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Population structure and reproductive status of two *Banksia* shrubs at various times after fire

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Abstract

Populations of the obligate-seeder, *Banksia ericifolia,* were even-aged. Seedling recruitment occurred only after fire. Mean genet size (height + canopy diameter; H + D) increased progressively with elapsed time since fire in stands last burnt 2–23 years before 1981. Populations of a co-occurring resprouter, *B. oblongifolia,* were mixed-aged. Genet size varied significantly between stands, but this variation was not explained by regressions of H + D on years since fire. In addition *B. oblongifolia* seedlings were recruited both after fire and in patches of heath unburnt for 16 years.

Most flower and seed production in *B. oblongifolia* occurred in the stands last burnt less than 10 years previously. More than 30% of genets had not produced cones since the last fire, irrespective of how many years had elapsed. In contrast, few *B. ericifolia* genets had produced cones five years after fire, but by 16 years after fire nearly 100% had. Overall, about 51% of *B. ericifolia* inflorescences and about 28% of *B. oblongifolia* inflorescences set seed. The number of seeds in seed-bearing cones was not significantly different between species.

Resprouting *B. oblongifolia* genets began flowering sooner after fire, but *B. ericifolia* subsequently overtook them in accumulating a bank of serotinous seeds. In the stand unburnt for 23 years the largest *B. ericifolia* genets had more than twice as many cones as the largest co-occurring *B. oblongifolia.* However, when accumulated cone production was compared for genets of equal H + D over all stands, there was no difference between species.

Introduction

There have been two general approaches to ecological studies of fire effects on vegetation. Community ecologists have monitored regeneration of species assemblages after single fires in Australia (Hill & Read, 1984; Purdie & Slatyer, 1976; Siddiqi *et al.,* 1976; Specht *et al.,* 1958), or studied floristic changes by sampling from communities of known ages (Bell & Koch, 1980; Russell & Parsons, 1978). On the other hand population biologists have examined the effects of fire on population structure (Ashton, 1976; Griffin & Friedel, 1984), seedling recruitment (Bradstock & Myerscough, 1981; Scalan & O'Rourke, 1982) and flowering (Gill & Ingwersen, 1976; Pyke, 1983). A recent volume summarises these and other aspects of the nature, impact and management of fires in the Australian biota (Gill *et al.,* 1981).

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Here we compare the population characteristics, in relation to time elapsed since fire, of two co-occurring *Banksia* (Proteaceae) shrub species common in the fire-prone scrublands of the Sydney Basin. *Banksia ericifolia* L.f. is an obligate-seeder. Individuals (genets) are killed by fire and so depend entirely on successfully recruiting seedlings for the persistence of lineages. Genets are single stemmed and can be up to 5 m tall. Ericoid leaves are arranged in a roughly spherical, continuous canopy, which covers up to 8 m^2 at maturity. In contrast, *B. oblongifolia* Cav. resprouts from a lignotuber after fire. In this species there are two levels of demographic response to fire: the mortality and recruitment of genets (lignotubers) and the mortality and recruitment of ramets (resprouting stems) on each genet. Individual shrubs seldom grow taller than 2 m in the heathlands of the Sydney Basin. However their canopies, made up of discontinuous clusters of large serrate leaves, may span up to 5 m^2. Both of these *Banksia* shrubs produce a variable number of persistent flowering spikes annually, each of which supports 500-2500+ flowers. A single winged seed is stored in each woody follicle, and follicles are clustered along the flowering spike to form a seed-bearing cone retained in the canopy. Seed release occurs mainly after fire ruptures the follicle, a trait known as serotiny.

Our aim in this comparative survey was to investigate how size frequency distributions and reproductive activity changed during the interval between fires in the two species. By choosing two species which are closely related but differ in the fundamental fire-response characteristic of resprouting vs obligate-seeding, we hoped to develop hypotheses about how other aspects of life history are associated with these characteristics.

Study area and methods

All surveys were done during March-August 1981 in the Lambert Peninsula region of Ku-ring-gai Chase National Park (33°55′S, 151°10′E), about 40 km north of Sydney, Australia. This landscape is part of the Hornsby Plateau, a mid-Triassic formation made up of eroded quartz sandstones interspersed with shales: it supports a number of vegetation types (Thomas & Benson, 1985). Shallow soils, some with impeded drainage, support the heath and scrub (sensu Specht, 1981) common on the plateaus of the peninsula. *Banksia ericifolia* and *B. oblongifolia* are common in the heath, scrub and some woodlands of this region (Thomas & Benson, 1985) and they also co-occur in other sandstone scrublands in the Sydney Basin (Siddiqi *et al.,* 1972).

Fire history records (New South Wales National Parks and Wildlife Service; Northern Metropolitan Office) were used to compile maps of all fire boundaries recorded within the Lambert Peninsula (about 70 km^2) between 1943–1980. All areas burnt between 1943 and 1957 had been burnt at least once again after 1958. The oldest scrub stand had been unburnt for 23 years. Areas which were last burnt in 1958, 1965, 1973, 1975 and 1979 were selected to represent a time-since-fire sequence. Their boundaries were validated against aerial photographs taken within a few years of the fires (New South Wales Lands Dept. Cumberland series; 1956, 1960, 1970, 1978). This comparison confirmed the overall reliability of the fire records, but highlighted the patchy nature of some fires. The sizes of suitable study areas varied widely. The 1973 and 1975 fires were confined, and only a small portion of the area burnt in 1958 had not been burnt again. The 1965 and 1979 fires burnt through large areas of the park and substantial areas had not been burnt again. Stands which supported both *B. ericifolia* and *B. oblongifolia* and which were similar in topography and vegetation structure were selected as survey sites (Table 1). We chose stands which were on ridgetops or north facing upper slopes. We avoided areas of excessive exposed rock: most transects had less than 10% exposed rock. We generally avoided stands which supported trees, however scattered trees were present in some restricted sites.

Up to five 30 m transects were randomly positioned in each of these sites. Along each transect we examined all plants rooted within 2 m on either side. We recorded height, two maximum canopy diameters, the number of current (1981) inflorescences, the number of seed-bearing cones and the number of barren, old inflorescence spikes. *Banksia ericifolia* at the site last burnt in 1979 were more abundant, and transects 1 m wide were examined. Current inflorescences were always intact. We found no evidence of destruction by insectivorous birds, as reported by Scott & Black (1981) and McFarland (1985).

We could distinguish entire lignotubers for most *B. oblongifolia* genets. However, when this proved difficult because parts of the lignotuber were buried, or when large lignotubers had rotted out in part, we probed the lignotuber perimeter with a metal spike. It is possible that on a few occasions we incorrectly classified several smaller, separate lignotubers as a single larger lignotuber. We counted the number of attached live and dead ramets on each genet.

We calculated several measures of the size of plants, using

Table 1. The locations and main features of the five surveyed stands in the Lambert Peninsula area (33° 55′S, 151° 10′E) of Ku-ring-gai Chase National Park, New South Wales, Australia.

Age[1]	Map Reference[2]		Fire[3]	Topography	Physiognomy[4]
1979	Hornsby 9130-IV-S	73000-74200N, 35500-35700E	W	plateau-ridgetop	closed heathland
1975	Hornsby 9130-IV-S	77100-77500N, 33500-33800E	C	upper slope N-facing	closed heathland
1973	Broken Bay 9130-I-N	79400-79600N, 41600-41800E	W	ridgetop & NW slopes	closed heath & open woodland
1965	Broken Bay 9139-I-N	79800-82800N, 39300-40700E	W	ridgetop & NE slopes	closed scrub
1958	Monavale 9139-I-S	76000-76600N, 39300-39700E	W	ridgetops N-NE	closed scrub & open woodland

[1] The year the stand last burnt (see Methods)

[2] From New South Wales (Australia) 1:25000 Orthophotomap Series.

[3] W = Wildfire, C = Control.

[4] After Specht (1981).

canopy height, mean canopy diameter, lignotuber area and stem basal area in various combinations. These were all highly intercorrelated (Zammit, 1986). Here we use height plus mean diameter ($H+D$) as a size measure, having found no evidence that other measures were more meaningful. In other perennial species $H+D$ is well correlated with plant age and stem diameter (Crisp & Lange, 1976), and with above ground biomass (Grice, 1984). We also harvested seed-bearing cones from nearby individuals of both species and compared their lengths and seed numbers.

In this survey we followed many other workers by examining populations which had been burnt at different times in the past, and interpreting these results as indicating how one population would behave over time. It is desirable to make explicit the reasoning involved. Strictly, our statistics only test for significant differences between different stands created in different fire-years. Because of the restricted area available for some fire-years, we did not study replicate sites within each fire-year. However, even if we had studied replicate sites for each fire, the difficulty would not have been removed, because the sites burnt in any given year are likely to be a very nonrandom sample from all sites. The problem cannot be solved by means of statistics. It is unavoidably a matter of interpretation whether effects are due to differences between site locations, or to differences in time elapsed since fire. Our approach has been to analyse the results in relation to time since fire, and to regard time elapsed as the likely cause when it seems improbable that such a pattern could arise accidentally from differences among site locations. It should be noted that since both species were sampled at the same sites, differences between species cannot be attributed to between-site effects.

Results

Genet size and reproductive status

Seed-bearing *B. ericifolia* cones were significantly longer than *B. oblongifolia* (12.2±3.8 cm vs 10.2±2.6 cm, $F_{1,29}=7.03$, $p<0.001$), however, there was no difference in seed number per cone (*B. ericifolia* 42±20; *B. oblongifolia* 39±16, $F_{1,29}=0.5$, ns). A direct count of the number of seed-bearing cones per genet therefore provided a nondestructive and comparative index of the number of seeds stored in serotinous cones.

In *B. ericifolia* differences among stands in mean H+D, mean cones accumulated, and mean seed-bearing cones accumulated were well described by linear regressions on years since fire (Figs. 1a, b, c). The distribution of *B. ericifolia* H+D size classes between stands followed the expected pattern for the obligate seeding strategy; a single cohort of seedlings was recruited after fire and a new population of genets established (Fig. 2). Sizes of the members of a cohort were normally distributed, but there was wider variance as populations thinned and reached reproductive maturity (Fig. 2). These patterns support the view that populations of the obligate-seeder, *B. ericifolia,* are even-aged.

Mean H+D for *B. oblongifolia* genets did not increase consistently with time since fire. However stands had different frequency distributions of $H+D$ (Fig. 2) and different means (Fig. 1a), which may be due to different long term fire histories of particular sites. On the other hand mean cones accumulated and mean seed-bearing cones accumu-

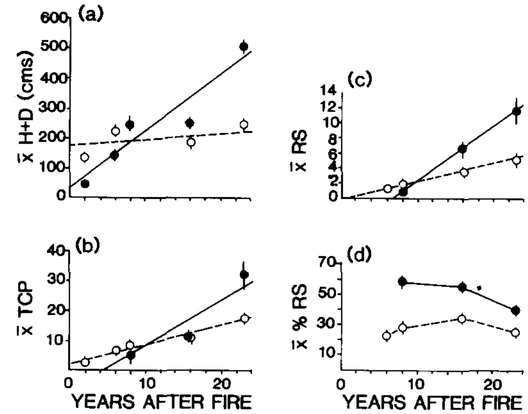

Fig. 1. Linear regressions of H+D and components of reproductive status on years after fire ($\bar{x} \pm se$). (a) Mean H+D of *B. ericifolia* (●) genets increased significantly (H+D=29.33+19.19 yrs; $r^2=0.88$, $p<0.001$). The sizes of *B. oblongifolia* (○) genets were not influenced by the elapsed time since fire ($r^2=0.06$, ns). (b) Mean cones accumulated (TCP) increased significantly in both species (*B. ericifolia:* TCP=−6.22+1.46 yrs; $r^2=0.90$, $p<0.013$; *B. oblongifolia:* TCP=2.29+0.63 yrs; $r^2=0.96$, $p<0.003$). (c) Mean seed-bearing cones accumulated (RS) increased significantly in both species (*B. ericifolia:* RS=−4.59+0.70 yrs; $r^2=0.98$, $p<0.018$; *B. oblongifolia:* RS=0.09+0.21 yrs; $r^2=0.99$, $p<0.004$). (d) The proportion of TCP which produced seed-bearing cones (%RS) declined significantly in *B. ericifolia* (%RS=69.6−1.2 yrs; $r^2=0.90$, $p<0.02$), and did not vary over time in *B. oblongifolia* ($r^2=0.31$, ns).

lated increased progressively with years after fire for *B. oblongifolia* (Figs. 1b, c).

Genet density

The density of *B. oblongifolia* genets did not vary systematically with increasing time since fire. Some transects from the 1965 stand, however, supported about twice as many genets as those from all other transects (Fig. 3). Most of these were from the smallest size class (Fig. 2). In contrast, the density of *B. ericifolia* genets was higher in the 1979 stand (2 years after fire) than in the rest.

Influence of time since fire on reproductive status

Flowering response in 1981 was different between

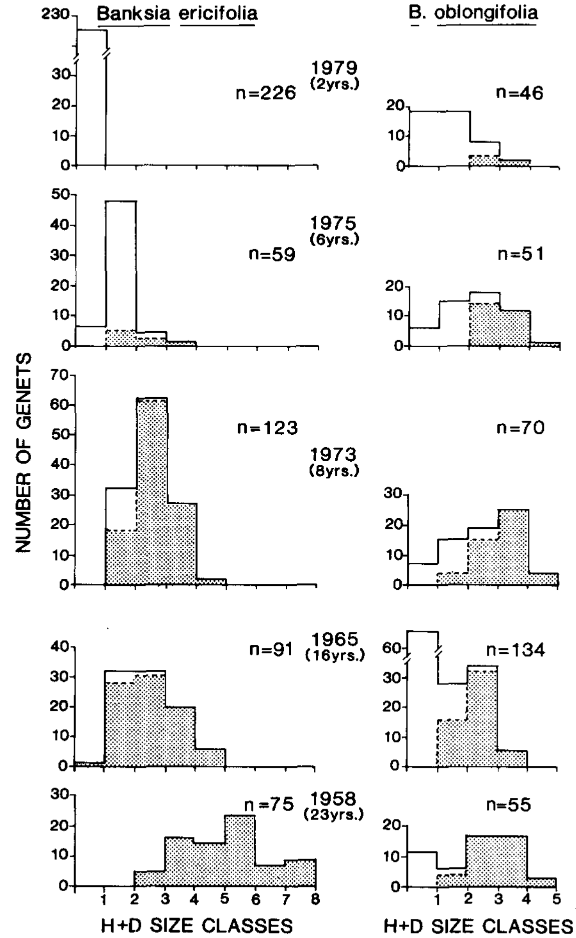

Fig. 2. The size distribution (1.0 m H+D interval) of *B. ericifolia* and *B. oblongifolia* populations from stands last burnt 2–23 years before 1981. The stippled area represents the distribution of reproductive genets. Mean H+D was significantly different between stands for both species: for *B. ericifolia* $X^2=38.3$, for *B. oblongifolia* $X^2=18.8$, $p<0.001$; analysis was by a mixed-model ANOVA which relaxed some requirements for balanced design and equality of variances. The test statistic is a maximum likelihood estimate of the variance components of the general mixed-model ANOVA (BMDP3V; Dixon *et al.,* 1983).

species from the same stand, and also between stands. Current *B. oblongifolia* inflorescences were most abundant in genets from the stand burnt in 1979, while current inflorescence abundance on *B. ericifolia* genets was highest in the stand burnt in 1958 (Table 2). The percentage of genets flowering in 1981, out of all genets which had flowered at some time since the last fire, is given in parentheses

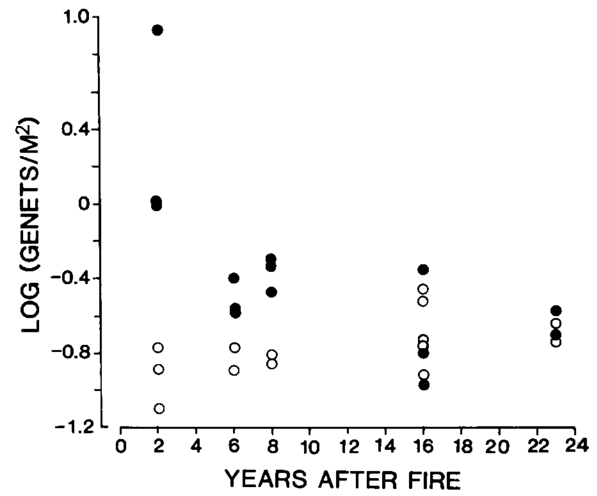

Fig. 3. The density of *B. ericifolia* (●) and *B. oblongifolia* (○) genets from each transect. Densities were based on the number of genets rooted in 120 m², except *B. ericifolia* in the 1979 stand, which were from 1 m² quadrats.

Table 2. Mean number of inflorescences per genet, ± standard deviation, produced in 1981 for *B. ericifolia* and *B. oblongifolia* populations from five stands last burnt between 2 and 23 years previously. Percentage of the reproductive population which flowered in 1981 is given in brackets.

Year of last fire	*B. ericifolia*	*B. oblongifolia*
1979	0	2.80 ± 1.79 (100)
1975	1.00 (52)	1.85 ± 0.80 (46)
1973	3.90 ± 3.00 (75)	1.91 ± 1.19 (71)
1965	3.41 ± 3.90 (68)	0
1958	5.00 ± 5.50 (59)	1.66 ± 1.00 (12)

in Table 2. For *B. oblongifolia,* this quantity was high at the site recently burnt, and progressively less in stands last burnt a longer time ago. For *B. ericifolia,* the quantity was in the order of two-thirds irrespective of time since fire.

The proportion of genets which had flowered at some time in a stand was also different between species. About 70% of *B. oblongifolia* genets had flowered in the 1973 stand, while a smaller proportion had flowered in other stands irrespective of when they last burnt (Fig. 2). In contrast, the proportion of *B. ericifolia* genets which had flowered increased with increasing time since fire. About 90% of all plants in the 1973 stand had flowered, and in the 1958 stand all genets had produced inflorescences at some time (Fig. 2).

Resprouting *B. oblongifolia* genets flowered sooner than *B. ericifolia,* but they added new cones more slowly thereafter. In the 1958 stand *B. ericifolia* genets, averaged over all individuals which had flowered, supported about 2.5 times as many cones as *B. oblongifolia* (Fig. 1b).

Averaged over genets in all stands, a significantly lower percentage of cones bore seed in *B. oblongifolia* (28%) than in *B. ericifolia* (51%) ($F_{1,449} = 58.7$, $p < 0.001$). Percentage of cones bearing seeds from *B. oblongifolia* genets did not differ between stands (Fig. 1d). Percentage of cones bearing seeds declined significantly in *B. ericifolia* with increasing time since fire (Fig. 1d). However this effect was not strong enough to offset *B. ericifolia's* increase in accumulated cone production with time since fire.

Except for *B. ericifolia* in the stand last burnt in 1958, most genets of both *Banksia* species supported less than twenty cones in total. Only a few genets carried more than 10 seed-bearing cones (Fig. 4). Accumulated seed production over about 20 years for most genets therefore added up to less than 500 seeds.

Genet size and reproductive status

For many plant species size is a better predictor of ecological performance than age (White, 1980). Larger genets of both species were the first to support reproductive structures. As the even-aged populations of *B. ericifolia* matured all plants reached a reproductive size (Fig. 2). This was not the case in the *B. oblongifolia* populations, where even in a stand unburnt for 23 years the smallest genets had never been reproductive (Fig. 2). For both *Banksia* species mean accumulated cone production was strongly related to genet size in all stands, irrespective of time elapsed since fire (Fig. 5). Averaged over all stands, cone production was very similar between species for any given H + D (Fig. 5).

There was no difference in the proportion of cones which bore seed between different sized ge-

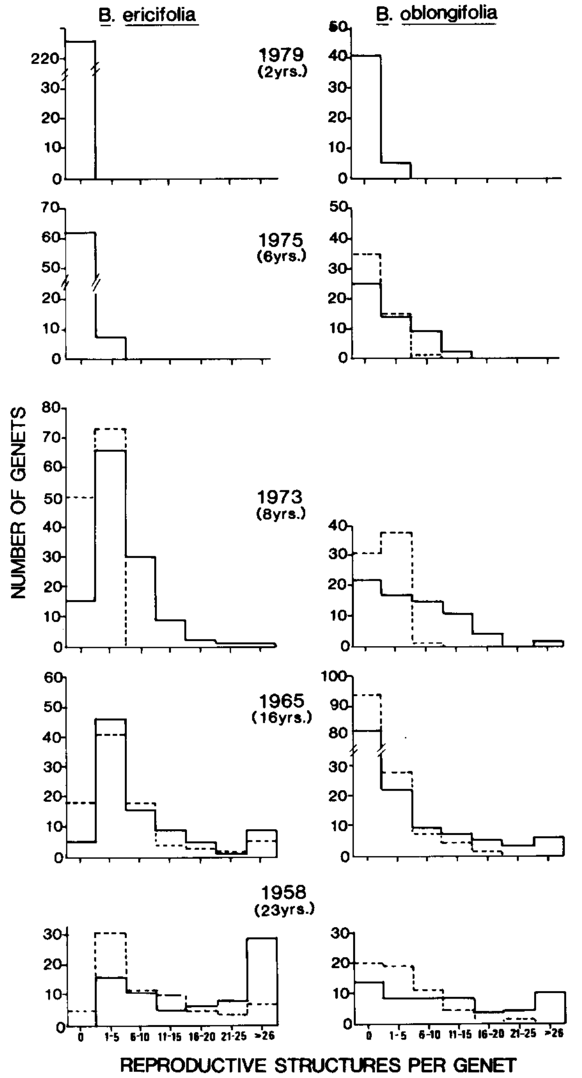

Fig. 4. Frequency distributions of cones accumulated (———), and seed-bearing cones accumulated (– – –) for *B. ericifolia* and *B. oblongifolia* from stands last burnt 2–23 years before 1981.

nets of either species in the 1975 and 1973 stands. In the 1965 and 1958 stands the smaller genets of both species had a lower percentage of seed-bearing cones (Fig. 6). Perhaps in older stands larger genets are more efficient at producing seeds, or more inflorescences in larger shrubs escape the damaging effects of predators (Zammit & Hood, 1986). Generally *B. ericifolia* cones were about twice as likely to bear seed, although this difference was less clear at the site last burnt in 1958 (Fig. 6).

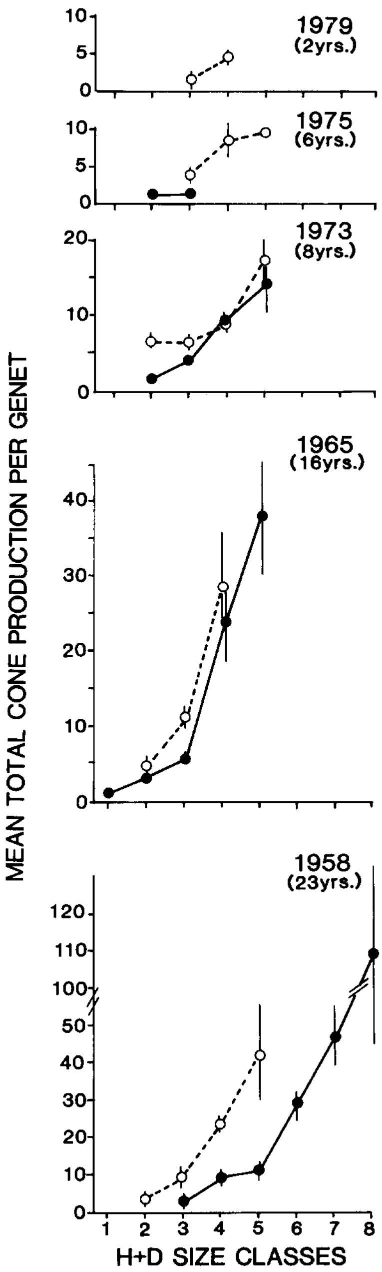

Fig. 5. Mean cone accumulation ($\bar{x}+se$) of different sized *B. ericifolia (———) and B. oblongifolia* (– – –) genets from stands last burnt 2–23 years before 1981.

The outcome of these various effects was that the accumulation of seed-bearing cones in the two species reflected patterns of change in H + D with time elapsed since fire. *Banksia oblongifolia* produced

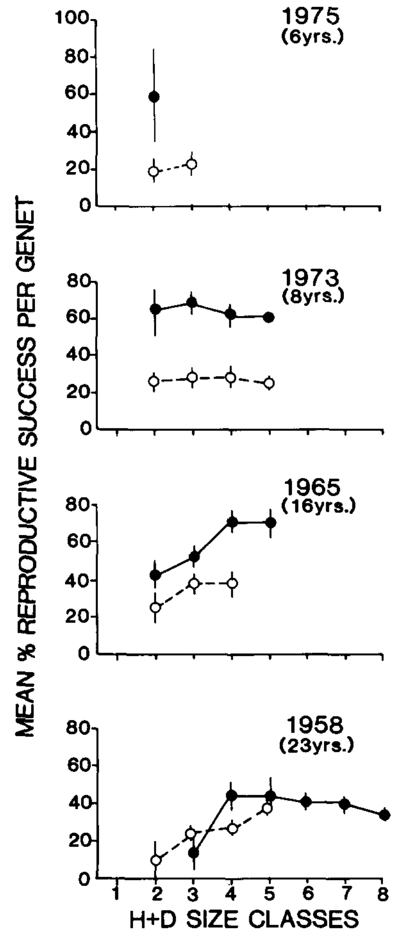

Fig. 6. Percent reproductive success ($\bar{x}+se$), defined as the percent seed-bearing cones accumulated on different sized *B. ericifolia* (———) and *B. oblongifolia* (– – –) genets from stands last burnt 2–23 years before 1981.

seed sooner after fire, but *B. ericifolia* overtook it about 10 yr after fire and continued to accumulate seed-bearing cones faster thereafter (Fig. 1c).

Influence of time since fire and genet size on populations of B. oblongifolia *ramets*

Both genet size and elapsed time since fire were significant influences on the proportion of live ramets a lignotuber supported. The proportion of live ramets per genet declined significantly with increasing $H+D$ ($r^2=0.12$; $F_{1,354}=47.7$, $p<0.001$). Time since fire added significantly to this regression ($r^2=0.35$; $F_{1,354}=94.7$, $p<0.001$). When the order of fit was reversed the result remained unchanged. The proportion of dead ramets per genet declined by 50% over the five stands spanning 23 years since fire (Fig. 7).

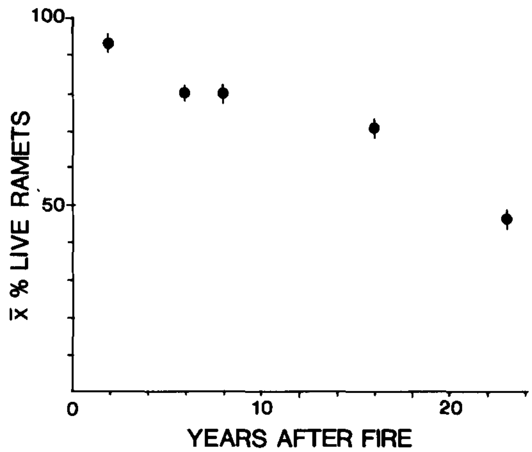

Fig. 7. Proportion of live *B. oblongifolia* ramets supported by genets from stands last burnt 2–23 years before 1981.

Discussion

Population structure in obligate-seeding and resprouting Banksia *genets*

Populations of the obligate-seeder, *B. ericifolia*, were even-aged and therefore well described by the elapsed time since the stand last burnt. Frequency distributions of genet H + D were unimodal. Distributions of this form are common in even-aged populations in which genetic and environmental differences between genets produce differences in relative growth rates over time (Ford, 1975). In contrast, population structures of the resprouter, *B. oblongifolia*, bore little relationship to when the stand last burnt. The wide range of *B. oblongifolia* lignotuber sizes clearly reflects the persistence of genets over an unknown number of past fires (Zammit, 1986). Growth since the last fire, at least as reflected by changes to $H+D$, seems to have little impact on the distribution of sizes in stands of this species.

Regeneration after fire in *B. oblongifolia* occurs both by resprouting and by seedling establishment (Siddiqi *et al.,* 1976). It was interesting, therefore, to find a high proportion of small genets in a stand unburnt for 16 years (Fig. 2; 1965). Most of the small *B. oblongifolia* genets found in some transects in the 1965 stand supported single ramets and had small lignotubers (<2 cm diameter) which showed no evidence of fire scars. This suggests an influx of new genets in the absence of fire.

Seedling establishment in mature stands has been reported for resprouting species in California coastal sage communities (Malanson & Westman, 1985), and in coastal scrub from southern Australia (Specht *et al.,* 1958). Two different mechanisms might permit the establishment of *B. oblongifolia* seedlings in mature stands. First, seeds released after fire might be dormant and so require further treatment before germinating. There is no evidence of this; *B. oblongifolia* seeds germinate readily (Zammit 1984). Alternatively there might be leakage of seeds from cones between fires. Some *Banksia* follicles, including *B. oblongifolia,* are reported to open in the absence of fire (George, 1981). Whether seed release between fires is an adaptive trait or an accidental consequence of other cone characters remains unclear.

The density of *B. ericifolia* genets declined with increasing stand age. Similar mortality patterns occur in even-aged populations of the chaparral obligate-seeder *Ceanothus megacarpus* (Schlesinger & Gill, 1978), even-aged populations of *Ceratiola ericoides* (Johnson, 1982) and monospecific *B. ericifolia* stands in a different heath area on Hawkesbury Sandstone (Morris & Myerscough, 1983).

The density of *B. oblongifolia* genets did not vary significantly between stands. Stable densities of resprouters over stands spanning 23 years suggests that populations of this species are not expanding immediately after fire then contracting over time as genets die. Because we did not survey populations during the first 12 months after fire, the time when most new genets are recruited and subsequent mortality occurs (Bradstock & Myerscough, 1981; Zammit, 1986), the impression of relative stability of *B. oblongifolia* numbers reported here excludes the mortality of seedling genets. Nevertheless, these results suggest resprouting *B. oblongifolia* are better able to withstand competitive and other forces which kill established genets.

Reproductive status in obligate-seeding and resprouting Banksia *genets*

Resprouting *B. oblongifolia* genets reach sexual maturity sooner than *B. ericifolia* regenerating from seeds. However, the size of resprouting *B. oblongifolia* ramets and *B. ericifolia* genets were similar at first flowering. Pyke (1983) has also reported flower and seed production 2–3 years after fire in resprouting proteaceaous shrubs in this environment. Resprouters in chaparral and garrigue communities begin flowering in the first year after fire and recruit seedlings 2–3 years after fire from the seeds produced (Keeley & Keeley, 1984; Trabaud & de Chanterac, 1985). This contrasts with serotinous species such as *Banksia* which recruit seedlings mostly in the first year after fire (Zammit, 1986). The adaptive significance of this difference is unclear. Possibly the immediate post-fire environment is not the optimal germination time for all species of fire-prone landscapes, or possibly the pattern of flowering and then recruiting seedlings 2–3 years after fire is found where high seed mortality militates against accumulating a seed bank which must be maintained until the next fire.

A substantial proportion of resprouting *B. oblongifolia* genets never flowered, a pattern that did not change with increasing time since fire. As in other studies (e.g., Pinero *et al.,* 1982; Grice, 1984), it was always the smallest genets in the population which were not reproductive. If we assume that the smallest *B. oblongifolia* genets are also recent additions to the population, it follows that new genets take more than 23 years to reach reproductive maturity. Observations from glasshouse experiments suggest that lignotubers are formed within 12 months, and lignotubers as small as 1–2 cm in diameter are capable of resprouting (C. Zammit, unpublished data). In the field most genets with lignotuber areas less than about 1.0 dm^2 at the soil surface have never flowered. The requirement for flowering is clearly more than a minimum lignotuber size capable of resprouting.

It might reasonably be predicted that genets of the obligate-seeder *B. ericifolia* would produce seeds earlier and more copiously than the resprouter *B. oblongifolia,* for either of two reasons. First lineages of *B. ericifolia* persist through fires by seed only, so they are vulnerable during the period before they develop a seed bank. Selection might be expected to abbreviate this period as much as possible. Second, the resource allocation hypothesis (Harper & Ogden, 1970) argues that as genets develop there are competing demands for limited resources between vegetative and reproductive functions. This has led to the prediction that obligate-seeders ought to produce more seeds than resprouters (Carpenter & Recher, 1979) per unit growth.

Considered over the whole life of genets, it appears to be true that *B. ericifolia* produces seed earlier, since *B. oblongifolia* genets did not appear to flower in their first fire cycle. On the other hand within each fire cycle, resprouting *B. oblongifolia* produced seeds sooner, contradicting the argument that obligate-seeders should be selected to seed quickly in order to tolerate short between-fire intervals. Further, there was little evidence that differences between the two species could be attributed to differences in the allocation of resources between growth and reproductive activity. On the contrary, the overall relationship between cone production and H+D was very similar in the two species. The essential difference between the two species seems to lie in the timing of their shoot growth in relation to the fire cycle. The obligate-seeder *B. ericifolia* continues growth much more vigorously than the resprouter *B. oblongifolia* from 5–10 years after fire onwards. On the other hand the resprouter grows more quickly than the obligate-seeder during the first five years after fire, except during the first fire-cycle it experiences as a seedling. Patterns of seed production mirror these patterns of shoot growth, rather than being an alternative activity.

For this pair of species it appears that resprouting and obligate-seeding are not alternative ways of dealing with the same fire regime, but are suited to rather different fire regimes. Our data, like those of Benson (1985), suggest *B. ericifolia* would be strongly disadvantaged by short between-fire intervals, and this has recently been observed (Nieuwenhuis, 1985). In contrast, the long-term persistence of *B. oblongifolia* does not seem to be influenced by the frequency of fires. However, the decline in percent live *B. oblongifolia* ramets in the 1958 stand suggests that the absence of a disturbance which stimulates resprouting for extended periods may result in gradual genet senescence.

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