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# Improvement of phosphorus efficiency in rice on the basis of understanding phosphate signaling and homeostasis

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Rice is one of the most important cereal crops feeding a large segment of the world's population. Inefficient utilization of phosphate (Pi) fertilizer by the plant in rice production increases cost and pollution. Developing cultivars with improved Pi use efficiency is essential for the sustainability of agriculture. Pi uptake, translocation and remobilization are regulated by complex molecular mechanisms through the functions of Pi transporters (PTs) and other downstream Pi Starvation Induced (PSI) genes. Expressions of these PSI genes are regulated by the Pi Starvation Response Regulator (OsPHR2)-mediated transcriptional control and/or PHO2-mediated ubiquitination. SPX-domain containing proteins and the type I $H^+$-PPase AVP1 involved in the maintenance and utilization of the internal phosphate. The potential application of posttranscriptional regulation of PT1 through OsPHF1 for Pi efficiency is proposed.

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## Introduction

Developing crop cultivars with increased yield and less dependence on the heavy application of fertilizers is essential for the sustainability of agriculture. Phosphorus (P) is an essential macronutrient for plant growth and development. Plants take up P exclusively in the form of inorganic phosphate (Pi). The high chemical fixation rate, slow diffusion and substantial fractions of organically bound P of Pi render it one of the least available nutrients for crop [1]. To obtain maximum crop yield, P fertilizer is often over-applied, which led to accelerating soil degradation and water eutrophication [2]. Rice is one of the most important cereal crops feeding a large segment of the world's population. Developing rice cultivars with higher efficiency in P use is increasingly important for sustainable food production.

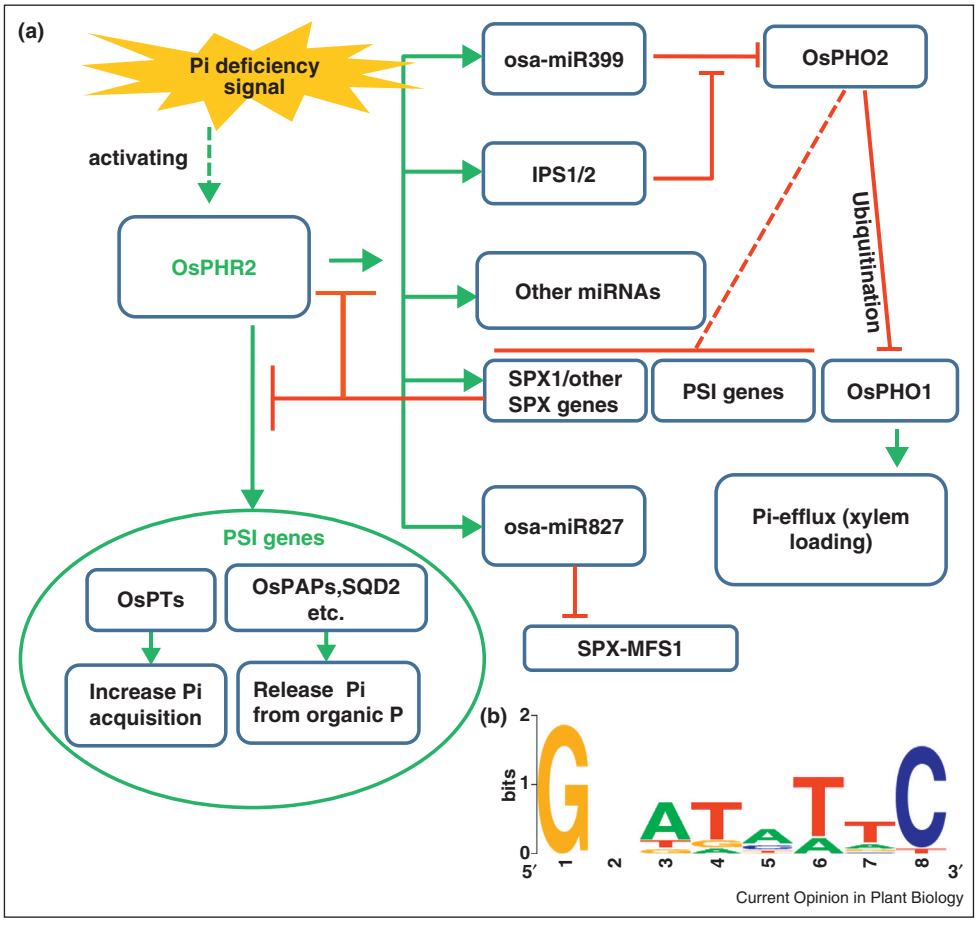
Over the past decades, many scientific studies aimed at elucidating the complex molecular mechanisms and crucial regulators underlying Pi signaling and Pi homeostasis in plants have been performed. In this article, we focus on progress in understanding the molecular regulation of Pi acquisition and homeostasis in the major cereal crop rice. In particular, this review summarizes the recent progress in determining the signal networks of PSI, the functions and regulation of rice PT, and the roles of SPX domain-containing proteins in Pi homeostasis. In addition, we provide new data showing the application of Pi-transporter posttranslational regulation to improve tolerance to low Pi stress in rice.

## Phosphate signaling under the control of the central transcription factor OsPHR2

The Arabidopsis Phosphate Starvation Response Regulator 1 (PHR1) is a MYB transcription factor, playing a key role in Pi starvation signaling by binding to a cis-element of GNATATNC, named the PHR1 binding sequences (P1BS) [3]. Genes downstream of PHR1 include genes encoding the signal molecules AtIPS1/At4 [4,5], miRNAs [6], SPXs [7,8••,9,10], biosynthetic genes of sulfolipids and galactolipids [11], PTs [12–14] and purple acid phosphatases (PAPs) [15–17] (Figure 1a). In addition to P1BS, there are other consensus sequences adjacent to P1BS that have proved to be essential to the Pi starvation response [18•,19].

OsPHR1 and OsPHR2 are homologous proteins of PHR1 in rice [20]. Overexpression of *OsPHR2* in rice mimicked the Pi starvation signal. It induced PSI gene expression and resulted in the enhancement of Pi acquisition. The PSI genes that are activated by the overexpression of *OsPHR2* include genes encoding the signaling molecules *OsIPS1/2*, microRNA osa-miR399 and osa-miR827 [20,21,22•,23], and SPX1-3 and SPX5-6 [8••,9,10,22•]; PTs for Pi uptake and translocation; PAPs for releasing Pi from organic P [20,24]; sulfoquinovosyldiacylglycerol 2 (SQD2) for recycling Pi from membrane phospholipids [12–14] (Table 1 and Figure 1a). Analysis of the 2.0 kb sequence upstream of the initiating ATG of the listed PSI genes and a yeast one-hybridization assay showed that at least one additional motif (Figure 1b), named as P1BS-like, adjacent to the PIBS elements at a certain distance is

**Figure 1**




**(a)** Regulation of phosphate starvation signal through the transcription factor, OsPHR2. Green arrows represent positive effects, whereas red lines ending with a short bar indicate negative effects. The dotted red line indicates unknown mechanism. **(b)** Weblogo presentation of sequence of P1BS-like motif.

required for OsPHR2 binding. The requirement for the existence of P1BS and P1BS-like sequences in the promoter region of PSI genes is consistent with the fact that OsPHR2 acts as a heterodimer or homodimer.

As was initially shown in Arabidopsis [25–29], the expression of both *osa-miR399* and its antagonists *OsIPS1/2* are induced by *OsPHR2* overexpression, regardless of the status of Pi supply. osa-miRNA399 targets an E2 ubiquitin-conjugase, OsPHO2 [30]. OsIPS1/2 mimics the osa-miR399 target to attenuate the suppressive effect of miR399 on PHO2 mRNA. Overexpression of *OsPHR2* and loss of function of *OsPHO2* lead to excessive accumulation of Pi in the shoot tissue [9,20,30].

A number of rice PTs have been shown to be induced by Pi starvation [8••,13,20,31,32••,33]. While 9 out of the 13 rice PTs contain P1BS sequences in their promoter region, only OsPT2/3/7/10/11 contains the adjacent P1BS-like motif (Table 1). The physical binding of OsPHR2 to the promoter of the *OsPT2* gene, which encodes a low-affinity PT, has been shown [8••]. Whether the Pi starvation-induced PTs, that lack the adjacent P1BS-like element, are regulated by the transcription factor OsPHR2 in conjugation with other protein factors or by other transcription factors needs to be clarified.

The expression levels of 10 out of the 25 identified rice *PAP* genes were upregulated by both phosphate deprivation or overexpression of the transcription factor OsPHR2 [24]. In addition to the 10 PSI PAP genes in the root, the promoters of *OsPAP9a* and *OsPAP15* contained P1BS and the adjacent P1BS-like elements (Table 1). It is not clear why the expression of the two PAP genes does not respond to Pi starvation. In addition, *OsPAP1d* and *OsPAP10a* have only P1BS element(s), not the adjacent P1BS-like element. Whether the induction of these two genes by Pi starvation requires factors other than OsPHR2 needs further analysis.