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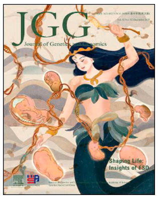

Review

The interplay between phosphorus nutrition and abiotic stresses in plants

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ABSTRACT

Phosphorus (P) is an essential macronutrient required for plant growth, development, and resilience to environmental stresses. Its availability in soil and homeostasis within plants are strongly influenced by environmental conditions, with unfavorable environments and soil factors disrupting phosphate availability, absorption, transport, and utilization. Optimizing phosphate supply can alleviate the detrimental impacts of abiotic stresses, thereby supporting growth and improving stress tolerance. Recent studies reveal that abiotic stresses modulate phosphate signaling pathways and alter the expression of phosphate-responsive genes, often affecting key regulators of P homeostasis. Strategic manipulation of phosphate transporters and their regulatory pathways offers a promising approach to enhance plant adaptation to challenging environments. This review highlights current advances in understanding the molecular mechanisms that coordinate P-responsive gene expression and homeostasis pathways under fluctuating P availability and stress conditions. It emphasizes the critical role of P nutrition in enhancing plant stress tolerance through antioxidant activation, osmolyte accumulation, membrane stabilization, and metal-phosphate complex formation. An in-depth mechanistic understanding of P-stress interactions will inform the development of P-efficient and stress-resistant crop varieties and guide more sustainable P fertilizer management in agriculture.

Introduction

Phosphorus (P) is a crucial macronutrient for plants, playing a vital role in respiration, energy metabolism, signal transduction, biomacromolecule synthesis, and photosynthesis (Chiou and Lin, 2011). Plants primarily absorb P as inorganic phosphate (Pi), in the forms of $H_2PO_4^-$ and HPO_4^{2-}, from the soil. However, Pi readily binds with cations such as calcium (Ca^{2+}) and magnesium (Mg^{2+}) in alkaline soils, or with aluminum (Al^{3+}) and iron (Fe^{2+}/Fe^{3+}) in acidic soils, forming insoluble compounds (Hinsinger, 2001). As a result, P is often a limiting nutrient in soils, with nearly one-third of the world's cultivated soils being Pi-deficient (Vance et al., 2003). The fraction of soil Pi that plants can absorb, termed "available Pi", is influenced by environmental conditions. Low soil Pi significantly impacts crop yield and quality. Conventional agriculture often addresses Pi deficiency by applying Pi fertilizer. Although higher Pi fertilization can alleviate low Pi (LP) levels, much of the excess Pi becomes fixed in soils, reducing its utilization efficiency. Moreover, the extensive use of Pi fertilizer depletes finite Pi rock resources, leads to environmental pollution, disrupts the ecological balance, and increases crop susceptibility to pathogens (Campos-Soriano et al., 2020; Lü et al., 2025).

The escalating impacts of climate change are intensifying pressure on global ecosystems, exposing crops to a complex interplay of

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environmental, biological, and nutritional stresses (Dai et al., 2023; Singh et al., 2024). Climate changes, such as global warming and elevation of atmospheric CO_2 concentration, have been known to affect the availability of nutrients in the soil and the concentrations of mineral nutrients in plant tissues (Gojon et al., 2023; Tian et al., 2023; Lee et al., 2024). Addressing these challenges requires the development of crop varieties with enhanced stress and/or climate resistance and efficient nutrient utilization. A significant interaction between P nutrition and environmental stress responses has been reported (Chan et al., 2021; Ueda et al., 2021). Certain abiotic stresses can significantly reduce the availability of Pi in soils, thereby limiting Pi uptake and utilization in plants. Application of Pi fertilizers enhances Pi uptake and significantly strengthens plant tolerance to abiotic stresses (Bechtaoui et al., 2021). Despite these findings, comprehensive insights into how P nutrition mitigates abiotic stress are still lacking. This review examines the interplay between P nutrition and abiotic stresses, focusing on Pi-responsive genes, the impact of stress on Pi homeostasis, and the regulatory mechanisms by which P nutrition enhances plant stress responses and tolerance.

Molecular mechanisms involved in phosphate starvation and homeostasis in plants

To overcome Pi scarcity in soil, mainly caused by fixation with cations and conversion into organic compounds, plants have developed diverse adaptive strategies to maintain steady cellular Pi concentration (Pi homeostasis). These responses to LP stress include altering biomembrane composition, enhancing Pi uptake and transport, modifying root architecture, inhibiting shoot growth and branching or tillering, reducing leaf angle, releasing organic acids and acid phosphatases, forming symbiotic associations with arbuscular mycorrhizal fungi, and reallocating Pi from older to younger tissues (Umehara et al., 2010; Baker et al., 2015; Chen and Liao, 2016; Ruan et al., 2018; Liu, 2021; Guo et al., 2025). Pi homeostasis is maintained through the coordinated regulation of rhizosphere Pi uptake, xylem loading, and its transport and reutilization among plant organs, involving complex signaling networks between tissues (Baker et al., 2015; Gu et al., 2016; Yang et al., 2024a). Phosphate transporters mainly mediate Pi uptake in plant roots, particularly members of the PHOSPHATE TRANSPORTER 1 (PHT1) family (Gu et al., 2016; Chang et al., 2019). After the uptake, Pi needs to be loaded into xylem vessels for transport to the shoots. Since the xylem consists of non-living cells, it functions as part of the apoplastic pathway. Therefore, Pi export is necessary to move intracellular Pi from the roots into the extracellular xylem space, and this process is facilitated by expression of PHOSPHATE 1 (PHO1) Pi exporter in xylem parenchyma cells (Arpat et al., 2012; Poirier et al., 2022; Dai et al., 2024). Arabidopsis PHO1 is mainly localized in the Golgi and *trans*-Golgi network, with occasional localization to the plasma membrane under high external Pi conditions (Arpat et al., 2012), while its homolog in rice, OsPHO1;2, mainly localizes in the plasma membrane (Che et al., 2020; Ma et al., 2021). Rice OsPHO1;1 and OsPHO1;2 are suggested to function as Pi influx transporters driven by proton gradient, which differs from the mechanism of Arabidopsis PHO1 (Che et al., 2020). Excess Pi is sequestered in vacuoles, with Vacuolar Phosphate Transporter 1 (VPT1/PHT5; 1) mediating Pi influx, while Vacuolar Pi Efflux transporters (VPEs) facilitate Pi efflux (Liu et al., 2015, 2016; Xu et al., 2019) (Fig. 1).

Many key regulators of Pi homeostasis and the phosphate starvation response (PSR) pathways have been well characterized in plants. Pi-responsive genes are regulated both genetically and epigenetically through various mechanisms. The PSR is primarily

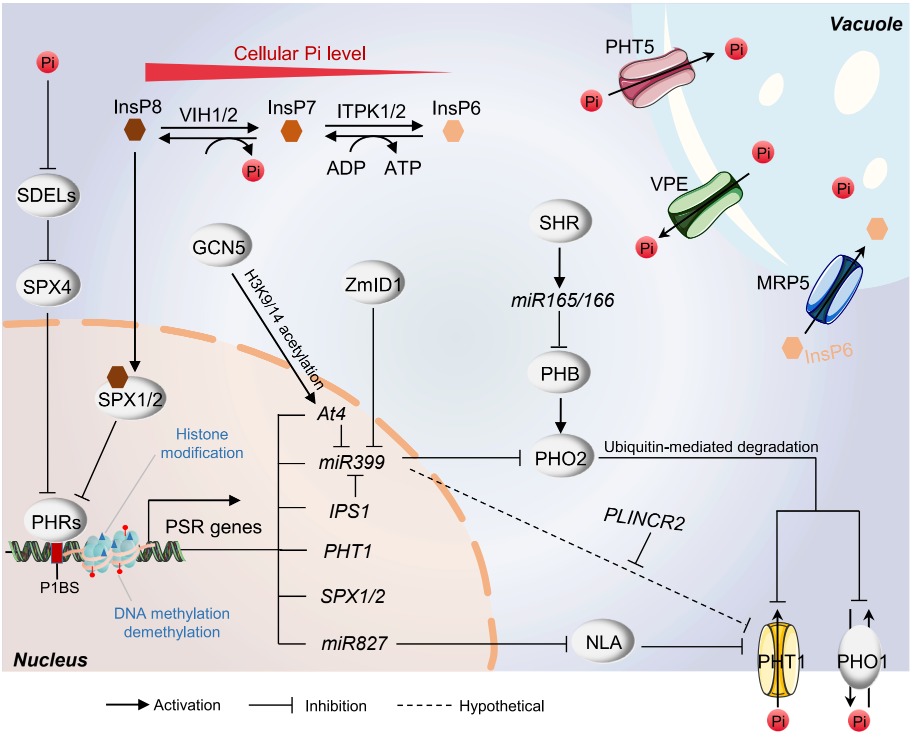


Fig. 1. Schematic representation of the molecular mechanisms involved in Pi homeostasis regulation of plants. The key components involved in Pi sensing, uptake, transport, and storage are depicted in the figure. SPX proteins (such as SPX1/2/4) are crucial for Pi sensing, and regulate Pi-responsive gene expression by interacting with the PHR transcription factors. The SPX-InsP8 complex regulates PHR activity under Pi-sufficient conditions, while Pi deficiency triggers the release of PHRs, which subsequently activate PSR genes, including *PHT1* and miRNAs like miR399. miR399 regulates Pi homeostasis by down-regulating *PHO2*, which encodes a ubiquitin E2 conjugating enzyme. Vacuolar Pi storage is mediated by transporters like PHT5 and MRP5, while VPEs control Pi efflux. Non-coding RNAs like *IPS1* and *PILNCR2* contribute to Pi homeostasis. Additionally, epigenetic mechanisms, such as histone modification and DNA methylation, regulate the expression of Pi-responsive genes. PSR, phosphate starvation reponse.

controlled by transcription factors, including MYB coiled-coil (MYB-CC) family members, such as Phosphate Starvation Response 1 (PHR1), PHR1-Like 1 (PHL1), and PHL2, along with other transcription factors from families like WRKY, bHLH, and ARF (Bustos et al., 2010; Paz-Ares et al., 2022; Wang et al., 2023a). PHR transcription factors activate the PSR by binding to PHR1-binding sites (P1BS) in the promoters of Pi starvation-responsive genes, thereby regulating their expression. SPX (named after yeast Syg1 and Pho81 proteins, and mammalian XPR1 protein) domain-containing proteins act as Pi sensors that interact with PHR1 and its homologs to inhibit their transcriptional activity under Pi-sufficient conditions, preventing excessive Pi accumulation and toxicity (Puga et al., 2014; Wang et al., 2014) (Fig. 1). SPX proteins are thought to sense soluble inositol polyphosphates (InsPs) rather than Pi itself (Wild et al., 2016). InsP8 binds to SPX proteins, and the resulting InsP8-SPX complex regulates Pi homeostasis by binding to the CC domain of PHR transcription factors (Dong et al., 2019; Zhu et al., 2019). The biosynthesis of InsP8 is modulated by a bifunctional enzyme named VIP1 homologs (VIHs), which have an N-terminal kinase domain to synthesize InsP8 from InsP7 and a C-terminal phosphatase domain to hydrolyze InsP8 into InsP7 (Zhu et al., 2019). Inositol tris/tetrakisphosphate kinase 1 (ITPK1) also functions as a bifunctional enzyme, which is capable of catalyzing reversible reactions to synthesize and hydrolyze InsP7 according to the cellular Pi level and the following ATP/ADP ratio (Whitfield et al., 2020; Riemer et al., 2021). The amount of InsP7 and InsP8 synthesized in plant tissues is also dependent on Multidrug Resistance-associated Protein 5 (MRP5)-mediated InsP6 compartmentalization (Riemer et al., 2021) (Fig. 1). Under Pi deficiency, InsP8 levels decrease, releasing PHR factors to activate Pi starvation-responsive genes (Ried et al., 2021). In rice, InsP6-SPX1 or InsP6-SPX2 complex interacts with MYB and CC domains of PHR2, disrupting PHR2 dimer formation and its activity (Zhou et al., 2021; Guan et al., 2022). Rice nitrate transporter OsNRT1.1B can interact with and promote the degradation of OsSPX4, which can control the cytoplasmic-nuclear shuttling of both OsPHR2 and OsNLP3, the central transcription factors of Pi and nitrate signaling; thereby, the OsNRT1.1B–OsSPX4 cascade acts as a molecular bridge to integrate nitrogen (N) and P signaling (Hu et al., 2019). Additionally, malate secretion via the Sensitive to Proton Rhizotoxicity 1 (STOP1)-Aluminum-activated Malate Transporter 1 (ALMT1) transcription module, along with Fe oxidation mediated by the Low Phosphate Root 1/2 (LPR1/2)-Phosphate Deficiency Response 2 (PDR2) module, plays an important role in inhibiting primary root growth under LP conditions (Balzergue et al., 2017; Tian et al., 2021). Under Pi deprivation, the upregulation of *ALMT1* increases malate exudation, while LPR1/2 ferroxidase-dependent Fe redox cycling promotes Fe^{3+} aggregation and reactive oxygen species (ROS) generation in root tips. This process further results in callose deposition in the meristem, which adjusts cell-to-cell communication and modulates root growth (Abel, 2017). In addition, blue light-mediated photo-Fenton reaction plays a critical role in the inhibition of Arabidopsis primary root growth under LP by promoting Fe^{3+} to react with malate to produce Fe^{2+} and then generate harmful hydroxyl radicals in the root apoplast (Zheng et al., 2019; Liu, 2021).

Small RNA-mediated post-transcriptional regulation plays a crucial role in fine-tuning the PSR and maintaining Pi homeostasis. The expression of miR399 is induced under Pi deficiency and is positively regulated by PHR1 (Bari et al., 2006). miR399 suppresses its target gene *PHO2*, which encodes a ubiquitin E2 conjugating enzyme, leading to increased levels of PHO1 and PHT1 proteins downstream of PHO2, thereby promoting Pi uptake and translocation (Liu et al., 2012). Additionally, the PHO2–PHO1 pathway is regulated by the Short-Root (SHR)-miR165/166-PHABULOSA (PHB) transcriptional module in Arabidopsis. Under prolonged Pi deficiency, SHR accumulation in roots decreases, enabling PHB-mediated regulation of *PHO2*, which reduces PHO1-mediated Pi transport from roots to shoots (Xiao et al., 2021) (Fig. 1). The miR399-PHO2 regulatory module is conserved across higher plants (Hu et al., 2011; Ouyang et al., 2016). For example, maize (*Zea mays*) miR399 is specifically induced by LP stress and post-transcriptionally represses the expression of *PHO2*, and overexpression of *miR399b* leads to Pi overaccumulation in shoots (Du et al., 2018). Interestingly, maize miR399 also negatively regulates the expression of phosphate transporter genes, such as *ZmPHT1;1*, *ZmPHT1;3*, and *ZmPHT1;13*. Pi modulates this regulation by starvation-induced long non-coding RNA *PILNCR2*, which interacts with *ZmPHTs* to form RNA/RNA dimers, thus disrupting the targeting effect of miR399 on *ZmPHTs* (Wang et al., 2023d) (Fig. 1). But it is still unclear whether miR399 targets *PHT* genes in other plants. Notably, miR399 is negatively regulated by INDETERMINATE1 (ID1) in maize, which is a monocotyledon-specific zinc-finger transcription factor playing an indispensable role in regulating the floral transition; ZmID1 counteracts the inhibitory effect of miR399 on *ZmPHO2* by suppressing the production of miR399, thus contributing to the maintenance of Pi homeostasis (Wang et al., 2023c) (Fig. 1). The expression of miR827 is also induced in response to Pi deficiency, targeting the *Nitrogen Limitation Adaptation (NLA)* gene, which encodes a ubiquitin E3 ligase responsible for the degradation of PHT1 and PHR1, thereby modulating Pi uptake and PSR (Lin et al., 2013; Park et al., 2023) (Fig. 1).

Under Pi deficiency, plants undergo extensive epigenetic reprogramming, including histone modifications and DNA methylation, to regulate the expression of Pi starvation-induced (PSI) genes. Arabidopsis histone acetyltransferase GENERAL CONTROL NON-REPRESSIBLE 5 (GCN5) activates gene expression, including that of long non-coding RNA *At4*, under LP conditions by directly binding to these loci and modulating histone H3 lysine 9 acetylation (H3K9ac) and/or H3K14ac levels (Wang et al., 2019a). The histone variant H2A.Z also plays a crucial role in PSR by modulating the transcription of PSI genes (Smith et al., 2010; Zahraeifard et al., 2018). The Arabidopsis HISTONE DEACETYLASE COMPLEX1 (HDC1), a component of the histone deacetylase complex, regulates H3 acetylation levels in the 5′ untranslated regions of *LPR1* and *LPR2*, thereby inhibiting primary root growth under Pi deficiency (Xu et al., 2020; Li et al., 2022b). Pi starvation induces global DNA methylation remodeling, and Pi-responsive genes such as *SPX2* and *miR827* are activated through demethylation, suggesting that dynamic DNA methylation is a crucial regulatory mechanism in PSR (Secco et al., 2015; Yong-Villalobos et al., 2015). Interestingly, Arabidopsis transcription factors PHR1 and PHL2 play an important role in remodeling chromatin accessibility in response to Pi starvation (Barragán-Rosillo et al., 2021). Therefore, histone modification and DNA methylation constitute an integrated epigenetic network, enabling plants to dynamically regulate PSI genes and adapt to Pi deficiency (Fig. 1). In addition, a recent study indicated that extrachromosomal circular DNAs (eccDNAs) respond to nutrient stresses, including LP. It could function in the PSR by contributing to genome plasticity and potentially regulating the expression of chromosomal genes in rice (Ni et al., 2025).

Plant hormones play critical roles in orchestrating Pi homeostasis and the PSR. Recent studies have revealed the molecular mechanism by which strigolactones (SLs), a class of carotenoid-derived phytohormones, modulate the PSR (Gu et al., 2023; Yuan et al., 2023). In rice grown under Pi deficiency, PHR2 induces the transcription of *NODULATION SIGNALING PATHWAY1 (NSP1)* and *NSP2*, two GRAS family transcription factors that directly bind to the promoters of SL biosynthesis genes, leading to increased SL biosynthesis (Yuan et al., 2023). The enhanced SL levels trigger the degradation of D53 and SPX4 proteins and modulate multiple PSR pathways, including reduced tiller number and increased Pi uptake and translocation (Gu et al., 2023; Yuan et al., 2023). *Sorghum bicolor* strigolactones transporter 1 (SbSLT1) and SbSLT2, members of the ABC transporter G (ABCG) family and induced under LP conditions, facilitate the export of SL from sorghum roots. Knockout mutants of *SbSLT1/2* exhibit reduced SL exudation, conferring resistance to *Striga* parasitism (Shi et al., 2025). Pi homeostasis and PSR are also influenced by other plant hormones, including auxin, cytokinin, ethylene, gibberellins, and abscisic acid (ABA) (Song et al., 2016b; Zhang et al., 2019; Zhang et al., 2022b).

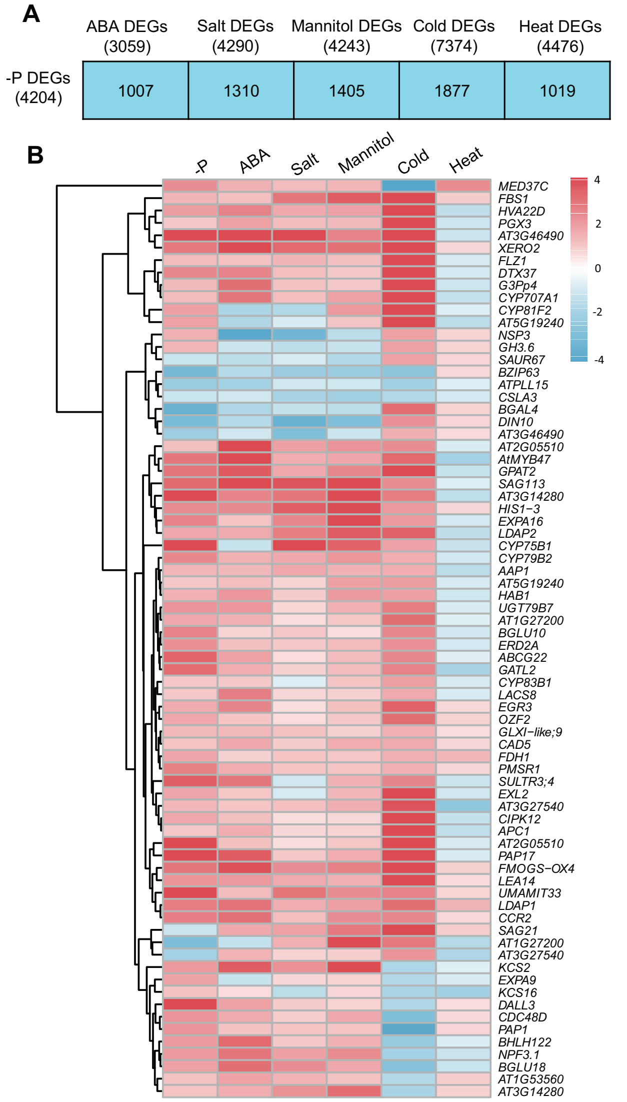
Pi deficiency and abiotic stresses show significant overlap in differentially expressed genes

Transcriptome studies have shown that numerous genes are differentially expressed in response to Pi deficiency (Bustos et al., 2010; Barragán-Rosillo et al., 2021). Functional enrichment analysis indicated that genes associated with osmotic stress response, water deprivation response, and oxidative stress response were significantly enriched among differentially expressed genes (DEGs) in both roots and shoots of Arabidopsis (Chen et al., 2025). Based on these findings, it was hypothesized that there is likely convergence between Pi deficiency and abiotic stresses. The published RNA-sequencing data from *Arabidopsis* subjected to various abiotic stresses were utilized, including salt stress (Gonzalez et al., 2024), mannitol-induced osmotic stress (Gonzalez et al., 2024), cold stress (Lantzouni et al., 2020), heat stress (Huang et al., 2021), and ABA treatment (Song et al., 2016a), an important hormone involved in abiotic stress responses. Meta-analysis indicates that 24%–45% of genes responsive to Pi deficiency in roots and shoots are also affected by salt (31.1%), mannitol (33.4%), cold (44.6%), heat (24.2%), and ABA (24.0%) treatments (Fig. 2A) (Tables S1–S7). At least 72 genes were commonly differentially expressed under Pi deficiency and various abiotic stresses or ABA treatment (Table S7). Most of these DEGs showed similar expression patterns across various stresses, except that the majority showed a reversed pattern under heat stress (Fig. 2B). The substantial overlap between Pi-regulated genes and those responsive to abiotic stresses and ABA suggests a significant crosstalk between Pi nutrition and abiotic stress responses.

Interplay between P nutrition and drought stress

Impact of drought stress on soil Pi availability and Pi acquisition in plants

Soil Pi availability is strongly influenced by drought stress. Reduced soil moisture during drought leads to the conversion of soluble Pi into immobile solid forms, which restricts its mobility in the soil and limits diffusion to the root surface (He and Dijkstra, 2014) (Fig. 3A). The reduction of soil water availability also impairs root function, making it more difficult for plants to access the limited Pi in the soil (Ahanger et al., 2016). This phenomenon is accompanied by a decline in soil microbial activity under drought, which plays a pivotal role in breaking down organic P compounds (Ahanger et al., 2016) (Fig. 3A). Prolonged drought can lower soil pH, accelerate the degradation of calcium phosphate, reduce the proportion of P in calcium phosphate, and increase the binding of inorganic and organic P to aluminum or iron oxides (Fig. 3A). These drought-induced P transformations are likely tied to reduced soil pH, which promotes the release of calcium phosphate (Zhang et al., 2020). During prolonged drought, soil Pi levels decrease sharply, whereas organic P levels increase significantly (O'Connell et al., 2018). In both drought-sensitive species like barley (*Hordeum vulgare*) and maize (*Zea mays*), and drought-tolerant species such as *Andropogon gerardii*, drought stress negatively impacts Pi uptake and reduces P content, possibly by decreasing the abundance of PHT proteins (Bista et al., 2018).



	ABA DEGs (3059)	Salt DEGs (4290)	Mannitol DEGs (4243)	Cold DEGs (7374)	Heat DEGs (4476)
-P DEGs (4204)	1007	1310	1405	1877	1019

Fig. 2. The common genes differentially expressed between Pi deficiency and various abiotic stress treatments. **A**: Transcriptomic data sets representing Pi deficiency-regulated (Bustos et al., 2010), ABA-regulated genes (Song et al., 2016a), salt-regulated genes (Gonzalez et al., 2024), mannitol-regulated genes (Gonzalez et al., 2024), cold-regulated genes (Lantzouni et al., 2020) and heat-regulated genes (Huang et al., 2021) were collected. The common differentially expressed genes (DEGs) between Pi-deficiency DEGs and DEGs under diverse abiotic stress conditions were shown. DEGs were identified based on the criteria of fold change ≥ 1.5, and adjusted P-values (or FDR) ≤ 0.05, as reported in the referenced studies. The number of DEGs for each treatment is shown in parentheses. **B**: A total of 74 common DEGs were identified across all treatments, including Pi deficiency, ABA, and various abiotic stresses. The expression levels of these genes are shown in the heatmap.

Role of P nutrition in drought stress resistance

Pi application enhances drought resilience in crops (Fig. 3A). In wheat under drought stress, a split Pi fertilizer treatment (40% at spring green-up, 30% at jointing, and 30% at grain filling) enhances Pi absorption and utilization, and delays endosperm programmed cell death. It raises grain weight and protein content (Li et al., 2024). Pi application can also enhance the morphological, physiological, and biochemical responses to drought stress in plants like *Alnus*

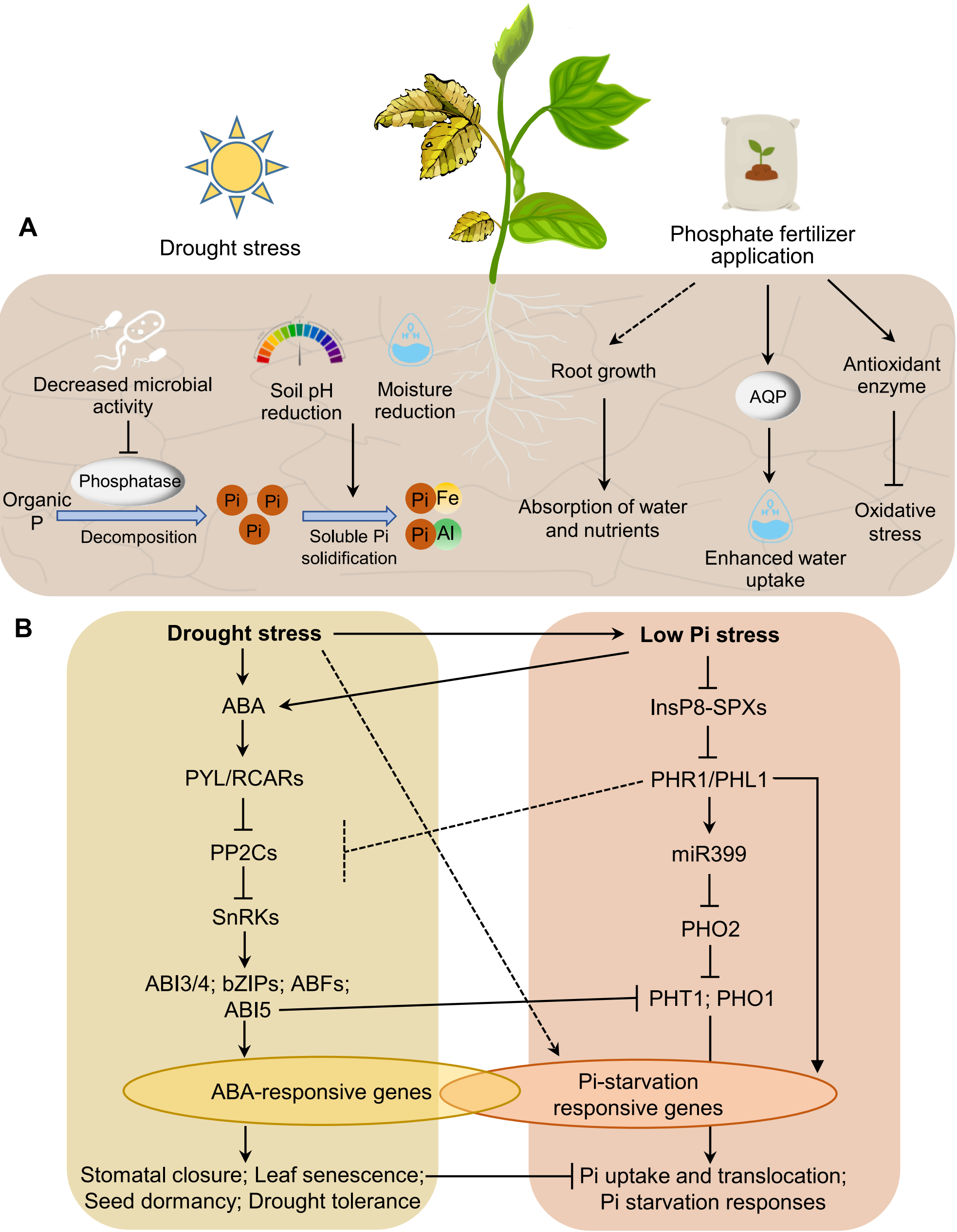


Fig. 3. Interplay between drought stress and P nutrition. **A**: The influence of drought stress on the availability of Pi (inorganic phosphate) in the soil, and the role of Pi fertilizer in enhancing drought stress tolerance by supporting root growth and drought-responsive signaling pathways. **B**: The molecular mechanism underlying the interplay between drought-induced ABA signaling and Pi starvation responses, involving key regulatory proteins and transporters. Arrowheads indicate activation, a line with a 'T' head indicates suppression, and dashed lines suggest hypothetical or indirect regulatory relationships that may require further investigation.

cremastogyne and *Eucalyptus grandis* (Tariq et al., 2018, 2019), promoting root growth and enhancing root capacity for water and nutrient absorption (Razaq et al., 2017). In sheep grass (*Leymus chinensis* L.), LP stress was found to repress root hydraulic conductivity and the expression of aquaporin genes (Li et al., 2020), suggesting that Pi supply may improve water uptake and transport in roots. Similarly, in soybean (*Glycine max*), Pi application promotes root growth and significantly increases both root and shoot dry weight under drought conditions, indicating that Pi plays a crucial role in mitigating the negative effects of drought stress on plant growth (Siregar et al., 2021). Root growth is usually inhibited by Pi starvation in plants like Arabidopsis, although in certain cases, root growth can be promoted by Pi starvation in plants like rice (Péret et al., 2014; Liu, 2021). Plants grown in soil with low water levels typically develop an extended taproot that can reach deeper soil layers, as water is generally more abundant in these regions. By contrast, a shallow root system is better suited for scavenging Pi in the topsoil, because soil Pi content is usually higher in the upper layers and decreases with soil depth (Lynch, 2019; Liu, 2021). Low soil Pi availability usually reduces the gravitropic response of basal roots of plants like legumes and results in the generation of a shallow root system (Liu, 2021). The shallow root system can repress water capture in the deeper soil. Therefore, Pi application could promote plant growth by relieving the root growth inhibition induced by Pi deficiency, and may modify the root system architecture to facilitate water capture. It is also worth investigating whether the effect of Pi application in the subsoil on drought stress resilience outperforms that of Pi application in the topsoil. In addition, Pi application alleviates drought stress by modulating the biosynthesis of hormones, such as ABA and indoleacetic acid (IAA) (Begum et al., 2020; Bechtaoui et al., 2021), and reducing ROS production by modulating antioxidant enzyme activities, ROS metabolism, and redox homeostasis (Begum et al., 2020) (Fig. 3A). For example, in rice, Pi supplementation significantly alleviates drought-induced oxidative stress by enhancing the activity of antioxidant defense systems, such as catalase (CAT), superoxide dismutase (SOD), and ascorbate peroxidase, thereby reducing ROS accumulation (Barbhuiya et al., 2023). Pi fertilizer application during drought stress lowers superoxide anion (O^{2-}) and malondialdehyde levels, markers of oxidative stress, thus indicating that Pi mitigates ROS damage in plants like *A. cremastogyne* and *E. grandis* (Tariq et al., 2018, 2019). Moreover, Pi supply treatment in wheat seedlings enhances drought stress tolerance by increasing antioxidant enzyme activity, improving sugar metabolism related to osmotic stress, and promoting organic acid accumulation to maintain intracellular ion homeostasis (Li et al., 2022a).

Molecular mechanism underlying the interplay between P nutrition and drought stress

Recent study shows that moderate drought stress lowers plant Pi levels and activates the PSR in plants such as Arabidopsis, soybean, and maize. Interestingly, the PSR is activated before the ABA-mediated response under mild drought stress (Nagatoshi et al., 2023; Tian et al., 2024). Mannitol treatment, which induces osmotic stress, significantly alters the expression of certain Pi starvation-responsive genes in Arabidopsis, including members of the *PHT1* subfamily such as *PHT1;4* and *PHT1;8* (Fig. 2; Table S4). Plant PHT1 subfamily proteins, which belong to the Pi/H^+ symporter family, localize to the plasma membrane. Most members of this subfamily are predominantly expressed in roots and are induced by LP stress (Gu et al., 2016). Several *PHT1* subfamily genes were also found to be induced by moderate and severe water stress in leaves and roots of *Lycium barbarum* (Hu et al., 2017). In *Populus trichocarpa*, the expression of *PtPHT1.2* increases remarkably under drought conditions (Zhang et al., 2016). In apples (*Malus domestica*), *MdPHT1;5* and *MdPHT1;7* were found to be remarkably increased in roots under the treatment of polyethylene glycol (PEG, osmotic stress) (Sun et al., 2017). Overexpression of *MdPHT1;7* has been shown to play an important role in enhancing Pi uptake and improving resistance to LP and drought stress in plants (Sun et al., 2021). Among the 49 *PHT1* subfamily genes in rapeseed (*Brassica napus*), 18 genes were found to be up-regulated in leaves, while 11 genes were down-regulated in roots under PEG treatment (Li et al., 2019), suggesting that *PHT* genes have differential responses to drought in different tissues. In addition to *PHT1* subfamily, other PHT subfamily genes may also respond to drought. For example, soybean GmPHT4;10, which belongs to PHT4 subfamily of phosphate transporters and is localized in the chloroplast, was found to be induced by drought in leaves and to participate in drought stress response. Overexpression of *GmPHT4;10* improves photosynthesis and drought resistance by increasing the accumulation of Pi in chloroplasts and catalase activity (Liu et al., 2023). The expression of *PHT* genes in response to drought or osmotic stress can vary depending on several factors, including growth conditions (soil vs. hydroponic), the Pi level in the growth medium, the type of treatment (drought, PEG, or mannitol), duration of treatment, specific plant tissues, and the drought sensitive or tolerance of the plant species. Different responses of various *PHT* genes suggest that plants deploy strategies to manage Pi acquisition, translocation, and remobilization under varying degrees of water and LP stresses. Notably, the promoter regions of *PHT* genes usually contain drought-responsive regulatory elements, such as the MYB-binding sequence (T/CAACTG) for drought induction, the dehydration-responsive element (DRE, TGGCCGAC), and the ABA-responsive element (ABRE, ACGTG) (Liu et al., 2011; Li et al., 2019). Further studies are required to reveal the molecular mechanisms underlying the drought-responsiveness of *PHT* genes and identify the upstream regulators.

In Arabidopsis, drought-responsive genes, such as *DRIR* (long non-coding RNA), *AT12CYS-2*, and *PYL10*, are also activated by LP, likely through PHR1 and PHL1 regulation (Scheible et al., 2023). Proline accumulation is an adaptive response to osmotic stress, with *Delta-1-Pyrroline-5-Carboxylate Synthase 1* (*P5CS1*) expression induced by drought and ABA (Szekely et al., 2008). Notably, PHR1 positively regulates *P5CS1* (Aleksza et al., 2017), linking Pi nutrition with osmotic stress response (Table 1). Maize ZmPHR1 was found to serve as a central regulator of PSR by activating genes involved in Pi acquisition, signaling, and redistribution, which are crucial under both Pi-deficient and drought conditions (Tian et al., 2024). ZmPHR1-regulated PSR genes are significantly upregulated under drought stress, and overexpression of *ZmPHR1* enhances drought resistance by reducing stomatal aperture and delaying water loss (Tian et al., 2024). Several other transcription factors and transporters have also been known to function in both LP and drought stress responses. PalERF2, an ERF transcription factor from *Populus alba* var. pyramidalis, positively regulates responses to both LP and drought stresses by modulating the expression of PSI and drought-responsive genes (Chen et al., 2022a). Arabidopsis type I proton-pumping pyrophosphatase (AVP1), an inorganic pyrophosphatase (H^+-PPase) located on the tonoplast, enhances plant resilience to LP and drought conditions (Schilling et al., 2017) (Table 1). Overexpression of *AVP1* increases Pi absorption by expanding the root absorption area and acidifying the rhizosphere (Yang et al., 2007; Pei et al., 2012; Pizzio et al., 2015). In genetically modified tomato plants, increased *AVP1* expression enhances Pi transport from leaves to fruits under LP conditions, improving fruit development and yield (Yang et al., 2014). Overexpression of *AVP1* has conferred drought tolerance in Arabidopsis, tobacco, and cotton (*Gossypium hirsutum*) (Gaxiola et al., 2001; Pasapula et al., 2011; Manzoor et al., 2022).

ABA plays a critical role in regulating plant responses to abiotic stresses, including drought, by modulating key physiological processes such as stomatal closure and root development (Liu et al., 2024). In the core ABA signaling pathway, ABA binds to its receptors, PYR/PYL/RCARs, which then interact with and inhibit type 2C protein phosphatases (PP2Cs). This inhibition prevents the dephosphorylation of SNF1-RELATED PROTEIN KINASE 2s (SnRK2s), thereby sustaining SnRK2 activity (Chen et al., 2020). Subsequently, the activated SnRK2s phosphorylate downstream target proteins, including ABSCISIC ACID INSENSITIVE 3 (ABI3), ABI4, ABI5, and transcription factors from the ABRE-BINDING FACTOR (ABF), AP2/ERF, or bZIP families. This phosphorylation mediates ABA signaling to regulate guard cell turgor as well as seed maturation and dormancy (Chen et al., 2020) (Fig. 3B). Recent studies suggest that Pi availability significantly influences ABA signaling pathways, which in turn regulate drought stress response and tolerance (Fig. 3B). Pi deficiency typically increases ABA accumulation in plants (Jaschke et al., 1997; Castro-Valdecantos et al., 2023), which may enhance water and Pi use efficiency by promoting stomatal closure and reducing transpiration under drought stress (Khan et al., 2023). ABI5, a key regulator in ABA signaling, was found to regulate Pi uptake by regulating the expression of PSI genes like *PHT1;5* (Lei et al., 2022; Zhang et al., 2022b) (Fig. 3B). Interestingly, Arabidopsis PHR1 and PHL1 play a negative role in ABA-mediated inhibition of seed germination and stomatal opening, as well as in drought stress tolerance, by potentially regulating the expression of a group of genes associated with ABA signaling, including the PP2C

Table 1
Roles of P nutrition-related genes in abiotic stress responses in plants.

Plant species	Gene name (Gene ID)	Protein annotation	Stress-related function	References
Arabidopsis thaliana	*AtPHR1* (At4g28610)	MYB-CC transcription factor	Proline accumulation	Aleksza et al. (2017)
			Arsenic stress	Navarro et al. (2021)
			Hypoxia stress	Klecker et al. (2014)
			Strong light stress	Nilsson et al. (2012)
			ABA response	Chen et al. (2025)
	AtPHL1 (At5g29000)	MYB-CC transcription factor	Proline accumulation	Aleksza et al. (2017)
	AtPHT1;1 (At5g43350)	Phosphate transporter	Arsenic stress	Castrillo et al. (2013)
	AtPHT4;6 (At5g44370)	Phosphate transporter	Salt stress	Cubero et al. (2009)
	AtPHO1 (At3g23430)	Phosphate transporter	ABA signaling	Zimmerli et al., (2012); Huang et al., (2017)
			Cold acclimatization	Hurry et al. (2000)
	AtPHO2 (At2g33770)	E2 ubiquitin-conjugating enzyme	Salt stress	Miura et al. (2011)
			Cold acclimatization	Hurry et al. (2000)
	AtMYB2 (At2g47190)	MYB-CC transcription factor	Salt/ABA/LP stress	Abe et al., (1997); Baek et al., (2013)
	AtmiR399f (At2g34208)	Non-coding RNA	Salt/drought/ABA stress	Baek et al. (2016)
	AtSPX1 (At5g20150)	SPX protein	Cold stress	Zhao et al. (2009)
	AtWRKY6 (At1g62300)	WRKY transcription factor	Arsenic stress	Castrillo et al. (2013)
	AtZAT6 (At5g04340)	C2H2-type zinc-finger transcription factors	Salt stress	Liu et al. (2013)
	AtMPT2 (At3g48850)	Mitochondrial phosphate transporter	Salt stress	Zhu et al. (2012)
	AtAVP1 (At1g15690)	Vacuolar H^+-pyrophosphatase	Low P stress	Yang et al. (2007); Pei et al., (2012); Pizzio et al., (2015)
			Drought stress	Gaxiola et al., (2001); Pasapula et al. (2011); Manzoor et al., (2022)
			Salt stress	Gaxiola et al., (2001); Kim et al., (2014); Schilling et al., (2014)
Hordeum vulgare	*HvPHO1* (KF195562)	Phosphate transporter	Heat stress	Pacak et al. (2016)
	HvPHO2 (KF147849)	E2 ubiquitin-conjugating enzyme	Heat stress	Pacak et al. (2016)
Oryza sativa	*OsSPX1* (Os06g40120)	SPX protein	Cold stress	Wang et al. (2013)
	OsPHR2 (Os07g25710)	MYB-CC transcription factor	UV stress	Ren et al. (2024)
	OsPHL7 (Os06g0609500)	MYB-CC transcription factor	Salt stress	Yang et al. (2024b)
	OsMPT3;1 (Os04g0448800)	Mitochondrial phosphate transporter	Salt stress	Huang et al. (2020)
	OsMPT3;2 (Os06g0210500)	Mitochondrial phosphate transporter	Salt stress	Huang et al. (2020)
Populus alba	*PtPHT1.2* (Potri.005g223600)	Phosphate transporter	Drought stress	Zhang et al. (2016)
	PalERF2 (PAYT003289)	ERF transcription factor	LP and drought	Chen et al. (2022a)
Solanum tuberosum	*StPHT1;7* (PGSC0003DMG400017226)	Phosphate transporter	Drought stress	Cao et al. (2020)
Malus domestica	*MdPHT1;7* (MDP0000261121)	Phosphate transporter	Drought stress	Sun et al. (2021)
Eutrema salsugineum	*EsPHT1;9* (Thhalv10018375m)	Phosphate transporter	Salt stress	Lv et al. (2021)
	EsPHT1;5 (Thhalv10016483m)	Phosphate transporter	Salt stress	Wang et al. (2024)
Glycine max	*GmPHT4;10* (Glyma.17g108300)	Chloroplast phosphate transporter	Drought	Liu et al. (2023)
	GmPHO1;H8 (Glyma_20g206900)	Phosphate transporter	Salt stress	Wang et al. (2019c)
Zea mays	*ZmPHR1* (Zm00001d029020)	MYB-CC transcription factor	Drought stress	Tian et al. (2024)
	ZmPHR2 (Zm00001d019536)	MYB-CC transcription factor	Drought stress	Tian et al. (2024)
Pteris vittata	*PvPht1;3* (KM192137)	Phosphate transporter	Arsenic stress	Cao et al. (2019)
	PvPht2;1 (MT043283)	Phosphate transporter	Arsenic stress	Feng et al. (2021)

gene *HAI1* (Chen et al., 2025) (Fig. 3B). ABA may also play an important role in plant resistance to combined Pi deficiency and drought stress by modulating water retention and Pi uptake (Chen et al., 2025). Thus, on one hand, Pi deficiency increases ABA biosynthesis by the mechanisms that are still unclear (Fig. 3B). On the other hand, ABA signaling is suppressed by PHR1 and PHL1. Elevated ABA concentrations could trigger enhanced stomatal closure and decelerate the growth rate, thereby facilitating Pi retention under Pi limitation (Fig. 3B). However, it may also hinder Pi uptake and transport, because reduced stomatal opening may decrease transpiration and the uptake of nutrients including Pi (Fig. 3B). It has also been revealed that genes associated with Pi uptake and transport, including *PHO1*, *PHO1;H1*, and *PHT1;1*, are suppressed by ABA through an ABI1-dependent pathway (Ribot et al., 2008). Under LP stress, activated PHR1 and PHL1 may suppress ABA signaling to maintain optimal ABA levels, thereby enhancing Pi acquisition and potentially delaying ABA-induced leaf senescence (Fig. 3B). In addition, ABA-mediated stomatal closure has been found to interact with Pi nutrition through PHO1, a key transporter involved in root-to-shoot translocation of Pi in Arabidopsis (Zimmerli et al., 2012). PHO1 is also involved in ABA-mediated seed germination and early seedling development through transcriptional regulation by ABI5 (Huang et al., 2017) (Fig. 3B). However, the role of *PHO1* in drought resistance remains to be fully elucidated.

Interplay between P nutrition and salt stress

Effect of salinity on Pi availability and Pi homeostasis

High salt concentrations in the soil reduce the solubility of P compounds, decreasing their availability to plants (Khan et al., 2023). High salinity disrupts the uptake of essential mineral nutrients, including Pi, by plant roots, leading to nutrient imbalances (Parihar et al., 2015). High salinity decreases Pi availability in soils, with over 75% of soil Pi reacting with Ca^{2+}, Mg^{2+}, and other ions to form insoluble compounds (Xie et al., 2022). Salt stress inhibits Pi uptake in various plants, including lupine (*Lupinus luteus*) and cotton, thereby reducing overall nutrient absorption efficiency under saline conditions (Treeby and van Steveninck, 1988; Martinez and Läuchli,

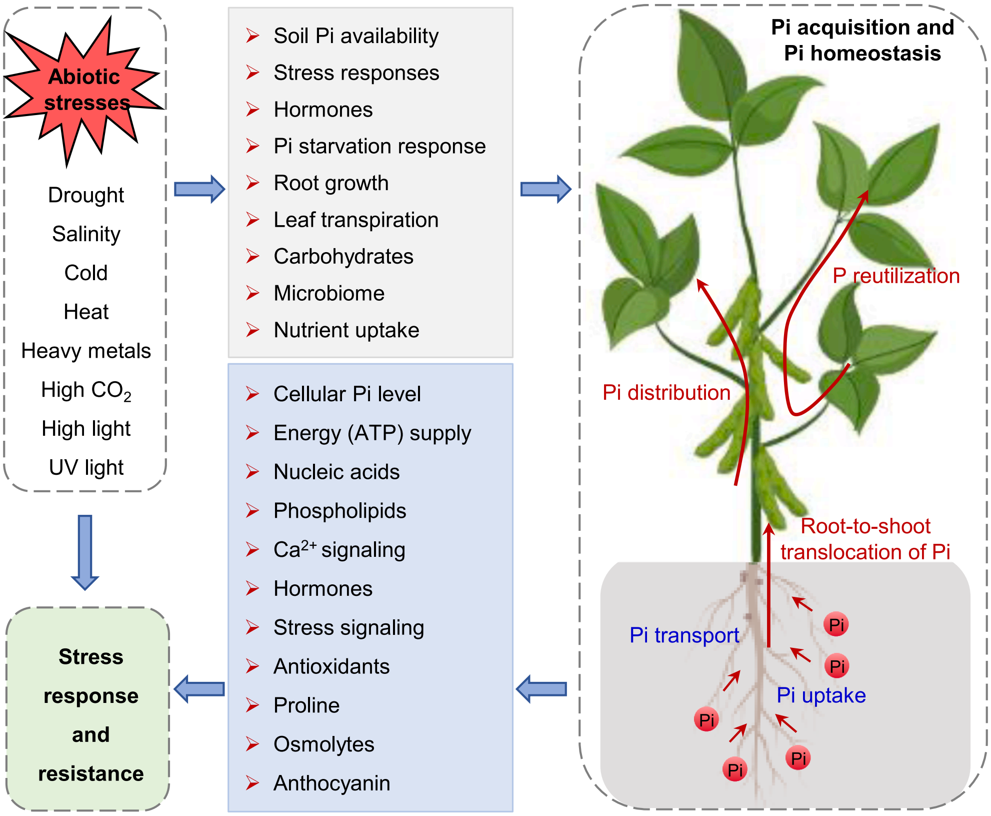


Fig. 4. Interaction between P nutrition and abiotic stress responses. Soil Pi availability, root Pi uptake, root-to-shoot Pi translocation, and Pi distribution and redistribution within plant tissues are all influenced by various abiotic stresses, including drought, salinity, heavy metals, heat, and high light. These abiotic stress responses are closely interconnected with Pi acquisition and homeostasis, with alterations in Pi transporters, signaling pathways, and Pi remobilization mechanisms playing key roles in stress adaptation.

1994). Salt stress can impair root growth, thereby further limiting the plant's ability to acquire Pi from the soil (Fig. 4). Furthermore, the impact of salt stress on phosphate transporters is linked to decreased Pi absorption (Talbi Zribi et al., 2015). Salt cress (*Eutrema salsugineum*) exhibits remarkable adaptability to both salinity and Pi limitation by expanding and differentially regulating *PHT* genes (Lv et al., 2021). Most *PHT1* genes are up-regulated in salt cress under salinity (Lv et al., 2021). Overexpression of *EsPHT1;9* was found to enhance plant tolerance to LP and salinity (Lv et al., 2021). EsPHT1;5 was found to be involved in plant response to salinity, possibly by mediating Pi mobilization from rosettes to siliques under salt stress (Wang et al., 2024). EsANT (AINTEGUMENTA), a transcription factor containing two AP2 domains and belonging to the AP2 subfamily, was shown to repress the expression of *EsPHT1;5* and negatively regulate LP and salinity tolerance in salt cress (Wang et al., 2024). Salt stress also influences the expression of *PHT* genes in other plants. For instance, 24 of the 49 *PHT1* family genes in leaves and 19 in roots respond to salt stress in rapeseed (Li et al., 2019). These results suggest that salt stress has an impact on Pi homeostasis and the roles of PHTs in the salt stress response. However, the molecular mechanism underlying the transcriptional responses of *PHT* genes to salt stress and their functions in the salt stress response remains to be determined.

Role of P nutrition in enhancing salt stress resistance

Increasing Pi supply enhances P and N uptake, promoting proline accumulation in sorghum under salt stress (Belouchrani et al., 2019). Additionally, Pi supplementation increases root length and surface area in tomatoes (Loudari et al., 2020) and improves growth and productivity in wheat under salt stress (Loudari et al., 2022). Increased Pi fertilizer supply also promotes the uptake of essential nutrients in salt-stressed plants, such as quinoa (*Chenopodium quinoa* Willd.) (Bouras et al., 2022). High-P conditions can enhance salt stress tolerance by improving the Na$^+$/K$^+$ balance, boosting antioxidant enzyme activities, and preserving cell membrane integrity in plants like *Robinia pseudoacacia* (Gan et al., 2025). Salt stress tolerance depends on the effective efflux of Na$^+$, which is mediated by Na$^+$/H$^+$ antiporter, and the maintenance of K$^+$ homeostasis, relying on energy from H$^+$-ATPase activity (Assaha et al., 2017). However, Pi availability appears to have a limited effect on salt excretion in the facultative halophyte *Aeluropus littoralis* (Talbi Zribi et al., 2015), indicating that the impact of Pi on salt tolerance may vary by plant species and salt concentration.

Ca^{2+}, a second messenger in plant cells, participates in signal transduction processes in response to various stresses (Zeng et al., 2023). Under abiotic stresses, the interplay of Ca^{2+} influx and efflux triggers fluctuations in cytoplasmic free Ca^{2+} concentration ($[Ca^{2+}]_{cyt}$) (Dong et al., 2022). Pi availability can modulate $[Ca^{2+}]_{cyt}$ response under salt and osmotic stress (Matthus et al., 2019) (Fig. 4). For instance, salt stress induces rapid $[Ca^{2+}]_{cyt}$ elevation, but Pi deficiency may inhibit these fluctuations, potentially impacting the Ca^{2+}-dependent salt overly sensitive (SOS) signaling pathway. Further studies are warranted to elucidate how P nutrition regulates Ca^{2+}-mediated salt stress signaling.

Molecular studies suggest a mechanism linking P nutrition and salt stress responses. In Arabidopsis*,* the transcription factor MYB2, known for regulating salt and drought responses (Abe et al., 1997), also promotes Pi homeostasis by upregulating *miR399f* (Baek et al., 2013). Loss of functional mutation of *PHO2,* a key Pi homeostasis regulator, leads to Pi accumulation, reduced Na^+ uptake, and improved salt tolerance (Miura et al., 2011). The vacuolar H^+-pyrophosphatase AVP1 is critical for both Pi deficiency and salt stress. Overexpression of *AVP1* can enhance biomass under saline conditions by promoting the sequestration of Na^+ into vacuoles via Na^+/H^+ antiporters (Gaxiola et al., 2001; Kim et al., 2014; Schilling et al., 2014). The C2H2 zinc finger transcription factor ZAT6 influences Pi-responsive root architecture and enhances salt tolerance during seed germination (Devaiah et al., 2007; Liu et al., 2013), though its role in PSR remains unclear. Phosphate transporters also contribute to salt adaptation. For instance, a Na^+-dependent high-affinity Pi uptake system in *Zostera marina* suggests a synergy between Na^+ and Pi transport (Rubio et al., 2005). In Arabidopsis, the Golgi-localized PHT4;6 supports salt tolerance by recycling Pi from glycosylation, thereby affecting protein glycosylation and cell wall biosynthesis. The *pht4;6* mutants exhibit root swelling and growth cessation under salt stress (Cubero et al., 2009) (Table 1). Functional analyses of knockout mutants of two mitochondrial phosphate transporters, OsMPT3;1 and OsMPT3;2, suggested that they play positive roles in salt stress resistance, possibly by modulating Pi transport and ATP synthesis in the mitochondrial matrix and triggering changes in the accumulation of ions and metabolites associated with salt stress response (Huang et al., 2020). Similarly, overexpression of the soybean *GmPHO1;H8*, a homolog of *PHO1*, increases salt stress tolerance in Arabidopsis (Wang et al., 2019c), though its link to Pi nutrition remains unclear.

Current studies have primarily examined the effects of either high salinity or LP alone on plant growth and nutrient absorption, whereas the effects and underlying mechanisms of combined salt and LP stresses are still elusive. It has been shown that the impact of salt stress and LP stress on plant growth is not additive, and the response of plants to the combined salinity and Pi deficiency is similar to that of plants grown under salinity alone (Talbi Zribi et al., 2015; Tang et al., 2019). In maize, Pi deficiency under salt stress increases osmolytes such as proline and soluble sugars, while decreasing Na^+ accumulation (Tang et al., 2019). Pi deficiency may also alleviate the inhibitory effect of mild salt stress on root growth (Kawa et al., 2016). Under combined salt stress and Pi deficiency stresses, phytohormones (such as auxin and ABA), and ROS are integrated into signaling pathways to regulate both the initiation and elongation of root hairs (Ibeas et al., 2024). In addition, inoculation of some plant growth-promoting bacteria that are both salt-tolerant and phosphate-solubilizing can enhance salinity stress tolerance and P-deficiency recovery in plants through mechanisms that avoid elevating cellular Na^+ accumulation. For example, inoculation of *Bacillus licheniformis* QA1 and *Enterobacter asburiae* QF11 can alleviate high salinity stress in *Chenopodium quinoa* by increasing Pi and K^+ uptake and reducing Na^+ uptake (Mahdi et al., 2020). Similarly, *Bacillus altitudinis* WR10 can increase wheat productivity under combined salinity and Pi deficiency stresses by restricting Na^+ uptake and enhancing available Pi through the production of phosphatases and phytases (Yue et al., 2019). Further investigation into the underlying interactions between P nutrition and salt tolerance mechanisms is necessary to comprehend the complexity of Pi's role in salt stress resilience.

Interplay between P nutrition and temperature stress

Global warming significantly alters soil temperatures, affecting the availability of essential nutrients such as P and N (Tian et al., 2023). In temperate forest soil, long-term warming can reduce bioavailable P through substantial losses of total soil P, increased Pi sorption, and the accumulation of recalcitrant P fractions (Tian et al., 2023). Soil temperature has been suggested to play a crucial role in regulating phosphatase activity, which is responsible for releasing Pi from organic compounds in the soil (Margalef et al., 2021). Rising temperatures have been shown to affect the efficiency of soil phosphatase enzymes, with warmer conditions generally increasing their activity (Margalef et al., 2021). However, extreme heat can also induce oxidative stress in soil microorganisms, potentially reducing the overall activity of these critical enzymes (Margalef et al., 2021) (Fig. 4). Rising temperatures can also hinder plants' ability to absorb and utilize essential nutrients, including Pi (Fahad et al., 2017). It has been reported that high-temperature stress reduces N, P, potassium (K), and proline levels in tomato leaves (Guo et al., 2022b) and significantly impairs the transport efficiency of N, P, and K in rice (Liu et al., 2018). It has been known that plants respond to high ambient temperature with a developmental program termed thermomorphogenesis. Root thermomorphogenesis has recently been found to be conserved across angiosperms such as Arabidopsis, rice, and soybean. It is regulated by the availability of N and P, with thermomorphogenesis responses linked to decreased levels of these nutrients. A key regulatory module involving ELONGATED HYPOCOTYL 5 (HY5) and the nitrate transceptor NITRATE TRANSPORTER 1.1 (NRT1.1) plays a central role in this process (Lee et al., 2024). High temperature stress may also alter Pi homeostasis by affecting the expression of Pi-responsive genes (Pacak et al., 2016). In barley, high-temperature exposure led to the reduced expression of root-specific Pi transporters *PHT1;1*, *PHT1;4*, and *PHT1;6*, along with lower *PHO1* expression, which possibly mediates Pi translocation from roots to shoots. Despite this, root Pi levels remained stable, likely due to reduced Pi translocation from roots to shoots caused by the downregulation of *PHO1*, which may compensate for the decreased Pi uptake by roots (Pacak et al., 2016). The application of Pi fertilizer can enhance photosynthesis, water use efficiency, and grain yield in rice when subjected to high temperatures (Fahad et al., 2016). Furthermore, applying Pi fertilizer to soils can enhance heat resistance by promoting the synthesis of lipids and proteins while diminishing lipid oxidation in maize (Zhang et al., 2022a). Therefore, Pi supplementation can alleviate plant damage caused by high-temperature stress and enhance resilience to such conditions (Fig. 4).

Low-temperature stress, a major constraint on plant growth and crop yield, can be categorized into cold (0°C–15°C) and freezing stress (below 0°C) (Ding et al., 2019). Low temperatures cause soil freezing and thawing, leading to Pi movement with soil moisture and subsequent Pi loss, thereby reducing the available Pi content in the soil (Zhao et al., 2021). Some Pi starvation-responsive genes, including *AtSPX1* and six *OsSPX* genes, were found to be induced by cold stress in plants. Interestingly, the low-temperature response element is found in promoter regions of many Pi starvation-responsive genes, indicating that these genes may be co-regulated by both low temperature and Pi starvation (Baek et al., 2017). Pi fertilizer is widely used to enhance plants' ability to withstand low-temperature stress (Noor et al., 2022). Pi fertilizer enhances plasma membrane permeability and increases antioxidant enzyme activities, including SOD, peroxidase (POD), and CAT, thus improving cold tolerance in rice and other plants (Ihtisham et al., 2023). Cold-tolerant chickpea varieties, for example, are better able to maintain Pi homeostasis under low-temperature stress, thereby supporting flower and pod development (Mehra et al., 2018). However, studies also indicate that LP promotes cold acclimatization by comparing the responses of *pho1* mutant with decreased leaf Pi level and *pho2* mutant with increased leaf Pi level in Arabidopsis (Hurry et al., 2000). The *pho1* mutant is more sensitive to freezing stress than wild-type by measuring the electrolyte leakage, but its cold acclimatization is improved (Hurry et al., 2000). The activity and protein levels of sucrose phosphate synthase and cytoplasmic fructose-1,6-

bisphosphatase are promoted in *pho1* but attenuated in *pho2*, suggesting a linkage between Pi and cold acclimatization that is associated with photosynthetic carbon metabolism (Hurry et al., 2000). Overexpression of *OsSPX1,* a negative regulator of Pi homeostasis in rice, enhances cold stress tolerance in Arabidopsis and tobacco, accompanied by reduced leaf total P content (Zhao et al., 2009). By contrast, silencing of *OsSPX1* increases the sensitivity of rice seedlings to cold and oxidative stresses, which may be caused by the down-regulation of some oxidative stress-related genes and an increase in H_2O_2 accumulation (Wang et al., 2013). The mechanism underlying how *OsSPX1* promotes cold stress resistance still needs to be revealed. It has been reported that knockdown of *OsSPX1* results in excessive Pi accumulation and Pi toxicity in rice seedling leaves (Wang et al., 2009). However, whether and how the cold stress sensitivity of *OsSPX1*-silencing plants is linked to Pi toxicity is still unclear. Severe Pi deficiency can lead to alterations in the photosynthetic apparatus and reductions in CO_2 assimilation rates, and cause potential photo-oxidative stress (Hernández and Munné-Bosch, 2015), while excessive Pi accumulation or Pi toxicity could also induce oxidative stress. Therefore, maintaining cellular Pi at a moderate level is critical for plant resistance to cold and other stresses.

Interplay between P nutrition and metal ion stress

Effects of metal ion stresses on Pi homeostasis

Excessive metal ions in soils adversely affect plant growth, development, and metabolism. Arsenic (As), cadmium (Cd), manganese (Mn), and lead (Pb) are among the metals that disrupt plant Pi

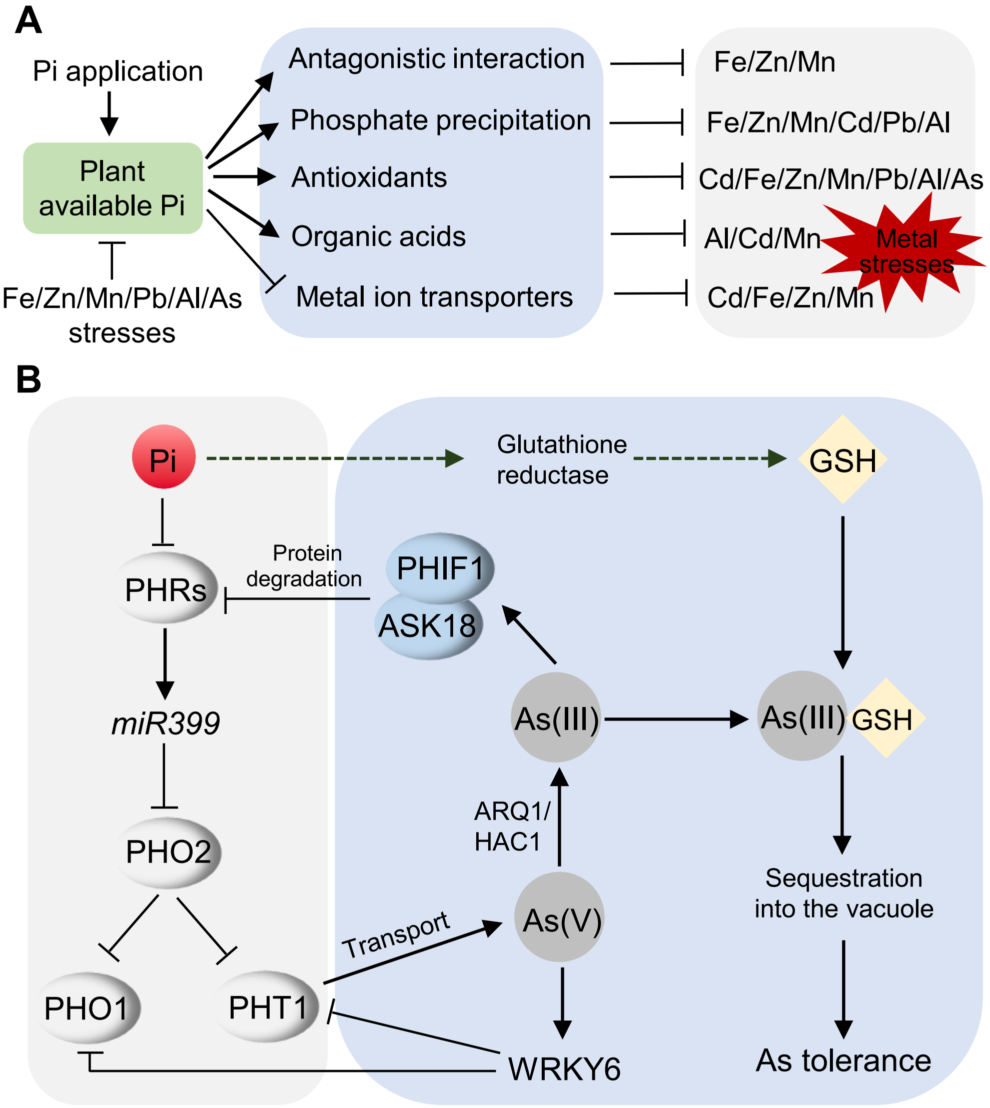


Fig. 5. Schematic illustration of Pi-mediated metal ion stress tolerance mechanisms in plants. **A**: Plant-available Pi mediates several defense mechanisms against metal ion stresses, including those induced by Fe, Zn, Pb, Al, and As. These mechanisms include antagonistic interactions that reduce metal ion uptake, phosphate precipitation to form metal-phosphate complexes, activation of antioxidant systems, biosynthesis of organic acids, and regulation of metal ion transporters, all contributing to enhanced metal ion stress tolerance. **B**: The molecular pathway illustrating Pi–As interactions reveals a complex regulatory network through which Pi influences As tolerance. Pi availability modulates metal ion responses by affecting PHR activity and the expression of downstream Pi-responsive genes. Under As(V) stress, PHR degradation is induced through an As(III)-triggered pathway involving ASK18 and PHIF1. This process limits PHT1 expression and As(V) uptake. Arsenate (As(V)) is reduced to arsenite (As(III)) by ARQ1 and HAC1, after which As(III) is detoxified by conjugation with glutathione (GSH) and sequestration into vacuoles. WRKY6 plays a critical role in transcriptionally repressing *PHT1;1*, thereby reducing As(V) uptake. Additionally, Pi promotes GSH biosynthesis, further enhancing the detoxification of As(III). Arrowheads indicate activation, a line with a ‘T’ head indicates suppression, and dashed lines suggest hypothetical or indirect regulation.

homeostasis. Arsenic primarily exists in two forms: arsenate (As(V)) and arsenite (As(III)), both of which impair plant metabolic processes. As(V), a carcinogenic substance, enters plant cells and can convert to the more toxic As(III). Since As(V) resembles Pi, it can enter the cell through PHT1 transporters and substitute phosphate in ATP phosphorylation, disrupting metabolism (Awasthi et al., 2017; Cao et al., 2019) (Fig. 5). As(III), predominantly formed in anaerobic conditions, is more toxic and enters via Nod-26-like aquaporin, binding to protein sulfhydryl groups and disrupting protein functions (Bienert et al., 2008). Exposure to As(V) has been shown to increase susceptibility to Pi deprivation in Arabidopsis (Shukla et al., 2015).

Elevated Cd levels induce toxicity in plants, causing leaf curling, chlorosis, stunted root growth, and reduction in photosynthetic pigment content (Rizwan et al., 2019). In *Aeluropus littoralis*, P levels increase under Cd stress (Rezvani et al., 2012). In rice, Cd exposure also increases P levels in shoots, possibly by activating Pi-responsive genes such as *OsIPS1*, *OsPT6*, and *OsPT10* (Wang et al., 2019b). However, Cd exposure does not affect P levels in some plants such as carrots and lettuce (Yang et al., 2016). These studies suggest that the effect of Cd on P nutrition varies among plant species, but the underlying mechanisms remain to be investigated.

Excessive Pb disrupts plasma membrane permeability, binds to enzyme active sites, interacts with the phosphate groups of ADP and ATP, and displaces essential nutrient ions, causing toxicity (Pourrut et al., 2011). Increased soil Pb significantly decreases shoot P concentration in plants like tomato (Cheyns et al., 2012). Pb accumulation in cabbage tissues is proportional to supplied Pb levels, but P concentration demonstrates the reverse trend with Pb concentration (Sinha et al., 2006). Similarly, in rice, Pb exposure restricts P accumulation in shoots likely due to the complexation and precipitation of Pb with Pi, which limits Pi transport from roots to shoots (Khan et al., 2018; Yang et al., 2021).

Role of P nutrition in metal ion stress resistance

Pi availability in the growth medium directly affects plant resistance to metal ion stress (Wang et al., 2023b). Adequate P nutrition can counteract the negative effects of metal ions by regulating plant metabolism and chemically interacting with metal ions in soils or within plants, thereby decreasing their bioavailability (Bechtaoui et al., 2021). Studies have shown that Pi application can inhibit the uptake of both As(V) and As(III) by plants (Huang et al., 2007). In plants, As(V) is reduced to As(III) by the enzyme arsenate reductase QTL1 (ARQ1)/High Arsenic Content 1 (HAC1), after which As(III) can form a complex with glutathione (GSH) and be sequestered into the vacuole, thereby reducing cytoplasmic As toxicity (Bali and Sidhu, 2021). High Pi levels may increase glutathione reductase (GR) activity by promoting GSH biosynthesis, facilitating the binding of As(III) with GSH and thus reducing As absorption (Souri et al., 2018). These studies, conducted in hydroponic systems, highlight the strong effect of Pi–As interactions in aqueous environments, where Pi application significantly reduces As uptake and toxicity in plants (Vromman et al., 2017). However, Pi and As concentrations in soils are generally much lower than in hydroponic systems (Anawar et al., 2018), suggesting that Pi–As interactions in hydroponics may not fully capture the complexities of soil environments. The role and mechanism of Pi in inhibiting As toxicity in soils remains unclear. The uptake of As(V) is regulated transcriptionally by modulating *PHT1* expression and transporter activity. Under As(V) stress, transcription factor WRKY6 quickly inhibits *PHT1;1*, encoding a transporter for both As(V) and Pi, and causes the internalization of *PHT1;1* into vesicles, reducing As uptake (Castrillo et al., 2013) (Fig. 5). Additionally, both As(V) and As(III) promote the degradation of PHR1 through an As(III)-induced pathway involving the SKP1-like protein ASK18 and F-box protein PHIF1, further limiting As(V) uptake by inhibiting the expression of *PHT1* (Navarro et al., 2021). Thus, Pi signaling helps restrict As(V) absorption and reduce its toxicity by inhibiting Pi signaling pathway under As(V) stress (Fig. 5).

Applying exogenous Pi can alleviate Cd stress in plants such as wheat and soybean (Sajwan et al., 2006; Kumar et al., 2018). Pi supplementation could enhance the insolubility and immobilization of Cd, likely by forming insoluble cadmium phosphate complexes in the rhizosphere (Qiu et al., 2011; Du et al., 2014) (Fig. 5). High Pi application has been shown to reduce Cd content in both roots and shoots and limit Cd translocation from roots to shoots in plants like Chinese flowering cabbage (*Brassica parachinensis*) (Qiu et al., 2011). In rice, application of calcium magnesium phosphate fertilizer effectively reduces Cd accumulation in roots, flag leaves, and grains, possibly by promoting iron plaque formation on the root surface and increasing soil solution pH (Zhao et al., 2020). Interestingly, exogenous Pi addition downregulated the expression of Cd transporter genes like *OsHMA2*, *OsIRT1*, and *OsABCC1* in rice seedlings (Chen et al., 2022b), suggesting that Pi improves Cd resistance by reducing Cd accumulation via regulating metal transporter genes. While increasing Pi fertilizer application can enhance the detoxification of both As and Cd in rice seedlings under combined stress, it also increases the risk of As and Cd accumulation in rice tissues (Wang et al., 2015). In wheat, Pi boosts antioxidant enzymes (SOD, POD, and CAT) and non-enzymatic antioxidants like α-tocopherol and ascorbic acid (AsA), improving Cd stress tolerance (Arshad et al., 2015). Additionally, Pi application increases organic acid accumulation, aiding Cd sequestration and detoxification in roots (Lu et al., 2007; Du et al., 2014). In contrast, Pi deficiency reduces Cd accumulation but increases Cd translocation from roots to shoots and reduces phytochelatin synthesis, thereby exacerbating the symptoms of Cd toxicity in rice seedlings grown under hydroponic culture (Yang et al., 2015). Although Pi plays a crucial role in alleviating Cd toxicity, the detailed molecular mechanism requires further investigation.

The Pi application has been shown to reduce Pb uptake in plants by forming less bioavailable Pb-Pi complexes in the soil, thereby decreasing the mobility and availability of Pb (Park et al., 2011) (Fig. 5). In maize plants grown in Pb-contaminated soils, Pi amendments significantly reduce Pb concentrations in both shoots and roots, accompanied by decreases in oxidative stress indicators (He et al., 2024). In Pb-polluted soils, Pi application not only reduces Pb bioavailability but also improves plant growth and yield (Zhang et al., 2024). Therefore, the Pi application plays a vital role in mitigating Pb toxicity by enhancing the antioxidant defenses and reducing Pb-induced toxicity.

Iron (Fe) is an essential micronutrient; however, excessive iron is toxic to plants. P and Fe exhibit an antagonistic interaction, where Pi in the rhizosphere can form insoluble compounds with Fe^{2+} or Fe^{3+}, limiting the Fe availability. The Pi application can mitigate the damage caused by excessive Fe in the growth media (Ohkama-Ohtsu and Wasaki, 2010). In Arabidopsis, PHR1 and PHL1, two core transcription factors regulating Pi homeostasis, also function in Fe homeostasis. Mutants deficient in both PHR1 and PHL1 show altered Fe distribution and misregulation of Fe-related genes, while PHR1 can upregulate *FER1*, a Fe storage protein, to modulate Fe levels (Bournier et al., 2013). Additionally, the Fe deficiency-induced E3 ligases, Hemerythrin RING Zinc finger 1/2 (HRZ1/2), interact with PHR2 to promote the ubiquitination of PHR2 in rice (Guo et al., 2022a).

Due to the antagonistic relationship between P and zinc (Zn), Pi application can alleviate Zn toxicity, while Zn supplementation has been shown to reduce Pi concentrations in plants (Verma and Minhas, 1987). In barley, Zn deficiency induces the expression of *HvPT1* and *HvPT2*, high-affinity Pi transporters under both Pi-sufficient and Pi-deficient conditions (Huang et al., 2000). In

Arabidopsis, *PHO1;H3*, a potential Pi exporter, is upregulated by Zn deficiency, which may limit Pi translocation from roots to shoots, helping to maintain Pi homeostasis under Zn-deficient conditions (Khan et al., 2014). High Pi levels reduce Zn bioavailability by forming stable Zn-Pi complexes, limiting Zn uptake and alleviating Zn toxicity in Zn-contaminated soils by reducing harmful free Zn^{2+} (Ding et al., 2021). Pi supply also boosts antioxidant production, which enhances defenses against Zn-induced oxidative stress (Bechtaoui et al., 2021; Kaur and Garg, 2021) (Fig. 5). However, excessive Pi can disrupt Zn homeostasis, potentially causing Zn deficiency even in Zn-rich soils due to inhibited Zn transport (Khan et al., 2014). High P levels may reduce arbuscular mycorrhizal fungi colonization, potentially exacerbating Zn stress (Bindraban et al., 2020).

Excessive Mn can disrupt the absorption, transport, and utilization of other nutrients, including P. On the other hand, Pi supply can mitigate Mn toxicity in plants such as potato (*Solanum tuberosum*), white clover (*Trifolium repens*), and perennial ryegrass (*Lolium perenne*) (Sarkar et al., 2004; Rosas et al., 2011). In barley grown under both hydroponic and soil conditions, increasing Pi supply decreases leaf Mn concentrations (Pedas et al., 2011). The alleviating effect of Pi on Mn toxicity could be associated with the formation of insoluble complexes between Pi and Mn in both soils and plants, as well as the reduced oxidative stress and enhanced photosynthetic capacity (Noor et al., 2022). Moreover, P deficiency significantly increases Mn accumulation in soybean leaves and roots grown in acidic soils, with the transcription factor GmSTOP1-3 playing a crucial role in regulating LP-mediated Mn accumulation (Liu et al., 2025). Pi deficiency-induced exudation of organic acids can mobilise not only soil P, but also micronutrient Mn (Pang et al., 2018). Notably, high Mn concentrations in leaves have been suggested to serve as a useful indicator for screening plant genotypes with high P acquisition efficiency (Lambers et al., 2015). The catalytic hydrolysis of phytates by phytase could release Mn from phytates in the soil (George et al., 2014). Therefore, Pi supply may reduce Mn availability in the soil and limit Mn uptake by possibly impairing the exudation of organic acids and phytase from plant roots.

Pi deficiency and Al toxicity often coexist in acidic soils. Al stress reduces P levels in plants, but Pi application can mitigate Al toxicity by facilitating Al fixation in roots as observed in plants like soybean and pummelo (*Citrus grandis*) (Liao et al., 2006; Jiang et al., 2009). In *Camellia oleifera* seedlings, Pi addition significantly reduces Al content in roots, potentially by promoting protein synthesis and carbohydrate accumulation (Qu et al., 2020). Pi also influences Al detoxification by forming Al-phosphate complexes that are less soluble and, therefore, less toxic to root tissues. In addition, Pi supplementation enhances the production of organic acids, which bind to Al^{3+} and further reduce its mobility and uptake (Bojórquez-Quintal et al., 2017). Consistently, P-efficient varieties have been shown to have higher Al tolerance than P-inefficient varieties under hydroponic culture in legume plants, which is possibly a result of the increased exudation of organic acids from the roots of P-efficient varieties (Liao et al., 2006; Du et al., 2009). On the other hand, Al-tolerant cultivars of plants like buckwheat (*Fagopyrum esculentum* M.) and ryegrass (*Lolium perenne* L.) were suggested to acquire P more effectively than Al-sensitive cultivars (Zheng et al., 2005; Parra-Almuna et al., 2018), which may be associated with the enhanced Pi uptake and precipitation and immobilization of Al in roots of Al-tolerant cultivars. However, Pi deficiency can also enhance Al tolerance by reducing Al-binding phospholipids and pectin in root cell walls, inducing the utilization of phosphoenolpyruvate carboxylase (PEPC)-derived organic acids for Al detoxification, and minimizing Al uptake and accumulation in plants like rice and tomato (Ward et al., 2011; Maejima et al., 2014; Pradhan et al., 2023). Thus, the effect of Pi nutrition on Al tolerance may be dependent on Pi status and plant species.

Conclusions and perspectives

Phosphate homeostasis and abiotic stress responses are intrinsically interconnected processes that significantly impact plant growth, development, and survival. This review summarizes current knowledge of these complex interactions across multiple levels, from physiological responses to molecular mechanisms. Abiotic stresses significantly alter Pi availability, uptake, and utilization through various mechanisms, such as changes in soil chemistry, disruptions in membrane transport, and modulation of Pi-responsive gene expression. Conversely, adequate Pi nutrition plays a central role in enhancing plant tolerance to abiotic stresses by improving antioxidant capacity, osmolyte accumulation, and membrane stability. At the molecular level, extensive crosstalk between Pi signaling and stress response pathways, involving key regulators like ABA signaling, PHR transcription factors, SPX proteins, and various transporters. Protective effects of Pi against abiotic stresses are mediated by complex mechanisms, including metal-phosphate complexes formation, enhanced antioxidant systems, and modulation of hormone signaling. Understanding how Pi interacts with abiotic stress responses is crucial, particularly in the context of growing environmental challenges and the need to develop stress-resilient crops while optimizing fertilizer use.

Despite significant advances, important questions remain. Most current research focuses on the effects of soil chemistry and plant physiology, yet the signaling pathways and molecular mechanisms underlying the interactions between plant P nutrition and abiotic stress are still not well defined. The ecological and evolutionary implications of these interactions are also poorly understood. A major challenge lies in improving both crop resistance to abiotic stress and the efficiency of P utilization. Achieving this requires a deeper understanding of how abiotic stress and P nutrition interact, which could be modulated through advanced tools such as genome editing, synthetic biology, and genetic transformation. Additionally, P nutrition influences soil microbiomes, and abiotic stresses alter the rhizosphere microbial community, which plays a vital role in P cycling. However, the precise mechanisms linking microorganisms with the interaction between P nutrition and abiotic stress remain elusive. Addressing these knowledge gaps is crucial for advancing our understanding of the molecular mechanisms that govern the interplay between P nutrition and abiotic stress responses. This will have significant implications for improving agricultural productivity. Furthermore, modulating the expression of specific genes could offer a means to enhance crop resilience to LP conditions and simultaneously mitigate abiotic stresses. Exploring genetic resources that enhance Pi uptake, transport, and utilization, along with environmental stress resistance, through modern molecular breeding and gene editing approaches is urgently needed. Technologies such as genomics, transcriptomics, proteomics, and single-cell sequencing can aid in the discovery of these critical genes. Moreover, employing gene editing, promoter editing, synthetic biology, and artificial intelligence AI-assisted analysis can facilitate the development of crops with enhanced nutrient use efficiency, improved stress resistance, and increased yield potential.

Conflict of interest

The authors declare that they have no conflict of interest.

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Supplementary data

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References

Abe, H., Yamaguchi-Shinozaki, K., Urao, T., Iwasaki, T., Hosokawa, D., Shinozaki, K., 1997. Role of Arabidopsis MYC and MYB homologs in drought- and abscisic acid-regulated gene expression. Plant Cell 9, 1859–1868.

Abel, S., 2017. Phosphate scouting by root tips. Curr. Opin. Plant Biol. 39, 168–177.

Ahanger, M.A., Morad-Talab, N., Abd-Allah, E.F., Ahmad, P., Hajiboland, R., 2016. Plant growth under drought stress: Significance of mineral nutrients, in: Ahmad, P. (ed), Water Stress and Crop Plants, pp. 649–668.

Aleksza, D., Horvath, G.V., Sandor, G., Szabados, L., 2017. Proline accumulation is regulated by transcription factors associated with phosphate starvation. Plant Physiol. 175, 555–567.

Anawar, H.M., Rengel, Z., Damon, P., Tibbett, M., 2018. Arsenic-phosphorus interactions in the soil-plant-microbe system: dynamics of uptake, suppression and toxicity to plants. Environ. Pollut. 233, 1003–1012.

Arpat, A.B., Magliano, P., Wege, S., Rouached, H., Stefanovic, A., Poirier, Y., 2012. Functional expression of PHO1 to the Golgi and *trans*-Golgi network and its role in export of inorganic phosphate. Plant J. 71, 479–491.

Arshad, M., Ali, S., Noman, A., Ali, Q., Rizwan, M., Farid, M., Irshad, M.K., 2015. Phosphorus amendment decreased cadmium (Cd) uptake and ameliorates chlorophyll contents, gas exchange attributes, antioxidants, and mineral nutrients in wheat (*Triticum aestivum* L.) under Cd stress. Arch. Agron Soil Sci. 62, 533–546.

Assaha, D.V.M., Ueda, A., Saneoka, H., Al-Yahyai, R., Yaish, M.W., 2017. The role of Na^+ and K^+ transporters in salt stress adaptation in glycophytes. Front. Physiol. 8, 509.

Awasthi, S., Chauhan, R., Srivastava, S., Tripathi, R.D., 2017. The journey of arsenic from soil to grain in rice. Front. Plant Sci. 8, 1007.

Baek, D., Chun, H.J., Kang, S., Shin, G., Park, S.J., Hong, H., Kim, C., Kim, D.H., Lee, S.Y., Kim, M.C., et al., 2016. A role for Arabidopsis *miR399f* in salt, drought, and ABA signaling. Mol. Cells 39, 111–118.

Baek, D., Chun, H.J., Yun, D.J., Kim, M.C., 2017. Cross-talk between phosphate starvation and other environmental stress signaling pathways in plants. Mol. Cells 40, 697–705.

Baek, D., Kim, M.C., Chun, H.J., Kang, S., Park, H.C., Shin, G., Park, J., Shen, M., Hong, H., Kim, W.Y., et al., 2013. Regulation of *miR399f* transcription by AtMYB2 affects phosphate starvation responses in Arabidopsis. Plant Physiol. 161, 362–373.

Baker, A., Ceasar, S.A., Palmer, A.J., Paterson, J.B., Qi, W., Muench, S.P., Baldwin, S.A., 2015. Replace, reuse, recycle: improving the sustainable use of phosphorus by plants. J. Exp. Bot. 66, 3523–3540.

Bali, A.S., Sidhu, G.P.S., 2021. Arsenic acquisition, toxicity and tolerance in plants - from physiology to remediation: a review. Chemosphere 283, 131050.

Balzergue, C., Dartevelle, T., Godon, C., Laugier, E., Meisrimler, C., Teulon, J.M., Creff, A., Bissler, M., Brouchoud, C., Hagege, A., et al., 2017. Low phosphate activates STOP1-ALMT1 to rapidly inhibit root cell elongation. Nat. Commun. 8, 15300.

Barbhuiya, I.H., Moulick, D., Hossian, A., Choudhury, S., 2023. Role of phosphate in drought stress regulation in developing rice (*Oryza sativa* L.) seedlings. Cereal Res. Commun. 52, 531–544.

Bari, R., Datt Pant, B., Stitt, M., Scheible, W.R., 2006. PHO2, microRNA399, and PHR1 define a phosphate-signaling pathway in plants. Plant Physiol. 141, 988–999.

Barragán-Rosillo, A.C., Peralta-Alvarez, C.A., Ojeda-Rivera, J.O., Arzate-Mejía, R.G., Recillas-Targa, F., Herrera-Estrella, L., 2021. Genome accessibility dynamics in response to phosphate limitation is controlled by the PHR1 family of transcription factors in Arabidopsis. Proc. Natl. Acad. Sci. U. S. A. 118, e2107558118.

Bechtaoui, N., Rabiu, M.K., Raklami, A., Oufdou, K., Hafidi, M., Jemo, M., 2021. Phosphate-dependent regulation of growth and stresses management in plants. Front. Plant Sci. 12, 679916.

Begum, N., Ahanger, M.A., Zhang, L., 2020. AMF inoculation and phosphorus supplementation alleviates drought induced growth and photosynthetic decline in *Nicotiana tabacum* by up-regulating antioxidant metabolism and osmolyte accumulation. Environ. Exp. Bot. 176, 104088.

Belouchrani, A.S., Latati, M., Ounane, S.M., Drouiche, N., Lounici, H., 2019. Study of the interaction salinity: phosphorus fertilization on sorghum. J. Plant Growth Regul. 39, 1205–1210.

Bienert, G.P., Thorsen, M., Schussler, M.D., Nilsson, H.R., Wagner, A., Tamas, M.J., Jahn, T.P., 2008. A subgroup of plant aquaporins facilitate the bi-directional diffusion of $As(OH)_3$ and $Sb(OH)_3$ across membranes. BMC Biol. 6, 26.

Bindraban, P.S., Dimkpa, C.O., Pandey, R., 2020. Exploring phosphorus fertilizers and fertilization strategies for improved human and environmental health. Biol. Fertil. Soils 56, 299–317.

Bista, D.R., Heckathorn, S.A., Jayawardena, D.M., Mishra, S., Boldt, J.K., 2018. Effects of drought on nutrient uptake and the levels of nutrient-uptake proteins in roots of drought-sensitive and -tolerant grasses. Plants (Basel) 7, 28.

Bojórquez-Quintal, E., Escalante-Magaña, C., Echevarría-Machado, I., Martínez-Estévez, M., 2017. Aluminum, a friend or foe of higher plants in acid soils. Front. Plant Sci. 8, 1767.

Bouras, H., Choukr-Allah, R., Amouaouch, Y., Bouaziz, A., Devkota, K.P., El Mouttaqi, A., Bouazzama, B., Hirich, A., 2022. How does quinoa (*Chenopodium quinoa* Willd.) respond to phosphorus fertilization and irrigation water salinity? Plants (Basel) 11, 216.

Bournier, M., Tissot, N., Mari, S., Boucherez, J., Lacombe, E., Briat, J.F., Gaymard, F., 2013. Arabidopsis ferritin 1 *(AtFer1)* gene regulation by the phosphate starvation response 1 (AtPHR1) transcription factor reveals a direct molecular link between iron and phosphate homeostasis. J. Biol. Chem. 288, 22670–22680.

Bustos, R., Castrillo, G., Linhares, F., Puga, M.I., Rubio, V., Perez-Perez, J., Solano, R., Leyva, A., Paz-Ares, J., 2010. A central regulatory system largely controls transcriptional activation and repression responses to phosphate starvation in Arabidopsis. PLoS Genet. 6, e1001102.

Campos-Soriano, L., Bundo, M., Bach-Pages, M., Chiang, S.F., Chiou, T.J., San Segundo, B., 2020. Phosphate excess increases susceptibility to pathogen infection in rice. Mol. Plant Pathol. 21, 555–570.

Cao, M., Liu, H., Zhang, C., Wang, D., Liu, X., Chen, Q., 2020. Functional analysis of *StPHT1;7*, a *Solanum tuberosum* L. phosphate transporter gene, in growth and drought tolerance. Plants (Basel) 9, 1384.

Cao, Y., Feng, H., Sun, D., Xu, G., Rathinasabapathi, B., Chen, Y., Ma, L.Q., 2019. Heterologous expression of *Pteris vittata* phosphate transporter PvPht1;3 enhances arsenic translocation to and accumulation in tobacco shoots. Environ. Sci. Technol. 53, 10636–10644.

Castrillo, G., Sanchez-Bermejo, E., de Lorenzo, L., Crevillen, P., Fraile-Escanciano, A., Tc, M., Mouriz, A., Catarecha, P., Sobrino-Plata, J., Olsson, S., et al., 2013. WRKY6 transcription factor restricts arsenate uptake and transposon activation in Arabidopsis. Plant Cell 25, 2944–2957.

Castro-Valdecantos, P., Martínez-Melgarejo, P.A., Pérez-Alfocea, F., Tian, J., Dodd, I. C., 2023. Stem girdling enhances ABA-induced stomatal closure of phosphorus-deprived soybean plants. Environ. Exp. Bot. 208, 105266.

Chan, C., Liao, Y.Y., Chiou, T.J., 2021. The impact of phosphorus on plant immunity. Plant Cell Physiol. 62, 582–589.

Chang, M.X., Gu, M., Xia, Y.W., Dai, X.L., Dai, C.R., Zhang, J., Wang, S.C., Qu, H.Y., Yamaji, N., Feng Ma, J., et al., 2019. OsPHT1;3 mediates uptake, translocation, and remobilization of phosphate under extremely low phosphate regimes. Plant Physiol. 179, 656–670.

Che, J., Yamaji, N., Miyaji, T., Mitani-Ueno, N., Kato, Y., Shen, R.F., Ma, J.F., 2020. Node-localized transporters of phosphorus essential for seed development in rice. Plant Cell Physiol. 61, 1387–1398.

Chen, H., Du, J., Wang, Y., Chao, K., Wang, Z., Ali, S., Zeng, H., 2025. Transcription factors PHR1 and PHR1-like 1 regulate ABA-mediated inhibition of seed germination and stomatal opening in Arabidopsis. Plant Sci. 352, 112389.

Chen, K., Li, G.J., Bressan, R.A., Song, C.P., Zhu, J.K., Zhao, Y., 2020. Abscisic acid dynamics, signaling, and functions in plants. J. Integr. Plant Biol. 62, 25–54.

Chen, N., Qin, J., Tong, S., Wang, W., Jiang, Y., 2022a. One AP2/ERF transcription factor positively regulates Pi uptake and drought tolerance in poplar. Int. J. Mol. Sci. 23, 5241.

Chen, Q., Hu, Y., Yang, L., Zhu, B., Luo, F., 2022b. Phosphorus regulates the level of signaling molecules in rice to reduce cadmium toxicity. Curr. Issues Mol. Biol. 44, 4070–4086.

Chen, Z.C., Liao, H., 2016. Organic acid anions: an effective defensive weapon for plants against aluminum toxicity and phosphorus deficiency in acidic soils. J. Genet. Genomics 43, 631–638.

Cheyns, K., Peeters, S., Delcourt, D., Smolders, E., 2012. Lead phytotoxicity in soils and nutrient solutions is related to lead induced phosphorus deficiency. Environ. Pollut. 164, 242–247.

Chiou, T.J., Lin, S.I., 2011. Signaling network in sensing phosphate availability in plants. Annu. Rev. Plant Biol. 62, 185–206.

Cubero, B., Nakagawa, Y., Jiang, X.Y., Miura, K.J., Li, F., Raghothama, K.G., Bressan, R.A., Hasegawa, P.M., Pardo, J.M., 2009. The phosphate transporter PHT4;6 is a determinant of salt tolerance that is localized to the Golgi apparatus of Arabidopsis. Mol. Plant 2, 535–552.

Dai, S., Wu, H., Chen, H., Wang, Z., Yu, X., Wang, L., Jia, X., Qin, C., Zhu, Y., Yi, K., et al., 2023. Comparative transcriptome analyses under individual and combined nutrient starvations provide insights into N/P/K interactions in rice. Plant Physiol. Biochem. 197, 107642.

Dai, S.H., Chen, H.Y., Shi, Y.T., Xiao, X.L., Xu, L., Qin, C., Zhu, Y.Y., Yi, K.K., Lei, M. G., Zeng, H.Q., 2024. PHOSPHATE1-mediated phosphate translocation from roots to shoots regulates floral transition in plants. J. Exp. Bot. 75, 5054–5075.

Devaiah, B.N., Nagarajan, V.K., Raghothama, K.G., 2007. Phosphate homeostasis and root development in Arabidopsis are synchronized by the zinc finger transcription factor ZAT6. Plant Physiol. 145, 147–159.

Ding, J., Liu, L., Wang, C., Shi, L., Xu, F., Cai, H., 2021. High level of zinc triggers phosphorus starvation by inhibiting root-to-shoot translocation and preferential distribution of phosphorus in rice plants. Environ. Pollut. 277, 116778.

Ding, Y., Shi, Y., Yang, S., 2019. Advances and challenges in uncovering cold tolerance regulatory mechanisms in plants. New Phytol. 222, 1690–1704.

Dong, Q., Wallrad, L., Almutairi, B.O., Kudla, J., 2022. Ca^{2+} signaling in plant responses to abiotic stresses. J. Integr. Plant Biol. 64, 287–300.

Du, J., Yan, C., Li, Z., 2014. Phosphorus and cadmium interactions in *Kandelia obovata* (S. L.) in relation to cadmium tolerance. Environ. Sci. Pollut. Res. Int. 21, 355–365.

Du, Q., Wang, K., Zou, C., Xu, C., Li, W.X., 2018. The *PILNCR1*-miR399 regulatory module is important for low phosphate tolerance in maize. Plant Physiol. 177, 1743–1753.

Du, Y.M., Tian, J., Liao, H., Bai, C.J., Yan, X.L., Liu, G.D., 2009. Aluminium tolerance and high phosphorus efficiency helps *Stylosanthes* better adapt to low-P acid soils. Ann. Bot. 103, 1239–1247.

Fahad, S., Bajwa, A.A., Nazir, U., Anjum, S.A., Farooq, A., Zohaib, A., Sadia, S., Nasim, W., Adkins, S., Saud, S., et al., 2017. Crop production under drought and heat stress: plant responses and management options. Front. Plant Sci. 8, 1147.

Fahad, S., Hussain, S., Saud, S., Hassan, S., Tanveer, M., Ihsan, M.Z., Shah, A.N., Ullah, A., Nasrullah, Khan, F., et al., 2016. A combined application of biochar and phosphorus alleviates heat-induced adversities on physiological, agronomical and quality attributes of rice. Plant Physiol. Biochem. 103, 191–198.

Feng, H., Li, X., Sun, D., Chen, Y., Xu, G., Cao, Y., Ma, L.Q., 2021. Expressing phosphate transporter PvPht2;1 enhances P transport to the chloroplasts and increases arsenic tolerance in *Arabidopsis thaliana*. Environ. Sci. Technol. 55, 2276–2284.

Gan, H., Chu, J., Sun, J., Wang, Q., 2025. High concentration of phosphate treatment increased the tolerance of *Robinia pseudoacacia* roots to salt stress. Plant Cell Rep. 44, 53.

Gaxiola, R.A., Li, J., Undurraga, S., Dang, L.M., Allen, G.J., Alper, S.L., Fink, G.R., 2001. Drought- and salt-tolerant plants result from overexpression of the AVP1 H^+-pump. Proc. Natl. Acad. Sci. U. S. A. 98, 11444–11449.

George, T.S., French, A.S., Brown, L.K., Karley, A.J., White, P.J., Ramsay, L., Daniell, T.J., 2014. Genotypic variation in the ability of landraces and commercial cereal varieties to avoid manganese deficiency in soils with limited manganese availability: is there a role for root-exuded phytases? Physiol. Plantarum 151, 243–256.

Gojon, A., Cassan, O., Bach, L., Lejay, L., Martin, A., 2023. The decline of plant mineral nutrition under rising CO_2: physiological and molecular aspects of a bad deal. Trends Plant Sci. 28, 185–198.

Gonzalez, S., Swift, J., Yaaran, A., Xu, J., Miller, C., Illouz-Eliaz, N., Nery, J.R., Busch, W., Zait, Y., Ecker, J.R., 2024. Arabidopsis transcriptome responses to low water potential using high-throughput plate assays. Elife 12, RP84747.

Gu, M., Chen, A., Sun, S., Xu, G., 2016. Complex regulation of plant phosphate transporters and the gap between molecular mechanisms and practical application: what are missing? Mol. Plant 9, 396–416.

Gu, P., Tao, W., Tao, J., Sun, H., Hu, R., Wang, D., Zong, G., Xie, X., Ruan, W., Xu, G., et al., 2023. The D14-SDEL1-SPX4 cascade integrates the strigolactone and phosphate signalling networks in rice. New Phytol. 239, 673–686.

Guan, Z., Zhang, Q., Zhang, Z., Zuo, J., Chen, J., Liu, R., Savarin, J., Broger, L., Cheng, P., Wang, Q., et al., 2022. Mechanistic insights into the regulation of plant phosphate homeostasis by the rice SPX2-PHR2 complex. Nat. Commun. 13, 1581.

Guo, H.L., Tian, M.Z., Ri, X., Chen, Y.F., 2025. Phosphorus acquisition, translocation, and redistribution in maize. J. Genet. Genomics 52, 287–296.

Guo, M., Ruan, W., Zhang, Y., Zhang, Y., Wang, X., Guo, Z., Wang, L., Zhou, T., Paz-Ares, J., Yi, K., 2022a. A reciprocal inhibitory module for Pi and iron signaling. Mol. Plant 15, 138–150.

Guo, T., Gull, S., Ali, M.M., Yousef, A.F., Ercisli, S., Kalaji, H.M., Telesinski, A., Auriga, A., Wrobel, J., Radwan, N.S., et al., 2022b. Heat stress mitigation in tomato (*Solanum lycopersicum* L.) through foliar application of gibberellic acid. Sci. Rep. 12, 11324.

He, M., Dijkstra, F.A., 2014. Drought effect on plant nitrogen and phosphorus: a meta-analysis. New Phytol. 204, 924–931.

He, Y., Jiang, R., Jiang, R., Zhu, C., Cao, Y., Xia, T., Hou, X., 2024. The effects of phosphate application in Pb-contaminated soil on the oxidative stress of leaves, Pb accumulation in maize biomass and Pb speciation in rhizosphere soil. Cereal Res. Commun. 52, 1855–1862.

Hernández, I., Munné-Bosch, S., 2015. Linking phosphorus availability with photo-oxidative stress in plants. J. Exp. Bot. 66, 2889–2900.

Hinsinger, P., 2001. Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: a review. Plant Soil 237, 173–195.

Hu, B., Jiang, Z., Wang, W., Qiu, Y., Zhang, Z., Liu, Y., Li, A., Gao, X., Liu, L., Qian, Y., et al., 2019. Nitrate–NRT1.1B–SPX4 cascade integrates nitrogen and phosphorus signalling networks in plants. Nat. Plants 5, 401–413.

Hu, B., Zhu, C., Li, F., Tang, J., Wang, Y., Lin, A., Liu, L., Che, R., Chu, C., 2011. *LEAF TIP NECROSIS1* plays a pivotal role in the regulation of multiple phosphate starvation responses in rice. Plant Physiol. 156, 1101–1115.

Hu, W., Zhang, H., Zhang, X., Chen, H., Tang, M., 2017. Characterization of six PHT1 members in *Lycium barbarum* and their response to arbuscular mycorrhiza and water stress. Tree Physiol. 37, 351–366.

Huang, C., Barker, S.J., Langridge, P., Smith, F.W., Graham, R.D., 2000. Zinc deficiency up-regulates expression of high-affinity phosphate transporter genes in both phosphate-sufficient and-deficient barley roots. Plant Physiol. 124, 415–422.

Huang, J., Zhao, X., Bürger, M., Wang, Y., Chory, J., 2021. Two interacting ethylene response factors regulate heat stress response. Plant Cell 33, 338–357.

Huang, S., Xin, S., Xie, G., Han, J., Liu, Z., Wang, B., Zhang, S., Wu, Q., Cheng, X., 2020. Mutagenesis reveals that the rice *OsMPT3* gene is an important osmotic regulatory factor. Crop J. 8, 465–479.

Huang, Y., Sun, M.M., Ye, Q., Wu, X.Q., Wu, W.H., Chen, Y.F., 2017. Abscisic acid modulates seed germination via ABA INSENSITIVE5-mediated PHOSPHATE1. Plant Physiol. 175, 1661–1668.

Huang, Z.C., An, Z.Z., Chen, T.B., Lei, M., Xiao, X.Y., Liao, X.Y., 2007. Arsenic uptake and transport of *Pteris vittata* L. as influenced by phosphate and inorganic arsenic species under sand culture. J. Environ. Sci. (China) 19, 714–718.

Hurry, V., Strand, A., Furbank, R., Stitt, M., 2000. The role of inorganic phosphate in the development of freezing tolerance and the acclimatization of photosynthesis to low temperature is revealed by the pho mutants of *Arabidopsis thaliana*. Plant J. 24, 383–396.

Ibeas, M.A., Salinas-Grenet, H., Johnson, N.R., Pérez-Díaz, J., Vidal, E.A., Alvarez, J. M., Estevez, J.M., 2024. Filling the gaps on root hair development under salt stress and phosphate starvation using current evidence coupled with a meta-analysis approach. Plant Physiol. 196, 2140–2149.

Ihtisham, M., Hasanuzzaman, M., El-Sappah, A.H., Zaman, F., Khan, N., Raza, A., Sarraf, M., Khan, S., Abbas, M., Hassan, M.J., et al., 2023. Primary plant nutrients modulate the reactive oxygen species metabolism and mitigate the impact of cold stress in overseeded perennial ryegrass. Front. Plant Sci. 14, 1149832.

Jaschke, W.D., Peuke, A.D., Pate, J.S., Hartung, W., 1997. Transport, synthesis and catabolism of abscisic acid (ABA) in intact plants of *Ricinus communis* L. under phosphate deficiency and moderate salinity. J. Exp. Bot. 48, 1737–1747.

Jiang, H.X., Tang, N., Zheng, J.G., Li, Y., Chen, L.S., 2009. Phosphorus alleviates aluminum-induced inhibition of growth and photosynthesis in *Citrus grandis* seedlings. Physiol. Plantarum 137, 298–311.

Kaur, H., Garg, N., 2021. Zinc toxicity in plants: a review. Planta 253, 129.

Kawa, D., Julkowska, M.M., Sommerfeld, H.M., ter Horst, A., Haring, M.A., Testerink, C., 2016. Phosphate-dependent root system architecture responses to salt stress. Plant Physiol. 172, 690–706.

Khan, F., Hussain, S., Tanveer, M., Khan, S., Hussain, H.A., Iqbal, B., Geng, M., 2018. Coordinated effects of lead toxicity and nutrient deprivation on growth, oxidative status, and elemental composition of primed and non-primed rice seedlings. Environ. Sci. Pollut. Res. Int. 25, 21185–21194.

Khan, F., Siddique, A.B., Shabala, S., Zhou, M., Zhao, C., 2023. Phosphorus plays key roles in regulating plants' physiological responses to abiotic stresses. Plants (Basel) 12, 2861.

Khan, G.A., Bouraine, S., Wege, S., Li, Y., de Carbonnel, M., Berthomieu, P., Poirier, Y., Rouached, H., 2014. Coordination between zinc and phosphate homeostasis involves the transcription factor PHR1, the phosphate exporter PHO1, and its homologue PHO1;H3 in Arabidopsis. J. Exp. Bot. 65, 871–884.

Kim, Y.S., Kim, I.S., Choe, Y.H., Bae, M.J., Shin, S.Y., Park, S.K., Kang, H.G., Kim, Y. H., Yoon, H.S., 2014. Overexpression of the Arabidopsis vacuolar H^+-pyrophosphatase *AVP1* gene in rice plants improves grain yield under paddy field conditions. J. Agric. Sci. 152, 941–953.

Klecker, M., Gasch, P., Peisker, H., Dormann, P., Schlicke, H., Grimm, B., Mustroph, A., 2014. A shoot-specific hypoxic response of Arabidopsis sheds light on the role of the phosphate-responsive transcription factor PHOSPHATE STARVATION RESPONSE1. Plant Physiol. 165, 774–790.

Kumar, R., Gopal, R., Sharma, Y.K., 2018. Influence of cadmium and phosphorus enhance absorption and membrane damage in wheat seedlings grown in nutrient medium. J. Plant Nutr. 41, 793–805.

Lambers, H., Hayes, P.E., Laliberte, E., Oliveira, R.S., Turner, B.L., 2015. Leaf manganese accumulation and phosphorus-acquisition efficiency. Trends Plant Sci. 20, 83–90.

Lantzouni, O., Alkofer, A., Falter-Braun, P., Schwechheimer, C., 2020. GROWTH-REGULATING FACTORS interact with DELLAs and regulate growth in cold stress. Plant Cell 32, 1018–1034.

Lee, S., Showalter, J., Zhang, L., Cassin-Ross, G., Rouached, H., Busch, W., 2024. Nutrient levels control root growth responses to high ambient temperature in plants. Nat. Commun. 15, 4689.

Lei, K.J., Zhou, H., Gu, D.L., An, G.Y., 2022. The involvement of abscisic acid-insensitive mutants in low phosphate stress responses during rhizosphere acidification, anthocyanin accumulation and Pi homeostasis in Arabidopsis. Plant Sci. 322, 111358.

Li, C., Zhang, X., Li, C., Li, C., 2022a. Ionomic and metabolic responses of wheat seedlings to PEG-6000-simulated drought stress under two phosphorus levels. PLoS ONE 17, e0274915.

Li, G., Wang, Y., Fu, K., Li, C., Wei, J., Zhu, J., Wang, Y., Li, C., Li, C., 2024. Split application of phosphorus fertilizer increased wheat grain weight under post-anthesis drought stress by delaying programmed cell death of endosperm. Environ. Exp. Bot. 226.

Li, L., Pan, S., Melzer, R., Fricke, W., 2020. Apoplastic barriers, aquaporin gene expression and root and cell hydraulic conductivity in phosphate-limited sheepgrass plants. Physiol. Plantarum 168, 118–132.

Li, T., Zhang, R., Satheesh, V., Wang, P., Ma, G., Guo, J., An, G.Y., Lei, M., 2022b. The chromatin remodeler BRAHMA recruits HISTONE DEACETYLASE6 to regulate root growth inhibition in response to phosphate starvation in Arabidopsis. J. Integr. Plant Biol. 64, 2314–2326.

Li, Y., Wang, X., Zhang, H., Wang, S., Ye, X., Shi, L., Xu, F., Ding, G., 2019. Molecular identification of the phosphate transporter family 1 (PHT1) genes and their expression profiles in response to phosphorus deprivation and other abiotic stresses in *Brassica napus*. PLoS ONE 14, e0220374.

Liao, H., Wan, H., Shaff, J., Wang, X., Yan, X., Kochian, L.V., 2006. Phosphorus and aluminum interactions in soybean in relation to aluminum tolerance. Exudation of specific organic acids from different regions of the intact root system. Plant Physiol. 141, 674–684.

Lin, W.Y., Huang, T.K., Chiou, T.J., 2013. Nitrogen limitation adaptation, a target of microRNA827, mediates degradation of plasma membrane-localized phosphate transporters to maintain phosphate homeostasis in Arabidopsis. Plant Cell 25, 4061–4074.

Liu, D., 2021. Root developmental responses to phosphorus nutrition. J. Integr. Plant Biol. 63, 1065–1090.

Liu, F., Chang, X.J., Ye, Y., Xie, W.B., Wu, P., Lian, X.M., 2011. Comprehensive sequence and whole-life-cycle expression profile analysis of the phosphate transporter gene family in rice. Mol. Plant 4, 1105–1122.

Liu, G., Chen, Q., Li, D., Mai, H., Zhou, Y., Lin, M., Feng, X., Lin, X., Lu, X., Chen, K., et al., 2025. GmSTOP1-3 increases soybean manganese accumulation under phosphorus deficiency by regulating *GmMATE2/13* and *GmZIP6/GmIREG3*. Plant Cell Environ. 48, 1812–1828.

Liu, J., Yang, L., Luan, M., Wang, Y., Zhang, C., Zhang, B., Shi, J., Zhao, F.G., Lan, W., Luan, S., 2015. A vacuolar phosphate transporter essential for phosphate homeostasis in Arabidopsis. Proc. Natl. Acad. Sci. U. S. A. 112, E6571–E6578.

Liu, L.W., He, X., Wang, S.W., Qin, X.T., Che, S.H., Wu, L., Wang, D.C., Tian, P., Wei, X.S., Wu, Z.H., et al., 2023. The role of the chloroplast localised phosphate transporter *GmPHT4;10* gene in plant growth, photosynthesis and drought resistance. Funct. Plant Biol. 50, 649–662.

Liu, Q.Q., Xia, J.Q., Wu, J., Han, Y., Zhang, G.Q., Zhao, P.X., Xiang, C.B., 2024. Root-derived long-distance signals trigger ABA synthesis and enhance drought resistance in Arabidopsis. J. Genet. Genomics 51, 749–761.

Liu, Q., Ma, H., Sun, Z., Lin, X., Zhou, X., 2018. Translocation efficiencies and allocation of nitrogen, phosphorous and potassium in rice as affected by silicon fertilizer under high daytime temperature. J. Agron. Crop Sci. 205, 188–201.

Liu, T.Y., Huang, T.K., Tseng, C.Y., Lai, Y.S., Lin, S.I., Lin, W.Y., Chen, J.W., Chiou, T. J., 2012. PHO2-dependent degradation of PHO1 modulates phosphate homeostasis in Arabidopsis. Plant Cell 24, 2168–2183.

Liu, T.Y., Huang, T.K., Yang, S.Y., Hong, Y.T., Huang, S.M., Wang, F.N., Chiang, S.F., Tsai, S.Y., Lu, W.C., Chiou, T.J., 2016. Identification of plant vacuolar transporters mediating phosphate storage. Nat. Commun. 7, 11095.

Liu, X.M., Nguyen, X.C., Kim, K.E., Han, H.J., Yoo, J., Lee, K., Kim, M.C., Yun, D.J., Chung, W.S., 2013. Phosphorylation of the zinc finger transcriptional regulator ZAT6 by MPK6 regulates Arabidopsis seed germination under salt and osmotic stress. Biochem. Biophys. Res. Commun. 430, 1054–1059.

Loudari, A., Benadis, C., Naciri, R., Soulaimani, A., Zeroual, Y., Gharous, M.E., Kalaji, H.M., Oukarroum, A., 2020. Salt stress affects mineral nutrition in shoots and roots and chlorophyll a fluorescence of tomato plants grown in hydroponic culture. J. Plant Interact. 15, 398–405.

Loudari, A., Mayane, A., Zeroual, Y., Colinet, G., Oukarroum, A., 2022. Photosynthetic performance and nutrient uptake under salt stress: differential responses of wheat plants to contrasting phosphorus forms and rates. Front. Plant Sci. 13, 1038672.

Lu, H., Yan, C., Liu, J., 2007. Low-molecular-weight organic acids exuded by mangrove (*Kandelia candel* (L.) Druce) roots and their effect on cadmium species change in the rhizosphere. Environ. Exp. Bot. 61, 159–166.

Lü, S., Yu, X., Wu, X., Hu, Q., Zhu, X., Wu, M., Hu, Q., Zhao, S., Hu, J., Wu, J., et al., 2025. The microRNA399d-PHOSPHATE2 module alters rice sensitivity to rice ragged stunt virus by manipulating phosphate uptake. Plant Physiol. 197, kiae517.

Lv, S., Wang, D., Jiang, P., Jia, W., Li, Y., 2021. Variation of *PHT* families adapts salt cress to phosphate limitation under salinity. Plant Cell Environ. 44, 1549–1564.

Lynch, J.P., 2019. Root phenotypes for improved nutrient capture: an underexploited opportunity for global agriculture. New Phytol. 223, 548–564.

Ma, B., Zhang, L., Gao, Q., Wang, J., Li, X., Wang, H., Liu, Y., Lin, H., Liu, J., Wang, X., et al., 2021. A plasma membrane transporter coordinates phosphate reallocation and grain filling in cereals. Nat. Genet. 53, 906–915.

Maejima, E., Watanabe, T., Osaki, M., Wagatsuma, T., 2014. Phosphorus deficiency enhances aluminum tolerance of rice (*Oryza sativa*) by changing the physicochemical characteristics of root plasma membranes and cell walls. J. Plant Physiol. 171, 9–15.

Mahdi, I., Fahsi, N., Hafidi, M., Allaoui, A., Biskri, L., 2020. Plant growth enhancement using rhizospheric halotolerant phosphate solubilizing bacterium *Bacillus licheniformis* QA1 and *Enterobacter asburiae* QF11 isolated from *Chenopodium quinoa* Willd. Microorganisms 8, 948.

Manzoor, H., Anjam, M.S., Saeed, F., Rasul, S., Yousaf, S., Kirn, A., Qureshi, M.K., Zafar, Z.U., Ashraf, M., Athar, H.u.R., 2022. Photosynthetic efficiency and antioxidant defense potential are key players in inducing drought tolerance in transgenic tobacco plants over-expressing *AVP1*. J. Plant Growth Regul. 41, 2653–2668.

Margalef, O., Sardans, J., Maspons, J., Molowny-Horas, R., Fernández-Martínez, M., Janssens, I.A., Richter, A., Ciais, P., Obersteiner, M., Peñuelas, J., 2021. The effect of global change on soil phosphatase activity. Glob. Change Biol. 27, 5989–6003.

Martinez, V., Läuchli, A., 1994. Salt-induced inhibition of phosphate uptake in plants of cotton (*Gossypium hirsutum* L.). New Phytol. 126, 609–614.

Matthus, E., Wilkins, K.A., Swarbreck, S.M., Doddrell, N.H., Doccula, F.G., Costa, A., Davies, J.M., 2019. Phosphate starvation alters abiotic-stress-induced cytosolic free calcium increases in roots. Plant Physiol. 179, 1754–1767.

Mehra, P., Singh, A.P., Bhadouria, J., Verma, L., Panchal, P., Giri, J., 2018. Phosphate homeostasis: links with seed quality and stress tolerance in chickpea, in: Wani, S., Jain, M. (eds.), Pulse Improvement, pp. 191–217.

Miura, K., Sato, A., Ohta, M., Furukawa, J., 2011. Increased tolerance to salt stress in the phosphate-accumulating Arabidopsis mutants *siz1* and *pho2*. Planta 234, 1191–1199.

Nagatoshi, Y., Ikazaki, K., Kobayashi, Y., Mizuno, N., Sugita, R., Takebayashi, Y., Kojima, M., Sakakibara, H., Kobayashi, N.I., Tanoi, K., et al., 2023. Phosphate starvation response precedes abscisic acid response under progressive mild drought in plants. Nat. Commun. 14, 5047.

Navarro, C., Mateo-Elizalde, C., Mohan, T.C., Sanchez-Bermejo, E., Urrutia, O., Fernandez-Muniz, M.N., Garcia-Mina, J.M., Munoz, R., Paz-Ares, J., Castrillo, G., et al., 2021. Arsenite provides a selective signal that coordinates arsenate uptake and detoxification through the regulation of PHR1 stability in Arabidopsis. Mol. Plant 14, 1489–1507.

Ni, H., Yong-Villalobos, L., Gu, M., López-Arredondo, D.L., Chen, M., Geng, L., Xu, G., Herrera-Estrella, L.R., 2025. Adaptive dynamics of extrachromosomal circular DNA in rice under nutrient stress. Nat. Commun. 16, 4150.

Nilsson, L., Lundmark, M., Jensen, P.E., Nielsen, T.H., 2012. The Arabidopsis transcription factor PHR1 is essential for adaptation to high light and retaining functional photosynthesis during phosphate starvation. Physiol. Plantarum 144, 35–47.

Noor, I., Sohail, H., Hasanuzzaman, M., Hussain, S., Li, G., Liu, J., 2022. Phosphorus confers tolerance against manganese toxicity in *Prunus persica* by reducing oxidative stress and improving chloroplast ultrastructure. Chemosphere 291, 132999.

O'Connell, C.S., Ruan, L., Silver, W.L., 2018. Drought drives rapid shifts in tropical rainforest soil biogeochemistry and greenhouse gas emissions. Nat. Commun. 9, 1348.

Ohkama-Ohtsu, N., Wasaki, J., 2010. Recent progress in plant nutrition research: cross-talk between nutrients, plant physiology and soil microorganisms. Plant Cell Physiol. 51, 1255–1264.

Ouyang, X., Hong, X., Zhao, X.Q., Zhang, W., He, X., Ma, W.Y., Teng, W., Tong, Y.P., 2016. Knock out of the *PHOSPHATE 2* gene *TaPHO2-A1* improves phosphorus uptake and grain yield under low phosphorus conditions in common wheat. Sci. Rep. 6, 29850.

Pacak, A., Barciszewska-Pacak, M., Swida-Barteczka, A., Kruszka, K., Sega, P., Milanowska, K., Jakobsen, I., Jarmolowski, A., Szweykowska-Kulinska, Z., 2016. Heat stress affects Pi-related genes expression and inorganic phosphate deposition/accumulation in barley. Front. Plant Sci. 7, 926.

Pang, J., Bansal, R., Zhao, H., Bohuon, E., Lambers, H., Ryan, M.H., Ranathunge, K., Siddique, K.H.M., 2018. The carboxylate-releasing phosphorus-mobilizing strategy can be proxied by foliar manganese concentration in a large set of chickpea germplasm under low phosphorus supply. New Phytol. 219, 518–529.

Parihar, P., Singh, S., Singh, R., Singh, V.P., Prasad, S.M., 2015. Effect of salinity stress on plants and its tolerance strategies: a review. Environ. Sci. Pollut. Res. Int. 22, 4056–4075.

Park, J.H., Bolan, N., Megharaj, M., Naidu, R., 2011. Relative value of phosphate compounds in reducing the bioavailability and toxicity of lead in contaminated soils. Water Air Soil Pollut. 223, 599–608.

Park, S.H., Jeong, J.S., Huang, C.H., Park, B.S., Chua, N.H., 2023. Inositol polyphosphates-regulated polyubiquitination of PHR1 by NLA E3 ligase during phosphate starvation response in Arabidopsis. New Phytol. 237, 1215–1228.

Parra-Almuna, L., Diaz-Cortez, A., Ferrol, N., Mora, M.d.l.L., 2018. Aluminium toxicity and phosphate deficiency activates antioxidant systems and up-regulates expression of phosphate transporters gene in ryegrass (*Lolium perenne* L.) plants. Plant Physiol. Biochem. 130, 445–454.

Pasapula, V., Shen, G., Kuppu, S., Paez-Valencia, J., Mendoza, M., Hou, P., Chen, J., Qiu, X., Zhu, L., Zhang, X., et al., 2011. Expression of an Arabidopsis vacuolar H^+-pyrophosphatase gene *(AVP1)* in cotton improves drought- and salt tolerance and increases fibre yield in the field conditions. Plant Biotechnol. J. 9, 88–99.

Paz-Ares, J., Puga, M.I., Rojas-Triana, M., Martinez-Hevia, I., Diaz, S., Poza-Carrion, C., Minambres, M., Leyva, A., 2022. Plant adaptation to low phosphorus availability: core signaling, crosstalks, and applied implications. Mol. Plant 15, 104–124.

Pedas, P., Husted, S., Skytte, K., Schjoerring, J.K., 2011. Elevated phosphorus impedes manganese acquisition by barley plants. Front. Plant Sci. 2, 37.

Pei, L., Wang, J., Li, K., Li, Y., Li, B., Gao, F., Yang, A., 2012. Overexpression of *Thellungiella halophila* H^+-pyrophosphatase gene improves low phosphate tolerance in maize. PLoS ONE 7, e43501.

Péret, B., Desnos, T., Jost, R., Kanno, S., Berkowitz, O., Nussaume, L., 2014. Root architecture responses: in search of phosphate. Plant Physiol. 166, 1713–1723.

Pizzio, G.A., Paez-Valencia, J., Khadilkar, A.S., Regmi, K., Patron-Soberano, A., Zhang, S., Sanchez-Lares, J., Furstenau, T., Li, J., Sanchez-Gomez, C., et al., 2015. Arabidopsis type I proton-pumping pyrophosphatase expresses strongly in phloem, where it is required for pyrophosphate metabolism and photosynthate partitioning. Plant Physiol. 167, 1541–1553.

Poirier, Y., Jaskolowski, A., Clúa, J., 2022. Phosphate acquisition and metabolism in plants. Curr. Biol. 32, R623–R629.

Pourrut, B., Shahid, M., Dumat, C., Winterton, P., Pinelli, E., 2011. Lead uptake, toxicity, and detoxification in plants. Rev. Environ. Contam. Toxicol. 213, 113–136.

Pradhan, A.K., Shandilya, Z.M., Sarma, P., Bora, R.K., Regon, P., Vemireddy, L.N.R., Tanti, B., 2023. Concurrent effect of aluminum toxicity and phosphorus deficiency in the root growth of aluminum tolerant and sensitive rice cultivars. Acta Physiol. Plant. 45, 33.

Puga, M.I., Mateos, I., Charukesi, R., Wang, Z., Franco-Zorrilla, J.M., de Lorenzo, L., Irigoyen, M.L., Masiero, S., Bustos, R., Rodriguez, J., et al., 2014. SPX1 is a phosphate-dependent inhibitor of Phosphate starvation response 1 in Arabidopsis. Proc. Natl. Acad. Sci. U. S. A. 111, 14947–14952.

Qiu, Q., Wang, Y., Yang, Z., Yuan, J., 2011. Effects of phosphorus supplied in soil on subcellular distribution and chemical forms of cadmium in two Chinese flowering cabbage (*Brassica parachinensis* L.) cultivars differing in cadmium accumulation. Food Chem. Toxicol. 49, 2260–2267.

Qu, X., Zhou, J., Masabni, J., Yuan, J., 2020. Phosphorus relieves aluminum toxicity in oil tea seedlings by regulating the metabolic profiling in the roots. Plant Physiol. Biochem. 152, 12–22.

Razaq, M., Zhang, P., Shen, H.L., Salahuddin, 2017. Influence of nitrogen and phosphorous on the growth and root morphology of *Acer mono*. PLoS ONE 12, e0171321.

Ren, J., Li, T., Guo, M., Zhang, Q., Ren, S., Wang, L., Wu, Q., Niu, S., Yi, K., Ruan, W., 2024. A PHR-dependent reciprocal antagonistic interplay between UV response and P-deficiency adaptation in plants. Plant Commun 6, 101140.

Rezvani, M., Zaefarian, F., Miransari, M., Nematzadeh, G.A., 2012. Uptake and translocation of cadmium and nutrients by *Aeluropus littoralis*. Arch. Agron Soil Sci. 58, 1413–1425.

Ribot, C., Wang, Y., Poirier, Y., 2008. Expression analyses of three members of the *AtPHO1* family reveal differential interactions between signaling pathways involved in phosphate deficiency and the responses to auxin, cytokinin, and abscisic acid. Planta 227, 1025–1036.

Ried, M.K., Wild, R., Zhu, J., Pipercevic, J., Sturm, K., Broger, L., Harmel, R.K., Abriata, L.A., Hothorn, L.A., Fiedler, D., et al., 2021. Inositol pyrophosphates promote the interaction of SPX domains with the coiled-coil motif of PHR transcription factors to regulate plant phosphate homeostasis. Nat. Commun. 12, 384.

Riemer, E., Qiu, D.Y., Laha, D., Harmel, R.K., Gaugler, P., Gaugler, V., Frei, M., Hajirezaei, M.R., Laha, N.P., Krusenbaum, L., et al., 2021. ITPK1 is an InsP_6/ADP phosphotransferase that controls phosphate signaling in Arabidopsis. Mol. Plant 14, 1864–1880.

Rizwan, M., Ali, S., Rehman, M.Z.U., Maqbool, A., 2019. A critical review on the effects of zinc at toxic levels of cadmium in plants. Environ. Sci. Pollut. Res. Int. 26, 6279–6289.

Rosas, A., Rengel, Z., Ribera, A., de La Luz Mora, M., 2011. Phosphorus nutrition alleviates manganese toxicity in *Lolium perenne* and *Trifolium repens*. J. Plant Nutr. Soil Sci. 174, 210–219.

Ruan, W., Guo, M., Xu, L., Wang, X., Zhao, H., Wang, J., Yi, K., 2018. An SPX-RLI1 module regulates leaf inclination in response to phosphate availability in rice. Plant Cell 30, 853–870.

Rubio, L., Linares-Rueda, A., García-Sánchez, M.J., Fernández, J.A., 2005. Physiological evidence for a sodium-dependent high-affinity phosphate and nitrate transport at the plasma membrane of leaf and root cells of *Zostera marina* L. J. Exp. Bot. 56, 613–622.

Sajwan, K.S., Paramasivam, S., Richardson, J.P., Alva, A.K., 2006. Phosphorus alleviation of cadmium phytotoxicity. J. Plant Nutr. 25, 2027–2034.

Sarkar, D., Pandey, S.K., Sud, K.C., Chanemougasoundharam, A., 2004. In vitro characterization of manganese toxicity in relation to phosphorus nutrition in potato (*Solanum tuberosum* L.). Plant Sci. 167, 977–986.

Scheible, W.R., Pant, P., Pant, B.D., Krom, N., Allen, R.D., Mysore, K.S., 2023. Elucidating the unknown transcriptional responses and PHR1-mediated biotic and abiotic stress tolerance during phosphorus limitation. J. Exp. Bot. 74, 2083–2111.

Schilling, R.K., Marschner, P., Shavrukov, Y., Berger, B., Tester, M., Roy, S.J., Plett, D.C., 2014. Expression of the Arabidopsis vacuolar H^+-pyrophosphatase gene *(AVP1)* improves the shoot biomass of transgenic barley and increases grain yield in a saline field. Plant Biotechnol. J. 12, 378–386.

Schilling, R.K., Tester, M., Marschner, P., Plett, D.C., Roy, S.J., 2017. AVP1: one protein, many roles. Trends Plant Sci. 22, 154–162.

Secco, D., Wang, C., Shou, H.X., Schultz, M.D., Chiarenza, S., Nussaume, L., Ecker, J.R., Whelan, J., Lister, R., 2015. Stress induced gene expression drives transient DNA methylation changes at adjacent repetitive elements. Elife 4, e09343.

Shi, J., Mei, C., Ge, F., Hu, Q., Ban, X., Xia, R., Xin, P., Cheng, S., Zhang, G., Nie, J., et al., 2025. Resistance to *Striga* parasitism through reduction of strigolactone exudation. Cell 188, 1955–1966.

Shukla, T., Kumar, S., Khare, R., Tripathi, R.D., Trivedi, P.K., 2015. Natural variations in expression of regulatory and detoxification related genes under limiting phosphate and arsenate stress in *Arabidopsis thaliana*. Front. Plant Sci. 6, 898.

Singh, K., Gupta, S., Singh, A.P., 2024. Review: Nutrient-nutrient interactions governing underground plant adaptation strategies in a heterogeneous environment. Plant Sci. 342, 112024.

Sinha, P., Dube, B.K., Srivastava, P., Chatterjee, C., 2006. Alteration in uptake and translocation of essential nutrients in cabbage by excess lead. Chemosphere 65, 651–656.

Siregar, A.O., Hanum, C., Hanafiah, D.S., 2021. Morphological characterization of soybean (*Glycine max* L. Merril) in drought stress condition and P fertilizer application. IOP Conf. Ser. Earth Environ. Sci. 713, 012019.

Smith, A.P., Jain, A., Deal, R.B., Nagarajan, V.K., Poling, M.D., Raghothama, K.G., Meagher, R.B., 2010. Histone H2A.Z regulates the expression of several classes of phosphate starvation response genes but not as a transcriptional activator. Plant Physiol. 152, 217–225.

Song, L., Huang, S.C., Wise, A., Castanon, R., Nery, J.R., Chen, H., Watanabe, M., Thomas, J., Bar-Joseph, Z., Ecker, J.R., 2016a. A transcription factor hierarchy defines an environmental stress response network. Science 354, aag1550.

Song, L., Yu, H., Dong, J., Che, X., Jiao, Y., Liu, D., 2016b. The molecular mechanism of ethylene-mediated root hair development induced by phosphate starvation. PLoS Genet. 12, e1006194.

Souri, Z., Karimi, N., de Oliveira, L.M., 2018. Antioxidant enzymes responses in shoots of arsenic hyperaccumulator, *Isatis cappadocica* Desv., under interaction of arsenate and phosphate. Environ. Technol. 39, 1316–1327.

Sun, T., Li, M., Shao, Y., Yu, L., Ma, F., 2017. Comprehensive genomic identification and expression analysis of the phosphate transporter (PHT) gene family in apple. Front. Plant Sci. 8, 426.

Sun, T., Zhou, B., Pei, T., Meng, H., Zhang, J., Ma, F., Wei, Q., 2021. Phosphate transporter MdPHT1;7 enhances phosphorus accumulation and improves low phosphorus and drought tolerance. J. Plant Biol. 64, 403–416.

Szekely, G., Abraham, E., Cseplo, A., Rigo, G., Zsigmond, L., Csiszar, J., Ayaydin, F., Strizhov, N., Jasik, J., Schmelzer, E., et al., 2008. Duplicated *P5CS* genes of Arabidopsis play distinct roles in stress regulation and developmental control of proline biosynthesis. Plant J. 53, 11–28.

Talbi Zribi, O., Barhoumi, Z., Kouas, S., Ghandour, M., Slama, I., Abdelly, C., 2015. Insights into the physiological responses of the facultative halophyte *Aeluropus littoralis* to the combined effects of salinity and phosphorus availability. J. Plant Physiol. 189, 1–10.

Tang, H., Niu, L., Wei, J., Chen, X., Chen, Y., 2019. Phosphorus limitation improved salt tolerance in maize through tissue mass density increase, osmolytes accumulation, and Na^+ uptake inhibition. Front. Plant Sci. 10, 856.

Tariq, A., Pan, K., Olatunji, O.A., Graciano, C., Li, Z., Li, N., Song, D., Sun, F., Wu, X., Dakhil, M.A., et al., 2019. Impact of phosphorus application on drought resistant responses of *Eucalyptus grandis* seedlings. Physiol. Plantarum 166, 894–908.

Tariq, A., Pan, K., Olatunji, O.A., Graciano, C., Li, Z., Sun, F., Zhang, L., Wu, X., Chen, W., Song, D., et al., 2018. Phosphorous fertilization alleviates drought effects on *Alnus cremastogyne* by regulating its antioxidant and osmotic potential. Sci. Rep. 8, 5644.

Tian, M.Z., Wang, H.F., Tian, Y., Hao, J., Guo, H.L., Chen, L.M., Wei, Y.K., Zhan, S.H., Yu, H.T., Chen, Y.F., 2024. ZmPHR1 contributes to drought resistance by modulating phosphate homeostasis in maize. Plant Biotechnol. J. 22, 3085–3098.

Tian, W.H., Ye, J.Y., Cui, M.Q., Chang, J.B., Liu, Y., Li, G.X., Wu, Y.R., Xu, J.M., Harberd, N.P., Mao, C.Z., et al., 2021. A transcription factor STOP1-centered pathway coordinates ammonium and phosphate acquisition in Arabidopsis. Mol. Plant 14, 1554–1568.

Tian, Y., Shi, C., Malo, C.U., Kwatcho Kengdo, S., Heinzle, J., Inselsbacher, E., Ottner, F., Borken, W., Michel, K., Schindlbacher, A., et al., 2023. Long-term soil warming decreases microbial phosphorus utilization by increasing abiotic phosphorus sorption and phosphorus losses. Nat. Commun. 14, 864.

Treeby, M.T., van Steveninck, R.F.M., 1988. The influence of salinity on phosphate uptake and distribution in lupin roots. Physiol. Plantarum 72, 617–622.

Ueda, Y., Sakuraba, Y., Yanagisawa, S., 2021. Environmental control of phosphorus acquisition: a piece of the molecular framework underlying nutritional homeostasis. Plant Cell Physiol. 62, 573–581.

Umehara, M., Hanada, A., Magome, H., Takeda-Kamiya, N., Yamaguchi, S., 2010. Contribution of strigolactones to the inhibition of tiller bud outgrowth under phosphate deficiency in rice. Plant Cell Physiol. 51, 1118–1126.

Vance, C.P., Uhde-Stone, C., Allan, D.L., 2003. Phosphorus acquisition and use: critical adaptations by plants for securing a nonrenewable resource. New Phytol. 157, 423–447.

Verma, T.S., Minhas, R.S., 1987. Zinc and phosphorus interaction in a wheat-maize cropping system. Fertil. Res. 13, 77–86.

Vromman, D., Martinez, J.P., Lutts, S., 2017. Phosphorus deficiency modifies as translocation in the halophyte plant species *Atriplex atacamensis*. Ecotoxicol. Environ. Saf. 139, 344–351.

Wang, C., Wei, Q., Zhang, K., Wang, L., Liu, F., Zhao, L., Tan, Y., Di, C., Yan, H., Yu, J., et al., 2013. Down-regulation of *OsSPX1* causes high sensitivity to cold and oxidative stresses in rice seedlings. PLoS ONE 8, e81849.

Wang, C., Ying, S., Huang, H., Li, K., Wu, P., Shou, H., 2009. Involvement of *OsSPX1* in phosphate homeostasis in rice. Plant J. 57, 895–904.

Wang, D., Lv, S., Guo, Z., Lin, K., Zhang, X., Jiang, P., Lou, T., Yi, Z., Zhang, B., Xie, W., et al., 2024. *PHT1;5* repressed by ANT mediates Pi acquisition and distribution under low Pi and salinity in salt cress. Plant Cell Physiol. 65, 20–34.

Wang, H., Wang, T., Ahmad, I., 2015. Involvement of phosphate supplies in different transcriptional regulation pathway of *Oryza sativa* L.'s antioxidative system in response to arsenite and cadmium stress. Ecotoxicology 24, 1259–1268.

Wang, R., Liu, X., Zhu, H., Yang, Y., Cui, R., Fan, Y., Zhai, X., Yang, Y., Zhang, S., Zhang, J., et al., 2023a. Transcription factors GmERF1 and GmWRKY6 synergistically regulate low phosphorus tolerance in soybean. Plant Physiol. 192, 1099–1114.

Wang, T., Xing, J., Liu, Z., Zheng, M., Yao, Y., Hu, Z., Peng, H., Xin, M., Zhou, D., Ni, Z., et al., 2019a. Histone acetyltransferase GCN5-mediated regulation of long non-coding RNA *At4* contributes to phosphate starvation response in Arabidopsis. J. Exp. Bot. 70, 6337–6348.

Wang, X., Ai, S., Liao, H., 2023b. Deciphering interactions between phosphorus status and toxic metal exposure in plants and rhizospheres to improve crops reared on acid soil. Cells 12, 441.

Wang, X., Yuan, D., Liu, Y., Liang, Y., He, J., Yang, X., Hang, R., Jia, H., Mo, B., Tian, F., et al., 2023c. INDETERMINATE1 autonomously regulates phosphate homeostasis upstream of the miR399-*ZmPHO2* signaling module in maize. Plant Cell 35, 2208–2231.

Wang, X.Q., Ruan, W.Y., Yi, K.K., 2019b. Internal phosphate starvation signaling and external phosphate availability have no obvious effect on the accumulation of cadmium in rice. J. Integr. Agric. 18, 2153–2161.

Wang, Y., Gao, H., He, L., Zhu, W., Yan, L., Chen, Q., He, C., 2019c. The *PHOSPHATE1* genes participate in salt and Pi signaling pathways and play adaptive roles during soybean evolution. BMC Plant Biol. 19, 353.

Wang, Y., Wang, Z., Du, Q., Wang, K., Zou, C., Li, W.X., 2023d. The long non-coding RNA *PILNCR2* increases low phosphate tolerance in maize by interfering with miRNA399-guided cleavage of *ZmPHT1s*. Mol. Plant 16, 1146–1159.

Wang, Z., Ruan, W., Shi, J., Zhang, L., Xiang, D., Yang, C., Li, C., Wu, Z., Liu, Y., Yu, Y., et al., 2014. Rice SPX1 and SPX2 inhibit phosphate starvation responses through interacting with PHR2 in a phosphate-dependent manner. Proc. Natl. Acad. Sci. U. S. A. 111, 14953–14958.

Ward, C.L., Kleinert, A., Scortecci, K.C., Benedito, V.A., Valentine, A.J., 2011. Phosphorus-deficiency reduces aluminium toxicity by altering uptake and metabolism of root zone carbon dioxide. J. Plant Physiol. 168, 459–465.

Whitfield, H., White, G., Sprigg, C., Riley, A.M., Potter, B.V.L., Hemmings, A.M., Brearley, C.A., 2020. An ATP-responsive metabolic cassette comprised of inositol tris/tetrakisphosphate kinase 1 (ITPK1) and inositol pentakisphosphate 2-kinase (IPK1) buffers diphosphosphoinositol phosphate levels. Biochem. J. 477, 2621–2638.

Wild, R., Gerasimaite, R., Jung, J.Y., Truffault, V., Pavlovic, I., Schmidt, A., Saiardi, A., Jessen, H.J., Poirier, Y., Hothorn, M., et al., 2016. Control of eukaryotic phosphate homeostasis by inositol polyphosphate sensor domains. Science 352, 986–990.

Xiao, X.L., Zhang, J.Q., Satheesh, V., Meng, F.X., Gao, W.L., Dong, J.S., Zheng, Z., An, G.Y., Nussaume, L., Liu, D., et al., 2021. SHORT-ROOT stabilizes PHOSPHATE1 to regulate phosphate allocation in Arabidopsis. Nat. Plants 8, 1074–1081.

Xie, W., Yang, J., Gao, S., Yao, R., Wang, X., 2022. The effect and influence mechanism of soil salinity on phosphorus availability in coastal salt-affected soils. Water 14, 2804.

Xu, J.M., Wang, Z.Q., Wang, J.Y., Li, P.F., Jin, J.F., Chen, W.W., Fan, W., Kochian, L. V., Zheng, S.J., Yang, J.L., 2020. Low phosphate represses histone deacetylase complex1 to regulate root system architecture remodeling in Arabidopsis. New Phytol. 225, 1732–1745.

Xu, L., Zhao, H., Wan, R., Liu, Y., Xu, Z., Tian, W., Ruan, W., Wang, F., Deng, M., Wang, J., et al., 2019. Identification of vacuolar phosphate efflux transporters in land plants. Nat. Plants 5, 84–94.

Yang, D., Guo, Z., Green, I.D., Xie, D., 2016. Effect of cadmium accumulation on mineral nutrient levels in vegetable crops: potential implications for human health. Environ. Sci. Pollut. Res. Int. 23, 19744–19753.

Yang, H., Knapp, J., Koirala, P., Rajagopal, D., Peer, W.A., Silbart, L.K., Murphy, A., Gaxiola, R.A., 2007. Enhanced phosphorus nutrition in monocots and dicots over-expressing a phosphorus-responsive type I H^+-pyrophosphatase. Plant Biotechnol. J. 5, 735–745.

Yang, H., Zhang, X., Gaxiola, R.A., Xu, G., Peer, W.A., Murphy, A.S., 2014. Over-expression of the Arabidopsis proton-pyrophosphatase *AVP1* enhances transplant survival, root mass, and fruit development under limiting phosphorus conditions. J. Exp. Bot. 65, 3045–3053.

Yang, S.Y., Lin, W.Y., Hsiao, Y.M., Chiou, T.J., 2024a. Milestones in understanding transport, sensing, and signaling of the plant nutrient phosphorus. Plant Cell 36, 1504–1523.

Yang, W., Luo, L., Bostick, B.C., Wiita, E., Cheng, Y., Shen, Y., 2021. Effect of combined arsenic and lead exposure on their uptake and translocation in Indian mustard. Environ. Pollut. 274, 116549.

Yang, W.T., Bae, K.D., Lee, S.W., Jung, K.H., Moon, S., Basnet, P., Choi, I.Y., Um, T., Kim, D.H., 2024b. The MYB-CC transcription factor PHOSPHATE STARVATION RESPONSE-LIKE 7 (PHL7) functions in phosphate homeostasis and affects salt stress tolerance in rice. Plants (Basel) 13, 637.

Yang, Y., Chen, R., Fu, G., Xiong, J., Tao, L., 2015. Phosphate deprivation decreases cadmium (Cd) uptake but enhances sensitivity to Cd by increasing iron (Fe) uptake and inhibiting phytochelatins synthesis in rice (*Oryza sativa*). Acta Physiol. Plant. 38, 28.

Yong-Villalobos, L., Gonzalez-Morales, S.I., Wrobel, K., Gutierrez-Alanis, D., Cervantes-Perez, S.A., Hayano-Kanashiro, C., Oropeza-Aburto, A., Cruz-Ramirez, A., Martinez, O., Herrera-Estrella, L., 2015. Methylome analysis reveals an important role for epigenetic changes in the regulation of the Arabidopsis response to phosphate starvation. Proc. Natl. Acad. Sci. U. S. A. 112, E7293–E7302.

Yuan, K., Zhang, H., Yu, C.J., Luo, N., Yan, J.J., Zheng, S., Hu, Q.L., Zhang, D.H., Kou, L.Q., Meng, X.B., et al., 2023. Low phosphorus promotes NSP1–NSP2 heterodimerization to enhance strigolactone biosynthesis and regulate shoot and root architecture in rice. Mol. Plant 16, 1811–1831.

Yue, Z., Shen, Y., Chen, Y., Liang, A., Chu, C., Chen, C., Sun, Z., 2019. Microbiological insights into the stress-alleviating property of an endophytic *Bacillus altitudinis* WR10 in wheat under low-phosphorus and high-salinity stresses. Microorganisms 7, 508.

Zahraeifard, S., Foroozani, M., Sepehri, A., Oh, D.H., Wang, G., Mangu, V., Chen, B., Baisakh, N., Dassanayake, M., Smith, A.P., 2018. Rice H2A.Z negatively regulates genes responsive to nutrient starvation but promotes expression of key housekeeping genes. J. Exp. Bot. 69, 4907–4919.

Zeng, H.Q., Zhu, Q.Q., Yuan, P.G., Yan, Y., Yi, K.K., Du, L.Q., 2023. Calmodulin and calmodulin-like protein-mediated plant responses to biotic stresses. Plant Cell Environ. 46, 3680–3703.

Zhang, C., Meng, S., Li, M., Zhao, Z., 2016. Genomic identification and expression analysis of the phosphate transporter gene family in poplar. Front. Plant Sci. 7, 1398.

Zhang, H., Shi, L., Lu, H., Shao, Y., Liu, S., Fu, S., 2020. Drought promotes soil phosphorus transformation and reduces phosphorus bioavailability in a temperate forest. Sci. Total Environ. 732, 139295.

Zhang, T., Yang, X., Zeng, Z., Li, Q., Yu, J., Deng, H., Shi, Y., Zhang, H., Gerson, A.R., Pi, K., 2024. Combined remediation effects of sewage sludge and phosphate fertilizer on Pb-polluted soil from a Pb-acid battery plant. Environ. Manag. 74, 928–941.

Zhang, X., Gao, Y., Zhuang, L., Huang, B., 2022a. Phosphatidic acid priming-enhanced heat tolerance in tall fescue (*Festuca arundinacea*) involves lipidomic reprogramming of lipids for membrane stability and stress signaling. Plant Growth Regul. 99, 527–538.

Zhang, X.R., Wang, B.M., Zhao, Y.J., Zhang, J.R., Li, Z.X., 2019. Auxin and GA signaling play important roles in the maize response to phosphate deficiency. Plant Sci. 283, 177–188.

Zhang, Y., Li, T.T., Wang, L.F., Guo, J.X., Lu, K.K., Song, R.F., Zuo, J.X., Chen, H.H., Liu, W.C., 2022b. Abscisic acid facilitates phosphate acquisition through the transcription factor ABA INSENSITIVE5 in Arabidopsis. Plant J. 111, 269–281.

Zhao, L., Liu, F., Xu, W., Di, C., Zhou, S., Xue, Y., Yu, J., Su, Z., 2009. Increased expression of *OsSPX1* enhances cold/subfreezing tolerance in tobacco and *Arabidopsis thaliana*. Plant Biotechnol. J. 7, 550–561.

Zhao, Y., Li, Y., Yang, F., 2021. Critical review on soil phosphorus migration and transformation under freezing-thawing cycles and typical regulatory measurements. Sci. Total Environ. 751, 141614.

Zhao, Y., Zhang, C., Wang, C., Huang, Y., Liu, Z., 2020. Increasing phosphate inhibits cadmium uptake in plants and promotes synthesis of amino acids in grains of rice. Environ. Pollut. 257, 113496.

Zheng, S.J., Yang, J.L., He, Y.F., Yu, X.H., Zhang, L., You, J.F., Shen, R.F., Matsumoto, H., 2005. Immobilization of aluminum with phosphorus in roots is associated with high aluminum resistance in buckwheat. Plant Physiol. 138, 297–303.

Zheng, Z., Wang, Z., Wang, X., Liu, D., 2019. Blue light-triggered chemical reactions underlie phosphate deficiency-induced inhibition of root elongation of Arabidopsis seedlings grown in petri dishes. Mol. Plant 12, 1515–1523.

Zhou, J., Hu, Q., Xiao, X., Yao, D., Ge, S., Ye, J., Li, H., Cai, R., Liu, R., Meng, F., et al., 2021. Mechanism of phosphate sensing and signaling revealed by rice SPX1-PHR2 complex structure. Nat. Commun. 12, 7040.

Zhu, J., Lau, K., Puschmann, R., Harmel, R.K., Zhang, Y., Pries, V., Gaugler, P., Broger, L., Dutta, A.K., Jessen, H.J., et al., 2019. Two bifunctional inositol pyrophosphate kinases/phosphatases control plant phosphate homeostasis. Elife 8, e43582.

Zhu, W., Miao, Q., Sun, D., Yang, G., Wu, C., Huang, J., Zheng, C., 2012. The mitochondrial phosphate transporters modulate plant responses to salt stress via affecting ATP and gibberellin metabolism in *Arabidopsis thaliana*. PLoS ONE 7, e43530.

Zimmerli, C., Ribot, C., Vavasseur, A., Bauer, H., Hedrich, R., Poirier, Y., 2012. *PHO1* expression in guard cells mediates the stomatal response to abscisic acid in Arabidopsis. Plant J. 72, 199–211.