

Plant nutrient-acquisition strategies change with soil age

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Nitrogen (N) tends to limit plant productivity on young soils; phosphorus (P) becomes increasingly limiting in ancient soils because it gradually disappears through leaching and erosion. Plant traits that are regarded as adaptations to N- and P-limited conditions include mycorrhizas and cluster roots. Mycorrhizas ‘scavenge’ P from solution or ‘mine’ insoluble organic N. Cluster roots function in severely P-impooverished landscapes, ‘mining’ P fixed as insoluble inorganic phosphates. The ‘scavenging’ and ‘mining’ strategies of mycorrhizal species without and non-mycorrhizal species with cluster roots, respectively, allow functioning on soils that differ markedly in P availability. Based on recent advances in our understanding of these contrasting strategies of nutrient acquisition, we provide an explanation for the distribution of mycorrhizal species on less P-impooverished soils, and for why, globally, cluster-bearing species dominate on severely P-impooverished, ancient soils, where P sensitivity is relatively common.

Introduction

Nitrogen (N) and phosphorus (P) are essential elements that limit plant growth in many ecosystems [1,2]. Terrestrial plants exhibit a wide array of traits that are regarded as adaptations for overcoming these limitations, and these include effective mechanisms of resorption, internal recycling, and allocation and use of N and P in growth [3]. For most plant species, however, the principal limitation occurs in the total uptake of N and P into the growing plant.

There has been a strong bias in the ecological literature towards N as the nutrient that usually limits plant productivity, because most plant ecologists have worked in Western Europe or North America, focusing on relatively young postglacial landscapes, where N is scarce. By contrast, in ancient and hence severely nutrient-impooverished soils, P is the limiting resource (Figure 1), and recognition of this important fact is emerging in ecological literature [4–8]. At the same time, the importance of plant strategies that increase access to different forms of nutrients is increasingly acknowledged (Box 1). These strategies are complementary, allowing plants to use the N and P resources that occur in soils that are at different stages of soil development (Figure 1). The focus of this review is on

P, as well as N, and on species with strategies that are highly efficient at accessing a range of chemical forms that change in availability as soils develop and are subsequently weathered and eroded (Box 2).

A conventional view of plant N and P acquisition is that the majority of the uptake occurs from soluble inorganic sources in the soil solution (N is sourced from nitrate and ammonium, and P from phosphate) (see Glossary). Three major factors limit this N and P uptake: the concentration of N or P at the absorbing root surface; the total surface

Glossary

Arbuscular mycorrhiza: common symbiotic association between 80% of higher plant species and particular soil fungi in the Glomeromycota, involved in plant acquisition of P and some other relatively immobile nutrients (e.g. zinc, copper and ammonium).

Chronosequence: series of soils that originated over various geological time-scales.

Cluster roots: bottle-brush-like or Christmas-tree-like structures in roots with a dense packing of root hairs; these structures release carboxylates into the rhizosphere, thus solubilizing poorly available nutrients (e.g. P) within the soil.

Disturbed soils: soils affected by human activities such as cultivation or logging, or by natural events such as animal digging, flooding, storms and burning

Ectomycorrhiza: symbiotic association between some tree or shrub species and particular soil fungi mainly in Basidiomycota and Ascomycota, involved in plant acquisition of P, N and other nutrients.

Ericaceae: plant family of heath species.

Ericoid mycorrhiza: symbiotic association between heath plants (Ericaceae) and particular soil fungi in the Ascomycota, involved in plant acquisition of P and N.

Inorganic N sources for plants: soil N that is available for uptake for plants (i.e. predominantly ammonium and nitrate).

Inorganic P source for plants: the only soil P that is taken up by plant roots.

Mining: nutrient-acquisition strategy wherein nutrients that are poorly available, because of their very low concentration in the soil solution, are accessed following release from roots of nutrient-solubilizing or hydrolysing exudates.

Non-mycorrhizal species: species unable to establish a symbiotic association with any type of mycorrhizal fungus; examples include most species belonging to Brassicaceae (cabbage family), Cyperaceae (sedge family) and Proteaceae.

Organic N sources for plants: soil N that is available for uptake by some mycorrhizal plants that have the capacity to hydrolyse proteins upon release of proteases from fungal mycelium; the products of the hydrolytic process (i.e. amino acids, small peptides) are available for uptake by plants roots and mycorrhizal hyphae.

Organic P sources for plants: soil P that is available for uptake for plants after hydrolysis by phosphatases that release inorganic P.

Rhizosphere: zone of soil influenced by the presence of a root.

Rock phosphate: naturally occurring ground rock that contains as much as 30% inorganic phosphate with very low solubility; the material from which phosphatic fertilizers are manufactured.

Scavenging: nutrient-acquisition strategy wherein nutrients at sites unavailable to the roots are accessed through a symbiosis with mycorrhizal fungi.

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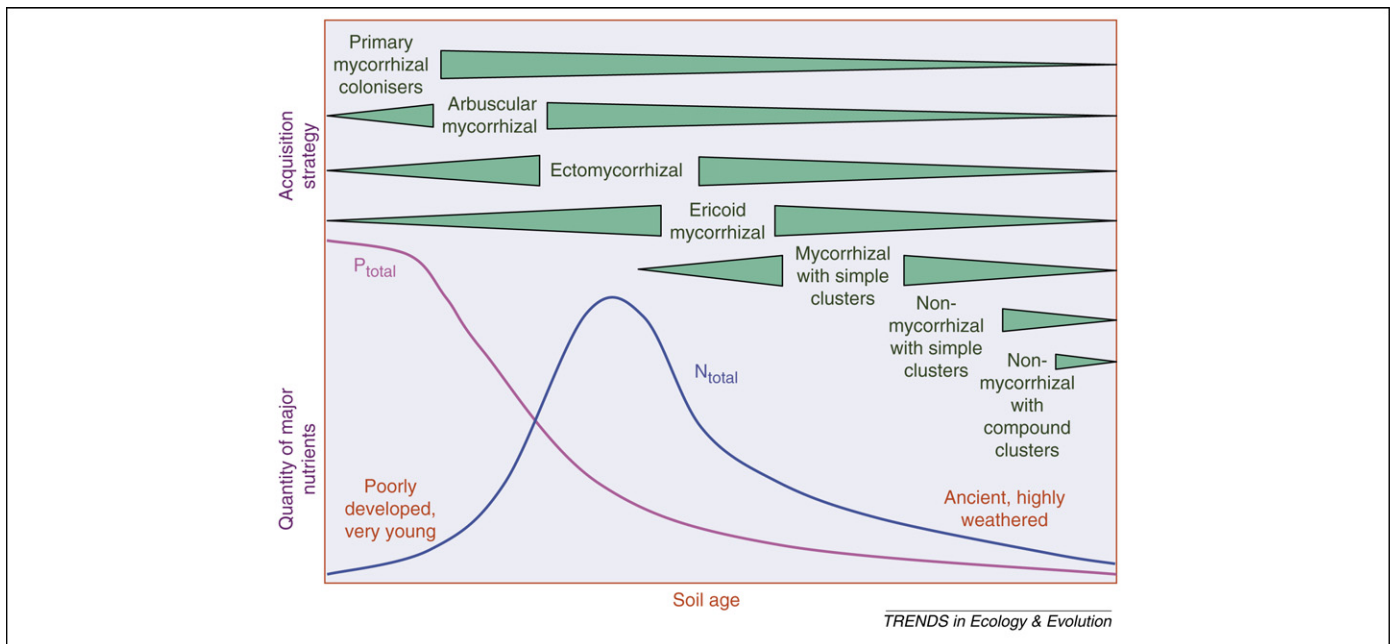


Figure 1. Changes in total soil P (purple) and N (blue) and in plant nutrient-acquisition strategies (green) as dependent on soil age, based on data in various studies [5,11,36]. ‘Poorly developed, very young soils’ refers to soils that result from recent volcanic eruptions; ‘ancient, highly weathered soils’ refers to soils that have been above sea level and have not been glaciated for millions of years. Although never becoming dominant in severely P-impoorished soils, some mycorrhizal species do co-occur with non-mycorrhizal cluster-bearing species. The highest and lowest total P levels in young and ancient soils are $\sim 800 \text{ mg kg}^{-1}$ soil and 30 mg kg^{-1} soil, respectively. Peak total N levels are 8000 mg kg^{-1} soil, whereas total N levels in the very youngest soils shown here are $<5 \text{ mg kg}^{-1}$. The width of the triangles referring to the different ecological strategies provides a (relative) measurement of the abundance of these strategies as dependent on soil age.

area of roots available for uptake; and the distribution of roots in the soil. Specific properties of the ‘transporters’ involved in nutrient uptake might be important for nitrate [9], but are much less so for inorganic phosphate (Pi), because Pi moves very slowly in soil [10]. Because roots can take up Pi much faster than Pi moves in soil, uptake results in a marked reduction of the Pi concentration at the absorbing surface. Therefore, the rate of production of more root surface available for uptake of Pi is more important than the properties of the proteins that are responsible for uptake [9].

It is becoming increasingly evident that a wider array of acquisition strategies meeting plant N and P requirements have evolved than was previously believed (see Box 1) [11,12]. These include mechanisms that increase the number of chemical forms that can be accessed [12–15], the supply rate of those forms from the soil [9], and both the effective absorbing area and its dispersal through the soil [16–18]. Thus, availability of a nutrient in soil is not only a function of its chemical form, but also of the capabilities of the plants growing in that soil to mobilize and absorb it. As our understanding of the range and diversity of uptake strategies grows, it is becoming apparent that their distribution is predictable, with respect to both ecosystems and families of plant species, and involves both benefits and costs to the plants. This review summarizes current knowledge of the geographical distribution and benefits of diverse N- and P-acquisition strategies, and we incorporate this information into a conceptual model along a chronosequence (see Glossary) of soil age and nutrient availabilities.

Acquisition of different sources of N and P

The quantitative contributions of different sources of nutrients and the pathways and mechanisms by which they are

absorbed are poorly established for different ecosystems. Probably the most effective predictor of these contributions in any particular environment is the incidence and frequency of the different strategies that are involved in acquisition of nutrients of different forms. Non-mycorrhizal and arbuscular mycorrhizal (see Glossary) plants access soluble inorganic, and some soluble organic, N sources from soil, with the relative importance of the uptake of nitrate or ammonium depending on the soil pH and aeration. The supply of these soluble forms depends on the rate of mobilization from organic sources (see Glossary) by the soil microflora, and this will vary with soil and climatic conditions as well as with the nature of the plant litter. There is rather little evidence for the involvement of arbuscular mycorrhizal symbioses in increasing N acquisition even from inorganic sources. However, new work has shown that the arbuscular mycorrhizal symbiotic pathway (see Box 1) can be involved in inorganic N uptake [19–21], but the quantitative contribution to plant nutrition is currently unknown. Ectomycorrhizal and ericoid mycorrhizal species (see Glossary) can take up the same soluble inorganic sources, and they have access to an additional source of N, namely insoluble organic forms. Because ectomycorrhizal roots are completely ensheathed by symbiotic fungal mycelium, all nutrients must enter the roots through the mycorrhizal pathway. In any ecosystem, the balance in use of inorganic and organic N will thus depend largely on the extent of mycorrhizal development of the plant species present. The importance of ectomycorrhizas and ericoid mycorrhizas has been appreciated for some time [15] and is further emphasized by a recent study showing that, in the arctic tundra of Alaska, between 61% and 86% of plant N is delivered by these symbioses [22].

Box 1. Below-ground nutrient-acquisition strategies

Nutrient acquisition from nutrient-impoverished soils frequently involves specialized root structures (i.e. cluster roots) or symbiotic structures (e.g. mycorrhizas, root nodules). Probably <10% of all plant species have root systems that have no specialized features enhancing nutrient uptake. Even those that do not form any apparently specialized structures or symbioses might actually have characteristics that are commonly associated with efficient nutrient uptake from the soil solution, for example rapid growth, proliferation in response to localized nutrient sources, and development of long root-hairs.

Specialized, symbiotic root-structures

The differences among mycorrhizal strategies are becoming more widely appreciated. The vast majority of plants form arbuscular mycorrhizas [45]. Extensive mycelial development extends the volume of soil from which the symbiotic root system can scavenge nutrients and transport them over relatively long distances (up to 25 cm has been measured). Major roles in inorganic P uptake are well established, and evidence for involvement in inorganic N nutrition is building [45]. However, the fungi probably have rather low capacity to release nutrients either from sorbed inorganic forms or from organic combination; they 'scavenge' but do not 'mine' the soil. By contrast, both ectomycorrhizas and ericoid mycorrhizas play major roles both in uptake of inorganic nutrients from the soil solution and in releasing P and N from organic forms through hydrolysis. Coupled with this hydrolytic ability, the proliferation of hyphae in nutrient-rich patches provides both 'mining' and 'scavenging' capacities to the symbiotic root systems (Figure 2).

Specialized, non-symbiotic root-structures

Cluster roots combine specialized structure and specialized physiology to maximize Pi acquisition from soils of low P availability, particularly when P is present in insoluble complexes [e.g. iron phosphate and rock phosphate (see Glossary)]. They occur in monocots (e.g. 'dauciform' roots in Cyperaceae) as well as dicots (e.g. 'proteoid' roots in numerous families, including Proteaceae). Dauciform roots are carrot-shaped roots with long root-hairs. Proteoid roots consist of clusters of longitudinal rows of extremely hairy rootlets, which originate during root development, 1–3 cm from the root tip; one lateral branch can contain one, two or several clusters, centimetres apart from each other. Proteoid roots in Proteaceae can be 'simple', bottle-brush-like structures, or 'compound' Christmas-tree-like structures (Figure 3). Cluster roots produce large amounts of carboxylates, which release P from strongly sorbed forms by either replacing P bound to Al or Fe in acid soils or to Ca in alkaline soils or by local reduction of pH in highly alkaline soils. Production of phosphatases releases P from organic sources, but evidence for release of N is scanty. *Banksia* and *Dryandra* species produce compound clusters; the vast majority of these species occur in Western Australia [80], the most ancient and P-impoverished part of the continent (Figure 1 in main text). Their mat-forming structures might allow more intensive 'mining' of mineral soil and recycling of litter; we hypothesize that this strategy comes at a high carbon-cost, thus excluding the strategy from environments where P is slightly more available.

The situation with P is somewhat different because organic P is a smaller fraction of the total amount of P in soil, in comparison with the fraction of total N composed of organic N, and it is equally unavailable to most plants. Again, plant species that are non-mycorrhizal, without cluster roots (see Glossary) or arbuscular mycorrhizal, access soluble inorganic P from the very low concentrations in the soil solution and have no access to the major insoluble forms, whether organic or inorganic. However, new work has shown that plants often switch from direct root uptake to mycorrhizal uptake when colonized by arbuscular mycorrhizal fungi [23–25], and it is very likely that the

Box 2. Properties of soil that depend on soil age

Soil properties that are relevant for nutrient acquisition of plants change dramatically as soils develop with increasing age. Young soils that originate from volcanic activity contain high levels of P and very low levels of N. Such soils are found on recently formed islands in New Zealand, Hawaii and Korea. As these soils age, P gradually disappears through erosion and leaching, and N levels increase, owing to microbial N₂ fixation and atmospheric N deposition. Ancient soils in landscapes that have been above sea level and which have not been glaciated for many millions of years occur in Western Australia, the southwest of South Africa and the Pantepui Mountains in Brazil and Venezuela. The rate at which soils develop depends on rainfall and temperature because these factors affect underlying processes such as erosion, root metabolism and microbial activity.

Soils can be rejuvenated and nutrient contents increased (e.g. by glaciation, import of dust blown in with strong winds, deposition of material from the ocean and arrival of eroded material from higher up in the landscape). Such rejuvenated soils occur in those parts of Europe and North America that were covered in glaciers during the last ice age. Rejuvenated soils also occur on Pacific islands that receive dust from the Loess Plateau in Asia. Deposits along rivers in ancient landscapes can also be considered rejuvenated soils. The concept of 'soil age' is therefore complicated, because younger and rejuvenated soils do occur in ancient landscapes dominated by old soils, forming a patchwork. The concept is nonetheless extremely useful to understand vegetation processes and composition across landscapes in a global context.

Chronosequences are series of soils that originated over various geological time-scales. Although some rejuvenation of these soils will occur at any time, the soils that originated most recently show distinctly different properties from those that are thousands or millions of years old. The most widely studied chronosequences with numerous data on soil microbial activities and vegetation functioning are in New Zealand and Hawaii. These studies have been very informative about the close links between soils and vegetation. None of the studied chronosequences include truly ancient soils, but the existing data can be extrapolated from a soil's perspective. To this extrapolated information, numerous data on vegetation functioning can be added to enhance our insight to how vegetation changes with soil age.

contribution of arbuscular mycorrhizal fungi to P acquisition by plants in general has been seriously underestimated. Absence of a positive effect of mycorrhizas on plant growth cannot be interpreted as a consequence of a lack of significant P uptake through the mycorrhizal hyphae [23]. As with N, both ectomycorrhizal and ericoid mycorrhizal plants access insoluble organic forms of P, and again where roots are completely ensheathed by fungus the mycorrhizal uptake pathway is the only one that is important for P uptake, regardless of the form of the nutrient. Importantly, as we have emphasized, plants with cluster roots are able to make significant use of the insoluble inorganic forms of P that are not available to plants with other acquisition strategies.

Here, we provide a novel perspective on where species with these different nutrient-acquisition strategies fit along gradients of soil age, chemical forms and amounts of N and P and soil pH.

Availability and chemistry of soil N and P as dependent on soil age

The term chronosequence is used to describe a series of soils that originated over various geological time-scales (Figure 1). Such sequences are informative about the



Figure 2. Nutrient-acquisition strategies involving mycorrhizal symbioses. Mycorrhizal fungi extend beyond the root zone and increase the volume of soil

amounts and chemical forms of both N and P that occur in young soils of only several decades old to old soils up to ~4 million years old [5,6,26]. Much more ancient soils are found in Australia [27,28], and the southwest of South Africa [29,30]. Chronosequences in both New Zealand [26] and Hawaii [31] show that, initially, N availability is very low, and P is relatively abundant compared with that in old soils from which nutrients have been lost by leaching and weathering (Figure 1). As vegetation becomes established early in the chronosequence, inputs from N₂ fixation increase, resulting in increases in soil N, N:P ratio and the proportion of the organic forms of both these nutrients. Accumulation of organic sources of N and P depends on local climatic and soil factors that affect organic matter turnover, but in any case the organic pool is more important for N than it is for P [3].

Phosphate diffuses very slowly in the soil solution and is rapidly sorbed as iron and aluminium phosphates in soils of low pH, or as calcium phosphates where the pH is high; that is, P is either adsorbed onto or absorbed into soil particles [32]. Because these P compounds have very low solubility, concentrations of P in the soil solution are very low and rarely exceed 10 μM [32,33]. By contrast, inorganic N compounds are generally soluble; nitrate is highly mobile, with concentrations in the soil solution sometimes in the millimolar range, and organic N is crucial for a continuous delivery of plant-available N [34,35]. As soils age, erosion, weathering, leaching and denitrification result in a general decline of nutrient status; and, importantly, both total P and available P decline [5,36], and P therefore becomes severely limiting. Indeed, the availability of P can limit N₂ fixation, and some legumes do not nodulate in P-deficient soils unless they are also colonized by arbuscular mycorrhizal fungi, which increase P uptake [37,38]. The apparent additional requirement for P in N₂ fixation is still mechanistically unresolved [38], and occurs despite substitution in some components of N₂-fixing nodules of phospholipids by galactolipids, which do not contain P [39].

Plants, as is increasingly appreciated, have several contrasting and complementary strategies for increasing the acquisition of both N and P, and for broadening the options of uptake from resources of different chemical composition (see above in this section, and Box 1). However, these strategies do not occur randomly across terrestrial biomes, but rather are very closely associated with soils of particular ages. Nutrient-acquisition strategies such as the various types of mycorrhizas (Figure 2),

that is explored and accessed for P or N uptake. All mycorrhizas (arbuscular mycorrhizas, ectomycorrhizas and ericoid mycorrhizas) are involved in uptake of soluble inorganic P. Ericoid mycorrhizas and ectomycorrhizas are also involved in mobilising P and N from inorganic and organic sources in soil. (a) Hyphae of the arbuscular mycorrhizal fungus *Glomus caledonium* growing into soil from a host root of *Trifolium repens*. Photo by Iver Jakobsen; reprinted with permission of Springer-Verlag [79]. (b) A seedling of *Pinus sylvestris* growing in a microcosm in association with the ectomycorrhizal fungus *Suillus bovinus*. The fungal mycelium can be seen spreading in the soil in the microcosm (arrowhead) and proliferating locally to form well-defined dense patches (arrows). Photograph courtesy Sari Timonen, Department of Applied Chemistry and Microbiology, University of Helsinki, Finland. (c). Ericoid mycorrhizal root of *Woolfsia pungens*, showing epidermal cells colonized by coils of an ericoid mycorrhizal fungus (stained blue, arrowed). Photograph courtesy of Susan Chambers and John Cairney, Centre for Plant and Food Science, University of Western Sydney, Australia.



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Figure 3. Root morphology of Australian Proteaceae and South African Cyperaceae species grown hydroponically at extremely low P supply ($\leq 1 \mu\text{M}$). (a) *Dryandra sessilis* (Proteaceae) root system with 'compound' 'proteoid' root clusters. (b) *Hakea prostrata* (Proteaceae) root system with 'simple' 'proteoid' root clusters. (c) *Tetraria* species (Cyperaceae) root system with 'dauciform' root clusters. (d) Compound proteoid root cluster of *Banksia grandis* (Proteaceae, Western Australia) terminate with third-order branch rootlets. (e) Simple proteoid root cluster of *Hakea sericea* (Proteaceae, eastern Australia) terminate with second-order branch rootlets. (f) Root hairs at very high density on individual dauciform root clusters (higher magnification of *Tetraria* species in photograph (c) above). Photographic plate courtesy Michael W. Shane (School of Plant Biology, the University of Western Australia).

N_2 -fixing symbioses and cluster roots (Figure 3) have often been discussed separately [11,40,41]. Moreover, the phenomenon of P toxicity (i.e. revealed as leaf necrosis and senescence) is relatively common when P is applied to plants in Australian ancient landscapes [42], compared with the situation for plants occurring on young soils. This distribution has not yet been discussed in the ecological and evolutionary context of nutrient-acquisition strategies. There has been little appreciation that these strategies might augment each other's activities, nor has there been much evaluation of the mix of strategies that are deployed by plants able to grow and compete under a wide range of conditions, including extremely impoverished soils, such as those existing in the ancient landscapes of much of Australia and southwestern Africa (but see [43]).

Plant strategies of 'scavenging' and 'mining' broaden options for nutrient acquisition

Nutrient uptake from soil is beset by many problems, which have resulted in the evolution of many plant strategies (Box 1). The low solubility and mobility of inorganic P sources means that effective uptake usually requires 'scavenging' (see Glossary) from large soil volumes, which is achieved by rapid root growth, localized root proliferation in enriched zones, development of root hairs, or establishment of symbioses with mycorrhizal fungi. Extensive development of extraradical mycorrhizal mycelium extends the volume of soil from which plants access P (from the soil solution and readily exchangeable pools), thus overcoming depletion close to roots (Figure 2) [3].

In some plants (notably some *Lupinus* (lupin) species, some Betulaceae, Myricaceae, Casuarinaceae and most Proteaceae) development of cluster roots (Figure 3), coupled with exudation of large amounts of carboxylates, results in mobilization of sorbed P from highly P-deficient soils [11,44]. This ‘mining’ process (see Glossary) occurs locally around the root clusters, as opposed to the long-distance scavenging achieved by roots, root hairs and mycorrhizas. As outlined earlier, the different types of mycorrhizal symbioses (Figure 2) vary in the chemical forms of nutrients that they can access, with arbuscular mycorrhizal fungi able to take up predominantly inorganic P from the soil solution, whereas both ectomycorrhizas and ericoid mycorrhizas can also exploit insoluble organic forms, owing to exudation of phosphatases [25]; they might thus be both ‘miners’ and ‘scavengers’.

The potential importance of arbuscular mycorrhizal symbioses in N uptake from soluble inorganic forms is now receiving recognition, but there is no doubt that both ectomycorrhizas and ericoid mycorrhizas play key roles in delivering N from both soluble inorganic and soluble and insoluble organic sources [45]. For the fungi in these symbioses, mobilization of organic nutrients does not depend on the C:N (or C:P) ratios of the substrates, because their C source is recent photosynthate from the plant partners. Additional strategies for N uptake are adopted by insectivorous plants (e.g. sundews, Droseraceae) (probably almost as important for P acquisition as for N) [46–48] and parasitic plants [49] (e.g. mistletoes, Loranthaceae); these essentially avoid soil problems [3], as do N₂-fixing symbioses. Many species adopt more than one strategy, so that it is common to find mycorrhizas (often arbuscular mycorrhizas) in plants with N₂-fixing symbioses; a few, such as *Casuarina* (sheoak; Casuarinaceae), *Alnus* (alder; Betulaceae), *Myrica* (e.g. bayberry, sweetgale; Myricaceae) and *Viminaria* (native broom; Fabaceae), form cluster roots as well as both arbuscular mycorrhizal and N₂-fixing symbioses [50]. However, a large number of cluster-root-forming species (e.g. most Proteaceae and many Cyperaceae) do not form any type of mycorrhiza, suggesting either that the mining and scavenging strategies do not always work effectively in the same soil environments or that, for them, the cost of deploying both strategies is too expensive. The mining strategy dominates in ancient soils, where most P is sorbed to soil particles, and little P is in solution; the scavenging strategy is common in younger soils, where the P concentration in the soil solution is sufficient to support mycorrhizal symbioses.

We know of no analysis of data on C:N:P or N:P ratios (‘ecological stoichiometry’) in plants that has focused on seeking interactions among the evolutionary history of plants, their occurrence in habitats with low N and (especially) low P availability, and the occurrence of the various N- and P-acquisition strategies [51–53]. This would be a profitable area for further research.

Variation in both P sensitivity among plant species and P status of the natural habitat

Why are plants from severely P-impoorished soils very sensitive to P fertilization, showing signs of P toxicity in comparison with plants in young landscapes? When P is in

short supply, plants tend to show a compensatory response in that their maximum P-inflow capacity (I_{\max}) is increased, generally over a 2 to 15 day period [54,55]. Compensatory changes in I_{\max} for P involve synthesis of additional P-transport proteins, and an upregulation of mRNA levels coding for a high-affinity P-uptake system in root epidermis and root hairs [54,56]. The consequence of the upregulation of the plant’s nutrient-uptake system is, in general, that the concentration of the limiting nutrient at the root surface is decreased. This in turn increases the concentration gradient, and hence the rate of diffusion of the limiting nutrient from the bulk soil to the root surface [57]. However, the significance of such upregulation for plants growing in soil is, at most, very small for immobile ions such as P, when compared with that for mobile ions such as nitrate [3,9,10]. For immobile ions, it is the mobility in the soil, rather than the I_{\max} of the roots, that determines the rate at which roots can acquire this nutrient from the rhizosphere (see Glossary).

Recent work on the molecular and physiological integration of root and arbuscular mycorrhizal fungal P-uptake systems has shown that the epidermal uptake systems play a much reduced role in arbuscular mycorrhizal plants compared with plants that have not been inoculated. The root’s P-uptake function is replaced (in whole or in part) with uptake into the hyphae through fungal P-transporters. Rapid P-movement along the hyphae towards the root compensates for the slow diffusion in the soil, and is followed by transfer to the roots through arbuscular mycorrhiza-inducible P-transporters in root cortical cells [58] which are crucial for the actual operation of the arbuscular mycorrhizal uptake pathway [24]. It seems likely that upregulation of I_{\max} for P uptake at a low P-availability is not functionally important, but it has been proposed that a downregulation at higher P-supply is important in avoiding P toxicity [42,59,60].

P toxicity symptoms (P sensitivity) in plants are, generally speaking, rare but are frequently observed in species from severely nutrient-impoorished soils in ancient landscapes when plants are exposed to slightly elevated P-supply [42,60–62]. P sensitivity is associated with a very low capacity of these plants to downregulate their P-uptake capacity [42]. Given that P sensitivity occurs in several plant families [28,63], both in Australia [28,60] and in South Africa [64,65], it must have evolved several times. What might be the molecular event that led to P sensitivity, and what would be its ecological advantage?

MicroRNAs (miRNAs) are a class of single-stranded RNA molecules of ~20 nucleotides that regulate gene expression by targeting mRNAs for translational repression. Recent results have shown that P homeostasis in plants involves a role for novel functions of miRNAs in regulating adaptive responses of plants to nutrient stresses [66]. Upregulation of a specific, miR399, during P deficiency results in the downregulation of *UBC24*, a gene involved in targeted protein-degradation. Plants either overexpressing miR399 or defective in *UBC24* display P toxicity because of increased P uptake, enhanced root-to-shoot translocation, and retention of P in their old leaves; these symptoms are very similar to those found in P-sensitive species. Plants with a nonsense mutation in

UBC24 also accumulate P to toxic levels [67]. Therefore, the miR399-mediated regulation of *UBC24* expression appears to be crucial in P homeostasis. The existence and conservation of miRNAs and their target genes involved in P uptake among many plant species reveals the evolutionary importance of these miRNA-mediated nutrient-stress responses [68]. P-sensitive species from P-impooverished soils might well have evolved in a manner to exhibit the same traits as the mutants referred to above, but this has not yet been studied.

P toxicity is inevitable when P concentrations in soil solution are high and when the system responsible for P uptake is not downregulated. Considering that species showing P sensitivity are typically found growing in P-impooverished soils in old landscapes [28,59], we argue that there are likely to be selective advantages associated with this trait. Continuous expression of the gene(s) involved in P uptake from the rhizosphere might allow uptake of P that could be lost to competitors if these genes were under tight control by the internal P status. Considering the low P availability in the natural environment of these species, there would be no selective disadvantage associated with continuous expression of the genes involved in P uptake. However, the trait would restrict these species to the most P-impooverished locations in the landscape, as found for *Hakea prostrata*, which naturally occurs in such soils in Australia [59].

P sensitivity is not exclusively found in non-mycorrhizal, cluster-root-bearing species, but also occurs in mycorrhizal species without cluster roots (e.g. *Acacia* species [69]). Certainly, many types of mycorrhizas store P in the fungal component [70,71], which might protect against toxicity in the short term but ensure that the P remains available for later use. In this context, it has been widely held that the reduction in arbuscular mycorrhizal colonization that often (but not always) occurs when P supply is high is evidence for plant 'control' of the symbiosis when fungal uptake 'is not needed', thus reducing the carbon costs of maintaining the fungal symbiont [72]. Although evidence for such direct control is slight, the outcome might also help to avoid accumulation of P to toxic levels when the P is highly available. Plant species vary considerably in the extent to which P affects arbuscular mycorrhizal colonization in their roots. It might be instructive to assess the correlations between sensitivity of arbuscular mycorrhizal colonization to external P supply and the availability of P in the soils where plants of different sensitivities occur, and also to search for a possible correlation with soil age. Furthermore, little is known of the responses of the arbuscular mycorrhizal pathway of P uptake to P supply, which again would provide an interesting line for future research.

Changes in the strategy-mix from young to ancient soils

It is broadly held that mycorrhizas are relatively unimportant in disturbed (see Glossary) and N-limited soils dominated by fast-growing species (e.g. many species belonging to Brassicaceae and Chenopodiaceae), which flourish on disturbed sites and complete their life cycle rapidly; these species exhibit no special strategies other than rapid growth of roots, and formation of root hairs [40].

They persist in disturbed and nutrient-rich patches, irrespective of the age of the landscape. N₂-fixing plant species are certainly of importance in such environments, but root clusters are not [73].

Plants with the potential to form mycorrhizas occur in most ecosystems. Indeed, of the species chosen by Vitousek *et al.* [4] because they occurred at all stages of the Hawaiian chronosequence, the majority are potentially mycorrhizal, mainly arbuscular mycorrhizal; as expected, none are likely to form root clusters, and none have been reported to be highly P sensitive. At least one species belonging to the Ericaceae (heath family) is in this list, emphasizing that the strategies — in this case ericoid mycorrhizal strategies — do not restrict plants to sites with particular resources, but rather broaden their options.

As soil development proceeds and as N accumulates, arbuscular mycorrhizas continue to be important for plants subject to continually diminishing P sources. The progressive sequestration of both N and P in soil organic matter and increase in N:P ratios are associated with an increase in the number of strategies that co-exist, including arbuscular mycorrhizas, ectomycorrhizas and ericoid mycorrhizas as well as N₂-fixing symbioses of various types. In combination, these permit exploitation of the full range of N and P sources likely to be present, whether organic or inorganic, and are associated with considerable plant diversity. It is possible that mining strategies release nutrients that are then acquired through scavenging strategies by the same plant or by neighbouring plants [3], but confirmation of this requires experimental investigation. The relative costs associated with the different strategies, and hence their advantages and disadvantages in either acquiring particular resources or in escaping competition, need to be determined.

As soils become more severely weathered and leached, both N and P decline over very long geological time-scales. Depending on the mix of chemical forms, mycorrhizal and N₂-fixing strategies remain important [74], the incidence of plants with cluster roots increases [11,75], and extreme P sensitivity is relatively common [28,60,65]. The cluster-root strategy is not restricted to ancient landscapes, but also occurs in many species in North America and Europe [11], where it tends to increase in importance in either relatively acidic or calcareous soils, where P is immobilized (see Box 1).

There are thus many ecosystems where plants with all the possible N- and P-acquisition strategies co-exist. These are not in the most nutrient-deficient environments, but they are nevertheless nutrient-poor in comparison with many of the young soils typical of recently glaciated environments, such as those in Europe and North America. Little attention has been paid to ancient and highly weathered soils. Here, as shown by McArthur [76], soil P is extremely low, with total P in the range 30–40 mg kg⁻¹, but available and readily exchangeable P is much lower and often below the detection limit of 2 mg kg⁻¹. Cluster-root strategies that allow access to the strongly sorbed P pool will be highly advantageous, as shown by the predominance of members of the Proteaceae, Cyperaceae and Restionaceae families in such ecosystems. Mycorrhizal strategies are relatively less important in ancient and

highly weathered soils, presumably because arbuscular mycorrhizas are not able to change the pool of P that plants exploit; however, a few mycorrhizal plants persist together with both N₂-fixing and insectivorous species. Parasites are also common, capitalizing on the abilities of other plants to extract nutrients from the soil. The outcome is that some of the most floristically diverse ecosystems in the world occur where nutrients, particularly P, are least available [77,78]. This agrees with the recent finding by Wassen *et al.* [1] that many more endangered plant species persist under P-limited rather than under N-limited conditions, at least in a transect of varying N deposition across temperate Eurasia, where N deposition has shifted nutrient constraints on plant growth from predominantly N- to increasingly P-limitation.

Concluding remarks

The aim of this review was to explore where different nutrient-acquisition strategies of plants are predominantly found across the globe. We show that distinct patterns exist, with nutrient-acquisition strategies dependent on age of the landscape and soil nutrient status. Nutrient-mining strategies of cluster-root-bearing species typically occur in ancient landscapes and severely nutrient-impooverished soils. N-mining involves mycorrhizas, particularly ectomycorrhizas, whereas P-mining strategies require the release of large amounts of exudates from root clusters.

In addition to P-mining strategies dominating in the most P-impooverished soils, P sensitivity is a relatively common trait among species in these landscapes, particularly in Australia. Recent discoveries on the control of P uptake in higher plants offer excellent tools for making major progress in this area. Although there are no disadvantages of being P sensitive when growing in severely P-impooverished soils, possible advantages have yet to be explored. There is a great deal to learn about the evolutionary events that have allowed the occurrence of cluster roots and P sensitivity in various taxonomic groups. Both traits have evolved several times, in relation to specific soil factors, but the molecular mechanisms remain to be elucidated.

The global biodiversity hotspot in south-western Australia is characterized by plant life exhibiting a range of nutrient-acquisition strategies. These strategies do not occur randomly across the landscape, but show a distinct pattern. Nutrient status of the soil accounts for a major component of the biodiversity as explored in this review; that is, the diversity in nutrient-acquisition strategies explains a major component of the observed plant species richness.

Our global perspective of where nutrient-acquisition strategies fit in relation to soil age offers a host of challenging questions. Future studies should include a careful analysis of the functioning of species that have both cluster roots and mycorrhiza, investigating in which soils and at what P availability these strategies confer significant advantages. A molecular investigation of P sensitivity also provides a major challenge, because it requires an integration of evolutionary and physiological analyses.

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