

REVIEW PAPER

Plant phosphate status influences root biotic interactions

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Abstract

Phosphorus (P) deficiency stress in combination with biotic stress(es) severely impacts crop yield. Plant responses to P deficiency overlapping with that of other stresses exhibit a high degree of complexity involving different signaling pathways. On the one hand, plants engage with rhizosphere microbiome/arbuscular mycorrhizal fungi for improved phosphate (Pi) acquisition and plant stress response upon Pi deficiency; on the other hand, this association is gets disturbed under Pi sufficiency. This nutrient-dependent response is highly regulated by the phosphate starvation response (PSR) mediated by the master regulator, *PHR1*, and its homolog, *PHL*. It is interesting to note that Pi status (deficiency/sufficiency) has a varying response (positive/negative) to different biotic encounters (beneficial microbes/opportunistic pathogens/insect herbivory) through a coupled PSR-*PHR1* immune system. This also involves cross-talk among multiple players including transcription factors, defense hormones, miRNAs, and Pi transporters, among others influencing the plant-biotic-phosphate interactions. We provide a comprehensive view of these key players involved in maintaining a delicate balance between Pi homeostasis and plant immunity. Finally, we propose strategies to utilize this information to improve crop resilience to Pi deficiency in combination with biotic stresses.

Keywords: Biotic stress, defense, immunity, phosphate starvation response, PHR, phytohormones.

Introduction

Most crops grow under suboptimal conditions where they frequently encounter different combinations of abiotic and/or biotic stresses (Bray *et al.*, 2000). These stresses are a major hurdle in maximizing crop yield and thus remain a constant threat to global food security. Plant response to these combinatorial stresses is complex as it is not simply an additive effect of individual stresses but rather has a reduced or enhanced susceptibility to biotic or abiotic stress. This is because combined stresses are largely controlled by different signaling pathways which often act antagonistically and engage in crosstalk (Asselbergh *et al.*, 2008; Atkinson and Urwin, 2012; Suzuki *et al.*, 2014). It has been found that abiotic stresses strongly affect the biotic stress response by altering the plant-microbial

interactions in a dynamic manner (see Saijo and Loo, 2020). For instance, a positive regulator of drought stress (calmodulin-binding transcription activator) negatively regulates the defense response against *Botrytis cinerea* and *Pseudomonas syringae* DC3000 in *Solanum lycopersicum* (Li *et al.*, 2014). Similarly, the hormone-like peptides AtPep3/AT13 capable of enhancing salinity tolerance were shown to induce biotic stress tolerance in *Arabidopsis* (Huffaker *et al.*, 2006; Suzuki *et al.*, 2014; Nakaminami *et al.*, 2018). Among various abiotic stresses, there has been a rising concern over mineral nutrient depletion in most agricultural soils (Alewell *et al.*, 2020). It has also been established that plants' response to microbes (both harmful and beneficial) gets altered according to their mineral nutrient

status (Bostock *et al.*, 2014; Suzuki *et al.*, 2014). It is therefore interesting to understand how crops prioritize growth versus defense and how plants modulate their immune response according to nutritional status, especially under soil phosphate (Pi) deficiency.

Phosphorus (P) is an essential mineral nutrient for crop growth, yield, and performance; however, its availability is limited due to low solubility and mobility in soil (Vitousek *et al.*, 2010; Johnston *et al.*, 2014; Oldroyd and Leyser, 2020; Ma *et al.*, 2021). Lack of sufficient P fertilizers is anticipated to affect the availability of food and feed in the future (Alewell *et al.*, 2020; Oldroyd and Leyser, 2020). Also, P deficiency cannot be alleviated entirely even with external supplementation with P fertilizers as most of the applied P is quickly precipitated to form metal-cation complexes with soil minerals, and soil microbes incorporate Pi in the organic matter. Consequently, only a fraction of the P becomes available for root uptake in the form of plant utilizable orthophosphate (Pi; van de Wiel *et al.*, 2016). To ensure adequate Pi supply, plants invoke various adaptive strategies for enhanced acquisition, efficient utilization, and remobilization regulated by comprehensive transcriptomic changes (Rouached *et al.*, 2010; Das *et al.*, 2022). These strategies include root system architecture (RSA) remodeling (López-Bucio *et al.*, 2003; Lynch *et al.*, 2022), induced expression of Pi transport genes (Raghothama, 2000; Nussaume *et al.*, 2011; Wang *et al.*, 2018), and exudation of Pi-solubilizing substances such as organic acids which act as anion exchangers that release the tightly bound Pi (Mehra *et al.*, 2017; Bhadouria and Giri, 2021; Isidra-Arellano *et al.*, 2021; Panchal *et al.*, 2021). Furthermore, plants also engage with rhizosphere microbiome and arbuscular mycorrhizal fungi (AMF) to improve Pi acquisition (Hiruma *et al.*, 2016; Castrillo *et al.*, 2017; Finkel *et al.*, 2019; Isidra-Arellano *et al.*, 2021). These adaptations involving morphological, physiological, metabolic, and transcriptomic changes in response to Pi deprivation are collectively known as the phosphate starvation response (PSR; Rubio *et al.*, 2001; Nilsson *et al.*, 2010; Rouached *et al.*, 2010; Yang and Finnegan, 2010; Das *et al.*, 2022). Interestingly, signaling components of PSR crosstalk with the biotic stress response including interactions with microbes for Pi acquisition (Chan *et al.*, 2021). In general, there seems to be a profound influence of biotic and abiotic stresses on each other in the manifestation of stress responses. It has been suggested that the genotypes having a superior response to abiotic stress may have a compromised biotic defense response (Demmig-Adams *et al.*, 2013). However, this understanding is fragmentary and the complete picture is still unclear (Atkinson and Urwin, 2012). While in specific cases, abiotic stress provides enhanced biotic stress resistance to plants, for others plants prioritize their response to tackle one of the combinatorial stresses (Atkinson *et al.*, 2013). The molecular intersection between these combinatorial stress responses and their regulatory principles are only beginning to be uncovered through recent studies (see Saijo and Loo, 2020). There have been gaps in the current understanding of

the molecular players involved in the crosstalk for mitigating Pi stress along with plant microbial interactions. In this review, we attempt to develop a comprehensive view of plant biotic interactions influenced by plant P status. Different key players, their crosstalk, and their involvement in molecular mechanisms that underpin plant-biotic-phosphate interactions have been outlined. This is crucial to the development of climate-resilient crops using genetic manipulation or molecular/conventional breeding or an integrated approach. Finally, a few strategies that could be utilized for developing climate-ready crops with high Pi efficiency and defense against biotic stress have been proposed.

Biotic interactions to mitigate phosphate deficiency stress

To improve Pi uptake, plant roots form symbiotic associations with the soil microbiome which are greatly dependent on the host Pi status (Fig. 1). Pi deficiency conditions trigger microbial associations, while Pi-sufficient plants restrict interactions with soil microbes (Kobae *et al.*, 2016; Campos-Soriano *et al.*, 2020). These associations are highly regulated through the activation of the PSR system (Oldroyd and Leyser, 2020). PHR1, a MYB-type coiled-coil (MYB-CC) transcription factor (TF) initially identified from Arabidopsis, is the core TF that regulates the PSR transcriptome (Riechmann *et al.*, 2000; Zhou *et al.*, 2008). A part of the PHR-driven P-starvation induced (PSI) genes is also involved in initiation, development, and maintenance of root microbial interactions (Das *et al.*, 2022). In Arabidopsis, it has been shown that PHR1 could directly activate microbiome-enhanced responses to limited P conditions; however, at the same time it represses a subset of genes involved in microbially driven immune system outputs (Castrillo *et al.*, 2017; Bai *et al.*, 2022). Furthermore, plant immune response has been shown to alter the root microbiome assemblage, indicating their close functional link (Liu *et al.*, 2020). A sophisticated chemical communication exists between the plant immune system and the root microbiome in the rhizosphere that results in an induced systemic resistance (ISR) in the host plant (Berendsen *et al.*, 2012). This takes place primarily through root exudates, and plants are known to secrete up to 40% of the photosynthetically fixed carbon as exudates (Walker *et al.*, 2003; Bais *et al.*, 2006; Bai *et al.*, 2022). Root exudates play a critical role in solubilizing phosphates as well as in regulating microbes that could interfere with the Pi uptake through the release of isoflavonoids, protons, and cell wall-degrading enzymes besides organic acids (Sasse *et al.*, 2018). Also, the aromatic organic acids (cinnamic, indole-3-acetic, salicylic, shikimic, and nicotinic acids) that are secreted as exudates also attract the rhizosphere bacterial community (Zhalnina *et al.*, 2018). This suggests that plants recruit soil microbes through root exudates, the composition of which becomes altered under plant nutrient status and influences rhizosphere microbiome

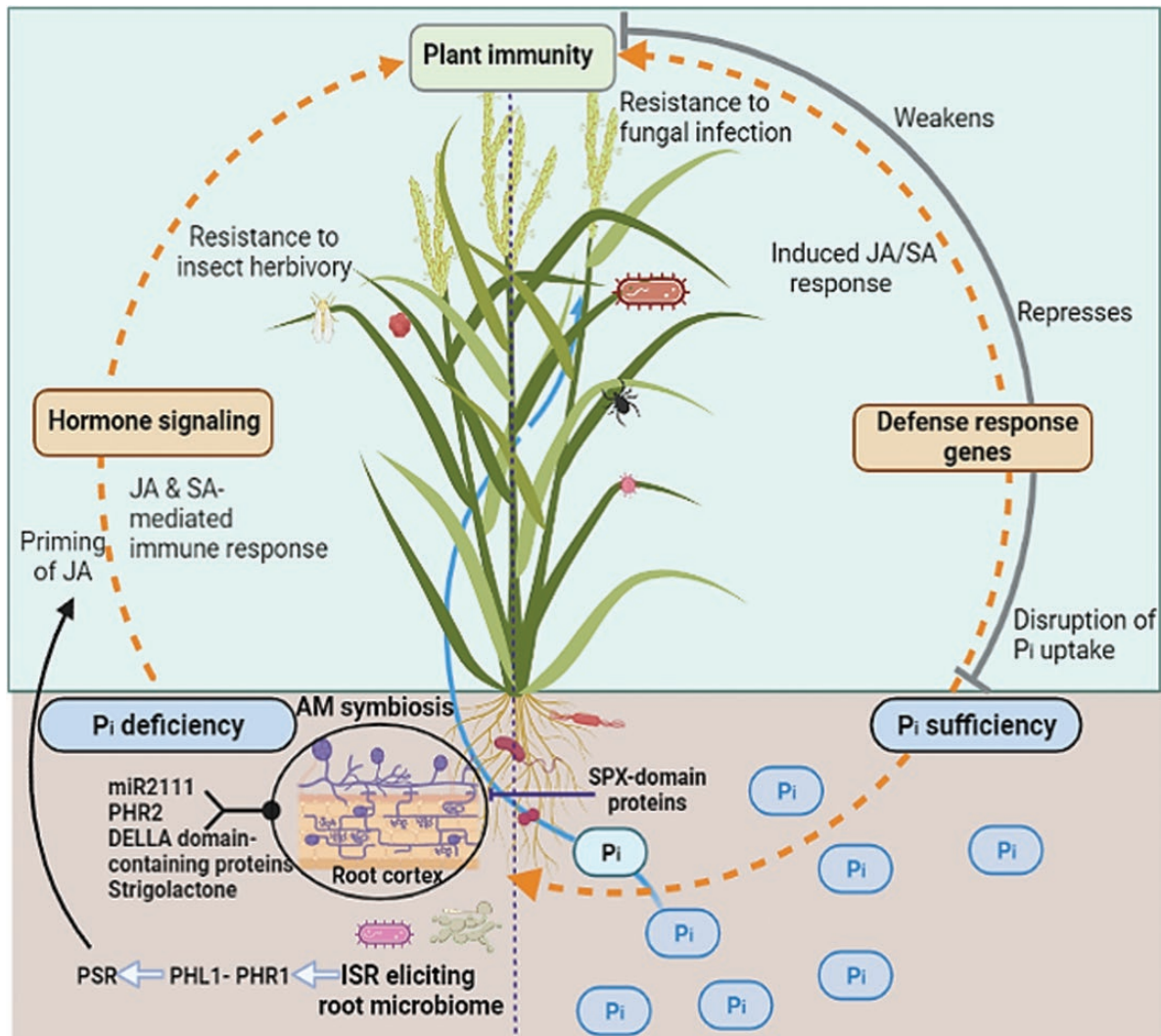


Fig. 1. Plant-biotic-phosphate interactions in crops. The diagram provides a comprehensive view of the inter-relationship between phosphate (Pi) status and plant immunity. Plants engage in an arbuscular mycorrhizal (AM) symbiosis and rhizobial symbiosis under Pi deficiency for enhanced Pi uptake depicted towards the left-hand side. Induced systemic resistance (ISR) elicited by the root microbiome triggers priming of jasmonic acid (JA), leading to resistance to insect herbivory. Plants coordinate with hormone signaling to trigger plant immunity to pathogen attack and is greatly affected by Pi status. Towards the right-hand side, plants under Pi sufficiency show both enhanced as well as repressed immune response depending on the kind of biotic encounters. Val-Torregrosa *et al.* (2022a) reported enhanced resistance to fungal pathogens upon sufficient Pi status in plants (*Arabidopsis*), while an excess of Pi has been reported to show increased susceptibility to pathogenic infection (Campos-Soriano *et al.*, 2020). The effect of Pi status (deficiency/sufficiency) on immunity is depicted by broken arrows. The positive regulation is represented by solid black arrows, while negative regulation is shown by gray blunt-ended arrows. The diagram was created using BioRender (BioRender.com).

community structure (Xu *et al.*, 2018; Bai *et al.*, 2022). Thus, root exudates could be the link between the nutritional cues, microbial assemblage, and immune response through ISR. Table 1 lists a few selected examples where rhizobium and/or AM symbiotic associations provided a comparative advantage to the host crop species in terms of enhanced Pi uptake, higher photosynthetic rate, growth, and development. However, in this process of establishing the symbiotic association, distinguishing friend from foe is a key characteristic for plant survival. The plant innate immune system involving pattern recognition receptors (PRRs) recognizes conserved

molecular patterns referred to as microbe/pathogen-associated molecular patterns (MAMPs/PAMPs). This MAMP/PRR recognition system serves as a checkpoint after which the bidirectional nutrient exchange interface is established wherein Pi and carbon exchange takes place, especially in the case of AMF (Wang *et al.*, 2022). Importantly, plants compromise their immunity to some extent to form associations with beneficial microbes for enhanced Pi uptake while remaining protected from the deleterious microbiota (Castillo *et al.*, 2017). This implies that plants prioritize Pi over immune response since Pi shortage could possibly be more

Table 1. Effect of arbuscular mycorrhizal fungi (AMF) and the rhizobial microbiome (RM) on host crop species

Host crop species	Biotic interaction	Advantage	References
<i>Triticum aestivum</i> <i>Festuca arundinacea</i> <i>Ocimum basilicum</i> <i>Capsicum annuum</i> <i>Solanum lycopersicum</i>	<i>Comamonas testosteroni</i> , <i>Pseudomonas putida</i> , <i>Enterobacter cloacae</i> , and <i>Citrobacter freundii</i>	Phosphate-solubilizing and doubling of growth and productivity	Baas et al. (2016)
<i>Medicago truncatula</i> <i>Medicago sativa</i> <i>Medicago sativa</i>	<i>Rhizophagus irregularis</i>	Improved phosphate uptake	Püschel et al. (2017)
<i>Glycine max</i> (L.) Merr	<i>Rhizobium meliloti</i> , <i>Glomus mosseae</i> (Nicol. and Gerd.) Gerd. and Trappe, and <i>Enterobacter</i> sp. Co-inoculation with rhizobia and AMF	Unavailable phosphorus sources utilization Better nodulation with high phosphate supply	Barea et al. (2002) X. Wang et al. (2011)
<i>Cajanus cajan</i>	Mycorrhizal fungal inoculum, <i>Gigaspora margarita</i> Becker & Hall.	Increased phosphate uptake	Shibata and Yano (2003)
<i>Arachis hypogaea</i>	Mycorrhizal fungal inoculum, <i>Gigaspora margarita</i> Becker & Hall.	Increased phosphate uptake	Shibata and Yano (2003)
<i>Vicia faba</i>	Rhizobium and AMF symbiotic associations	Higher photosynthetic rates per unit leaf area.	Jia et al. (2004)
<i>Glycyrrhiza</i>	<i>Mesorhizobium tianshanense</i> Chen and an AM fungus, <i>Rhizophagus irregularis</i>	Promote plant growth and enhancing drought tolerance	Hao et al. (2019)
<i>Vicia faba</i>	<i>R. leguminosarum</i> bv. <i>viciae</i> STDF-Egypt 19 and mixture of AMF (<i>Acaulospora laevis</i> , <i>Glomus geosporum</i> , <i>Glomus mosseae</i> , and <i>Scutellospora armeniacae</i>)	Promote growth in alkaline soils	Abd-Alla et al. (2014)

detrimental than infections ([Motte and Beeckman, 2017](#); [Tang et al., 2022](#)). In the following sections, the mechanisms involved in plant–microbial symbiosis for Pi and their associated trade-offs are discussed.

Rhizobial associations for phosphate acquisition

During Pi starvation, plants modulate their immune response to alter the root microbiome community structure for their own advantage. However, it is not clear how plants form a selective microbial assemblage in response to nutritional cues ([Bakker et al., 2018](#)). [Castrillo et al. \(2017\)](#) demonstrated using a synthetic bacterial community which competes with the plant for nutrients exerting Pi deficiency, that PSR is induced through the activity of PHR1, which in turn negatively regulated immunity in Arabidopsis. It has also been observed that some of the members of the commensal root microbiome facilitate nutrient acquisition. For example, *Colletotrichum tofeldiae* could facilitate Pi acquisition through direct delivery of Pi to roots, while many of its closely related species are plant pathogens. It is interesting to note that the components controlling the immune response to nutrient status regulate these commensal associations. It has been shown that *C. tofeldiae* infection and rhizosphere bacterial communities are dependent on PHR1-regulated signaling, suggesting a common component regulating both commensal association and response to nutrient status, particularly Pi ([Hiruma et al., 2016](#); [Castrillo et al., 2017](#); [Oldroyd and Leyser, 2020](#)). This symbiosis is influenced by the biosynthesis of tryptophan-derived secondary metabolites such as indole glucosinolates ([Hiruma et al., 2016](#); [Frerigmann et al., 2021](#)).

In brief, Pi status in plants is monitored by the PSR which determines the fate of the plant biotic interaction. This involves a highly regulated process of sensing and response. Under sufficient Pi growth conditions, intracellular levels of inositol polyphosphates (InsPs) are high. InsP binds to the SPX domain (Syt1/Pho81/XprI) found in various proteins involved in regulating Pi homeostasis. One group of such protein are named SPX proteins because they only contain an SPX domain. Under high Pi growth conditions, InsP promotes the interaction between SPX and the PHR1, inhibiting its activity as a TF ([Puga et al., 2014](#); [Wild et al., 2016](#)). In Pi deficiency, the levels of InsPs, especially InsP8, becomes low, and thus could not facilitate binding of SPXs with PHR. Incidentally, InsP8 is generated from its precursor, InsP7, through the kinase activity of VIH1 and VIH2, which is allosterically regulated under Pi-sufficient conditions allowing InsP8–SPX–PHR complex formation ([Laha et al., 2015](#); [Gu et al., 2017](#); [J. Dong et al., 2019](#); [Zhu et al., 2019](#); [Satheesh et al., 2022](#)). SPX proteins are eventually degraded, allowing PHRs to activate PSR ([J. Dong et al., 2019](#); [Ruan et al., 2019](#)). However, upon Pi starvation, how the levels of InP become low and PHR1–SPX dissociation takes place is not completely understood ([Motte and Beeckman, 2017](#)). In a recent finding, under Pi-starvation conditions, PHR1 is shown to bind to the promoter of a rapid alkalization factor (RALF) gene to activate its expression. This in turn suppresses a PAMP-triggered immunity (PTI) receptor via FERONIA, a PTI modulator known to enhance pathogen resistance ([Tang et al., 2022](#)). This PHR1–RALF–FERONIA axis suppresses immunity in order to facilitate colonization by specialized root microbiota to alleviate Pi starvation via the

expression of PSR genes (Tang *et al.*, 2022; Xie *et al.*, 2022). This was also reiterated by Castrillo *et al.* (2017) where, in *Arabidopsis*, PHR1 and its paralog, PHL1, were also found to repress the immune response under Pi depletion. This implies that plants find it difficult to cope with dual stress, namely nutrient starvation and pathogenic infection at the same time. During Pi depletion, plants suppress immunity through PHR1 and associate with microbes that help in nutrient uptake (Motte and Beeckman, 2017; Oldroyd and Leyser, 2020). However, our understanding of the crosstalk between mutualism and immunity with mediator molecules playing an important role is limited. A study showed that under Pi-sufficient conditions, *Arabidopsis* facilitated a mutualistic association with *Bacillus amyloliquefaciens* strain GB03, but triggers the salicylic acid (SA)-mediated immune response to the bacterium under Pi-deficient conditions. The study revealed that the nature of plant association is actually in response to the diacetyl, a microbial volatile compound produced by the bacterial strain. This rhizobacterium-derived compound promotes plant growth under Pi sufficiency by partially suppressing reactive oxygen species (ROS) and enhancing symbiont colonization. However, upon Pi deficiency, it becomes deleterious, causing leaf cell death and impaired photosynthesis (Morcillo *et al.*, 2020). Further, plants also recruit beneficial microbes for their defense response and confer immunity to a variety of diseases. This notion is supported by a recent study where an enhanced defense against the fungal pathogen *Fusarium oxysporum* was established by specific families of the rhizosphere microbiome in common beans (*Phaseolus vulgaris*; Mendes *et al.*, 2018). However, it is interesting to note that Pi-starved *Arabidopsis* roots establish a beneficial relationship with *C. tofieldiae*, prioritizing root growth and Pi metabolism, but activate a defense response under Pi sufficiency. This implies that the plant response to microbes varies with their Pi status. In addition, a study demonstrated that *Arabidopsis*, when inoculated with a synthetic bacterial community (SynCom), induces the PSR and mediates systemic plant immunity, controlled by the master regulator, PHR1 (Castrillo *et al.*, 2017; Rolfe *et al.*, 2019). If this holds true for other plant species, then PSR induced by the ISR-eliciting microbiota could enhance the biosynthesis of strigolactone (SL) which in turn facilitates the recruitment of AMF to plant roots (Cameron *et al.*, 2013; Rolfe *et al.*, 2019). Thus, during the course of evolution, PSR has been found to be coupled to the immune response, maintaining a delicate balance between Pi status and innate immunity (Motte and Beeckman, 2017).

Symbiotic associations for phosphate acquisition

To support survival, stress resistance, and performance, plants also engage in AM symbiosis, where fungal colonization is promoted under soil Pi deficiency conditions. About 80% of vascular plant families are colonized by mycorrhiza (Wang *et al.*, 2017) and acquire Pi through the fungi, an association which is

~469 million years old (Redecker *et al.*, 2000). Interestingly, fungi provide wide coverage of the soil, extending between 25 cm and a few meters for efficient Pi mobilization, and could directly transfer Pi to the host root cells due to endophytic colonization (Chan *et al.*, 2021; Poirer *et al.*, 2022). Crops such as maize (*Zea mays*) depend ~33% more on mycorrhizal association than on root hairs for enhanced Pi acquisition (Ma *et al.*, 2021). In addition to facilitating Pi uptake, AMF have been reported to induce systemic resistance that suppresses a wide range of plant pests and diseases in the host (Jung *et al.*, 2012; Cameron *et al.*, 2013). Mycorrhizal tomato (*Solanum lycopersicum*) plants showed lesser *Alternaria solani* symptoms compared with the control plants, but symptoms became pronounced upon external Pi application (Fritz *et al.*, 2006; Cameron *et al.*, 2013). This study suggests that the mycorrhiza played an important role in providing resistance to *A. solani* which upon Pi sufficiency was possibly attenuated, manifesting disease symptoms. However, mycorrhization turns out to be costly to the host as the fungi depend on its photosynthetically fixed carbon and compromise its immunity to facilitate colonization. Mycorrhization is, therefore, highly regulated in accordance with the Pi status, similar to the case of rhizosphere microbiome association. A complex network of cell-cell and organ-organ communication enables plants to regulate symbiotic association with respect to the nutritional status involving phytohormones (SLs), signaling protein (DELLA proteins and karrikin-like molecules), and miRNAs (Müller and Harrison, 2019; Oldroyd and Leyser, 2020). Phytohormones play a critical role in integrating P status with establishment of AM symbiosis. The role of SL in linking plant Pi status with AM symbiosis has become increasingly apparent recently through several studies. In addition, it also serves as a hub for integrating inputs from other hormones such as auxins, gibberellin (GA), and ethylene (reviewed in Müller and Harrison, 2019). PHR2 has been shown to be required for pre-contact signaling, root colonization, and AM function in rice (Isidra-Arellano *et al.*, 2021; Shi *et al.*, 2021; Das *et al.*, 2022). During Pi starvation, PHR2 binds to the P1BS motifs (GNATATNC) in the promoter regions of PSI genes and transcriptionally activates genes important for AM including for biosynthesis of SL that is perceived by the Myc factors which include lipochitooligosaccharides and chitooligosaccharides secreted by the AMF in the rhizosphere (Kobae *et al.*, 2016). Other genes involved are those encoding CERK1 and SYMRK receptors for the perception of fungal signals (Stracke *et al.*, 2002; Zhang *et al.*, 2015), and NSP2 TFs involved in root colonization (Lauressergues *et al.*, 2012). In addition, various PHT1 transporter genes specifically induced by mycorrhiza such as *PT4* in *Medicago truncatula* and *OsPT11* in rice facilitate symbiotic Pi uptake (Javot *et al.*, 2007; Yang *et al.*, 2012; Garcia *et al.*, 2016). Under sufficient Pi conditions, SPX proteins inhibit mycorrhizal infection through suppression of PHR2-mediated activation of symbiosis-related genes (Oldroyd and Leyser, 2020; Shi *et al.*, 2021). In rice, SPX1 and SPX2 inhibit the activity of OsPHR2 and subsequent PSR in a Pi-dependent manner (Wang *et al.*, 2014). Recently, a yeast one-hybrid

assay was used to reveal a PHR-centered regulatory network that controls AM symbiosis composed of 266 TFs and 47 target promoters controlling hormone signaling pathways [ethylene, auxin, and jasmonic acid (JA) signaling], Pi homeostasis, and Pi starvation (Shi *et al.*, 2021). Thus, it is quite evident that there exists an extensive regulation of AM symbiosis involving various endogenous and exogenous signals with precise Pi sensing.

Nexus between components controlling phosphate status and immunity

Crops experience a plethora of biotic stresses in natural and agricultural ecosystems. While Pi deficiency limits plant growth and development, pathogen infection and insect herbivory account for major losses in crop productivity (Khan *et al.*, 2017; Kim *et al.*, 2021). Stress response pathways evoked in plants are greatly influenced by their nutritional status (Snoeijers *et al.*, 2000; Ballini *et al.*, 2013; Val-Torregrosa *et al.*, 2022a, b). Since Pi homeostasis and immunity are linked, Pi status can directly influence the plant immune response through PSR involving common molecular players of signaling pathways (Fig. 2). Recent studies revealed that the Pi level (InsP8) serves as a signal, and its accumulation represses the expression of genes involved in defense response. For instance, high Pi status weakens the plant defense against foliar pathogens in rice (Campos-Soriano *et al.*, 2020). This inverse relationship between Pi availability and defense response was also evident in the case of cotton (*Gossypium hirsutum*) where Pi deficiency leads to resistance against *Verticillium dahliae* (Luo *et al.*, 2021). Pi deficiency can directly impact the immune response through the induction of phytohormones such as SA and JA, which further mediate the biosynthesis of defense-related secondary metabolites (Chan *et al.*, 2021). Low Pi also triggers PSI gene expression regulated by the TFs PHR1/PHL1, which directly regulate the expression of SA-responsive gene expression (Castrillo *et al.*, 2017).

The soil microbiome could elicit ISR in the host plant (Rudrappa *et al.*, 2008; Rolf *et al.*, 2019). The external soil Pi availability and internal cellular Pi in plants have been known to influence the response to biotic stress through a crosstalk between Pi starvation signaling machinery and various key components including phosphate transporters (PHTs) in biotic interactions. The Pi transporter, PHT1;4, mediating Pi acquisition and transport into roots (Shin *et al.*, 2004; Ye *et al.*, 2015) is inhibited with the activation of PTI. On the other hand, PHT1;4-mediated Pi uptake negatively regulates antibacterial immunity in roots (Dindas *et al.*, 2022). During Pi deficiency, the Pi starvation signaling pathway including various TFs, miRNAs, and transporters plays a crucial role in mediating the plant immune response modulated by sugar and defense hormones such as SA and JA (Khan *et al.*, 2016; Castrillo *et al.*, 2017). Additionally, various secondary metabolites with antimicrobial activities including flavonoids and glucosinolate are also induced, which provide enhanced immunity against pathogen attack (Pant *et al.*, 2015). Table 2 lists selected examples demonstrating the influence of different (a)biotic stresses

involving various signaling pathways on the biotic stress response in crops. Multiple stress responses, involving a complex regulatory network controlled by a range of key components such as TFs, Pi transporters, defense phytohormones, miRNA, and sugar transporters are discussed in the following section.

PHRs modulate phosphate starvation-induced resistance to biotic stress

PHRs form the nexus between Pi homeostasis and the plant immune responses by transcriptionally regulating about two-thirds of Pi-responsive genes (Motte and Beeckman, 2017; Chan *et al.*, 2021; Isidra-Arellano *et al.*, 2021; Tang *et al.*, 2022). Under Pi-deficient conditions, PHR1 has been shown to negatively regulate the SA-mediated immune response. Repression of SA-responsive genes by PHR1 was shown through *phr1* and *phr1phl1* Arabidopsis mutant studies (Castrillo *et al.*, 2017). This corroborates well with the fact that, in order to associate with the root microbiome, plants have to compromise their immunity to alleviate low Pi conditions. Through the molecular analysis of *phr1-1* mutant, it has also been found that the activation of the JA signaling pathway is partially controlled by PHR1 under Pi-deficient conditions. In rice, *OsPHR2*, which is expressed mainly in roots and is involved in Pi-dependent alteration of root architecture, has recently been implicated in enhancing JA response and antibacterial resistance, especially to *Xanthomonas oryzae* pv. *oryzae* (Xoo). The study indicated the *OsPHR2*–*OsMYC2* engage in crosstalk in modulating an enhanced JA response and antibacterial resistance (Kong *et al.*, 2021). However, in rice *phr2* mutants, AMF colonization is drastically reduced (Das *et al.*, 2022), but does not cease completely, implying that it could be co-regulated by other TFs (Khan *et al.*, 2016). Apart from the MYB/MYC TFs, WRKY family TFs could also play a crucial role in crosstalk between Pi starvation response, phytohormones, and biotic stress signaling (Baek *et al.*, 2017). There are a few WRKY TFs localized in the nucleus and primarily expressed in the roots that have been reported to modulate Pi starvation responses and root development. WRKY75 is one such TF that enhances the expression of PSI genes and JA marker genes while reducing SA marker gene expression (Devaiah *et al.*, 2007; Chen *et al.*, 2013; Baek *et al.*, 2017). Similarly, AtWRKY45 is known to activate the expression of *PHT1;1* by binding to its two W-boxes in the promoter region during Pi starvation (Wang *et al.*, 2014). Also, AtWRKY42 modulates Pi homeostasis through the regulation of *PHO1* and *PHT1;1* expression and subsequently modulating Pi translocation and acquisition according to Pi status (Su *et al.*, 2015). The role of these WRKYs in the crosstalk between Pi availability and biotic stress needs to be investigated in detail.

PHT1 is the major facilitator in regulating Pi uptake and AM association

The survival of Pi-deprived plants depends on the efficient utilization of limited Pi for maximum agronomic benefit. This greatly depends on the Pi transport system for Pi uptake and

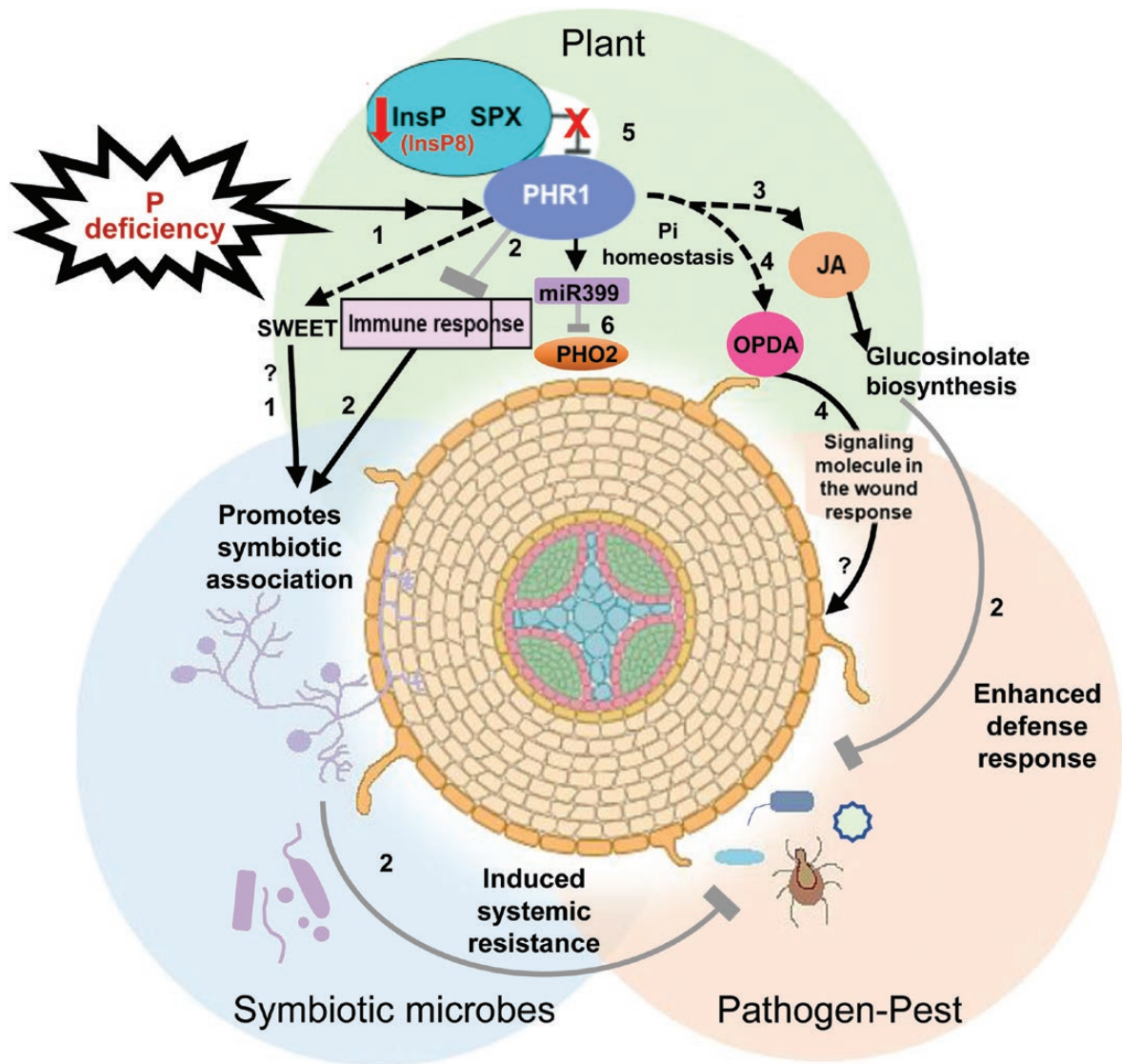


Fig. 2. An illustration depicting key molecular players involved in plant-biotic-phosphate interaction. PHR1 is a major regulator of the transcriptional activation of PSR and plant immunity. Plant immunity is suppressed transiently through PHR1 to facilitate association with symbiotic microbes for enhanced Pi acquisition under its deficiency. However, plants acquire AMF- and RM-induced ISR to pathogenic microbes and insect herbivory. Pi deficiency also activates JA which induces disease resistance in crops like cotton. Upon attaining Pi sufficiency, inositol polyphosphate (InsP) signaling molecules regulate Pi homeostasis in plants by binding to SPX-domain-containing proteins. InsP8 binding allows SPX proteins to interact with PHR1 and inhibit Pi starvation-response gene transcription. Under Pi starvation, the level of InsP8 drops to release PHR1 allowing expression of PSI genes. Pi homeostasis is also regulated by miR399. miR399 is induced upon Pi deprivation which in turn represses PHO2 for Pi accumulation. This miR399–PHO2 pathway operates downstream of PHR1 and forms a subcomponent of the Pi signaling network in Arabidopsis. Other crucial players such as OPDA and SWEET have also been indicated to have a role in the nexus between Pi availability and biotic stress response. Pi, inorganic phosphate; PSR, phosphate starvation response; PHR1, PHOSPHATE STARVATION RESPONSE1; PHO2, Phosphate overaccumulator2; JA, jasmonic acid; AMF, arbuscular mycorrhizal fungi; RM, rhizobial microbiome. References are provided as numbers, 1–6. 1, [Hennion et al., 2019](#); 2, [Castrillo et al., 2017](#); 3, [Khan et al., 2016](#); 4, [Taki et al., 2005](#); 5, [Puga et al., 2014](#); 6, [Bari et al., 2006](#). Black dotted lines represent induction, while black solid arrows depict direct activation. The gray blunt-ended line and the red cross represents inhibition. Question marks (?) are provided at places where we find a missing link between the nexus between the phosphate status and plant immunity.

distribution within the plant ([Javot et al., 2007](#)). High-affinity Pi transporters localized in the root epidermis and root hairs generally take up Pi from the plant–soil interface, whereas there is an additional and more predominant route of Pi up-take in AM plants via the AM at the plant–fungal interface after

colonization ([Smith et al., 2003, 2004](#); [Chen et al., 2011](#)). Among the Pi transporters, PHT1, belonging to a multigene family, utilizes the proton motive force across the plasma membrane to transport the Pi anion into the cytosol ([Liu et al., 2021](#); [Dindas et al., 2022](#)). Besides Arabidopsis (nine members;

Table 2. Influence of different stresses on biotic stress response in crops

Crop	Genes involved	Induced by	Pathways involved	Biotic stress resistance	Reference
<i>Zea mays</i>	<i>ZmOPR1</i> <i>ZmOPR2</i>	<i>Cochliobolus carbonum</i> , <i>Cochliobolus heterostrophus</i> , <i>Fusarium verticillioides</i>	Octadecanoid pathway	Resistance to <i>C. heterostrophus</i>	Zhang et al. (2005)
<i>Oryza sativa</i>	<i>OsMYC2</i>	Pi starvation	Jasmonate pathway	<i>Xanthomonas oryzae</i> pv. <i>oryzae</i>	Kong et al. (2021)
<i>Solanum tuberosum</i>	<i>NaPLP</i>	<i>Alternaria alternata</i>	Jasmonate signaling Ethylene signaling	Negative role in <i>Nicotiana attenuata</i> resistance	Cheng et al. (2019)
<i>Nicotiana tabacum</i>	<i>NtPat1</i> <i>NtPat2</i> <i>NtPat3</i>	12-Oxo-phyto-dienoic acid	Oxylipin signaling	Tobacco mosaic virus	Dhondt et al. (2000)
<i>Solanum lycopersicum</i>	<i>JAZ10</i>	Pi deficiency	Jasmonate signaling	Resistance to <i>S. littoralis</i>	Khan et al. (2016)
<i>Nicotiana benthamiana</i>	<i>JAZ10</i>	Pi deficiency	Jasmonate signaling	Resistance to <i>S. littoralis</i>	Khan et al. (2016)
<i>Gossypium hirsutum</i>	<i>GhAOS</i>	Pi deficiency	Jasmonic acid biosynthesis Phenylpro-panoid pathway	Resistance to <i>Verticillium dahlia</i>	Luo et al. (2021)
<i>Solanum lycopersicum</i>		<i>Bemisia argentifolii</i>	–	Resistance to powdery mildew	Mayer et al. (2002)
<i>Capsicum annuum</i>		<i>Bemisia tabaci</i>	–	Resistance to <i>Xanthomonas axonopodis</i> pv. <i>Vesicatoria</i> and <i>Ralstonia solanacearum</i>	Yang and Wan (2011)
<i>Solanum lycopersicum</i>	SR/CAMTA transcription factors	Drought stress		Negatively regulates defense response against <i>B. cinerea</i> and <i>Pseudomonas syringae</i> DC3000	Li et al. (2014)

Mudge et al., 2002; Shin et al., 2004), it has also been reported in many of the crop species including *Oryza sativa* (13 members; Paszkowski et al., 2002; Liu et al., 2011), *Zea mays* (13 members; Nagy et al., 2006; Liu et al., 2016), *Hordeum vulgare* (11 members; Srivastava et al., 2021), *Glycine max* (15 members; Qin et al., 2012; Fan et al., 2013), and *Solanum lycopersicum* (eight members; Chen et al., 2014) to mediate Pi uptake and translocation. In AM symbiosis, Pi uptake through the periarbuscular membrane is reported to be mediated by mycorrhiza-inducible Pi transporters (MPTs) and has been found to be regulated by RAM1 and DELLA proteins (Ferrol et al., 2019). A study showed that the fungus failed to proliferate inside the roots when the functioning of MtPT4 was lost in *Medicago truncatula* (Javot et al., 2007). In several crop species, AM-inducible Pi transporters belonging to the PHT1 family have been identified and shown to repress arbuscule formation when Pi transporters were knocked out, suggesting a conserved mycorrhiza-regulated pathway across plant species (Javot et al., 2007).

Dindas et al. (2022) reported that Pi uptake in roots is actively repressed upon immune activation through direct phosphorylation of key PHTs by receptor-like cytoplasmic kinases, BOTRYTIS-INDUCED KINASE 1 (BIK1) and PBS1-LIKE KINASE 1 (PBL1), leading to enhanced anti-bacterial immunity. PHT4;1 is implicated in regulating innate immunity and functions as a negative regulator of Arabidopsis defense (G.Y. Wang et al., 2011; Wang et al., 2014). The Golgi Pi transporter, PHT4;6, on the other hand, has been reported to be a negative regulator of SA-mediated defense and thus suppresses disease resistance to the virulent *Pseudomonas syringae* strain DC3000 in Arabidopsis (Hassler et al., 2012). Over-expression of OsPT8, a rice Pi transporter gene, suppresses disease resistance against *Magnaporthe oryzae* and Xoo, thus regulating immunity negatively (Z. Dong et al., 2019). Thus, Pi transporters, involved in Pi uptake, could also be implicated in modulating immunity in plants (Hassler et al., 2012; Chan et al., 2021).

JA as a critical component in Pi deficiency adaptations and plant immunity

Phytohormones play a primary role in mediating signaling between environmental stimuli (biotic/abiotic) and the transcriptomic response for acclimation (Chan *et al.*, 2021). They orchestrate the interaction between biotic and abiotic stresses by exerting either an antagonistic or a synergistic effect (Asselbergh *et al.*, 2008; Atkinson and Urwin, 2012). Under varying Pi status, crops respond differently to biotic stresses. In this regard, phytohormones such as SLs, SA, JA, and ethylene play a critical role (Chan *et al.*, 2021). Pi starvation represses the level of GA and cytokinin (CK), while elevating the level of abscisic acid (ABA) in Arabidopsis and barley roots (Vysotskaya *et al.*, 2016) and of ethylene (Chapin and Jones, 2009; Chiou and Lin, 2011). In studying the nutrient–immunity trade-off, crosstalk between these hormones seems critical. While SLs are an important phytohormone regulating PSR and rhizosphere signaling molecules, plants trigger systemic defense responses involving SA and JA when exposed to pathogenic infection (Robert-Seilaniantz *et al.*, 2011; Pieterse *et al.*, 2012; Wang *et al.*, 2021). SA mediates defense against biotrophic pathogens such as downy mildew, whereas JA mediates immune response against insect herbivores and necrotrophic pathogens. All these phytohormones directly or indirectly play an important role in shaping the root microbiome (Lebeis, 2014; Carvalhais *et al.*, 2015). GAs regulates AM association in accordance with the Pi status. Using solanaceous model systems, high Pi was shown to cause an increase in GA levels in the mycorrhizal roots, leading to an inhibitory effect on the AM symbiosis (Nouri *et al.*, 2021). Similarly, in rice, a GA receptor, GIBBERELLIN INSENSITIVE DWARF1 (GID1), was shown to perceive GA which then interacts with a rice DELLA ortholog, SLR1, causing its degradation by polyubiquitination (Yu *et al.*, 2014). However, high activity of GA2 oxidase keeps the relative levels of GA low under low Pi conditions due to which DELLA protein remains protected from degradation (Nouri *et al.*, 2021). A repressed level of GA leads to DELLA protein accumulation, which in turn promotes AM symbiosis (Wang *et al.*, 2022). In addition to these, a crosstalk also exists among SA, JA, and ethylene which provides resistance against pathogens and herbivory (Yang *et al.*, 2019).

Interestingly, traits observed in Pi-starved plants such as growth retardation and anthocyanin accumulation, are also found during JA induction, suggesting a link between the two signaling pathways (Li *et al.*, 2018). Recently, a rapid rise in the level of endogenous JA along with the genes involved in its biosynthesis (*LOX2*, *AOS1*, and *AOS2*) was shown within 1 h of transfer of rice seedlings to Pi-deficient media (Tao *et al.*, 2022). Exogenous application of JA in roots resulted in an altered exudate profile that would allow rhizobial associations and mycorrhization for better Pi acquisition (Carvalhais *et al.*, 2015; Das *et al.*, 2022). In the leaves and roots of Arabidopsis, higher levels of JA led to enhanced defense response to insect

herbivory (Khan *et al.*, 2016; Kong *et al.*, 2021). It has been indicated that the induction of the JA signaling pathway by Pi deficiency was partially controlled by PHR1. Studies with the *phr1* mutants found a delayed activation of the JA signaling pathway but it was not abolished completely (Khan *et al.*, 2016), indicating the possible role of other signaling components such as InsPs. InsP5 and InsP8 have been known to act as co-activators of the JA signaling pathway by binding to the co-receptor complex, COI1–JAZ (Sheard *et al.*, 2010; Laha *et al.*, 2015; Khan *et al.*, 2016).

In Arabidopsis and tomato, Pi deficiency has been shown to enhance the resistance to *Spodoptera littoralis* (Khan *et al.*, 2016). Castrillo *et al.* (2017) revealed clusters of SA- related genes significantly enriched as in the case of plant defense in Arabidopsis using global ChIP-seq. In another study, Arabidopsis grown under high Pi conditions exhibited resistance to necrotrophic and hemibiotrophic fungal infections. In the absence of any infection, plants grown under high Pi supply displayed an induced expression of genes involved in SA- and JA-dependent signaling pathways. However, in the event of pathogen infection, these plants showed opposite regulation in the two branches of the JA signaling pathway (the ERF and MYC branch). This was indicated by an enhanced expression of a defense marker gene of the ERF branch, *Plant Defensin 1.2* (*PDF1.2*) and a reduced expression of a commonly used marker gene of the MYC branch, *Vegetative Storage Protein 2* (*VSP2*) (Val-Torregrosa *et al.*, 2022a). These studies clearly indicated JA as a core component in modulating Pi adaptation and plant innate immunity.

Pi starvation-induced miR399 plays an important role in fine-tuning immunity

miRNAs have been implicated in the regulation of reproductive development (Wang *et al.*, 2020), nutrient homeostasis (Sunkar and Zhu, 2007; Shukla *et al.*, 2008; Simon *et al.*, 2009), and plant immunity (Staiger *et al.*, 2013; Song *et al.*, 2021). The first miRNA reported to be involved in response to Pi starvation was Arabidopsis miR399. It is induced specifically under Pi-deficient conditions and controls Pi homeostasis in several plants including Arabidopsis (Fujii *et al.*, 2005; Chiou *et al.*, 2006), rice (Hu *et al.*, 2015), soybean (Xu *et al.*, 2013), and maize (Du *et al.*, 2018). While moving from shoots to roots, miR399 regulates Pi homeostasis by repressing its target gene, *PHOSPHATE2* (*PHO2*), involved in the ubiquitination of PHTs (Lin *et al.*, 2008). Further, its induction under Pi deficiency is significantly reduced in the *atphr1* mutant, suggesting a conserved signaling pathway involving the PHR1–miR399–PHO2 system (Bari *et al.*, 2006). However, this is not the case with rice as no reciprocal expression of *OsmiR399* and *OsPHO2* was identified, suggesting different regulatory circuitry controlling Pi homeostasis, downstream of miRNA399 in rice and Arabidopsis (Zhou *et al.*, 2008). Over the last few years, several studies were conducted to identify

miRNAs that exert regulatory functions either positively or negatively at the transcriptional level for disease resistance, not only in model plants but also in crop species. Arabidopsis miR393 was the first miRNA reported for plant immunity, imparting bacterial pathogen resistance (Navarro *et al.*, 2006). Others involved in fine-tuning immunity based on their target genes include rice miR812w for blast resistance (Campo *et al.*, 2021), miR858 which negatively regulates PTI in Arabidopsis (Camargo-Ramírez *et al.*, 2018), and miR160 in potato (*Solanum tuberosum*) which elicits systemic acquired resistance to *P. infestans* (Natarajan *et al.*, 2018). Interestingly, miR399, in addition to regulating Pi homeostasis, affected resistance to necrotrophic (*Plectosphaerella cucumerina*) and hemibiotrophic (*Colletotrichum higginsianum*) fungal pathogens in Arabidopsis. Val-Torregrosa *et al.* (2022a) observed severe infection in wild-type plants, while an enhanced resistance was exhibited by miR399-overexpressing plants in an Arabidopsis–*P. cucumerina* pathotype system. However, overexpression of *MIR399f* was shown to cause Pi accumulation in rice which led to an enhanced susceptibility to *M. oryzae* (Campos-Soriano *et al.*, 2020). These studies suggested that different disease suppression mechanisms respond differently to nutrient status and depend on the coordinated manner in which nutrient signaling and defense signaling operate (Campos-Soriano *et al.*, 2020; Val-Torregrosa *et al.*, 2022a).

SWEET transporters might play a crucial role in plant-biotic-phosphate interactions

Pi starvation is accompanied by an increase in sugar accumulation, predominantly sucrose and starch, in the leaves of many plant species. In Arabidopsis, sugar signaling has been found to mediate PSR (Karthikeyan *et al.*, 2007; Baek *et al.*, 2017). Substantial evidence provides the link between Pi starvation responses and sugar homeostasis (Karthikeyan *et al.*, 2007; Hammond and White, 2008; Rouached *et al.*, 2010; Yan *et al.*, 2022). A significant portion of sucrose allocated to roots is exuded and plays an important role in engaging beneficial microbes to deliver Pi from non-utilizable sources (Hennion *et al.*, 2019). Also, sugars are known to integrate different environmental stimuli and act as signaling molecules that could modulate the root system (Valifard *et al.*, 2021). The distribution of sugars within plant cells and movement between tissues (source to sink) are facilitated by plasma membrane- and organelle membrane-localized sugar transport proteins and is a highly regulated process (Salvi *et al.*, 2022). Sugar transport proteins including SUGAR WILL EVENTUALLY BE EXPORTED TRANSPORTER (SWEET), sucrose transporters/sucrose carriers (SUT/SUC), and monosaccharide sugar transporter (MST) families facilitate the movement of sugars to the roots, consequently enhancing the up-regulation of Pi transporters, phosphatases, and metabolic enzymes, mediated by a PHR1 transcriptional cascade (Hermans *et al.*, 2006; Pérez-Torres *et al.*, 2008; Hammond and White, 2011;

Baek *et al.*, 2017). Plasma membrane SUT1-type or STP transporters carry sugars to the plant cells containing the arbuscule, while sucrose effluxers of the SWEET family export sugar across the peri-arbuscular membrane towards the AM (Hennion *et al.*, 2019). Transport of sugars within the plant cells and towards the rhizosphere-associated microbes mainly takes place through SWEET transporters (Chen *et al.*, 2010; Chen *et al.*, 2014; Hennion *et al.*, 2019). SWEET transporters could be regarded as a core component for Pi starvation-induced mycorrhizal association. Besides their role in mycorrhizal association, SWEETs have been implicated in plant response to pathogens (Yamada *et al.*, 2016; Hennion *et al.*, 2019). Restricting sugar uptake is one of the strategies plants employ against microbial infection and is regulated by sugar transporters. For instance, AtSWEET2 and AtSWEET11 have been shown to restrict *Pythium irregulare* and *Plasmodiophora brassicae* infections, respectively, through this mechanism (Chen *et al.*, 2015; Li *et al.*, 2018). This duelling for sugar shapes the plant biotic interactions (Yamada *et al.*, 2016; Breia *et al.*, 2021). On the contrary, SWEET transporters are also targeted by pathogens and therefore are a key player in plant–pathogen interaction. In different crops such as rice, cassava (*Manihot esculenta*), and cotton, *Xanthomonas* species causing bacterial blight disease-enhanced expression of specific SWEET genes through transcription activator-like (TAL) effectors to hijack its activity for its growth and proliferation (Breia *et al.*, 2021). In response to AMF, SWEET transporters have been shown to be differentially expressed in potato (*S. tuberosum*), suggesting their role in regulating the export of sugar to the symbiotic interface (Manck-Gotzenberger and Requena, 2016). Similarly, in chickpea (*Cicer arietinum*), expression of *CaSWEET* genes has been found to be induced when subjected to Pi deficiency (La *et al.*, 2022).

Thus, the relevance of SWEET in Pi starvation-induced mycorrhizal association and plant biotic interactions is evident through these studies. However, the clear understanding of their potential role in the crosstalk between the Pi stress and biotic stress, their metabolic signatures, and their regulatory principles still needs to be elucidated.

12-Oxo-phytodienoic acid as a signal mediator for Pi and biotic stress response

Plant oxylipins are cellular messengers to initialize the defense response to biotic stresses and are derived from oxidatively modified polyunsaturated fatty acids (Demmig-Adams *et al.*, 2013). There have been a growing number of oxylipins identified as signal mediators in addition to JAs (Blée, 2002). Thus, oxylipins have also emerged as a potential candidate for the crosstalk between biotic stress and Pi deficiency in plants (Dhondt *et al.*, 2000). Though JA has been widely accepted to have a role in Pi and biotic stress, we are focusing here on the new role of 12-oxo-phytodienoic acid (OPDA), apart from its role as a cyclopentenone JA precursor

in triggering plant defense responses under Pi-deprived conditions. In Arabidopsis, this intermediate molecule formed via the plastidial 13-LOX (lipoxygenase) possesses signaling functions triggering a set of genes encoding TFs, signaling components, and stress-responsive proteins. These genes referred to as OPDA-specific response genes (ORGs) contain one-half of wound-induced genes specifically responding to OPDA and not JAs. Through mutant studies, their role as signaling molecules in response to wounding was ascertained in a CORONATINE INSENSITIVE 1-independent manner, indicating that the OPDA signaling pathway is independent of that of JAs (Taki *et al.*, 2005). Its role in signaling could be attributed to its α,β -unsaturated carbonyl group characteristic of reactive carbonyl species (Alméras *et al.*, 2003; Taki *et al.*, 2005; Biswas and Mano, 2021). Again, in Arabidopsis, *AtPHO1;H10* belonging to the *PHO1* gene family involved in Pi homeostasis has been shown to be induced upon application of OPDA but not JAs or coronatine (Ribot *et al.*, 2008; Shikha *et al.*, 2022). These results thus led us to suspect OPDA involvement in Pi and biotic stress response which needs to be explored further.

Concluding remarks and future perspectives

There is substantial evidence that abiotic stresses modulate the expression of plant defense and pathogen virulence genes (Rizhsky *et al.*, 2004). Plants prioritize and balance resource allocation between growth and defense response as responding to stresses can prove costly in terms of growth and crop yield (Tian *et al.*, 2003). Depletion of P and nitrogen triggers defense responses at molecular and biochemical levels in plants (Zarattini *et al.*, 2021). In the case of Pi depletion, PHR1 is reportedly known to directly integrate PSR and plant immunity, also activating a microbiome-enhanced response. Very recently, Tang *et al.* (2022) demonstrated that Pi starvation and plant immunity are balanced through the RALF-FERONIA module in Arabidopsis. Additionally, Castillo *et al.* (2017) demonstrated the role of PHR1 in suppressing SA-induced response under Pi starvation while activating JA-responsive genes including those mediating the biosynthesis of defense-related glucosinolates in Arabidopsis. This study indicates that PHR1 shuts a part of but not the entire immune response system. Arabidopsis, unlike rice and *Lotus japonicus*, is a non-mycorrhizal plant, and whether this immune suppression theory in Arabidopsis applies to mycorrhizal-driven responses is something that still needs to be explored. Furthermore, soil Pi uptake and its distribution within the plant take place mainly through *PHT1*. Some of these genes are also known to be regulated in response to beneficial microbes, especially AMF. However, these fungus-inducible *PHT1* genes such as soybean *PT10* and *PT11* seem to be lacking in non-mycorrhizal plant such as Arabidopsis. Most of the *PHT1* transporter genes have been reported to show mild or no response to a beneficial endophytic fungus, *Piriformospora indica*, irrespective of

the Pi status (Sisaphaithong *et al.*, 2012; Tamura *et al.*, 2012). These studies indicate that there are different immune system outputs for different biotic interactions modulated by the Pi status. In addition, experiencing long-term abiotic stress can cause a weakening of the immune response subsequently causing pathogen infection (Amtmann *et al.*, 2008; Mittler and Blumwald, 2010; Atkinson and Urwin, 2012). Further, a recent study in Arabidopsis demonstrated that plants with high Pi status exhibited resistance to infections by fungal pathogens. This suggests that the plant modulates different defense response circuitry in accordance with the nutritional clues for varying biotic encounters such as fungal, bacterial, and insect herbivory. The understanding of the direct coupling of PSR to the immune response opens up new avenues to deploy resistance strategies in crops. Also, it would be interesting to explore a similar coupling of the starvation response of other minerals with plant immunity. For instance, the *NITROGEN LIMITATION ADAPTATION* (*NLA*) gene, having an important role in nitrogen limitation responses in Arabidopsis (Peng *et al.*, 2007), also mediates degradation of Pi transporters to maintain Pi homeostasis (Lin *et al.*, 2013; Park *et al.*, 2014; Yue *et al.*, 2017). A recent study revealed that *nla* mutants show resistance to necrotrophic and hemibiotrophic fungal infections through the enhanced accumulation of SA, JA, and camalexin levels in Arabidopsis. Several independent studies suggest the role of *NLA* in regulating adaptation under nitrogen limitation, PSR, and immunity (Peng *et al.*, 2007; Val-Torregrosa *et al.*, 2022b). This indicates the existence of a crosstalk between various nutrient signaling pathways and immune responses in plants. Our understanding of this crosstalk would help to devise strategies to improve crop resilience under a natural environment where nutrient deficiency is coupled with other stresses especially biotic stresses. Though a holistic approach would be required to mitigate such a situation, there are instances where manipulating a single gene or a combination of key genes was demonstrated to enhance yield (Delhaize *et al.*, 2009; Baker *et al.*, 2015; Cho *et al.*, 2021). A majority of such studies have been conducted in model plants; however, similar studies need to be conducted in other crop species as well which would allow engineering cultivars, for instance with more efficient utilization of available Pi and enhanced Pi acquisition strategies with the defense response. These require a mechanistic understanding of stress responses and utilization of stress acclimation networks. Several key molecular components including TFs, phosphate transporters, defense phytohormones, miRNA, and sugar transporters have been identified. Many of these genes have been characterized for a key role in low Pi tolerance and modulating plant immunity (Fig. 2) through either overexpression or suppression. Some of these genes encoding SWEET, WRKY TFs, and the OPDA have been suggested to have a new role in the nexus between Pi status and immunity which could be explored further. Attempts have also been made to determine their positive effects on Pi acquisition and/or utilization efficiency (López-Arredondo *et al.*, 2014). In the context of the present article, there could be two rational strategies to reduce over-reliance on Pi fertilizers; firstly, to ameliorate negative effects of Pi deficiency on plants through adaptive metabolic responses

and efficient utilization of available Pi, and secondly including maintaining Pi homeostasis by mobilizing recalcitrant P in plant. In the case of multiple stress responses, attention has to be paid to applying strategies that are synergistic to the plant immune response. It is highly critical to understand the negative interactions of multiple stresses and the complexity involved in stress response signaling during stress combination (Suzuki et al., 2014). Targeting and utilizing these molecular players through genetic engineering approaches, utilizing SynCom, integrating quantitative trait locus mapping with other genetic and conventional breeding approaches would be the way forward.

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Author contributions

JG: conceptualization and design of the outline; LTP: literature survey and writing. Both authors prepared the final draft.

Conflict of interest

The authors declare no conflict of interest.

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