

CHAPTER 19

ROLE OF ROOT CLUSTERS IN PHOSPHORUS ACQUISITION AND INCREASING BIOLOGICAL DIVERSITY IN AGRICULTURE

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Abstract. Soils in the south-west of Western Australia and South Africa are among the most phosphorus-impooverished in the world, and at the same time both of these regions are Global Biodiversity Hotspots. This unique combination offers an excellent opportunity to study root adaptations that are significant in phosphorus (P) acquisition. A large proportion of species from these P-poor environments cannot produce an association with mycorrhizal fungi, but, instead, produce 'root clusters'. In Western Australia, root-cluster-bearing Proteaceae occur on the most P-impooverished soils, whereas the mycorrhizal Myrtaceae tend to inhabit the less P-impooverished soils in this region. Root clusters are an adaptation both in structure and in functioning; characterized by high densities of short lateral roots that release large amounts of exudates, in particular carboxylates (anions of di- and tri-carboxylic acids). The functioning of root clusters in Proteaceae ('proteoid' roots) and Fabaceae ('cluster' roots) has received considerable attention, but that of 'dauciform' root clusters developed by species in Cyperaceae has barely been explored. Research on the physiology of 'capillaroid' root clusters formed by species in Restionaceae has yet to be published. Root-cluster initiation and growth in species of the Cyperaceae, Fabaceae and Proteaceae are systemically stimulated when plants are grown at a very low P supply, and are suppressed as leaf P concentrations increase. Root clusters in Proteaceae, Fabaceae and Cyperaceae are short-lived structures, which release large amounts of carboxylates, briefly, at a particular stage of root development. The rates of carboxylate release are considerably faster than reported for non-specialized roots of a wide range of species. Root clusters play a pivotal role in mobilization of P from P-sorbing soil. Because the world P reserves are being depleted whilst vast amounts of P are stored in fertilized soils, there is a growing need for crops with a high efficiency of P acquisition. Some Australian and African native species as well as some existing crops have traits that would be highly desirable for future crops. The possibilities of introducing P-acquisition-efficient species in new cropping and pasture systems are explored. In addition, possible strategies to introduce traits associated with a high P-acquisition efficiency into future crop species are discussed.

INTRODUCTION

Phosphorus (P) is an essential inorganic nutrient for all living beings. After nitrogen (N), P is quantitatively the most important inorganic nutrient for plant growth. Phosphorus is a non-renewable resource, unlike N, which can be assimilated from N_2 into NH_3 by free-living and symbiotic N_2 -fixing micro-organisms or converted into NH_3 , NO_3^- or urea industrially. Global P reserves are rapidly being depleted; current reserves will be halved (relative to the reserves at the turn of the 20th century) by 2040–2060 (Steen 1998). Whilst global P reserves are being depleted, P levels in many P-sorbing, agricultural soils are accumulating (Parfitt 1979), because 80–90% of P applied as fertilizer is sorbed by soil particles, rendering it unavailable for plants without specific adaptations to access sorbed P (Parfitt 1979; Jones 1998). With decreasing global P reserves, P-fertilizer prices are bound to increase. There is an urgent need to develop crops that are more efficient in acquiring P from soil and/or in using P more efficiently. Equally, it is becoming increasingly important to use crops that reduce the off-site effects of P fertilization, thus reducing the risks of pollution of streams and rivers. This chapter focuses on traits associated with efficient P acquisition.

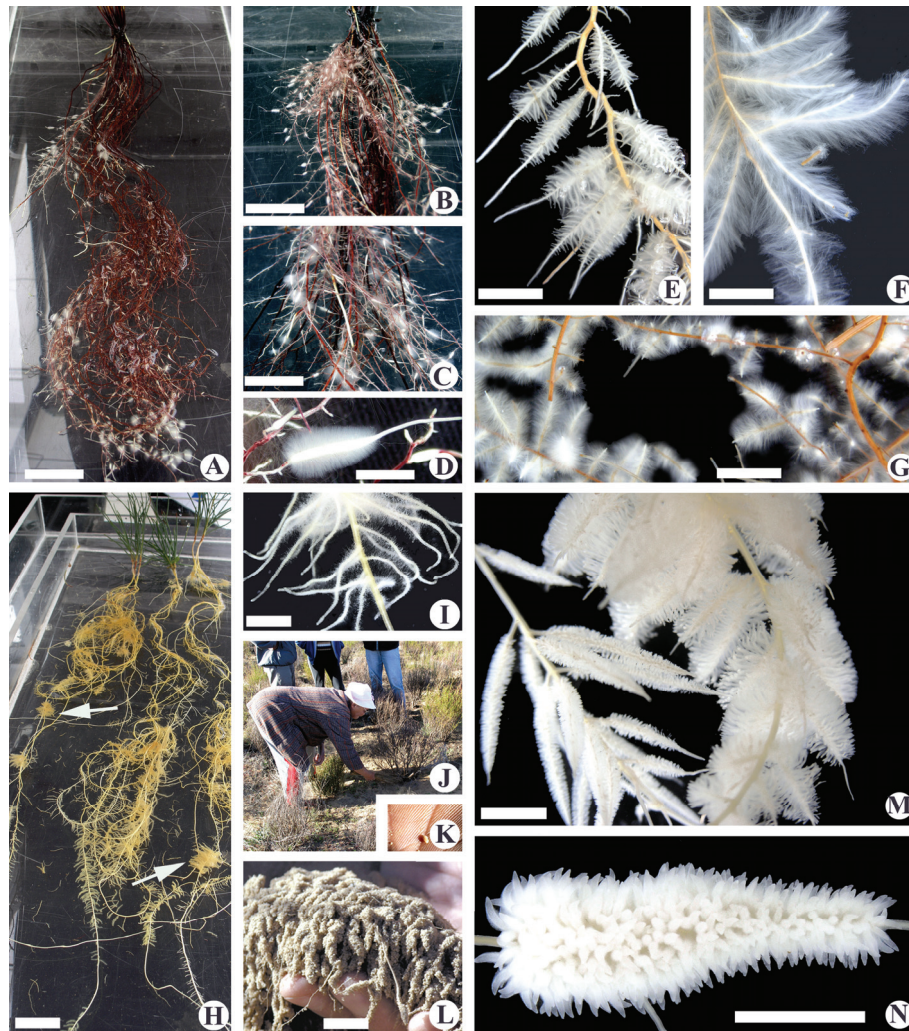
Unlike nitrate, which readily moves in soil towards the roots via both mass flow and diffusion, phosphate is highly immobile in soil. Mass flow typically delivers as little as 1–5% of a plant's P demand, and the amount intercepted by growing roots is only half of that (Lambers et al. 1998). The rest of all required P has to reach the root surface via diffusion; diffusion coefficients for phosphate in soil are typically very low, compared with those for other nutrients: $0.3\text{--}3.3 \times 10^{-13} \text{ m}^2 \text{ s}^{-1}$ (Clarkson 1981). Diffusion is particularly slow in dry soil (e.g., Turner and Gilliam 1976; Bhadoria et al. 1991). Increasing P delivery to roots via mass flow can be achieved by enhanced transpiration rates, but this cannot have a major effect, and would be at the expense of a plant's water-use efficiency. Root interception of P can be increased by root proliferation, increased frequency and length of root hairs, a root architecture that leads to enhanced root growth and root foraging in upper soil horizons (where nutrients are often relatively enriched), and mycorrhizal symbioses (Lambers et al. 2006). When the P concentration in soil solution is very low, an effective mechanism to increase acquisition of P is to enhance P diffusion. In dry soil, this can be achieved by increasing the moisture content of the soil, involving 'hydraulic redistribution'; it can also be driven effectively by increasing the concentration of inorganic P in the rhizosphere (Lambers et al. 2006). This review focuses on specific structural and functional root traits that enhance P acquisition from soil(s) with restricted availability of P. In particular, we discuss the traits of naturally occurring species taken from two of the world's 25 hotspots of biodiversity, the south-west corner of Western Australia and South Africa. These two regions have soils that are nutrient-impoverished, and the soils in Western Australia are exceptionally ancient and deeply weathered. Consequently, a host of species have evolved in these two regions with very efficient root adaptations to acquire sparingly available soil P. We further explore possibilities these traits may offer to future crop plants, and include pertinent information on several crop species that form root clusters.

Table 1. Families with root clusters (Shane and Lambers 2005a; Lambers et al. 2006) and examples of their present and potential commercial use (numerous sources)

Family	Genus	Species	Type of root cluster	Commercial use
Betulaceae	<i>Alnus</i>	<i>incana</i>	simple	timber
Casuarinaceae	<i>Allocasuarina</i>	<i>huegeliana</i>	simple	bio-energy
		<i>luehmannii</i>	simple	timber, fodder
	<i>Casuarina</i>	<i>cristata</i>	simple	fodder for browsing sheep
		<i>cunninghamiana</i>	simple	timber
	<i>Gymnostoma</i>	<i>papuanum</i>	simple	timber
Cucurbitaceae	<i>Cucurbita</i>	<i>pepo</i>	cluster-like	vegetable
Cyperaceae	<i>Carex</i>	<i>flava</i>	dauciform	fodder
		<i>flacca</i>	dauciform	fodder
	<i>Caustis</i>	<i>blakei</i>	dauciform	ornamental
Elaeagnaceae	<i>Hippophae</i>	<i>rhamnoides</i>	simple	fruit juice, health tea, source of flavonoids and vitamin C
Fabaceae	<i>Aspalathus</i>	<i>linearis</i>	simple	tea
	<i>Hakea</i>	<i>oleifolia</i>	simple	pulpwood
	<i>Lupinus</i>	<i>albus</i>	simple	protein
	<i>Viminaria</i>	<i>juncea</i>	simple	pulpwood
Moraceae	<i>Ficus</i>	<i>benjamina</i>	cluster-like	indoor plant
Myricaceae	<i>Myrica</i>	<i>cerifera</i>	simple	bayberry candles
		<i>esculenta</i>	simple	fruit
		<i>gale</i>	simple	insect repellent
Proteaceae	<i>Banksia</i>	<i>coccinea</i>	compound	flowers
	<i>Grevillea</i>	<i>robusta</i>	simple	timber
		<i>leucopteris</i>	simple	fine paper, pulpwood
				cut-flower
	<i>Leucadendron</i>	<i>L. laureolum</i> × <i>L. salignum</i> . cv. safari sunset	compound	
	<i>Protea</i>	<i>Eximia</i> × <i>susannae</i> cv. sylvia	simple	cut-flower
	<i>Macadamia</i>	<i>integrifolia</i>	simple	nuts
Restionaceae	<i>Telopea</i>	<i>speciosissima</i>	simple	flowers
	<i>Chondropetalum</i>	<i>tectorum</i>	capillaroid	ornamental plant, thatch
	<i>Calopsis</i>	<i>paniculata</i> (silk koala)	capillaroid	ornamental
	<i>Desmocladus Baloskion</i>	<i>flexuosus tetraphyllum</i>	capillaroid	restoration ornamental, landscaping

ROOT-CLUSTER STRUCTURE AND CARBOXYLATE RELEASE

Root clusters are formed by species belonging to eight families of dicotyledonous plants and also by species in two families of monocotyledonous plants (Table 1, Shane and Lambers 2005a; Lambers et al. 2006). Root clusters were first described in Australian Proteaceae (therefore termed 'proteoid' roots, Purnell 1960) but 'cluster' root is now a preferred general term following their subsequent identification in the other families (Lamont 1982). In terms of their structure, cluster roots can be identified as belonging to one of two broad types, i.e., 'simple' or 'compound' (Figure 1A–N). Many species in the families listed in Table 1 form the



simple root cluster that has a distinct bottlebrush-like appearance (e.g., *Leucadendron meridianum*, Figure 1N). There are several quite distinct morphologies of simple cluster roots among the species, and especially between species of the Proteaceae (e.g., *Leucadendron*) and those in other families, e.g., Fabaceae species (e.g., *Aspalathus linearis* (rooibos), Figure 1H and 1I). This difference likely reflects differences in anatomical structure related directly to the number of primary xylem poles as described for *Hakea prostrata* (Proteaceae) and *Lupinus albus* (Fabaceae). The number of longitudinal rows of short lateral roots (rootlets) developed within each cluster root reflects the number of xylem poles, of which there are more in *Hakea prostrata* (6 to 8) than in *Lupinus albus* (2 poles) (Lamont 1982; Watt and Evans 1999; Shane and Lambers 2005a). Within the Proteaceae, a few genera also produce (alone or in combination with the simple type) a 'compound' type of cluster roots (Table 1, *Protea* sp. Figure 1M), which are essentially 'branched simple cluster roots'. The compound type of cluster root is known for a couple of Australian genera (e.g., *Banksia*) and several South African genera (e.g., *Leucadendron* and *Protea*) (Lamont 1982; 1983). It is not clear what the significance is for some species to form preferentially the compound type of root cluster. Lamont (1983) has suggested that compound cluster roots are perhaps ontogenetically and phylogenetically more advanced than simple cluster roots, but whether or not these two types of cluster root preferentially access specific fractions of soil nutrients (e.g., inorganic and organic P) has yet to be determined.

Root clusters have been described in the monocotyledonous plant families Cyperaceae (sedges) and Restionaceae (rushes). In the Cyperaceae 'dauciform' root clusters were first described by Russian plant scientists (Selivanov and Utemova 1969, and references cited therein). They were subsequently found in cyperacean species around the world (Lamont 1982; Shane et al. 2006; Lambers et al. 2006). Lamont (1974) coined the term 'dauciform', because of the carrot shape of these

Figure 1. Roots and root systems of South African species of Cyperaceae, Restionaceae, Fabaceae and Proteaceae grown under conditions of low P availability. (A-D) sedge roots, *Tetraria* sp. (A) whole root system; bar is 45 mm. (B and C) higher magnification showing cotton-ball-like dauciform roots; bars are 36 and 24 mm, respectively. (D) specialized 'dauciform' root showing abundant, long root hairs; bar is 4 mm. (E-G) capillaroid roots of rush species, (E) *Mastersiella digitata*; bar is 15 mm. (F) *Thamnochortus fraternus*; bar is 8 mm, and (G) *Chondropetalum tectorum*; bar is 9 mm. (H-L) *Aspalathus linearis* (Fabaceae, rooibos), (H and I) roots were from plants grown in hydroponics, (H) whole root system containing cluster roots (arrows); bar is 35 mm. (I) single cluster root; bar is 3 mm. (J) seed being collected from beneath wild rooibos plants. (K) very small (ca. 2 mm length) rooibos seed in the palm of a hand. (L) soil, tightly bound to mature rootlets of root cluster from field-grown rooibos plants; bar is 23 mm. Images of proteoid roots in M and N are from the species in the genus *Leucadendron*. (M) abundant proteoid-root development in *L.* var. *chameleon* (*L. laurum* × *L. salignum*), groups of ca. 15 individual proteoid roots on the left side of the image are at an earlier stage of development than the group of proteoid roots on the right side of the image; bar is 6 mm. (N) individual proteoid root of *L. meridianum* (limestone cone bush), with hundreds of growing rootlets that had yet to develop root hairs; bar is 10 mm

root clusters (e.g., South African *Tetraria* sp. Figure 1A–D). It is apparent that dauciform roots are developed in two tribes of the Cyperaceae (i.e. Cariceae and Rhynchosporae) (Lamont 1982). Dauciform root clusters occur in groups of up to 20 to 30 but their most remarkable external feature is the very dense formation of long root hairs over the carrot-shaped axis (Figure 1D). The Restionaceae (the ‘Southern Hemisphere rushes’) are mostly distributed in Australia and South Africa (as are Proteaceae). Root clusters in this family are termed ‘capillaroid’ and are characterized by dense numbers of rootlets densely covered with long root hairs (Figure 1E, F and G). The term ‘capillaroid’ stems from their sponge-like properties on holding soil water (Lamont 1982).

In terms of the functioning of root clusters for nutrient acquisition we summarize the literature concerning root exudation of carboxylates (e.g., citrate), and the reader is referred to Lambers et al. (2006) for more information about the other exudates, such as phosphatases released by root clusters. The cluster roots of Fabaceae (*L. albus*, Watt and Evans 1999) and Proteaceae (*Hakea prostrata*, Shane et al. 2004) release citrate in a developmentally programmed exudation event that lasts for a brief time (ca. 1 to 2 days) once the roots mature. The dense ‘root mats’ in the field developed by the compound-cluster-root-forming Proteaceae also release carboxylates (Grierson 1992; Roelofs et al. 2001), but there are no reports on the exact time course of carboxylate exudation in these root-mat-forming species. Pate and Watt (2002) calculated that citrate in the cluster-root rhizosphere of *Banksia prionotes* (Proteaceae) accumulates to levels of 35–72 μmol per gram soil. Such concentrations are sufficiently high to mobilize P. The authors calculated that the clusters mobilized 44% of the total P in the soil trapped by their clusters, or 250% of the ‘available’ P.

Though morphologically and anatomically very distinct, dauciform roots function in a way very similar to proteoid roots (Davies et al. 1973; Lamont 1974; Shane et al. 2005; 2006; Playsted et al. 2006). That is, dauciform-root formation is suppressed when plants have a relatively high P status (Shane et al. 2005; Playsted et al. 2006) and carboxylates (e.g., citrate) are released during a brief interval once the dauciform root has matured (Figure 1D, Shane et al. 2005; 2006). This brief time interval when large amounts of carboxylates are released from the roots is considered important to mobilize P before microbial activity builds up. Microbial activity in the rhizosphere of root clusters of *L. albus* is slowed down by rhizosphere acidification and by exudation of flavonoids that promote fungal sporulation (Weisskopf et al. 2006). Finally, release of anti-fungal cell-wall-degrading enzymes (chitinase and glucanase) prior to the release of carboxylates would inhibit fungal growth (Weisskopf et al. 2006). We have yet to assess whether the capillaroid roots of species within the Restionaceae function like proteoid roots, but based on our own preliminary observations, we hypothesize that they do.

In summary, root clusters differ greatly in their anatomy and morphology. Proteoid root clusters and dauciform root clusters release carboxylates in a developmentally programmed, brief exudative event, a pattern that is considered vital for their functioning (Lambers et al. 2006).

EFFECTS OF PLANT P STATUS ON DEVELOPMENT AND FUNCTIONING OF ROOT CLUSTERS

Root clusters in species of the Casuarinaceae (Racette et al. 1990; Reddell et al. 1997), Cyperaceae (Shane et al. 2005; Playsted et al. 2006), Fabaceae (Gardner et al. 1983; Keerthisinghe et al. 1998), Myricaceae (Louis et al. 1990) and Proteaceae (Lamont 1982; Aitken et al. 1992; Shane et al. 2003a; 2003b) are suppressed when adding P to the root environment. Feeding P to leaves also suppresses cluster-root formation in *L. albus* (Marschner et al. 1986; Gilbert et al. 2000; Shane et al. 2003a), showing that the signal(s) that leads to suppression of cluster-root initiation and growth originate in the shoot, most likely in young leaves (Keerthisinghe et al. 1998).

Root clusters are relatively short-lived (approx. 1 to 3 weeks) and intermittent development of new root clusters produces spacing between old and new cluster roots (see Figure 1 in Shane and Lambers 2005a), which are typically separated by unbranched regions along the root axis. In experiments using plants with a split-root system, where one root half received a low and the other a high P supply, depending on species, cluster roots are either produced equally on both root halves (i.e., *L. albus*, Shane et al. 2003b; *Grevillea crithmifolia*, Shane and Lambers 2006), or predominantly on low-P root halves (*H. prostrata*, Shane et al. 2003a). This suggests that there are local signals as well as systemic ones. Therefore, there is evidence for both systemic and local signals controlling root cluster formation and functioning (Watt and Evans 1999; Shane and Lambers 2005a). Local signals may be stronger for some processes (exudation) and may also vary among species.

Since auxin-transport inhibitors suppress root-cluster formation in P-deficient *L. albus* plants (Gilbert et al. 2000), whereas auxins stimulate root-cluster formation in P-sufficient *L. albus* (Gilbert et al. 2000; Skene and James 2000), it is very likely that auxin is a component of the signal-transduction path between plant P status ('P-sensing') and cluster-root formation. Shane et al. (2003a) showed that various processes in cluster roots of *Hakea prostrata* (Proteaceae) have different sensitivities to plant P status, with carboxylate exudation from cluster roots being the most sensitive, followed by cluster-root growth, and then cluster-root initiation. Interestingly, application of auxins leads to cluster-root formation in P-sufficient *L. albus* plants, but does not lead to carboxylate exudation from those clusters (Hocking and Jeffery 2004). This suggests that, whilst systemic signals account (in part) for production of root clusters in *L. albus*, exudation of carboxylates from cluster roots in this species may be controlled by (additional) local signals. Root-produced cytokinins probably play an antagonistic role in the transduction pathway (Neumann et al. 2000).

Liu et al. (2005) showed that sugars are related to P-deficiency-induced gene expression in *L. albus*. Interruption of phloem supply to P-deficient roots resulted in a rapid decline in accumulation of gene products induced by P deficiency. Regulation of P-deficiency-induced genes appears to be conserved across plant species and sugars are crucial for P-deficiency signal transduction.

Much remains to be discovered about signalling molecules and signalling pathways involved in the development and functioning of cluster roots. Systemic

and local signals involved in nodule formation may guide us towards a model for cluster-root formation (e.g., Ferguson and Mathesius 2003). Auxins and other phytohormones play a role in nodule initiation and development; nitrate locally inhibits nodule formation. Figure 2 summarizes our current thinking; it has components that are firmly established (auxins, cytokinins) as well as aspects that are speculative (direct P effects). What is currently lacking is a sound understanding of specific genes that are responsible for the synchronous development of numerous rootlets that form a root cluster. Nothing about their development appears to be cluster-specific; what makes the process special is the synchronization of rootlet development and metabolism. Identification of the gene(s) controlling that synchronous development would be a major step in the direction of future crops with root clusters.

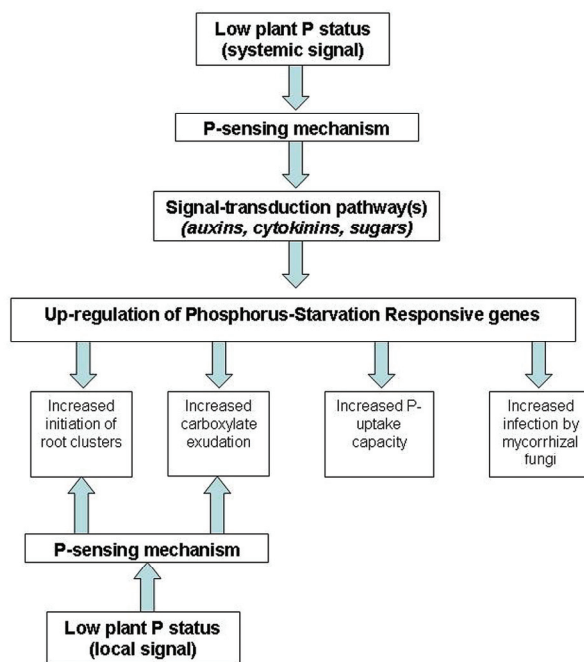


Figure 2. Plant responses to P limitation. A low external P availability decreases the plant's internal P status. When the plant senses a low P status, P-starvation responses are induced. P-starvation responses, depending on the species, include increased root-hair formation, root-cluster initiation and development, carboxylate exudation, P-uptake capacity, and mycorrhiza formation. Apart from systemic signals, most likely originating in young leaves, there are local signals. Systemic and local signals may interact

EXISTING CROP PLANTS WITH A HIGH P-ACQUISITION EFFICIENCY

Many species occurring on severely P-impooverished soil have the capacity to produce root clusters that enhance the availability of P in the rhizosphere. At one stage, a plant's capacity to produce root clusters was considered an alternative to the mycorrhizal habit. For example, proteacean (Purnell 1960), cyperacean (Powell 1975) and *Lupinus* (Trinick 1977) species are non-mycorrhizal (or weakly at most, Shane and Lambers 2005a). However, it has since been discovered that there are also many species that can produce both root clusters and mycorrhizas (reviewed in Lambers et al. 2006).

Root clusters combine adaptive structures with adaptive functioning. Root clusters occur in a large number of species belonging to 10 families (Lambers et al. 2006). Root-cluster-bearing plants include several species used for the production of food, fodder, fibre, timber, tea or bayberry candles: *Grevillea* and *Macadamia* species (Proteaceae), *Aspalathus linearis* (rooibos) and *Lupinus* species (Fabaceae), *Myrica cerifera* (wax myrtle) (Myricaceae), *Carex* species (Cyperaceae), *Allocasuarina* and *Casuarina* species (Casuarinaceae), *Cucurbita pepo* (Cucurbitaceae) and *Hippophae rhamnoides* (sea buckthorn) (Elaeagnaceae). Many are also used for horticultural purposes (Betulaceae, Cyperaceae, Elaeagnaceae, Fabaceae, Moraceae, Proteaceae, Restionaceae) and in restoration. Considering that P reserves are rapidly being depleted (Steen 1998), whilst vast amounts are present in soils that have been fertilized for decades (Singh and Gilkes 1991), we should consider options for incorporating root clusters in new crop species or cropping systems.

There are several advantages of a large capacity to mobilize P in the rhizosphere, especially by root clusters, and the downsides are limited (Lambers et al. 2006). Provided the risks of enhanced cadmium uptake and eutrophication are carefully managed, P-acquisition-efficient new crops, especially high-exuding, cluster-bearing crops, offer tremendous potential. To apply information gleaned from the study of native plants for cropping and pasture systems, we should be willing to consider new crop species. Equally, we should consider new cropping systems where combinations of species in intercropping systems and ideal rotations are used to maximize the acquisitions of P from low-P soils (Lambers et al. 2006). These approaches should lead to more sustainable cropping systems with less off-site risks of eutrophication of streams and rivers.

PERSPECTIVES FOR EXISTING AND FUTURE P-ACQUISITION-EFFICIENT CROP PLANTS

Root clusters allow plants to grow in soils where the total amount and availability of P is restricted (Neumann and Martinoia 2002). Root clusters can mobilize sparingly available P, and hence support plant growth where mycorrhizas are less effective (Lambers et al. 2006). As such, the cluster-root-bearing habit contributes to the biodiversity in natural systems, allowing cluster-root-bearing species to compete successfully on the poorest soils, whilst being less competitive on slightly less P-impooverished soils. Do nearest neighbours of root-cluster-bearing plants in natural

systems benefit from the P-solubilizing ability of their neighbours? There are no hard data available to answer this question, but there is information from pot experiments on growth-enhancing effects of root-cluster-bearing *L. albus* plants on neighbouring *Triticum aestivum* plants (Horst and Waschkies 1987; Cu et al. 2005). In this section, we explore how the cluster-bearing habit might be valuable in new cropping and pasture species and systems.

Biodiversity in western agricultural systems has been reduced dramatically over the last few decades, but is now increasingly considered important for a variety of reasons: it provides ecosystem services beyond production of food, fibre, fuel and income (Altieri 1999; Van Elsen 2000). Enhanced biodiversity may also allow more efficient acquisition of P from P-sorbing soils. The results from pot experiments with cluster-root-bearing *L. albus* and low-carboxylate-exuding *T. aestivum* (Horst and Waschkies 1987; Cu et al. 2005), as cited in the preceding paragraph, are promising, but the experiments need to be followed up using more realistic root densities under field conditions. Intercropping is common practice in large parts of China (Zhang and Li 2003), and some combinations greatly enhance the efficiency of nutrient acquisition (Zuo et al. 2000), but so far no combinations include the use of cluster-root-bearing species. The cluster-root-bearing proteaceous tree, *Grevillea robusta*, is frequently intercropped with *Zea mays* (e.g., Smith et al. 1999; Smith and Roberts 2003), but Radersma and Grierson (2004) concluded that it is unlikely that the extent of P mobilization by *G. robusta* will benefit adjacent crop plants, unless crop roots actually share the rhizosphere with tree roots. However, Kumar et al. (1999) found that *G. robusta* enhanced ^{32}P uptake by *Cocos nucifera* (coconut) when the two species were interplanted in coconut plantations. Since cluster-root-bearing plants mobilize not only P but also micronutrients (Shane and Lambers (2005b) and references cited therein), intercropping also has beneficial effects on Mn uptake (Gardner and Boundy 1983). Since cluster roots can also be induced by Fe deficiency (Arahou and Diem 1997; Hagström et al. 2001), it is envisaged that Fe uptake might also be enhanced by intercropping with a cluster-root-bearing species. Generally speaking, it is anticipated that species with complementary nutrient-acquisition strategies will do well in intercropping systems (Zhang and Li 2003); for example, the combination of a monocotyledonous species that mobilizes Fe in calcareous soil and a legume that fixes dinitrogen symbiotically.

Beneficial effects of cluster-root-bearing species with a large capacity to mobilize soil P are not restricted to increased P uptake by neighbouring plants, but may extend to enhanced P acquisition and growth by the following crop (Kamh et al. 1999). Little et al. (2004) showed that Olsen-extractable P in plots 8 weeks after sowing potatoes was enhanced after growing *L. albus* or a combination of *L. albus* and *B. napus* as a cover-crop relative to that after *Avena sativa* or *B. napus* alone. These results provide evidence that cover-crops containing the cluster-bearing *L. albus* potentially enhance the P availability for the following crop. Similarly, other fast-exuding plants can have a beneficial effect on the following crop (Lambers et al. 2006).

Incorporation of root-cluster-bearing species into cropping, pasture and forestry systems need not be restricted to the introduction of new species. Interspecific crosses between root-cluster-bearing *Lupinus* species and congeneric species

without root clusters might be a valuable approach that has yet to be explored. Combined with molecular-marker-assisted breeding, this might allow the development of new lupin crops that are excellent at acquiring P from P-sorbing soils. Alternatively, a better understanding of the genes and molecular events involved in root-cluster formation might lead to the isolation of genes that could be introduced in existing crop species that lack root clusters.

There are risks associated with the introduction of new crop species. One of these risks is the potential for any introduced species to become an invasive weed. Some of the highly P-acquisition-efficient proteacean species, e.g., *Hakea drupacea*, *H. gibbosa* and *H. sericea*, are serious weeds outside Australia, e.g., in South Africa (e.g., Dyer and Richardson 1992). However, we do not know if this is accounted for, in part, by their P-acquisition strategy. Another risk of P-mobilizing species is that the mobilized P might leach and reach the groundwater and then streams and rivers, contributing to their eutrophication (Djodjic et al. 2004). This risk should be managed by measuring both agronomic and environmental soil P saturation, and fertilizing accordingly (Maguire and Sims 2002).

FUTURE RESEARCH

P-acquisition-efficient plants offer potential as future crops and cropping systems. Future research should aim at identification of the genes involved in the development and functioning of root clusters, in an attempt to transfer these to other species. Equally, the potential of 'new' species should be explored, e.g., Australian cluster-root-bearing *Kennedia* species (Adams et al. 2002) for introduction as food (Rivett et al. 1983) or pasture plants (Cohen and Wilson 1981; Cocks 2001).

Much still needs to be learned about how P is made available for the subsequent crop. Beneficial effects on P acquisition have been found on several occasions, but the mechanism that accounts for these beneficial effects is not known. It is highly unlikely that released carboxylates are still present when the next crop is growing. Rather, the effects may be via P-containing crop residues (Nuruzzaman et al. 2005), but this needs further investigation.

CONCLUDING REMARKS

Global P reserves are rapidly being depleted, whilst agricultural soils that have been fertilized for decades contain substantial amounts of P that cannot be accessed by plants lacking specific root adaptations. To acquire soil P more efficiently, new crops need to be developed, and there should be a strong focus on species with root clusters, as these represent a combination of plant root form and function that is highly desirable in a world where P will be harder to obtain. There is still much to be learned on the role of root clusters in natural systems, and it is envisaged that new knowledge based on investigations of such systems will further enhance our potential to develop new crops and cropping systems that use P more efficiently.

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