

# *Emerging roles of inositol pyrophosphates in signaling plant phosphorus status and phytohormone signaling*

Article

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1 REVIEW ARTICLE

2 **Emerging roles of inositol pyrophosphates in signaling plant phosphorus status**  
3 **and phytohormone signaling**

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21 *Abbreviations*—P, phosphorus; Pi, phosphate; PUpE, phosphate uptake efficiency; PUtE, phosphate  
22 utilization efficiency; P1BS, PHR1-binding sequence; InsPs, inositol phosphates; PP-InsPs,  
23 inositol pyrophosphates; PA, phytic acid; PSR, phosphate starvation response; PSI genes,  
24 phosphate starvation induced genes; PAGE, polyacrylamide gel electrophoresis; IAA, auxin; JA,  
25 jasmonic acid; SA, salicylic acid.

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28 **ABSTRACT**

29 Phosphorus (P) is an indispensable macronutrient serving a variety of functions in plants. Inositol  
30 pyrophosphates (PP-InsPs) nutrient messengers play vital roles in the signaling of P status and  
31 plant growth and development. In this review, we summarize (1) the biosynthetic pathway of  
32 PP-InsPs and their regulation by plant P status, (2) the effects of PP-InsPs on the function of the  
33 SPX-domain containing proteins in signaling plant P status, (3) the effects of inositol  
34 pyrophosphates on auxin signaling through TIR1 and on jasmonate signaling through COI1, and  
35 (4) the potential crosstalk between P status signaling and phytohormone signaling in plants  
36 mediated by inositol pyrophosphates. It is concluded that the interactions between inositol  
37 pyrophosphates and their binding proteins are central to plant P status and developmental  
38 responses to different P supply.

39 **Keywords:** inositol phosphates; inositol pyrophosphates; the SPX-domain containing proteins;  
40 TIR1; COI1; phosphorus status; auxin; jasmonic acid

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## 57 INTRODUCTION

58 Phosphorus (P) is an indispensable macronutrient for plants (White and Hammond 2008). It is  
59 largely present in nucleic acids, phospholipids and phosphorylated metabolites (White and  
60 Hammond 2008; Scheible and Rojas-Triana 2015). Although the total amount of P in soil is often  
61 abundant, it mainly exists in the form of organic P and insoluble P, while the quantity and  
62 concentration of inorganic phosphate (Pi) that can be taken up directly by plants in the soil  
63 solution is small (Raghothama and Karthikeyan 2005; White and Hammond 2008; Peret et al.  
64 2011; Lopez-Arredondo et al. 2014; Wang et al. 2018). The application of inorganic Pi fertilizer is  
65 the main agronomic method to increase Pi phytoavailability, but only 30-60% of the applied Pi  
66 fertilizer is utilized by crops in the year that it is applied (Schachtman et al. 1998; Syers et al.  
67 2008). Excessive application of Pi fertilizers not only increases the cost of agricultural activities,  
68 but also increases the flow of P into rivers, lakes, and oceans, causing environmental problems  
69 (Scheible and Rojas-Triana 2015).

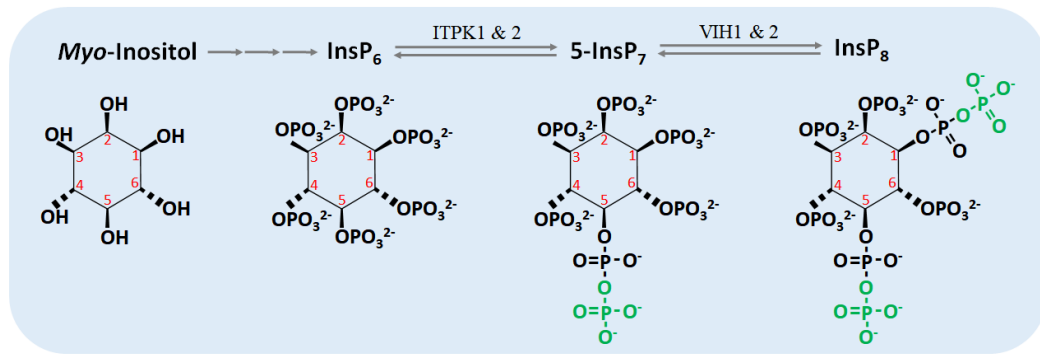
70 Through evolution, plants have developed a series of morphological, physiological and  
71 molecular mechanisms to improve Pi uptake efficiency (PUpE) and Pi utilization efficiency (PUtE)  
72 (White and Hammond 2008; Veneklaas et al. 2012; Wang et al. 2019b; Han et al. 2022b; Wen et al.  
73 2022). Low Pi availability promotes the elongation of lateral roots and formation of root hairs  
74 (Lynch 2011; Peret et al. 2011), as well as the establishment of mycorrhizal symbiosis  
75 (Lopez-Arredondo et al. 2014; Wen et al. 2022), enabling greater access to the soil volume. The  
76 synthesis and secretion of plant acid phosphatases, ribonucleases, and organic acids are induced  
77 by low Pi availability, which release Pi from organophosphates, RNA, and Pi-metal ion complexes,  
78 respectively (Fang et al. 2009; Du et al. 2022; Wen et al. 2022). Low Pi availability also increases  
79 the abundance of Pi transporters to improve Pi uptake by plants (White and Hammond 2008;  
80 Lopez-Arredondo et al. 2014). The glycolysis- and oxidative-phosphorylation pathways in plant  
81 cells are severely curtailed under low Pi availability, decreasing the P demand of metabolism  
82 (Plaxton and Tran 2011) and the phospholipid content of lipid membranes, while the  
83 non-phospholipid content is increased, thereby decreasing tissue P requirements (White and  
84 Hammond 2008; Sun et al. 2021; Yang et al. 2021). The redistribution of P from old leaves to  
85 developing tissues is also enhanced in plants lacking P to maintain photosynthetic capacity  
86 (Scheible and Rojas-Triana 2015).

87 An elaborate signaling network regulates the morphological, physiological and biochemical  
88 adaptations to fluctuations in Pi supply, which has been well reviewed (Franco-Zorrilla et al. 2004;  
89 Secco et al. 2012; Liu et al. 2014; Gu et al. 2016; Wang and Liu 2018; Pan et al. 2019). In  
90 particular, fluctuations in Pi supply alter hormone biosynthesis, transport, and signaling, which  
91 have been implicated in plant acclimation to vagaries in Pi availability (Chiou and Lin 2011).  
92 Although substantial insights into the molecular biology of the regulatory networks regulating  
93 plant P status and phytohormone signaling have been obtained, exact knowledge is limited on how  
94 plants sense external Pi availability and to evoke proper intracellular responses.

95 This review summarizes the biosynthetic pathway of inositol (pyro)phosphates and their  
96 regulation by plant P status, and the functions of the SPX-domain containing proteins that bind  
97 inositol (pyro)phosphates in signaling plant P status and co-receptors in phytohormone response  
98 pathways. It highlights the possible new roles of inositol (pyro)phosphates in mediating plant P  
99 status, and the crosstalk between P status and phytohormone signaling.

## 100 **BIOSYNTHESIS OF INOSITOL PYROPHOSPHATES IN PLANTS**

101 *Myo*-, *D-chiro*-, *L-chiro*-, *muco*-, *scyllo*-, and *neo*- inositol are naturally occurring isomers, of  
102 which *myo*-inositol is the most abundant form (Michell 2008; Pani et al. 2020). The *myo*-inositol  
103 isomer is the skeleton for inositol phosphates (InsPs), which are a series of phosphorylated inositol  
104 metabolites synthesized by the multi-step phosphorylation of *myo*-inositol. Phytic acid (PA) is the  
105 fully phosphorylated *myo*-inositol (Fig. 1). PA is synthesized via lipid-dependent or  
106 lipid-independent pathways (Wang et al. 2022). Both lipid-dependent and lipid-independent  
107 pathways rely on phosphorylation of several kinases to produce InsP<sub>5</sub>, which is subsequently  
108 phosphorylated by IPK1 (inositol pentakisphosphate 2-kinase) to yield PA (Wang et al. 2022). PA  
109 can be (1) transported via a multidrug-resistance-associated protein (MRP) to protein storage  
110 vacuoles (PSV) where it is accumulated into globoids in the form of PA salts (Otegui et al. 2002;  
111 Shi et al. 2007; Krishnan 2008; Regvar et al. 2011); (2) decomposed by phytase to release Pi,  
112 inositol and associated cations; or (3) used as a precursor to be further phosphorylated into inositol  
113 pyrophosphates (PP-InsPs). PA plays a central role in the synthesis of PP-InsPs (Fig. 1).



114

115 **Fig. 1** The chemical structure of *myo*-inositol, phytic acid (InsP<sub>6</sub>), and inositol pyrophosphates (5-InsP<sub>7</sub> and  
 116 InsP<sub>8</sub>). ITPK1 & 2, Inositol tetrakisphosphate kinase 1 & 2; VIH1 & 2, Diphosphoinositol pentakisphosphate  
 117 kinase 1 & 2.

118 The biosynthesis of PP-InsPs in plants is mainly catalyzed by two types of bifunctional  
 119 enzymes, inositol tetrakisphosphate kinase (ITPK) and diphosphoinositol pentakisphosphate  
 120 kinase (VIH) (Fig. 1). In *Arabidopsis*, PA can be phosphorylated at the 5-position phosphate group  
 121 by ITPK1 to yield InsP<sub>7</sub>, and kinetic analysis revealed that ITPK1 exhibits an extremely high K<sub>M</sub>  
 122 for ATP of approximately 520 μM (Laha et al. 2019; Riemer et al. 2021). ITPK1 not only  
 123 phosphorylates InsP<sub>6</sub> to generate InsP<sub>7</sub>, but also mediates the decomposition of 5-InsP<sub>7</sub> (Riemer et  
 124 al. 2021). An interesting question regarding bifunctional enzyme is how ITPK1 catalyzes the  
 125 reverse reaction of the kinase activity as there is no phosphatase domain within ITPK1 protein.  
 126 Kinetic analyses demonstrate that ITPK1 has comparable K<sub>M</sub> values for ATP and ADP, and ITPK1  
 127 can shift its activity to an ADP-phosphotransferase that can transfer Pi from the 5-position  
 128 phosphate group of 5-InsP<sub>7</sub> to ADP at low ATP/ADP ratio conditions (Riemer et al. 2021).  
 129 Additionally, there was no ADP-phosphotransferase activity of ITPK1 with any other InsP<sub>7</sub> isomer,  
 130 suggesting a substrate specificity for the reaction. Collectively, Pi-dependent changes in ATP  
 131 concentration and the ATP/ADP ratio may ultimately determine the production of 5-InsP<sub>7</sub> by  
 132 shifting ITPK1-mediated InsP<sub>6</sub> kinase and ADP-phosphotransferase activities (Riemer et al. 2021).

133 InsP<sub>7</sub> is phosphorylated by VIH1 and VIH2 to generate InsP<sub>8</sub>. The products of InsP<sub>8</sub> are likely  
 134 1,5-InsP<sub>8</sub> and its enantiomeric isomer 3,5-InsP<sub>8</sub>, but the enantiomer identity has not been resolved  
 135 (Fig. 1; Dong et al. 2019; Zhu et al. 2019; Laha et al. 2019). Both VIH1 and VIH2 are bifunctional  
 136 enzymes that synthesize and decompose InsP<sub>8</sub>. Although VIHs contain both kinase and  
 137 phosphatase domains, only mutating the kinase active center, but not the phosphatase active center,  
 138 leads to constitutive P starvation responses (PSR) and P accumulation (Dong et al. 2019). *In vitro*

139 experiments show that  $Mg^{2+}$ -ATP concentrations control the relative kinase and phosphatase  
140 activities of VIH1 and VIH2 and that Pi inhibits the phosphatase activity of the enzyme (Zhu et al.  
141 2019). Thus, VIH1 and VIH2 regulate the production of InsP<sub>8</sub> depending on intracellular ATP and  
142 Pi concentrations, which vary with external P supply (Zhu et al. 2019).

## 143 **INOSITOL PYROPHOSPHATES SIGNALING OF PLANT**

### 144 **PHOSPHORUS STATUS**

#### 145 **Inositol pyrophosphates control phosphorus status**

146 The SPX (SYG1, Pho81 and XPR1) domain (PfamPF03105) were named after a homologous  
147 sequence shared by yeast SYG1, PHO81 and human XPR1 (Secco et al. 2012). In plants, the SPX  
148 domain-containing proteins can be divided into four subfamilies: SPX proteins, SPX-EXS (EXS,  
149 named after the yeast ERD1, the human XPR1 and the yeast SYG1) proteins, SPX-MFS (MFS,  
150 the major facilitator superfamily) proteins, and SPX-RING (RING, the really interesting new gene)  
151 proteins (Secco et al. 2012). The SPX domain in the SPX domain-containing proteins contains a  
152 putative binding site for PP-InsPs, which could play a key role in signaling plant P status and  
153 affecting the regulation of plant P as an intracellular sensor in plants (Fig. 2A, Fig. 2B, Table1).  
154 Since many InsPs and PP-InsPs exist in plant cells, one question is which molecules are involved  
155 in signaling plant P status and affecting internal P concentrations. Using titanium dioxide  
156 (TiO<sub>2</sub>)-based pull-down followed by PAGE, and capillary electrophoresis electrospray ionization  
157 mass spectrometry (CE-ESI-MS), different species of InsP<sub>6</sub>, InsP<sub>7</sub>, and InsP<sub>8</sub> were quantified  
158 under P-sufficient and -deficient conditions (Riemer et al. 2021). In *Arabidopsis thaliana*, the  
159 concentrations of InsP<sub>6</sub>, InsP<sub>7</sub> and InsP<sub>8</sub> decreased significantly upon P deficiency. After  
160 resupplying P, the increase of InsP<sub>7</sub> and InsP<sub>8</sub> concentrations were significantly larger than that of  
161 InsP<sub>6</sub> concentration, with the concentration of InsP<sub>8</sub> increasing approximately 100-fold, greatly  
162 exceeding the concentration detected in plants grown continuously with an adequate P supply  
163 (Riemer et al. 2021). InsP<sub>7</sub> and InsP<sub>8</sub> are most sensitive to fluctuations in external P supply,  
164 suggesting that they may be intracellular signaling molecules allowing plants to respond to  
165 external P supply. Similar responses are also observed in rice and *Physcomitrium patens*,  
166 suggesting that the response to P availability in the biosynthesis of InsP<sub>7</sub> and InsP<sub>8</sub> is  
167 evolutionarily conserved in plant kingdom (Riemer et al. 2021).



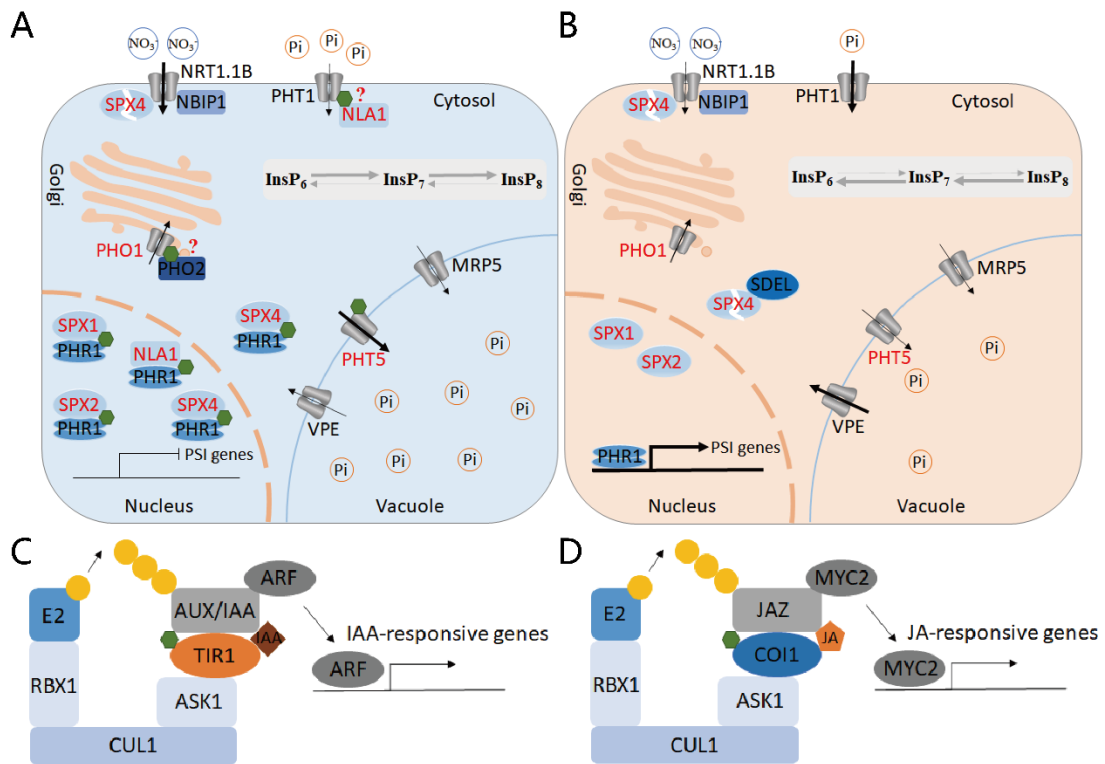
168 Similar to IPK1, ITPK1 is widely distributed at the tissue level, localized to the cytoplasm  
169 and nucleus, and the expression of *ITPK1* is not induced by P deficiency (Kuo et al. 2018). The  
170 *ipk1-1/itpk1* double mutant exhibits more severe growth reduction than single mutants and plants  
171 that proceeded to the reproductive stage have aborted seeds (Kuo et al. 2018). Although tissue P  
172 concentrations are greater in the *ipk1-1/itpk1* double mutant than in single mutants, by 50~70%,  
173 this might be attributed to the relative 50~80% reduction in fresh weight of the former. The  
174 expression of phosphate starvation induced (PSI) genes in *ipk1-1/itpk1* double and single mutants  
175 was comparable, indicating that ITPK1 and IPK1 are in a common response pathway to plant P  
176 status (Kuo et al. 2018).

177 *In vitro* assays have shown that ITPK2 also has InsP<sub>6</sub> kinase activity, however, only the  
178 disruption of ITPK1, but not of ITPK2, results in growth defects and constitutive P  
179 overaccumulation (Riemer et al. 2021). Concentrations of 5-InsP<sub>7</sub>, InsP<sub>8</sub>, and other inositol  
180 (pyro)phosphates in the *itpk2* mutant were similar to wild-type (Laha et al. 2019; Riemer et al.  
181 2021). Despite the different phenotypes of the *itpk2* and *itpk1* mutants, the growth reduction and P  
182 hyperaccumulation in *itpk1* are not as severe as *vih1/vih2* mutants, which is unable to catalyze the  
183 conversion of InsP<sub>7</sub> to InsP<sub>8</sub> (Fig. 1), suggesting partial functional redundancy of *ITPK2* and  
184 *ITPK1* (Dong et al. 2019; Zhu et al. 2019; Riemer et al. 2021). However, when grown in  
185 P-sufficient conditions, the *itpk1/itpk2* double mutant exhibits severe growth reduction, and its  
186 shoot P concentration was approximately 3.5-fold and 2.1-fold higher than wild-type and *itpk1*,  
187 respectively, suggesting that ITPK2 plays a relatively minor role in signaling plant P status in the  
188 presence of a functional ITPK1 (Riemer et al. 2021).

189 Among a series of mutants in the PA and PP-InsPs biosynthesis pathways, only *ipk1-1* and  
190 *itpk1* show significant increases in shoot P concentration from seedlings to the mature plant (Kuo  
191 et al. 2018). PHOSPHATE2 (PHO2) is an ubiquitin-conjugating enzyme (UBC24) that  
192 ubiquitinates the SPX-EXS Pi transporter PHOSPHATE1 (PHO1), resulting in its degradation and a  
193 decrease in xylem Pi loading (Liu et al. 2012). Compared with *ipk1-1* and *pho2* single mutants, the  
194 *ipk1-1/pho2* double mutant showed additive shoot P accumulation, suggesting that P  
195 hyperaccumulation in the *ipk1-1* mutant was mainly independent of the PHO2 regulatory pathway  
196 (Kuo et al. 2014). In comparison with the *ipk1-1* single mutant, the P concentration and the  
197 expression of several genes regulated directly by the transcription factor PHOSPHATE

198 STARVATION RESPONSE1 (PHR1) and PHR1-like 1 (PHL1) in the *ipk1-1/phr1* double and  
199 *ipk1-1/phr1/phl1* triple mutants were significantly decreased, but they were still greater than those  
200 in *phr1* and *phr1/phl1* mutants, respectively, indicating that PHR1 (PHL1) plays a partial role in  
201 upregulating the expression of PSI genes and P hyperaccumulation in the *ipk1-1* mutant (Kuo et al.  
202 2014). Similarly, the shoot P concentration of the *itpk1/pho2* double mutant was approximately  
203 twice that of *itpk1* and *pho2* mutants, suggesting that P hyperaccumulation in the *itpk1* mutant is  
204 also independent of the PHO2 regulatory pathway (Riemer et al. 2021). Although *phr1/itpk1* and  
205 *phr1/phl1/itpk1* mutants accumulate more P than *phl1* and *phr1/phl1* mutants, respectively, the  
206 relative increments are smaller than in the presence of functional PHR1 and PHL1, suggesting that  
207 PHR1 (PHL1) is tightly linked to ITPK1-mediated regulation of plant P status (Riemer et al.  
208 2021).

209 The growth of *vih2/itpk1* is slower than *itpk1*, and shoot P accumulation in *vih2/itpk1* is  
210 greater by about 27%, suggesting that VIH2 and ITPK1 are located in the same regulatory  
211 pathway affecting plant P status (Riemer et al. 2021). The concentration of InsP<sub>8</sub> was decreased in  
212 *vih2* and undetectable in the *vih1/vih2* double mutants (Dong et al. 2019). Although *vih1* and *vih2*  
213 single mutants have similar P concentrations to wild-type plants, *vih1/vih2* double mutants have  
214 severely restricted growth and significantly increased P accumulation, indicating that VIH1 and  
215 VIH2 are functionally redundant in Arabidopsis (Dong et al. 2019; Zhu et al. 2019). Knockout of  
216 PHR1 in the *vih1/vih2* mutant partially complements its phenotype, suggesting that VIH1/VIH2  
217 functions in signaling and regulating plant P status (Dong et al. 2019; Zhu et al. 2019).



**Fig. 2 Inositol pyrophosphates binding proteins in plant cells and their function.**

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219

220 (A) Under P sufficient conditions, Pi stimulates the synthesis of PP-InsPs, and PP-InsPs involved in signaling plant

221 P status by regulating the function of the SPX domain-containing proteins. (B) Under P deficient conditions,

222 PP-InsPs are hydrolyzed and their actions on the SPX-domain containing proteins are abolished. (C) InsPs and

223 PP-InsPs involved in auxin signaling by regulating the function of TIR1 in plants. (D) InsPs and PP-InsPs involved

224 in jasmonic acid signaling by regulating the function of COI1 in plants. Green hexagons indicate InsPs or PP-InsPs,

225 and yellow circle indicates ubiquitin.

226

**Table 1 Inositol pyrophosphates binding proteins in plants and their functions**

PP-InsPs binding proteins	Interaction protein	InsPs/PP-InsPs dependency	Consequence of interaction	References
<b>SPX</b> (AtSPX1~AtSPX4; OsSPX1~OsSPX6)	AtPHR1/OsPHR2	Yes (InsP <sub>6/7/8</sub> )	Block PHR-mediated transcription activation of PSI genes	Puga et al. 2014; Wang et al. 2014b; Wild et al. 2016; Dong et al. 2019; Zhou et al. 2021; Guan et al. 2022
	OsSDEL1/2	No	Degrade SPX4 to release PHR	Ruan et al. 2019
	OsNRT1.1B	No	Recruit NBIP1 to degrade SPX4	Hu et al. 2019
	OsNBIP1	No	Degrade SPX4 to release PHR and NLP	Hu et al. 2019
	OsNLP3	No	Block NLP-mediated transcription activation of nitrate responsive genes	Hu et al. 2019
	OsRLI1	Unknown	Inhibit RLI1 to regulate leaf inclination	Ruan et al. 2018; Zhang et al. 2021

	AtPAP1	Yes (InsP <sub>6</sub> )	Block PAP1-mediated transcription activation of anthocyanin biosynthesis	He et al. 2020b
<b>SPX-EXS</b> (AtPHO1; AtPHO1;H1~H10; OsPHO1;1~1;3)	OsBHLH6	Unknown	Block the effect of SPX4 on PHR2	He et al. 2021a
	AtPHO2	Unknown	Degrade AtPHO1 to reduce Pi loading	Liu et al. 2012
	Within VPT1 protein (i.e., SPX domain and MFS domain)	Yes (InsP <sub>6</sub> )	Activate the transport activity of VPT1	Luan et al. 2022
<b>SPX-MFS</b> (AtSPX-MFS1~3; OsSPX-MFS1~4; FaVPT1)	AtPHT1	Unknown	Degrade AtPHT1 to reduce Pi uptake	Kant et al. 2011; Lin et al. 2013
	OsPHT1	Unknown	Degrade OsPHT1 to reduce Pi uptake	Yue et al. 2017; Yang et al. 2020
	AtNRT1.7	Unknown	Degrade NRT1;7 to reduce nitrate redistribution	Liu et al. 2017
<b>SPX-RING</b> (AtNLA1~AtNLA2; OsNLA1~OsNLA2)	AtORE1	Unknown	Degrade ORE1 to alleviate leaf senescence	Park et al. 2018
	AtPHR1	Yes (InsP <sub>6</sub> )	Degrade PHR1 to block transcription activation of PSI genes	Park et al. 2022
<b>TIR1</b>	IAA7	Yes (InsP <sub>6/7</sub> )	Degrade IAAs to release ARFs	Tan et al. 2007; Calderon Villalobos et al. 2012; Laha et al. 2022
<b>COI1</b>	JAZ	Yes (InsP <sub>6</sub> )	Degrade JAZs to release MYCs	Sheard et al. 2010; Mosblech et al. 2011; Laha et al. 2015; Laha et al. 2016

## 227 **SPX protein subfamily**

228 There are four members in *Arabidopsis* SPX protein subfamily, known as *AtSPX1~AtSPX4*  
229 (Duan et al. 2008). Except for *AtSPX4*, the expression of other members is induced by P  
230 deficiency, among which *AtSPX1* and *AtSPX3* are strongly induced while *AtSPX2* is only slightly  
231 induced (Duan et al. 2008). The *spx1/spx2* double mutant exhibits an increased activity of PHR1  
232 in plants grown in P-sufficient conditions but only a minor alteration of PHR1 activity in  
233 P-deficient plants, indicating that the inhibitory effect on PHR1 of SPX1 and SPX2 is cellular  
234 Pi-dependent (Puga et al. 2014). The interaction of SPX1 and PHR1 is compromised under  
235 P-sufficient conditions in the *vih1/vih2* mutant, leading to a constitutive activation of PSI genes.  
236 Furthermore, isothermal titration calorimetry shows that InsP<sub>8</sub> binds directly to SPX1 proteins and  
237 co-immunoprecipitation demonstrates that the interaction of SPX1 and PHR1 is Pi- and  
238 InsP<sub>8</sub>-dependent (Dong et al. 2019). Recently, it was reported that the KHR motif (PHR1<sup>K325</sup>,  
239 PHR1<sup>H328</sup>, and PHR1<sup>R335</sup>) at the surface of the coiled-coil (CC) domain of AtPHR1 is essential for

240 its interaction with AtSPX1 (Ried et al. 2021). The Pi-InsP<sub>8</sub>-SPX1-PHR1 working model indicates  
241 that InsP<sub>8</sub> is an intracellular signaling molecule which is sensitive to Pi concentration, and SPX1  
242 suppresses the activities of PHR1 in an InsP<sub>8</sub>-dependent manner as an intracellular sensor (Fig. 2  
243 A and B).

244 AtSPX4 functions as a repressor not only in PHR1-dependent but also in PHR1-independent  
245 pathways in P-sufficient plants. Gene regulatory network analyses revealed that SPX4 interacts  
246 with several regulators of shoot development, such as SUPPRESSOR OF OVEREXPRESSION  
247 OF CONSTANS1 (SOC1) and ARABIDOPSIS NAC DOMAIN CONTAINING PROTEIN55  
248 (ANAC055) (Osorio et al. 2019). SPX4 acts as a regulator not only in signaling P status, but also  
249 in transmitting the P deficiency signal to anthocyanin biosynthesis. The MYB transcription factor  
250 PRODUCTION OF ANTHOCYANIN PIGMENTS1 (PAP1) controls the synthesis of anthocyanin  
251 by activating the expression of genes encoding the proteins in the synthesis pathway (He et al.  
252 2021b). SPX4 interacts with PAP1 to inhibit the binding of PAP1 to the promoter of its  
253 downstream genes in a PP-InsPs -dependent manner under P-sufficient conditions, conversely, in  
254 the absence of PP-InsPs under P-deficient conditions, the interaction between SPX4 and PAP1 is  
255 compromised, and PAP1 is released to initiate anthocyanin biosynthesis (He et al. 2021b).

256 In rice, there are six members in SPX protein subfamily, namely OsSPX1~OsSPX6 (Zhong  
257 et al. 2018). Except for *OsSPX4*, which is not responsive to P deficiency, the other five *SPX* genes  
258 are all induced significantly after 7 days of P deficiency (Zhong et al. 2018). Rice transcription  
259 factor PHR2 is composed of transcriptional activation domain, MYB domain responsible for DNA  
260 binding, and CC domain responsible for dimerization, from N- to C-terminal (Wang et al. 2014b).  
261 Nuclear-localized OsSPX1 and OsSPX2 regulate P status by inhibiting the activity of PHR2 in a  
262 Pi-dependent manner (Wang et al. 2014b). Unexpectedly, PHR2 binds to P1BS elements in  
263 dimerized form *in vivo* to activate the expression of PSI genes in P-deficient conditions (Zhou et al.  
264 2021). When two OsSPX1 proteins approach a dimerized PHR2 in P-sufficient conditions, their  
265 helix  $\alpha 1$  will be sterically hindered, resulting in the inability of the OsSPX1s bind to the PHR2  
266 dimer (Zhou et al. 2021). Upon binding PP-InsPs, an allosteric effect is produced so that OsSPX1s  
267 can disrupt PHR2 dimers and form a SPX1-PHR2 complex in a 1:1 ratio. In this instance, the  
268 DNA binding activities of PHR2 will be sterically blocked (Zhou et al. 2021). Similarly, in the  
269 OsSPX2-InsP<sub>6</sub>-PHR2 complex, the InsP<sub>6</sub>-binding OsSPX2 proteins assemble into a dimer and

270 binds two molecules of PHR2, making the MYB domain of PHR2 severely allosteric turned and  
271 unable to bind DNA molecules (Guan et al. 2022).

272 Rice REGULATOR OF LEAF INCLINATION1 (OsRLI1) is a transcription factor positively  
273 regulating leaf inclination by affecting lamina joint cell elongation in rice (Zhang et al. 2021).  
274 OsRLI1 directly activates the downstream genes OsBU1 and OsBU1-LIKE1 COMPLEX1 to  
275 regulate elongation of the lamina joint cells (Ruan et al. 2018). OsSPX1 protein interacts directly  
276 with OsRLI1, which could prevent OsRLI1 binding to the promoter of its downstream genes. In  
277 this way, OsSPX1 can also regulate leaf inclination by inhibiting the transcriptional activity of  
278 OsRLI1 in rice, whether this process is dependent on PP-InsPs remains to be further investigated  
279 (Ruan et al. 2018).

280 OsSPX4 can interact with OsPHR2 to prevent the latter from entering the nucleus or binding  
281 to P1BS elements in downstream genes, thereby regulating P status (Lv et al. 2014). Although  
282 OsSPX4 does not respond to changes in external P availabilities at the transcriptional level, its  
283 protein stability is reduced under P-deficient conditions (Lv et al. 2014). RING-type E3 ubiquitin  
284 ligases OsSDEL1 and OsSDEL2 induced by P deficiency are involved in the degradation of  
285 OsSPX4 protein, resulting in the release of OsPHR2, allowing plants to adapt to P deficiency  
286 (Ruan et al. 2019). Furthermore, OsPHR2 competes with OsSDELS by interacting with OsSPX4  
287 under P-sufficient conditions, which protects OsSPX4 from ubiquitination and degradation (Ruan  
288 et al. 2019). *In vitro* assays provide a more detailed working model of  
289 PP-InsPs-SDELS-SPX4-PHR2 complex in rice (Ruan et al. 2019). The presence of PP-InsPs  
290 promotes the interaction of OsSPX4 and OsPHR2, which prevents OsSDELS from interacting  
291 with OsSPX4 and mediating its degradation under P-sufficient conditions, reversely, the  
292 dissociation of the OsSPX4-OsPHR2 in the absence of PP-InsPs releases OsSPX4 to OsSDELS,  
293 leading to ubiquitination and degradation of OsSPX4 under P-deficient conditions (Ruan et al.  
294 2019).

295 Nuclear- and cytoplasm-localized OsbHLH6 exclusively interacts with OsSPX4 but not with  
296 other OsSPX proteins, moreover, OsbHLH6 has higher binding affinity with OsSPX4 than  
297 OsPHR2. Therefore, OsbHLH6 can alleviate the blocking effect of OsSPX4 on OsPHR2 (He et al.  
298 2021a). The interaction between OsbHLH6 and OsSPX4 mainly occurs under P-sufficient  
299 conditions, however, it remains unknown whether the interaction is PP-InsPs-dependent. Under

300 nitrate-sufficient conditions, nitrate perception strengthens the interaction of OsNRT1.1B and  
301 OsSPX4, and OsNRT1.1B interacting protein 1 (OsNBIP1) is recruited to degrade OsSPX4,  
302 therefore releasing OsPHR2 and OsNLP3 to promote Pi and nitrate acquisition; while under low  
303 nitrate conditions, OsSPX4 interacts with OsPHR2 and OsNLP3 and inhibits the function of  
304 OsPHR2 and OsNLP3 in P and nitrate signaling and regulation (Hu et al. 2019).

305 OsSPX3 and OsSPX5 redundantly regulate plant P status, and genetic analysis indicates that  
306 both are repressors of OsPHR2 (Shi et al. 2014). OsSPX6 is localized in cytoplasm and nucleus  
307 The interaction of OsSPX6 with OsPHR2 blocks the translocation of OsPHR2 from cytoplasm  
308 into the nucleus, and inhibits OsPHR2 binding to the P1BS elements in downstream genes. Thus,  
309 OsSPX6 negatively regulates the PSR through suppression of PHR2 (Zhong et al. 2018). In  
310 addition, SPX proteins in other species are also involved in plant P status through similar  
311 mechanisms, such as GmSPX1 and GmSPX3 in soybean, BnaSPX1 in rapeseed, and MtSPX1 and  
312 MtSPX3 in *Medicago truncatula* (Yao et al. 2014; Zhang et al. 2016; Du et al. 2017; Wang et al.  
313 2021).

#### 314 **SPX-EXS protein subfamily**

315 PHOSPHATE1 (PHO1), identified by map-based cloning, shows very low homology to  
316 H<sup>+</sup>-Pi co-transporters, belonging to a new class of ion transporters in plants (Hamburger et al.  
317 2002). The *PHO1* family has 11 members in the Arabidopsis genome, namely *PHO1* and  
318 *PHO1;H1~PHO1;H10* (*PHO1* homologs), most of which are expressed in the vascular tissues of  
319 roots, stems, leaves and flowers (Wang et al. 2004). PHO1 and PHO1;H1 are responsible for the  
320 loading of Pi from root epidermal cells and cortical cells to xylem vessels (Stefanovic et al. 2007).  
321 Loss of PHO1 function can hinder the long-distance transport of Pi from roots to shoots, resulting  
322 in the decline of Pi concentrations in the shoot (Stefanovic et al. 2007). There are three  
323 homologous genes of *PHO1* in rice, known as *OsPHO1;1*, *OsPHO1;2*, and *OsPHO1;3*, among  
324 which OsPHO1;1 and OsPHO1;2 are located in the plasma membrane and mainly expressed in  
325 node I, being responsible for the transportation of Pi to grains (Che et al. 2020; Chiou 2020; Ma et  
326 al. 2021). Additionally, OsPHO1;2 is also responsible for the long-distance transport of Pi from  
327 roots to shoots in rice (Secco et al. 2010). It is worth noting that the regulation of expression of  
328 PHO1 occurs at different levels in Arabidopsis. Firstly, there are W-box cis-acting elements in the  
329 promoter region of *PHO1*, to which transcription factors WRKY6 and WRKY42 can bind to

330 inhibit the expression of *PHO1* (Chen et al. al 2009; Su et al. 2015). Secondly, the  
331 ubiquitin-conjugating enzyme PHO2 (UBC24) is involved in the ubiquitination of PHO1,  
332 resulting in the degradation of PHO1 protein (Liu et al. 2012). Finally, there is an upstream open  
333 reading frame (uORF) in the 5' untranslated region of *PHO1*, which can also regulate the protein  
334 abundance of PHO1 (Reis et al. 2020).

335 Pi efflux in human cells is highly dependent on Xenotropic and Polytopic Retrovirus  
336 Receptor 1 (XPR1) (Wilson et al. 2019). Isothermal titration calorimetry shows that InsP<sub>8</sub> has a  
337 very high affinity for the XPR1 protein (K<sub>d</sub>=180 nM), and diphosphoinositol pentakisphosphate  
338 kinases (PPIP5Ks) mutant cell lines have reduced Pi efflux, while the XPR1 mutant cell lines  
339 exhibit a similar phenotype (Li et al. 2020). By mutating PPIP5Ks or adding an inhibitor of  
340 inositol hexakisphosphate kinases (IP6Ks), intracellular synthesis of InsP<sub>8</sub> can be reduced, thereby  
341 inhibiting XPR1-mediated Pi efflux in human cells (Wilson et al. 2019; Li et al. 2020). In  
342 *Arabidopsis thaliana*, topological analysis reveals that the N-terminus of the PHO1 protein  
343 contains an SPX domain, followed by four transmembrane motifs and an EXS domain (Wege et al.  
344 2016). The SPX domain of PHO1 contains no transmembrane motif and is located in the  
345 cytoplasmic side of the cell, providing a putative anchor site to be regulated (Wege et al. 2016).  
346 Using a tobacco transient expression system, it was found that the EXS domain of PHO1 is  
347 necessary for its Pi transport activity and subcellular localization, but the EXS domain alone  
348 cannot transport Pi. Expression of the EXS domain in the *pho1* background rescues the shoot  
349 growth defect, while the P concentration remains the same as in *pho1* mutant, suggesting that the  
350 SPX domain is indispensable for a functional PHO1 (Wege et al. 2016). Although the mutation of  
351 the PP-InsPs binding site in the Arabidopsis PHO1 protein did not affect its subcellular  
352 localization, the mutated PHO1 proteins driven by the native promoter are unable to rescue the  
353 reduced shoot P concentration of the *pho1* mutant, suggesting that the binding of PP-InsPs is also  
354 critical for a functional PHO1 protein (Wild et al. 2016). AtPHO1 was previously identified as a Pi  
355 efflux transporter (Arpat et al. 2012; Vogiatzaki et al. 2017), but OsPHO1;1 and OsPHO1;2 were  
356 recently identified as Pi influx transporters (Che et al. 2020). The influx activity of PHO1 cannot  
357 explain its prominent role in the xylem loading, which requires efflux activity to move Pi out of  
358 cells (Stefanovic et al. 2007). Alternatively, it cannot be ruled out that PHO1 is able to mediate  
359 bi-directional transport of Pi. The N-terminal part of PHO1, which contains the SPX domain, is



360 required for the recognition, interaction, and subsequent ubiquitination by PHO2 (Liu et al. 2012).  
361 There exists a possibility that the transport direction/activity of PHO1 and the interaction between  
362 PHO1 and PHO2 are controlled finely by the concentration of PP-InsPs in plant cells.

### 363 **SPX-MFS protein subfamily**

364 Plant vacuoles are the main organelle for storing Pi, and vacuole Pi transporter (VPT), also  
365 known as SPX-MFS or PHT5, mediates Pi transport between cytosol and vacuole (Yang et al.  
366 2017). The PHT5 family in Arabidopsis includes three members, known as AtPHT5;1, AtPHT5;2  
367 and AtPHT5;3, of which AtPHT5;1 plays a major role in Pi accumulation (Liu et al. 2015; Liu et  
368 al. 2016). The SPX-MFS family in rice includes four members, namely OsSPX-MFS1,  
369 OsSPX-MFS2 OsSPX-MFS3 and OsSPX-MFS4, among which *OsSPX-MFS1* and *OsSPX-MFS3*  
370 are downregulated under P deficiency, whereas *OsSPX-MFS2* is induced (Wang et al. 2012). All  
371 the OsSPX-MFS proteins transport Pi from the cytosol to the vacuole, among which  
372 OsSPX-MFS3 plays dominant role while OsSPX-MFS2 has the weakest function (Lin et al. 2010;  
373 Wang et al. 2015; Xu et al. 2019; Guo et al. 2022). Recently, we identified two vacuolar Pi influx  
374 transporters in *B. napus*, and revealed the distinct and conserved roles of BnaPHT5;1bs in cellular  
375 Pi status in this plant species (Han et al. 2022a).

376 Yeast VTC (Vacuolar Transporter Chaperone) is a type of inorganic polyphosphate (polyP)  
377 polymerase localized on the tonoplast (Gerasimaite et al. 2017). 5-PP-InsP<sub>5</sub> bind specifically to  
378 the SPX domain of the VTC protein and acts as the main activator of intracellular VTC, indicating  
379 that the SPX domain may integrate PP-InsPs to adapt to cytoplasmic Pi levels under different  
380 metabolic conditions (Gerasimaite et al. 2017). When PP-InsPs is binding to the SPX domain  
381 within the VTC protein, the catalytic polymerase domain at the entrance of the trans-membrane  
382 channel is oriented, both activating the enzyme and coupling polyP synthesis and membrane  
383 translocation (Guan et al. 2023). Rice OsSPX-MFS1, OsSPX-MFS2 and OsSPX-MFS3 localize to  
384 the tonoplast, and their truncated proteins ΔMFS1, ΔMFS2 and ΔMFS3 with the SPX domain  
385 deleted still localized to the tonoplast, suggesting that the transmembrane domain and C-terminal  
386 motif are critical for the localization of SPX-MFSs, while the SPX domain probably plays a  
387 regulatory role (Wang et al. 2015). The SPX domain of the strawberry FaVPT1 protein shows a  
388 high affinity for InsP<sub>6</sub> (K<sub>d</sub>=3.5 μM), moreover, the SPX-MFS family proteins share highly  
389 conserved PP-InsPs binding sites, suggesting that PP-InsPs may also act on SPX-MFS proteins to

390 control intracellular P homeostasis (Secco et al. 2012; Huang et al. 2019). The auto-inhibitory  
391 domain in the VPT1 protein suppresses its transport activity under P deficient conditions.  
392 However, under P sufficient conditions activity of VPT1 is activated to transport excess Pi into  
393 vacuole upon binding of InsP<sub>8</sub> through the SPX domain (Luan et al. 2022).

#### 394 **SPX-RING protein subfamily**

395 Proteins containing the RING domain generally possess ubiquitin ligase (E3) activity, which  
396 can transfer ubiquitin from ubiquitin-conjugating enzyme (E2) to specific substrate proteins (Kraft  
397 et al. 2005; Stone et al. 2005). In the Arabidopsis and rice genomes, there are only two genes  
398 encoding proteins containing both SPX and RING domains, namely NLA1 and NLA2 (Secco et al.  
399 2012; Jung et al. 2018). Screening of 200 T-DNA insertion lines identified a line that failed to  
400 develop the essential adaptive responses to low nitrogen conditions, and senesced earlier and more  
401 rapidly than wild type under nitrogen deficiency, so it was named NITROGEN LIMITATION  
402 ADAPATATION1 (NLA1) (Peng et al. 2007). Two suppressors of *nla1* (*nla1*-Suppressor1 and  
403 *nla1*-Suppressor2) were identified by genetic approaches, both of which can rescue the phenotype  
404 of *nla1* mutants failing to adapt to nitrogen deficiency. It was found that the two suppressors were  
405 *PHF1* and *PHT1;1* mutations after map-based cloning, moreover, the *nla1/phf1* or *nla1/pht1;1*  
406 double mutant can also restore the phenotype of *nla1* (Kant et al. 2011). NLA1 co-localizes with  
407 PHT1;1 and PHT1;4 in the plasma membrane, and NLA1 regulates P status by mediating the  
408 ubiquitination and degradation of PHT1;1 and PHT1;4 in Arabidopsis (Lin et al. 2013). OsNLA1  
409 also controls P status by ubiquitinating several OsPHT1s in rice, notably, the main difference  
410 between two species is that *AtNLA1* is regulated by the microRNA *miR827* at the  
411 post-transcriptional level, while *OsNLA1* is not regulated in this manner (Yue et al. 2017; Yang et  
412 al. 2020). Interestingly, the phenotype of *nla1* mutant whilst failing to adapt to low nitrogen  
413 conditions can not only attribute to Pi toxicity, but also excessive nitrogen transfer from old leaves  
414 to new leaves under nitrate deficiency. NLA1 mediates the ubiquitination and degradation of  
415 nitrate transporter NRT1;7, and regulates the redistribution of nitrate from source to sink in plants  
416 under low nitrogen conditions (Liu et al. 2017). ORE1 is a core transcription factor that controls  
417 leaf senescence under nitrate deficient conditions, and NLA1 also regulates leaf senescence under  
418 nitrogen limitation by mediating ORE1 ubiquitination and degradation (Park et al. 2018).

419 Sequence alignment shows that the binding site of PP-InsPs in NLA1 is highly conserved

420 (Secco et al. 2012). Furthermore, both mutation in genes related to PP-InsPs synthesis (e.g., *IPK1*,  
421 *ITPK1*, and *VIHs*) and *NLA1* leads to P overaccumulation (Lin et al. 2013; Kuo et al. 2018; Dong  
422 et al. 2019). It was shown that the SPX domain of *NLA1* not only interacts with the Pi transporter  
423 *PHT1s*, but also with the nitrate transporter *NRT1;7* (Lin et al. 2013; Liu et al. 2017). Although it  
424 was revealed that *NLA1* mediates the ubiquitination of *PHR1* in a PP-InsPs-dependent manner  
425 (Park et al. 2022), it remains largely unknown whether PP-InsPs affect the *NLA1*-*PHT1s* module  
426 to control Pi uptake, or on the *NLA1*-*NRT1;7* module to regulate nitrate status in plants. The SPX  
427 domain of *NLA2* also contains a conserved PP-InsPs binding site, suggesting that *NLA2* may also  
428 work coordinately with PP-InsPs to control P status in plants (Secco et al. 2012; Jung et al. 2018).

## 429 **INOSITOL (PYRO)PHOSPHATES MEDIATED AUXIN** 430 **SIGNALING PATHWAY**

### 431 **Inositol (pyro)phosphates and auxin co-receptor TIR1**

432 Auxin is widely involved in plant growth, development, and stress adaptation (Salehin et al.  
433 2015). There are four types of auxins derived from plants, of which indole-3-acetic acid (IAA) is  
434 the most abundant form (Lavy and Estelle 2016). The distribution of auxin within plant tissues is  
435 controlled by biosynthesis, transport and inactivation, and once sensed by its receptors in the  
436 nucleus, triggers a series of downstream reactions (Zazimalova et al. 2010; Kasahara 2016). The  
437 core auxin sensing complex includes three parts: the F-box type auxin co-receptor **TRANSPORT**  
438 **INHIBITOR RESPONSE 1/AUXIN SIGNALING F-BOX PROTEIN (TIR1/AFB)**, the  
439 transcriptional repressor **Auxin/INDOLE-3-ACETIC ACID (Aux/IAA)**, and **AUXIN RESPONSE**  
440 **FACTOR (ARF)** (Salehin et al. 2015; Fig. 2C). Auxin enhances the interaction between the  
441 **TIR1/AFB** complex and **Aux/IAA** proteins, leading to degradation of **Aux/IAA** and release of **ARF**  
442 to regulate auxin-mediated transcriptional activation or repression of downstream genes  
443 (Okushima et al. 2005; Badescu and Napier 2006; Hagen 2015).

444 Inositol (pyro)phosphates not only play an important role in signaling P status, but are also  
445 involved in the auxin signaling pathway (Fig. 2C, Table1). **TIR1** is an F-box protein containing a  
446 leucine-rich-repeat (LRR) that forms part of a **SKP1/Cullin/F-box (SCF)** type E3 ubiquitin ligase  
447 complex. Specifically, **SKP1** (e.g., **SKP1-like protein ASK1**) links **TIR1** to the **Cullin** (e.g., **CUL1**),  
448 which in turn interacts with **RBX1**, **SCF-type ubiquitin ligases** catalyze the transfer of activated

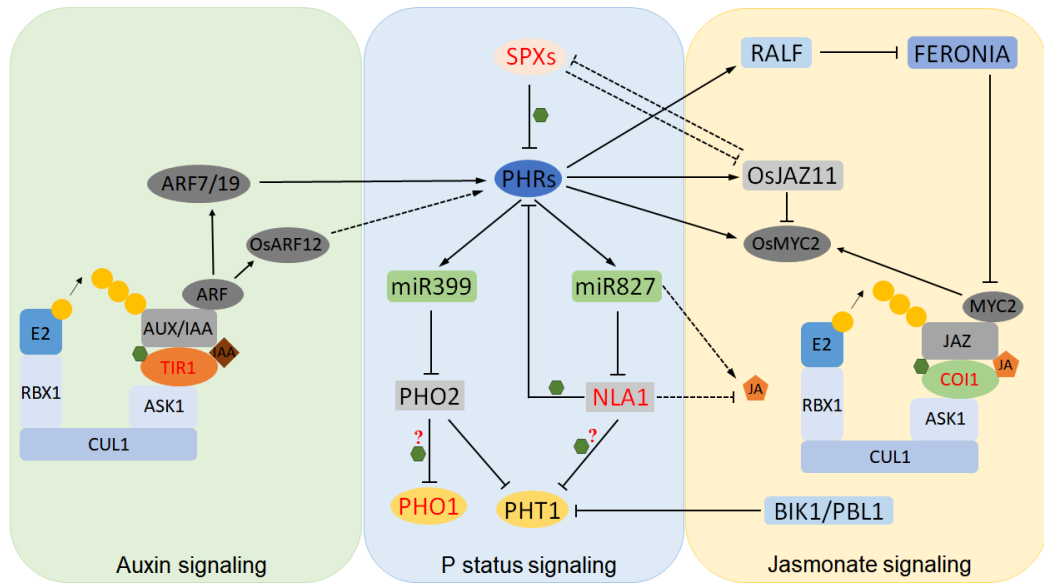
449 ubiquitin from a ubiquitin-conjugating enzyme (E2) to a target protein (i.e., Aux/IAAs) (Fig. 2C,  
450 Kepinski and Leyser 2005). The TIR1 protein expressed and purified from insect cells  
451 co-crystallized with InsP<sub>6</sub>, while mutation of the InsPs/PP-InsPs binding site of TIR1 resulted in  
452 failure of the auxin-TIR1-Aux/IAA complex to form, suggesting that InsPs/PP-InsPs are directly  
453 involved in the auxin signaling pathway (Tan et al. 2007; Calderon Villalobos et al. 2012).

454 Addition of exogenous auxin induced the expression of the Arabidopsis *ITPK1* gene, and  
455 ITPK1 played an important role in auxin-mediated processes, including primary root elongation,  
456 leaf vein development, thermomorphogenesis and gravitropism (Laha et al. 2022). 5-InsP<sub>7</sub>  
457 produced by ITPK1 has a very high affinity for the auxin receptor TIR1, furthermore, 5-InsP<sub>7</sub>  
458 promotes the interaction between AFB1/AFB2 and Aux/IAA in yeast, suggesting that PP-InsPs are  
459 involved in auxin signaling (Laha et al. 2022).

#### 460 **Crosstalk between P status- and auxin- signaling**

461 Root architecture undergoes adaptive changes, including the inhibition of primary root  
462 growth and the increase in the number and length of lateral roots under P-deficient conditions  
463 (Peret et al. 2011). It was reported that P deficiency changes the sensitivity of plant roots to auxin,  
464 which in turn causes the morphogenesis of plant lateral roots. Specifically, the expression of the  
465 auxin receptor gene *TIR1* is induced after P deficiency. As a result, the degradation of the repressor  
466 Aux/IAAs are accelerated, releasing ARF19, which further activates the expression of genes  
467 related to lateral root morphogenesis (Pérez-Torres et al. 2008). *AtPHR1*, a target gene of AtARF7  
468 and AtARF19, is positively regulated by auxin signaling, and both AtPHR1 and its downstream  
469 PSI genes are down-regulated in *arf7*, *arf19*, and *arf7/arf19* mutants (Huang et al. 2018). In rice,  
470 knocking out *OsARF12* affected the transcript abundance of *OsPHR2* and its downstream genes,  
471 moreover, knocking out *OsARF16* resulted in the loss of primary root, lateral root and root hairs  
472 responses in response to auxin and P deficiency signals (Shen et al. 2013; Wang et al. 2014a),  
473 indicating that ARF family members are involved in the crosstalk between auxin signaling and P  
474 status. Although the *pho2* mutant (with high concentrations of Pi and InsP<sub>8</sub>, Liu et al. 2012; Dong  
475 et al. 2019) and wild-type display similar phenotypes with respect to auxin responsiveness, the  
476 auxin insensitive primary root growth of *itpk1* plants is not observed anymore when plants are  
477 grown under P deficiency, indicating that both P overaccumulation and defective auxin  
478 responsiveness are independent consequences of impaired ITPK1 activity (Laha et al. 2022).

479 Given that InsP<sub>7</sub> and InsP<sub>8</sub> are sensitive to fluctuations in external P supply, whether P status  
 480 affects the interaction between TIR1 and Aux/IAA at the protein level by controlling the synthesis  
 481 of PP-InsPs, and then regulates plant growth and development is still elusive. It seems  
 482 contradictory that P deficiency induces the expression of *TIR1*, but inhibits the synthesis of  
 483 PP-InsPs, as they are both essential for the degradation of Aux/IAA and the release of ARFs.  
 484 However, the underlying complex regulation mode is worthy of investigation (Fig. 2; Fig. 3).



485  
 486 **Fig. 3 The crosstalk among P status, auxin, and jasmonate signaling pathways in plants.** Core transcription  
 487 factor PHRs play major roles in the signaling crosstalk of P status, auxin, and JA. Firstly, PHRs regulate  
 488 multi-pathways in P status signaling including microRNA-mediated surveillance of Pi uptake and transport.  
 489 Secondly, *PHRs* targeted directly by ARF proteins so that auxin signaling is able to affect P status signaling.  
 490 Thirdly, PHRs activate the expression of genes associated with JA signaling (e.g., *rapid alkalization factor*  
 491 (*RALF*), *OsJAZ11*, and *OsMYC2*), in turn, protein kinases BIK1 and PBL1 in JA signaling regulate Pi uptake  
 492 directly. Green hexagons indicate InsPs or PP-InsPs, and yellow circle indicates ubiquitin.

## 493 INOSITOL (PYRO)PHOSPHATES MEDIATED JASMONIC ACID 494 SIGNALING PATHWAY

### 495 Inositol (pyro)phosphates and JA co-receptor COI1

496 Jasmonic acid (JA) is widely involved in plant growth and development, including root  
 497 elongation, leaf senescence, and pollen fertility, and is also essential for plants to resist insect  
 498 infestation, low temperature, drought and other stresses (Hu et al. 2017; Huang et al. 2017; Wang

499 et al. 2019a). JA is synthesized in chloroplasts and peroxisomes, and then chemically modified in  
500 the cytoplasm (Huang et al. 2017; Wang et al. 2019a). Methyl jasmonate (MeJA), JA-isoleucine  
501 complex (JA-Ile) and cis-jasmone (CJ) are biologically active JA derivatives, in which JA-Ile  
502 possesses the highest biological activity, and JASMONATE RESISTANT1 (JAR1) is responsible  
503 for its chemical modification (Wasternack and Strnad 2016; Wasternack and Song 2017).

504 When JA-Ile is accumulated in plants, the COI1-JAZ protein complex acts as a JA  
505 co-receptor to bind to JA-Ile, promoting the ubiquitination of the repressor JAZ proteins by the  
506 SCF-COI1 complex (Fig. 2D). After JAZ proteins are degraded by the 26S proteasome, the  
507 transcription factor MYCs are released and bind to the promoters of a series of JA-responsive  
508 genes, thereby turning on the expression of downstream genes (Fig. 2D). Similar to TIR1, COI1 is  
509 an F-box protein that forms part of a SKP1/Cullin/F-box (SCF) type E3 ubiquitin ligase complex  
510 (Chini et al. 2009; Kazan and Manners 2012; 2013). The COI1-JAZ co-receptor contains not only  
511 a JA-Ile binding site, but also a InsPs or PP-InsPs binding site, indicating InsPs and PP-InsPs play  
512 important regulatory roles in the JA signaling pathway (Sheard et al. 2010; Laha et al. 2015; Fig.  
513 2D, Table 1). Yeast two-hybrid experiments showed that the COI1 protein, mutated at the InsPs or  
514 PP-InsPs binding site, had a reduced interaction with the JAZ9 protein, and its mutant version also  
515 had a reduced degree of rescue to the inhibited phenotype of root growth and silique development  
516 in the *coil* mutant, indicating that InsPs or PP-InsPs is indispensable for a functional COI1  
517 (Mosblech et al. 2011). Yeast *ipk1Δ* strongly accumulates PP-InsP<sub>4</sub> (an inositol pyrophosphate),  
518 and the interaction between COI1 and JAZ9 is enhanced in yeast *ipk1Δ* mutant lines (Saiardi et al.  
519 2002; Mosblech et al. 2011). Both the *ipk1* mutant and *vih2* mutants display a strong reduction of  
520 InsP<sub>8</sub>, moreover, the phenotypes of *ipk1* mutant are similar to that of *vih2* plants that display  
521 compromised JA-dependent defenses (Laha et al. 2015; Laha et al. 2016). Based on bioinformatics  
522 analysis and radioligand reconstitution experiments, InsP<sub>8</sub> and COI1-JAZ co-receptor show a very  
523 high binding ability (Cui et al. 2018). The above findings indicate PP-InsPs, in particular InsP<sub>8</sub>, is  
524 a co-ligand of the COI1-JAZ co-receptor and is essential for JA-mediated plant immune  
525 responses.

526 The content of PA in the mutants of genes related to PA synthesis pathway is decreased, and  
527 the immunity of the mutant lines to pathogenic bacteria is also decreased (Murphy et al. 2008).  
528 Potato inositol-3-phosphate synthase (MIPS) RNAi lines have reduced InsP<sub>6</sub> content and reduced

529 immunity to potato Y virus and tobacco mosaic virus (TMV), suggesting that InsP<sub>6</sub> maintains  
530 plant resistance to basic immunity to pathogens (Murphy et al. 2008). The function of multiple  
531 immune pathways in plants depends on the biosynthesis of InsPs and PP-InsPs. In *ipk1*, *itpk1* and  
532 *vih2* mutants, constitutive activation of immune signaling results in enhanced resistance to  
533 *Pseudomonas syringae*, indicating that Arabidopsis IPK1, ITPK1, and VIH2 inhibited  
534 SA-dependent immune responses (Gulabani et al. 2022). After JA treatment, the biosynthesis of  
535 InsP<sub>8</sub> is induced in plants, and *VIH2* regulates the plant's ability to sense JA and resist to  
536 herbivorous insects and disease fungi (Laha et al. 2015).

### 537 **Crosstalk between P status- and JA- signaling**

538 There exists a crosstalk between P status- and JA- signaling in plants, enabling plants to  
539 coordinately adapt to stresses such as P deficiency, pest invasion, and diseases (Fig. 3). In  
540 Arabidopsis, P deficiency signals can enhance JA synthesis and affect signaling pathways, thereby  
541 enhancing plant resistance to herbivorous insects (Khan et al. 2016). In cotton, JA synthesis is also  
542 increased under P deficiency, and the resistance of cotton to *Verticillium wilt* is greatly enhanced  
543 (Luo et al. 2021). The *GhAOS* gene RNAi lines have a weakened resistance to *Verticillium wilt*  
544 under P deficiency, indicating that P deficiency signals enhanced cotton's resistance to *Verticillium*  
545 *wilt* by activating JA biosynthesis (Luo et al. 2021). Transcriptome analysis revealed that the  
546 differential expression of JA- and SA-related genes during P deficiency is dependent on PHR1,  
547 suggesting that PHR1 can regulate plant immune responses at the transcriptional level (Castrillo et  
548 al. 2017). Recently, it was reported that AtPHR1 activates the expression of *rapid alkalization*  
549 *factor* (*RALF*) under P-deficient conditions, subsequently, RALF inhibits the complex formation  
550 of pathogen-associated molecular pattern (PAMP)-triggered immunity (PTI) receptor through the  
551 PTI modulator FERONIA (Tang et al. 2022). Impairment of the plant immune response via the  
552 PHR1-RALF-FERONIA pathway allows the colonization of root-specific microbial communities,  
553 which in turn alleviate the PSR (Tang et al. 2022). The resistance of rice to *Xanthomonas oryzae*  
554 *pv. oryzae* is enhanced under P deficiency, which is achieved via OsPHR2 by activating the  
555 expression of the core transcription factor MYC2 in the JA signaling pathway (Kong et al. 2021).  
556 After benzoic acid treatment or inoculation with *Pseudomonas syringae* *pv. tomato* DC3000, SA  
557 accumulated in *nla1* (*bah1*) mutants, suggesting that *NLA1/BAH1* (*benzoic acid hypersensitive1*)  
558 is involved in plant immune responses by regulating benzoic acid- and pathogen-induced SA

559 accumulation (Yaeno and Iba 2008). The P concentration in the *nla1* mutant and  
560 *miR827*-overexpressing lines was elevated, resulting in increased resistance to *Plectosphaerella*  
561 *cucumerina* (Val-Torregrosa et al. 2022). When infected with pathogenic bacteria or treated with  
562 fungal inducers, the expression of *miR827* is induced, while the expression of *NLA1* is  
563 down-regulated. Moreover, the concentrations of callose, phytoalexin, SA and JA in the leaves of  
564 *nla1* mutants are increased, indicating that *NLA1* may be a negative regulator involved in plant  
565 immunity (Val-Torregrosa et al. 2022). *NLA1* may control the JA signaling pathway by regulating  
566 the protein level of *PHR1* with a PP-InsPs-dependent manner (Park et al. 2022; Fig. 3).

567 P deficiency signals can affect JA biosynthesis and signaling pathways, and the key genes of  
568 JA biosynthesis and signaling pathways are also involved in the PSR of plants (Khan et al. 2016;  
569 Pandey et al. 2021; Fig. 3). The P deficiency inducible gene *OsJAZ11* is regulated by *OsPHR1* at  
570 the transcriptional level, and overexpression of *OsJAZ11* alleviates the inhibitory effect of JA on  
571 rice root growth (Pandey et al. 2021). *OsJAZ11* overexpression lines have an increased primary  
572 and seminal root elongation, and their ability to forage P is enhanced (Pandey et al. 2021). The PSI  
573 genes are significantly down-regulated in *OsJAZ11*-overexpressing lines, whereas they are  
574 significantly up-regulated in RNAi lines, indicating that *OsJAZ11* suppressed the PSR (Pandey et  
575 al. 2021). *OsJAZ11* protein can interact with *OsSPX1* protein, which may be another way of  
576 regulating PSR (Pandey et al. 2021). Recently, it was reported that protein kinases *BIK1* and  
577 *PBL1* functioning in immune pathway inhibit the activity of *PHT1;4* via phosphorylation,  
578 suggesting that activation of immune signaling can directly inhibit Pi uptake in plants (Dindas et  
579 al. 2022).

## 580 **CONCLUSION AND FUTURE PERSPECTIVE**

581 In the past two decades, great progress has been achieved in the biosynthetic pathways of  
582 InsPs and PP-InsPs and their emerging roles in P status, auxin and JA signaling pathways in plants.  
583 The regulation of PP-InsPs on the SPX domain protein subfamily has been clearly elucidated.  
584 However, the dependence of the SPX-EXS, SPX-MFS and SPX-RING subfamily members on  
585 PP-InsPs still needs further study to understand their molecular mechanisms of controlling plant P  
586 status. In addition, given that PP-InsPs are essential for signaling P status, auxin and JA signaling  
587 pathways, whether P status acts on phytohormone signaling pathway by controlling the synthesis



588 of PP-InsPs, and in turn phytohormone signaling affects the growth and development of plants  
589 under different P supply also warrants further study. Although it is becoming clearer that the SPX  
590 domain containing proteins are intracellular sensors, it is largely unknown what kind of proteins  
591 act as local P sensors. Understanding of whether and how PP-InsPs integrate local and systemic  
592 signaling pathways to module plant P status will be beneficial for genetic improvement of crop P  
593 efficiency.

594

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599

## 600 **Author contributions**

601 T.W. and L.S.: drafting and correcting the manuscript; C.W., B.H., Z.L., X.Y., W.W., G.D.,  
602 J.P.H., P.J.W. and F.X.: editing and improving the manuscript, and contributing to specific  
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604

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