FUTURE DIRECTIONS   No. 3

Resource partitioning for soil phosphorus: a hypothesis

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Summary

1. Organic phosphorus is abundant in soil and its turnover can supply a considerable fraction of the phosphorus taken up by natural vegetation. Despite this, the ecological significance of organic phosphorus remains poorly understood, which is remarkable given the biological importance of phosphorus in terrestrial environments.

2. Of particular interest is the possibility that coexisting plant species partition soil organic phosphorus to reduce competition. This seems likely given the large number of biologically available phosphorus compounds that occur in soil and the variety of mechanisms by which plants can utilize them.

3. Here I propose a conceptual model of resource partitioning for soil phosphorus. The model describes a hypothetical example of four coexisting plant species that differ in their ability to access soil organic phosphorus compounds, which are grouped to form a gradient of biological availability based on the processes involved in their utilization by plants.

4. *Synthesis*: Resource partitioning for soil phosphorus could provide an additional mechanism to explain the coexistence and distribution of plant species. It is likely to occur widely in terrestrial environments, but should have greatest ecological significance wherever productivity is limited by the availability of soil phosphorus. This includes freshwater wetlands, super-humid temperate regions and ecosystems developed on strongly-weathered soils that cover vast areas of ancient landscapes in Africa, Australia and South America.

Key-words: arbuscular mycorrhiza, ectomycorrhiza, ericoid mycorrhiza, inositol phosphates, phosphatase, phosphate diesters, phosphate monoesters, phytase, plant nutrition, resource partitioning, soil organic phosphorus

Studies of plant nutrition often consider only inorganic phosphate to be biologically available, yet organic phosphorus is abundant in soils (typically between 30% and 65%, but sometimes > 90%, of the total soil phosphorus; Harrison 1987) and its turnover can account for the majority of the phosphorus taken up by natural vegetation (e.g. Cole *et al.* 1977; Attiwill & Adams 1993). In fact, only a small fraction of the soil organic phosphorus need be hydrolyzed to provide a substantial proportion of the annual phosphorus requirement of plants (Harrison 1987). Despite this, ecological aspects of organic phosphorus acquisition have received little explicit attention, which is surprising given the extent to which phosphorus availability limits or co-limits primary productivity in terrestrial environments (Elser *et al.* 2007).

Of particular interest is the possibility of resource partitioning for soil phosphorus; in other words, that coexisting plants use different forms of soil phosphorus to minimize competition. Such a phenomenon has been demonstrated for soil nitrogen in an arctic tundra community (McKane *et al.* 2002), in which the most productive plants use the most abundant forms of nitrogen, while less productive plants use less abundant forms. The same process also seems to occur for nitrogen in some (Weigelt *et al.* 2005; Kahmen *et al.* 2006), but not all (Harrison *et al.* 2007), temperate grasslands.

Resource partitioning for phosphorus seems likely to occur for two reasons. First, soil phosphorus exists in a range of inorganic and organic compounds that differ markedly in their biological availability in the soil environment (Condron *et al.* 2005). For example, the organic phosphorus in most soils is dominated by a mixture of phosphate monoesters (e.g. mononucleotides, inositol phosphates) and phosphate diesters (mainly nucleic acids and phospholipids), with smaller amounts of phosphonates (compounds with a direct carbon–phosphorus bond) and organic polyphosphates (e.g. adenosine triphosphate).

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Second, plants can manipulate their acquisition of phosphorus from organic compounds through a variety of mechanisms, which in some cases allows them to utilize organic phosphorus as efficiently as inorganic phosphate (Tarafdar & Claassen 1988; Adams & Pate 1992). These include the synthesis of phosphatase enzymes, secretion of organic anions, formation of proteoid roots and symbiotic association with mycorrhizal fungi (Richardson *et al.* 2005b). Of particular significance is the synthesis of extracellular phosphatase enzymes, which catalyze the release of inorganic phosphate from phosphate esters – a key step in the utilization of soil organic phosphorus. This ubiquitous response of higher plants, bryophytes and algae to phosphorus stress provides a clear indication of the importance of organic phosphorus in the nutrition of natural vegetation (Duff *et al.* 1994; Whitton *et al.* 2005).

Mycorrhizal fungi also synthesize phosphatase enzymes and are therefore likely to be involved in the acquisition of organic phosphorus by plants. Of the main mycorrhizal groups, the ectomycorrhizas are well-known to access phosphate esters, including the inositol phosphates (Antibus *et al.* 1992), while ericoid mycorrhizas can efficiently utilize phosphate diesters (Leake & Miles 1996), which tend to be abundant in soils supporting ericaceous plants (Turner *et al.* 2004). Arbuscular mycorrhizas, which form associations with the majority of terrestrial plant species, have been widely assumed to utilize only inorganic phosphate (Smith & Read, 1997). However, it is now clear that they can also use organic phosphorus, including inositol phosphates, as a sole source of phosphorus (Joner *et al.* 2000; Koide & Kabir 2000). Presumably there are also considerable differences in the ability of species within each of the major mycorrhizal groups to use the various forms of soil organic phosphorus (e.g. Antibus *et al.* 1992). If so, this could contribute to phosphorus partitioning and might be an additional factor by which mycorrhizal diversity influences plant diversity (van der Heijden *et al.* 1998). Mycorrhizas are therefore likely to play a central role in phosphorus partitioning by plants. It should be noted, however, that proteoid-root forming species adapted to infertile soils do not usually associate with mycorrhizas (Lambers *et al.* 2008), yet they synthesize phosphatase enzymes and appear able to readily exploit soil organic phosphorus (Adams & Pate 1992; Watts & Evans 1999).

A conceptual model of how resource partitioning for soil phosphorus could occur is shown in Fig. 1. It describes a hypothetical example of four coexisting plant species that differ in their ability to access soil organic phosphorus compounds, which are grouped by the processes involved in their utilization by plants and/or their mycorrhizal symbionts. In other words, the groups of phosphorus compounds constitute a gradient of biological availability based on the investment that must be made to access the phosphate ion.

Species A uses mainly inorganic phosphate dissolved in soil solution, the most biologically available form of soil phosphorus. Like most plants, it can also access some simple phosphate monoesters (see below). Dissolved phosphate is the form of phosphorus taken up directly by plants, so it must be released from all organic phosphorus compounds prior to uptake. In most natural ecosystems the concentration of free phosphate in solution is vanishingly small, but its turnover rate can be rapid.

Species B competes with Species A for dissolved phosphate, but is best-adapted to access simple phosphate monoesters. These compounds are abundant in soil and are the most available form of organic phosphorus, being weakly sorbed and requiring only hydrolysis by phosphomonoesterase, a common plant enzyme, to release phosphate for plant uptake (Condron *et al.* 2005). Species B can also use phosphate diesters through the synthesis of phosphodiesterase enzymes, but cannot utilize the inositol phosphates, which require a specialized enzyme (see below).

Species C can acquire phosphate from a range of organic phosphate esters, but specializes in the use of phosphate diesters, including nucleic acids and phospholipids. These compounds are abundant in biological tissue and therefore constitute most of the organic phosphorus inputs to soils, although they tend to degrade rapidly and do not usually accumulate (Bowman & Cole 1978). Despite this, they are less available than simple phosphate monoesters because they must be hydrolyzed by a series of phosphatase enzymes, including phosphomonoesterase and phosphodiesterase, to release phosphate for plant uptake. Because Species C synthesizes both these enzymes, it can also utilize simple phosphate monoesters and, to a limited extent, the inositol phosphates.

Species D uses the least biologically available group of soil organic phosphorus compounds – the inositol phosphates. These constitute only a small fraction of the organic phosphorus input to soils, occurring mainly in plant seeds, but they are stabilized strongly through sorption and precipitation reactions and often accumulate to form a considerable fraction of the soil organic phosphorus (Turner 2007). Species D specializes in the acquisition of these refractory organic phosphates, probably through the synthesis of a combination of phytase enzymes (phosphatases that catalyze the release of phosphate from *myo*-inositol hexakisphosphate) and a solubilizing agent such as an organic acid to release inositol phosphates from binding sites. The secretion of organic acids is often assumed to release only inorganic phosphate, although they also solubilize organic phosphorus (Hayes *et al.* 2000) and appear to be of key importance in the utilization of inositol phosphates by plants (George *et al.* 2004). Note that Species C and D can also use dissolved phosphate (not indicated on the figure), although this probably makes only a small contribution to their phosphorus nutrition in environments where these species are abundant.

The model includes four groups of common phosphorus compounds, but other inorganic and organic phosphorus compounds also occur in soils and are biologically available. Of particular significance is that inorganic phosphate occurs in a range of relatively stable chemical forms in soil (e.g. primary mineral phosphate, metal precipitates, sorbed to the surfaces of metal oxides, occluded within mineral matrices, etc.). These are often considered to be of limited biological
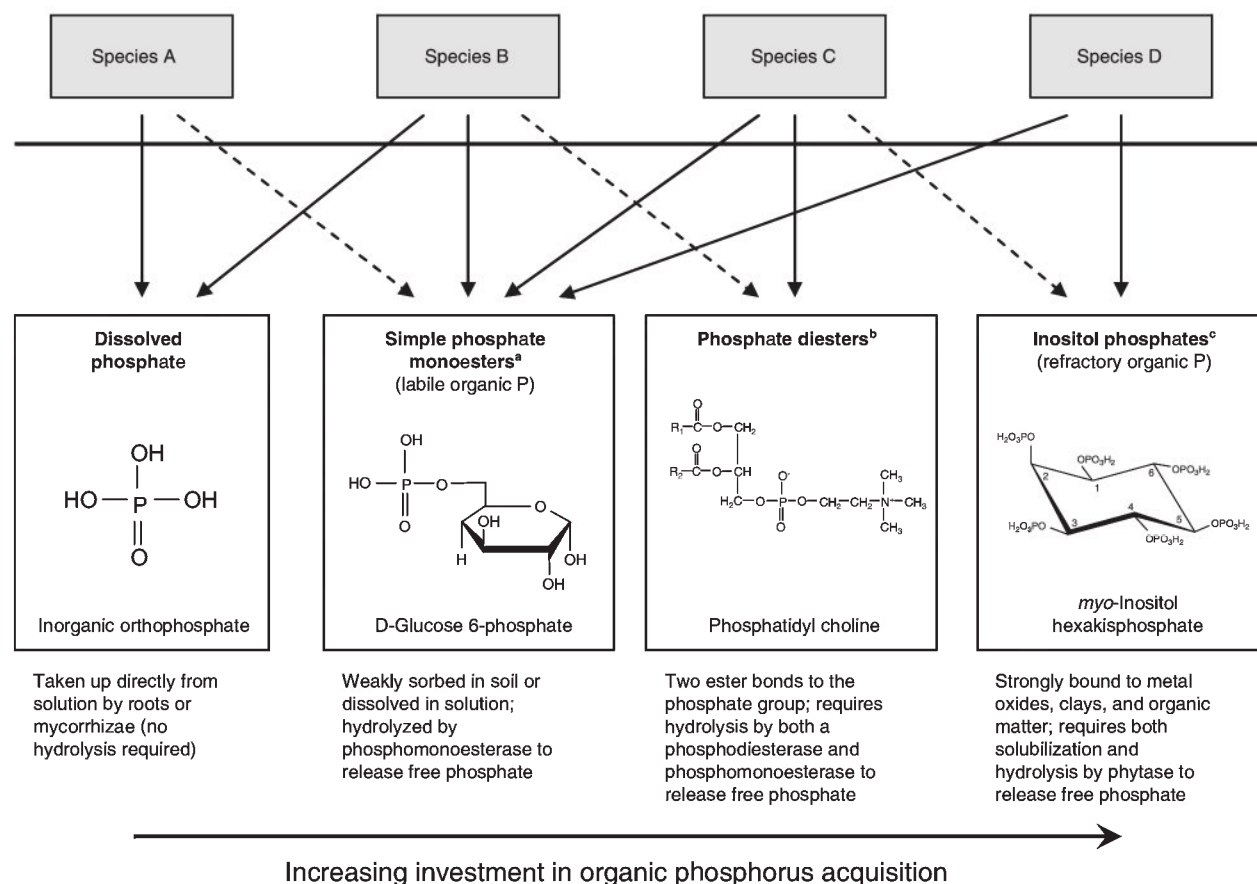
Fig. 1. A conceptual model of resource partitioning for phosphorus. The model contains four plant species with differing degrees of adaptation to accessing four groups of soil phosphorus compounds (a representative compound is demonstrated in each case) with differing degrees of biological availability. Species A uses mainly dissolved inorganic phosphate from soil solution, the most readily available form of phosphorus, and can also access some simple phosphate monoesters through phosphomonoesterase enzymes. Species B competes with Species A for dissolved phosphate, but is best-adapted to accessing simple phosphate monoesters. It can also use phosphate diesters through phosphodiesterase enzymes, but cannot utilize the inositol phosphates. Species C specializes in the acquisition of a range of organic phosphate esters; it mainly uses phosphate diesters, but can also use simple phosphate monoesters and inositol phosphates through phytase enzymes. Species D specializes in the acquisition of refractory organic phosphate in the form of inositol phosphates; these compounds are stabilized strongly by association with clays and metal oxides, so it is likely that Species D can synthesize phytase enzymes as well as organic anions that can solubilize inositol phosphates from binding sites. Species C and D can also use dissolved phosphate (not indicated), although this is likely to make only a small contribution to their nutrition. Note that the acquisition of phosphorus by the four species described above could be direct via roots or, more likely, indirect through association with mycorrhizal fungi.
[a]Simple phosphate monoesters include adenosine monophosphate and other mononucleotides, sugar phosphates (including the one shown) and the breakdown products of phospholipids (e.g. choline phosphate). Note that phosphomonoesterase enzymes also catalyze the hydrolysis of condensed inorganic and organic phosphates, including adenosine di- and triphosphates, pyrophosphate and long-chain polyphosphate.
[b]Phosphate diesters, which include the nucleic acids (DNA, RNA), phospholipids (including the one shown), and some cyclic phosphates (e.g. cyclic adenosine monophosphate), are the major group of organic phosphorus added to soils in natural ecosystems.
[c]The inositol phosphates accumulate in soils mainly as penta- and hexakisphosphate esters and include *myo*-inositol hexakisphosphate (also known as phytic acid or phytate) as well as a series of stereoisomeric forms (*scyllo*, D-*chiro*, *neo*) that are extremely rare elsewhere in nature (Turner 2007).

availability, but there is evidence that some plants can deplete stable forms of inorganic phosphate as readily as more soluble forms (Gahoonia & Nielsen 1992). In particular, species that form proteoid roots (e.g. the Proteaceae) can solubilize sparingly soluble phosphate minerals through the secretion of organic acids, which allows them to grow on extremely infertile soils (Watts & Evans 1999). Inclusion of stable inorganic phosphates in the model would therefore increase the potential for resource partitioning by adding further niches for specialized plants.

Resource partitioning for soil phosphorus is likely to occur widely, but should have greatest ecological significance wherever primary productivity is limited or co-limited by phosphorus availability. Evidence from fertilization experiments indicates that co-limitation by phosphorus and nitrogen is widespread in terrestrial ecosystems (Elser *et al.* 2007), while phosphorus limitation is expected in freshwater wetlands, super-humid temperate regions (e.g. in Chile, New Zealand, etc.) and ecosystems developed on strongly weathered soils that cover vast areas of ancient landscapes in Africa,

Australia and South America (Richardson *et al.* 2004; Wardle *et al.* 2004; Wassen *et al.* 2005; Lambers *et al.* 2008). These areas are of considerable global extent and many are botanically diverse – for example, lowland tropical rainforests growing on strongly weathered soils contain large numbers of plant species coexisting in apparently similar environmental niches (Wright 2002).

The model could also explain in part the distribution of plants across gradients of phosphorus availability. In a relatively phosphorus-rich soil with abundant dissolved phosphate Species A would be expected to dominate, whereas in a low-phosphorus soil in which the turnover of organic phosphorus is of key importance for plant nutrition Species D would be most abundant. Phosphorus gradients occur naturally along soil chronosequences, in which the gradual loss of phosphorus during pedogenesis leads to a long-term decline in phosphorus availability (Walker & Syers 1976). For example, along the Franz Josef chronosequence in New Zealand, increasing phosphorus limitation as soils age causes a shift in the composition of the plant community, from dominance by angiosperms on younger soils towards conifers of the Podocarpaceae on old soils where productivity is limited strongly by phosphorus availability (Richardson *et al.* 2004). This coincides with changes in the soil organic phosphorus composition, including a marked decline in the concentration of inositol phosphates in older soils (Turner *et al.* 2007). Although podocarps possess a variety of features that allow them to compete effectively under nutrient-poor conditions (Richardson *et al.* 2005a), an additional factor may therefore be that they are efficient at acquiring phosphorus from refractory soil organic phosphorus compounds.

The model may also have significance for understanding the response of plant communities to perturbation in nutrient availability. The enrichment of a soil with phosphorus, for example by runoff from agricultural land, would be expected to shift the plant community towards species that are adapted to using dissolved inorganic phosphate (Species A). In contrast, a decline in phosphorus availability, such as following atmospheric nitrogen deposition, would be expected to shift the plant community towards species that can utilize refractory forms of soil organic phosphorus (Species D). High rates of nitrogen deposition cause a marked increase in the phosphatase activity of plants and microbes (Johnson *et al.* 1999; Turner *et al.* 2001), a clear sign of phosphorus stress and an increase in the demand for phosphorus from organic compounds. This ultimately leads to a switch from nitrogen to phosphorus limitation and a shift in plant community composition (Bobbink *et al.* 1998), although the emphasis has often been on nitrogen-related mechanisms (e.g. Fenn *et al.* 2003) rather than the enhancement of phosphorus limitation as a causative factor driving such changes (Wassen *et al.* 2005).

In summary, the variety of phosphorus compounds that occur in soil, coupled with the range of adaptations by which plants can manipulate their access to such compounds, suggests that coexisting plants partition soil phosphorus to minimize competition. This could provide an additional mechanism to explain the abundance and distribution of

plants in the environment and is likely to have particular ecological significance wherever productivity is limited or co-limited by the availability of soil phosphorus.

Acknowledgements

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