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Arabidopsis Pht1;5 plays an integral role in phosphate homeostasis

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The mobilization of inorganic phosphate (Pi) in planta is a complex process regulated by a number of developmental and environmental cues. Plants possess many Pi transporters that acquire Pi from the rhizosphere and translocate it throughout the plant. A few members of the high-affinity Pht1 family of Pi transporters have been functionally characterized and, for the most part, have been shown to be involved in Pi acquisition. We recently demonstrated that the Arabidopsis Pi transporter, Pht1;5, plays a key role in translocating Pi between tissues. Loss-of-function *pht1;5* mutant seedlings accumulated more P in shoots relative to wild type but less in roots. In contrast, overexpression of *Pht1;5* resulted in a lower P shoot:root ratio compared with wild type. Also, the rosette leaves of *Pht1;5*-overexpression plants senesced early and contained less P, whereas reproductive organs accumulated more P than those of wild type. Herein we report the molecular response of disrupting *Pht1;5* expression on other factors known to modulate P distribution. The results reveal reciprocal mis-regulation of *PHO1*, *miR399d* and *At4* in the *pht1;5* mutant and *Pht1;5*-overexpressor, consistent with the corresponding changes in P distribution in these lines. Together our studies reveal a complex role for Pht1;5 in regulating Pi homeostasis.

Phosphorus (P) is a major macronutrient for plants that is vital to a number of processes. Thus, plants must acquire large quantities of P from the soil and coordinate its distribution to satisfy the developmental requirements of each tissue. P is acquired as inorganic phosphate (Pi) via Pi transporters, which also distribute Pi throughout the plant.[1] A number of plant Pi transporters have been identified based on their homology to the *Saccharomyces cerevisiae* Pho84p Pi transporter. These proteins, which are localized to the plasma-membrane and have 12 membrane-spanning domains, comprise the PHOSPHATE TRANSPORTER 1 (Pht1) family and are presumed to be high-affinity transporters.[2] The Arabidopsis Pht1 family contains 9 members, Pht1;1 through Pht1;9.[2] Of these, only Pht1;1 and Pht1;4 had previously been functionally characterized, and were shown to be involved in Pi acquisition.[3] Recently, we described the characterization of *Pht1;5* via analyses of loss-of-function mutants and overexpression transgenics.[4] We found that Pht1;5 plays key roles in Pi translocation and remobilization. Herein we provide additional evidence that Pht1;5 is required for normal Pi homeostasis in Arabidopsis by examining the expression of other factors known to control P distribution in *Pht1;5*-mutant and overexpression lines.

In plants, Pi acquisition occurs via Pi transporters present in root epidermal and cortical cells (**Fig. 1-I**).[5-10] From the cortex, Pi must be loaded into the xylem for subsequent translocation to shoot tissues (**Fig. 1-II**). The PHO1 protein plays a role in root Pi xylem loading in Arabidopsis.[11,12] Via the phloem, Pi is retranslocated to root tissues (**Fig. 1-III**) and across shoot tissues (**Fig. 1-IV and V**) in accordance with developmental cues and Pi status. Our recent report in reference 4, demonstrated that Arabidopsis Pht1;5 is involved in (1) P retranslocation between shoots and roots of young seedlings (**Fig. 1-III**) and (2) mobilization/remobilization of P from shoot sources (i.e., mature and senescing leaves) to sinks (i.e., young leaves and inflorescence tissues; **Fig. 1-IV and V**).[4] Interestingly, loss of *Pht1;5* led to an increase in the shoot:root ratio of P relative to wild type, whereas *Pht1;5*-overexpression resulted in a decrease. To gain insight into the influence of *Pht1;5* disruption on other factors known to impact P distribution, we measured the transcript levels of *PHO1* and *At4*, as well as primary transcripts of *miR399d*, in the roots of the *pht1;5-1* loss-of-function mutant and a *Pht1;5*-overexpression line. As shown in **Figure 2**, *PHO1* transcript levels were lower in *pht1;5-1* mutant roots compared with wild type, but were higher in roots of the *Pht1;5*-overexpressor. This is consistent with the mutant exhibiting downregulation of *PHO1* in an attempt to decrease Pi xylem loading in roots and subsequent translocation to shoots, whereas upregulation of *PHO1* in the *Pht1;5*-overexpression line may result from the increased mobilization of Pi to roots. The microRNA *miR399* and *At4* are two antagonistic components of a circuit that functions to modulate multiple Pi starvation responses including distribution of P.[13-17] As with *PHO1*, the expression of *miR399d* (one representative of the miR399 family) and *At4* show reciprocal changes in the *pht1;5-1*

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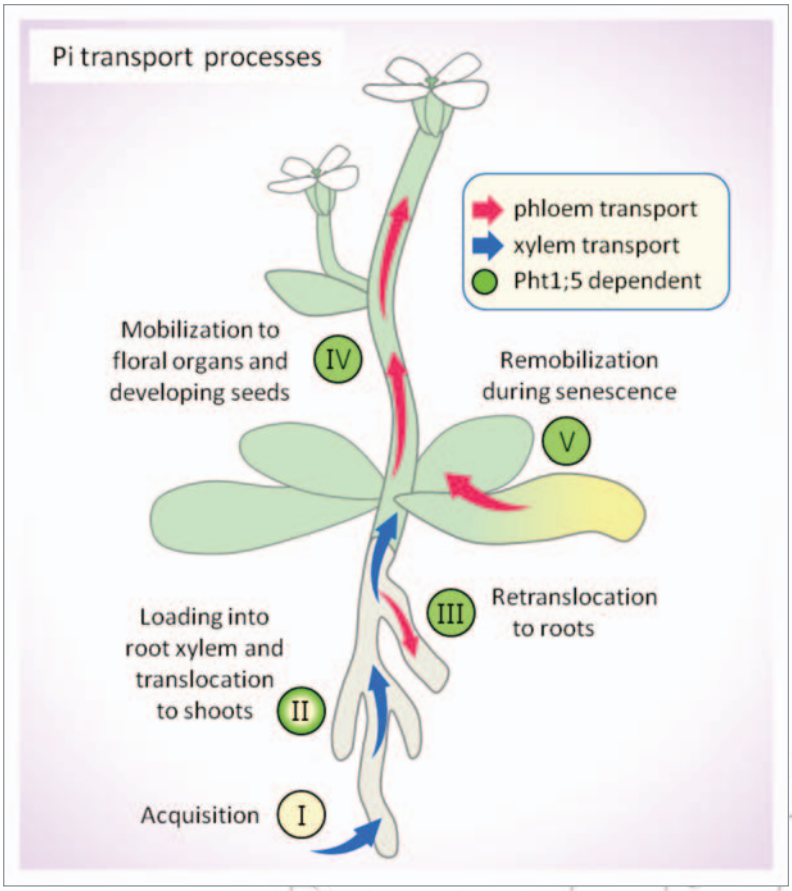

Figure 1. Proposed role for Pht1;5 in Pi mobilization. The processes of Pi transport are shown following its acquisition from the rhizosphere. Green labels show processes in which Pht1;5 likely plays a role. The arrows indicate the movement of Pi via the xylem (blue) and phloem (red).

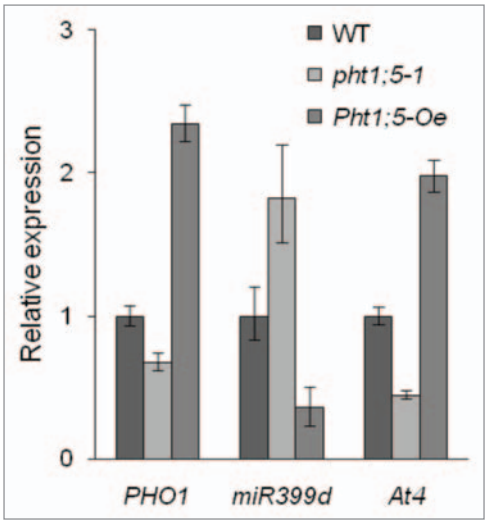

Figure 2. Quantitative RT-PCR analysis of genes associated with P distribution. Wild-type (WT), *pht1;5-1* mutant and *Pht1;5*-overexpression (*Pht1;5-Oe*) seedlings were grown hydroponically for three weeks in high-Pi (1.25 mM Pi) media. Total RNA isolated from these plants was used for qRT-PCR. *At4g26410* was used as an internal reference gene, and the values, normalized to WT levels, are the means ± SE of two independent biological replicates run in triplicate.

mutant and *Pht1;5*-overexpressor (**Fig. 2**). Transcript levels for *miR399d* and *At4* were higher and lower, respectfully, in *pht1;5-1* roots compared with wild type, whereas the *Pht1;5*-overexpressor accumulated less *miR399d* and more *At4* transcripts relative to wild type. This also indicates that loss of *Pht1;5* affects the shoot-derived Pi starvation signal thereby systemically upregulating the expression of *miR399d* in the roots. Taken together these results suggest that disruption of *Pht1;5* expression causes atypical Pi mobilization, which leads to the initiation of other signal transduction events that attempt to overcome the alterations in P distribution.

Our recent report also indicated that Pht1;5 contributes to mobilization of Pi from mature and senescing leaves to metabolically active tissues. The leaves of transgenic Arabidopsis plants overexpressing *Pht1;5* senesced earlier than those of wild type and contained lower levels of P.[4] However, the *Pht1;5*-overexpressor accumulated more P in floral stalks and siliques compared with wild type.[4] These results are consistent with Pht1;5 functioning in retranslocation of Pi from P source to sink organs (**Fig. 1-IV and V**). A similar function was recently proposed for the rice Pi transporter, OsPht1;8. Overexpression of *OsPht1;8* led to increased P content in the panicles and hulls of transgenic rice.[18] OsPht1;8 was also implicated in root-to-shoot transport of Pi due to its expression at root-shoot junctions.[18] Similarly, *Pht1;5* is expressed in root stele cells of Pi-starved Arabidopsis,[8] and mutation of *Pht1;5* led to a drop in Pi root-to-shoot translocation under Pi-deficient conditions.[4] These results suggest that Pht1;5 may also contribute to the loading of Pi into root xylem for subsequent translocation to shoots during low Pi conditions (**Fig. 1, II**).

In conclusion, our work on Pht1;5 highlights intricate regulation of Pi mobilization and distribution in higher plants. In addition to Pi acquisition from soil, high-affinity Pi transporters are also needed for internal Pi mobilization, which is controlled by the coordination of developmental and environmental (i.e., P availability) cues. Our work thus gives credence to the notion that Pi transporters are not simply downstream components of Pi signaling pathways, but rather influence gene expression and signaling events by regulating Pi homeostasis in tissues and organs.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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