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EDITORIAL

Phosphate as a limiting resource: introduction

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Global context

Phosphorus (P) is commonly a limiting nutrient for both terrestrial and aquatic productivity, with the consequence that it is considered important in determining the biodiversity and biomass of natural ecosystems. P-limitation of terrestrial plants is not a recent development. Karandashov and Bucher (2005) argued that the evolutionary transition of plants from the aquatic to terrestrial habitats was contingent on the presence of arbuscular mycorrhiza, which facilitated P acquisition. As a consequence of persistent P-limitations, terrestrial plants have evolved a wide range of P acquisition strategies, including mechanisms that increase the range of chemical forms that can be accessed, the range of concentrations that can be taken up and the effective absorbing area of the roots (Lambers et al. 2008). Likewise, plants have a range of strategies for conserving P that enable them to persist in P-deficient habitats, including sclerophyllous leaves and serotinous cones. In order to ensure successful recruitment in P-limited environments they also produce P-rich seeds (e.g. Groom and Lamont 2010, this volume).

P is also often a limiting nutrient in agriculture (e.g. Sánchez 2010), deficiency being redressed through applications of P-fertilisers (globally *ca.* 20×10^9 kg P annum^{-1}; Smit et al. 2009). Alarmingly, the finite global stocks of P ($2{,}400\times10^9$ kg P) are likely to be depleted within 125 years (Smit et al. 2009; Vaccari 2009). Anthropogenic modification of the global P cycle by fertiliser use as well as waste streams and detergent use have effectively doubled global P cycling since the mid-19th century (Filippelli 2002). A consequence is that many natural ecosystems are threatened by super-abundance of a formerly limiting resource, with resulting biodiversity losses (e.g. Tilman et al. 2001). This is likely to be especially true in systems where P was formerly most-limiting, such as in Mediterranean terrestrial ecosystems (Sala et al. 2000), oligotrophic lakes (Schindler et al. 2008) and nutrient-impoverished oceans (Rabalais et al. 2008). Apart from the direct biodiversity consequences of P-eutrophication, release from P-limitation combined with increased atmospheric CO_2 concentration and N deposition may exacerbate the loss of biodiversity.

Regional context

The global importance of P as a limiting resource, prompted the compilation of this Special Issue of Plant

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and Soil, following a workshop held in Stellenbosch (South Africa) in January 2009. Stellenbosch is situated in the Cape Floristic Region (CFR). The CFR, located at the south-western tip of Africa, is a Mediterranean ecosystem occupying a relatively small area of 90 000 km^2, but with some of the highest levels of plant diversity in the world (9,000 vascular plant species, of which 69% are endemic) (Cowling et al. 1992). This high γ diversity of the CFR is the product of a moderately-high α-diversity, which is similar to that of other Mediterranean-ecosystems at the 1,000 m^2 scale (*ca* 70 species per 1,000 m^2; Cowling et al. 1996) and a very high β-diversity among habitats. The component biomes are floristically distinct and associated with equally distinct soil-types: Afrotemperate Forest, Albany Thicket, Fynbos and Succulent Karoo, that make up the CFR (Cowling et al. 1992; Cowling et al. 1997; Goldblatt and Manning 2000; Rebelo et al. 2006). The highly species-rich Fynbos biome occupies the largest area (56% of the CFR) and consists of three vegetation types; fynbos, renosterveld and western strandveld, of which fynbos is the dominant type (Cowling et al. 1997; Rebelo et al. 2006). Fynbos vegetation type is a fire-prone heathland, containing small-leaved, evergreen, sclerophyllous shrubs (Kruger 1983; Cowling et al. 1992; Cowling et al. 1997; Rebelo et al. 2006) and occurs on ancient sandstone-derived soils which are coarse-grained, highly leached and extremely deficient in exchangeable bases, total N (1 to 2 mgN g^{-1}) and available P (0.4 to 3.7 μg P g^{-1}) (Kruger 1979; Stock and Lewis 1986; Witkowski and Mitchell 1987).

The particularly high diversity of fynbos, combined with low aboveground biomass prompted the hosting of the workshop within the CFR, to stimulate discussion of what determines the ecophysiological and ecological characteristics of such ecosystems. Over many decades, comparative research has been carried out between the CFR and the South West Botanical Province (SWBP) of Australia. This has been based on the fact that these highly biodiverse Mediterranean-ecosystems share several families in common, and that many of the functional traits of the native plants are similar (e.g. serotiny, resprouting, sclerophyllous leaves, cluster roots). The soils of the two regions are also both extremely P-impoverished. Despite the similarities, there are also striking differences. For example, SWBP Proteaceae are generally taller (personal observation), more sclerophyllous (Beard et al. 2000) and have more serotinous cones with more P (Groom and Lamont 2010). This has sparked much debate over the relative availabilities of nutrients in the two geographic regions. This debate is complicated by the climatic and edaphic variability of the two regions, making comparisons highly dependent on the rather sparse data. In this volume, Lambers et al. (2010) have gathered data showing that foliar [N], [P] and N:P ratios of fynbos and west-Australian kwongan plants are relatively similar. In contrast, leaf mass per unit area (LMA), a proxy for sclerophylly, was *ca.* 1.7-fold higher in kwongan than in fynbos. Also in this volume, Groom and Lamont (2010) report that the plants native to kwongan have seeds with 2.2-fold higher [P] and 4.7-fold greater P contents than those of fynbos plants, and concluded that P must be more limiting in kwongan. However, plants in kwongan have their own challenges not related to P and peculiar to Australia; voracious graminivorous cockatoos (Groom and Lamont 1997). While this does not deny the importance of P-rich seeds for successful recruitment, the occurrence of graminivores and the extinct Australian megafauna (Miller 2005) may have contributed to a high degree of serotiny (measured as duration of seed retention and extent of protection) coupled with low numbers of P-rich seeds and high LMA.

Field excursion to investigate the role of P in determining forest-fynbos boundaries

At the workshop there was considerable discussion of the importance of P in determining the biodiversity (see Lambers et al. 2010, this volume) and structure of vegetation (see Bond 2010, this volume). This was highlighted by a field excursion to the Swartboskloof valley (Fig. 1) where both Kogelberg Sandstone fynbos and evergreen Southern Afrotemperate Forest (Mucina and Rutherford 2006) occur in close proximity on soils derived from the same geology (sandstone). This sharp (tens of metres) vegetation disjunction has commonly been ascribed to protection from fire by boulders (e.g. Moll et al. 1980; Manders 1990). Fire does enter the forests, although infrequently (van Wilgen et al. 1990), and the forest patches are often also associated with landscape drainage lines and rock scree (Manders 1990). The soils associated with forest are considerably more nutrient-rich than those asso-

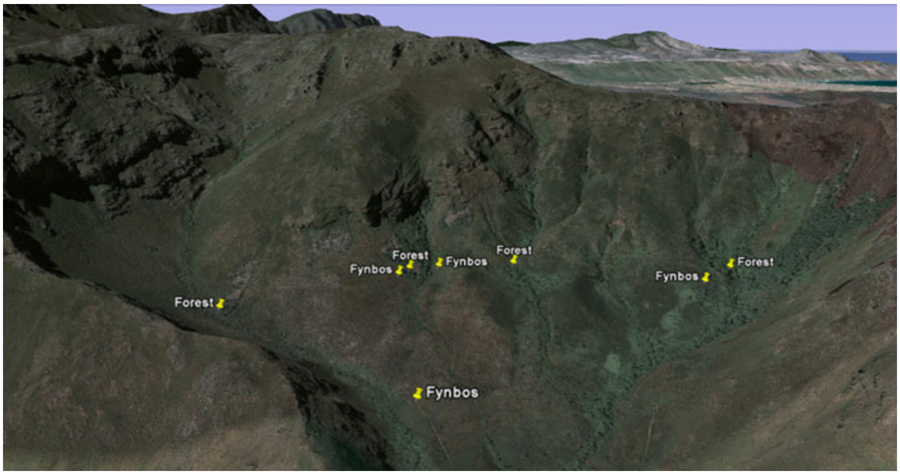

Fig. 1 Swartboskloof (33° 59′45.53″S, 18°57′23.29″E, South Africa) from low elevation (1 130 m above sea level) looking south and showing sites sampled (Table 1) in forest and fynbos patches (image from Google Earth, Sep 2009). The forests are restricted to ravines (all except leftmost patch) or associated with rocky scree (leftmost forest patch). Evidence of a recent fire is visible at top right

ciated with fynbos (Table 1). These distinct forest and fynbos soils have scarcely changed over the 20 years since Manders (1990) sampled the same region. Nevertheless, forest expansion into formerly fynbos areas protected from fire, such as in Orange Kloof (Luger and Moll 1993) is often cited as evidence that soil properties are not influential. It should be noted, however, that the Orange Kloof site is on granitic soils (Luger and Moll 1993) which are considerably more nutrient rich than sandstone-derived soils in the same region (e.g. Witkowski and Mitchell 1987). Thus the Orange Kloof case may not be appropriate for understanding forest-fynbos dynamics on sandstone-derived soils. The consensus amongst field excursion participants (see acknowledgements for participants) was that this forest-fynbos disjunction is probably the product of 'niche construction' (reviewed by Day et al. 2003), in which frequent fires in fynbos mobilise nutrients, allowing these to 'leak' out of the ecosystem (through volatilization, ash loss or leaching), whereas forests may act as nutrient collectors trapping dust and ash and taking up nutrients and water from deep in the soil. Forests were probably originally more widespread in the region before the onset of global cooling and aridification in the Pliocene, and were replaced (off the drainage lines/rock scree) by fire-prone sclerophyllous vegetation and dry woodlands, especially during the Quaternary when seasonal Mediterranean-type climates developed (Cowling et al. 1996). Thus the floristic composition and structure of the closed-canopied forests may be a consequence of greater water and nutrient availability, which is in turn the product of long-term soil development in the relative absence of fire. In contrast, the neighbouring open-canopied, highly sclerophyllous fynbos is associated with nutrient poor soils, particularly impoverished in P, which are the product of long-term losses of nutrients driven by repeated fires.

Biodiversity

Although the turnover in lineages between vegetation types such as afrotemperate forest and fynbos

Table 1 Comparison of the soil characteristics of forest and fynbos soils at sites (Fig. 1) sampled at Swartboskloof in Jonkershoek, South Africa (Feb 2007). Soil was analysed as described in Cramer et al. (2008). Means±SE are followed by letters indicating significant differences between biome measures determined using Student's t-tests. Results are ranked using an "effect size" measure (Hedges's*g*; Hedges and Olkin 1985), $g = t\sqrt{(n_1+n_2)}/\sqrt{(n_1 n_2)}$, where *t* is the value of the Student's *t* test of the differences between the two groups and *n* is the number of samples ($n=4$)

Measure	Unit	Forest	Fynbos	*g*
Ca	cmol kg^{-1}	9.8±2.2 b	0.6±0.1 a	7.4
EC	mS m^{-1}	32±227 b	6±38 a	5.7
pH	(in 1 M KCl)	5.2±0.2 b	3.7±0.1 a	5.0
T-Value	cmol kg^{-1}	15±2 b	5±1 a	3.4
Mg	cmol kg^{-1}	3.3±0.3 b	0.5±0.2 a	3.3
Bray II P	mgkg^{-1}	22.5±8.6 b	4.8±0.9 a	2.7
Total N	mgg^{-1}	3.9±0.8 b	1.3±0.6 a	2.0
K	mgkg^{-1}	188±41 a	79±30 a	1.6
Na	cmol kg^{-1}	0.12±0.02 a	0.07±0.02 a	1.4
C	mgg^{-1}	39±6 a	22±1 a	1.3
H^+	cmol kg^{-1}	1.4±0.4 a	3.2±0.9 b	−1.8

contributes to biodiversity of the CFR, the α-diversity the Kogelberg Sandstone fynbos is much greater than that of the Southern Afrotemperate forest (Mucina and Rutherford 2006). The high fynbos biodiversity has been extensively discussed in the literature (e.g. Linder 2003; Verboom et al. 2009). The association of high biodiversity in the CFR and SWBP with nutrient-limited habitats is well established (e.g. Hopper 2009). Species diversity in such regions has been linked to what is referred to as old, climatically buffered, infertile landscapes (OCBILs). The OCBIL concept of speciation does need to accommodate a role for disturbance (e.g. fire) and also probably applies more generally to the SWBP than to the CFR; in the latter the diversity of soils is associated with topographic diversity, resulting in a patchwork of young and ancient soils (Cowling et al. 2009). Whether the link between low fertility and biodiversity is causal, or just the consequence of a climatically stable region, combined with speciation and the persistence of lineages (e.g. Verboom et al. 2009), is still debatable. In this volume, Lambers et al. (2010) provide a link between P availability in OCBILs and biodiversity. Although the link between P and biodiversity has been explored, it is also notable that soil [N] and [P] are highly correlated within the SWBP. Nevertheless, in both the CFR and SWBP, leaf [P] is *ca.* one-third of the world average, while [N] is *ca.* half of the world average. This is partially a consequence of high LMA in these regions relative to global averages. Lambers et al. (2010) argue that high biodiversity is causally linked to low fertility through the increased diversity of plants with specialised nutritional adaptations, such as various forms of mycorrhizal association, cluster roots for acquiring P and the occurrence of parasitic and carnivorous plants. The idea is that as nutritional availability decreases in OCBILs, particularly with respect to P, there is greater selection pressure for strategies to acquire the resources, with the consequence of niche segregation. How this niche segregation is linked to speciation through reproductive isolation has not, however, been expressly considered.

The importance of P to biodiversity is also suggested by the linkage of weak legume persistence in the CFR (Cocks and Stock 2001) to post-fire decline in P availability (Power et al. 2010, this volume). Legumes also do not persist through post-fire succession in other Mediterranean-type ecosystems (e.g. chaparral of California, Westman 1981; Jarrah forests of South West Australia, Bell and Koch 1980). The relative lack of persistence of indigenous legumes (there are 761 species, 627 of which are endemic to the CFR, Goldblatt and Manning 2000) during post-fire succession in fynbos vegetation of the CFR may partially be a consequence of the fact that most legumes lack the highly effective root adaptations required for acquisition of P (i.e. cluster roots of size and functional activity of the Proteaceae) from soils with scarce sparingly soluble P late in post-fire succession (Power et al. 2010). However, this raises the question of how Australian legume species, such as *Acacia saligna* and *A. cyclops*, are able to persist successfully after fire in the CFR where they often dominate areas previously occupied by fynbos vegetation. Power et al. (2010) argued that alien *Acacia* species possess extensive root systems and associated mycorrhizal networks compared to fynbos legumes (e.g. Hoffman and Mitchell 1986), which would allow them to access a greater pool of P. An alternative possibility is that the deep root systems of alien Australian legumes combined with a high capacity for water transport (Le Maitre et al. 1996) allows them to trade water for nutrient access (e.g. Field et al. 1983; Wright et al. 2003) by using transpiration-driven mass-flow to extend the foraging range of roots away from the immediate vicinity of the roots (Cramer et al. 2009).

Biomass

The obvious differences in vegetation biomass associated with the forest-fynbos discontinuity could be due to the ability of forests to escape fire or to differences in their ability to access water and/or nutrients. The link between declining nutrients, in particular P, and declining woody biomass has been strongly demonstrated across several chronosequences in which P and biomass decrease with soil age (e.g. Richardson et al. 2004; Wardle et al. 2008). In this volume, Bond (2010) has issued a challenge to the view that nutrients, particularly P, determine woody biomass, by estimating the available stocks of major nutrients (excluding N) in the soil, and the nutrient stocks required to produce woody biomass. Due to limitations of data availability, this estimation required several assumptions; for example, adequate nutritional data are not generally available for soils below 0.3 to 0.5 m, soil and rooting depth is seldom reported and there are uncertainties about the actual available fraction of total P and other cations. Nevertheless, Bond (2010) estimated that total P (and available P) is adequate for the formation of woody biomass, even in some of the most impoverished soils; instead he makes a case for K and Ca limitation. Bond (2010) cites an example from the CFR where above-ground biomass of fynbos shrublands is *ca.* 15 000 kg ha^{-1}, compared *ca.* 170 000 kg ha^{-1} for adjacent conifer plantations, supporting the notion that nutrients alone are not a constraint. It may be informative to note that in African savannas, woody cover (a measure of canopy closure by woody species) is strongly correlated with rainfall, followed by fire frequency and then soil total P, with soil N playing only a minor role (Sankaran et al. 2008). Although woody cover is not directly related to woody biomass, interactions of several factors may be important in determining final woody biomass, but further definitive work is required.

Reproductive strategies

For plants from habitats with limited P availability, the investment of nutrients in reproduction can be enormous. One might expect that when nutrients are limiting, nutrient allocation to any process would be under tight selection pressure and as low as possible. In this volume, Groom and Lamont (2010) review the investment of P in seeds of plants from P-impoverished habitats. Those from South Western Australia (SWA) allocated up to *ca.* 50% of above ground P to seeds, with less allocation to seeds in more nutrient replete areas. The high [P] in seeds relative to leaves and other plant structures may be required because of the edaphic constraints on germination and seedling survival. The high concentrations translate into large amounts of P per seed (up to 15 mg P per seed), giving the seedlings a better chance of establishing in soils in which the P concentration is low. Serotiny limits the nutrient losses associated with seed dispersal by ensuring that seeds are shed in the post-fire environment, when the chance of germination is higher. Does serotiny, which protects P-investment in seed result in more P-rich seeds? Groom and Lamont (2010) show that the amount of P in serotinous seeds is greater than in non-serotinous seeds. This may be because serotiny is a lower-risk seeding strategy, or alternatively because more P-rich seeds are required in P-impoverished habitats for successful recruitment. Recurring fires and nutrient limitations have also resulted in a large number of resprouting plants in P-limited regions in which regrowth takes advantage of pre-existing roots. In resprouters, the investment in seed is generally lower than in plants that are reseeders, because the resprouters only require sufficient seed to offset parental mortalities, whereas obligate reseeders rely entirely on seed production (Meney et al. 1994). Indeed, Groom and Lamont (2010) found that resprouters produced fewer, but larger seeds, with more total seed P than co-occurring reseeders. Thus reproductive strategies, like those of P acquisition and P conservation, are clearly geared to the degree of P-limitation imposed by the habitat,

N:P interactions

Although absolute soil [P] is an important determinant of vegetation properties, plants do maintain N:P ratios within certain bounds, and thus the relative N and P availabilities are important for determining growth (Ågren 2008). Although species that dominate areas with low N availability share similarities with those that dominate areas with low P availability, N- and P-limitations should not just be merely considered as ‘infertile conditions’, but rather as independent, but interacting, specific limitations (Ostertag 2010, this volume) that interact with each other. Plants native to the most P-impoverished soils, such as those characteristic of the CFR and SWBP, seem unlikely to show growth responses to N supplied without added P. Contrary to expectations, when Craine and Jackson (2010, this volume) amended 98 North American soils by supplying NH_4NO_3 and Na_2HPO_4 either individually or in a N:P ratio of 22:1, N and P were co-limiting for the grass *Schizachyrium scoparium* grown on many low-P soils. These authors concluded that low P may alter the N cycle to limit N availability to the plants. Isotopic evidence suggested that this might occur through greater gaseous N losses from low-P soils. Thus, even on low-P soils, they needed additional N to respond to P addition. It remains to be seen whether this also applies to plants native to low-P soils from the CFR and SWBP.

Unlike grasslands which are commonly co-limited by N and P (Craine et al. 2008; Craine and Jackson

2010) there was no evidence of co-limitation in the classic work of Vitousek (2004), who reported on fertilization experiments across an Hawaiian chronosequence. In that work single-resource limitation (see Craine and Jackson 2010) was evident both at younger (0.3 ky) N-limited and at older (4,100 ky) P-limited sites, although there was some response of plants at the younger site to N as well (Fig. 2a). It seems likely, however, that the lack of requirement for additional N in the work of Vitousek (2004) compared to that of Craine and Jackson (2010) stems from either differences in the degree of N-limitation or the life-forms used (i.e. shrubs versus grasses). In this volume, Ostertag (2010) examined the interesting phenomenon that foliar [N] responds little to fertilization (Fig. 2b) while foliar [P] is much more responsive (Fig. 2c). Both inorganic and organic P accumulated when plants were fertilized with P, indicating that this was not simply a case of passive accumulation of P (Ostertag 2010). This author concluded that the plants may be incapable of down-regulation of P uptake. A lack of down-regulation of P uptake capacity has been proposed to account for the sensitivity of plants from P-impoverished Mediterranean ecosystems to P-toxicity (Shane and Lambers 2005; Shane et al. 2008; Hawkins et al. 2008). Whether this lack of down-regulation is more widespread and contributes to tissue P-accumulation requires examination of the P-uptake kinetics of the plants in question.

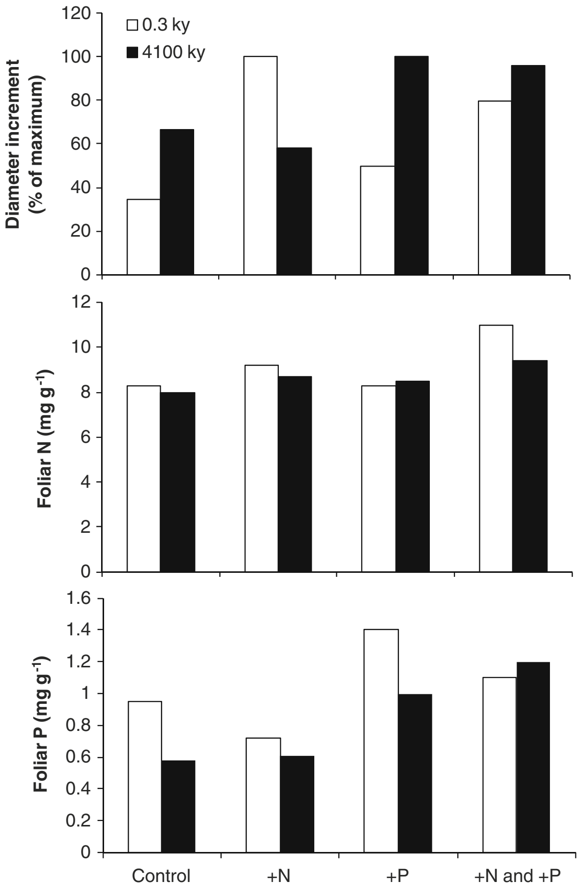

Fig. 2 Fertilization responses after 2 years for two of the six sites reported on by Vitousek (2004), and for which foliar N and P have been reanalysed for several species by Ostertag (2010). Diameter increment was expressed as a percentage of the maximum (0.3 ky maximum=13.3 and 4,100 ky maximum=2.4 mm annum^{-1}) across the four treatments for a particular site (data from Vitousek 2004). Plots were fertilized with 100 kg ha^{-1}N and/or P twice annually since 1985 (N-limited site) or 1991 (P-limited site)

Whilst low N availability may limit plant responses to P fertilization, when the N:P ratios become very high, plants seem to be unable to utilise P, even when this is supplied at concentrations that are suitable for growth at lower N:P ratios. In this volume Fujita et al. (2010) studied the effect of increased N:P ratios (from 1.7 to 135) supplied as KNO_3/$Ca(NO_3)_2$ and KH_2PO_4 in quartz sand on 5 European grass and 3 herb species. High N:P ratios resulted in decreased overall growth over 2 years, independent of the overall amount of nutrient supplied. This decreased growth was attributable to root death at the higher N:P ratios, triggered by P-limitation and consequent P-starvation in the root tissue. Fujita et al. (2010) suggested that low mycorrhizal infections may play a role in this P-limitation. However, an alternative explanation is that the higher N:P ratios limit transpiration driven mass-flow, and this reduces access to P. A signalling role for NO_3^- in regulating transpiration through decreased stomatal conductances (Cramer et al. 2009) could result in reduced mass-flow of P through the relatively inert quartz sand used (e.g. Cramer et al. 2008), resulting in the observed P-starvation of the plants at high N:P ratios.

One lesson from these N×P interaction experiments in this volume (Craine and Jackson 2010; Fujita et al. 2010; Ostertag 2010) is that consideration of a single limitation (e.g. P) in isolation is misleading. The importance of N×P interactions is also pertinent when considering the consequences of how climate change influences plant processes (e.g. through effects on transpiration) and also how nutrient deposition may influence plant communities by changing the N:P ratios.

Resource acquisition

Apart from mechanisms that conserve P (e.g. sclerophylly, serotiny, efficient P remobilisation from senescing tissue), plants native to P-limited habitats also have several mechanisms (e.g. cluster roots, mycorrhiza, phosphatase exudation) for ensuring P acquisition from low concentration resources and from forms of P that are not readily available to other plants (reviewed by Lambers et al. 2006; Lambers et al. 2010). Cluster roots are relatively rare outside of Australia and South Africa. However, in this volume Zúñiga-Feest et al. (2010) have found that cluster roots of South American Proteaceae responded to P-deprivation, similar to Proteaceae from South Africa and Australia (reviewed by Lambers et al. 2006). This ubiquitous induction of cluster root formation by P-deficiency has been used to argue that these roots function mostly in P acquisition. Due to the mobilisation of P from inorganic complexes such as Ca-P, Mg-P, Mn-P, Zn-P and Fe-P by carboxylates, cluster roots do also take up the associated cations (Lamont 2003). Cluster roots can also absorb ^{15}N-glycine (Schmidt and Stewart 1997), possibly indicating that they have a role in N-uptake. Indeed, low levels of N have been reported to induce cluster root formation under P-deficiency, whereas high N levels were inhibitory (Lamont 1972; 1973; Dinkelaker et al. 1995). In contrast, Sas et al. (2002) showed that NH_4^+ stimulated cluster root formation and proton excretion under P deficiency more than did NO_3^-. Although cluster roots do take up N, the consensus today is that cluster roots function mostly for P-acquisition and the reasons for N linked cluster root induction may be due to perceived P deficiency in response to N supply. The work of Rath et al. (2010) in this volume using 2,102 white lupin ESTs to analyze gene expression of cluster roots in white lupin in response to P, N, and Fe deprivations may challenge the stereotyping of cluster roots as solely a P-acquisition strategy. They identified 19 genes in cluster roots that displayed up-regulation in response to both N and P deprivation (N normally supplied as KNO_3), six of which were glycolytic enzymes and one was sucrose synthase. The increased expression of sucrose synthase and changes in glycolysis are intriguing because sugar signalling has been shown to mediate plant responses to N and P deprivation (e.g. Müller et al. 2005; Hammond and White 2008; Liu et al. 2005), and has been demonstrated to be involved in the formation of proteoid roots (Zhou et al. 2008). Thus the work of Rath et al. (2010) indicates that there may be cross-talk between signalling mechanisms reporting N and P deficiencies, leading to cluster root induction.

In the absence of soil-resetting disturbance, soil weathering leads to long-term reduction of P availability. The decline in total P with soil age has been firmly established from chronoseqeunces (e.g. Stevens and Walker 1970). This decline of total P is also associated with increasing contribution of a variety of organic P forms to the total P pool (Turner et al. 2007). The contribution of organic P may be especially important in the most P-impoverished ecosystems. For example, in fynbos up to 76% of the total P (total $P=46\ \mathrm{mg\,kg^{-1}}$) was in the organic P fraction (Mitchell et al. 1984). For this reason, direct root facilitated access to organic P, rather than indirect access via microbial mineralisation, is a potentially important, but relatively little studied mechanism. Phosphatases hydrolytically remove P from organic substrates, and are thought to play an important role in P acquisition (e.g. Vance et al. 2003). A microRNA (miR399) thought to target mRNAs coding for a phosphatase transporter was originally identified in both *Arabidopsis thaliana* and *Oryza sativa* (Jones-Rhoades and Bartel 2004). miR399-overexpressing *Arabidopsis* accumulates 4 to 6-fold more P, with greater P-transporter mRNA abundance (Bari et al. 2006). In this volume Gao et al. (2010) have shown that transgenic tomato overexpressing miR399 had higher P uptake due to increased expression of P-transporters, combined with increased acidification of the root medium and exudation of acid phosphatase. Thus miR399 seems to co-ordinate a suite of P-acquisition traits that is garnering it considerable research attention, and work with cluster-root forming species is an obvious next step.

Concluding remark

Phosphate as a limiting resource is an important and specific constraint that plants have co-evolved with ever since making the transition to the terrestrial environment. There has been substantial progress in identifying how plants meet the challenge of acquiring and conserving this resource. However, the responses of plant species richness and plant production to P-limitation can only be understood when the interactions of this limitation with multiple other abiotic resources (e.g. N, water, light) and biotic interactions (e.g. competition, fire, herbivoury) are taken into consideration.

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