Plant Soil (2022) 476:133–160
https://doi.org/10.1007/s11104-022-05464-8

REVIEW ARTICLE

Strategies to acquire and use phosphorus in phosphorus-impoverished and fire-prone environments

Hans Lambers · Patrícia de Britto Costa · Gregory R. Cawthray · Matthew D. Denton · Patrick M. Finnegan · Patrick E. Hayes · Rafael S. Oliveira · Simon C. Power · Kosala Ranathunge · Qi Shen · Xiao Wang · Hongtao Zhong

Received: 23 December 2021 / Accepted: 26 April 2022 / Published online: 19 May 2022
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Abstract
Background Unveiling the diversity of plant strategies to acquire and use phosphorus (P) is crucial to understand factors promoting their coexistence in hyperdiverse P-impoverished communities within fire-prone landscapes such as in cerrado (South America), fynbos (South Africa) and kwongan (Australia).

Scope We explore the diversity of P-acquisition strategies, highlighting one that has received little attention: acquisition of P following fires that temporarily enrich soil with P. This strategy is expressed by fire ephemerals as well as fast-resprouting perennial shrubs. A plant's leaf manganese concentration ([Mn]) provides significant clues on P-acquisition strategies. High leaf [Mn] indicates carboxylate-releasing P-acquisition strategies, but other exudates may play the same role as carboxylates in P acquisition. Intermediate leaf [Mn] suggests facilitation of P acquisition by P-mobilising neighbours, through release of carboxylates or functionally similar compounds. Very low leaf [Mn] indicates that carboxylates play no immediate role in P acquisition. Release of phosphatases also represents a P-mining strategy, mobilising organic P. Some species may express multiple strategies, depending on time since germination or since fire, or on position in the landscape. In severely P-impoverished landscapes, photosynthetic P-use efficiency converges among species. Efficient species exhibit rapid rates of photosynthesis at low leaf P concentrations. A high P-remobilisation efficiency from senescing organs is another way to use P efficiently, as is extended longevity of plant organs.

Conclusions Many P-acquisition strategies coexist in P-impoverished landscapes, but P-use strategies tend to converge. Common strategies of which we know little are those expressed by ephemeral or perennial species that are the first to respond after a fire. We surmise that carboxylate-releasing P-mobilising

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Responsible Editor: Alexia Stokes.

H. Lambers (✉) · P. de Britto Costa · G. R. Cawthray · P. M. Finnegan · P. E. Hayes · K. Ranathunge · Q. Shen · X. Wang · H. Zhong
School of Biological Sciences, The University of Western Australia, 6009 Perth, WA, Australia
e-mail: hans.lambers@uwa.edu.au

P. de Britto Costa
Programa de Pós Graduação em Biologia Vegetal, Institute of Biology, University of Campinas, Campinas, Brazil

M. D. Denton
School of Agriculture, Food and Wine, The University of Adelaide, 5064 Glen Osmond, SA, Australia

R. S. Oliveira
Departamento de Biologia Vegetal, Institute of Biology, University of Campinas – UNICAMP, P.O. Box: 6109, Campinas, SP, Brazil

S. C. Power
School of Environment and Natural Resources, Kottman Hall, The Ohio State University, Columbus, OH 43210, USA

strategies are far more widespread than envisaged so far, and likely expressed by species that accumulate metals, exemplified by Mn, metalloids, such as selenium, fluorine, in the form of fluoroacetate, or silicon. Some carboxylate-releasing strategies are likely important to consider when restoring sites in biodiverse regions as well as in cropping systems on P-impoverished or strongly P-sorbing soils, because some species may only be able to establish themselves next to neighbours that mobilise P.

Keywords Carboxylates · Cluster roots · Dauciform roots · Facilitation · Fire · Hyperdiverse ecosystems · Mycorrhizas · Non-mycorrhizal plants · Phosphorus · Phosphorus-acquisition efficiency · Phosphorus-use efficiency · Sand-binding roots

Introduction

Many global biodiversity hotspots for conservation priorities (sensu Myers et al. 2000) are located in nutrient-impoverished climatically-buffered fire-prone regions, including fynbos in South Africa (Allsopp et al. 2014; Cowling et al. 1996), kwongan in Australia (Hopper 2009; Lambers 2014) and campos rupestres, which is part of the cerrado in Brazil (Oliveira et al. 2015; Silveira et al. 2016; Villarroel Segarra and Wood 2011). Fire is a key component of all these ecosystems, and some species have evolved strategies to acquire nutrients that are released in ash during a fire (Orians and Milewski 2007). Phosphorus (P) is a key nutrient that limits primary productivity in all these environments, mainly because of their age, allowing extensive erosion and leaching over time, and lack of major rejuvenating processes (Hopper 2009; Hopper et al. 2021). The availability of soil P declines steadily with increasing soil age (Walker and Syers 1976), with further losses of P in fire-prone environments on long time scales due to convection losses and volatilisation during hot fire events (> 500˚C) (Butler et al. 2018; Giardina et al. 2000; Leitch et al. 1983; Raison et al. 1985). In addition, the low P content of parent material plays a role (Porder and Ramachandran 2013). Here, we explore some of the diversity in P-acquisition and P-use strategies that contribute to the hyperdiversity in these landscapes. We highlight the coexistence of, and interactions among, species expressing different strategies and explore how this knowledge may be applied in restoration of disturbed landscapes and in intercropping agroecosystems (Homulle et al. 2022).

We acknowledge that there are more P-acquisition strategies in P-impoverished landscapes than discussed in this review, especially carnivory, which is very common in P-impoverished habitats, coprophagy and parasitism, which is relatively uncommon in these habitats if they are seasonally dry. Since these strategies have been discussed in detail before (Cramer et al. 2014; Lambers et al. 2014; Oliveira et al. 2016), we do not deal with them in this review. Table 1 summarises the P-acquisition strategies we discuss in this review. Note that some species may express multiple

Table 1 A summary of phosphorus (P)-acquisition strategies discussed in this review

Strategy	Key plant trait
Fire ephemeral phosphophile	Germination stimulated after a fire (e.g., in response to smoke or heat); rapid growth and P acquisition following a fire event, with a relatively short life cycle
Resprouting within days to weeks after a fire	Rapid growth, dependent on stored reserves and P acquisition following a fire event, followed by slow growth and efficient recycling of P
Mycorrhizal scavenging	Access P that is beyond the zone available for roots and root hairs, thus enhancing the soil volume that is available for P uptake
Phosphorus-mining based on exudation of P-mobilising low-molecular weight compounds	Exudation of low-molecular weight compounds; these are often carboxylates, but in Poaceae they may also be phytosiderophores
Phosphorus-mining based on the release of phosphatases	Exudation of enzymes that hydrolyse organic P; access to phytate requires exudation of phytases
Facilitation by P-mobilising neighbours	Phosphorus acquisition is enhanced by neighbours that mobilise P through their own P-mining strategy

Some species may express multiple strategies, depending on time since germination or since fire, or on position in the landscape strategies, depending on time since germination or since fire, or on position in the landscape.

Phosphophiles as post-fire ephemerals

When soils are relatively fertile, non-mycorrhizal plants such as most Amaranthaceae, Brassicaceae, Caryophyllaceae, Chenopodiaceae, Polygonaceae and Urticaceae are common (Brundrett 2009; Brundrett and Tedersoo 2018). Some of these non-mycorrhizal species produce abundant long root hairs, e.g., *Brassica oleracea* (Dechassa et al. 2003) and *Spinacia oleracea* (Föhse et al. 1991). For these plants, only P that is close to the surface of roots or root hairs is available (Lambers et al. 2008). These plants typically occur in nutrient-rich habitats with a high P concentration in the soil solution; they are commonly referred to as nitrophiles (Braun-Blanquet 1949), but in the present context, the term 'phosphophiles' is more appropriate (Lambers 2022).

In nutrient-poor, fire-prone environments, phosphophiles are common in the early stages of post-fire succession, during which a temporary (4–6 months) flush in soil P availability occurs (Brown and Mitchell 1986; Hester and Hobbs 1992). Although some P is volatilised during hot fires (> 500°C) (Giardina et al. 2000; Raison et al. 1985), the burning of vegetation can increase plant-available P relative to pre-fire levels; burning to black carbon increases plant-available P c. 10-fold and burning to ash c. 2- to 7.5-fold (Schaller et al. 2015). Phosphophiles in these environments often represent a significant fraction of the flora (Cowling et al. 1997), with examples typically monocarpic and fast-growing fire ephemerals, such as *Stipa elegantissima* (Poaceae), and *Macarthuria apetala* (formerly Aizoaceae, but now Macarthuriaceae) in kwongan (Pate et al. 1985); and *Itasina filifolia* (Apiaceae) in fynbos (Rutherford et al. 2011). While many of these species complete their lifecycle within the first year post-fire, other species such as those in the genera *Aspalathus* (Fabaceae) (Cocks 1994), *Kennedia* (Fabaceae) and *Comesperma* (Polygalaceae) (Miller and Dixon 2014) tend to live up to five years post-fire and are referred to as multi-year fire ephemerals.

Unlike longer-lived late post-fire succession species (e.g., Cyperaceae, Proteaceae, Restionaceae), phosphophiles do not need to acquire P from poorly soluble sources that dominate in such environments (McArthur 1991; Witkowski and Mitchell 1987). Species adapted to such conditions often rely upon root specialisations such as cluster roots in Proteaceae and some Fabaceae or dauciform roots in many Cyperaceae to 'mine' poorly soluble P (Lambers et al. 2008). Although not commonly reported for fire ephemerals, cluster roots do occur in several legume genera, for example, *Aspalathus* in fynbos (MacAlister et al. 2018; Power et al. 2010), and *Daviesia*, *Kennedia* and *Viminaria* in kwongan (Adams et al. 2002; Lamont 1972; Nge et al. 2020); Power et al. (2010), however, found that for fynbos species, these cluster roots are relatively rudimentary. They release smaller amounts and have lower rhizosphere concentrations of carboxylates compared with most Proteaceae, resulting in a low capacity to mobilise P from sparingly soluble sources. This restriction may explain why these fire ephemerals are limited to the immediate post-fire environment where sufficient P is available to support fast growth; beyond the early stage after a fire, a capacity to fix N_2 in the case of leguminous fire ephemerals offers little competitive advantage (Power et al. 2011).

The recent observation that fynbos plants belong to the world's thinnest-rooted plant community (Lu et al. 2022) may be highly relevant for fire ephemerals in that system. These thin roots possibly function like the roots of phosphophiles such as *Brassica oleracea* (Dechassa et al. 2003) and *Spinacia oleracea* (Föhse et al. 1991), as discussed above. It is highly unlikely that these very thin roots function as scavengers long after a fire, because, as we discuss below, even mycorrhizal hyphae are ineffective at extremely low P availability. If these hyphae are ineffective, it is hard to imagine how roots that are much thicker than fungal hyphae, even the thinnest roots in the world, could be effective at acquiring P from severely P-impoverished soils (Raven et al. 2018).

Post-fire P acquisition in resprouting perennial species

In addition to the classical mycorrhizal and non-mycorrhizal P-acquisition strategies discussed below, some species appear not to strongly depend on these strategies but acquire P when it is relatively available following a fire (Giardina et al. 2000). This strategy is expressed in both non-mycorrhizal [e.g., *Stirlingia latifolia* (Proteaceae) (Bowen and Pate 2004), *Adenanthos barbiger* (Proteaceae) (Q. Shen & H. Lambers, pers. obs.)] and mycorrhizal [e.g., *Macrozamia riedlei* (Zamiaceae) (Grove et al. 1980), *Xanthorrhoea preissii* (Xanthorrhoeaceae) (Korczynskyj and Lamont 2005)] pyrophilous species. While possibly not essential, mycorrhizas might play a role in P acquisition immediately after a wildfire.

Fire is a key determinant of P cycling in P-impoverished fire-prone ecosystems, because it enhances nutrient cycling and the soil P to carbon ratio (Brown and Mitchell 1986; Giardina et al. 2000; Kutiel and Shaviv 1989). A temporary increase of the total P concentration in the top soil post-fire (Brown and Mitchell 1986) likely benefits specific species (i.e. phosphophiles) that can take up P rapidly. Brown and Mitchell (1986) showed a 26% increase of the total P concentration and the resin-extractable P concentration increased more than five-fold. These concentrations returned to pre-fire levels within four months. The strategy to quickly acquire P immediately after a fire may be exhibited in all fire-prone ecosystems but might be successful only in P-impoverished habitats, since it requires considerable plasticity in growth, as exhibited by *S. latifolia* (Bowen and Pate 1993). The remarkable 'bubble roots' exhibited by this species likely contribute to its plasticity (Fig. 1). These structures not only store starch (Bowen and Pate 1993), but also P, albeit at similar concentration as in non-bubble roots (Fig. 1). These plants only increase their biomass when nutrient (especially P) availability increases, and thus do not need a scavenging or mining strategy, because P is abundant in a short window of time (van Blerk et al. 2021). Non-mycorrhizal *S. latifolia* does not produce cluster roots when mature (Lambers et al. 2021), but quickly resprouts after a fire (Fig. 1a, b) and rapidly accumulates biomass, but then stops increasing in size (Bowen and Pate 1993). Leaf [Mn] in mature *S. latifolia* plants is low, presumably due to low carboxylate concentrations in the rhizosheath (Lambers et al. 2021). In contrast to mature plants, seedlings of *S. latifolia* do produce cluster roots (Fig. 2). Similarly, based on a comparison of leaf [Mn] of *Stirlingia anethifolia* with that of co-occurring *Synaphea oligantha* (Proteaceae) (Fig. 3), we surmise that this *Stirlingia* species functions in a similar manner to *S. latifolia*. The leaf [Mn] of *Xanthorrhoea preissii* (Zhong et al. 2021), a mycorrhizal species (Brundrett and Abbott 1991) that rapidly resprouts after a wildfire (Fig. 4), suggests it functions in a very similar manner as non-mycorrhizal *Stirlingia* species. The same likely pertains to mycorrhizal *Kingia australis* (Dasypogonaceae), *Macrozamia riedlei* and *Xanthorrhoea gracilis* which also exhibit low mature leaf [Mn] (X.M. Zhou, K. Ranathunge & H. Lambers, pers. obs.). They are among the first to resprout and grow fast after a wildfire (Fig. 5), and then their growth declines to very slow rates (Grove et al. 1980; Korczynskyj and Lamont 2005; Lamont and Downes 1979).

In the cerrado of eastern Bolivia, the newly described *Plantago pyrophila* (Plantaginaceae), also resprouts and flowers quickly after a fire (Villarroel Segarra and Wood 2011). The same pattern is found in *Byrsonima verbascifolia* (Malpighiaceae), a common shrub in the cerrado biome of Brazil that exhibits low leaf [Mn] (Lambers et al. 2015b) and resprouts as quickly as six days after fire (Fig. 6). In campos rupestres, many Velloziaceae species (Conceição et al. 2013) and lineages of Fabaceae and Melastomataceae (Simon et al. 2009) rapidly resprout and flower after a fire, and this trait is also expressed in Cyperaceae, for example, *Bulbostylis paradoxa* in campos rupestres (Fidelis and Zirondi 2021); Oliveira et al. (1996) found that 44 orchid species in campos rupestres flower just two weeks after fire events. Indeed, several reviews conclude that a high diversity of species exhibit post-fire flowering in cerrado (Fidelis and Zirondi 2021), kwongan and fynbos (Lamont and Downes 2011), indicating that fire is an important factor influencing flowering in these fire-prone regions. Although the links between post-fire flowering, resprouting and P-acquisition strategies are yet to be fully explored in these communities, the combination of defoliation and fertilisation, mimicking the effects of fire, significantly increases flowering (e.g., in the geophytic fynbos grass *Erharta capensis*; Verboom et al. 2002).

In summary, acquiring P after its availability is temporarily increased is a common strategy in fire-prone P-impoverished ecosystems. We know next to nothing about what traits are required to ensure rapid uptake of P during a short window of enhanced P availability (Box 1). We envisage that the very thin

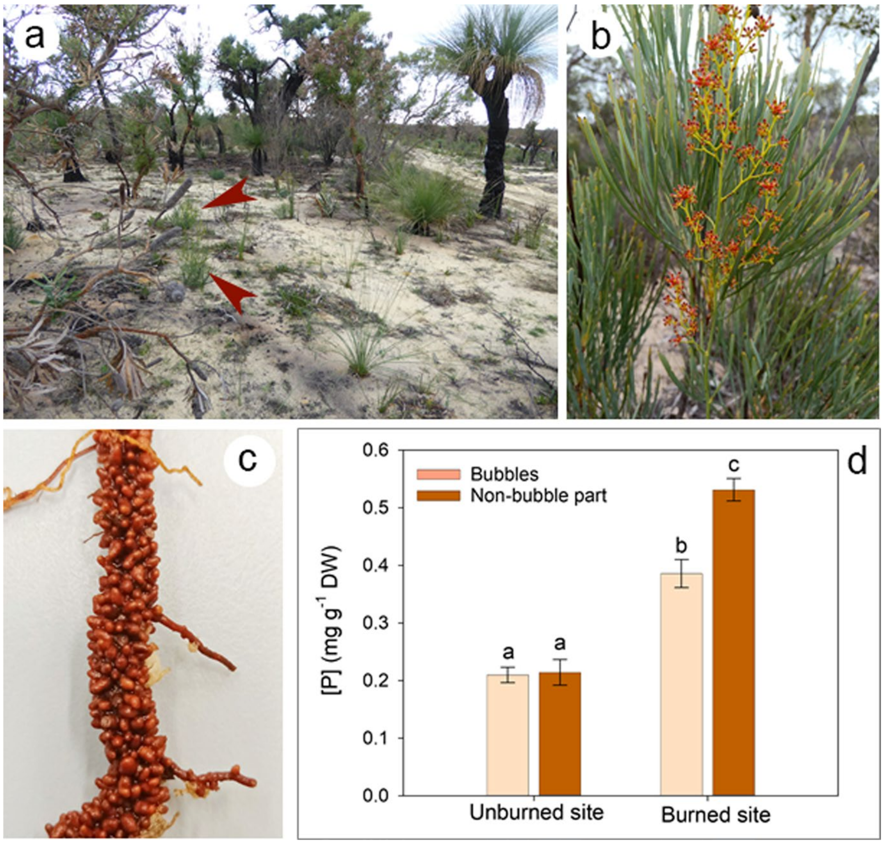


Fig. 1 *Stirlingia latifolia* (blueboy). (**a**) Habitat near Yanchep, south-western Australia, a few months after a wildfire showing vigorously resprouting plants (arrows). (**b**) Flowering, triggered by a fire. (**c**) Bubble roots. (**d**) Phosphorus (P) concentrations ([P]) expressed per unit dry weight (DW) in bubbles and non-bubble parts of the roots at both an unburned and a burned site. Different letters indicate significantly different means determined by ANOVA ($p < 0.05$). Photos: Hans Lambers (**a**) and Kosala Ranathunge (**b**, **c**)

roots observed in fynbos (Lu et al. 2022) may well play a role.

Interestingly, *Dasypogon bromeliifolius* (Dasypogonaceae), another species in the same family as *Kingia australis* that is among the first to resprout and flower after a fire (Rudall and Conran 2012), exhibits a relatively high leaf [Mn], similar to co-occurring *Banksia* species, and therefore likely releases carboxylates to access P in the time between fires (Fig. 6). Cyperaceae, like Proteaceae, are typically non-mycorrhizal (Brundrett 2009; Wang and Qiu 2006) and release carboxylates, with or without producing dauciform roots (Güsewell and Schroth 2017; Masuda et al. 2021). As a result, they tend to exhibit high leaf [Mn] (Hayes et al. 2014). However, there are clear exceptions (Hayes et al. 2014), and some of them may show a similar strategy as Proteaceae that resprout vigorously after disturbance by fire, without depending on carboxylates, e.g., *Lepidosperma tetraquetrum* (Cyperaceae) (X.M. Zhou, K. Ranathunge & H. Lambers, pers. obs.). In campos rupestres, *Bulbostylis paradoxa* (Cyperaceae) flowers three days after a fire

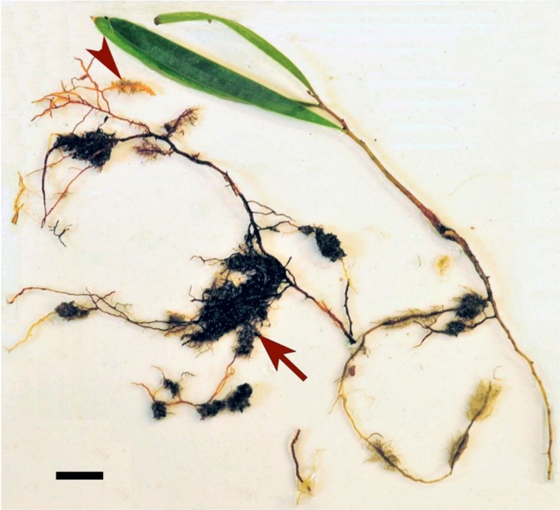


Fig. 2 Seedling of *Stirlingia latifolia* (blueboy) excavated from a natural habitat in Alison Baird Reserve, City of Gosnells in south-western Australia (Tauss et al. 2019), showing many cluster roots; arrowhead points towards a developing cluster and the arrow points towards a senesced cluster; scale bar = 20 mm. Photo: Kosala Ranathunge

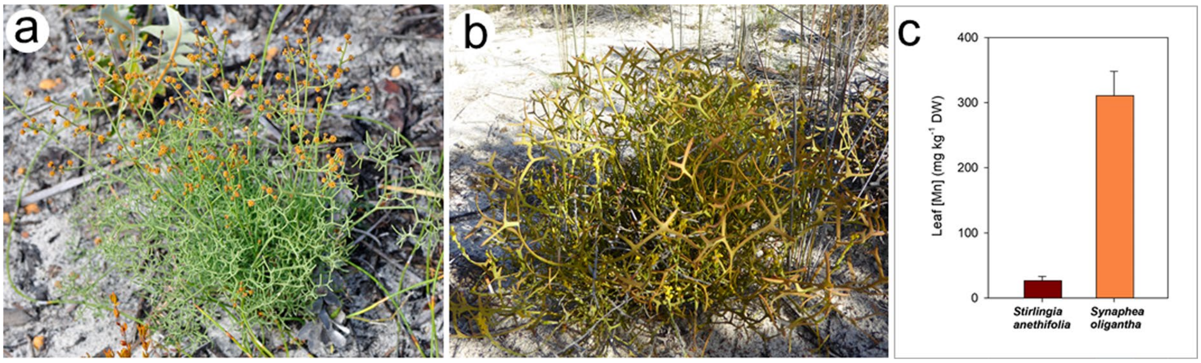


Fig. 3 *Stirlingia anethifolia* (Proteaceae). (**a**) Plant growing in its natural habitat in close proximity of (**b**) *Synaphea oligantha* (Proteaceae) near Hopetoun, south-western Australia. (**c**) Leaf manganese concentrations ([Mn]) expressed per unit dry weight (DW) of *S. anethifolia* growing in its natural habitat, shared with *S. oligantha*, used as a positive reference. Positive references comprise co-occurring species that are known to release abundant amounts of carboxylates (Zhong et al. 2021; Zhou et al. 2020). *** indicates significantly different means ($p < 0.001$). Photos: Hongtao Zhong

event (Fig. 5a), with inflorescences already starting to emerge within 24 h after the passage of fire (Fidelis et al. 2019). It would be worthwhile to further study Cyperaceae with low leaf [Mn] in low-P environments (Hayes et al. 2014; X.M. Zhou, K. Ranathunge & H. Lambers, pers. obs.) to determine how they acquire P.

The strategy to capitalise on nutrients released during a fire is likely confounded by other mechanisms that act together in this event. For instance, we are dealing only with resprouter species and not fire ephemerals, whose germination is triggered by karrikins in smoke (Flematti et al. 2004, 2015) or heat (Cocks and Stock 1997); we discussed these when covering phosphophile species. Resprouter species usually rely on non-structural carbohydrates to build new organs rapidly (Bowen and Pate 1993; Hansen et al. 1991; Pate et al. 1990, 1991); however, concurrent P acquisition is also essential, since P is part of the tissues. In Brazilian savannahs, fire stimulates absorptive root biomass, correlated with shoot regrowth (Oliveras et al. 2013). Variation in morphological root parameters reflect differences in soil chemistry, especially soil P and graminoid biomass changes (Le Stradic et al. 2021). To acquire P from ash, the P in the soil must be in solution. This may be the case when fire events are followed by rain, which is likely, because wildfires are usually started by lighting. Alternatively, hydraulic lift is a mechanism to bring P in solution (Pang et al. 2013) by bringing up water from deeper in the profile where plant-available P concentrations are very low (Turner et al. 2018) to shallow layers, where most of the P is located (Turner et al. 2018), especially after a fire (Giardina et al. 2000; Resende et al. 2011). Hydraulic lift is exhibited by a wide range of species (Belovitch et al. 2022). Indeed, *Byrsonima verbascifolia*, which resprouts very quickly after a fire exhibits hydraulic lift (Oliveira 2004). Once P is in solution and in the rhizosphere of these species, they likely take it up rapidly, but some may be sorbed onto soil particles. We have no information on the dynamics of the various fates of P in ash.

In summary, the remarkable strategy of post-fire active functional types is to switch from a typical nutrient-stress-tolerating (Grime 1977) or a *K* strategy (McArthur and Wilson 1967; Parry 1981) between fires, to an opportunistic ruderal (Grime 1977) or *r* strategy (McArthur and Wilson 1967; Parry 1981) immediately after a fire, nomenclature depending on which ecological theory is adopted. We are aware of minor shifts in strategy during plant ontogeny (Dayrell et al. 2018), but know virtually nothing about what underpins major shifts in strategy following a wildfire.

Mycorrhizas: P-scavenging strategies

The vast majority of terrestrial plant species can establish a symbiotic association with mycorrhizal fungi (Smith and Read 2008). Mycorrhizal associations can enhance plant P acquisition in moderately

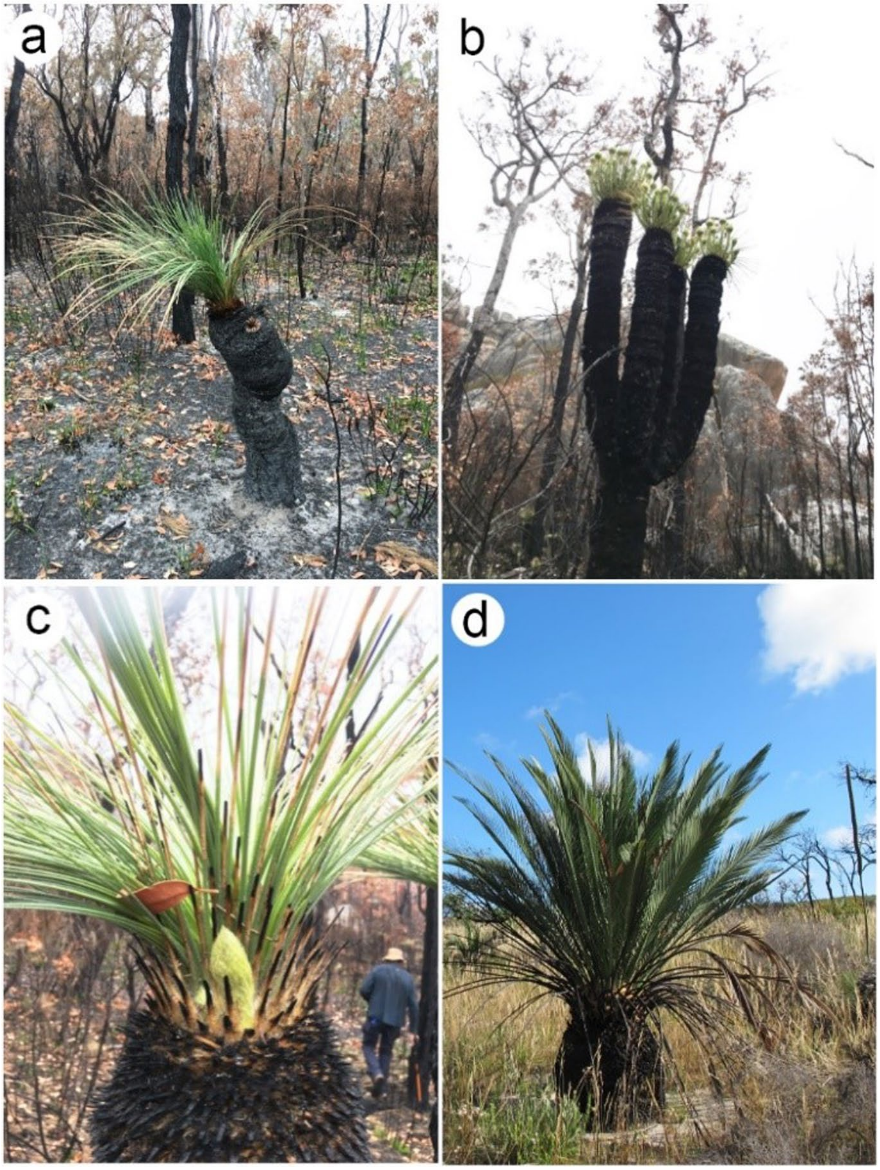


Fig. 4 Photos of plant species that are among the first to resprout and flower after a wildfire. (**a**) *Xanthorrhoea preissii* (balga or grasstree) (Xanthorrhoeaceae); (**b**, **c**) *Kingia australis* (kingia) (Dasypogonaceae); photos a-c were taken in Mount Lindesay National Park, south-western Australia; (**d**) *Macrozamia riedlei* in Lesueur National Park in south-western Australia, 10 months after a fire when its entire canopy of about 40 fronds had grown back. Photos: Hans Lambers

infertile soils (0.5-2 µM P in the soil solution), but when soils are severely P-impoverished (<0.5 µM P in solution), mycorrhizas are less effective (Lambers et al. 2015a; Parfitt 1979) and tend to be suppressed (Abbott et al. 1984; Chu et al. 2013; Treseder and Allen 2002). The soil solutions presented by Parfitt (1979) cannot be converted into mg P kg^{-1} soil, but we can compare these soil solution concentrations with those in a range of agricultural soils, representing a wide range in texture and organic matter content. The average inorganic P concentration ([Pi]) in the soil solution is 3 µM (range: 0.6 to 11 µM) (Lambers 2022). That range equates to concentrations of readily available P (i.e. resin-P, Bray-P or Colwell-P) of approximately 5 to 13 mg P kg^{-1} in agricultural soils (Sandral et al. 2019; Waddell et al. 2016). Concentrations of readily available P in old kwongan soils are 0.2 to 0.6 mg P kg^{-1} on low-rainfall sites (Gao et al. 2020; Laliberté et al. 2012), with rare values of about 5 mg P kg^{-1} soil at high-rainfall sites (Turner et al. 2018). In fynbos, which predominantly occupies sandstone-derived soils, a similar range of 0.4 to 2.7 mg P kg^{-1} occurs (Witkowski and Mitchell 1987). For a range of

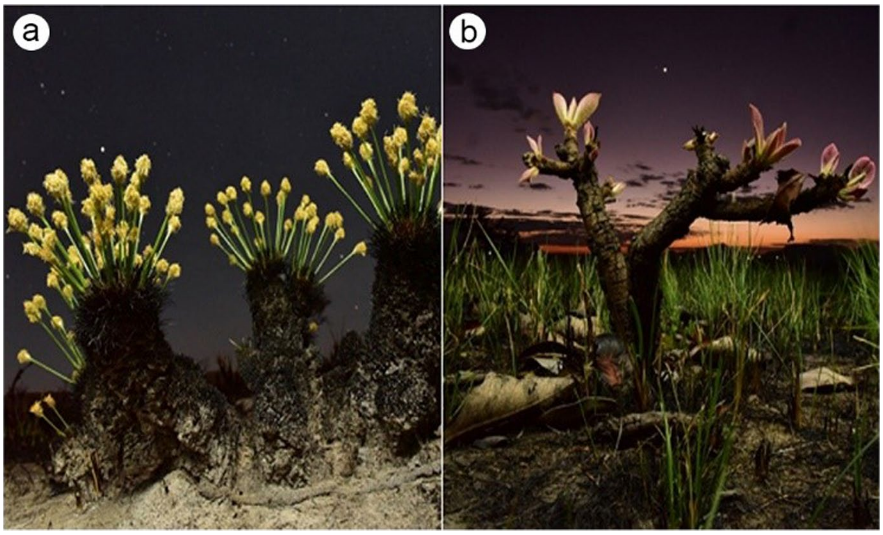


Fig. 5 (**a**) *Bulbostylis paradoxa* (Cyperaceae) flowering three days after a wildfire. (**b**) *Byrsonima verbascifolia* (Malpighiaceae) resprouting six days after a fire. Both plants were growing in their natural habitat in Chapada dos Veadeiros, Goiás, Brazil. Photos: Rafael S. Oliveira

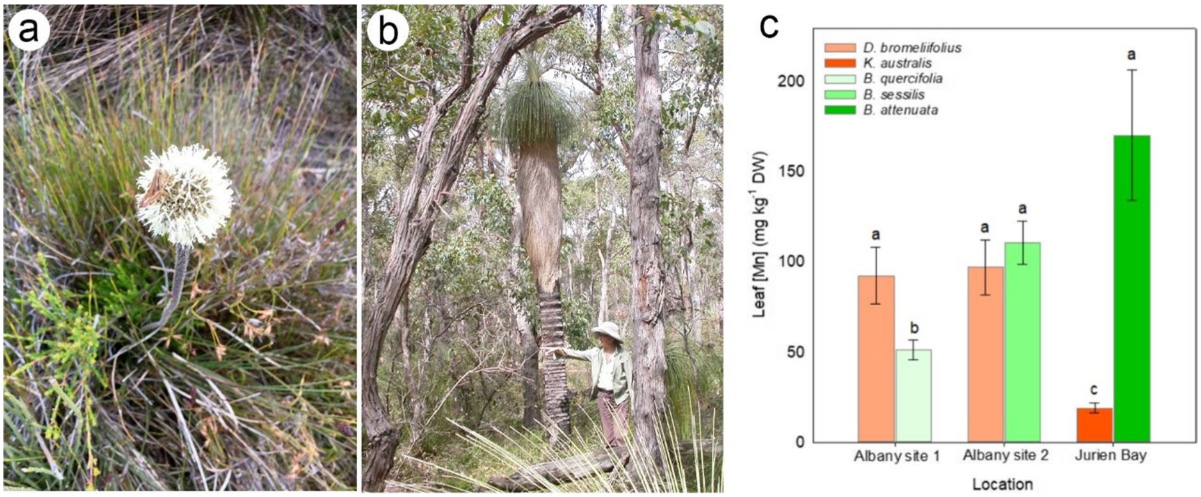


Fig. 6 (**a**) *Dasypogon bromeliifolius* (pineapple bush), (**b**) *Kingia australis* (kingia) (both Dasypogonaceae, growing at Karrak Reserve in Rosa Brook, south-western Australia), and (**c**) leaf manganese concentrations ([Mn]) expressed per unit dry weight (DW) of both Dasypogonaceae and three co-occurring *Banksia* species, which were used as positive references; all leaf material was collected in natural habitats of the species. Positive references comprise co-occurring species that are known to release abundant amounts of carboxylates (Zhong et al. 2021). Different letters indicate significantly different means determined by ANOVA ($p < 0.05$). Photos: Hans Lambers

campos rupestres sites, soil P is about 2.6 mg P kg^{-1} (Zemunik et al. 2018). That leads to the conclusion that in the range for agricultural soils (0.6 to 11 μM or 5 to 13 mg P kg^{-1}) mycorrhizas are expected to be effective at enhancing P acquisition. However, on the poorest sites in kwongan, fynbos and campos rupestres, mycorrhizas are likely ineffective, explaining a shift from mycorrhizal to non-mycorrhizal carboxylate-releasing strategies on the poorest sites (Zemunik et al. 2015, 2018). If mycorrhizal hyphae are ineffective at scavenging P at such a low P availability, the world's thinnest roots found in fynbos (Lu et al. 2022), which are much thicker and shorter than fungal hyphae (Raven et al. 2018), cannot then be expected to be effective as scavengers.

An important point to make here is that the observation that a plant forms a mycorrhizal association does not provide evidence that it actually depends on mycorrhizas to acquire P (Albornoz et al. 2021). In severely P-impoverished environments, the significance of mycorrhizal associations is likely that of protection against pathogens, rather than P acquisition (Albornoz et al. 2017; Lambers et al. 2018).

Phosphorus-mining strategies based on release of low-molecular-weight exudates are associated with mobilisation of a range of other elements

Mycorrhizal symbioses are crucial to scavenge P when the soil P availability is relatively low (Smith and Read 2008). However, as discussed above, mycorrhizas are rather ineffective when soil P availability is very low (Lambers et al. 2015a; Parfitt 1979). Under such conditions, P-mining strategies are more effective; an aspect of these P-mining strategies involves the release of P-mobilising low-molecular weight carboxylates or molecules with similar effects (Lambers et al. 2018; Nagarajah et al. 1970). Here we discuss how P-mobilising exudates not only release P, but also a range of other elements. For Mn and silicon (Si), this has been explored before (de Tombeur et al. 2021a; Lambers et al. 2015b), but here we present evidence that it is likely equally relevant for a range of other elements.

Phosphorus-mining strategies include cluster roots in Proteaceae (Delgado et al. 2014; Purnell 1960; Shane and Lambers 2005), Fabaceae (Allsop and Stock 1993; Brundrett and Abbott 1991; Gardner et al. 1981; Lamont 1972) and a range of actinorhizal families (Hurd and Schwintzer 1996; Louis et al. 1990; Reddell et al. 1997), dauciform roots in many Cyperaceae (Güsewell 2017; Selivanov and Utemova 1969; Shane et al. 2006), capillaroid roots in Restionaceae and Anarthriaceae (Hayes et al. 2014; Lambers et al. 2019; Lamont 1982), sand-binding roots in Haemodoraceae and a range of other families (Abrahão et al. 2014; Hayes et al. 2014; Smith et al. 2011), vellozioid roots in Velloziaceae (Abrahão et al. 2020; Teodoro et al. 2019), and carboxylate-releasing roots without obvious specialised structures, e.g., in *Cicer arietinum* (Fabaceae) (Neumann and Römheld 1999; Pang et al. 2018), *Vicia faba* (Fabaceae) (Li et al. 2013; Wen et al. 2019), *Lotus corniculatus* (Fabaceae) (Kidd et al. 2018) and *Kennedia* (Fabaceae) (Pang et al. 2010; Ryan et al. 2012), *Artemisia* (Asteraceae) and *Potentilla* (Rosaceae) species (Tian et al. 2021). The discovery of cluster roots in species or genera previously unknown to produce these specialised structures continues, e.g., in the *Daviesia* group (Mirbelioids; Fabaceae) (Lambers et al. 2019; Nge et al. 2020). Likewise, functionally-equivalent structures continue to be discovered, most recently in Cactaceae (Abrahão et al. 2014) and Velloziaceae (Abrahão et al. 2020; Teodoro et al. 2019).

The recent observation that fynbos plants belong to the world's thinnest-rooted plant community (Lu et al. 2022) may be relevant in the context of a P-mining strategy as well. We have no information on ultrathin roots in campos rupestres, but we do know that *Discocactus placentiformis* (Cactaceae) is a non-mycorrhizal species that produces abundant root hairs from roots with 200 µm diameter that are more than 1 mm long (Abrahão et al. 2014). These root hairs are thinner than ultrathin fynbos roots. *Discocactus placentiformis* exhibits a very high shoot [Mn] and plants grown in nutrient solution release carboxylates; hence it exhibits a mining, rather than a scavenging strategy. Likewise, *Persoonia* (Proteaceae), a large genus of 101 species, lacks cluster roots, but *Persoonia* species in kwongan produce abundant long root hairs (P.E. Hayes, unpubl.) and show high leaf [Mn] (Lambers et al. 2021). Again, these ultrathin structures convey a mining strategy, rather than being important to a scavenging approach. Capillaroid roots in Restionaceae are also ultrathin and express a mining strategy (Lambers et al. 2019).

In contrast to numerous angiosperms that release carboxylates either from specialised root structures or from non-specialised roots, as discussed above, Poaceae generally do not release large amounts of carboxylates (Lambers et al. 2018). There are exceptions among Poaceae, e.g., *Avena sativa* (Wang et al. 2016, 2018) and *Sorghum bicolor* (Leiser et al. 2014; Magalhaes et al. 2007). Release of carboxylates in small quantities tends to be associated with aluminium (Al) resistance, e.g., malate release in *Triticum aestivum* (Poaceae) (Delhaize et al. 1993) and citrate and malate in a *Eucalyptus* (Myrtaceae) clone (Li et al. 2021). However, Poaceae, which exhibit Strategy II to acquire iron (Fe) (Lambers and Oliveira 2019), do release phytosiderophores, generally in response to a low availability of Fe or zinc (Zn) (Ma 2005; Römheld and Schaaf 2004), but they also mobilise Mn (Zhang 1993). *Microlaena stipoides* (Poaceae) is a perennial grass with high leaf [Mn] when grown in a low-P habitat (X.M. Zhou, K. Ranathunge & H. Lambers, pers. obs.), but it does not release carboxylates in a low-P nutrient solution. Rather, this grass releases phytosiderophores when Fe sufficient, but P starved (X.M. Zhou, K. Ranathunge & H. Lambers, pers. obs.), suggesting that phytosiderophores may play a role in P acquisition under low-P conditions. Since Fe-deficient *Zea mays* (Poaceae) plants accumulate more P in their roots and shoots than Fe-sufficient ones (Zanin et al. 2017), phytosiderophores likely enhance P availability in soil. Because much inorganic P in soil is sorbed onto oxides and hydroxides of Fe in acid soils (Barrow et al. 2021), we may expect phytosiderophores to mobilise both Fe and P, as well as Mn, but this requires further investigation (Box 1).

Di- and tricarboxylates are effective at desorbing P sorbed onto oxides and hydroxides of Al and Fe, mobilising Al and Fe at the same time (Earl et al. 1979; Geelhoed et al. 1998; Lopez-Hernandez et al. 1979). It is therefore not surprising that there is a strong correlation between leaf [P] and leaf [Al] in carboxylate-releasing *Banksia* species (Proteaceae) grown in a range of soils collected in natural *Banksia* habitats (Fig. 7). The slope of the regression lines strongly depends on the species, because some *Banksia* species, e.g., *B. laricina*, are clearly Al-accumulating species, whereas others, e.g., *B. chaemaephyton*, exclude Al. For Fe, no such correlation is found, because Fe uptake in plants tends to be tightly regulated (Baxter et al. 2008; Jeong and Guerinot 2009). This tight regulation thus avoids Fe toxicity (Fageria et al. 2008). Although Fe acquisition is also tightly controlled in *Banksia* species, unlike that in non-graminaceous plants (i.e. typical Strategy I species (Ma 2005)), this control in *Banksia* is not based on regulation of Fe reductase (Cawthray et al. 2021). This finding challenges the model that is commonly accepted for species that exhibit Strategy I to acquire Fe.

In cerrado, *Miconia albicans* (Melastomataceae) accumulates large amounts of Al in its fruits (Pasta et al. 2019). This plant likely exhibits a carboxylate-releasing P-mobilising strategy, as do other Al-accumulating species in cerrado (Amaury de Medeiros and Haridasan 1985; de Andrade et al. 2011; Haridasan and De Araújo 1988).

A carboxylate-releasing strategy may well play a role in other severely P-impoverished systems in the tropics, but we have very little hard evidence to draw a strong conclusion (Box 1). The recent observation that many species (51 species in 24 genera, belonging to 12 families) in tropical forests on P-impoverished soils in Borneo hyperaccumulate Mn (van der Ent et al. 2019) suggests that these likely depend on carboxylate release to acquire P. One might also expect carboxylate-releasing strategies to be pervasive in Amazonia, but this has yet to be explored (Reichert et al. 2022).

We envisage that many species that accumulate Si, which is co-mobilised by P-mobilising carboxylates (de Tombeur et al. 2021a), will likely release carboxylates, e.g., *Equisetum* species (Equisetaceae) (Hodson and Evans 1995; Husby 2013) and *Phyllostachys heterocycla* (Poaceae) (Lux et al. 2003); alternatively, phytosiderophores may mobilise Si in Poaceae (Gattullo et al. 2016). The acquisition of P from the C horizon by *Equisetum* in an Alaskan shrub wetland brings it to the soil surface, increasing the amount of P in the O horizon (Marsh et al. 2000). This ability of *Equisetum* to act as a nutrient pump, and its accumulation of Si might be accounted for by carboxylate release.

Carboxylates may also be indirectly involved in mobilising non-essential elements. For example, species that accumulate fluoroacetate may be expected to release P-mobilising carboxylates, because the fluoride (F) availability in the natural habitats of these species tends to be very low (Twigg and King 1991; Vickery and Vickery 1972). Carboxylates may mobilise F from substrates that have low F availability. Examples of genera that comprise such species include *Gastrolobium* (Fabaceae) in south-western Australia (Aplin 1969; Twigg 2014), *Amorimia* (Malpighiaceae), *Arrabidaea* (Bignoniaceae) and *Palicourea* (Rubiaceae) in Brazil (Cook et al. 2014; Krebs et al. 1994; Lee et al. 2012) and *Dichapetalum* (Dichapetalaceae) in southern Africa (Peters et al. 1960; Vickery and Vickery 1972). *Palicourea rigida* (Rubiaceae) is one of the species in its genus that does not accumulate fluoroacetate (Cook et al. 2014). Its leaf [Mn] is low compared with that of other species in the same habitat (<50 mg kg^{-1}) (Lambers et al. 2015b), but it is the only *Palicourea* species for which leaf [Mn] is available. de Tombeur et al. (2021b) reported low leaf [Mn] for both *Gastrolobium linearifolium* and

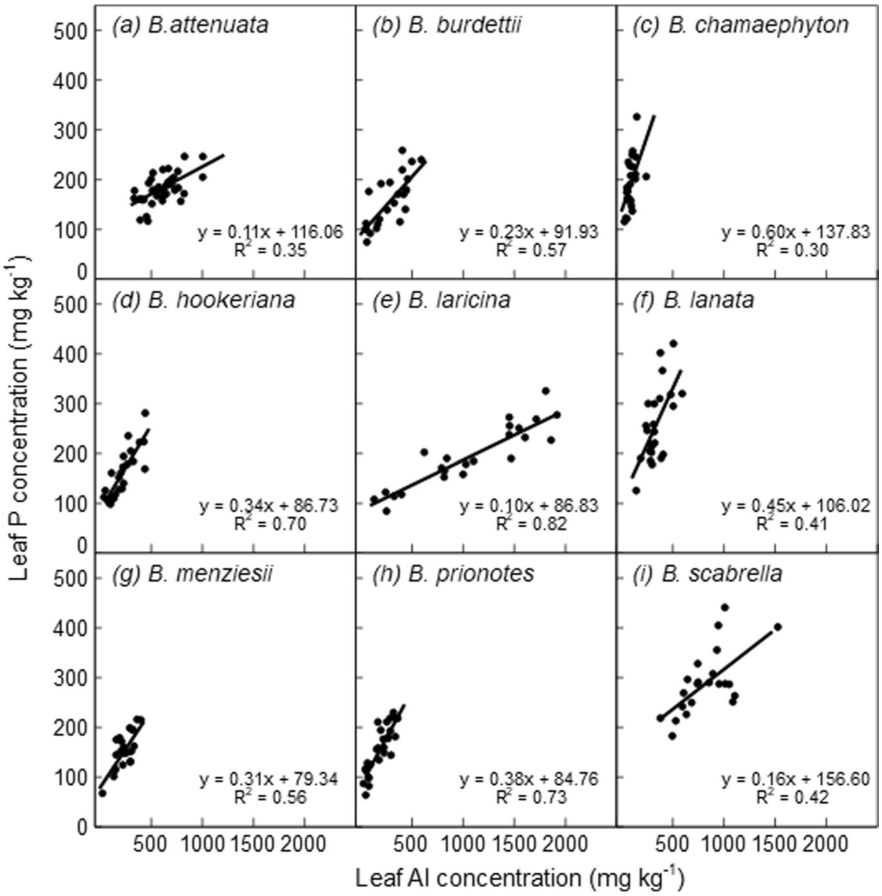


Fig. 7 Correlation between leaf phosphorus (P) and leaf aluminium (Al) concentrations expressed on a dry weight basis for nine *Banksia* species grown in soil collected from the natural habitats of the species. For further details, see Denton et al. (2007a, b)

G. nervosum, but for neither is toxicity due to fluoroacetate known (Chandler et al. 2002). The leaf [Mn] in the highly toxic *G. bilobum* (Chandler et al. 2002) is high (100 mg kg^{-1}), compared with the negative reference but not as high (200 mg kg^{-1}) as that of the cluster-rooted positive reference (Fig. 8). This indicates that *G. bilobum* depends on a carboxylate-releasing P-mobilising strategy. Further studies on leaf [Mn] and fluoroacetate accumulation in other *Gastrolobium* species as well as species in other fluoroacetate-bearing genera are needed to test the hypothesis that carboxylates play a role in F mobilisation.

DeGroote et al. (2018) suggested that hyperaccumulation of Mn in *Phytolacca americana* (Phytolaccaceae) may be a side effect of a P-acquisition mechanism, rather than an adaptation in its own right. Likewise, *Astragalus* (Fabaceae) and *Neptunia* (Fabaceae) species that hyperaccumulate selenium (Se) (Pinto Irish et al. 2021; Sors et al. 2005), and *Anacardium occidentale* (Anacardiaceae) that is known for its high [Se] in both reproductive (edible) and vegetative parts (Lim 2012), might take up Se because they mobilise it as a result of the release of carboxylates under P deficiency (Lan et al. 2012). Although Se is not an essential plant nutrient, it is sometimes considered a beneficial element (Silva et al. 2020). It may act as an antioxidant in plants at low concentrations (1 to 10 μg Se g^{-1} dry weight) because of its capacity to enhance the activity of radical-scavenging enzymes and the synthesis of non-enzymatic antioxidant compounds (Chauhan et al. 2019). The possible role of carboxylates in mobilising Se also warrants further investigation.

We surmise that species that hyperaccumulate elements such as Al, nickel (Ni), Zn, cadmium (Cd), Mn, arsenic (As), Se or rare earth elements (Li et al. 2018; Liu et al. 2021; Severne and Brooks 1972; Van der Ent et al. 2013, 2019; Webb 1954) do so because these elements are co-mobilised by carboxylates or functionally similar compounds that are released as a strategy to mobilise and acquire P. This is in line with results reviewed by de Tombeur et al. (2021a) on co-mobilisation of Si and P. This is not to say that all species that release carboxylates and co-mobilise metals and Si will accumulate these elements, because their uptake may involve transporters that are either not very specific (Baxter et al. 2008) or require specific transporters that do not occur in all species, as for Si (Coskun et al. 2019). When these transporters are not specific, accumulation is expected; when specific transporters are required, we only expect accumulation in species that express these specific transporters.

Phosphorus-mining strategies based on the release of phosphatases

Some plants access organic P, following release of acid phosphatases, without concomitant release of carboxylates. This is particularly prominent in Fabaceae (Houlton et al. 2008; Olde Venterink 2011), including Fabaceae in severely P-impoverished habitats (Png et al. 2017). This strategy is only effective when the organic P in soil is relatively mobile, e.g., breakdown products of phospholipids and nucleic acids (Doolette et al. 2011; Zhong et al. 2021), and would not work to access phytate, which strongly sorbs to soil particles (Anderson et al. 1974; Turner 2007). For example, in P-impoverished soil, *Adenanthos cygnorum* (Proteaceae), which only produces short-lived tiny ineffective cluster roots, can hydrolyse organic P that is less tightly bound by releasing acid phosphatases without large amounts of carboxylates (Q. Shen & H. Lambers, pers. obs.). Interestingly, this species exhibits an alternative P-acquisition strategy in more severely P-impoverished soil. Rather than producing cluster roots, it is facilitated by neighbouring cluster-root producing *Banksia attenuata* to acquire P (Q. Shen & H. Lambers, pers. obs.).

Facilitation by P-mobilising neighbours

Facilitation occurs when one plant enhances the growth, survival and/or fitness of another plant (Callaway 1995;

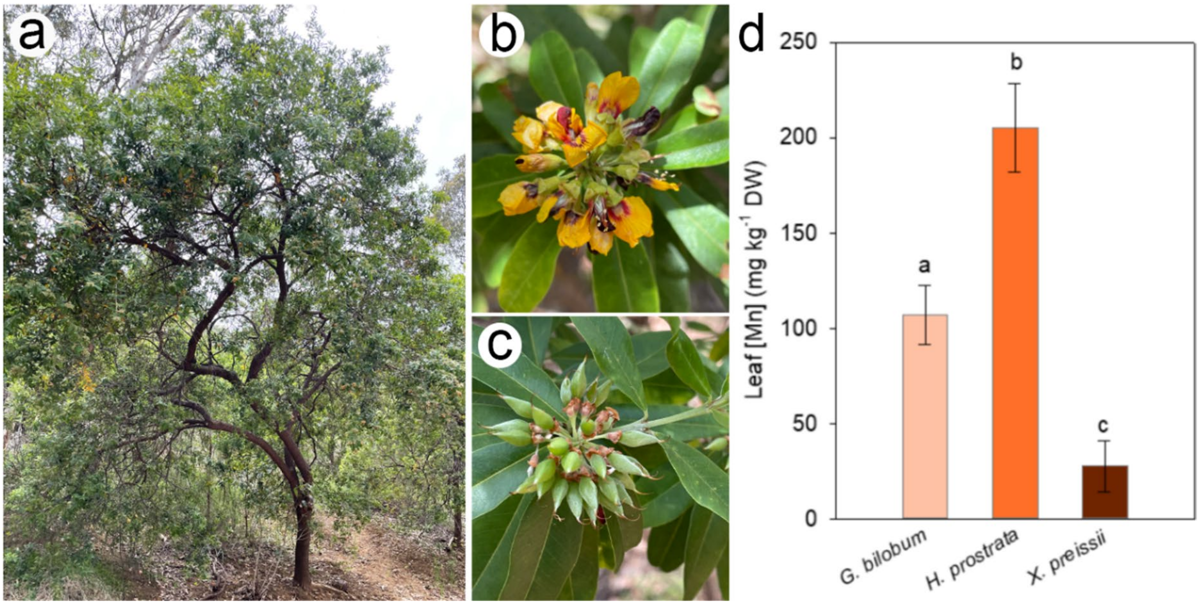


Fig. 8 *Gastrolobium bilobum* (heart-leaf poison; Fabaceae), which grows on soils with a low fluoride (F) availability and accumulates F as the highly toxic fluoroacetate (Chandler et al. 2002; Twigg 2014). (**a**) A tree in its natural habitat in Roley Pool Reserve near Perth in south-western Australia; (**b**) flowers and (**c**) developing fruits of *G. bilobum*. (**d**) Leaf manganese concentrations ([Mn]) expressed per unit dry weight (DW) of *G. bilobum* and two references species, *Hakea prostrata* (Proteaceae) as positive and *Xanthorrhoea preissii* (Xanthorrhoeaceae) as negative reference. The positive reference is known to release abundant amounts of carboxylates (Shane et al. 2004a), whereas the negative reference is a species that releases very few carboxylates (Zhong et al. 2021). Different letters indicate significantly different means determined by ANOVA ($p < 0.05$). Photos: Hans Lambers

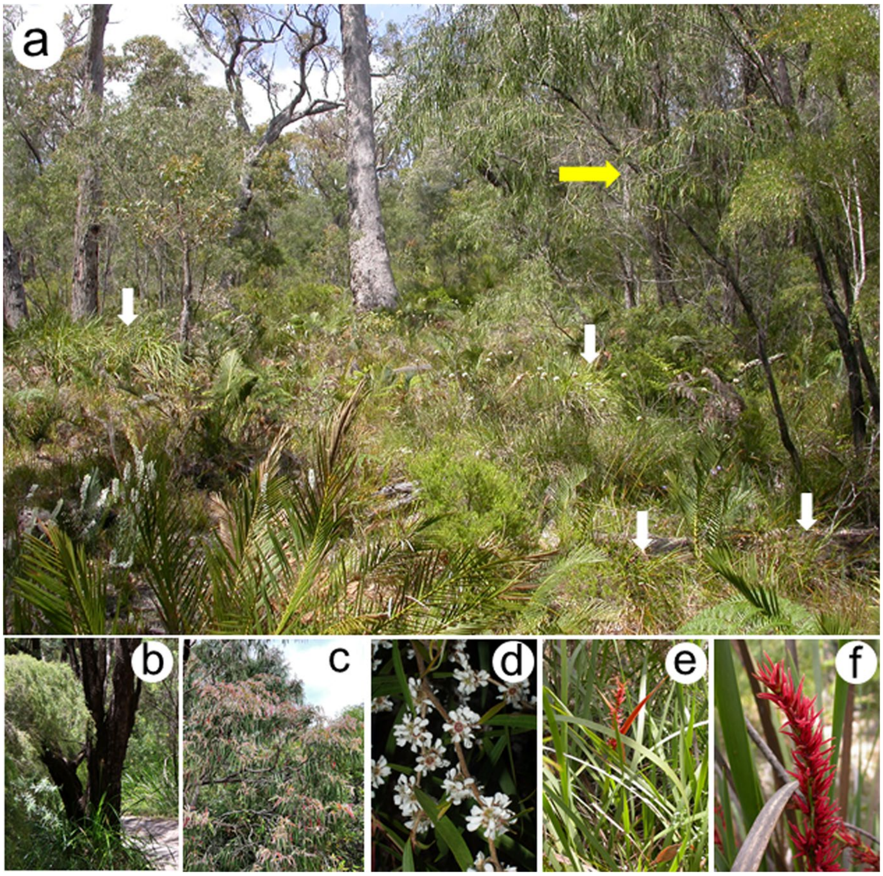
Fletcher et al. 2016). Facilitation based on P mobilisation by carboxylates released by P-efficient neighbours is increasingly acknowledged as a strategy to acquire P by P-inefficient neighbours (Lambers et al. 2018; Li et al. 2014; Yu et al. 2021). A promising way to explore this kind of facilitation is by comparing leaf [Mn] of targeted plants with those of neighbouring reference species (Muler et al. 2014; Zhou et al. 2020). Reference species should include both a positive reference, known to release large amounts of carboxylates and to have high leaf [Mn], and a negative reference that releases virtually no carboxylates and has low leaf [Mn] (Zhong et al. 2021; Zhou et al. 2020). Based on this approach, it is likely that P uptake in *Agonis flexuosa* (Myrtaceae) in south-western Australia which does not release carboxylates when P availability is low (Huang et al. 2017), is facilitated, possibly by Anarthriaceae, Cyperaceae and Restionaceae in the understorey (Fig. 9). Likewise, *Bossiaea* species (Fabaceae) that do not release carboxylates are likely facilitated in a similar manner, possibly by Proteaceae (Abrahão et al. 2018). Interestingly, *Bossiaea aquifolium* exhibits a high leaf [Mn], when compared with a positive reference (*Banksia grandis*) and a negative reference (*Xanthorrhoea preissii*) (X.M. Zhou, K. Ranathunge & H. Lambers, pers. obs.), so it likely releases P-mobilising carboxylates. *Hibbertia hypericoides* (Dilleniaceae) is also likely facilitated by Proteaceae (Zhong et al. 2021). When digging around its roots, it is common to find cluster roots of an adjacent Proteaceae (Fig. 10). In overgrazed Inner Mongolian steppes, Cyperaceae function as facilitators of some grasses (Yu et al. 2020a, b). Likewise, when these systems are fertilised with N, mimicking N deposition in acid rain, carboxylate release from *Artemisia frigida* (Asteraceae) will likely facilitate P uptake in some neighbouring grasses (Tian et al. 2021). Since not all grasses are facilitated in these systems, the facilitated species are also exhibiting a strategy; their traits must somehow match those of the facilitator. When roots of *Cleistogenes squarrosa* and *Bromus inermis* (both Poaceae) interact with a facilitating neighbour, they tend to show greater plasticity of root proliferation or rhizosheath acid phosphatase activity compared with other non-P-mobilising species (Yu et al. 2020a). Greater variation in these root traits strongly correlates with increased performance in the presence of a facilitator. In rhizobox experiments involving two species, *Hibbertia racemosa* (Dilleniaceae) exhibits more root growth towards its carboxylate-releasing *Banksia attenuata* (Proteaceae) neighbour than towards another *Hibbertia racemosa* plant (de Britto Costa et al. 2021). The facilitated plants may be responding to highly mobile allelochemicals released from the facilitator (Delory et al. 2016; Kong et al. 2018; Li et al. 2020) or microorganisms in its rhizosphere (Peñuelas et al. 2014; van Dam and Bouwmeester 2016), but we do not know what these signals might be. Thus, we can consider plasticity in specific root traits or directing growth towards a facilitator as a strategy to acquire P mobilised by a P-efficient neighbour, rather than concluding that these species lack a strategy (Yu et al. 2021).

Facilitation of P acquisition by carboxylate-releasing species may be indirect, as proposed for southern South American species on rich volcanic soils with low P availability (Lambers et al. 2012a). This facilitation involves shedding P-rich litter, and neighbours accessing organic P mediated by exuded or microbial phosphatases. This strategy can be expected to work only if the organic P is not strongly sorbed onto litter or soil. To access compounds like phytate, which strongly sorbs onto soil (Anderson et al. 1974; Turner et al. 2002), release of phosphatases or phytases alone would not work (Giles et al. 2017). However, in highly-weathered soils, very little organic P occurs as phytate (Turner et al. 2014; Zhong et al. 2021), and the organic P compounds that occur in these soils are more readily hydrolysed by rhizosheath phosphatases (Zhong et al. 2021).

Phosphorus-use efficiency: photosynthetic P-use efficiency

Whereas plants may express a range of divergent strategies to acquire P in habitats with low P availability, they appear to converge when it comes to their photosynthetic P-use efficiency (Denton et al. 2007a; Guilherme Pereira et al. 2019; Lambers et al. 2012b; Sulpice et al. 2014) and P-remobilisation efficiency and proficiency (Denton et al. 2007a; Guilherme Pereira et al. 2019; Hayes et al. 2014; Tsujii et al. 2017b; Zhong et al. 2021). Photosynthetic P-use efficiency (PPUE) is the rate of carbon-fixation per unit leaf P; a higher PPUE indicates a more efficient use of P for photosynthesis. Species from severely P-impoverished habitats tend to have a very low total leaf [P] (~0.3 mg g^{-1} in south-western Australia), yet maintain photosynthetic rates similar to many crop plants, thus achieving a high PPUE (Guilherme Pereira et al. 2019). Along the Jurien Bay chronosequence in south-western Australia, PPUE is much higher in species on the oldest most severely P-impoverished sites (~200 µmol CO_2 g^{-1} P s^{-1}), compared with that in species on younger P-richer

Fig. 9 A severely phosphorus (P)-impoverished habitat on a c. 2-million-year-old dune along the Warren chronosequence near Pemberton in south-western Australia (Turner et al. 2018). (**a**) *Agonis flexuosa* (Western Australian peppermint, yellow horizontal arrow) (Myrtaceae) is a significant overstorey tree that is likely facilitated by species in the understorey, for example Anarthriaceae, Cyperaceae or Restionaceae (white vertical arrows) (Huang et al. 2017). (**b**), (**c**), (**d**) Details of *A. flexuosa*. (**e**), (**f**) Female flowers of *Anarthria scabra* (Anarthriaceae), a significant component of the understorey. Photos: a, c-f: Hans Lambers; b; Graham Zemunik



sites (~90 µmol CO_2 g^{-1} P s^{-1}) (Guilherme Pereira et al. 2019). This is consistent across a range of species, indicating convergence in P-use efficiency. In contrast with the variation in P-acquisition strategies, convergent P-use strategies have been identified across a range of P-efficient species, including low mature leaf lipid-P concentrations, achieved through lipid remodelling, low investment in ribosomal RNA (rRNA), low inorganic-P concentrations, and a preferential allocation of P to photosynthetically active mesophyll cells (Guilherme Pereira et al. 2018; Hayes et al. 2018; Lambers et al. 2012b; Sulpice et al. 2014).

Lipid remodelling is the substitution of phospholipids with lipids that do not contain P (e.g., sulfolipids or galactolipids), thus reducing total leaf P (Tjellström et al. 2008). Phosphorus-efficient Proteaceae from south-western Australia show high levels of lipid remodelling during leaf development, thus reducing their mature leaf [P] without compromising photosynthetic capacity (Kuppusamy et al. 2014; Lambers et al. 2012b). In rice (*Oryza sativa* (Poaceae)) plants grown under low-P conditions, a low investment in phospholipids is strongly associated with a high PPUE, again, with no reduction in photosynthetic capacity (Hayes et al. 2022). We surmise that lipid remodelling has little impact on photosynthesis, because most phospholipids are found outside the chloroplasts and can be remodelled without impacting photosynthesis (Mamode Cassim et al. 2019; Nakamura 2017).

Nucleic acid P (predominantly rRNA) is generally the largest leaf fraction of organic P in plants grown at adequate P supply; 30% in *Hordeum vulgare* (barley; Poaceae) (Chapin and Bieleski 1982), 40% in *Oryza sativa* (Jeong et al. 2017) and as high as 50% in rice grown under low-P conditions (Hayes et al. 2022). The latter increase in relative allocation under low-P conditions reflects a reduction in other P fractions (mainly lipid P and inorganic P), rather than an increase in nucleic acid P (Hayes et al. 2022; Jeong et al. 2017). Phosphorus-efficient species allocate ~ 30–40% of total P to nucleic-acids, but this represents a very low concentration, < 0.1 mg g^{-1} (*Melaleuca systena* (Myrtaceae) and *Hakea prostrata*); thus investment in nucleic acid P (predominantly

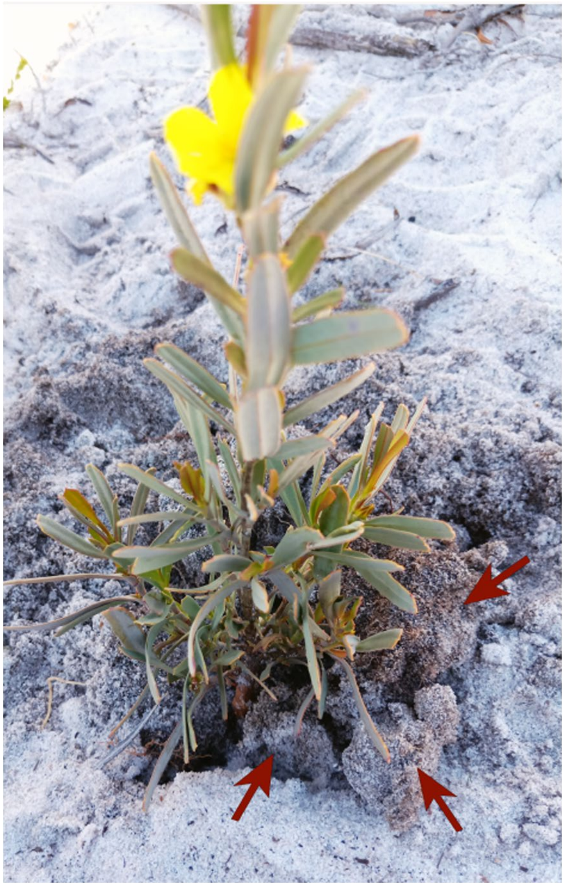


Fig. 10 *Hibbertia hypericoides* (Dilleniaceae) surrounded by cluster roots (pointed at by arrows) produced by a *Banksia* species (Proteaceae) in its natural habitat in Alison Baird Reserve in the City of Gosnells, south-western Australia (Tauss et al. 2019). Photo: Kosala Ranathunge

rRNA) is very low in highly P-efficient species (Sulpice et al. 2014; Yan et al. 2019). A low investment in rRNA significantly reduces total leaf [P], but is not associated with slow rates of photosynthesis; however, it may result in slower rates of protein turnover, which may impact the plant's ability to rapidly respond to environmental stresses (Lambers 2022). This needs further investigation.

Inorganic phosphate is often the largest P fraction when P supply is abundant. It closely reflects P supply in a range of crop and pasture plants such as *Brassica napus* (Brassicaceae), *Cucurbita maxima* (Cucurbitaceae) (Pant et al. 2008), *Oryza sativa* (Hayes et al. 2022; Jeong et al. 2017), *Medicago truncatula* (Fabaceae) (Branscheid et al. 2010), as well as plants such as *Hakea prostrata* and *Melaleuca systena* (Shane et al. 2004b; Yan et al. 2019) that are native to south-western Australia. Rice plants grown under low-P conditions show a significant decrease in inorganic-P concentration, from 30 to 18% of total P (Hayes et al. 2022), and similar reductions occur in field-collected *Melaleuca systena* and *Hakea prostrata*, when compared across sites of decreasing soil P availability within their natural range (Yan et al. 2019).

In addition to efficient investment of P into chemical P fractions, it is also important to consider where within a leaf P is actually invested. Phosphorus is preferentially allocated to specific leaf cells (Conn and Gilliham 2010). Many dicots allocate leaf P preferentially to epidermal cells (Conn and Gilliham 2010), whereas eudicots from severely P-impoverished habitats (Guilherme Pereira et al. 2018; Hawkins et al. 2008; Hayes et al. 2018; Shane et al. 2004b) and monocots (Boursier and Läuchli 1989; Dietz et al. 1992; Karley et al. 2000) preferentially allocate P to mesophyll cells. By preferentially allocating P to where it is needed in the greatest amount, photosynthetically active mesophyll cells, rather than metabolically inactive epidermal cells, these species are more P-efficient (Stitt et al. 2010; Tsujii et al. 2017a). This efficient P allocation is not restricted to species from kwongan, cerrado and fynbos (Guilherme Pereira et al. 2018; Hayes et al. 2018; Lambers et al. 2015a), but has also been found in a tropical tree species from a P-impoverished site in Borneo (Tsujii et al. 2017a). Proteaceae from severely P-impoverished south-western Australia (high PPUE) allocate P to mesophyll cells, whereas Proteaceae from P-richer regions in Chile (low PPUE) do not (Hayes et al. 2018), with similar observations made for other eudicot families (Guilherme Pereira et al. 2018). This P-use strategy therefore reflects the habitat in which species have evolved, rather than their phylogeny, and is an excellent example of a common P-use strategy in P-efficient species.

Phosphorus-use efficiency: P-remobilisation efficiency

A high remobilisation of P from senescing organs (mainly leaves) is important to reduce P loss, making that P available for growth elsewhere in the plant and preventing its loss to the environment, increasing overall P-use efficiency. Leaf P-resorption efficiency is the proportion of P resorbed, while P-resorption proficiency is the final concentration to which P is reduced in senescing leaves (Aerts and Chapin 1999; Killingbeck 1996). High levels of P-resorption efficiency and proficiency are common among species from severely P-impoverished systems, with as much as 90% being resorbed from senescing leaves in highly P-efficient Proteaceae and a community average of 79% in the most P-limited stage of the Jurien Bay chronosequence (south-western Australia) (Denton et al. 2007a; Hayes et al. 2014). Furthermore, species that preferentially allocate P to mesophyll cells also tend to have a more efficient P remobilisation, suggesting a possible link between these two strategies and emphasising the commonality of these traits among species from P-impoverished systems.

Results on cerrado species indicate a highly efficient P remobilisation, supporting the idea that cerrado plants, like those in fynbos and kwongan, are limited by P (Kozovits et al. 2007). However, that does not mean that P addition can be expected to enhance the productivity of individual plants in this system, as Lu et al. (2022) hypothesised for fynbos plants. Rather, P addition shifts the ecosystem, replacing slow-growing highly P-efficient species by faster-growing less efficient ones (Specht 1963). Heath species are excluded from more fertile soils by harmful effects on seedlings (P toxicity; Lambers et al. 2013; Nichols et al. 1979) and competition from more vigorous herbaceous plants in this environment (Heddle and Specht 1975).

In tropical tree species on Mount Kinabalu, Borneo, at severely P-impoverished sites, P-remobilisation efficiency was 93% in species from the most severely P-impoverished site (Tsujii et al. 2017b). Phosphorus remobilisation was greatest from the phospholipid and nucleic acid fractions, and least for the easily soluble fraction, possibly because breakdown of phospholipids and nucleic acids produces compounds captured in the easily soluble fraction. The residual fraction was also remobilised to a smaller extent. For species with higher P-remobilisation efficiency, resorption from the residual fraction was relatively high and similar in magnitude to that of labile fractions. This suggests that tree species inhabiting P-impoverished habitats increase their P-remobilisation efficiency by greater degradation of recalcitrant compounds, which are likely phosphorylated proteins (Tsujii et al. 2017b).

Phosphorus-use efficiency: leaf longevity

Whilst PPUE gives an indication of instantaneous P-use efficiency and P remobilisation provides insight into how much P is remobilised from senescing organs to be used elsewhere in the plant, as opposed to being lost in litter, neither provides information on the use of P over the lifetime of a leaf. To capture this, we need to know how long a leaf functions and uses the P invested in it. A low PPUE and P-remobilisation efficiency can be compensated by a long leaf longevity (Berendse and Aerts 1987). Leaf longevity varies substantially among species growing at the same site in kwongan. For a *Banksia* woodland with a kwongan understorey Veneklaas and Poot (2003) found

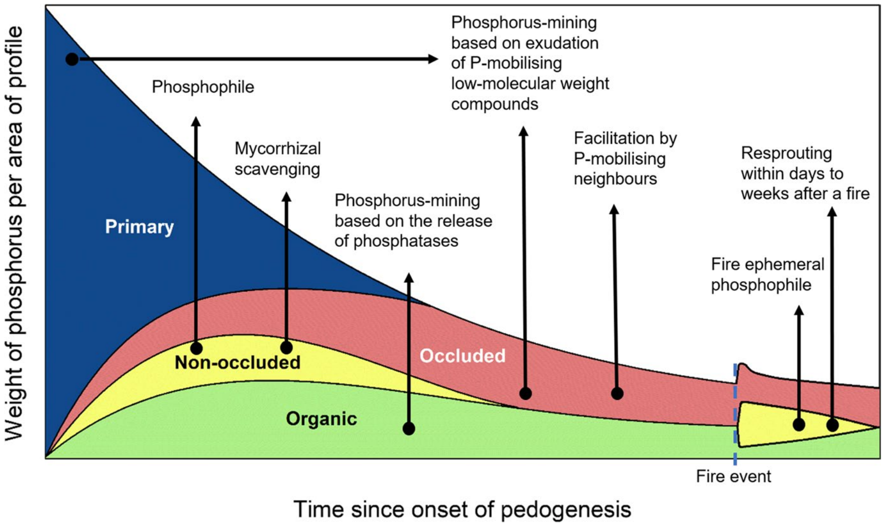

Weight of phosphorus per area of profile
Phosphophile
Phosphorus-mining based on exudation of P-mobilising low-molecular weight compounds
Mycorrhizal scavenging
Phosphorus-mining based on the release of phosphatases
Facilitation by P-mobilising neighbours
Resprouting within days to weeks after a fire
Fire ephemeral phosphophile
Primary
Non-occluded
Occluded
Organic
Fire event
Time since onset of pedogenesis

Fig. 11 Phosphorus (P)-acquisition strategies as dependent on soil age and time since fire in ancient landscapes. The changes in soil P with soil age are based on Walker and Syers (1976) as modified by Turner and Condron (2013). The P-acquisition strategies and effects of fire on soil P are discussed in detail in this review. Note that some species may express multiple strategies, for example, dependent on their developmental stage, time since a major disturbance such as fire, or location in the landscape, as discussed in this review

an average leaf longevity of 2.8 years for trees (deep-rooted), 3.1 years for other deep-rooted species, and 1.7 years for shallow-rooted species. The highest value was found for *Macrozamia riedlei* (Zamiaceae), 8.8 years, compensating for its low PPUE (57 μmol CO_2 g^{-1} P s^{-1}) because of its modest rates of photosynthesis (11.6 μmol CO_2 m^{-2} s^{-1}) and relatively high leaf [P] (600 μg g^{-1} DW) (P.E. Hayes and H. Lambers, unpubl.).

Perspectives and knowledge gaps

The diversity of P-acquisition and P-use strategies is one aspect contributing to the hyperdiversity in biodiversity hotspots. Many of these hyperdiverse systems are fire-prone and some species express strategies to acquire P after a fire that temporarily increases the soil P availability (Fig. 11). While fire is able to provide a temporary flush in soil P, we know very little about the dynamics of soil P in the first few months after a fire and what root traits allow rapid access to P in ash (Box 1; Fig. 12).

The P-acquisition strategies discussed in this review are equally relevant for ecosystems where P is increasingly becoming limiting for primary productivity, because of either overgrazing (Yu et al. 2020a, b), atmospheric N deposition (Tian et al. 2021, 2022) or global warming (Zhou et al. 2021). Many highly P-efficient species are excluded from more fertile soils by harmful effects on seedling growth (Lambers et al. 2013; Nichols et al. 1979) and competition from more vigorous herbaceous plants in this environment (Heddle and Specht 1975). A recent global meta-analysis revealed that P limitation of aboveground primary productivity in natural terrestrial ecosystems is far more common than widely acknowledged (Hou et al. 2020). Therefore, P-acquisition mechanisms, including those that maximise benefits resulting from facilitation based on P-mobilisation by neighbours, are likely pervasive and worth further consideration. Facilitation of a plant's P uptake by P-mobilising neighbours is a

Box 1 Outstanding questions

1. What is the role of 'ultrathin' roots of fynbos plants (Lu et al. 2022), given that it is unlikely they can act as scavengers (Raven et al. 2018) after the P concentrations that have increased after a fire have declined to their very low pre-fire values (Fig. 12; Brown and Mitchell 1986)?
2. What are the root traits that allow fast-growing fire ephemerals (Cowling et al. 1997; Pate et al. 1985) to rapidly acquire P that has become available after a fire?
3. What are the root traits that allow plants that are the first to resprout after a fire (Grove et al. 1980; Korczynskyj and Lamont 2005) to rapidly acquire P that is made available during a fire event? Does hydraulic lift play a role (Oliveira 2004)?
4. How common are carboxylate-releasing P-mobilising strategies in other biodiverse P-impoverished regions such as Amazonia (Reichert et al. 2022) and Borneo (van der Ent et al. 2019)?
5. What are the root traits that favour being facilitated by carboxylate-releasing P-mobilising species (Yu et al. 2021)?
6. What are the signals that play a role in positioning roots near those of a facilitating P-mobilising neighbour (Cramer et al. 2014; de Britto Costa et al. 2021)?
7. How widespread among Poaceae is the release of phytosiderophores in response to P deficiency (X.M. Zhou, K. Ranathunge & H. Lambers, pers. obs.)?

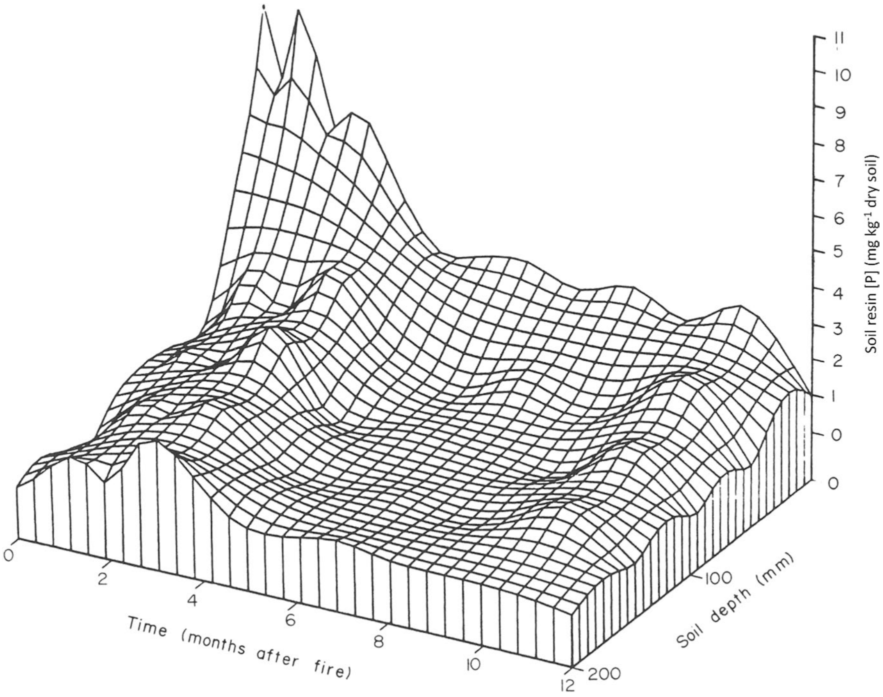


Fig. 12 Variation in plant-available phosphorus concentrations ([P]), measured as resin-P, expressed on a soil dry weight (DW) basis with time after fire, and soil depth in the < 2-mm fraction at a sandplain lowland fynbos location (Pella, South Africa). Reproduced with permission, with minor modification, from Brown and Mitchell (1986)

P-acquisition strategy in itself, and we still understand very little about the root traits that favour facilitation and what allows a plant to preferentially position its roots near those of a facilitating neighbour (de Britto Costa et al. 2021) (Box 1).

Analyses of leaf [Mn] as a proxy for rhizosphere carboxylate concentrations or functionally similar compounds in combination with glasshouse studies on selected species to verify the proxy, provide a novel tool to explore belowground interactions (Lambers et al. 2021; Zhong et al. 2021; Zhou et al. 2020). This has led to the conclusion that phytosiderophores, which are well known to be released by grass roots and to mobilise Fe, Zn and Mn, are also released in response to P deficiency in *Microlaena stipoides* (Poaceae) (X.M. Zhou, K. Ranathunge & H. Lambers, pers. obs.). We do not know how widespread this strategy is among grasses and how it is controlled by P deficiency (Box 1).

The interactions we discussed when focusing on P-impoverished landscapes are also highly relevant in agroecosystems based on intercropping (Dowling et al. 2021; Homulle et al. 2022; Li et al. 2014). As we are beginning to understand the subtleties of belowground interactions involving P-acquisition strategies (Yu et al. 2021), we can work towards optimisation of combinations of crop species and genotypes (Cong et al. 2020; Dowling et al. 2021). When aiming to restore disturbed sites in landscapes where P availability is very low, for example after mining or farming, the mechanisms discussed in this review, especially those focusing on facilitation of P acquisition based on carboxylate release, are highly relevant. Without suitable facilitators, species that depend on facilitation may never make it and hence be lacking from restored sites. It will be a challenge to identify suitable combinations of facilitators and facilitates species (Box 1).

In summary, in ancient landscapes there are a range of P-acquisition strategies that plants exhibit, some of which have been given little attention so far, especially those involving the use of P from ash (Box 1) and P released by facilitators (Box 1). Understanding this variation of strategies will inform management and restoration of hyperdiverse systems in P-impoverished fire-prone landscapes and contribute to greater P-use efficiency in managed landscapes.

Acknowledgements We thank Xue-Meng Zhou for her comments on an earlier version of this manuscript and three anonymous Reviewers for their constructive feedback on the first submission of this manuscript. Funding was provided by Australian Research Council Grants (DP0985685, DP110101120, DP130100005, DP140100148, DP200101013, LP200100341, FT170100195 and IH140100013) and by the Deputy Vice Chancellor (Research) at the University of Western Australia.

Funding Open Access funding enabled and organized by CAUL and its Member Institutions

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