Initial conditions can have long-term effects on plant species diversity in jarrah forest restored after bauxite mining

Conference or Workshop Item

Published Version

Daws, M. I., Grigg, A. H., Blackburn, C., Barker, J. M., Standish, R. J. and Tibbett, M. ORCID: https://orcid.org/0000-0003-0143-2190 (2022) Initial conditions can have long-term effects on plant species diversity in jarrah forest restored after bauxite mining. In: Mine Closure 2022: Proceeding of the 15th International Conference on Mine Closure, 4-6th Oct 2022, Brisbane, Australia, pp. 857-868. doi: https://doi.org/10.36487/ACG_repo/2215_62 (ISBN 9780645093841) Available at https://centaur.reading.ac.uk/108529/

Published version at: http://dx.doi.org/10.36487/ACG_repo/2215_62
Identification Number/DOI: https://doi.org/10.36487/ACG_repo/2215_62 <https://doi.org/10.36487/ACG_repo/2215_62>

Mine Closure 2022 - M Tibbett, AB Fourie & G Boggs (eds)
© 2022 Australian Centre for Geomechanics, Perth, ISBN 978-0-6450938-4-1
doi:10.36487/ACG_repo/2215_62

Initial conditions can have long-term effects on plant species diversity in jarrah forest restored after bauxite mining

MI Daws *Alcoa of Australia, Australia*

AH Grigg *Alcoa of Australia, Australia*

C Blackburn *Alcoa of Australia, Australia*

JM Barker *Alcoa of Australia, Australia*

RJ Standish *Murdoch University, Australia*

M Tibbett *University of Reading, UK*

Abstract

Much of the remarkable plant species diversity of the Southwest Australian Floristic Region can be attributed to high diversity of the understorey in its forests and woodlands, including 400–600 understorey species per km^2 *in the Northern Jarrah Forest alone. Consequently, returning species diversity is a key challenge for post-mining ecological restoration in the region. Each year, Alcoa of Australia undertakes restoration of mined areas within the Northern Jarrah Forest with a goal of returning a self-sustaining jarrah forest ecosystem. To meet this goal, it is important to understand long-term (i.e. > 20 years) trajectories of vegetation development and the restoration practices that direct species diversity outcomes. Here, we report the results of several experiments, the oldest of which is 45 years of age, which together demonstrate significant longer-term effects on understorey species diversity of restoration practices determining initial conditions including topsoil handling, fertiliser application, seeding rates of large legumes, and tree (overstorey) species stocking rates. Our research highlights (1) that 'historical contingency' can determine the trajectory of jarrah forest restoration and (2) that longer-term studies are critical as they give a different, sometimes conflicting, perspective to short-term datasets. Notably, after 27 years, we found an inverse relationship between plant cover and P fertilisation, where plant cover was highest in the in the absence of P fertiliser and lowest at the uppermost P amendment rate. We also found that the long-accepted Initial Floristics Model of succession does not fit well with our data. Our overall findings are likely useful to restore understorey diversity to woodlands, forests, and abandoned farmlands elsewhere in the region.*

Keywords: *fertiliser, legumes, phosphorus, productivity, topsoil, species richness, tree stocking*

1 Introduction

The restoration of native ecosystems following mining-related disturbances is a key requirement for many mining operations in Australia and elsewhere. However, longer-term (> 10 years post-establishment) data to understand the trajectories of vegetation development following restoration are limited (but see Daws et al. 2021; Standish et al. 2021) and, consequently, prescriptions for restoration are often based on results from short-term (≤3 years) monitoring (e.g. Daws et al. 2013; Golos et al. 2016; Standish et al. 2015; Tibbett et al. 2020; Waryszak et al. 2021).

Key elements for post-mining restoration advocated across the literature are broad. Since the seminal study of Tacey & Glossop (1980), the use of fresh topsoil to maximise the value of the in situ soil seed bank has been confirmed by numerous studies to become recommended best practice (e.g. DFAT 2016; Koch et al. 1996; Standish et al. 2015; Waryszak et al. 2021). Similarly, applying fertiliser to increase plant growth and improve establishment, often combined with a strategy of seeding N_2-fixing legume species, to increase nutrient cycling and facilitate successional processes (Grant et al. 2007), is also recommended best practice (Bell 2001; DFAT 2016; Environment Protection Agency 1995; Tibbett 2010).

While fresh topsoil can increase the initial species richness and similarity of the vegetation community to reference communities, the influence of fresh topsoil beyond 2–3 years after establishment has received less attention (e.g. Tacey & Glossop 1980; Waryszak et al. 2021).

The use of large growth form understorey legumes combined with fertiliser (especially phosphate, P) application can increase N_2-fixation and increase initial plant cover in re-establishing vegetation after mining (Koch 1987). Conversely, negative impacts of legumes on understorey diversity have been shown to persist for 15 years (Daws et al. 2019). However, since legumes senesce over time (Daws & Koch 2015; Daws et al. 2019), it is unclear whether their impacts persist beyond senescence, for example, via legacy effects to soil or vegetation dynamics.

A further key input for re-establishing forest ecosystems is the number of trees that are established at the outset. However, tree stocking rates can affect re-establishing understorey due to competition for water, light and nutrients. For example, in rehabilitated coal mines in the USA, a rapid increase in cover of *Pinus strobus* to achieve tree growth negatively affected herbaceous understorey species, with most understorey found in gaps between trees (Holl 2002). Similarly, Chan et al. (2006), in regrowth Douglas fir (*Pseudotsuga menziesii*) stands, reported a 64% increase in understorey diversity and a more than doubling in understorey cover when tree density was reduced from ~550 to 75 trees ha^{-1}. However, potential impacts of tree stocking rates on mine restoration in Australia have received minimal attention.

Long-term experiments of the effects of management practice on the success of mine restoration are rare. In this paper, we take advantage of three long-term (27–45 years of age) experiments in jarrah forest restored after bauxite mining. In the first experiment, the effects of three initial P-fertiliser application rates, applied at the outset of restoration, were assessed early in the restoration process (approx. one year of age) and then at 27 years of age. In the second, the effects of stocking densities of the primary overstorey tree, jarrah (*Eucalyptus marginata*), in factorial combination with seeding different amounts of large understorey legumes, were tested and monitored at 15 and 32 years of age. In the final experiment, the effects of three initial topsoil handling treatments were monitored over 45 years.

2 Materials and methods

2.1 Study site

The experiments were established within the Alcoa of Australia Ltd (Alcoa), bauxite mining lease in the Northern Jarrah Forest, located between 60 and 100 km southeast of Perth, Western Australia. The area has a Mediterranean-type climate with cool, wet winters and hot, dry summers. Annual rainfall is ~1,200 mm, with average summer maximum temperatures of 29°C and average winter minimum temperatures of 6°C (Australian Bureau of Meteorology 2015).

The forest vegetation comprises the dominant overstorey species *Eucalyptus marginata* (jarrah), which constitutes around 80% of stems in both restored and unmined forest (Daws et al. 2015). The remaining stems are mostly marri (*Corymbia calophylla*). In addition, there is a mid-storey layer dominated by *Banksia grandis*, *Allocasuarina fraseriana* and *Xanthorrhoea preisii*, with large woody shrubs of *Bossiaea aquifolium*, various *Acacia* species and a diverse understorey (Gardner & Bell 2007).

Mine pits range from 1 to 20 ha in size and are surrounded by intact forest. Restoration involves reshaping the mine pit, ripping to alleviate compaction and spreading topsoil. Subsequently, seeds of local plants are spread over the restored mine pits, planting of nursery-grown plants occurs and finally an aerial fertiliser application occurs. However, in the experiments reported here, topsoil spreading (Experiment 3), seeding and planting (Experiments 2 and 3) and fertiliser application (Experiments 1 and 3) were modified from standard restoration protocols.

2.2 Experiment 1: long-term effects of fertiliser on understorey richness

In 1994, an experiment was established in five restored mine pits. Within each pit, four treatment plots of 25 m × 25 m were established. Following contour ripping, plots were seeded during summer 1994 (January to April) with 1.44 kg ha^{-1} jarrah seed, 0.60 kg ha^{-1} marri seed and an understorey seed mix containing 0.72 kg ha^{-1} of legume species and 0.20 kg ha^{-1} of non-legume species. For three of the plots, fertiliser was applied, after contour ripping, at 0, 80 or 120 kg ha^{-1} for P (as double superphosphate) and 80 kg ha^{-1} for N (as ammonium sulphate) (hereafter 0P, 80P and 120P). Fertiliser was broadcast by hand as a surface dressing. In the fourth treatment plot, fertiliser at 80 kg ha^{-1} of N and P was applied prior to contour ripping (hereafter '80P incorporated'). Ripping incorporated the fertiliser into the soil profile to a maximum of 0.8 m (the depth of the ripping tines). For more details on the experimental design, see Daws et al. (2021).

In September 1995, one year after the establishment of the experiment, a 20 m × 20 m plot was established within the centre of each 25 m × 25 m plot and subdivided into twenty 2 m × 2 m quadrats with a total of 80 m^2 sampled per plot (Figure 1). Species identity and density of all shrub and understorey species in each quadrat were recorded, with density summed for the entire plot. Plots were re-monitored in October 2021 at 27 years of age. All presented data is for native jarrah forest species only.

2.3 Experiment 2: long-term effects of legumes and tree spacing

In 1988, an experiment was established across five restored mine pits. A factorial combination of three planted jarrah tree densities on either a 4 × 4, 2 × 4 or 1 m × 1 m spacing (equivalent to stand stockings of 625, 1,250 and 10,000 stems ha^{-1}) and two seed treatments (plus and minus a vigorous native legume seed mix) were applied across the five sites. The chosen tree stocking rates span the historic range of established tree densities in mine restoration at this site (Grigg 2012; Koch & Ward 2005). Each treatment consisted of 100 trees in 10 rows and columns, resulting in treatment areas of 40 × 40, 20 × 40, 20 × 20 or 10 m × 10 m as the tree density increased. The vigorous native legume seed mix, applied at 0.9 kg ha^{-1}, consisted of 14 plant species, predominantly acacias, but also other legumes that are fast growing and tall shrubs (2–4 m in height). All sites were seeded with an understorey seed mix, applied at 0.5 kg ha^{-1}, of 78 species that are small shrubs and herbs usually less than 0.5 m tall. Each plot was fertilised with 500 kg ha^{-1} of superphosphate (41 kg ha^{-1} P, 3.3 kg ha^{-1} Cu, 1.5 kg ha^{-1} Zn, and 0.2 kg ha^{-1} Mo) and 250 kg ha^{-1} diammonium phosphate (43.75 kg ha^{-1} N and 50 kg ha^{-1} P). For more details, see Ward & Koch (1995).

Within each of the 30 treatment areas, twenty 2 m × 2 m quadrats (a total of 80 m^2) were established in September 2003. Within each 2 m × 2 m quadrat, the density and cover of each plant species was monitored and recorded in September 2003 and September 2020, 15- and 32-years post-establishment, respectively. All presented data is for native jarrah forest species only.

2.4 Experiment 3: long-term effects of topsoil handling on species richness

In summer (December–February) 1976, an experiment was established in three restored mine pits. In one pit, unmined forest topsoil that had been stripped from an average depth of 40 cm and stockpiled for two years in a heap approx. 10 m high was respread at 40 cm depth (hereafter 'stockpiled'). The second pit received unmined forest topsoil that had been stripped to 40 cm depth in an adjacent area and then immediately respread to 40 cm deep (hereafter 'single-stripped direct-return'). The third pit received unmined forest topsoil stripped to an average depth of 5 cm respread immediately over 40 cm deep of stockpiled topsoil (hereafter 'double-stripped direct-return'). Following topsoil return, the three pits were ripped on contour to a depth of ca. 1 m using a single tine attached to a bulldozer. In the first winter (June–August) following topsoil spreading, marri seedlings (*C. calophylla*) were planted on a 4 m × 4 m spacing (approx. 625 trees ha^{-1}). Neither a seed mix nor fertiliser was applied to the experimental areas. See Tacey & Glossop (1980) for further details.

In spring 1979, 1982, 1985, 1988, 1992, 1996 and 2021, each stem within fifty 1 m × 1 m quadrats was recorded in each pit. In addition, in 1979, fifty 1 m × 1 m quadrats were established and monitored in adjacent non-mined jarrah forest. All presented data is for native jarrah forest species only.

A dissimilarity matrix, using Sorensen dissimilarity index based on species abundance data for the 50 non-mined forest quadrats, was created using PC-ORD v. 6.0 (MjM Software, Gleneden Beach, OR, US). The matrix provided pairwise forest quadrat–forest quadrat similarity values (1 – dissimilarity). Subsequently, for each experimental quadrat, pairwise similarity values were determined by comparison with each forest quadrat, resulting in 50 pairwise similarity values per experimental quadrat; the average of these values was then expressed as a percentage of the overall forest quadrat–forest quadrat similarity value.

3 Results

3.1 Experiment 1: long-term impacts of fertiliser on understorey responses

One year after restoration was initiated, understorey plant cover was significantly increased by the addition of P (i.e. 80P, 120P; Table 1). In addition, incorporation of the fertiliser approximately doubled plant cover compared with applying the same amount of fertiliser to the surface (Table 1). Further, native species richness increased with the application of fertiliser and was significantly higher than 0P when the fertiliser was incorporated (Table 1).

At 27 years of age, plant cover was highest in the 0P and 80P treatment and lowest in the 120P treatment. Species richness and cover were no different between 80P and 80P incorporated. Soil Colwell-P concentrations were significantly elevated in 80P and 120P after 27 years compared with the 0P control. For 80P incorporated, Colwell-P concentrations at 0–5 cm depth were intermediate between the 0P and surface applied 80P treatments (Table 1).

Table 1 The effect of fertiliser-P application rate on species richness and plant cover one year and 27 years after an initial once-off application either applied as a surface top-dressing or incorporated in the soil profile by ripping. Also presented is soil Colwell-P concentration at 0–5 cm depth 27 years after the initial once-off application. Values are means

Fertiliser-P application rate (kg ha^{-1})	1 year of age		27 years of age		
	Understorey plant cover (%)	Number of native species	Understorey plant cover (%)	Number of native species	Available/ Colwell-P (mg P kg^{-1} soil)
0	0.42^{a}	20^{a}	37^{b}	29^{a}	2.5^{a}
80	3.7^{b}	24^{ab}	37^{b}	25^{ab}	4.5^{b}
80 (incorporated)	7.2^{c}	26^{b}	34^{ab}	25^{ab}	3.5^{ab}
120	4.0^{b}	23^{ab}	32^{a}	22^{b}	4.6^{b}

Note: within each column, different superscripts indicate a significant difference (Tukey's post hoc test, $p < 0.05$) between values.

3.2 Experiment 2: long-term impacts of legumes and tree spacing on understorey responses

At the 15-year monitoring point, understorey plant cover was higher both when large legumes were seeded and as the tree density reduced. Understorey plant richness increased as tree density decreased. For example, in the large legume treatment, richness increased from 19 at 1 m × 1 m spacing to 27 at 4 m × 4 m spacing (Table 1). However, understorey richness was lower in the large legume seeding treatment even though an additional 14 species were seeded compared with the treatment where large legumes were not seeded. These responses were reflected in significant main effects of tree spacing and legumes on both cover and species richness (two-way ANOVA, $p < 0.05$).

At the 32-year monitoring point, the effect of seeding large legumes on understorey cover was less pronounced and was no longer significant (two-way ANOVA, $p > 0.05$). Again, species richness increased significantly as tree stocking rates decreased and when large legumes were not seeded (two-way ANOVA, $p < 0.05$; Table 2).

Table 2 The effects of including large legumes in the seed mix and tree stocking rates on plant cover and species richness at 15 and 32 years after the onset of restoration. Data are the means of five replicates. Bold font shows high values of each response variable

Seeding treatment	15 years of age		32 years of age	
	Total understorey cover (%)	Species count	Total understorey cover (%)	Species count
Large legumes seeded	46^{a}	19^{a}	43^{a}	16^{a}
	66^{ab}	19^{a}	57^{ab}	20^{a}
	73^{b}	**27^{ab}**	**72^{b}**	**22^{ab}**
Large legumes not seeded	35^{a}	24^{a}	53^{a}	16^{a}
	46^{a}	32^{b}	61^{b}	23^{ab}
	45^{a}	**39^{b}**	**63^{b}**	**28^{b}**

Note: within each column, different superscripts indicate a significant difference (Tukey's post hoc test, $p < 0.05$) between values.

3.3 Experiment 3: long-term effects of soil handling on understorey responses

Topsoil handling impacted species richness in the restored areas with approximately twice as many species present after two years in the site that received double-stripped direct-return topsoil compared with the site that received stockpiled topsoil (Figure 1a). The site that received single-stripped direct-return topsoil was intermediate in response. These differences were maintained over the 45-year duration of the experiment and became more pronounced for the double-stripped site, as it increased in species richness while the other two sites stabilised, over the last 25 years (Figure 1a).

The compositional similarity of the vegetation in the restored sites compared with unmined reference forest was highest in the double-stripped direct-return site and lowest in the stockpiled topsoil treatment (Figure 1b). Similarity increased over time in all three treatments, but the ranking of the treatments stayed constant. These differences in understorey/mid-storey plant cover and diversity between the double-stripped and stockpiled sites were clearly visible after 45 years (Figure 2).

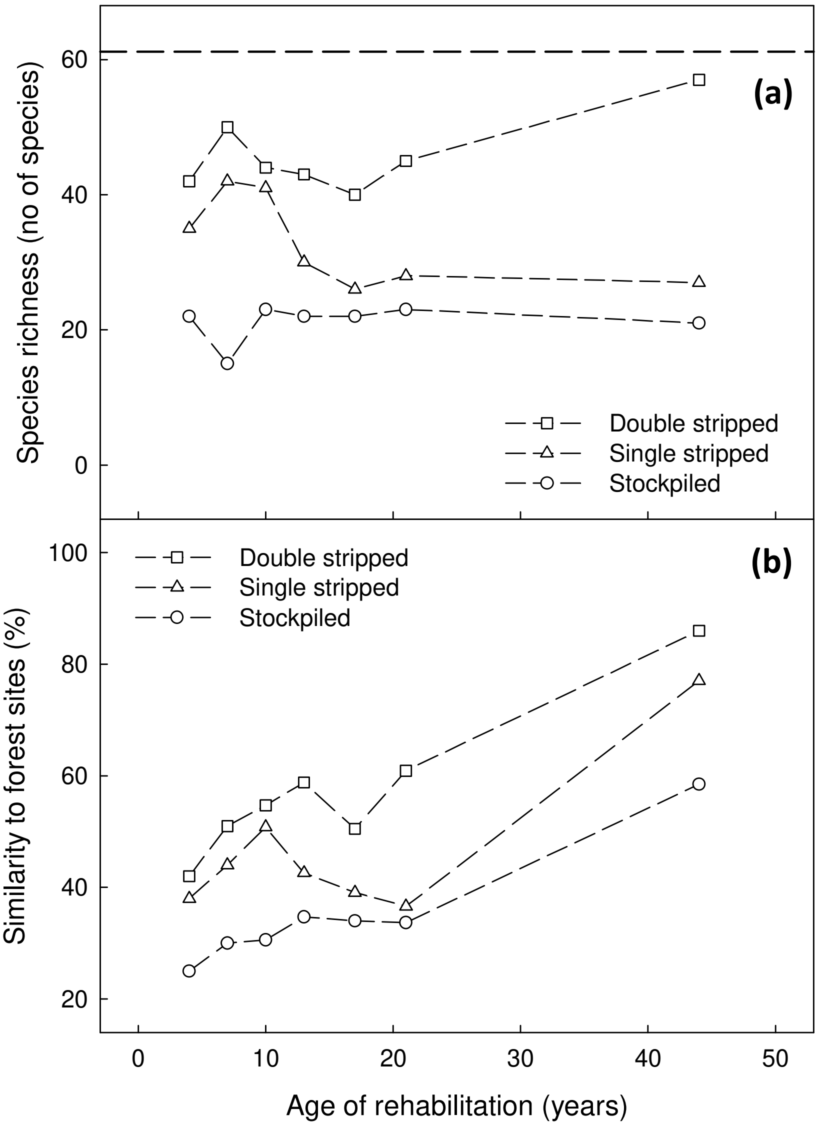

Figure 1 The effect of topsoil handling on the long-term restoration trajectory of (a) species richness (summed across the fifty 1 m × 1 m plots) and (b) similarity of restored sites compared with reference forest sites in restored bauxite mines in the jarrah forest. The horizontal dashed line in (a) is the total number of plant species recorded in the reference forest plots when monitored at the start of the experiment

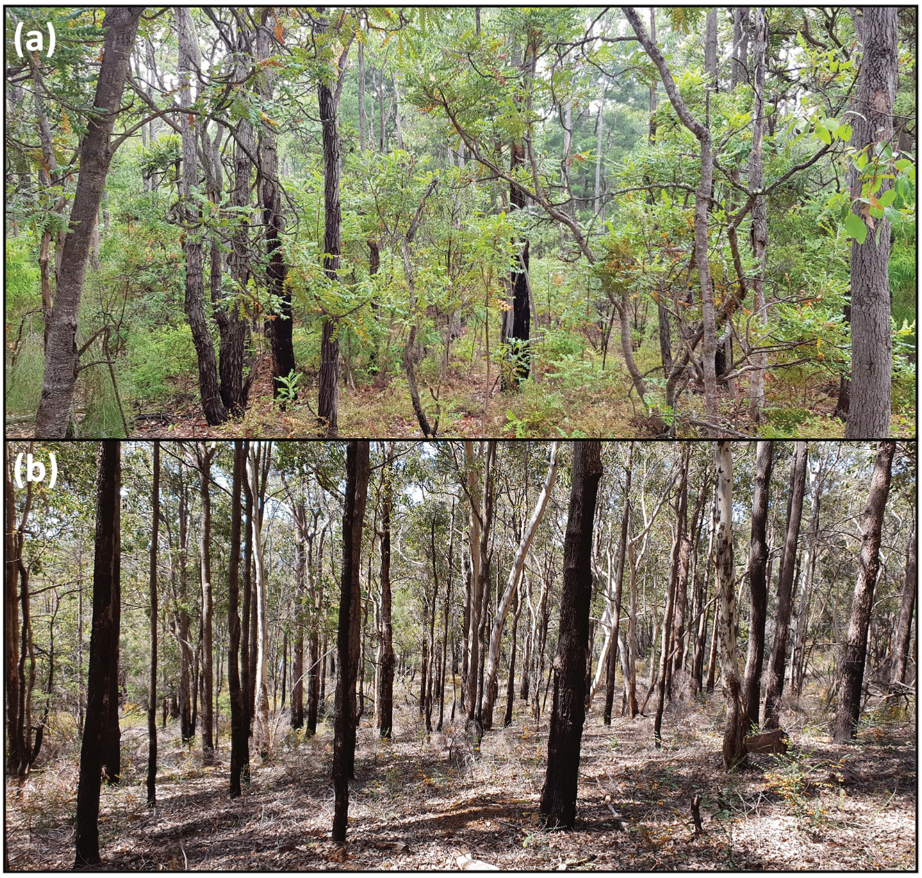

Figure 2 Comparison of 45-year-old sites that (a) received double-stripped direct-return and (b) received topsoil that had been stockpiled for two years prior to being used in restoration in jarrah forest restored after bauxite mining

4 Discussion

The results from the three experiments reported here demonstrate that the initial conditions at the outset of restoration can significantly influence the resulting plant communities for up to 45 years. Importantly, these impacts were not always evident early in restoration, and later findings sometimes even contradicted earlier findings. Our experimental results suggest significant 'historical contingencies' – that is, effects of the order and timing of past events, here triggered by restoration practices, on community reassembly (*sensu* Fukami 2015). These events can be biotic or abiotic and our data suggest the importance of both, and that some effects were amplified over time and space due to plant growth and interactions (e.g. presumed competition with jarrah; Experiment 2). Abiotic contingencies were evident in Experiment 1 where the legacy of a single dose of P fertiliser was evident in soils and plant cover 27 years later. There was evidence of biotic contingencies in the form of priority effects, whereby the arrival of species, either via topsoil (Experiment 3) or seeding in the case of large legumes (Experiment 2), resulted in different trajectories of community development. The latter is notable because legumes are often assumed to facilitate, rather than inhibit, the establishment of later-arriving species in restoration (Young et al. 2005). Overall, our data provide a rare insight into the influences of common restoration practices on long-term community development.

Applying fertiliser to mine restoration is widely advocated as best practice (e.g. Bell 2001; DFAT 2016; Environment Protection Agency 1995; Tibbett 2010). However, while consistent with previous studies in regard to the short-term effects of fertiliser application on plant cover and species richness (e.g. Daws et al. 2013, 2015; Tibbett et al. 2020), our data indicate that these benefits disappear over the longer term. Furthermore, fertiliser application can have long-term negative impacts on species richness, with the ongoing impacts of applied fertiliser potentially related to the long-term persistence of applied P in restored sites (i.e. ongoing elevated soil P even after 32 years; Table 1).

In one-year-old restored sites fertiliser increased plant growth and species richness. These benefits were maximised when fertiliser availability to plants was increased via incorporation within the soil profile. Similarly, Tibbett et al. (2020) reported that incorporating fertiliser maximised the initial growth response to fertiliser in two-year-old restored jarrah forest. Where fertiliser is required as part of the restoration with a goal of maximising early surface stabilisation, these data suggest that incorporation within the profile can maximise 'bang for buck'. However, these initial growth increases from using fertiliser disappeared, with no ongoing longer-term benefits for plant cover. However, if the goal is to maximise long-term species richness, our data suggest fertiliser use should be approached with caution.

There are several possible mechanisms whereby fertiliser application results in a long-term reduction in species richness. First, as demonstrated in Experiment 2, large legumes can, at least up to 15 years of age, reduce species richness, presumably by outcompeting and smothering smaller, slower growing understorey species. When fertiliser containing P is applied, it is these N_2-fixing legume species that are most growth responsive. Consequently, applying P may potentially shift community composition in favour of more rapidly growing and P-responsive species (e.g. Daws et al. 2019). A second explanation is that in the naturally P-deficient soils in the jarrah forest (Tibbett et al. 2020), there are a range of species with specialised P-acquisition mechanisms that are potentially susceptible to P toxicity due to an inability to regulate P uptake at high external P concentrations (e.g. de Campos et al. 2013). While P toxicity is traditionally thought of as the expression of visible symptoms such as leaf chlorosis, necrosis and death (e.g. Shane et al. 2004a, 2004b), P toxicity can, at least in pot experiments, also be expressed as a reduction in growth rates with increasing external P-application rates (Standish et al. 2022; Tibbett et al. 2022; Williams et al. 2019). A further reduction in growth rates of already slow-growing species when P is applied may further tip the balance of competition in favour of P-responsive species like legumes. Taken together, the data suggest P fertiliser modifies the niche space of species adapted to low-P soils.

Experiment 2 indicates that including large understorey legumes can have negative impacts on restoration trajectories for at least 15 years by reducing overall plant species richness. For example, when large legumes were seeded, there was an average reduction in native species richness of 10 species at 15 years and three species at 32 years. For future studies, it would be of interest to understand if there is a consistent suite of species most impacted by the legumes or whether all species are negatively affected. This reduction occurred despite the seed mix in the large legume treatment containing an additional 14 species. In effect, seeding 14 extra species in the large legume treatment reduced richness by 24 and 17 species at the two-time intervals, respectively. While maximising initial plant cover and stimulating N_2-fixation may have potential benefits, such as landform stabilisation and potentially increased growth of tree species through increased soil-N supply (Ward et al. 1990; Ward & Koch 1996), our data show that negative impacts on understorey diversity can be significant.

The intent of applying fertiliser and seeding large understorey legumes is to maximise early site productivity and plant growth. An additional key input for restoring forest ecosystems is applied tree seed (or planted tubestock). Site productivity can also be manipulated by altering the quantity of applied tree seed/number of planted tubestock since, for jarrah forest restoration, the resulting stand basal area increases with increasing tree density (e.g. Grigg et al. 2008) – maximising basal area may be an important objective if the final land use includes timber production. Analogous to the negative impact of increased productivity resulting from applied fertiliser and large legumes, we observed that understorey species richness and native plant cover also declined with increasing numbers of planted trees. This negative effect was maintained over the 32-year duration of the experiment. Similar effects have been reported elsewhere in both mine restoration and forestry systems (Chan et al. 2006; Holl 2002; Zangy et al. 2021). To maximise the diversity of the re-establishing jarrah forest community following bauxite mining, lower levels of productivity and presumably competition (i.e. fewer large legumes, fewer trees and judicious use of fertiliser) may be appropriate.

Experiment 3 indicated that irrespective of topsoil handling, the similarity of the restored sites to unmined forest increases over time. However, using fresh topsoil, and in particular double stripping, increased the starting point (in terms of similarity) and appears to reduce the time for full recovery to occur. Topsoil seed banks exhibit a negative exponential decline in seed numbers with depth: for the jarrah forest, 77% of the seeds are in the top 20 mm (Tacey & Glossop 1980). Consequently, double stripping, where the surface layers are removed and replaced as the surface in restoration, maximises the contribution of the soil seed bank to restoration success. In contrast, in the single stripping treatment, the entire soil profile was removed and returned to an adjacent site; in this scenario, the seed-rich surface layer was 'diluted' and 'mixed' across the returned profile, with many seeds likely buried to depths from which they were unable to emerge (Daws et al. 2007). This is evident from our results, where the double-stripped site performed significantly better than the single-stripped site, even after 45 years. Further, our data indicate that stockpiling significantly reduces the value of topsoil for restoration – approximately half the number of species occurred in the site that received stockpiled soil compared with the double-stripped direct-return site. This is consistent with the understanding that stockpiling topsoil can result in significant loss of seed viability due to the anaerobic conditions that can exist within stockpiles (e.g. Golos & Dixon 2014).

Researchers have suggested that the Initial Floristics Model (IFM) of succession is followed in jarrah forest restoration (*sensu* Egler 1954; Wilson et al. 1992), whereby the restored community in large part reflects what was established at the outset with little ongoing dispersal and recruitment of new species (Norman et al. 2006). In contrast, Experiment 1 indicates that species richness can increase over time when fertiliser is not added. Similarly, for Experiment 3, where no fertiliser or seed mix was applied, species richness also increased over time in the double-stripped treatment. Indeed, even in the single-stripped and stockpiled treatments where species richness was stable over time, the similarity to surrounding forest communities increased, implying a significant degree of immigration and turnover in species composition. Taken together, this suggests (1) that, in contrast to the suggestion of Norman et al. (2006), the IFM is at best a poor description of jarrah forest dynamics, (2) species do recolonise restored jarrah forest over time and without further intervention, and that (3) restored jarrah forest communities are likely to converge with those in surrounding reference forest sites given sufficient time.

5 Conclusion

Our data indicate that to restore diverse jarrah forest plant communities, moderation of key inputs, such as fertiliser application, the use of large legumes and the number of trees, may be appropriate. These data indicate the value of long-term experiments and monitoring. Our data also indicate that both time and the starting conditions at the outset of restoration are important. Interestingly, our data indicate that the starting conditions can affect the re-establishing plant community for a period of decades. The results of these and other experiments have enabled optimisation of Alcoa's ongoing progressive restoration program in the jarrah forest and provide important tests of ecological theory and its relevance to the practice of ecological restoration.

Acknowledgement

This work was in part funded by the Australian Research Council. We thank a range of previous Alcoa employees, including Warren Tacey, Beverly Koch, John Koch, Sam Ward, Carl Grant and Melanie Norman for establishing and/or undertaking some of the monitoring reported here.

References

Australian Bureau of Meteorology 2015, *Monthly Climate Statistics for Dwellingup*, Melbourne, viewed November 2015, http://www.bom.gov.au/climate/averages/tables/cw_009538.shtml

Bell, IC 2001, 'Establishment of native ecosystems after mining - Australian experience across diverse biogeographic zones', *Ecological Engineering*, vol. 17, pp. 179–186.

Chan, SS, Larson, DJ, Maas-Hebner, KG, Emmingham, WH, Johnston, SR & Mikowski, DA 2006, 'Overstory and understory development in thinned and underplanted Oregon Coast Range Douglas-fir stands', *Canadian Journal of Forest Research*, vol. 36, pp. 2696–2711.

Daws, MI, Ballard, C, Mullins, CE, Garwood, NC, Murray, B, Pearson, TRH & Burslem, DFRP 2007, 'Allometric relationships between seed mass and seedling characteristics reveal trade-offs for neotropical gap-dependent species', *Oecologia*, vol. 54, pp. 445–454.

Daws, MI, Grigg, AH, Tibbett, M & Standish, RJ 2019, 'Enduring effects of large legumes and phosphorus fertiliser on jarrah forest restoration 15 years after bauxite mining', *Forest Ecology and Management*, vol. 438, pp. 204–214.

Daws, MI & Koch, JM 2015, 'Long-term restoration success of re-sprouter understorey species is facilitated by protection from herbivory and a reduction in competition', *Plant Ecology*, vol. 216, pp. 565–576.

Daws, MI, Standish, RJ, Koch, JM & Morald, TK 2013, 'Nitrogen and phosphorus fertiliser regime affect jarrah forest restoration after bauxite mining in Western Australia', *Applied Vegetation Science*, vol. 16, pp. 610–618.

Daws, MI, Standish, RJ, Koch, JM, Morald, TK, Tibbett, M & Hobbs, RJ 2015, 'Phosphorus fertilisation and large legume species affect jarrah forest restoration after bauxite mining', *Forest Ecology and Management*, vol. 354, pp. 10–17.

Daws, MI, Walters, SJ, Harris, RJ, Tibbett, M, Grigg, AH, Morald, TK, Hobbs, RJ & Standish, RJ 2021, 'Nutrient enrichment diminishes plant diversity and density, and alters long-term ecological trajectories, in a biodiverse forest restoration', *Ecological Engineering*, vol. 165, 106222.

de Campos, MCR, Pearse, SJ, Oliveira, RS & Lambers, H 2013, 'Downregulation of net phosphorus-uptake capacity is inversely related to leaf phosphorus-resorption proficiency in four species from a phosphorus-impoverished environment'*, Annals of Botany*, vol. 111, pp. 445–454.

DFAT 2016, *Mine Rehabilitation: Leading Practice Sustainable Development Program for the Mining Industry*, Department of Foreign Affairs and Trade, Commonwealth Government of Australia, Canberra.

Egler, FE 1954, 'Vegetation science concepts. I. Initial floristic composition, a factor in oldfield vegetation development', *Vegetatio*, vol. 4, pp. 412–417.

Environment Protection Agency 1995, 'Rehabilitation and revegetation', *Best Practice Environmental Management in Mining*, Commonwealth of Australia, Canberra.

Fukami, T 2015, 'Historical contingency in community assembly: integrating niches, species pools, and priority effects', *Annual Review of Ecology, Evolution, and Systematics*, vol. 46, pp. 1–23.

Gardner, JH & Bell, DT 2007, 'Bauxite mining restoration by Alcoa World Alumina Australia in Western Australia: social, political, historical, and environmental contexts', *Restoration Ecology*, vol. 15, pp. S3–S10.

Golos, PJ & Dixon, KW 2014, 'Waterproofing topsoil stockpiles minimizes viability decline in the soil seed bank in an arid environment', *Restoration Ecology*, vol. 22, pp. 495–501.

Golos, PJ, Dixon, KW & Erickson, TE 2016, 'Plant recruitment from the soil seed bank depends on topsoil stockpile age, height, and storage history in an arid environment', *Restoration Ecology*, vol. 24, pp. S53–S61.

Grant, CD, Ward, SC & Morley, SC 2007, 'Return of ecosystem function to restored bauxite mines in Western Australia', *Restoration Ecology*, vol. 15, pp. S94–S103.

Grigg, A 2012, 'Adaptive rehabilitation management and a drying climate: unique challenges for Alcoa's bauxite mine rehabilitation in southwestern Australia', Mine Closure 2012 - A.B. Fourie and M. Tibbett (eds), Australian Centre for Geomechanics, Perth.

Grigg, AH, MacFarlane, C, Evangelista, C, Eamus, D & Adams, MA 2008, 'Does initial spacing influence crown and hydraulic architecture of *Eucalyptus marginata*?', *Tree Physiology*, vol. 28, pp. 753–760.

Holl, KD 2002, 'Long-term vegetation recovery on reclaimed coal surface mines in the eastern USA', *Journal of Applied Ecology*, vol. 39, pp. 960–970.

Koch, JM 1987, 'Nitrogen accumulation in a rehabilitated bauxite-mined area in the Darling Range, Western Australia', *Australian Forestry Research*, vol. 17, pp. 59–72.

Koch, JM & Ward, SC 2005, 'Thirteen-year growth of jarrah (*Eucalyptus marginata*) on rehabilitated bauxite mines in south-western Australia', *Australian Forestry*, vol. 68, pp. 176–185.

Koch, JM, Ward, SC, Grant, CD & Ainsworth, GL 1996, 'Effects of bauxite mine restoration operations on topsoil seed reserves in the jarrah forest of Western Australia', *Restoration Ecology*, vol. 4, pp. 368–376.

Norman, MA, Koch, JM, Grant, CD, Morald, TK & Ward, SC 2006, 'Vegetation succession after bauxite mining in Western Australia', *Restoration Ecology*, vol. 14, pp. 278–288.

Shane, MW, McCully, ME & Lambers, H 2004b, 'Tissue and cellular phosphorus storage during development of phosphorus toxicity in *Hakea prostrata* (Proteaceae)', *Journal of Experimental Botany*, 55, pp. 1033–1044.

Shane, MW, Szota, C & Lambers, H 2004a, 'A root trait accounting for the extreme phosphorus sensitivity of *Hakea prostrata* (Proteaceae)', *Plant Cell and Environment*, vol. 27, pp. 991–1004.

Standish, RJ, Daws, MI, Gove AD, Didham, RK, Grigg, AH, Koch, JM & Hobbs, RJ 2015, 'Long-term data suggest jarrah-forest establishment at restored mine sites is resistant to climate variability', *Journal of Ecology*, vol. 103, pp. 78–89.

Standish, R.J, Daws, MI, Morald, TK, Speijers, J, Koch, JM, Hobbs, RJ & Tibbett, M 2022, 'Phosphorus supply affects seedling growth of mycorrhizal but not cluster-root forming jarrah-forest species', *Plant and Soil*, vol. 472, pp. 577–594.

Standish, RJ, Gove, AD, Grigg, AH & Daws, MI 2021, 'Beyond species richness and community composition: using plant functional diversity to measure restoration success in jarrah forest', *Applied Vegetation Science*, vol. 24, e12607.

Tacey, WH & Glossop, BL 1980, 'Assessment of topsoil handling techniques for rehabilitation of sites mined for bauxite within the jarrah forest of Western Australia', *Journal of Applied Ecology*, vol. 17, pp. 195–201.

Tibbett, M 2010, 'Large-scale mine site restoration of Australian eucalypt forests after bauxite mining: soil management and ecosystem development', in LC Batty & K Hallberg (eds), *Ecology of Industrial Pollution*, Cambridge University Press, Cambridge, pp. 309–326.

Tibbett, M, Daws, MI, George, SJ & Ryan, MH 2020, 'The where, when and what of phosphorus fertilisation for seedling establishment in a biodiverse jarrah forest restoration after bauxite mining in Western Australia', *Ecological Engineering*, vol. 153, 105907.

Tibbett, M, Daws, MI & Ryan, MH 2022, 'Phosphorus uptake and toxicity is delimited by mycorrhizal symbiosis in P-sensitive *Eucalyptus marginata* but not in P-tolerant *Acacia celastrifolia*', *AoB Plants*, plac037.

Ward, SC & Koch, JM 1995, ‘Early growth of jarrah (*Eucalyptus marginata* Donn ex Smith) on rehabilitated bauxite minesites in south-west Australia’, *Australian Forestry*, vol. 58, pp. 65–71.

Ward, SC, & Koch, JM 1996, ‘Biomass and nutrient distribution in a 15.5 year old forest growing on a rehabilitated bauxite mine’, *Australian Journal of Ecology*, vol. 21, pp. 309–315.

Ward, SC, Koch, JM & Nichols, OG 1990, ‘Bauxite mine rehabilitation in the Darling Range, Western Australia’, *Proceedings of the Ecological Society of Australia*, vol. 16, pp. 557–565.

Waryszak, P, Standish, RJ, Ladd, PG, Enright, NJ, Brundrett, M & Fontaine, JB 2021, ’Best served deep: the seedbank from salvaged topsoil underscores the role of the dispersal filter in restoration practice’, *Applied Vegetation Science*, vol. 24, e12539.

Williams, A, George, S, Birt, HWG, Daws, MI & Tibbett, M 2019, ‘Sensitivity of seedling growth to phosphorus supply in six tree species of the Australian Great Western Woodlands’, *Australian Journal of Botany*, vol. 67, pp. 390–396.

Wilson, JB, Gitay, H, Roxburgh, SH, King, WM & Tangney, RS 1992, ‘Egler’s concept of 'Initial Floristic Composition' in succession: ecologists citing it don't agree what it means’, *Oikos*, vol. 64, pp. 591–593.

Young, TP, Petersen, DA & Clary, JJ 2005, ‘The ecology of restoration: historical links, emerging issues and unexplored realms’, *Ecology Letters*, vol. 8, pp. 662–673.

Zangy, E, Kigel, J, Cohen, S, Moshe, Y, Ashkenazi, M, Fragman-Sapir, O & Osem, Y 2021, ‘Understory plant diversity under variable overstory cover in Mediterranean forests at different spatial scales’, *Forest Ecology and Management*, vol. 494, 119319.