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Enduring effects of large legumes and phosphorus fertiliser on jarrah forest restoration 15 years after bauxite mining

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ABSTRACT

Restoring nutrients lost in the mining process and re-establishing nutrient-cycling are often key goals of mine restoration. One common strategy to facilitate these goals is to seed fast-growing legumes combined with one application of P-fertiliser to maximise legume growth and increase soil-N. However, the longer term effects of this strategy have received little attention. Here we report the results of a 15-year-old experiment that was established to test the effects of fertiliser-P application and seeding large understorey legumes, both singly and in combination, on jarrah forest restoration after bauxite mining.

Fifteen years after the establishment of this experiment, the majority of the seeded legumes had senesced, with total legume cover having declined significantly compared with results of the same experiment at 5-years-of-age. Yet, despite the legumes having senesced there were still negative effects of both large legumes and P-fertiliser on species richness and abundance of non-leguminous understorey species. These negative effects may be mediated by the persistent effects of legume competition that was evident at 5 years and the accumulation of significant quantities of leaf litter and fine woody debris in the large legume × P-addition treatments. Compared with the 0kg P ha^{-1} treatment, application of 20 kg P ha^{-1} significantly increased jarrah tree growth, but there was no additional benefit of 80 kg P ha^{-1}. These data suggest that moderation of P-fertiliser and large understorey legumes could maximise understorey cover, tree growth and understorey species richness, and therefore simultaneously address multiple key restoration goals.

Key words: *Acacia*, competition, fertilizer, nitrogen, rehabilitation

1. Introduction

Mining operations result in the removal of both above-ground vegetation and topsoil, with the topsoil generally being stockpiled (often for a number of years) between mining and rehabilitation. These disturbances result in a significant loss of nutrients and replacing these nutrients is a goal of both mine rehabilitation and restoration (*sensu* McDonald et al., 2016). Whilst for both rehabilitation and restoration these nutrients are replaced to increase plant productivity and cover, for mine restoration there are additional ecosystem dynamics to consider, including interspecific competition, plant-soil feedbacks and nutrient-cycling, given the focus to restore historic (pre-mining) native ecosystems

Planting or seeding fast-growing legumes has been a key component of restoring productivity and re-establishing nutrient-cycling in many mine restoration (Ward et al., 1990) and reafforestation operations (e.g. Siddique et al., 2008). Planting legumes has the advantage of N_2-fixation, potentially increasing soil-N availability to other species such as trees. In addition, fast growing legumes may help to minimise soil erosion of newly rehabilitated (bare) sites (Ward et al., 1990). This strategy has been widely applied in Australia (Langkamp et al., 1979; Todd et al., 2000; Grant et al., 2007; Brady and Noske, 2010) and elsewhere including the United Kingdom (Bradshaw, 1983) and Brazil (Parrotta and Knowles, 1999, 2001). Growth and N-fixation of legumes can be maximised by applying P-fertiliser to low-P soils since legumes are generally P-, but not N-limited. For example, adding the equivalent of 50 kg P ha^{-1} to mined and restored jarrah forest soils increased annual N-fixation by *Acacia pulchella* from 12 kg N ha^{-1} to 85 kg N ha^{-1} (Hingston et al., 1982). Taken together, the available evidence suggests a beneficial role of legumes in restoration projects.

There are, however, a number of potential disadvantages to a restoration strategy based on establishment of leguminous species facilitated by high P-application rates. These include: (1) increased competition due to the rapid growth and dense vegetation that can result (Koch, 1987), (2) an increase in N-responsive weed species (e.g. Nichols and Carpenter, 2006), (3) elevated fuel loads, particularly for fine fuels from both live and senesced legumes (Todd et al., 2000; Grant et al., 2007), and (4) many legumes produce a thick leaf litter layer that can physically retard the establishment of other understorey species (Boyes et al., 2011; le Stradic, 2014). While applying fertiliser, and particularly P, maximises the initial growth of leguminous species, it can also have negative impacts on the re-establishing plant community. Elevated P on ancient soils lacking P can favour annual species, including weeds, while negatively affecting slow growing species and those with specialised P-acquisition strategies, such as Proteaceae (Lambers et al., 2008; Shane et al., 2004). For example, in fynbos restoration in South Africa after a simulated mining disturbance, Holmes (2001) found that adding 26 kg P ha^{-1} increased overall plant density and cover. However, this effect was mainly limited to exotic weeds, and P-addition increased the mortality of native Proteaceae. Similarly, Daws et al. (2013) found that for jarrah forest restored after mining, annual species (weeds and natives) were the main beneficiaries of applied P-fertiliser. Furthermore, while the growth and density of native Proteaceae was insensitive to P application, the overall species richness of native species was reduced at P-application rates greater than 20 kg ha^{-1}. Overall, these studies highlight the need for more detailed understanding of the combined effects of P-fertiliser and legumes.

In an experimental test of the effects of seeding large understorey legumes combined with P-addition on jarrah forest restoration, Daws et al. (2015) found that five years after restoration both legume seeding and P-addition resulted in significantly higher plant cover, although cover was dominated by large legumes. P addition also significantly increased the growth of the dominant tree species *Eucalyptus marginata* (jarrah): seeding legumes had no impact on tree growth. However, by 10-13 years of age jarrah stands in restored forest are, based on stand thinning experiments, more constrained by water- than P-availability (Grigg and Grant, 2009). Consequently, any initial growth benefit for jarrah from P-application might reduce over-time as water availability becomes more limiting. However, this remains to be tested. For non-leguminous understorey species, both cover and density were negatively affected by seeding large legumes and P-addition. However, previous studies in restored jarrah forest indicate that many larger understorey legumes reach their maximum size at around 5-years-of-age (Daws and Koch, 2015), and that beyond this point, many of these legumes senesce (Daws and Koch, 2015; Grant et al., 2007). The longer-term implications of legume senescence for the trajectory of restoration, and particularly community composition, are unknown.

There are two possible outcomes of legume senescence. Firstly, the debris and litter on the soil surface from senescing legumes may further negatively impact small understorey species, due to either an inability to germinate through deep litter (e.g. small seeded ephemerals; Daws et al., 2005), or by plants being physically buried. For example, in quarry restoration in Brazil Le Stradic et al. (2014) indicated that understorey legume shrubs resulted in a thick litter layer that limited herbaceous species establishment. Secondly, the senescence of these larger species may increase opportunities for recruitment and growth of smaller and slower growing species. These potential longer-term effects of seeding large legumes and P-addition on assembly trajectories of restored jarrah forest remain to be tested.

In this study, we report on a 15-year-old experiment in restored jarrah forest that had a factorial combination of three P-fertiliser addition rates combined with additional seeding of large legume shrubs. We test, approximately 10 years after the onset of legume senescence whether, (1) understorey cover, density and species richness for non-leguminous species are affected by the initial inclusion of large legumes in the seed mix, (2) whether there are persistent effects of initial P-application on community assembly, and (3) whether there are long-term effects of legume seeding and P-application on tree growth.

2. Materials and methods

2.1. Study site

Alcoa of Australia Ltd. (hereafter Alcoa) mines and restores ca. 550 ha of forest each year (Koch, 2007a). The experiment described here was established in 2001 within the Alcoa mining lease located within the Darling Range of Southwest Western Australia (32°35'06" S, 116°06'44" E). The climate of the region is Mediterranean with hot, dry summers and cool, wet winters. Annual rainfall is 1,200 mm, the average summer monthly maximum temperature is 28 °C and the average winter minimum is 5 °C. The overstorey vegetation is dominated by jarrah (*Eucalyptus marginata*). The understorey consists of shrubs and herbs predominantly in the families Myrtaceae, Proteaceae, Fabaceae, Restionaceae, Orchidaceae, Apiaceae, Liliaceae (*sensu lato*), Ericaceae, Asteraceae and Cyperaceae.

Mine pits range from 1 to 20 ha in size and are surrounded by intact forest. The aim of Alcoa's restoration is to establish a self-sustaining jarrah forest ecosystem that fulfils pre-mining land uses including nature conservation, recreation, timber production and water catchments. Restoration involves reshaping the mine pit, ripping to alleviate compaction and spreading fresh topsoil (Koch, 2007a). Restored areas receive fresh topsoil sourced from adjacent areas that have been cleared of vegetation in advance of being mined. This restoration practice ensures availability of soil stored seeds such as legumes (Grant et al., 2007), and microorganisms including the rhizobia that form nitrogen-fixing symbioses with native legumes (Jasper, 2007).

Seeds of local plants are spread over the restored mine pits and planting of nursery grown plants occurs for species where seed application is not a viable establishment method (Koch 2007b). A fertiliser mix is applied by helicopter in late winter or early spring after the completion of restoration. In 2001, this mix contained the equivalent of 80 kg elemental P ha^{-1} and 80 kg elemental N ha^{-1}. The mine pits used for the experiment reported here were excluded from this routine fertiliser application.

2.2. Experimental design

In March 2001 within each of six newly restored mine pits, a block containing six 40 m × 50 m plots was established. A factorial design with two factors was used: with and without seeding of 7 large understorey legume species (a combined total of 217 g ha^{-1} of *Acacia drummondii*, *A. extensa*, *A. lateriticola*, *A. pulchella*, *A. urophylla*, *Bossiaea aquifolium* and *Mirbelia dilatata* seeds); and P-fertiliser application, including none, 20 kg elemental P ha^{-1} and 80 kg elemental P ha^{-1}. Each experimental plot also received a generic seed mix containing seeds of 108 jarrah forest species which was broadcast by hand in March 2001 (see Appendix 1 for individual species seeding rates). This mix included the dominant tree species jarrah. After seeding, P was applied once as di-ammonium phosphate, and nitrogen (urea) was added once to each plot at an application rate of 80 kg elemental N ha^{-1}. Further details of the experimental design are provided in Daws et al. (2015).

Fifteen months after seeding there were, on average, 0.39 more legume seedlings m^{-2} in the legume seeding treatment (for more details see Daws et al., 2015). Treatments were allocated randomly to the 40 m × 50 m plots within each block.

2.3. Botanical monitoring

Within each experimental plot, a previously selected central 20 m × 20 m quadrat (Daws et al. 2015) was surveyed for jarrah trees. In December 2015, for all individual jarrah trees >2m in height we recorded diameter at breast height, bark thickness and tree height. Data for multiple stems was recorded if stems were >1 cm diameter.

In October 2015, five 4 m × 4 m quadrats in the four corners and the centre of the 20 m × 20 m plot (a total of 80 m^2) were surveyed for shrubs and herbaceous species; the number, identity and percentage cover (a visual estimate that included overhang) of these species was recorded. Estimation of cover took place using frames within the monitoring quadrats, and for each species took into account vertical structuring of the understorey. As a result, it was possible for the sum of all cover estimates to exceed 100%.

2.4. Leaf litter depth measurements

Leaf litter depth was measured to assess whether there was increased accumulation of leaf litter when large legumes were included in the seed mix since this is one potential mechanism for large legumes to exhibit an ongoing impact on vegetation composition (hypothesis 1). For three of the six restored mine pits measurements of leaf litter depth were recorded at 45 random locations per plot in February 2016. It was not possible to take measurements of the other three sites due to an intense wild-fire burning these sites in January 2016. Leaf litter depth was also sampled in three 20 m × 20 m quadrats in non-mined forest. Based on fire history data from the Department of Parks and Wildlife, these sites had not been burnt within the previous 15-year period, i.e. leaf litter had been accumulating for at least the 15-year duration of the current experiment.

2.5. Soil nutrient analyses

Soil samples were analysed for plant available-P to allow an assessment of whether potential long-term impacts of a single initial P application (hypothesis 2) result from greater ongoing availability of soil-P. Soil sampling was planned to take place in January 2016. However, this was delayed to 2018 due to wildfires burning three of the experimental blocks in January 2016 and a further two blocks in 2017. While Ward et al. (1991) reported that wildfire can result in significant losses of N from jarrah forest soils, they found no effect on the main focus of our present study - soil P. In January 2018, soil samples were collected from the six experimental blocks. Within each of the six plots within each block, six samples were taken from 0 to 10 cm depth randomly across each plot. All samples were collected from the bottom of the furrows caused by contour ripping at the outset of restoration. The six samples per plot were then bulked to form a composite sample, air dried and passed through a 2 mm sieve to remove the gravel fraction before being sent to a commercial laboratory for nutrient analyses (CSBP Soil and Plant Laboratories, Bibra Lake, Perth). Total N, ammonium (NH_4^+), total organic carbon and Colwell P were determined using the methodology of Rayment and Higginson (1992).

2.6. Statistical analyses

For analysis of the effects of seeding the seven large legumes (hypothesis 1), and application of phosphorus (hypothesis 2) on species richness, stem density and cover, each plant species was assigned to one of five categories reflecting hypothesised responses to P. We predicted that non-native weeds and ephemerals would respond positively to fertiliser application (Prober and Wiehl, 2012), re-sprouters and Proteaceae would respond negatively (Lambers et al., 2008) and that long-lived re-seeders would be mixed in their responses. Plants were categorised as either: (1) ephemerals (short-lived native species), (2) non-native species (weeds), (3) Proteaceae, (4) re-sprouters or (5) re-seeders (see Appendix 2 for species assignment to the five categories). Following Bell (2001), re-seeders must re-establish through germination and establishment of seedlings, whereas re-sprouters can re-establish by sprouting from surviving underground structures. It should be noted that in Bell's categorisation, used for fire response, ephemerals and weeds are also re-seeders; whereas the re-seeder category used here consisted only of longer-lived species.

In addition, proteaceous species were all re-sprouters and were therefore excluded from the re-sprouter category. Since the large seeded legumes are all in the re-seeder category, these species were excluded from analyses of the effect of P and large legumes on re-seeder species. Species were classified as re-sprouters and re-seeders based on published literature (Bellairs and Bell, 1990; Bell et al., 1993; Ward et al., 1997; Smith et al., 2000; Norman et al., 2006a; Burrows et al., 2008). Native ephemerals and weed species were classified based on the FloraBase database (Western Australian Herbarium, 2012).

We used MANOVA (implemented in Minitab 16) to assess effects of P and seeding legumes on percentage cover and the number of species and stems within the various growth form categories. In this analysis, ‘Pit’ was included as a random factor. For significant terms in the MANOVA model, uni-variate GLMs were used to assess differences among the growth-form categories. In all analyses, the three P-application rates (0, 20 and 80 kg ha^{-1}) were treated as levels of a single treatment and a critical alpha of 0.05 was used to assess significance.

3. Results

3.1. Soil chemical analyses

Seventeen years after the establishment of this experiment, there were no effects of either experimental treatment on total soil N, total organic carbon or soil NH_4^+ (Table 1). The addition of P-fertiliser resulted in significantly elevated soil Colwell-P, while legume seeding had no effect on soil-P (Table 1).

3.2. *Accumulation of fine woody debris in response to fertiliser and legume seed addition*

The depth of fine debris and leaf litter increased significantly with both P-application and seeding large legumes (Table 1). This resulted in leaf litter depth being greater than in unmined forest in the legume seeding treatment when either 20 or 80 kg P ha^{-1} were applied (Table 1). There was also a significant P × legume interaction indicating that the effect of seeding legumes on litter accumulation was greatest when P was also applied.

3.3. Legume responses to fertiliser and legume seed addition

The inclusion of 7 additional legume species in the seed mix had no significant effect on the total number of legume species present after 15 years (Fig 1A). However, there were significantly fewer legume species present when P was applied at a rate of 80 kg ha^{-1} compared with either 0 or 20 kg ha^{-1}: there was at least one fewer species present at 80 kg P ha^{-1} compared with the other application rates (Fig 1A). There was no effect of either seeding large legumes or P-application rate on the density of legumes 15 years after the onset of rehabilitation (Fig 1B). However, total legume cover was significantly increased by the inclusion of large legumes in the seed mix, the addition of P fertiliser, and the interaction between seeding and fertiliser addition (Fig 1C).

3.4. Understorey responses to fertiliser and legume seed addition

The addition of P-fertiliser resulted in a highly significant reduction in the species richness of non-leguminous understorey species (Fig 2AB). For example, in the absence of large legumes species richness decreased from 38.6 species at 0 kg ha^{-1} P to 29.6 species at 80 kg ha^{-1} P. Similarly, the addition of large legumes resulted in a significant reduction in non-legume species richness: at 0 kg P ha^{-1} there were seven additional non-legume species present when the seven large legumes were not included in the seed mix. In the MANOVA analysis, there was a significant effect of both seeding large legumes and addition of P-fertiliser on the distribution of species across the five growth-form categories. Based on univariate tests, phosphorus addition had a significant negative effect on the number of species of re-seeders and a positive effect on the number of weed species. Seeding large legumes had a significant negative effect on the number of re-sprouter and Proteaceous species.

Application of P-fertiliser significantly affected both the density of non-leguminous understorey plants and their distribution across the five growth-form categories (Fig 2CD). For example, in the absence of seeded large legumes, total plant density declined from 2.85 to 2.16 stems m^{-2} as the P-application rate increased from 0 to 80 kg ha^{-1} (Fig 2C). There was no significant effect of legume seeding on plant density. The effect of P on plant density was driven predominantly by significant reductions in the density of re-sprouter and Proteaceous species.

P-addition resulted in a significant decrease in the understorey cover attributable to non-legume species (Fig 2EF). For example, in the absence of seeding large legumes cover declined from 42.6 to 22.9 % as P application rates increased from 0 to 80 kg ha^{-1}. Seeding large legumes had no effect on the distribution of plant cover within the five growth form categories (Fig 2EF). The reduction in cover, in relation to P, was driven primarily by the cover of re-sprouter species declining by approximately 50% as P increased (Fig 2EF).

3.5. Jarrah growth responses to fertiliser and legume seed addition

Increasing P from 0 to 20 kg ha^{-1} significantly increased growth of jarrah in terms of both stand basal area under bark (BAUB) and tree height. As P increased from 0 to 20 kg ha^{-1}, BAUB increased from approximately 13 m^{2} ha^{-1} to 16 m^{2} ha^{-1} (Fig. 3A) and tree height from 9.5 to 11 m (Fig 3B). At 80 kg P ha^{-1} there was no further benefit for tree growth compared with 20 kg ha^{-1}. There was no effect of seeding large legumes on either BAUB (Fig 3A) or tree height (Fig 3B).

4. Discussion

Fifteen years after the establishment of this experiment, application of P-fertiliser increased the growth of legumes and jarrah trees in restored jarrah forest. Including large legumes in the seed mix also increased the cover attributable to legumes. However, the combination of large legumes and high P-application rates significantly reduced the species richness, density and cover of non-legume understorey species.

While we found that after 15 years legumes were still a significant component of the total understorey cover, total legume cover was less than at 5-years-of-age (Daws et al., 2015). For example, in the 80 kg P ha^{-1} and legume seeding treatment legume cover was ~50 % at 5-years-of-age and had declined to ~18 % by 15 years. This result is consistent with previous studies (Daws and Koch, 2015; Grant et al., 2007), which indicated that from about five years of age onwards, many large understorey legumes senesce. Legume senescence was also evident in the leaf litter depth measurements, which indicate a significant accumulation of fine woody debris and leaf litter on the soil surface related to seeding legumes and applying P. Increased litter depth and masses related to legume senescence have been reported in other P fertilised eucalypt forest restoration schemes (George et al. 2010; Tibbett, 2010; Spain et al., 2015) where greater production of litter compared to native forests is a common phenomenon.

It has been hypothesised that seeding a high density of legumes combined with P-application may increase N-availability to other species and result in, for example, more rapid tree growth (Palaniappan et al., 1979; Ward and Koch, 1996). However, we found no evidence of any benefit of large legumes to tree growth, total soil N or to NH_4^+ in restored jarrah forest. While increased growth of *Eucalyptus* species when in mixed plantings with legumes is commonly observed, it is by no means a ubiquitous feature of mixed species plantings. For example, Forrester et al. (2006) reported that the effect of legumes on *Eucalyptus* growth can depend on factors including the proportion of legumes in the mix and species selection . Conversely, while also not evident in this study, high densities of large understorey legumes can reduce tree growth in both restored sites and forestry plantations (Turvey et al., 1983; Koch, 1987; Forrester et al., 2011). Taken together, these data suggest that in a restoration context, a strategy that includes legumes to increase N-availability may have unpredictable outcomes.

Our current data suggest, at least for the first 15 years of restoration, there are few benefits of a strategy that includes large understorey legumes. Thus, despite an additional seven species being included in the seed mix in the large legume treatment, even the species richness of legumes was not increased: smaller legume species were potentially outcompeted by the seven larger species. Including the seven large legumes in the seed mix also decreased the species richness of non-legume understorey species, presumably due to increased competition. However, the rapid establishment of plant cover, which may minimise initial soil erosion is a potential benefit of seeding large legumes, although for Alcoa's operations, ripping on contour is the primary means of erosion control (Koch 2007a).

In our previous study (Daws et al., 2015), applied-P was still present in the soil and impacting vegetation dynamics 5 years after fertiliser addition. While overall soil P levels have declined in the 12 years between this study and our earlier study (Daws et al., 2015), soil-P was still significantly higher in the applied-P treatments 17 years after a single initial application. Furthermore, these levels of soil P were still higher than the approx. 2 mg kg^{-1} P typically observed in reference jarrah forest soils (Standish et al., 2008). Similarly, soil-P levels in restored jarrah forest, and other post-mining environments can remain elevated for at least 26-years after fertiliser addition (Spain et al., 2006; Banning et al., 2008; Standish et al., 2008; Spain et al., 2015). Indeed, a recent study of forest soil P dynamics in a restored tropical eucalypt forest found ongoing net increases in near-surface concentrations of P over 26 years, potentially storing up future difference between fertilised restored and native forest systems (Spain et al., 2015). Therefore, while P-addition may have mid- to long-term positive impacts on, for example, legume growth (as shown in this current study), there is a potential for ongoing persistent negative effects on other understorey species.

In earlier studies of this system, elevated P significantly increased the abundance of weeds and ephemerals (Daws et al., 2013, 2015). This effect was less apparent at 15-years-of-age: presumably these species have declined in abundance as the forest canopy has closed. However, there was still a negative effect of applied-P on species richness, abundance and cover attributable to non-leguminous native species. These negative effects potentially result from direct toxicity of applied P to native species since many species in the jarrah forest (e.g. Proteaceae) have specialised adaptations for P-acquisition in this naturally P-deficient system (Lambers et al., 2008; Shane et al., 2004). However, direct toxicity of applied-P in jarrah forest soils may be tempered by the strong P-binding properties of the iron and aluminium hydroxides that are abundant in these soils (Bolan et al., 1983; Handreck, 1997). Additionally, or alternatively, the reduction in species richness of understorey species may be mediated through increased competition from species that respond vigorously to applied-P such as the larger legumes and establishing jarrah trees: indeed, the negative effects of applied-P were most evident for re-sprouter species (including the Proteaceae), which are generally slow growing (Pate et al., 1990; Bowen, 1991; Bowen and Pate, 1993) and some of which exhibited no growth response to applied fertiliser in other studies (e.g. Daws et al., 2013). The relative importance of direct P-toxicity and competitive effects for the negative effects of P-addition require further study.

Furthermore, a negative effect of P on non-leguminous understorey species was evident after 15 years despite an overall reduction in both the density and cover of the highly P-responsive legumes due to senescence. While it is probable that legume senescence will have reduced competition in the understorey, an ongoing negative effect of P may result from the associated increase in accumulation of fine woody debris and litter from senescing legumes. Accumulation of litter may continue to hinder the recruitment of small seeded species (Daws et al., 2005) even after many of the larger legumes have senesced. In addition, jarrah forest restoration has been reported to generally follow the initial floristics model of succession due to a limited ability for most species to colonise into restored mine pits (Norman et al., 2006b). This means that even if the legumes senesce, colonisation of the restored forest by additional species may be limited.

There were significant benefits of applied-P (20 or 80 kg ha^{-1}) for tree growth albeit with no difference between 20 and 80 kg ha^{-1}. Although the response to P was significant, the magnitude of the difference in growth between 0 and 20 kg P ha^{-1} was substantially less than when the trees were measured at 5-years-of-age (Daws et al., 2015). Thus, in our present study stand basal area and average tree height were only 23% and 16% greater at 20 compared with the 0 kg P ha^{-1} treatment. In contrast, at 5-years-of-age there was a 230 % and 170% difference between 0 and 20 kg P ha^{-1} for basal area and tree height, respectively (Daws et al., 2015). This reduction in the relative benefit of adding P-fertiliser suggests that the benefit of P application for tree growth may disappear over time, although this suggestion remains to be tested. Nonetheless, this result is consistent with other studies that have shown growth of jarrah to be constrained primarily by water availability primarily rather than P-availability. For example, studies in both 10-13-year-old rehabilitated jarrah forest and unmined forest have shown no growth response to fertiliser addition unless water availability is increased by thinning the stands (Stoneman et al., 1997; Grigg and Grant, 2009).

A trade-off between productivity and diversity has been observed in a range of ecosystems with nutrient enrichment reducing species richness (e.g. Wheeler and Shaw, 1991; Tilman et al. 2001; Wassen et al., 2005). In addition, for a range of vegetation types, fertiliser addition can increase growth and diversity of non-native weeds and decrease the diversity of native understorey plants in post-mining restoration, e.g. boreal sites in Canada

(Errington and Pinno, 2015) and fynbos in South Africa (Holmes, 2001). Combined with our current data, this suggests that a restoration strategy based on maximising early growth and site productivity may not be optimal for re-establishing diverse understorey communities. In a jarrah forest context, although applied P fertiliser did increase early tree growth this benefit also declined markedly over time. Interestingly, mining and clearing operations prior to mining in the jarrah forest result in the loss of ~20 kg P ha^{-1} (Hingston et al., 1980) and it appears that an application rate close to this value may provide an appropriate balance between restoring lost nutrient capital and maximising native plant species richness.

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Table 1. The effects of phosphorus addition and seeding large legumes on the soil properties in the experimental plots in January 2018, 17 years after phosphorus addition and seeding of large legumes in a fully factorial experiment. Also shown is the depth of accumulated leaf litter and fine woody debris measured in 2016, 15 years after establishment of the experiment.

P-application rate (kg ha^{-1})	Large legumes seeded?	Total N (%)	Colwell P mg kg^{-1}	Total organic carbon (%)	NH_4-N mg kg^{-1}	Litter layer depth (mm)
Experimental treatments						
0	Yes	0.16 ± 0.02	3.67 ± 0.33	2.53 ± 0.36	6.17 ± 0.83	29.2 ± 8.7
	No	0.14 ± 0.03	3.67 ± 0.71	2.71 ± 0.29	6.83 ± 2.15	57.4 ± 8.8
20	Yes	0.16 ± 0.01	4.00 ± 0.52	3.13 ± 0.36	11.50 ± 3.49	112.4 ± 13.4
	No	0.14 ± 0.02	4.33 ± 0.76	2.77 ± 0.34	9.17 ± 2.70	54.5 ± 4.3
80	Yes	0.19 ± 0.04	7.83 ± 0.83	3.70 ± 0.10	16.83 ± 3.82	93.9 ± 19.5
	No	0.14 ± 0.03	7.00 ± 0.58	2.78 ± 0.30	10.17 ± 3.04	50.9 ± 10.7
Unmined forest						
Nil	**N/A**	**n.d.**	**n.d.**	**n.d.**	**n.d.**	68.1 ± 7.5

Means ± 1SE of the mean.

n.d. = not determined.

Figure legends:

Fig. 1. The effects of phosphorus fertiliser application rate and seeding large legumes on: (A) the species richness, (B) the number of individual plants, and (C) total cover of legume species, 15 years after seeding and fertiliser addition. Error bars are +1SE of the mean.

Fig. 2. The effect of phosphorus application rate and seeding large legumes on, (A, B) established species richness, (C, D) seedling density, and (E, F) plant cover in each of five growth form categories (weeds, native ephemerals, Proteaceae, re-sprouter and re-seeder species). Legume species are excluded from these plots. Note that Proteaceae are hardly visible on C and D due to low overall plant densities and that ephemerals and weeds are not visible on E and F due to very low overall cover associated with these groups. Error bars are –1SE of the mean.

Fig. 3. The effect of phosphorus fertiliser application rate and seeding additional large legumes on: (A) the basal area, and (B) height, for the tree species jarrah (*Eucalyptus marginata*), 15 years after seeding and fertiliser addition. Error bars are +1SE of the mean.

578 Fig. 1

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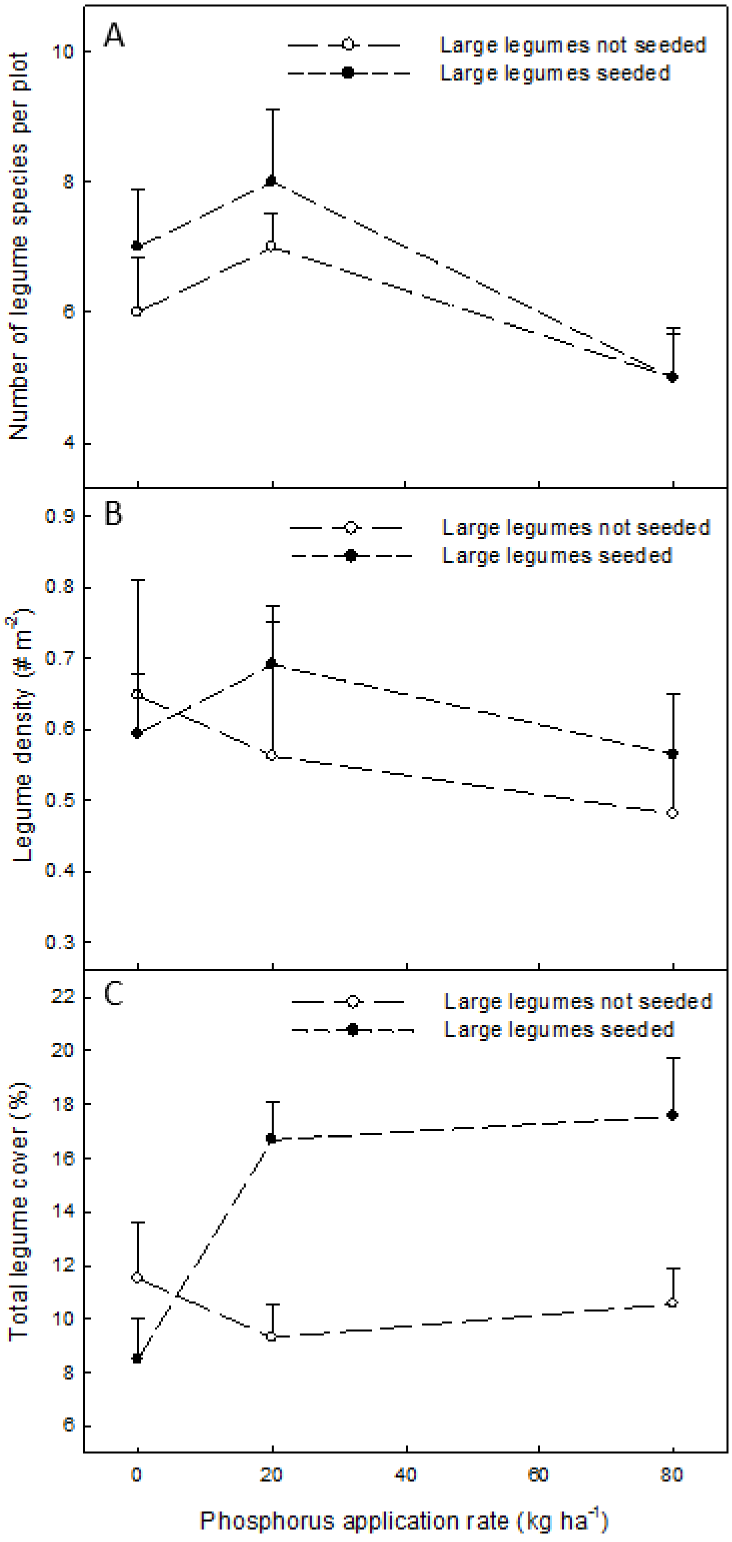

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582 Fig. 2

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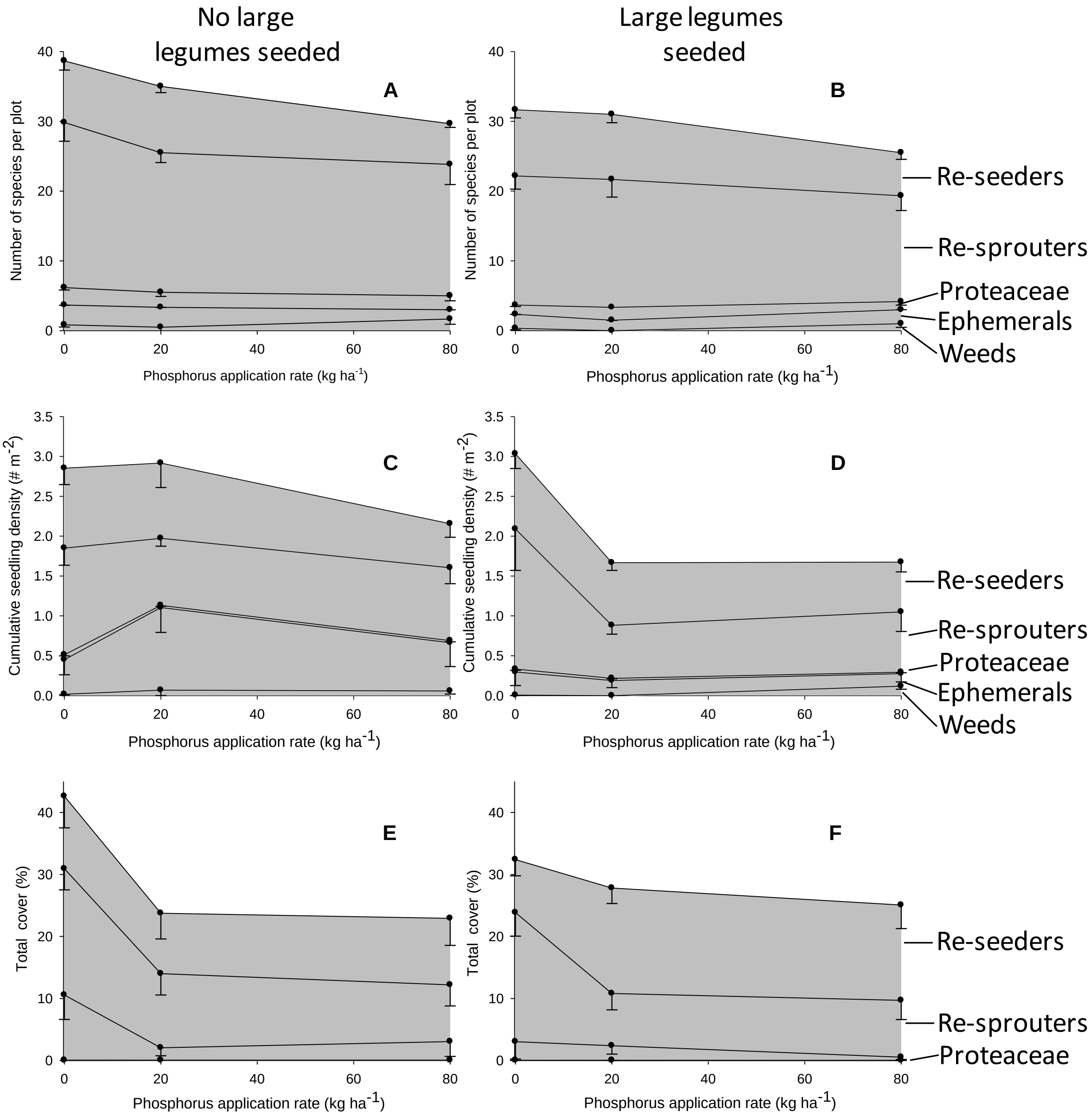

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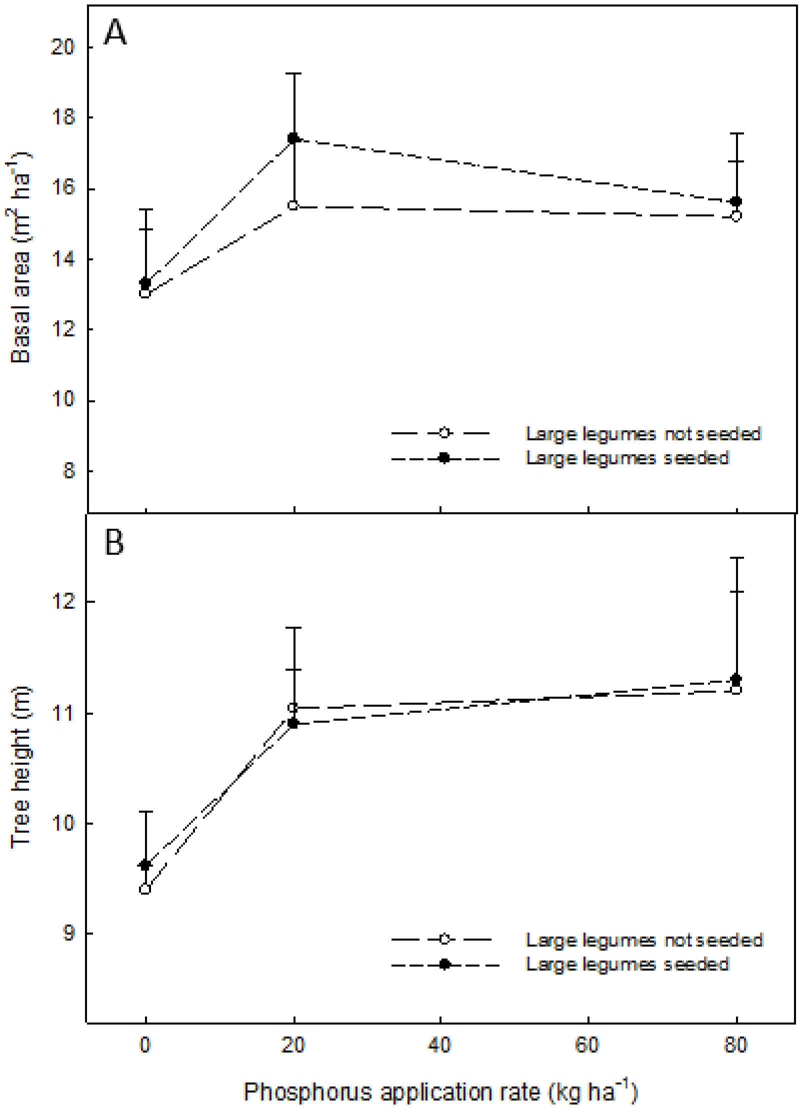
Fig 3.


A
Basal area (m^2 ha^{-1})
20
18
16
14
12
10
8
Large legumes not seeded
Large legumes seeded
B
Tree height (m)
12
11
10
9
Large legumes not seeded
Large legumes seeded
0
20
40
60
80
Phosphorus application rate (kg ha^{-1})

593 Appendix 1: Seeding rates used in the experiment.

Species	Family	Seed application rate (#ha^{-1})
*Acacia drummondii**	Fabaceae	15881
*Acacia extensa**	Fabaceae	1791
Acacia horridula	Fabaceae	114
*Acacia lateriticola**	Fabaceae	5516
Acacia nervosa	Fabaceae	139
*Acacia pulchella**	Fabaceae	1455
*Acacia urophylla**	Fabaceae	1966
Agrosticrinum scabrum	Anthericaceae	663
Allocasuaria fraseriana	Casuarinaceae	736
Amphipogon amphipogonoides	Poaceae	697
Andersonia involucrata	Epacridaceae	7896
Andersonia latiflora	Epacridaceae	11171
Anigozanthos manglesii	Haemodoraceae	1026
Astroloma ciliata	Epacridaceae	10
Austrodanthonia caespitosa	Poaceae	895
Banksia grandis	Proteaceae	426
Billardiera floribunda	Pittosporaceae	179
Billardiera fraseri	Pittosporaceae	33
Billardiera heterophylla	Pittosporaceae	571
Billardiera variifolia	Pittosporaceae	145
Boronia fastigiatus	Rutaceae	216
*Bossiaea aquifolium**	Fabaceae	5111
Bossiaea ornata	Fabaceae	13844
Burchardia congesta	Colchicaceae	1967
Chamaescilla corymbosa	Anthericaceae	298
Chorizema dicksonii	Fabaceae	1258
Chorizema ilicifolium	Fabaceae	2884
Clematis pubescens	Ranunculaceae	96
Conostylis aculeata	Haemodoraceae	767
Corymbia calophylla	Myrtaceae	3169
Craspedia variabilis	Asteraceae	23
Cryptandra arbutiflora	Rhamnaceae	99
Cyathochaeta avenecea	Cyperaceae	1312
Daviesia cordata	Fabaceae	523
Daviesia decurrens	Fabaceae	37
Daviesia physodes	Fabaceae	13
Daviesia preissii	Fabaceae	11

Dianella revoluta	Phormiaceae	198
Dryandra lindleyana	Proteaceae	7
Dryandra sessilis	Proteaceae	1
Eryngium pinnatifidum	Apiaceae	1082
Eucalyptus marginata	Myrtaceae	49645
Glischrocaryon aureum	Haloragaceae	257
Gompholobium knightianum	Fabaceae	2417
Gompholobium marginatum	Fabaceae	5693
Gompholobium polymorphum	Fabaceae	181
Gompholobium preisii	Fabaceae	378
Gonocarpus cordiger	Haloragaceae	50
Grevillea pilulifera	Proteaceae	7
Grevillea quercifolia	Proteaceae	7
Grevillea wilsonii	Proteaceae	10
Haemodorum paniculatum	Haemodoraceae	5
Haemodorum spicata	Haemodoraceae	76
Hakea amplexicauis	Proteaceae	40
Hakea cyclocarpa	Proteaceae	21
Hakea lissocarpa	Proteaceae	78
Hakea ruscifolia	Proteaceae	2
Hakea stenocarpa	Proteaceae	9
Hakea undulata	Proteaceae	96
Hemigenia rigidum	Labiaceae	802
Hemigenia sericea	Labiaceae	170
Hibbertia commutata	Dilleniaceae	263
Hibbertia huegelii	Dilleniaceae	196
Hovea chorizemifolia	Fabaceae	50
Hovea trisperma	Fabaceae	166
Hyalosperma cotula	Asteraceae	745
Hybanthus calycinus	Violaceae	39
Hybanthus floribunda	Violaceae	14
Hypocalymma angustifolium	Myrtaceae	4223
Isotoma hypocrateriformis	Campanulaceae	1768
Kennedia coccinea	Fabaceae	92
Labichea punctata	Fabaceae	876
Lagenophora huegelii	Asteraceae	3401
Lechenaultia biloba	Goodeniaceae	819
Leucopogon propinquus	Epacridaceae	54
Leucopogon verticillatus	Epacridaceae	146
Lomandra nigricans	Dasypogonaceae	16
Lomandra preissii	Dasypogonaceae	0.47
Lomandra purpurea	Dasypogonaceae	39

Lomandra sonderi	Dasypogonaceae	39
Macrozamia reidlii	Zamiaceae	155
Marianthus bicolor	Pittosporaceae	191
*Mirbelia dilatata**	Fabaceae	1442
Neurachne alopecuroidea	Poaceae	10974
Orthosanthus laxus	Iridaceae	85
Persoonia elliptica	Proteaceae	1
Persoonia longifolia	Proteaceae	1
Phyllanthus calycinus	Euphorbiaceae	2085
Pimelia ciliata	Thymelaceae	320
Pimelia suaveolens	Thymelaceae	47
Ptilotheca spicata	Rutaceae	29
Ptilotus manglessii	Ameranthaceae	396
Stackhousia pubescens	Celastraceae	62
Stylidium amoenum	Stylidiaceae	7934
Stylidium calcaratum	Stylidiaceae	5408
Stylidium diuroides	Stylidiaceae	5408
Stylidium junceum	Stylidiaceae	453
Stylidium schoenoides	Stylidiaceae	133
Tetrarrhena laevis	Poaceae	1536
Tetratheca hirsuta	Tremandraceae	317
Thysanotus multiflorus	Anthericaceae	261
Trichocline spathulata	Asteraceae	62
Tricoryne elatior	Anthericaceae	65
Tripterococcus brunonis	Celastraceae	1214
Trymalium ledifolium	Rhamnaceae	1955
Velleia trinervis	Goodeniaceae	784
Xanthorrhoea gracilis	Xanthorrhoeaceae	2415
Xanthorrhoea preissii	Xanthorrhoeaceae	529

*only seeded in the large legume treatment.

Appendix 2: Species recorded in the experiment, and the growth form they were assigned in analyses.

Species	Family	Growth form
Acacia drummondii	Fabaceae	Re-seeder
Acacia extensa	Fabaceae	Re-seeder
Acacia lateriticola	Fabaceae	Re-seeder
Acacia pulchella	Fabaceae	Re-seeder
Acacia saligna	Fabaceae	Re-seeder
Acacia urophylla	Fabaceae	Re-seeder
Adenanthos barbiger	Proteaceae*	Re-sprouter
Aira caryophyllea	Poaceae	Non-native weed
Allocasuarina fraseriana	Casuarinaceae	Re-sprouter
Amphipogon amphipogonoides	Poaceae	Re-sprouter
Andersonia lehmanniana	Epacridaceae	Re-seeder
Austrodanthonia caespitosa	Poaceae	Re-sprouter
Banksia grandis	Proteaceae*	Re-sprouter
Billardiera heterophylla	Pittosporaceae	Re-sprouter
Boronia fastigiatus	Rutaceae	Re-sprouter
Bossiaea aquifolium	Fabaceae	Re-seeder
Bossiaea ornata	Fabaceae	Re-sprouter
Burchardia congesta	Colchicaceae	Re-sprouter
Caladenia flava	Orchidaceae	Re-sprouter
Chamaescilla corymbosa	Anthericaceae	Re-sprouter
Chorizema cordatum	Fabaceae	Re-sprouter
Chorizema dicksonii	Fabaceae	Re-sprouter
Chorizema ilicifolium	Fabaceae	Re-sprouter
Comesperma calymega	Polygalaceae	Ephemeral
Comesperma virgatum	Polygalaceae	Re-sprouter
Conostylis serrulata	Haemodoraceae	Re-sprouter
Conostylis setigera	Haemodoraceae	Re-sprouter
Conostylis setosa	Haemodoraceae	Re-sprouter
Conyza bonariensis	Asteraceae	Non-native weed
Corymbia calophylla	Myrtaceae	Re-sprouter
Cyathochaeta avenacea	Cyperaceae	Re-sprouter
Daviesia decurrens	Fabaceae	Re-sprouter
Dianella revoluta	Phormiaceae	Re-sprouter
Disa bracteata	Orchidaceae	Non-native weed
Diuris longifolia	Orchidaceae	Re-sprouter
Drosera stolonifera	Droseraceae	Re-sprouter
Eucalyptus maculata	Myrtaceae	Re-sprouter
Eucalyptus marginata	Myrtaceae	Re-sprouter
Gastrolobium spinosum	Fabaceae	Re-sprouter
Gompholobium knightianum	Fabaceae	Re-seeder
Gompholobium marginatum	Fabaceae	Re-seeder

Gompholobium polymorphum	Fabaceae	Re-seeder
Gompholobium preissii	Fabaceae	Re-seeder
Hakea amplexicaulis	Proteaceae*	Re-sprouter
Hakea lissocarpha	Proteaceae*	Re-sprouter
Hakea prostrata	Proteaceae*	Re-sprouter
Hakea ruscifolia	Proteaceae*	Re-sprouter
Hakea stenocarpa	Proteaceae*	Re-sprouter
Hakea undulata	Proteaceae*	Re-sprouter
Hardenbergia comptoniana	Fabaceae	Re-sprouter
Hemigenia rigida	Lamiaceae	Re-seeder
Hibbertia acerosa	Dilleniaceae	Re-sprouter
Hibbertia amplexicaulis	Dilleniaceae	Re-sprouter
Hibbertia commutata	Dilleniaceae	Re-sprouter
Hibbertia quadricolor	Dilleniaceae	Re-sprouter
Hovea chorizemifolia	Fabaceae	Re-sprouter
Hovea trisperma	Fabaceae	Re-sprouter
Hybanthus calycinus	Violaceae	Re-sprouter
Hybanthus floribundus	Violaceae	Re-sprouter
Hypocalymma angustifolium	Myrtaceae	Re-sprouter
Hypocalymma cordifolium	Myrtaceae	Re-sprouter
Hypochaeris glabra	Asteraceae	Non-native weed
Hypolaena exsulca	Restionaceae	Re-sprouter
Kennedia coccinea	Fabaceae	Re-seeder
Labichea punctata	Fabaceae	Re-sprouter
Lagenophora huegelii	Asteraceae	Re-sprouter
Lasiopetalum floribundum	Sterculiaceae	Re-sprouter
Lepidosperma gracile	Cyperaceae	Re-sprouter
Lepidosperma squamatum	Cyperaceae	Re-sprouter
Lepidosperma tenue	Cyperaceae	Re-sprouter
Leucopogon nutans	Epacridaceae	Re-seeder
Leucopogon propinquus	Epacridaceae	Re-sprouter
Leucopogon verticillatus	Epacridaceae	Re-sprouter
Levenhookia pusilla	Stylidiaceae	Ephemeral
Lomandra caespitosa	Dasypogonaceae	Re-sprouter
Lomandra drummondii	Dasypogonaceae	Re-sprouter
Lomandra hermaphrodita	Dasypogonaceae	Re-sprouter
Lomandra preissii	Dasypogonaceae	Re-sprouter
Lomandra sericea	Dasypogonaceae	Re-sprouter
Lomandra sonderi	Dasypogonaceae	Re-sprouter
Lomandra spartea	Dasypogonaceae	Re-sprouter
Macrozamia riedlei	Zamiaceae	Re-sprouter
Microtis media	Orchidaceae	Re-sprouter
Millotia tenuifolia	Asteraceae	Ephemeral
Mirbelia dilatata	Fabaceae	Re-seeder
Neurachne alopecuroidea	Poaceae	Re-sprouter
Opercularia apiciflora	Rubiaceae	Re-seeder

Opercularia echinocephala	Rubiaceae	Re-seeder
Orthrosanthus laxus	Iridaceae	Re-sprouter
Patersonia rudis	Iridaceae	Re-sprouter
Pentapeltis peltigera	Apiaceae	Re-sprouter
Persoonia longifolia	Proteaceae*	Re-sprouter
Phyllanthus calycinus	Euphorbiaceae	Re-sprouter
Platysace compressa	Apiaceae	Re-sprouter
Platysace tenuissima	Apiaceae	Ephemeral
Podolepis gracilis	Asteraceae	Ephemeral
Pseudognaphalium luteo-album	Asteraceae	Non-native weed
Pterochaeta paniculata	Asteraceae	Ephemeral
Pterostylis pyramidalis	Orchidaceae	Re-sprouter
Ranunculus colonorum	Ranunculaceae	Re-sprouter
Rhodanthe citrina	Asteraceae	Ephemeral
Scaevola calliptera	Goodeniaceae	Re-sprouter
Senecio diaschides	Asteraceae	Non-native weed
Senecio hispidulus	Asteraceae	Ephemeral
Senecio quadridentatus	Asteraceae	Ephemeral
Sonchus oleraceus	Asteraceae	Non-native weed
Sphaerolobium medium	Fabaceae	Re-sprouter
Stylidium amoenum	Stylidiaceae	Ephemeral
Stylidium calcaratum	Stylidiaceae	Ephemeral
Stylidium hispidum	Stylidiaceae	Ephemeral
Stylidium junceum	Stylidiaceae	Ephemeral
Styphelia tenuiflora	Epacridaceae	Re-sprouter
Tetraria capillaris	Cyperaceae	Re-sprouter
Tetrarrhena laevis	Poaceae	Re-sprouter
Tetratheca hirsuta	Tremandraceae	Re-sprouter
Thelymitra macrophylla	Orchidaceae	Re-sprouter
Thysanotus fastigiatus	Anthericaceae	Re-sprouter
Thysanotus multiflorus	Anthericaceae	Re-seeder
Thysanotus thyrsoideus	Anthericaceae	Re-sprouter
Trachymene pilosa	Apiaceae	Ephemeral
Trymalium ledifolium	Rhamnaceae	Re-seeder
Velleia trinervis	Goodeniaceae	Ephemeral
Vellereophyton dealbatum	Asteraceae	Non-native weed
Viminaria juncea	Fabaceae	Re-seeder
Xanthorrhoea gracilis	Xanthorrhoeaceae	Re-sprouter
Xanthorrhoea preissii	Xanthorrhoeaceae	Re-sprouter
Xanthosia atkinsoniana	Apiaceae	Re-seeder
Xanthosia candida	Apiaceae	Re-seeder
Xanthosia huegelii	Apiaceae	Re-seeder

*Although all are re-sprouters, Proteaceae were treated as a separate grouping in analyses.