ISSN:2790-1688 Volume-14-(2025)

The Role of Small Peptide Signals in Regulating Plant Reproductive Development

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Abstract. Plant reproductive development is a key stage in the plant life cycle, with small peptides serving as crucial signaling molecules that play a key regulatory role. During sexual reproduction, small peptides regulate various processes, including floral organ formation, pollination, fertilization, and seed development. For instance, small peptides from the CLV3/ESR-related (CLE) family regulate stem cell proliferation, precisely controlling the morphogenesis of floral organs; RALF family peptides mediate the signaling between pollen tubes and the pistil, ensuring accurate fertilization; and EPF/EPFL family peptides are involved in regulating ovule development and fruit maturation. In asexual reproduction, the MpCLE1 peptide in Marchantia is involved in gametophyte development, while vvi-miPEP171d1 peptides in grapevines promote adventitious root formation. Small peptide signaling relies on specific interactions with receptor kinases and co-receptors, exhibiting complex patterns such as “multiple ligands - single receptor”, “single ligand - multiple receptors”, and co-receptor integration across multiple pathways. However, current research still faces significant limitations, including the large number of functionally uncharacterized small peptides and unclear mechanisms in the upstream and downstream signaling pathways. Future research should employ advanced technologies to further elucidate the mechanisms of small peptide action and explore their potential applications in crop breeding and agricultural production.

Keywords: Plant Small Peptides; Reproductive Development; Signal Transduction; Receptor Kinases.

1. Introduction

Plants regulate their growth, development, and responses to external environmental signals with high precision through the recognition of various signaling molecules. Among these, plant peptides, as small molecular signaling entities, are capable of efficiently and accurately transmitting signals, rapidly initiating responses within a short time frame. They exhibit strong specificity and greater flexibility in regulatory capacity, playing a critical role at various stages of plant growth and development. Peptides are short-chain polypeptides, typically encoded by genes with fewer than 120 amino acids, and function similarly to hormones in signaling. The genes encoding peptides first express precursor proteins, which typically contain an N-terminal signal peptide, a variable region in the middle, a conserved functional domain, and a C-terminal processing signal region. Following a series of translation and post-translational processing steps, the precursor proteins are ultimately cleaved to release bioactive mature peptides.

In recent years, through systematic genomic analysis and experimental validation, more than 3,000 distinct peptides have been successfully identified, demonstrating their significant roles in various plant processes[1]. In the peptide signaling cascade, these peptides function as ligands, interacting with receptors and co-receptors to form complex and well-organized signaling pathways. Plants have evolved a unique family of membrane-bound receptor kinases (Receptor Kinases, RKs), or receptor-like kinases, located on the cell membrane. These receptors are composed of an extracellular ligand-binding domain, a single transmembrane helix, and a cytoplasmic kinase domain, enabling the transmission of extracellular signals across the membrane[2]. Additionally, the SERK family, as a representative co-receptor family, works in concert within peptide signaling pathways. SERKs belong to the LRR-RLK II group (Leucine-Rich Repeat Receptor-Like Kinase II Group), characterized by a smaller extracellular domain composed of leucine-rich repeats[3]. Although the peptide-receptor-co-receptor signaling network has been shown to play a pivotal role in plant growth and development,

significant gaps remain in current research. On one hand, the roles of certain peptides in plant life processes are still not fully understood. On the other hand, the regulatory mechanisms governing the upstream and downstream processes of peptide signaling pathways remain largely unexplored.

The reproductive development of plants is of paramount importance throughout their life cycle, encompassing both sexual and asexual reproduction. Sexual reproduction begins with the formation of floral organs, which arise from the apical meristem. This process progresses through the stages of pollination and fertilization. Upon pollen landing on the stigma of the pistil, it interacts with the secretions of the stigma, leading to the germination of the pollen tube. The sperm cells then travel through the pollen tube to the ovule, where fertilization occurs with the egg cell, resulting in the formation of a zygote. Following fertilization, the ovary develops into a fruit, and the ovule within the ovary matures into a seed. The seed consists of the seed coat, the embryo, and the endosperm. The embryo, derived from the fertilized egg, germinates under suitable conditions, and a new plant begins to grow. In contrast, asexual reproduction does not require the fusion of male and female reproductive cells. Instead, it relies on processes such as cell division, budding, spore formation, or vegetative propagation (e.g., cutting, grafting, and layering), whereby new individuals are directly generated from the parent organism. This mode of reproduction facilitates rapid propagation and ensures the retention of the parent's favorable traits.

This review focuses on the functional roles of small peptides in plant reproductive development, synthesizing recent research on plant peptides and reproduction. Through a comprehensive analysis, it consolidates the mechanisms by which small peptides influence various stages of plant reproductive development. It provides a robust theoretical framework for future studies and offers insights into both emerging research directions and practical applications.

2. The Role of Small Peptides in Plant Sexual Reproduction

2.1 The Role of Small Peptides in Regulating Floral Organ Formation in Plants

Plant reproductive development encompasses both sexual and asexual reproduction. Sexual reproduction in plants begins with the formation of floral organs. When the plant reaches a certain developmental stage, the apical meristem undergoes a transition to form the floral meristem. This floral meristem then gradually differentiates into various floral organs, including sepals, petals, stamens, and carpels, which develop in a specific sequence. As a crucial step in sexual reproduction, floral organ formation is regulated not only by plant hormones, such as auxins, and environmental factors but also by small peptide signals, which play an essential role in the fine-tuning of this process. Together, these factors ensure the precise development of reproductive structures, optimize pollination efficiency, and contribute to ecological adaptability.

The CLV3/ESR-related (CLE) family, the largest family identified to date, is one of the most significant. It was first discovered in the shoot apical meristem (SAM) of Arabidopsis thaliana. *CLV3*, in conjunction with genes such as *CLV1*, is of vital importance in maintaining the balance between stem cell proliferation and differentiation, which is essential for the proper function of the SAM. Mutations in the *CLV3* gene result in an enlarged SAM and excessive growth of the floral meristem, leading to the formation of additional floral organs, particularly stamens and carpels[4]. CLV3 is involved in the CLV-WUS signaling pathway, where WUS functions as a positive regulator that promotes stem cell formation and maintenance. The WUS protein activates CLV3 expression, which, after processing and maturation, is secreted. CLV3 then transmits signals through the CLV1/CLV2 receptor kinase complex to negatively regulate WUS activity, thereby limiting its expression domain and maintaining the balance of stem cell populations[5]. Moreover, studies have revealed that in addition to binding with CLV1, CLV3 also interacts with a heterodimer formed by CLV2 and CORYNE (CRN), which plays a role in CLV3 signal perception, with CRN functioning as a co-receptor of CLV2. Additionally, BARELY ANY MERISTEM1-3 (BAM1-3), RECEPTOR-LIKE PROTEIN KINASE2 (RPK2), and CLAVATA3 INSENSITIVE RECEPTOR KINASES (CIKs) are involved in CLV3 signal transduction, with BAM1 and BAM2 directly binding to the CLV3 peptide[6].

Studies have also indicated that CLV2/CRN signal transduction requires the involvement of CIK family co-receptors. Under cold or ambient temperature conditions, the CLV2/CRN-CIK signaling pathway promotes auxin-dependent floral meristem growth. At elevated temperatures, CLV2/CRN signaling, in conjunction with heat-induced auxin biosynthesis, collaboratively supports floral development, ensuring the stability of reproductive processes in Arabidopsis across varying temperature environments. This mechanism ensures the proper growth and development of floral meristems and is of considerable importance in ensuring reproductive success in plants under diverse environmental conditions[7]. In this signaling pathway, the KNU regulatory factor not only directly binds to and represses the expression of CLV3 and CLV1, but also inhibits WUS-mediated activation of CLV3 through its interaction with WUS. This, in turn, affects the activity of stem cells in the floral meristem, thereby providing an additional layer of regulation to the CLV3-WUS signaling pathway[8].

In rice, the CLE family peptide FON4 interacts with receptor FON1 to regulate the size of the apical meristem, including the shoot apical meristem, inflorescence meristem, and floral meristem. *FON4* gene mutations cause excessive proliferation of the meristem, leading to an abnormal increase in the number of floral organs, particularly a significant enlargement in the number of stamens and carpels[9]. In rice, the CLE family peptide FON2 regulates the size of the floral and inflorescence meristems through its receptor FON1, which is homologous to Arabidopsis CLV1. Mutations in FON2 cause excessive meristem proliferation, leading to a significant increase in the number of floral organs[10]. The rice CLE family peptide FCP1 (OsCLE402) regulates the maintenance of the shoot apical meristem (SAM) and root apical meristem (RAM). Constitutive expression of FCP1 leads to SAM depletion, causing premature senescence of the plant. Furthermore, exogenous application of FCP1 disrupts root development by inhibiting elongation, altering root morphology, and inducing mis-specification of RAM cell fate, ultimately depleting meristematic activity[11]. The rice CLE family genes FOS1 and FON2 redundantly regulate the maintenance of floral meristem stem cells. The CLE proteins encoded by these genes may act through receptors that are distinct from those of FON2[12].

In maize, CLV3 interacts with the receptor FEA2 (Fasciated Ear2) and the co-receptor CT2 (COMPACT PLANT2), regulating stem cell proliferation in the shoot apical meristem via the CLV-WUS signaling pathway. This interaction is crucial for maintaining the normal size and morphology of the meristem[13]. The ZmCLE7 peptide in maize interacts with the FEA2 receptor and co-receptors CT2 and ZmCRN, transmitting signals through the FEA2-CT2-G protein complex. This interaction regulates the expression of genes associated with shoot apical meristem development, thereby maintaining meristem homeostasis via the FEA2-ZmCRN interaction. Additionally, the ZmFCP1 peptide from the same family interacts with the FEA3 receptor to inhibit the expression of ZmWUS1 in specific regions. Together, these peptides contribute to the CLV-WUS signaling pathway, where they mediate negative feedback regulation by restricting the expression domain of the WUS gene through their interactions with receptors and co-receptors[6].

In tomatoes, a peptide homologous to Arabidopsis CLV3, termed SlCLV3, interacts with the receptor SlCLV1, which is encoded by FAB, and is involved in the CLV-WUS signaling pathway. It inhibits the expression of the SlWUS gene, limiting the excessive proliferation of stem cells and maintaining the homeostasis of shoot apical meristem size. SlCLV2, a homolog of Arabidopsis CLV2, functions redundantly with SlCLV1[14]. Studies have also shown that in tomato, FIN, FAB2, and SlRRA3a, as CLV3-modified arabinosyltransferase genes, are involved in the CLV signaling pathway, influencing CLV3 modification and signal transduction[6]. Furthermore, studies in tomato have revealed that the plant sulfopeptide PSK functions as a drought-specific signaling molecule. Phytaspase 2 (SlPhyt2) in the tomato pedicel processes the PSK precursor through aspartic acid-specific cleavage, generating mature PSK. This, in turn, induces the expression of cell wall hydrolases and facilitates flower abscission[15].

2.2 The Role of Small Peptides in Regulating Plant Pollination and Fertilization

Following the establishment of male and female reproductive structures during floral organ formation, small peptides, as intercellular signaling molecules, further mediate critical events in the pollination and fertilization process, including the interaction between pollen and the stigma, pollen tube guidance, and gametophyte recognition. These processes facilitate the transition from reproductive organ development to the initiation of fertilization. As a central mechanism of sexual reproduction, plant pollination and fertilization involve a highly regulated sequence—from pollen release and germination to double fertilization. This sequence is orchestrated through the synergistic regulation of calcium signaling, redox balance, hormones, and small peptide-receptor pathways, ensuring genetic recombination, ovule development, and population continuity, thereby preserving offspring diversity.

In 2001, Gregory Pearce, Daniel S. Moura, and their team isolated a substance from tobacco that belongs to the Rapid Alkalinization Factor (RALF) peptide family. Initial studies demonstrated that this substance significantly affects plant growth, notably inhibiting the growth and development of new roots in both tomato and Arabidopsis[16]. During fertilization in Arabidopsis, RALF family peptides regulate pollen tube behavior through CrRLK1L receptor kinases, such as FER in the female gametophyte, and ANXUR1/2 and BUPS1/2 in the pollen tube. RALF4/19, in association with the BUPS/ANXUR complex, sustains pollen tube growth, while ovule-derived RALF34 triggers structural changes by competitively binding to the receptor complex. This binding activates FER-mediated signaling, initiating downstream events that ultimately result in pollen tube rupture and the release of sperm, completing double fertilization[17]. Studies have demonstrated that the peptide RALF4/19 not only interacts with the receptors BUPS1/2 and ANX1/2 but also binds to the co-receptors LLG2/3 (Lorelai-like glycosylphosphatidylinositol-anchored proteins 2/3). This interaction plays a crucial role in maintaining pollen tube integrity, thereby ensuring the proper transport and release of sperm[18]. In addition, the self-secreted peptide RALF33 in Arabidopsis stigma interacts with the FER/ANJ receptor kinases and the co-receptor LLG1, thereby activating the ROP2-RBOHD pathway. This activation induces the production of reactive oxygen species in papillary cells and helps maintain homeostasis, ultimately inhibiting pollen hydration[19].

Studies have shown that members of the RALF6/7/16/36/37 peptide family secreted by Arabidopsis pollen tubes interact with various receptor kinases, including FERONIA (FER), ANJEA (ANJ), and HERCULES RECEPTOR KINASE 1 (HERK1), to form specific ligand-receptor complexes. Once the pollen tube successfully reaches the ovule and is received and ruptured by the synergid cells, the RALF peptides, which originally maintain the mechanism that blocks multiple pollen tubes, are rapidly reduced, resulting in the release of this blockage mechanism[20]. The RALF4 and RALF19 peptides in Arabidopsis pollen tubes bind to the FER-LRE (LORELEI) receptor complex, which subsequently recruits NORTIA (NTA) to the plasma membrane, forming a receptor-channel complex. This complex establishes a functional calcium ion channel, activating the NTA channel and facilitating calcium ion influx. The resulting increase in Ca2+ concentration in the synergid cells triggers pollen tube rupture and sperm release. RALF6, RALF7, RALF16, RALF36, and RALF37 exhibit redundant functions in pollen tube blockage and reception[21]. Self-secreted RALF peptides (sRALFs) in Arabidopsis stigma can prevent non-compatible pollen from penetrating by disrupting the complex formed between the receptor-like kinases FER/CURVY1/ANJEA/HERK1 and the cell wall proteins LRX3/4/5. In contrast, RALF peptides released by compatible pollen (pRALFs) can competitively relieve this barrier, thereby revealing a "lock-and-key" regulatory mechanism underlying plant reproductive isolation[22].

In the self-incompatibility system of the Brassica genus, the male determinant SP11/SCR binds to the female receptor kinase SRK through S-haplotype-specific recognition, thereby activating downstream signaling pathways that inhibit the germination or growth of self-pollen[23]. In Brassica species, self-incompatibility is initiated by the interaction between the pollen protein SP11, encoded by the S-locus gene, and the stigma receptor kinase SRK. This interaction activates downstream signaling pathways, and through direct binding with SRK on the plasma membrane of stigma papilla

cells via MLPKf1/f2 isoforms, they collaboratively transduce the self-incompatibility signal, thereby inhibiting the germination of self-pollen[24].

In Arabidopsis thaliana, small peptides from the PCP-Bs family on the pollen surface (e.g., PCP-Bγ) regulate reactive oxygen species (ROS) homeostasis by interacting with the FER/ANJ receptor kinase and the co-receptor LLG1 on the plasma membrane of stigma papilla cells. Prior to pollination, the self-secreted RALF33 from the stigma binds to FER/ANJ, inhibiting pollen hydration. Following pollination, pollen-secreted PCP-Bγ competitively replaces RALF33, binding to the receptor complex, relieving the inhibition, and reducing ROS levels, thereby promoting pollen hydration and the fertilization process[19].

In Arabidopsis thaliana, small peptides derived from the EPFL family have been identified. Peptides EPFL4, EPFL5, and EPFL6 from the EPFL family interact with the ERECTA family (ERECTA, ERL1, and ERL2) and the co-receptor SERK family (including SERK1, BAK1, and SERK4) to form receptor complexes. This interaction promotes the proliferation of anther cells, leading to filament elongation, which facilitates pollen access to the stigma and thereby ensures the completion of self-pollination, thus supporting proper reproductive processes in Arabidopsis thaliana[25].

In rice research, small peptides derived from the Arabinogalactan Proteins (AGP) family and the FCS-like zinc finger (FLZ) family have been identified. Two peptides, OsAGP16 and OsFLZ13, specifically expressed in rice from these families, have been found to exert distinct effects. OsAGP16 reduces plant height, causes leaf drooping during the seedling stage, and negatively affects pollen grain development and maturation, resulting in decreased pollen viability. This, in turn, leads to a significant reduction in seed setting rate and a notable decrease in thousand-grain weight. In contrast, Osflz13 mutant plants show a significant decline in seed setting rate, with most pollen losing viability. OsFLZ13 plays a crucial role in the development and maturation of rice pollen and is essential for producing fertile and viable pollen[26].

Plant sulfated peptide-α (PSKα), a non-classical small peptide signal, mediates transmembrane signal transduction through its receptor PSKR. In tobacco, it activates downstream pathways at low concentrations, serving as a key regulator of pollen collective behavior and significantly enhancing pollen germination[27]. In Brassica napus and Arabidopsis, the small peptide Exo70A1 mediates ubiquitin-dependent degradation through its receptor ARC1, bidirectionally regulating both compatible pollination (by promoting pollen hydration and growth) and self-incompatibility reactions (by enhancing self-pollen rejection through degradation of Exo70A1), thereby coordinating the maintenance of pollination compatibility[28].

In Arabidopsis, the GPI-anchored proteins LORELEI (LRE) and LLG1 interact with the receptor kinase FER, facilitating its transport from the endoplasmic reticulum to the plasma membrane, where it participates in the RAC/ROP signaling pathway. This interaction regulates various plant processes, including growth, defense, and reproduction, with the LRE-FER interaction particularly essential for pollen tube-ovule recognition and fertilization[29]. The AtLURE1 peptides secreted by the synergid cells of Arabidopsis ovules mediate species-specific pollen tube guidance through the PRK6 receptor, thereby promoting the competitive growth of same-species pollen tubes to enhance reproductive isolation. In contrast, the XIUQIU1-4 peptides attract heterospecific pollen tubes in a non-species-specific manner, independent of PRK6. Together, these peptides coordinate the balance between reproductive isolation and heterospecific fertilization, with their gene knockout resulting in a significant reduction in plant fertility[30]. In further studies on Arabidopsis, researchers have also identified that the central cell selectively secretes the peptide substances SALVAGER1 and SALVAGER2. These peptides attract pollen tubes in a directional manner to regulate the restoration of fertilization when the pollen tube, dependent on the synergid cells, either fails to attract or carries infertile sperm cells, resulting in its termination[31].

2.3 The Role of Small Peptides in Regulating Seed Development and Fruit Formation in Plants

Following successful pollination and fertilization, the fertilized egg develops into the embryo, the fertilized central cell develops into the endosperm, and the integument forms the seed coat, collectively completing seed development. Meanwhile, the ovary gradually expands, and the ovary wall develops into the pericarp, resulting in fruit formation. Both seed development and fruit maturation are influenced by a range of factors, with small peptides serving as key signaling molecules that play an indispensable role in these processes.

Small peptides from the Epidermal Patterning Factor (EPF) / Epidermal Patterning Factor-Like (EPFL) family play a pivotal role throughout the entire seed development cycle. In Arabidopsis, two peptides involved in ovule patterning have been identified, each associated with distinct signaling pathways. The EPFL9 secreted peptide promotes fruit growth by activating receptor kinases ER, ERL1, and ERL2, while the small peptide EPFL2 regulates ovule spacing in the carpel wall and placenta tissue through the receptors ERL1 and ERL2, thereby modulating ovule initiation patterns and influencing the regularity of ovule initiation. These two peptides not only function during fruit maturation but also play an integral part in the ovule initiation process prior to pollination, thereby controlling the growth of the ovary and fruit[32]. In rice, small peptides from this family, GAD1 and OsEPFL2, are involved in regulating the development of the awn, which facilitates seed dispersal and further increases seed germination rates in natural environments. Additionally, they also promote seed germination by inhibiting the biosynthesis and signaling pathways of abscisic acid (ABA), thereby enhancing α-amylase activity and the release of soluble sugars[33].

In Arabidopsis, researchers have identified a small molecule signaling peptide family with sulfation modifications, known as the CASPARIAN STRIP INTEGRITY FACTORS (CIFs) family. TWS1, acting as a ligand for GASSHO, plays a role in the formation of the cuticle. The serine protease ALE1, produced in the endosperm, mediates the processing of the TWS1 precursor generated in the embryo, leading to the release of the active peptide TWS1. This, in turn, triggers the GASSHO-dependent reinforcement of the wax layer in the embryo. The bidirectional molecular communication between the embryo and the endosperm ensures the integrity of the wax layer prior to germination, thereby protecting the seedling from water loss[34]. In mature Arabidopsis seeds, tyrosylprotein sulfotransferase (TPST) in the endosperm sulfates CIF2 and PSY1 peptides, which in turn promote the formation and development of the seedling cuticle[35].

Additionally, two other small peptides are involved in seed development and fruit ripening. In 2024, Hanmo Fang and Jinhua Zuo's team discovered that the plant peptide hormone Plant Sulfated Peptide (PSK) is recognized by its receptor PSKR1 in tomatoes, thereby activating the PSKR1-mediated signaling pathway. This pathway interacts with the transcription factor DREB2F, enhancing DREB2F phosphorylation and facilitating the transition towards fruit ripening[36]. The second discovery comes from research on maize and its close relatives, where it was found that qKDR1, as a silencer, can bind to the transcription factors ZmMYBST1 and ZmMYBR43, inhibiting the expression of the downstream gene RPG. The micropeptide microRPG1 encoded by RPG regulates the expression of ZmEIL1 and ZmEIL3 genes in the ethylene signaling pathway, thereby affecting the maize kernel dehydration rate (KDR), which influences mechanized harvesting and grain quality[37].

3. The Role of Small Peptides in Regulating Asexual Reproduction in Plants

Plants can also reproduce asexually (with offspring directly produced by the parent through fission, budding and other forms), which can shorten the reproduction cycle and maintain genetic superiority.While the molecular regulatory networks of small peptides in sexual reproduction are well-established, the functional roles of small peptides in asexual reproduction remain underexplored.

A small peptide, MpCLE1, belonging to the CLE family and the H/TDIF-type subfamily, has been identified in Marchantia polymorpha. MpCLE1 interacts with the receptor MpTDR, an LRR-RK type

receptor kinase, to inhibit cell proliferation in the apical meristem of the haploid gametophyte, thereby regulating thallus growth and the development of reproductive organs (gametangiophores)[38]. In grapevine research, scientists have identified vvi-miPEP171d1, a member of the miPEPs family, which promotes the formation of adventitious roots. Exogenous application of vvi-miPEP171d1 activates the expression of vvi-MIR171d, thereby enhancing adventitious root development and increasing the number of adventitious roots, although this results in a significant reduction in root length[39].

4. Summary and Future Outlook

4.1 Functional Diversification of Small Peptides through Binding to the Same Receptor

Various small peptides in plants bind to the same receptor during plant reproductive development. In rice, FON4 and FON2 interact with the receptor FON1 to regulate the size of the shoot apical meristem and the number of floral organs. In maize, CLV3 and ZmCLE7 bind to the receptor FEA2, contributing to the regulation of stem cell proliferation in the shoot apical meristem. Small peptides, including RALF4, RALF19, RALF6, RALF7, RALF16, RALF36, and RALF37, expressed in the pollen tube, interact with receptor kinases such as FER and ANJ. During pollen tube growth, RALF4 and RALF19 interact with BUPS1, BUPS2, and ANX1/2 to maintain pollen tube integrity. Upon reaching the female gametophyte, RALF34 competes for receptor binding, promoting pollen tube rupture and fertilization.

The "multiple ligands binding to a single receptor" model suggests that receptor kinases may exhibit multifunctionality. A single receptor can bind to various small peptides, recruit distinct downstream signaling molecules, or form different signaling complexes, thereby eliciting diverse cellular responses. This allows a limited number of receptors to effectively respond to complex and diverse environmental signals and survival demands. At the same time, it increases the complexity and flexibility of the plant signaling network, providing essential support for the regulation of plant growth, development, and environmental adaptation.

4.2 A Single Peptide Mediates Its Function Through Different Receptors

A single peptide can mediate distinct signaling pathways in plants by binding to different receptors, executing various biological functions. The receptor for CLV3 includes not only CLV1 but also BAM1 and BAM2, involved in the CLV-WUS signaling pathway and playing a pivotal role in maintaining stem cell homeostasis in the shoot apical meristem (SAM). The ability of a single peptide to interact with different receptors and produce diverse functions reveals the intricate regulatory mechanisms of plant signaling. The interaction between peptides and their receptors is highly specific, and the expression and activity of particular receptors can vary across different tissues, developmental stages, or environmental conditions, determining the peptide's functional outcome. This mechanism enables plants to utilize a limited repertoire of peptide molecules to construct a complex and precise signaling network, responding to diverse physiological demands and environmental changes. It enhances plant adaptability and survival while providing new perspectives on the regulatory mechanisms underlying plant growth and development.

4.3 Integration of Multiple Signaling Pathways and Functional Output Mediated by Co-receptors

In plant peptide signaling, co-receptors play a pivotal role in the integration and transmission of signals. A single co-receptor can participate in multiple signaling pathways and generate distinct outputs. LLG1, as a co-receptor, performs different roles in various signaling pathways, such as pollen hydration and the multi-pollen tube blockage mechanism. Acting as a "hub" in signal transduction, it integrates multiple signal inputs by interacting with different receptors and peptide ligands, thereby activating diverse downstream signaling pathways and eliciting a wide range of biological effects. The multifunctionality of co-receptors underpins the complexity and plasticity of

plant signaling networks, enabling plants to coordinate various physiological processes and achieve precise regulation of reproductive development.

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