INVITED REVIEW: PART OF A SPECIAL ISSUE ON ROOT BIOLOGY

Phosphorus-mobilization ecosystem engineering: the roles of cluster roots and carboxylate exudation in young P-limited ecosystems

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Received: 2 March 2012 Returned for revision: 25 April 2012 Accepted: 17 May 2012 Published electronically: 13 June 2012

• Background Carboxylate-releasing cluster roots of Proteaceae play a key role in acquiring phosphorus (P) from ancient nutrient-impoverished soils in Australia. However, cluster roots are also found in Proteaceae on young, P-rich soils in Chile where they allow P acquisition from soils that strongly sorb P.

• Scope Unlike Proteaceae in Australia that tend to proficiently remobilize P from senescent leaves, Chilean Proteaceae produce leaf litter rich in P. Consequently, they may act as ecosystem engineers, providing P for plants without specialized roots to access sorbed P. We propose a similar ecosystem-engineering role for species that release large amounts of carboxylates in other relatively young, strongly P-sorbing substrates, e.g. young acidic volcanic deposits and calcareous dunes. Many of these species also fix atmospheric nitrogen and release nutrient-rich litter, but their role as ecosystem engineers is commonly ascribed only to their diazotrophic nature.

• Conclusions We propose that the P-mobilizing capacity of Proteaceae on young soils, which contain an abundance of P, but where P is poorly available, in combination with inefficient nutrient remobilization from senescing leaves allows these species to function as ecosystem engineers. We suggest that diazotrophic species that colonize young soils with strong P-sorption potential should be considered for their positive effect on P availability, as well as their widely accepted role in nitrogen fixation. Their P-mobilizing activity possibly also enhances their nitrogen-fixing capacity. These diazotrophic species may therefore facilitate the establishment and growth of species with less-efficient P-uptake strategies on more-developed soils with low P availability through similar mechanisms. We argue that the significance of cluster roots and high carboxylate exudation in the development of young ecosystems is probably far more important than has been envisaged thus far.

Key words: Actinorhizal species, carboxylates, cluster roots, phosphorus nutrition, Cyperaceae, ecosystem engineering, facilitation, Lupinus, Proteaceae.

INTRODUCTION

In a recent review on nutrient-acquisition strategies in a global context, with a focus on phosphorus (P), it was highlighted that the non-mycorrhizal ‘P-mining’ strategy of species with carboxylate-releasing cluster roots (especially Proteaceae species; see Appendix for glossary of terms used in this paper) is particularly successful on the world’s most ancient soils, where P is a key limiting nutrient (Lambers et al., 2008b). The strategy is based on the release of large amounts of carboxylates (organic anions) into a small volume of soil, where their high concentration allows them to strongly compete for binding sites, thus moving P into solution.

P limitation in ancient soils is primarily caused by P depletion due to prolonged weathering (Walker and Syers, 1976). However, P limitation is not restricted to ancient soils and can arise through different mechanisms in younger soils (Vitousek et al., 2010), such as: (a) low P availability relative to that of other nutrients, (b) low-P parent material, (c) inorganic (i.e. sorption) or biological (i.e. P immobilization in biomass or humus) P sinks, and (d) human-driven increases in other nutrients, particularly N (Wassen et al., 2005). The P-mining strategy of species with carboxylate-releasing cluster roots is very successful on the world’s most ancient, P-impoverished soils (Lambers et al., 2008b). However, cluster roots also occur in many species in the Americas and Europe (Skene, 1998; Lambers et al., 2006). In these younger landscapes in which P is not depleted through prolonged weathering, cluster- and dauciform-rooted species tend to increase in importance in either acidic (Crocker and Schwintzer, 1993; Skene et al., 2000) or calcareous soils (Oremus and Otten, 1981; Bakker et al., 2005), where P is immobilized by oxides of iron (Fe) and aluminium (Al), or by calcium (Ca), respectively. We explore this in more detail at the end of this review, under ‘Ecosystem engineering through P mobilization in other young landscapes’.

This review aims to explore the role of cluster-rooted species, and others that release large amounts of carboxylates, in P cycling in young soils with high total P but low P availability. First, we focus on the poorly studied cluster-rooted species of the Proteaceae family found in Chile and western...
Argentina, where they grow on comparatively young soils rich in P, but with poor P availability (Beinroth et al., 1985; Borie and Rubio, 2003). As a means of understanding the physiological and ecological function of these species and their cluster roots, we compare them with the relatively well-studied Proteaceae found on the ancient, P-impoverished soils of south-western Australia. Our analysis of Patagonian Proteaceae then prompts us to explore the role of species outside the Proteaceae from genera known to form cluster roots and/or expected to release large amounts of carboxylates in young, poorly developed soils, to propose a more general role for these species in ecosystem engineering and facilitation. In contrast to the Proteaceae, most other species with these traits also form symbiotic associations with N-fixing bacteria (Skene, 1998), potentially coupling N and P cycling at the individual plant level in a manner not previously appreciated. Many of the examples we present are incomplete; our intention is therefore to identify current gaps in our knowledge of the function and ecological consequences of these P-mobilizing functional traits, and highlight areas in need of further investigation.

Clusters roots are only one of many traits that characterize species that evolved in old, climatically buffered, infertile landscapes (OCBILs, *sensu* Hopper, 2009). The great age and relative stability of OCBILs has led to highly specialized adaptations to nutrient-impoverished soils, which contrast with those of species in younger, P-rich landscapes. In this review, we therefore aim to explore pertinent traits in a single family (Proteaceae) with many representatives in two vastly contrasting landscapes (south-western Australia and Chile) that are united by low P-availability, but where P limitation is driven by completely different mechanisms. We include as many traits that are relevant for the present comparison of OCBIL (P-impoverished) vs. young, potentially fertile (P-rich, but with low P availability) landscapes as we can find sufficient data for, highlighting major gaps in our present knowledge. A striking result of our survey is the notable lack of nutrient-conservation strategies in the Proteaceae of young landscapes, e.g. a low nutrient-resorption efficiency and proficiency. Consequently, Proteaceae in these young landscapes may play a key role in P cycling, converting poorly available forms of P (sorbed P) to more readily available forms (organic P). Our survey leads us to explore further the role of carboxylate-exuding cluster roots in combination with a very low P-resorption efficiency from senescing leaves in P cycling in young, P-rich soils with strong P-sorption potential. We refer to this process as ‘P-mobilization ecosystem engineering’.

**PROTEACEAE IN AUSTRALIA AND CHILE**

Australia and South America were once part of Gondwana (Fig. 1). About 180 million years ago, this ancient continent started to break up, and the geological fate of south-western Australia and Chile turned out to be vastly different (McLoughlin, 2001; Veevers, 2004; Ali and Aitchison, 2008). Prolonged weathering in the absence of major soil rejuvenating processes led to severe nutrient impoverishment in south-western Australia (Beadle, 1962). Therefore, the flora evolved on highly infertile soils (Hopper and Gioia, 2004). On the other hand, orogenic uplift, volcanic activity, earthquakes, landslides, glaciation and associated landscape rejuvenation characterize Chile (Tralli et al., 2005). As a result, leaf P concentrations are considerably higher in plants in Chile compared with those in south-western Australia (Lambers et al., 2011). Obviously, plant species were subjected to significantly different evolutionary forces in these contrasting landscapes. Nonetheless, cluster-rooted Proteaceae occur in both Chile and south-western Australia.

The Proteaceae are a plant family of ancient Gondwanan origins, and their common ancestor is estimated to be 118-5 million years old (Weston et al., 2007; Fig. 2). Ancestors of extant new-world species were either isolated in South America by continental drift when the Gondwanan continent broke up (Fig. 1; e.g. *Embothrium*, *Gevuina*, *Lomatia*, *Orites*) or arrived via long-distance, transoceanic dispersal (e.g. *Panopsis*) (Barker et al., 2007).

In a recent review, the mineral nutrition and growth strategies of a wide range of species in the OCBILs within southwest Australia and South Africa were compared with those elsewhere in the world (Lambers et al., 2010). Here we first explore information on a single Gondwanan family (Proteaceae) in the two contrasting landscapes of south-western Australia and Chile. South-western Australia is dominated by typical OCBILs where hundreds of Proteaceae species are found, generally on the most nutrient-impoverished soils (Pate et al., 2001; Lambers et al., 2010). Southern and central Chile, on the other hand, is covered in relatively young soils; it is home to six Proteaceae species. In Chile, Proteaceae are commonly found on P-rich volcanically derived soils, but with an abundance of Al and Fe and a low pH (4.7–5.2) (Borie and Rubio, 2003; Redel et al., 2008), rendering P poorly available for most plants (Fig. 3). Chilean Proteaceae can also be found colonizing recently formed glacial moraines, whose soils have yet to be characterized. Some Chilean Proteaceae (*Orites myroidea* and *Embothrium coccineum*) also grow on rocky young soils and volcanic material.

We suggest that the biochemical and physiological mechanisms of cluster roots in Australia and Chile are similar, but that their ecological role in P cycling is fundamentally different. In Australia, cluster roots of Proteaceae and other families allow efficient P uptake on extremely P-impoverished soils; the acquired P is used very efficiently and tightly recycled (Denton et al., 2007). Conversely, in Chile, cluster-rooted Proteaceae tap into a very large (but not readily available) pool of P, do not recycle P efficiently, and therefore are likely to release large quantities of P in litter (a much more readily available P pool) (Diehl et al., 2003). This conversion of a poorly available P pool into a more readily available P pool is a clear form of ecosystem engineering. Based on a review of data in the literature, we propose a similar ecosystem-engineering role for species with cluster roots and others with a potentially high capacity to release carboxylates (organic anions) from their roots in young, poorly developed soils. Where P is strongly sorbed, due to high or low pH during the early stages of primary succession, e.g. on calcareous mobile dunes, acidic lava flows, and glacial moraines, we propose that these species play a vital role in P cycling, converting sorbed P to more readily available forms.
MINERAL NUTRITION

Proteoid or cluster roots and mycorrhizal status

The root systems of species that form cluster roots have a unique capacity for altered branch-root development. Large numbers of branch roots ('rootlets') are initiated and compacted into specific regions along the axes of growing lateral roots (Shane and Lambers, 2005). Cluster-root development represents the epitome of many common root traits that are effective in enhancing the acquisition of nutrients that are often poorly available, especially mineral-bound inorganic or organic P (Lambers et al., 2002, 2006).

Most Proteaceae species in the Southwest Australian Floristic Region (SWAFR, sensu Hopper and Gioia, 2004) produce cluster roots; the only exception being Persoonia (Lamont, 1982). Almost all are non-mycorrhizal, but there are exceptions, e.g. Hakea verrucosa, which grows on ultramafic soils that contain high concentrations of nickel (Boulet and Lambers, 2005). Mycorrhizal species in typically non-mycorrhizal families have been found more often on soils that are rich in nickel, e.g. serpentine soils (Lambers et al., 2009; Lagrange et al., 2011). Presumably, the release of carboxylates and associated protons enhances the availability of nickel (Ni); this heavy metal is highly inhibitory to root growth, including the growth of cluster roots of Hakea verrucosa (F. Boulet & H. Lambers, pers. obs.). In that case, the mycorrhizal strategy would confer greater fitness, not by enhancing P uptake, but by preventing Ni toxicity. This suggests there are trade-offs in the strategy of large carboxylate release.

In the SWAFR with a Mediterranean climate, cluster roots are produced in the wet season (winter) only, predominantly very close to the soil surface, in the litter layer or just below the ash of a recent fire (Lamont, 2003; Shane and Lambers, 2005). This is a response to the higher levels of P in the top layer and litter, as demonstrated for the crop species Lupinus albus (Li et al., 2010).

Six Proteaceae species naturally occur in Chile: Embothrium coccineum, Gruviua avellana, Lomatia dentata, L. ferruginea, L. hirsuta and Orites myrtoides (Zapata, 1981). Embothrium coccineum, Lomatia ferruginea and Lomatia hirsuta have been described as non-mycorrhizal (Godoy et al., 1994; Fontenla et al., 1998). Cluster roots have been described for Gruviua avellana (Ramirez et al., 2004); its rootlets on mature clusters are characterized by a ‘claviform’ structure (Figs 4 and 5) whose functional significance is unknown. Embothrium coccineum produces cluster roots (Fig. 6D) that strongly acidify their rhizosphere (Zúñiga-Feest et al., 2010) and release citrate and malate (E. Pen˜aloza, Instituto de Investigaciones Agropecuarias, Temuco, Chile, pers. comm.). All Chilean Lomatia species produce cluster roots (Fig. 6D), as does Orites myrtoides. Distinctly different from the situation in SWAFR, cluster roots are predominantly found deeper in the soil profile, but rarely in the litter layer (Fig. 5); very few cluster roots appear intermingled with the roots of neighbouring plants, and interspecific root interaction appears to suppress cluster-root formation (Donoso-Nanculao et al., 2010). If substantiated, these observations imply that unlike examples for cluster-rooted white lupin, which makes P and manganese available to neighbouring plants when their roots intermingle (Gardner and Boundy, 1983; Horst and Waschkies, 1987; Cu et al., 2005), P ‘mined’ by Chilean Proteaceae would be made available to neighbouring species only indirectly, through the release of P-rich litter.

Leaf P concentrations

Leaves of many SWAFR Proteaceae species are characterized by very low leaf P concentrations ([P]) (Wright et al., 2005; Denton et al., 2007) and by both efficient and proficient P resorption (sensu Killingbeck, 1996) from senescent leaves (Denton et al., 2007). In contrast, in a study of Andean–Patagonian species, including Lomatia hirsuta (Diehl et al., 2003, 2008), senesced leaves of all investigated species exhibited a higher [P] than the green leaves of Banksia species in SWAFR studied by Denton et al. (2007), indicating comparatively poor P resorption proficiency.

Based on currently available, albeit limited, information (Table 1), we conclude that leaf [P] in Proteaceae species in the SWAFR are much lower than those in Chilean species. Phosphorus resorption is considerably more efficient and proficient in SWAFR Proteaceae than in Chilean ones (Table 1). The total P concentration in young Chilean volcanic soils...
Fig. 2. Chronogram of divergences in the Proteaceae, as determined using four internal calibration points (marked by numbered black diamonds) set as minimal ages and the mean prior age of the root set to 93 million years ago (Myr) (± 37 Myr). Numbers above the branches are maximum-likelihood bootstrap values; numbers below the branches represent Bayesian clade credibility values (values >0.85 are shown). Nodes marked with circles correspond to transoceanic disjunctions for which estimated ages of lineage diversification pre-date continental break-up. Nodes marked with squares correspond to transoceanic disjunctions that post-date continental break-up and thus infer long-distance dispersal. Genera listed in bold occur in south-western Australia or Chile; blue (not bold) refers to exclusively Australian; blue (bold) refers to exclusively south-western Australian; red refers to exclusively Chilean; green refers to both Chilean and Australian (but not south-western Australian). Shaded horizontal bars indicate standard deviation estimates of key nodes. Key tectonic events are indicated below the time line. Key to Tertiary epochs: Pa, Palaeocene; Eo, Eocene; Ol, Oligocene; Mi, Miocene; Pl, Pliocene. Modified with permission of the senior author (Barker et al., 2007).
may be high, but their ‘readily available’ P concentrations are relatively low (Pinochet et al., 2001; Borie and Rubio, 2003). However, the cluster roots of Proteaceae should allow abundant acquisition of ‘unavailable’ P, and hence efficient and proficient resorption of P from senescent leaves may not be strongly selected for in the Chilean environment.

Leaf and leaf litter N : P ratios

N : P ratios of leaves of SWAFR species in general are very high compared with those in Chile (Lambers et al., 2010), reflecting the P-impoverished soils of SWAFR. Comparing N : P ratios of leaves of SWAFR Proteaceae with those of Lomatia hirsuta and Embothrium coccineum (the only species for which data are available) from Patagonia shows a similar difference (Table 1). Due to highly proficient resorption of P from senescent leaves in many SWAFR Proteaceae (Denton et al., 2007), the N : P ratio is higher for leaf litter than for green leaves. However, N resorption in SWAFR Proteaceae is low, decreasing from 8.7 mg g⁻¹ dry mass (DM) in green leaves to 6.1 mg g⁻¹ DM in leaf litter (A. Boonman and E. J. Veneklaas, University of Western Australia, pers. comm.). In contrast, Proteaceae in Patagonia resorb very little N or P (Diehl et al., 2003, 2008). This difference in resorption between the two geographic regions, driven by differences in the scarcity of total P, combined with a major difference in leaf mass per unit area (LMA) (Table 1), should impact on the cycling of nutrients in the two systems.

Phosphate sensitivity

When fertilized with a readily available source of P, leaf [P] can become very high in many SWAFR Proteaceae, sometimes reaching toxic levels (Handreck, 1991; Lambers et al., 2002; Shane et al., 2004b). The same holds for South African Proteaceae (Hawkins et al., 2008; Shane et al., 2008). This is accounted for by the low capacity of these species to down-regulate their P uptake (Shane et al., 2004c; Shane and Lambers, 2006). The down-regulation of the expression of P transporters is ecologically significant to avoid P toxicity, whereas their up-regulation at low P would do little to acquire more P when soil properties, rather than kinetic properties of root P transporters, are major rate-limiting steps to P uptake (Lambers et al., 2006).

There is no evidence for P sensitivity in Chilean Proteaceae. Embothrium coccineum does not show any signs of P toxicity when grown in sand and watered with a nutrient solution containing 1 mM P, which would readily kill any P-sensitive Australian Proteaceae. Similarly, hydroponic cultures of Orites myrtoidea and Embothrium coccineum produce healthy plants at P concentration of 250 μM after 3 months in a growth chamber (Ochoa, 2010). The lack of P toxicity in Chilean Proteaceae explains why they can persist in soils with high total P, whereas many SWAFR Proteaceae cannot.

Leaf gas exchange

Rates of photosynthesis per unit leaf area of SWAFR species in general are relatively high compared with those in the rest of the world (Lambers et al., 2010). Comparing photosynthesis of SWAFR Proteaceae with those from Chile shows a similar but far less pronounced difference (Table 1).

Rates of photosynthesis per unit leaf P (PPUE) are exceptionally high for SWAFR Banksia species (Denton et al., 2007); there are no data on PPUE in the literature for Chilean species, but given the information on leaf [P] and gas exchange in Table 1, PPUE is expected to be quite low in Chilean Proteaceae. This is confirmed by recent data on Embothrium coccineum (A. Zúñiga-Feest, unpubl. res.) (Table 1). Rates of photosynthesis per unit leaf N are somewhat lower for SWAFR Proteaceae compared with the ones
in Chile (Table 1). The low PNUE reflects a high investment in Rubisco and other photosynthetic enzymes, which represent a major component of all organic N in C3 leaves (Evans, 1989). This might allow a higher water-use efficiency or allow the Calvin cycle to operate at lower levels of phosphorylated intermediates (thus potentially increasing PPUE), but this apparent trade-off between PNUE and PPUE remains to be explored further (Lambers et al., 2011).

Values for LMA of SWAFR species are exceptionally high compared with those from the rest of the world (Lambers et al., 2010). A similar difference is found when comparing Proteaceae from south-western Australia and Chile (Table 1). The high LMA of SWAFR Proteaceae is partly accounted for by their thickness, up to 700 µm for some SWAFR Banksia species (Hassiotou et al., 2009a). Leaves of Chilean

**FIG. 4.** Cluster roots of *Gevuina avellana* grown in a glasshouse of Universidad Austral de Chile, Valdivia, Chile. (A) Entire sapling removed from the pot in which it was grown, with some of the soil removed. (B) Two immature clusters of different developmental stages, showing ‘normal’ root tips. (C) Mature cluster rootlets showing the ‘claviform’ shape, whose function is unknown. Photographs: Marion Cambridge.
Proteaceae tend to be thinner, 400–500 μm (Torres, 1998). Given the very large difference in LMA when compared with that in leaf thickness, most of the difference in LMA between SWAFR and Chilean Proteaceae must be accounted for by the very high amount of dry mass per unit leaf volume of the leaves of SWAFR Proteaceae (Lambers et al., 2011). Therefore, one would expect leaf lifespan to be greater in SWAFR Proteaceae. Whilst that is the case when looking at average values (Table 1), it should be noted that the range for Chilean species is very large: a lifespan of 7 months only for Embothrium coccineum, with the thinnest leaves, and as long as 64 months for Gevuina avellana, with thicker leaves (Lusk and Corcuera, 2011). This variation in leaf lifespan reflects contrasting ecological strategies that will have equally contrasting effects on ecosystem function, e.g. litter decomposition (Garnier et al., 2004; Laliberté and Tylianakis, 2012).

Leaf anatomy and morphology

Sunken stomata are common though not universal in SWAFR Proteaceae (Jordan et al., 2008; Hassiotou et al., 2009a; Groom and Lamont, 2010). Stomata in Chilean Proteaceae are invariably at the leaf surface (Torres, 1998). In the Australian genus Banksia, the depth of stomatal crypts increases with increasing leaf thickness (Hassiotou et al., 2009a) and the role of the crypts is supposedly in facilitating diffusion of CO₂ to the mesophyll cells, rather than in enhancing water-use efficiency (Hassiotou et al., 2009b; Roth-Nebelsick et al., 2009). Given that leaves of Chilean Proteaceae are thinner, there may not be a need for sunken stomata to allow rapid gas exchange. As argued by Hassiotou et al. (2009b) and Roth-Nebelsick et al. (2009), sunken stomata are an integral part of thick, structurally defended leaves. Such leaves, with a high LMA, are part of the growth strategy in OCBILs; they decompose very slowly, so nutrients are released predominantly during a fire.

The contrasting role of cluster roots in P cycling in OCBILs and young soils

In young soils, N is widely thought to be the nutrient most limiting to plant growth, based on a long history of nutrient-addition experiments, and because parent material is generally devoid of N (Walker and Syers, 1976; Vitousek and Howarth, 1991; Lambers et al., 2008b). Symbiotic N₂ fixation allows a build-up of soil N in young soils as they develop. However, it is becoming increasingly clear that P limitation or N/P co-limitation of terrestrial primary production is widespread, even in young ecosystems (Wassen et al., 2005; Elser et al., 2007; Harpole et al., 2011). While the role of long-term depletion of P in OCBILs and other old ecosystems is well recognized, P limitation in young ecosystems may also result from a variety of other mechanisms (Vitousek et al., 2010). In particular, P can be limiting if it is strongly bound in complexes with aluminium, iron,
calcium or allophane clay, as occurs when pH is either relatively high or low (Fig. 3), and thus P is poorly soluble even if total amounts of P in the soil are high. The strategy to release large amounts of carboxylates in an exudative burst from cluster roots (Watt and Evans, 1999b; Shane and Lambers, 2005) is particularly effective at mobilizing sorbed P (Fox et al., 1990; Geelhoed et al., 1998). We therefore expect an advantage for species that exude carboxylates, usually in association with cluster roots, cluster-like roots or dauciform roots, relative to P-scavenging, mycorrhizal species (Lambers et al., 2006, 2008b) in this context.

The key question we address next is: what is the role of cluster roots in young landscapes where Proteaceae frequently occur on P-rich volcanic soils? To answer this question requires a further analysis of young volcanic soils in southern South America (Borie and Rubio, 2003; Satti et al., 2007). Phosphorus concentrations in newly deposited volcanic materials in this region ranges over an order of magnitude, depending on the type of magma (from 350 mg P kg⁻¹ in rhyolite up to 3300 mg P kg⁻¹ in basalt) (Ruggieri et al., 2011). These materials are deposited over an extreme precipitation gradient, ranging from >6000 mm on parts of the coast range on Chiloé Island to 300 mm in shrublands east of the cordillera (Austin and Sala, 2002). Dissolution of P is rapid in rhyolitic and dacitic deposits (Dahlgren et al., 2004), such as those from recent eruptions of Chaiten and Puyehue Cordon-Caulle volcanoes, and high precipitation may cause rapid depletion of readily available P (Nanzyo et al., 1997). In basaltic and andesitic materials, dissolution is slower, but low pH and high levels of activated Al and Fe cause high retention of P and relatively rapid occlusion in Al–humus complexes, where it is unavailable to most plants (Beinroth et al., 1985; Satti et al., 2007). Soil ‘Olsen-P’ concentrations (a measure of P availability) of young volcanic soils on the drier Argentinean side of the Andes (39–41°S) ranges from 2–12 mg P kg⁻¹ soil (Satti et al., 2007). While these values are low, more coastal populations of *Embothrium coccineum* in the vicinity of Chiloé, Temuco and Puerto Montt (38–43°S), where volcanic ash deposition is much less frequent, are generally on soils with even lower Olsen-P, often less than 1 mg P kg⁻¹ (Souto et al., 2009).

*Embothrium coccineum* is a frequent colonist on young deposits of Patagonian volcanoes, and also commonly colonizes glacial moraines, clearcuts, roadsides, agricultural margins, and other disturbed areas across a latitudinal span of 20°, where it often grows on soils with low P availability (median Olsen-P from 25 populations was 1.8 mg P kg⁻¹; >25 % of all populations were growing on soils with Olsen-P <1.0 mg P kg⁻¹) (Souto et al., 2009). The ‘mining’ strategy of the cluster roots of *Embothrium coccineum* (Lambers et al., 2008b), however, may allow access to the fraction of P that is largely unavailable for most other plants. In this context it is noteworthy that cluster roots in Chile penetrate deep into the soil profile (Fig. 5) and thus avoid roots...
TABLE 1. Characteristics of mature and senesced leaves of Proteaceae in south-western Australia and in Patagonia (Argentina or Chile)

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<thead>
<tr>
<th>Characteristics</th>
<th>South-western Australia</th>
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<td>Chile</td>
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<td>References</td>
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<td>Mature leaf [P] (mg g⁻¹ D.M.)</td>
<td>250 ± 1</td>
<td>Wright et al., 2004; Denton et al., 2004; Mitchell et al., 2008</td>
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<tr>
<td>Senesced leaf [P] (mg g⁻¹ D.M.)</td>
<td>5.2 ± 0.2</td>
<td>Wright et al., 2004; Mitchell et al., 2008</td>
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<tr>
<td>Mature leaf [N] (mg g⁻¹ D.M.)</td>
<td>1.2 ± 0.1</td>
<td>Wright et al., 2004; Mitchell et al., 2008</td>
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<tr>
<td>Senesced leaf [N] (mg g⁻¹ D.M.)</td>
<td>0.9 ± 0.1</td>
<td>Wright et al., 2004; Mitchell et al., 2008</td>
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<tr>
<td>Rate of photosynthesis (µmol CO₂ g⁻¹ Nₙs⁻¹)</td>
<td>8.4 ± 0.6</td>
<td>Wright et al., 2004</td>
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<tr>
<td>PPUE (µmol CO₂ g⁻¹ Nₙs⁻¹)</td>
<td>8.9 ± 2.1</td>
<td>Wright et al., 2004; Mitchell et al., 2008</td>
</tr>
<tr>
<td>PNUE (µmol CO₂ g⁻¹ Nₙs⁻¹)</td>
<td>337 ± 14</td>
<td>Wright et al., 2004; Mitchell et al., 2008</td>
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All data are based on plants grown in their natural habitat. Note that all data (Piper and A. Zúñiga-Feest, unpubl. res.) are for Embothrium coccineum (from Argentina) only, whereas the data used in Wright et al. (2004) for Lambers et al. — Phosphorus-mobilization ecosystem engineering 337

of neighbours. Cluster-root formation by Embothrium coccineum is relatively high on very young volcanic deposits, where cluster roots make up >50% of seedling biomass (F. Piper and A. Zúñiga-Feest, unpubl. res.). While its green leaf and senescent leaf [P] and [N] are not exceptionally high compared with other rainforest trees (Lusk and Contreras, 1999; Diehl et al., 2008), we infer that Embothrium coccineum accelerates cycling of both nutrients. However, this requires further experimental testing. In a comparison of 11 rainforest trees, Embothrium coccineum had the highest foliage P pool among seven shade-intolerant species, and much higher annual litter N deposition than the other species, owing to its short leaf lifespan (Lusk and Contreras, 1999; Lusk and Corcuera, 2011). Given that the leaf P resorption of Embothrium coccineum is also low (Table 1), its short leaf lifespan is likely to lead to substantial contributions to P in litter. Thus, we hypothesize that P mobilized by cluster roots of Proteaceae from the poorly available fraction low in the profile in Chilean soils is made available, through decomposition of low-LMA leaf litter, for plants lacking similar root specializations, and available N is also increased, though its ultimate source is as yet unknown. This implies that some Patagonian Proteaceae act as ecosystem engineers during early succession by increasing the pool of available P and its rate of cycling (Figs 7 and 8). Although symbiotic N₂ fixation is heralded as a classic case of ecosystem engineering and a key mechanism of facilitation in early primary succession (Van Breemen and Finzi, 1998; Walker and del Moral, 2003), facilitation by cluster-rooted species is likely to involve improved P nutrition.

The potential for other Chilean Proteaceae to play a similar ecosystem-engineering role is less clear (Diehl et al., 2008). Lomatia ferruginea and Gevuina avellana are often later colonists on the same soil types as Embothrium coccineum, with the order of colonization reflecting higher shade tolerance and lower dispersal ability of Gevuina avellana. Orites myrtoidae colonizes andesitic and dacitic lava flows and outcrops in central Chile that are nearly devoid of soil (Pfanzelt et al., 2008); its cluster roots may be critical to P nutrition and may increase P availability to other colonists. Lomatia hirsuta is also a common colonist of drier forests and shrublands on volcanic soils that are disturbed by burning and grazing. It resprouts after fire and is unpalatable to introduced herbivores. Its leaves are poor in P and rich in lignin, relative to other species in these communities, and hence it may not strongly accelerate P cycling (Satti et al., 2003; Diehl et al., 2008). However, with its low resorption proficiency, its senescent leaves are even richer in N (>10 mg g⁻¹ dry weight) than those of Embothrium coccineum and, unlike other tree species in these communities, it appears not to be N limited (Diehl et al., 2008). The surprising role of Chilean Proteaceae in N cycling and its relationship to their mode of P nutrition is worth further investigation. Embothrium coccineum frequently co-occurs with N₂-fixing Gunnera spp. and cyanolichens (J. G. Bishop, unpubl. res.), providing the potential for mutualistic interactions via N and P exchange.

The height of the vegetation where Proteaceae are found in Chile is approximately ten times greater than that where Proteaceae dominate in south-western Australia: typically 3–30 m or more in Chile (Huber and Iroumé, 2001; Pujana,
ECOSYSTEM ENGINEERING AND FACILITATION THROUGH P MOBILIZATION IN OTHER YOUNG LANDSCAPES

Proteaceae are restricted to the southern hemisphere, and hence cannot be expected to play a role in ecosystem engineering in young ecosystems in the northern hemisphere. However, are there functionally equivalent species that may play a similar role there? Few convincing demonstrations have yet to be described; to stimulate further investigation, here we identify several systems in which P-mobilization might be especially likely or advantageous.

Does carboxylate exudation play a role in ecosystem engineering on Mount St Helens?

Primary succession following the unusual lateral eruption of Mount St Helens, Washington, USA, in 1980 has been monitored in detail (Wood and del Moral, 1988; del Moral and Lacher, 2005; Marleau et al., 2011; del Moral et al., 2012). Primary surfaces were rapidly colonized by Lupinus lepidus within the first two years after the eruption (del Moral et al., 1995). On the infertile pyroclastic flows, with an acidic pH of 4.3–6.4 (del Moral and Clamptt, 1985; Halvorson et al., 2005), Lupinus lepidus formed localized monospecific patches with high population growth rates and densities (Bishop, 2002) and has acted as a facilitator for many subsequently invading species, although the interactions can be complex (Morris and Wood, 1989). The nitrogen-fixing capacity of this legume has received ample attention (Halvorson et al., 1992; del Moral and Rozzell, 2005; del Moral, 2009), and it is also acknowledged that, as a result of its presence, chemical weathering is enhanced in soils occupying the ‘islands of soil fertility’ in the vicinity of the individual lupin plants (Ugolini and Dahlgren, 2002; Dahlgren et al., 2004). However, the possibility that Lupinus lepidus might also enhance the availability of P in the acidic pyroclastic substrate (Fig. 3) through the release of carboxylates has largely been ignored. While many old-world lupins produce cluster roots, new-world lupin species such as Lupinus lepidus, do not (Clements et al., 1993; Skene, 2000; Lambers et al., 2003). However, Lupinus species without specialized cluster-root structures may also release relatively large amounts of P-mobilizing carboxylates, as is common in Lupinus angustifolius and L. sericeus (Weir et al., 2006; Pearse et al., 2007), or they may make cluster-like roots, as in Lupinus luteus and L. mutabilis (Hocking and Jeffery, 2004). These traits are common in a wide range of lupin species that are superior at accessing sorbed P (Bolland et al., 1999; Pearse et al., 2006). Indeed, Lupinus lepidus does produce zones of enhanced lateral root development under P-deficient conditions that acidify surrounding soil to an extent similar to that in other lupins (N. J. Frein and J. G. Bishop, unpubl. res.). ‘Plant-available’ P, as determined by the Mehlich III method, increased by approx. 45 % under dead Lupinus lepidus (Halvorson and Smith, 2009). We suggest that the significance of Lupinus lepidus as an ecosystem engineer is not only that it builds up soil organic matter and N, but also that it enhances the availability of P. Enhanced P availability may directly facilitate subsequently invading pioneer species, and also indirectly facilitate them through increasing the rate of N2 fixation (Bishop et al., 2010), which is often P limited (Houlton et al., 2008; Vitousek et al., 2010). Alnus viridis and A. rubra, woody pioneers on Mount St Helens (del Moral and Grishin, 1999; Titus, 2009), might play a similar role, given that Alnus species are also known to produce cluster roots (Hurd and Schwintzer, 1996), as do many other actinorhizal species (Skene, 1998; Lambers et al., 2006).

Could carboxylate exudation play a role in ecosystem engineering on other nutrient-poor volcanic soils?

Lupinus spp. and Alnus spp. are common colonists in many other nutrient-poor, early-successional volcanic systems. On lava flows on Miyakejima, Japan, Alnus sieboldiana is an important pioneer species (Hiroki and Ichino, 1993). Lupinus angustifolius, a species that exudes large amounts of carboxylates (Pearse et al., 2007), which enhance P availability (Lopez-Hernandez et al., 1979; Gerke et al., 2000), has been one of the dominant species on 60-year-old ash deposits on Santorini, Greece for at least 30 years (Dimopoulos et al., 2010). Lupinus smithianus plays a prominent role in early succession of high-altitude Andean vegetation on lahars of Volcán Cotopaxi, Ecuador, and Lupinus microphyllus on older lahars (Sklenář et al., 2010). Lupinus nootkatensis has been widely planted to facilitate forest re-establishment on severely eroded, bare, low available-P (Olsen-P < 0-9 mg P kg–1) volcanic soils in Iceland (Magnusson et al., 2004; Oskarsson and Sigurjónsson, 2004). It is also a prominent colonist on the 2008 eruptive materials of Kasatochi Island, Alaska (Talbot et al., 2010), and at non-volcanic restoration sites in Sweden is known to facilitate birch and double available P (Myrold and Huss-Danell, 2003). Most authors would readily suggest a link with the N2-fixation abilities of these species, because of the generally N-limited habitat in which volcanic primary succession takes place (Vitousek et al., 1987; Scherer-Lorenzen et al., 2007) and, in many cases, dramatic increases in soil N have indeed been documented. However, there may well be an additional explanation for the presence of these species during early-successional stages, if other Alnus and Lupinus species have the ability to release large amounts of carboxylates and make sorbed P available (Lambers et al.,
2006); this seems particularly likely since N$_2$ fixation requires relatively large amounts of P (Vitousek et al., 2010). This possibility warrants further investigation.

**Is there a role for carboxylate exudation in ecosystem engineering on other nutrient-poor young soils?**

Within California coastal prairie, invasion and alternative vegetation states are facilitated by a native N$_2$-fixing shrub, *Lupinus arboreus* (Maron and Connors, 1996; Maron and Jefferies, 1999). *Lupinus arboreus* can fix significant amounts of N$_2$ on a variety of acidic, P-poor soils, ranging from dunes to mine wastes (Davis, 1991; Maron and Jefferies, 1999; Gosling, 2005). However, it does not produce cluster roots (Skene and James, 2000); no information is available on its rate of carboxylate exudation, but, like *Lupinus polyphyllus*, it performs much better at lower P supply, and achieves higher foliar [P], than a range of other temperate legumes (Davis, 1991; Scott, 2001, 2007). Another lupin species, *Lupinus chamissonis*, plays a role as ecosystem engineer on coastal dunes in northern California (Cushman et al., 2010). Whilst the authors rightly stress the role of these lupins in building up soil N, they might also be important in rendering soil P more available, given the acidic nature of the dune soils (pH 4.9–5.6; Jaffee et al., 1996) and the high P concentrations in leaf litter (Diehl et al., 2003). For further explanations, see text. Photographs: (A) Etienne Laliberté; (B–F) Marion Cambridge.
bushes, occupied by herbaceous vegetation. Litter inputs beneath *Lupinus arboreus* are more than two and a half times higher in terms of P than in areas between bushes, accounting for the higher soil P concentration. A glasshouse trial showed that in the absence of N and P fertilizer, *Urtica dioica* grows poorly on soil collected from areas between bushes of *Lupinus arboreus*, while its growth on soil from beneath *Lupinus arboreus* is more than four times higher.

Amendment of the soil collected under *Lupinus arboreus* with N significantly increases growth of *Urtica dioica*, but amendment with P does not. This clearly indicates that the growth of *Urtica dioica* on soil under *Lupinus arboreus* is not limited by P, even when amended with N. Facilitation of colonization by *Urtica dioica* can therefore be attributed to increased soil P as well as soil N, derived from litter of *Lupinus arboreus* (Gosling, 2005). The proposed role of *Lupinus* species in ecosystem engineering by mobilizing P following release of carboxylates (Hocking and Jeffery, 2004) warrants further experimental investigation.

As pointed out in a recent review (Wheeler et al., 2008), ‘the primary colonization of deglaciated areas in Alaska, first by *Dryas drummondi* and then by *Alnus sinuata*, both actinorhizal species, provided a benchmark chronosequence that has served as a paradigm for the role of actinorhizal plants as pioneer species and facilitators of fixed-nitrogen accretion in nutrient-poor habitats.’ However, Chapin and co-workers demonstrated that plant growth at the earliest successional stages of these deglaciated soils was limited by both N and P, and that facilitation of spruce by *Dryas drummondi* was associated with both higher uptake and concentrations of both nutrients (Chapin et al., 1994). Despite the paradigm that N is limiting on young soils (Crews et al., 1995; Richardson et al., 2004), on recessional moraines of the Athabasca Glacier, Alberta, Canada, *Dryas drummondi* was found not to be nodulated (Fitter and Parsons, 1987). Similarly, its north-western European counterpart, *Dryas octopetala*, a classic colonizer in late-glacial/postglacial times, is invariably not diazotrophic (Becking, 1970; Stewart, 1977; Walker, 1993). We believe that the role of these actinorhizal species in P acquisition has so far been largely overlooked and that this should receive further attention.

![Diagram](image-url)

**Fig. 8.** Schematic diagram describing the contrasting functioning of Proteaceae in OCBILs (left) and young nutrient-rich landscapes (right). Note the stark contrast in mature and senesced leaf [P] and the much greater percentage reduction in leaf [P] during senescence Proteaceae in the SWAFR. Values for leaf mass per unit leaf area (LMA) are considerably higher for SWAFR Proteaceae, reflecting greater leaf density and leading to slower breakdown of leaf litter. Whilst the total soil P is considerably higher in Chilean soils, the ‘readily available P pool’ is still relatively low, thus favouring the production of cluster roots, which access this large pool. Whilst a vast amount of information is available on Proteaceae in SWAFR, it should be stressed that data for Chile are rather limited at this stage and further research is warranted to substantiate the proposed model. For further explanations, see text.
Another example of P mobilization during primary succession comes from the rehabilitation of an abandoned limestone quarry in Kenya, where planted *Casuarina glauca* rapidly established a dense vegetation cover, with abundant litterfall creating a humus layer that promoted the establishment of other plant species [C. V. Wood, 1987 (as cited in Diem et al., 2000)]. Diem et al. (2000) attribute the success of *Casuarina glauca* on that site to its ability to make cluster roots, which in turn allows P and Fe uptake from calcareous soils and promotes nodulation and N$_2$ fixation. Indeed, in the absence of cluster roots in calcareous soils, *C. glauca* shows leaf chlorosis, slow growth and poor nodulation, whereas cluster roots alleviate these symptoms (Arahou and Diem, 1997). This suggests that the role of cluster roots in mobilizing P and Fe precedes N fixation and is central to the success of *Casuarina glauca* in colonizing calcareous substrates.

*Morella* (formerly *Myrica*) (Louis et al., 1990; Crocker and Schwintzer, 1993), *Comptonia* (Hurd and Schwintzer, 1997) and *Alnus* (Hurd and Schwintzer, 1996) are all actinorhizal genera, each comprising species that typically grow in acidic peat soils or bogs (Torrey, 1978; Skene et al., 2000), where the low pH renders P poorly available for most plants (Fig. 3). These species are capable of making cluster roots (Table 2), and hence they have access to a P source that is of limited availability to other plants. In acidic bog soils, this P source might be iron phosphate, which is readily available to plants releasing large amounts of carboxylates (Earl et al., 1979; Gerke et al., 2000). Thus, these cluster-forming plants may act as ecosystem engineers as discussed above for *Lupinus lepidus* and *Lupinus arboreus*, or simply provide access to P for their neighbours (facilitation), without acting as ecosystem engineers in these habitats. In ombrotrophic bogs and mires in New Zealand, a similar role is possibly played by Restionaceae (Clarkson et al., 2005). Many of these produce cluster roots (Hodges and Rapson, 2010) (Table 2).

*Hippophae rhamnoides* (Oremus and Otten, 1981) and *Morella cordifolia* (Cramer and Hawkins, 2009) are both actinorhizal species inhabiting calcareous dunes, and both produce cluster roots (Table 2). Because P is poorly available in calcareous soils (Fig. 3), these species may play a similar role as discussed above for *Lupinus lepidus* and *Lupinus arboreus*. They may act as ecosystem engineers, not only by increasing soil N, but also by enhancing the availability of P for themselves and neighbouring plants. This may well account, in part, for the strongly competitive and invasive nature of *Hippophae rhamnoides* on nutrient-poor, calcareous dunes (Isersen et al., 2007; Richards and Burningham, 2010). Interestingly, several species whose invasive nature is readily ascribed to their N$_2$-fixing capacity are also known for their cluster roots, but this is rarely acknowledged (Hejda et al., 2009; Vollstad Shah et al., 2010). For example, *Morella* (formerly *Myrica*) *faya* is an invasive that radically transforms ecosystem development on young volcanic soils in Hawaii through its input of N-rich litter (Vitousek et al., 1987; Vitousek and Walker, 1989). These soils have extremely low P availability and N$_2$ fixation on them is P limited (Vitousek et al., 1987; Vitousek and Walker, 1989; Raich et al., 1996). Similarly, *Morella cerifera* is a recent invader on young lava flows in Hawaii with a similar potential for ecosystem transformation via N$_2$ fixation, despite available P being undetectable (Kurten et al., 2008). *Casuarina equisetifolia*, *C. glauca* and *C. cunninghamiana* have invaded coastal habitats in Florida, USA (Wheeler et al., 2010). *Elaeagnus angustifolia* has invaded riparian corridors of interior western United States (Vollstad Shah et al., 2010) and into the desert steppe communities of southern Ukraine (Sudnik-Wójcikowska et al., 2009).

It should be noted, however, that the production of cluster roots in *Elaeagnus angustifolia*, unlike that of the other actinorhizal species mentioned here, is inferred from its taxonomic position (*Elaeagnaceae*; Table 2); we are unaware of any papers actually reporting cluster roots for this particular species. It would be worth exploring if the capacity to produce cluster roots is universal of all actinorhizal species or whether it is restricted to certain genera. Until recently, the >20 actinorhizal genera in eight families of angiosperms were considered taxonomically unrelated, but they have now been placed in one rosid clade, comprising taxa with a predisposition to nodular symbiosis with diazotrophs, including rhizobia (Benson and Dawson, 2007).

Ca- and Fe-rich seepage in calcareous, wet dune slacks often sustains oligotrophic vegetation as a result of reduced P availability, where the seepage can lower P availability in soils with a strong pH buffer (Fig. 3). In the long term, this may lead to favourable conditions for species that exhibit efficient P uptake, e.g. Cyperaceae with dauciform roots (Davies et al., 1973; Bakker et al., 2005) (Table 2). Conceivably, these Cyperaceae act as facilitators in dune slacks and peat and moist grasslands (Davies et al., 1973), much the same as we discussed above for *Alnus*, *Comptonia* and *Morella* (*Myrica*) species.

**CONCLUDING REMARKS**

Within young, often disturbed, P-rich landscapes, there are still areas where the P availability for plants lacking specialized roots is low. There is clear evidence that P can be either limiting, or N and P co-limiting, for plant production in such landscapes (Elser et al., 2007; Harpole et al., 2011), e.g. on acidic or calcareous soils (Fig. 3). Based on our review of the literature, this is where we expect that species with cluster or dauciform roots, which release large amounts of P-mobilizing carboxylates, will have a competitive advantage over mycorrhizal species (Lambers et al., 2008b). These cluster-rooted species with a P-mining strategy are superior at accessing sorbed P (Lambers et al., 2008b) and may even act as ecosystem engineers and/or facilitators by converting poorly available P to more readily available forms and enhancing P uptake of neighbouring plants, as demonstrated for *Lupinus albus* in pot experiments (Horst and Waschkes, 1987; Cu et al., 2005). Moreover, many of these species are diazotrophs whose rate of N$_2$ fixation may depend on an ability to access scarce P, such that P, and not N, is the ultimate limiting nutrient. Such species may form an important link that couples P and N cycling in recently-developed systems.

Cyperaceae in P-impoverished landscapes are well adapted to cope with P-impoverished soils. They acquire and recycle P very efficiently; they also photosynthesize at relatively fast rates at very low leaf P concentrations and produce seeds with large P reserves (Groom and Lamont, 2010;
**Table 2.** Species with specialized roots (cluster roots or dauciform roots), or without mycorrhizas or specialized roots that are known to be capable of exudation of large amounts of carboxylates, in young landscapes; their habitat characteristics and their geographical and taxonomic distribution

<table>
<thead>
<tr>
<th>Species</th>
<th>Family</th>
<th>(Potentially) diazotrophic*</th>
<th>Habitat characteristics</th>
<th>Geographical origin</th>
<th>References for carboxylate exudation and either presence of cluster/dauciform roots, or habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Alnus</em> species</td>
<td>Betulaceae</td>
<td>Yes</td>
<td>Poor soils, sand hills/dunes, glacial till, wet bogs, mine dumps, gravel, wasteland, volcanic ash</td>
<td>Europe, Siberia, North America, Japan, Andes</td>
<td>Torrey, 1978; Hurd and Schwintzer, 1996</td>
</tr>
<tr>
<td><em>Carex flacca</em></td>
<td>Cyperaceae</td>
<td>No</td>
<td>Wet dune slacks, with Ca- and Fe-rich dune seepage; calcareous grasslands</td>
<td>Europe</td>
<td>Willis, 1963; Davies et al., 1973; Barbaro et al., 2001; Bakker et al., 2005</td>
</tr>
<tr>
<td><em>Carex atrofusca</em></td>
<td>Cyperaceae</td>
<td>No</td>
<td>Alpine and circumpolar distribution; nutrient-poor soils</td>
<td>Eurasia and Greenland</td>
<td>Schönwetter et al., 2006; Yano et al., 2011</td>
</tr>
<tr>
<td><em>Hippophaë rhamnoides</em></td>
<td>Elaeagnaceae</td>
<td>Yes</td>
<td>Calcareous sand dunes, coastal areas</td>
<td>Asia, Europe, from Himalayas to Arctic Circle</td>
<td>Oremus and Otten, 1981; Gardner et al., 1984; Kallio et al., 2002; Chen et al., 2009</td>
</tr>
<tr>
<td><em>Lupinus albus</em></td>
<td>Fabaceae</td>
<td>Yes</td>
<td>Poor sandy soils</td>
<td>Mediterranean basin</td>
<td>Gardner et al., 1981; White, 1990</td>
</tr>
<tr>
<td><em>Lupinus angustifolius</em></td>
<td>Fabaceae</td>
<td>Yes</td>
<td>Young volcanic ash deposits</td>
<td>Mediterranean basin</td>
<td>Clements et al., 1993; Pearse et al., 2007; Dimopoulos et al., 2010</td>
</tr>
<tr>
<td><em>Lupinus luteus</em></td>
<td>Fabaceae</td>
<td>Yes</td>
<td>Sandy, acidic soils</td>
<td>Mediterranean basin</td>
<td>Hocking and Jeffery, 2004; Wolko et al., 2011</td>
</tr>
<tr>
<td><em>Lupinus mutabilis</em></td>
<td>Fabaceae</td>
<td>Yes</td>
<td>Unknown, as natural populations no longer exist</td>
<td>Andes</td>
<td>Hocking and Jeffery, 2004; Wolko et al., 2011</td>
</tr>
<tr>
<td><em>Lupinus sericeus</em></td>
<td>Fabaceae</td>
<td>Yes</td>
<td>Wide range of soils</td>
<td>Western North America</td>
<td>Welsh, 1978; Weir et al., 2006</td>
</tr>
<tr>
<td><em>Morella cordifolia</em></td>
<td>Myricaceae</td>
<td>Yes</td>
<td>Calcareous sand dunes</td>
<td>South Africa</td>
<td>Cramer and Hawkins, 2009</td>
</tr>
<tr>
<td><em>Morella</em> (formerly <em>Myrica</em>) species</td>
<td>Myricaceae</td>
<td>Yes</td>
<td>Acidic bogs, sand dunes, mine wastes</td>
<td>Many tropical, subtropical and temperate regions, extending nearly to Arctic Circle</td>
<td>Torrey, 1978; Crocker and Schwintzer, 1993</td>
</tr>
<tr>
<td><em>Embothrium coccineum</em></td>
<td>Proteaceae</td>
<td>No</td>
<td>Acid volcanic soil</td>
<td>Southern South America</td>
<td>Prance and Plana, 1998; Zúñiga-Feest et al., 2010</td>
</tr>
<tr>
<td><em>Gevuina avellana</em></td>
<td>Proteaceae</td>
<td>No</td>
<td>Acid volcanic soil</td>
<td>Southern South America</td>
<td>Prance and Plana, 1998; Ramirez et al., 2004</td>
</tr>
<tr>
<td><em>Empodisma minus, Sporadanthus ferrugineus, Sporadanthus traversii</em></td>
<td>Restionaceae</td>
<td>No</td>
<td>Ombrotrophic bogs</td>
<td>New Zealand</td>
<td>Agnew et al., 1993; Clarkson et al., 2005; Hodges and Rapson, 2010</td>
</tr>
</tbody>
</table>

Most plants release a small amount of carboxylates under some conditions, but these species have been excluded from the table. Only those that release carboxylates as much as cluster root-forming species do have been included in the table. *Potentially diazotrophic indicates that the species or members of the genus are known to form a symbiotic association with N₂-fixing bacteria in some contexts, based on the literature.*
Lambers et al., 2010, 2011). In P-rich Chilean soils, on the other hand, we propose that Proteaceae may function as ecosystem engineers, making P that is locked up in acidic, volcanic soils available for neighbouring plants by providing P-rich litter (Fig. 8). This role of cluster roots, in combination with inefficient P resorption from senescing leaves and higher leaf-turnover, of Proteaceae in P-rich soils is most likely not unique. Whilst the functioning of carboxylate-releasing cluster roots is firmly established, the data on nutrient resorption are limited, warranting further investigation.

We can expect examples of P-mobilization ecosystem engineering, similar to what we propose for Chilean Proteaceae species, in other young soils where P is present in relatively large amounts, but in poorly available forms. Little solid information is available to reach a firm conclusion, but a summary of information from the literature on other families with cluster roots and the habitats in which these are found (Table 2) suggests the role of cluster roots and dauciform roots in P-mobilization ecosystem engineering may be far more common than envisaged so far. Moreover, it is quite possible that many *Lupinus* species, even those that lack cluster roots, can act in a similar manner, as this genus is well known for its species exhibiting high carboxylate-exudation rates (Hocking and Jeffery, 2004; Wang et al., 2008).

Further research on the role of species with cluster/dauciform roots and other species that release large amounts of carboxylates in P-rich soils is required to explore further the role of such species in P cycling, N cycling, P-mobilization ecosystem engineering and facilitation. Ecosystem engineering has frequently been associated with the diazotrophic nature of plants. However, many diazotrophic species are also known or expected to have cluster roots or release large amounts of carboxylates without having specialized root structures. The possibility that their role as ecosystem engineers is also linked with their P-mobilizing capacity warrants further investigation.

**ACKNOWLEDGEMENTS**

We thank Dr Marion Cambridge for providing several photographs used in this publication, and Professor Luis Corcuera for being a great host while H.L. visited Parque Katalapi. We also acknowledge valuable feedback provided by Prof. John Raven. H.L. was supported by the Australian Research Council (ARC) and A.Z.-F by Fondecyt Grant 11080162. A.Z.-F also thanks Frida Piper and Mabel Delgado for their valuable information on Chilean Proteaceae. S.D.H. is grateful for being a great host while H.L. visited Parque Katalapi.

**LITERATURE CITED**


Lammers et al. — Phosphorus-mobilization ecosystem engineering


**APPENDIX**

**Glossary of terms**

**Cluster roots and dauciform roots**

There are at least two main types of non-mycorrhizal, specialized roots involved in phosphorus (P) acquisition: cluster roots and dauciform roots (Lambers et al., 2006). Cluster roots (or proteoid roots, named after the family in which they were first discovered: Proteaceae; Purnell, 1960) are an adaptation for nutrient acquisition from soils with a low availability of nutrients, particularly P. In many species, the growth of cluster roots is suppressed by a high P supply (Lamont, 1972; Gardner et al., 1982; Keerthisinghe et al., 1998; Skene and James, 2000; Shane et al., 2003; Shane and Lambers, 2006; Zúñiga-Feest et al., 2010). Cluster roots occur in several plant families (e.g. Proteaceae, Casuarinaceae, Fabaceae and Myricaceae) (Skene, 1998). Their morphology is variable, but typically, large numbers of determinate branch roots develop over very short distances of root axes (Shane and Lambers, 2005). Dauciform roots, named for their carrot shape (Lamont, 1974), are typical in the tribes Cariceae and Rhynchosporaee of Cyperaceae only; while active, they have a cotton-ball appearance, because of their abundance of root hairs (Shane et al., 2005). Both dauciform roots and cluster roots are seasonal and ephemeral, living for approx. 2 and 3 weeks, respectively. Under the appropriate seasonal conditions, new cluster roots or dauciform roots are produced along extending lateral roots or on other lateral roots (Shane and Lambers, 2005; Lambers et al., 2006). During a brief developmental window of a few days, carboxylates (organic anions) are released both from cluster roots (Watt and Evans, 1999a; Shane et al., 2004a) and dauciform roots (Playsted et al., 2006; Shane et al., 2006) at very fast rates during a short period, referred to as an ‘exudative burst’.

**Carboxylate exudation**

Carboxylate exudation has been detected from the cluster and dauciform roots of all species studied so far, including taxa in the Fabaceae, Proteaceae, Cyperaceae and Myricaceae (Lambers et al., 2008a). Release of carboxylates (such as malate and citrate) also occurs in a wide range of species that lack such specialized structures, e.g. *Lupinus* and *Brassica* species (Weir et al., 2006; Pearse et al., 2007; Wang et al., 2008). Carboxylate exudation is often accompanied by exudation of acid phosphatases and other compounds that may confer the ability to obtain P from a variety of...
sources (Pearse, 2011), and sometimes by defensive enzymes and secondary compounds that protect exudates from soil microbes (Weisskopf et al., 2006).

**Ecosystem engineering**

The process by which a species significantly alters the habitat in which other species live (Jones et al., 1994). Ecosystem engineering operates at broader spatial and temporal scales than the scale of individual interactions between organisms (Hastings et al., 2007). A key feature of ecosystem engineering is that the effects of an engineer on other species persist well beyond the lifespan of the engineer, thus leaving a 'legacy' that can either be positive or negative (Hastings et al., 2007). Autogenic engineers affect the environment through their own morphological structures (e.g. coral reefs), whereas allogenic engineers convert inorganic or organic materials from one state to another (e.g. earthworms, diazotrophs) (Jones et al., 1994).

**Facilitation**

Facilitation is a positive interaction between two organisms where at least one is favoured and neither is harmed (Callaway, 1995). Facilitation may strongly influence community and ecosystem dynamics, including ecological succession (Clements, 1916; Connell and Slatyer, 1977). Positive and negative (e.g. resource competition or allelopathy) interactions between plants occur simultaneously in plant communities, leading to a complex balance between competition and facilitation (Callaway and Walker, 1997).

**OCBILs**

These are old, climatically buffered, infertile landscapes (Hopper, 2009). They are ancient landscapes having extremely low nutrient availability, due to prolonged weathering and the absence of nutrient-rejuvenating mechanisms, such as glaci-ation or volcanic deposition. OCBILs today are old-shield landscapes, located away from the poles continuously since the early Cretaceous, adjacent to oceans that buffered the land from climatic extremes since the Jurassic. They have endured weathering ever since; consequently, their soils are among the most nutrient-poor on Earth, with P being most limiting (Lambers et al., 2010). OCBILs are prominent and widespread in the SWAFR, South Africa’s Greater Cape and Venezuela’s Pantepui Highlands, as well as other regions, and may have been more evident globally prior to Pleistocene glaciations and associated landscape rejuvenation.