Journal of Experimental Botany, Vol. 76, No. 7 pp. 1907–1920, 2025
https://doi.org/10.1093/jxb/eraf071 Advance Access Publication 20 February 2025

REVIEW PAPER

Jack of all trades: crosstalk between FERONIA signaling and hormone pathways

Jie Tang and Hongqing Guo*

Department of Genetics, Development and Cell Biology, Iowa State University, Ames, IA 50011, USA

* Correspondence: hguo@iastate.edu

Received 17 July 2024; Editorial decision 14 February 2025; Accepted 14 February 2025

Editor: Paula McSteen, University of Missouri, USA

Abstract

The receptor kinase FERONIA (FER) is a multifaceted regulator of plant growth, development, reproduction, and stress responses. FER is functionally connected to many plant hormones in diverse biological processes. This review summarizes the current understanding of the interplay between FER and phytohormones, with a focus on abscisic acid, ethylene, jasmonic acid, auxin, and brassinosteroid. The mutual regulation between FER and plant hormones happens at multiple levels including ligands, receptors, and downstream signaling components. Plant hormones can regulate the expression of genes encoding FER and its ligands RAPID ALKALINIZATION FACTORs (RALFs) as well as the abundance and kinase activity of FER proteins. On the other hand, FER can regulate hormone biosynthesis, transport, perception, and downstream signaling components such as transcription factors. Evidence of the crosstalk between FER and phytohormones is also emerging in crop species. Despite the rapid progress made in this field, more mechanistic studies are still needed to gain a comprehensive understanding of the FER–phytohormone crosstalk. Future research prospects and potential approaches are also discussed in this review.

Keywords: Abscisic acid, auxin, brassinosteroid, ethylene, FERONIA receptor kinase, jasmonic acid, peptide ligand, plant growth and stress responses, plant hormones.

Introduction

As sessile organisms, plants constantly sense the environment and reprogram their biological processes to adapt to the environment and survive challenging conditions. During this process, receptor-like kinases (RLKs) are important components that perceive environmental cues, transduce extracellular signals into the cell, and regulate downstream pathways, which eventually leads to changes in plant growth and development as well as responses to various stresses.

In Arabidopsis, there are >300 genes encoding RLKs (Shiu and Bleecker, 2001). A typical RLK has three major domains: an extracellular domain that is usually diverse among different families of RLKs; a single transmembrane domain, and an intracellular kinase domain that usually phosphorylates and modulates downstream targets to control cellular responses (Jose *et al.*, 2020). In Arabidopsis, FERONIA (FER) was the first characterized member of an RLK subfamily designated as *Catharanthus roseus* Receptor-like kinase 1-like (CrRLK1-like) or Malectin-like receptor kinases (MLRs) due to the presence of two tandem malectin-like domains in the extracellular region (Huck *et al.*, 2003; Rotman *et al.*, 2003; Escobar-Restrepo *et al.*, 2007). This subfamily includes 17 members in Arabidopsis with diverse biological functions (Huck et al., 2003; Escobar-Restrepo et al., 2007; Hematy et al., 2007; Boisson-Dernier et al., 2009; Guo et al., 2009a, b; Miyazaki et al., 2009; Deslauriers and Larsen, 2010; Duan et al., 2010; Bai et al., 2014; Gachomo et al., 2014; Ge et al., 2017; Richter et al., 2018; Galindo-Trigo et al., 2020; Huang et al., 2020; Liu et al., 2020). FERONIA, named after the Etruscan goddess of fertility, was first identified with a critical role in female reproduction, with pollen tube overgrowth and failure to release sperm for fertilization in loss-of-function mutants, leading to compromised fertility (Huck et al., 2003; Escobar-Restrepo et al., 2007). In the past two decades, tremendous progress has been made in deciphering the functions and underlying molecular mechanisms of FER. FER has been established as a multifaceted receptor kinase playing important roles in many aspects of the life of plants, including reproduction (Huck et al., 2003; Escobar-Restrepo et al., 2007; Duan et al., 2014, 2020; Ge et al., 2017; Galindo-Trigo et al., 2020; Liu et al., 2021; Zhong et al., 2022; Huang et al., 2023; Lan et al., 2023), vegetative growth (Guo et al., 2009a), root development (Duan et al., 2010; Yu et al., 2020; Zhu et al., 2020a, b; Xu et al., 2024a), pavement cell development (Lin et al., 2022; Tang et al., 2022), mechanosensing (Shih et al., 2014; Malivert et al., 2021; Darwish et al., 2022; Tang et al., 2022), responses to abiotic stresses, such as salt (Feng et al., 2018; Zhao et al., 2018; Liu et al., 2023) and heat (Yin et al., 2018), and responses to biotic stresses, such as bacteria (Keinath et al., 2010; Stegmann et al., 2017; Guo et al., 2018; Song et al., 2021), fungal pathogens (Kessler et al., 2010; Masachis et al., 2016), and nematodes (Zhang et al., 2020).

Our current understanding on the FER receptor kinase signaling pathway is that FER and co-receptors LORELEI (LRE) and LORELEI-LIKE GLYCOSYLPHOSPHATIDYLINOSITOL-ANCHORED PROTEIN 1/2/3 (LLG1/2/3) perceive the extracellular RAPID ALKALINIZATION FACTOR (RALF) family peptide ligands at the plasma membrane to form the FER/LRE(LLG)/RALF tripartite complex (Haruta et al., 2014; Li et al., 2015; Xiao et al., 2019; Cheung, 2024), which functions through other membrane and cytoplasmic proteins to regulate diverse biological processes. At the plasma membrane, in addition to the FER/LRE(LLG)/RALF tripartite complex, cell wall-associated proteins LEUCINE-RICH REPEAT EXTENSINs (LRXs) also play important roles in FER-mediated signaling, by interacting with ligand RALFs or the FER receptor (Mecchia et al., 2017; Zhao et al., 2018; Dunser et al., 2019; Herger et al., 2020; Moussu et al., 2020, 2023; Schoenaers et al., 2024). Moreover, the cell wall component pectin is involved in FER signaling by associating with LRXs, RALFs, and/or FER directly (Feng et al., 2018; Gigli-Bisceglia et al., 2022; Tang et al., 2022; Moussu et al., 2023; Liu et al., 2024). *FER* is expressed broadly, and tissue-specific assembly of this signaling complex is a major way in which FER can carry out diverse functions. FER and the RALF23 complex play important roles in plant immunity (Stegmann et al., 2017; Guo et al., 2018). FER, RALF23, and the LRX3/4/5 complex regulate salt stress response (Zhao et al., 2018, 2021). FER and the LRX3/4/5 complex regulate vacuolar expansion, root hair growth, and vegetative growth (Dunser et al., 2019; Herger et al., 2020). In the process of pollen tube reception at the ovule, during which the pollen tube enters the female gametophyte and bursts to release sperm cells, male- and female-specific FER signaling complexes are involved (Kessler and Grossniklaus, 2011; Ogawa and Kessler, 2023; Baillie et al., 2024; Cheung, 2024; Zhong et al., 2024). In the female gametophyte, FER functions together with homologs HERCULES1 (HERK1)/ANJEA, co-receptor LRE, and pollen-derived ligands RALF6/7/16/36/37 to regulate pollen tube reception by mediating pollen tube rupture, polytubey block, and fertilization recovery (Galindo-Trigo et al., 2020; Zhong et al., 2022). On the other hand, pollen-specific homologs ANXUR1 (ANX1)/ANX2/BUDDHAS PAPER SEAL 1 (BUPS1)/BUPS2 function with co-receptors LLG2/3 (Ge et al., 2019). Pollen-derived ligands RALF4/19 bind to the receptors to maintain pollen tube integrity during pollen tube growth, while female-derived ligand RALF34 competes with RALF4/19 during pollen tube reception to induce pollen tube bursting (Ge et al., 2017, 2019). Recent studies have shown that LRX8, RALF4, and pectin form a compact complex for cell wall patterning in pollen tube growth (Moussu et al., 2023), and the LRX1/2, RALF22, and pectin complex leads to pectin compaction at the root hair tip to form periodic rings to regulate polar growth. RALF1/23 and pectin association can lead to liquid–liquid phase separation (LLPS) and form condensates with LLG1 and FER to trigger extensive endocytosis, including FER, LLG1, and membrane proteins involved in other signaling pathways such as brassinosteroid (BR) receptor, BRASSINOSTEROID INSENSITIVE 1 (BRI1), and auxin transporters PIN-FORMED 2 (PIN2) and AUXIN RESISTANT 1 (AUX1), potentially mediating the crosstalk between FER and these signaling pathways (Liu et al., 2024). It is worth noting that in addition to the 17 FER receptor kinase homologs in Arabidopsis, there are four co-receptor genes (*LRE/LLG1/2/3*) (Li et al., 2015; Noble et al., 2022), 37 ligand *RALF* genes (Abarca et al., 2021), and 11 *LRX* genes (Herger et al., 2019) which, together with cell wall pectin, can form diverse signaling complexes at the cell membrane.

FER signaling perceived at the plasma membrane is further mediated by many downstream effector proteins. It has been shown that FER interacts with a family of guanine nucleotide exchange factors (GEFs) to activate RHO GTPases to regulate root hair growth, abscisic acid (ABA) signaling, pavement cell development, and reactive oxygen species (ROS)-mediated pollen tube rupture (Duan et al., 2010, 2014; Yu et al., 2012; Lin et al., 2022; Tang et al., 2022). Another well-characterized downstream component is NORTIA (NTA), also known as MILDEW RESISTANCE LOCUS O 7 (MLO7) (Kessler et al., 2010; Jones et al., 2017; Ju et al., 2021; Gao et al., 2022). NTA was originally identified in a forward genetic screen for pollen overgrowth phenotype, downstream of the *fer-1* mutant

(Kessler *et al.*, 2010). NTA belongs to a family of 15 members in Arabidopsis and is localized on the Golgi apparatus. Upon pollen tube arrival, NTA re-localizes to the filiform apparatus in the synergid cells in a FER-dependent manner (Ju *et al.*, 2021). It was further demonstrated that NTA is a calmodulin-gated Ca^{2+} channel and is relocated to the plasma membrane in the synergid cells by the RALF4/19–FER–LRE signaling complex to increase the amplitude of Ca^{2+} oscillations, which is critical for pollen tube reception (Ngo *et al.*, 2014; Gao *et al.*, 2022). A genetic screen also identified that *TURAN* and *EVAN*, involved in protein *N*-glycosylation in the endoplasmic reticulum (ER), function downstream of *FER* in mediating pollen tube reception (Lindner *et al.*, 2015). Moreover, FER regulates the TARGET OF RAPAMYCIN (TOR) signaling pathway, a major pathway for nutrient homeostasis, to regulate autophagy and root hair growth under low temperature (Wang *et al.*, 2022b; Pacheco *et al.*, 2023).

Many other proteins including transcription factors (TFs) have been shown to play important roles in FER signaling. An integrated multiomic study showed that FER regulates ~500 TFs at transcription, protein, and/or phosphorylation levels, which is consistent with the finding that FER signaling involves major transcriptome reprogramming by mediating the expression of thousands of genes (Guo *et al.*, 2018; Wang *et al.*, 2022a). FER was shown to phosphorylate and stabilize PHYTOCHROME INTERACTING FACTOR 3 (PIF3) to promote root penetration (Xu *et al.*, 2024a). RNA-binding protein GLYCINE-RICH RNA BINDING PROTEIN 7 (GRP7) regulates FER-mediated temperature stress through LLPS in a FER phosphorylation-dependent manner (Wang *et al.*, 2020; Xu *et al.*, 2024b). FER also regulates initiation factor EUKARYOTIC TRANSLATION INITIATION FACTOR 4E1 (eIF4E1) and tRNA-binding protein YUELAO for protein synthesis (Zhu *et al.*, 2020a, 2023). More recently, it has been shown that FER phosphorylates the red light receptor phytochrome B (phyB) to promote its dark conversion from the active form (Pfr) to the inactive form (Pr) to regulate plant growth and salt stress response (Liu *et al.*, 2023).

FER receptor kinase plays diverse roles in the life of a plant and has been established as a critical regulator in coordinating plant growth, development, stress responses, and reproduction. Many recent excellent reviews covered different aspects of the exciting progress in understanding the functions of FER and the underlying molecular mechanisms (Xie *et al.*, 2022; Malivert and Hamant, 2023; Ogawa and Kessler, 2023; Baillie *et al.*, 2024; Cheung, 2024; Zhong *et al.*, 2024). In this review, we will focus on the crosstalk between FER signaling and phytohormone pathways. FER is functionally connected with various plant hormones, such as auxin, ABA, BRs, ethylene (ET), and jasmonic acid (JA). The crosstalk between FER and plant hormones plays important roles in plant growth and stress responses (Guo *et al.*, 2009a, b, 2018; Deslauriers and Larsen, 2010; Duan *et al.*, 2010; Yu *et al.*, 2012; Chen *et al.*, 2016; Dong *et al.*, 2019; Li *et al.*, 2020; Lu *et al.*, 2024). Here, we summarize recent findings on the connections between FER and various hormone pathways, and discuss directions for future research.

FERONIA and abscisic acid

ABA is an important plant hormone that regulates plant development and stress responses (Raghavendra *et al.*, 2010). The perception of ABA in plants is mediated by a family of intracellular receptors named PYRABACTIN RESISTANCE/PYRABACTIN RESISTANCE-LIKE/REGULATORY COMPONENTS OF ABA RECEPTOR (PYR/PYL/RCAR) (Ma *et al.*, 2009; Park *et al.*, 2009). In the presence of ABA, ABA-bound PYR/PYL/RCARs form a complex with clade A protein phosphatase 2C (PP2C), ABA INSENSITIVE 1 (ABI1), and ABI2, and suppress its function, leading to the activation of SNF1-RELATED PROTEIN KINASE 2 (SnRK2) and downstream responses (Fujii *et al.*, 2009; Ma *et al.*, 2009; Park *et al.*, 2009).

Three *fer* mutants, namely *fer-4*, *fer-5*, and *srn*, are more sensitive to ABA treatment than wild-type (WT) plants, with enhanced growth inhibition, stomatal closure, and decreased germination rate (Yu *et al.*, 2012; Wang *et al.*, 2022a). It has been shown that RHO-RELATED GTPASES FROM PLANTS (ROPs) play a role in ABA signaling (Zheng *et al.*, 2002) (Fig. 1A; Table 1). ROPs are RHO GTPases that mediate responses to developmental stimuli and environmental stresses (Feiguelman *et al.*, 2018). A family of GEFs called ROPGEFs is responsible for converting GDP-bound inactive ROPs to GTP-bound active ROPs (Ou and Yi, 2022). FER is known to interact with ROPGEFs and is necessary for activating ROPs (Duan *et al.*, 2010). ROP11 binds to FER-interacting ROPGEFs including GEF1, GEF4, and GEF10 (Yu *et al.*, 2012). The active form of ROP11 interacts with ABI2, a member of PP2C and the ABA receptor complex, and activates its phosphatase activity (Yu *et al.*, 2012). Taken together, FER inhibits ABA signaling by activating ABI2 through the the FER–ROPGEF–ROP11 pathway (Fig. 1A). On the other hand, ABI2 directly interacts with and dephosphorylates FER, indicating the existence of a feedback regulation mechanism (Chen *et al.*, 2016) (Fig. 1A; Table 1). It remains to be determined if FER phosphorylation of ABI2 affects ABA perception by the ABI2/PYR/PYL/RCAR receptor complex.

FER can affect ABA signaling and responses through not only ABI2 but also other mechanisms. Multi-omics data showed that FER phosphorylates ABA-related TFs, ABSCISIC ACID RESPONSIVE ELEMENT0S-BINDING FACTOR 3 (ABF3) and ABI5, suggesting that FER can regulate ABA signaling through these TFs (Wang *et al.*, 2022a). Indeed, FER negatively regulates ABI5 by directly phosphorylating ABI5 at Ser145 and destabilizing ABI5 protein, leading to FER-regulated seed germination (Wang *et al.*, 2022a) (Fig. 1A; Table 1). The mechanism underlying FER phosphorylation of ABI5 leading to its instability is currently unknown.

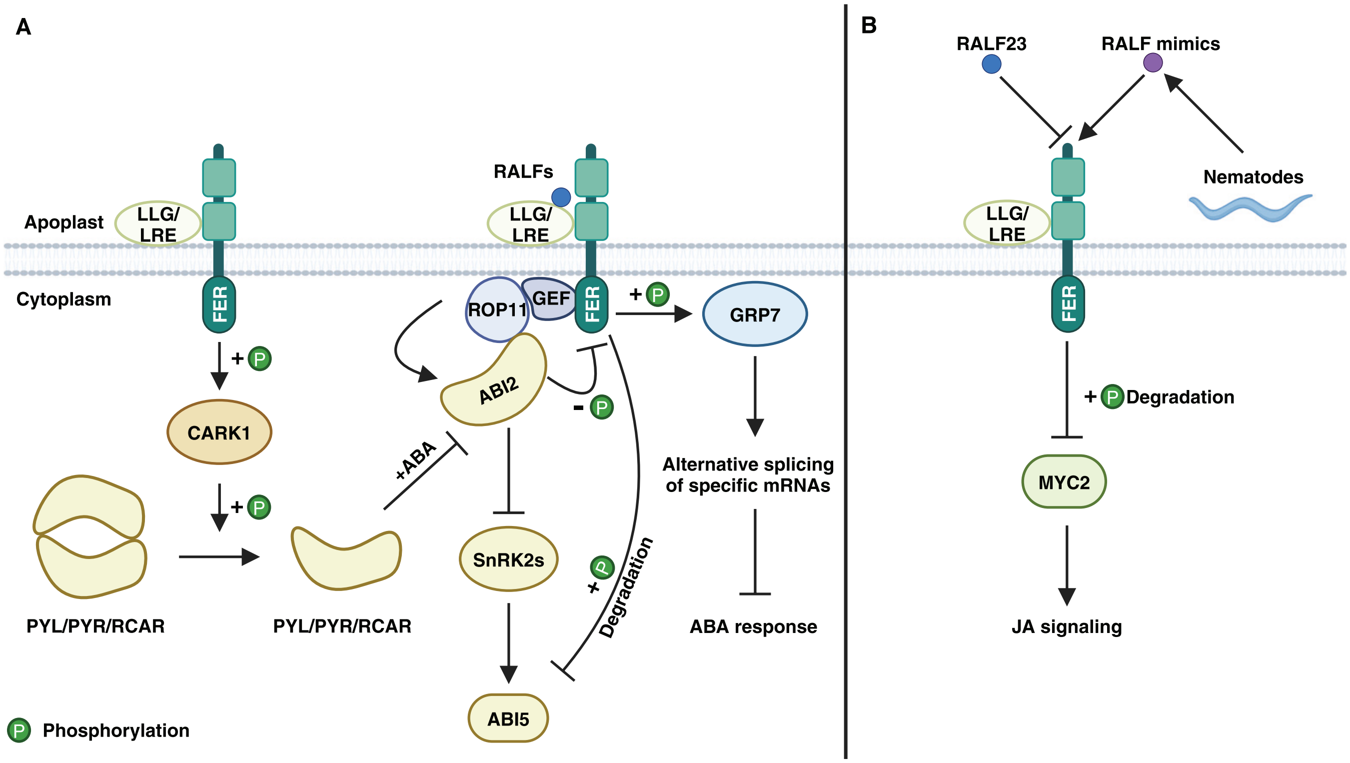

Fig. 1. The crosstalk between FER and ABA and JA pathways. (A) The crosstalk between FER and ABA. In the presence of ABA, ABA-bound PYR/PYL/RCARs form a complex with ABI2 and suppress its phosphatase activity, leading to the activation of SnRK2s and downstream responses including transcriptional responses mediated by transcription factor ABI5. FER can activate ABI2 through the FER–GEF1/4/10–ROP11 module to inhibit ABA signaling. ABI2 can dephosphorylate FER as a negative feedback mechanism. In addition, FER can directly phosphorylate and destabilize ABI5 to inhibit ABA signaling. RALF1–FER binding triggers phosphorylation of GRP7, which promotes GRP7-mediated alternative splicing of ABA-related mRNAs, leading to negative regulation of ABA signaling. FER phosphorylates CARK1 and activates CARK1-mediated phosphorylation of ABA receptors PYR/PYL/RCARs to promote their monomerization, which enhances ABA binding and signaling. (B) The crosstalk between FER and JA. FER phosphorylates and destabilizes MYC2, a master transcription factor that promotes JA signaling. RALF23 inhibits FER function to stabilize MYC2. Parasitic nematodes can secrete RALF mimics to activate FER-mediated MYC2 degradation, which promotes parasitism. Created in BioRender. Tang, J. (2025) https://BioRender.com/w89v501.

It has also been shown that FER negatively regulates ABA biosynthesis. The *fer-4* mutant has an elevated ABA level, which can be suppressed by the ABA DEFICIENT 2 (ABA2) mutation that disrupts ABA biosynthesis (Zhao *et al.*, 2021) (Table 1). Recently, it was reported that FER interacts with and phosphorylates GRP7, which promotes the association of GRP7 with the spliceosome and modulates alternative splicing of many genes involved in ABA signaling (Wang *et al.*, 2020). Similar to the *fer-4* mutant, the loss-of-function *grp7* mutant shows hypersensitivity to ABA treatment (Wang *et al.*, 2020). Further analysis showed that the role of GRP7 in ABA signaling is dependent on FER phosphorylation (Wang *et al.*, 2020) (Fig. 1A). Transcriptome analysis showed that FER-regulated genes heavily overlap with ABA-regulated genes (Guo *et al.*, 2018), and FER regulates many biological processes involving ABA signaling such as seed germination and salt stress response (Zhao *et al.*, 2018, 2021; Wang *et al.*, 2022a). Systematic analysis of how FER modulates major TFs in the ABA pathway to regulate downstream gene expression and ABA responses will expand our understanding of the crosstalk of these two major pathways.

Moreover, MARIS, a receptor-like cytoplasmic kinase, originally identified as a downstream signaling component of ANX1/2 in regulating pollen tube elongation, also functions downstream of FER to regulate root hair growth (Boisson-Dernier *et al.*, 2015). It was shown that MARIS/CYTOSOLIC ABA RECEPTOR KINASES 4 (CARK4) functions together with other CARK homologs CARK5/2/7/11 to phosphorylate homo- or heterodimerized ABA receptors RCAR3/11/12/13/14 to promote their monomerization, leading to enhanced ABA binding and signaling (X. Li et al., 2022). More recently, it was reported that FER interacts with and phosphorylates CARK1 to activate CARK1 kinase activity, which positively regulates ABA-mediated early seed germination, signified by radicle protrusion (Wang *et al.*, 2024) (Fig. 1A; Table 1). This is opposite to the role that FER plays during late-stage seed germination (cotyledon greening) and post-germination growth, where FER negatively regulates

Table 1. Crosstalk between FER and plant hormones

Regulation of plant hormone signaling pathways by FER				
Hormones	Processes regulated by FER	Genes/proteins regulated by FER	Functions of FER	References
ABA	Biosynthesis	Unknown	Negatively regulating ABA biosynthesis	Zhao *et al.* (2021)
	Perception	PYLs/PYRs/RCARs	Positively regulating ABA signaling by phosphorylating CARK1 and activating CARK1-mediated phosphorylation of PYLs/PYRs/RCARs	Wang *et al.* (2024)
	Dephosphorylation of SnRK2s	ABI2	Negatively regulating ABA signaling by phosphorylating ABI2 and activating its phosphatase activity	Yu *et al.* (2012)
	Transcriptional responses	ABI5	Negatively regulating ABA signaling by phosphorylating ABI5 and destabilizing ABI5 protein	Wang *et al.* (2022a)
JA	Biosynthesis	LIPOXYGENASE 3/4 (LOX3/4), ALLENE OXIDE CYCLASE 3 (AOC3), OXOPHYTODIENOATE-REDUCTASE 3 (OPR3)	Negatively regulating JA biosynthesis by suppressing the expression of JA biosynthetic genes	Zhao *et al.* (2021); Darwish *et al.* (2022)
	JAZ-mediated repression	JAZ1, JAZ7, JAZ8	Possibly regulating the expression of *JAZ* genes and stability of JAZ proteins	Zhao *et al.* (2021); Darwish *et al.* (2022)
	Transcriptional responses	MYC2	Negatively regulating JA signaling by phosphorylating MYC2 and destabilizing MYC2 protein	Guo *et al.* (2018)
Auxin	Biosynthesis	YUC5/6/11	Positively regulating the expression of *YUCCA* genes	L. Li *et al.* (2022)
	Transport	PIN2/3	Required for proper cellular trafficking and distribution of PINs	Dong *et al.* (2019; Li *et al.* (2020); C.Y. Li et al. (2022)
	Perception	TIR1, AFB2	Positively regulating auxin signaling by promoting TIR1/AFB2 oxidation	Lu *et al.* (2024)
ET	Biosynthesis	SAM1/2	Interacting with SAMs and negatively regulating ET biosynthesis	Mao *et al.* (2015)
SA	Biosynthesis	Unknown	Negatively regulating SA biosynthesis	Zhao *et al.* (2021); Jing *et al.* (2022)
Regulation of FER/RALFs by plant hormones				
Hormones	Processes regulated by hormones	Hormone signaling components involved	Mechanisms	References
ABA	FER phosphorylation	ABI2	ABI2 interacts with FER and dephosphorylates FER	Chen *et al.*, 2016)
BR	Expression of *FER* and *RALF23*	BES1/BZR1	BES1/BZR1 binds to the promoter of FER and possibly the promoter of *RALF23* to regulate expression	Srivastava *et al.* (2009); Yin *et al.* (2018)
ET	Expression of *FER*	Unknown	ET induces the expression of *FER*	Deslauriers and Larsen (2010)
GA	Expression of *FER*	Unknown	GA induces the expression of *FER*	Guo *et al.* (2009a)

ABA signaling (Yu *et al.*, 2012; Wang *et al.*, 2022a). How FER differentially regulates ABA signaling at different development stages remains to be elucidated.

FERONIA and jasmonic acid

JA is a major stress-related plant hormone mediating responses to pathogens and herbivores (Carvalhais *et al.*, 2017). JA signaling is a repressor degradation-type pathway. When the level of the active form of JA, JA-isoleucine (JA-Ile), is low, repressor proteins JASMONATE-ZIM DOMAIN PROTEINs (JAZs) bind to and repress TFs such as MYC2, MYC3, and MYC4 (Chini *et al.*, 2007; Fernandez-Calvo *et al.*, 2011). When levels of JA-Ile are high, JA-Ile triggers the formation of a ligand–receptor complex with the F-box protein CORONATINE INSENSITIVE1 (COI1) and JAZs, leading to ubiquitination and degradation of JAZs (Sheard *et al.*, 2010). Thus, TFs are released to regulate JA-responsive genes. The JA signaling pathway can be hijacked by pathogens to promote virulence. For instance, the bacterial pathogen *Pseudomonas syringae* produces a toxin coronatine (COR), a mimic of JA-Ile, to activate TFs ANAC019, ANAC055, and ANAC072 via MYC2, leading to stomatal reopening and inhibition of salicylic acid (SA) accumulation to promote bacterial infection (Zheng *et al.*, 2012).

A transcriptome comparison between the WT and *fer-4* mutant identified that JA and FER pathways antagonistically regulate a large number of genes (Table 1). The *fer-4* mutant has constitutive expression of JA-responsive genes and is more susceptible to *P. syringae* (Guo *et al.*, 2018). Mechanistic analysis showed that FER interacts with and phosphorylates MYC2, causing the destabilization of MYC2 (Guo *et al.*, 2018) (Fig. 1B; Table 1). Mature RALF23 peptide, induced by bacterial pathogens (Stegmann *et al.*, 2017), is also involved in the crosstalk between FER and MYC2-mediated JA signaling.

RALF23-overexpressing plants showed similar phenotypes to the *fer-4* mutant, including hypersensitivity to JA, higher susceptibility to *P. syringae*, and higher accumulation of MYC2 proteins, providing evidence that RALF23 negatively regulates FER function in FER and JA crosstalk (Guo *et al.*, 2018). Taken together, FER negatively regulates JA signaling by phosphorylating and destabilizing MYC2, and contributes to bacterial defense. However, how FER phosphorylation of MYC2 leads to its instability needs further examination.

RALF-like genes have been identified in fungal pathogens. *Fusarium oxysporum* produces RALF peptide which interacts with host FER to achieve virulence (Masachis *et al.*, 2016; Thynne *et al.*, 2017). Therefore, it is conceivable that a FER–MYC2 module is also involved in the fungus–plant interaction. A similar RALF–FER–MYC2 mechanism also exists in the parasitism of the root-knot nematode (RKN) *Meloidogyne incognita*. When compared with WT plants, multiple *fer* mutants, including *fer-4*, *fer-5*, and *srn*, are more resistant to *M. incognita*, suggesting that FER is negatively involved in RKN resistance (Zhang *et al.*, 2020). Eighteen RALF-like genes were identified across genomes of six different *Meloidogyne* species (Zhang *et al.*, 2020). These nematode *RALF* genes are expressed in the esophageal gland at the parasitic stages and display similar activities to Arabidopsis RALF1, such as inhibition of root growth, alkalization of the extracellular medium, and global gene expression changes in plants treated with RALFs (Zhang *et al.*, 2020). Nematode RALFs also bind to FER, and the protein levels of MYC2 are reduced in plants treated with nematode RALFs, suggesting that nematodes can suppress JA signaling via FER-mediated MYC2 degradation (Zhang *et al.*, 2020) (Fig. 1B). Whether or not this trans-kingdom RALF–FER interaction is a common mechanism underlying plant biotic interactions needs further investigation.

Apart from plant–pathogen interactions, there is evidence suggesting that the crosstalk between FER and JA signaling may play an important role in touch signaling and thigmomorphogenesis. Thigmomorphogenesis refers to mechanically induced responses in plants. Some typical changes are reduced shoot elongation, increased radial expansion, and delayed flowering (Chehab *et al.*, 2009). In *fer-2* and *fer-4* mutants, mechanically induced Ca^{2+} signals are either blocked or show different signatures (Shih *et al.*, 2014). Touch-responsive genes, such as *TOUCH 4* (*TCH4*), are less induced in *fer-2* and *fer-4* mutants in response to mechanical stimuli (Shih *et al.*, 2014). However, the expression of JA-associated touch-inducible genes, such as *JAZ8* and many JA biosynthesis components, is significantly up-regulated in *fer-4* mutant under both untouched and touched conditions, suggesting that FER is a negative regulator of JA signaling in the context of the touch response (Darwish *et al.*, 2022) (Table 1). Transcriptome analysis of the *fer-4* mutant and *myc2myc3myc4* triple mutant suggested that *fer-4* and *myc2myc3myc4* showed almost completely opposite responses to touching, especially in the expression of JA-associated genes, suggesting that FER may negatively regulate JA signaling through MYC TFs during touching response.(Darwish *et al.*, 2022).

FERONIA and auxin

Auxin plays important roles in regulating plant growth and development. One well-characterized auxin signaling pathway involves ubiquitin-mediated degradation of repressor proteins (Leyser, 2018). In this pathway, auxin response is mainly mediated through genes activated by a family of TFs named AUXIN RESPONSE FACTOR (ARF). When auxin is not present, Aux/IAA transcription repressors bind to ARFs and inhibit their transcription activity. In the presence of auxin, auxin mediates the binding of Aux/IAAs to F-box proteins of the TRANSPORT INHIBITOR RESPONSE 1/AUXIN SIGNALING F-BOX (TIR1/AFB) family, leading to the ubiquitination and degradation of Aux/IAAs and hence activation of ARF-induced genes (Gray *et al.*, 2001; Tan *et al.*, 2007; Maraschin Fdos *et al.*, 2009). A plasma membrane-localized rapid auxin response pathway involving AUXIN BINDING PROTEIN 1 (ABP1) and TRANSMEMBRANE KINASE 1 (TMK1) has been characterized (Xu *et al.*, 2014; Friml *et al.*, 2022; Yu *et al.*, 2023). In this pathway, secreted ABP1/ABL1/ABL2 bind to extracellular auxin in the acidic apoplast and associate with TMK1 (Xu *et al.*, 2014; Friml *et al.*, 2022; Yu *et al.*, 2023). TMK1 phosphorylates >1000 substrate proteins, such as plasma membrane H^+-ATPases (AHAs), myosin XI, PIN auxin transporters, and members of the MITOGEN-ACTIVATED PROTEIN KINASE (MAPK) cascade, resulting in rapid responses including apoplast acidification and polar auxin transport (Li *et al.*, 2021; Lin *et al.*, 2021; Friml *et al.*, 2022; Fiedler and Friml, 2023).

FER was first connected to auxin when it was identified as an important player in root hair growth (Fig. 2A; Table 1). Under normal growth conditions, *fer-4* and *fer-5* mutants show a higher percentage of collapsed, arrested, or short root hairs when compared with WT plants (Duan *et al.*, 2010). When treated with auxin, WT plants showed further stimulated root hair growth, but *fer-4* and *fer-5* mutants did not respond (Duan *et al.*, 2010). It is known that root hair growth is triggered by auxin and ROS, which are both regulated by ROP GTPase signaling (Kanaoka and Torii, 2010). Overexpression of ROP2 in the *fer-5* mutant rescued the defective root hair phenotype, suggesting that ROP2 functions downstream of FER (Duan *et al.*, 2010). The level of GTP-bound active ROP2 is reduced in *fer-4* and *fer-5* mutants when compared with that in the WT, indicating that FER is necessary for ROP2 activation (Duan *et al.*, 2010). It was further demonstrated that the FER, ROPGEFs, and ROP2 module promoted the NADPH oxidase-dependent accumulation of ROS in roots and root hairs in response to auxin (Duan *et al.*, 2010) (Fig. 2A).

In addition, the co-receptor LLG1 is required for the FER-mediated ROS accumulation in response to auxin (Li *et al.*, 2015). An *llg1* mutant showed similar phenotypes to those

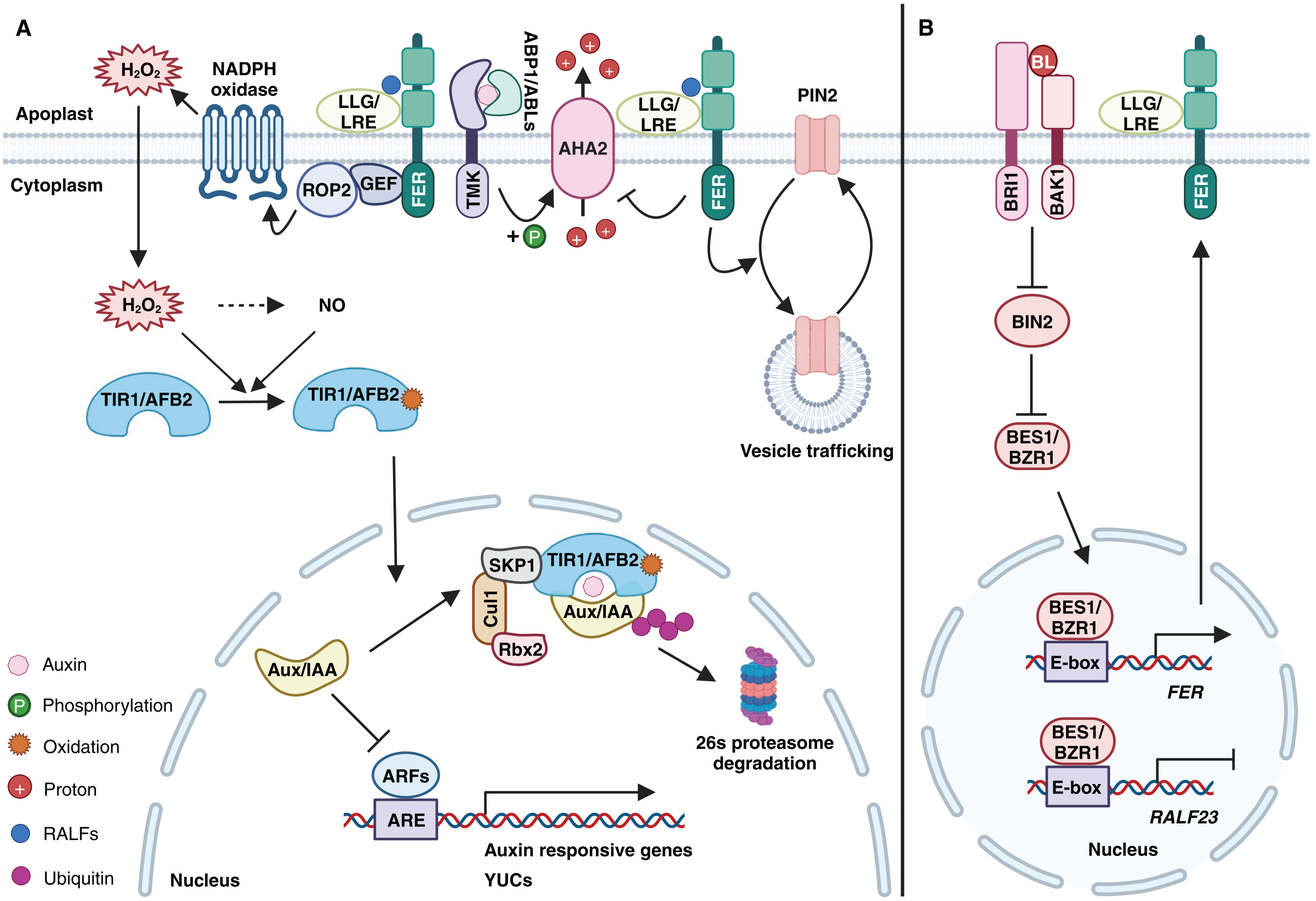

Fig. 2. The crosstalk between FER and auxin and BR pathways. (A) The crosstalk between FER and auxin. FER activates ROP2 through GEFs to promote NADPH oxidase-mediated ROS production and possibly NO production. ROS and NO are critical for oxidation of auxin receptors TIR1 and AFB2, which is important for their translocation from cytoplasm to nucleus. TIR1 and AFB2 are F-box proteins that form a complex with Cul1, Rbx2, and SKP1 to ubiquitinate and destabilize transcriptional repressors Aux/IAAs, leading to the activation of auxin-responsive genes. RALF1 treatment increases the expression of the auxin biosynthesis genes YUCs in a FER-dependent manner. RALF1–FER binding triggers phosphorylation of AHA2 and inhibits its activity. AHA2 is also phosphorylated and activated by TMKs, a family of receptor-like kinases that sense extracellular auxin together with ABP1/ABLs. In addition, FER is needed for proper cellular trafficking of the auxin transporter PIN2. (B) The crosstalk between FER and BR. In the presence of BR, BR perception by receptor BRI1 and co-receptor BAK1 leads to inhibition of BIN2 and activation of master transcription factors BES1/BZR1. In tomato, BZR1 binds to the promoters of *FER* genes and promotes *FER* expression, leading to enhanced FER function. In Arabidopsis, *RALF23* expression is reduced by BL treatment or in a gain-of-function *bes1-D* mutant. BES1-binding sites are identified in the promoter of the *RALF23* gene but whether BES1 directly regulate *RALF23* expression is not known. Created in BioRender. Tang, J. (2025) https://BioRender.com/u17o471.

observed in the *fer-4* mutant, including root hair defects and reduced ROS accumulation in response to auxin (Li *et al.*, 2015). A recent mechanistic study showed that the FER–LLG1–ROP2 module promoted ROS- and nitric oxide (NO)-mediated oxidation or *S*-nitrosylation of auxin receptors TIR1 and AFB2, which is important for translocation of TIR1 and AFB2 from the cytoplasm to the nucleus (Lu *et al.*, 2024). In the *fer-4* mutant, the oxidation levels of both TIR1 and AFB2 are reduced, leading to the retention of these proteins in the cytoplasm and reduced transcriptional auxin response (Lu *et al.*, 2024) (Fig. 2A; Table 1). It is worth further investigating whether FER-mediated TIR1/AFB2 oxidation is spontaneous or catalyzed by certain nitrosylases.

FER potentially regulates polar auxin transport. When compared with WT plants, the loss-of-function *fer-4* mutant displays reduced angles of curvature in response to a gravitropic stimulus due to deficient auxin redistribution (Barbez *et al.*, 2017; Dong *et al.*, 2019). It was found that the auxin efflux transporter PIN2 showed abnormal localization in the *fer-4* mutant, which is related to deficient membrane recycling of PIN2 and reduced stability of actin filaments (Dong *et al.*, 2019) (Fig. 2A; Table 1). In addition, the *fer-4* mutant showed enhanced asymmetrical root growth, indicated by the root growth behavior of anti-clockwise coils when grown on horizontal plates (Li *et al.*, 2020). This phenotype is related to asymmetric auxin distribution and can be suppressed by applying auxin transport inhibitors or introducing mutations in PIN2 or auxin influx transporter AUX1 (Li *et al.*, 2020). Altered PIN2 localization was also observed as the future concave side had more PIN2 proteins than the future convex side in the *fer-4* mutant root (Li *et al.*, 2020).

A similar mechanism may also exist in the context of phototropism. The Arabidopsis *fer-4* mutant showed attenuated phototropic hypocotyl bending in response to lateral blue light (C.Y. Li et al., 2022). This is partly due to the disrupted PIN3 localization that results in a disrupted auxin gradient (C.Y. Li et al., 2022) (Table 1). However, how FER regulates PIN localization and activity remains unknown. It has been shown that the MAP KINASE KINASE 7 (MKK7)–MAP KINASE 6 (MPK6) cascade phosphorylates PIN1 and determines its polarization (Jia *et al.*, 2016). PIN1 can also be phosphorylated by two receptor kinases, leading to altered subcellular trafficking and polarization during canalization (Hajny *et al.*, 2020). It is conceivable that FER can modify auxin transport and distribution through phosphorylating the transporters. Furthermore, RALF1–FER signaling can trigger auxin biosynthesis by up-regulating the transcription of the auxin biosynthesis genes, YUCCAs (YUCs), to inhibit root growth (L. Li *et al.*, 2022) (Fig. 2A; Table 1).

It is intriguing that the FER signaling pathway and the TMK-regulated pathway have a large degree of overlap. First, both TMKs and FER regulate ROP GTPases, and both FER and TMKs are required for the activation of ROP2 and ROP6 (Xu *et al.*, 2014). The level of activated ROP2 is also reduced in *fer* mutants (Duan *et al.*, 2010). Secondly, TMKs interact with and phosphorylate MKK4/5 to activate MKK4/5–MPK3/6 signaling in response to auxin, thus regulating lateral root development (Huang *et al.*, 2019). Several members of the MAPK cascade, including MPK3 and MPK6, have altered phosphorylation levels in the *fer-4* mutant, suggesting that the MAPK cascade could be involved in FER signaling (Wang *et al.*, 2022b).

Thirdly, both TMKs and FER have been shown to regulate apoplast pH through AHAs, although in an antagonistic manner. TMKs phosphorylate and activate AHAs, leading to rapid acidification of the apoplast (Li *et al.*, 2021; Lin *et al.*, 2021; Friml *et al.*, 2022). In contrast, RALF1–FER binding triggers phosphorylation of AHA2 at a different site, leading to reduced AHA2 activity (Haruta *et al.*, 2014) (Fig. 2A), although it was also shown that AHAs do not play a major role in RALF1–FER-mediated root growth inhibition (L. Li *et al.*, 2022). It has been shown that increasing the endogenous auxin level or applying exogenous auxin triggers a transient alkalinization of the apoplast, and this process is dependent on FER (Barbez *et al.*, 2017).

Finally, another connecting point is ABI2. It is reported that a high level of auxin enhances the ABA response through TMK1 (Yang *et al.*, 2021). TMK1 directly interacts with and phosphorylates ABI2, inhibiting the phosphatase activity of ABI2 (Yang *et al.*, 2021). Studies have also shown that FER activates ABI2, and ABI2 interacts with and dephosphorylates FER to inhibit its function through a feedback loop (Yu *et al.*, 2012; Chen *et al.*, 2016). Considering the extensive functional overlaps, it would be interesting to know how the two pathways interact and coordinate at the receptor and co-receptor level during auxin and other responses.

FERONIA and brassinosteroids

BRs are plant steroid hormones that play important roles in plant growth and development as well as responses to abiotic and biotic stresses (Nolan *et al.*, 2020). Tremendous progress has been made in understanding the BR signaling pathway. In short, when BR levels are low, a glycogen synthase kinase 3 (GSK3)-like kinase BRASSINOSTEROID INSENSITIVE 2 (BIN2) phosphorylates and inhibits the function of BRI1-EMS-SUPPRESSOR1 (BES1) and BRASSINAZOLE-RESISTANT1 (BZR1), two key TFs that control BR-related gene expression (Li and Nam, 2002). In the presence of BRs, they are perceived by plasma membrane-located receptor BRI1 and its co-receptor BRI1-ASSOCIATED KINASE 1 (BAK1), leading to the inhibition of BIN2 and activation of BES1 and BZR1 and BR signaling (Li and Chory, 1997; Z.Y. Wang et al., 2002; Yin *et al.*, 2002, 2005).

BR signaling can regulate *FER* gene expression. In Arabidopsis seedlings and adult plants, the expression of *FER* is induced by treatment of brassinolide (BL), the most active BR (Guo *et al.*, 2009a). When compared with that in WT plants, the expression of *FER* is down-regulated in a loss-of-function *bri1-5* mutant and up-regulated in the *bes1-D* mutant, a gain-of-function mutant with a constitutive BR response (Guo *et al.*, 2009a). Similarly, in tomato (*Solanum lycopersicum*), the expression of *FER* homologs is reduced in the *bzr1* mutant or *BRI1*-silenced plants but increased in *BZR1*-overexpressing plants (Yin *et al.*, 2018). The tomato BZR1 binds to the promoters of tomato *FER2* and *FER3* genes and induces their expression (Yin *et al.*, 2018) (Fig. 2B; Table 1).

Moreover, FER plays important roles in BR signaling and responses. In Arabidopsis, under light-grown conditions, a *fer-2* knockout mutant displays hypersensitivity to 24-epibrassinolide (EBL) when compared with WT plants, indicated by enhanced hypocotyl growth (Deslauriers and Larsen, 2010). This suggests that FER negatively regulates BR response. In contrast, under dark-grown conditions, the *fer-2* mutant is less responsive to EBL (Deslauriers and Larsen, 2010). In tomato, FER is also required for BR-induced ROS accumulation and heat stress tolerance (Yin *et al.*, 2018). These results suggest that the role of FER in the BR response is more complex and context dependent.

The crosstalk between FER and BR signaling also involves the peptide ligands, RALFs. The expression of *RALF23* is reduced in the *bes1-D* mutant when compared with WT plants, and treatment with BL further down-regulates *RALF23* expression in both WT and *bes1-D* plants (Srivastava *et al.*, 2009) (Fig. 2B; Table 1). Overexpressing *RALF23* reduces plant growth and compromises BL-induced hypocotyl elongation (Srivastava *et al.*, 2009). Similarly, BL-induced hypocotyl elongation is attenuated in *RALF1*-overexpressing plants (Bergonci *et al.*, 2014). These results indicate that RALF and BR function antagonistically (Srivastava *et al.*, 2009; Bergonci *et al.*, 2014; Haruta *et al.*, 2014; Stegmann *et al.*, 2017).

Although many reports have suggested a crosstalk between FER and BR signaling, detailed mechanisms remain to be fully defined. ABI1 and ABI2 have been shown to interact with and dephosphorylate BIN2 to inhibit its kinase activity (Wang *et al.*, 2018), and FER can activate the phosphatase activity of ABI2 (Yu *et al.*, 2012). Whether FER could regulate BIN2 and BR signaling via ABI2 is worth investigating.

BR induces the production of ROS to regulate stomata and stress responses (Xia *et al.*, 2014; Shi *et al.*, 2015; Tian *et al.*, 2018; Yin *et al.*, 2018). BR-induced NADPH oxidase-dependent ROS production leads to the oxidation of BZR1 and BES1 (Tian *et al.*, 2018). The oxidation of BZR1 enhances its interaction with specific companion TFs, such as ARF6 and PIF4, to promote its transcriptional activity (Tian *et al.*, 2018). Interestingly, FER is known to mediate NADPH oxidase-dependent ROS production in response to both auxin and BR (Duan *et al.*, 2010; Yin *et al.*, 2018; Lu *et al.*, 2024). Determining whether FER is involved in oxidation of BZR1 to regulate its transcriptional activity would be an interesting topic.

FERONIA and ethylene

ET is a gaseous plant hormone that plays important roles during the whole life cycle of a plant. It is involved in processes such as the ET triple response, fruit ripening, and stress responses (Johnson and Ecker, 1998). The biosynthesis of ET starts from the production of *S*-adenosylmethionine (SAM) from methionine, which is catalyzed by SAM synthetase (K.L.C. Wang *et al.*, 2002). 1-Aminocyclopropane-1-carboxylic acid (ACC) synthase converts SAM to ACC, the immediate precursor of ET (K.L.C. Wang *et al.*, 2002). ACC is finally utilized as substrate by ACC oxidase to generate ET (K.L.C. Wang *et al.*, 2002). A classic ET response is the triple response in etiolated seedlings, with inhibited growth of root and hypocotyl, an exaggerated apical hook, and thickened hypocotyl (Binder, 2020). The canonical ET signaling pathway involves major components including five ET receptors on the ER membrane, a protein kinase named CONSTITUTIVE TRIPLE RESPONSE 1 (CTR1), a transmembrane protein on the ER called ETHYLENE-INSENSITIVE 2 (EIN2), and TFs such as EIN3, EIN3-LIKE 1 (EIL1), and ETHYLENE RESPONSE FACTORs (ERFs) (Binder, 2020). In the absence of ET, the ET receptors promote CTR1 phosphorylation of EIN2, leading to ubiquitination-mediated degradation of EIN2 and downstream TFs (Binder, 2020). When ET is present, it inhibits the receptors and thus reduces CTR1 activity to release the inhibition of EIN2 and TFs, leading to the ET response (Binder, 2020).

In Arabidopsis, the expression of FER can be induced by ET, and several *fer* mutants, including *fer-1*, *fer-2*, *fer-3*, and *fer-4*, are hyper-responsive to ET treatment (Table 1), indicated by severely shortened hypocotyl and increased expression of ET-responsive genes, such as *PLANT DEFENSIN 1.2* (*PDF1.2*) (Deslauriers and Larsen, 2010; Kessler *et al.*, 2010; Mao *et al.*, 2015). Analyses of various higher order mutants harboring mutations in the *FER* gene and genes encoding one of the ET signaling components provided some clues as to how FER interacts with the ET signaling pathway. Treatment with the ET perception inhibitor $AgNO_3$ reversed the shortened hypocotyl phenotype in the *fer-2* mutant, suggesting that this phenotype is dependent on ET signaling (Deslauriers and Larsen, 2010). This is further supported by the loss of the phenotype in an *etr1-1fer-2* double mutant harboring a mutation that disrupts the ET receptor ETHYLENE RESPONSE 1 (ETR1) (Deslauriers and Larsen, 2010). $AgNO_3$ treatment does not reverse hypocotyl shortening in a *ctr1-3fer-2* double mutant, suggesting that FER functions at or downstream of CTR1 (Deslauriers and Larsen, 2010). Introducing the *fer-2* mutation into an *ein2-5* mutant background partially restores the ET response, indicating that FER may function in a different ET signaling pathway that bypasses EIN2 (Deslauriers and Larsen, 2010). More interestingly, the same study showed that the *ein3-1 eil1-1* double mutant was able to largely suppress the hypersensitivity of *fer-2* to ET, suggesting that EIN3 and EIL1 are important TFs mediating FER and ET crosstalk. It is worth further investigation to determine how FER modulates EIN3 and EIL1 to regulate ET signaling.

A screen using immunoprecipitation and MS identified SAM synthetases, including SAM1, SAM2, and METK3, as FER-interacting proteins (Mao *et al.*, 2015). When compared with the WT, the *fer-4* mutant is more sensitive to ethionine, a toxic analog of methionine that can be utilized by enzymes such as SAM synthetase and be incorporated into methionine metabolic pathways such as SAM synthesis (Mao *et al.*, 2015). This indicated that the *fer* mutant has higher SAM synthetase activity, which is further supported by the higher levels of SAM and ET in the *fer-4* mutant (Mao *et al.*, 2015). The *sam1sam2* double mutant is more resistant to ethionine and has lower levels of ET, while plants overexpressing *SAM1* behave in the opposite way (Mao *et al.*, 2015). Taken together, FER interacts with SAMs to negatively regulate ET biosynthesis (Table 1). However, a detailed mechanism, such as whether FER could phosphorylate SAM to regulate its activity, is not known.

FERONIA and other hormone pathways

Substantial progress has been made to understand how FER integrates with various plant hormones such as auxin, ABA, BR, ET, and JA. Considering the diverse roles FER plays in a plant life cycle, the more substantial connections between FER and other hormones, such as gibberellin (GA), SA, and cytokinin will be likely to emerge. GA has been shown to induce FER expression (Guo *et al.*, 2009a) (Table 1). In addition, TFs mediating GA signaling, such as PIF3 and PIF5, have been shown to function downstream of FER signaling in root penetration and salt stress response (Liu *et al.*, 2023; Xu *et al.*, 2024a).

For SA, it has been reported that SA content is increased in the *fer-4* mutant when compared with the WT (Zhao *et al.*, 2021). In apple (*Malus domestica*), overexpressing a homolog of *FER* reduced SA levels (Jing *et al.*, 2022) (Table 1). It is known that MYC2 activates the expression of several NAC TFs (Zheng *et al.*, 2012), and NACs repress the expression of *ISOCHORISMATE SYNTHASE GENE 1* (*ICS1*), a gene encoding a key SA biosynthesis enzyme, and induces the expression of *SA GLUCOSYL TRANSFERASE GENE 1* (*SAGT1*), a gene encoding an enzyme that converts SA to inactive forms (Zheng *et al.*, 2012). Thus, it is possible that FER regulates SA biosynthesis and activity through the MYC2–NAC–ICS1/SAGT1 module.

Recently, an enlarged root apical meristem phenotype was reported in the *fer-4* mutant (Xu *et al.*, 2024a). It is well known that the control of meristem size needs the orchestration of auxin and cytokinin (Yamoune *et al.*, 2021). Thus, it would be interesting to know if cytokinin plays a role in FER-mediated meristem control.

The FERONIA–phytohormone crosstalk in crop species

Considering that FER plays important roles in plant growth, development, and stress responses, a better understanding of FER in crop species would be beneficial for potential agricultural applications and crop improvement. Homologs of FER have been identified and characterized in various crop species, such as maize (*Zea mays*) (Yu *et al.*, 2022), rice (*Oryza sativa*) (Li *et al.*, 2016; Yang *et al.*, 2020; Wang *et al.*, 2021; He *et al.*, 2023; Kwon *et al.*, 2024), tomato (Yin *et al.*, 2018; Fan *et al.*, 2024), apple (Jia *et al.*, 2017b; Jing *et al.*, 2022, 2023a, b), and strawberry (*Fragaria×ananassa*) (Jia *et al.*, 2017a). In these crop species, FER homologs function in plant immunity (Yang *et al.*, 2020; Jing *et al.*, 2022; Yu *et al.*, 2022; Fan *et al.*, 2024; Kwon *et al.*, 2024), vegetative growth (Li *et al.*, 2016; Fan *et al.*, 2024), abiotic stress response (Yin *et al.*, 2018; Jing *et al.*, 2023a, b), grain yield and quality (Li *et al.*, 2016; Wang *et al.*, 2021; He *et al.*, 2023), fruit ripening (Jia *et al.*, 2017a, b), and fertility (Li *et al.*, 2016). There is also evidence connecting FER and phytohormones, such as ABA, BR, SA, and ET (Jia *et al.*, 2017a; Yin *et al.*, 2018; Jing *et al.*, 2022). Some molecular mechanisms established in Arabidopsis, by which FER regulates phytohormone signaling pathways, could be conserved in crop species. For example, in strawberry, the FER homolog FaMRLK47 interacts with PP2C protein FaABI1 (Jia *et al.*, 2017a). However, more research is still needed to gain a more comprehensive understanding of the functional interactions between FER and various plant hormones in crop plants.

Conclusions and future perspectives

The study of crosstalk between receptor kinase FER signaling and plant hormones has been progressing rapidly. It is clear that mutual regulation between FER and phytohormones exists at the levels of ligands, receptor kinase, as well as downstream signaling components. On the one hand, phytohormones can regulate the expression of *FER*, the abundance of FER protein, and its kinase activity (Deslauriers and Larsen, 2010; Chen *et al.*, 2016; Guo *et al.*, 2018; Yin *et al.*, 2018). The expression of peptide ligand *RALF* genes can also be regulated (Srivastava *et al.*, 2009). On the other hand, FER can regulate hormone biosynthesis (Mao *et al.*, 2015; Zhao *et al.*, 2021; Darwish *et al.*, 2022; L. Li *et al.*, 2022), hormone transport (Dong *et al.*, 2019; Li *et al.*, 2020, C.Y. Li et al., 2022), post-translational modification of receptors (Lu *et al.*, 2024), and downstream components including TFs (Guo *et al.*, 2018; Wang *et al.*, 2022a) (Table 1).

Studies on multi-level crosstalk have greatly enhanced our understanding on how plants manage their growth under stress conditions and established FER as a critical regulator and a convergence point in regulating diverse biological processes (Guo *et al.*, 2009a, 2018; Srivastava *et al.*, 2009; Deslauriers and Larsen, 2010; Duan *et al.*, 2010; Yu *et al.*, 2012; Chen *et al.*, 2016; Zhao *et al.*, 2021; L. Li *et al.*, 2022).

The potential combinations of 17 members in the FER family, four LRE/LLGs, and 37 RALF family peptides provide many potential signaling scenarios and may very well explain the diverse functions of this family of receptor kinases, and signify the importance of their roles in regulating plant growth, development, and stress responses. It is worth noting that FER function does not seem to always require its kinase activity. It has been shown that the kinase-dead FER (FER^{K565R}, Lys565 to Arg mutation in the kinase domain) was able to fully complement the infertility of *fer-1* (Kessler *et al.*, 2015), and partially rescue the primary root mechano-sensing defect (Shih *et al.*, 2014), stomatal opening, vegetative dwarfism (Chakravorty *et al.*, 2018), and primary root growth under dim light of *fer-4* (Haruta *et al.*, 2018). It is also worth mentioning that FER^{K565R} showed autophosphorylation at a much higher protein level in an *in vitro* kinase assay, suggesting that residual kinase activity remains in FER^{K565R} (Wang *et al.*, 2022a).

Here are some considerations for future research. (i) FER–hormone crosstalk has been largely studied in isolation, one hormone at a time. How does FER signaling coordinate different hormones at the same time? Extensive transcriptomics and gene regulatory network analysis will be helpful to examine multiple FER–hormone crosstalk simultaneously. (ii) Studies have shown that highly specific ligand–receptor signaling complexes are involved in male–female interaction, and FER complexes with other homologs in this process. FER can also perceive different RALF peptides to either activate or inhibit its own function (see the Introduction). Does FER–hormone crosstalk employ similar logistics in plant growth and stress responses? The loss-of-function *fer* mutant displays highly pleiotropic phenotypes, which hinders studies in FER signaling specificity. Single-cell transcriptomics in a well-defined root system could help overcome the pleiotropy and redundancy by identifying cell type-specific FER signaling modules (Nolan *et al.*, 2023). (iii) Transcription reprogramming is a major part of FER-mediated signaling, and FER can mediate ~500 TFs. Does the FER signaling pathway employ 'master transcription factors' similar to BES1 in BR signaling and MYC2 in the JA pathway? Targeted screening using a TF CRISPR library could help address this question (Hu *et al.*, 2023). (iv) FER has been shown to phosphorylate many substrates, which leads to their altered properties, such as protein stability (Guo *et al.*, 2018; Wang *et al.*, 2022a; Liu *et al.*, 2023; Xu *et al.*, 2024a, b). How does FER phosphorylation lead to altered protein stability? Using proximity labeling coupled with MS could help identify proteins including E3 ubiquitin ligases that are involved in this process (Cho *et al.*, 2020).

Acknowledgements

We apologize for not being able to reference all FERONIA receptor kinase-related publications in this review. We thank BioRender.com for providing tools to create figures.

Author contributions

JT: wrote the main text and generated the figures and table; JT and HG: co-wrote the Introduction and the Conclusions and future perspectives, and edited the manuscript.

Conflict of interest

The authors declare no conflict of interest.

Funding

The authors are supported by startup funds from Iowa State University and the National Institutes of Health (1R35GM155200).

References

Abarca A, Franck CM, Zipfel C. 2021. Family-wide evaluation of RAPID ALKALINIZATION FACTOR peptides. Plant Physiology **187**, 996–1010.

Bai L, Zhou Y, Ma X, Gao L, Song CP. 2014. Arabidopsis CAP1-mediated ammonium sensing required reactive oxygen species in plant cell growth. Plant Signaling & Behavior **9**, e29582.

Baillie AL, Sloan J, Qu LJ, Smith LM. 2024. Signalling between the sexes during pollen tube reception. Trends in Plant Science **29**, 343–354.

Barbez E, Dunser K, Gaidora A, Lendl T, Busch W. 2017. Auxin steers root cell expansion via apoplastic pH regulation in *Arabidopsis thaliana*. Proceedings of the National Academy of Sciences, USA **114**, E4884–E4893.

Bergonci T, Ribeiro B, Ceciliato PH, Guerrero-Abad JC, Silva-Filho MC, Moura DS. 2014. *Arabidopsis thaliana* RALF1 opposes brassinosteroid effects on root cell elongation and lateral root formation. Journal of Experimental Botany **65**, 2219–2230.

Binder BM. 2020. Ethylene signaling in plants. Journal of Biological Chemistry **295**, 7710–7725.

Boisson-Dernier A, Franck CM, Lituiev DS, Grossniklaus U. 2015. Receptor-like cytoplasmic kinase MARIS functions downstream of CrRLK1L-dependent signaling during tip growth. Proceedings of the National Academy of Sciences, USA **112**, 12211–12216.

Boisson-Dernier A, Roy S, Kritsas K, Grobei MA, Jaciubek M, Schroeder JI, Grossniklaus U. 2009. Disruption of the pollen-expressed FERONIA homologs ANXUR1 and ANXUR2 triggers pollen tube discharge. Development **136**, 3279–3288.

Carvalhais LC, Schenk PM, Dennis PG. 2017. Jasmonic acid signalling and the plant holobiont. Current Opinion in Microbiology **37**, 42–47.

Chakravorty D, Yu Y, Assmann SM. 2018. A kinase-dead version of FERONIA receptor-like kinase has dose-dependent impacts on rosette morphology and RALF1-mediated stomatal movements. FEBS Letters **592**, 3429–3437.

Chehab EW, Eich E, Braam J. 2009. Thigmomorphogenesis: a complex plant response to mechano-stimulation. Journal of Experimental Botany **60**, 43–56.

Chen J, Yu F, Liu Y, *et al*. 2016. FERONIA interacts with ABI2-type phosphatases to facilitate signaling cross-talk between abscisic acid and RALF peptide in Arabidopsis. Proceedings of the National Academy of Sciences, USA **113**, E5519–E5527.

Cheung AY. 2024. FERONIA: a receptor kinase at the core of a global signaling network. Annual Review of Plant Biology **75**, 345–375.

Chini A, Fonseca S, Fernandez G, *et al*. 2007. The JAZ family of repressors is the missing link in jasmonate signalling. Nature **448**, 666–671.

Cho KF, Branon TC, Udeshi ND, Myers SA, Carr SA, Ting AY. 2020. Proximity labeling in mammalian cells with TurboID and split-TurboID. Nature Protocols **15**, 3971–3999.

Darwish E, Ghosh R, Ontiveros-Cisneros A, *et al*. 2022. Touch signaling and thigmomorphogenesis are regulated by complementary CAMTA3- and JA-dependent pathways. Science Advances **8**, eabm2091.

Deslauriers SD, Larsen PB. 2010. FERONIA is a key modulator of brassinosteroid and ethylene responsiveness in Arabidopsis hypocotyls. Molecular Plant **3**, 626–640.

Dong Q, Zhang Z, Liu Y, Tao LZ, Liu H. 2019. FERONIA regulates auxin-mediated lateral root development and primary root gravitropism. FEBS Letters **593**, 97–106.

Duan Q, Kita D, Johnson EA, Aggarwal M, Gates L, Wu HM, Cheung AY. 2014. Reactive oxygen species mediate pollen tube rupture to release sperm for fertilization in Arabidopsis. Nature Communications **5**, 3129.

Duan Q, Kita D, Li C, Cheung AY, Wu HM. 2010. FERONIA receptor-like kinase regulates RHO GTPase signaling of root hair development. Proceedings of the National Academy of Sciences, USA **107**, 17821–17826.

Duan Q, Liu MJ, Kita D, *et al*. 2020. FERONIA controls pectin- and nitric oxide-mediated male–female interaction. Nature **579**, 561–566.

Dunser K, Gupta S, Herger A, Feraru MI, Ringli C, Kleine-Vehn J. 2019. Extracellular matrix sensing by FERONIA and leucine-rich repeat extensins controls vacuolar expansion during cellular elongation in *Arabidopsis thaliana*. The EMBO Journal **38**, e100353.

Escobar-Restrepo JM, Huck N, Kessler S, Gagliardini V, Gheyselinck J, Yang WC, Grossniklaus U. 2007. The FERONIA receptor-like kinase mediates male–female interactions during pollen tube reception. Science **317**, 656–660.

Fan Y, Bai J, Wu S, *et al*. 2024. The RALF2–FERONIA–MYB63 module orchestrates growth and defense in tomato roots. New Phytologist **243**, 1123–1136.

Feiguelman G, Fu Y, Yalovsky S. 2018. ROP GTPases structure–function and signaling pathways. Plant Physiology **176**, 57–79.

Feng W, Kita D, Peaucelle A, *et al*. 2018. The FERONIA receptor kinase maintains cell-wall integrity during salt stress through Ca^{2+} signaling. Current Biology **28**, 666–675.e5.

Fernandez-Calvo P, Chini A, Fernandez-Barbero G, *et al*. 2011. The Arabidopsis bHLH transcription factors MYC3 and MYC4 are targets of JAZ repressors and act additively with MYC2 in the activation of jasmonate responses. The Plant Cell **23**, 701–715.

Fiedler L, Friml J. 2023. Rapid auxin signaling: unknowns old and new. Current Opinion in Plant Biology **75**, 102443.

Friml J, Gallei M, Gelova Z, *et al*. 2022. ABP1–TMK auxin perception for global phosphorylation and auxin canalization. Nature **609**, 575–581.

Fujii H, Chinnusamy V, Rodrigues A, Rubio S, Antoni R, Park SY, Cutler SR, Sheen J, Rodriguez PL, Zhu JK. 2009. In vitro reconstitution of an abscisic acid signalling pathway. Nature **462**, 660–664.

Gachomo EW, Jno Baptiste L, Kefela T, Saidel WM, Kotchoni SO. 2014. The Arabidopsis CURVY1 (CVY1) gene encoding a novel receptor-like protein kinase regulates cell morphogenesis, flowering time and seed production. BMC Plant Biology **14**, 221.

Galindo-Trigo S, Blanco-Tourinan N, DeFalco TA, Wells ES, Gray JE, Zipfel C, Smith LM. 2020. CrRLK1L receptor-like kinases HERK1 and ANJEA are female determinants of pollen tube reception. EMBO Reports **21**, e48466.

Gao Q, Wang C, Xi Y, Shao Q, Li L, Luan S. 2022. A receptor–channel trio conducts Ca^{2+} signalling for pollen tube reception. Nature **607**, 534–539.

Ge Z, Bergonci T, Zhao Y, *et al*. 2017. Arabidopsis pollen tube integrity and sperm release are regulated by RALF-mediated signaling. Science **358**, 1596–1600.

Ge Z, Zhao Y, Liu MC, *et al*. 2019. LLG2/3 are co-receptors in BUPS/ANX–RALF signaling to regulate Arabidopsis pollen tube integrity. Current Biology **29**, 3256–3265.

Gigli-Bisceglia N, van Zelm E, Huo W, Lamers J, Testerink C. 2022. Arabidopsis root responses to salinity depend on pectin modification and cell wall sensing. Development **149**, dev200363.

Gray WM, Kepinski S, Rouse D, Leyser O, Estelle M. 2001. Auxin regulates SCF(TIR1)-dependent degradation of AUX/IAA proteins. Nature **414**, 271–276.

Guo H, Li L, Ye H, Yu X, Algreen A, Yin Y. 2009a. Three related receptor-like kinases are required for optimal cell elongation in *Arabidopsis thaliana*. Proceedings of the National Academy of Sciences, USA **106**, 7648–7653.

Guo H, Nolan TM, Song G, Liu S, Xie Z, Chen J, Schnable PS, Walley JW, Yin Y. 2018. FERONIA receptor kinase contributes to plant immunity by suppressing jasmonic acid signaling in *Arabidopsis thaliana*. Current Biology **28**, 3316–3324.

Guo H, Ye H, Li L, Yin Y. 2009b. A family of receptor-like kinases are regulated by BES1 and involved in plant growth in *Arabidopsis thaliana*. Plant Signaling & Behavior **4**, 784–786.

Hajny J, Prat T, Rydza N, *et al*. 2020. Receptor kinase module targets PIN-dependent auxin transport during canalization. Science **370**, 550–557.

Haruta M, Gaddameedi V, Burch H, Fernandez D, Sussman MR. 2018. Comparison of the effects of a kinase-dead mutation of FERONIA on ovule fertilization and root growth of Arabidopsis. FEBS Letters **592**, 2395–2402.

Haruta M, Sabat G, Stecker K, Minkoff BB, Sussman MR. 2014. A peptide hormone and its receptor protein kinase regulate plant cell expansion. Science **343**, 408–411.

He W, Li W, Luo X, Tang Y, Wang L, Yu F, Lin Q. 2023. Rice FERONIA-LIKE RECEPTOR 3 and 14 affect grain quality by regulating redox homeostasis during endosperm development. Journal of Experimental Botany **74**, 3003–3018.

Hematy K, Sado PE, Van Tuinen A, Rochange S, Desnos T, Balzergue S, Pelletier S, Renou JP, Hofte H. 2007. A receptor-like kinase mediates the response of Arabidopsis cells to the inhibition of cellulose synthesis. Current Biology **17**, 922–931.

Herger A, Dunser K, Kleine-Vehn J, Ringli C. 2019. Leucine-rich repeat extensin proteins and their role in cell wall sensing. Current Biology **29**, R851–R858.

Herger A, Gupta S, Kadler G, Franck CM, Boisson-Dernier A, Ringli C. 2020. Overlapping functions and protein–protein interactions of LRR-extensins in Arabidopsis. PLoS Genetics **16**, e1008847.

Hu Y, Patra P, Pisanty O, *et al*. 2023. Multi-Knock—a multi-targeted genome-scale CRISPR toolbox to overcome functional redundancy in plants. Nature Plants **9**, 572–587.

Huang J, Yang L, Yang L, *et al*. 2023. Stigma receptors control intraspecies and interspecies barriers in Brassicaceae. Nature **614**, 303–308.

Huang R, Zheng R, He J, Zhou Z, Wang J, Xiong Y, Xu T. 2019. Noncanonical auxin signaling regulates cell division pattern during lateral root development. Proceedings of the National Academy of Sciences, USA **116**, 21285–21290.

Huang Y, Yin C, Liu J, *et al*. 2020. A trimeric CrRLK1L–LLG1 complex genetically modulates SUMM2-mediated autoimmunity. Nature Communications **11**, 4859.

Huck N, Moore JM, Federer M, Grossniklaus U. 2003. The Arabidopsis mutant feronia disrupts the female gametophytic control of pollen tube reception. Development **130**, 2149–2159.

Jia M, Ding N, Zhang Q, *et al*. 2017a. A FERONIA-like receptor kinase regulates strawberry (*Fragaria* × *ananassa*) fruit ripening and quality formation. Frontiers in Plant Science **8**, 1099.

Jia M, Du P, Ding N, *et al*. 2017b. Two FERONIA-like receptor kinases regulate apple fruit ripening by modulating ethylene production. Frontiers in Plant Science **8**, 1406.

Jia W, Li B, Li S, *et al*. 2016. Mitogen-activated protein kinase cascade MKK7–MPK6 plays important roles in plant development and regulates shoot branching by phosphorylating PIN1 in Arabidopsis. PLoS Biology **14**, e1002550.

Jing Y, Liu C, Liu B, Pei T, Zhan M, Li C, Wang D, Li P, Ma F. 2023a. Overexpression of the FERONIA receptor kinase MdMRLK2 confers apple drought tolerance by regulating energy metabolism and free amino acids production. Tree Physiology **43**, 154–168.

Jing Y, Pei T, Li C, Wang D, Wang Q, Chen Y, Li P, Liu C, Ma F. 2023b. Overexpression of the FERONIA receptor kinase MdMRLK2 enhances apple cold tolerance. The Plant Journal **115**, 236–252.

Jing Y, Zhan M, Li C, Pei T, Wang Q, Li P, Ma F, Liu C. 2022. The apple FERONIA receptor-like kinase MdMRLK2 negatively regulates Valsa canker resistance by suppressing defence responses and hypersensitive reaction. Molecular Plant Pathology **23**, 1170–1186.

Johnson PR, Ecker JR. 1998. The ethylene gas signal transduction pathway: a molecular perspective. Annual Review of Genetics **32**, 227–254.

Jones DS, Yuan J, Smith BE, Willoughby AC, Kumimoto EL, Kessler SA. 2017. MILDEW RESISTANCE LOCUS O function in pollen tube reception is linked to its oligomerization and subcellular distribution. Plant Physiology **175**, 172–185.

Jose J, Ghantasala S, Roy Choudhury S. 2020. Arabidopsis transmembrane receptor-like kinases (RLKs): a bridge between extracellular signal and intracellular regulatory machinery. International Journal of Molecular Sciences **21**, 4000.

Ju Y, Yuan J, Jones DS, Zhang W, Staiger CJ, Kessler SA. 2021. Polarized NORTIA accumulation in response to pollen tube arrival at synergids promotes fertilization. Developmental Cell **56**, 2938–2951.

Kanaoka MM, Torii KU. 2010. FERONIA as an upstream receptor kinase for polar cell growth in plants. Proceedings of the National Academy of Sciences, USA **107**, 17461–17462.

Keinath NF, Kierszniowska S, Lorek J, Bourdais G, Kessler SA, Shimosato-Asano H, Grossniklaus U, Schulze WX, Robatzek S, Panstruga R. 2010. PAMP (pathogen-associated molecular pattern)-induced changes in plasma membrane compartmentalization reveal novel components of plant immunity. Journal of Biological Chemistry **285**, 39140–39149.

Kessler SA, Grossniklaus U. 2011. She's the boss: signaling in pollen tube reception. Current Opinion in Plant Biology **14**, 622–627.

Kessler SA, Lindner H, Jones DS, Grossniklaus U. 2015. Functional analysis of related CrRLK1L receptor-like kinases in pollen tube reception. EMBO Reports **16**, 107–115.

Kessler SA, Shimosato-Asano H, Keinath NF, Wuest SE, Ingram G, Panstruga R, Grossniklaus U. 2010. Conserved molecular components for pollen tube reception and fungal invasion. Science **330**, 968–971.

Kwon OK, Moon H, Jeong AR, Yeom G, Park CJ. 2024. Rice small secreted peptide, OsRALF26, recognized by FERONIA-like receptor 1 induces immunity in rice and Arabidopsis. The Plant Journal **118**, 1528–1549.

Lan Z, Song Z, Wang Z, *et al*. 2023. Antagonistic RALF peptides control an intergeneric hybridization barrier on Brassicaceae stigmas. Cell **186**, 4773–4787.

Leyser O. 2018. Auxin signaling. Plant Physiology **176**, 465–479.

Li C, Yeh FL, Cheung AY, *et al*. 2015. Glycosylphosphatidylinositol-anchored proteins as chaperones and co-receptors for FERONIA receptor kinase signaling in Arabidopsis. eLife **4**, e06587.

Li CY, Chen J, Li XY, *et al*. 2022. FERONIA is involved in phototropin 1-mediated blue light phototropic growth in Arabidopsis. Journal of Integrative Plant Biology **64**, 1901–1915.

Li CY, Wang L, Cui YC, *et al*. 2016. Two FERONIA-like receptor (FLR) genes are required to maintain architecture, fertility, and seed yield in rice. Molecular Breeding **36**, 151.

Li E, Wang G, Zhang YL, Kong Z, Li S. 2020. FERONIA mediates root nutating growth. The Plant Journal **104**, 1105–1116.

Li J, Chory J. 1997. A putative leucine-rich repeat receptor kinase involved in brassinosteroid signal transduction. Cell **90**, 929–938.

Li J, Nam KH. 2002. Regulation of brassinosteroid signaling by a GSK3/SHAGGY-like kinase. Science **295**, 1299–1301.

Li L, Chen H, Alotaibi SS, Pencik A, Adamowski M, Novak O, Friml J. 2022. RALF1 peptide triggers biphasic root growth inhibition upstream of auxin biosynthesis. Proceedings of the National Academy of Sciences, USA **119**, e2121058119.

Li L, Verstraeten I, Roosjen M, *et al*. 2021. Cell surface and intracellular auxin signalling for H^+ fluxes in root growth. Nature **599**, 273–277.

Li X, Xie Y, Zhang Q, *et al*. 2022. Monomerization of abscisic acid receptors through CARKs-mediated phosphorylation. New Phytologist **235**, 533–549.

Lin W, Tang W, Pan X, Huang A, Gao X, Anderson CT, Yang Z. 2022. Arabidopsis pavement cell morphogenesis requires FERONIA binding to pectin for activation of ROP GTPase signaling. Current Biology **32**, 497–507.

Lin W, Zhou X, Tang W, *et al*. 2021. TMK-based cell-surface auxin signalling activates cell-wall acidification. Nature **599**, 278–282.

Lindner H, Kessler SA, Muller LM, Shimosato-Asano H, Boisson-Dernier A, Grossniklaus U. 2015. TURAN and EVAN mediate pollen tube reception in Arabidopsis synergids through protein glycosylation. PLoS Biology **13**, e1002139.

Liu C, Shen L, Xiao Y, *et al*. 2021. Pollen PCP-B peptides unlock a stigma peptide–receptor kinase gating mechanism for pollination. Science **372**, 171–175.

Liu J, Huang Y, Kong L, *et al*. 2020. The malectin-like receptor-like kinase LETUM1 modulates NLR protein SUMM2 activation via MEKK2 scaffolding. Nature Plants **6**, 1106–1115.

Liu MJ, Yeh FJ, Yvon R, Simpson K, Jordan S, Chambers J, Wu HM, Cheung AY. 2024. Extracellular pectin–RALF phase separation mediates FERONIA global signaling function. Cell **187**, 312–330.e22.

Liu X, Jiang W, Li Y, *et al*. 2023. FERONIA coordinates plant growth and salt tolerance via the phosphorylation of phyB. Nature Plants **9**, 645–660.

Lu B, Wang S, Feng H, *et al*. 2024. FERONIA-mediated TIR1/AFB2 oxidation stimulates auxin signaling in Arabidopsis. Molecular Plant **17**, 772–787.

Ma Y, Szostkiewicz I, Korte A, Moes D, Yang Y, Christmann A, Grill E. 2009. Regulators of PP2C phosphatase activity function as abscisic acid sensors. Science **324**, 1064–1068.

Malivert A, Erguvan O, Chevallier A, Dehem A, Friaud R, Liu M, Martin M, Peyraud T, Hamant O, Verger S. 2021. FERONIA and microtubules independently contribute to mechanical integrity in the Arabidopsis shoot. PLoS Biology **19**, e3001454.

Malivert A, Hamant O. 2023. Why is FERONIA pleiotropic? Nature Plants **9**, 1018–1025.

Mao D, Yu F, Li J, *et al*. 2015. FERONIA receptor kinase interacts with S-adenosylmethionine synthetase and suppresses S-adenosylmethionine production and ethylene biosynthesis in Arabidopsis. Plant, Cell & Environment **38**, 2566–2574.

Maraschin Fdos S, Memelink J, Offringa R. 2009. Auxin-induced, SCF(TIR1)-mediated poly-ubiquitination marks AUX/IAA proteins for degradation. The Plant Journal **59**, 100–109.

Masachis S, Segorbe D, Turra D, *et al*. 2016. A fungal pathogen secretes plant alkalinizing peptides to increase infection. Nature Microbiology **1**, 16043.

Mecchia MA, Santos-Fernandez G, Duss NN, *et al*. 2017. RALF4/19 peptides interact with LRX proteins to control pollen tube growth in Arabidopsis. Science **358**, 1600–1603.

Miyazaki S, Murata T, Sakurai-Ozato N, Kubo M, Demura T, Fukuda H, Hasebe M. 2009. ANXUR1 and 2, sister genes to FERONIA/SIRENE, are male factors for coordinated fertilization. Current Biology **19**, 1327–1331.

Moussu S, Broyart C, Santos-Fernandez G, Augustin S, Wehrle S, Grossniklaus U, Santiago J. 2020. Structural basis for recognition of RALF peptides by LRX proteins during pollen tube growth. Proceedings of the National Academy of Sciences, USA **117**, 7494–7503.

Moussu S, Lee HK, Haas KT, *et al*. 2023. Plant cell wall patterning and expansion mediated by protein–peptide–polysaccharide interaction. Science **382**, 719–725.

Ngo QA, Vogler H, Lituiev DS, Nestorova A, Grossniklaus U. 2014. A calcium dialog mediated by the FERONIA signal transduction pathway controls plant sperm delivery. Developmental Cell **29**, 491–500.

Noble JA, Bielski NV, Liu MJ, *et al*. 2022. Evolutionary analysis of the LORELEI gene family in plants reveals regulatory subfunctionalization. Plant Physiology **190**, 2539–2556.

Nolan TM, Vukasinovic N, Hsu CW, *et al*. 2023. Brassinosteroid gene regulatory networks at cellular resolution in the Arabidopsis root. Science **379**, eadf4721.

Nolan TM, Vukasinovic N, Liu D, Russinova E, Yin Y. 2020. Brassinosteroids: multidimensional regulators of plant growth, development, and stress responses. The Plant Cell **32**, 295–318.

Ogawa ST, Kessler SA. 2023. Update on signaling pathways regulating polarized intercellular communication in Arabidopsis reproduction. Plant Physiology **193**, 1732–1744.

Ou H, Yi P. 2022. ROP GTPase-dependent polarity establishment during tip growth in plants. New Phytologist **236**, 49–57.

Pacheco JM, Song L, Kubenova L, *et al*. 2023. Cell surface receptor kinase FERONIA linked to nutrient sensor TORC signaling controls root hair growth at low temperature linked to low nitrate in *Arabidopsis thaliana*. New Phytologist **238**, 169–185.

Park SY, Fung P, Nishimura N, *et al*. 2009. Abscisic acid inhibits type 2C protein phosphatases via the PYR/PYL family of START proteins. Science **324**, 1068–1071.

Raghavendra AS, Gonugunta VK, Christmann A, Grill E. 2010. ABA perception and signalling. Trends in Plant Science **15**, 395–401.

Richter J, Watson JM, Stasnik P, Borowska M, Neuhold J, Berger M, Stolt-Bergner P, Schoft V, Hauser MT. 2018. Multiplex mutagenesis of four clustered CrRLK1L with CRISPR/Cas9 exposes their growth regulatory roles in response to metal ions. Scientific Reports **8**, 12182.

Rotman N, Rozier F, Boavida L, Dumas C, Berger F, Faure JE. 2003. Female control of male gamete delivery during fertilization in *Arabidopsis thaliana*. Current Biology **13**, 432–436.

Schoenaers S, Lee HK, Gonneau M, *et al*. 2024. Rapid alkalinization factor 22 has a structural and signalling role in root hair cell wall assembly. Nature Plants **10**, 494–511.

Sheard LB, Tan X, Mao H, *et al*. 2010. Jasmonate perception by inositol-phosphate-potentiated COI1–JAZ co-receptor. Nature **468**, 400–405.

Shi CY, Qi C, Ren HY, Huang AX, Hei SM, She XP. 2015. Ethylene mediates brassinosteroid-induced stomatal closure via Gα protein-activated hydrogen peroxide and nitric oxide production in Arabidopsis. The Plant Journal **82**, 280–301.

Shih HW, Miller ND, Dai C, Spalding EP, Monshausen GB. 2014. The receptor-like kinase FERONIA is required for mechanical signal transduction in Arabidopsis seedlings. Current Biology **24**, 1887–1892.

Shiu S-H, Bleecker AB. 2001. Plant receptor-like kinase gene family: diversity, function, and signaling. Science's STKE **2001**, re22.

Song Y, Wilson AJ, Zhang XC, *et al*. 2021. FERONIA restricts *Pseudomonas* in the rhizosphere microbiome via regulation of reactive oxygen species. Nature Plants **7**, 644–654.

Srivastava R, Liu JX, Guo H, Yin Y, Howell SH. 2009. Regulation and processing of a plant peptide hormone, AtRALF23, in Arabidopsis. The Plant Journal **59**, 930–939.

Stegmann M, Monaghan J, Smakowska-Luzan E, Rovenich H, Lehner A, Holton N, Belkhadir Y, Zipfel C. 2017. The receptor kinase FER is a RALF-regulated scaffold controlling plant immune signaling. Science **355**, 287–289.

Tan X, Calderon-Villalobos LI, Sharon M, Zheng C, Robinson CV, Estelle M, Zheng N. 2007. Mechanism of auxin perception by the TIR1 ubiquitin ligase. Nature **446**, 640–645.

Tang W, Lin W, Zhou X, Guo J, Dang X, Li B, Lin D, Yang Z. 2022. Mechanotransduction via the pectin–FERONIA complex activates ROP6 GTPase signaling in Arabidopsis pavement cell morphogenesis. Current Biology **32**, 508–517.

Thynne E, Saur IML, Simbaqueba J, *et al*. 2017. Fungal phytopathogens encode functional homologues of plant rapid alkalinization factor (RALF) peptides. Molecular Plant Pathology **18**, 811–824.

Tian Y, Fan M, Qin Z, *et al*. 2018. Hydrogen peroxide positively regulates brassinosteroid signaling through oxidation of the BRASSINAZOLE-RESISTANT1 transcription factor. Nature Communications **9**, 1063.

Wang HJ, Tang J, Liu J, Hu J, Liu JJ, Chen YX, Cai ZY, Wang XL. 2018. Abscisic acid signaling inhibits brassinosteroid signaling through dampening the dephosphorylation of BIN2 by ABI1 and ABI2. Molecular Plant **11**, 315–325.

Wang KLC, Li H, Ecker JR. 2002. Ethylene biosynthesis and signaling networks. The Plant Cell **14**, S131–S151.

Wang L, Wang D, Yang Z, *et al*. 2021. Roles of FERONIA-like receptor genes in regulating grain size and quality in rice. Science China Life Sciences **64**, 294–310.

Wang L, Yang T, Wang B, *et al*. 2020. RALF1–FERONIA complex affects splicing dynamics to modulate stress responses and growth in plants. Science Advances **6**, eaaz1622.

Wang P, Clark NM, Nolan TM, *et al*. 2022a. Integrated omics reveal novel functions and underlying mechanisms of the receptor kinase FERONIA in *Arabidopsis thaliana*. The Plant Cell **34**, 2594–2614.

Wang P, Clark NM, Nolan TM, *et al*. 2022b. FERONIA functions through Target of Rapamycin (TOR) to negatively regulate autophagy. Frontiers in Plant Science **13**, 961096.

Wang X, Liu J, Wang M, Liu L, Liu X, Zhao C. 2024. FERONIA controls ABA-mediated seed germination via the regulation of CARK1 kinase activity. Cell Reports **43**, 114843.

Wang ZY, Nakano T, Gendron J, *et al*. 2002. Nuclear-localized BZR1 mediates brassinosteroid-induced growth and feedback suppression of brassinosteroid biosynthesis. Developmental Cell **2**, 505–513.

Xia XJ, Gao CJ, Song LX, Zhou YH, Shi K, Yu JQ. 2014. Role of H_2O_2 dynamics in brassinosteroid-induced stomatal closure and opening in *Solanum lycopersicum*. Plant, Cell & Environment **37**, 2036–2050.

Xiao Y, Stegmann M, Han Z, DeFalco TA, Parys K, Xu L, Belkhadir Y, Zipfel C, Chai J. 2019. Mechanisms of RALF peptide perception by a heterotypic receptor complex. Nature **572**, 270–274.

Xie Y, Sun P, Li Z, Zhang F, You C, Zhang Z. 2022. FERONIA receptor kinase integrates with hormone signaling to regulate plant growth, development, and responses to environmental stimuli. International Journal of Molecular Sciences **23**, 3730.

Xu F, Chen J, Li Y, Ouyang S, Yu M, Wang Y, Fang X, He K, Yu F. 2024a. The soil emergence-related transcription factor PIF3 controls root penetration by interacting with the receptor kinase FER. Developmental Cell **59**, 434–447.

Xu F, Wang L, Li Y, Shi J, Staiger D, Yu F. 2024b. Phase separation of GRP7 facilitated by FERONIA-mediated phosphorylation inhibits mRNA translation to modulate plant temperature resilience. Molecular Plant **17**, 460–477.

Xu T, Dai N, Chen J, *et al*. 2014. Cell surface ABP1–TMK auxin-sensing complex activates ROP GTPase signaling. Science **343**, 1025–1028.

Yamoune A, Cuyacot AR, Zdarska M, Hejatko J. 2021. Hormonal orchestration of root apical meristem formation and maintenance in Arabidopsis. Journal of Experimental Botany **72**, 6768–6788.

Yang J, He H, He Y, *et al*. 2021. TMK1-based auxin signaling regulates abscisic acid responses via phosphorylating ABI1/2 in Arabidopsis. Proceedings of the National Academy of Sciences, USA **118**, e2102544118.

Yang Z, Xing J, Wang L, Liu Y, Qu J, Tan Y, Fu X, Lin Q, Deng H, Yu F. 2020. Mutations of two FERONIA-like receptor genes enhance rice blast resistance without growth penalty. Journal of Experimental Botany **71**, 2112–2126.

Yin Y, Qin K, Song X, Zhang Q, Zhou Y, Xia X, Yu J. 2018. BZR1 transcription factor regulates heat stress tolerance through FERONIA receptor-like kinase-mediated reactive oxygen species signaling in tomato. Plant and Cell Physiology **59**, 2239–2254.

Yin Y, Vafeados D, Tao Y, Yoshida S, Asami T, Chory J. 2005. A new class of transcription factors mediates brassinosteroid-regulated gene expression in Arabidopsis. Cell **120**, 249–259.

Yin Y, Wang ZY, Mora-Garcia S, Li J, Yoshida S, Asami T, Chory J. 2002. BES1 accumulates in the nucleus in response to brassinosteroids to regulate gene expression and promote stem elongation. Cell **109**, 181–191.

Yu F, Qian L, Nibau C, *et al*. 2012. FERONIA receptor kinase pathway suppresses abscisic acid signaling in Arabidopsis by activating ABI2 phosphatase. Proceedings of the National Academy of Sciences, USA **109**, 14693–14698.

Yu H, Ruan H, Xia X, Chicowski AS, Whitham SA, Li Z, Wang G, Liu W. 2022. Maize FERONIA-like receptor genes are involved in the response of multiple disease resistance in maize. Molecular Plant Pathology **23**, 1331–1345.

Yu M, Li R, Cui Y, *et al*. 2020. The RALF1–FERONIA interaction modulates endocytosis to mediate control of root growth in Arabidopsis. Development **147**, dev189902.

Yu Y, Tang W, Lin W, *et al*. 2023. ABLs and TMKs are co-receptors for extracellular auxin. Cell **186**, 5457–5471.

Zhang X, Peng H, Zhu S, *et al*. 2020. Nematode-encoded RALF peptide mimics facilitate parasitism of plants through the FERONIA receptor kinase. Molecular Plant **13**, 1434–1454.

Zhao C, Jiang W, Zayed O, *et al*. 2021. The LRXs–RALFs–FER module controls plant growth and salt stress responses by modulating multiple plant hormones. National Science Review **8**, nwaa149.

Zhao C, Zayed O, Yu Z, Jiang W, Zhu P, Hsu CC, Zhang L, Tao WA, Lozano-Duran R, Zhu JK. 2018. Leucine-rich repeat extensin proteins regulate plant salt tolerance in Arabidopsis. Proceedings of the National Academy of Sciences, USA **115**, 13123–13128.

Zheng XY, Spivey NW, Zeng W, Liu PP, Fu ZQ, Klessig DF, He SY, Dong X. 2012. Coronatine promotes *Pseudomonas syringae* virulence in plants by activating a signaling cascade that inhibits salicylic acid accumulation. Cell Host & Microbe **11**, 587–596.

Zheng ZL, Nafisi M, Tam A, Li H, Crowell DN, Chary SN, Schroeder JI, Shen J, Yang Z. 2002. Plasma membrane-associated ROP10 small GTPase is a specific negative regulator of abscisic acid responses in Arabidopsis. The Plant Cell **14**, 2787–2797.

Zhong S, Li L, Wang Z, *et al*. 2022. RALF peptide signaling controls the polytubey block in Arabidopsis. Science **375**, 290–296.

Zhong S, Zhao P, Peng X, Li HJ, Duan Q, Cheung AY. 2024. From gametes to zygote: mechanistic advances and emerging possibilities in plant reproduction. Plant Physiology **195**, 4–35.

Zhu S, Estevez JM, Liao H, *et al*. 2020a. The RALF1–FERONIA complex phosphorylates eIF4E1 to promote protein synthesis and polar root hair growth. Molecular Plant **13**, 698–716.

Zhu S, Li Y, Wu Y, *et al*. 2023. The FERONIA–YUELAO module participates in translational control by modulating the abundance of tRNA fragments in Arabidopsis. Developmental Cell **58**, 2930–2946.

Zhu S, Martinez Pacheco J, Estevez JM, Yu F. 2020b. Autocrine regulation of root hair size by the RALF–FERONIA–RSL4 signaling pathway. New Phytologist **227**, 45–49.