Box 1. Main Alternatives to Effectively Reduce the Need for Chemical Phosphate (Pi)- Fertilizers

The development of crop varieties with increased Pi utilization efficiencies, i.e., crops (e.g., grain, fruit) that can produce more desirable biomass per gram of Pi absorbed.

Systems that increase the capacity of the plant to extract immobile Pi from the soil. This can be achieved by producing microbial inoculants that solubilize Pi and promote plant growth.

The development of alternative P-fertilizer formulations that solve the problems associated with the chemical properties of orthophosphate.

that are not readily available for plant uptake is converted into Pi that is available for plant assimilation. Recently, plant nutrition studies have focused on identifying the microbes present in the rhizosphere or those present as endophytes that can increase biomass production with the same or lower amounts of fertilizer [6]. Many bacterial and fungal strains have been isolated that, at least under controlled conditions, promote plant growth and enhance nutrient use efficiency. However, commercial use of these bio-inoculants has produced mixed results, probably because specific soil microbes associate with particular plant species and inoculated bacteria must compete with native strains that are potentially better adapted to the local soil. Advances in the technology used to study microbiomes may yield information that facilitates future design of microbial consortia that are well adapted to different types of soils and can efficiently associate with the crop of interest [6].

Sattari et al. [2] estimated that 45-50 million tons of mineral P fertilizer will be required per year by 2050 for crop and grass production, requiring the mining of 350 million tons of phosphate rock. This scenario is unfeasible, not only because P reserves would be rapidly diminished, but also because an increase in the release of Pi from agricultural effluents into lakes and the ocean would enhance the already critical problem of toxic algae blooms. Hypoxia caused by Pi-promoted algae blooms already account for over 400 zones of death sea, of which one of the most prominent is the 5000 square kilometer ocean death zone in the Mexican Gulf in the delta of the Mississippi river [7,8]. Therefore, P fertilizer use must be urgently optimized, requiring integration of the different strategies briefly described above to avoid a severe food production crisis and a rapid increase in feed prices as P reserves diminish. Although a global problem, it would be interesting to see how this critical scenario is addressed at the national scale.

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Spotlight

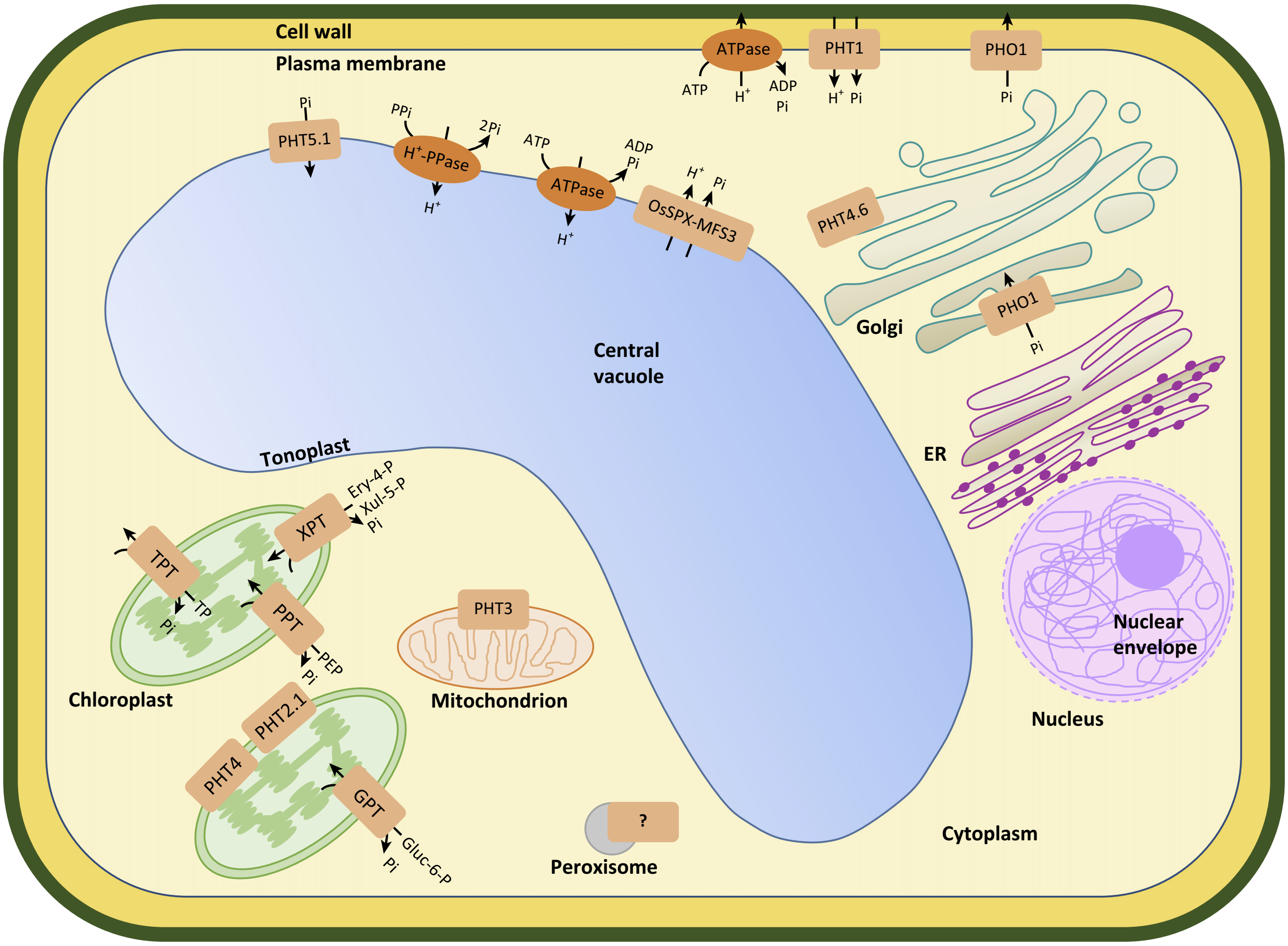
Long-Sought Vacuolar Phosphate Transporters Identified

Marcel Bucher[1,]* and Izabela Fabiańska[1]

The vacuole is an important subcellular compartment that serves as main phosphate storage in plants among other functions. Three recent studies shed light on the underlying molecular mechanisms for vacuolar phosphate transport that had long remained unknown.

Cellular Compartmentation in Eukaryotes

Biological membranes consist mainly of phospholipids and are a prerequisite for cellular life. The formation of the plasma membrane which surrounds the cytoplasm is common to prokaryotes and eukaryotes separating the interior of the cell from its external environment. In contrast to prokaryotes, eukaryotic cells, which evolved from a common prokaryotic ancestor at least 2.7 billion years ago, exhibit a high level of subcellular compartmentalization and contain a nucleus, a cytoskeleton, and a variety of cytoplasmic membrane-enclosed organelles [1]. While serving many biological functions, most of these endomembrane systems enable single cells to accumulate hydrophilic compounds, such as most nutrients and metabolites, on either side of the membrane. This intricate internal organization supports metabolic, reproductive, and developmental activities under stable physico-chemical conditions. Chloroplasts are typical organelles of photoautotrophic plants, whereas vacuoles are present in all cells of plants and fungi and in cells of some bacteria, protists [2], and animals [3].



Trends in Plant Science

Figure 1. Cellular Localization of Main Plant Pi Transport Systems. Arrows indicate the direction of Pi transport validated *in situ*. Plasma membrane localized PHT1 transporters require proton ATPase activity to facilitate proton-coupled Pi transport. The transport mechanisms of chloroplastidic PHT2.1 and PHT4, and mitochondrial PHT3 was studied in heterologous systems [5]. PHO1 protein localizes to Golgi and plasma membrane and PHO1-mediated Pi transport does not require a H^+ gradient across the membrane. There are four types of Pi translocators localized in the inner envelope membrane of plastids that can transport Pi in counter exchange with different substrates: TPT accepts triose-phosphates (TP), GPT accepts glucose-6-phosphate (Gluc-6-P), triose-phosphate and 3-phosphoglycerate, XPT has a broad substrate specificity: xylulose-5-phosphate (Xul-5-P), erythrose-4-phosphate, (Ery-4-P), ribulose-5-phosphate (Ru 5-P) and triose-phosphates (TP), and PTP mediates the import of phosphoenolpyruvate (PEP) [12]. Tonoplast localized PHT5.1 (or VPT1) is assumed to be an ion channel mediating vacuolar Pi import, similarly to its homolog in rice OsSPX-MFS1. Another rice protein at the tonoplast, OsSPX-MFS3 is proposed to export Pi in exchange with protons. Abbreviations: AtPHT5.1 = AtVPT1, *A. thaliana* phosphate transporter 5.1 = vacuolar phosphate transporter 1; PHT1, phosphate transporter family 1; PHT2;1, phosphate transporter 2;1; PHT3, phosphate transporter family 3; PHT4, phosphate transporter family 4; TPT, triose-phosphate/phosphate translocator; PPT, phosphate/phosphoenolpyruvate translocator; GPT1, glucose 6-phosphate/phosphate translocator 1; OsSPX-MFS1, *O. sativa* (SPX)-major facility superfamily 1, OsSPX-MFS3, *O. sativa* (SPX)-major facility superfamily 3; PHO1, phosphate 1; XPT, xylulose 5-phosphate/phosphate translocator.

Functions of Vacuoles in Plant Cells

Form, function and significance of vacuoles vary greatly dependent on the species, the organisms metabolic and physiological status, and the cell type in which they are contained. Plant vacuoles mainly serve the following functions [4]: turgor-driven cell growth; ion and protein storage; storage of primary and secondary metabolites and potentially toxic compounds; turnover of cellular compounds (protein and RNA); and regulation of cellular phosphate homeostasis.

Phosphorus (P) is an essential plant nutrient which is usually limiting plant productivity in natural habitats but also in agricultural soils world-wide, if not added as fertilizer. Orthophosphates, $H_2PO_4^-$ and HPO_4^{2-} (Pi), are the primary forms of P taken up by plants dependent on soil pH. Root uptake, xylem loading with and subsequent allocation in aboveground organs of Pi and its subcellular distributions are mediated by several families of Pi transport proteins [5]. The molecular mechanisms underlying