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Plant Biology: Unravelling the Transient Physiological Role for PHO1 in the Seed

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Summary

During seed development, an important transfer of nutrients occurs between the seed coat and the embryo. A new study reveals that, for inorganic phosphate (Pi), this function is transiently performed by PHO1, a protein associated previously with Pi loading into the xylem.

Main Text

Phosphorus is an essential macronutrient for plant development and signalling. It is acquired in the plants exclusively in the form of Pi from the environment by the PHT1 family of Pi/H+ cotransporters [1], which mediates its transport across the plasma membrane. Interestingly, this family of transporters is involved in both the direct uptake of Pi from soils and the exchanges with arbuscular myccorhizal fungi (a trait shared by 80% of vascular flowering plants [2]). All of these transporters are mainly associated with the influx activities of Pi into the cell, and many additional Pi transporters have been identified for the allocation of this crucial resource in the different plant cell compartments [2].

For the efflux activity, other key components for Pi homeostasis are the members of the PHO1 family. Their physiological activity was difficult to demonstrate, as they exhibit no homology to known transporters [3], but show similarities with the yeast Syg1 protein (a component of the mating pheromone signal transduction pathway) or with the Rcm1 mammalian receptor for xenotropic murine leukemia retrovirus. Another problem with studying these proteins is the difficulty to detect the PHO1 protein at the plasma membrane. A GFP-labeled PHO1 can complement the *pho1* mutant but is observed only in the Golgi and trans-Golgi network [4]. This may be due to fine control of the level of this protein at the plasma membrane level through important recycling at the trans-Golgi network level.

Until now, PHO1 proteins were only known to support the Pi transfer from root to shoot [5]. Indeed the *pho1* mutant exhibits a strong reduction of Pi content in the leaves due to a failure in the loading of Pi into the xylem [6,7]. Experiments overexpressing this protein in plant tissue where it was normally not detected triggered Pi export, suggesting a direct role in Pi export for the PHO1 protein [3,4].

In *Arabidopsis*, where they were first identified, the PHO1 family comprises 11 members. They share important homologies (47–94% [8]) but phylogenetic studies have revealed that PHO1 and PHO1;H1 belong to a distinct clade from all other PHO1 family members, which would suggest a distinct role independent of Pi homeostasis [9]. Such analysis is reinforced by genetic studies

revealing that mutants affecting these other members of the PHO1 family exhibited abnormal hypocotyl growth [10], seed size [11] or flowering [12]. Besides, only PHO1;H1 can also complement the *pho1* mutant, supporting a similar physiological role for these two proteins [5].

Since the pioneering work on the gene expression map of the *Arabidopsis* root [13], the transcriptomes of many plant tissues have been analysed. They revealed unexpected and specific locations for many genes, offering the opportunity to investigate their physiological relevance in these tissues. So for phosphate, the recent identification of PHT1 proteins in the root cap offered the opportunity to identify the important contribution of this cell layer to Pi uptake [14]. In this issue of *Current Biology*, Yves Poirier's team found a new physiological role for PHO1 — the transfer of Pi between the chalazal seed coat and the embryo [15]. Using several reporters such as GFP or GUS fused to PHO1 or PHO1;H1 genes under the control of their own promoters, the authors detected strong expression in the chalazal seed coat. It also revealed a novel level of complexity, as in this system, PHO1;H1 cannot complement PHO1 phenotype, suggesting distinct features between these two proteins, which have been unknown so far [15]. Such results can appear surprising, as PHO1;H1 is also expressed in the same tissues. However, both genetic studies of mutants and specific tissue complementation confirmed this surprising result.

As *pho1* mutation impacts Pi distribution in plants (including the seed), the authors circumvented this problem elegantly by grafting wild-type root stock onto *pho1*(*pho1;H1,* or double mutant) mutants to produce plants with normal Pi distribution from root to shoot, but with *pho1* background for the seed development [15].

The other difficulty in the study of Pi is the lack of a technique to visualize the cellular resolution of Pi distribution [16] and the velocity of the transport of this ion. Most physical techniques offering access to ion distribution, for example, synchrotron x-ray fluorescencemicrotomography used to localize iron in the seed [17], can only detect total phosphorus and therefore are not accurate for visualizing the phosphate pool. The main tool remains the labeling of the tissues with radioisotope (^{32}P or ^{33}P), which can be measured either by real-time imaging [18] or microdissection when high resolution is requested. This latter solution has been used here [15]. I must underline the difficulty of such experiments, as the role of PHO1 protein during seed development appears to be only transient, and the phenotype can be found only at the mature green stage. The absence of a strong seed phenotype may be due to compensatory mechanisms resulting from the activity of other members of the PHO1 family (distinct from PHO1;H1) or to physiological adaptations that remain to be discovered.

This role for PHO1 may also require specific conditions, as illustrated by the study of iron allocation in the seed. Indeed, the role of VIT1 for primary allocation of iron in the provascular strands of the embryo was revealed by specific pH conditions, which promoted an impact at the germination level between the mutant and the wild-type [17]. For phosphate, similar

mechanisms may exist, especially since abnormal growth is only observed when Pi absorption is reduced by more than 80% in normal growth conditions [19], highlighting the capacity of the plant to adapt.

Nevertheless, the analysis reported in the present issue provides novel evidence supporting the role of the PHO1 family in Pi export.

Unravelling the molecular mechanisms involved remains an exciting but very difficult challenge, as all attempts to understand PHO1 transport activities in non-plant systems have failed so far. Nevertheless, the increasing pace of research in the field of Pi homeostasis should help to fill this gap in the near future.

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