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A molecular perspective on the role of FERONIA in root growth, nutrient uptake, stress sensing and microbiome assembly

Sajad Ali [a,b,1], Anshika Tyagi [a,1], Suvin Park [a,1], Rajeev K. Varshney [c,d,*], Hanhong Bae [a,*]

[a] Department of Biotechnology, Yeungnam University, Gyeongsan Gyeongbuk 38541, Republic of Korea
[b] Department of Biological Sciences, College of Science, King Faisal University, Al-Ahsa 31982, Saudi Arabia
[c] Center of Excellence in Genomics &, Systems Biology, International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Hyderabad, India
[d] Murdoch's Centre for Crop and Food Innovation, WA State Agricultural Biotechnology Centre, Food Futures Institute, Murdoch University, Murdoch, Western Australia, Australia

HIGHLIGHTS

- Roots play multifaceted role in plants which are crucial for their growth ad survival.
- Receptor like kinases are important cell wall sensors for detecting intrinsic and external cues.
- FERONIA a multitasking sensor regulates diverse root growth and adaptive traits.
- FERONIA activation modulates calcium, ROS and hormonal signaling cascades in roots.
- FERONIA regulates nutrient uptake and microbiome assembly.

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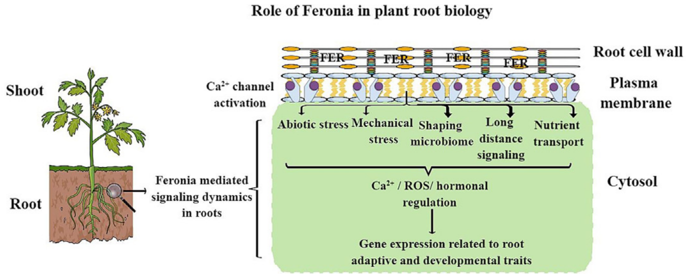
GRAPHICAL ABSTRACT



ABSTRACT

Background: Roots perform multifaceted functions in plants such as movement of nutrients and water, sensing stressors, shaping microbiome, and providing structural support. How roots perceive and respond above traits at the molecular level remains largely unknown. Despite the enormous advancements in crop improvement, the majority of recent efforts have concentrated on above-ground traits leaving significant knowledge gaps in root biology. Also, studying root system architecture (RSA) is more difficult due to its intricacy and the difficulties of observing them during plant life cycle which has made it difficult to identify desired root traits for the crop improvement. However, with the aid of high-throughput phenotyping and genotyping tools many developmental and stress-mediated regulation of RSA has emerged in both model and crop plants leading to new insights in root biology. Our current understanding of upstream signaling events (cell wall, apoplast) in roots and how they are interconnected with downstream signaling cascades has largely been constrained by the fact that most research in plant systems concentrate on cytosolic signal transduction pathways while ignoring the early perception by cells' exterior parts. In this regard, we discussed the role of FERONIA (FER) a cell wall receptor-like kinase (RLK) which acts as a sensor and a bridge between apoplast and cytosolic signaling pathways in root biology.

Aim of the review: The goal of this review is to provide valuable insights into present understanding and future research perspectives on how FER regulates distinct root responses related to growth and stress adaptation.

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[*] Corresponding authors at: Center of Excellence in Genomics &, Systems Biology, International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Hyderabad, India (R.K. Varshney); Department of Biotechnology, Yeungnam University, Gyeongsan Gyeongbuk 38541, Republic of Korea (H. Bae).

E-mail addresses: Rajeev.Varshney@murdoch.edu.au (R.K. Varshney), hanhongbae@ynu.ac.kr (H. Bae).

[1] These authors contributed equally.

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Key scientific concepts of review: In plants, FER is a unique RLK because it can act as a multitasking sensor and regulates diverse growth, and adaptive traits. In this review, we mainly highlighted its role in root biology like how it modulates distinct root responses such as root development, sensing abiotic stressors, mechanical stimuli, nutrient transport, and shaping microbiome. Further, we provided an update on how FER controls root traits by involving Rapid Alkalinization Factor (RALF) peptides, calcium, reactive oxygen species (ROS) and hormonal signaling pathways.. We also highlight number of outstanding questions in FER mediated root responses that warrants future investigation. To sum up, this review provides a comprehsive information on the role of FER in root biology which can be utilized for the development of future climate resilient and high yielding crops based on the modified root system.

Contents

Introduction

Climate change poses significant threat to agricultural productivity, economy and nutritional security especially in developing countries [1,2]. The impact of climate change driven extremes like drought, heat waves, floods, storms on agricultural production as well as dwindling agricultural land makes it harder to meet the 2050 goal of producing more food for increasing global population [1]. Also, achieving 2050 food security mission, crop input must rise by 2.4 % yearly, while the present pace is just 1.3 % [3,4]. In the past there have been reports that climate change driven multifactorial environmental stressors have significantly affected the major food crops such as rice, wheat and maize which had huge impact on human diet and economy [5,6]. According to FAO [7], hunger affected over 828 million people worldwide which are projected to exacerbate as agricultural output declines. Therefore, a paradigm-shifting innovation for crop improvement is required to develop climate-resilient and high-yielding smart crops for safeguarding future food security. One such approach is developing robust root system that is more resilient to environmental abrasions, sequesters more carbon in the soil, and effectively captures water and nutrients [8]. In plants, roots are the first organs to respond multifactorial abiotic stresses such drought, floods, salt stress, heavy metals, and nutrient depletion, therefore, strengthening the RSA will be crucial to enhancing global food production [9]. Crop improvement has advanced significantly during the past two decades, but the majority of current efforts have focused mostly on the above-ground features, leaving significant knowledge gaps in the field of root biology [9–12]. Because roots were generally considered as the 'hidden half 'and have been least explored for developing future resilient smart crops owing to their complexity, time-consuming, labor-intensive, and difficulties of observing them throughout their life cycle [13]. In the past, researchers using conventional breeding or biotechnological advancements for crop improvements using root traits were facing challenges due to the difficulties on phenotypic selection to select superior lines possessing promising RSAs to adapted to biotic and abiotic stressors stress [14–16]. Additionally, the genetic regulation of root traits for genetic recombination and selection is not well understood. This challenge has impeded advancements in the study of root traits genetics to understand how they are expressed in terms of phenotype and genotype [17]. Also, the complexity of root structure in monocots and dicots were also challenging for identifying key root traits for the crop improvement [17]. Roots can alter their form and purpose over time due to factors such as root age and season [18]. The development stage of root systems influences various root traits, including root branching density and coarse root to fine root ratio [19]. It is becoming increasingly evident that root trait values change over time at both the species and community levels, alongside seasonal shifts in environmental factors like soil resource availability or soil organism community composition and activity [20]. Hence, the tactics for changing root architecture need to be tailored to each crop, which poses a difficult challenge for biotechnological and breeding crop improvement programs. Therefore, a thorough comprehension of root phenotyping and genetic control is crucial for accurately measuring root trait values and using them for crop improvement programs. With the advent of new technologies such as computed tomography, computer simulation modeling, hydroponics, high-throughput phenotyping, and genotyping, many developmental and stress-mediated regulations of different root traits have emerged in both model and crop plants leading to new insights into the field of root biology [21–25]. Given the magnitude of the climate change challenge and increased food demand, holistic approach is needed to explore RSA and how they respond to multifactorial stressors with more emphasized on wild plant root system which may open up new possibilities for breeders to develop future robust crops.

Roots are of essential biological importance since they serve as the sites of an array of biological, environmental and chemical processes such as nutrient and water intake, interactions with microbiome, mycorrhizas, pathogens, pests, and abiotic stressors [26,27]. Additionally, it also offers a vital experimental framework for exploring various facets of plant organogenesis, such as the control of pattern formation, cell division and differentiation as well as intercellular local and systemic signaling [12]. In general, there are two different kinds of roots: (i) those that develop during embryonic development, like tap or primary roots in beans and primary and seminal roots in maize, and (ii) those that develop post-embryonically from adjacent nodes on shoots, which are typically denoted as adventitious roots (ARs) [28,29]. Interestingly, roots have a great degree of developmental plasticity and frequently adapt to their surroundings. RSA consists of structural features including root length, shape, type, spread, and the quantity and length of lateral roots [30]. RSA displays both robustness and plasticity-oriented responses against abiotic stressors therefore they can be a viable source for crop improvement [10,30]. However, long-term advancements in RSA characterization and the link between RSA and function traits are necessary for the creation of crop genotypes with enhanced root phenotypes. In this regard, integration of high-throughput phenotyping and genotyping tools is required to underpin the detailed mechanism of RSA development under diverse environmental conditions [11,31]**.** Interestingly, Arabidopsis roots have served as a model for understanding the intricacy and unexplored realm of root biology due to its simple root architecture, and availability of huge mutant collections which have contributed to a better understanding of developmental and adaptive responses at the cellular level [32]. Nevertheless, despite significant advancements in Arabidopsis, there are still many knowledge gaps in understanding trait functioning in wild or crop root systems.

Plant roots face number of challenges including nutrient depletion, abiotic/biotic stressors, and mechanical pressures which affects their growth and functional traits [11,33,34]. However, roots are constantly tailoring their responses to above environmental cues via a complex array of chemical signaling pathways that integrate both developmental and adaptive traits in order to ensure plant survival [11]**.** Plants have evolved their root system as one of the multifaceted sensing tool kit that plays a key role in sensing and responding to diverse environmental and nutritional factors [35]**.** However, most researchers focus on intracellular signal transduction pathways while ignoring the early perception by cell's exterior parts, such as the cell wall or apoplast, which has limited our understanding of early signaling events and how they relate to downstream signaling cascades in root signaling dynamics. Interestingly, roots may use different sensors or receptors, which can sense external environmental cues and trigger intracellular physiological and biochemical signaling cascades to maintain cellular growth and stress adaptability. One such type of sensors is cell wall receptor-like kinase (RLKs), which act as bridge between signal perception and transduction [36]. RLKs are of paramount importance in cell wall- and membrane-mediated signaling that regulate plant growth, reproduction, and adaptation to environmental stressors [37]. The first RLK was discovered in maize (*ZmPK1*) [38], subsequently with genome-sequencing research in numerous plant species showed a considerable number of RLKs in higher plant genomes [39–41]. RLKs have unique cell surface sensing capabilities of different biotic, abiotic, and mechanical stress which makes them important players in plant signal transduction [42]**.** Owing to their multifaceted functions in plants they act as molecular switches of various plant signal transduction pathways associated with growth and adaptive responses. Structural profiling of RLKs have revealed that they contain serine/threonine kinases with a single transmembrane spanning from their C-terminal cytoplasmic kinase domain to their N-terminal extracellular domain [37,43]. Interestingly, some RLKs that lack a N-terminal extracellular domain are called receptor-like cytoplasmic kinases (RLCKs). RLCKs typically have an intracellular kinase domain, although some may also include a transmembrane domain [44].

With over 600 members, RLKs are the largest protein family in Arabidopsis, and few of them have been identified as crucial cell wall sensors. [45]. Generally, *Arabidopsis* transmembrane RLKs are divided into 14 categories based on the hallmark motifs in the ectodomains of receptor kinases, viz., leucine-rich repeats (LRRs), *Catharanthus roseus* receptor-like kinase (CrRLKs), lectin receptors (C-type and L-type lectin), wall-associated kinases (WAKs), extension-like proteins, S-domain receptor-like kinase (SD RLKs), proline-rich extension-like kinase (PERK), CRINKLY-like (CR-like), the domain of unknown function 26 (DUF26), thaumatin-like protein kinases (TLPKs), leaf rust kinase-like (LRK), lysin motif (LysM), receptor-like kinase in flowers (RKF), and unknown receptor kinase (URK) [46]. However, the biological role of these RLKs is not fully understood. Additionally, ligands or upstream and downstream signaling components are also missing for most of the RLKs in plants. For in depth information on RLKs readers are referred to reviews [44,47–49].

In this review, we focused on FER which belongs to CrRLK1 family, and its multifaceted role in root biology as well as their signaling dynamics. The CrRLK1 family was named following the discovery of CrRLK1 in *C. roseus* [43]. The CrRLKs are distinguished by one or two malectin-like domains, a transmembrane domain, and an intracellular Ser/Thr kinase domain [44]. Among CrRLK1 family, FER has become a multifunctional player, controlling a variety of growth and development functions as well as responses to pathogens and environmental variables [50–55]. In search of primary regulator of female fertility in Arabidopsis, FER was discovered to be the master regulator and later identified as receptor kinase [56,57]. FER, which was named after the Etruscan goddess of fertility, acts as a node for the crosstalk between environmental signals and plant growth. Rapid Alkalization Factor (RALF) peptides function as ligands for CrRLK1-like FER and THESUS1 [50,53]. RALFs were given that name because they quickly raised the medium's pH, when introduced to *Nicotiana tabacum* cell cultures [58]. RALFs have been found in a variety of land plants but not in charophytes. In Arabidopsis, 34–39 RALFs have been predicted in its genome [50,53,59]. Recent researches have shown that RALF peptides have significant roles in numerous physiological processes [60–62]. In addition to RALF, FER can also bind to oligosaccharides such as pectin fragments through interactions between its malectin domain and polygalacturonic acid to detect cell wall defects during stress, and triggers calcium (Ca^{2+}) transients that maintain cell wall integrity [63]. Therefore, FER activation can be either RALF dependent or RALF independent, which can have different effects on plant signal transduction (Fig. 1). However, there are still many questions that remain unanswered in RALF- or pectin-dependent FER activation such RALF peptide activation, oligosaccharide formation, activation of Ca^{2+} channels, hormonal regulation, and reactive oxygen species (ROS) homeostasis during different plant developmental and stress conditions. Mutant studies have revealed that FER plays a variety of roles in plant development, including the elongating of hypocotyl and root, leaf development, developing root hairs, and regulating flower timing and seed development [64–67]. Recent studies have reported that FER is a key player for sensing and regulating various process in *Arabidopsis*, including cell wall stress responses, hormonal crosstalk and mechanical signaling [65,68–72]. FER is a crucial component of cell wall integrity and detects any changes in the cell wall caused by abiotic or biotic stimuli as well as mechanical stress [37,63]. Further, we have summarized the role of FER in numerous plant developmental and adaptation responses (Fig. 2).

Owing to its multifaceted roles in plant development and stress biology, FER is considered as a multifactorial sensor and regulator

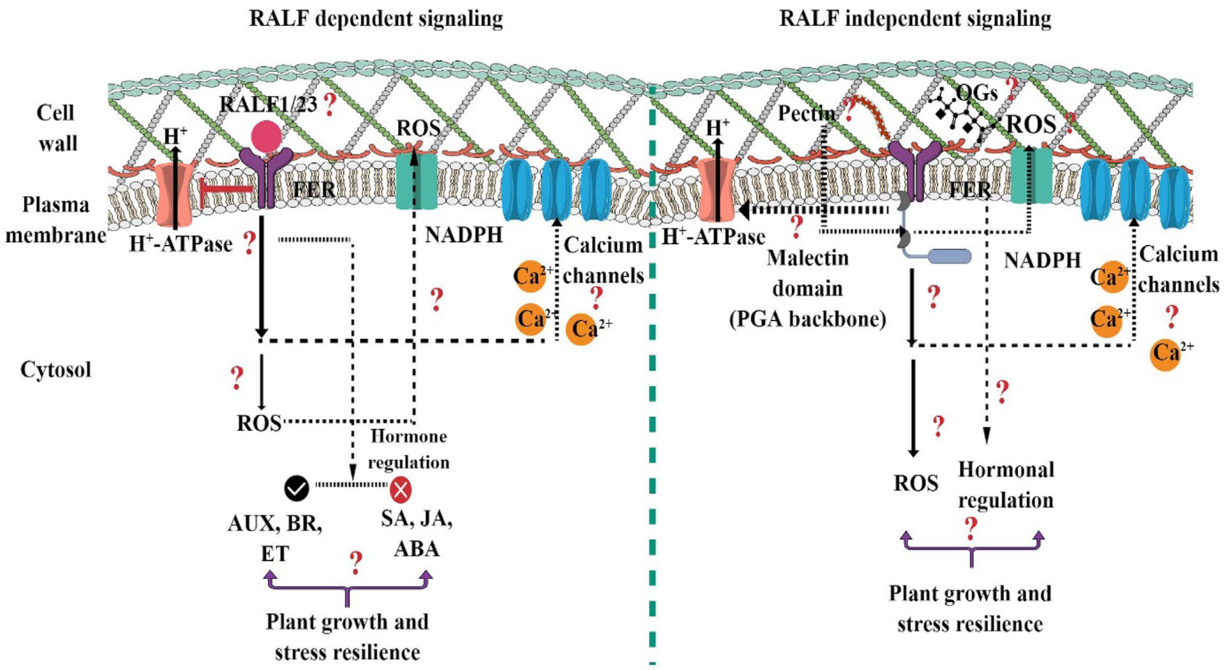

Fig. 1. Schematic diagram shows FER activation by RALFs or oligosacrides which can modulate diverse plant signaling transduction pathways. Activation of FER can trigger calcium, ROS and hormones signaling cascades that can regulate different plant signaling pathways related to growth and stress responses.

of numerous upstream and downstream signaling pathways related to different traits [50–55]. In this review, we provided a multiscale viewpoint on FER-mediated regulation of root signaling dynamics. We primarily focused on how FER regulates different aspects of root development and also how it aids in perceiving the mechanical and environmental stresses. We also discussed the new directions of root microbiome dynamics by highlighting the role of FER in shaping root microbiome. We have also highlighted the knowledge gaps and outstanding questions that warrant future investigation in order to fully understand the complexity of FER-mediated root-signaling dynamics.

FER a key regulator of root development

Root developmental processes are very complex, which involve the coordination of diverse signaling players such as hormones, genes, transcriptional factors, and small peptides. From the last few decades, significant advancement has been made in deciphering the regulatory mechanisms of root development, leading the identification of different signatures such as hormones [auxin (AUX), cytokinin (CK), brassinosteroid (BR), abscisic acid (ABA)], small peptides [CLE (CLAVATA3/ESR-related), RGF (ROOT GROWTH FACTOR), CEP (C-TERMINALLY ENCODED PEPTIDE), IDA (INFLORESCENCE DEFICIENT IN ABCISSION)], cyclin-dependent-kinases (CDKs), and D-type cyclin (CYCD) as well as transcription factors (TFs) [73–79]. Recent studies have reported the role of additional components namely RLKs in regulating different aspects of root developmental biology which have emerged a new research frontier in root biology [67,69,80,81]. RLKs regulates the growth of different root types such as primary, lateral, adventitious and hair formation [82–84]. However, our current understanding on how RLKs regulate different root traits is still at early stage. In this review, we are focusing on the role of FER as one of the elegant members of RLKs in root developmental biology and also highlighting new paradigms that suggest their involvement in root signaling dynamics.

Plants require regulated formative cell divisions and proper cell specification in order to produce many tissues and organs that make up the adult body [85]**.** These mechanisms are primarily regulated by transcriptional networks and phytohormones. Recently, it has been discovered that ligand-induced RLK signaling pathways are yet another potential essential regulator of plant cell specification [82]. Among them, FER is emerging as one of the key modulators of root developmental biology. Many studies have shown that FER acts as both positive and negative regulator of root development that is mainly relied on different cellular signatures like RALFs, AUX, ABA, protein kinases (PTKs), ROS, Ca^{2+} and various TFs as well as the nature of stress and nutritional conditions [50,86]. For example, FER is necessary for RALF1-induced Ca^{2+} spikes, which further limit root development. A crosstalk between RALF and ABA through FER phosphorylation is indicated by the fact that its peptide ligands RALF and ABA both activate FER and limit root development [86]. Previous study has shown that exogenous treatment of RALF peptides in wild type Arabidopsis significantly inhibits root growth but not in FER mutants, which highlights the importance of FER in RALF-mediated root inhibition. Arabidopsis RALF1 peptides, when binds to the FER receptor, stimulate its kinase activity which inhibits H^+-ATPase activity and proton transport, thus causing apoplast alkalization and suppression of root elongation [50]. FER can also inhibit primary root growth by phosphorylating receptor interacting protein kinases (RIPKs) in a RALF1-dependent manner [80].

On the other hand, FER positively regulates root hair (RH) development by involving multiple signaling routes. RHs are tubular protrusions that appear on the root's outermost layer and may make up as much as 50 % of the root's surface area. RH size has paramount physiological and adaptive significances since it affects the root's surface area and, consequently, the plant's capacity to absorb nutrients and water from the soil [67]. There are various environmental signals and internal growth regulators that regulate the formation of RHs. Nevertheless, numerous genes have been identified so far that regulate RH development. However, Arabidopsis ROOT HAIR DEFECTIVE 6-LIKE 4 (RSL4), a *bHLH* transcription factor, is one of the major players that regulates the transcription of number of *RH* genes related to RH elongation [87]. Further, *Arabidopsis* plants deficient in *RSL4* are impaired in

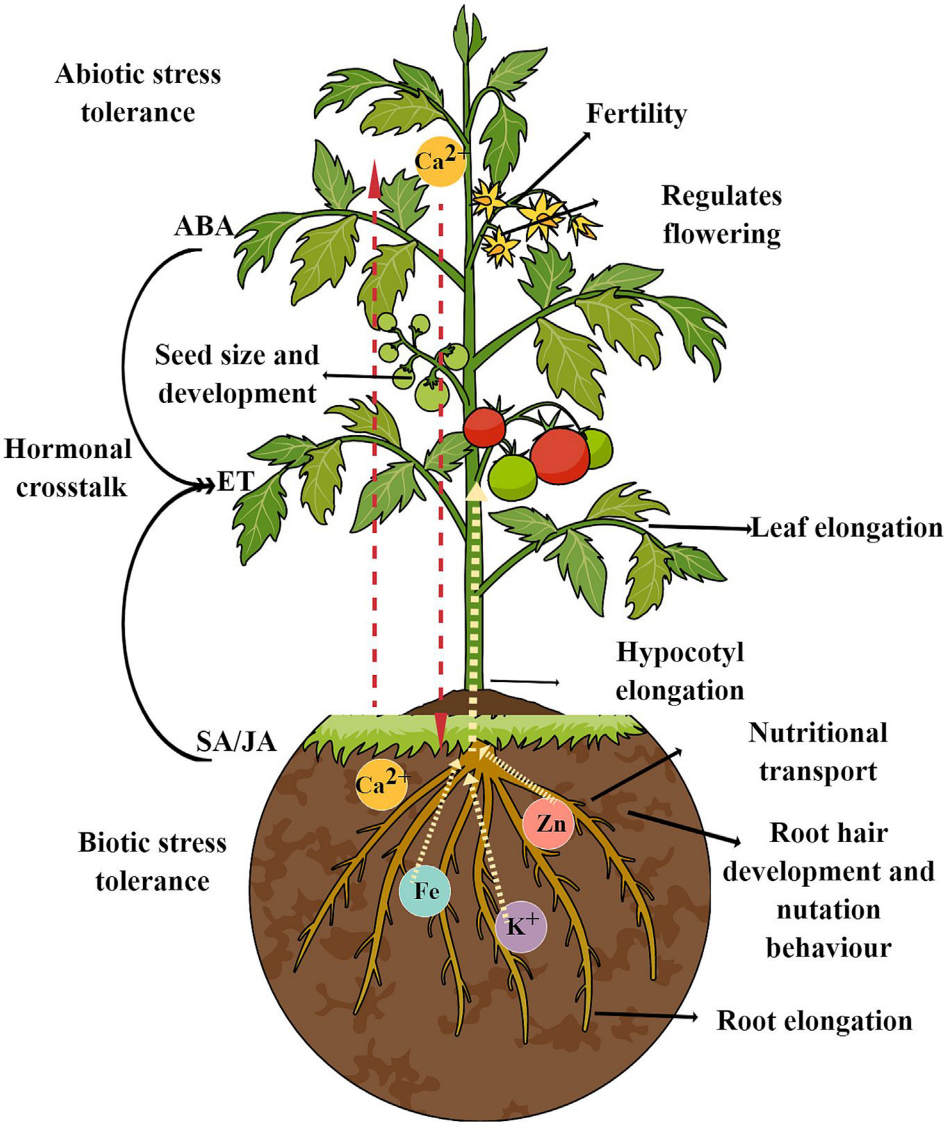

Fig. 2. A schematic diagram highlights the role of FER in regulating different plant growth and adaptive traits. FER regulates various growth traits (e.g., pollen development, root and shoot elongation, leaf size, root development, seed size and development, and flowering). Additionally, FER plays key role in sensing different environmental stressors.

hairy root development, while as overexpression of *RSL4* are sufficient to promote root hair growth. Recently, RALF1-FER was identified as a central hub of RH development between the upstream cell surface and downstream signaling events. Activation of RALF1-FER leads to the phosphorylation of an early translation initiation factor (eIF4E1) that modulates the expression of numerous RH genes including *RSL4* all of which promotes the RH growth [87]. In other words, the RALF1-FER-eIF4E1 trio promotes RSL4 protein synthesis, which modulates RH growth. Interestingly, higher levels of RSL4 also display negative feedback regulation of RALF1 gene mainly by binding its promoter *cis* elements which ultimately balancing RH growth and size. RALF1 also interacts with Lorelei-like-GPI anchored protein 1 (LLG1) in addition to FER and forms a trio complex RALF1-LLG/FER that induces GEF–ROP/ARAC pathway, which in turn modulates auxin-mediated RH development [87]. However, it will be interesting to find out how RALF1-FER controls RH development during environmental stressors, nutrient depletion and other factors. On the other hand, FER enhances RH growth by another pathway. For instance, Duan et al. [65] reported that FER triggers the guanine nucleotide exchange factor (GEF)-plant RHO GTPase (ROP/ARAC) pathway to generate ROS, which is vital for RH growth. In addition to FER, another CrRLK1 so called ERULUS (ERU) is also found in RH tips and its activation is reliant on the auxin signaling pathway [88]. In contrast, *fer* mutant seedlings' root hairs have significant faults, with the majority collapsing upon emergence and the remainder either growth-retarded or growth-arrested [65]. Additionally, *fer* mutant seedlings were found to be insensitive to AUX triggered root hair elongation [65]. It will be interesting to decipher how FER, ERULUS and auxin trio can modulate RH development, which will provide novel avenues not only unravelling the intricacy of RH development but also for developing stress resilient crops with different RH traits. As a matter of fact, a variety of environmental factors, including the availability of phosphorus, nitrogen and other micronutrients as well as different hormonal cascades like AUX, ABA and ethylene (ET) affect the cell destiny and proliferation of root hairs. ABA and ET are very often considered as negative regulators of cellular growth including root. However, FER is known to suppress both ABA and ET pathways [64,69]. As a result, the interaction between FER and hormones (ABA, ET, AUX) will be an exciting research area to

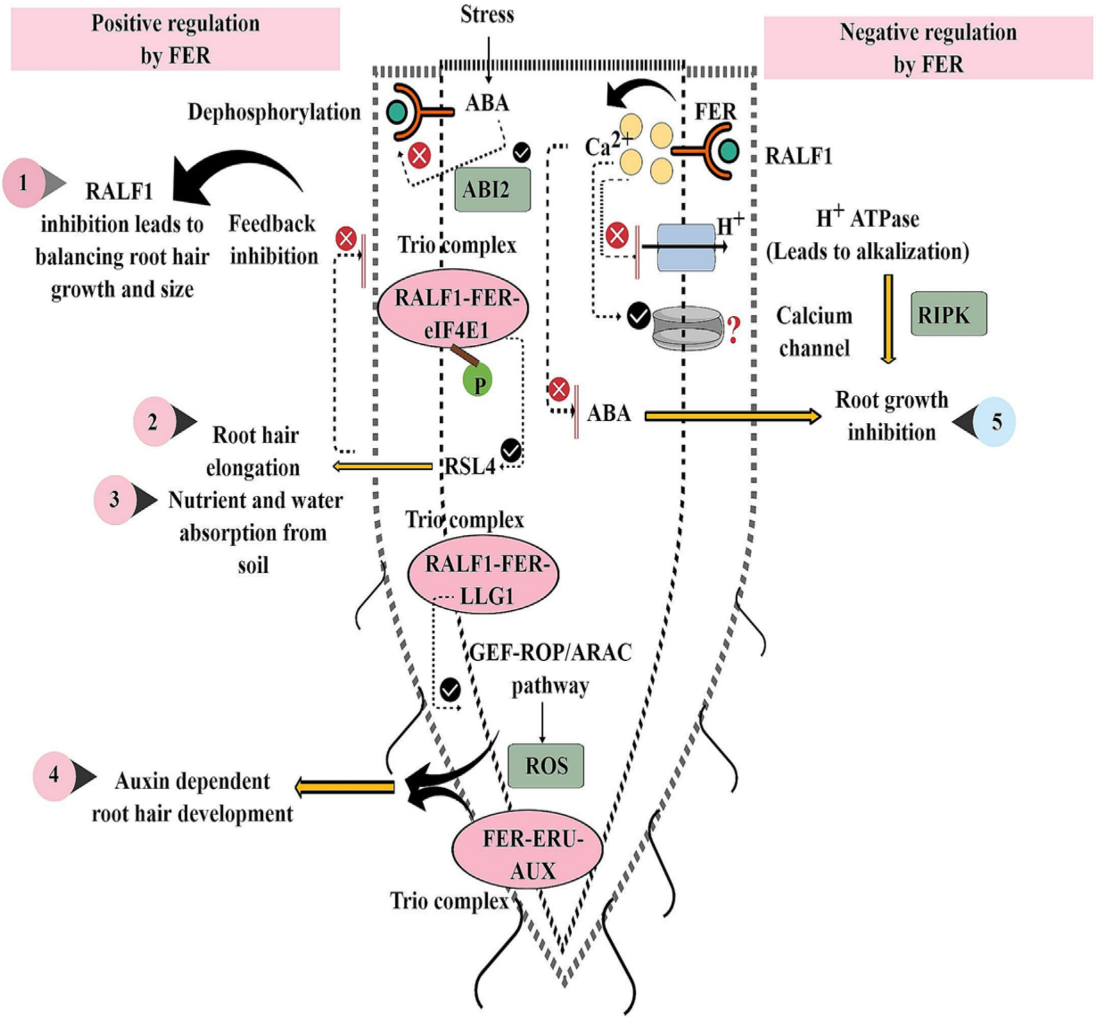

Fig. 3. Regulation of root development by FER. This model depicts how RALF/FER and other key signaling players drive root hair development, enhance nutrient, and water absorption (1–4). Many important molecular players (e.g., RALF-FER/eIF4E1, RSL4, RALF1-FER-LLG1, and FER-ERU-AUX) have been identified to drive root hair development. This model shows how RALF/FER activation leads root growth inhibition via calcium burst and apoplast alkalization (5). It also highlights the missing players that are involved in RALF/FER-controlled root developmental traits.

explore in root developmental biology given their significance in controlling a variety of root traits. This complexity raises the possibility that FER functions as a central node that coordinates signals and mediates root growth responses at the junction of the plasma membrane and the cell wall. In conclusion, RALF1-FER stimulates root hair cell proliferation, while inhibiting primary root cell growth. Further, we have summarized the FER signaling cascades in regulating root development (Fig. 3). The concept that FER has cell-type- and/or growth environment-dependent function is supported by the mounting evidence that RALF1 and FER cooperate to restrict primary root growth [50], while promoting root hair growth [67]. However, it is difficult to comprehend how FER positively and negatively regulates a variety of root cellular processes that have different outcome. Additional investigation into FER root regulatory networks may produce helpful insights in deciphering its complexity that will be helpful for developing crops with distinct root system.

Another important aspect of root developmental biology is the root nutation. Root nutation is form of asymmetric root growth (ARG) describes how roots grow in a wave and skewing manner as a result of uneven growth rates on different sides [89]. The PIN-FORMED2 (PIN2) and AUXIN RESISTANT1 (AUX1)-mediated polar auxin transport are recognized to be essential roles in carrying out asymmetry as the absence of either PIN2 or AUX1 gene inhibited ARG [90,91]. FER has been discovered as a key player in defining the root nutating behavior (Fig. 3). For example, FER loss of function (*fer-4*) showed increased root waviness on tilted plates as well as formed anti-clockwise coils on horizontal plates, which further shows FER in controlling root nutating behavior [81]. This study also reported that FER modulates root nutating behavior through Ca^{2+}, PIN2- and AUX1-mediated auxin transport signaling and microtubule organization. Recent studies have revealed that *fer-4* mutant seedlings had abnormal columella root cell patterns, grew more lateral root (LR) branches, and took longer to respond to gravitropic signals in the primary root than their wild-type counterparts [92]. This study provided incredible finding on the involvement of polar auxin transport (PAT) in *fer-4* mutant lines responsible for having abnormal columella root cell patterns, more lateral root (LR) branches, and delayed response to gravitropic signals. They highlighted that FER regulates PAT by modulating ACTIN-mediated PIN2 polar localization which could further display distinct root traits [92]. Additionally, we have outlined the significant findings regarding the function of FER controlled root developmental features (Table 1).

Table 1
Regulation of root morphological and structural traits by FERONIA.

Root		Regulation	Species	References
Structure	Root (↓) Primary root (↓)	RALF-mediated growth inhibition (cell expansion) (7 days old *fer-4 mutant* has longer root than WT) By negatively regulating JA signaling	*Arabidopsis thaliana*	[50,93]
	Primary root (↓)	Comparable to that in wild type (no regulation)	*A. thaliana*	[92]
	Lateral root (↓)	Activation of ERF114 and ERF115Negatively regulates lateral root formation related genes (ERF114 and ERF115) Abnormal polarized PIN2 induced by F-actin cytoskeleton yielding auxin accumulation	*A. thaliana*	[92,94]
	Root hair (↑)	Auxin mediated RHO GTPase signalingHas a role in autocrine regulation with RALF1 and root hair defective 6-like4 (RSL4) Involved in ERU-mediated root hair tip growth with AHA1/2	*A. thaliana*	[65,88,95]
	Xylem (↑)	Negatively regulates xylem maturation related genes (ERF114 and ERF115)	*A. thaliana*	[94]
Morphology	Skewing / nutating	Component for nutation polar auxin (PIN and AUX1), Ca^{2+} signaling Increased screwing angle in *fer-4 mutant*	*A. thaliana*	[70,81]

↑, positive regulation; ↓, negative regulation.

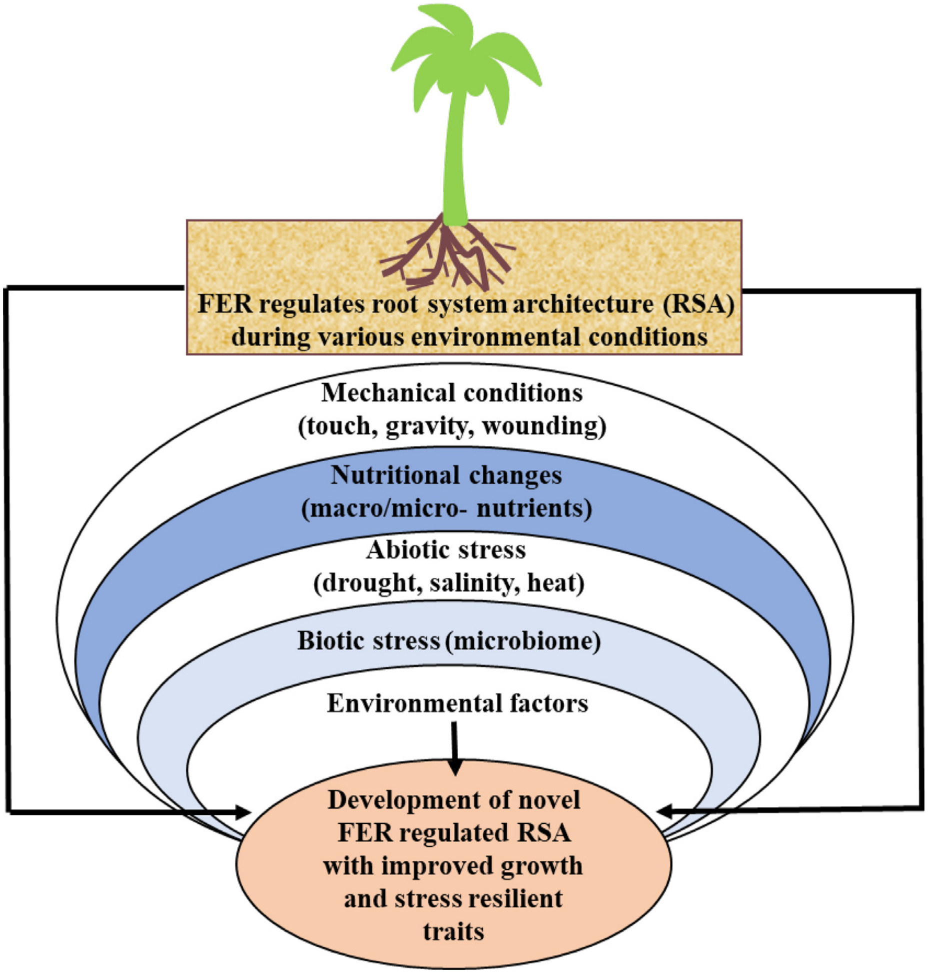

Fig. 4. Modulation of root system architecture (RSA) by FER during different environmental, mechanical and nutritional conditions in plants.

Role of FER in stress perception and regulation in roots

Plants are capable of sensing and responding to diverse environmental and mechanical cues as well as nutrients in order to survive and reproduce. The majority of research to date has been concentrated on above-ground shoot-related phenotypes, which have been helpful in understanding the intricate interactions between plants and their environment, and have successfully been translated into the development of high-yielding and resilient crops through molecular breeding and genetic engineering. However, the plant roots are still an underutilized source of crop development [96]. The root system is responsible for essential plant processes such as water and nutrient intake, substrate anchoring, and communication with symbiotic species. Roots face different external factors *viz.,* environmental (biotic and abiotic stressors, microbiota), nutritional (macro and micronutrients), and mechanical conditions (gravity, touch, sound, wounding), all of which have significant impact on above-ground parts and crop yield Fig. 4. However, it remains largely unknown how roots sense above factors at molecular level. In this review, discussed how FER plays a key role in root sensing and signal dynamics during abiotic and mechanical stressors as well as nutrient homeostasis (macro and micronutrients).

Role of FER in abiotic stress responses in roots

Roots are very often exposed to various abiotic stressors such as drought, salinity, cold, heat, and heavy metals which affect their development and overall crop yield [97]. For instance, drought stress directly inhibits root growth and development, and reduces water intake which increases stress on xylem tissue [98]. Without proper acclimatization, this could result in xylem embolism, which would lead to hydraulic failure [99]. Drought also affects root's capacity to absorb nutrients, change their microbiota, decrease their penetrability, and also place mechanical strains on them, all of which endanger plant survival [100]. Similarly salt and heavy metal stressors impede root growth and their essential functions by leading to nutritional imbalances, osmotic stress, and inhibiting enzyme activity [101]. High and low temperature stress also affects root system and its key traits [102]. Similar to other stresses, flooding has a detrimental effect on a plant's root system by blocking gas diffusion, which causes hypoxia, altering root microbiome, nutrient imbalance and promoting root diseases, all of which contributes to plant death [103–105]. However, plants use their elegant responsive system in order to confront or survive these conditions. For instance, the role of calcium channels, ROS, hormones, nitric oxide (NO) and small peptides have been reported to play key role in abiotic stress signaling responses in plants. However, their apoplastic activation or regulation remains largely unknown thereby leaving major knowledge gaps in cells interior and exterior signaling responses. However, recent studies have shown that cell wall sensors play vital role in stress sensing and signal transduction by detecting early damages caused by abiotic or biotic stressors, and triggers a variety of downstream signaling cascades. Here, we focused on the existing knowledge on how cell wall sensor FER is perceiving various abiotic stressors, and regulates different upstream and downstream signaling cascades. Previous study has shown that FER maintains the cell wall integrity in roots by detecting the defects caused by salinity stress [63]. This was confirmed by subjecting *fer* mutants to salinity stress, which causes a dramatic burst of root cells. Interestingly, in this study, FER extracellular domain binds with pectin fragments during salinity stress and triggers Ca^{2+} transients that maintain cell-wall integrity. This study also proved that FER is required for the recovery of root growth after exposure to salt stress. The most striking feature of this study was the FER/RALF1-independent response towards salinity stress. However, there are other RALF peptides that may be important during salinity stress. For instance, Zhao et al. [106] identified new FER-mediated salinity tolerance pathways which involve the association of three players leucine rich extensin LRX3/4/5, RALF22/23 and FER, which control ROS production and hormone homeostasis. The main finding of this trio regulatory complex was the negative regulation of ABA, jasmonic acid (JA), and salicylic acid (SA). Although many new findings have emerged from these studies but how RALF peptides are activated that bind to FER as well as which calcium channel is involved remains largely unknown. In addition, how FER controls ATPase, NADPH activity and other downstream signaling events during salt stress warrants future consideration. How FER interacts with other signaling cascades that is prominent during salinity stress needs further attention for developing salinity resilient smart crops. Finally, it requires to identify the other players involved in cell wall reprograming during salinity stress and how they are connected with FER. Recently, Xie et al. [107] reported that FER positively regulates salt tolerance and reduces ABA sensitivity in *Malus domestica*. These studies highlight the importance of FER in salinity stress perception and signal transduction.

Roots are the main organs that detect drought stress and relay this signal to other organs which forms a long-distance signaling communication with above ground parts [108]. Under drought stress root undergo various adaptive changes such as deeper root formation, root diameter and root respiration [109]. For instance, under drought stress increased number of thinner and deeper roots are formed, which facilitates roots to absorb nutrients and water due to more surface area [109]**.** The bending of roots toward areas of water, or positive hydrotropism, is another element that affects drought tolerance and RSA [110]. Since the accumulation of ABA is a hallmark of drought stress and root adaptive responses and has been studied on deciphering the intricacy of drought stress mediating signaling [111]. There is evidence that exogenous treatments of ABA enhance drought tolerance, which further supports the strong link between ABA accumulation and drought tolerance [112]. ABA signaling triggers a number of defensive responses in plants, such as stomatal closure and transcriptional/translational reprograming of stress response genes [111]. Recently, it was found that FER suppresses ABA by activating ABI2 phosphatase (a negative regulator of ABA) through FER–RopGEF1/4/10–ARAC10/ROP11 that further inhibits ROS production [69]. Further, *fer* mutants were found to be more hypersensitive to ABA and produce high levels of ROS which inhibited stomata closure, seedling and root development, and ultimately led to cell death [69]. This study also provides novel findings on the upstream regulation of ABA signaling and its ally ROS by linking the FER pathway with the inhibition of ABA signaling. However, further studies are required to unravel how FER controls ABA signaling cascades when plants are exposed to drought either individually or in combination with other stressors. The role of FER in root development and adaptive traits during drought stress warrants future investigation. Additionally, how FER controls ABA regulatory signaling molecules such as calcium, potassium, nitrate, malate channels and peptides in roots and their impact on long distance signaling during drought stress needs further consideration. Future studies are required to unwire the role of FER in ABA independent regulatory responses during drought stress which will offer new insights on drought signaling mechanisms in root biology. On the other hand, role of oligosaccharide mediated FER activation during drought stress warrants future investigation.

Recently, FER was identified as important player for regulating cold and heat stress responses in Arabidopsis [113]. As *fer* mutants showed more hypersensitivity to cold and heat with low survival rate when compared to wild-type plants [86]. This study provides the crucial role of FER in plant response to RALF1 and ABA during cold or heat signaling dynamics. Another study found that the *BZR1* transcription factor controls heat stress tolerance in tomato by ROS signaling mediated by FER [114]. However, the core signaling players that are involved during FER-mediated cold and heat response have not yet been identified. Hence, identifying other components such as FER co-receptors and downstream molecules will enable us to better understand how FER regulates cold or heat stress responses in plants. Owing to the complexity of cold and heat signal transduction in plants, it is important to examine how FER regulates different cold or heat responsive hormonal cascades, calcium channels, ROS and NO which will provide novel avenues for developing cold or heat tolerant crops. Plant growth and crop production are severely hampered by excess heavy metals and trace elements as well as nutrient deficiencies in soils [115]**.** There-

Table 2
The role of FER in sensing different environmental cues and its regulatory mechanism in plants.

Stress		Regulation	Species	References
Abiotic stress	Salt	Sense the defects occurred by stress at cell wall (root growth recovery) Involved in RALFs and LRXsInvolved in RALF1 and AGB1 (heterotrimeric Gβ subunit) Increased sensitivity to stress in *fer-4 mutant*Negatively regulates touch regulated genes (TCHs)	*A. thaliana*	[63,70,118,119]
		Increased tolerance to stress and reduced sensitivity to ABA in *oxFER*	*Malus domestica*	[107]
	Drought	Involved in relieve photosystem damage and accumulation of free amino acid	*M. domestica*	[120]
	Heat	Involved in ROS and brassinosteroid-mediated process (brassinazole resistant 1, BZR1)	*Solanum lycopersicum*	[114]
		Increased sensitivity to stress in *fer-4 mutant*	*A. thaliana*	[86]
	Cold	Increased sensitivity to stress in *fer-4 mutant*	*A. thaliana*	[86]
	Light (phototropism)			
	Photo-oxidative	Regulates light-induced stress genes, ROS ($^1O_2$), photosystem Ⅱ	*A. thaliana*	[121]
	Blue light	Regulates phototropin 1 (PHOT1)	*A. thaliana*	[122]
	Red	Involved in phytochrome B-regulated Fe deficiency tolerance pathway	*S. lycopersicum*	[123]
	Far-red	Involved in canonical shade response strategies (SAS)-associated gene network	*A. thaliana*	[124]
	C/N	Response to stress by regulating E3 ubiquitin ATL6	*A. thaliana*	[125]
	Heavy metals	Negatively respond to Cd, Ni, Pb Positively respond to Cu, Zn	*A. thaliana*	[117]
		Negatively regulates Cd toxicity via Fe uptaking pathway (tolerance in *fer-4 mutant*)	*A. thaliana*	[126]
Mechanical stress	Touch	Negatively regulates Jasmonic acid-mediated stress response Involved in CAMTA3 regulation Mediated by Ca^{2+} signaling (impaired in *fer-4 mutant*)	*A. thaliana*	[70,127]
	Gravitropism	Inhibits root cell elongation (alkalization in apoplast) Regulates columella cell, PIN2, auxin, and F-actin	*A. thaliana*	[92]
	Cell wall damage (wounding)	Negatively regulates ERF114 and ERF115 expression	*A. thaliana*	[94]
		Involved in root tip regeneration with RALF33 under stress	*A. thaliana*	[128]
Biotic stress	*Pseudomonas syringae*	Inhibit jasmonic acid signaling (plant immunity)	*A. thaliana*	[93]
	P. syringae & *Bacillus subtilis*	Alleviate phosphate starvation together with PHR1 and RALF	*A. thaliana*	[129]
	Pseudomonas fluorescens	Inhibit Pseudomonas in the rhizosphere pseudomonads through ROS regulation	*A. thaliana*	[130]
	Valsa mali	Negatively regulates pathogen infection by ABA, SA, and polyphenol accumulation	*M. domestica*	[131]
	Pyricularia oryzae	FLR2 and FLR11 (FER –like receptor, FLR) is related to ROS production and defense-related genes	*Oryza rufipogon*	[132]

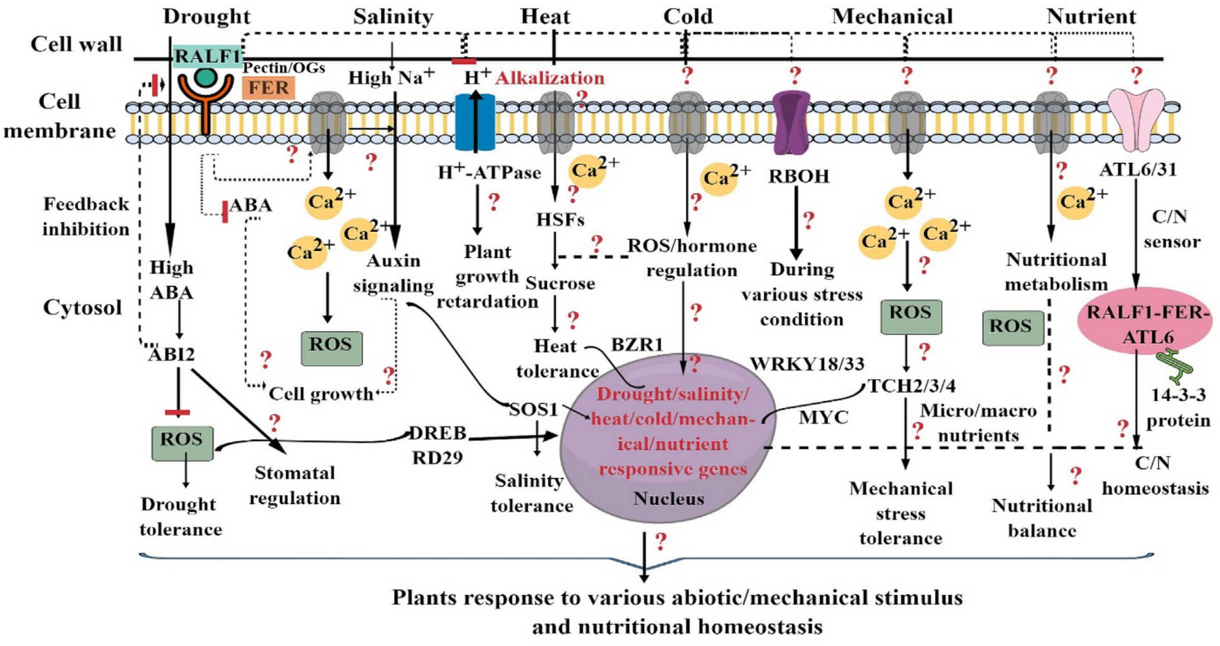

Fig. 5. A schematic model shows the signaling pathways regulated by FER. This model provides a summary of the existing knowledge regarding the unique regulation of several signaling cascades by FER during the detection and signal transduction of abiotic and mechanical stressors. This figure shows some of the key players (e.g., ABA, JA, Ca^{2+}, ROS and ATPase, TFs) which are either directly or indirectly regulated by RALF1 or PECTIN/FER activation that in turn triggers different downstream signaling cascades depending on the nature of stress. This model also highlights various missing links in FER-mediated signal transduction (e.g., activation of calcium channels and their sensors, ROS regulation, hormonal crosstalk, sensing different abiotic and mechanical stimuli and their signal transduction). It also highlights the role of FER in nutrient homeostasis such C/N ratio. The role of trio complex RALF1-FER-ATL6 and their interaction with 14–3-3 family has been identified as primary molecular switches of maintaining C/N ratio.

fore, plants must maintain the ion homeostasis in order to maintain the cell integrity and cellular functions. In the past, various players (e.g.,carriers, transporters, hormonal signatures, ROS, NO, and different gene networks) have been identified that govern the ion regulation in plants [115,116]. However, the recent studies have reported the role of cell wall sensors such as FER, THESEUS1, and HERCULES1 in monitoring the defects triggered by presence of excessive or low heavy metals as well as growth adaption [117]. This study also reported that *fer*-4 knock-out showed a greater tolerance to cadmium (Cd), copper (Cu), lead (Pb), and (zinc) Zn, but a hypersensitivity to nickel (Ni). This indicates that, FER seems to be an important player for underpinning the heavy metal sensing in root biology. Future studies are required to identify FER mediated signaling players during heavy metal stress in roots. Further, we summarized the overall information on how FER regulates different abiotic stressors (Table 2), based on available literature we have shown how FER senses different abiotic and mechanical stresses and regulates signaling transduction pathways in Fig. 5. We have also highlighted the missing gaps in FER-mediated signaling which warrants future investigation.

FER a key sensor in root mechanobiology

Plant mechanobiology has emerged as one of the most prominent field in plant sensory biology in the recent times [36]. Plants are very often exposed to different mechanostimulli such as touch, rain, wind, gravity, sound, wounding and other cellular mechanical signals (turgor pressure) which have significant impact on their growth and development [133–135]. However, plants have well-structured mechanosensing system that allows them to detect these diverse mechanostimuli and translate them into biochemical responses [136]. Nevertheless, mechanosensing in plants depends on various intrinsic and extrinsic factors, such as the type of mechanostimulus, duration, plant species, organ, physical properties, cells, and environmental conditions [136]. Although the biochemical and molecular components of plant responses to other environmental cues have been well recognized, but it remains largely unknown in plant mechano perception and signal transduction. Roots face wide ranges of mechanical perturbations during drought or heterogeneous soil particles that impact root penetration and extension [137]**.** Root caps, which are dynamic organs at the very tip of main roots, are crucial for development through harder media and heterogenous soils [138]**.** It is well documented that bending or poking of root tips elicits a transient Ca^{2+} influx and using mechanical channel calcium inhibitors further supports that presence of mechanical sensing system in roots [139]. Roots are generally considered as an elegant model to explore the molecular underpinnings that govern gravitropism. Many studies have reported an array of gene families such as inositol 1, 4, 5-trisphosphate (InsP3), auxin influx (AUXI and LAX family), efflux transporters (PIN family and P-glycoprotein-type transporters), ALTERED RESPONSE TO GRAVITY 1 (ARG1), ARG1-LIKE2 (ARL2), PID-like protein kinases (WAG1 and WAG2), and signaling molecules (Ca^{2+}, ROS, NO), which have provided novel insights into the molecular intricacy of root gravitrophism [140–146]. However, it remains largely unknown how gravity sensing occurs in the upstream cellular compartment like cell wall and plasma membrane, and how it triggers downstream signaling into different cytosolic intracellular and organelle signaling cascades. Calcium burst has become a hallmark of root gravitropism but still no mechanosensitive channels has been identified in response to gravitropism. There are many mechanosensitive channels [MSL, Mid1-Complementing Activity (MCA) proteins, reduced hyperosmolality-induced $[Ca^{2+}]_i$ increase (OSCA) channel, two-pore K^+ (TPK), PIEZO], and cell wall receptor-like kinase (FER, THESEUS1, ANXUR1, ANXUR2 and WAKS) which are considered important sensors for perceiving different mechanical or other stresses in plant system [13]. Recent studies have reported the role of mechanosensitive channels in root responses to different mechano stimuli hence provided novel insights into plant mechanobiology [13,147,148].

In this review, we focused on the role of FER in plant mechanostimulation. Owing to its multifaceted functions, FER is one of the best candidates to explore in root mechanobiology. As we have already discussed how FER controls various root signaling aspects using different signaling cascades thus further proves that how important FER is for root developmental and sensing stressors. However, the role of FER as a mechanosensor is not fully explored therefor remains many knowledge gaps. Shih et al. [70] reported that FER controls touch response in roots. Mutant of *fer* shows abolished Ca^{2+} activation pathways and the reduced expression of touch responsive genes such as *TCH4*, *TCH2*, *TCH3*, *CPK28*, *CML49*, *WRKY33*, *WRKY18* and *ZAT10* than wild-type touch treated plants. This study highlight the role of FER in modulating the touch signaling cascades in Arabidopsis [70]. Many questions remain unanswered in FER mechanosensing. For instance, i) whether RALF-dependent or RALF-independent FER activation occurs in roots after mechanical stress. ii) How FER activation further modulates Ca^{2+} channels, NADPH, H^+-ATPase and hormonal crosstalk that form central hub of mechanosignal transduction in plants. How FER aids roots in sensing different mechanical cues like sound, gravity, wind, touch, rain, etc. warrants future investigation. In this regard there is needs to integrate forward and reverse genetics, genome-wide association studies (GWAS), multiomics, and real-time imaging using different sensors approaches to address above questions with an aim of unravelling the molecular intricacy of root mechanosignal transduction. Additionally, future research should focus on other cell wall sensors like THESEUS1 in root mechanobiology. Further we have shown the role of FER in root mechanosensing in (Fig. 5).

FER and root-nutrient signaling dynamics

Plants being sessile are highly reliant on their root system in order to locate and uptake nutrients more efficiently and economically from the soil systems for their existence [149]. Numerous studies have demonstrated that nutrients directly affect RSA, making it an intriguing area for researchers to investigate the complex relationships between nutrient dynamics and root development [150]**.** As a result, modifying RSA has become a key tactic to improve nutrient uptake, particularly in low input agricultural systems. Root hairs are the major parts to uptake nutrients from the soil, and have become an obvious sites to examine the molecular underpinnings of nutrient transport activities in the root [151]**.** Nevertheless, molecular candidates that act as modulators or regulators of different stages of root hair development are beginning to emerge. One such molecular candidate is FER that controls an array of signaling events during root hair development and its functions. Recent study has shown that FER plays a major role in regulating carbon/nitrogen ratio in Arabidopsis [125]. Nutrients such as carbon (C) and nitrogen (N) are crucial to maintain routine and fundamental cellular functions. For example, C is the primary structural component in the production of enormous molecules like amino acids [152]. Similarly, N is also critical for normal growth, cellular metabolism and energy homeostasis [153]. Numerous studies have demonstrated that synchronization of the C and N ratio controls a number of crucial pathways in plants, including glycolysis/gluconeogenesis, protein targeting, and metabolism, all of which are crucial for plant growth and development [154,155]. Despite playing a vital function in plants, C and N molecular sensing and regulation remain a mystery. Previous studies have identified many potential candidates that could play vital role in C/N ratio regulation. For example, ATL (Arabidopsis Tóxicos en Levadura) family encodes plant-specific E3 ubiquitin ligase proteins, and associates with 14–3-3 proteins for ubiquitination [125]. It is known that 14–3-3 proteins regulate many enzymes (glutamine synthetase, trehalose-phosphate synthase, sucrose-phosphate synthase, nitrate reductase) involved in C/N ratio. ATL31 and its closest homolog, ATL6, have been found among the ATL gene family to interact with 14–3-3 proteins to regulate C/N ratio. FER controls the upstream regulation of signaling cascades that are mediated by ATL6 [125]. According to their findings, overexpression of FER increased resistance while *fer* mutants displayed hypersensitivity to high C/N ratio in Arabidopsis. The core mechanism behind the FER-mediated ATL6/14–3-3 signaling was FER kinase activity of ATL6, and RALF1/FER activation that increases the stability of 14–3-3 proteins. The discovery of the RALF1/FER/ATL6 trio regulatory pathway as a novel regulatory mechanism of the C/N ratio in Arabidopsis thus opens up new avenues in the dynamics of nutrient signaling in plants (Fig. 5). The connection between FER and the nutrient sensor TOR Complex 1 (TORC1) signaling 2 to control root hair growth under low temperatures has recently been discovered to be a new avenue of FER-mediated nutrient signaling in Arabidopsis [156]. This study also provides the evidence on the role FER under low nutrient condition and could be a promising area for future research in root-nutrient dynamics. These studies further support the notion that FER has important role of FER in plant-nutrient signaling dynamics. Therefore, additional research is required to decipher how FER controls various root-nutrient signals in plants (including macro- and micro-nutrients), as this may open up new opportunities for crop development in environments with low soil nutrient levels and changing conditions (Fig. 5). It is important to decode how FER controls the intracellular and extracellular activity of various channels or transporters, hormones, calcium waves, ROS, NO, and transcriptional factors that are involved in the regulation of macro- and micro-nutrient transportation and translocation. Additionally, which pathways FER will evolve in response to macro- or micro-nutrient absorption in roots. How FER can maintain the macro- or micro-nutrient ratio for proper growth and functions of RHs. It will be interesting to study how FER can control root-nutrient dynamics during biotic and abiotic stressors. Finally, researchers need to also focus on other allies of FER such as THESEUS1 and their peptides (RALFs) in order to examine their role in root-nutrient dynamics.

FER: A bridge between upstream and downstream signaling pathways

The initial line of defense between plant cells and their surroundings is the cell wall, which preserves not only the shape of plant cells but also senses environmental cues [157]. From the last decade, significant findings have emerged on cell wall-mediated growth and stress resilience in Arabidopsis, which has led new perspectives on plant signal transduction system [158]. For example, role of various RLKs as sensors and their modulatory or regulatory functionaries has opened new platforms in plant developmental and stress biology [159,160]. Plants produce numerous structurally diverse biochemical signaling molecules such as Ca^{2+} waves, ROS, hormones, peptides that modulate their growth and adaptive responses [134]. The functional role of these signaling molecules have been well studied in both model and crop systems. However, their regulation by RLKs and other apoplastic players is not fully understood. Here, we are updating the recent developments on how FER modulates plant cellular signaling cascades and highlighting knowledge gaps. In plants, FER controls diverse growth and adaptive traits mainly by modulating Ca^{2+} waves, hormonal crosstalk, ROS burst, H^+-ATPase activity, and cell wall integrity [161]. These signaling pathways are controlled by both RALF-FER-dependent and independent manner, and their activation is largely reliant on the nature of stress and site [60,63]. FER modulates calcium signaling during growth and mechanical stress. For example, Ngo et al., [162] showed that FER controls Ca^{2+} waves during pollen development as *fer* mutants were severely altered in the dynamics of calcium waves. Similarly, in Arabidopsis it was found that FER controls cytosolic Ca^{2+} waves during touch treatment as *fer* knock-out mutants totally inhibit the calcium burst and decrease the expression of touch marker genes [70]. Under salt stress, the FER protects cell-wall integrity in Arabidopsis via Ca^{2+} dependent signaling [63]. These studies further support the notion that FER controls calcium channels however, how it triggers their activation remains largely unknow. Also, which calcium channel (e.g., GLR, CNGC, MCA, MSL, OSCA, and PIEZO) is regulated by FER during stress perception remains unknown. Additionally, calcium sensors that are involved in the calcium signal transduction induced by RALF1-FER remains enigmatic. Therefore, future studies are required to decode how FER activates calcium channels and to identify sensors that translate environmental triggered signals into biochemical responses which will provide novel insights on apoplast mediated signaling in plants. FER also act as master regulator of ROS production during growth and stress [163]. However, it largely depends on the organ type and nature of the stress. For example, FER positively controls auxin-induced ROS production, which in turn controls the growth of root hair polar [65]. FER also regulates pathogen-triggered ROS during plant defense responses [69]. In contrast, FER inhibits the production of ROS in guard cells in response to ABA [69]. How NADPH oxidases are regulated by FER is not fully understood therefore warrant future investigation.

Numerous studies have shown that RALF1-FER activation modulates both growth and stress related hormonal cascades such as AUX [65,164], BR [64,68], JA [93], ET [72], and ABA [69,86]. All of them have huge impact on plant growth and stress resilience. For example, FER is a regulator of auxin-regulated root hair growth and participates in the ROPGEF1/RAC/ROP2 signaling pathway [65]. FER also modulates auxin transportation and regulate auxin triggered ROS in root hair cells. In a similar manner, FER phosphorylates MYC2, a critical element of JA signaling, resulting in its inactivation to counteract high JA levels in situations when the pathogen uses JA to promote disease [93]. According to Deslauriers and Larsen [64], FER is an important modulator of ET signaling pathway in Arabidopsis because it suppresses the expression of inhibitors of ET synthesis like S-adenosylmethionine (SAM) via SAM1 and SAM2 [72]. Recent research has shown that FER controls ABA signaling by interacting with ABA INSENSITIVE 2 (ABI2), a PP2C member operating upstream in the ABA response [69]. However, as a potential feedback control mechanism, ABI2 dephosphorylates FER for its RALF activation [86]. This study also highlights the crosstalk between ABA and RALF peptides during FER-mediated growth and stress resilience. In future, it will be interesting to explore new horizons of ABA-RALF1-FER regulatory mechanism in biotic and abiotic stressors, and how this trio will balance trade-off between growth and stress in plants. We speculate that this trio system may have additional hidden players upstream and downstream that could control a variety of growth and stress responses. Recent study has demonstrated that FER plays a role in plant growth and resistance that is mediated by BR. First, BRs induce *FER* genes, and BR mutants show altered gene expression patterns of *FER* and *CrRLK1L* subfamily members (*HERCULES1* and *THESEUS1*). All of these studies provide concrete evidence that FER controls hormonal crosstalk and forms a central node between growth and stress hormonal pathways. In future, major players in the upstream and downstream RALF1-FER signaling need to be identified to fully decipher its role in plant growth and signal transduction. Here, we have summarized how FER modulates different signaling signatures in plants (Fig. 5).

FER and root microbiome assembly: A new paradigm in root microbiome dynamics

Roots offer a very desirable and nutrient-rich niche that support diverse microbial communities which are beneficial to plant health and nutrient availability [13,165]**.** Additionally, root microbiome has huge impact on plant stress resilience and soil fertility. At the soil-root interface, roots offer a variety of microhabitats, such as endorhizosphere, rhizosphere, and rhizosphere soil. Therefore, a critical first step in the logical use of the microbiota for agricultural objectives will be the analysis of the molecular mechanisms behind plant–microbe community relationships at the root-soil interface. Enrichment of particular microbial taxa in plants has been linked to growth promotion and stress resilience, while dysbiosis microbiome have been linked to disease in both plants and animals [166]. Many studies have shown that plants under stress can shape their beneficial microbial taxa in the rhizosphere to increase the resilience to future stressors [167,168]. Likewise, under field or lab conditions, synthetic enrichment of particular of tailored beneficial consortia can support not only growth traits but also increase stress resilience to biotic and abiotic stressors [169,170]. These findings imply that, to maximize fitness, plants may be able to control the particular or a few beneficial microbes. Hence, maintaining microbiome structure is one of the most important function of roots, and has become research frontier in root biology for the crop improvement. However, little is known about the genetic controls and methods which plants utilize to manage the structure of such beneficial microbes. Nevertheless, there are plenty of data that highlight the role of diverse factors for driving the structure of root microbiome [165,171]. Some of the important drivers for microbiome assembly are host-based factors are root exudate chemistry, plant age, genotypes, plant species, and canopy type which can greatly influence the root microbiome. For example, in the same soil potato and rice showed diversified root microbiome composition at subspecies level. Based on the next-generation sequencing approaches a distinct microbiome was identified in Arabidopsis and other crop plants grown under same soil conditions. Interestingly phylogenetically different plants show greater variation in shaping microbiome which provides the evidence that plant phylogeny plays important role in structuring root microbiomes [172]. On the other hand, genotype-based microbiome structure was found in different crops such as pea, wheat, oats, and potato [173,174]. Previous reports have shown that wild and transgenic line of Populus with different genetic clones shaped distinct microbiomes [175]. Additionally, developmental stage and plant age also influences root microbiome. For example, previous studies have shown that root growth, root architecture, root morphology and root length influence microbiome structure [176,177]. Root exudates have the major influence on root microbiome structure. Generally, roots produce a diverse blend of chemicals known as exudates such as amino acids, carbohydrates, vitamins; organic acid and ions which not only provide nutrient riche niche but also influence in shaping microbiome [178,179]. Similarly, environmental factors (e.g., organic matter, soil pH, temperature, soil type, depth, porosity, oxygen, and carbon dioxide concentration) are important signatures for root microbiome assembly [165,171]. On the other hand, microbe based factors [e.g., microbe-microbe interaction, biofilm formation, exopolysaccharide (EPS) secretion, biosurfactant compounds, quorum sensing signals, adhesion molecules, flagellum, antibiotics, and free radical detoxifying proteins] also determine the overall outcome of root microbiome assembly [165,171]. Till date, most of the studies have focused on the external factors that drive root microbiome assembly which indeed has broaden our understanding of the complexity of root microbiome dynamics. Generally, roots act as filters for selecting unique microbiota in plants. However, it is still unknown how roots sense microbiome.

From last two decades, significant progress has been made on how plants sense pathogens with different lifestyles which have provided novel findings in molecular plant-pathogen interactions. For example, many cell wall-based sensors, trichomes, plasma membrane channels and other intracellular signaling cascades have been identified that drive early pathogen perception signaling as well as late transcriptional, translational, and posttranslational modifications [101]. However, it remains largely unknown how they sense different beneficial microbial taxa at molecular level. Plants have different sensors, which are located both above- and below-ground parts. For instance, trichomes, leaves and root hairs have different sensors that can play key roles in plant microbiome structure assembly and signaling dynamics. In this review, we address the role of FER in root-microbiome signaling dynamics and highlight the future directions and knowledge gaps. RLKs and RLPs are crucial players for pathogen recognition and activation of plant immune responses. However, their role in microbiome shaping or functioning is not fully understood. Recently, it was discovered that FER acts as most versatile cell wall sensor that can drive the assembly of particular beneficial taxa in root microbiome [129,130]. For instance, Song et al., [130] reported that that loss of FER robustly enriches rhizosphere *pseudomonads* due to low ROS production. Additionally, they demonstrated that a novel mechanism necessary for the negative regulation of rhizosphere *Pseudomonas* is FER-regulated basal ROS buildup through ROP2-dependent NADPH oxidase activity [130]. In another study, it was found that FER-RALF and PHR1(transcriptional regulator of P starvation) intersects with FLS2/BAK1 to suppress Arabidopsis immunity, thereby allowing specific beneficial root microbiota (*Flavobacterium, Pseudomonas and Delftia*) to colonize which in turn helps to relieve phosphate deprivation. Previous studies have revealed that *Flavobacterium, Pseudomonas and Delftia* were among the most predominant beneficial bacterial in plants during stress [180–182]. These studies open new directions in plant microbiome research. Further research is required to determine how RALF/FER pathway can regulate calcium, ROS, hormones and root exudates and their role in the selection of beneficial bacteria by sensing the integrity of the cell wall. Also, the role of FER in shaping plant microbiome at different plant compartments under diverse environmental conditions warrants future attention, which will provide novel avenues for exploring new paradigms of plant microbiome interactions. Future studies should also focus on other cell wall RLKs (e.g., THESEUS1, ANUX, WAKS, and LRRs) to decipher their role in root microbiome dynamics. Deciphering the significance of FER in forming the root microbiome will require more research into how FER and other RLKS control plasma membrane ion channels, ATPase, NADPH, and hormone dynamics, as well as their influence on plant root exudate production. We have presented the model which shows the role of FER in microbiome assembly as well as its interconnected networks (Fig. 6).

Conclusion and perspectives

Plants with superior root systems may effectively gather water and nutrients, and store more carbon in the soil, potentially making them more resistant to climate change and enhancing production stability. Even though roots are essential for plant productivity and adaptability and their role in crop improvement and yield productivity has not been fully explored in contrast to above ground traits. Roots are the first organ that faces many environmental

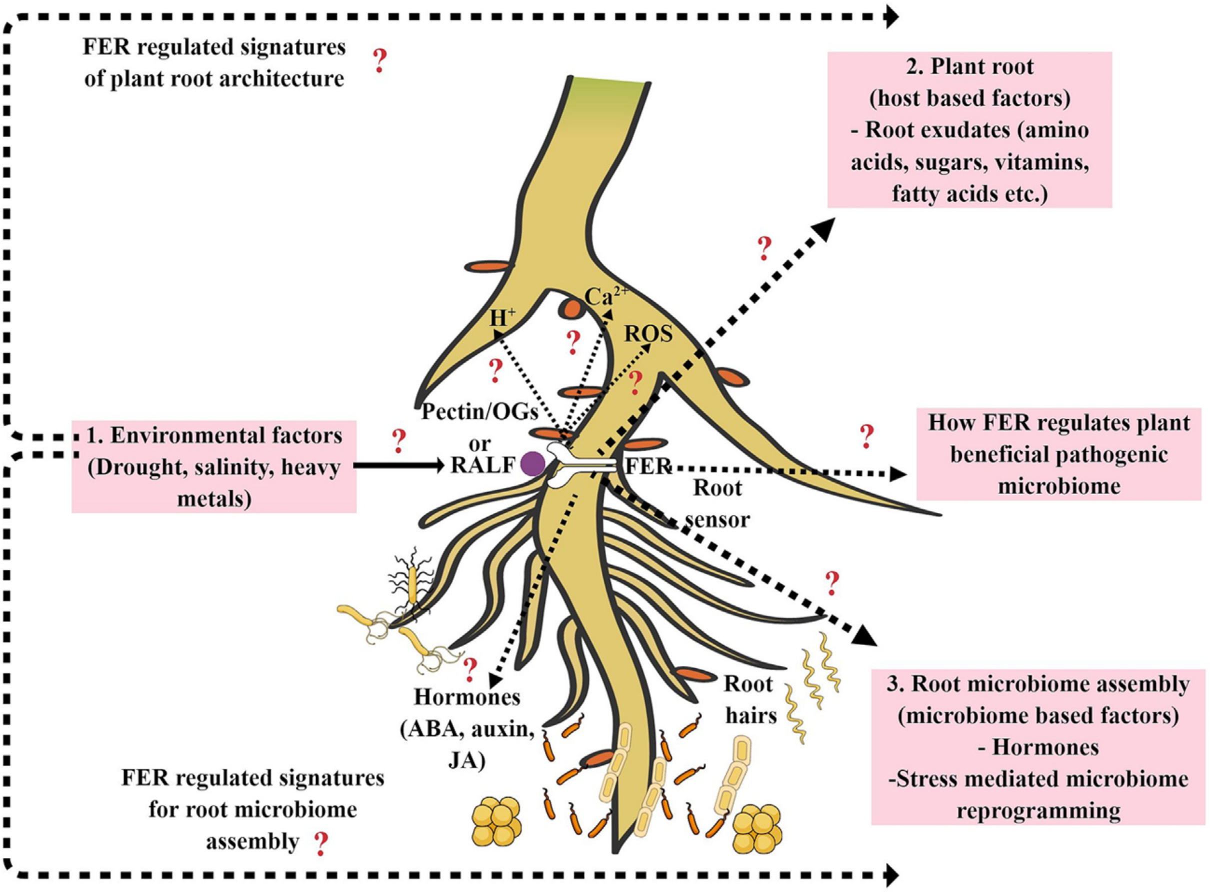

Fig. 6. Schematic diagram shows how FER mediated signaling molecules influence root microbiome assembly. FER can affect root microbiome assembly by regulating different root traits (e.g., pH, ROS, calcium, and hormonal signatures). This figure shows FER activation may be triggered by either RALF peptide or pectin/oligosaccharide that will affect microbial taxa during different environmental conditions. It also highlights the missing links in FER-mediated root microbiome signaling dynamics.

obstacles like salinity stress, drought, and heavy metal stressors that have significant impact on whole plant. Signal perception via cell surface receptors is a characteristic shared by all living things. Recent studies on cell wall sensors such as RLKs have provided novel insights on how plants detect various stimuli (e.g., mechanical, biotic, abiotic, and cellular development) and translate them into biochemical responses to balance growth and adaptive responses. Considering this, we provided a multiscale viewpoint on the role of most prominent cell wall sensor FER which has emerged a master player in sensing both growth and stress responses. We also discussed how they modulate or regulate different aspects of root biology. However, there are many questions that need to be addressed in future, which will provide new research directions in the field of root biology (See outstanding questions). How FER regulates root development by modulating key root signaling players (AUX, CK, BR, and ABA), small peptides [CLE, RGF, CEP, IDA cyclin-dependent-kinases (CDKs), D-type cyclin (CYCD)], as well as TFs that regulate different root developmental processes. How FER modulates root adaption to biotic and abiotic stressors, and how it protects and promotes their root growth. How FER senses diverse mechanical stress is the most exciting research in root mechanobiology. How FER regulate root growth and stress responses, and balance their trade-offs? How FER regulate root Ca^{2+} channels and their signaling events, which is RALF-dependent and RALF-independent? How FER control ROS, pH, and hormonal crosstalk that influence different root traits? How FER perceive individual or multiple root abiotic and mechanostimulli, and how it differs in their perception and transduction? How FER regulate root RSA and adaptive responses? Do FER have any role for the signaling from root to shoot? How FER influence root microbiome during mechanical and abiotic stresses? Addressing these questions requires integration of forward and reverse genetics, GWAS, multiomics, and real-time imaging using different sensors with an aim of unravelling the molecular intricacy of FER-mediated root signaling dynamics. Due to its diverse, fundamental, and tissue-specific roles in plant development, yield regulation, and numerous stress responses, FER can be ideal candidate for plant breeding to improve plant growth, yield and adaptive traits.

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CRediT authorship contribution statement

Sajad Ali: Conceptualization, Methodology, Writing – original draft, Writing – review & editing. **Anshika Tyagi:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing. **Suvin Park:** Methodology, Writing – original draft, Writing – review & editing. **Rajeev K. Varshney:** Conceptualization, Writing – review & editing. **Hanhong Bae:** Supervision, Conceptualization, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

[1] Habib-ur-Rahman M, Ahmad A, Raza A, Hasnain MU, Alharby HF, Alzahrani YM, et al. Impact of climate change on agricultural production; Issues, challenges, and opportunities in Asia. Front Plant Sci 2022;13:. doi: https://doi.org/10.3389/fpls.2022.925548925548.

[2] Benitez-Alfonso Y, Soanes BK, Zimba S, Sinanaj B, German L, Sharma V, et al. Enhancing climate change resilience in agricultural crops. Curr Biol 2023;33: R1246–61. doi: https://doi.org/10.1016/j.cub.2023.10.028.

[3] Tilman D, Balzer C, Hill J, Befort BL. Global food demand and the sustainable intensification of agriculture. Proc Natl Acad Sci U S A 2011;108:20260–4. doi: https://doi.org/10.1073/pnas.1116437108.

[4] Ray DK, Ramankutty N, Mueller ND, West PC, Foley JA. Recent patterns of crop yield growth and stagnation. Nat Commun 2012;3:1–7. doi: https://doi.org/10.1038/ncomms2296.

[5] Daryanto S, Wang L, Jacinthe PA. Global synthesis of drought effects on maize and wheat production. PLoS One 2016;11:e0156362.

[6] Brás TA, Seixas J, Carvalhais N, Jagermeyr J. Severity of drought and heatwave crop losses tripled over the last five decades in Europe. Environ Res Lett 2021;16:. doi: https://doi.org/10.1088/1748-9326/abf004065012.

[7] FAO, IFAD, UNICEF, WFP, WHO. The State of Food Security and Nutrition in the World 2022. 2022. doi: 10.4060/cc0639en.

[8] Calleja-Cabrera J, Boter M, Oñate-Sánchez L, Pernas M. Root Growth Adaptation to Climate Change in Crops. Front Plant Sci 2020;11:. doi: https://doi.org/10.3389/fpls.2020.00544523645.

[9] Uga Y. Challenges to design-oriented breeding of root system architecture adapted to climate change. Breed Sci 2021;71:3–12. doi: https://doi.org/10.1270/jsbbs.20118.

[10] Khan MA, Gemenet DC, Villordon A. Root system architecture and abiotic stress tolerance: current knowledge in root and tuber crops. Front Plant Sci 2016;7:1584.

[11] Koevoets IT, Venema JH, Elzenga JTM, Testerink C. Roots withstanding their environment: Exploiting root system architecture responses to abiotic stress to improve crop tolerance. Front Plant Sci 2016;7:1335. doi: https://doi.org/10.3389/fpls.2016.01335.

[12] Wachsman G, Sparks EE, Benfey PN. Genes and networks regulating root anatomy and architecture. New Phytol 2015;208:26–38. doi: https://doi.org/10.1111/nph.13469.

[13] Tyagi A, Ali S, Park S, Bae H. Deciphering the role of mechanosensitive channels in plant root biology: perception, signaling, and adaptive responses. Planta 2023;258:105.

[14] Richard CAI, Hickey LT, Fletcher S, Jennings R, Chenu K, Christopher JT. High-throughput phenotyping of seminal root traits in wheat. Plant Methods 2015;11:1–11. doi: https://doi.org/10.1186/s13007-015-0055-9.

[15] Lynch JP. Root phenes for enhanced soil exploration and phosphorus acquisition: Tools for future crops. Plant Physiol 2011;156:1041–9. doi: https://doi.org/10.1104/pp.111.175414.

[16] Rose TJ, Impa SM, Rose MT, Pariasca-Tanaka J, Mori A, Heuer S, et al. Enhancing phosphorus and zinc acquisition efficiency in rice: A critical review of root traits and their potential utility in rice breeding. Ann Bot 2013;112:331–45. doi: https://doi.org/10.1093/aob/mcs217.

[17] Meister R, Rajani MS, Ruzicka D, Schachtman DP. Challenges of modifying root traits in crops for agriculture. Trends Plant Sci 2014;19:779–88. doi: https://doi.org/10.1016/j.tplants.2014.08.005.

[18] Volder A, Smart DR, Bloom AJ, Eissenstat DM. Rapid decline in nitrate uptake and respiration with age in fine lateral roots of grape: Implications for root efficiency and competitive effectiveness. New Phytol 2005;165:493–502. doi: https://doi.org/10.1111/j.1469-8137.2004.01222.x.

[19] Freschet GT, Pagès L, Iversen CM, Comas LH, Rewald B, Roumet C, et al. A starting guide to root ecology: strengthening ecological concepts and standardising root classification, sampling, processing and trait measurements. New Phytol 2021;232:973–1122. doi: https://doi.org/10.1111/nph.17572.

[20] Zadworny M, McCormack ML, Rawlik K, Jagodziński AM. Seasonal variation in chemistry, but not morphology, in roots of Quercus robur growing in different soil types. Tree Physiol 2015;35:644–52. doi: https://doi.org/10.1093/treephys/tpv018.

[21] Trachsel S, Kaeppler SM, Brown KM, Shovelomics LJP. High throughput phenotyping of maize (Zea mays L.) root architecture in the field. Plant Soil 2011;341:75–87. doi: https://doi.org/10.1007/s11104-010-0623-8.

[22] Bucksch A, Burridge J, York LM, Das A, Nord E, Weitz JS, et al. Image-based high-throughput field phenotyping of crop roots. Plant Physiol 2014;166:470–86. doi: https://doi.org/10.1104/pp.114.243519.

[23] Dunbabin VM, Postma JA, Schnepf A, Pagès L, Javaux M, Wu L, et al. Modelling root-soil interactions using three-dimensional models of root growth, architecture and function. Plant Soil 2013;372:93–124. doi: https://doi.org/10.1007/s11104-013-1769-y.

[24] Rogers ED, Monaenkova D, Mijar M, Nori A, Goldman DI, Benfey PN. X-ray computed tomography reveals the response of root system architecture to soil texture. Plant Physiol 2016;171:2028–40. doi: https://doi.org/10.1104/pp.16.00397.

[25] Teramoto S, Takayasu S, Kitomi Y, Arai-Sanoh Y, Tanabata T, Uga Y. High-throughput three-dimensional visualization of root system architecture of rice using X-ray computed tomography. Plant Methods 2020;16:1–14. doi: https://doi.org/10.1186/s13007-020-00612-6.

[26] Meng F, Xiang D, Zhu J, Li Y, Mao C. Molecular mechanisms of root development in rice. Rice 2019;12:1–10. doi: https://doi.org/10.1186/s12284-018-0262-x.

[27] Torres-Martínez HH, Rodríguez-Alonso G, Shishkova S, Dubrovsky JG. Lateral root primordium morphogenesis in angiosperms. Front Plant Sci 2019;10:206. doi: https://doi.org/10.3389/fpls.2019.00206.

[28] Hochholdinger F. The maize root system: Morphology, anatomy, and genetics. Handb Maize Its Biol 2009:145–60. doi: https://doi.org/10.1007/978-0-387-79418-1_8.

[29] Lynch JP, Brown KM. New roots for agriculture: Exploiting the root phenome. Philos Trans R Soc B Biol Sci 2012;367:1598–604. doi: https://doi.org/10.1098/rstb.2011.0243.

[30] Schneider HM, Lynch JP. Should root plasticity be a crop breeding target? Front Plant Sci 2020;11:546. doi: https://doi.org/10.3389/fpls.2020.00546.

[31] Bayuelo-Jiménez JS, Gallardo-Valdéz M, Pérez-Decelis VA, Magdaleno-Armas L, Ochoa I, Lynch JP. Genotypic variation for root traits of maize (Zea mays L.) from the Purhepecha Plateau under contrasting phosphorus availability. F Crop Res 2011;121:350–62. doi: https://doi.org/10.1016/j.fcr.2011.01.001.

[32] Scheres B, Wolkenfelt H, Willemsen V, Terlouw M, Lawson E, Dean C, et al. Embryonic origin of the Arabidopsis primary root and root meristem initials. Development 1994;120:2475–87. doi: https://doi.org/10.1242/dev.120.9.2475.

[33] Karlova R, Boer D, Hayes S, Testerink C. Root plasticity under abiotic stress. Plant Physiol 2021;187:1057–70. doi: https://doi.org/10.1093/plphys/kiab392.

[34] Okamoto T, Takatani S, Motose H, Iida H, Takahashi T. The root growth reduction in response to mechanical stress involves ethylene-mediated microtubule reorganization and transmembrane receptor-mediated signal transduction in Arabidopsis. Plant Cell Rep 2021;40:575–82. doi: https://doi.org/10.1007/s00299-020-02653-6.

[35] Gandullo J, Ahmad S, Darwish E, Karlova R, Testerink C. Phenotyping tomato root developmental plasticity in response to salinity in soil rhizotrons. Plant Phenomics 2021;2021:2760532. doi: https://doi.org/10.34133/2021/2760532.

[36] Ali S, Tyagi A, Park S, Bae H. Understanding the mechanobiology of phytoacoustics through molecular Lens: Mechanisms and future perspectives. J Adv Res 2023. doi: https://doi.org/10.1016/j.jare.2023.12.011.

[37] Zhang X, Yang Z, Wu D, Yu F. RALF–FERONIA signaling: Linking plant immune response with cell growth. Plant Commun 2020;1:. doi: https://doi.org/10.1016/j.xplc.2020.100084100084.

[38] Walker JC, Zhang R. Relationship of a putative receptor protein kinase from maize to the S-locus glycoproteins of Brassica. Nature 1990;345:743–6. doi: https://doi.org/10.1038/345743a0.

[39] Lehti-Shiu MD, Zou C, Shiu S-H. Origin, Diversity, Expansion History, and Functional Evolution of the Plant Receptor-Like Kinase/Pelle Family. Recept kinases plants from Dev to Def 2012:1–22. doi: https://doi.org/10.1007/978-3-642-23044-8_1.

[40] Fischer I, Diévart A, Droc G, Dufayard JF, Chantret N. Evolutionary dynamics of the leucine-rich repeat receptor-like kinase (LRR-RLK) subfamily in angiosperms. Plant Physiol 2016;170:1595–610. doi: https://doi.org/10.1104/pp.15.01470.

[41] Yan J, Su P, Meng X, Liu P. Phylogeny of the plant receptor-like kinase (RLK) gene family and expression analysis of wheat RLK genes in response to biotic and abiotic stresses. BMC Genomics 2023;24:224. doi: https://doi.org/10.1186/s12864-023-09303-7.

[42] Rui Y, Dinneny JR. A wall with integrity: surveillance and maintenance of the plant cell wall under stress. New Phytol 2020;225:1428–39. doi: https://doi.org/10.1111/nph.16166.

[43] Schulze-Muth P, Irmler S, Schröder G, Schröder J. Novel type of receptor-like protein kinase from a higher plant (Catharanthus roseus): cDNA, gene, intramolecular autophosphorylation, and identification of a threonine important for auto- and substrate phosphorylation. J Biol Chem 1996;271:26684–9. doi: https://doi.org/10.1074/jbc.271.43.26684.

[44] Shiu SH, Bleecker AB. Receptor-like kinases from Arabidopsis form a monophyletic gene family related to animal receptor kinases. Proc Natl Acad Sci U S A 2001;98:10763–8. doi: https://doi.org/10.1073/pnas.181141598.

[45] Jose J, Ghantasala S, Choudhury SR. Arabidopsis transmembrane receptor-like kinases (RLKS): A bridge between extracellular signal and intracellular regulatory machinery. Int J Mol Sci 2020;21:1–29. doi: https://doi.org/10.3390/ijms21114000.

[46] Sun L, Zhang J. Regulatory role of receptor-like cytoplasmic kinases in early immune signaling events in plants. FEMS Microbiol Rev 2020;44:845–56. doi: https://doi.org/10.1093/femsre/fuaa035.

[47] Ye Y, Ding Y, Jiang Q, Wang F, Sun J, Zhu C. The role of receptor-like protein kinases (RLKs) in abiotic stress response in plants. Plant Cell Rep 2017;36:235–42. doi: https://doi.org/10.1007/s00299-016-2084-x.

[48] Macho AP, Lozano-Duran R. Molecular dialogues between viruses and receptor-like kinases in plants. Mol Plant Pathol 2019;20:1191–5. doi: https://doi.org/10.1111/mpp.12812.

[49] Soltabayeva A, Dauletova N, Serik S, Sandybek M, Omondi JO, Kurmanbayeva A, et al. Receptor-like Kinases (LRR-RLKs) in response of plants to biotic and abiotic stresses. Plants 2022;11:2660.

[50] Haruta M, Sabat G, Stecker K, Minkoff BB, Sussman MR. A peptide hormone and its receptor protein kinase regulate plant cell expansion. Science 2014;343:408–11. doi: https://doi.org/10.1126/science.1244454.

[51] Li C, Wu HM, Cheung AY. FERONIA and her pals: Functions and mechanisms. Plant Physiol 2016;171. doi: https://doi.org/10.1104/pp.16.00667.

[52] Liao H, Tang R, Zhang X, Luan S, Yu F. FERONIA receptor kinase at the crossroads of hormone signaling and stress responses. Plant Cell Physiol 2017;58:1143–50. doi: https://doi.org/10.1093/pcp/pcx048.

[53] Stegmann M, Monaghan J, Smakowska-Luzan E, Rovenich H, Lehner A, Holton N, et al. The receptor kinase FER is a RALF-regulated scaffold controlling plant immune signaling. Science 2017;355:287–9. doi: https://doi.org/10.1126/science.aal2541.

[54] Xiao Y, Stegmann M, Han Z, DeFalco TA, Parys K, Xu L, et al. Mechanisms of RALF peptide perception by a heterotypic receptor complex. Nature 2019;572. doi: https://doi.org/10.1038/s41586-019-1409-7.

[55] Duan Q, Liu MCJ, Kita D, Jordan SS, Yeh FLJ, Yvon R, et al. FERONIA controls pectin- and nitric oxide-mediated male–female interaction. Nature 2020;579:561–6. doi: https://doi.org/10.1038/s41586-020-2106-2.

[56] Huck N, Moore JM, Federer M, Grossniklaus U. The Arabidopsis mutant feronia disrupts the female gametophytic control of pollen tube receptor. Development 2003;130:2149–59. doi: https://doi.org/10.1242/dev.00458.

[57] Escobar-Restrepo JM, Huck N, Kessler S, Gagliardini V, Gheyselinck J, Yang WC, et al. The Feronia receptor-like kinase mediates male-female interactions during pollen tube reception. Science 2007;317:656–60. doi: https://doi.org/10.1126/science.1143562.

[58] Pearce G, Moura DS, Stratmann J, Ryan CA. RALF, a 5-kDa ubiquitous polypeptide in plants, arrests root growth and development. Proc Natl Acad Sci U S A 2001;98:12843–7. doi: https://doi.org/10.1073/pnas.201416998.

[59] Cao J, Shi F. Evolution of the RALF gene family in plants: Gene duplication and selection patterns. Evol Bioinforma 2012;2012:271–92. doi: https://doi.org/10.4137/EBO.S9652.

[60] Murphy E, De Smet I. Understanding the RALF family: A tale of many species. Trends Plant Sci 2014;19:664–71. doi: https://doi.org/10.1016/j.tplants.2014.06.005.

[61] Campbell L, Turner SR. A comprehensive analysis of RALF proteins in green plants suggests there are two distinct functional groups. Front Plant Sci 2017;8:37. doi: https://doi.org/10.3389/fpls.2017.00037.

[62] Gonneau M, Desprez T, Martin M, Doblas VG, Bacete L, Miart F, et al. Receptor kinase THESEUS1 is a rapid alkalinization factor 34 receptor in Arabidopsis. Curr Biol 2018;28:2452–8. doi: https://doi.org/10.1016/j.cub.2018.05.075.

[63] Feng W, Kita D, Peaucelle A, Cartwright HN, Doan V, Duan Q, et al. The FERONIA receptor kinase maintains cell-wall integrity during salt stress through Ca2+ signaling. Curr Biol 2018;28:666–75. doi: https://doi.org/10.1016/j.cub.2018.01.023.

[64] Deslauriers SD, Larsen PB. FERONIA is a key modulator of brassinosteroid and ethylene responsiveness in arabidopsis hypocotyls. Mol Plant 2010;3:626–40. doi: https://doi.org/10.1093/mp/ssq015.

[65] Duan Q, Kita D, Li C, Cheung AY, Wu HM. FERONIA receptor-like kinase regulates RHO GTPase signaling of root hair development. Proc Natl Acad Sci U S A 2010;107:17821–6. doi: https://doi.org/10.1073/pnas.1005366107.

[66] Wang L, Yang T, Lin Q, Wang B, Li X, Luan S, et al. Receptor kinase FERONIA regulates flowering time in Arabidopsis. BMC Plant Biol 2020;20:1–16. doi: https://doi.org/10.1186/s12870-019-2223-y.

[67] Zhu S, Estévez JM, Liao H, Zhu Y, Yang T, Li C, et al. The RALF1–FERONIA complex phosphorylates eIF4E1 to promote protein synthesis and polar root hair growth. Mol Plant 2020;13:698–716. doi: https://doi.org/10.1016/j.molp.2019.12.014.

[68] Guo H, Li L, Ye H, Yu X, Algreen A, Yin Y. Three related receptor-like kinases are required for optimal cell elongation in Arabidopsis thaliana. Proc Natl Acad Sci U S A 2009;106:7648–53. doi: https://doi.org/10.1073/pnas.0812346106.

[69] Yu F, Qian L, Nibau C, Duan Q, Kita D, Levasseur K, et al. FERONIA receptor kinase pathway suppresses abscisic acid signaling in Arabidopsis by activating ABI2 phosphatase. Proc Natl Acad Sci U S A 2012;109:14693–8. doi: https://doi.org/10.1073/pnas.1212547109.

[70] Shih HW, Miller ND, Dai C, Spalding EP, Monshausen GB. The receptor-like kinase FERONIA is required for mechanical signal transduction in Arabidopsis seedlings. Curr Biol 2014;24:1887–92. doi: https://doi.org/10.1016/j.cub.2014.06.064.

[71] Yu F, Li J, Huang Y, Liu L, Li D, Chen L, et al. FERONIA receptor kinase controls seed size in Arabidopsis thaliana. Mol Plant 2014;7:920–2. doi: https://doi.org/10.1093/mp/ssu010.

[72] Mao D, Yu F, Li J, Van de poel B, Tan D, Li J, et al. FERONIA receptor kinase interacts with S-adenosylmethionine synthetase and suppresses S-adenosylmethionine production and ethylene biosynthesis in Arabidopsis. Plant Cell Environ 2015;38:2566–74. doi: 10.1111/pce.12570.

[73] Stenvik GE, Tandstad NM, Guo Y, Shi CL, Kristiansen W, Holmgren A, et al. The EPIP peptide of inflorescence deficient in abscission is sufficient to induce abscission in Arabidopsis through the receptor-like kinases HAESA and HAESA-LIKE2. Plant Cell 2008;20:1805–17. doi: https://doi.org/10.1105/tpc.108.059139.

[74] Fukaki H, Tasaka M. Hormone interactions during lateral root formation. Plant Mol Biol 2009;69:437–49. doi: https://doi.org/10.1007/s11103-008-9417-2.

[75] Overvoorde P, Fukaki H, Beeckman T. Auxin control of root development. Cold Spring Harb Perspect Biol 2010;2:. doi: https://doi.org/10.1101/cshperspect.a001537a001537.

[76] Ni J, Guo Y, Jin H, Hartsell J, Clark SE. Characterization of a CLE processing activity. Plant Mol Biol 2011;75:67–75. doi: https://doi.org/10.1007/s11103-010-9708-2.

[77] Whitford R, Fernandez A, Tejos R, Pérez AC, Kleine-Vehn J, Vanneste S, et al. GOLVEN secretory peptides regulate auxin carrier turnover during plant gravitropic responses. Dev Cell 2012;22:678–85. doi: https://doi.org/10.1016/j.devcel.2012.02.002.

[78] Delay C, Imin N, Djordjevic MA. Regulation of Arabidopsis root development by small signaling peptides. Front Plant Sci 2013;4:352. doi: https://doi.org/10.3389/fpls.2013.00352.

[79] Okamoto S, Shinohara H, Mori T, Matsubayashi Y, Kawaguchi M. Root-derived CLE glycopeptides control nodulation by direct binding to HAR1 receptor kinase. Nat Commun 2013;4:1–7. doi: https://doi.org/10.1038/ncomms3191.

[80] Du C, Li X, Chen J, Chen W, Li B, Li C, et al. Receptor kinase complex transmits RALF peptide signal to inhibit root growth in Arabidopsis. Proc Natl Acad Sci U S A 2016;113:E8326–34. doi: https://doi.org/10.1073/pnas.1609626113.

[81] Li E, Wang G, Zhang YL, Kong Z, Li S. FERONIA mediates root nutating growth. Plant J 2020;104:1105–16. doi: https://doi.org/10.1111/tpj.14984.

[82] De Smet I, Voß U, Jürgens G, Beeckman T. Receptor-like kinases shape the plant. Nat Cell Biol 2009;11:1166–73. doi: https://doi.org/10.1038/ncb1009-1166.

[83] Song L, Huang SSC, Wise A, Castanoz R, Nery JR, Chen H, et al. A transcription factor hierarchy defines an environmental stress response network. Science 2016;354. doi: https://doi.org/10.1126/science.aag1550.

[84] Ou Y, Kui H, Li J. Receptor-like kinases in root development: Current progress and future directions. Mol Plant 2021;14:166–85. doi: https://doi.org/10.1016/j.molp.2020.12.004.

[85] Smolarkiewicz M, Dhonukshe P. Formative cell divisions: Principal determinants of plant morphogenesis. Plant Cell Physiol 2013;54:333–42. doi: https://doi.org/10.1093/pcp/pcs175.

[86] Chen J, Yu F, Liu Y, Du C, Li X, Zhu S, et al. FERONIA interacts with ABI2-type phosphatases to facilitate signaling cross-talk between abscisic acid and RALF peptide in Arabidopsis. Proc Natl Acad Sci U S A 2016;113:E5519–27. doi: https://doi.org/10.1073/pnas.1608449113.

[87] Li C, Yeh FL, Cheung AY, Duan Q, Kita D, Liu MC, et al. Glycosylphosphatidylinositol-anchored proteins as chaperones and co-receptors for FERONIA receptor kinase signaling in Arabidopsis. Elife 2015;4:1–21. doi: https://doi.org/10.7554/eLife.06587.

[88] Schoenaers S, Balcerowicz D, Breen G, Hill K, Zdanio M, Mouille G, et al. The auxin-regulated CrRLK1L kinase ERULUS controls cell wall composition during root hair tip growth. Curr Biol 2018;28:722–732.e6. doi: https://doi.org/10.1016/j.cub.2018.01.050.

[89] Migliaccio F, Tassone P, Fortunati A. Circumnutation as an autonomous root movement in plants. Am J Bot 2013;100:4–13. doi: https://doi.org/10.3732/ajb.1200314.

[90] Qi B, Zheng H. Modulation of root-skewing responses by KNAT1 in Arabidopsis thaliana. Plant J 2013;76:380–92. doi: https://doi.org/10.1111/tpj.12295.

[91] Bidzinski P, Noir S, Shahi S, Reinstädler A, Gratkowska DM, Panstruga R. Physiological characterization and genetic modifiers of aberrant root thigmomorphogenesis in mutants of Arabidopsis thaliana MILDEW LOCUS O genes. Plant Cell Environ 2014;37:2738–53. doi: https://doi.org/10.1111/pce.12353.

[92] Dong QK, Zhang ZW, Liu YT, Tao LZ, Liu HL. FERONIA regulates auxin-mediated lateral root development and primary root gravitropism. FEBS Lett 2019;593:97–106. doi: https://doi.org/10.1002/1873-3468.13292.

[93] Guo H, Nolan TM, Song G, Liu S, Xie Z, Chen J, et al. FERONIA receptor kinase contributes to plant immunity by suppressing jasmonic acid signaling in Arabidopsis thaliana. Curr Biol 2018;28:3316–3324.e6. doi: https://doi.org/10.1016/j.cub.2018.07.078.

[94] Canher B, Lanssens F, Zhang A, Bisht A, Mazumdar S, Heyman J, et al. The regeneration factors ERF114 and ERF115 regulate auxin-mediated lateral root development in response to mechanical cues. Mol Plant 2022;15:1543–57. doi: https://doi.org/10.1016/j.molp.2022.08.008.

[95] Zhu S, Martínez Pacheco J, Estevez JM, Yu F. Autocrine regulation of root hair size by the RALF-FERONIA-RSL4 signaling pathway. New Phytol 2020;227:45–9. doi: https://doi.org/10.1111/nph.16497.

[96] Den HG, Van Isterdael G, Beeckman T, De Smet I. The roots of a new green revolution. Trends Plant Sci 2010;15:600–7. doi: https://doi.org/10.1016/j.tplants.2010.08.009.

[97] Zhou G, Zhou X, Nie Y, Bai SH, Zhou L, Shao J, et al. Drought-induced changes in root biomass largely result from altered root morphological traits: Evidence from a synthesis of global field trials. Plant Cell Environ 2018;41:2589–99. doi: https://doi.org/10.1111/pce.13356.

[98] Gupta A, Rico-Medina A, Caño-Delgado AI. The physiology of plant responses to drought. Science 2020;368:266–9. doi: https://doi.org/10.1126/science.aaz7614.

[99] Li H, Testerink C, Zhang Y. How roots and shoots communicate through stressful times. Trends Plant Sci 2021;26:940–52. doi: https://doi.org/10.1016/j.tplants.2021.03.005.

[100] Correa J, Postma JA, Watt M, Wojciechowski T. Soil compaction and the architectural plasticity of root systems. J Exp Bot 2019;70:6019–34. doi: https://doi.org/10.1093/jxb/erz383.

[101] Van Zelm E, Zhang Y, Testerink C. Salt tolerance mechanisms of plants. Annu Rev Plant Biol 2020;71:403–33. doi: https://doi.org/10.1146/annurev-arplant-050718-100005.

[102] Yang Y, Guo Y, Zhong J, Zhang T, Li D, Ba T, et al. Root physiological traits and transcriptome analyses reveal that root zone water retention confers drought tolerance to Opisthopappus taihangensis. Sci Rep 2020;10:2627. doi: https://doi.org/10.1038/s41598-020-59399-0.

[103] Martínez-Alcántara B, Jover S, Quiñones A, Forner-Giner M ángeles, Rodríguez-Gamir J, Legaz F, et al. Flooding affects uptake and distribution of carbon and nitrogen in citrus seedlings. J Plant Physiol 2012;169:1150–7. doi: 10.1016/j.jplph.2012.03.016.

[104] Tyagi A, Sharma S, Srivastava H, Singh A, Kaila T, Ali S, et al. Transcriptome profiling of two contrasting pigeon pea (Cajanus cajan) genotypes in response to waterloging stress. Front Genet 2023;13:3757.

[105] Tyagi A, Sharma S, Ali S, Gaikwad K. Crosstalk between H2S and NO: an emerging signalling pathway during waterlogging stress in legume crops. Plant Biol 2022;24:576–86. doi: https://doi.org/10.1111/plb.13319.

[106] Zhao C, Jiang W, Zayed O, Liu X, Tang K, Nie W, et al. The LRXs-RALFs-FER module controls plant growth and salt stress responses by modulating multiple plant hormones. Natl Sci Rev 2021;8. doi: https://doi.org/10.1093/nsr/nwaa149.

[107] Xie YH, Zhang FJ, Sun P, Li ZY, Zheng PF, Di GK, et al. Apple receptor-like kinase FERONIA regulates salt tolerance and ABA sensitivity in Malus domestica. J Plant Physiol 2022;270:. doi: https://doi.org/10.1016/j.jplph.2022.153616153616.

[108] Ko D, Helariutta Y. Shoot–root communication in flowering plants. Curr Biol 2017;27:R973–8. doi: https://doi.org/10.1016/j.cub.2017.06.054.

[109] Ma Z, Guo D, Xu X, Lu M, Bardgett RD, Eissenstat DM, et al. Evolutionary history resolves global organization of root functional traits. Nature 2018;555:94–7. doi: https://doi.org/10.1038/nature25783.

[110] Dinneny JR. Developmental responses to water and salinity in root systems. Annu Rev Cell Dev Biol 2019;35:239–57. doi: https://doi.org/10.1146/annurev-cellbio-100617-062949.

[111] Todaka D, Takahashi F, Yamaguchi-Shinozaki K, Shinozaki K. ABA-responsive gene expression in response to drought stress: cellular regulation and long-distance signaling. Adv Bot Res 2019;92:83–113. doi: https://doi.org/10.1016/bs.abr.2019.05.001.

[112] Waterland NL, Campbell CA, Finer JJ, Jones ML. Abscisic acid application enhances drought stress tolerance in bedding plants. HortSci 2010;45:409–13. doi: https://doi.org/10.21273/hortsci.45.3.409.

[113] Wang N, Wu X, Ku L, Chen Y, Wang W. Evaluation of Three Protein-Extraction Methods for Proteome Analysis of Maize Leaf Midrib, a Compound Tissue Rich in Sclerenchyma Cells 2016;7:1–12. doi: https://doi.org/10.3389/fpls.2016.00856.

[114] Yin Y, Qin K, Song X, Zhang Q, Zhou Y, Xia X, et al. BZR1 transcription factor regulates heat stress tolerance through FERONIA receptor-like kinase-mediated reactive oxygen species signaling in tomato. Plant Cell Physiol 2018;59:2239–54. doi: https://doi.org/10.1093/pcp/pcy146.

[115] Ali S, Tyagi A, Bae H. Ionomic approaches for discovery of novel stress-resilient genes in plants. Int J Mol Sci 2021;22:7182. doi: https://doi.org/10.3390/ijms22137182.

[116] Chen J, Zou W, Meng L, Fan X, Xu G, Ye G. Advances in the uptake and transport mechanisms and QTLs mapping of cadmium in rice. Int J Mol Sci 2019;20:3417. doi: https://doi.org/10.3390/ijms20143417.

[117] Richter J, Ploderer M, Mongelard G, Gutierrez L, Hauser M-T. Role of CrRLK1L cell wall sensors HERCULES1 and 2, THESEUS1, and FERONIA in growth adaptation triggered by heavy metals and trace elements. Front Plant Sci 2017;8:1554. doi: https://doi.org/10.3389/fpls.2017.01554.

[118] Zhao C, Zayed O, Yu Z, Jiang W, Zhu P, Hsu CC, et al. Leucine-rich repeat extensin proteins regulate plant salt tolerance in Arabidopsis. Proc Natl Acad Sci U S A 2018;115:13123–8. doi: https://doi.org/10.1073/pnas.1816991115.

[119] Yu Y, Assmann SM. Inter-relationships between the heterotrimeric Gβ subunit AGB1, the receptor-like kinase FERONIA, and RALF1 in salinity response. Plant Cell Environ 2018;41:2475–89. doi: https://doi.org/10.1111/pce.13370.

[120] Jing Y, Liu C, Liu B, Pei T, Zhan M, Li C, et al. Overexpression of the FERONIA receptor kinase MdMRLK2 confers apple drought tolerance by regulating energy metabolism and free amino acids production. Tree Physiol 2022; tpac100.. doi: https://doi.org/10.1093/treephys/tpac100.

[121] Shin SY, Park JS, Park H Bin, Moon KB, Kim HS, Jeon JH, et al. FERONIA confers resistance to photooxidative stress in Arabidopsis. Front Plant Sci 2021;12:714938. doi: 10.3389/fpls.2021.714938.

[122] Li C, Chen J, Li X, Zhang X, Liu Y, Zhu S, et al. FERONIA is involved in phototropin 1-mediated blue light phototropic growth in Arabidopsis. J Integr Plant Biol 2022;64:1901–15. doi: https://doi.org/10.1111/jipb.13336.

[123] Guo Z, Xu J, Wang Y, Hu C, Shi K, Zhou J, et al. The phyB-dependent induction of HY5 promotes iron uptake by systemically activating FER expression. EMBO Rep 2021;22:e51944.

[124] Gommers CMM, Keuskamp DH, Buti S, van Veen H, Koevoets IT, Reinen E, et al. Molecular profiles of contrasting shade response strategies in wild plants: Differential control of immunity and shoot elongation. Plant Cell 2017;29:331–44. doi: https://doi.org/10.1105/tpc.16.00790.

[125] Xu G, Chen W, Song L, Chen Q, Zhang H, Liao H, et al. FERONIA phosphorylates E3 ubiquitin ligase ATL6 to modulate the stability of 14–3-3 proteins in response to the carbon/nitrogen ratio. J Exp Bot 2019;70:6375–88. doi: https://doi.org/10.1093/jxb/erz378.

[126] Zhou M, Zhang LL, Ye JY, Zhu QY, Du WX, Zhu YX, et al. Knockout of FER decreases cadmium concentration in roots of Arabidopsis thaliana by inhibiting the pathway related to iron uptake. Sci Total Environ 2021;798:. doi: https://doi.org/10.1016/j.scitotenv.2021.149285149285.

[127] Darwish E, Ghosh R, Ontiveros-Cisneros A, Tran HC, Petersson M, De Milde L, et al. Touch signaling and thigmomorphogenesis are regulated by complementary CAMTA3-and JA-dependent pathways. Sci Adv 2022;8: eabm2091.. doi: https://doi.org/10.1126/sciadv.abm2091.

[128] Xie Q, Chen W, Xu F, Ouyang S, Chen J, Wang X, et al. Wounding promotes root regeneration through a cell wall integrity sensor, the receptor kinase FERONIA. BioRxiv 2022.

[129] Tang J, Wu D, Li X, Wang L, Xu L, Zhang Y, et al. Plant immunity suppression via PHR1-RALF-FERONIA shapes the root microbiome to alleviate phosphate starvation. EMBO J 2022;41:e109102.

[130] Song Y, Wilson AJ, Zhang XC, Thoms D, Sohrabi R, Song S, et al. FERONIA restricts Pseudomonas in the rhizosphere microbiome via regulation of reactive oxygen species. Nat Plants 2021;7:644–54. doi: https://doi.org/10.1038/s41477-021-00914-0.

[131] Jing Y, Zhan M, Li C, Pei T, Wang Q, Li P, et al. The apple FERONIA receptor-like kinase MdMRLK2 negatively regulates Valsa canker resistance by suppressing defence responses and hypersensitive reaction. Mol Plant Pathol 2022;23:1170–86. doi: https://doi.org/10.1111/mpp.13218.

[132] Yang Z, Xing J, Wang L, Liu Y, Qu J, Tan Y, et al. Mutations of two FERONIA-like receptor genes enhance rice blast resistance without growth penalty. J Exp Bot 2020;71:2112–26. doi: https://doi.org/10.1093/jxb/erz541.

[133] Tyagi A, Ali S, Park S, Bae H. Assessing the effect of sound vibrations on plant neurotransmitters in Arabidopsis. J Plant Growth Regul 2023;42:5216–23. doi: https://doi.org/10.1007/s00344-023-10918-z.

[134] Ali S, Tyagi A, Bae H. ROS interplay between plant growth and stress biology: Challenges and future perspectives. Plant Physiol Biochem 2023;203:. doi: https://doi.org/10.1016/j.plaphy.2023.108032108032.

[135] Ghosh R, Gururani MA, Ponpandian LN, Mishra RC, Park SC, Jeong MJ, et al. Expression analysis of sound vibration-regulated genes by touch treatment in arabidopsis. Front Plant Sci 2017;8. doi: 10.3389/fpls.2017.00100.

[136] Huynh TP, Haick H. Learning from an intelligent mechanosensing system of plants. Adv Mater Technol 2019;4:1800464. doi: https://doi.org/10.1002/admt.201800464.

[137] Bengough AG, McKenzie BM, Hallett PD, Valentine TA. Root elongation, water stress, and mechanical impedance: A review of limiting stresses and beneficial root tip traits. J Exp Bot 2011;62:59–68. doi: https://doi.org/10.1093/jxb/erq350.

[138] Kumpf RP, Nowack MK. The root cap: A short story of life and death. J Exp Bot 2015;66:5651–62. doi: https://doi.org/10.1093/jxb/erv295.

[139] Toyota M, Furuichi T, Tatsumi H, Sokabe M. Cytoplasmic calcium increases in response to changes in the gravity vector in hypocotyls and petioles of arabidopsis seedlings. Plant Physiol 2008;146:505–14. doi: https://doi.org/10.1104/pp.107.106450.

[140] Bennett MJ, Marchant A, Green HG, May ST, Ward SP, Millner PA, et al. Arabidopsis AUX1 gene: A permease-like regulator of root gravitropism. Science 1996;273:948–50. doi: https://doi.org/10.1126/science.273.5277.948.

[141] Sinclair W, Trewavas AJ. Calcium in gravitropism. A re-examination. Planta 1997;203:S85–90. doi: https://doi.org/10.1007/pl00008120.

[142] Noh B, Murphy AS, Spalding EP. Multidrug resistance-like genes of Arabidopsis required for auxin transport and auxin-mediated development. Plant Cell 2001;13:2441–54. doi: https://doi.org/10.1105/tpc.13.11.2441.

[143] Geisler M, Blakeslee JJ, Bouchard R, Lee OR, Vincenzetti V, Bandyopadhyay A, et al. Cellular efflux of auxin catalyzed by the Arabidopsis MDR/PGP transporter AtPGP1. Plant J 2005;44:179–94. doi: https://doi.org/10.1111/j.1365-313X.2005.02519.x.

[144] Perera IY, Hung CY, Brady S, Muday GK, Boss WF. A universal role for inositol 1,4,5-trisphosphate-mediated signaling in plant gravitropism. Plant Physiol 2006;140:746–60. doi: https://doi.org/10.1104/pp.105.075119.

[145] Harrison BR, Masson PH. ARL2, ARG1 and PIN3 define a gravity signal transduction pathway in root statocytes. Plant J 2008;53:380–92. doi: https://doi.org/10.1111/j.1365-313X.2007.03351.x.

[146] Terrile MC, París R, Calderõn-Villalobos LIA, Iglesias MJ, Lamattina L, Estelle M, et al. Nitric oxide influences auxin signaling through S-nitrosylation of the Arabidopsis TRANSPORT INHIBITOR RESPONSE 1 auxin receptor. Plant J 2012;70:492–500. doi: https://doi.org/10.1111/j.1365-313X.2011.04885.x.

[147] Mousavi SAR, Dubin AE, Zeng WZ, Coombs AM, Do K, Ghadiri DA, et al. PIEZO ion channel is required for root mechanotransduction in Arabidopsis thaliana. Proc Natl Acad Sci U S A 2021;118. doi: https://doi.org/10.1073/pnas.2102188118. e2102188118.

[148] Basu D, Haswell ES. Plant mechanosensitive ion channels: an ocean of possibilities. Curr Opin Plant Biol 2017;40:43–8. doi: https://doi.org/10.1016/j.pbi.2017.07.002.

[149] Smith S, de Smet I. Root system architecture: Insights from Arabidopsis and cereal crops. Philos Trans R Soc B Biol Sci 2012;367:1441–52. doi: https://doi.org/10.1098/rstb.2011.0234.

[150] Dong J, Jones RH, Mou P. Relationships between nutrient heterogeneity, root growth, and hormones: Evidence for interspecific variation. Plants 2018;7:15. doi: https://doi.org/10.3390/plants7010015.

[151] Cui S, Suzaki T, Tominaga-Wada R, Yoshida S. Regulation and functional diversification of root hairs. Semin Cell Dev Biol 2018;83:115–22. doi: https://doi.org/10.1016/j.semcdb.2017.10.003.

[152] Coruzzi GM, Zhou L. Carbon and nitrogen sensing and signaling in plants: Emerging "matrix effects". Curr Opin Plant Biol 2001;4:247–53. doi: https://doi.org/10.1016/S1369-5266(00)00168-0.

[153] Frink CR, Waggoner PE, Ausubel JH. Nitrogen fertilizer: Retrospect and prospect. Proc Natl Acad Sci U S A 1999;96:1175–80. doi: https://doi.org/10.1073/pnas.96.4.1175.

[154] Palenchar PM, Kouranov A, Lejay LV, Coruzzi GM. Genome-wide patterns of carbon and nitrogen regulation of gene expression validate the combined carbon and nitrogen (CN)-signaling hypothesis in plants. Genome Biol 2004;5:1–15. doi: https://doi.org/10.1186/gb-2004-5-11-r91.

[155] Gutiérrez RA, Lejay LV, Dean A, Chiaromonte F, Shasha DE, Coruzzi GM. Qualitative network models and genome-wide expression data define carbon/ nitrogen-responsive molecular machines in Arabidopsis. Genome Biol 2007;8:1–13. doi: https://doi.org/10.1186/gb-2007-8-1-r7.

[156] Martínez Pacheco J, Song L, Kuběnová L, Ovečka M, Gabarain VB, Peralta JM, et al. 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 2022.01.10.475584. BioRxiv 2022. doi: https://doi.org/10.1101/2022.01.10.475584.

[157] Anderson CT, Kieber JJ. Dynamic construction, perception, and remodeling of plant cell walls. Annu Rev Plant Biol 2020;71:39–69. doi: https://doi.org/10.1146/annurev-arplant-081519-035846.

[158] Novaković L, Guo T, Bacic A, Sampathkumar A, Johnson KL. Hitting the wall—sensing and signaling pathways involved in plant cell wall remodeling in response to abiotic stress. Plants 2018;7:89. doi: https://doi.org/10.3390/plants7040089.

[159] Miller G, Schlauch K, Tam R, Cortes D, Torres MA, Shulaev V, et al. The plant NADPH oxidase RBOHD mediates rapid systemic signaling in response to diverse stimuli. Sci Signal 2009;2. doi: https://doi.org/10.1126/scisignal.2000448. ra45 –ra45.

[160] Kesten C, Menna A, Sánchez-Rodríguez C. Regulation of cellulose synthesis in response to stress. Curr Opin Plant Biol 2017;40:106–13. doi: https://doi.org/10.1016/j.pbi.2017.08.010.

[161] Wang L, Wang L, Yang T, Wang B, Lin Q, Zhu S, et al. RALF1-FERONIA complex affects splicing dynamics to modulate stress responses and growth in plants. Sci Adv 2020;6:eaaz1622. doi: https://doi.org/10.1126/sciadv.aaz1622.

[162] Ngo QA, Vogler H, Lituiev DS, Nestorova A, Grossniklaus U. A calcium dialog mediated by the FERONIA signal transduction pathway controls plant sperm delivery. Dev Cell 2014;29:491–500. doi: https://doi.org/10.1016/j.devcel.2014.04.008.

[163] Chapman JM, Muhlemann JK, Gayomba SR, Muday GK. RBOH-Dependent ROS Synthesis and ROS Scavenging by Plant Specialized Metabolites to Modulate Plant Development and Stress Responses. Chem Res Toxicol 2019;32:370–96. doi: https://doi.org/10.1021/acs.chemrestox.9b00028.

[164] Barbez E, Dünser K, Gaidora A, Lendl T, Busch W. Auxin steers root cell expansion via apoplastic pH regulation in Arabidopsis thaliana. Proc Natl Acad Sci U S A 2017;114:E4884–93. doi: https://doi.org/10.1073/pnas.1613499114.

[165] Ali S, Tyagi A, Park S, Mir RA, Mushtaq M, Bhat B, et al. Deciphering the plant microbiome to improve drought tolerance: Mechanisms and perspectives. Environ Exp Bot 2022;201:104933.

[166] Chen T, Nomura K, Wang X, Sohrabi R, Xu J, Yao L, et al. A plant genetic network for preventing dysbiosis in the phyllosphere. Nature 2020;580:653–7. doi: https://doi.org/10.1038/s41586-020-2185-0.

[167] Mendes R, Kruijt M, De Bruijn I, Dekkers E, Van Der Voort M, Schneider JHM, et al. Deciphering the rhizosphere microbiome for disease-suppressive bacteria. Science 2011;332:1097–100. doi: https://doi.org/10.1126/science.1203980.

[168] Berendsen RL, Vismans G, Yu K, Song Y, De Jonge R, Burgman WP, et al. Disease-induced assemblage of a plant-beneficial bacterial consortium. ISME J 2018;12:1496–507. doi: https://doi.org/10.1038/s41396-018-0093-1.

[169] Pradhan S, Tyagi R, Sharma S. Combating biotic stresses in plants by synthetic microbial communities: Principles, applications and challenges. J Appl Microbiol 2022;133:2742–59. doi: https://doi.org/10.1111/jam.15799.

[170] Schmitz L, Yan Z, Schneijderberg M, de Roij M, Pijnenburg R, Zheng Q, et al. Synthetic bacterial community derived from a desert rhizosphere confers salt stress resilience to tomato in the presence of a soil microbiome. ISME J 2022;16:1907–20. doi: https://doi.org/10.1038/s41396-022-01238-3.

[171] Ali S, Tyagi A, Mushtaq M, Al-Mahmoudi H, Bae H. Harnessing plant microbiome for mitigating arsenic toxicity in sustainable agriculture. Environ Pollut 2022;300:. doi: https://doi.org/10.1016/J.ENVPOL.2022.118940118940.

[172] Bouffaud ML, Poirier MA, Muller D, Moënne-Loccoz Y. Root microbiome relates to plant host evolution in maize and other Poaceae. Environ Microbiol 2014;16:2804–14. doi: https://doi.org/10.1111/1462-2920.12442.

[173] Marques JM, da Silva TF, Vollu RE, Blank AF, Ding GC, Seldin L, et al. Plant age and genotype affect the bacterial community composition in the tuber rhizosphere of field-grown sweet potato plants. FEMS Microbiol Ecol 2014;88:424–35. doi: https://doi.org/10.1111/1574-6941.12313.

[174] Turner TR, James EK, Poole PS. The plant microbiome. Genome Biol 2013;14:1–10.

[175] Hacquard S, Schadt CW. Towards a holistic understanding of the beneficial interactions across the Populus microbiome. New Phytol 2015;205:1424–30. doi: https://doi.org/10.1111/nph.13133.

[176] Sugiyama A, Ueda Y, Zushi T, Takase H, Yazaki K. Changes in the bacterial community of soybean rhizospheres during growth in the field. PLoS One 2014;9:e100709.

[177] Chaparro JM, Badri DV, Vivanco JM. Rhizosphere microbiome assemblage is affected by plant development. ISME J 2014;8:790–803. doi: https://doi.org/10.1038/ismej.2013.196.

[178] Bais HP, Weir TL, Perry LG, Gilroy S, Vivanco JM. The role of root exudates in rhizosphere interactions with plants and other organisms. Annu Rev Plant Biol 2006;57:233–66. doi: https://doi.org/10.1146/annurev.arplant.57.032905.105159.

[179] Bertin C, Yang X, Weston LA. The role of root exudates and allelochemicals in the rhizosphere. Plant Soil 2003;256:67–83. doi: https://doi.org/10.1023/A:1026290508166.

[180] Bernal P, Allsopp LP, Filloux A, Llamas MA. The Pseudomonas putida T6SS is a plant warden against phytopathogens. ISME J 2017;11:972–87. doi: https://doi.org/10.1038/ismej.2016.169.

[181] Lally RD, Galbally P, Moreira AS, Spink J, Ryan D, Germaine KJ, et al. Application of endophytic pseudomonas fluorescens and a bacterial consortium to brassica napus can increase plant height and biomass under greenhouse and field conditions. Front Plant Sci 2017;8:2193. doi: https://doi.org/10.3389/fpls.2017.02193.

[182] Melnyk RA, Hossain SS, Haney CH. Convergent gain and loss of genomic islands drive lifestyle changes in plant-associated Pseudomonas. ISME J 2019;13:1575–88. doi: https://doi.org/10.1038/s41396-019-0372-5.

Sajad Ali is currently working as Assistant Professor in the Department of Biotechnology, Yeungnam University, Republic of Korea. He completed his Ph.D. Microbiology from University of Madras India. He worked as a postdoctoral scientist at Centre of Research for Development University of Kashmir, India on disease improvement in saffron using functional genomics. His research line focuses on the plant molecular biology, host microbe interactions and plant mechanobiology. Currently, he is working on plant-sound vibration interactions and its ecological perspectives.

Anshika Tyagi is working as Assistant Professor in the Department of Biotechnology, Yeungnam University, Republic of Korea. Earlier she worked at ICAR-National Institute for Plant Biotechnology, New Delhi, India as a postdoctoral fellow. She has made great research achievement in the field of plant stress biology, plant mechanobiology and developmental biology. Currently, her research is focused on decoding the molecular mechanism of plant-sound vibration interactions using highthrouput tools

Suvin Park is currently doing an integrated MS and PhD course in Biotechnology Department of Yeungnam University, Republic of Korea. She is working on decoding the molecular mechanism of plant-sound vibration interactions using Arabidopsis as model.

Rajeev K. Varshney Director, Western Australian State Agricultural Biotechnology Center, University of Western Australia (UWA), Perth, Australia. He has a background in molecular genetics and possesses more than 15 years research experience in international agriculture. His research is focused on structural, functional, comparative, and translational genomics for improving the crop productivity of legume crops.

Hanhong Bae Professor of Biotechnology at Yeungnam University. Former research fellow at USDA-ARS in Beltsville, Maryland, USA; holds Ph.D in Genetics from Iowa State University, Ames, IA, USA. Professor Bae is a molecular biologist specialized in plant and endophytes. His main research interests are focused on the study of plant-sound vibration interactions, using conventional tools and multi-omics approaches to understand the sound vibration signal perception and transduction in plant.