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Plant adaptations to severely phosphorus-impoverished soils

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Mycorrhizas play a pivotal role in phosphorus (P) acquisition of plant roots, by enhancing the soil volume that can be explored. Non-mycorrhizal plant species typically occur either in relatively fertile soil or on soil with a very low P availability, where there is insufficient P in the soil solution for mycorrhizal hyphae to be effective. Soils with a very low P availability are either old and severely weathered or relatively young with high concentrations of oxides and hydroxides of aluminium and iron that sorb P. In such soils, cluster roots and other specialised roots that release P-mobilising carboxylates are more effective than mycorrhizas. Cluster roots are ephemeral structures that release carboxylates in an exudative burst. The carboxylates mobilise sparingly-available sources of soil P. The relative investment of biomass in cluster roots and the amount of carboxylates that are released during the exudative burst differ between species on severely weathered soils with a low total P concentration and species on young soils with high total P concentrations but low P availability. Taking a modelling approach, we explore how the optimal cluster-root strategy depends on soil characteristics, thus offering insights for plant breeders interested in developing crop plants with optimal cluster-root strategies.

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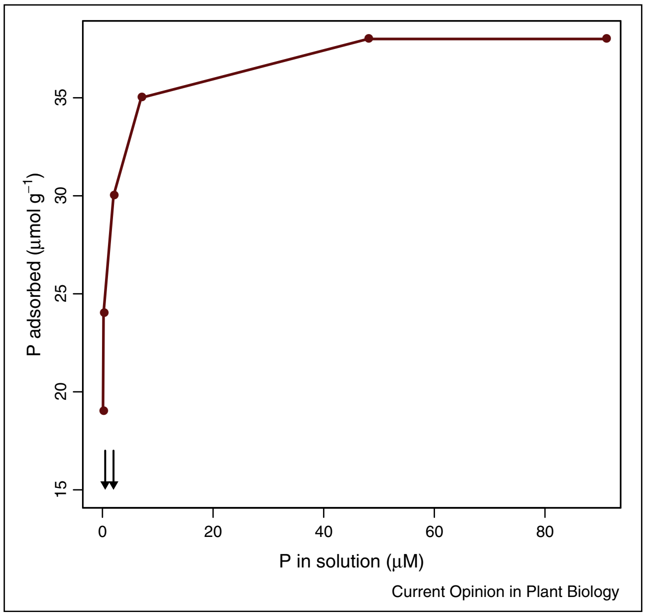
Strategies of phosphorus acquisition in mycorrhizal and non-mycorrhizal species

Mycorrhizal structures, which arise from symbiotic associations between plants and fungi, occur in most terrestrial higher plants [1]. They play a pivotal role in acquisition of poorly-mobile nutrients, in particular phosphorus (P). Non-mycorrhizal species are relatively common in young landscapes on sites that contain the most exchangeable P, for example, in Swedish rocky habitats [2]. These are referred to as the 'Brassicaceae type' [3•], after a well-known non-mycorrhizal family. Conversely, on the world's most P-impoverished soils such as the sandplains in south-western Australia [4], the Cape Floristic Region in South Africa [4], and the *campos rupestres* in Brazil [5••], non-mycorrhizal species are also very common. In south-western Australia, their frequency increases with decreasing soil P concentration [6]. This group of non-mycorrhizal species is referred to as the 'Proteaceae type' [3•], after a family common on severely P-impoverished soils in Australia and South Africa. In summary, non-mycorrhizal species occur at both ends of a soil fertility gradient. The Brassicaceae type is associated with fertile soils, whereas the Proteaceae type is found on severely P-impoverished soils [3•].

To understand why non-mycorrhizal species are common on severely P-impoverished soils requires knowledge about P in soil. Only some of this P is in the soil solution; the rest is adsorbed onto or absorbed by soil particles. Since adsorption and absorption are hard to separate, the process is usually referred to as 'sorption', a non-committal term coined by McBain [7]. In soil, goethite, named after the German poet and philosopher J.W. von Goethe, who had a keen interest in minerals, is an iron-bearing hydroxide mineral that tightly sorbs P. When phosphate is added to goethite, most of the added P is sorbed to the mineral, until a significant fraction of the sites that can bind P are occupied (Figure 1) [8]. Adding more P then increases the concentration of P in solution. When *Lolium perenne* (ryegrass) is grown in pots with goethite, no P is readily available to ryegrass until >40% of the goethite surface is covered with phosphate ions. The P availability then increases till the concentration in solution reaches 2 μM, when 75% of all the P-binding sites of goethite are covered. Arbuscular mycorrhizal fungi increase the P availability for ryegrass at a concentration between 0.5 and 2 μM (60–70% coverage of the goethite surface). Neither below nor above that concentration range do arbuscular mycorrhizal fungi promote the growth of ryegrass. Above the range, the uninoculated ryegrass roots are just as effective as mycorrhizal roots at taking up P. Below that range, the mycorrhizal fungi are ineffective, but an alternative P-mining strategy based on displacing P from soil surfaces with citrate is more effective [8,9].

Figure 1



Phosphate-adsorption isotherm on goethite at pH 6.3 after two days shaking using $Ca(H_2PO_4)_2$, 0.01 M $CaCl_2$ at 20 °C. Following this, the phosphorus (P) concentration in the solution was measured as well as the amount of P sorbed to the goethite. The arrows denote the range over which inoculation of *Lolium perenne* (ryegrass) with an arbuscular mycorrhizal fungus enhances plant growth. Redrawn based on data in [8].

Figure 2

Cluster roots of *Hakea* species. Top: Active cluster roots of *Hakea ceratophylla*, photographed *in situ* in winter in Allison Baird reserve, Yule Brook. Bottom: Cluster roots of an unidentified *Hakea* species photographed after excavation close to the soil surface in Lesueur National Park, near Jurien Bay. Both locations are in south-western Australia. Photos: Hans Lambers.

Cluster roots are common in Proteaceae, but functionally similar roots occur in other families

If arbuscular mycorrhizas are ineffective at very low soil P concentrations, is there evidence that plants that release citrate from roots can be more effective in soils that either contain very little total P or in which P is strongly sorbed? Indeed there is. Most Proteaceae are non-mycorrhizal, and in south-western Australia they predominantly occur on ancient soils that contain very little P [4]. These species produce proteoid or cluster roots (Figure 2) [10]; *Hakea prostrata* (Proteaceae) releases carboxylates (organic anions) in an exudative burst [11]. In southern South America, Proteaceae occur on young acidic soils with very high total P concentrations, but with a low P availability, due to strong sorption of P to oxides and hydroxides of iron and aluminium [12••]; *Embothrium coccineum* releases predominantly citrate [13••]. In tropical rainforests in north-eastern Australia, a mycorrhizal species without cluster roots, *Placospermum coriaceum*, occurs, together with non-mycorrhizal species with cluster roots [14]. When grown at a very low soil P concentration, the non-mycorrhizal species with cluster roots grow better than the mycorrhizal species without cluster roots (Figure 3), confirming that cluster roots are better than mycorrhizas at very low soil P availability. Similar results are found with crop species. Comparing the response to applied soil P of a non-mycorrhizal crop species with cluster roots, that is, *Lupinus albus* (white lupin), with that of a mycorrhizal species without cluster roots, that is, *Triticum aestivum* (wheat), shows similar results to those in Figure 3 [15]. The genus *Lupinus* is non-mycorrhizal, with only a small number known to produce cluster roots [16•]. However, many that do not produce cluster roots do produce relatively large amounts of carboxylates, for example, *L. angustifolius* (narrow-leaf lupin) [17]. Narrow-leaf lupin produces more biomass at a low P supply than wheat does, but not as much as white lupin [16•]. That is, the combination of programmed production and release of carboxylates and the structure that allows the local build-up of high concentrations of released carboxylates in the rhizosphere is ideally suited to access soil P when the P concentration in the soil solution is very low [18].

Cluster roots do not only occur in Proteaceae and some Fabaceae, but are also common in actinorhizal families [9,10]. Moreover, there are other structures that are morphologically very different, but functionally similar to cluster roots, for example, dauciform roots in many non-mycorrhizal Cyperaceae [19,20], non-mycorrhizal sand-binding roots in *Discocactus placentiformis* (Cactaceae) [21], and capillaroid roots in *Lyginia barbata* (Anarthriaceae) (M.W. Shane, unpublished data). Where