Patterns of native and exotic species establishment in banksia woodland after fire

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Summary Plant invasions have become a worldwide problem as the introduction of aliens often cause negative effects on ecosystem structure and functioning. Plant-recruitment models are useful to make quantitative predictions of the impact of the aliens on native floras. One such model is the lottery. This study investigated whether lottery or non-lottery mechanisms might explain how exotic species are able to replace native species recruiting together in *Banksia* woodlands in Western Australia. The demography of the nineteen studied species (ten native and nine exotic) was assessed on a plot basis from number of initial seeds and seedlings (emerged germinants), survivors per month, survivors at the end of the growing season and number of seeds produced per species. The study was conducted in three unrelated sites that had recently been burnt. Variables were measured in plots within the burnt area and in adjacent non-burnt plots over ten consecutive months and at the end of the next growing season. We hypothesised that recruitment after fire of native and introduced species follows a lottery pattern. We showed that both groups followed biased lotteries, with abundance of exotics exceeding that expected by chance alone, and abundance of native species less than expected, based on their numbers of seeds. Most of the exotics produced seeds by the end of the growing season but none of the natives had. These processes help provide a mechanism to explain how exotics are gradually replacing natives in a system subjected to recurrent fire.

Keywords Plant invasions, native vs. exotic species, recruitment patterns, lottery.

INTRODUCTION

Plant invasion and the spread of exotic species threatens the structure and functioning of many ecosystems worldwide (Drake *et al*. 1989). Syntheses of knowledge on the topic have not yet been able to develop predictive theories of alien invasions and up until now, little is known about the rates, spatial patterns and determinants of invasive plant spread (Higgins *et al*. 1996).

The mechanisms accounting for co-occurrence of similar plant species remain unresolved in many ecosystems. The empirical studies on plant recruitment propose deterministic and stochastic processes. The former ones are said to occur when recruitment success for a species is related to biotic factors and environmental effects are not random. In the latter, stochastic recruitment processes govern success for a species and are proportional to its relative frequency in the pool of propagules (Chesson and Warner 1981). Thus, lottery recruitment can be identified by plotting the proportion of individuals at one stage against the corresponding proportions at the previous stage on a per species basis (Lamont and Witkowski 1995).

Lottery models can fit a simple lottery, when a given species have equal proportions of individuals at both stages and it follows a line passing through the origin. A biased lottery would apply when species attributes are superimposed on the simple lottery process (Lamont and Witkowski 1995). A lottery with storage takes place when the proportion of recruits relative to the initial number of individuals fluctuates widely over space and/or time, but the overall mean remains equal to one. This indicates strong but random environmental effects on plant recruitment.

In this paper we analyse seedling recruitment patterns of 14 species common in a *Banksia* woodland by examining seedling/seed ratios at three phenological stages. We also investigate the relative ability of native and exotic species to recruit in a post-fire soil.

As hypotheses to explain why the exotics eventually replace the native species, we tested were that weed species are quickly able to replace native species after a fire because they show (i) greater germinability, (ii) greater survival and (iii) earlier seed production.

MATERIALS AND METHODS

Plant species and experimental design Three typical *Banksia* woodland sites were chosen in the Perth Coastal Plain that were burnt in the summer of 1996. Sites were Kings Park and Jandakot airport in the vicinity of Perth and Yanchep, 80 km North of Perth. The vegetation at these three sites was *Banksia attenuata* with patches of *Banksia menziesii*, *Allocasuarina fraseriana* and *Eucalyptus todtiana*, with up to 20% cover Jandakot, up to 30% cover in Kings Park, and up to 40% cover in Yanchep.

The understorey was made up of woody shrubs and herbs, including *Allocasuarina humilis*, *Acacia pulchella*, *Bossiaea eriocarpa* and *Gompholobium tomentosum* and annual native and exotic species, including all the species studied here. Soils were deep acid sands.

The experiment was set up on 29 May, 4 June and 6 June 1997 at Jandakot, Kings Park and Yanchept respectively. At each site, two sub-sites were chosen, one in the burnt area and the other in an adjacent unburnt area. In each sub-site, two plots of 10 × 5 m subdivided into subplots of 2 × 1 m were set up. All plots were established within a fenced area to exclude mammal herbivores. Plots were sown with 50 seeds of each of the following set of native and exotic species.

Native species were *Banksia attenuata*, *Allocasuarina humilis*, *Acacia pulchella*, *Bossiaea eriocarpa*, *Gompholobium tomentosum* and *Podotheca gnaphalioides*. All species but the last are perennial and resprout after fire. Additionally, *B. eriocarpa* and *G. tomentosum* may be both resprouters and nonsprouters. *Nuytsia floribunda*, *Eremaea fimbriata*, *Eucalyptus todtiana* and *Anigozanthos manglesii* failed to produce many seedlings and were omitted from the analysis.

Exotic species were *Hypochaeris glabra*, *Urospermum pycroides*, *Ursinia anthemoides*, *Petrorhagia velutina*, *Briza maxima*, *Avena barbata*, *Ehrharta calycina* and *Gladiolus caryophyllaceus*. All species but *U. pycroides*, *E. calycina* and *G. caryophyllaceus* are annuals with the last two resprouters. *Romulea rosea* produced insufficient seedlings for analysis.

Sub-plots were selected randomly and seeded with 50 seeds of each species per sub-plot; seeds were covered with a 1–2 mm layer of soil from each sub-plot. All seeds were surface-sterilised with 1% sodium hypochlorite (Cochrane *et al*. 1999) and then soaked for a period of 24 hours prior to sowing. No other treatment was applied to the seeds, with the exception of the three legumes, *Acacia pulchella*, *Bossiaea eriocarpa* and *Gompholobium tomentosum*, which were pre-soaked for eight hours in boiling water and immediately allowed to cool to room temperature to break their innate dormancy. This was to simulate the effect of fire, which is the usual way that dormancy is broken in these species (Bell and Bellairs 1992, Bell *et al.* 1993). Germination, as measured by seedling emergence, and seedling recruitment was recorded over a period of 10 months. Monitoring was done every fortnight for the first two months and every month from then to the end of the experiment.

Data analyses and test for lottery Lottery pattern of recruitment was tested in a three stage statistical approach following Groom *et al*. (2001).

RESULTS AND DISCUSSION

The ratios of proportion of initial recruits (Table 1) show that, on average, the exotic annual species proportionally recruit more individuals than the exotic perennials, while the proportions shown by the native species (one annual and five perennials) is very variable.

The pattern of recruitment varied between species when comparing the proportion of initial seedlings with proportions of seed sown. Thus the patterns followed by the exotic species (Table 2) indicates high variability dependent on the kind of substrate where the seeds were sown. Specifically, in the unburnt sites there were five lotteries with storage (*A. barbata*, *B. maxima*, *G. caryophyllaceus*, *P. velutina* and *U. anthemoides*), three non-lotteries (*E. calycina*, *U. pycroides*) and one biased lottery (*P. velutina*). In the burnt sites, non-lottery (*A. barbata*, *E. calycina* and *U. anthemoides*), biased lottery (*B. maxima*, *H. glabra* and *U. pycroides*) and lottery with storage (*G. caryophyllaceus* and *P. velutina*) patterns were observed for the same comparisons.

Similar variations in the patterns of recruitment were observed in the native species (Table 3). Thus, in the unburnt sites there were five lotteries with storage (*A. pulchella*, *A. humilis*, *B. attenuata*, *B. eriocarpa* and *G. tomentosum*) and one non-lottery with storage (*P. gnaphalioides*). In the burnt sites, there were three lotteries with storage (*A. pulchella*, *A. humilis* and *P. gnaphalioides*), one non-lottery with storage

Table 1. Ratio of proportion of initial recruits (July, 1997) to proportions of seeds sown.

	Unburnt	Burnt
Exotic annuals	1.35–3.72	0.87–3.67
Exotic perennials	0.71–1.27	0.37–0.72
Native annual	2.25	2.51
Native perennials	0.38–2.93	0.33–2.54

Table 2. Patterns of recruitment of exotic species comparing initial individuals (July 1997) and final recruits in spring (October 1997). Lott = lottery, st = storage.

Species	Unburnt	Burnt
A. barbata	Lott with st 2.3	Non-lott 1.4
B. maxima	Lott with st 1.1	Biased lott 0.8
E. calycina	Non-lott with st 0.6	Non-lott 1.5
G. caryophyllaceus	Lott with st 0.7	Lott with St 1
H. glabra	Biased lott 0.6	Biased lott 0.7
P. velutina	Lott with st 1.1	Lott with St 1
U. pycroides	Non-lott with st 0.4	Biased lott 0.8
U. anthemoides	Lott with st 1.4	Non-lott 1.6

(*B. aquifolium*), one non-lottery (*G. tomentosum*) and one simple lottery (*B. attenuata*).

When comparing changes in patterns of recruitment by looking at the proportions in both spring and ten months after the beginning of the Sites (burnt and unburnt) three and ten months after the beginning of the recruitment process (Table 4), one can see that the patterns tend to move towards models with storage and biased lottery.

In summary, for the burnt sites simple or biased lotteries were more likely to occur. Both exotics and natives displayed a mixture of lottery and non-lottery responses.

In particular, the exotic annuals displayed either biased (below lottery line indicating equal proportion of individuals at two states of recruitment). The exotic annuals consistently produced proportionally more initial seedlings in relation to the proportion of seeds sown in both burnt and unburnt sites. Recruits had produced and set seed after ten months of establishment.

For the unburnt sites in ten months time, most species exhibited storage models or recruitment, according to the protocol used (Groom *et al*. 2001). Strong stochastic environmental effects characterise storage, indicating strong responses to the patchiness of the environment in plant establishment.

However, these are not the final results and further investigations on recruitment patterns are required. Still needed are answers to such questions as: is the invasive nature of exotic annuals due to their ability to take greater advantage of resource-rich microsites and what are the implications for the native species?

Table 3. Patterns of recruitment of native species after comparing the proportions of initial individuals (July 1997) and the final recruits in spring (October 1997).

Species	Unburnt	Burnt
A. pulchella	Lott with st 1.4	Lott with St 0.6
A. humilis	Lott with st 1.6	Lott with St 0.6
B. attenuata	Lott with st 1.3	Simple 1.4
B. eriocarpa	Lott with st 0.9	Non-lott with St 1.5
G. tomentosum	Lott with st 1.6	Non-lott 1.5
P. gnaphalioides	Non-lott with st 1.1	Lott with St 0.9

Table 4. Evaluation of the patterns of recruitment of exotic and native species grown in burnt and unburnt sites at two stages: after three and ten months of establishment respectively.

	Initial (July 1997) vs. spring (October 1997)			
	Unburnt		Burnt	
	Native	Exotic	Native	Exotic
Non-lottery			1	3
Non-lottery with storage	1	2	1	
Lottery with storage	5	5	3	2
Simple lottery			1	
Biased lottery	1			3
	Initial (July 1997) vs. next autumn (May 1998)			
	Unburnt		Burnt	
	Native	Exotic	Native	Exotic
Non-lottery				1
Non-lottery with storage	2	4	2	1
Lottery with storage	4	1	1	2
Simple lottery			1	2
Biased lottery	3		2	2

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REFERENCES

Bell, D.T. and Bellairs, S.M. (1992). Effect of temperature on the germination of selected Australian native species used in the rehabilitation of bauxite mining disturbance in Western Australia. *Seed Science and Technology* 20, 47-55.

Bell, D.T., Plummer, J.A. and Taylor, S.K. (1993). Seed germination ecology in southwestern Western Australia. *The Botanical Review* 59, 24-73.

Chesson, P.L. and Warner, R. (1981). Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist* 117, 923-943.

Cochrane, A., Brown, K., Meeson, N. and Harding, C. (1999). The germination requirements of *Hemigenia exilis* (Lamiaceae) – seed plug removal and gibberellic acid as a successful technique to break dormancy in an arid zone shrub from Western Australia. *CALMScience* 3, 21-30.

Drake, J.A., Mooney, H.A., Di Castri, F., Groves, R.H., Kruger, F.J., Rejmanek, M. and Williamson, M. (1989). Biological invasions: a global perspective. (John Wiley and Sons, Chichester, England).

Groom, P.K., Lamont, B.B. and Wright, I.W. (2001). Lottery (stochastic) and non-lottery (biological) processes explain recruitment patterns among eight congeneric shrub species in southwestern Australia. *Journal of Mediterranean Ecology* 2, 1-14.

Lamont, B.B. and Witkowski, E.T.F. (1995). A test for lottery recruitment among four *Banksia* species based on their demography and biological attributes. *Oecologia* 101, 299-308.