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Phosphorus Acquisition and Utilization in Plants

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Abstract

Tremendous progress has been made on molecular aspects of plant phosphorus (P) nutrition, often without heeding information provided by soil scientists, ecophysiologists, and crop physiologists. This review suggests ways to integrate information from different disciplines.

When soil P availability is very low, P-mobilizing strategies are more effective than mycorrhizal strategies. Soil parameters largely determine how much P roots can acquire from P-impoverished soil, and kinetic properties of P transporters are less important. Changes in the expression of P transporters avoid P toxicity.

Plants vary widely in photosynthetic P-use efficiency, photosynthesis per unit leaf P. The challenge is to discover what the trade-offs are of different patterns of investment in P fractions. Less investment may save P, but are costs incurred? Are these costs acceptable for crops? These questions can be resolved only by the concerted action of scientists working at both molecular and physiological levels, rather than pursuing these problems independently.

Contents

1. INTRODUCTION

Phosphorus (P) is essential for all life on Earth and, for plants, a key element in photosynthesis, respiration, and the biosynthesis of nucleic acids and membranes (68). It also plays an important role in the regulation of many enzymes (189). As a plant macronutrient, P frequently limits productivity in both natural and agricultural systems, especially crop production in low input systems worldwide (35). Plants take up P as orthophosphate, and this has been a thoroughly studied aspect of plant nutrition, with an extensive literature on molecular, biochemical, morphological, and physiological effects of P deficiency reviewed in this journal (18, 32, 103, 134).

There are excellent reviews on the role of P in several aspects of plant metabolism in this journal (31, 103, 134, 157). These provide a comprehensive overview of the complex nature of P acquisition and utilization by plants. An outstanding reference source for an overall understanding of P in soil and plants is *Marschner's Mineral Nutrition of Plants* (139).

This review provides an overview of physiological and biochemical acclimations and adaptations of plants to acquire and utilize P, emphasizing recent developments in ecophysiological aspects of P acquisition and utilization. This is an exciting period for those studying plant nutrition. After significant progress on molecular aspects of P acquisition and utilization, we can now begin to explore the opportunities for crop improvement and move toward a better understanding of ecological functioning in the context of global change. However, we stand on the shoulders of giants (119) and must not forget the work done before us. Sometimes, old but insightful papers appear to be slipping into oblivion; at these moments, it is time to put the spotlight on them again. Integration of new molecular evidence with more traditional plant and soil science information

will be pivotal to achieve a comprehensive understanding of P nutrition in plants and applied outcomes of enhanced P-use efficiency in crops. To quote Grant W. Thomas (170), "Old age and a certain lack of patience have prompted me to write a few thoughts on our practice of science both for the edification and the annoyance of my colleagues and friends."

2. PHOSPHORUS IN THE SOIL SOLUTION AND SOIL

Roots and mycorrhizal fungi acquire P from the soil solution as orthophosphate P (P_i), as $H_2PO_4^-$ (66, 131, 147). The P_i concentration [P_i] in the soil solution is invariably very low, as detailed in Section 2.1.

2.1. Inorganic and Organic Phosphorus in the Soil Solution

Pierre & Parker (130) studied 21 agricultural soils from the United States, representing a wide range in texture and organic matter content, and measured an average [P_i] in the soil solution of 3 μM (range: <0.6 to 11 μM). More recent publications have included soils fertilized with P at rates that are common agronomic practice, and they corroborate the range of soil [P_i] reported in the earlier work (99). Plants can be grown at these low P_i concentrations, provided that the concentration is maintained. This is exactly what Asher & Loneragan (10) did, using a facility that was locally known as their Ashertron (A.D. Robson, personal communication). A similar approach has also been used elsewhere (23). Maximum plant growth is reached at a wide range of [P_i], but all concentrations are very low. It is 1 μM for of *Vulpia myuros* (silver grass), whereas *Erodium botrys* (erodium), *Trifolium subterraneum* (subclover), and *Bromus rigidus* (ripgut brome grass) reach maximum yield at 5 μM, and this is sufficient to reach 90% of the maximum biomass for *Arctotheca calendula* (capeweed). Interestingly, 24 μM produces significantly more growth in *Medicago tribuloides* (barrel medic) and *Hypochaeris glabra* (smooth cat's-ear) than does any lower [P_i], but this concentration produces severe necrosis in leaves of *V. myuros* and inhibits its growth. Likewise, it produces necrosis in leaves of *T. subterraneum* and *Lupinus digitatus* (blue lupin). At the highest P supply, the P concentration in the shoots of the three P-sensitive species ranges from 9 to 18 mg P g^{-1} dry weight (10).

When investigating effects of P availability on growth and metabolism of *Arabidopsis thaliana* and *Solanum lycopersicum* (tomato), 250 μM (116), 1 mM (117), or 2.5 mM (188) is typically used to grow normal P-sufficient plants, and plants are commonly grown at 0 mM to provide P-limiting conditions. Depending on the hypotheses to be addressed, it might be worth considering the Ashertron approach, referred to above (10), as an alternative. For small plants like *A. thaliana*, this would not require a major investment but would allow investigation of plants at a more realistic P_i availability.

The average organic P concentration in the 21 different soils studied by Pierre & Parker (130) was 15 μM, considerably greater than the average [P_i]. Organic P cannot be taken up by roots or mycorrhizal fungi, but it can be made available following hydrolysis by root-released or microbial phosphatases (57, 106). Most P in soil is not in the soil solution and not readily available for roots or mycorrhizal fungi. Some organic P is relatively mobile and may leach far more readily than P_i (76). Other organic P molecules are at least as tightly bound as P_i, for example, phytate, also known as inositol hexakisphosphate (7, 191).

2.2. Phosphorus Fractions in Soil

Soil scientists have long chemically partitioned P in soil in different fractions (29, 77), but the relevance of most of these fractions for plants has never been demonstrated. More importantly,

Sorption: soil process comprising adsorption (precipitation) onto soil particles and absorption inside particles; sorption strength is expressed as phosphorus buffer capacity

Nonmycorrhizal plant species: plants that are incapable of establishing a mycorrhizal symbiosis; they occur at both extremes of the soil fertility spectrum

Phosphophile: plant species that naturally occur in habitats that contain large amounts of plant-available phosphorus

Carboxylate: the organic anion component of an organic acid

Phosphorus-scavenging strategy: a phosphorus-acquisition mechanism based on exploring a large soil volume and acquiring phosphorus from the soil solution

the fractionation procedures may detect discrete compounds, even when they are absent; for example, calcium phosphate is detected when no calcium is present because goethite or aluminum oxide is used, rather than real soil (15). Some of these fractions are useful, however. These include the readily plant-available fractions, but what is unavailable for some plants is readily available for others that exhibit different P-acquisition strategies, as discussed in Section 2.3. These plant-available fractions are referred to as Resin P, Colwell P, Bray P, or Mehlich P (34, 177, 186), depending on the extraction procedure that is followed. Soil P_i is mostly adsorbed and penetrates heterogeneous variable-charge particles (14). Removal of P by plants initially depletes the soil solution, inducing desorption of adsorbed phosphate, and this enhances backward diffusion of the penetrated phosphate. Thus, P supply in soils exceeds the amount of P in solution. Nevertheless, many scientists hold to the precipitate-particulate theory and accordingly attempt to partition soil P into different fractions, many of which are often interpreted as discrete iron, aluminum, or calcium phosphates. Research has recently shown that when these fractionation procedures were applied to iron or aluminum phosphate in which the phosphate was only present in adsorbed or penetrated forms, discrete fractions were detected, and often these were wrong: Iron, aluminum, and calcium phosphates were detected where there were none (15).

It is very important to consider organic P, which can be a major fraction, especially in old soils, even when the total P concentration is very low (176). Other molecules, such as phytate (7), strongly sorb onto soil particles and can be accessed only following the release of phytases (80), while at the same time providing a mechanism to avoid sorption of the released P_i onto soil particles (54). If we aim to understand which P molecules exist in soil, ^{31}P-nuclear magnetic resonance (^{31}P-NMR) (27, 112) or P K-edge X-ray absorption near-edge structure (XANES) spectroscopy (62) should be used, rather than classical fractionation techniques only.

Whatever technique is used to measure P-containing molecules in soil, we can be absolutely certain to find no P_2O_5, which exists neither in soil nor in fertilizer bags. It would be helpful if users were informed about what form of P exists in the bag. Common forms are (single, ordinary, or normal) superphosphate [$Ca(H_2PO_4)_2$], which is produced by the action of concentrated sulfuric acid on powdered phosphate rock or (originally) ground animal bones, and triple superphosphate, which is produced by exposing rock phosphate to phosphoric acid and therefore has a higher P content (**http://www.ipni.net/specifics**). Other forms of P fertilizer include potassium phosphate, monoammonium phosphate, and diammonium phosphate (82, 164). Yet, most fertilizer manufacturers, and even some scientists, continue to pervasively use what Berzelius (16) believed was the correct formula more than 200 years ago. It is high time we stopped using P_2O_5 in current writing; it belongs to the nineteenth, rather than the twentieth or twenty-first, century (92).

2.3. Plant Availability of Soil Phosphorus

The availability for a plant of soil P strongly depends on its P-acquisition strategy. For nonmycorrhizal plant species without any specific strategy, such as most Brassicaceae, Caryophyllaceae, Chenopodiaceae, and Urticaceae (25), only P that is close to the surface of roots or root hairs can be accessed (100). These plants typically occur in nutrient-rich habitats with a high P concentration in the soil solution; they are commonly referred to as nitrophiles (21) but can also be considered phosphophiles. For arbuscular mycorrhizal and ectomycorrhizal plants, P_i that is in the soil solution but beyond the root depletion zone can also be accessed (107). For ectomycorrhizal plants, some of the organic P in solution is available as well, and if they release carboxylates, some sorbed P can be accessed (156). Mycorrhizal plants exhibit a P-scavenging strategy (100). For nonmycorrhizal plants that release large amounts of carboxylates and phosphatases, P that

is sorbed onto soil particles is made available, including organic P. This strategy is typically expressed in plants on severely P-impoverished or strongly P-sorbing soils. They exhibit a P-mining strategy (100).

Phosphorus-mining strategies have been the most profoundly studied in nonmycorrhizal *Lupinus albus* (55, 146, 196) and Proteaceae (149, 153); most of these species produce carboxylate-releasing cluster roots. These strategies are also common in nonmycorrhizal Cyperaceae, some of which produce dauciform roots (65, 148); Restionaceae and Anarthriaceae, which produce capillaroid roots (90, 101); Haemodoraceae, which produce sand-binding roots (155, 195); and Velloziaceae, some of which produce vellozioid roots (2, 167) (**Figure 1**). Some roots release substantial amounts of carboxylates without obvious specialized structures, for instance, *Cicer arietinum* (chickpea) (125) and *Eucalyptus patens* (blackbutt) (95), which are both mycorrhizal plant species. Comparing both growth and grain yield of cluster-rooted species with those of noncluster-rooted *Lupinus* species, all of which are nonmycorrhizal and release carboxylates, cluster-rooted species perform better at the lowest P availabilities in soil (20, 126). This indicates that the combination of structure and physiology leads to the best performance of crop lupines when P availability is very low. Comparing a mycorrhizal Proteaceae species without cluster roots (*Placospermum coriaceum*) with three nonmycorrhizal ones that produce cluster roots also showed that the species with cluster roots produced more biomass at very low availability of P (94). In contrast, comparisons of carboxylate-releasing Cyperaceae species that do and do not produce dauciform roots have not shown an unambiguous advantage of a combination of structure and physiology (65, 86), possibly because they have not been compared over the same wide range as *Lupinus* and Proteaceae species have (20). Alternatively, Cyperaceae species without dauciform roots may compensate for a lower P-acquisition capacity by a greater internal P-use efficiency (65) or express functionally similar root strategies, such as typical long root hairs (86).

Parfitt (127) carried out an experiment using goethite, which strongly sorbs P. Goethite is an iron oxyhydroxide mineral that is common in soil; in 1806, it was named after Johan Wolfgang von Goethe, who is best known as a German poet but also had a keen interest in geology and mineralogy (175). Parfitt (127) added increasing amounts of P to goethite. No P was readily available to *Lolium perenne* (ryegrass) until the P-sorbing sites on the goethite surface were >40% covered with P_i. The P availability for ryegrass increased as the P concentration in solution increased. Maximum P availability was attained when the P concentration in solution was 2 μM, which occurred at about 75% coverage of P-sorbing sites on goethite. Most importantly, mycorrhizas increase the P availability for ryegrass at a concentration range of about 0.5–2 μM P (60–70% coverage of the sorbing sites on the goethite surface). This experiment clearly shows that P-scavenging mycorrhizas can contribute to P uptake when soil P availability is low, but when soils are severely P impoverished, P-mining strategies are more effective to acquire P. That is the situation in soils with a very low total P concentration as well as in soils where P is strongly sorbed onto hydroxides or oxides of iron or aluminum (at low pH) or onto calcium-containing compounds (at high pH). In fact, at very low P availability, the arbuscular mycorrhizal symbiosis is typically suppressed (1, 174). Further evidence to support the contention that P-mining strategies are more effective than P-scavenging strategies at extremely low soil P availabilities is provided by an experiment that compared an unusual mycorrhizal Proteaceae species that does not make cluster roots (*P. coriaceum*) with three other Proteaceae species that are nonmycorrhizal but do produce cluster roots (94). The nonmycorrhizal species perform better at the lowest soil P concentration than the mycorrhizal *P. coriaceum*. It would be worthwhile to repeat Parfitt's experiment with goethite using ectomycorrhizal species as well as nonmycorrhizal carboxylate-releasing plants.

Phosphorus-mining strategy: a phosphorus-acquisition mechanism based on mobilizing sorbed inorganic phosphorus or organic phosphorus following the release of, e.g., carboxylates or phosphatases, respectively

Cluster roots: specialized root structures with abundant root hairs that release carboxylates into the rhizosphere, thus solubilizing poorly available soil nutrients (e.g., phosphate)

Mycorrhizal plant species: plants that can establish a mycorrhizal symbiosis; mycorrhizal colonization cannot be used as evidence that the mycorrhizas supported phosphorus acquisition

(*Caption appears on following page*)

Figure 1 (*Figure appears on preceding page*)

Specialized root structures involved in carboxylate release and phosphorus mobilization. (*a*) Simple cluster roots of *Hakea prostrata* and (*b*) compound cluster roots of *Banksia grandis*, grown in nutrient solution at 1 μM phosphorus (P). Both species belong to the Proteaceae, and these roots were therefore originally called proteoid roots, but since they also occur in other families, the term cluster roots is now more common. (*c*) Simple cluster roots of *Daviesia physodes* (Fabaceae) freshly dug up in its natural habitat. (*d*) Simple cluster roots of *Aspalathus linearis* (rooibos tea, Fabaceae) freshly dug up in a farmer's field. (*e*) Dauciform roots of *Schoenus* sp. (*left*) and *Carex* sp. (Cyperaceae), grown in nutrient solution at 1 μM P. (*f*) Capillaroid roots of *Mastersiella digitata* (Restionaceae) grown in nutrient solution at 1 μM P. (*g*) Vellozioid roots of *Barbacenia tomentosa* (Velloziaceae). (*h*) Sand-binding roots of *Lyginia barbata* (Anarthriaceae), freshly dug up in its natural habitat. Photos provided by Michael W. Shane (*a*, *b*, *d*, *e*, *f*, *h*), Hongtao Zhong (*c*), and Grazielle S. Teodoro (*g*).

2.4. Uptake of Manganese and Silicon as Affected by Phosphorus-Acquisition Strategy

Plants that produce cluster roots, which we now know to release carboxylates, have long been known to have high leaf manganese concentrations ([Mn]) (56, 81), but only recently has leaf [Mn] been considered as a proxy for rhizosheath carboxylates (95, 96, 125). This tool is now available to identify genotypes with desirable P-acquisition traits (125, 184) as well as to screen for P-acquisition strategies of plants growing in their natural habitat (194, 195).

Somewhat surprisingly, de Tombeur et al. (40, 41) found an increase in leaf silicon (Si) concentration ([Si]), correlated with an increase in leaf [Mn], with increasing soil age and decreasing soil P availability along a long-term chronosequence. This contrasted with decreasing plant-available concentrations of nutrients and the beneficial element Si in soil (**Figure 2**). It is very likely that increased carboxylate release with increasing soil age and decreasing soil P concentration mobilized not only P and Mn but also Si because the rates of dissolution and amounts of Si released from Si-bearing minerals increase in the presence of chelating substances (19, 22, 28, 40, 182). This would explain the increase in leaf [Si] in those species that are capable of Si uptake, for example, in Cyperaceae species (41, 43). This offers tremendous potential, because Si is a beneficial element (51, 52) that offers protection against both biotic and abiotic stresses (4, 37, 44, 79, 159).

Rhizosheath: the physical rhizosphere zone where soil particles are bound together by root exudates and root hairs

Silicon (Si): a nonessential beneficial plant element; effects of Si include regulation of plant development and protection against abiotic stresses, pathogens, and herbivory

Phosphorus buffer capacity: the amount of phosphorus sorbed when the phosphorus concentration in the equilibrium solution is raised

2.5. Soil Characteristics Are Major Determinants for Plant Orthophosphate Uptake

Soil pH is considered a major determinant of P availability for plants, but this is not quite straightforward because plant traits determine the response of P uptake to pH and soil characteristics affect the sorption of P as dependent on soil pH. Root P_i uptake increases with decreasing pH, as studied most carefully in *Zea mays* (maize), where all processes involved in P_i uptake were considered (147). For P uptake in roots of *Trifolium repens* (white clover), Dunlop & Bowling (50) found a pH optimum of 4.3 on one hand. Sorption, on the other hand, also increases at decreasing soil pH (13), thus counteracting the potential of roots. Clearly, textbook figures, including one in Lambers & Oliveira (98), are an oversimplification and should be taken with a grain of salt. Does that mean that farmers should not lime acid soils to enhance the availability of P? No, because liming may not enhance the P availability because of a change in pH, but it does decrease the sorption of P onto soil (158).

It has long been known that at a low P availability, soil characteristics such as the P buffer capacity and P diffusion coefficient have major impacts well beyond that of the kinetic properties of the roots' P-uptake system (12, 124, 154). The rate of root elongation and root hairs also play

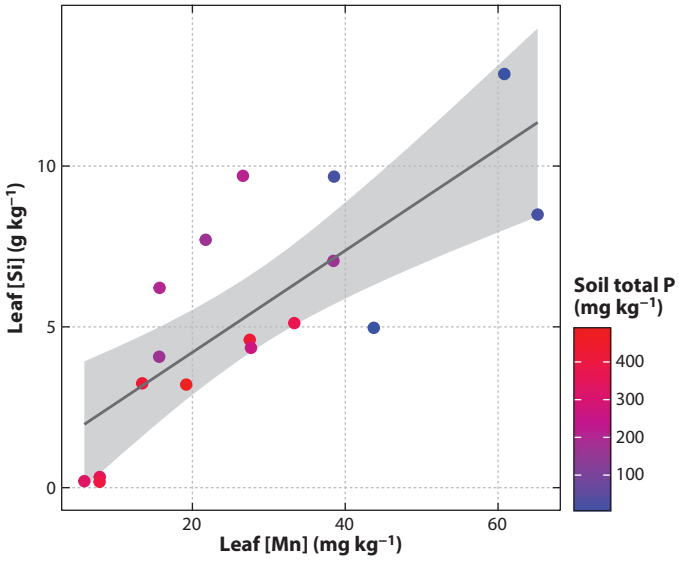

Figure 2

Correlation between the concentrations of silicon ([Si]) and manganese ([Mn]) in leaves of a range of Cyperaceae species along a 2-million-year dune chronosequence in Jurien Bay in southwestern Australia. The chronosequence exhibits a very strong natural gradient of soil phosphorus (P) concentrations, declining with increasing soil age. With declining soil P availability, plants that acquire P using a carboxylate-releasing P-acquisition strategy become more common. Many Cyperaceae species produce carboxylate-releasing dauciform or sand-binding roots (**Figure 1**). Leaf [Mn] is a proxy for carboxylate concentration in the rhizosheath (96, 125). Data from References 40 and 41.

important roles (45, 123), but kinetic parameters such as I_{max} and K_m do not (59, 154). Yet, several research groups have attempted to change the kinetic properties of the plant P-uptake system, believing that plants upregulate their P-uptake system under P starvation, so it must be important. Do they really upregulate their P-uptake system under P starvation, though, or do they, in fact, downregulate their P-uptake systems when they have sufficient P? A simple change in expression will not answer that question, but this is exactly what is explored in Section 3.2. In accordance with the low impact of kinetic parameters of the P-uptake system, overexpression of the gene encoding a P transporter in *Hordeum vulgare* (barley) does not increase P uptake under any of the conditions tested (133).

Rhizosphere: conceptual zone of soil influenced by a root; the zone is smallest for phosphate, greater for nitrate, and even greater for water, and thus is physically ill-defined, unlike the rhizosheath

3. UPTAKE OF PHOSPHORUS FROM THE RHIZOSPHERE, LONG-DISTANCE TRANSPORT, AND PHOSPHORUS TOXICITY

Plants only take up P_i, as $H_2PO_4^-$ (131, 147), from their rhizosphere, and no organic P. Claims that they do take up complex P molecules such as DNA (129) have not been substantiated in subsequent experiments. Likewise, plants or fungi do not have a system to take up P linked to quantum dots (181). It remains puzzling how these P-linked quantum dots enter plants or fungi. However, until it has been demonstrated that these P-linked quantum dots abide by the same rules as P that is taken up as P_i, we must be careful when interpreting the colorful images produced by this technique based on P linked to quantum dots.

3.1. Phosphorus Transport

Phosphorus toxicity: occurs when plants take up too much phosphorus; symptoms include premature leaf senescence, chlorosis and necrosis, and stunted growth

Plants rely on root phosphate transporters (PHTs) to acquire P_i from the soil solution and transport it inside the plant, inside cells, between cells, and between plant organs, as covered in recent reviews (47, 103, 122). Under P-sufficient conditions, the [P_i] in the cytosol is in the millimolar range (114), and, therefore, roots take up P_i from the soil solution against a steep electrochemical potential gradient. The uptake of $H_2PO_4^-$ is an energy-mediated process, driven by a protonmotive force (180) that increases the pH of the external solution, indicating that P_i uptake involves a P_i/H^+ cotransport (178). The stoichiometry of the P_i/H^+ cotransport is two to four protons per $H_2PO_4^-$ (143, 179).

The vast majority of vascular plants can form a symbiotic association with mycorrhizal fungi, which may be responsible for the lion's share of P uptake under low P conditions (as reviewed in 157), but these fungi tend to contribute little in terms of P uptake in severely P-impoverished habitats (91, 168). Even under low levels of root colonization of *Glycine max* (soybean), the arbuscular mycorrhizal symbiosis suppresses the expression of several *PHT1* genes in roots and nodules under P starvation (26).

The internal plant [P_i] is a major factor in the control of *PHT1* expression (122). Expression is generally greater at low internal [P_i], with upregulation of the expression of the *PHT1* gene (26, 102, 103, 169), and this is commonly interpreted as a P-starvation response. This is at odds with the minor role of kinetic properties of the P-uptake system in determining plant P_i-uptake capacity from soil (12, 124, 154). In fact, all that can be concluded is that the expression of P_i transporters differs between P-starved and P-sufficient plants, but whether this shows upregulation or whether this actually indicates downregulation under P-sufficient conditions requires a physiological approach, as outlined in Section 3.2.

3.2. Phosphorus Toxicity

Using their Ashertron facility, Asher & Loneragan (10) showed that for P-sensitive crop plants, P can become toxic at twice the concentration that can be expected in the soil solution of a fertilized field. While P toxicity is known for crop plants (10, 141), it is relatively uncommon, except when the P supply to P-starved plants is increased suddenly (33, 58). However, it is fairly common in species adapted to P-impoverished habitats when exposed to P availability slightly higher than that in their natural habitat (60, 70, 97, 121). Shane et al. (152) showed that P sensitivity in *Hakea prostrata* (Proteaceae) is associated with a very low capacity of this species to downregulate its P-uptake system, and similar results were obtained for two *Banksia* species (Proteaceae) (39). Conversely, *Grevillea crithmifolia* in the same family is P insensitive and shows strong downregulation of its P-uptake system (150) (**Figure 3**). This indicates that the differential expression of P transporters is a mechanism to avoid P toxicity rather than an acclimation to acquire more P at low availability. Next, I discuss the phenomenon of P toxicity, beginning from the accumulation of P_i within cells to death in terrestrial plants.

A low capacity to downregulate P-uptake systems is only part of the explanation for P sensitivity in some Proteaceae species. In addition, their preferential allocation of P to mesophyll cells plays a role (69, 72, 151). Many dicots from high P habitats allocate substantial amounts of P to their epidermal cells, thus avoiding accumulation in mesophyll cells (36, 63, 72). A high calcium supply aggravates the P toxicity symptoms of P-sensitive species (61, 121). Calcium-enhanced P toxicity provides an explanation for the calcifuge habit of most Proteaceae species (73). Calcium enhances the preferential allocation of P to palisade mesophyll cells under high P conditions, without a change in whole leaf P concentration (**Figure 4**). Calcifuge Proteaceae species show a greater P concentration in their palisade mesophyll than soil-indifferent species do, in accordance

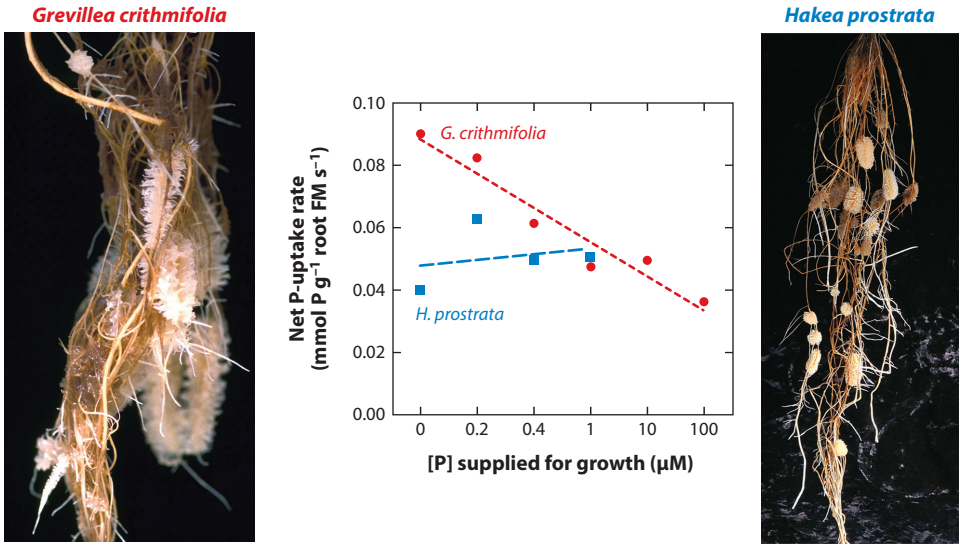

Figure 3

Net uptake rates of inorganic phosphorus (P) of intact whole root systems, calculated from P-depletion curves. The nutrient solution for the uptake studies contained 5 μM P. Uptake rates are plotted against the external P concentration ([P]) during plant growth for two Proteaceae species. *Grevillea crithmifolia* (*left*) is P insensitive and *Hakea prostrata* (*right*) is P sensitive. The P-insensitive species shows downregulation of its P-uptake capacity (the common response in most investigated species), whereas the P-sensitive species does not show downregulation of its net P-uptake rates. Some species may show an intermediate response, i.e., some degree of downregulation. Both species produce cluster roots at low P availability, and cluster root formation in both species is systemically suppressed at a high P supply, showing that P sensitivity is not associated with the formation of cluster roots. Figure adapted from Reference 98 based on data on *Grevillea crithmifolia* from Reference 150 and on *Hakea prostrata* from Reference 152. Photos provided by Michael W. Shane.

with their greater P sensitivity (71). In *Oryza sativa* (rice), P toxicity is associated with phytic acid accumulation in leaf cells that reduces metal availability and the activity of superoxide dismutase, which requires these metals, thus triggering lipid peroxidation (166).

In summary, the significance of differential expression of P transporters involved in P_i uptake from the soil solution is the avoidance of P toxicity, rather than enhancement of P uptake under low P conditions. Under low soil P conditions, soil characteristics, rather than kinetic properties of the roots' P-uptake system, dominate the uptake capacity of P from soil. To make further progress in this area requires concerted efforts of molecular plant biologists and ecophysiologists.

4. PHOSPHORUS UTILIZATION: BEYOND PHOSPHORUS FRACTIONATION

Phospholipids: lipids with a hydrophilic head, containing a phosphate group, and two hydrophobic tails derived from fatty acids, joined by glycerol

The total P concentration in plants comprises four major fractions—orthophosphate (P_i), metabolite P, P in phospholipids, and P in nucleic acids (183)—and a residual fraction, which is poorly defined and thought to include phosphorylated proteins (183). These fractions are based on chemical separations of plant material, usually leaves, but they also play an important role in the plant's physiology. Many Proteaceae species function at very low leaf P concentration (~0.2 mg g^{-1} dry weight) (74), well below the concentration considered adequate for crop growth (2 mg g^{-1} dry weight) (53). Species from other families in the same P-impoverished habitats exhibit similarly low leaf P concentration (64, 75). Despite low leaf P concentration, these

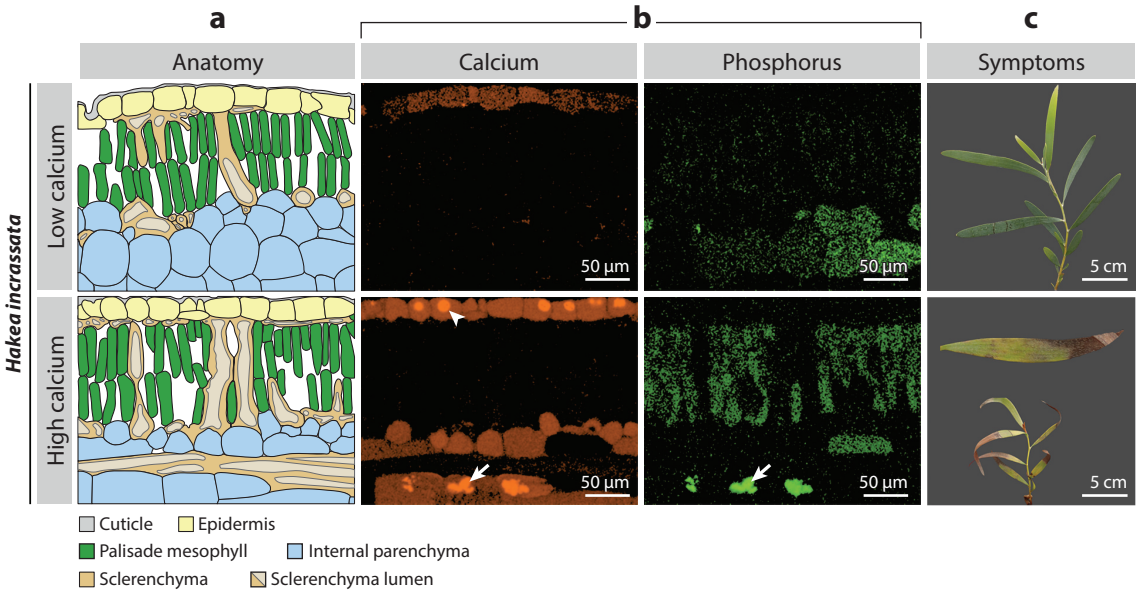

Figure 4

Calcium (Ca)-enhanced phosphorus (P) toxicity in *Hakea incrassata*, a P-sensitive Proteaceae species. (*a*) Leaf anatomical structure corresponding to the (*b*) qualitative energy-dispersive X-ray image maps showing the distribution of Ca and P in the upper part of a transverse leaf section. Note that Ca modulates cell-specific P allocation. (*c*) Visual symptoms of the two treatments. In this experiment, plants were grown in nutrient solution; low and high Ca treatments were 0 and 600 µM Ca, respectively, and the P supply was 10 µM. The leaf P concentrations in the two treatments were not statistically different (6.9 ± 1.1 and 7.4 ± 1.2 mg g^{-1} dry weight, respectively), despite a substantial increase in P concentration in the palisade mesophyll cells (cellular P concentration increased from 9 to 100 µmol g^{-1} fresh weight). Arrows indicate Ca-phosphate deposits; the arrowhead indicates Ca-based crystals. Panels *a* and *b* adapted with permission from Reference 71. Panel *c* adapted with permission from Reference 73.

species exhibit rates of photosynthesis similar to those of crop plants and hence show very high photosynthetic P-use efficiency (PPUE) (46, 64, 93). To achieve this, they must have invested considerably less P in one or more of the P fractions referred to above. If the aim is to understand why some species achieve a very high PPUE and explore whether this is desirable in crop plants, we need to understand in which of the fractions less P is invested and whether this occurs at the expense of desirable traits.

4.1. Orthophosphate: Preferential Allocation to Specific Leaf Cells

The plant [P_i] strongly depends on P availability, more so than the concentration of any other plant P fraction (183). The P that is not required for metabolism accumulates in cell vacuoles (192). According to Conn & Gilliham (36), monocots allocate P preferentially to mesophyll cells, whereas dicots show preferential P allocation to epidermal cells. However, most Proteaceae species do not exhibit this pattern because those that evolved in P-impoverished landscapes show preferential allocation to mesophyll cells (72, 94, 151). Since most of the leaf P is organic when plants grow at a low P availability (67, 190), there will be very little P in vacuoles. Within the same family, species that evolved in landscapes with volcanic soils that contain vast amounts of P do show preferential allocation to epidermal cells. Guilherme Pereira et al. (63) found the same pattern for several other eudicot families. Therefore, the preferential allocation of P to mesophyll cells has evolved in species of several eudicot families, and this trait reflects the P availability in landscapes where species evolved, rather than their phylogeny.

Photosynthetic phosphorus-use efficiency (PPUE): the rate of photosynthesis per unit of leaf phosphorus

Endoplasmic reticulum: an interconnected network of tubular and planar membranes that supports the synthesis and export of proteins, carbohydrates, and lipids

Preferential P allocation to metabolically active mesophyll cells, rather than metabolically inactive epidermal cells, contributes to the high PPUE of species from severely P-impoverished habitats (64). When grasslands in Inner Mongolia are exposed to simulated nitrogen (N) deposition, which makes P limiting for their productivity, forbs respond with a greater acquisition of P, whereas grasses show greater P-use efficiency in their leaves than forbs do (171). This is likely partly accounted for by the differential P-allocation patterns in monocots and dicots.

4.2. Phospholipids

Phospholipids are important components of the tonoplast; endoplasmic reticulum; Golgi apparatus (8, 83); and nuclear, plasma, and mitochondrial membranes and also play a role in signaling during plant development and in responses to stress (38). Under P starvation, some plants, including *A. thaliana* and *H. vulgare*, replace some of their phospholipids with lipids that do not contain P (9, 49).

Remarkably, several Proteaceae species that exhibit a very high PPUE replace most of their phospholipids by galactolipids and sulfolipids during leaf development; this pattern is hardwired, rather than a P-starvation response (93). While the lipid fraction of young, expanding leaves, on average, contains 46% phospholipids, mature leaves show as little as 9.6% phospholipids. Based on an analysis of leaf P fractions, mature leaves of *Melaleuca systena* (Myrtaceae), which occurs in the same habitat as Proteaceae species, also function at low phospholipid concentrations (190). In addition to preferential allocation of P to mesophyll cells, the replacement of phospholipids during leaf development contributes to a high PPUE.

In young leaves of P-limited *H. prostrata* (Proteaceae) plants, phosphatidylcholine/phosphatidylethanolamine and associated transcript levels are higher, while phosphatidylglycerol and sulfolipid levels are lower than in mature leaves (88). Phosphate reduces galactolipid and increases phospholipid concentrations in mature leaves, with concomitant changes in the expression of four *H. prostrata* genes. A regulatory network with a small number of central hubs underpins extensive phospholipid replacement during leaf development in this P-efficient Proteaceae species. This framework allows a high PPUE in a low P environment.

Why young leaves of P-efficient Proteaceae species start off producing phospholipids and then replace them, rather than producing galactolipids and sulfolipids to begin with, remains an open question (but see Section 4.3). During development, organelles other than chloroplasts, in which phospholipids are only a minor component (11), are built up, and in the nonchloroplast membranes phospholipids must have been replaced by other lipids. The Proteaceae may have adapted to low P situations, minimizing membrane perturbation resulting from phospholipid replacement in a manner that deserves further investigation. The plasma membrane leaflet facing the apoplast (probably the major water permeability barrier) contains only trace amounts of galactolipids (173), and phospholipids possibly play a vital role in the plasma membrane and tonoplast during leaf expansion when they require a high degree of lipid order. This aspect deserves further study, and if we seek to exploit this trait linked to a high PPUE in P-efficient crop plants, it will require the concerted action of physiologists and molecular plant biologists.

4.3. Nucleic Acids

Nucleic acids are the largest organic P fraction in leaves, generally comprising 40–60% of total organic P in leaves (183) and approximately 0.3–2 mg P g^{-1} dry weight, depending on species and P supply (17, 183). This fraction tends to contain at least 85% RNA, with the remainder being DNA (17, 165). Most RNA is ribosomal RNA (rRNA): *Cucurbita ficifolia* seedling roots contain approximately 94% rRNA, 4% transfer RNA, and 2% messenger RNA (84). In eukaryotes,

ribosomes comprise 79 to 80 ribosomal proteins and 4 main ribosomal RNAs (185). Ribosomes continually turn over, and *A. thaliana* uses selective mechanisms to transport rRNA or ribosomes to the vacuole, where rRNA is degraded using autophagy-like mechanisms; breakdown products are recycled (108).

The major difference between P-efficient Proteaceae and inefficient species, such as *A. thaliana*, is their low abundance of rRNA (163), and, based on an analysis of leaf P fractions, this is also the case in *M. systena* (Myrtaceae), which grows in similar P-impoverished habitats (190). In *A. thaliana*, 31% of the genome encodes membrane proteins (162) that will be synthesized on ribosomes attached to the phospholipid-containing endoplasmic reticulum (142). Among eukaryotes, the proportion of the genome that codes for membrane proteins is relatively constant at approximately 30% (138), and hence we expect the proportion of total ribosomes attached to the endoplasmic reticulum to be relatively constant as well. Given that the endoplasmic reticulum accounts for >60% of the phospholipid mass in a variety of cell types (89), it is possible that the decline in phospholipids is associated with less endoplasmic reticulum being required to support ribosomal protein synthesis in highly P-efficient Proteaceae and co-occurring species. However, since the lipid fraction of young leaves of P-efficient Proteaceae species contains 46% phospholipids, compared with 9.6% in mature leaves (93), this decline cannot be entirely accounted for by changes in the endoplasmic reticulum, even if it contains >60% of the phospholipid mass (89).

A low investment in rRNA obviously saves P, but what might this be traded off against? Based on an analysis of an *A. thaliana* mutant hyperaccumulating subunits of nontranslating ribosomes, Cheong et al. (30) suggested that a greater abundance of ribosomes may buffer fluctuating translation by preexisting nontranslating ribosomes before de novo synthesis meets temperature-induced changes in demands. Using a cell culture of *A. thaliana*, Salih et al. (144) induced oxidative stress, showing that ribosome content on a total-cell-protein basis decreases, but overall protein synthesis rates on a ribosome-abundance basis show that the resident ribosomes retain their function. The degradation and synthesis rates of most ribosomal proteins slow following oxidative stress, leading to an aging population of ribosomes in stressed cells. Overall, ribosome abundance decreases, and their age increases with oxidative stress, but the function of the aging ribosomes appears to be maintained concomitantly with differences in turnover and abundance of specific ribosomal proteins. Differences in turnover and abundance of ribosomes under oxidative stress may contribute to plant cytosolic ribosome resilience to oxidative stress (144). The turnover rates of 26 40S subunit ribosomal proteins and 29 60S subunit ribosomal proteins show that half of the ribosome population in cell cultures of *A. thaliana* is replaced every 3–4 days (145). Historically, the multiprotein ribosome complexes have been considered static protein synthesis machines that are not subject to extensive regulation but only read messenger RNA (mRNA) and produce polypeptides accordingly. Recent evidence, however, shows the heterogeneous nature of ribosomes. A prominent example of ribosome heterogeneity is shown in *A. thaliana*, revealing genome duplications and multiple paralogs of each ribosomal protein gene (109).

The genes encoding rRNA are the most abundant genes in the eukaryotic genome, residing in tandem repetitive clusters, sometimes with hundreds of copies. A unique gene amplification system compensates for loss of copies, thus maintaining copy number, albeit with some fluctuations. The repeat number determines sensitivity to DNA damage (85). Plant genomes contain tandem arrays of rRNA genes, many of which are transcriptionally silenced. Silent recombinant DNA (rDNA) repeats may act as backup copies for ribosome biogenesis and have nuclear organization roles. Following genome editing in the *A. thaliana* female gametophyte, Lopez et al. (104) reduced 45S rDNA copy numbers to ~10%. Despite drastic reduction of rDNA copies, rRNA transcriptional rates and steady-state levels remained the same as those in wild-type plants. Gene dosage compensation of rRNA transcript levels is associated with reduction of silencing histone

Ribosome: macromolecular machines in cells performing protein synthesis, linking amino acids in the order specified by the codons of messenger RNA

Autophagy: degradation pathway in which substrates are wrapped in vesicles (autophagosomes) and delivered to the vacuole, where they are broken down

Nontranslating ribosomes: fully intact ribosomes that are not involved in mRNA translation and protein synthesis; they may become active under stress conditions

marks at rDNA. Genome editing of rRNA repeats offers a powerful technique to elucidate rDNA dosage compensation mechanisms and impacts of low rDNA copy number on genome stability, development, and cellular processes (104).

What can be gleaned from the molecular information about model plants for our understanding of native plants in P-impoverished habitats and strategies to develop more P-efficient crop plants? For small organisms, such as slow-growing freshwater copepods and fast-growing cladocerans, the relationship between growth rate, P investment, and N:P ratio has been explained by the growth rate hypothesis, which proposes that fast growth rates are associated with a proportionally greater requirement for P than for N because organisms must allocate a disproportionately greater amount of P to rRNA to meet the protein synthesis demands to support rapid growth (138, 161). Nucleic acids have an N:P stoichiometry of 4:1 (137), much lower than that of leaves (187). However, the P-efficient leaves referred to above were mature and nongrowing, and hence the growth rate hypothesis cannot explain major differences among plant species. Matzek & Vitousek (111) compared N:P ratios and protein:RNA ratios in *Pinus contorta* and *Pinus muricata* growing at different rates, depending on nutrient supply. The faster-growing plants had higher RNA, N, and P concentrations and lower protein:RNA ratios, but there was no correlation between growth rate and leaf N:P or protein:RNA ratios when comparing species of different inherent growth rates. Comparing mature leaves of the inherently faster-growing *Banksia sessilis* with those of the slower-growing *Banksia attenuata*, Han et al. (67) showed greater N:nucleic acid P ratios in the faster-growing species. However, since they also studied mature nongrowing leaves, faster rates of protein synthesis must have been balanced by faster rates of protein breakdown and, hence, protein turnover. The greater nucleic acid P concentration relative to the N concentration suggests a faster protein turnover in the slower-growing plants. Differences in rRNA in *Pinus* or nucleic acid P in *Banksia* leaves likely reflect protein turnover, rather than association with plant growth rates. Different proteins in leaves of *H. vulgare* (barley) turn over at 100-fold different rates (118). Abundant proteins in photosynthesis, photorespiration, and specific subunits of chlorophyll biosynthesis turn over much faster than the average protein in leaves. Therefore, differences among species might reflect differences in investment in proteins that exhibit a rapid turnover.

A low abundance of ribosomes and associated low concentration of the nucleic acid P fraction in leaves are the main reasons for a high PPUE in P-efficient Proteaceae species. Plant investments in ribosomes are like cities' investments in fire engines: They may invest in them in proportion to their long-term average needs, or they may overinvest, allowing them to not function for some of the time but jump into action when the alarm bells ring. It may be that less-P-efficient plants overinvest to a greater extent, and hence are better protected against stress (**Figure 5**). For example, they may limit plant vulnerabilities, which are still poorly known, to heat waves, particularly heat-wave-driven sudden plant death (24, 110). Exposure to or recovery from water stress will require the synthesis of proteins involved in the production or breakdown of compatible solutes and in the transport of solutes between different compartments inside and outside of the cell (98). The questions for those who seek to develop more-P-efficient crops are how safe they need to be and whether that safety margin can be reduced if the plants are well managed. This requires careful studies integrating physiology and molecular biology.

4.4. Phosphorus-Containing Metabolites

Sulpice et al. (163) were unable to measure all of the major molecules that make up the metabolite P fraction (phosphate esters and anhydrides) in six P-efficient Proteaceae due to interfering substances with the enzyme-linked assays in the leaf material. However, one of the major molecules,

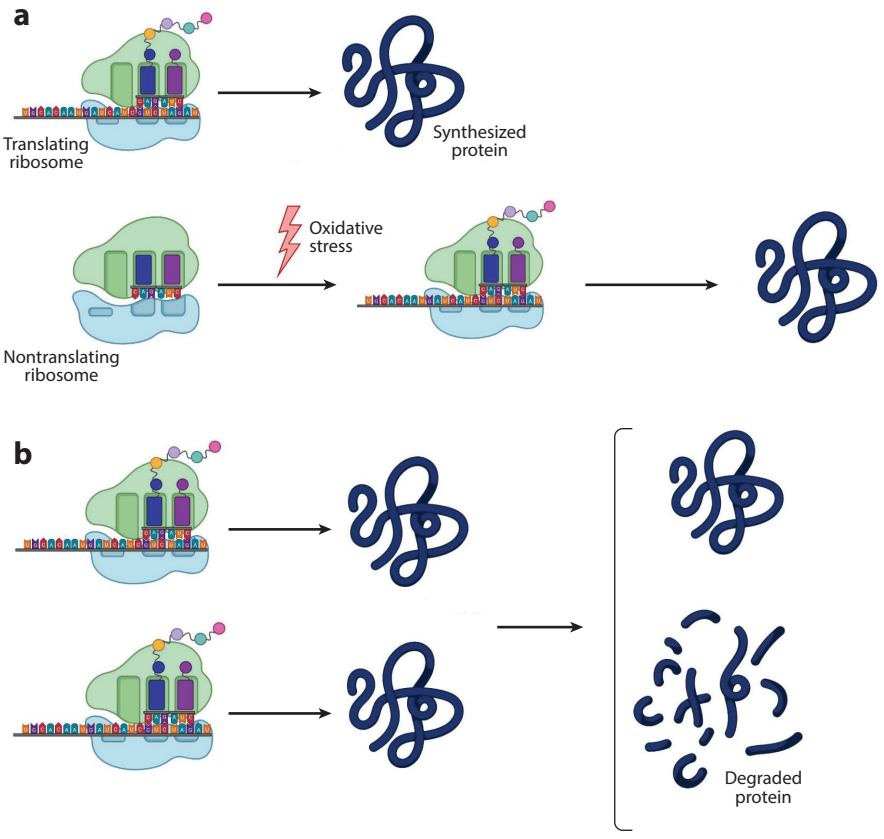

Figure 5

A conceptual diagram exploring what a high ratio between the concentrations of foliar ribosomal RNA (involved in the structures on the left) and of leaf protein (dark blue structures on the right, synthesized on ribosomes) might mean for leaf functioning. Ribosomal RNA can be approximated by the nucleic acid phosphorus (P) fraction, and leaf protein can be approximated by nitrogen (N). A high ratio might reflect (*a*) a relatively large proportion of nontranslating ribosomes, which might become active under oxidative stress (144). Alternatively, (*b*) most ribosomes might be translating, and the reason why the ratio is low might be that the synthesized proteins turn over at a rapid rate (shown for one of the proteins, leaving only one intact) (78, 172), allowing a complement of proteins that suits a changing environment. Figure adapted from images created with BioRender.com.

glucose 6-phosphate, clearly did not exhibit low concentrations in comparison with that in *A. thaliana*. Accordingly, the metabolite P fraction did not reveal a low concentration in one of these Proteaceae, *H. prostrata* (190). We can therefore safely conclude that metabolite P is the only one of the four fractions that is not low, relative to other measured species, in P-efficient Proteaceae. This is possible because these metabolites are predominantly substrates for enzymes in glycolysis and the Calvin-Benson cycle, and a decrease in substrate concentration might decrease the activity of these pathways, unless compensated by a greater abundance of the enzymes. However, a greater abundance of enzymes would incur P costs associated with rRNA and thus not lead to a more efficient use of P. This suggests a trade-off of metabolite (enzyme substrate) and protein (enzyme) concentrations in achieving rapid metabolic fluxes (135).

Trade-off: the balancing of investment in mutually exclusive traits (e.g., protective structures versus photosynthetic machinery in leaves)

4.5. What Does the Variation in Leaf Phosphorus Fractions Really Mean?

There is insufficient information to arrive at firm conclusions about differences in P fractions in contrasting species. We do know that some Fabaceae function at higher leaf P concentrations than global averages (115, 187), but there are distinct exceptions of Fabaceae from P-impoverished habitats that exhibit low leaf P concentration (64, 75, 160). In a comparison of *H. prostrata* (Proteaceae) and *Acacia rostellifera* (Fabaceae), the P-efficient Proteaceae showed a low nucleic acid P concentration and relatively high metabolite P concentration, whereas the P-inefficient legume showed the opposite (190). A high nucleic acid P concentration would support high protein concentration in legumes, but a lower metabolite P concentration might curtail the activity of some of the glycolytic and Calvin-Benson cycle enzymes that use these metabolites as substrates. Does that mean they have greater control over the activity of their enzymes, because they do not function at full capacity, so a change in substrate concentration may quickly change their activity? If so, efficiency might be traded off against metabolic flexibility. It would be interesting to find out more about the allocation of P to the leaf P fractions in other Fabaceae that function at low leaf P concentration, for example, *Jacksonia* (75), *Bossiaea* (3), *Gompholobium* (128), and *Daviesia* (120), especially since cluster roots appear to be pervasive in the *Daviesia* group, which includes *Daviesia*, *Gompholobium*, *Sphaerolobium*, and *Viminaria* (120).

4.6. The Way Forward

To fully understand the significance of different patterns in allocation of P to major leaf P fractions, we need broader and targeted comparisons. We require a better understanding of the replacement of phospholipids in membranes and in which membranes phospholipid replacement does or does not occur. We also need more details about the metabolite P fraction to find out exactly which molecules differ among species. This is particularly important because this fraction also contains phytate, which is a storage compound, rather than a metabolically active molecule. Phytate is widely known as a storage compound in seeds (87, 105, 132) but also occurs in leaves, albeit at much lower concentrations. Phytate concentrations in leaves vary widely and tend to increase with decreasing leaf P concentrations (6).

We need to improve our methods to measure P-containing metabolites, by either solving issues with interfering substances that have been encountered before (163) or developing an alternative approach involving ^{31}P-NMR (48, 113, 140). A modeling approach might also be useful to explore possible trade-offs involving investment in different P fractions. Finally, we need to explore what greater investment in ribosomes really means for plants in natural habitats and in agroecosystems (**Figure 5**).

5. PERSPECTIVES

When soils contain very little P or when P is strongly sorbed to soil particles, carboxylate-releasing P-mobilizing strategies are more effective than mycorrhizal strategies (100, 136). Mycorrhizal strategies are effective when soils are moderately infertile, and their persistence on severely P-impoverished soils is likely accounted for by mycorrhizas playing alternative roles, especially in defense against pathogens (5, 91). The facilitation of P uptake by carboxylate-releasing neighbors plays an important role in natural as well as managed systems when P limits plant productivity. Leaf [Mn] can be used to explore the role of carboxylate exudation, including that by facilitating neighbors (194). A challenge will be to identify matching root traits that enhance the chances of a plant to be facilitated (193). Facilitation may also involve mobilization of Si by P-mobilizing carboxylate-releasing neighbors and confer greater resistance to abiotic and biotic stresses (40, 42).

Soil constraints and root traits such as root hairs and root elongation play a pivotal role in plant P acquisition when soil P concentrations are low, whereas the kinetic properties of the roots' P-uptake system are relatively unimportant and sometimes overrated (12). Variation in the expression of P transporters as dependent on P availability reflects downregulation when P is readily available, rather than upregulation when P is scarce (150).

Analyses of major P fractions in leaves can provide insight into a plant's PPUE, but to make progress we need to explore these fractions in more detail and find out which metabolites are affected, in which membranes phospholipids are replaced, and what it means for a leaf to function at high or low protein:rRNA ratios (**Figure 5**). These explorations require measurements of translating and nontranslating ribosomes and protein turnover rates under steady-state conditions as well as following exposure to stress. Progress requires concerted action from molecular plant scientists and ecophysiologists.

To capture the tremendous progress made on molecular aspects of plant P nutrition in the past decades, that information needs to be integrated with more traditional insights developed by soil scientists, ecologists, and plant physiologists. Plants typically grow in soil and in a dynamic environment. We can learn much from plants grown in nutrient solution in controlled environments, but, to fully understand a native or crop plant growing in a natural habitat or a farmer's field, that knowledge must be scrutinized in the real world.

SUMMARY POINTS

1. Nonmycorrhizal plants occur in soil with either a very high availability of soil phosphorus (P) (e.g., phosphophiles) or very low concentrations of plant-available P (e.g., carboxylate-releasing P-mining species).
2. P-scavenging mycorrhizas are very effective at enhancing plant P acquisition at relatively low P availability but are ineffective at very low P availability.
3. When the availability of P in soil is low, soil characteristics (P diffusion coefficient, P buffer capacity) and root morphology (root hairs, length, and architecture) dominate the rate of plant P acquisition, whereas kinetic properties of the P-uptake system are relatively unimportant.
4. Phosphorus toxicity in plants results from a low capacity of roots to downregulate their P-uptake systems. When plants exhibit preferential allocation of P to mesophyll cells in general or to specific mesophyll cells in the presence of calcium, P becomes toxic at even lower leaf P concentrations because it has become concentrated.
5. A high photosynthetic P-use efficiency is associated with the preferential allocation of P to photosynthetically active mesophyll cells and a low investment of P in ribosomal RNA and phospholipids.
6. We have a very poor understanding of possible trade-offs between the efficient use of P and physiological plasticity; a better understanding would be pivotal to defining breeding targets.
7. To further understand what differences in P fractions among species really mean, we need better methods to measure P-containing metabolites; nuclear magnetic resonance (NMR) is a promising tool.

8. We need much more information on the activity of ribosomes, and the fraction that is nontranslating, in intact plants under different environmental conditions, including stress.

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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