

Seedling emergence and summer survival after direct seeding for woodland restoration on old fields in south-western Australia

By Lauren M. Hallett, Rachel J. Standish, Justin Jonson and Richard J. Hobbs

Lauren M. Hallett was a masters student at the University of Western Australia (School of Plant Biology, Crawley, WA 6009, Australia) and is currently at PhD candidate at the University of California (Department of Environmental Science, Policy & Management, 130 Mulford Hall #3144, Berkeley, CA 94720, USA; Email: lauren.hallett@berkeley.edu). *Rachel J. Standish* is a research assistant professor at the School of Plant Biology, University of Western Australia; (Email: rachel.standish@uwa.edu.au). *Justin Jonson* was a restoration manager with Greening Australia and is currently the managing director of Threshold Environmental (PO Box 1124, Albany, WA 6331, Australia; Email: jjonson@thresholdenvironmental.com.au). *Richard J. Hobbs* is a professor at the School of Plant Biology, University of Western Australia (Email: richard.hobbs@uwa.edu.au).

Summary Restoration opportunities provided by an emerging carbon market have largely focused on large-scale woodland restoration projects. Gondwana Link is one such project operating in a 1000-km corridor in south-western Australia. We identified environmental factors affecting the success of woody-species restoration at a dry-woodland Gondwana Link site, Peniup, by relating the emergence and survival of 1522 seedlings to abiotic and biotic variables, including soil conditions and weed cover. We found soil conditions were highly variable across the site and, together with the dry Mediterranean-climate summer, affected seedling emergence and summer survival. Seedling emergence was higher in sandy soils, but summer survival was higher in clay soils. Most of the seedlings that emerged and survived the summer were in either the Fabales or Myrtaceae family. We concluded that attempts to analyse restoration outcomes that do not consider how the influence of primary abiotic and biotic factors changes over time may mask the mechanisms driving seedling establishment.

Key words: agricultural legacies, carbon projects, Gondwana Link, large-scale restoration, Mediterranean climate, recruitment bottlenecks.

Introduction

Large-scale woodland restoration projects in postagricultural lands are on the rise in Australia (McDonald & Williams 2009), in part due to a growing carbon economy (Bradshaw *et al.* 2013). Direct seeding is a common method for large-scale ecological restoration because it is more cost effective than containerised plantings (Carr *et al.* 2009). There is a long history of direct-seeding woody perennial species in North America and Europe, stretching back to the Middle Ages (Willoughby *et al.* 2004), and yet the practice is relatively recent in Australia (Carr *et al.* 2009). Moreover, there are few published accounts on the outcome of direct-seeding efforts that have occurred in Australia in the last few decades (i.e.

Doust *et al.* 2008; Geeves *et al.* 2008; Jonson 2010; and Woodall 2010 for woody perennials). Promoting seedling establishment from seeds is inherently difficult as this phase is a major bottleneck in the regeneration of long-lived plants such as trees and shrubs (Fenner 1987). Monitoring studies that track the success of direct seeding over time can help identify factors that limit recruitment and seedling establishment, informing future management strategies.

Land-use legacies can affect direct-seeding recruitment patterns in old-field restoration projects. For example, phosphorus (P) enrichment can affect native Australian woody species directly and indirectly by altering competitive hierarchies with agricultural weeds (Dorrough & Moxham 2005; Standish *et al.* 2006, 2008; Wong

et al. 2010; Scott & Morgan 2012). Regional climatic patterns can further affect which direct-seeded species survive to form the restored community. In particular, dry summers are a primary filter to seedling establishment in Australia, particularly in the temperate zone where rainfall is usually in winter (e.g. Cowling & Lamont 1987).

Here, we tracked seedling survival over time at a restoration site in south-western Australia to understand the interplay between climate and local abiotic and biotic factors and the establishment of woody seedlings. We predicted that land-use legacies associated with wheat cultivation and sheep grazing might vary with soil type to become important abiotic or biotic factors – for example soil P enrichment (Standish *et al.* 2006) and agricultural weeds (Standish *et al.* 2008). Thus, we

related seedling emergence and summer survival of native, predominantly woody perennial species, to variation in soil type, soil nutrient concentration and weed cover (after herbicide application) across the restoration site. We focused on first-year survival, a critical window for seedling establishment in ecosystems that experience dry summers. Our first goal was to determine the primary abiotic and biotic factors to seedling emergence and summer survival. Second, we asked whether the effects of these local-scale factors change with the onset of the Mediterranean climate summer.

Methods

Study site

Our field site is located at Peniup in south-western Australia (S 34°5'17.55" E 118°51'44.47"; Fig. 1). Peniup is 2406 ha in area and was purchased by Greening Australia and Bush Heritage Australia as part of the Gondwana Link initiative (www.gondwanalink.org). Peniup was farmed for wheat and sheep, in rotation across all soil types, for 30 years prior to its ecological restoration in 2008 (Sid Dowset, pers. comm., 2008). The climate is Mediterranean, with hot, dry summers (December–February) and cool, wet winters (June–August). Average annual rainfall is 456 mm but can vary considerably by year. Rainfall over the year of study (June 2008–May 2009) was 440 mm (Bureau of Meteorology, unpubl. data, 2009). Mean maximum temperature for the period of study (June 08 to May 09) was 21.8°C; mean minimum for the same period was 9.8°C. The long-term annual averages of these two statistics are 21.73 and 9.43°C, respectively (Bureau of Meteorology, unpubl. data, 2009).

In July 2008, 250 hectares were direct-seeded at Peniup using a modified agricultural seeder, which sowed native species into five scalped rows spaced 1.4 m apart (Jonson 2010). Prior to sowing, one pesticide treatment was applied to control Red-legged Earth Mite (*Halotydeus destructor*) and four herbicide treatments were applied to control agricultural weeds – primarily Wimmera Ryegrass (*Lolium rigidum*),

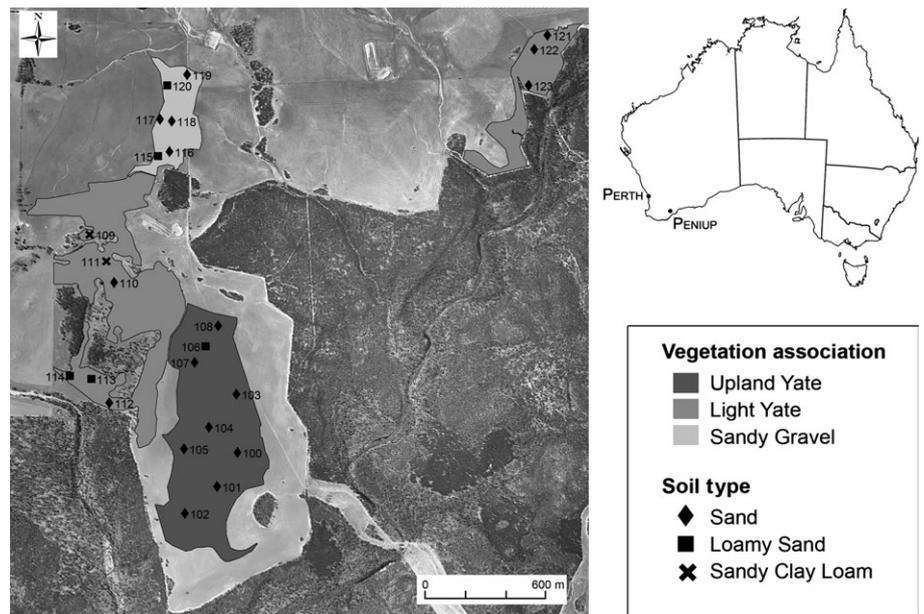


Figure 1. Aerial map of Peniup restoration site, and the location of Peniup in relation to Perth, south-western Australia.

Cape Weed (*Arctotheca calendula*), Yellow Catsear (*Hypochaeris radicata*), Mintweed (*Salvia reflexa*) and Prickly Paddy Melon (*Cucumis myriocarpus*) (Jonson 2010). Locally collected native seeds were pretreated where required with smoke, heat or gibberellic acid to break dormancy, then measured and mixed into seven different seed mixes based on soil type. Mixes were combined with a bulking agent (vermiculite fines) to ensure an even application of seeds (Jonson 2010). Seed viability was not assessed as it was locally collected and assumed to be as high as can be practically achieved having been collected and stored according to Florabank protocols (<http://www.florabank.org.au>; accessed 27 June 2007). Seeding depth varied from 0 to 20 mm depending on soil type (Jonson 2010), with most areas seeded at a depth of 5–10 mm.

For this study, we focused on three similar vegetation associations (seed mixes) comprised primarily of woody perennial species (Jonson 2010): (i) *Upland Yate*, open woodland dominated by swamp yate (*Eucalyptus occidentalis*) and rock sheoak (*Allocasuarina huegeliana*) in dark-granitic loam soils; (ii) *Mallee Heath*, heath dominated by mallees (*E. captiosa*, *E. thamnooides* and *E. falcata*) and an understory of acacias (*Acacia* spp.) and

melaleucas (*Melaleuca* spp.) in sandy gravel soils; and (iii) *Light Yate*, an ecotone (mix) of upland yate and mallee heath species in sandy gravels (Table 1). Seeding rates for individual species reflected their proportional representation in the local vegetation associations as well as seed availability (Table 2).

Data collection

We recorded seedling emergence within 24 10 × 14 m plots across the three vegetation associations (Fig. 1). Plots were located along a gradual south-east facing slope, and each vegetation association/slope combination was replicated three times (Fig. 1). Soil type broadly reflected the vegetation associations (Fig. 1). In November 2008, we recorded the location and genus of each seedling within the plots. Given similarities in seedling morphology, it was not possible to identify all seedlings to species. Using a 25 × 25 cm grid, we estimated per cent weed cover (to the nearest 10%) around each seedling. Weeds were primarily exotic species that had germinated after the herbicide application and sowing.

In early June 2009, we recorded which seedlings had persisted through the summer. We also collected three randomly located surface soil samples (to 10 cm

Table 1. For the three vegetation associations that were studied at Peniup, a comparison of seeding rates with the number of individuals that emerged and survived the summer by genus. Seedling emergents and survivors as a percentage of the approximate number of seeds sown is given in brackets

Genus	Family	Approx. number seeds sown	Number of species seeded	Number of emergents (%)	Number of summer survivors (%)
<i>Acacia</i>	Fabaceae	6000	11	777 (13)	443 (7)
<i>Allocasuarina</i>	Casuarinaceae	4000	2	145 (4)	83 (2)
<i>Alyogyne</i>	Malvaceae	50	1	0	0
<i>Anigozanthos</i>	Haemodoraceae	3000	1	2 (<1)	1 (<1)
<i>Callistemon</i>	Myrtaceae	50 000	1	11 (<1)	7 (<1)
<i>Calothamnus</i>	Myrtaceae	40 000	1	37 (<1)	31 (<1)
<i>Daviesia</i>	Fabaceae	50	1	0	0
<i>Eremaea</i>	Myrtaceae	2000	1	5 (<1)	4 (<1)
<i>Eucalyptus</i>	Myrtaceae	50 000	7	358 (<1)	155 (<1)
<i>Gastrolobium</i>	Fabaceae	500	2	18 (4)	12 (2)
<i>Hakea</i>	Proteaceae	50	4	10 (20)	2 (4)
<i>Kennedia</i>	Fabaceae	700	2	42 (6)	28 (4)
<i>Melaleuca</i>	Myrtaceae	100 000	7	92 (<1)	48 (<1)
<i>Senna</i>	Fabaceae	50	1	0	0
<i>Templetonia</i>	Fabaceae	300	1	27 (9)	7 (2)

depth) from each plot using a standard soil core. We air-dried soil samples for 1 week, sieved them to remove coarse particles (>2 mm) and weighed them to determine per cent coarse particle content. Samples were bulked by plot and analysed by CSBP Wesfarmers, Perth, for soil texture, particle size, nitrate nitrogen, plant-available phosphorus (Colwell), potassium (Colwell), sulphur, percentage organic carbon, conductivity and pH (in a CaCl₂ solution) according to the methods detailed in Stan-dish *et al.* (2006). Conductivity was calculated as a one part soil to five parts water (EC_{1:5}) and converted to EC_e by multiplying by a soil texture factor (Slavich & Petterson 1993).

We assumed that soil type and competition with weeds were the primary variables driving differences in seedling emergence and summer survival across the site. Because young seedlings were sparsely distributed (i.e. 10–120 seedlings per 10 × 14 m plot), we assumed that competition among them was minimal (Moles & Westoby 2004). Seed predation is typically low in old fields because of a lack of protective canopy cover (Mittelbach & Gross 1984).

Data analysis

Relationships among site variables

To visualize the relationships among environmental variables, we performed a PCA ordination using the *rda* command in the

vegan package, R version their 2.10.1 (R Development Core Team 2009; Oksanen *et al.* 2010). We tested variables for collinearity prior to their inclusion in the ordination: slope, percentage clay, percentage sand, percentage silt, percentage coarse particles (rock), concentrations of nitrate nitrogen, phosphorus, potassium and sulphur, percentage organic carbon, EC_e, pH and weed cover. We averaged weed cover scores by plot for this analysis. All variables were standardized (ranged from 0 to 1) but otherwise untransformed prior to analysis.

Seedling emergence and summer survival

To relate environmental factors with seedling emergence, we used multilevel logistic regression with the proportion of emergents from added seeds as the response variable, PC1 and PC2 as continuous variables, family and vegetation association as fixed factors and plot as a random effect. We included family as an explanatory variable to test for the influence of differences associated with species groups at this taxonomic level (e.g. seed-size, growth form; Table 2). The model was fitted with binomial errors using the *lmer* command in R (Bates *et al.* 2013). To determine whether the same environmental factors associated with seedling emergence also affected summer survival, we used a similar model but with

the proportion of emergents that survived the summer as the response variable. In this model, we also included weed cover as a continuous variable, as this was measured around each emergent seedling. Finally, to determine whether ultimate success was more related to factors governing emergence or survival, we repeated the original model using the proportion of added seeds that both recruited and survived the summer as the response variable.

Results

Overall, we recorded 1522 seedlings across the 24 plots, of which 820 (53%) survived the summer. The majority of seedlings were in the *Acacia*, *Eucalyptus*, *Allocasuarina* and *Melaleuca* genera, while many of the other seeded genera produced few seedlings (Table 1). Three seeded genera had no seedlings emerge within the sampled plots (Table 1).

Site variables

All plots had high sand content (64.8–94.2%) and correspondingly low clay (27.6–2.9%) and very low silt (10.1–0.01%) contents. The cumulative variance explained by the first two axes of the PCA ordination was 68% (Fig. 2). The first axis (PC1), which explained 51.7% of the variance, was associated with increasing soil clay content, increasing soil nutrient concentration (phosphorus, percentage

Table 2. Details of the species that were seeded and surveyed for emergence and summer survival at Peniup. Vegetation associations: L = Light Yate, M = Mallee Heath, U = Upland Yate. Under growth form, 'mallee' refers to the multistemmed habit of some *Eucalyptus* species. Species nomenclature follows Paczkowska & Chapman (2000). Seed mass data from Kew Seed Information database (available at <http://data.kew.org/sid/>; accessed 9 September 2013) and R. J. Standish, T. K. Morald and M. I. Daws (unpubl. data); means are 13.94 mg for Fabaceae, 18.48 mg for Proteaceae and 1.14 mg for Myrtaceae. NA = data not available

Species	Family	Vegetation association	Growth form	Seed mass (mg)
<i>Acacia acuminata</i>	Fabaceae	U	Shrub or tree	5.92
<i>Acacia aemula</i>	Fabaceae	L, M	Shrub	NA
<i>Acacia cupularis</i>	Fabaceae	U	Shrub	16.23
<i>Acacia cyclops</i>	Fabaceae	U	Shrub	30.3
<i>Acacia gonophylla</i>	Fabaceae	L, M	Shrub	NA
<i>Acacia lasiocarpa</i>	Fabaceae	L, M	Shrub	4.61
<i>Acacia moirii</i>	Fabaceae	L, M	Shrub	NA
<i>Acacia myrtifolia</i>	Fabaceae	L, M, U	Shrub	13.96
<i>Acacia puchella</i>	Fabaceae	L, M, U	Shrub	11.0
<i>Acacia saligna</i>	Fabaceae	U	Shrub or tree	14.71
<i>Acacia varia</i>	Fabaceae	L, M	Shrub	1.84
<i>Allocasuarina huegeliana</i>	Casuarinaceae	L, U	Tree	4.83
<i>Allocasuarina humilis</i>	Casuarinaceae	M	Shrub	2.7
<i>Alyogyne huegelii</i>	Malvaceae	U	Shrub	6.07
<i>Anigozanthos humilis</i>	Haemodoraceae	L, M	Herb	0.51
<i>Callistemon phoeniceus</i>	Myrtaceae	L	Shrub or tree	0.05
<i>Calothamnus quadrifidus</i>	Myrtaceae	U	Shrub	0.84
<i>Daviesia purpurascens</i>	Fabaceae	L, M	Shrub	NA
<i>Eremaea pauciflora</i>	Myrtaceae	M	Shrub	1.11
<i>Eucalyptus captiosa</i>	Myrtaceae	L, M	Mallee or tree	NA
<i>Eucalyptus occidentalis</i>	Myrtaceae	U	Tree	7.85
<i>Eucalyptus phaenophylla</i>	Myrtaceae	L, U	Mallee	0.05
<i>Eucalyptus pleurocarpa</i>	Myrtaceae	L	Mallee	4.4
<i>Eucalyptus pluricaulis</i>	Myrtaceae	L	Mallee	0.71
<i>Eucalyptus thamnoides</i>	Myrtaceae	L, U	Mallee	NA
<i>Eucalyptus xanthonema</i>	Myrtaceae	L	Mallee	0.39
<i>Gastrolobium spinosum</i>	Fabaceae	L, M	Shrub	10.3
<i>Hakea corymbosa</i>	Proteaceae	L	Shrub	6.8
<i>Hakea laurina</i>	Proteaceae	L, M, U	Shrub or tree	25.0
<i>Hakea lissocarpha</i>	Proteaceae	U	Shrub	23.9
<i>Hakea nitida</i>	Proteaceae	L, M	Shrub	18.2
<i>Kennedia eximia</i>	Fabaceae	L, M	Shrub	6.15
<i>Kennedia prostrata</i>	Fabaceae	L, M, U	Shrub	19.48
<i>Melaleuca acuminata</i>	Myrtaceae	U	Shrub	0.19
<i>Melaleuca bracteosa</i>	Myrtaceae	M	Shrub	0.08
<i>Melaleuca hamata</i>	Myrtaceae	U	Shrub or tree	0.04
<i>Melaleuca pauperiflora</i>	Myrtaceae	U	Shrub or tree	0.41
<i>Melaleuca subfalcata</i>	Myrtaceae	M	Shrub	0.09
<i>Melaleuca tuberculata</i>	Myrtaceae	L, M	Shrub	0.17
<i>Melaleuca undulata</i>	Myrtaceae	U	Shrub	0.66
<i>Senna artemisioides</i>	Fabaceae	U	Shrub	18.16
<i>Templetonia retusa</i>	Fabaceae	L, U	Shrub	28.5

organic carbon, nitrate nitrogen, potassium and sulphur), increasing weed cover and higher position on the slope. The second axis (PC2) explained 16.4% of the variance and described slope position and coarse particle content. All variables had a score of ≥ 0.5 on at least one of the two axes, and so we retained axis scores as opposed to individual variables in subsequent analyses. Clay and sand had

high loadings on PC1 and were strongly negatively correlated ($r = -0.97$); consequently, much of the variation along PC1 can be attributed to changes in soil type.

Seedling emergence and summer survival

Seedling emergence was significantly and negatively associated with PC1, indicating that the number of seedlings was highest

in sandy, low-nutrient plots and decreased along an axis associated with increasing clay content, nutrient concentration and weed cover (Fig. 3a, $\beta = -0.33$, $P = 0.04$), but was not significantly related to PC2 or vegetation association. Emergence was significantly higher for the Fabaceae ($\beta = 2.7$, $P < 0.0001$) and Proteaceae ($\beta = 3.0$, $P < 0.0001$) and lower for Myrtaceae ($\beta = -2.9$,

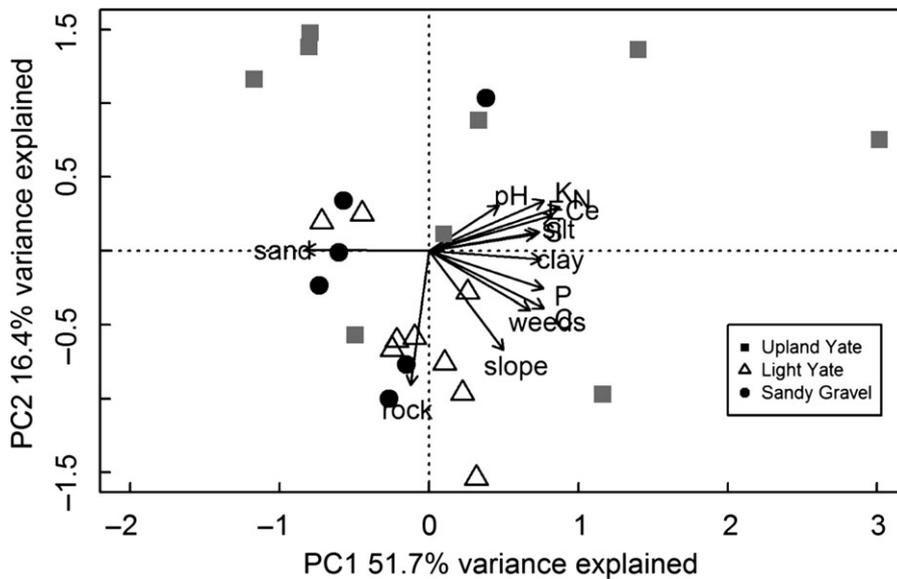


Figure 2. PCA ordination of 13 environmental variables for 24 plots representing three different vegetation associations across the restoration site at Peniup.

$P < 0.001$), when contrasted with Casuarinaceae (Table 1). In contrast to seedling emergence, summer survival was significantly positively associated with PC1, indicating that survival was higher in plots with high-nutrient clay soils ($\beta = 0.64$, $P = 0.004$). Summer survival was significantly negatively associated with weed cover ($\beta = -0.078$, $P = 0.01$) and with PC2 (Fig. 3b, $\beta = -0.61$, $P = 0.002$), indicating that seedling survival was decreased in lower-slope soils with fewer rocks. Summer survival did not significantly differ with family or vegetation association.

Unlike seedling emergence and summer survival, neither PCA axis significantly explained the post-summer establishment success of the added seeds (Fig. 3c). However, differences in emergence rates among families persisted to affect postsummer establishment rates, with significantly greater success rates for Fabaceae ($\beta = 2.7$, $P < 0.001$) and Proteaceae ($\beta = 2.1$, $P = 0.01$) and lower success rates for Myrtaceae ($\beta = -3.1$, $P < 0.001$) when compared with Casuarinaceae. Despite high rates of seedling establishment per seed, the absolute number of established Proteaceae seedlings was low (Table 1).

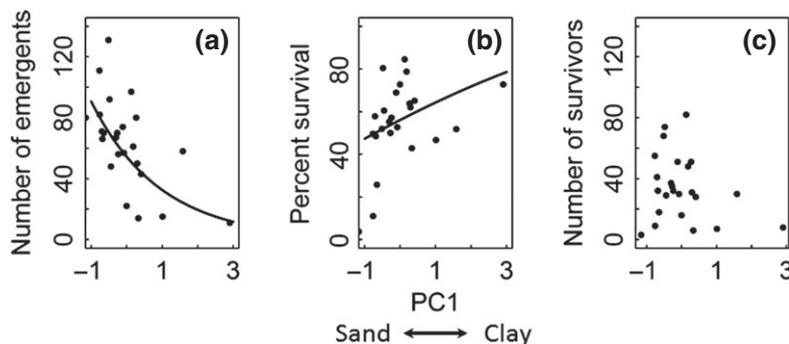


Figure 3. Seedling emergence and summer survival in relation to the first axis of the PCA presented in Fig. 2. Low PC1 scores reflect high sand, low-nutrient conditions, high PC1 scores reflect high-clay, high-nutrient conditions. (a) Number of individuals that emerged per plot by PC1 ($y = e^{4.0-51x}$; $R^2 = 0.44$), (b) percentage of emergents that survived the summer by PC1 ($y = \sin(0.60 + 0.10x)$; $R^2 = 0.28$), (c) number of individuals per plot that survived the summer by PC1 (relationship was not significant and fit line is therefore omitted).

Because PC1 was strongly associated with soil texture, we repeated all models with soil texture (sand or clay) as the fixed explanatory variable. Results were qualitatively similar, with a significant positive effect of sand on the proportion seeds that emerged ($\beta = 0.07$, $P < 0.001$); a significant positive effect of clay on the proportion of emergents that survived the summer ($\beta = 0.10$, $P = 0.004$); no significant effect of either sand or clay on the proportion of seeds that emerged and persisted through the summer.

Discussion

Despite an increase in direct-seeding restoration efforts in Australia and elsewhere, few studies have investigated the factors that affect seedling establishment over time in restored sites (Nuttall 2007). Our study identified the factors that influence seedling emergence and summer survival in a restoration project on a south-western Australian old field. We observed limited emergence within the majority of genera seeded, and of the seedlings that emerged, approximately half survived the summer. We found that local site conditions had opposing effects on seedling emergence and summer survival, with emergence higher in sandy, low-nutrient soils with lower weed cover and summer survival higher in clay soils with high nutrient concentration. Our findings indicate that the processes through which local factors filter individuals may change over time and with plant life stage and that focusing solely on factors associated with final establishment may mask the processes governing seedling survival over time (Gómez-Aparicio 2008; James *et al.* 2011; Pérez-Ramos & Marañón 2012).

Soil sand vs. clay content stood out as a strong determinant of seedling emergence. Our plots had the typically high sand content of soils found in south-western Australia (Harper & Gilkes 2004), ranging from 65% to 94% sand content. The strength of the positive relationship between seedling emergence and high sand content, low-nutrient soils was steep within this relatively narrow range of soil types, suggesting that even slightly higher

levels of sand content may be important for seedling emergence.

Seedling emergence rates may be greater in sandier soils for several reasons. First, the strength of sandy soils increases rapidly with slight increases in clay content (Harper & Gilkes 2004), and seedling roots may have difficulty in penetrating lower sand, higher clay soils (Bassett *et al.* 2005). Soil compaction due to heavy agricultural machinery may exacerbate this effect. Compaction may be particularly pronounced in higher clay soils, both because their soil structure can be reduced by cultivation to much smaller particles and they can have a higher water-holding capacity (Drewry *et al.* 2008). Consequently, the very low numbers of recruits in plots with high clay content may be due to combined effects of soil physical constraints and agricultural legacy.

Second, sandy soils have high water infiltration rates that may increase seed germination and enable emerging plants to readily extract water after rainfall (Maestre & Cortina 2002). Rainfall is regular and reliable in the period of seed germination and seedling emergence in regions with a Mediterranean climate, particularly south-western Australia (Cowling *et al.* 2005). Consequently, water infiltration may be more important than soil water retention for seedling emergence (Schutz *et al.* 2002), and an interaction between soil type and climate may be an additional reason why seedling emergence rates were higher in sandy soils. Finally, emergence rates may be higher in sandy soils because of reduced competition with weeds. Sandy soils had lower nutrient concentrations, and fewer weeds compared with clay soils. Competition with weeds may suppress seedling emergence in high-nutrient plots. Conversely, low nutrient availability is unlikely to impact seedling emergence of large-seeded species because seedlings are initially reliant on seed resources (Milberg & Lamont 1997). Having large seeds may help to explain the higher rates of post-summer establishment for species belonging to the families Fabaceae and Proteaceae compared with those belonging to the Myrtaceae and the Casuarinaceae (Hallett *et al.* 2011).

In contrast, summer survival rates were higher in clay soils with high nutrient concentration and weed cover. Seedlings are highly susceptible to dry conditions relative to adult trees and shrubs (Milberg *et al.* 1998), and soil water retention may be particularly important for seedling summer survival. Soil water-holding capacity is generally higher in soils with high clay and low sand content (Rawls *et al.* 1982), and greater water retention in clay soils may directly mitigate the effect of the summer dry period on seedling survival.

Moreover, higher nutrient retention in clay soils may increase seedling root growth relative to sandy soils, allowing seedlings to extract water from a deeper soil profile in these soil types (Woodall 2010). In particular, phosphorus is the primary nutrient limiting plant growth in ancient soils such as those in south-western Australia and is critical for root growth (Milberg *et al.* 1998). Higher summer survival in clay, high-nutrient soils may therefore be enhanced by an indirect effect of phosphorus for drought avoidance. Nitrogen too may be important for drought avoidance in some eucalypts (Woodall 2010). More research is needed to determine the effects of nutrient availability on seedling emergence and growth for a range of native woody species representing different families and field conditions (e.g. soil types, land-use legacies) to assess the benefits of fertilizer addition for improving the success of direct-seeding efforts in old fields. The potential effect of fertilizer addition on the competitive dynamics among seedlings as they mature also needs to be considered (e.g. Daws *et al.* 2013).

Conclusions

Documenting the ecological factors that influence seedling establishment is a critical first step to maximizing the effectiveness of ecological restoration (Hobbs & Norton 2004; Nuttle 2007), and this is particularly true of large-scale efforts such as direct seeding. We found it helpful to conceptualize the ecological factors as filters that affect seedling emergence and post-summer survival (Keddy 1992). Ecological filter models are often depicted as a

hierarchical set of static filters through which the species pool is reduced until an end community is formed (Keddy 1992). In reality, the strength of particular filters may vary through time (Fattorini & Halle 2004) and affect species to a small or large degree depending on their age (Stokes & Archer 2010). We found support for this idea in the importance of factors differentially affecting the sequential phases of seedling emergence and survival. More generally, our data support the evidence for ecological filters associated with seedling emergence and establishment having significant effects on the assembly of woody-plant communities (e.g. Gómez-Aparicio 2008).

Once filters are identified, and they can be used to improve restoration practice as managers can strategically manipulate filters, modify seeding rates or select species with the traits necessary to pass through these filters (Hobbs & Norton 2004). In our case, sand vs. clay was a significant indicator of when recruitment bottlenecks might occur. This general pattern suggests different management strategies for different soil types. For example, if the positive relationship between emergence and sandy soils was because seed radicles could not penetrate clay soils, then restoration treatments should include site preparation and seeding techniques to increase friability of areas with high clay content. A manipulative study is needed to determine whether the relationship between sand and emergence was primarily a consequence of reduced weed cover in sandy plots, and the results of which could be used to focus weed management efforts. Outlining the dynamic filters governing seedling survival therefore provides a basis for further experimental studies to improve future restoration practice.

Acknowledgements

Lauren Hallett was funded by a Fulbright Postgraduate Fellowship, the University of Western Australia and the Mary Janet Lindsay of Yanchep Memorial Fund. We thank Greening Australia and Bush Heritage Australia for access to Peniup, Dylan Chapple, Sara Jo Dickens, Emily Farrer, Joe Fontaine, David Freudenberger,

Joanna Hsu, Lorelee Larios, Claudia Stein and Katharine Suding for comments on a draft version of this manuscript, Heather Gordon for Figure 1 and Luke Barrett, Kellie Maher, Tim Morald and Rebecca Parsons for field assistance.

References

- Bassett I. E., Simcock R. C. and Mitchell N. D. (2005) Consequences of soil compaction for seedling establishment: implications for natural regeneration and restoration. *Austral Ecology* **30**, 827–833.
- Bates D., Maechler M. and Bolker B. (2013). lme4: Linear mixed-effects models using Eigen and Eigen. R package version 0.999999-2.
- Bradshaw C. J. A., Bowman D. M. J. S., Bond N. R. *et al.* (2013) Brave new green world – Consequences of a carbon economy for the conservation of Australian biodiversity. *Biological Conservation* **161**, 79–90.
- Carr D., Bonney N., Huxtable D. and Bartle J. (2009) *Improving Direct Seeding for Woody Crops in Temperate Australia: A Review*. RIRDC Publication No. 09/047. RIRDC, Canberra.
- Cowling R. M. and Lamont B. B. (1987) Post-fire recruitment of four co-occurring *Banksia* species. *Journal of Applied Ecology* **24**, 645–658.
- Cowling R. M., Ojeda F., Lamont B. B., Rundel P. W. and Lechmere-Oertel R. (2005) Rainfall reliability, a neglected factor in explaining convergence and divergence of plant traits in fire-prone mediterranean-climate ecosystems. *Global Ecology & Biogeography* **14**, 509–519.
- Daws M. I., Standish R. J., Koch J. M. and Morald T. K. (2013) Nitrogen and phosphorus fertilizer regime affect jarrah forest restoration after bauxite mining in Western Australia. *Applied Vegetation Science* **16**, 610–618.
- Dorrrough J. and Moxham C. (2005) Eucalypt establishment in agricultural landscapes and implications for landscape-scale restoration. *Biological Conservation* **123**, 55–66.
- Doust S. J., Erskine P. D. and Lamb D. (2008) Restoring rainforest species by direct seeding: tree seedling establishment and growth performance on degraded land in the wet tropics of Australia. *Forest Ecology & Management* **256**, 1178–1188.
- Drewry J. J., Cameron K. C. and Buchan G. D. (2008) Pasture yield and soil physical property responses to soil compaction from treading and grazing – a review. *Australian Journal of Soil Research* **46**, 237–256.
- Fattorini M. and Halle S. (2004) The dynamic environmental filter model: how do filtering effects change in assembling communities after disturbance? In: *Assembly Rules and Restoration Ecology: Bridging the Gap between Theory and Practice*. (eds V. M. Temperton, R. J. Hobbs, T. Nuttle and S. Halle) pp. 96–114. Island Press, Washington, DC.
- Fenner M. (1987) Seedlings. *New Phytologist* **106**, 35–47.
- Geeves G., Semple B. and Johnston D. (2008) Improving the reliability of direct seeding for revegetation in the Central West of New South Wales. *Ecological Management & Restoration* **9**, 68–71.
- Gómez-Aparicio L. (2008) Spatial patterns of recruitment in Mediterranean plant species: linking the fate of seeds, seedlings and saplings in heterogeneous landscapes at different scales. *Journal of Ecology* **96**, 1128–1140.
- Hallett L. M., Standish R. J. and Hobbs R. J. (2011) Seed mass and summer drought survival in a Mediterranean-climate ecosystem. *Plant Ecology* **212**, 1479–1489.
- Harper R. J. and Gilkes R. J. (2004) The effects of clay and sand additions on the strength of sandy topsoils. *Australian Journal of Soil Research* **42**, 39–44.
- Hobbs R. J. and Norton D. A. (2004) Ecological filters, thresholds and gradients in resistance to ecosystem reassembly. In: *Assembly Rules and Restoration Ecology: Bridging the Gap between Theory and Practice*. (eds V. M. Temperton, R. J. Hobbs, T. Nuttle and S. Halle) pp. 72–95. Island Press, Washington, DC.
- James J. J., Svejcar T. J. and Rinella M. J. (2011) Demographic processes limiting seedling recruitment in arid grassland restoration. *Journal of Applied Ecology* **48**, 961–969.
- Jonson J. (2010) Ecological restoration of cleared agricultural land in Gondwana Link: lifting the bar at 'Peniup'. *Ecological Management & Restoration* **11**, 16–26.
- Keddy P. A. (1992) Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science* **3**, 157–164.
- Maestre F. T. and Cortina J. (2002) Spatial patterns of surface soil properties and vegetation in a Mediterranean semi-arid steppe. *Plant & Soil* **241**, 279–291.
- McDonald T. and Williams J. (2009) A perspective on the evolving science and practice of ecological restoration in Australia. *Ecological Management & Restoration* **10**, 113–125.
- Milberg P. and Lamont B. B. (1997) Seed/cotyledon size and nutrient content play a major role in early performance of species on nutrient-poor soils. *New Phytologist* **137**, 665–672.
- Milberg P., Perez-Fernandez M. A. and Lamont B. B. (1998) Seedling growth response to added nutrients depends on seed size in three woody genera. *Journal of Ecology* **86**, 624–632.
- Mittelbach G. G. and Gross K. L. (1984) Experimental studies of seed predation in old-fields. *Oecologia* **65**, 7–13.
- Moles A. T. and Westoby M. (2004) What do seedlings die from and what are the implications for evolution of seed size? *Oikos* **106**, 193–199.
- Nuttle T. (2007) Evaluation of restoration practice based on environmental filters. *Restoration Ecology* **15**, 330–333.
- Oksanen J., Blanchet F. G., Kindt R. *et al.* (2010) *vegan: Community Ecology Package*. R package version 1.18-3/r11173.
- Paczkowska G. and Chapman A. R. (2000) *The Western Australian Flora: A Descriptive Catalogue*. Wildflower Society of Western Australia (Inc.), Western Australian Herbarium, CALM and the Botanic Gardens & Park Authority, Perth.
- Pérez-Ramos I. M. and Marañón T. (2012) Community-level seedling dynamics in Mediterranean forests: uncoupling between the canopy and the seedling layers. *Journal of Vegetation Science* **23**, 526–540.
- R Development Core Team (2009) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rawls W. J., Brakensiek D. L. and Saxton K. E. (1982) Estimation of soil-water properties. *Transactions of the ASAE* **25**, 1316–1320 & 1328.
- Schutz W., Milberg P. and Lamont B. B. (2002) Germination requirements and seedling responses to water availability and soil type in four eucalypt species. *Acta Oecologica* **23**, 23–30.
- Scott A. J. and Morgan J. W. (2012) Recovery of soil and vegetation in semi-arid Australian old fields. *Journal of Arid Environments* **76**, 61–71.
- Slavich P. G. and Petterson G. H. (1993) Estimating the electrical-conductivity of saturated paste extracts from 1–5 soil, water suspensions and texture. *Australian Journal of Soil Research* **31**, 73–81.
- Standish R. J., Cramer V. A., Hobbs R. J. and Kobryn H. T. (2006) Legacy of land-use evident in soils of Western Australia's wheatbelt. *Plant & Soil* **280**, 189–207.
- Standish R. J., Cramer V. A. and Hobbs R. J. (2008) Land-use legacy and the persistence of invasive *Avena barbata* on abandoned farmland. *Journal of Applied Ecology* **45**, 1576–1583.
- Stokes C. J. and Archer S. R. (2010) Niche differentiation and neutral theory: an integrated perspective on shrub assemblages in a parkland savanna. *Ecology* **91**, 1152–1162.
- Willoughby I., Jinks R. L., Kerr G. and Gosling P. G. (2004) Factors affecting the success of direct seeding for lowland afforestation in the UK. *Forestry* **77**, 467–482.
- Wong N. K., Morgan J. W. and Dorrrough J. (2010) A conceptual model of plant community changes following cessation of cultivation in semi-arid grassland. *Applied Vegetation Science* **13**, 389–402.
- Woodall G. S. (2010) Improving the direct sowing of commercial native plants in agricultural lands of southern Australia. Report to the Joint Venture Agroforestry Program (JVAP). RIRDC Publication No. 10/061. RIRDC: Canberra.