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The role of the *P1BS* element containing promoter-driven genes in Pi transport and homeostasis in plants

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Inorganic phosphate (Pi) is an easily accessible form of phosphorus for plants. Plant Pi uptake is usually limited however by slow Pi diffusion through the soil which strongly adsorps phosphate species. Plants have developed mechanisms to increase Pi availability. There are also abiotic (phosphate level) and biotic (e.g., mycorrhizal) factors regulating the expression of Pi-responsive genes. Transcription factors binding to the promoters of Pi-responsive genes activate different pathways of Pi transport, distribution, and homeostasis maintenance. Pi metabolism involves not only functional proteins but also microRNAs and other non-coding RNAs.

Keywords: phosphate, Pi-responsiveness, *P1BS*, microRNA

INTRODUCTION

Phosphorus (P) is one of the most important macronutrients in the plant lifecycle. It is involved in the synthesis of nucleic acids and phospholipids, in reactions of phosphorylation, and also in energy delivery (ATP). Lack of phosphate (inorganic phosphate, Pi) inhibits plant growth, whereas excessive phosphate levels are toxic to plants and stimulate algal bloom in water reservoirs (reviewed by Scott, 2008). Here we describe genes and their products involved in Pi transport and maintenance of Pi homeostasis (**Figure 1A**). Phosphate and its role in plant life have both scientific and economic importance. **Figure 1B** shows the effect of Pi-deprivation on plant growth: the barley plants grown without Pi in the absence (−Pi) or presence (−Pi, Myc) of mycorrhizal fungi had shoot weights 35.2 and 33% lower, respectively, than the plant grown in Pi replete soil (+Pi) at 23 days post-sowing.

TRANSCRIPTION FACTORS INVOLVED IN Pi ACQUISITION

The mechanisms of Pi acquisition include secretion of carbon dioxide, and plant enzymes, e.g., acid phosphatases and organic acids (citric and malic acids), which target organic and inorganic soil P species, respectively, and release Pi from the soil particles (Scott, 2008; Richardson et al., 2011). Phosphate starvation induces expression of transcription factors (TFs) like *phosphorus starvation response 1* (*Psr1*), which shows at least 10-fold increase of expression during Pi deficiency in *Chlamydomonas reinhardtii* (AF174532; Wykoff et al., 1999). In contrast, the related *Arabidopsis thaliana* ortholog *phosphate starvation response 1* (*AtPHR1*, At4g28610) is only weakly responsive to Pi starvation (Rubio et al., 2001). The key regulatory functions of AtPHR1 and other TFs involved in Pi response have been reviewed by Nilsson et al. (2010) and Rouached et al. (2010). Signaling networks including TFs, Pi-responsive microRNAs, hormones, and sugars implicated in Pi sensing have been recently extensively reviewed by Chiou and Lin (2011). Located in the nucleus AtPHR1 can bind as a dimer via its MYB domain to the PHR1 binding site (*P1BS*, sequence GNATATNC), a motif present in the promoters of crucial Pi-responsive genes (Rubio et al., 2001; Schünmann et al., 2004a; Bustos et al., 2010; Nilsson et al., 2010; Oropeza-Aburto et al., 2012). A set of Pi-responsive genes with *P1BS* elements in their promoters is outlined in **Figure 1A**. This motif is frequent and considerably enriched in the promoters of Pi-responsive genes of *Arabidopsis* compared with the entire genome (Müller et al., 2007; Bustos et al., 2010). *AtPHR1* also regulates genes not directly involved in phosphate metabolism but possessing the *P1BS* element: e.g., *P1BS* occurs in the promoter of the *Arabidopsis sulfate transporter 1;3* gene (*AtSULTR1;3*, At1g22150), which is up-regulated during Pi-deficient conditions in wild-type plants but much less in *phr1* mutant plants (Rouached et al., 2011). Bustos et al. (2010) showed that expression of Pi-responsive genes in *Arabidopsis* also requires the PHR1-LIKE1 TF (*AtPHL1*, At5g29000), which also contains a MYB domain. The double mutant *phr1 phl1* exhibited lower expression levels of Pi transporter *AtPht1;1* (U62330, At5g43350, three *P1BS* elements) compared with either of the single mutants *phr1* and *phl1* or wild-type plants (Franco-Zorrilla et al., 2004; Bustos et al., 2010). Since the expression of neither *AtPHR1* nor *AtPHL1* is strongly induced by Pi starvation, it is still unclear how Pi-limitation influences Pi-responsive genes. It has been shown in *Arabidopsis* that there are at least four MYB-CC (CC – coiled coil domain) proteins highly similar to both AtPHR1 and AtPHL1, i.e., At2g20400, At3g04450, At3g13040, and At5g06800 (Bustos et al.,

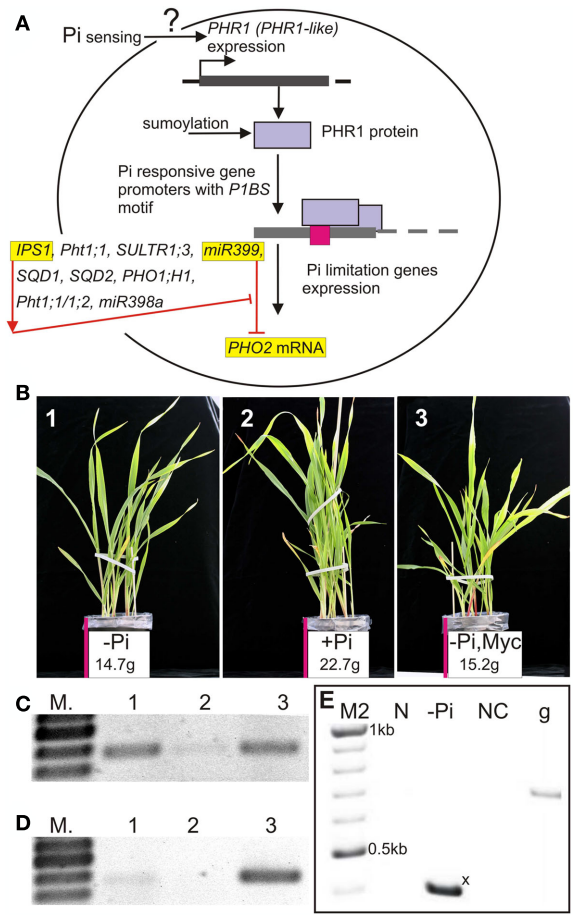

FIGURE 1 | (A) Schematic representation of the relation between *Arabidopsis* PHR1 or its orthologs and examples of Pi-responsive genes possessing PHR1 binding sites in their promoters. *Arabidopsis*: *IPS1* and *Pht1;1* genes have been described by Martin et al. (2000) and Muchhal et al. (1996), respectively; *SULTR1;3* by Rouached et al. (2011); miR399 by Pant et al. (2009) and Kuo and Chiou (2011); *SQD1*, *SQD2* (involved in sulfolipid biosynthesis) by Franco-Zorrilla et al. (2004); *PHO1;H1* (involved in Pi loading to the root xylem) by Stefanovic et al. (2007); barley *Pht1;1/1;2* by Schünmann et al. (2004a); rice miR398a by Gu et al. (2010); **(B)** Barley grown without or with inorganic phosphate (−Pi, +Pi) or without Pi but in the presence of mycorrhizal fungi (−Pi Myc); **(C)** Barley *HvPht1;1/1;2* expression in roots under different soil Pi and mycorrhiza conditions; **(D)** Barley *HvPht1;8* expression in roots under different soil Pi and mycorrhiza conditions; **(E)** *Arabidopsis* pri-miR399a isoform expression under Pi sufficient growing conditions (N) and during Pi starvation (−Pi). The short pri-microRNA399a isoform is marked with an x (see **Figure 2B**). Lanes/pictures 1, 3 (−Pi), lane/picture 2 (+Pi), lane/picture 3 depicts roots colonized by the mycorrhizal fungus *Glomus intraradices* (28A). N, sufficient Pi conditions; −Pi, phosphate starvation; NC, negative control; g, genomic DNA positive control. M – GeneRuler 100 bp DNA ladder, M2 – GeneRuler 100 bp Plus DNA ladder (Thermo Scientific, formerly Fermentas). Barley – *Hordeum vulgare* cv. Black Hulless. Presented data: **(B–D)** Pacak et al., unpublished data, **(E)** Sobkowiak, unpublished data.

2010). It is possible that these proteins are also involved in regulating the Pi-deprivation response. Furthermore, the AtPHR1 protein is a target for sumoylation by the SUMO E3 ligase, AtSIZ1 (At5g60410), which is also needed for Pi starvation-dependent responses (Miura et al., 2005). The expression of *AtSIZ1* is not strongly induced by Pi starvation, however (Miura et al., 2005).

PHOSPHATE TRANSPORT

There are four Pi transporter classes, Pht1, Pht2, Pht3, and Pht4, which are responsible for phosphate transport across membranes of cells, chloroplasts, mitochondria, and Golgi, respectively (Karandashov and Bucher, 2005; Rouached et al., 2010). Analysis of six barley (*Hordeum vulgare*) *Pht1* gene promoters revealed that all analyzed promoters possess *P1BS* elements (Schünmann et al., 2004a). These genes encode proteins belonging to the Pht1 family of phosphate transporters, which represents plasma membrane phosphate-H^+ symporters, containing 12 trans-membrane helices connected by a hydrophilic loop (reviewed by Karandashov and Bucher, 2005). Expression of the *AtPht1;1*, *HvPht1;1*, *HvPht1;2* (almost identical *CDS* to *HvPht1;1*), *Triticum aestivum Pht1;2* (AJ344241) gene members of the *Pht1* family, is largely restricted to roots (Muchhal et al., 1996; Davies et al., 2002; Schünmann et al., 2004a). The *HvPht1;1* (AF543197) and *HvPht1;2* (AY187019) promoters possess three and two *P1BS*-like motifs, respectively, and are Pi-limitation induced genes (Schünmann et al., 2004a,b; Glassop et al., 2005; Pacak et al., unpublished data; **Figure 1C**). Mutations in two out of three *P1BS* elements present in the *HvPht1;1* rearranged promoter completely abolished promoter completely abolished low-Pi induction (Schünmann et al., 2004b). Expression of the *TaPht1;2* gene is induced by Pi starvation in the wheat cultivar Dalcahue, although the full *P1BS* motif is not present in the promoter. Instead, four other conserved motifs have been identified. Three of them are also present in the promoter of *HvPht1;1*, whereas the fourth one is similar to the *P1BS* element (motif4; ATATRCA sequence; Tittarelli et al., 2007). Some phosphate transporter genes are expressed only in the presence of mycorrhizal fungi (reviewed by Javot et al., 2007; Smith et al., 2011). Mycorrhizal fungi do not colonize the roots of *Arabidopsis*, and no mycorrhiza-specific Pi transporter genes have been discovered in this species. They are, however, present in barley (*HvPht1;8*, AY187023; Glassop et al., 2005; Pacak et al., unpublished data; **Figure 1D**). Chen et al. (2011) described a set of mycorrhiza-activated phosphate transporters from eudicots. Apart from a *mycorrhiza* transcription factor binding *sequence* (MYCS), *P1BS* motifs were also found in the promoters of these genes. Mutation or deletion of either of these motifs resulted in a remarkable decrease or even the complete absence of gene expression (Chen et al., 2011).

Pi LEVEL REGULATION IN PLANTS BY microRNAs 399 AND *IPS1*

Among the Pi-responsive microRNAs which have been described in the latest review published by Kuo and Chiou (2011), miR399 is especially interesting owing to its interaction with an RNA molecule named *induced by phosphate starvation 1* (*IPS1*). The miR399 promoters possess the *P1BS* motif (Kuo and Chiou, 2011) and expression of their primary transcripts (pri-microRNAs) is activated by Pi starvation (Pant et al., 2009; Sobkowiak, unpublished data; **Figure 1E**). Two *P1BS* elements were found in the promoter of the *Arabidopsis* gene *AtIPS1* (AF236376, At3g09922; Martin et al., 2000; Rubio et al., 2001; Bustos et al., 2010). Originally *AtIPS1*

was described as a highly Pi starvation inducible gene belonging to the *Mt4*/*TPSI1* family, which possesses a conserved nucleotide motif and encodes only short open reading frames (Martin et al., 2000). Excellent work done by Franco-Zorrilla et al. (2007) showed that *AtIPS1* sequesters miR399, which is bound to the mentioned conserved region, thereby preventing complete degradation of miR399 targets such as the mRNA for the phosphate2 protein (*PHO2*, At2g33770). *AtIPS1* itself is not cleaved by miR399 owing to the sequence mismatches (**Figure 2A**). As we showed in our previous report about *miR* gene structures and the processing of *Arabidopsis* HYL1-dependent pri-microRNAs, alternative splicing events and alternative polyadenylation of microRNA precursors are often observed (Szarzynska et al., 2009). Interestingly, the *Arabidopsis* pri-microRNA399a transcript undergoes alternative splicing, with 3′ alternative splice site selection resulting in completely different sequences of the 3′ exons in the two pri-miR399a isoforms as well as different polyadenylation sites (**Figure 2B**; Sobkowiak, unpublished data). The role of these processes in miR399a expression regulation is still elusive.

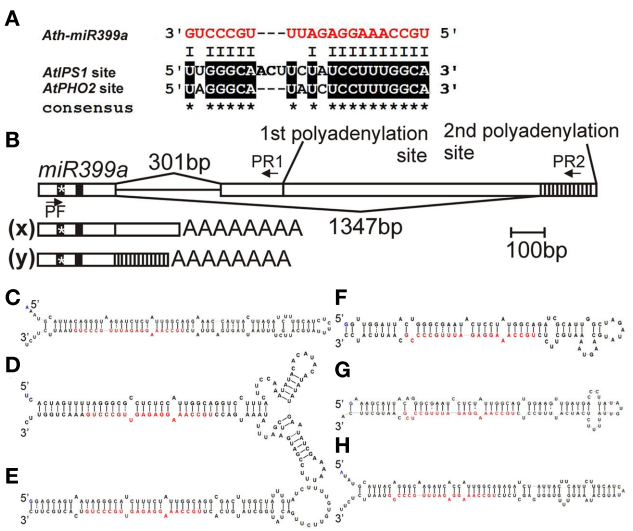

FIGURE 2 | (A) Alignment of mature *Arabidopsis* miR399a with miR399 binding site present in *AtIPS1* sequence and in 5′ UTR of *AtPHO2* mRNA (binding site no. 2 according to Lin et al., 2008); **(B)** *Arabidopsis* miR399a gene structure and its pri-miRNA species. The position of primers used for amplification of both pri-miR399a isoforms is marked by arrows. (x) pri-microRNA399a isoform marked in **Figure 1E** with an x (primers: PF and PR1), (y) second pri-microRNA399a isoform (primers: PF and PR2), after alternative 3′ splice site recognition. The position of mature microRNA is depicted by a vertical black line, the position of the microRNA* is depicted by * symbol on a vertical black line; **(C–H)** Stem-loop structures of *Arabidopsis* microRNA399 precursors with Minimum folding Free Energy (MFE); mature microRNA399 is marked by red fonts; **(C)** pre-miR399a (dG = −51.60 kcal/mol, one of two structures with the same energy, MI0001020 – accession number in the miRBase, www.mirbase.org); **(D)** pre-miR399b (dG = −61.70 kcal/mol, MI0001021); **(E)** pre-miR399c (dG = −57.89 kcal/mol, MI0001022); **(F)** pre-miR399d (dG = −45.40 kcal/mol, MI0001023); **(G)** pre-miR399e (dG = −48.70, one of six structures with the same energy, MI0001024); **(H)** pre-miR399f (dG = −49.60, one of two structures with the same energy, MI0001025); structures were designed with Folder v. 1.11 beta software, algorithm RNAfold (Hansen, 2007).

The six microRNA399 species (a–f) in *Arabidopsis* are considered as the immediate mediators of *PHO2* mRNA silencing. They are derived from six pre-microRNAs that differ in structure and sequence (**Figures 2C–H**). Mature miR399s can bind to five predicted target sites (differing in sequence from each other) present in the 5′ UTR of the *PHO2* mRNA (Allen et al., 2005; Bari et al., 2006). Only miR399a and miR399f have full complementarity (including GU base pairings) with target sequences – sites 1 and 3 in the 5′ UTR of *PHO2* mRNA, respectively (Lin et al., 2008). In *Arabidopsis*, an overexpression of miR399f leads to overaccumulation of Pi in shoots resembling the *pho2* mutant phenotype (Chiou et al., 2006). Suppression of *PHO2* by overexpressed miR399b/c is less efficient (Lin et al., 2008). The differences in microRNA affinity for the *PHO2* mRNA are probably owed to a nucleotide substitution at position 13 in the miR399b/c sequence, which reduces base pairing between microRNA399b/c and the target sites (Lin et al., 2008). Interestingly, the same nucleotide substitution improves base pairing of miR399b/c with the conserved region of the *At4*/*IPS1* family. A similar variation in miR399 sequences has been found in rice, *Medicago*, and *Populus*, where certain miR399 variants show reduced base pairing with target sequences in *PHO2* but improved base pairing with the *IPS1* homolog of the respective species (Lin et al., 2008).

The *Arabidopsis* PHO2 protein is responsible for the Pi level decrease in shoots and Pi remobilization. *pho2* mutants grown under Pi replete conditions accumulate Pi in shoots, but not in roots, and show induction of some phosphate starvation-induced genes, e.g., acid phosphatase 5 (*AtACP5*, At3g17790) and *AtPht1;4* – At2g38940 (Delhaize and Randall, 1995; Bari et al., 2006). Down-regulation of *PHO2* expression in barley produced a similar effect of increased Pi levels in shoots and decreased Pi levels in roots (Pacak et al., 2010). PHO2 possesses the UBiquitin-Conjugating E2 enzyme catalytic domain (UBCc domain). Since other UBC domain-containing proteins are usually smaller, 20 vs. 100 kDa (Bari et al., 2006), PHO2 may contain unidentified additional domains. Such domains may interact with phosphate-related proteins, e.g., targeting them for degradation. Degradation of these proteins may affect the phosphate homeostasis. Bioinformatic analysis showed that, apart from *PHO2* mRNA, other transcripts derived from the following genes, At3g11130 (encoding Clathrin, heavy chain), At3g25905 (clavata3/ESR-related27 protein), At3g54700 (*AtPht1;7*), At4g00170 (vesicle-associated membrane protein, VAMP), and At4g09730 (DEAD-box protein), are potential targets for miR399 (Pant et al., 2009; Kuo and Chiou, 2011). These complex connections between the miR399 family members and their targets can explain the fact that miR399b-overexpressing plants and a *pho2* mutant exhibited not only Pi-related changes, but also an early flowering phenotype observed only at normal temperature (23°C; Kim et al., 2011).

FUTURE PROSPECTS

The data presented above show that the presence of one or more *P1BS* elements in a gene promoter is associated with low-Pi induction. Other factors, however, can modulate the response. In the promoter of the *Arabidopsis* phospholipase *DZ2* gene (*PLDZ2*, At3g05630), apart from five *P1BS* copies, elements such as *SRE* (*sugar-repressive element*) have been found. A 65-bp promoter

fragment spanning two of the *P1BS* motifs (the *EZ2* region) has been identified as particularly important for the Pi-limitation response but strong induction also required sucrose and was negatively affected by cytokinins (Oropeza-Aburto et al., 2012). Exactly how the information carried by the *P1BS* elements and by the various sugar and hormone responsive promoter elements is integrated by the MYB-CC TFs *PHR1* and *PHL1* and possibly others is still unknown. Furthermore, additional studies are necessary to find out how Pi-limitation directly affects the function and/or expression of Pi-related TFs. Finally, the influence of other factors which can modulate the Pi response of genes containing *P1BS* elements should be further investigated.

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