

Plant coexistence in coastal heaths: Habitat segregation in the post-fire environment

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Abstract Previous studies of heaths on Pleistocene coastal sands showed consistent variation in patterns of floristic composition between areas on ridges and slopes but not within them. A large wild-fire that swept this system provided an opportunity to observe temporal processes in habitat segregation of species. Ridges and slopes were found to differ in species richness of seedlings in 0.0625 m² quadrats and there was no evidence that the species richness in the two habitats was converging over 3 years. This suggests that initially these processes differ in space between the two habitats with more species in the wet heath being packed into a smaller area than in the dry heath. Seed-banks of species did not saturate available space for recruitment in either habitat, but seedling densities differed asymmetrically between habitats across two pairs of species studied. Experimental manipulation of seeds among habitats also showed distinct differences in establishment and survival among representative species from different habitats. The presence of seed-banks of wet-heath species in dry heath suggested that recruitment of their seedlings may occur there, but experiments showed that seedlings that arise from them do not survive there. Conversely, although no seed-bank of either dry-heath species studied was found in wet heath, our manipulations showed that their seedlings could grow there. Thus, superficially, physiological tolerance appeared to limit regeneration of wet-heath species in dry heath. However, there appeared to be no physiological limit for dry-heath plants to survive in wet heath. This paper shows that segregation of species may operate at either of two stages of the life cycle: at dispersal when safe sites for establishment are required, and at recruitment after seedlings have established. These findings highlight the importance of the regeneration niche in structuring community composition in coastal heaths, and contrast with traditional explanations of species segregation invoking physiological tolerance and competition at later life-history stages.

Key words: fire, floristic composition, physiological tolerance, plant coexistence, seed-banks.

INTRODUCTION

Previous studies of heaths on Pleistocene coastal sands showed consistent variation in patterns of floristic composition, between areas on ridges and slopes over a wide range of spatial scales (Myerscough *et al.* 1995). The processes that produce these vegetation patterns are likely to be strongly influenced by episodic fires because many of the species have pulsed recruitment of either seedlings or resprouted shoots in the post-fire environment (e.g. Bradstock & Myerscough 1981; Enright & Lamont 1989). A large wild-fire in January 1991 that followed preliminary studies of community patterns pro-

vided an opportunity to observe temporal processes and to test hypotheses about habitat segregation of species.

In this paper we describe post-fire patterns in water tables, seed-banks and species richness, between ridges and slopes (i.e. between habitats) and among transects and plots (i.e. within habitats). Seed-banks might be expected to vary between and within habitats, but species richness for plants regenerating from seed and for those resprouting was expected to be similar among habitats, given that similar patterns of species richness were detected in the two habitats before the fire (Myerscough *et al.* 1995).

Approximately 60 days after the fire, we experimentally manipulated a representative range of species from the two major habitats by sowing their seed between and within habitats to test hypotheses that (i) habitats were unsaturated with these seed, and (ii) species differ in

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their germination, seedling establishment and survival between and within habitats in space and time. The species used were two resprouting shrubs (*Banksia aemula* and *Banksia oblongifolia*) and two obligate seeding shrubs (*Acacia ulicifolia* and *Dillwynia floribunda*). Both *B. aemula* and *A. ulicifolia* are usually found in dry heath whereas *B. oblongifolia* and *D. floribunda* are mainly confined to wet heath (Myerscough & Carolin 1986; Myerscough *et al.* 1995). Under controlled glasshouse conditions we also tested the response of seedlings to water table variation, which could not be controlled in the field.

METHODS

Water table and soil heterogeneity

Water tables were measured at regular intervals over 2 years starting in June 1991. The central two of the four transects described in Myerscough *et al.* (1995) were selected and in each transect plots on two ridges (dry heath) and two slopes (wet heath) were sampled (Fig. 1). Both the transects and plots were selected on the basis of being representative of the floristic variation found on the land system (see Myerscough *et al.* 1995); within each of these plots, measuring 5 × 30 m, four shafts were sunk. Polythene pipes (8 cm diameter and up to 2 m long) were then inserted into the holes and depth to water tables measured using a tape-measure inserted into the pipe. Data were analysed using a nested ANOVA model where physiography (ridges and slopes) was a fixed factor, transects were nested within physiography and plots were nested within physiography and transects. The relationship between water table depths and monthly

rainfall at Williamstown (20 km south of the study area) was assessed via correlation analysis.

Soil organic content was measured from the A horizon (to 10 cm) 30 months after the wild-fire. Four samples of 500 cm² volume were removed from each of the eight plots. Organic content was determined by loss on ignition at 400°C.

Seed-banks

Seed-bank differences were not directly measured; rather an attempt was made to assess differences in seed-banks between habitats for a selected range of species. Direct comparison of differences in seedlings establishing between habitats is confounded by differences in germinability and post-germination survival between habitats. Instead, the proportion of sown seeds that successfully established was used to estimate the natural seed-bank, in unsown areas, as a function of natural seedling establishment. This approach makes two assumptions; first, that the added seeds behave in the same way as the natural seed-bank and, second, that seedling recruitment is not already saturated by an abundant natural seed-bank.

Seeds of the two legumes were collected in December of 1990 when they were ripe but before they were shed from their fruit. They were heat-treated in the laboratory before being sown in the field. Seeds of *B. aemula* and *B. oblongifolia* were collected from woody fruit after they had opened following the fire in January 1991. Sets of approximately equal weights of seeds of the two species of *Banksia* were prepared (*B. aemula* five seeds; *B. oblongifolia* 20 seeds) and then each sown into a disturbed soil surface in a quadrat (25 × 25 cm), three of which were randomly positioned in each plot (30 × 5 m). Sets of seeds of *A. ulicifolia* (13 seeds) and *D. floribunda* (50 seeds) were similarly prepared and sown. Two ridge plots (dry heath) and two slope plots (wet heath) were selected within each of two transects (Fig. 1). The influence of predators was controlled by caging quadrats with stiff plastic mesh with 6 mm holes. Thus the habitat factor was heath type (fixed factor), and the within-habitat factors were transects (random factor), and plots nested within transects and heath type. A nested ANOVA was used to analyse the relative difference in establishment. Data were log-transformed before analysis.

Post-fire recruitment of seedlings and resprouting plants

Species richness of seedlings arising from natural seed-banks, and species richness of resprouting plants were measured in three quadrats (25 × 25 cm) randomly positioned in each plot (30 × 5 m). There were four ridge plots and four slope plots as outlined previously. Species richness was measured at regular intervals during 3 years. Data for each type of species richness were analysed by four-factor ANOVA for each observation through time.

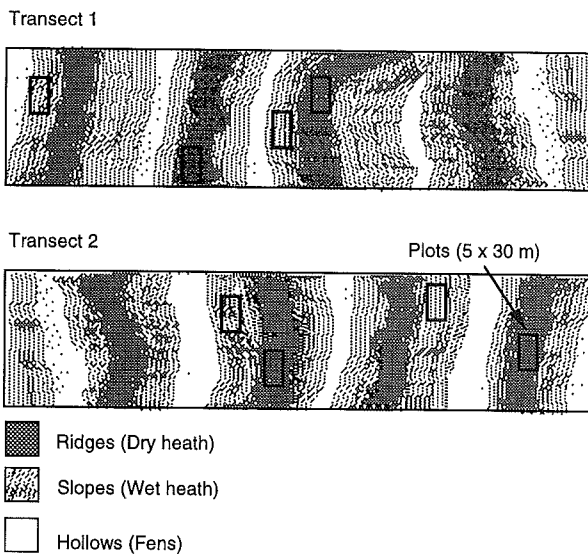


Fig. 1. Diagrammatic representation of the spatial arrangement of plots in transects and on ridges and slopes.

No attempt was made to incorporate time in the analysis as these observations are not independent of each other.

Post-fire recruitment from seeds sown

Ongoing survival of seedlings was followed from seeds sown as described previously for assessing seed-banks, and number of seedlings was analysed using nested ANOVA.

Glasshouse experiment

A glasshouse experiment was designed to assess indirectly the effect of a falling water table on survival and growth of seedlings of species sown in the field, as water tables could not readily be manipulated in the field. Two dry-heath species (*B. aemula* and *Dillwynia retorta*) and two wet-heath species (*B. oblongifolia* and *D. floribunda*) were sown independently into 2 m columns of soil from ridges (dry heath). Seeds collected for the field experiment were

used in the glasshouse experiment. After seedlings had been established for 3 months, two water table treatments were applied. These treatments mimicked rates of fall and final levels of water tables observed in the field on slopes (wet heath) and on ridges (dry heath) over the first 250 days (see Fig. 2a). Three replicate pots of each species in each of two blocks were treated. After 8 months, seedlings were harvested and their root lengths measured.

RESULTS

Water table and soil heterogeneity

Water tables were consistently lower on ridges (dry heath) than on slopes (wet heath) by about 50 cm (Fig. 2a). Considerable spatial variation in water tables also occurred among plots within transects and physiography, but not among transects (i.e. spatial differences were consistent over the Pleistocene ridge system; Table 1). Two episodes of water table rise and fall occurred over the 2 years and these corresponded to periods of high and low rainfall. Correlations between rainfall over the previous month and water table depth (Fig. 2b) indicate the obvious effect of rainfall on water table rise. Soil loss on ignition correlated with average water table depth (Fig. 3) indicating higher soil organic content in areas susceptible to waterlogging.

Seed-banks

Based on the establishment success of a known sown seed-bank and the numbers of seedlings found in unsown

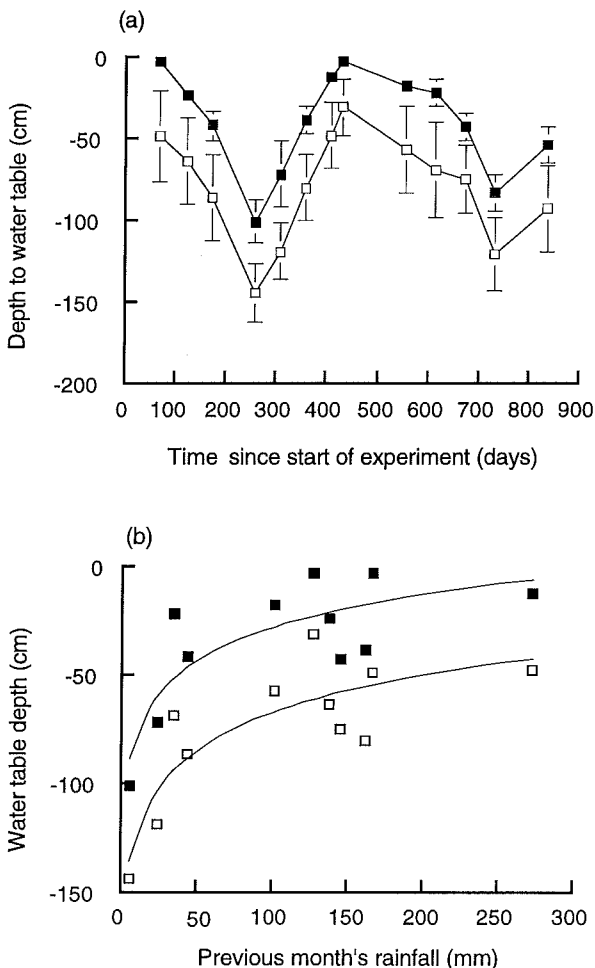


Fig. 2. (a) Mean depth (\pm SE) to water table on slopes (wet heath; \blacksquare) and ridges (dry heath; \square). (b) Correlation of depth to water table and the previous month's rainfall. Dry heath, $y = 51.8 \log x - 132.1$, $r^2 = 0.67$; wet heath $y = 58.7 \log x - 185.3$, $r^2 = 0.72$.

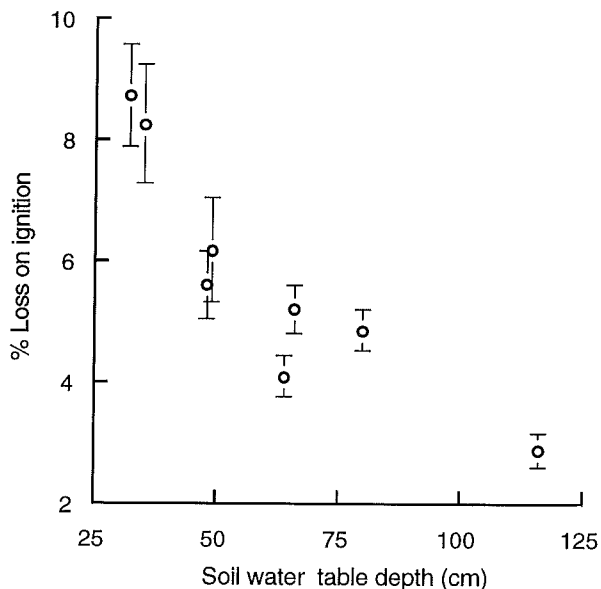


Fig. 3. Correlation between mean (\pm SE) percentage loss on ignition and water table levels.

Table 1. Summary of ANOVA results for water tables on ridges (dry heath) and slopes (wet heath)

Factor	Time since start of experiment (days)					
	84	171	308	405	555	675
Heath type	*	*	*	*	*	*
Plot (heath type)	**	**	**	**	**	**

Transects have been pooled with plots ($P > 0.25$); * $P < 0.05$; ** $P < 0.001$.

Table 2. Summary of ANOVA results for significant spatial effects on number of species arising from naturally establishing seedlings and resprouting plants

Factor	Time since start of experiment (months)					
	4	Resprouting		4	Seedlings	
		12	24		12	24
Heath (A)	—	***	***	—	—	***
Transects (B)	—	NS	NS	—	—	NS
A × B	*	NS	NS	***	***	NS
C (A × B) plots	***	***	***	***	***	**

NS, not significant; ** $P < 0.01$; *** $P < 0.001$.

areas, the estimated average number of seeds in the soil 6 months after the wild-fire is shown in Fig. 4. This indicates that there were no seed-banks of *B. aemula* and *A. ulicifolia* in the wet heath. Both species of wet-heath seedlings were present in unsown plots on dry heath indicating they can disperse to the dry heath, but their estimated seed-banks were significantly lower than those in the wet heath.

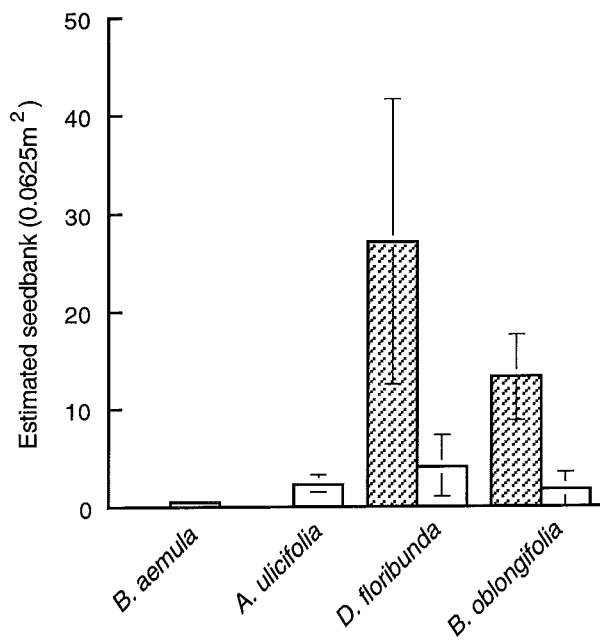


Fig. 4. Estimated mean seed-bank (\pm SE) size in dry-heath (unhatched) and wet-heath (hatched) sites.

Post-fire recruitment of seedlings and resprouting plants

More species of seedlings and resprouting plants were found in the area sampled in wet heath than in dry heath (Fig. 5). These patterns were consistent across the Pleistocene system for resprouting plants (Table 2) and were consistent through time (Fig. 5). However, within the wet heath and the dry heath, plots were significantly different in species richness of seedlings and resprouting plants (Table 2). Differences among plots for numbers of resprouting plants correlate with depth to the water table (Fig. 6), but species richness of seedlings was not as well correlated with water table depth (Fig. 6).

Post-fire recruitment from seeds sown

More seedlings were found in quadrats where seeds were sown versus unsown areas for all species except *D. floribunda* (Fig. 7); that is, the natural seed-bank does not saturate available space for establishment. Seed sown of both wet-heath species showed better establishment on slopes than on the ridges (Fig. 8a–d) and this was consistent over the Pleistocene system as there were no transect effects (Table 3). Few seedlings of the two wet-heath species established on ridges (dry heath), and those that did often died within the first year (Fig. 8b,d). Those seedlings established in the wet heath, however, showed less post-establishment mortality. Some patchy mortality due to the effects of an unknown herbivore was observed at the last sampling for *D. floribunda*. There was also considerable variation in establishment among plots for *B. oblongifolia* (i.e. spatial variation within slopes and ridges; Fig. 8b, Table 3). Initial establishment

differences among plots (4 months) were found to correlate with water table level for the two wet-heath species (Fig. 9). Thereafter, mortality of wet-heath species in the wet heath appeared to be unrelated to water table movements, because this fluctuated to high and low levels during the following year.

In contrast to the wet-heath species, both dry-heath species showed no particular preference for a particular habitat (Table 3, Fig. 8a,c). Some preference for wet-heath habitats may be present for *A. ulicifolia*, but this may not have been detected due to the very low numbers of seedlings that established. Large differences in establishment among plots did not correlate with initial water table conditions as it did for wet-heath species (Fig. 9).

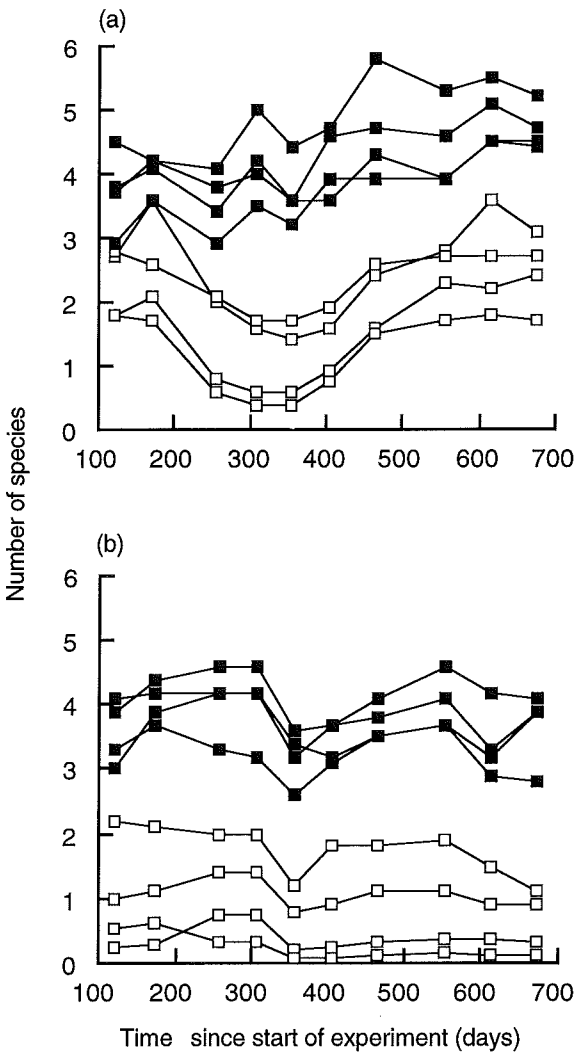


Fig. 5. Mean numbers of post-fire species per 0.0625 m² establishing and surviving in wet-heath (■) and dry-heath (□) areas not sown with seed. (a) Seedlings; (b) resprouting plants from rhizomes, tubers and basal stems.

Glasshouse experiment

Under conditions of falling water tables that mimicked conditions found in the field experiment both legume species showed similar mortality to that shown in the field (i.e. about 40% mortality in the first 6 months). Similarly, both *Banksia* species had low levels of mortality that corresponded to observations in the field during the first 6 months. Root lengths of both legume species were

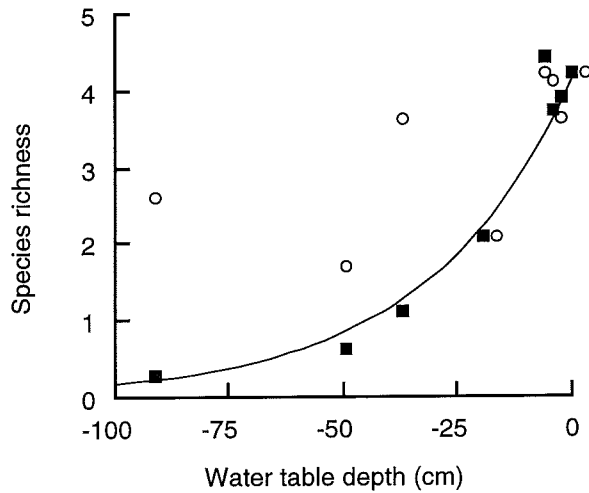


Fig. 6. Correlation between depth to water table and numbers of species per 0.0625 m² of seedlings (○), and of resprouting plants (■) 171 days ($y = 4.12 \times 10^{0.014x}$, $r^2 = 0.97$) after the start of the experiment.

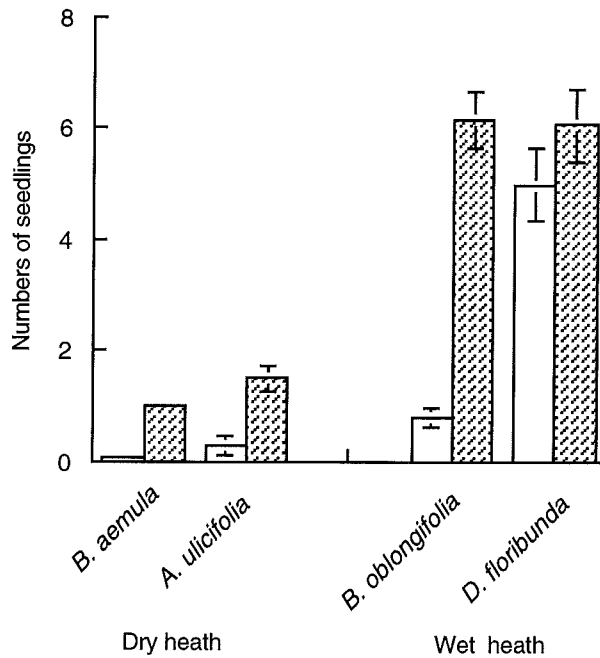


Fig. 7. Mean number (\pm SE) of seedlings per 0.0625 m² establishing in natural habitats from seed sown (hatched) and natural germination (unhatched).

Table 3. Summary of ANOVA results for significant spatial effects

Factor	<i>B. aemula</i>				<i>B. oblongifolia</i>				<i>A. ulicifolia</i>				<i>D. floribunda</i>			
	4	12	24	30	4	12	24	30	4	12	24	30	4	12	24	30
Heath (A)	NS	NS	NS	NS	NS	***	***	***	NS	NS	NS	NS	***	***	***	***
Transects (B)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
A × B	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
C(A × B) plots	**	***	***	**	*	***	***	***	*	*	NS	NS	NS	NS	NS	NS

NS, not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Seed sown onto caged soils.

Table 4. ANOVA for effects of water table on root length

Factor	d.f.	<i>B. aemula</i>		<i>B. oblongifolia</i>		<i>A. ulicifolia</i>		<i>D. floribunda</i>	
		MS	<i>P</i>	MS	<i>P</i>	MS	<i>P</i>	MS	<i>P</i>
Watertable	1	7239	***	1653	*	722	NS	68	NS
Residual	8	101		234		596		51	

NS, not significant; * $P < 0.05$; *** $P < 0.001$.

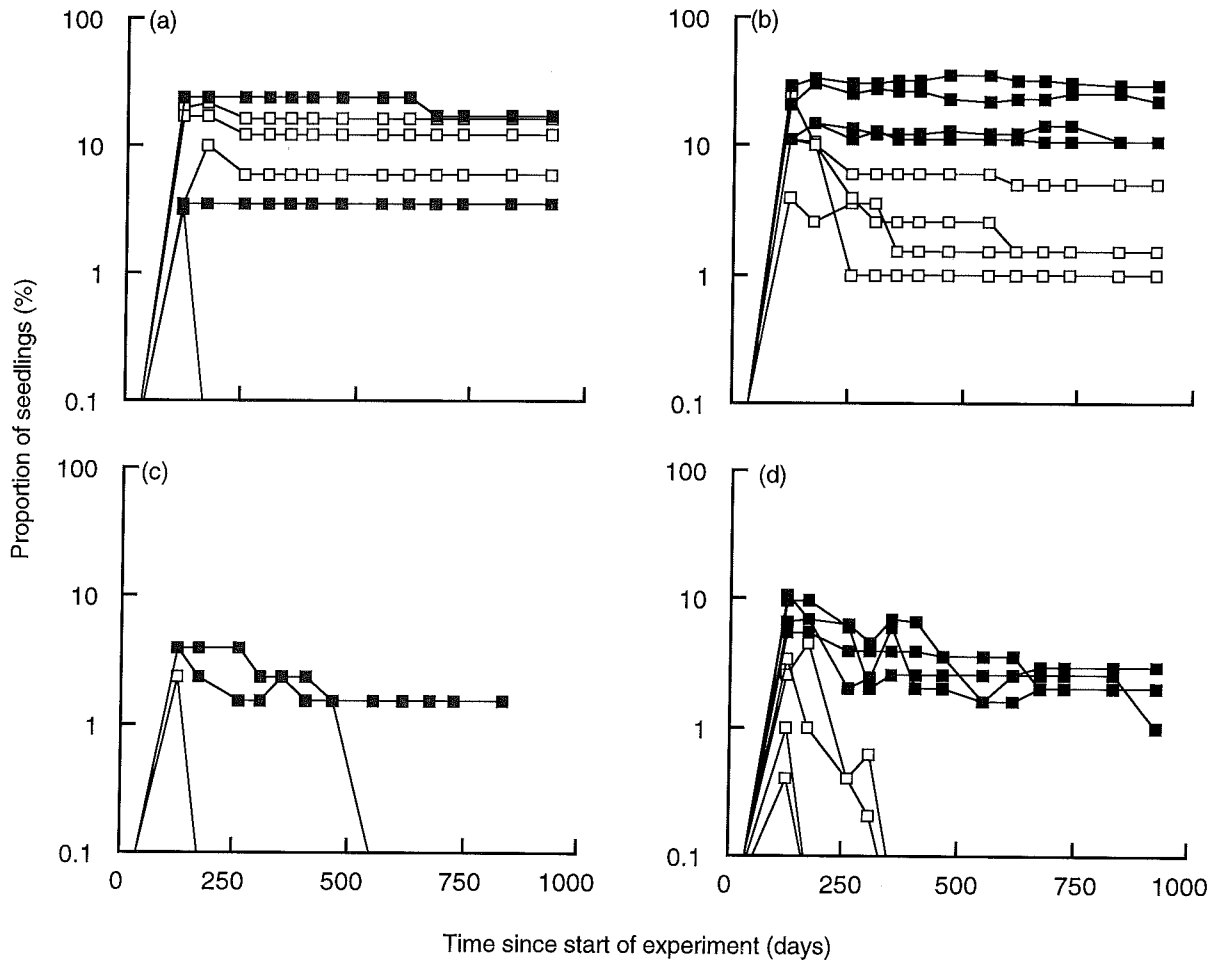


Fig. 8. Mean proportion (as percentage of number of seeds sown) of seedlings per 0.0625 m² establishing and surviving from seed sown in wet heath (■) and dry heath (□). (a) *Banksia aemula*, 5 seeds per replicate; (b) *Banksia oblongifolia*, 20 seeds per replicate; (c) *Acacia ulicifolia*, 13 seeds per replicate; (d) *Dillwynia floribunda*, 50 seeds per replicate.

not significantly different among water table levels (Table 4) but overall they were significantly shorter than the *Banksia* species (Fig. 10). Both *Banksia* species grew significantly longer roots in low water tables (Table 4) but *B. aemula* was able to extend its roots further down the profile than *B. oblongifolia* (Fig. 10).

DISCUSSION

Seed-banks

The two assumptions upon which our method of assessing native seed-banks is based require some examination. First, the equivalence of the sown seed-bank to the natural seed-bank was not tested. However, sown seeds from the two *Banksia* species belong to exactly the same cohort as those in the natural seed-bank. In contrast the natural legume seed-bank is characterized by cohorts of differing ages (e.g. Auld 1986). This, together with the artificial heat treatment of seeds sown, may affect the reliability of estimating seed-banks from seedlings recruited from sown seeds. Nevertheless, the enhanced seedling recruitment observed with the addition of sown seed indicates that there were more sites available for seedling recruitment than the native seed-bank filled. It is possible that where species' seed-banks are insufficient to saturate sites for seedling recruitment the variable seedling recruitment hypothesis may apply to coexistence in a spatial sense in this system rather than in a temporal sense that may apply in other systems (cf. Hubbell & Foster 1986).

The expectation, however, that the distribution of seed-banks was random between habitats has to be

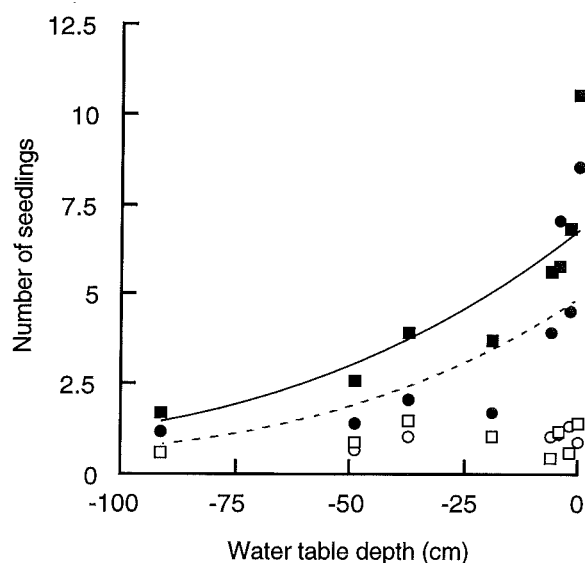


Fig. 9. Correlation in June 1991 between water table and numbers of seedlings arising from seed sown: (■) *Banksia oblongifolia* ($y = 6.84 + 10^{0.007x}$, $r^2 = 0.85$); (●) *Dillwynia floribunda* ($y = 4.9 \times 10^{0.008x}$, $r^2 = 0.69$); (□) *Banksia aemula*; (○) *Acacia ulicifolia*.

rejected for the two pairs of species examined. Seed-banks of dry-heath species were never found in the wet heath while wet-heath seed-banks were depressed in the dry heath. Hypotheses that account for these differences may include patterns of dispersal, predation of seeds, and microsite disturbance and interspecific competition.

Post-fire recruitment of seedlings and resprouting plants

The expectation of similar species richness in seedlings and resprouting plants in the two habitats after fire has to be rejected. The numbers of seedling species and resprouting plants were higher in wet heath than in the dry heath. The considerable plot variation for resprouting plants within heath types also correlated with depth to water table, although it would appear that moisture conditions in the post-fire environment do not explain differences in the numbers of seedling species among plots. Mortality of seedlings was low during the 3 years, in contrast to mortality of seedlings in the Kwongan of Western Australia (Cowling & Lamont 1987).

The contrast between pre- and post-fire species packing may be explained by spatial scales in the regenerative process differing between the two habitats or its rate differing between them. As there was no evidence that the species richness in the two habitats was converging during the period of observation we suggest that the process differs in scale between the two habitats, with more species in the wet heath per unit area than in the dry heath. The study of the pre-fire condition of the area (Myerscough *et al.* 1995) used a much larger unit sampling area than this study. The habitats may eventually

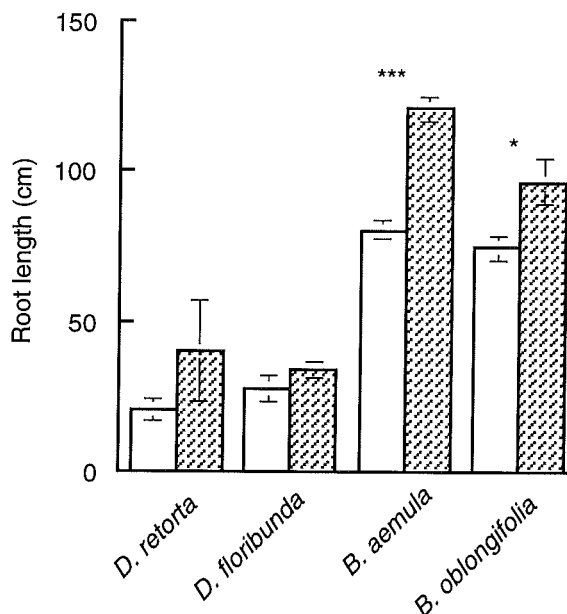


Fig. 10. Mean root lengths (\pm SE) of seedlings grown under low water tables (hatched) and higher water tables (unhatched). Significant differences indicated *** $P < 0.001$, * $P < 0.05$.

converge in species richness at the scales examined in this study, but only after more than 3 years when competition may be of greater importance in regulating species packing. Alternatively, the finer grain of species packing in wet heath may persist between fires.

Post-fire recruitment from seeds sown

Differences in recruitment from seed sown and natural recruitment were marked for all species except one legume in its own habitat where seedling density approaches habitat saturation. Clear asymmetric habitat preferences were shown for recruitment from seeds sown into differing habitats.

Wet-heath species appear to be able to disperse into dry heath and germinate there as they have seed-banks in the dry heath, but the converse is not so. We suggest that seeds of dry-heath species are unable to find safe sites for germination in the wet heath. Experimental manipulations of sown seed support the general observations of poor post-fire regeneration and seedling establishment in the dry heath. As with species richness there were also significant plot differences in establishment and survival. For the wet-heath species, this could be correlated to depth to the water table during the germination and establishment phase, but no such correlation was evident for the dry-heath species. This is partially supported by glasshouse experiments on water table levels where dry-heath species were able to extend their roots deeper than congeneric wet-heath species. This result differs from the mechanism proposed by Siddiqi and Carolin (1975) who suggested that competition excludes *B. oblongifolia* from the dry heath by the congener *B. aemula*.

The reason for lack of dry-heath species in wet heath when they can grow there requires experimentation to examine factors that provide safe sites for germination and establishment. Clearly, however, there appears to be no physiological inhibition for dry-heath seedling growth in the wet heath if they are established there. Glasshouse experiments to confirm this pattern were conducted and the results will be reported elsewhere.

While moisture conditions appear to influence early establishment, seedling survival in either dry-heath or wet-heath species during 3 years of observation was not correlated with water table conditions. This suggests, along with within-habitat variation, that other local site factors such as disturbance and predation may be important and not only mediate between-habitat differences but also influence coexistence within habitats.

In conclusion, the work presented in this paper shows that spatial segregation of species may operate at either of two stages of the life cycle. The first of these is dispersal of seeds, in that seeds of species in one habitat may not reach the other habitat even though they are capable of germinating there and seedlings arising survive there, as in *B. aemula* and *A. ulicifolia*. The second is the survival of seedlings, in that seeds may reach the other

habitat but seedlings arising from them may not survive there, as in *B. oblongifolia* and *D. floribunda* in the experiment described here. These findings highlight the importance of the 'regeneration niche' (Grubb 1977) in structuring plant community composition in coastal heaths, and contrast with traditional explanations of species segregation invoking physiological tolerance and competition at later life-history stages.

Similar points may be made about within-habitat segregation of species to explain their coexistence. In this paper, we have shown there is considerable variation of within-habitat recruitment of seedlings and, at the earlier stage in the life cycle, seed-banks are insufficient to fill all spaces available for successful recruitment of seedlings. In short, within habitats dispersal and recruitment are spatially variable at the plot scale, but structuring mechanisms, such as predation, disturbance and competition, operating at this scale, require further field studies.

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