Foliar nutrient-allocation patterns in Banksia attenuata and Banksia sessilis differing in growth rate and adaptation to low-phosphorus habitats

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Abstract

We compared the use of phosphorus (P) and nitrogen (N) in slow-growing Banksia attenuata (Proteaceae), which resprouts after fire and naturally occurs on deep sand, with faster-growing opportunistic B. sessilis, which is killed by fire and occurs on shallow sand over laterite or limestone. We carried out pot experiments with plants on substrates with different P availability. We measured foliar nutrient concentrations, and P allocated to major biochemical fractions. The two species had similar foliar total P concentrations, but distinct patterns of P allocation to P-containing fractions. The foliar total N concentration of B. sessilis was greater than that of B. attenuata on all substrates. The foliar total P and N concentrations in both species decreased with decreasing P availability. The relative growth rate of both species was positively correlated with both foliar nucleic acid P and total N concentrations, but there was no correlation with other P and N fractions. Faster-growing B. sessilis allocated more P to nucleic acids than B. attenuata did, but other fractions were similar. We conclude that the nutrient-allocation patterns in faster-growing opportunistic B. sessilis and slower-growing B. attenuata revealed different strategies in response to soil P availability, which matched their contrasting growth strategy.

INTRODUCTION

Understanding strategies of nutrient allocation and their underlying mechanisms in plants adapted to phosphorus (P)-impoverished soils is an important topic in plant physiological ecology (Lambers *et al.* , 2006, Veneklaas *et al.* , 2012). Phosphorus-impoverished soils limit the growth and yield of crops, pastures and forests throughout the world (Conroy *et al.* , 1990, Fujita *et al.* , 2003, Herbert & Fownes, 1995, Seneweera & Conroy, 1997, Thomas *et al.* , 2006). Moreover, a recent meta-analysis showed that P limitation of above-ground plant production is pervasive in natural terrestrial ecosystems (Hou *et al.* , 2020). Low soil P availability is widespread in Australia (Kooyman *et al.* , 2016, Viscarra Rossel & Bui, 2016), and plants generally respond to low soil P availability by having a low foliar P concentration (Epstein & Bloom, 2005).

Foliar P concentration is the sum of the concentrations of several major P fractions in leaf cells including inorganic P (Pi) and various P-containing organic compounds (i.e. nucleic acids, phospholipids and small phosphate esters (Veneklaas *et al.* , 2012). Therefore, variation in foliar P concentration among plant species or due to environmental conditions will reflect differences in both the concentrations of the foliar P fractions and the relative proportions among these fractions. The allocation of P to foliar fractions is likely related to life-history strategy, because these fractions are functionally related to growth, reproduction, and stress

tolerance. Shifting P-allocation patterns in leaves is an important mechanism for plants to acclimate to low soil P availability (Hidaka & Kitayama, 2011, Yan *et al.* , 2019). If strong P limitation occurs, plants shift the allocation of P among foliar P fractions, and this might increase plant fitness under the prevailing conditions (Hidaka & Kitayama, 2011).

Chapin III & Kedrowski (1983) investigated foliar P fractions of four Alaskan tree species and found that nucleic acid P was the largest pool throughout the growing season, and that there was no difference in the proportion of foliar P concentrations between different forest types. However, these species demonstrated a relatively high foliar P concentration (1.3–2.1 mg g^{-1} dry mass (DM)), so no adaptation of the tree species to P limitation can be expected. Hidaka & Kitayama (2009) found that plants growing on P-impoverished tropical soils increased both leaf mass per area (LMA) and photosynthetic P-use efficiency (PPUE) compared with plants on P-richer soil. These authors suggested that a greater proportion of cellular P may be allocated to metabolic P, rather than to structural P to maintain high PPUE. Yan*et al.* (2019) investigated foliar P fractions of three species along a two-million-year chronosequence with a strong gradient of available P in south-western Australia, and found that their P allocation pattern was associated with their distribution along the chronosequence, and concluded that the differences are likely adaptive. How plants allocate P among foliar P fractions and exhibit adaptive strategies to efficiently use P in two species in the same genus with contrasting life-history strategies in extremely P-impoverished ecosystems with a Mediterranean climate remains unclear.

The relationship between growth rate and P investment, and the rapidly-emerging field of ecological stoichiometry have shown that species with fast growth rates have low N:P ratios (Reef *et al.* , 2010). This pattern has been explained by the Growth Rate Hypothesis (GRH), which proposes that fast growth rates are associated with a proportionally greater requirement for P than for N, because organisms must allocate a disproportionately greater proportion of P to P-rich ribosomal RNA (rRNA) to meet the protein synthesis demands needed to support the rapid growth rates (Elser & Hamilton, 2007, Elser *et al.* , 1996, Sterner & Elser, 2002). Nucleic acids have an N:P stoichiometry of 4:1 (Reef *et al.* , 2010), and are a major fraction of organic P, with RNA by far the largest proportion (Geider & La Roche, 2002). Within the RNA pool, rRNA is the largest P fraction.

Tree species in ancient landscapes have experienced long-term low soil P status; thus, they likely possess adaptations to P limitation. Non-mycorrhizal Proteaceae are an important component of the vegetation on severely P-impoverished soils in south-western Australia (Hayes*et al.* , 2014, Lambers *et al.* , 2013, Pate *et al.* , 2001). Species in this family typically form cluster roots that effectively mine soil P by releasing large amounts of low-molecular-weight carboxylates to desorb P from soil particles (Shane & Lambers, 2005). It is striking that mature leaves of Proteaceae species from south-western Australia exhibit relatively fast rates of area-based photosynthesis, despite having extremely low leaf P concentrations (Denton *et al.* , 2007, Lambers *et al.* , 2012, Sulpice *et al.* , 2014), while leaves of P-starved crop plants tend to have slow rates of photosynthesis per unit leaf area (Brooks *et al.* , 1988, Fredeen*et al.* , 1990, Rao *et al.* , 1989). Consequently, some of these Proteaceae exhibit a very high photosynthetic P-use efficiency (PPUE, Denton *et al.* , 2007, Lambers *et al.* , 2010, Sulpice*et al.* , 2014). This high PPUE in Proteaceae from severely P-impoverished habitats is brought about mainly by low foliar rRNA concentrations (Sulpice *et al.* , 2014) and extensive replacement of phospholipids with galactolipids and sulfolipids during leaf development (Lambers *et al.* , 2012).

The slow-growing resprouter *Banksia attenuata* and the faster-growing seeder *B. sessilis* (Pate *et al.* , 1991) both produce compound cluster roots (Shane & Lambers, 2005), but have different life histories (Shi *et al.* , 2020). *Banksia sessilis* is a short-lived obligate seeder that occurs on shallow sand over laterite or limestone (Hayes *et al.* , 2019, Pate & Bell, 1999) and allocates more biomass to cluster roots than *B. attenuata* , which invests more in deep roots (Shi *et al.* , 2020). This strategy enhances P mobilisation from laterite or limestone by releasing more carboxylates and/or exuding these at a faster rate than*B. attenuata* (Shi *et al.* , 2020). In contrast to *B. sessilis* , *B. attenuata* is restricted to deep sand (FloraBase, http://florabase.dpaw.wa.gov.au/) and does not grow fast and complete its life cycle quickly (Bowen &

Pate, 2017, Knox & Clarke, 2005, Pate*et al.* , 1990). McArthur & Wilson (1967) coined the terms*r* strategy and *K* strategy to describe selection for rapid population growth in uncrowded populations and selection for competitive ability in crowded populations, respectively. Over time, the meaning of these terms has broadened (Parry, 1981), and according to the broader context, *B. sessilis* is an *r* strategist, while *B. attenuata* is a *K* strategist. We do not know the physiological pattern of allocating P among foliar P fractions that allows species to exhibit a particular life-history strategy and efficient use of P in contrasting low-P environments. Therefore, we aimed to compare P-allocation patterns in these two *Banksia* species with contrasting life history. Thus, we measured leaf P and N concentrations, LMA, and concentrations and proportions of P in foliar P-containing fractions in *B. attenuata* and *B. sessilis* grown with different soil P availability.

We hypothesised that:

1) With decreasing soil P availability, the foliar total P concentrations of both *B. attenuata* and *B. sessilis* would decrease.

2) *Banksia sessilis* , which exhibits a more opportunistic*r* -life strategy than *B. attenuata* , would have a higher foliar N_{Total} : P_{Total} ratio and invest more P in nucleic acids than *B. attenuata* when grown on the same substrate.

MATERIALS AND METHODS

Sowing method

Seeds of *Banksia attenuata* R.Br. and *B. sessilis* (Knight) A. R. Mast & K. R. Thiele (purchased from Nindethana Seed Company, King River, Western Australia), were sown on filter paper. One seedling was transferred into each experimental pot on 22nd May, 2016. According to the supplier, the seeds of *B. sessilis* were collected from a coastal population, growing over limestone near Jurien Bay, Western Australia (30°18 S, 115°3' E). The provenance of the *B. attenuata* seed was unknown.

Experimental design

A pot experiment was carried out in a glasshouse at the University of Western Australia, Perth, Australia (31°59' S, 115°53' E) using a randomised complete block design. Glasshouse temperature fluctuated between 13 and 33°C over a whole year, and transmission of radiation into the glasshouse was 60% of natural light. The experiment was designed to explore why *B. sessilis* is able to grow across a wider range of P-impoverished soil types and maintain a greater relative growth rate (RGR) than *B. attenuata* by comparing the use and allocation of P among foliar P fractions in the two species. Three soil treatments were imposed, based on washed river sand: sand only, sand + laterite (SLAT), and sand + limestone (SLIM). The substrate total P availability was sand > SLAT > SLIM (Fig. S1, Shi *et al.* , 2020). The pots (100 mm inner diameter x 400 mm tall PVC cylinder) were lined with plastic bags. For each soil treatment, 3.0 kg substrate was added to the pots. For the SLAT and SLIM treatment, a 100 mm layer of laterite or limestone gravel, respectively, was added 50 mm below the soil surface, and other layers were filled with sand. There were ten replicates for each species in each treatment. Field capacity of soils in each treatment was calculated as [(wet mass – dry mass) / dry mass] × 100%. The pots were watered to a constant weight of 80% of field capacity three times a week. A 20 ml aliquot of basal liquid nutrient solution lacking P and containing (per kilogram of soil): 217.5 mg KNO_3; 74 mg $CaCl_2$; 140 mg K_2SO_4; 80 mg $MgSO_4.7H_2O$; 28.9 mg $MnSO_4.H_2O$; 10 mg $ZnSO_4.7H_2O$; 5 mg $CuSO_4.5H_2O$; 0.7 mg H_3BO_3; 0.5 mg $CoSO_4.7H_2O$; 0.4 mg $Na_2MoO_4.2H_2O$; 20 mg FeNaEDTA, was applied to each pot once every second week.

Photosynthesis measurement

Prior to the final harvest, net photosynthetic rate (P_n) of attached leaves was measured between 10:00 and 11:00 on March 7th, 9th 2017 using a red/blue LED light source (LI-6400, LI-COR Inc., Lincoln, NE, USA). The plants were watered on the day before the photosynthesis measurement. One mature leaf of each plant was measured under a photosynthetic photon flux density of 1500 μmol m^{-2} s^{-1} and a CO_2 concentration of 400 μmol mol^{-1}. The leaves used for photosynthesis measurement were sampled, and the projected leaf area measured at 200 dpi (Epson 1680, Long Beach, CA, USA) and calculated (ImageJ 1.4, NIH, Bethesda, MD, USA). Leaves were then dried at 70 °C for 72 h to measure dry mass (DM).

Harvest

After 50 weeks of growing in pots, a total of 20 fully-expanded leaves with no visible damage or discolouration were harvested from each plant. The leaves were immediately scanned at 200 dpi to calculate leaf area (LA_1), submerged in liquid nitrogen and stored at -80°C. Frozen leaves were freeze dried for seven days (VirTis Benchtop "K", New York, USA) and dry mass (DM) was determined (DM_1). The remaining leaves on each plant were harvested and scanned at 200 dpi to calculate the remaining leaf area (LA_2). Total LA = LA_1 + LA_2. The remaining leaves, stem and roots were separated and dried at 70°C for 72 h. The DM was determined for the remaining leaves (DM_2) and for stems plus roots (DM_3). Total leaf DM = DM_1 + DM_2. Total plant dry mass M_2 = DM_1 + DM_2 + DM_3. Leaf mass per area (LMA) was calculated as total leaf DM / total LA. Seed weight (W_1) was measured using four lots of 10 (*B. attenuata*) or 30 (*B. sessilis*) seeds that were dried (70@C, 48hr) and weighed before calculating the average seed weight. Relative growth rate (RGR) was calculated as $(\ln M_2 - \ln W_1) / (T_2 - T_1)$, where T_1 and T_2 were the dates of sowing and harvesting, respectively, expressed in weeks.

Leaf nutrient analyses

Freeze-dried leaves were ground to a fine powder (Geno/Grinder 2010, Spex SamplePrep, Metuchen, New Jersey, USA). A 50 mg sample was used to determine inorganic P (Pi) described by Yan*et al.* (2019).

The P allocated to nucleic acids, lipids, small metabolites (Pi + other metabolites) and a residual fraction was determined in a 50 mg portion of powdered leaves using the differential solubility method described by Hidaka & Kitayama (2013), as modified in Yan *et al.*(2019). Metabolite P is defined here as small metabolite P – Pi.

Phosphorus concentrations in extracts and residues from the above procedures were measured as in described by Matusiewicz & Golik (2004) using a molybdenum blue method (Ames, 1966). Total leaf P is the sum of Pi, nucleic acids, lipids, small metabolites and residual fraction. Total leaf P was confirmed by acid digestion of ground leaf material, followed by Pi assay. Total foliar N concentration was determined by combustion of approx. 30 mg of dried leaf sample (Vario Macro Combustion Analyser, Elementar Analysensysteme GmbH, Langenselbold, Germany).

Leaf area-based P concentration was calculated as Total leaf P mass concentration×LMA; PPUE was calculated as the ratio of photosynthesis rate to area-based P concentration; Leaf area-based N concentration was calculated as Leaf N mass concentration×LMA, and photosynthetic nitrogen-use efficiency (PNUE) was calculated as the ratio of photosynthesis rates to area-based N concentration.

Statistics

The differences in means between *B. attenuata* and *B. sessilis* on the same substrate were analysed by t test, while the differences in means within each species across substrate types were analysed by one-way ANOVA with 95% confidence intervals. The relationships of foliar P fractions to total foliar P concentration, leaf mass per area, relative growth rate (RGR) to nucleic acid phosphorus (P), foliar nitrogen (N) and foliar N

to nucleic acid P were determined by linear regression analysis, the correlation coefficients were analysed by Student's T-test. All statistical analyses were performed using the SPSS Statistics 19.0 (SPSS Inc., Chicago, US), and graphed with OriginPro 9.5 (OriginLab Corporation, Northampton, MA, USA).

RESULTS

Leaf phosphorus and nitrogen concentrations

The effect of P availability on P and N relations in leaves of *B. attenuata* and *B. sessilis* was tested by growing plants in sand, sand + laterite (SLAT) and sand + limestone (SLIM). Foliar total P concentrations on a mass basis for both *B. attenuata* and *B. sessilis* were highest when grown in sand, and lowest in SLIM (Fig. 1A). However, there were no significant differences between *B. attenuata* and *B. sessilis* in foliar total P concentrations for any substrate type (Fig. 1A). Mass-based foliar total P concentration for *B. attenuata* differed on all three substrates ($P < 0.05$): sand > SLAT > SLIM. In contrast to foliar total P concentration, foliar total N concentration on a mass basis for *B. sessilis* was greater than that for *B. attenuata* in each substrate type (Fig. 1B). The leaf total N concentrations on a mass basis for both species were the same in sand and SLAT, and higher than when grown in SLIM ($P < 0.05$).

The differences in mass-based foliar total P across substrates for both*B. attenuata* and *B. sessilis* were also apparent when P concentrations were expressed on an area basis ($P < 0.05$, Fig. 1C). However, on an area basis, the foliar P concentration for *B. attenuata* was higher than for *B. sessilis* in all substrates. There were also substrate-dependent differences in area-based foliar total N concentration for *B. attenuata* , but not for *B. sessilis*(Fig. 1D). In contrast to higher mass-based foliar N concentration in*B. sessilis* than in *B. attenuata* in all substrates, the area-based foliar N concentration was higher in *B. attenuata* in SLAT, or was not distinguishable (Fig. 1D).

The concentration ratio of foliar total N to foliar total P ($N_{Total} : P_{Total}$) had the same pattern for the two species across the three substrate types (Table 1). The $N_{Total} : P_{Total}$ ratio for both species was lower when grown in sand than when grown in SLAT or SLIM ($P < 0.05$). However, there was no significant difference for either species when grown in SLAT or SLIM. The $N_{Total} : P_{Total}$ ratio in *B. sessilis* was significantly higher than that in *B. attenuata* in every substrate.

Photosynthetic rates, PPUE and PNUE

Net photosynthetic rates (P_n) for *B. attenuata* grown in SLIM were lower than for plants grown in sand or SLAT, while there were no substrate-dependent differences for *B. sessilis* ($P< 0.05$, Table 2). There were no differences in photosynthesis rate between the two species in any substrate ($P > 0.05$). Moreover, there were no substrate-dependent differences in PPUE within either species (Table 2). However, the PPUE of *B. sessilis*was significantly higher than that of *B. attenuata* in all three substrates ($P < 0.05$, Table 2). The PNUE for *B. attenuata* grown in sand was higher than that of plants grown in SLIM ($P < 0.05$, Table 2), while PNUE for *B. sessilis*was the same in all substrate types (Table 2). Moreover, there were no significant differences in PNUE between *B. attenuata* and *B. sessilis* for any substrate type (Table 2).

Leaf phosphorus fractions

Banksia attenuata and *B. sessilis* had different patterns of allocating leaf P to lipid, metabolite, nucleic acid and residual fractions in all substrates (Fig. 2). The lipid P concentrations of *B. attenuata*grown in SLIM were lower than in plants grown in sand and SLAT (Fig. 2A), while the differences in metabolite P concentration in *B. attenuata* grown in the three substrate types was sand > SLAT > SLIM (Fig. 2B). The nucleic acid P concentrations of*B. attenuata* grown in SLIM were lower than in plants grown in sand and

SLAT (Fig. 2C). The lipid P, metabolite P, nucleic acid P and Pi concentrations of *B. sessilis* grown in sand were greater than those in plants grown in SLAT and SLIM (Fig. 2A, B, C, E).

The lipid P concentration of *B. attenuata* was greater than that of *B. sessilis* in SLAT and SLIM (Fig. 2A). The metabolite P and nucleic acid P concentrations of *B. attenuata* were lower than those of *B. sessilis* in both sand and SLIM, but were the same in SLAT (Fig. 2B, C). The residual P concentration only differed between the species when grown in SLAT, with the concentration in *B. attenuata* being lower than that in *B. sessilis* (Fig. 2D). The Pi concentrations of *B. attenuata* were greater than those of*B. sessilis* in sand and SLAT, but not SLIM (Fig. 2E).

The $N_{Total} : P_{Fraction}$ ratios for metabolite P and Pi for *B. attenuata* were significantly lower in sand than in SLAT or SLIM, while the ratios for the other fractions were indistinguishable among the substrates (Table 1). This result shows that metabolite P and Pi fractions were drivers for the observed difference in leaf $N_{Total} : P_{Total}$ ratio for*B. attenuata* in the three substrates. For *B. sessilis* , all P factions except residual P contributed to the lower leaf $N_{Total} : P_{Total}$ ratio in sand. The ratios of leaf $N_{Total} : P_{Fraction}$ in each P fraction were lower in *B. attenuata* than in *B. sessilis* for plants grown in any of the three substrates (Table 2).

The proportions of foliar P fractions to total foliar P

The proportions of lipid P and nucleic acid P in *B. attenuata*were significantly lower for plants grown in sand than when grown in SLAT or SLIM ($P < 0.05$, Fig. 3A, C). Conversely, the proportion of total P in Pi for *B. attenuata* was greater for plants grown in sand than for plants grown in SLAT or SLIM ($P< 0.05$, Fig. 3E). There was no significant difference in the proportions of total P in lipids , metabolites, nucleic acid and Pi for *B. sessilis* grown in any of the three substrates (Fig. 3A).

The proportion of total P in lipid P in *B. attenuata* was greater than that of *B. sessilis*in SLAT and SLIM ($P < 0.05$, Fig. 3A). Conversely, the proportion of total P in nucleic acid P in *B. sessilis* was significantly greater than that in *B. attenuata* in all substrates ($P < 0.01$); likewise, the proportion of metabolite P in*B. sessilis* was greater than in *B. attenuata* in SLIM (Fig. 3B, C). The proportion of residual P was below 10% in all substrates, except for *B. sessilis* grown in SLAT (Fig. 3D). The proportion of total P in Pi in *B. attenuata* was greater than that of *B. sessilis* in all three substrates ($P < 0.05$, Fig. 3E).

The relationships of RGR and foliar nutrient concentrations, foliar P fractions, and leaf mass per area

The RGR of *B. attenuata* was lower than for *B. sessilis* in all substrates (Table 1). In *B. attenuata,* the RGR was the same in sand and SLAT, but lower in SLIM, while in *B. sessilis,* RGR was also highest in sand, but lower and equal in both SLAT and SLIM. The RGR of *B. attenuata* and *B. sessilis* was positively correlated with foliar nucleic acid P concentration (Fig. 4A) and foliar N concentration (Fig. 4B). There was also a positive correlation between foliar N concentration and nucleic acid P concentration for both species (Fig. 4C). No other correlations were detected in any other pairwise comparison of P concentration with N concentration. In both species, the concentration P in lipid, metabolite, nucleic acid, residual and Pi fractions were all correlated positively with foliar total P concentration (Fig. 5).

Leaf mass per area varied from 240 to 267 g m^{-2} in *B. attenuata* and 119 to 131 g m^{-2} in *B. sessilis* depending on the growth substrate (Fig. 5, Table 2). The concentrations of the P fractions and total P generally decreased with increasing LMA (Fig. 5). This relationship was not significant for lipid P and nucleic acid P in*B. sessilis* . The only exception to a negative correlation between leaf P fraction and LMA was the lack of a relationship between residual P and LMA in *B. attenuata* .

DISCUSSION

Foliar total phosphorus and nitrogen concentrations

Our first hypothesis was that with decreasing soil P availability, the mass-based foliar total P concentrations of both *B. attenuata* and *B. sessilis* would decrease in response to decreased P availability, and this was supported. An important finding was that the area-based foliar P concentrations was higher in *B. attenuata* than in *B. sessilis* in all three substrates, but there was no significant difference in mass-based foliar P concentration in any of the three substrates. We found the same patterns of mass-based foliar total P concentration for both *B. attenuata* and *B. sessilis* grown in all three substrates; the foliar total P concentrations of both species were greatest in sand, and about 35% lower in SLIM. The greatest carboxylate-extractable P concentration was in sand, and the lowest was in limestone gravel (Fig. S1).

In contrast to the similar mass-based foliar total P concentrations in the two species in each substrate, the mass-based foliar total N concentration of *B. sessilis* was almost twice that of *B. attenuata* grown in the same substrate. Leaf N concentrations in *B. attenuata* and *B. sessilis* grown on SLIM were approx. 20% lower than those in plants grown in sand and SLAT. Our result differ results on *Hakea prostrata* (Proteaceae) showing that P availability did not influence leaf N concentration (Prodhan *et al.* , 2016). The foliar total N concentrations of both species were very low compared with those of plants from other environments (Reich *et al.* , 1991), which reflects the low foliar rRNA concentration in *B. attenuata* (Sulpice *et al.* , 2014), and, presumably, in *B. sessilis* , based on the similar size of their nucleic acid P pools. In our study, the relatively low foliar N concentrations in *B. attenuata* and *B. sessilis* indicate that protein concentrations were very low, which implies a low demand for rRNA and, thus, P.

Whilst the leaf N concentrations in both species were low compared with the global average (Reich *et al.* , 1991), they were distinctly higher in*B. sessilis* than in *B. attenuata* . The higher N concentration correlated with greater allocation of P to the nucleic acid fraction in*B. sessilis* . However, rates of photosynthesis and leaf N concentrations expressed on an area basis were similar for the two species, and hence so was the photosynthetic N-use efficiency (PNUE). Therefore, the 'extra' N in *B. sessilis* on a mass basis was a reflection of a lower investment in sclerenchymatic tissue, as evidenced by its lower LMA). A low ribosome abundance can be expected to decrease the rate of protein synthesis, and hence the protein and N concentrations. Therefore, lower leaf N concentrations in *B. attenuata* compared with *B. sessilis* on the three substrates tested is consistent with lower rRNA concentrations and lower rates of protein synthesis. However, since we studied mature non-growing leaves, which do not rapidly change in protein concentration (Kuppusamy *et al.* , 2014), the faster rate of protein synthesis must have been balanced by faster rate of protein breakdown, and hence protein turnover.

We found that RGR was strongly correlated with leaf N and nucleic acid P concentrations in both species, and that RGR and N concentration in*B. sessilis* were significantly greater than those in *B. attenuata* . This supports our second hypothesis that *B. sessilis* , which exhibits a more opportunistic growth strategy than *B. attenuata* (Shi *et al.* , 2020), will have a higher foliar $N_{Total} : P_{Total}$ ratio than *B. attenuata* and invest more P in nucleic acid P to support the higher N concentration. The higher leaf N concentration found here and higher capacity to acquire P (Shi *et al.* , 2020) in *B. sessilis*than in *B. attenuata* when grown in the more P-limiting SLIM may explain the different distribution patterns of the two species in the environment. This higher capacity to acquire P presumably allows it to colonise and become established on different P-impoverished soils (sand over laterite or over limestone), compared with *B. attenuata,*which is restricted to deep sand (FloraBase, http://florabase. dpaw.wa.gov.au/).

Foliar traits and P fractions

The different foliar P-allocation patterns combined with differences in LMA between the two species reflects differences in their life history strategies and resource requirements. Plants like *B. sessilis*with an *r* selection life history typically grow fast (Clarke*et al.* , 2013) and produce seeds before the next catastrophe,*i.e.* fire or

drought (Bowen & Pate, 2017, Knox & Clarke, 2005, Pate *et al.* , 1990). This strategy may require relatively greater investment in P-rich rRNA and, thus, ribosomes, to support rapid protein synthesis and turnover, including replacement of damaged proteins (Raven, 2012). A high protein synthesis capacity may provide flexibility to acclimate to variable and changing environments (*i.e.* shallow sand over laterite or limestone, where water availability may fluctuate) and complete the life cycle quickly. Unlike *B. sessilis* , *B. attenuata* with larger seeds (Shi *et al.* , 2020) and higher LMA, has the ability to resprout from epicormic buds or lignotubers (Groom & Lamont, 2011, Pate *et al.* , 1991), a strategy associated with a slower RGR (Bowen & Pate, 2017, Knox & Clarke, 2005, Pate *et al.* , 1990). Thus, selection in*B. attenuata* was based on a lower investment in nucleic acid P, as well as the ability to allocate more biomass to deep roots compared with *B. sessilis* (Shi*et al.* , 2020). Thus, it does not need to grow fast and complete its life cycle quickly (Bowen & Pate, 2017, Knox & Clarke, 2005, Pate*et al.* , 1990).

The Pi concentration in slow-growing *B. attenuata* was higher than that in the faster-growing *B. sessilis* when grown in sand and SLAT, slightly higher than when grown in SLIM. Cell vacuoles serve as a reservoir for excess Pi in most plants, which can then be drawn upon as P availability decreases (Mimura, 1995). Changes in total foliar P concentration with Pi supply generally reflect the accumulation of Pi in vacuoles, which is typically greater in slow-growing species than in fast-growing ones (Güsewell, 2004). Thus, fast-growing species convert Pi into growth-sustaining organic P, rather than accumulate Pi, as in slow-growing species.

The metabolite P concentrations and the proportions of total P in metabolites for *B. sessilis*were significantly higher than those for *B. attenuata* for plants grown in SLIM. Moreover, the PPUE of *B. sessilis* was greater than that of *B. attenuata* grown on all substrates. Hidaka & Kitayama (2009) suggested that high PPUE is sustained by the allocation of a greater proportion of P to metabolic P (metabolite P + Pi) than to structural P, as we have showed here. In addition, *B. sessilis* had a lower LMA than *B. attenuata* on all substrates tested; however, *B. attenuata* had higher lipid P concentrations when grown in SLAT and SLIM in response to the lower P availability compared with sand alone. This finding was partially in line with a study that showed that the concentration of structural P is greater in slow-growing plants with high LMA than in fast-growing plants with low LMA (Villar *et al.* , 2006). In other words, a greater proportion of nucleic acid P, a lower proportion of lipid P and a lower LMA in *B. sessilis* than in *B. attenuata* are all traits associated with a higher RGR and shorter leaf life-span (Veneklaas*et al.* , 2012). Overall, the unique foliar traits of the two species revealed different patterns of P allocation in response to soil P availability and associated with growth strategy that may define the ecological niches in which they are found (Figure 6).

CONCLUSIONS

Both *B. attenuata* and *B. sessilis* exhibited a unique pattern of allocating P to different P fractions within the leaves under P limitation. *Banksia sessilis* allocated more P to nucleic acids than *B. attenuata* . This investment in nucleic acid may support greater protein synthesis, which is likely needed for greater protein turnover. The observations that *B. attenuata* had a higher LMA and lower N concentration, PPUE, allocation of P to nucleic acids and N:P ratios than *B. sessilis* are possibly adaptive traits to growth in more severely P-impoverished soils, and may account for the different distributions of the two species. We surmise that P-allocation patterns are likely the functional basis explaining why plants can reduce foliar P concentrations on P-poor soils. The foliar nutrient-allocation patterns and distinct foliar traits of the two *Banksia* species reveal different adaptive strategies in response to soil P availability and match their differences in growth strategies.

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Figure legends

Fig. 1 Leaf mass-based total P **(A),** and N concentrations **(B),** and area-based P **(C)** and N**(D)** concentrations of *Banksia attenuata* and *B. sessilis* grown in three substrates. Values are means ± SE ($n = 10$); asterisks show significant differences between the two species by$t$ test. ^{ns} not significant,** $P < 0.01$, *** $P < 0.001$. Different letters represent significant differences among substrates ($P < 0.05$). SLAT: sand plus laterite, SLIM: sand plus limestone.

Fig. 2 The lipid phosphorus (P) **(A)** , metabolite P (**B**), nucleic acid P **(C),** residual P **(D)** and inorganic P (Pi) concentrations **(E)** in leaves of *Banksia attenuata* and *B. sessilis* grown in three substrates. Values are means ± SE ($n = 10$); asterisks show significant differences between the two species by t test. ns not significant, * $P< 0.05$, ** $P < 0.01$, *** $P < 0.001$. Different letters represent significant differences for the two species among substrates ($P < 0.05$). SLAT: sand plus laterite, SLIM: sand plus limestone

Fig. 3 The proportions of total foliar phosphorus (P) as lipid P **(A)** , metabolite P (**B**), nucleic acid P **(C),**residual P **(D)** and inorganic P (Pi) **(E)** for*Banksia attenuata* and *B. sessilis* grown in three substrates. Values are means ± SE ($n = 10$); asterisks show significant differences between the two species by t test. ns means not significant, * $P < 0.05$, ** $P< 0.01$, *** $P < 0.001$. Different letters represent significant differences for the two species among substrate types ($P < 0.05$). SLAT: sand plus laterite, SLIM: sand plus limestone

Fig. 4 Relationships of relative growth rate (RGR) to foliar nucleic acid phosphorus (P), foliar nitrogen (N), and foliar N to nucleic acid P for *Banksia attenuata* and *B. sessilis* . Values are means ± SE ($n = 10$). Individual data can be found in Figures 1 and 2, and Table 1.

Fig. 5 Relationships between foliar phosphorus (P) fractions and total foliar P concentration (left), and leaf mass per area (LMA) (right) for *Banksia attenuata* and *B. sessilis* grown in three substrates ($n = 30$). Each symbol represents an individual plant. BA: *B. attenuata* , BS: *B. sessilis* , SLAT: sand plus laterite, SLIM: sand plus limestone

Fig. 6 Diagrams summarising foliar traits affecting relative growth rates for the resprouter *Banksia attenuata* (a) and the seeder *Banksia sessilis* (b). Solid lines indicate connections between factors; dashed arrows indicate factors that affect another factor; red dashed arrow indicates that the factor affects the relative growth rate. P: phosphorus, LMA: leaf mass per area, PPUE: photosynthetic P-use efficiency

Table 1 . Mass ratios for total foliar nitrogen (N) to total foliar phosphorus (P) and to P in each foliar P-containing fraction, and relative growth rate (RGR) for *Banksia attenuata* and *B. sessilis* in three substrates. Values are means ± SE ($n = 10$); asterisks show significant differences between the two species by$t$ test. ** $P < 0.01$,*** $P < 0.001$. Different letters represent significant differences for the two species among the substrates ($P < 0.05$). SLAT: sand plus laterite, SLIM: sand plus limestone.

Items	*Banksia attenuata*	*Banksia attenuata*	*Banksia attenuata*	*Banksia attenuata*	*Banksia sessilis*	*Banksia sessilis*	*Banksia sessilis*
	Sand	SLAT	SLIM	Sand	Sand	SLAT	SLIM
Leaf N / Total leaf P	27.1±1.8 b	33.4±2.5 a	33.1±3.6 a	45.9±8.9 b***	45.9±8.9 b***	63.2±7.4 a***	56.9±7.72 a***
Leaf N / Pi	100±14 b	161±46 a	176±46 a	253±86 b***	253±86 b***	390±67 a***	356±80 a***
Leaf N / Lipid P	159±25 a	168±27 a	158±23 a	294±76 b***	294±76 b***	436±127 a***	398±95 ab***
Leaf N / Metabolic P	119±10 b	168±36 a	177±38 a	189±29 b***	189±29 b***	274±41 a***	239±54 a**

Items	*Banksia attenuata*	*Banksia attenuata*	*Banksia attenuata*	*Banksia attenuata*	*Banksia sessilis*	*Banksia sessilis*	*Banksia sessilis*
Leaf N / Nucleic acid P	105±9 a	114±11 a	108±13 a	136±29 b**	136±29 b**	186±28 a***	159±25 ab***
Leaf N / Residual P	416±94 a	447±94 a	375±66 a	692±195 a***	692±195 a***	607±98 a**	772±258 a***
Nucleic acid P / Lipid P	1.52±0.28 a	1.48±0.25 a	1.46±0.16 a	2.19±0.44 a**	2.19±0.44 a**	2.35±0.55 a***	2.53±0.58 a***
RGR (mg g^{-1} week^{-1})	95±2.6 a	93±3.7 a	86±4.6 b	123±4 a***	123±4 a***	115±7.6 b***	110±6.1 b***

Table 2. Photosynthesis rates, photosynthetic phosphorus-use efficiency (PPUE), photosynthetic nitrogen-use efficiency (PNUE), foliar mass per area (LMA) and the foliar ratio of nucleic acid phosphorus (P) to organic P of *Banksia attenuata* and *B. sessilis* grown in three substrates. Values are means ± SE ($n = 10$); asterisks show significant differences between the two species by t test.^{ns} not significant, * $P< 0.05$, ** $P < 0.01$,*** $P < 0.001$. Different letters represent significant differences for the two species among the substrates ($P < 0.05$). SLAT: sand plus laterite, SLIM: sand plus limestone.

	Banksia attenuata	*Banksia attenuata*	*Banksia attenuata*	*Banksia sessilis*	*Banksia sessilis*	*Banksia sessilis*
	Sand	SLAT	SLIM	Sand	SLAT	SLIM
Photosynthesis rates (μmol m^{-2} s^{-1})	15.3±3 a	15.4±1.3 a	10.8±1.8 b	13.4±2.2 a^{ns}	13.2±6.2 a^{ns}	10.7±2.3 a^{ns}
PPUE (μmol g^{-1} P s^{-1})	234±53 a	264±38 a	223±52 a	377±86.4 a***	506±269 a*	410±116 a***
PNUE (μmol g^{-1} N s^{-1})	8.9±2.2 a	7.9±1.0 ab	6.7±1.0 b	8.6±2.4 a^{ns}	7.9±3.5 a^{ns}	7.3±1.9 a^{ns}
LMA (g m^{-2})	240±15 b	248±21 b	267±24 a	119±7 b**	121±9 b**	131±6 a**
The ratio of nucleic acid P to organic P	0.355±0.026 a	0.378±0.042 a	0.382±0.023 a	0.420±0.044 a**	0.411±0.043 a^{ns}	0.434±0.041 a^{ns}

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