

Effects of inter-fire intervals on the reproductive output of resprouters and obligate seeders in the Proteaceae

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Abstract Fire is often used as a management tool in fire-prone communities to reduce fuel loads with the intention of reducing the severity and extent of unplanned fires, often resulting in the increased occurrence of fire in the dry sclerophyll vegetation of Australia. This study examined the effects of fire frequency (length of the inter-fire interval) on the reproductive output of seven plant species in the Proteaceae, including obligate seeding shrubs (*Hakea teretifolia*, *Petrophile pulchella*), resprouting shrubs (*Banksia spinulosa*, *Isopogon anemonifolius*, *Lambertia formosa*) and resprouting trees (*Banksia serrata*, *Xylomelum pyrifforme*). Reproductive output (measured as either number of confructescences or follicles) and relative size were estimated for 100 individuals at each of five sample sites, covering a range of past fire frequencies over 26 years including repeated short inter-fire intervals. Patterns in reproductive output (after standardizing for size) were related to the life-history attributes of the species. In areas that had experienced short inter-fire intervals, obligate seeders had greater reproductive output compared with longer intervals, and the reproductive output of resprouting shrubs was less. Fire frequency did not affect reproductive output of the resprouting trees. The decreased reproductive output of the resprouting shrubs could be due to the allocation of resources to regrowth following fire rather than to reproduction. It is less clear what process resulted in the increased reproductive output of obligate seeders in high fire frequency areas, but it could be due to the most recent fires being more patchy in the areas experiencing shorter inter-fire intervals, or it may have resulted from the selection for early reproduction in the high fire frequency areas. These results highlight the need to take into account past fire frequency at a site, in addition to time since the last fire, when planning prescribed fires.

Key words: fire ecology, fire frequency, obligate seeders, Proteaceae, reproduction, resprouters.

INTRODUCTION

Fire is a recurring event in many plant communities in Australia, and is particularly frequent in sclerophyllous vegetation (Keith 1996; Bradstock *et al.* 2002). Fire is often used as a management tool in the Sydney region to reduce fuel loads, with the intention of reducing the extent and severity of unplanned fires. However, the use of fire as a management tool has resulted in altered fire regimes, particularly with increased occurrence of fire (Morrison *et al.* 1996). An understanding of the effects of increased fire frequency on plant population dynamics is important for the conservation of biodiversity in these fire-prone communities.

The response of plant populations to fire can be broadly categorized based upon whether the adults of

a species usually survive fire (e.g. >50% survival of adults subject to 100% leaf scorch) or not. Species in which the adults are generally killed by fire are dependent upon seed for regeneration at a site, and are termed obligate seeders (Gill 1981). Species with protected dormant vegetative buds regenerate at a site following fire through adult persistence (and often also through seedling recruitment) and are termed resprouters (Gill 1981). These two life-history traits result in contrasting population dynamics. The co-occurrence of these life-history traits in communities has been explained in part by the principle of resource allocation (Wells 1968; Keeley & Keeley 1977; Bond & Midgley 2001), which suggests that plants have only a limited amount of resources that need to be shared between growth, maintenance and reproduction (Silvertown & Charlesworth 2001). This principle has led to the general theory that obligate seeders maximize their fitness by allocating more resources to early reproduction than do resprouters, thereby increasing their chances of being reproductively mature before the next fire. Conversely, resprouters maximize fitness by allocating more resources to root reserves and structures that will increase their chances of surviving the next fire (Clark 1991; Bond & Van Wilgen 1996).

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Accepted for publication September 2004.

Increased fire frequency influences the floristic composition and species richness of dry sclerophyll vegetation (Cary & Morrison 1995; Morrison *et al.* 1995, 1996). Obligate seeders are particularly prone to population decline under increased fire frequency when the interval between fires is shorter than the time taken to accumulate a seed bank adequate for persistence (Noble & Slatyer 1981; Keith & Bradstock 1994; Cary & Morrison 1995; Morrison *et al.* 1995; Bradstock *et al.* 1997; Enright *et al.* 1998). Moreover, obligate seeders with canopy-stored serotinous seed banks are most susceptible to short inter-fire intervals due to their whole seed bank being released post-fire (Bradstock & Myerscough 1981; Enright & Lamont 1989). Species with soil-stored seed banks may be buffered to some degree from short inter-fire intervals, because not all of their seeds are stimulated to germinate post-fire and therefore a residual seed bank remains (Bradstock & Myerscough 1981; Enright & Lamont 1989).

While the effects of fire frequency on floristic composition and species richness have been relatively well studied, the effects of past fire frequency on reproductive output have been poorly studied. This is surprising, given the importance of the reproduction life-history stage for the persistence of species at a site. Allocation theory predicts that obligate seeders and resprouters have contrasting fecundity in response to increased fire frequency, given their differences in allocation of resources.

Currently, predictions of the optimal fire frequency for a site are often based on the relationship between the age of a population and the rate of seed accumulation of the most susceptible species (i.e. the obligate seeders) (see Whelan 1995). This focuses attention on the demographic effects of the time since the most recent fire, with less concern for the effects of the prior fire history of a site. Past fire history may, however, affect the rate of seed bank accumulation. Therefore, our study examined the effects of fire frequencies in the recent past on the reproductive output of several co-occurring Proteaceae species with contrasting life histories. In particular, we examined to what extent: (i) occurrence of short inter-fire intervals affects the reproductive output of members of the Proteaceae; and (ii) changes in reproductive output due to fire frequency (inter-fire interval) are related to the life-history attributes of these species.

METHODS

Study sites

Five study sites (2–10 ha) were located in open forest alongside Patonga Road, adjacent to the Warrah Trig. Road in Brisbane Water National Park north of Sydney

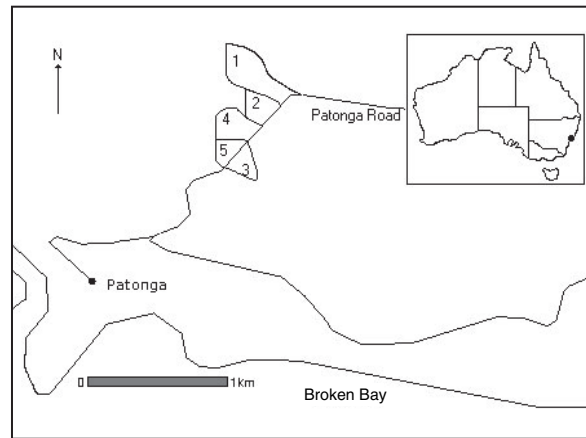


Fig. 1. The spatial arrangement of study sites. Sites 1 and 2 are characterized by no short inter-fire intervals, site 3 by one short inter-fire interval and sites 4 and 5 by two short inter-fire intervals.

(latitude 33°30'S, longitude 151°E) (see Fig. 1). The dominant tree species in the area were *Angophora costata*, *Corymbia gummifera*, *Eucalyptus haemastoma* and *Banksia serrata*, growing in a deep yellow podzolic soil (Benson & Fallding 1981). This area was chosen because it contained a number of sites with differing fire histories in close proximity, was a uniform landscape unit (plant community 4P of Benson & Fallding 1981), and contained a range of species with different life histories within the same family (thus reducing taxonomic variation). This latter point is important for comparative biology. The particular plant community chosen is well known for its unusual abundance of Proteaceae species, and by choosing to study co-occurring species in this relatively uniform community we effectively eliminated many environmental factors as potential confounding variables, allowing us to focus on reproductive variation attributable to fire history.

An unplanned fire, the 'first' known fire in the recent past, burned all five study sites in 1964 (Table 1). Since that time, the area had been burnt by a series of partially overlapping fires, forming a mosaic of areas with different fire histories in terms of time between successive fires (inter-fire intervals). Sites 1 and 2 had only long inter-fire intervals since 1964 (defined as >7 years between consecutive fires; Cary & Morrison 1995). Site 3 had one, and sites 4 and 5 had two short inter-fire intervals after 1964 (Table 1). All sites were last burnt by a wildfire in 1990, and thus time since the most recent fire was equal across sites. This experimental design was fortuitous rather than planned, but it effectively dealt with many of the potentially confounding effects that can lead to non-independence of the experimental comparisons in a descriptive experiment such as this (i.e. pseudoreplication). For example, the study sites were interspersed (Fig. 1) and far

Table 1. Fire histories of the five sample sites used to study the effects of varying inter-fire intervals on reproductive output

Sample site	Inter-fire intervals since 1964 (years)	Important characteristic
One	13, 13	No short inter-fire intervals
Two	12, 14	No short inter-fire intervals
Three	13, 3, 10	One short inter-fire interval
Four	11, 4, 7, 4	Two short inter-fire intervals
Five	11, 4, 7, 4	Two short inter-fire intervals

The sequences of inter-fire intervals of all fires occurring between 1964 and 1990 and the important fire characteristic of each site are given.

enough apart (300–500 m) to avoid local confounding ecological effects, and the sites were delineated in areas burnt by different fires, so that they could be considered to be independent applications of the experimental treatments (i.e. numbers of short inter-fire intervals). In this sense, only the experimental treatment represented by site 3 could not be replicated in the study area (Table 1).

Study species and sampling

Seven serotinous species in the Proteaceae family were examined to test the effects of short inter-fire intervals on reproductive output (Table 2). Species with serotinous seed banks were used because the reproductive output could more easily be quantified than for species with soil-stored seed banks. Also, species with serotinous seed banks accumulate reproductive output over a number of years, reducing variation due to yearly fluctuations in climatic conditions. Five of the species were resprouters while two were obligate seeders, so that we had replicate species for each of the three fire-regeneration life histories being studied (Table 2).

Approximately 100 individuals of six of the species were sampled at each of the five sites, but *Hakea teretifolia* was not abundant enough at site 3 (54 individuals) or site 2 (67 individuals). For each individual, estimates of the reproductive output (as total number of 'woody fruits') and relative plant size were recorded (Table 2). Confructescences and follicles were recorded irrespective of whether they held seed. Data from five species were collected in June to July 1997, while *B. serrata* and *Xylomelum pyrifforme* were sampled in August 1998.

Data analysis

The reproductive output of each species was compared among sites by analysis of covariance (ANCOVA) using the general linear model function in SYSTAT (Wilkinson 1989), with site as the factor, reproductive output as the dependent variable and plant size as the

covariate. Plant size was included because plants of different size or age may vary in reproductive output. The *F*-statistic for the covariate was significant in all analyses, indicating that plant size would be an important confounding variable if its effect was not removed. Plant size and the reproductive output of each plant were log transformed ($\log(x + 1)$), in order to improve the homogeneity of slopes (Sokal & Rohlf 1981). Homogeneity of slopes was determined by testing the interaction between the covariate and the main factor (Wilkinson 1989).

A priori orthogonal comparisons (Wilkinson 1989) were carried out to determine whether: (i) the reproductive output of each species was different at sites that had experienced 0–1 short inter-fire intervals compared with sites that had experienced two short inter-fire intervals (i.e. sites 1, 2 and 3 *vs.* sites 4 and 5); and (ii) the reproductive output of each species was different at sites that had experienced no short inter-fire intervals compared with sites that had one short inter-fire interval (i.e. sites 1 and 2 *vs.* site 3).

RESULTS

For all species except *X. pyriforme* the reproductive output differed significantly between at least two of the sites. Orthogonal comparisons of sites showed that the obligate seeding species (*Petrophile pulchella* and *H. teretifolia*) had significantly greater reproductive output at sites that experienced two short inter-fire intervals compared with sites with 0–1 short inter-fire interval (Table 3). Furthermore, the reproductive output was significantly greater in the area that had experienced one short inter-fire interval compared with sites experiencing no short inter-fire intervals for *P. pulchella*, but not for *H. teretifolia*.

The resprouting shrub species (*Banksia spinulosa*, *Isopogon anemonifolius* and *Lambertia formosa*) had a significantly higher reproductive output at sites that experienced no short inter-fire intervals or one short inter-fire interval compared with sites that experienced two short inter-fire intervals. (NB: the value of $P = 0.052$ for *I. anemonifolius* in the comparison is

Table 2. The mode of recovery, life form and the method for determining relative size and reproductive output of each study species

Species	Life form	Mode of regeneration	Measure of relative size	Measure of reproductive output
<i>Banksia serrata</i> L.f.	Tree	Epicormic resprouting	Circumference at breast height (cm)	No. of confructescences
<i>Xylomelum pyriforme</i> (Gaertn.) Knight	Tree	Epicormic resprouting	Circumference at breast height (cm)	No. of follicles
<i>Banksia spinulosa</i> Sm.	Shrub	Lignotuber resprouting	No. of resprouting shoots	No. of confructescences
<i>Isoopogon anemonifolius</i> Knight	Shrub	Lignotuber resprouting	No. of resprouting shoots	No. of follicles
<i>Lambertia formosa</i> Sm.	Shrub	Lignotuber resprouting	No. of resprouting shoots	No. of follicles
<i>Hakea teretifolia</i> (Salisb.) Britten	Shrub	Obligate seeding	Height (cm)	No. of follicles
<i>Petrophile pulchella</i> (Schrad.) R.Br	Shrub	Obligate seeding	Height (cm)	No. of confructescences

interpreted to be biologically significant.) *I. anemonifolius* had greater reproductive output at sites experiencing no short inter-fire intervals compared with the sites experiencing one short inter-fire interval, but this pattern was not found for *B. spinulosa* or *L. formosa*.

Fire frequency had no significant effect on the reproductive output of either of the resprouting tree species (*B. serrata* and *X. pyriforme*).

DISCUSSION

Fire frequency apparently influenced the reproductive output of all species studied with the exception of the resprouting trees. In summary we found that: (i) shrubs resprouting from lignotubers had greater reproductive output at sites with longer rather than shorter inter-fire intervals; (ii) the reproductive output of trees resprouting from epicormic buds was not affected by the fire frequencies involved in this study; and (iii) obligate seeders had greater reproductive output at sites with short inter-fire intervals than at sites with longer intervals. Since the observed patterns in reproductive output were consistent across those species with similar life-history attributes, we suggest that these patterns may be general for other species with the same attributes. A number of hypotheses can be proposed regarding the potential causes of these correlative patterns.

Those shrubs resprouting from lignotubers were observed to have lower reproductive output in areas of greater fire frequency. Following fire, resprouting shrubs use stored carbohydrate reserves to facilitate the regrowth of vegetative structures. Reduced reproductive output in high fire frequency areas is thus presumably a result of the repeated burning leading to a depletion of carbohydrate reserves (Keith 1996), with energy that would otherwise be mobilized for sexual reproduction being allocated instead to the regrowth of vegetative structures. Reproductive structures generally require a lot of resources but contribute little to their own carbohydrate requirements (Bloom *et al.* 1985), and this is likely to be particularly true for serotinous species because woody cones require a large amount of structural tissue. It is unclear from our results whether the lower reproductive output of resprouting shrubs in high fire frequency areas is a result of delayed reproduction or alternatively a reduction in reproductive rate. Distinguishing between these two possibilities would help to further elucidate cause and effect.

The observed decline in reproductive output of resprouting species when burnt at high fire frequencies potentially has implications for the density of post-fire seedling establishment. The reduction of reproductive output in areas with high fire frequency will presum-

Table 3. Means of the log of the reproductive output per plant, and a priori orthogonal comparisons from the analyses of covariance

Site	Obligate seeders		Lignotuber resprouters			Epicormic resprouters	
	<i>Hakea teretifolia</i>	<i>Petrophile pulchella</i>	<i>Banksia spinulosa</i>	<i>Isopogon anemonifolius</i>	<i>Lambertia formosa</i>	<i>Banksia serrata</i>	<i>Xylomelum pyriforme</i>
1	0.168	0.128	0.558	1.183	0.778	0.481	0.050
2	0.084	0.232	0.631	1.078	0.861	0.325	0.074
3	0.193	0.321	0.564	0.868	0.821	0.356	0.092
4	0.578	0.661	0.383	0.919	0.625	0.289	0.059
5	0.389	0.485	0.416	1.001	0.618	0.510	0.059
SE [†]	0.043	0.026	0.033	0.053	0.042	0.037	0.059
<i>Orthogonal comparisons of site means (probability)</i>							
1 + 2 + 3 vs. 4 + 5	<0.001	<0.001	<0.001	0.052	<0.001	0.712	0.440
1 + 2 vs. 3	0.273	<0.001	0.439	<0.001	0.977	0.290	0.193

[†]Pooled standard error from the ANCOVA.

Sites 1 and 2 are characterized by no short inter-fire intervals, site 3 by one short inter-fire interval and sites 4 and 5 by two short inter-fire intervals. Means are adjusted for the covariate (plant size).

Table 4. Mean sizes of plants (with standard deviation)

Site	Obligate seeders (height, cm)		Lignotuber resprouters (number of shoots)			Epicormic resprouters (stem circumference, cm)	
	<i>Hakea teretifolia</i>	<i>Petrophile pulchella</i>	<i>Banksia spinulosa</i>	<i>Isopogon anemonifolius</i>	<i>Lambertia formosa</i>	<i>Banksia serrata</i>	<i>Xylomelum pyriforme</i>
1	175.0 (36.5)	146.7 (23.0)	5.6 (3.3)	7.9 (4.4)	8.6 (5.2)	43.3 (27.3)	13.0 (10.4)
2	165.6 (35.7)	156.4 (33.7)	6.3 (3.3)	6.3 (3.1)	9.6 (6.2)	26.9 (20.9)	12.8 (11.5)
3	154.9 (27.5)	142.2 (32.5)	6.6 (5.1)	9.7 (4.7)	8.1 (5.4)	28.6 (25.3)	10.9 (10.8)
4	170.3 (41.4)	181.2 (40.2)	5.9 (3.6)	7.6 (5.2)	10.8 (6.4)	34.2 (20.6)	10.9 (9.8)
5	154.5 (36.5)	173.1 (31.5)	6.6 (4.3)	7.8 (4.2)	9.7 (5.2)	34.1 (24.6)	9.5 (11.5)

Sites 1 and 2 are characterized by no short inter-fire intervals, site 3 by one short inter-fire interval and sites 4 and 5 by two short inter-fire intervals.

ably result in a subsequent reduction in the post-fire seedling establishment for the resprouting shrub species. This process may explain why some resprouters decline in abundance under repeated burning at short inter-fire intervals (e.g. Watson & Wardell-Johnson 2004).

The reproductive output of the resprouting trees was not observed to be affected by the fire frequencies involved in this study. The lack of a significant effect on the reproductive output of resprouting trees may be due to the fire regimes in this study not affecting their energy budgets. By definition, species capable of resprouting via epicormic buds do not lose all of their above-ground biomass following fire (cf. species that resprout via lignotubers), and the canopy may not even receive 100% leaf scorch in any particular fire (Morrison & Renwick 2000). Therefore it would be expected that short inter-fire intervals would have a greater effect on the resource allocation of the resprouting shrubs than that of the tree species. Alternatively, for *X. pyriforme* the statistical tests have relatively low power because the average number of

follicles per plant is very low (Table 3), and so even a sample size of 100 may be inadequate to detect trends for this species.

The greater reproductive output of obligate seeders observed at sites with high fire frequency is more difficult to explain. This is because several alternative explanations present themselves, and our correlative observations cannot necessarily be used to distinguish among them.

One possible explanation for obligate seeders having greater reproductive output at sites experiencing high fire frequency is that the most recent fire was patchy and therefore some highly fecund individuals escaped fire. Such a suggestion seems unlikely for several reasons. First, and most importantly, if a large number of individuals escaped burning in the high fire frequency areas, it would be expected that the individuals would be on average larger in size than those in the less frequently burnt areas. This pattern was observed in our data only for *P. pulchella* but not for *H. teretifolia* (Table 4). Furthermore, we observed no size heterogeneity suggestive of multiple cohorts, as would be

expected if the plants were different ages. Second, the interval of 4 years between fires is enough time to allow sufficient fuel to accumulate to pose a severe fire hazard (Morrison *et al.* 1996), thus reducing the probability of a fire being patchy enough to affect these shrub species differentially.

An alternative explanation as to why the obligate seeders have more fruits at sites with shorter inter-fire intervals is that these sites might have a lower population density than do sites with longer intervals. Density has been shown to affect fecundity in some Proteaceae (Morris & Myerscough 1988). As a heuristic (but not definitive) test of this hypothesis, we carried out Pearson correlations comparing fruit abundance data from our study with the plant density data of Cary (1992), which were collected for six of the species at four of the same sites after the 1990 fire. We examined a log–log relationship, as the scatterplots indicated that there was no linear relationship between fruit numbers and plant density. For the density data, the variation between sites was only 5–35% for the resprouter species, but was >150% for the obligate seeders. However, density and the number of fruits were found not to be correlated across sites for any of the species ($P = 0.087–0.604$). Thus, we conclude that plant density cannot be used to explain the observed variation in fruit numbers between sites with different fire histories.

A more intriguing explanation is that the higher reproductive output of obligate seeders at sites with high fire frequency could be due to differential survival of individuals with earlier reproduction at those sites. In high fire frequency areas, individuals that reach reproductive maturity first may contribute the greatest proportion of propagules to the next generation. Those individuals that do not have a chance to produce offspring, because the inter-fire interval is shorter than the time taken to reach reproductive maturity, do not contribute to the next generation. Given that the time taken to reach reproductive maturity for 50% of the population for *H. teretifolia* and *P. pulchella* has been recorded as 6 and 9 years, respectively (Benson 1985), then few individuals would be reproductively mature when the short inter-fire intervals of 3 and 4 years occurred. Only those individuals reproductively mature at the time that the fires occurred could have contributed offspring to future generations, and if maturation time is genetically determined then there could be rapid selection for individuals with short primary juvenile periods. While it appears that this pattern has not been demonstrated for woody species in fire-prone environments, similar patterns have been found for annuals in disturbed environments (Rendon & Nunez-Farfan 2001; Satake *et al.* 2001).

Our findings also accord with the predictions of Clark's (1991) model of plant population dynamics under regular disturbance. This model predicts that

populations in high disturbance areas should flower earlier than in less frequently disturbed populations. Early flowering due to increased disturbance would be expected to affect obligate seeders more strongly than resprouters, as each fire event results in a new generation for obligate seeders but not necessarily for resprouters (Wells 1968). Clearly, future work is required to determine whether fire frequency influences the reproductive output of other obligate-seeder species and what is the underlying process influencing this pattern.

Finally, in this study we utilized areas that had fortuitously experienced different fire frequencies, and hence the study had a 'natural' descriptive design rather than a controlled manipulative design. It is impractical to perform a controlled experiment over the period of time that would be required for an experiment such as the one we have performed here, although we would certainly encourage anyone who is prepared to try. However, one potential problem with our descriptive design is that the variation in fire frequency may have been a result of landscape heterogeneity, and that this heterogeneity is the real underlying factor influencing the patterns found in this study rather than the fire frequencies of the sites. We therefore made an explicit attempt to minimize latent problems caused by such confounding variables. First, we chose to sample co-occurring species within a uniform landscape unit with a distinctive plant community. This should help eliminate the effects of many potentially confounding variables associated with site to site variation (e.g. Warton & Wardle 2003). Second, our study sites were separate and interspersed within the study area, so that local ecological factors were not confounded with the variation in fire frequency. Third, the study areas were delineated by partially overlapping fires that occurred at different times, so that the replicate study areas could be considered to result from independent applications of the experimental manipulations (i.e. fire frequencies). Fourth, we standardized the reproductive output using plant size, to help reduce the effect of variation in other post-fire growth characteristics. While these strategies cannot eliminate the problems entirely, their combined effect should be considerable.

ACKNOWLEDGEMENTS

We thank Scott King, Fiona Knox, Sheena Knox and Richard Snelson for assisting with the data collection. Dorothy Bell, Michael Bull, Peter Clarke, Andrew Denham, Belinda Kenny and Glenda Vaughton provided valuable comments on the manuscript. Sampling was performed under licence from the NSW National Parks and Wildlife Service. We also thank Geoff Cary for the use of unpublished data.

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