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Habitat Segregation by Serotinous Shrubs in Heaths: Post-fire Emergence and Seedling Survival

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Abstract

Seeds of two serotinous shrub species generally restricted to the drier edges, and two serotinous shrub species commonly confined to the wetter drainage channels of upland sedge–heaths were assessed for germinability and used in manipulative field experiments. In post-fire field experiments the effects of habitat and manipulated soil moisture were examined to test if the distribution of adult plants was influenced by soil moisture at seed germination. The effects of habitat on seedling survival for 11 months were also assessed. One species from the edge zone, *Banksia marginata* Cav., and one from the channel zone, *Hakea microcarpa* R.Br., had germination preferences corresponding to the distribution of adult plants. The other edge species, *Hakea dactyloides* (Gaertner) Cav., did not show a significant preference for either zone. The second channel species, *Callistemon pityoides* F.Muell., did not germinate in the field or in a laboratory germination trial. Some evidence for soil-stored dormancy related to temperature and or waterlogging was found in both *Hakea* species. Overall the results suggest that for two species habitat segregation occurs when seeds are incorporated into the seed-bed and germination occurs. No differential survival effects across habitats were found in the first year of growth.

Introduction

Sedge–heath communities, structural mixtures of sedgelands and heaths, occur along the coastal plains and plateaus of south-eastern mainland Australia and Tasmania, in areas of impeded drainage (Beadle 1981). Detailed accounts of some of these treeless communities in upland areas have recently become available (e.g. Keith and Myerscough 1993; Williams 1995; Keith 1996) and indicate that floristic patterns are related to edaphic and fire factors. However, the intercorrelated nature of the environmental gradients that occur in these heaths (see Keith and Myerscough 1993) makes the deduction of causal agents from field correlations intractable.

Habitat segregation of heath species along environmental gradients is a striking feature of a number of studies in south-eastern Australia (e.g. Siddiqi *et al.* 1972; Burrough *et al.* 1977; Buchanan 1980; Bowman *et al.* 1986; Myerscough and Carolin 1986; Keith and Myerscough 1993). Numerous causal agents have been suggested to account for habitat segregation, some of which include seed-bed conditions, physiological tolerance, competition, and predation. These effects are also related to the fire-prone nature of heaths and the influence of fire on demographic processes (Bond and van Wilgen 1996; Whelan 1995). Whilst there is an expanding literature on both interval-dependent and event-dependent effects of fire in heath species (e.g. Burgman and Lamont 1992), until recently there has been little focus on the effects of fire events across environmental gradients. In a series of experiments, Myerscough *et al*. (1996) and Clarke *et al*. (1996) have highlighted the importance of pre-emergence and emergence demographic events influencing the distribution of coastal heath dominants.

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In this paper, the effect of soil moisture on seed germination and survival of dominant serotinous shrub species in sedge–heaths of Gibraltar Range National Park is examined. Seeds of species restricted to either drier open-heaths or wetter closed-heaths on drainage channels were used in a post-fire field experiment to test the hypothesis that soil moisture differentially affects seed germination and survival. Field emergence results were also compared to laboratory germination and viability data to assess predation and dormancy effects. General field observation on the natural emergence of seedlings were also made in nearby burnt heaths and compared to laboratory and field experiments.

Methods

Study Area

Gibraltar Range National Park is located on the eastern edge of the Northern Tablelands, 70 km east of Glen Innes, New South Wales (29°32′ S 152°18′ E). Within the park the predominant geology is granitic and is described by Brunker and Chestnut (1976) as the Dandahra Granite intrusion. On this parent material, treeless sedge–heaths develop in waterlogged areas on hill sides and on flats. Those found on the flats usually contain a naturally formed drainage channel, providing a flow of water through the system. Distinct vegetation patterns occur on these flats which relate to topographic position and time since fire. From the better drained edges, open-heath grades into expanses of sedgeland which are broken by closed-heath along the wetter narrow drainage line (Williams 1995). Dominant shrubs found in the open-heath include *Leptospermum arachnoides*, *Epacris obtusifolia*, *Epacris microphylla*, *Banksia marginata* and *Hakea dactyloides*. Dominant shrubs found in the closed-heath include *Hakea microcarpa*, *Leptospermum gregarium*, *Baeckea* sp. ‘c’ and *Callistemon pityoides*. *Banksia marginata* is also found in these heaths but is not a dominant species (Williams 1995). Nomenclature follows Harden (1990–1993). Background descriptions of soil properties of the sedge–heaths has been reported by Williams (1995).

Field Germination Experiment

Four serotinous shrub species were used in this study allowing ease of seed collection and uniformity of seed bank type. Two species commonly associated with the better drained open-heath edges, *Banksia marginata* Cav. and *Hakea dactyloides* (Gaertner) Cav. and two from the wetter closed-heaths along drainage lines, *Hakea microcarpa* R.Br. and *Callistemon pityoides* F.Muell. were selected.

Fruits of each of the four species were collected from a large number of individual plants. Only *Banksia marginata* fruits required heat treatment to release seeds, the fruits of the others opening within days of collection. The fruits of *B. marginata* were placed inside an oven at 150°C for 15 min. Bradstock (1991) indicated that this has no effect on the germination of seeds of two other *Banksia* species. On removal from the fruits, the number of seeds that had been damaged by predators was noted for each species and all undamaged seed was pooled.

Three moisture treatments (waterlogging, free drained and background) were applied to shallowly buried seed in each of two habitats (well-drained open-heath, wetter closed-heaths). Spatial replication was achieved by placing four replicates of each treatment in two well-separated patches. Ten seeds of each species were sown per replicate. To avoid possible effects of cover and to approximate the time of natural recruitment, seeds were sown into an area that was burnt 7 months prior to the study (October 1994). Also, in order to minimise the confounding effect of naturally dispersed seed germinating in the treatments, sites were selected away from the burnt remains of adult plants.

Seeds of the four species were then buried to a depth of about 1 cm in the soil in all treatments, since Clarke *et al.* (1996) found that shallow burial of seeds of heath species allowed greater germination than placing seeds on the soil surface. The waterlogged treatment involved removing a cube of soil and replacing it inside a 4 L waterproof container placed inside the hole. The bucket was filled to the soil surface with water from the channel and topped up every fortnight. A free drained soil treatment was similar to the waterlogged treatment, except the bucket contained holes allowing drainage and was not filled with water. Note that in the channel the free drained treatment was placed on the channel surface and allowed to drain. The third treatment involved burying the seeds in unmodified soil. The hypothesis that seed germination would be enhanced for the drainage line species under waterlogged conditions and that the converse would apply for the drained open-heath species was tested.

The experiment commenced in mid-May 1995. Every fortnight the replicates were inspected for germination (emergence of cotyledons) and the waterlogged plots topped up with water from the channel. The germination experiment concluded after 4 months when all seed germination appeared to have ceased. Thereafter, watering of waterlogged plots ceased.

Survival of experimental seedlings was monitored in the untreated plots in the channel and on the edge in September 1995, November 1995, January 1996 and April 1996. Observations on seedling establishment in surrounding heaths were also made during this time by comprehensive searches of burnt heaths.

Laboratory Studies

In order to detect dormancy mechanisms and to assess the viability of the seeds of each species, two trials were performed in the laboratory. Firstly, 8 replicates of 10 seeds of each species were placed on moist germination paper within plastic germination trays. Cotyledon emergence was counted every week until germination appeared to be complete, after 2 months. Ungerminated seeds were subjected to a tetrazolium test to determine viability.

The second laboratory trial involved subjecting 8 replicates of 10 seeds of each species to a tetrazolium viability test. Seeds were soaked in deionised water for 2 days, deeply sliced and soaked in 2,3,5 triphenyl tetrazolium chloride for 2 days in the dark. The seeds were then examined for the presence of a red pigment indicating a viable embryo.

Data Analysis

Numbers of emergences were adjusted for initial seed viability of seed. These were compared among treatments, habitats and patches using a three-factor nested ANOVA. Treatments and habitats were fixed factors, whilst patches were a nested random factor. Data were tested for homogeneity of variance using Cochran’s test. Post-hoc multiple comparisons were done using the Bonferoni test. Comparison of proportions of germinating and viable seed were made using *z*-tests.

Results

Seedling Emergence

Of the four shrub species used in the field experiment, three germinated readily, but the fourth species, *Callistemon pityoides*, failed to germinate in the field under any treatment. Of the others *Banksia marginata* had the highest emergence followed by *Hakea microcarpa* and *Hakea dactyloides*. In each of these species, significant effects of site and or treatment were detected (Table 1). No patch effects were detected and these effects were pooled with the replicates for increased statistical power ($P > 0.25$).

Interactive effects of treatments and habitats were detected for the drier edge heath species *Banksia marginata* (Table 1). Emergences were clearly higher in the free-drained plots on both the edge, where it naturally occurs, and in the drained channel treatment. In both habitats, emergence was reduced by the waterlogged treatments (Fig. 1*a*). Thus there appears to be no soil factor other than waterlogging inhibiting germination of this in the wetter sites. Natural seedling emergence was observed in very low numbers around adult plants in burnt woodlands but no emergence was observed in the sedge–heaths.

Table 1. **Summary of ANOVA results for numbers of seedlings of *Banksia marginata*, *Hakea dactyloides* and *H. microcarpa* emerging after 4 months from seeds sown**
n.s., not significant at $P > 0.05$

Factor	d.f.	*Banksia marginata*	*Hakea dactyloides*	*Hakea microcarpa*
Habitat	2	n.s.	n.s.	$P < 0.01$
Treatment	3	$P < 0.001$	$P < 0.01$	$P < 0.01$
Interaction	6	$P < 0.01$	n.s.	$P < 0.01$

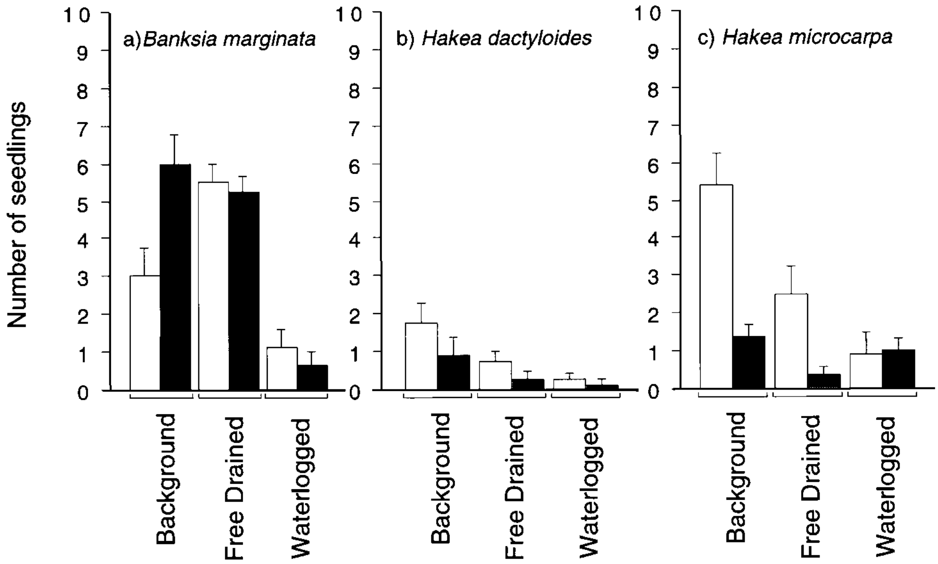

Fig. 1. The mean number (± SE) of seedlings of (*a*) *Banksia marginata*, (*b*) *Hakea dactyloides* and (*c*) *Hakea microcarpa* emerging 4 months after sowing in heath edges (■) and in drainage channels (□).

No interactive effects were found for the other drier edge species, *Hakea dactyloides*. Instead, only treatment effects were detected (Table 1). Emergences were clearly depressed by waterlogging treatment. However, emergences were often the highest on the moist undisturbed channel sites where it does not naturally occur (Fig. 1*b*). No natural seedling emergence was observed in the field.

Hakea microcarpa, one of the two species typically restricted to the channel and wet mid-slopes, showed interactive effects of treatment and habitat (Table 1). Significantly higher emergence in the undisturbed and drained channel plots was detected than in any of the edge sites and the waterlogged channel (Fig. 1*c*). This indicated a preference for soil conditions or microsites in the channel but not waterlogging. No natural seedling emergence was observed in the field.

Seedling Survival and Secondary Emergence

Seedlings of *Banksia marginata* all emerged within the first 4 months and thereafter exhibited slow mortality even though this was a period of very low rainfall. Rates of mortality appear to be similar in both swamp edges and in the drainage line (Fig. 2*a*). Both *Hakea* species showed 'secondary' emergence in the drying channel sites up to 9 months after seeds were sown (Fig. 2*b, c*). This effect was also pronounced in the abandoned waterlogging treatments where it was noted that seedlings emerged after these plots began to dry out (Fig. 3). Overall, there was little cumulative mortality of both *Hakea dactyloides* and *Hakea microcarpa* in either edge or channel plots (Fig. 2*b, c*).

Predispersal Seed Predation

Twenty one percent of seeds collected from *Banksia marginata* infructescences were damaged and rendered inviable by unknown insect larvae. Only 0.9% of the seed collected

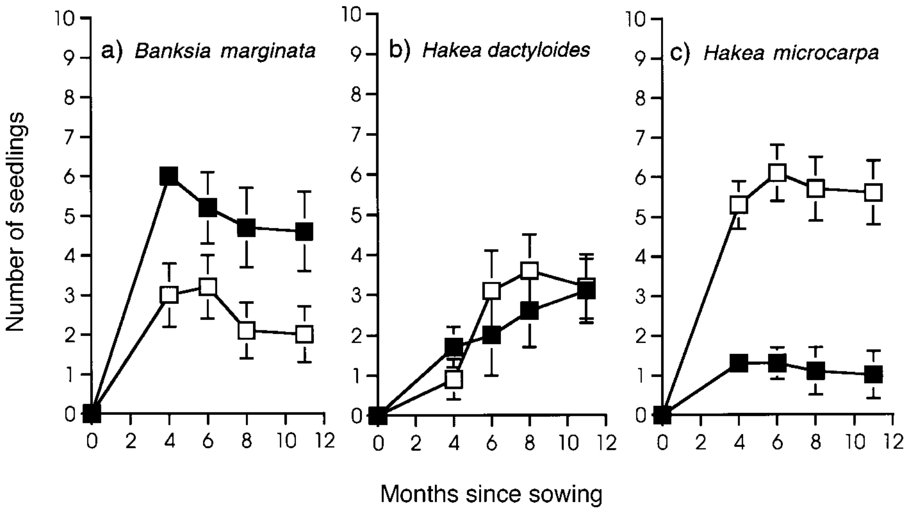

Fig. 2. The mean number (± SE) of seedlings of (*a*) *Banksia marginata*, (*b*) *Hakea dactyloides* and (*c*) *Hakea microcarpa* emerging and surviving in untreated 'natural' plots on heath edges (■) and in drainage channels (□).

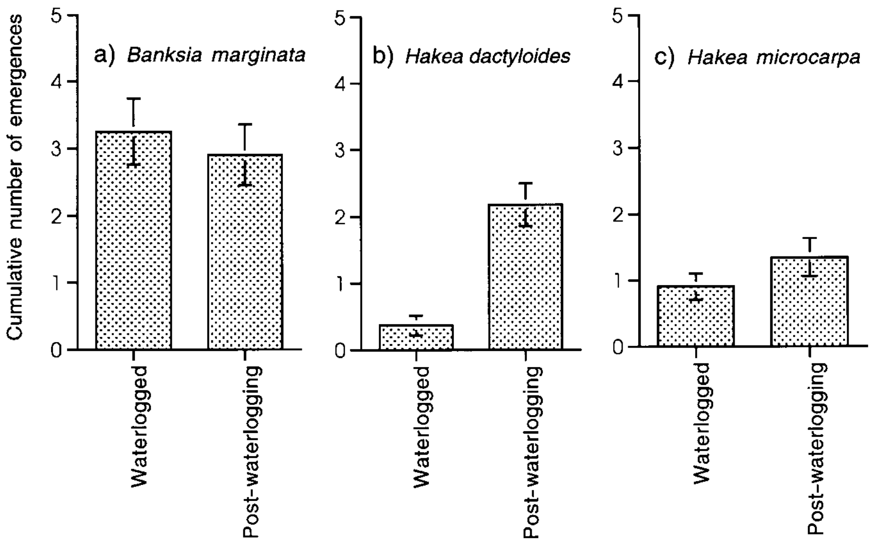

Fig. 3. The mean number (± SE) of seedlings of (*a*) *Banksia marginata*, (*b*) *Hakea dactyloides* and (*c*) *Hakea microcarpa* emerging in waterlogged treatments before (4 months, May–August) and after (September–January) treatments ceased.

from *Hakea dactyloides* fruits had been eaten by unknown insect larvae and, 0.6% of the *H. microcarpa* seeds were consumed or damaged. There appeared to be no predispersal predation of *Callistemon pityoides* seed.

Laboratory Studies

Seeds of *B. marginata* had the highest germination in the laboratory (96.3%). All ungerminated seeds were not viable and therefore seed appeared to have no innate dormancy. Viability from the tetrazolium test was 98.8% and was not significantly different from the germination test ($z = 0.2$, $P > 0.1$). This indicated that all the viable seeds germinated in the laboratory, but significantly less (60%) of the viable seeds germinated in the most favourable field environment (disturbed edges) ($z = 5.6$, $P < 0.001$).

The proportion of *H. dactyloides* seed germinating in the laboratory was 68.8%. All ungerminated seeds from the laboratory trial were not viable. This was significantly different from the independent tetrazolium (78.8% viability) ($z = 2.5$, $P < 0.01$) and suggests some innate dormancy. While most viable seed germinated in the laboratory, the highest germination in the field was 17.5%, about one third of that found in the laboratory ($z = 5.9$, $P < 0.001$).

Seeds of *H. microcarpa* germinated readily in the laboratory (85.0%). All ungerminated seeds from the laboratory trial were not viable and there appeared to be no innate dormancy as the viability from the tetrazolium test (81.2%) was not significantly different from the germinations ($z = 1.1$, $P > 0.1$). This indicated that all the viable seeds germinated in the laboratory but only 60% of the viable seeds germinated in the most favourable field environment (undisturbed channel) ($z = 4.3$, $P < 0.001$).

No seeds of *Callistemon pityoides* germinated in the laboratory. The tetrazolium test indicated that 10.0% of seed of this species was viable. A tetrazolium test of the seed used in the germination test, after it was finished, indicated that 6.0% of these seed were in fact viable. Therefore even though some of the seeds were viable, they did not germinate in the field or the laboratory suggesting the presence of an innate seed dormancy mechanism.

Discussion

Seed Viability and Natural Recruitment

Levels of pre-dispersal seed predation in *Banksia marginata* (> 20%) contrast with those found in adjacent fruits of the other serotinous species (< 1%). Interestingly, these losses may be compensated for by higher viability of the seeds in *Banksia marginata* relative to the two resprouting *Hakea* species. Populations of *Banksia marginata* at Gibraltar Range National Park are obligate seeders and enhanced recruitment might be expected relative to the other resprouting shrubs. Post-fire observations of natural seedling emergence were very low for *Banksia marginata* and were mainly confined to the woodland edges of sedge–heaths near burnt adult plants. Viability of seeds from both *Hakea* species although less than that of *Banksia* was still high and had low levels of pre-dispersal predation. These results together with those of the field experiment would lead to the expectation of some natural seedling emergence after a fire. In the present study, no seedlings were found under or around adult plants of either *Hakea* species in the field. Lack of seedlings may be related to the effects of fire on the canopy-stored seed bank. Bradstock *et al*. (1994) have shown that excessive heat can kill canopy-stored seed banks in *Hakea* species and that small-fruited species are more susceptible than large-fruited species. The effects of fire intensity on the viability of plant-stored seed banks may be important in terms of differential distribution of *Hakea* species distribution across environmental gradients. This effect might explain why the small-fruited species, *Hakea microcarpa*, has a patchy and restricted distribution in sedge–heath communities.

The viability of the small-seeded species, *Callistemon pityoides*, was very low compared with that of the large-seeded species and supports the idea that smaller seeds have less chance of establishing than larger seeds in heaths. Pickard and Jacobs (1983) also found that the small-seeded species, *Leptospermum scorparium*, had lower percentage germination than large-seeded Proteaceae species. Myerscough (pers. comm.) also found that a range of small-seeded Myrtaceae species had low levels of emergence in their field experiments at Myall Lakes, New South Wales. The general lack of germination in the field, either in the experimentally sown areas or in other areas where adult plants were fecund, is perplexing and indicates some innate dormancy mechanisms.

Emergence and Dormancy

All species that emerged in the field were inhibited by waterlogging in the treatments; the results of which are consistent with laboratory-based studies. Pickard and Jacobs (1983) found higher seed germination in a free-drained treatment than in wetter treatments in a glasshouse trials of both *Banksia ericifolia* and *Hakea teretifolia*, from heaths on Hawkesbury Sandstone.

Initial field emergences occurred over about a 6 week period and, when adjusted for the viability of seeds sown, were about one third less than laboratory germinations. This may be related to either mortality of buried seed or some soil stored seed dormancy. Nevertheless, it is likely that seed burial enhanced emergence due to moister soil conditions and the absence of ground foraging granivorous ants.

For *Banksia marginata*, the difference between observed and expected germination appears to related to decomposition or granivory of buried seed as little secondary emergence was recorded over spring or summer. There is also some suggestion that placing soil inside containers reduced seed germination. Free-drained edge treatments should have provided the same conditions as the undisturbed edge plots; however, the latter allowed a higher percentage seed germination than the free-drained edge treatment for all germinating species. This may have been due to the container walls reducing the natural movement of moisture into the pores of the soil within the container and therefore causing the soil to dry more than is natural.

In both *Hakea* species examined in the present study, there appears to be some soil-stored seed dormancy related to temperature as small numbers of seedlings were observed to emerge over spring and summer. Whilst seasonal effects on seedling emergence were not examined, these patterns are consistent with studies by Bradstock and Bedward (1992) which suggest that seasonal weather conditions affect emergence. Pronounced secondary emergences were also observed in treatments where waterlogging had ceased. This implies that waterlogging induced soil-stored seed dormancy and reiterates the warning by Whelan (1995, p. 172) over differences between laboratory and field germinations. Nevertheless, taking dormancy into account, about one third of the seeds are unaccounted for and appear to be either decomposed or removed by granivores.

Habitat Segregation

The high emergence of *Banksia marginata* seedings in the undisturbed edge plots, and in free-drained plots, suggests its most common distribution on the edge of open-heaths is related to seed germination on moist soils found on the edge of these sedge–heaths. These results contrast with those found by Pickard and Jacobs (1983) and Mustart and Cowling (1993) for related species, as they found post-emergence survival to be important in habitat segregation. Myerscough *et al.* (1996) have also shown that survival of seedlings segregates wet-heath species from the dry-heath. However, they have also shown that dry-heath species are segregated from the wet-heath during dispersal i.e. prior to germination. *Banksia marginata* is also capable of emerging and surviving in the channel sites when sown there. So why is it generally absent from sedgelands and channels? This difference could be explained by either initial dispersal events or by longer term seedling survival. Given that no differential survival effects were detected in the first year, it is suggested that at dispersal, seeds are less able to become incorporated into the seed-bed in the wetter areas than the dry ones.

The inhibiting effect of waterlogging was very pronounced in *Hakea dactyloides*. Nevertheless there was consistently better germination in the wet channel plots than the edge plots. These patterns of recruitment do not reflect the distribution of adult plants, as *Hakea dactyloides* has never been recorded from the sedgelands or channels at Gibraltar Range. It should be noted is that this experiment ran over the driest part of the year, during a succession of dry years; therefore, the channel, although wet, may usually be wet enough to inhibit germination. Early establishment may also be counteracted by low survival of seedlings, as Pickard and Jacobs (1983) and Mustart and Cowling (1993) found for other species in their studies. However, in the present study, no such effects were found for the first year of survival. Alternatively, assuming the seeds disperse into the channel, the necessary disturbance causing burial of seeds may not occur there and hence seeds of *H. dactyloides* may not be capable of germinating as suggested by Clarke *et al.* (1996).

The only species that showed very strong germination preference for the habitat in which it occurred was *Hakea microcarpa*. Significantly higher emergence was found in undisturbed and free drained channel plots than in those of the edge, reflecting its preference for the wetter channel habitat. This suggests that habitat segregation mainly occurs immediately after dispersal at the seed germination stage. The difference in seed germination between free-drained plots of the channel compared with the edge suggest that particular soil conditions stimulated seed germination. Raised ‘islands’ of post-fire debris often accumulate around the root burls of shrubs in the drainage channel and together with the loosely compacted peaty soil may be important sites for seed germination. Like *Banksia marginata, Hakea microcarpa* emerged in lower numbers in a habitat in which it does not normally occur. Subsequent high rates of survival were unexpected in *Hakea microcarpa* because of the prevailing drought conditions. Lamont *et al*. (1993) report drought induced mortality in other Proteaceous shrubs, while Myerscough *et al.* (1996) report that wet-heath seedlings establishing in dry heath show high rates of mortality.

Conclusion

The present research indicates that segregation of distribution of two serotinous shrub species (*Banksia marginata* and *Hakea microcarpa*) is primarily mediated by processes at germination and emergence. However, each is also capable of some emergence beyond the limits of their natural dominance when sown there. By contrast, the natural distribution of *Hakea dactyloides* is not reflected in the results of reciprocal sowing. Buried seeds have the capacity to germinate equally well beyond the natural distribution of adult plants as well as within that distribution. This lack of segregation could be explained by either the inability of seeds to be incorporated into the seed bank or differential seedling survival after the first year of growth.

Overall, this study highlights the importance of understanding the early stages of recruitment of serotinous shrub species. Some circumstantial evidence for differential influence of fire on seed viability in plant-stored seed banks has been gathered, but more definitive experimental studies are required. There is, however, clear experimental evidence that seed-bed conditions can act as an environmental sieve at germination and influence species distributions. The suggestion that soil-stored seed dormancy can occur in species that are conventionally described as having plant-stored seed banks points to greater emphasis being placed on understanding the fates of dispersed seed prior to establishment.

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