POST-FIRE LITTER MICROSITES: SAFE FOR SEEDS, UNSAFE FOR SEEDLINGS[1]

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Abstract. We explored the effect of post-fire microsites on seed and seedling distribution and hence their potential role in community restoration. A summer wildfire and control burn in a sclerophyll shrubland in mediterranean Australia produced mosaics of physically and chemically contrasting microsites of litter and sand. Most seeds (>75%) of all species released from the burnt canopies fell, or were redispersed by wind, into the litter patches after both fires. Data on microsite characteristics and wind exposure (fire intensity), height of fruits, time of release, and seed properties were required to interpret relative distribution between the litter and sand patches.

Seeds remained equally viable (up to 100%) over summer–autumn in the litter and sand and had equally high rates and levels (up to 100%) of subsequent winter germination. However, seedlings were 2–3 times less likely to survive in the litter and survivors were 35% smaller than those in the sand by the end of the first summer. *Banksia hookeriana* was particularly vulnerable to microsite properties, whereas the needle-leaved *Hakea polyanthema* showed only minor responses. Pre-summer thinning of seedlings in the litter increased survival of the remainder by 2 times and size of the survivors by 31%.

The fire-sensitive, small-seeded *B. hookeriana* had 17 times more seeds in the backburn litter than the resprouting, larger-seeded *B. attenuata,* which more than compensated for its 3 times greater seedling mortality levels over the dry summer. Recruitment of species prone to density-dependent mortality in the litter was enhanced by the retention of some seeds in the sand where competition for water was minimal, as indicated by the 2.2 times greater stomal conductance of their seedlings in early summer.

Key words: Banksia; competition for water vs. nutrients or light; drought; field trial; fire in sclerophyll scrub; germination; Hakea; seed and seedling distribution after fire; seed dispersal; seed size; serotiny; survival in litter vs. sand patches.

INTRODUCTION

Synchronized release of canopy-stored seeds after fire is a major device for ensuring recruitment of seedlings of many trees and shrubs in Australia, South Africa, and North America (O'Dowd and Gill 1984, Lamont et al. 1991). Most seedlings arise from litter/charcoal patches around obstacles, under canopies, and in depressions (Enright and Lamont 1989). Past studies on the role of favorable microsites have either been based on seed placement in artificially created patches (Harper et al. 1965, Evans and Young 1970, Hamrick and Lee 1987), casting uncertainty about the ecological significance of the results; or their existence inferred through the identification of clumps of soil-stored seeds or seedlings (Thompson 1986, Fowler 1988). Some authors concluded that genets of some species may be "safer" (more likely to survive) in high-density litter/ash patches than in low-density bare patches (Loneragan and Loneragan 1964, Evans and Young 1970, Fowler 1988), while others have shown the reverse

(Goldberg and Werner 1983, Winn 1985). If differential distribution between patch types occurs, actual abiotic conditions under which seedlings establish will be different from random samples of the site. The intensity of interactions and pattern of mortality between species will also be different, ultimately affecting community structure and composition. Thus, careful attention to the ecological implications of post-fire patches (microsites) is warranted.

We report on the effects of a wildfire, and a backburn started on the same day to stop the spread of the wildfire, on seed distribution and viability, and seedling distribution, mortality, and growth, in a sclerophyll shrubland in mediterranean southwestern Australia. Since there have been no previous attempts to describe properties of post-fire litter and bare-soil patches, special attention was given to this aspect. It was expected that the backburn would produce quite different patch effects than the wildfire (Hobbs and Atkins 1988). This would be similar to the effects of fires at different seasons but with the advantage of avoiding the problems of differential granivory and exposure over time (Bond 1984, Cowling and Lamont 1987). Our earlier work 60 km south of the current study site indicated most seedlings were distributed in the litter patches formed after spring and autumn fires (Enright and Lamont

1989). The spatial distribution and fate of both seeds and seedlings was the focus of this study.

Most seeds released belonged to *Banksia attenuata* R. Br. (Proteaceae), a broad-leaved, large-seeded, fire-tolerant shrub that grows to 1.5 m high; *B. hookeriana* Meissner, a broad-leaved, small-seeded, fire-sensitive shrub, height to 2.5 m; *Hakea polyanthema* Diels (Proteaceae), a needle-leaved, moderately large-seeded, fire-sensitive shrub, height to 1.2 m; and *Petrophile drummondii* Benth. (Proteaceae), a needle-leaved, very small-seeded, fire-sensitive shrub, height to 1.0 m. Most attention was given to the first three species, as they contributed most to the structure of the vegetation and were consistently present in all patch types. We tested the following hypotheses:

1) The physical and chemical composition and availability of microsites for seeds depends on the type of fire;

2) More seeds accumulate in litter (rough surface) than in bare sand (smooth surface) patches (Mortimer 1974), the extent depending on the type of fire (Enright and Lamont 1989) and species attributes (Bond 1988);

3) Seeds are safer in litter than in sand patches (deeper in soil, higher viability, greater rate and level of germination) (Evans and Young 1970, Fowler 1986, Cowling and Lamont 1987, Hamrick and Lee 1987, Zhang and Maun 1990);

4) More seedlings are located in litter patches, the extent depending on seed density, type of patch, and time since germination (Yeaton 1978, Wellington and Noble 1985, Hamrick and Lee 1987, Fowler 1988, Enright and Lamont 1989);

5) Seedlings are safer in the litter patches (greater emergence, lower mortality, higher growth rate) (Evans and Young 1970, Fowler 1986, 1988, Hamrick and Lee 1987, Enright and Lamont 1989);

6) Small-seeded species are more strongly aggregated in litter patches, but more likely to survive in the bare patches (Silvertown 1981, Winn 1985);

7) Seedlings of resprouting species are less likely to survive competition in the litter patches than the nonsprouting species (Frazer and Davis 1988);

8) Competition for water rather than nutrients or light controls the pattern of survival in the various microsites (Evans and Young 1970, Siddiqi et al. 1976, Wellington and Noble 1985, Fowler 1986, Lamont et al. 1989, Reader and Best 1989);

9) Needle-leaved (drought-resistant) species are less affected by microsite availability and properties than are broad-leaved species (Enright and Lamont 1989, 1992).

MATERIALS AND METHODS

Study area and fire types

The study sites were located in Yardonogo Nature Reserve (29°25' S, 114°58' E), 340 km north of Perth near Mount Adams Road, Western Australia. The re-serve is in the most northern section of the Swan Coastal Plain, with deep, infertile aeolian sands of late Tertiary/Pleistocene origin (Playford et al. 1976). Effective rainfall is almost confined to four winter months (Fig. 1) with a mean total of 487 mm at Dongara, 25 km northwest of the study area. Mean maximum temperature for the hottest month (January) is 32.8°C, and minimum temperature for the coolest month (July) is 8.9°C (Cowling and Lamont 1985a). Maximum temperatures >40°C are invariably recorded during December–March (Anonymous 1959). The vegetation is a sclerophyll shrubland, dominated in the 1.5–2.5 m stratum by the geographically restricted *Banksia hookeriana* and geographically widespread *B. attenuata* (Lamont et al. 1989), with patches of *Hakea polyanthema* and *Petrophile drummondii* in the 0–1.5 m stratum and occasional plants of *P. macrostachya, Calothamnus* sp., *Eremaea beaufortioides,* and *Casuarina humilis* (all with canopy-stored seeds), and *Verticordia grandis* and pea species (soil-stored seeds). The last fire was 21 yr ago (stem increment counts, Lamont 1985a).

On 11–12 February 1989 a lightning-initiated fire burnt 1700 ha of the reserve. Its progress to Mount Adams Road was stopped by a 5-ha strip ignited by the Department of Conservation and Land Management on 12 February. As this backburn was patchy not all canopy-held seeds in the *Banksia* spp. were released (Table 1) and it scorched rather than incinerated all leaves (Table 2). There were 10 d after the fires, and before the winter rains began, when winds reached ≥50 km/h (Fig. 1), including gusts of ≥86 km/h on 30 April at Geraldton (the closest meteorological station), 16 km nearer to the coast. At both sites and the unburnt control at their boundary, all open fruits on 10 representative plants of the four main species were inspected for the presence of seeds 4 mo after the fires. Seeds were dissected from 50 follicles or cones and their condition noted (intact, aborted, or eaten) and the means used to convert total seeds to intact seeds remaining per infructescence.

Patch description and seed distribution

May 1989 was the first month after the fire with effective rain and temperatures below 15°C (Fig. 1), both required for germination of the study species (Cowling and Lamont 1987). A field trial (described in *Seed attributes and viability,* below) showed no germination occurred before the May rains. In the laboratory, germination at 15°C commenced after 2 wk and was completed in 6 wk (Enright and Lamont 1989). On 13 June, after allowing for 6 wk of effective rain, we ran five transects of 10 × 0.15 m through each of the wildfire and backburn stands. Each was begun in an accessible bare patch 10–15 m from the previous transect and ran north–south. We removed all loose soil and debris by scraping an open hand (0.15 m wide) across the soil surface to a depth of 10–20 mm, depending on the uppermost location of the surface root

mat (Low and Lamont 1990). The boundary of each patch of litter (dark humic soil with much debris, Fig. 2) and sand (pale coarse sand grains with little debris) was noted on the measuring tape, and the litter and sand samples were placed in separate bags. The debris was separated from the soil by shaking in a 2-mm mesh sieve. The material retained by the sieve was washed and examined for all seeds, germinants (only radicle exposed), and emerged seedlings (exposed green cotyledons). These were identified to species and the embryos dissected from all seeds—those shrivelled, brown, and/or papery were considered non-viable. A search of the debris was made for damaged seeds or husks, which would indicate the activity of post-dispersal granivores (rodents, parrots).

The debris from each patch type per transect was dried at 65°C for 5 d, separated into leaves, fruits, and stems, and weighed. The associated soil was dried at 105°C for 24 h, weighed, tamped down in a measuring cylinder, and its volume noted for bulk density. Subsamples of ≈ 10 g were heated at 500°C for 3 h to estimate organic matter content. Total N was determined on 2-g subsamples by Kjeldahl digestion and titration; total P and K were determined on 0.5-g subsamples by digestion with a volumetric mixture of concentrated acids (10 $HNO_3 : 2$ $H_2SO_4 : 1$ $HClO_4$) fol-

FIG. 2. (A) The study site 2 wk after the wildfire showing dead *Banksia hookeriana* plants, ≈ 1.7 m high, with open cones and fallen seeds (dark points, arrowed) among the litter patches. (B) Litter patch, ≈ 300 mm long, 11 wk after the wildfire, showing numerous seedlings of *Hakea polyanthema* beginning to emerge from the debris after the opening winter rains 2 wk before. Note the distinct boundary from the surrounding sand and distribution of seedlings throughout the patch.

lowed by molybdenum blue colorimetry and flame photometry, respectively. Shading by the overstory was gauged with a forest densiometer held at a height of 0.1 m in the middle of 10 patches of the four microsite types.

Seed *location* (number in the litter or sand patches per square metre of transect) and seed *density* (number per square metre of litter or sand) were based on all potential propagules (seeds + germinants + seedlings). Germination *level* was based on the number of germinants compared with viable propagules (ungerminated viable seeds + germinants + seedlings). Germination *rate* was based on (emerged) seedlings
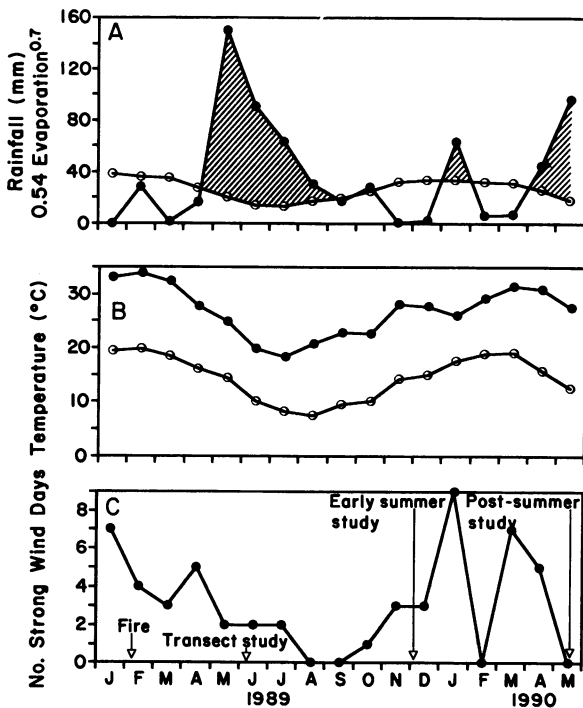

FIG. 1. Weather conditions at Geraldton, 60 km northwest of study site, throughout the study period. (A) Monthly rainfall (●), 0.54 evaporation$^{0.7}$ (O). Effective rainfall (the difference between these two values, Prescott's formula) is shaded. (B) Mean monthly maximum (●) and minimum (O) air temperatures. (C) Number of days per month when winds reached ≥ 50 km/h.
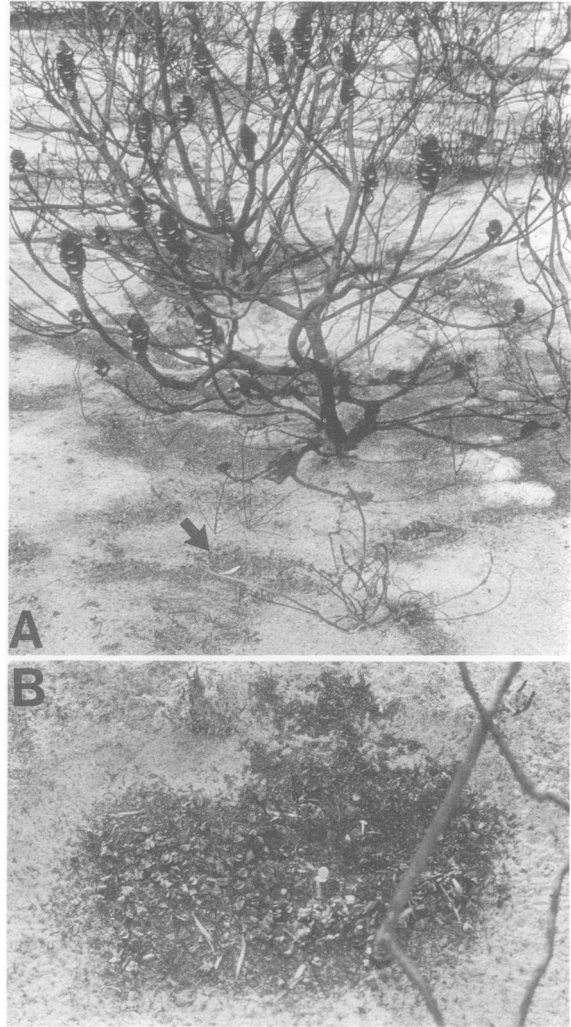
TABLE 1. Number of intact seeds remaining per infructescence 4 mo after adjacent intense (wildfire) and mild (backburn) fires compared with the unburnt control at Yardonogo Nature Reserve. Results are $\bar{X} \pm 1$ SD for all dispersal units on 10 plants each of the four species at each of the three sites.

Species*	Infructescence	Fire treatment		
		Unburnt	Wildfire	Backburn
Banksia attenuata	Cone	11.7 ± 5.7	0.2 ± 0.2	3.1 ± 4.6
B. hookeriana	Cone	12.2 ± 5.5	0.1 ± 0.1	3.3 ± 5.5
Hakea polyanthema	Follicle	2.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Petrophile drummondii	Cone	31.5 ± 21.5	1.4 ± 1.0	1.3 ± 0.8

* The first three species listed contributed most to the vegetative structure and were consistently present in all patch types.

compared with viable propagules; fast-germinating seeds would have existed as seedlings rather than as germinants or viable seeds at the time of harvest. The depth of seed burial per patch type was assessed on 100 seedlings of each of the three main species by measuring the length of the hypocotyl, as the cotyledons flatten flush with the soil surface on emergence (Brits 1987). Initial seedling location and density were based on germinants + seedlings.

Seed attributes and viability

A random sample of 30 intact seeds of the four major species was obtained from the post-fire seed release study (Table 1). They were weighed and their terminal velocity, as an index of air lift for ease of redistribution, assessed by dropping them individually from a height of 4.5 m in still air. Two observers gauged their time to fall with digital chronometers (accurate to 0.01 s). Since the wings of the *Banksia* spp. are readily dislodged (as would occur during redistribution by wind), the wings were removed, the seeds reweighed, and terminal velocity reassessed.

Additional intact seeds of the two *Banksia* spp. were divided into nine batches of 25 seeds each. Three batches of each species were retained in the laboratory at 23 ± 1°C, three were placed in white fiber glass mesh bags and covered with surface sand/litter to a depth of 15 ± 5 mm in the field trial area, Curtin University, over summer (mid-January to late April 1990) to simulate litter patch conditions prior to winter, and three were left on the soil surface in mesh bags. As no seeds had germinated by the end of this period, all were placed in moistened petri dishes at 15°C, and their germination after 6 wk used as an index of their viability (Cowling and Lamont 1987).

Seedling survival, stomatal conductance, growth, and response to thinning

Twenty litter patches were examined adjacent to the common boundary of the two fire types on 19 September 1989, when further germination was unlikely but before the dry season had started (Fig. 1). They were selected by walking in a northerly direction in each fire type and counting seedlings of the three major species (*B. attenuata, B. hookeriana, H. polyanthema*) in the 10 successive patches encountered. An additional 20

plots were treated in a similar way, except seedlings of the three species were thinned, so that each species remained well represented but the distance apart of adjacent plants was increased from 30 ± 10 mm ($\bar{X} \pm$ 1 SD) to 100 ± 20 mm (this mainly required removal of *B. hookeriana* seedlings). Fifty seedlings of each species in the surrounding sandy areas were marked with wire pegs.

On 7 December 1989 (start of summer) and 7 May 1990 (end of autumn), the numbers of plants of each species still alive in all the treatments were counted. The competitive ability of each species was gauged by its relative survival in the (high-density) litter patches compared with the (low-density) sand, while an attempt was made to identify the limiting resource for which they were competing (nutrients, light, or water). As an index of moisture availability, stomatal resistance of unshaded mature leaves was measured on three seedlings of each species in three replicate patches of the four microsite types. Readings were taken at 1000–1200 in the wildfire site (cloudless, air temperature 32.0 ± 1.5°C [$\bar{X} \pm$ 1 SD], relative humidity 37%) and 1300–1500 in the backburn site (cloudless 33.5 ± 1.5°C, 33 ± 1%) on 7 December. We used a dynamic diffusion porometer (Mk 3, Delta-T Devices, Burwell, England) and converted the results to stomatal conductance. On 10 May we harvested all living seedlings from the thinned patches, 25 of each species from both sandy areas and 20 ± 5 from five litter patches at both sites. The shoots were dried at 65°C for 3 d and weighed.

Statistical analyses

Where analyses of total species is given, it includes *B. attenuata, B. hookeriana,* and *H. polyanthema* as well as minor species (mostly *Petrophile drummondii* and *P. macrostachya*) in Tables 4 and 7, but only the first three species, in proportion to their presence in the patches, in Tables 8 and 10. Most of the data were suitable for analysis by two-way ANOVA (2 fire types, 2 patch types per fire type, 5 transects [replicates] with patches combined in each). In an attempt to pinpoint the significantly different treatments, we reasoned that the four treatments could also be viewed as randomly rather than dichotomously related since >2 variables actually distinguished each patch type (Peterson 1977), and we submitted the data to Ryan's multiple-range

TABLE 2. Patch dimensions and litter distribution between patches on 13 June 1989, 4 mo after adjacent intense (wildfire) and mild (backburn) fires at Yardonogo Nature Reserve. Results are $\bar{X} \pm 1$ SD for all patches combined in each of five 10 m long by 0.15 m wide transects in each post-fire type. Different superscript letters indicate significant differences between values for each attribute ($P < .05$, Ryan's Q test).

| Attribute | Wildfire | | Backburn | | ANOVA results† | | |
	Litter	Sand	Litter	Sand	Fire	Patch	Inter-action
Patch area (% of transect)	12.6 ± 6.7^b	87.4 ± 6.7^a	67.1 ± 11.2^a	32.9 ± 11.2^b	$\cdots$	$\cdots$	$\cdots$
Patch (intercept) width (m)	0.45 ± 0.21^b	2.56 ± 1.57^a	1.09 ± 0.86^b	0.57 ± 0.34^b	*	***	***
Debris location (g/m² transect)	24.9 ± 22.4^b	7.0 ± 2.0^b	84.0 ± 33.4^a	10.5 ± 4.5^b	**	***	**
Debris concentration (g/m² patch)	193.9 ± 108.8^a	7.9 ± 2.1^b	123.5 ± 34.8^a	31.9 ± 6.4^b	NS	***	NS
Leaf location (% of transect)	48.7 ± 23.1^b	52.4 ± 22.9^b	86.4 ± 9.0^a	11.4 ± 5.3^c	$\cdots$	$\cdots$	$\cdots$
Fruit location (% of transect)	79.2 ± 15.4^a	20.8 ± 15.4^b	90.6 ± 6.3^a	9.3 ± 6.1^b	$\cdots$	$\cdots$	$\cdots$
Stem location (% of transect)	32.5 ± 23.2^b	67.5 ± 23.2^a	76.8 ± 15.9^a	23.2 ± 15.9^b	$\cdots$	$\cdots$	$\cdots$
Leaf/litter (% of dry mass)	8.5 ± 4.6^c	29.3 ± 12.9^b	60.2 ± 10.7^a	56.6 ± 15.0^a	***	NS	*
Fruit/litter (% of dry mass)	87.3 ± 9.0^a	46.8 ± 29.5^b	24.4 ± 17.2^c	19.4 ± 5.9^c	***	***	**
Stem/litter (% of dry mass)	4.1 ± 4.5^b	23.7 ± 12.5^a	11.2 ± 3.6^{ab}	24.0 ± 14.2^a	NS	**	NS

† Results of the two-way ANOVA (2 fires × 2 patches × 5 reps) are shown by NS = not significant, * $P < .05$, ** $P < .01$, *** $P < .001$. Since % of transect data were not independent within fire types, only a one-way ANOVA was applied, with $P < .001$ in each case.

tests (Day and Quinn 1989). Normality of the data was checked and they were transformed as necessary, including arcsine treatment of percentages, before analysis. Results are given as means ± 1 standard deviation before transformation. Yates' correction was applied to the number of seedlings alive in each of the two patch types prior to χ^2 analysis. Since the 10 litter patches in this section were selected randomly, the numbers of survivors were summed to enable comparisons with the total survivors among the 50 tagged seedlings of each species assigned randomly in the sand.

RESULTS

Fire effects and patch descriptions

The fruits and cones released 74–100% of their seeds compared with the unburnt infructescences in response to both fire types (Table 1). Only the two banksias showed less than complete seed drop after the backburn. Seed release was negligible in the unburnt stand.

Litter patches were small and of very limited extent compared with the bare sand in the wildfire site, but covered twice the area of the sand in the backburn (Table 2). Most debris (80–90%) was located in the litter patches. Debris concentration in the litter patches was 4 times that in the backburn sand and 24 times that in the wildfire sand. The wildfire litter patches contained most of the woody fruit parts (80% of the total), whereas most of the stem fragments remained in the sand patches (68%). Litter patches accounted for

most of the dead leaves, fruits, and stem fragments (77–91%) in the backburn site. Most of the wildfire litter was made up of woody fruit parts (87%), whereas most of the backburn litter was composed of scorched leaves (60%).

There was a much greater concentration of loose surface soil in the litter patches, especially in the wildfire site (Table 3). The high humus and charcoal levels resulted in much higher levels of organic matter and lower ex situ bulk density in the soil beneath litter patches, with a tendency for the differences to be less marked in the backburn sites. Total nitrogen, phosphorus, and potassium concentrations were much higher in the litter patches (2–10 times those of the sand), especially in the wildfire site. There was little shading over any of the patches, although it was higher in the backburn (even after leaf drop from scorched plants was complete) and higher over both litter patch types (Table 3).

Seed distribution and attributes

For each species most of the seeds released by the fires (73–91%) were located in litter patches (Table 4). This was due to the much greater density of seeds in wildfire litter than in sand (from 18 times for B. attenuata up to 41 times for Petrophile spp.), and to both the larger patch area and greater density of seeds in backburn litter than in sand (from NS for Petrophile spp. up to 16 times for H. polyanthema). Overall, seed density was 36 times greater in the wildfire litter than

TABLE 3. Physical and chemical properties of loose soil (upper 10–20 mm) scraped from the litter and sand patches, and shading received from overhanging plants. Same transects and analyses as in Table 2, except shading is based on 10 replicates.

Attribute	Wildfire		Backburn		ANOVA results		
	Litter	Sand	Litter	Sand	Fire	Patch	Inter-action
Loose soil volume (L/m^2 patch)	6.75 ± 1.96[a]	1.89 ± 0.33[b]	2.69 ± 0.08[b]	1.63 ± 0.42[b]	***	***	**
Bulk density (ex situ) (kg/L)	0.71 ± 0.14[b]	1.35 ± 0.17[a]	0.85 ± 0.07[b]	1.15 ± 0.14[a]	NS	***	**
Organic matter (%)	11.7 ± 4.2[a]	1.9 ± 0.5[d]	7.1 ± 1.6[b]	3.4 ± 0.5[c]	NS	***	**
Nitrogen (mg/g)	3.3 ± 1.9[a]	0.3 ± 0.1[b]	2.1 ± 1.0[a]	0.5 ± 0.1[b]	NS	***	NS
Phosphorus (µg/g)	24.7 ± 3.1[a]	1.3 ± 1.0[b]	5.0 ± 3.1[b]	1.9 ± 1.2[b]	***	***	***
Potassium (µg/g)	28.4 ± 14.2[a]	6.7 ± 4.5[b]	14.1 ± 8.6[b]	6.1 ± 1.7[b]	NS	**	NS
Shading (%)	7.3 ± 4.6[ab]	0.5 ± 1.3[c]	9.5 ± 7.2[a]	4.4 ± 4.4[b]	*	***	NS

* $P < .05$, ** $P < .01$, *** $P < .001$, NS = not significant.

sand, and 5 times greater in the backburn litter than sand. Seed viability of each species was high (35–100%) in all patch types, but it was highest in the backburn patches. There was no evidence of post-dispersal granivory: no damaged seeds or husks were located in the soil or debris collected from the transects; no granivorous animals (mice, parrots) and few tracks or scratchings were observed. For all species, burial was greatest in the wildfire litter patches (2.5 times that in the other three patch types). The length of hypocotyls showed there was a tendency for *H. polyanthema* seeds to be buried deepest and *B. attenuata* seeds to be shallowest, especially in the sand and backburn litter patches.

The mass of *B. attenuata* seeds was twice that of *B. hookeriana* and 11 times that of *P. drummondii* (Table 5). Terminal velocity was in the same rank order of species as seed mass, though not as variable, except that of *H. polyanthema* was less than expected from values for the other three species. Removing the wings increased the terminal velocity in both banksias by 15%. The height of seed release in the field was greatest for *B. hookeriana* and least for *P. drummondii*.

Seeds of both *Banksia* spp. exposed on the soil surface over summer–autumn lost 2–3 times the viability of those buried (Table 6). The buried seeds retained 75% of the viability of seeds kept in the laboratory. There was no granivory, but air temperatures exceeded 40°C several days during that period, implying lethal soil temperatures may have been reached (Cowling and Lamont 1987).

TABLE 4. Distribution of seeds between patches, plus seed depth and viability, for *Banksia attenuata* (Ba), *B. hookeriana* (Bh), and *Hakea polyanthema* (Hp). Totals include these plus other species (mainly *Petrophile drummondii*). Same transects and analyses as in Table 2.

Attribute	Species	Wildfire		Backburn		ANOVA results		
		Litter	Sand	Litter	Sand	Fire	Patch	Inter-action
Seed location (no./m^2 of transect)	Ba	8.0 ± 5.9[a]	2.9 ± 2.6[ab]	5.9 ± 3.9[a]	0.3 ± 0.4[b]	NS	**	NS
	Bh	35.2 ± 26.4[a]	6.0 ± 4.4[b]	52.9 ± 22.1[a]	5.1 ± 3.7[b]	NS	***	NS
	Hp	4.1 ± 4.0[b]	1.2 ± 0.7[b]	18.4 ± 13.8[a]	0.7 ± 0.7[b]	*	***	*
	Other	82.1 ± 85.2[a]	11.1 ± 13.1[b]	5.6 ± 3.1[b]	1.5 ± 1.4[b]	**	*	NS
	Total	129.5 ± 120.5[a]	21.2 ± 18.1[b]	82.8 ± 39.5[a]	7.5 ± 4.8[b]	NS	***	NS
Seed density (no./m^2 of patch)	Ba	41.7 ± 15.5[a]	2.3 ± 2.1[b]	5.4 ± 3.1[b]	0.5 ± 0.6[b]	***	***	***
	Bh	188.6 ± 105.2[a]	4.8 ± 3.9[c]	53.7 ± 12.4[b]	12.9 ± 9.1[c]	*	***	**
	Hp	19.9 ± 12.6[a]	0.9 ± 0.5[b]	17.6 ± 9.5[a]	1.1 ± 1.2[b]	NS	***	NS
	Other	369.4 ± 267.0[a]	9.0 ± 11.1[b]	6.0 ± 2.7[b]	2.2 ± 2.2[b]	***	***	**
	Total	619.5 ± 373.1[a]	17.0 ± 15.6[b]	82.7 ± 22.0[b]	16.6 ± 7.2[b]	**	***	**
Viable seeds (%)	Ba	83.4 ± 17.0[a]	83.2 ± 21.2[a]	95.5 ± 9.1[a]	100.0 ± 0.0[a]	NS	NS	NS
	Bh	77.7 ± 4.4[a]	68.7 ± 19.9[a]	85.8 ± 13.3[a]	85.7 ± 21.1[a]	*	NS	NS
	Hp	100.0 ± 0.0[a]	100.0 ± 0.0[a]	76.9 ± 4.8[ab]	50.0 ± 50.0[b]	***	NS	NS
	Other	35.0 ± 24.0[a]	40.5 ± 35.4[a]	60.9 ± 9.9[a]	82.2 ± 16.8[a]	*	NS	NS
	Total	54.0 ± 18.0[a]	57.2 ± 18.7[a]	83.1 ± 8.7[a]	81.4 ± 16.6[a]	**	NS	NS
Depth of viable seeds (mm)	Ba	11.4 ± 7.0[a]	2.0 ± 0.9[b]	4.6 ± 1.5[b]	2.3 ± 0.8[b]	***	**	***
	Bh	13.3 ± 1.9[a]	5.1 ± 4.3[b]	4.3 ± 1.6[b]	5.4 ± 4.7[b]	**	***	***
	Hp	11.9 ± 9.0[a]	6.9 ± 5.1[b]	8.1 ± 3.7[b]	6.3 ± 2.4[b]	***	NS	NS
	Total	12.6 ± 8.6[a]	4.6 ± 4.4[b]	5.6 ± 3.0[b]	5.0 ± 3.7[b]	***	***	***

* $P < .05$, ** $P < .01$, *** $P < .001$, NS = not significant.

TABLE 5. Mass, terminal velocity (inverse of wind dispersability), and actual (potential) release height of seeds of *Banksia attenuata, B. hookeriana, Hakea polyanthema*, and *Petrophile drummondii*. Results are $\bar{X} \pm 1$ SD for 30 seeds and 10 plants. Different superscript letters indicate significant differences within columns ($P < .05$, Ryan's Q test).

Species	Seed appendages	Seed mass (mg)	Terminal velocity (m/s)	Actual field release height (m)
B. attenuata	+ wings	120 ± 15[a]	3.49 ± 0.55[b]	1.1 ± 0.4[b]
	− wings	112 ± 15[b]	4.08 ± 0.36[a]	
B. hookeriana	+ wings	59 ± 11[d]	2.83 ± 0.38[d]	1.6 ± 0.6[a]
	− wings	55 ± 10[e]	3.18 ± 0.21[c]	
H. polyanthema	+ wings	73 ± 13[c]	2.06 ± 0.25[e]	0.8 ± 0.3[c]
P. drummondii	+ hairs	11 ± 2[f]	1.60 ± 0.17[f]	0.7 ± 0.3[c]

Germination and seedling distribution

Almost all viable seeds had germinated by early winter (Table 7). There was a tendency for slightly higher germination levels in the litter for some species and fire types, but the overall differences were not significant. There was some evidence of faster germination rates in the litter patches on the basis of emerged seedlings at the time of harvest, but this was only significant for *B. hookeriana*. Most young seedlings of all species were located in the litter patches, varying from 74% of the total for *B. attenuata* in the wildfire to 98% for *H. polyanthema* in the backburn; overall, it was 85% for the wildfire and 93% for the backburn. There was also a marked difference in density, with 41 times more seedlings per unit area in the wildfire litter and 5 times more in the backburn litter. There was no marked herbivory of any of the study plants, although selective grazing of grasses by kangaroos was widespread in the wildfire site.

Seedling survival, stomatal conductance, growth and response to thinning

No seedling mortality was observed over winter–spring. Seedling death by early summer was only significant in the unthinned litter patches, especially the banksias in the wildfire litter (Table 8). There was considerable mortality by autumn at all microsites, especially the banksias in the backburn litter. Mortality was negligible for *H. polyanthema* at all microsites over summer. Over the entire period the banksias declined much more than the hakea. Survival of all species was

from NS to 4.7 times greater in the wildfire than backburn patches, and NS to 5 times greater in the sand than litter patches. Overall, almost twice as many seedlings survived on a percentage basis in the wildfire sand than in litter, and almost 4 times as many in the backburn sand than in litter. Survival in the thinned litter patches was either intermediate between the control litter and sand or not significantly different from the sand.

Stomatal conductance, as an index of transpiration, was usually lowest in *H. polyanthema* and highest in *B. hookeriana* (Table 9). It was always higher in the sand patches than in the litter. The difference was most marked between *B. hookeriana* in the backburn sand and litter (7 times) and least between *H. polyanthema* in the backburn sand and litter (no significant difference).

By autumn, the shoot mass of the hakea was greater than the banksias at all microsites, especially relative to *B. hookeriana* in the backburn litter (Table 10). There was no consistent difference in size between fire types, but plants of each species were 28–71% larger in the sand than in litter. Overall, plants were 46% larger in the wildfire sand and 63% larger in the backburn sand than in the corresponding control litter. The shoot mass of the thinned plants was intermediate between the control litter and sand, and always NS from either. Overall, thinned backburn plants were 59% larger than unthinned backburn plants.

DISCUSSION

Generally, the summer fires had three direct outcomes: they produced mobile ash, fine charcoal, incompletely combusted litter, fallen leaves and fruit parts; they resulted in the release of buoyant canopy-stored seeds from most species; and they exposed fixed obstacles (stumps, fallen branches, coarse charcoal, cones, and local mounds and depressions produced by animals before the fire). Recurrent windy days over the ensuing autumn would have redistributed the mobile debris, loose soil particles, and seeds simultaneously against the obstacles and into the depressions (Fig. 1; Mortimer 1974, Bond 1988). Thus a mosaic of rough surfaces, i.e., litter patches (sink), and smooth surfaces,

TABLE 6. Percentage viability of seeds of *Banksia attenuata* and *B. hookeriana* following three treatments: retention in the laboratory (control), placement on the soil surface, or burial over summer–autumn (January–April). Values are $\bar{X} \pm 1$ SD for three replicates of 25 seeds each. Different superscript letters indicate significant differences between treatments ($P < .05$, Ryan's Q test).

Species	Control	Exposed	Buried
	Percentage of seeds viable		
B. attenuata	90.7 ± 6.1[a]	33.3 ± 6.1[c]	67.7 ± 2.3[b]
B. hookeriana	90.1 ± 8.3[a]	25.8 ± 3.6[c]	67.8 ± 1.9[b]

TABLE 7. Seed germination and initial distribution of seedlings between patches on 13 June 1989 for *Banksia attenuata* (Ba), *B. hookeriana* (Bh), *Hakea polyanthema* (Hp). Totals include these plus other species (mainly *Petrophile drummondii*). Same transects and analyses as in Table 2.

| Attribute | Species | Wildfire | | Backburn | | ANOVA results | | |
		Litter	Sand	Litter	Sand	Fire	Patch	Inter-action
Germination level (seedlings and germinants as % of viable propagules)	Ba	100.0 ± 0.0^a	100.0 ± 0.0^a	95.8 ± 8.3^a	50.0 ± 50.0^b	*	NS	NS
	Bh	95.8 ± 3.9^a	82.5 ± 24.2^a	94.1 ± 7.9^a	92.5 ± 11.2^a	NS	NS	NS
	Hp	100.0 ± 0.0^a	100.0 ± 0.0^a	95.0 ± 6.8^a	100.0 ± 0.0^a	NS	NS	NS
	Other	91.3 ± 12.2^a	76.0 ± 33.6^a	100.0 ± 0.0^a	100.0 ± 0.0^a	NS	NS	NS
	Total	95.9 ± 2.7^a	86.8 ± 9.3^a	95.1 ± 6.8^a	94.0 ± 9.7^a	NS	NS	NS
Germination rate (seedlings as % of viable propagules)	Ba	35.6 ± 16.9^a	25.0 ± 43.3^a	16.9 ± 11.7^a	0.0 ± 0.0^a	NS	NS	NS
	Bh	28.0 ± 16.2^a	10.3 ± 14.2^a	24.2 ± 7.5^a	10.0 ± 22.4^a	NS	*	NS
	Hp	85.0 ± 20.5^a	60.0 ± 50.0^a	53.9 ± 32.6^a	50.0 ± 70.7^a	NS	NS	NS
	Other	82.5 ± 16.8^a	76.0 ± 33.6^a	96.7 ± 7.5^a	100.0 ± 0.0^a	NS	NS	NS
	Total	50.8 ± 16.0^a	34.5 ± 22.3^a	34.8 ± 6.7^a	29.0 ± 28.3^a	NS	NS	NS
Initial seedling location (no./ m² of transect)	Ba	7.1 ± 5.8^a	2.5 ± 2.5^{ab}	5.5 ± 3.9^a	0.1 ± 0.3^b	NS	**	NS
	Bh	26.0 ± 19.5^a	3.7 ± 3.6^b	43.6 ± 20.7^a	3.7 ± 2.6^b	NS	***	NS
	Hp	4.1 ± 4.0^b	1.2 ± 0.7^b	14.4 ± 12.0^a	0.3 ± 0.4^b	NS	***	*
	Other	13.5 ± 9.3^a	1.3 ± 0.7^b	3.6 ± 2.6^b	1.2 ± 1.2^b	*	***	NS
	Total	50.7 ± 33.2^a	8.8 ± 4.9^b	67.1 ± 38.5^a	5.3 ± 2.6^b	NS	***	NS
Initial seedling density (no./ m² of patch)	Ba	36.4 ± 17.5^a	2.0 ± 2.0^b	5.0 ± 3.1^b	0.2 ± 0.4^b	***	***	**
	Bh	138.5 ± 73.9^a	3.0 ± 3.1^c	44.0 ± 14.5^b	10.2 ± 8.9^c	NS	***	**
	Hp	19.9 ± 12.6^a	0.9 ± 0.5^b	13.5 ± 8.6^a	0.4 ± 0.6^b	NS	***	NS
	Other	89.4 ± 92.7^a	1.0 ± 0.5^b	3.8 ± 2.1^b	1.8 ± 2.0^b	**	**	**
	Total	284.1 ± 165.8^a	6.9 ± 4.3^c	66.3 ± 22.4^b	12.7 ± 7.2^c	**	***	**

* $P < .05$, ** $P < .01$, *** $P < .001$, NS = not significant.

i.e., sand patches (source), was built up by the start of the winter rains. Wind would not play such an important role in seed redistribution or creation of the patches in the backburn site, since it was much less exposed and most of the seeds and dead leaves falling from poorly combusted plants remained beneath the canopy.

Differences between species in depth of burial and relative distribution between the litter and sand microsites could be accounted for by the varying thickness of loose soil (depressions in the wildfire site were most-completely filled), asynchronous seed release (*Hakea* was almost immediate while *Banksia* was delayed, Cowling and Lamont 1985*b*), and different redispersal opportunities. The terminal velocity should have indicated the readiness with which the seed was redistributed by the wind after landing, since it is an index of uplift. However, it was of limited explanatory value because shape (tendency to tumble) and mass (overcoming inertia) are probably just as important, as well as height and time of release, wind exposure, microsite availability, and the texture of the surface on first landing (Mortimer 1974, Platt and Weiss 1977, Rabinowitz and Rapp 1981, Goldberg and Werner 1983, Lamont 1985*b*, Bond 1988). Only trials with post-fire debris and marked seeds in fruits, and study of their post-dispersal attributes, would reveal the relative importance of these constraints in fully explaining patch formation and seed distribution.

Seeds in the litter patches retained equally high viabilities as those in the sand, attributable to low exposure to summer heat through burial by loose sand and litter and absence of granivory (Table 6; Bond 1984, Cowling and Lamont 1987). The extra shading in the backburn site may have accounted for the higher seed viability in litter/sand patches compared with the wildfire site. The slightly higher germination levels and seedling emergence rates also showed that the litter patch types were as safe or safer for the viable seeds as the sand patches. This gave some support for previous studies showing greater viability (Enright and Lamont 1989) and germination (Fowler 1986) in nonbare patches, although emergence has sometimes been suppressed by thick litter (Goldberg and Werner 1983, Fowler 1988). Unlike the results for seeds released onto unburnt litter (Hamrick and Lee 1987), the post-fire litter did not deter seeds from reaching the soil (although some seeds of *Petrophile* did catch in the foliage). Burial was too shallow, even in the wildfire litter, and the seeds too large for emergence to be a problem (contrast Winn 1985). There was no tendency for seeds to be safer in the wildfire than backburn litter patches.

The combination of efficient redispersal of seeds into post-fire litter patches and their relative safeness resulted in an overall initial seedling density over 40 times that in the sand for the wildfire site and 5 times that for the backburn. Initial seed density was by far the main determinant of this difference. However,

TABLE 8. Percentage of seedling survival for *Banksia attenuata* (Ba), *B. hookeriana* (Bh), and *Hakea polyanthema* (Hp) within patches during (a) the initial 6 mo (winter to early summer, i.e., June–December), (b) the next 6 mo (early summer to late autumn, i.e., December–May) of the previous survivors, and (c) over the entire period (June–May).†

Species		Time interval	Wildfire Litter Control	Wildfire Litter Thinned	Wildfire Sand	Backburn Litter Control	Backburn Litter Thinned	Backburn Sand
Ba		*n*	90	46	50	112	38	50
	a)	Initial 6 mo	60	96***	100***	88	100^{NS}	98^{NS}
	b)	Next 6 mo	61	77^{NS}	68^{NS}	25	50*	62***
	c)	Overall	37	74***	68***	22	50**	62***
Bh		*n*	369	66	50	419	84	50
	a)	Initial 6 mo	43	100***	100***	77	89*	94*
	b)	Next 6 mo	77	58**	80^{NS}	9	39***	68***
	c)	Overall	33	58***	80***	7	35***	64***
Hp		*n*	115	36	50	89	40	50
	a)	Initial 6 mo	81	100*	98**	79	100**	96*
	b)	Next 6 mo	100	100^{NS}	94^{NS}	99	93^{NS}	100^{NS}
	c)	Overall	81	100*	92^{NS}	78	93^{NS}	96**
Total		*n*	574	148	150	620	162	150
	a)	Initial 6 mo	53	99***	99***	81	94***	96***
	b)	Next 6 mo	81	74^{NS}	81^{NS}	25	56***	77***
	c)	Overall	43	73***	80*** (78)	20	52***	74*** (65)

Three-way ANOVA treating overall values (%) per species above as replicates, i.e., 3 spp. × 2 fires × 3 patch types (no three-way interactions possible):

Species	Fire	Patch	Interactions
***	**	***	NS

* $P < .05$, ** $P < .01$, *** $P < .001$, NS = not significant.

† Ten litter patches were thinned in September and 10 were left intact in each post-fire area. The initial number of seedlings recorded (*n*) is also given. Superscripts refer to level of significance for χ^2 analysis between (a) control vs. thinned and (b) control vs. sand, performed on the raw data for each fire type. Same notation as in Table 2. Values in parentheses (in Total section) are corrected for the actual numbers of seedlings of each species in the sand initially (Table 7).

overall seedling mortality levels in the litter by the end of the first summer were almost 3 times that in the sand. Marked early (pre-summer) mortality in the wildfire litter was probably due to the unusually dry spring (Fig. 1) and earlier depletion of surface soil water in the presence of much higher seedling densities, less leaf mulch, and less shading from the overstory than in the backburn (Evans and Young 1970, Bradstock and Myerscough 1981, Goldberg and Werner 1983, Wellington and Noble 1985, Zammit and Westoby 1987, Lamont et al. 1989). The overriding influence of competition for water (rather than the possibility of its greater evaporation) was confirmed by negligible death in the thinned litter patches at this time. Nutrient availability can be dismissed as limiting survival since

the levels in the wildfire litter patches were much higher than at the other microsites and species in these genera do not demand soil nutrients in the first year as their seed nutrient contents are unusually high (Siddiqi et al. 1976, Barrow 1977, Mitchell and Allsopp 1984). The survivors were also smaller in the litter patches. This is the usual density-dependent effect of competition (Obied et al. 1967), in this case for water (Lamont et al. 1989) rather than for nutrients or light (Reader and Best 1989)—there was minor overlapping of the vertically oriented leaves by early summer, but no species overtopped others and they usually received full sunlight at least 90% of the time (Table 3).

We conclude that post-fire litter microsites are unsafe for seedlings relative to sand patches. This appar-

TABLE 9. Stomatal conductance (mm/s) of seedlings of three major species within patches in early summer. Data for the wildfire area obtained during mid-morning and for the backburn during mid-afternoon of the same day (7 Dec). Results are $\bar{X} \pm 1$ SD for nine plants. Significant differences based on *t* tests within each fire type. Same notation as in Table 2.

Species	Wildfire Litter	Wildfire Sand	Backburn Litter	Backburn Sand
Banksia attenuata	1.6 ± 1.2	3.7 ± 1.4***	0.8 ± 0.5	2.0 ± 1.0**
B. hookeriana	3.3 ± 1.9	4.9 ± 1.0*	0.6 ± 0.2	4.2 ± 2.1***
Hakea polyanthema	1.2 ± 0.6	3.0 ± 1.0***	1.2 ± 0.9	1.7 ± 0.8^{NS}

* $P < .05$, ** $P < .01$, *** $P < .001$, NS = not significant.

TABLE 10. Shoot dry mass (in grams) of *Banksia attenuata* (Ba), *B. hookeriana* (Bh), and *Hakea polyanthema* (Hp) seedlings within patches. Results are $\bar{X} \pm 1$ SD for 20 ± 5 plants. Total means are based on the proportion of each species at each microsite type. Same notation as Table 2.

| | Wildfire | | | Backburn | |
| | Litter | | | Litter | |
Species	Control	Thinned	Sand	Control	Thinned
Ba	1.04 ± 0.38[b]	1.27 ± 0.62[b]	1.71 ± 0.76[ab]	1.27 ± 0.50[b]	1.67 ± 0.93[ab]
Bh	1.25 ± 0.99[ab]	1.10 ± 0.76[ab]	1.60 ± 0.80[a]	0.85 ± 0.34[b]	1.24 ± 0.80[ab]
Hp	1.50 ± 0.56[b]	2.04 ± 1.02[ab]	2.53 ± 1.08[a]	1.58 ± 0.59[b]	2.08 ± 0.59[ab]
Total	1.28 ± 0.83[bc]	1.39 ± 0.85[abc]	1.87 ± 0.95[a]	0.98 ± 0.43[c]	1.56 ± 0.84[ab]

* $P < .05$, *** $P < .001$, NS = not significant.

ent contradiction with our earlier preliminary work (Enright and Lamont 1989) was due to the emphasis we gave to microsite contribution to total recruits without knowledge of their relative seed store. Here, wildfire litter patches continued to harbor the greatest proportion of seedlings after 12 mo, but this was not true for the backburn. We predict that with time the sand patches would make an increasing contribution to survivors at both sites. The ameliorating effects of the thinning treatments confirmed that the litter effect was not due to deleterious abiotic attributes, but to intensified competition for water induced by the high seedling densities there. Fowler (1986) also concluded that the relative safeness of a microsite depended on its effect on water availability. This underlines the need to take abiotic site factors and seedling interactions into account at the same time in order to correctly interpret subsequent community structure and composition.

With negligible effective rain and high temperatures over the summer there was a marked decline in survival at all microsites, attributable to low water availability generally (the climate factor). Superimposed on this was marked additional mortality in the backburn (the fire factor), due to heightened competition between the greater proportion of pre-summer surviving seedlings and probably adults not killed by the fire (Lamont and Bergl 1991), especially in litter patches since these tended to occur around existing plants. The exception was the needle-leaved hakea, which not only showed moderate stomatal conductance levels with no significant differences between the backburn litter and sand microsites, but also negligible mortality over summer in any of the patch types following some pre-summer deaths in the litter patches. With its faster emergence and growth rates (drought avoidance) and needle-leaves with strong xeromorphy (drought tolerance) compared with the broad-leaved banksias, *H. polyanthema* was largely insensitive to patch type in terms of its overall survival but its size was affected (contrast Winn [1985] and Fowler [1986] who found negligible differences between species).

B. hookeriana is killed by fire and thus solely dependent on seeds for its regeneration. Without substantially increasing hazards for the seeds, "escape" into competition-free sand patches promotes early sur-

vival and growth of its seedlings. Swamping of the litter patches with its seeds is a two-edged sword: it exacerbates self-thinning (especially in the backburn) but ensures some of the survivors are *B. hookeriana*. As an alternative strategy, the fire-sensitive hakea produced fewer larger seeds, which yielded highly competitive seedlings in the litter. By resprouting after fire, *B. attenuata* has been able to bypass the adaptive imperative to maximize the canopy seed store (Enright and Lamont 1989). This species released a few large seeds, which were less efficiently distributed into litter patches than the smaller seeds of *B. hookeriana*. *B. attenuata* seedlings were 3 times more likely to survive than *B. hookeriana* in the backburn litter but were no different in the sand. This is limited support for smaller-seeded species surviving better in less competitive bare patches (Silvertown 1981, Winn 1985). Thus, the relatively high density of post-summer seedlings of *B. hookeriana* in the four patch types was attributable to high initial seed density and not superior physiological or morphological attributes. This contrasts with Frazer and Davis (1988), who not only found seedlings of the fire-sensitive *Ceanothus megacarpus* survived summer better than the resprouting *Rhus laurina,* but were able to attribute it to greater drought tolerance. The equivalent pair here is the needle-leaved *H. polyanthema* and the broad-leaved *B. attenuata*.

In our study the interaction between properties of the post-fire patches, the reproductive biology of the component species, and the competitiveness of their seedlings affected the relative safeness of the microsites for seedlings independent of that for seeds. Though of restricted geographical distribution and a poor competitor (Lamont et al. 1989), *B. hookeriana* is able to take advantage of the varying mosaics of microsites after fire via its large canopy seed store, which ensures substantial representation in all patch types. Extreme self-thinning in the backburn litter microsites is preceded by less-efficient dispersal of seeds into them. This tends to buffer the effects of contrasting fire events, as concluded by Enright and Lamont (1989) for fires in different seasons.

TABLE 10. Continued.

Backburn	ANOVA results		
Sand	Fire	Patch	Interaction
1.97 ± 1.26^a	*	***	NS
1.45 ± 1.35^{ab}	NS	*	NS
2.32 ± 0.97^a	NS	***	NS
1.60 ± 1.27^{ab}	NS	***	NS

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