Minireview

Cross-talk between Phosphate Starvation and Other Environmental Stress Signaling Pathways in Plants

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INTRODUCTION

The availability of inorganic phosphate (Pi) in soil is a crucial determinant of plant growth and development as well as crop productivity (Raghothama, 1999). Plants have evolved morphological, physiological, biochemical, and molecular processes to improve the mobilization, acquisition, and efficient utilization of Pi under deficiency conditions (Poirier and Bucher, 2002; Yuan and Liu, 2008). Reports on the mechanisms that regulate sensing and the response to Pi starvation have identified Pi starvation signaling pathway components and the cross-talk between Pi starvation responses and other plant signaling pathways, including sugars, phytohormones, and photosynthesis (Franco-Zorrilla et al., 2005; Lei et al., 2011a; Rouached et al., 2010; Rubio et al., 2009).

Cross-regulation occurs between Pi starvation and other plant signaling pathways, such as sugars and phytohormones (Rouached et al., 2010; Yuan and Liu, 2008). Pi starvation often causes sugar accumulation in plant tissues; high sugar levels in roots induce root system architecture (RSA) changes under Pi deprivation (Ciereszko et al., 2005; Ham-
also acts as a direct transcriptional activator of the miR-399f gene, which plays a crucial role in maintaining Pi homeostasis in response to changing environmental conditions.

The signaling networks involved with plant responses to Pi starvation are well known, but the cross-talk between Pi starvation and other abiotic stress signaling pathways remains unclear. Recently, however, their cross-talk has been suggested in physiological, phenotypical, and molecular levels. In barley, heat stress affects the expression of PSI genes, which leads to maintenance of Pi homeostasis in plant tissues (Pacak et al., 2016). They suggest that retarded growth and accelerated senescence of barley under heat stress conditions is probably due to disturbances of the macronutrient, including Pi, homeostasis. Comparative root transcriptome analysis using rice cultivars exhibiting contrasting nutrient, including Pi, homeostasis. Comparative root transcriptome analysis using rice cultivars exhibiting contrasting...
Table 1. Transcription factors interconnecting Pi starvation and other stress-responsive signaling pathways in Arabidopsis

| Type of Factor | Transcription Name | Locus | Binding Motif | Sequence | Responses | References |
|---------------|--------------------|-------|---------------|----------|-----------|------------|
| MYB Family (R1-type) | MYB-CC | PHR1 At4g28610 P185 element | GNATATNC-AC/AAATTC/CC | Pi starvation, metals deficiency, oxygen deficiency | Brat et al., 2015; Bustos et al., 2010; Khan et al., 2014; Klecker et al., 2014; Nilsson et al., 2007; Rubio et al., 2001 |
| | | PHL1 At5g29000 | | Pi starvation | | |
| | | PHL2 At3g24120 | | Pi starvation | | |
| | | PHL3 At4g13640 | | Pi starvation | | |
| MYB-CC (R2R3-type) | MYB2 | At2g47190 MBS | TAACTG | Pi starvation, cytokinin response, salt/ABA/drought response | Abe et al., 1997; 2003; Baek et al., 2013; Guo and Gan, 2011; Yoo et al., 2005 |
| WRKY Family | WRKY6 | At1g62300 W box | TTGACT/C | Pi starvation, pathogen defense, ABA response | Robatzek and Somssich, 2002; Chen et al., 2009; Huang et al., 2016 |
| | WRKY42 | At4g04450 | | Pi starvation | Su et al., 2015 |
| | WRKY45 | At3g01970 | | Pi starvation | Wang et al., 2014c |
| | WRKY75 | At5g13080 | | Pi starvation, JA/SA response, pathogen defense | Chen et al., 2013; Devaiah et al., 2007a; Schmiesing et al., 2016 |
| Zinc Finger (C2H2-type) | ZAT6 | At5g04340 POS9A (GA)$_4$ repeat | TGTGAGAGA | Pi starvation, metals deficiency, salt/drought/osmotic stress response | Chen et al., 2009; Huang et al., 2016; Chen et al., 2013; Devaiah et al., 2007b; Liu et al., 2013; Nakashima and Yamaguchi-Shinozaki, 2006 |
| | | POS9B and POS9C | | | |
| | | DRE | TGGCCGAC | | |

and cross-regulation by modulating plant transcriptional processes in multiple stress signaling pathways (Banerjee and Roychoudhury, 2015; Phukan et al., 2016). WRKY transcription factors with a C2H2 zinc finger domain control target gene transcription by binding to W box (TTGACT/C) elements (Choi and Lin, 2011; Rushton et al., 2010). The WRKY6 transcription factor is a typical WRKY family member with roles in the responses to different stimuli, where it enhances the PR1 promoter activity in senescence and pathogen-defense signaling (Chen et al., 2009; Huang et al., 2016; Robatzek and Somssich, 2002). WRKY6 expression is also highly induced by bacterial pathogens and it increases the senescence-induced receptor-like kinase promoter’s activity in response to the bacterial elicitor flagellin (Robatzek and Somssich, 2002). WRKY6 directly binds to the W box within the RAV1 promoter and decreases its gene transcript level during ABA stress response (Huang et al., 2016). Thus, WRKY6 modulates the cross-talk among different stress responses by regulating the transcription of various target genes (Table 1).

WRKY6 negatively regulates PHO1 expression (Chen et al., 2009) and a WRKY6 homolog, WRKY42, positively regulates Pho1 and PHO1 transcription in the Pi starvation response (Table 1; Su et al., 2015). WRKY6 and WRKY42 are both degraded via 26S proteasome-mediated proteolysis in the Pi starvation response (Chen et al., 2009; Su et al., 2015). WRKY45 is specifically expressed in roots and binds to two W box elements in the promoter of Pho1 to regulate its transcription (Chen et al., 2009). WRKY45 is also specifically expressed in roots and binds to two W box elements in the promoter of Pho1 to regulate its transcription (Chen et al., 2009; Su et al., 2015). WRKY45 is specifically expressed in roots and binds to two W box elements in the promoter of Pho1 to regulate its transcription (Chen et al., 2009; Su et al., 2015). WRKY45 is specifically expressed in roots and binds to two W box elements in the promoter of Pho1 to regulate its transcription (Chen et al., 2009; Su et al., 2015). WRKY45 is specifically expressed in roots and binds to two W box elements in the promoter of Pho1 to regulate its transcription (Chen et al., 2009; Su et al., 2015).
Other transcription factors

There are numerous other transcription factors that are important components of the transcriptional regulatory system of stress-responsive genes (Nakashima et al., 2009). C2H2-type zinc finger protein transcription factors function as essential components in Pi starvation and other abiotic stresses (Sakamoto et al., 2000). ZAT6 binds to three different sequences of POS9 (P-INO-specific regions) motifs in target gene promoters during developmental processes and the Pi starvation response (Table 1; Devaiah et al., 2007b; Meister et al., 2004). ZAT6 is strongly induced and closely related to abiotic stress responses, such as salt, cold, osmotic, and drought stresses, by binding to DRE (dehydration-responsive element) in target gene promoter regions (Table 1; Liu et al., 2013; Vogel et al., 2005). ZAT6 is highly expressed under cold stress and it regulates CBF2 transcription by binding to

| Stress  | Motif Name          | Sequence                  | ApTIs                              | Gene Name (Number of sites in the promoter) | microRNAs                  | PSI  |
|---------|----------------------|---------------------------|------------------------------------|--------------------------------------------|-----------------------------|------|
| Auxin   | AuxRE               | TGTCTCAATAAG              | ApT1(1), ApT5(1)                   | miR2111a(1)                               | None                        |      |
| AuxRR-core | GGTCCAT           |                           | ApT1(1), ApT5(1)                   | miR156g(2)                                 | SPX1(1), LPR1(1)            |      |
| TGA-element | AACGAC            |                           | ApT1(1), ApT5(1)                   | miR156g(2), miR156g(1), miR156h(1),        | SPX4(2), PHR1(2), SCR1(1), RAP1(2) |      |
|          |                     |                           |                                    | miR2111a(1)                               | miR2111a(1)                 |      |
| TGA-box  | TGAACGTAA          |                           | None                               | miR156b(1)                                 | None                        |      |
| Ethylene | ERE                 | ATTCCAAA                  | GGTCCAT                            | miR156b(2), miR156b(1), miR156c(1),        | None                        |      |
|          |                     |                           |                                    | miR156(2), miR2111b(1)                     | AAmPS2(1), RAP1(2)         |      |
| GA P-box | CACTTGGA           |                           | GGTCCAT                            | miR156b(1), miR156b(1), miR156c(1),        | None                        |      |
| GARE-motif | GCCTTGTGAG       |                           | GGTCCAT                            | miR156b(1), miR156b(1), miR156c(1),        | None                        |      |
|          |                     |                           |                                    | miR156b(1), miR156b(1), miR156c(1),        | None                        |      |
|          |                     |                           |                                    | miR156b(1), miR156b(1), miR156c(1),        | None                        |      |
|          |                     |                           |                                    | miR156b(1), miR156b(1), miR156c(1),        | None                        |      |
|          |                     |                           |                                    | miR156b(1), miR156b(1), miR156c(1),        | None                        |      |
|          |                     |                           |                                    | miR156b(1), miR156b(1), miR156c(1),        | None                        |      |
| TATC-box | TATCCCA            |                           | GGTCCAT                            | miR156b(1), miR156b(1), miR156c(1),        | None                        |      |
| CGTCA-motif | CGTCA           |                           | GGTCCAT                            | miR156b(1), miR156b(1), miR156c(1),        | None                        |      |
|          |                     |                           |                                    | miR156b(1), miR156b(1), miR156c(1),        | None                        |      |
|          |                     |                           |                                    | miR156b(1), miR156b(1), miR156c(1),        | None                        |      |
|          |                     |                           |                                    | miR156b(1), miR156b(1), miR156c(1),        | None                        |      |
|          |                     |                           |                                    | miR156b(1), miR156b(1), miR156c(1),        | None                        |      |
|          |                     |                           |                                    | miR156b(1), miR156b(1), miR156c(1),        | None                        |      |

In silico analysis was conducted using 1.5 kb upstream promoter regions from first exon start site of each gene by the PlantCARE database (http://bioinformatics.psb.ugent.be/webtools/plantcare/html/).
DRE within its promoter (Vogel et al., 2005).

**IN SILICO ANALYSIS OF PUTATIVE CIS-ACTING REGULATORY ELEMENTS IN PI-RESPONSIVE GENE PROMOTERS**

**Phosphate transporters**

Plants have diverse biological mechanisms for enhancing the availability of external Pi in the soil via Pi transporters (Chiou et al., 2011: Raghothama, 2000). Pi transporters are encoded by members of PHT gene families, including nine Pht1 members, one Pht2 member, three Pht3 members, six Pht4 members, and three Pht5 members in Arabidopsis (Guo et al., 2008; Knappe et al., 2003; Liu et al., 2016: Rausch and Bucher, 2002). Pht1:1 transcription is positively regulated by PHR1 (Rubio et al., 2001), WRKY75 (Devaiah et al., 2007a), WRKY45 (Wang et al., 2014), and WRKY42 (Su et al., 2015) but negatively regulated by MYB62 (Devaiah et al., 2009) under Pi-deficient conditions. Several types of cis-acting regulatory elements exist in the Pht1:1 promoter, such as P1BS, W box, and MBs. To understand the transcriptional regulation of Pi transporters, we conducted in silico analysis based on the DNA sequences of Pi transporter promoter regions and showed that the expression of Pi transporters could be regulated by hormones and various other stresses as well as by Pi starvation (Tables 2 and 3).

In silico analysis suggest that Pht1:4, Pht1:7, Pht1:8, Pht1:9, Pht3:1, Pht3:2, Pht4:1, Pht4:5, Pht5:2 and Pht5:3 gene transcription is possibly regulated by auxin because their promoters contain auxin-related putative cis-acting regulatory elements such as AuxRE, AuxRR-core, TGA-element, and TGA-box (Table 2). The Pht1:3, Pht1:4, Pht1:6, Pht3:1, Pht3:3 and Pht4:2 gene promoters contain ethylene-responsive cis-acting elements, and a GA-responsive element is found in most Pi transporter genes except Pht1:6, Pht2:1, Pht3:3, Pht4:3, and Pht4:4 (Table 2). A previous report shows the induction of Pht4:4 expression by ethylene supporting the reliability of our in silico analysis for understanding the regulation of Pi starvation-responsive gene networks by other stresses (Lei et al., 2011b). Most Pi transporters contain putative cis-acting regulatory elements in their promoters, such as CGTCA-motif, TGAACG-motif, SARE, and TCA-element, which are related to SA- and JA-mediated plant defense signaling (Table 2). The ABA or drought stress-responsive elements ABRE, DRE, and MBS also exist in most Pi transporters, except Pht1:6, Pht1:7, Pht3:1, and Pht5:2, and the cold-responsive element LTR is found in the Pht1:5, Pht1:6, Pht2:1, Pht3:1, Pht3:3, Pht4:2, Pht4:5, Pht4:6, and Pht5:2 gene promoters (Table 3). Many Pi transporters have TC-rich repeats related to defense and stress responses, except the Pht1:8, Pht3:3, Pht4:4, Pht4:6, and Pht5:1 genes, and an HSE element for heat stress response, except the Pht1:2, Pht1:5, Pht3:1, Pht4:3, Pht4:5, Pht4:6, Pht5:2, and Pht5:3 genes (Table 3). Fungal stress-related Box-W1 elements are found in the Pht1:1, Pht1:3, Pht1:6, Pht1:9, Pht3:1, Pht3:3, Pht4:3, Pht4:4, Pht4:6, and Pht5:3 genes, and wounding stress-related WUN-motifs are predicted in the Pht1:4, Pht3:1, Pht4:1, and Pht4:6 gene promoters (Table 3).

**Phosphate starvation-inducible genes**

The expression of many Pi starvation-responsive genes is cross-regulated by Pi starvation and other stress signaling pathways. Plant phytohormones, such as cytokinin, ethylene, ABA, and auxin are associated with the transcription of genes involved in the Pi starvation response. PHO1 plays a crucial role in Pi starvation signaling and it is significantly down-regulated by auxin, cytokinin, and ABA (Ribot et al., 2008). RNS1 is a secreted ribonuclease and another Pi starvation-related gene that is significantly upregulated by ABA (Hillwig et al., 2008). The RNS1 promoter contains several putative cis-acting elements, including ABRE, MYB/MYC, W box, HSE, P-box, and TCA elements, which mediate various stress signaling pathways (Tables 2 and 3; Hillwig et al., 2008). SIZ1 is a small ubiquitin-like modifier E3 ligase paying important roles in enhancing the tolerance of environmental stresses such as salt, cold, drought, ABA, auxin, SA, and Pi starvation (Catala et al., 2007; Miura et al., 2005; 2007; 2009; 2010; 2011a; 2011b). Multiple functions of SIZ1 are known in various stress signaling pathways, but the transcriptional regulation of its expression remains unknown. Our in silico analysis indicates that the SIZ1 promoter contains various putative cis-acting regulatory elements, such as ABRE, LTR, TC-rich repeats, WUN-motif, box-W, and TCA elements, which function in diverse stress signal transduction cascades (Tables 2 and 3). Our results provide biological insights into the mechanisms that regulate SIZ1 expression as well as its biological functions in plant stress responses. In summary, findings of our in silico analysis of the regulatory regions of Pi starvation-related genes, such as Pi transporters, miRNAs, and PSI genes, suggest that their expression may be related to various environmental stresses to maintain Pi homeostasis in plants.
Table 3. Analysis of various stresses signaling-related putative cis-acting regulatory elements in Pi starvation-responsive gene promoters

| Stress | Motif Name Sequence | Gene Name (Number of sites in the promoter) | AtPIs | microRNAs | PSI |
|--------|---------------------|-------------------------------------------|-------|-----------|-----|
| ABA    | ACGTGCC             | AtPh4;1(1), AtPh4;4(1)                    |       | miR2111b(1) |     |
|        | AGTACGTCGCG         | None                                      |       | miR399e(1)  |     |
|        | CAGCCTGGGC          | AtPh4;1(1), AtPh4;2(1), AtPh4;3(1), AtPh4;4(1), AtPh4;5(1) |       | miR156b(2), miR156c(1), miR156e(1), miR156h(1), miR399e(1), miR2111a(1) |     |
|        | CGACGGTGCT          | None                                      |       | miR2111a(1) |     |
|        | GCAACGGTGTC         | AtPh5;5(1), AtPh5;3(1)                    |       | None       |     |
|        | GCCACGTACA          | AtPh3;3(1)                                |       | None       |     |
|        | GCCCGCTGGGC         | AtPh4;1(1), AtPh4;2(1)                    |       | None       |     |
|        | TACGTG              | AtPh1;1(1), AtPh1;2(1), AtPh1;3(1), AtPh1;4(1), AtPh1;5(1), AtPh1;6(1), AtPh1;7(1), AtPh1;8(1), AtPh2;1(1), AtPh3;2(1), AtPh3;3(1), AtPh4;1(1), AtPh4;2(1), AtPh4;4(1), AtPh4;6(1), AtPh4;8(1), AtPh5;1(1) |       | miR156a(1), miR156d(1), miR156h(1), miR399c(1) | LPR(1) |
| Drought | C-repeat/ DRE        | TGGCCGAC                                  |       | miR778a(1), miR827a(1) |     |
| CE3    | TAGCGTC              | None                                      |       | miR156h(1)  |     |
| MBS    | CGTCCGAC            | AtPh1;9(1)                                |       | None       |     |
| Cold   | CCGAAA               | AtPh1;5(1), AtPh1;6(1), AtPh1;7(1), AtPh1;8(2), AtPh1;9(1), AtPh2;1(3), AtPh3;1(2), AtPh3;3(1), AtPh4;2(1), AtPh4;5(1), AtPh4;6(1), AtPh4;7(1), AtPh4;8(1), AtPh4;9(1), AtPh5;2(1) |       | miR156b(1), miR156e(1), miR399c(1), miR827a(1) | LPR(1) |
| Defense | TC-rich repeats      | ATTCTCAA                                  |       | miR156c(1), miR156e(1), miR156h(1), miR2111a(1) |     |
|        | ATTTCCTCA           | AtPh1;3(2), AtPh1;4(2), AtPh1;5(1), AtPh1;6(2), AtPh1;7(2), AtPh2;1(1), AtPh2;2(1), AtPh2;3(1), AtPh2;4(1), AtPh4;1(1), AtPh4;2(1), AtPh4;3(1), AtPh4;4(1), AtPh4;5(1), AtPh4;6(1), AtPh4;7(1), AtPh4;8(1), AtPh4;9(1), AtPh5;2(1) |       | miR156b(1), miR156c(1), miR156h(1), miR399b(1), miR399c(1), miR399d(1), miR399e(1), miR399f(1), miR399g(1), miR399h(1), miR827a(1) | LPR(1), LPR(2) |
| Fungal | Box-W1               | TTGACC                                    |       | miR778a(1)  |     |
| Heat   | HSE                  | ATTTTTCTCCTA                              |       | PHR(1), PHF(1), LPR(2) |     |
| Wound  | WUN-motif            | GTTTTCTTCAC                               |       | IPS(1), AAAP(2), SCR(2) |     |
|        | TCATACGAA            | AtPh1;9(1)                                |       | None       |     |

In silico analysis was conducted using 1.5 kb upstream promoter regions from first exon start site of each gene by the PlantCARE database (http://bioinformatics.psb.ugent.be/webtools/plantcare/html/).

**CONCLUSION**

Phosphorus in the form of Pi is an essential nutrient for plant growth, development, and productivity, but Pi is one of the least available essential nutrients because of its insolubility and low available concentrations (Poirier and Bucher, 2002; Raghothama, 1999). To cope with Pi starvation, plants reprogram various cellular processes, including the reduction
of internal Pi usage and activation of external Pi acquisition and recycling. Studies on Pi starvation signaling in plants have identified signaling components, such as transcription factors, non-coding RNAs, and protein modifiers, but also cross-talk with other plant signaling pathways including phytohormones, sugars, and other nutrients (e.g., iron) (Rouached et al., 2010; Yuan and Liu, 2008). Biotic and abiotic stresses significantly affect plant growth, but the links between Pi starvation and other environmental stress signaling pathways remain unclear. Understanding the cross-regulation of gene expression by identifying the transcription factors involved in both Pi starvation and diverse environmental stress signaling pathways, as well as in silico analysis of cis-acting elements in the regulatory regions of Pi starvation signaling components, will provide molecular mechanisms of the connections between Pi starvation and other environmental stress signaling pathways.

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