Function of Small Peptides During Male-Female Crosstalk in Plants

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Plant peptides secreted as signal molecular to trigger cell-to-cell signaling are indispensable for plant growth and development. Successful sexual reproduction in plants requires extensive communication between male and female gametophytes, their gametes, and with the surrounding sporophytic tissues. In the past decade, it has been well-documented that small peptides participate in many important reproductive processes such as self-incompatibility, pollen tube growth, pollen tube guidance, and gamete interaction. Here, we provide a comprehensive overview of the peptides regulating the processes of male-female crosstalk in plant, aiming at systematizing the knowledge on the sexual reproduction, and signaling of plant peptides in future.

Keywords: small peptides, self-incompatibility, pollen germination, polar growth, male-female crosstalk

INTRODUCTION

Small peptides refer to proteins that are less than 100 amino acids broadly (Hsu and Benfey, 2018), which can be divided into three categories from the source: processed from the original precursor protein; directly translated from an independent small open reading frame (ORF); and encoded by a small ORF in the 5' or 3' untranslated region (UTR) within a normal size protein. Small peptides used as signals are usually secreted proteins which are mainly divided into post-translationally modified small peptides and small cysteine-rich peptides (CRPs; Matsubayashi, 2003). High-throughput sequencing has predicted a large number of small peptide-encoding genes in a variety of plant genomes, and their functions have gradually attracted attention. It is well-established that small peptides are involved in many growth and development processes such as cell proliferation (Imin et al., 2013; Djordjevic et al., 2015), root development (Delay et al., 2013a,b; Mohd-Radzman et al., 2015; Taleski et al., 2016, 2018; Patel et al., 2018), pollen fertility (Okuda et al., 2009; Takeuchi and Higashiyama, 2012, 2016; Higashiyama and Takeuchi, 2015), stomata opening (Takahashi et al., 2018; Qu et al., 2019), absorption and regulation of mineral elements (Taleski et al., 2018), resistance to pests and diseases (Stotz et al., 2009a,b; Ziemann et al., 2018), and environmental adaptation.

Fertilization is a process in which male-female cells interact and fuse with each other in plants. Pollen grains fall onto the stigma through pollination and germinate to form a pollen tube which transports sperm cells through the stigma and grows into the embryo sac along the transmitting tract (Figure 1). A sperm cell fuses with the egg cell to form a zygote which develops into an embryo; the other sperm cell fuses with the central cell to form a fertilized...
polar nucleus which develops into an endosperm (Hamamura et al., 2012). The successful completion of fertilization relies on the continuous recognition and interaction between female and male cells. The basis for completing these processes is signal communication.

In recent years, a good many of studies have demonstrated the important role of small peptides in male-female crosstalk in plants (Kim et al., 2021). Different small peptides involved in pollen grains-stigma recognition, pollen tube germination, polar growth and reception, ovule attraction, gamete activation, and other processes have been identified. The identification and functional analysis of small peptide during male-female crosstalks are helpful to reveal the formation mechanism of species in plants. Peptide-receptor interaction is the reason for the formation of inter-species isolation. Therefore, researches in this field have great significance for overcoming the reproductive barriers between different species.

**SMALL PEPTIDES INVOLVED IN IMPORTANT PROCESSES OF PLANT REPRODUCTION**

**Self-Incompatibility**
Self-incompatibility is the pre-fertilization reproductive barrier of many plants. The pollen grains fall on the stigma and recognize with the papilla cells quickly before germination, causing interspecific incompatibility and self-incompatibility, preventing different species from crossing and selfing decline (Takayama and Isogai, 2005). Self-incompatibility includes gametophyte self-incompatibility and sporophyte self-incompatibility. The sporophyte self-incompatibility reaction is controlled by the male and female substances encoded by the S locus gene, and the interaction of the S locus encoded protein of the same haplotype inhibits the growth of pollen (tube). Pollen-expressed small peptide ligand S-locus Cys-rich/S-locus protein 11 (SCR/SP11) and small peptide receptor kinase (SRK) on the stigma (Stein et al., 1991; Schopfer et al., 1999; Takayama et al., 2000) play an important role in the determination of sporophyte self-incompatibility in Brassica napus (Figure 2A). SCR/SP11 is a small CRP that is secreted into the pollen sac after translation, then transferred and adhered to the surface of the pollen, and interacted with SRK expressed in the stigma papillary cells after being pollinated (Table 1). After SCR/SP11 binds to SRK, the phosphorylation process of multiple factors recruits ubiquitin ligase to degrade the protein Exo70A1 involved in water absorption and hydration, and prevents the germination of pollen tubes (Samuel et al., 2009).

**Pollen Germination**
The nonmotile sperm cells must rely on the polar growth of the pollen tube to reach the embryo sac. Pollen tube germination and polar growth need the support and guidance of pistil tissue. The signal from the pollen or carpel is received by the receptor on the pollen tube and transmitted to the cell, changing the dynamic nature of the cytoskeleton and forming a pattern of polar growth (Guan et al., 2013).

It was found that PCP-Ba/β/γ/δ located in pollen coat are important for pollen germination because the pollen of pcp-ba/β/γ/δ displayed defects in pollen adhesion, pollen hydration, and pollen tube growth in vivo (Wang et al., 2017). In tomato, a small CRP LAT52 secreted by pollen is involved in pollen germination (Figure 2A). LAT52 can bind to the pollen tube receptor kinase LePRK2 specifically (Tang et al., 2002). This binding effect is strongest when the pollen tube germinates, and gradually weakens with the extension of the pollen tube. After the pollen tube germinates, substances from the carpel are needed to promote the growth of the pollen tube.

The small CRP LeSTIG1 expressed on stigma of tomato is involved in the regulation of pollen tube growth (Figure 2A). Application of LeSTIG1 can promote pollen tube elongation in vitro (Tang et al., 2004). After processing and maturation, LeSTIG1 is secreted out of the cell, combined with the receptor LePRK2, and enriched in the pollen tube. The intracellular domain of LePRK2 interacts with the plant-specific Rop GTPase guanylate exchange factor (GEF) family member KPP, and may regulate pollen tube growth through downstream ROP (Zhang et al., 2008). It has been discovered that the small peptide LeSTIG1 not only binds to receptors, but its C-terminal cysteine-rich domain can also bind to phospholipid molecules such as PI(3)P and participate in intracellular redox state regulation (Huang et al., 2014). Homologous genes of LeSTIG1 in other species may have other functions, such as regulating the secretion of petunia and tobacco stigma cells (Table 1; Verhoeven et al., 2005).
Pollen Tube Polar Growth

The polar growth of pollen tube is essential for the transportation of sperm cells to embryo sac to complete double fertilization. Small peptides can guide the pollen tube to grow in the transmitting tract of the style. Several CRPs expressed in pistil, such as stigma-style cysteine rich adhesin (SCA; Figure 2A), act as an adhesin binding the pollen tubes to the transmitting tract of the style (Park et al., 2000). The combination of SCA and pectic polysaccharide is necessary to induce pollen tube adhesion to other pollen tubes and to an in vitro style matrix (Lord, 2000). SCA is endocytosed into the pollen tube starting at the tip and subsequently moves through an endocytic route. This may be a process triggered by the ligand-receptor binding, but its receptor and the downstream events of the signal have not been clarified (Kim et al., 2006).

In addition, there are gradients formed by plantacyanin and other protein in pistil affect pollen tube elongation. Plantacyanins are secreted proteins with a size of about 10 kDa, with a distinctive gradient from the stigma to the ovule. The distribution may be regulated by the miRNA pathway (Maunoury and Vaucheret, 2011). The pollen tube will elongate at random in the papilla cells and the polar growth will be disrupted if overexpression of the plantacyanin gene to disrupt the gradient distribution pattern. Plantacyanin has properties of copper ion binding, which gives it a higher redox potential, and may participate in the metabolism of reactive oxygen species (ROS). Chemocyanin, the homologous protein of plantacyanin in Lily, is a similar chemotactic factor, which affects the polar growth of pollen tube (Kim et al., 2006).

Flowering plants in the breeding period are particularly susceptible to temperature. CLV3/ESR-related 45 (CLE45), a small modified peptide post-translationally, is involved in the process of maintaining seed yield under high temperature conditions. CLE45 is expressed in the stigma mainly at 22°C,
but its expression expands to the transmitting tract upon temperature rise to 30°C. The synthetic CLE domain of CLE45 promotes pollen tube elongation in vitro at 30°C. In vivo, CLE45 cannot promote elongation, but can prolong the time of pollen tube growth. CLE45 binds the leucine-rich repeat receptor-like kinase STERILITY-REGULATING KINASE MEMBER1 (SKM1) and STERILITY-REGULATING KINASE MEMBER2 (SKM2; Figure 2A). The activity of pollen is maintained through the CLE45-SKM1/SKM2 signaling pathway under high temperature to ensure successful double fertilization (Table 1; Endo et al., 2013).

Attraction to Ovules

In recent years, it has been confirmed that pollen tubes are attracted by guidance signals from the embryo sac (Palanivelu and Preuss, 2000; Hepler et al., 2001). With the help of laser ablation, Higashiyama et al. observed that a single pollen tube penetrated a synergid cell and discharged its two gametes into the embryo sac as the synergid cell ruptured in *Torenia fournieri*. At the same time, it was found that the effective attracting distance of the synergid cells was 100–200 μm. It implies that the attracting substance has a short diffusable distance and may be secreted small peptides (Higashiyama et al., 2001). LURE1 and LURE2 expressed in the synergid cell abundantly and predominantly are secreted to the surface of the egg apparatus (Figure 2B). LUREs contain six conserved cysteines and are about 65 amino acids in length (~9 KDa). Injection of morpholino antisense oligomers against the LUREs impaired pollen tube attraction, demonstrating that LUREs are the attractants derived from the synergid cells of *T. fournieri* (Okuda et al., 2009).

Studies found that there are more than 300 defensin-like (DEFL) genes involving in cell-to-cell communication during male-female gametes interactions in *Arabidopsis*. AtLURE1 peptides, expressed in egg-accompanying synergid cells specifically, and secreted toward the funicular surface through the micropyle, are pollen tube attractants guiding pollen tubes to the ovular micropyle (Takeuchi and Higashiyama, 2012). In addition, there are still a certain percentage of pollen tubes can be fertilized normally in AtLURE1 RNAi transgenic plants, suggesting that there are other substances involved in pollen tube guidance. *Lost In Pollen tube guidance 1* (LIP1) and 2 (LIP2) expressed in the membrane of pollen tube, interacted with PRK6 (Figure 2B), perceive the female signal AtLURE1 for micropylar pollen tube guidance (Liu et al., 2013). MALE DISCOVERER1-MDIS1 INTERACTING RECEPTOR LIKE KINASE1 (MDIS1-MIK; Figure 2B), a cell-surface receptor kinase, was identified to perceive AtLURE1 in *Arabidopsis* (Wang et al., 2016).

In the monocotyledonous maize, *Zea mays* EGG APPARATUS1 (ZmEA1; Figure 2B) expressed in the egg cell and two synergids, is required for pollen tube attraction by the female gametophyte. Transgenic downregulation of the ZmEA1 gene led to ovule sterility caused by loss of close-range pollen tube guidance to the micropyle (Marton et al., 2005). ZmEA1 is recognized specifically by the pollen tube after being secreted by egg apparatus and degraded subsequently (Table 1; Marton et al., 2012).

**Table 1** | Peptides and receptors involved in double fertilization.

| Biological process       | Small peptide | Receptor | References |
|--------------------------|---------------|----------|------------|
| Self-incompatibility     | SCR/SP11      | SKP      | Schopfer et al., 1999; Takayama et al., 2000 |
| Pollen germination       | LAT52         | LePRK2   | Tang et al., 2002 |
| Pollen tube polar growth | LeSTIG1       | LePRK2   | Tang et al., 2004 |
| Pollen tube polar growth | SCA           | Unknown  | Lord, 2000; Chae et al., 2010 |
| Pollen tube polar growth | Plantacyanin  | Unknown  | Maunoury and Vaughan, 2011 |
| Pollen tube polar growth | Chemocyanin   | Unknown  | Kim et al., 2006 |
| Pollen tube polar growth | CLE45         | SKM1/2   | Endo et al., 2013; Okuda et al., 2009; Takeuchi and Higashiyama, 2012; Liu et al., 2013; Wang et al., 2016 |
| Ovule attraction         | LUREs         | MDIS1-MIK; LIP1/2 | Marton et al., 2005, 2012 |
| Ovule attraction         | ZmEA1         | Unknown  | Pearce et al., 2001; Haruta and Constabel, 2003; Haruta et al., 2008; Ge et al., 2017 |
| Pollen tube reception    | RALFs         | BUPS/ANX | Amien et al., 2010 |
| Gamete activation        | ZmES1-4       | Unknown  | Sprunck et al., 2012 |

**Pollen Tube Reception**

The synergid cells not only are required for pollen tube guidance, but also regulate the reception of the pollen tube. The pollen tube enters the female gametophyte by growing into one of the synergid cell which undergoes programmed cell death to burst and release sperm cells (Weterings and Russell, 2004).

The receptor-like serine-threonine kinase FERONIA/SIRENE (FER/SRN) is located on the cell membrane of the synergid cell (Figure 2C). In *feronia* (Huck et al., 2003) and *sirene* (Rotman et al., 2003), pollen tubes of wild-type can enter the embryo sac but fail to cease growth, rupture, and release their contents. Similar pollen tube overgrowths occur in interspecific crosses of *Rhododendron* and in the *in vitro Torenia* system (Higashiyama et al., 1998). It was found that ANXUR1 (ANX1) and ANXUR2 (ANX2; Figure 2C), the pollen-expressed homologs most closely related to FER, function redundantly to control the timing of pollen tube discharge. The pollen tubes of the double-mutant anx1 anx2 cease growth and burst *in vitro* and fail to reach the embryo sac *in vivo* (Boisson-Dernier et al., 2009; Miyazaki et al., 2009).

Rapid alkalinization factor (RALF), a secreted peptide, suppresses cell elongation of the primary root by activating the cell surface receptor FER in *Arabidopsis* (Haruta et al., 2014). It was found that RALF can induce the signal of Ca²⁺, suggesting an important role in the reception of pollen tubes (Pearce et al., 2001; Haruta and Constabel, 2003; Haruta et al., 2008). BUDDHA’S PAPER SEAL1 and 2 (BUPS1/2) and their peptide ligands RALF4/19 (Figure 2C), are pollen tube-expressed and are required to maintain pollen tube integrity since...
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Mori et al., 2006)

Glucosyl synthase (glc + )

Sprunck et al., 2012

LUREs-LAT52-LePRK2 regulate pollen germination in tomato,

One sperm cell fuses with the egg cell, the other sperm cell

Fertilization is the premise of seed production. Improving the

**CONCLUSION AND PERSPECTIVES**

During the past decade, it has been established that small peptides

At present, there are many similar family members of small

**AUTHOR CONTRIBUTIONS**

JZ and LY wrote the manuscript. XW, HL, and WW provided

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REFERENCES

Amien, S., Kliwer, I., Marton, M. L., Debener, T., Geirger, D., Becker, D., et al. (2010). Defensin-like ZmES4 mediates pollen tube burst in maize via opening of the potassium channel KZM1. *PloS Biol.* 8(1):e1000388. doi: 10.1371/journal.pbio.1000388

Boisson-Dernier, A., Roy, S., Kritsas, K., Grobel, M. A., Jacubek, M., Schroeder, J. I., et al. (2009). Disruption of the pollen-expressed FERONIA homologs ANXUR1 and ANXUR2 triggers pollen tube discharge. Development 136, 3279–3288. doi: 10.1242/dev.040071

Chae, K., Gongong, B. J., Kim, S. C., Kishel, C. A., Morikis, D., Balasubramanian, S., et al. (2010). A multifaceted study of stigma/style cytokine-rich adhesion (SCA)-like Arabidopsis lipid transfer proteins (LTPs) suggests diversified roles for these LTPs in plant growth and reproduction. *J. Exp. Bot.* 61, 4277–4290. doi: 10.1093/jxb/erq228

Delay, C., Imim, N., and Djordjevic, M. A. (2013a). CEP genes regulate root and shoot development in response to environmental cues and are specific to seed plants. *J. Exp. Bot.* 64, 5383–5394. doi: 10.1093/jxb/ert332

Delay, C., Imim, N., and Djordjevic, M. A. (2013b). Regulation of Arabidopsis root development by small signaling peptides. *Front. Plant Sci.* 4:352. doi: 10.3389/fpls.2013.00352

Djordjevic, M. A., Mohd-Radzman, N. A., and Imin, N. (2015). Small peptide signals that direct root and shoot developmental and symbiotic. *J. Exp. Bot.* 66, 5171–5181. doi: 10.1093/jxb/erv357

Endo, S., Shinohara, H., Matsubayashi, Y., and Fukuda, H. (2013). A novel pollen-pistil interaction conferring high-temperature tolerance during reproduction via CLE45 signaling. *Carr. Biol.* 23, 1670–1676. doi: 10.1016/j.cub.2013.06.060

Ge, Z., Bergonci, T., Zhao, Y., Zou, Y., Du, S., Liu, M. C., et al. (2017). *Arabidopsis* pollen tube integrity and sperm release are regulated by RALF-mediated signaling. *Science* 358, 1596–1600. doi: 10.1126/science.aao3642

Guo, Y., Guo, J., Li, H., and Yang, Z. (2013). Signaling in pollen tube growth: crosstalk, feedback, and missing links. *Mol. Plant* 6, 1053–1064. doi: 10.1093/mp/mtt070

Hamamura, Y., Nagahara, S., and Higashiyama, T. (2012). Double fertilization on the move. *Curr. Opin. Plant Biol.* 15, 70–77. doi: 10.1016/j.copp.2011.11.001

Haruta, M., and Constabel, C. P. (2003). Rapid alkalinization factors in poplar cell cultures. Peptide isolation, CDNA cloning, and differential expression in leaves and methyl jasmonate-treated cells. *Plant Physiol.* 131, 814–823. doi: 10.1104/pp.014597

Haruta, M., Monshausen, G., Gilroy, S., and Sussman, M. R. (2008). A cytoplasmic Ca2+ functional assay for identifying and purifying endogenous cell signaling peptides in Arabidopsis seedlings: identification of AIRALF peptide. *Biochimica et biophysica acta* 1778, 6311–6321. doi: 10.1016/j.bbapap.2008.07.008

Haruta, M., Sabat, G., Stecker, K., Minkoff, B. B., and Sussman, M. R. (2014). A peptide hormone and its receptor protein kinase regulate plant cell expansion. *Science* 343, 408–411. doi: 10.1126/science.1244454

Hepler, P. K., Vidal, L., and Cheung, A. Y. (2001). Polarized cell growth in higher plants. *Annu. Rev. Cell Dev. Biol.* 17, 159–187. doi: 10.1146/annurev.cellbio.17.1.159

Higashiyama, T., Kuroiwa, H., Kawano, S., and Kuroiwa, T. (1998). Guidance in vitro of the pollen tube to the naked embryo sac of *Torenia fournieri*. *Plant Cell* 10, 2019–2032. doi: 10.1105/tpc.10.12.2019

Higashiyama, T., and Takeuchi, H. (2015). The mechanism and key molecules involved in pollen tube guidance. *Annu. Rev. Plant Biol.* 66, 393–413. doi: 10.1146/annurev-plant-033014-115635

Higashiyama, T., Yabe, S., Sasaki, N., Nishimura, Y., Miyagishima, S., Kuroiwa, H., et al. (2001). pollen tube attraction by the synergid cell. *Science* 293, 1480–1483. doi: 10.1126/science.1062429

Hsu, P. Y., and Benfey, P. N. (2018). Small but mighty: functional peptides encoded by small ORFs in plants. *Proteomics* 18: e1700038. doi: 10.1002/pmc.201700038

Huang, W. J., Liu, H. K., McCormick, S., and Tang, W. H. (2014). Tomato pistil factor STIG1 promotes in vivo pollen tube growth by binding to phosphotidylinositol 3-phosphate and the extracellular domain of the pollen receptor kinase LePRK2. *Plant Cell* 26, 2505–2523. doi: 10.1105/tpc.114.123281

Huck, N., Moore, J. M., Federer, M., and Grossniklaus, U. (2003). The Arabidopsis mutant feronia disrupts the female gametophytic control of pollen tube reception. *Development* 130, 2149–2159. doi: 10.1242/dev.00458

Imin, N., Mohd-Radzman, N. A., Ogilvie, H. A., and Djordjevic, M. A. (2013). The peptide-encoding CEP1 gene modulates lateral root development in *Medicago truncatula*. *J. Exp. Bot.* 64, 5395–5409. doi: 10.1093/jxb/ert369

Katsir, L., Davies, K. A., Bergmann, D. C., and Laux, T. (2011). Peptide signaling in plant development. *Curr. Biol.* 21, R356–R364. doi: 10.1011/cb.2011.03.012

Kim, M. J., Jeon, B. W., Oh, E., Seo, P. J., and Kim, J. (2021). Peptide signaling during plant reproduction. *Trends Plant Sci.* doi: 10.1016/j.tplants.2021.02.008

Kishel, C. A., Morikis, D., Balasubramanian, S., et al. (2010). A multifaceted study of stigma/style cytokine-rich adhesion (SCA)-like Arabidopsis lipid transfer proteins (LTPs) suggests diversified roles for these LTPs in plant growth and reproduction. *J. Exp. Bot.* 61, 4277–4290. doi: 10.1093/jxb/erq228

Zhang et al. Small Peptides in Male-Female Interaction
Samuel, M. A., Chong, Y. T., Haassen, K. E., Aldea-Brydges, M. G., Stone, S. L., and Goring, D. R. (2009). Cellular pathways regulating responses to compatible and self-incompatible pollen in *Brassica* and *Arabidopsis* stigmas intersect at Exo70A1, a putative component of the exocytosis complex. *Plant Cell* 21, 2653–2671. doi: 10.1105/tpc.109.0969740

Schopfer, C. R., Nasrallah, M. E., and Nasrallah, J. B. (1999). The male determinant of self-incompatibility in *Brassica*. *Science* 286, 1697–1700. doi: 10.1126/science.286.5445.1697

Sprunk, S., Rademacher, S., Vogler, F., Gheyseleinck, J., Grossniklaus, U., and Dresselhaus, T. (2012). Egg cell-secreted EC1 triggers sperm cell activation during double fertilization. *Science* 338, 1093–1097. doi: 10.1126/science.1223944

Stein, J. C., Howlett, B., Boyes, D. C., Nasrallah, M. E., and Nasrallah, J. B. (1991). Molecular cloning of a putative receptor protein kinase gene encoded at the self-incompatibility locus of *Brassica oleracea*. *Proc. Natl. Acad. Sci. U. S. A.* 88, 8816–8820. doi: 10.1073/pnas.88.19.8816

Stotz, H. U., Spence, B., and Wang, Y. (2009a). A defensin from tomato with dual function in defense and development. *Plant Mol. Biol.* 71, 131–143. doi: 10.1007/s11103-009-9512-z

Stotz, H. U., Thomson, J. G., and Wang, Y. (2009b). Plant defensins: defense, development and application. *Plant Signal. Behav.* 4, 1010–1012. doi: 10.4161/psb.4.11.9755

Takahashi, F., Suzuki, T., Osakabe, Y., Betsuyaku, S., Kondo, Y., Dohmee, N., et al. (2018). A small peptide modulates stomatal control via abscisic acid in long-distance signalling. *Nature* 556, 235–238. doi: 10.1038/s41586-018-0009-2

Takayama, S., and Iosogi, A. (2005). Self-incompatibility in plants. *Annu. Rev. Plant Biol.* 56, 467–489. doi: 10.1146/annurev.arplant.56.032604.144249

Takayama, S., Shiba, H., Iwano, M., Shimosato, H., Che, F. S., Kai, N., et al. (2000). The pollen determinant of self-incompatibility in *Brassica campestris*. *Proc. Natl. Acad. Sci. U. S. A.* 97, 1920–1925. doi: 10.1073/pnas.040556397

Takeuchi, H., and Higashiyama, T. (2012). A species-specific cluster of defensin-like genes encodes diffusible pollen tube attractants in *Arabidopsis*. *PLoS Biol.* 10:e1001449. doi: 10.1371/journal.pbio.1001449

Takeuchi, H., and Higashiyama, T. (2016). Tip-localized receptors control pollen tube growth and LURE sensing in *Arabidopsis*. *Nature* 331, 245–248. doi: 10.1038/nature17413

Taleski, M., Imin, N., and Djordjevic, M. A. (2016). New role for a CEP peptide and its receptor: complex control of lateral roots. *J. Exp. Bot.* 67, 4797–4799. doi: 10.1093/jxb/erw306

Taleski, M., Imin, N., and Djordjevic, M. A. (2018). CEP peptide hormones: key players in orchestrating nitrogen-demand signalling, root nodulation, and lateral root development. *J. Exp. Bot.* 69, 1829–1836. doi: 10.1093/jxb/erz037

Tang, W., Ezzurra, I., Muschietti, J., and McCormick, S. (2002). A cysteine-rich extracellular protein, LAT52, interacts with the extracellular domain of the pollen receptor kinase LePRK2. *Plant Cell* 14, 2277–2287. doi: 10.1105/tpc.016873

Tang, W., Kelley, D., Ezzurra, I., Cotter, R., and McCormick, S. (2004). LeSTIG1, an extracellular binding partner for the pollen receptor kinases LePRK1 and LePRK2, promotes pollen tube growth in vitro. *Plant J.* 39, 343–353. doi: 10.1111/j.1365-313X.2004.02139.x

Vehoheven, T., Feron, R., Wolters-Arts, M., Edqvist, J., Gerats, T., Derksen, J., et al. (2005). STIG1 controls exudate secretion in the pistil of petunia and tobacco. *Plant Physiol.* 138, 153–160. doi: 10.1104/pp.104.054809

von Besser, K., Frank, A. C., Johnson, M. A., and Preuss, D. (2006). *Arabidopsis HAP2* (GCS1) is a sperm-specific gene required for pollen tube guidance and fertilization. *Development* 133, 4761–4769. doi: 10.1242/dev.02683

Wang, L., Clarke, L. A., Eason, R. J., Parker, C. C., Qi, B., Scott, R. J., et al. (2017). PCP-B class pollen coat proteins are key regulators of the hydration checkpoint in *Arabidopsis thaliana* pollen-stigma interactions. *New Phytol.* 213, 764–777. doi: 10.1111/nph.14162

Wang, T., Liang, L., Xue, Y., Jia, P. F., Chen, W., Zhang, M. X., et al. (2016). A receptor heteromer mediates the male perception of female attractants in plants. *Nature* 531, 241–244. doi: 10.1038/nature16975

Wetters, K., and Russell, S. D. (2004). Experimental analysis of the fertilization process. *Plant Cell* 16(Suppl), S107–S118. doi: 10.1105/tpc.104.069740

Zhang, D., Wengier, D., Shuai, B., Gui, C. P., Muschietti, J., McCormick, S., et al. (2008). The pollen receptor kinase LePRK2 mediates growth-promoting signals and positively regulates pollen germination and tube growth. *Plant Physiol.* 148, 1368–1379. doi: 10.1104/pp.108.124420

Ziemann, S., van der Linde, K., Lahrmann, U., Acar, B., Kaschani, F., Colby, T., et al. (2018). An apoplastic peptide activates salicylic acid signalling in maize. *Nat. Plants* 4, 172–180. doi: 10.1038/s41477-018-0116-y

**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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