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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 \times 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 reforestation operations (e.g. Siddique *et al.*, 2008). Planting legumes has the advantage of N₂-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

107 in a thick litter layer that limited herbaceous species establishment. Secondly, the senescence
108 of these larger species may increase opportunities for recruitment and growth of smaller and
109 slower growing species. These potential longer-term effects of seeding large legumes and P-
110 addition on assembly trajectories of restored jarrah forest remain to be tested.

111 In this study, we report on a 15-year-old experiment in restored jarrah forest that had a
112 factorial combination of three P-fertiliser addition rates combined with additional seeding of
113 large legume shrubs. We test, approximately 10 years after the onset of legume senescence
114 whether, (1) understorey cover, density and species richness for non-leguminous species are
115 affected by the initial inclusion of large legumes in the seed mix, (2) whether there are
116 persistent effects of initial P-application on community assembly, and (3) whether there are
117 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 m²) 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.

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

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

230

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 m² ha⁻¹ to 16 m² 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 NH₄⁺ 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 $\sim 20 \text{ kg P ha}^{-1}$ (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:

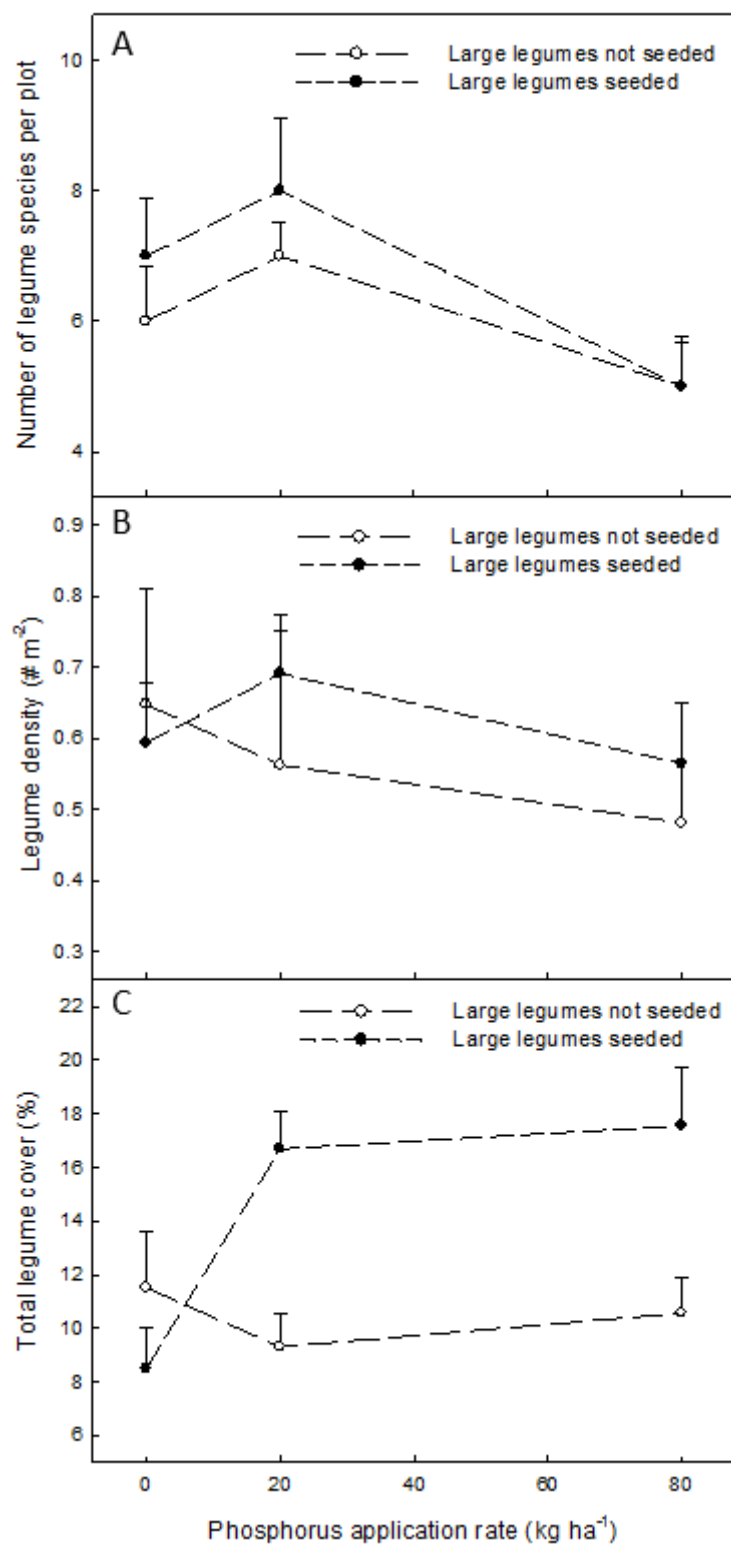
Fig. 1. The effects of phosphorus fertiliser application rate and seeding large legumes on: (A) the species richness, (B) the number of individual plants, and (C) total cover of legume species, 15 years after seeding and fertiliser addition. Error bars are +1SE of the mean.

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

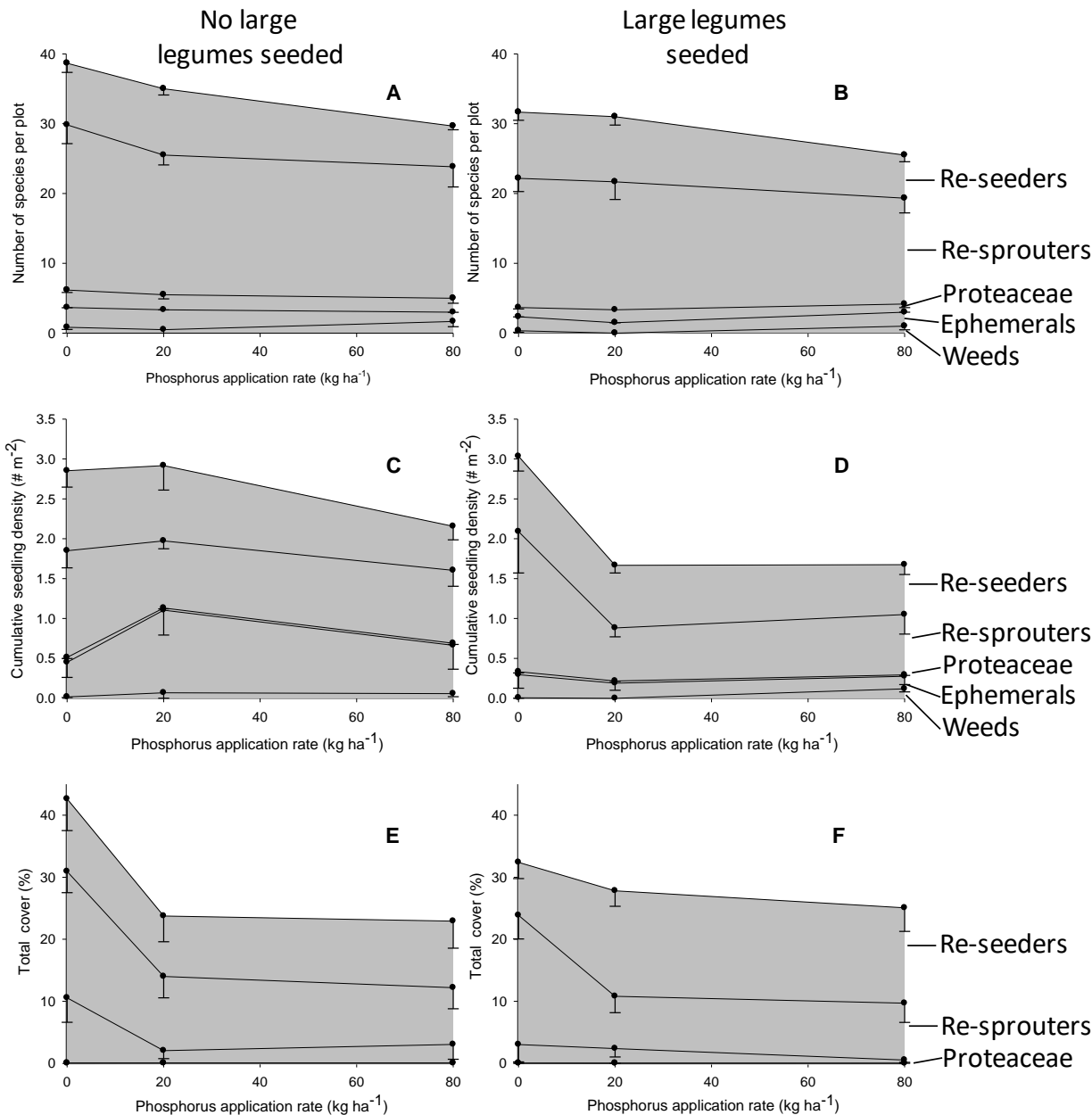
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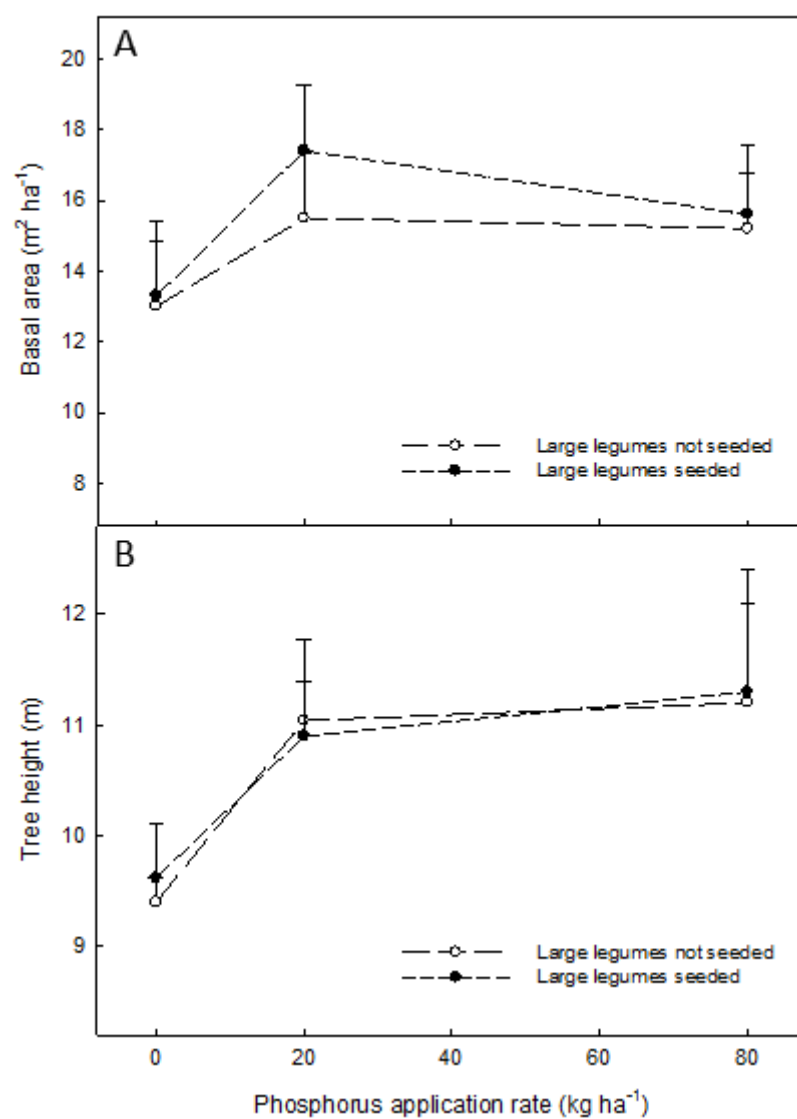
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Fig. 2



588 Fig 3.



593 Appendix 1: Seeding rates used in the experiment.

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

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

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

*only seeded in the large legume treatment.

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

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

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

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

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