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Insights into plant phosphate sensing and signaling

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Phosphorus (P) is a macronutrient essential for plant growth, therefore, soil P level is critical to crop yield potential in agriculture. As Pi levels limit crop yield under many soil conditions, it is crucial to understand the mechanisms by which plants adapt to low-phosphate (Pi) soil conditions and interact with their soil microbiome to improve crop P use efficiency, in order to ensure global food security. Recent advances have been made towards achieving this goal through advancing our understanding of the plant's response to limiting Pi conditions to maintain P homeostasis. In this review, we assess advances made in local and systemic Pi sensing and signaling, and in the molecular events for Pi absorption, redistribution and plant–symbiont interactions. These findings offer important avenues for bio-engineering of agricultural crops with traits for enhanced Pi acquisition and utilization.

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Introduction

In plants, phosphorus (P) is an essential macronutrient in pervasive biological processes. However, an acute conflict arises between increasing demand for agricultural output and inefficient application of finite and non-renewable phosphate (Pi), as a fertilizer. Thus, a deeper understanding of the regulatory mechanisms underlying P sensing and signaling in plants is a prerequisite for optimizing crop P use efficiency [1,2]. In the face of shifting edaphic conditions, plants must maintain cellular P homeostasis by employing a range of strategies. In response to low external Pi, *local* signals are produced that lead to adaptation of root system architecture (RSA) to enhance Pi absorption. For most plants, this generally involves a cessation of primary root (PR) growth and enhanced lateral root (LR) development, as wells as changes in root-microbiome interactions. Plant vacuoles also play an important function in the local maintenance of P homeostasis. *Systemic* or *long-distance* signals are responsive to internal Pi fluctuations, and are transported to distant target cells to execute their functions [3]. In this review, we address recent progress that has revealed elaborate molecular mechanisms underlying both local and systemic signaling pathways.

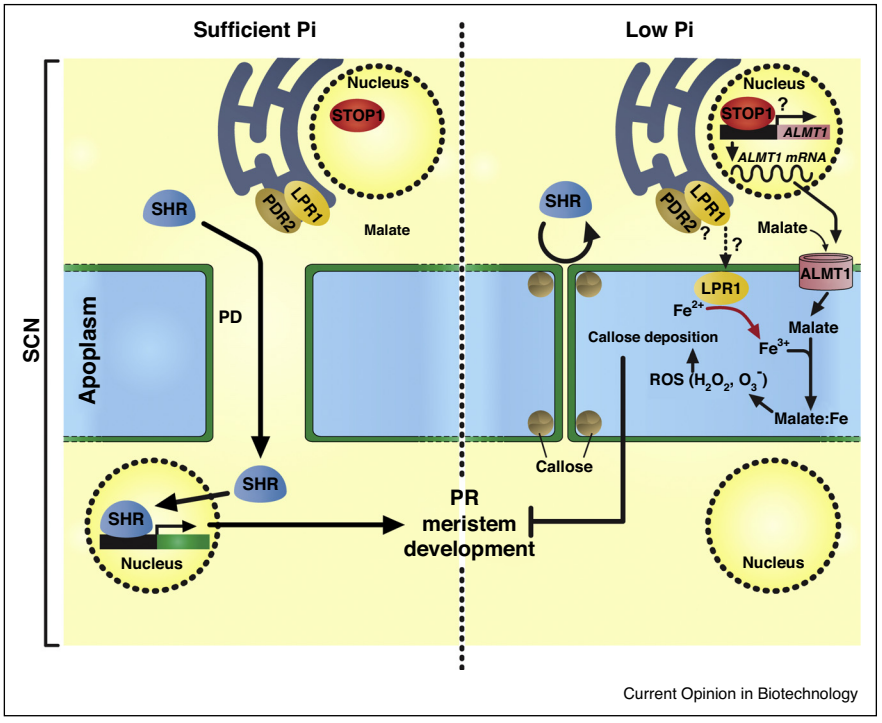
Local P sensing in the root tip

In Arabidopsis, the *PHOSPHATE DEFICIENCY RESPONSE 2* (*PDR2*) and *LOW PHOSPHATE ROOT* (*LPR*) genetically interact to arrest PR growth under Pi-limiting conditions [4]. Insight into the underlying mechanism was afforded by recent studies showing that, under Pi-stress, LPR1 acts locally to regulate primary root apical meristem (RAM) activity, by blocking symplasmic communication within the stem cell niche (SCN) [5••]. This involves the transcription factor, *SENSITIVE TO PROTON RHIZOTOXICITY* (*STOP1*), which controls expression of *ALUMINUM ACTIVATED MALATE TRANSPORTER 1* (*ALMT1*), a plasma membrane-localized malate secretion system. Next, malate released into the apoplasm mediates in the activation of a Fe-redox-cycling system to induce production of reactive oxygen species (ROS) [6,7•]. This rise in local ROS induces callose deposition in the primary root SCN, leading to a disruption in the plasmodesmal communication pathway, thereby causing a cessation in stem cell function and stoppage of PR growth [5••,6,8] (Figure 1). What remains unknown in this scenario is how the root tip cells sense the presence of low Pi levels, in the neighboring soil, and transduce this change to an activation of *ALMT1* expression mediated through the STOP1 signaling module.

Adaptations of RSA under Pi-stress

When grown under limited Pi availability, the root system of many plants becomes concentrated in the topsoil, due to an inhibition of PR elongation and the stimulation of LR initiation. These traits enhance topsoil foraging which generally contains both organic P and fertilizer-applied Pi. During the various stages of LR development, auxin gradients play a crucial role. Under Pi-limiting conditions, the trigger for LR proliferation, through an enhancement in auxin sensitivity, involves an increase in the expression of the auxin receptor, *TIR1* in the pericycle cells [9]. However, the process that controls TIR1 turnover, as a result of fluctuating Pi levels in the soil, has yet to be established. Interestingly, strigolactone (SL) also appears to participate both in the adaptation of RSA and root–microbiome interactions (discussed later), under limited Pi availability [10•,11], thereby allowing for targeted

Figure 1



Local Pi sensing and signaling controls primary root development. The stem cell niche (SCN) in the primary root (PR) requires plasmodesmata (PD)-mediated trafficking of transcription factors (TFs), such as SHORT ROOT (SHR), for normal developmental progression. Upon experiencing Pi-limiting conditions in the soil, two important pathways become activated in the PR SCN. The STOP1 pathway activates *ALMT1* expression and the subsequent insertion of ALMT1, a malate channel, into the plasma membrane then facilitates malate release into the apoplasm. In parallel, the endoplasmic reticulum (ER)-located PDR2 is inactivated, likely allowing for the intracellular trafficking of LPR1 from the ER to the plasma membrane, where it serves as a cell-wall associated ferroxidase that oxidizes Fe^{2+} to Fe^{3+}. This enzymatic activity of LPR1 results in Fe^{3+}accumulation in the apoplasm, where it forms a complex with the released malate to then activate ROS production which triggers callose deposition in SCN cell wall. This process blocks PD trafficking of SHR and other TFs, which leads to PR apical meristem exhaustion. These STOP1-ALMT1 and PDR2-LPR1 signaling pathways also play a role in cell wall stiffening in the root transition zone, leading to inhibition of cell expansion and subsequently root elongation [7•]. Collectively, these Pi-limiting conditions lead to a cessation of PR growth. The mechanisms underlying STOP1 activation of *ALMT1* expression, PDR2 inactivation and intracellular LPR1 transport remain to be elucidated.

rearrangements of the root system to optimize exploration of Pi enriched sites by the plant.

Mechanisms underlying P homeostasis

A complex sensing system is required to maintain the internal levels of P within the plant. In this regard, the initial uptake and subsequent remobilization of Pi is regulated by the PHOSPHATE TRANSPORTER 1 (PHT1) proteins. Endomembrane-mediated delivery of PHT1 proteins to the plasma membrane is mediated by PHOSPHATE TRANSPORTER TRAFFIC FACILITATOR1 (PHF1), and this process is negatively regulated by phosphorylation, which is relieved under Pi-limiting conditions [12]. In addition, PHT1 levels at the plasma membrane are fine-tuned by such proteins as PHOSPHATE2 (PHO2) and NITROGEN LIMITATION ADAPTATION (NLA) that mediate in PHT1 turnover, via ubiquitination [13–15], and this process involves receptor-based targeting to the vacuole for PHT1 degradation [16] (Figure 2a). Unfortunately, testing whether PHT1 acts as a plasma membrane sensor of external Pi levels has been complicated by the fact that interference of the PHT1 regulatory events also leads to a disturbance of P homeostasis [3].

In the plant, the vacuole serves as a primary Pi reservoir. Recently, vacuolar located SPX-MFS domain-containing proteins have been characterized that mediate Pi transport across the tonoplast. These vacuolar Pi transporters (VPTs) contain an N-terminal SPX (SYG1/PHO81/XPR1) domain and a C-terminal major facilitator superfamily (MFS) transporter domain. These domains are characteristics of the PHT5 protein family, for which in *Arabidopsis* there are three members. Patch-clamp studies performed on isolated vacuoles, combined with ^{31}P-magnetic resonance spectroscopy assays have demonstrated that PHT5;1 (also known as VPT1) functions as a major vacuolar Pi influx transporter [17••,18••].