Predicting seedbank decay rates: the effects of field conditions on seed longevity and seedling recruitment in *Echium plantagineum* L.

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Summary A field experiment was set up using a resident natural seedbank of the winter annual pasture weed *Echium plantagineum* subsequently subjected to a range of management conditions to address the questions:

a) How long do seedbanks live and is longevity affected by field conditions?
b) Are seedbank losses explained most by recruitment or seed mortality?
c) Can we predict the aboveground recruitment levels from the size of the seedbank? and
d) Is recruitment density dependent?

Seedbank decay without seed input was monitored over three years under cultivation, no ground cover and mature perennial grass. Seed germination in relation to local seedbank density was also monitored. *E. plantagineum* seedbank decay varied between treatments depending on access to germination cues, but peaked at about 35% per annum. Seedbank longevity was highly affected by field conditions and may last tens of years. As observed, seedlings explained most seedbank loss, burying seeds through cultivation may be counter-productive. Aboveground recruitment can be predicted reliably from known viable seedbank densities, but predictive capacity is complicated by interspecific competition for safe germination sites. Seedling recruitment is highly density dependent, both within and between years. Implications of this study for the long-term management of Paterson's curse are discussed.

Keywords Seedbank dynamics, density dependence, seedbed, density dependent recruitment, seed mortality.

INTRODUCTION

The seedbank is the population of seeds in the soil between production and germination. When seeds in the seedbank have dormancy mechanisms this allows seedlings to avoid unsuitable growing conditions or competitors by limiting the proportion of seed that germinate when suitable conditions arise (Rice 1985, Hamrick and Lee 1987). Seed dormancy mechanisms are a common survival mechanism in plants adapted to disturbed environments, where risk of death before maturity is high. Adaptation to high disturbance frequency is also a feature of most invasive plants. Seedbank dormancy is therefore a dominant survival mechanism in this group, particularly amongst agricultural weeds. Understanding seedbank dormancy is vital when developing management strategies to combat the survival strategies of weeds. This task is confused, however, by a poor understanding that to increase the chance that some progeny of a given parent will survive, seeds exhibit variable expression of dormancy mechanisms. Many consider that because some seeds of a given weed can survive in the seedbank for several years, all seeds of that species will survive this length of time and therefore most seedbanks are very long-lived and hard to combat. Little data is available, however, on how quickly seedbanks decay under field conditions. There is also rarely clear information on whether seedbank decay is direct seed mortality or failed germination.

Seed dormancy is divided into; innate dormancy, where the physical or physiological conditions of the seed preventing immediate germination (= after ripening); enforced dormancy, where an inability to germinate is due to the lack of suitable germination cues; and induced dormancy, where physiological dormancy is imposed by specific often fluctuating environmental conditions (e.g. increasing temperatures).

This study explored these issues with Paterson's curse, Australia's worst broadleaved temperate pasture weed. Paterson's curse is also a typical representative of a Mediterranean climate winter annual weed that invades crops and pastures throughout Australia. Through this study we also attempted to address whether aboveground weed recruitment levels can predict the size of the seedbank, as this would provide predictive help of weed outbreaks.

MATERIALS AND METHODS

Echium plantagineum is typical of agro-ecosystems in Mediterranean, summer-rain temperate areas on acid soils. It is cumulatively toxic to livestock and horses. Paterson's curse typically dominates poor pastures on improved soils. *Echium plantagineum* seeds have an innate after-ripening requirement of variable length (3 months +), seed germination requires moisture and soil temperatures of at least 12°C. Germinated seedlings fail to reach the soil surface from below 6 cm. Seed dormancy is enforced by experiencing low temperatures (preventing germination after June at the study site) and induced by increasing temperatures (spring conditions; Piggin and Sheppard 1995).

Seedbank experiment The experiment was set up in an ungrazed 10 × 100 m block running down the edge of permanent pasture near Jugiong, NSW. The block had been fenced off six years previously. The *E. plantagineum* seedbank had been monitored since being fenced and had decayed to approximately 1500 viable seeds m^{-2} in 3 years prior to the experiment and then showed little further decay under a thick turf of *Phalaris aquatica*. The block was divided into nine pairs of 5 × 5 m plots. Three initial seedbed treatments were randomly allocated to the 18 plots, using six replicates of each treatment. The three treatments were; a) ungrazed perennial grass cover (control), b) all vegetation cut and cleared to ground level and c) all vegetation removed and ground cultivated. Treatment b) was designed to represent as far as possible the conditions found in the adjoining grazed pasture, but without any grazing animals that would have upset other treatments, Treatment c) was designed to represent cropping systems the year before a pasture rotation.

A census of seedlings was carried out after each rainfall of greater than 20 mm each year (December – June) either by counting all seedlings in the plot or sub-sampling five 0.25 m^2 quadrats per visit. All vegetation was sprayed out of treatments b) and c) in July of each year using Glyphosate™ to prevent seed input and the buildup of heavy vegetation cover.

The seedbank was sampled with 10, 3.2 cm diameter soil cores per plot per year in January. Cores were wet sorted and extracted seeds were tested for viability using tetrazolium.

Nested seed-addition experiment Within each treatment plot, ten 0.25 m^2 permanent subplots were positioned at random and permanently marked. The equivalent of 0, 1600, 4000, 20,000 and 40,000 m^{-2} of fresh viable (checked by scoring samples of 100 seeds with tetrazolium) seed were sprinkled, in a handful of dry river sand, onto each of the subplots allowing two replicate subplots per seed addition treatment per plot. In addition two further similar sized subplots were set up in treatment c) in which the top soil was removed to a depth of 20 cm, sterilised in an autoclave to kill the resident seedbank and returned to the holes left in the subplots the following day. On to these plots the equivalent of 40,000 seeds m^{-2} were sprinkled in an identical manner to the other treatments.

Censuses were made of seedlings in the subplots at the same time as the plots and such seedlings were subsequently killed by the Glyphosate™ treatment.

Statistical analysis Data were analysed using regression analysis. Seed and seedling numbers were log transformed except when this had no significant impact on the analysis.

RESULTS

Seedbank experiment The initial seedbank densities (Figure 1) and the total number of seedlings observed (Figure 2) across seed bed treatments show that the grass turf had a significant suppressive effect on recruitment.

Over the first three years of the experiment the seedbank declined fastest in the cleared but not cultivated seedbed treatment where the seedbank is predicted to decline from 1000 viable seeds m^{-2} to 1 m^{-2} in four years from treatment application (Figure 3). Seedbank decline was next fastest in the cleared and cultivated seedbed treatment, but was four times slower than in the cleared only treatment. Seedbank

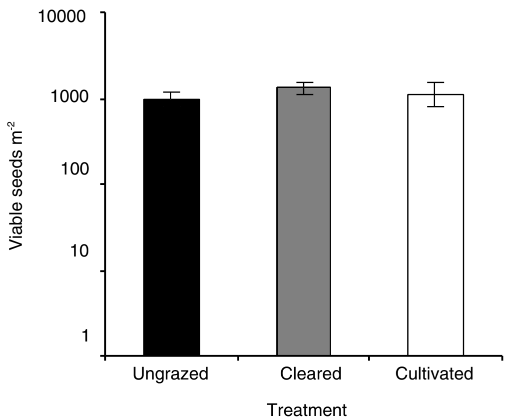

Figure 1. Initial seedbank densities across seedbed treatments.

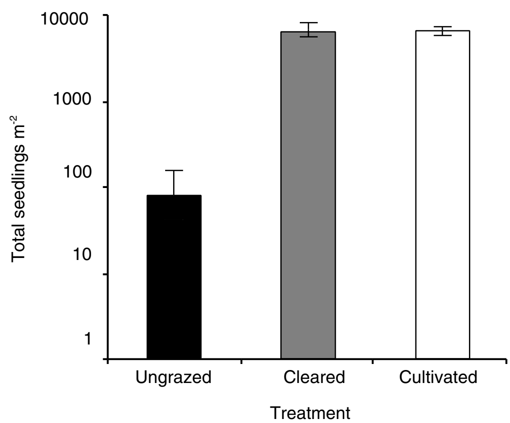

Figure 2. Total number of successful recruits by seedbed treatment.

decline in this treatment was predicted to reach one viable seeds m^{-2} in 16 years after treatment application. Lastly the control *P. aquatica* turf had a very significant suppressive effect on seed bank decline. Three years of data from this treatment suggested seedbank decline to one m^{-2} would take 70 years.

To see the degree to which seedbank decline could be explained by germination, the loss to the seedbank between years was regressed against the number of seedlings observed in that between year period (Figure 4). All seedbed treatments are included in the same figure to maximise the number of data points, as loss of the seedbank could not be accurately measured within each plot.

Figure 4 suggests that 70% of the variation in losses from the seedbank between years can be explained by the observed recruitment, suggesting that the vast majority of seedbank decline/decay was through germination.

Seed-addition experiment There was no significant difference in recruitment between unmanipulated subplots and those in which soil sterilisation was used. Results from the separate subplots of the seed addition experiment were used to see whether the size of the seedbank in any given subplot accurately predicted the number of observed seedlings across the three seedbed types.

Under a perennial grass turf there was no significant relationship between seedbank size and the number of observed seedlings over the three years of the experiment (Figure 5). In the cleared and cultivated plots, however, 70% of the variation in the number of observed seedlings was explained by the size of the initial seedbank. As the slope of this regression is much smaller than one this suggests that very large seedbanks produce proportionally fewer seedlings and is strong evidence for density dependent recruitment.

Data used in Figure 5 were converted from the number of seedlings observed to the probability a seed in the seedbank would produce a seed and re-graphed (Figure 6). Again while there was little evidence for any declining probability of recruitment with increasing seedbank size under the *P. aquatica* turf, there was a very rapid decline in seedling establishment probability from the seedbank over three years with increasing seedbank size in the other seedbed treatments.

DISCUSSION

This study has shown that seedbank decline in a typical winter annual broadleaved weed of Australian agro-ecosystems is strongly affected by the seedbed conditions within which the seedbank rests, declining much more rapidly in a situation similar to heavily

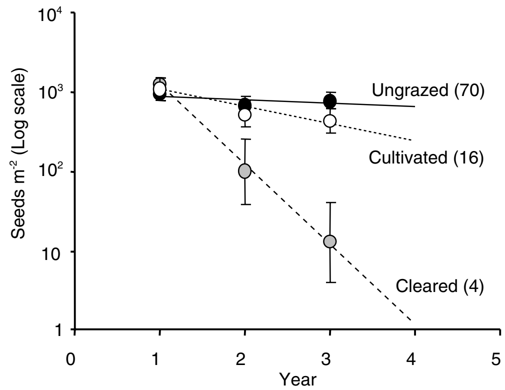

Figure 3. Seedbank decay by seedbed treatment (# years for seedbank to reach one seed m-^{2}).

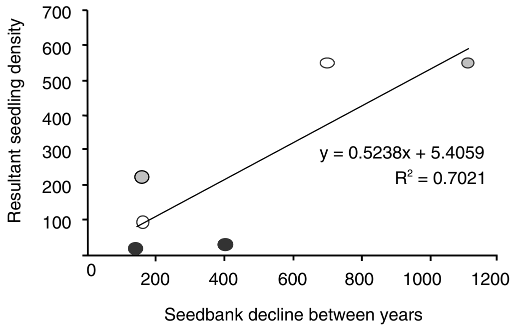

Figure 4. Observed annual seedling density as a function of the recorded loss to the seedbank within the same period (see Figure 3 for explanation of symbols).

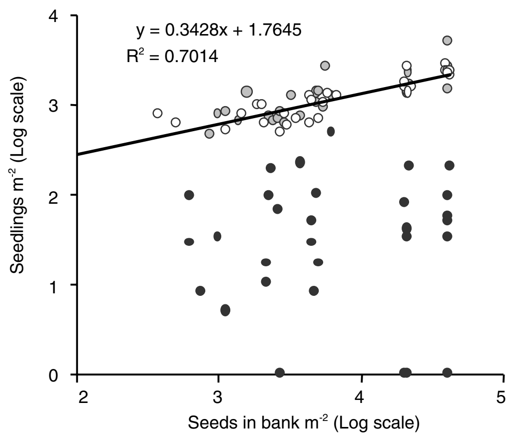

Figure 5. Number of seedlings observed over three years as a function of the initial seedbank size in the seed-addition experiment across three seedbed types (see Figure 3 for explanation of symbols). Regression line is fitted data from cleared and cultivated seedbed treatments only.

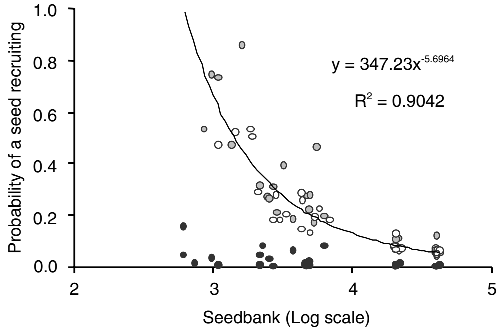

Figure 6. Regression of the probability a seed in the seedbank will be observed as a seedling against the size of the initial seedbank for three seedbed types (see Figure 3 for explanation of symbols). Regression line is fitted data from cleared and cultivated seedbed treatments only.

grazed pasture than in either of the other two situations i.e. ungrazed pasture of pre-cropping cultivation. The lack of significant seedbank decline observed under *Phalaris* both before and during this experiment is consistent with the hypothesis that such seedbanks are experiencing few germination cues, as *Echium* seeds do need temperature and moisture, but not light to germinate (Piggin and Sheppard 1995). A much more rapid decline in cleared versus cleared and cultivated pasture is consistent with higher proportion of the seedbank becoming buried during cultivation and thus being moved beyond the reach of most germination cues.

Depending on these field conditions, this experiment suggests seedbanks may persist for tens of years when prevented exposure to germination cues (burying seeds through cultivation may be counter-productive), but in most pasture situations decline appears more likely to be one order of magnitude per annum (Figure 3). Most seedbank loss was explained by attempted recruitment (Figure 4).

The nested seed-addition experiment also showed clearly that aboveground recruitment through seedlings can be predicted from known viable seedbank densities (Figure 5), but this predictive capacity is limited when there is significant interspecific competition from surrounding vegetation (i.e. perennial grass-cover seedbed treatment) or strong intraspecific competition (i.e. high seedbank densities) for germination sites.

Echium plantagineum recruitment was shown to be highly density dependent both within (not shown) and across all three years of this study. Evidence from other studies suggests that seed germination is not affected by the density of competitors (Grigulis *et al*. 2001).

Management implications This study shows that the seedbank of this weed declines very fast in a typical pasture setting, suggesting management strategies that prevent seed input are likely to be highly effective in the medium term at suppressing the densities of Paterson's curse in pastures. Attempts to smother out the weed with perennial grass or bury the seeds through cultivation are likely to be counter-productive. Perennial grass cover does occupy potential recruitment sites and so maintaining this component in realistic amounts in grazed systems would be beneficial. Management strategies aimed at suppressing this weed in the long-term through removing the capacity of the weed to set seed has a high-risk element. The year we stopped our experiment the low density of *Echium* plants that did recruit in that year went on unattended to become very large individuals producing thousands of seeds that would in one season have replenished the seedbank to pre-experimental levels.

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REFERENCES

Grigulis, K., Sheppard, A.W., Ash, J.E. and Groves, R.H. (2001). The comparative demography of the pasture weed *Echium plantagineum* between its native and invaded ranges. *Journal of Applied Ecology* 38, 281-290.

Hamrick, J.L. and Lee, J.M. (1987). Effect of soil surface topography and litter cover on the germination, survival, and growth of musk thistle (*Carduus nutans*). *American Journal of Botany* 74, 451-7.

Piggin, C.M. and Sheppard, A.W. (1995). *Echium plantagineum* L. *In* 'The biology of Australian weeds, Volume 1', eds R.H. Groves, R.C.H. Shepherd, and R.G. Richardson, pp. 87-110. (R.G. and F.J. Richardson, Melbourne).

Rice, K.J. (1985). Responses of *Erodium* to varying microsites: The role of germination cueing. *Ecology* 66, 1651-7.