



MICROREVIEW

Regulation of immune complex formation and signalling by FERONIA, a busy goddess in plant–microbe interactions

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Abstract

Being sessile in soil, plant cells rely on cell-surface receptors to sense and transduce environmental stimulus signals into intracellular responses. FERONIA (FER), a *Catharanthus roseus* receptor-like kinase 1-like protein, has emerged as a versatile regulator of plant growth, development, and stress responses. In recent years, accumulating studies have witnessed rapid advances in dissecting the mechanisms underlying the interaction between FER and its partners in response to pathogen invasion, particularly regulation of immune complex formation and signalling. Moreover, hormonal signalling, rhizosphere microbiota and other constituents are also extensively involved in these processes.

KEYWORDS

endocytosis, FERONIA, immune responses, plant–microbe interaction, protein dynamics

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1 | INTRODUCTION

Plants have evolved sophisticated immune systems that integrate the perception of complex danger signals with the activation of appropriate defence outputs for pathogen resistance. Plasma membrane-localized receptor-like kinases (RLKs) are responsible for sensing microbe- or host-derived molecular patterns and controlling transmembrane signal transduction (Zhang, Yang, et al., 2020; Zhou & Zhang, 2020). The immune signalling pathways are always initiated by regulated mechanisms for the activation or attenuation of membrane RLKs through specific protein–protein interaction, the formation of a microdomain-based signalling platform, or ligand-mediated internalization, eventually triggering efficient downstream defence reactions (Beck et al., 2012; Cui et al., 2018; Spallek et al., 2013; Xing et al., 2022).

The RLK FERONIA (FER) is a well-characterized member of the *Catharanthus roseus* RLK 1 (CrRLK1L) family and functions with its co-receptors LRE/LLGs (LORELEI/LORELEI-like GPI-anchored proteins) through binding with rapid alkalization factor (RALF) peptides. In recent decades, FER has emerged as an essential regulator in plant growth and development, biotic stress responses, and reproduction (Duan et al., 2020; Liu et al., 2021). Importantly, FER serves as a RALF-regulated scaffold that modulates the formation of an immune receptor kinase complex, providing new insights into the underlying mechanisms of FER in plant immunity (Stegmann et al., 2017). FER also functions in cell wall-integrity sensing, hormonal signalling, and controlling of the immune outputs of pattern recognition receptors (PRRs) (Dünser et al., 2019; Gronnier et al., 2022; Guo et al., 2018; Stegmann et al., 2017). Recent studies have revealed that membrane trafficking also modulates location-specific FER dynamics in the process of immune activation and root growth (Xing et al., 2022; Yu et al., 2020). Here, we discuss recent advances in understanding of the regulated mechanisms of FER in plant immune responses and highlight the mechanisms that mediate the integration of complex danger signals for proper defence responses.

2 | FERONIA CONTROLS LIGAND-INDUCED IMMUNE COMPLEX FORMATION

FER, as an important RLK on the plasma membrane, functions as an important constituent of the immune receptor complex involved in regulating the interaction between plants and pathogens (Escocard de Azevedo Manhães et al., 2021). As early as 2010, Keinath et al. performed a quantitative proteomics study to explore the early responses of plasma membrane proteins in $^{15}\text{N}/^{14}\text{N}$ -labelled *Arabidopsis* suspension cells following stimulus with flg22 (Keinath et al., 2010). A total of 64 proteins were significantly enriched in detergent-resistant membranes within 15 min, during which FER was co-detected with several plasma membrane-residing immune receptors and immunity-related proteins (including FLS2, ACA8, REM1.2 and REM1.3), thereby implying a potential role of FER as a new component in the flg22-induced defence responses (Figure 1).

In addition, the *fer4* mutant displays defects in flg22-induced reactive oxygen species (ROS) burst, mitogen-activated protein kinase (MAPK) activity and stomatal closure.

Several excellent studies in the following years further ascertained the important role of FER in ligand-induced immune complex formation (Stegmann et al., 2017; Xiao et al., 2019). Being negative regulators of the plant immune response, RALFs are small peptides that interact with malectin-like receptor kinases and the LEUCINE-RICH REPEAT EXTENSIN (LRX) family (Ge et al., 2017; Liu et al., 2021; Mecchia et al., 2017). Flg22 treatment enhances the interactions between FER, FLS2 and BAK1, while flg22-induced FLS2-BAK1 complex assembly is reduced in *fer-4*; the complex in FER-GFP/*fer-4* transgenic lines recovered to normal levels. Moreover, RALF23 overexpression had a similar effect on flg22-induced FLS2-BAK1 complex formation. Notably, the loss of RALF23 or FER did not affect the accumulation of FLS2, EFR or BAK1. These results suggest that FER promotes the association of FLS2/EFR to its co-receptor BAK1, while RALF23 inhibits this process, further confirming that FER is an important scaffold component regulating the formation of immune receptor complex (Figure 1) (Stegmann et al., 2017). The FER-RALF module may play a universal role in growth and development or environmental perception by regulating different receptor kinase complexes. Further structural and biochemical data indicate that LLG1 [LORELEI (LRE)-LIKE GLYCOSYLPHOSPHATIDYLINOSITOL (GPI)-ANCHORED PROTEIN 1] and LLG2 directly bind RALF23 to nucleate the assembly of RALF23-LLG1-FER and RALF23-LLG2-FER heterocomplexes, respectively, depending on the conserved N-terminal region of RALF23 (Xiao et al., 2019). Notably, combined variable angle total internal reflection fluorescence microscopy (VA-TIRFM) and single-particle tracking further confirmed that FER is required for controlling FLS2-GFP nanoscale organization accumulation at the plasma membrane, while FER knockout impairs the nanoscale organization of FLS2 and BAK1. FER-LLG1 and LRX3/4/5 may form distinct RALF23 receptor complexes, showing cell context-specific regulation of growth and immunity. Moreover, the inhibition of RALF23 on FLS2-BAK1 complex formation, elf18-induced ROS production all depend on FER kinase activity (Gronnier et al., 2022).

Aside from its function in immune complex formation during the interaction between host plants and bacteria, FER is also involved in the signalling in response to fungal invasion or elicitation. Homozygous *fer* mutants displayed higher resistance to powdery mildew *Golovinomyces* (syn. *Erysiphe*) *orontii*, but normal susceptibility to *Hyaloperonospora arabidopsidis* and *Colletotrichum higginsianum*. Interestingly, the unchallenged *fer* leaves displayed a phenotype similar to spontaneous cell death and H_2O_2 production (Kessler et al., 2010), while *fer-4* and *fer-5* roots had a lower ROS level as revealed by $\text{H}_2\text{DCF-DA}$ staining (Duan et al., 2010), suggesting that the functions of FER related to ROS homeostasis may be tissue- or cell context-specific (Figure 1). Notably, RALF homologues contributing to host infection ability have also been identified in different fungal pathogen genomes. *Fusarium oxysporium* secretes F-RALF, a small peptide similar to the RALF peptides from host plants, thereby inducing extracellular space alkalization and facilitating the

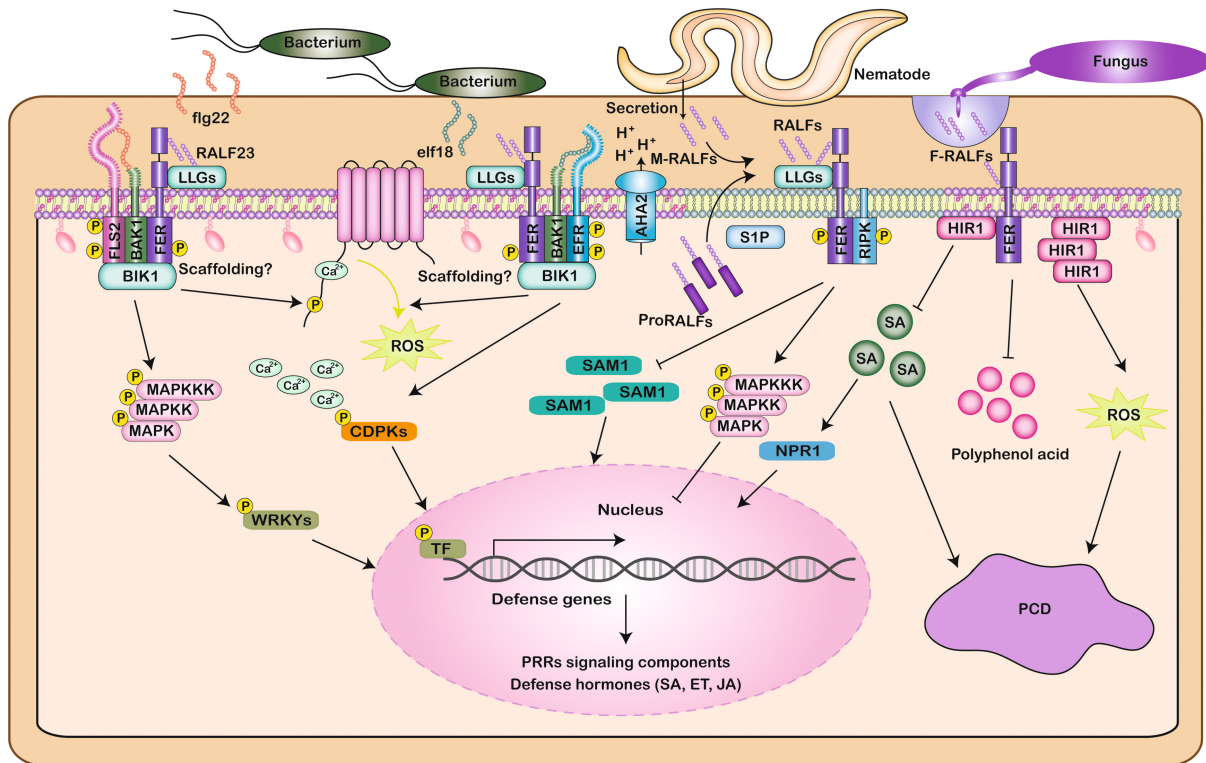


FIGURE 1 Various functions of FER in controlling the ligand-induced immune response. The bacterial flagellin (flg22) and elongation factor Tu (elf18) trigger the formation of FLS2-BAK1 and EFR-BAK1 immune complex, further activating downstream immune responses, such as Ca^{2+} oscillations, NADPH oxidase-induced oxidative burst, and mitogen-activated protein kinase cascades. FER destabilizes the FLS2-BAK1 and EFR-BAK1 immune complex by interacting with RALF23-LLGs, thereby modulating the plant immune response. FER also interacts with RIPK and phosphorylates it, thus regulating the activity of AHA2 and affecting the pH. F-RALF and M-RALFs peptides secreted by *Fusarium oxysporium* or nematodes can also bind FER and hijack the FER-RALF pathway. In Valsa canker resistance, FER interacts with a hypersensitive reaction (HR)-induced protein HIR1 and disrupts HIR self-interaction. The FER-HIR complex compromises resistance by altering the salicylic acid (SA) level, suppressing polyphenol accumulation and blocking the HIR1-mediated HR. ET, ethylene; JA, jasmonic acid; PCD, programmed cell death; ROS, reactive oxygen species; SA, salicylic acid; TF, transcription factor.

infection of hosts (Masachis et al., 2016). Moreover, *fer4* is insensitive to F-RALF. Further in-depth studies revealed that F-RALF binds to FER, blocks AHA2 (H^+ -ATPase 2)-mediated H^+ efflux, and elevates the extracellular pH of roots, thus facilitating *F. oxysporium* infection and negatively regulating immune responses (Figure 1). In a recent study, *MdMRLK2*, a FER homologous gene in apple, was found to be highly induced by *Valsa mali* in the susceptible *Malus mellana*, but not in the resistant *Malus yunnanensis*. *MdMRLK2* suppressed the hypersensitive reaction by interacting with *MdHIR1* and probably impairing *MdHIR1* oligomerization (Figure 1) (Jing et al., 2022). Thus, FER seems to have differential roles in the responses to biotrophic, hemibiotrophic and necrotrophic pathogens.

3 | FERONIA INTERNALIZATION REQUIRES ALTERNATIVE ENDOCYTIC ROUTES

Cell surface signalling is critical for perceiving a variety of immune signals and subsequently executing the resistance response against pathogens (Zhou & Zhang, 2020). Endocytic trafficking contributes

to plant basal resistance by modulating the abundance of immunity-related RLKs at the cell surface to control signalling activation or attenuation (Beck et al., 2012; Mbengue et al., 2016). A recent study showed that flg22 significantly promoted the lateral diffusion and concomitant endocytosis of FER from the plasma membrane, which was consistent with the internalization of FLS2 (Figure 2) (Cui et al., 2018; Xing et al., 2022). Notably, flg22 also triggered the rapid phosphorylation of FER, while the lateral diffusion of FER was abolished in the *fls2* mutant, suggesting that flg22 perception is essential for the function of FER (Benschop et al., 2007; Xing et al., 2022). Given that FER serves as a scaffold controlling the ligand-induced nanoscale organization of FLS2 and BAK1 (Gronnier et al., 2022), the flg22-triggered internalization of FER and FLS2 seems to be important for modulating the abundance of receptors during flg22 perception and immune activation.

Numerous reports also support the concept that membrane trafficking delivers active receptors to endosomes, while the recycling/signalling and the degradative fates are accomplished by constitutive and ligand-induced endocytosis (Geldner & Robatzek, 2008; Reyes et al., 2011; Xing et al., 2021). FER constitutively undergoes alternative endocytic pathways via clathrin-mediated endocytosis

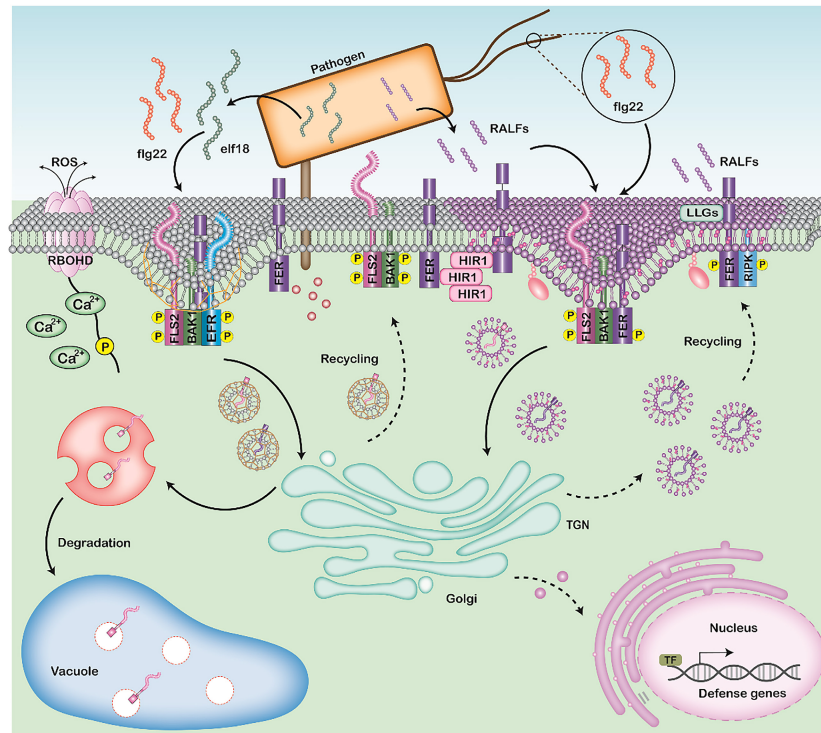


FIGURE 2 Schematic model illustrating the alternative endocytic routes of FER and other receptor-like kinases (RLKs) in plant immunity. On elicitation, FLS2 and EF-TU RECEPTOR (EFR) detect the bacterial flagellin (flg22) and elongation factor Tu (elf18), respectively. FER recognizes rapid alkalization factor (RALF) peptides or possibly other conserved microbial signatures from bacteria, fungi or nematodes. Plasma membrane (PM)-localized immune receptors, such as FLAGELLIN SENSING 2 (FLS2) and FER, undergo constitutive endocytosis and recycling between the PM and endosomes before activation. Once activated by cognate elicitors, pattern recognition receptors (PRRs) are internalized via clathrin-mediated endocytosis or clathrin-independent endocytosis, sorted to the trans-Golgi network (TGN), and finally recycled to the PM or degraded in the vacuole via multivesicular bodies. FLS2 and FER internalize via alternative endocytic routes, while activated FLS2 is mainly sorted to the central vacuole for signalling attenuation and FER might be delivered to the PM to stabilize the flg22-triggered immune complexes. ROS, reactive oxygen species; TF, transcription factor.

and clathrin-independent endocytosis (Figure 2) (Xing et al., 2022; Yu et al., 2020). After RALF1 treatment, FER mainly internalized by the clathrin-mediated endocytosis pathway, was then transported by the ARA7-positive endosome, and was finally delivered to the vacuole for degradation (Yu et al., 2020). flg22 triggered the sorting of FER to the trans-Golgi network and inhibited further trafficking to late endosomes, implying that flg22 probably promotes the recycling of FER from the trans-Golgi network to the plasma membrane (Xing et al., 2022). The distinct destinations of FER under RALF1 or flg22 treatment point to different functions of FER in plant growth and the immune response process. During flg22 perception, FLS2 localizes to bona fide endosomes via two distinct endocytic trafficking routes depending on its activation status, highlighting that receptor-mediated endocytosis is directed through different endosomal compartments (Beck et al., 2012; Spallek et al., 2013). The spatiotemporal dynamics of receptor-mediated endocytosis are critical to receptor function, and the recycling/degradative fates are always related to signalling activation or attenuation (Cui et al., 2018; Spallek et al., 2013). Because the inhibited endocytosis of ligand-bound FLS2 or PEPR1 (the Pep1 receptor) led to an impaired immune response (Mbengue et al., 2016; Ortiz-Morea et al., 2016; Yun & Kwon, 2017), further elucidation for the function of FER recycling

to the plasma membrane will provide deeper insights into the formation mechanisms of flg22-triggered immune complexes (Figure 2).

4 | FERONIA INTEGRATES MULTIPLE INTRACELLULAR AND EXTRACELLULAR SIGNALS TO REGULATE IMMUNE SIGNALLING

Besides cell surface signalling, FER may function as a hub to integrate various extracellular and intracellular signals in immune responses. An excellent example for extracellular signal perception is that *fer-4* displayed lower susceptibility to *Meloidogyne incognita* compared with wild-type seedlings. Further investigations revealed that MiRALF1 and MiRALF3, two RALF-like peptides, displayed typical activities of plant RALFs and could directly bind to the extracellular domain of FER to modulate parasitism-related immune responses to nematodes. The nematode-encoded RALFs may facilitate parasitism via FER, suggesting that the RALF-FER module is conserved but context-specific in host-pathogen interaction (Figure 1) (Zhang, Peng, et al., 2020). Interestingly, FER may adjust the rhizosphere microbiome to enrich *Pseudomonas fluorescens* by modulating

ROS. The *fer-8* mutant has lower levels of ROS in roots and elevated rhizosphere pseudomonads, independent of jasmonic acid signalling, while the addition of RALF23 was sufficient to enrich *P. fluorescens* (Figure 1) (Song et al., 2021). Similarly, PHR 1, a transcriptional regulator, directly binds to the promoter regions of RALFs and activates their expression under phosphate-starvation conditions in *Arabidopsis thaliana*. RALFs consequently suppress immune complex formation through FERONIA, thereby recruiting specialized root microbiota (such as *Flavobacterium*, *Pseudomonas* and *Delftia* spp.) to alleviate phosphate starvation by up-regulating the expression of phosphate starvation response genes (Tang et al., 2022).

Hormonal signalling is also closely correlated with FER function. Indeed, FER has been previously reported to be related to auxin, brassinosteroid, abscisic acid, and ethylene signalling during plant growth (Deslauriers & Larsen, 2010; Duan et al., 2010; Ji, et al., 2020; Mao et al., 2015; Yu et al., 2012). A recent study combined quantitative transcriptome, proteome and phosphoproteome profiling of *Arabidopsis* wild-type and *fer-4* mutant plants. Phytohormone signalling, abiotic stress and biotic stress genes were significantly enriched among differentially expressed transcripts, differentially abundant proteins and/or misphosphorylated proteins; in particular, some abscisic acid-induced transcription factors were hypophosphorylated in the *fer-4* mutant (Wang et al., 2022). Guo et al. reported a new mechanism by which plants use FER signalling to counteract coronatine (COR)-mediated host susceptibility. FER functions to inhibit jasmonic acid and coronatine signalling by phosphorylating and destabilizing MYC2, thereby positively regulating immunity. Conversely, RALF23 interacts with FER to stabilize MYC2 and elevate jasmonic acid signalling, negatively contributing to plant immunity (Figure 1) (Guo et al., 2018).

5 | CONCLUSIONS AND PERSPECTIVE

FER has enjoyed extensive research interest as a key molecule for its roles in various aspect of the life cycle of plants. The past few decades have witnessed considerable progress in dissecting the regulatory mechanisms of FER in immune responses. However, we still face some unsolved problems or challenges.

1. In addition to RALFs, could *Arabidopsis* FER and its homologues recognize other conserved microbial signatures and transduce danger signals into cells?
2. Identification of other constituents in the immune complexes in response to various microbial signatures may further broaden our insights into the functions of FER.
3. Further exploration of cell type- and context-specific kinase substrates and other interacting proteins may greatly facilitate our understanding of the diverse biological roles of FER.
4. Given that FER functions as an RLK, what are the mechanisms for signalling attenuation? What is the exact role for its endocytosis? Which types of posttranslational modifications are involved in these processes in addition to phosphorylation?

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DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analysed.

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