

NUTRIENT-ACQUISITION STRATEGIES

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INTRODUCTION

PLANT LIFE IN THE SOUTHWEST of Western Australia has evolved on some of the world's most nutrient-impooverished soils. The availability of phosphorus is particularly low, but soil nitrogen, potassium and micronutrients are also notoriously scarce (McArthur, 1991). The extreme infertility of most soils is primarily due to the low nutrient content of the parent materials that gave rise to the sands and clays that are present (Wyrwoll *et al.*, 2014; Lane & Evans, 2019), as well as to their old age and strong degree of weathering (Leopold & Zhong, 2019). Over time, weathering leads to the loss of rock-derived nutrients (*e.g.*, phosphorus) in the absence of major soil-rejuvenating processes (*e.g.*, glaciations, volcanic eruptions, landslides) (Walker & Syers, 1976). On the other hand, nitrogen is mainly derived from the atmosphere, and continuously lost from the system, predominantly as a result of fire, when most nitrogen is volatilised (Wittkuhn *et al.*, 2017). Therefore, biological fixation of atmospheric nitrogen is crucially important to compensate for losses due to fire.

Given that extreme soil infertility imposes a severe constraint to plant growth, one might expect the south-western Australian flora to show low diversity, composed of only a restricted number of plant species that evolved the necessary adaptations to successfully grow on these soils. Yet we find the exact opposite. A key feature of the flora is its exceptionally high degree of floristic and functional diversity (Lambers *et al.*, 2010; Zemunik *et al.*, 2016). Interestingly, the greatest biodiversity in the southwest is found

on the most severely phosphorus-impooverished soils (Lambers *et al.*, 2010; 2014; Zemunik *et al.*, 2016). In these environments, competition among plants tends to be less important than it is in more nutrient-rich habitats; instead, facilitation, where one plant benefits from its neighbour, is more common (Lekberg *et al.*, 2018).

In this chapter, we present the main nutrient-acquisition strategies displayed by plants in the region that The Beeliar Group proposed as the Yule Brook Regional Park, and discuss their functioning. First, we focus on non-mycorrhizal species with specialised root adaptations to acquire phosphorus, as they are relatively abundant, compared with plants in regions where soil phosphorus availability is greater (Lambers *et al.*, 2014). Many of these specialised root adaptations would also enhance the acquisition of micronutrients, as discussed below. Second, we present some of the mycorrhizal strategies that we can find in the region, with the exception of the strategy in orchids, as this is covered in a separate chapter (Swarts & Dixon, 2019). Third, we present several symbiotic systems that contribute to biological nitrogen fixation, including the nodules of the legume-rhizobium symbiosis, the rhizothamnia of sheoaks and associated *Frankia*, an actinomycete, and the coralloid roots of cycads and associated cyanobacteria (Lambers *et al.*, 2014). We will leave the specialised nutrient-acquisition strategies of the many carnivorous (Cross, 2019) and those of parasitic species (Ranathunge *et al.*, 2019) in the region for separate chapters in this book.

PHOSPHORUS-ACQUISITION STRATEGIES

Broadly speaking, there are mycorrhizal and non-mycorrhizal phosphorus-acquisition strategies. The vast majority of vascular plants are mycorrhizal, only 8% are completely non-mycorrhizal and 7% have inconsistent non-mycorrhizal-arbuscular mycorrhizal associations (Brundrett & Tedersoo, 2018). Although mycorrhizal phosphorus acquisition is common in vascular plants, on the severely phosphorus-impooverished soils of south-western Australia, non-mycorrhizal species are far more common than expected on the basis of global figures (Lambers *et al.*, 2010; 2014). Below, we explain this paradox.

Cluster roots in Proteaceae, Casuarinaceae and Fabaceae

Almost all Proteaceae are non-mycorrhizal and most of them produce cluster roots (Shane & Lambers, 2005). Originally, the term 'proteoid' roots was used, because these specialised roots were first discovered in Australian Proteaceae (Purnell, 1960). They

have since been found in other families including Casuarinaceae, *e.g.*, *Allocasuarina humilis* (Lambers *et al.*, 2014) and Fabaceae, *e.g.*, *Viminaria juncea* (swishbush) (Lamont, 1972) and *Daviesia cordata* (Brundrett & Kendrick, 1988). Thus, cluster roots is now the preferred term.

Most Proteaceae species as well as cluster-root forming species in other families produce 'simple' cluster roots (Fig. 1). Simple cluster roots have a bottlebrush-like morphology. The main root is perennial, while cluster roots are ephemeral. For example, rootlet initiation to senescence occurs over approximately three weeks in *Hakea prostrata* (harsh hakea) grown in hydroponics at low phosphorus concentrations (Shane *et al.*, 2004). When growing in soil, relatively large volumes of soil become tightly bound to maturing cluster roots (Fig. 1). The formation of simple cluster roots in *Hakea prostrata* and many other Proteaceae is suppressed when plants are supplied with even relatively low phosphorus levels (Shane *et al.*, 2003).

Some Fabaceae and Casuarinaceae also produce



FIGURE 1. Simple cluster roots of *Hakea ceratophylla* (horned leaf hakea). Photo: Hans Lambers.

cluster roots (Fig. 2). *Daviesia cordata* (bookleaf) and *Daviesia physodes* (prickly bitter pea) are both non-mycorrhizal and both produce cluster roots (Brundrett & Abbott, 1991). However, *Viminaria juncea* (swishbush) makes both cluster roots (Lamont, 1972) and symbiotic associations with arbuscular mycorrhizal fungi (Brundrett & Abbott, 1991). In an attempt to discover whether phosphorus supply would cause a switch between the two phosphorus-acquisition strategies, de Campos

et al. (2013) discovered that they never switch off either strategy. The presence of these two strategies is associated with remarkably low leaf phosphorus concentrations, independently of phosphorus supply. This situation had never been found in any other plant species; leaf phosphorus concentrations invariably increase with increasing phosphorus supply (Lambers *et al.*, 2008a). *Allocasuarina humilis* produces simple cluster roots (Fig. 2) as well as mycorrhizas. However, the mycorrhizal symbioses are

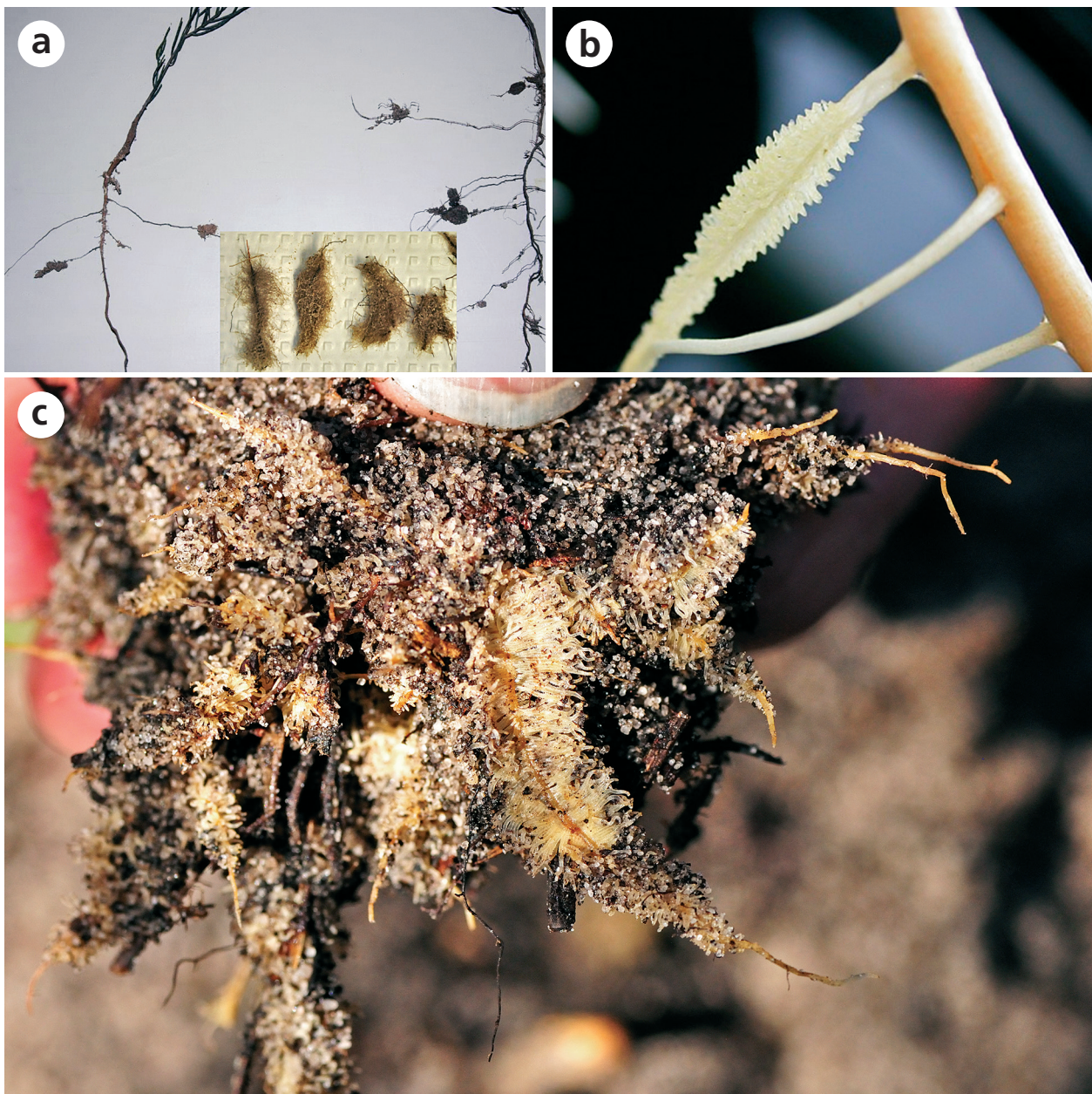


FIGURE 2. Simple cluster roots of (a) *Allocasuarina humilis* (dwarf sheoak) and (b) *Viminaria juncea* (swishbush). Previously unrecorded cluster roots of (c) *Daviesia physodes* (prickly bitter pea). Photos: a: Graham Zemunik; b: Michael W. Shane; a, inset, c: Hongtao Zhong.

unlikely to substantially assist phosphorus uptake by the Casuarinaceae in severely phosphorus-impo- verished soils of the Bassendean dunes. This is because roots of *Allocasuarina humilis* possess generally low levels of mycorrhizal colonisation (<20%) and colonisation does not significantly increase with decreasing soil phosphorus availability (Png *et al.*, 2017). The role of the mycorrhizas is likely to boost plant defence against pathogens, rather than en- hancing phosphorus uptake (Albornoz *et al.*, 2017; Lambers *et al.*, 2018).

‘Compound’ cluster roots are typical for all *Banksia* species (Fig. 3). Here, branched rootlets form cluster roots with a Christmas-tree-like mor- phology. In hydroponically-grown *Banksia attenuata* (slender banksia), the life span of a rootlet is over 15 days from initiation to maturity (Lambers *et al.*, 2014; Beeck, 2017). In field-grown banksias, a thick cluster-root mat typically develops just beneath the leaf litter or an ash bed (Fig. 3). As in the simple cluster roots of *Hakea prostrata*, the formation of compound cluster roots in banksias is suppressed when plants receive sufficient phosphorus, and induced when phosphorus supply is insufficient (Lambers *et al.*, 2002).

Both simple and compound cluster roots effectively ‘mine’ soil phosphorus. They release vast

amounts of carboxylates (the ionic component of organic acids) (Fig. 4). These are negatively charged, just like phosphate ions in soil. If the concentration of carboxylates is sufficiently high, they replace phosphate that is bound to soil particles, pushing phosphorus into solution, making it available for uptake by roots (Lambers *et al.*, 2015). *Hakea prostrata* and some other species with simple cluster roots release the carboxylates in an exudative burst, so the phosphorus is mobilised before microbes can build up and consume them (Watt & Evans, 1999; Shane *et al.*, 2004; Delgado *et al.*, 2014). In *Banksia attenuata* (slender banksia) and *Banksia sessilis* (parrot bush), the release of carboxylates is slower, but steady until they senesce, without an ‘exudative burst’ (Beeck, 2017). Cluster roots also release phosphatases, giving them access to organic phosphorus (Gilbert *et al.*, 1999; Grierson & Adams, 2000).

The costs associated with the formation and functioning of cluster roots are large, compared with those associated with maintaining mycorrhizas (Raven *et al.*, 2018). Cluster roots are a very effective strategy when the availability of phosphorus in soil is very low, based on their mining strategy. When soil phosphorus availability is greater, the mycorrhizal strategy is more effective, and far less costly. This

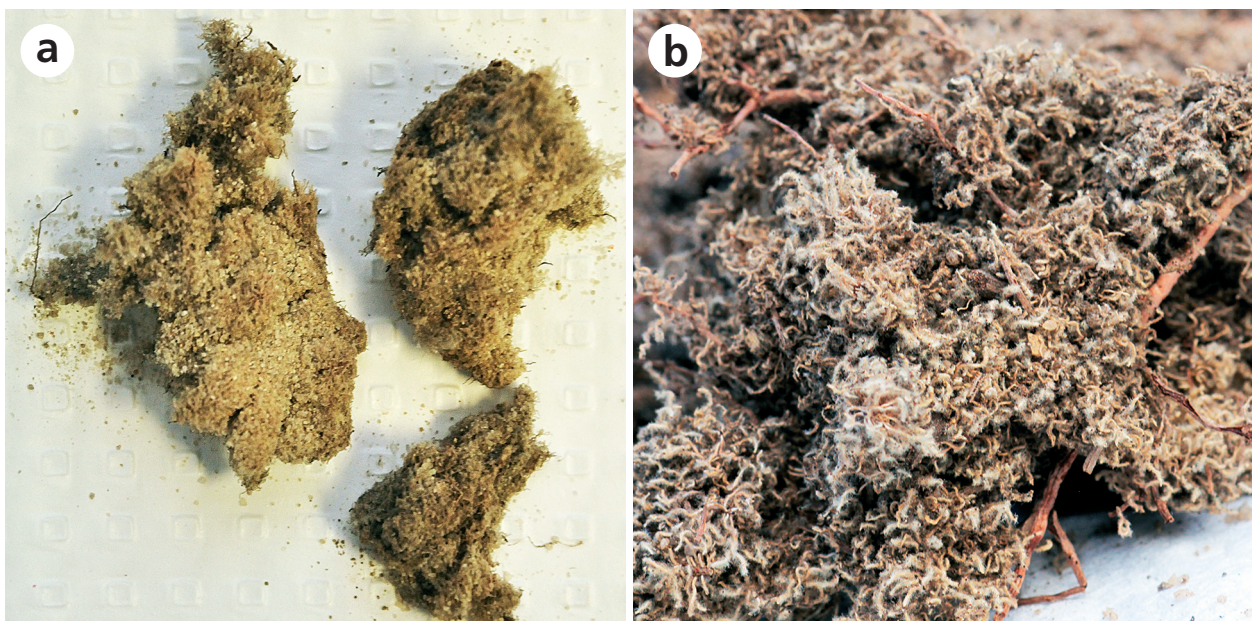


FIGURE 3. Compound cluster roots of (a) *Banksia attenuata* (slender banksia) and (b) *Banksia menziesii* (Menzies’ banksia). Photos: a: Hongtao Zhong; b: Graham Zemunik.

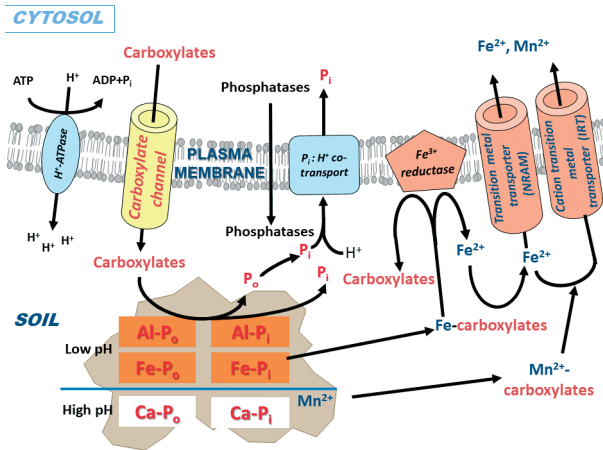


FIGURE 4. Effects of carboxylates (and other exudates) on inorganic (Pi) and organic phosphorus (Po) mobilisation in soil. Carboxylates (organic anions) are released via an anion channel. In the rhizosphere, carboxylates mobilise both inorganic and organic phosphorus, which both sorb onto soil particles. The carboxylates effectively take the place of phosphorus, thus pushing it in solution. Phosphatases hydrolyse organic phosphorus compounds, once these have been mobilised by carboxylates. Carboxylates will also chelate some of the cations that bind phosphorus, especially iron (Fe), and other micronutrients. Chelated Fe moves to the root surface, where it is reduced, followed by uptake by the roots, via a Fe^{2+} transporter. This transporter is not specific and also transports other micronutrients, especially manganese (Mn), which have been mobilised by carboxylates in soil. The carboxylates allow phosphorus to be ‘mined’, as opposed to the ‘scavenging’ strategy of mycorrhizas. For further explanation, see text (modified after Lambers *et al.*, 2015).

explains why cluster roots are common on phosphorus-impoveryished soils, whereas mycorrhizas are the norm when soils contain relatively larger amounts of phosphorus (Lambers *et al.*, 2014).

Dauciform roots in some Cyperaceae

Cyperaceae (sedges) is a largely non-mycorrhizal family (Brundrett & Tedersoo, 2018), although some sedge species produce arbuscular mycorrhizas (Lagrange *et al.*, 2013). Many Western Australian sedges produce dauciform roots (Fig. 5) (Lamont, 1974; Shane *et al.*, 2006b) as do many species in this family that occur elsewhere (Selivanov & Utemova, 1969; Davies *et al.*, 1973; Playsted *et al.*, 2006; Güsewell, 2017). These structures are much smaller than cluster roots and live for an even shorter time, about 10 days (Shane *et al.*, 2006a). Like simple cluster roots, they release carboxylates in an exudative burst. Like cluster roots, they also release phosphatases, giving them access to soil organic phosphorus (Playsted *et al.*, 2006). The formation of dauciform roots is suppressed when

plants contain sufficient phosphorus (Güsewell, 2017). Dauciform roots are the functional equivalent of simple cluster roots, despite major differences in morphology and anatomy. They only occur in some clades of Cyperaceae (Shane *et al.*, 2006b; Konoplenko *et al.*, 2017). Species of subgenus *Carex* form dauciform roots, while those of subgenus *Vignea* do not. Species with dauciform roots exude more citrate, but less oxalate and less total carboxylates than species without dauciform roots. They also allocate less biomass to roots. Species with and without dauciform roots show

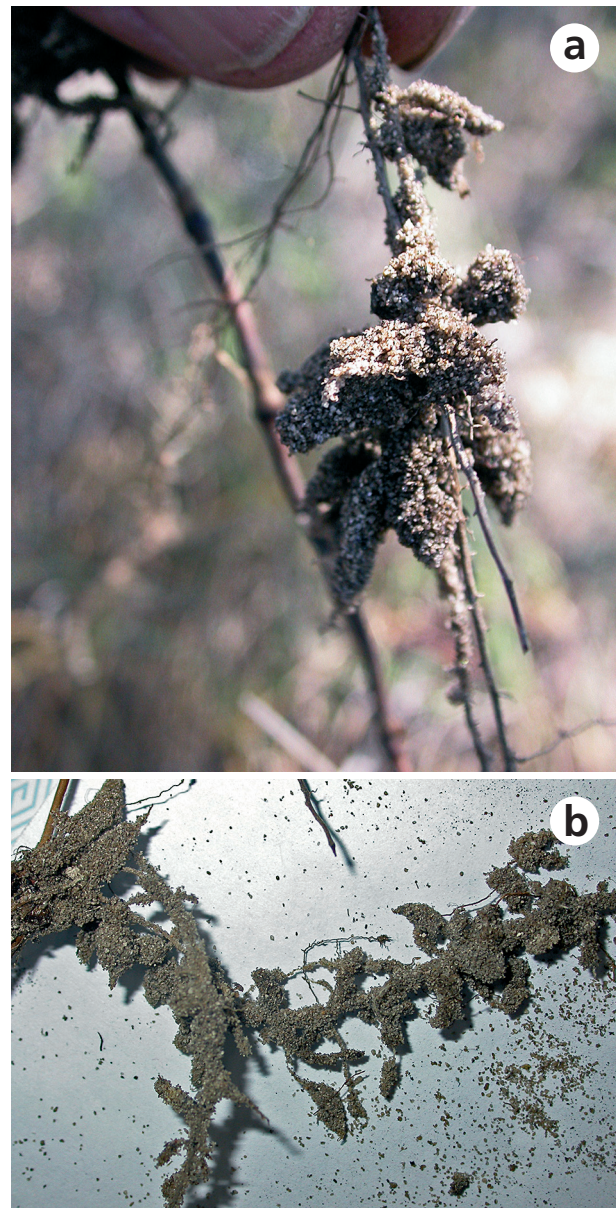


FIGURE 5. Dauciform roots of a sedge (a) freshly dug from the soil, and (b) after removing some of the adhering sand. Photos: Hans Lambers.

similar growth responses to different forms of phosphorus and different amounts of phosphorus supplied. This suggests that *Carex* species with and without dauciform roots do not exhibit distinct phosphorus-acquisition strategies (Güsewell & Schroth, 2017). What appears to matter most in this family is that they release carboxylates, rather than what specialised root structure they deploy to do so. Despite some differences in physiological function, dauciform roots in European *Carex* species do not influence the nutritional niche of this group of sedges (Güsewell & Schroth, 2017). Clearly, more research is warranted on this family that features prominently in our flora.

Capillaroid roots in Restionaceae and Anarthriaceae

Both Restionaceae and Anarthriaceae are non-mycorrhizal and both produce capillaroid roots (Lamont, 1982; Lambers *et al.*, 2014) (Fig. 6a). Like simple cluster roots and dauciform roots, these roots also release carboxylates in an exudative burst (Fig. 6b). There are no surveys to show how common this strategy is in these families.

Sand-binding roots in Haemodoraceae and other families

Sand grains are very tightly bound to the root surface by persistent root hairs in Haemodoraceae (Fig. 7). The majority of genera and species in the family worldwide possess sand-binding roots, but two of its 14 genera, *Conostylis* and *Tribonanthes*, have sister taxa with and without this trait (Smith *et al.*, 2011). The presence of sand-binding roots is the probable

ancestral condition for Haemodoraceae, associated with a high degree of phylogenetic conservation and some secondary loss, notably in *Conostylis*. Sand-binding roots in this non-mycorrhizal family likely function like cluster roots and other specialised roots discussed above (Hayes *et al.*, 2014), but further work is required to confirm this. Sand-binding roots in other families have not been studied systematically (Fig. 8), but this would be worth further exploration, taking advantage of surveys of leaf manganese (Mn) concentrations as a proxy for belowground carboxylate release (Lambers *et al.*, 2015; Pang *et al.*, 2018), as further explored below.

Mycorrhizas

The vast majority of vascular plants are mycorrhizal: 72% are arbuscular mycorrhizal (AM), 10% are orchid mycorrhizal, 2.0% are ectomycorrhizal (ECM), and 1.5% are ericoid mycorrhizal (Brundrett & Tedersoo, 2018)(Fig. 9). Mycorrhizal associations may enhance phosphorus acquisition from soils with low phosphorus availability by their ‘scavenging’ strategy, because fungal hyphae reach zones that are not accessible by roots or root hairs (Smith & Read, 2008). All mycorrhizal symbioses are capable of this, including the most widespread and ancient arbuscular mycorrhizal symbiosis.

Mycorrhizal fungi increase nutrient and water acquisition of plants as they significantly increase the volume of exploited soil. Arbuscular mycorrhizas enhance the acquisition of inorganic phosphorus and other relatively immobile nutrients (Smith *et al.*, 2015). There is growing evidence that arbuscular mycorrhizal fungi also provide protection to their hosts against pathogens (Wehner *et al.*, 2010) and can neutralise the negative effects of pathogens for seedling survival and growth (Liang *et al.*, 2015). Ectomycorrhizal fungi associate with far fewer plant species than arbuscular mycorrhizal fungi, but still provide the main nutrient-acquisition strategy in many ecosystems (*e.g.*, temperate forests) (Brundrett, 2009), and are thought to play a major role in nutrient cycling (Dickie *et al.*, 2014). Ectomycorrhizal fungi can access inorganic phosphorus as well as organic forms of both nitrogen and phosphorus due to their release of proteolytic enzymes and phosphatases (Smith *et al.*, 2015).

Plants can regulate mycorrhizal symbioses by either promoting or inhibiting them, depending

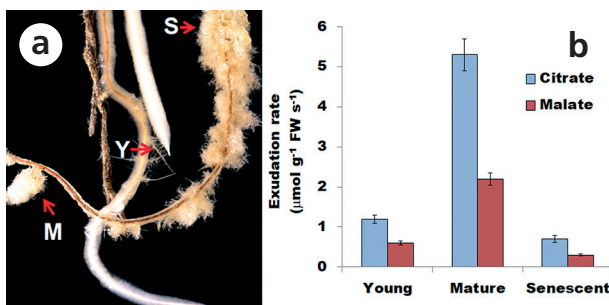


FIGURE 6. (a) Extremely fine short-lived capillaroid roots of *Lyginia barbata* (Anarthriaceae). Y, = young; M = mature; S = senescent (four weeks old). Photo: Michael W. Shane (Lambers *et al.*, 2014). (b) Carboxylate exudation from extremely fine capillaroid roots of *Lyginia barbata* (M.W. Shane, unpublished).



FIGURE 7. Sand-binding roots in Haemodoraceae. Photos: Michael W. Shane.

on nutrient availability (Lambers *et al.*, 2008b). For example, when soil phosphorus availability decreases, arbuscular mycorrhizal root colonisation increases, compensating for the low availability of phosphorus (Abbott *et al.*, 1984). On the other hand, when soil phosphorus is mainly in an organic form, ectomycorrhizal root colonisation tends to increase, because of their ability to obtain nutrients from organic matter (Antibus *et al.*, 1992). The ability of ectomycorrhizal hyphae to hydrolyse organic phosphorus via extracellular phosphatase enzymes (Smith & Read, 2008) might give them access to an important phosphorus fraction in the phosphorus-impooverished soils of Bassendean dunes (Turner & Laliberté, 2015). However, in the Bassendean dunes, ectomycorrhizal symbioses are unlikely to contribute substantially to the hydrolysis and acquisition of the available organic phosphorus fractions (Png *et al.*, 2017; Lambers *et al.*, 2018).

This is because ectomycorrhizal colonisation tends to be generally low for many co-occurring plant species on Bassendean dunes, and does not respond to decreasing soil phosphorus availability (Png *et al.*, 2017). Host identity (Martínez-García *et al.*, 2015) and interactions with other microbes (André *et al.*, 2003) can also have strong effects on mycorrhizal root associations. For example, several plant species can form dual associations with both arbuscular and ectomycorrhizal fungi (Pagano & Scotti, 2008). In these plants, colonisation by ectomycorrhizal fungi is thought to be detrimental for arbuscular mycorrhizal fungal colonisation. This has been attributed to competition between arbuscular and ectomycorrhizal fungi (Neville *et al.*, 2002).

Root infection by soil-borne pathogens can be inhibited when roots are colonised by either arbuscular (Wehner *et al.*, 2010) or ectomycorrhizal fungi (Branzanti *et al.*, 1999). The mechanisms by



FIGURE 8. Sand-binding roots of *Lyginia barbata* (Anarthriaceae). Photo: Hongtao Zhong.

which mycorrhizal fungi can provide defence against pathogens differ between arbuscular mycorrhizal and ectomycorrhizal fungi. Arbuscular mycorrhizal fungi induce systemic resistance against pathogens and trigger the formation of callose to surround infected root cells, possibly slowing pathogen invasion into surrounding cells (Herre *et al.*, 2007). Even though arbuscular mycorrhizal fungi may not produce antibiotic compounds themselves, there is some evidence that they alter their surrounding microbial communities in favour of microbes that are capable of producing these compounds (Wehner *et al.*, 2010). On the other hand, ectomycorrhizal fungi do not appear to induce systemic resistance to pathogens, but provide a physical barrier against infection by making a hyphal sheath around the root (Branzanti *et al.*, 1999) (Fig. 9a). In addition, they produce antibiotic compounds, for example diatretyne nitrile, a polyacetylene, diatretyne amide and diatretyne 3 (Marx, 1972).

In south-western Australian shrublands, Proteaceae are a prominent plant family (Zemunik *et al.*, 2015), because they produce cluster roots to

efficiently acquire phosphorus (Lambers *et al.*, 2014). Interestingly, despite their advantage in nutrient acquisition over other species with non-cluster-root strategies, they never dominate in this system (Zemunik *et al.*, 2015). In fact, other strategies, such as symbiotic associations with ectomycorrhizal fungi remain relatively abundant. Short-lived cluster roots lack an outer exodermal barrier immediately below their epidermis (Lambers *et al.*, 2018), thus potentially making them more susceptible to root pathogens (Laliberté *et al.*, 2015). Soil-borne pathogens may promote plant diversity by preferentially attacking, and therefore suppressing, species with superior phosphorus-acquisition strategies, rather than those with less effective strategies to acquire phosphorus (Lambers *et al.*, 2018). Recently, Laliberté *et al.* (2015) proposed that soil-borne pathogens promote plant diversity in phosphorus-impooverished soils as a result of a trade-off between phosphorus-acquisition efficiency and pathogen defence. On one hand, cluster-rooted species are highly efficient at phosphorus acquisition, but poorly defended against pathogens, and on the other hand, mycorrhizal

species are strongly defended against pathogens, but less efficient at acquiring phosphorus in severely phosphorus-impooverished soil. Hence, both mutualistic root symbionts and soil-borne pathogens would be key drivers of plant community structure and species diversity in hyperdiverse south-western Australian shrublands.

The ecological role of native soil-borne pathogens (especially oomycetes, or water moulds) in shaping plant diversity has received little attention in Mediterranean shrublands and this hypothesis requires further study (Albornoz *et al.*, 2017; Lambers *et al.*, 2018). This is particularly important, because the introduced oomycete *Phytophthora cinnamomi*, which has devastating effects on south-western Australian biodiversity (Davison & Rikli, 2019), is combated by spraying phosphite in national parks and reserves (Lambers *et al.*, 2013). This method of pathogen control likely also affects native oomycetes that may play a role in maintaining biodiversity in natural ecosystems. This situation makes it imperative to search for alternatives for phosphite to combat *Phytophthora cinnamomi*. A complementary hypothesis for the persistence of mycorrhizal plant species in this phosphorus-impooverished system is 'nutrient-mobilisation-based facilitation', where Proteaceae plants mobilise nutrients through the action of their cluster roots, and neighbouring plants 'tap into' this

resource before it is all taken up by the cluster roots (Muler *et al.*, 2014; Teste *et al.*, 2014). The available data support both of these hypotheses. For example, Teste *et al.* (2017) showed that the survival of non-mycorrhizal plant species is reduced when grown in live conspecific inoculum (*i.e.* soil collected from under the same species) compared with sterilised conspecific inoculum, while ectomycorrhizal plant species followed the opposite trend. This highlights the importance of ectomycorrhizal fungi in boosting the defence against plant pathogens. In accordance, Albornoz *et al.* (2017) showed that the presence of pathogens equalises the competitive ability of cluster-rooted and ectomycorrhizal plant species, providing a potential explanation for their coexistence and the high degree of plant diversity in south-western Australia.

Leaf manganese concentrations as a proxy for carboxylate-releasing roots

Exudation of carboxylates mobilise not only phosphorus, but also iron (Fe) and manganese (Mn) (Fig. 4). The uptake of iron is tightly controlled in roots, thus avoiding iron toxicity inside the plant, but the uptake of manganese is not (Lambers *et al.*, 2015). As a result, Proteaceae with functional cluster roots tend to have higher leaf manganese concentrations than their mycorrhizal neighbours (Hayes *et al.*, 2014). Mycorrhizas tend to intercept

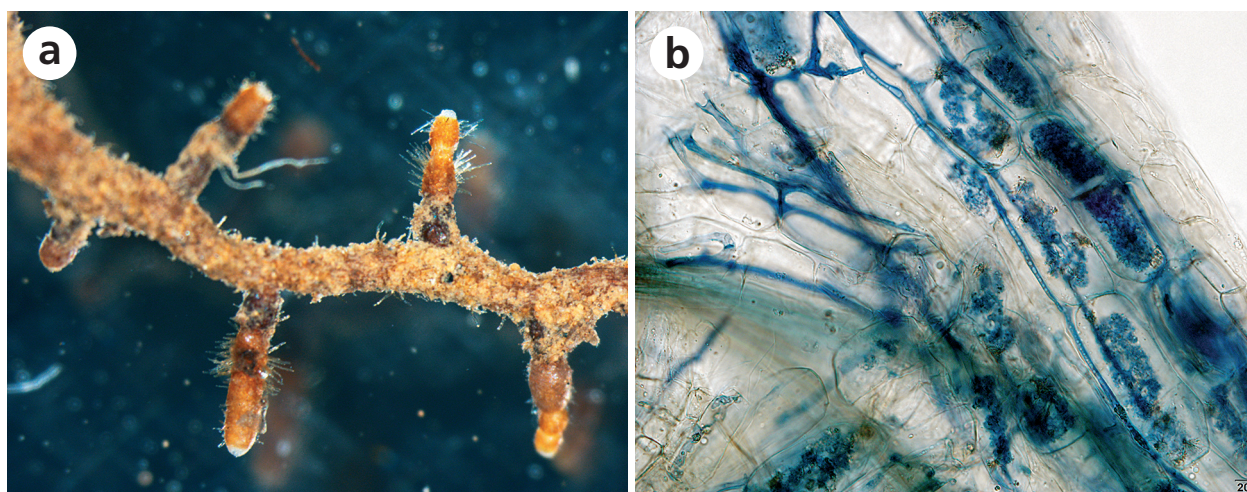


FIGURE 9. Roots colonised by mycorrhizal fungi. (a) Roots of *Pseudotsuga menziesii* (Douglas fir) heavily colonised by ectomycorrhizal fungi. A mantle covers root tips from the base and 'scavenging' extraradical hyphae can be seen around colonised root tips. (b) A root of *Melaleuca systema* (coastal honeymyrtle) colonised by arbuscular mycorrhizal fungi. Fungal structures were stained with ink and vinegar. Intraradical hyphae and arbuscules can be seen. Photos: Felipe E. Albornoz.

manganese, thus further adding to the contrast between species (Arines *et al.*, 1989; Lehmann & Rillig, 2015). High leaf manganese concentrations are not restricted to Proteaceae, but are also typical for other non-mycorrhizal carboxylate-releasing species (Hayes *et al.*, 2014; Oliveira *et al.*, 2015).

When growing next to *Banksia attenuata* (slender banksia) in pots in a glasshouse, *Scholtzia involucrata* shows higher leaf manganese concentrations than when grown alone, indicating that it benefits from the nutrients mobilised by its neighbour (Muler *et al.*, 2014). Leaf manganese concentration can therefore be used to explore belowground phosphorus-acquisition strategies without extensive digging and sampling of carboxylates (Hayes *et al.*, 2014). We can also use it to explore interactions between plants exhibiting different phosphorus-acquisition strategies, but this is still in its infancy. In agriculture, it can be used to select genotypes that differ in their release of carboxylates, thus allowing to breed cultivars for specific environments (Pang *et al.*, 2018).

Root anatomy of carboxylate-releasing Proteaceae and Fabaceae and of species in other families

Nutrient and water uptake from the soil solution is critical to any plant, and the functioning of a root relies on its anatomy and physiology (Ma & Peterson, 2003; Ranathunge *et al.*, 2011). At the same time, roots must be able to exclude potentially harmful substances, *e.g.*, toxic gases, organic acids and toxic metals, and prevent the entry of pathogens. This selectivity of roots is accompanied by a complex root structure (Esau, 1977; Schreiber *et al.*, 1999). Our knowledge of the root anatomy of south-western Australian native plants including Proteaceae is still scarce. We recently started exploring detailed comparative anatomical features of species endemic to south-western Australia from three families: Proteaceae, Fabaceae and Casuarinaceae, all producing roots with specialised phosphorus-mining clusters. Detailed anatomical and histochemical studies of cluster roots from these families revealed species-specific differences, but they all have a common and unique character – the lack of an exodermis, the outermost cortical layer and a barrier for the entry of water and pathogens in the roots (Fig. 10).

Not only Proteaceae, but also Fabaceae such as

Lupinus angustifolius, *Lupinus luteus*, *Cicer arietinum* and *Glycine max*, lack a suberised exodermis in their roots (Perumalla *et al.*, 1990; Hartung *et al.*, 2002; Ranathunge *et al.*, 2008; Bramley *et al.*, 2009). Most of these Fabaceae release large amounts of carboxylates (Watt & Evans, 1999; Veneklaas *et al.*, 2003; Pearse *et al.*, 2006). On the other hand, monocots such as *Oryza sativa* (rice), *Saccharum officinarum* (sugarcane), *Triticum aestivum* (wheat) and *Zea mays* (maize) do produce a suberised exodermis (Clark & Harris, 1981; Perumalla & Peterson, 1986; Perumalla *et al.*, 1990; Ranathunge *et al.*, 2003). Unlike many Proteaceae and Fabaceae, monocots often release some specific exudates, but do not release large amounts of carboxylates (Delhaize *et al.*, 1993; Ma *et al.*, 2003; Pearse *et al.*, 2006; Li *et al.*, 2013; Oburger *et al.*, 2014; Sun *et al.*, 2016). Myrtaceae such as *Calothamnus hirsutus* do not develop cluster roots and lack the capacity to release large amounts of carboxylates, as is common in Proteaceae (Shane & Lambers, 2005). However, this species develops a strong and complete ring of exodermis, which would shield pathogen entry into roots (Fig. 10). There is plenty of research on angiosperm species in specific families that do or do not produce an exodermis (Perumalla *et al.*, 1990; Hose *et al.*, 2001), but there is no research on their carboxylate exudation or their leaf manganese concentrations, which can be used as a proxy for carboxylate concentrations in the rhizosphere (Lambers *et al.*, 2015; Pang *et al.*, 2018). We surmise that species that release large amounts of exudates have evolved to strategically modify their root structure for rapid carboxylate exudation in order to efficiently take up phosphorus from nutrient-poor soils. This hypothesis requires further testing involving a wider range of plant families.

Absence of a suberised exodermis may have some negative consequences such as providing easy access for pathogens to enter the root tissues, and allowing loss of water and nutrients from the roots to the dry soil by back-flow (Hose *et al.*, 2001; Thomas *et al.*, 2007; Ranathunge *et al.*, 2008). In some plant species, such as *Glycine max* (soybean), ‘diffuse suberin’ in the epidermal cell walls fulfils the requirement of an exodermis, which is lacking in soybean. Diffuse suberin in the epidermis acts as a physical and chemical barrier for the penetration of *Phytophthora sojae*, an oomycete (water mould)

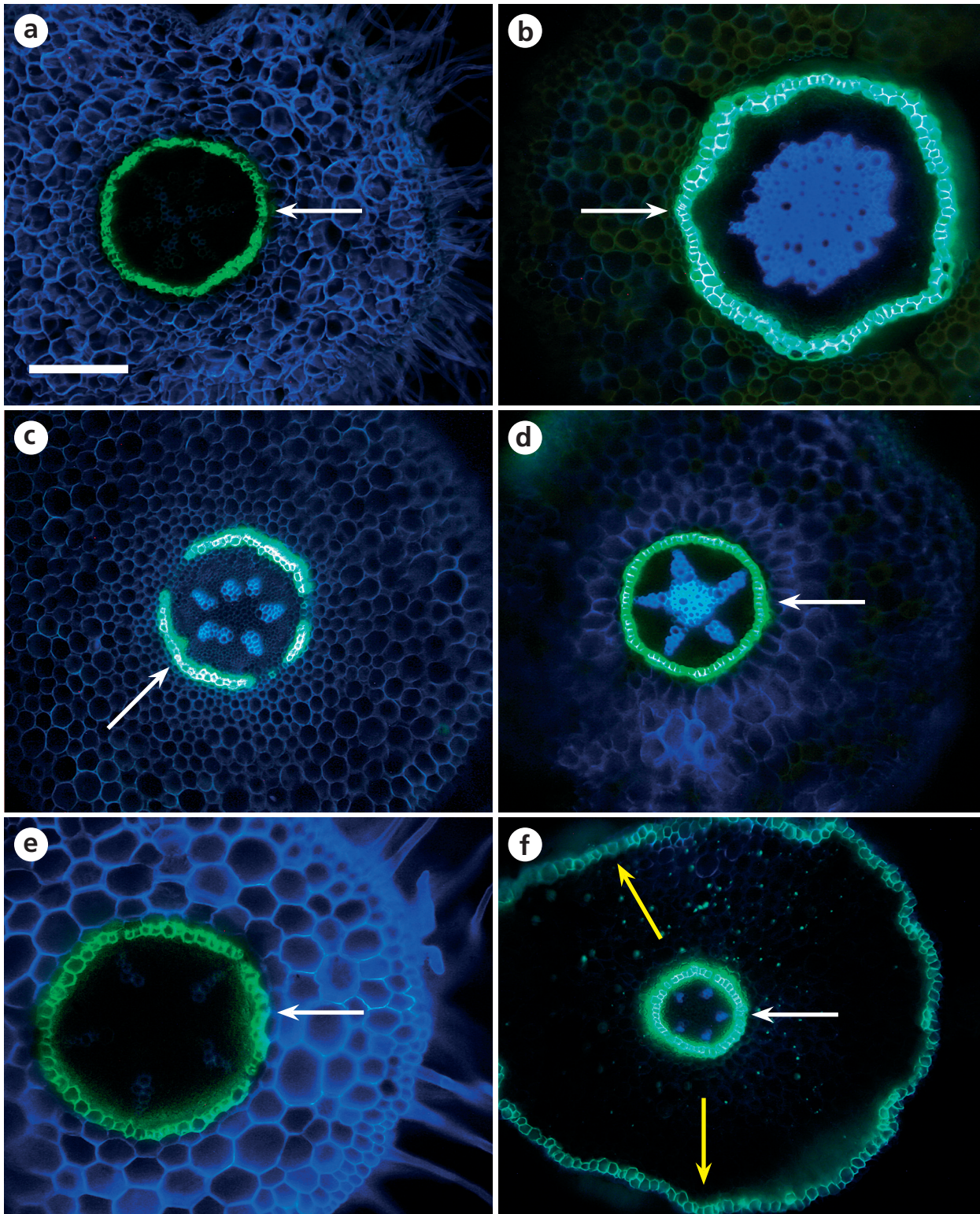


FIGURE 10. Deposition of suberin in the cell walls of endodermis and exodermis of plant species from different families collected in Alison Baird Reserve, south-western Australia. Roots of (a) *Banksia telmatiaea* and (b) *Grevillea thelemanniana* (spider net grevillea, Proteaceae), (c) *Daviesia physodes* (prickly bitter pea) and (d) *Jacksonia furcellata* (grey stinkwood) (both Fabaceae), and (e) *Allocasuarina humilis* (dwarf sheoak, Casuarinaceae) did not develop an exodermis. However, (f) *Calothamnus hirsutus* (Myrtaceae) developed a complete and strong exodermis, just below the epidermis (yellow arrows). All species developed an endodermis, the innermost barrier of the roots (white arrows). Cross-sections were taken at 50 - 70 mm from the root apex and stained with fluorol yellow 088. The presence of suberin lamellae was detected by yellow-green fluorescence (either white or yellow arrows). Bar = 100 μ m.

causing soybean root rot disease (Ranathunge *et al.*, 2008). However, there is no histochemical evidence indicating the presence of 'diffuse suberin' in the epidermal cell walls of cell walls of south-western Australian native species studied so far. Instead, the species without an exodermis in Proteaceae and Fabaceae exhibit intense deposition of phenolic compounds in the cell walls of the entire cortex, as indicated by bright autofluorescence (Fig. 10). Such soluble phenolic compounds, which are associated with suberin act as antifungal agents (Kolattukudy, 1984; Biggs & Miles, 1988; Lulai & Corsini, 1998; Thomas *et al.*, 2007). In contrast, such intense autofluorescence, which represent phenolic compounds, is lacking in the cortex of *Calothamnus birsutus* which develops a strong suberised exodermis. The presence of a suberised endodermis, on the other hand, serves as the last line of defence before pathogens invade the vascular cylinder and spread throughout the plant (Kolattukudy & Espelie, 1989; Enkerli *et al.*, 1997; Enstone *et al.*, 2003; Huitema *et al.*, 2004; Thomas *et al.*, 2007).

Cyperaceae do have an exodermis in roots (Perumalla *et al.*, 1990; Enstone *et al.*, 2003); we do not know the situation for Restionaceae and Anarthriaceae. These likely release carboxylates from their root hairs, and hence the absence of an exodermis may not be required. When considering the amounts of carboxylates exuded from cluster roots of Proteaceae, it is likely that they produce them not only in the epidermal cells, but also in the cortical cells, and release them from both.

Extracellular phosphatase enzymes of Fabaceae

Organic phosphorus represents a major fraction of total phosphorus in the severely phosphorus-impooverished soils of the Bassendean dunes (Turner & Laliberté, 2015). As such, the ability to acquire organic phosphorus could be important for many Bassendean species. Generally, plants are able to acquire organic phosphorus to varying extents by releasing root phosphatases, and, indirectly, via phosphatases synthesised by their root associates (*e.g.*, ectomycorrhizal fungi) (Richardson *et al.*, 2005; Turner, 2008). These phosphatase enzymes enhance phosphorus acquisition by hydrolysing organic phosphorus in soil to release inorganic phosphorus that is available for uptake by plant roots (Tarafdar & Claassen, 1988). Fabaceae

species show significantly greater root and soil phosphatase activity when compared with co-occurring non-Fabaceae species in many parts of the world (Houlton *et al.*, 2008; Olde Venterink, 2011; Png *et al.*, 2017). In particular, the roots of Fabaceae from the Bassendean dunes, such as those of *Acacia pulchella* (prickly Moses) and *Jacksonia floribunda* (holly pea), display exceptionally greater extracellular phosphatase activity than co-occurring non-Fabaceae species (Png *et al.*, 2017). This strategy of greater investment in root phosphatase enzymes may provide Fabaceae with a competitive advantage to persist in severely phosphorus-impooverished soils (Png *et al.*, 2017).

PHOSPHORUS-UTILISATION STRATEGIES

Proteaceae

Banksia and *Hakea* species function at very low leaf phosphorus concentrations, but show rates of photosynthesis that are similar to those of crop plants with phosphorus concentrations that are about 10 times greater (Denton *et al.*, 2007; Sulpice *et al.*, 2014). Low leaf phosphorus concentrations, similar to those found in several co-occurring *Banksia* species, have been found for *Stirlingia latifolia* (blueboy) growing on an ancient Bassendean dune in Alison Baird Reserve (Fig. 11). *Banksia* and *Hakea* species achieve their amazingly high photosynthetic phosphorus-use efficiency by allocating leaf phosphorus very effectively, compared with what we know about other plants. Most importantly, they function at very low levels of ribosomal RNA (Sulpice *et al.*, 2014), which is the largest organic phosphorus fraction in leaves (Veneklaas *et al.*, 2012). They also replace most of their phospholipids during leaf development by lipids that do not contain phosphorus, *e.g.*, sulfur-containing lipids (Lambers *et al.*, 2012; Kuppusamy *et al.*, 2014). In addition, they preferentially allocate leaf phosphorus to those cells that require it most for photosynthesis, the chloroplast-containing mesophyll cells (Hayes *et al.*, 2018).

Grevillea is an interesting genus in many ways. It is the genus from which *Hakea* descended in the Middle Eocene–Early Oligocene, 45 to 30 million years ago (Cardillo *et al.*, 2017). In terms of phosphorus nutrition, there are distinct differences between the two genera. *Grevillea* species in

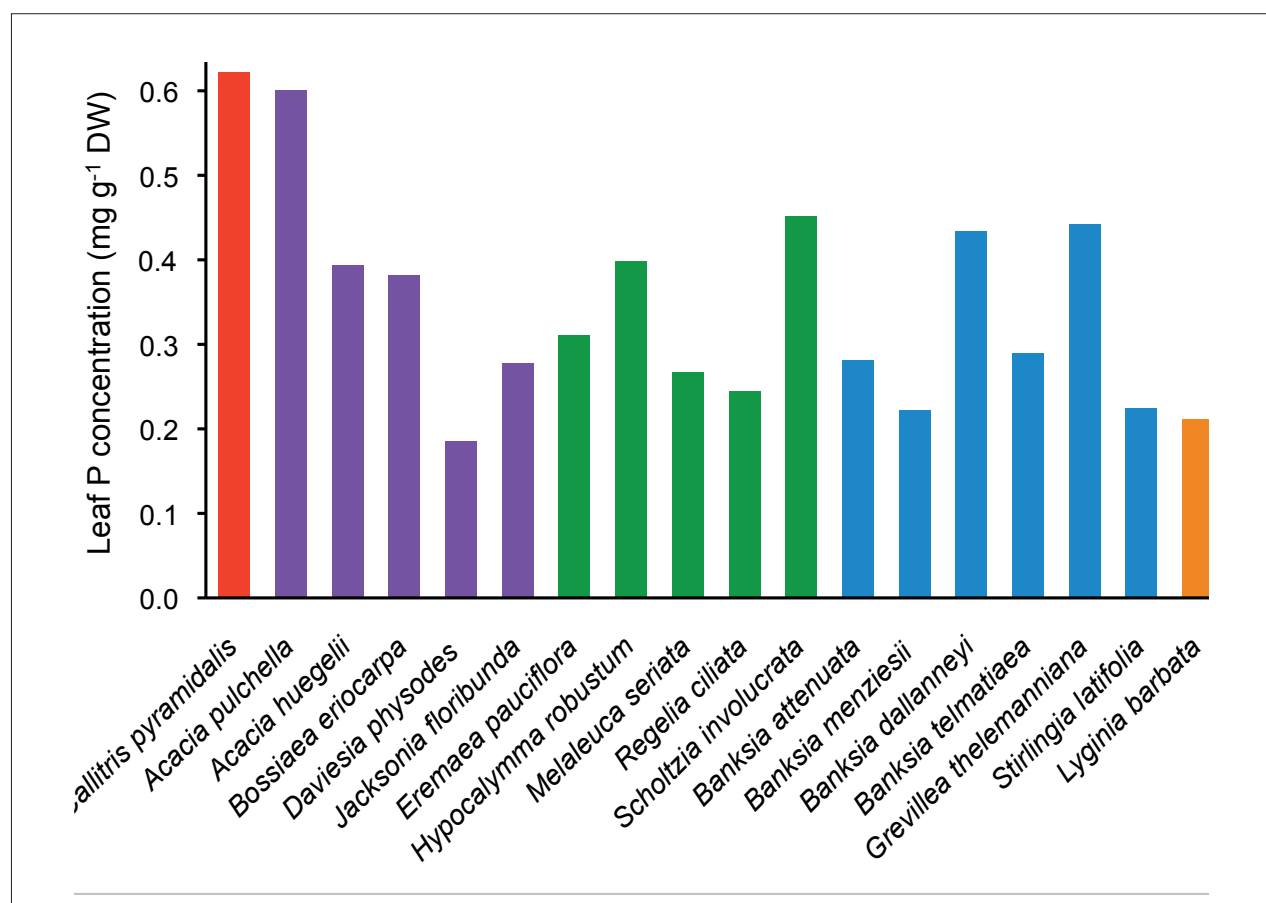


FIGURE 11. Total leaf phosphorus (P) concentrations for a range of species from five families: Cupressaceae (red), Fabaceae (purple), Myrtaceae (green); Proteaceae (blue) and Anarthriaceae (orange).

general, including *Grevillea thelemanniana* (spider net grevillea), a Declared Rare Flora (DRF) species in the Greater Brixton Street Wetlands, function at leaf phosphorus concentrations that are considerably greater than those in *Hakea* leaves (Wright *et al.*, 2004). The leaf phosphorus concentration in *Grevillea thelemanniana* (spider net grevillea) is among the highest among Proteaceae at Alison Baird Reserve (Fig. 11). The ‘innovation’ that arose in *Hakea* to separate it from *Grevillea* and allowed this genus to diversify on more severely phosphorus-impoverished soils was that *Hakea* functions at leaf phosphorus concentrations that are only 64% of those in *Grevillea*. In the proposed Yule Brook Regional Park, which is characterised by soils with a very low phosphorus availability, we can find numerous *Hakeas*, but very few *Grevillea* species (Fig. 12). *Grevillea* species typically grow in slightly richer habitats, and this makes them rare in the proposed Regional Park.

Myrtaceae

Myrtaceae species that co-occur with Proteaceae on ancient Bassendean dunes show leaf P concentrations that are similar to those of *Banksia menziesii* (firewood banksia) and *Stirlingia latifolia* (blueboy) (Fig. 11) and to the species referred to above (Denton *et al.*, 2007; Sulpice *et al.*, 2014). We have yet to find out if they also function at low ribosomal RNA levels and replace their phospholipids. However, we do know that Myrtaceae from severely phosphorus-impoverished habitats do allocate their leaf phosphorus preferentially to their mesophyll cells (Guilherme Pereira *et al.*, 2018), and also function with a low amount of phosphorus allocated to nucleic acids and lipids (Yan *et al.*, 2019).

Fabaceae

Fabaceae species that co-occur with Proteaceae on Bassendean dunes possess the ability to form symbiotic associations with nitrogen-fixing rhizobia.

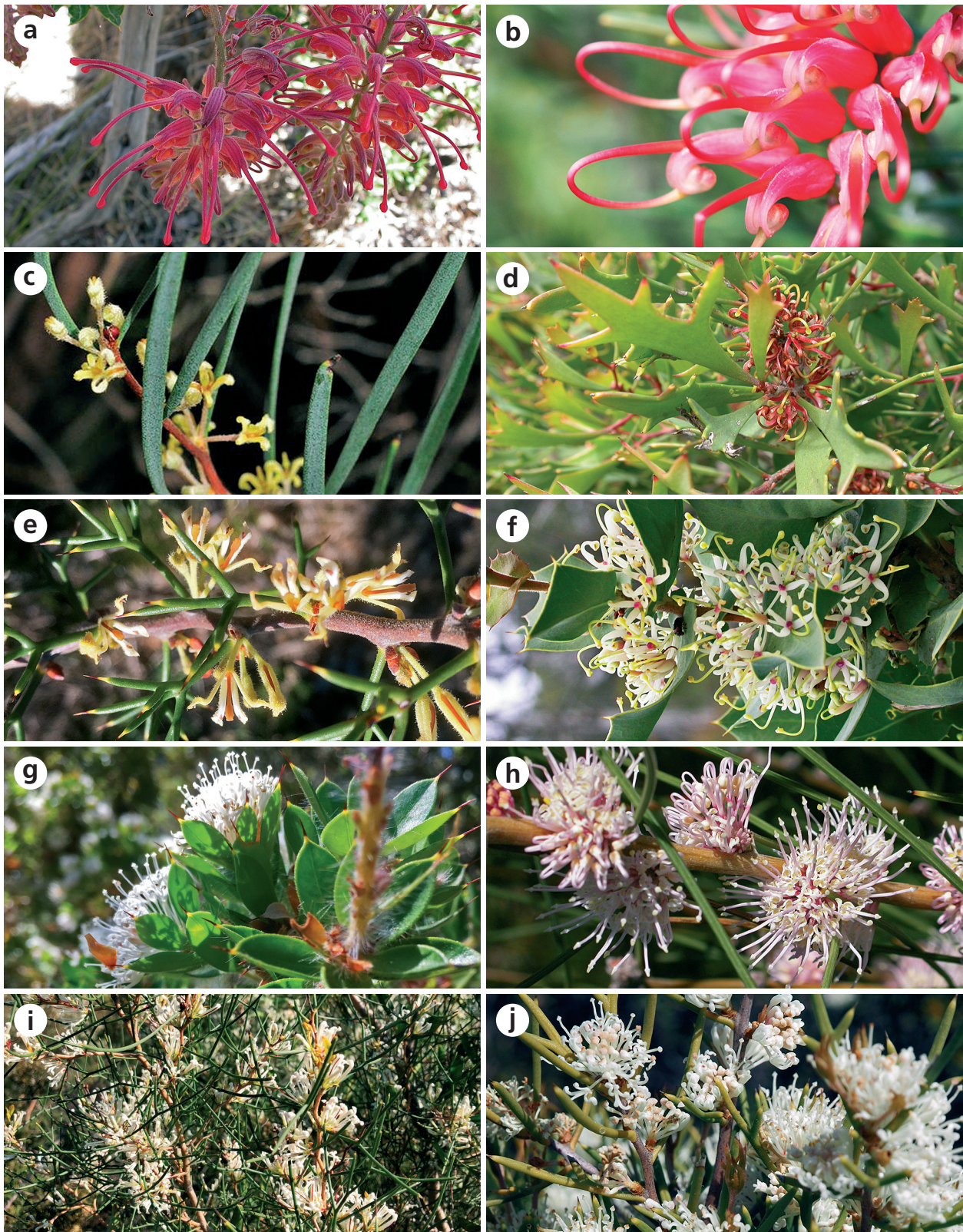


FIGURE 12. Examples of *Grevillea* and *Hakea* (sub)species that naturally occur in the proposed Yule Brook Regional Park. Note that the number of *Grevillea* species is far less than that of *Hakea* species. (a) *Grevillea bipinnatifida* ssp. *bipinnatifida* (fuchsia grevillea), (b) *Grevillea thelemanniana* (spider net grevillea), (c) *Hakea candolleana*, (d) *Hakea ceratophylla* (horned leaf hakea), (e) *Hakea lissocarpha* (honey bush), (f) *Hakea prostrata* (harsh hakea), (g) *Hakea ruscifolia* (candle hakea), (h) *Hakea sulcata* (furrowed hakea), (i) *Hakea trifurcata* (two-leaf hakea) and (j) *Hakea varia* (variable-leaved hakea). Photos: a, d, e, f, g, h: Hans Lambers; b, j: Angela Rossen; c: André Arruda; i: Roberta Dayrell.

However, nitrogen-fixing plants are generally thought to possess a nitrogen-demanding lifestyle (McKey, 1994), which has high phosphorus costs associated with it (Hartwig, 1998; Raven, 2012). Therefore, nitrogen-fixing plants are expected to be disadvantaged in severely phosphorus-impooverished soils (Houlton *et al.*, 2008). Yet, paradoxically, many nitrogen-fixing species co-occur with Proteaceae in the severely phosphorus-impooverished soils of the Bassendean dunes (Zemunik *et al.*, 2015; 2016). Their greater root-released phosphatase activity may give them greater access to organic phosphorus than some of their neighbours have (Png *et al.*, 2017).

In addition to some of the phosphorus-acquisition strategies discussed above, the remarkable persistence of the putative nitrogen-fixing species on the Bassendean dunes might also be associated with a variety of phosphorus-use strategies. Some Fabaceae that co-occur with Proteaceae species on Bassendean dunes show a fascinating pattern. Four of them, *Acacia huegelii* (Huegel's wattle), *Bossiaea eriocarpa* (common brown pea), *Daviesia physodes* (prickly bitter pea), and *Jacksonia floribunda* (holy pea), show low leaf phosphorus concentrations, similar to those exhibited by co-occurring Proteaceae and Myrtaceae (Fig. 11). By contrast, *Acacia pulchella* (prickly Moses) functions at much higher leaf phosphorus concentrations. This is a species that typically germinates in abundance after a fire (Monk *et al.*, 1981), the last of which was in 2006 at this location. Dense populations (10,000 plants per ha) may establish after a summer burn. Plant density declines to 30% of its initial value after four years, and to less than 8% after 13 years. Plants accumulate dry matter, nitrogen and phosphorus throughout a 13-year growth period. Seed production commences after two years, reaches a maximum (12,000 seeds per plant per year) at three or four years, and then declines to 2000 seeds per plant after 13 years (Monk *et al.*, 1981). To persist in severely phosphorus-impooverished soils, *Acacia pulchella* (prickly Moses) may compensate for its relatively high phosphorus requirements by down-regulating its symbiotic nitrogen fixation more effectively than Fabaceae species that occur on the younger dunes with greater soil phosphorus availability (Png, 2017). Png (2017) also observed this trait of conservative phosphorus use by down-regulating symbiotic nitrogen fixation very effectively in *Jacksonia floribunda* (holy pea),

which is common on the Bassendean dunes in Alison Baird Reserve. The trait is likely present in other nitrogen-fixing species that co-occur in these severely phosphorus-impooverished soils (Png *et al.*, 2017).

Other families

Little is known about the phosphorus-use strategies of species from other plant families in Alison Baird Reserve. *Callitris pyramidalis* (swamp cypress) is a coniferous tree native to south-western Australia. It has a leaf phosphorus concentration as high as that of *Acacia pulchella* (prickly Moses) (Fig. 11). In contrast, *Lyginia barbata* (Anarthriaceae) has a leaf phosphorus concentration in the low range of values known for plants in the reserve. It will be interesting to learn whether there has been convergence of phosphorus-efficiency traits among the various plant families in the reserve. Such convergence has been found for photosynthetic phosphorus-use efficiency traits and phosphorus-allocation patterns among different biochemical fractions as in plants on the phosphorus-impooverished soils of the Jurien Bay dune chronosequence (Guilherme Pereira *et al.*, 2019; Yan *et al.*, 2019).

Competition vs. facilitation

Non-mycorrhizal Proteaceae, Cyperaceae, Anarthriaceae and Haemodoraceae may have a superior carboxylate-releasing phosphorus-acquisition strategy on severely phosphorus-impooverished soils, but they do co-occur with mycorrhizal species that do not release carboxylates. In addition, they co-occur with species that exhibit both strategies, for example *Viminaria juncea* (swishbush). How can we account for this?

The current thinking in plant ecology is that competition among plants is fierce when resource levels are high and stress levels low (Lekberg *et al.*, 2018), and, *vice versa*, competition would be mild when resources are limited.

SYMBIOTIC NITROGEN FIXATION

Despite nitrogen not being the limiting nutrient for plant growth in the severely phosphorus-impooverished soils of the Bassendean dune systems (Laliberté *et al.*, 2012; Hayes *et al.*, 2014),

nitrogen input into the ecosystem remains an important ecological process that is essential for the maintenance of biodiversity and productivity. This is because nitrogen is continually lost from the ecosystem, for the most part, via natural (or anthropogenic) fire disturbance events (Orians & Milewski, 2007). While there is essentially an unlimited supply of nitrogen in the atmosphere (~78 % of atmospheric gases by volume), the gaseous form is not directly accessible by eukaryotes and has to be converted or 'fixed' into ammonia, which can then be further converted to other forms of nitrogen that can be assimilated by plants.

Nitrogen fixation in the natural world is done predominantly by free-living or symbiotic nitrogen-fixing bacteria (Vitousek & Farrington, 1997; Galloway *et al.*, 2004). In many terrestrial ecosystems, the greatest source of biological nitrogen fixation comes from nitrogen-fixing bacteria that form symbiotic associations with vascular plants (Cleveland *et al.*, 1999). Although these plants are commonly referred to as 'nitrogen-fixing plants', the 'fixing' of atmospheric nitrogen to other forms of nitrogen (primarily ammonia) is, in fact, not done by the plants. Rather, the conversion or 'fixing' of gaseous nitrogen is catalysed by the nitrogenase enzymes produced by the nitrogen-fixing microbial symbiont (Cooper & Scherer, 2012). However, this nitrogen fixation process only occurs effectively under anaerobic conditions due to nitrogenase being highly sensitive to damage by oxygen (Cooper & Scherer, 2012). As such, the plant symbiont provides this anaerobic environment to the nitrogen-fixing microorganism via the formation of specialised structures (*e.g.*, root nodules in Fabaceae, rhizothamnia in actinorhizal plants), which restrict oxygen diffusion (Cooper & Scherer, 2012). A great diversity of putative nitrogen-fixing vascular plant species found on the Bassendean dunes possess either one of the following three symbiotic nitrogen fixation systems (Lambers *et al.*, 2014). First, many Fabaceae species, including *Bossiaea eriocarpa* and *Acacia pulchella* (prickly Moses), form symbiotic associations with nitrogen-fixing rhizobia, giving rise to the formation of specialised root structures known as nodules (Monk *et al.*, 1981; Lambers *et al.*, 2014; Abrahão *et al.*, 2018) (Fig. 13). Most of the rhizobia species that form symbiotic

associations with Fabaceae occur in a few genera such as the *Rhizobium*, *Mesorhizobium*, *Ensifer* and *Bradyrhizobium* (Birnbaum *et al.*, 2018). However, Birnbaum and colleagues discovered that soils from the Bassendean dunes, compared with younger soils with greater phosphorus availability, contain a large proportion of unique rhizobia species that are likely adapted to the extremely phosphorus-impooverished Bassendean soils (Birnbaum *et al.*, 2018). The intriguing discovery of these unique rhizobia species warrants further research, as we may be able to apply it to identify highly phosphorus-efficient strains of rhizobia for leguminous crops. Second, the actinorhizal plants, such as the *Allocasuarina humilis* (dwarf sheoak) from the Casuarinaceae family, form symbioses with filamentous actinomycete nitrogen-fixing bacteria, *i.e.* *Frankia* (Chaia *et al.*, 2010; Lambers *et al.*, 2014). The symbiotic association between an actinorhizal plant and *Frankia* produces a specialised root structure known as rhizothamnia (Chaia *et al.*, 2010) (Fig. 14). Third, cycads, including *Macrozamia riedlei* (zamia palm), form symbiotic associations with the nitrogen-fixing *Nostoc* cyanobacteria (Halliday & Pate, 1976). The nitrogen-fixing *Nostoc* symbionts are enclosed within elongated, coral-like root structures known as coralloid roots (Halliday & Pate, 1976) (Fig. 15). Conversely, unlike rhizobia and *Frankia*, where nitrogen-fixation occurs exclusively within the specialised root structures of the Fabaceae and actinorhizal plants, respectively, the *Nostoc* cyanobacteria are also capable of non-symbiotic nitrogen-fixation in their free-living state and of symbiotic nitrogen-fixing associations with a wide range of non-vascular-plant-hosts (*e.g.*, lichens, bryophytes) (Svenning *et al.*, 2005). An interesting difference between nodules and rhizothamnia on one hand and coralloid roots on the other is that nodules and rhizothamnia are induced by the microsymbionts, while coralloid roots are produced whether there are cyanobacteria or not (Vessey *et al.*, 2005). The cyanobacteria enter at a later stage, in a manner that is not yet fully understood. Finally, while nitrogen-fixing actinorhizal plants and cycads are not as well represented as the Fabaceae in the Bassendean dunes (Zemunik *et al.*, 2016), these non-Fabaceae nitrogen-fixing plants still represent a significant nitrogen input into ecosystems (Halliday & Pate, 1976; Andrews *et al.*, 2011; Png *et al.*, 2017).



FIGURE 13. Nitrogen-fixing structures (nodules) of *Acacia saligna* (orange wattle). Photo: Hongtao Zhong.



FIGURE 14. Nitrogen-fixing structures (rhizothamnia) of *Allocasuarina humilis* (dwarf sheoak). Photo: Hans Lambers.

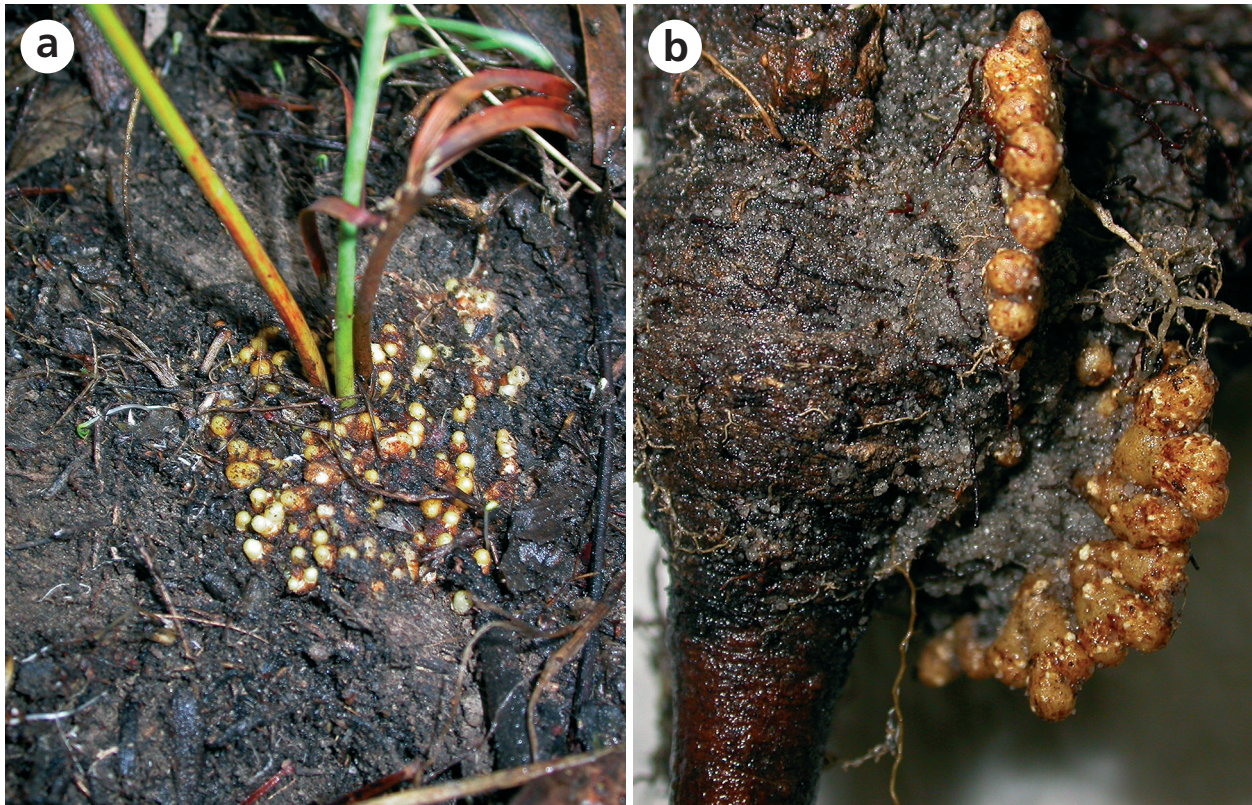


FIGURE 15. (a) Coralloid roots of a young plant of *Macrozamia riedlei* (zamia); (b) close-up of the coralloid roots. Photos: Hans Lambers.

GREVILLEA THELEMANNIANA, A DECLARED RARE FLORA (DRF) SPECIES IN THE GREATER BRITTON STREET WETLANDS

Figure 11 provides a clue why *Grevillea thelemanni-ana* (spider net grevillea) is rare, because it functions at higher leaf phosphorus concentrations than other Proteaceae do, and that extra phosphorus is rarely available in the Southwest Biodiversity Hotspot. Since it has this in common with other *Grevillea* species that have been studied (Wright *et al.*, 2004), phosphorus availability is only part of the story. It also requires a greater availability of water than most other species (Tauss *et al.*, 2019). Combined with its high demand for calcium (J. Gao, F. Wang, H. Lambers & K. Ranathunge, unpubl.), which is unusual among Proteaceae (Hayes *et al.*, 2019a; 2019b), it becomes evident why *Grevillea thelemanni-ana* is so rare. The combination of wet conditions and a high availability of both phosphorus and calcium is rare in south-western Australia which explains its rarity. The only way this species can be conserved in its natural habitat is by ensuring its habitat is looked after.

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