

Response of Resprouting Shrubs to Repeated Fires in the Dry Sclerophyll Forest of Gibraltar Range National Park

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Fire regimes affect survival and reproduction of shrub species in fire-prone vegetation such as occurs in Gibraltar Range National Park. The influence of fire regimes on resprouting shrubs is known for a range of species in coastal regions of Australia but is poorly known in montane sclerophyll communities. The fire responses of three Proteaceae shrubs (*Banksia spinulosa*, *Hakea laevipes*, *Petrophile canescens*) and a grasstree (*Xanthorrhoea johnsonii*) were measured after the wildfire of 2002 to determine whether: 1) storage organ size was related to post-fire growth and flowering response, 2) fire frequency influences post-fire mortality and if survival was related to the size of plant; 3) fire frequency influences the resprouting ability of plants, and 4) fire frequency affects pyrogenic flowering in the post-fire environment. We found the size of storage organs was positively related to post-fire sprouting in the three shrubs and to flowering in the grasstree. However, high fire frequency only affected the survival of *Banksia spinulosa* and decreased flowering in *Xanthorrhoea johnsonii*. Survival in all species ranged between 83 and 99% and it appears that the intervals between fires (7-22 years) had been sufficient for most adult plants to regain the ability to resprout. The ability of juvenile plants to develop the ability to resprout needs to be tested on seedlings that established after recent fires.

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INTRODUCTION

The fire response of species is often simplified into resprouters and obligate seeders, but in reality a continuum from 0-100% mortality of individuals within a population exists amongst species (Bellingham and Sparrow 2000; Vesk and Westoby 2004; Clarke et al. 2005). Characteristics of a particular fire, distribution of size-classes and the physiological and anatomical features of a species will affect the percentage mortality in a population after fire. Shrub species capable of resprouting generally resprout from subterranean buds (lignotubers and roots suckers), but also occasionally from epicormic buds on aerial stems. Grasstrees on the other hand resprout via apical buds. The ability of an individual to resprout following fire depends on having adequate dormant buds and carbohydrate storage to facilitate resprouting (Bell 2001; Knox and Clarke 2005). Variation in mortality has been observed for different size-classes within populations (Morrison 1995;

Bond and Van Wilgen 1996). Some species have been found to have greater resprouting potential in larger size-classes (e.g. Morrison 1995); in contrast, some species have been found to have greater resprouting potential in smaller size-classes (e.g. Burrows 1985).

Frequent fires with short inter-fire intervals may result in the exhaustion of buds or carbohydrates stored in the lignotuber, resulting in the mortality of resprouters (Zammit 1988; Bowen and Pate 1993). The intensity of a particular fire can influence what proportion of a population survives. Some obligate seeders may survive a low-intensity fire if 100% leaf scorch does not occur (Gill 1981; Bond and van Wilgen 1996). On the other hand a very high-intensity fire may result in the death of a large number of individuals within a population that usually resprouts following fire. The minimum fire-tolerant stem size of resprouters often increases with fire intensity for some species (Bradstock and Myerscough 1988; Morrison 1995; Morrison and Renwick 2000).

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Resprouters that recruit seedlings into populations following fire generally have seed stored in the soil or in the canopy in woody fruits. Hence, understanding the post-fire growth and reproductive response of resprouting shrubs is critical in determining appropriate fire regimes in landscapes dominated by resprouting species. Resprouting shrubs typically have greater growth and reproductive vigour in the year following a fire (e.g. Auld 1987; Bowen and Pate 2004). In many resprouting shrubs flowering occurs predominantly, or exclusively, following fire, e.g. *Telopea speciosissima* (Pyke 1983), *Lomatia silaifolia* (Denham and Whelan 2000), *Xanthorrhoea preissii* (Lamont et al. 2000), and *Stirlingia latifolia* (Bowen and Pate 2004). Little is known about the factors that influence reproductive output of pyrogenic flowering plants, although season of fire is known to strongly influence flowering in some Western Australian species (Lamont et al. 2000; Bowen and Pate 2004). One important component of fire regime that is likely to influence post-fire flowering is the frequency of burns as this may influence the starch storage capacity of plants.

Little quantitative work has been conducted to determine the effects of frequent fires on post-fire performance and mortality of shrubs that resprout following fire. The fire regime in Gibraltar Range National Park provided an opportunity to examine these questions because records date back to the 1960s and the number and extent of subsequent fires have spatially explicit records. Gibraltar Range National Park also has widespread and abundant populations of resprouting shrubs occurring within physiographically similar landscapes. In late 2002 an intensive crown fire burnt most of the dry sclerophyll forest in the National Park. This event afforded an opportunity to study the post-fire response of species, which have experienced different fire frequencies.

Evidence of an effect of fire frequency would show that more frequently burnt sites had more dead plants and surviving plants with reduced growth and reproduction. If, however, these sites had smaller plants, then these may appear to show reduced survival, growth and reproduction purely for allometric reasons. Hence we asked whether: 1) storage organ size was related to post-fire growth and flowering response, 2) fire frequency influences the resprouting ability of plants 3) fire frequency and/or size of the storage organ influences post-fire mortality 4) fire frequency affects pyrogenic flowering (flower or inflorescence production) in the post-fire environment.

METHODS

Fire regime maps of Gibraltar Range National Park were examined and dry sclerophyll forest areas that had been burnt twice, four and five times since 1964 were identified. All sites were burnt in November 2002 by an intense wildfire that removed most of the tree leaf canopy but did not totally incinerate the fruits of the target species. The minimum interval between fires was approximately seven years and the maximum 22 years. Fire records showed that all fires burnt in spring/summer, suggesting that all fires were of high intensity. All observations were at the same time since the last fire (8 months). In areas of each of the fire frequency regimes two patches were chosen that were at least 1 km apart. In each patch three 500 m transects were established and the post-fire response of three species of Proteaceae shrubs with canopy-held seed banks (*Banksia spinulosa*, *Hakea laevipes*, and *Petrophile canescens*) were measured. These species were selected because they are ubiquitous, easy to identify when dead, and they only recruit after fire, hence their minimum age can be estimated. For each species the number of shoots resprouted from the lignotuber, the length of the longest shoot resprouted and the basal girth of the lignotuber were measured for the first 20 (approx.) individuals encountered in each transect. Dead plants were also recorded and their basal girth measured. Individuals were identified by their 'skeletal' remains and their canopy-held woody fruits. In addition, the post-fire flowering of the grass tree *Xanthorrhoea johnsonii* was also recorded along each transect. For *Xanthorrhoea* basal girth and height of the caudex were measured and the presence and length of the inflorescence were recorded for the first 20 individuals encountered along each transect.

Data for this study were mainly collected by undergraduate students. All students collected the equivalent amount of data from each of the fire frequency areas. This was important so that the patterns in post-fire resprouting and flowering could be attributed to the different fire frequencies, and not to variation in sampling among different students. In each of the three species of shrubs, to test the relationship between storage organ size and post-fire response, basal girths were regressed against the number of shoots resprouted, height of shoots resprouted and size of inflorescence as independent variables. We then used analysis of covariance (ANCOVA) to test if number of shoots or stem height were reduced by fire frequency, with lignotuber size as the covariate. We also used ANCOVA in *Xanthorrhoea* to test if the inflorescence length was reduced by fire frequency, with the caudex size as a covariate. Plots of residuals

established that no transformations of raw data were necessary. Homogeneity of slopes was determined by testing the interaction between the covariate and the main factors. We next tested the hypothesis that storage organ size and/or fire frequency affects post-fire survival by logistic regression using likelihood ratio tests. In these analyses the response variable is the number of plants alive or dead. In *Xanthorrhoea*, we also tested the hypothesis that caudex volume and/or fire frequency affects post-fire flowering by logistic regression using likelihood ratio tests. In this

analysis the response variable was the number of plants flowering or not flowering.

RESULTS

Of the four species sampled, only the grasstree *Xanthorrhoea johnsonii* was observed to flower in the immediate post-fire period (August 2003), whilst the other species began to flower in the following year (August 2004). All resprouting Proteaceae shrub species had a positive and significant ($P < 0.05$)

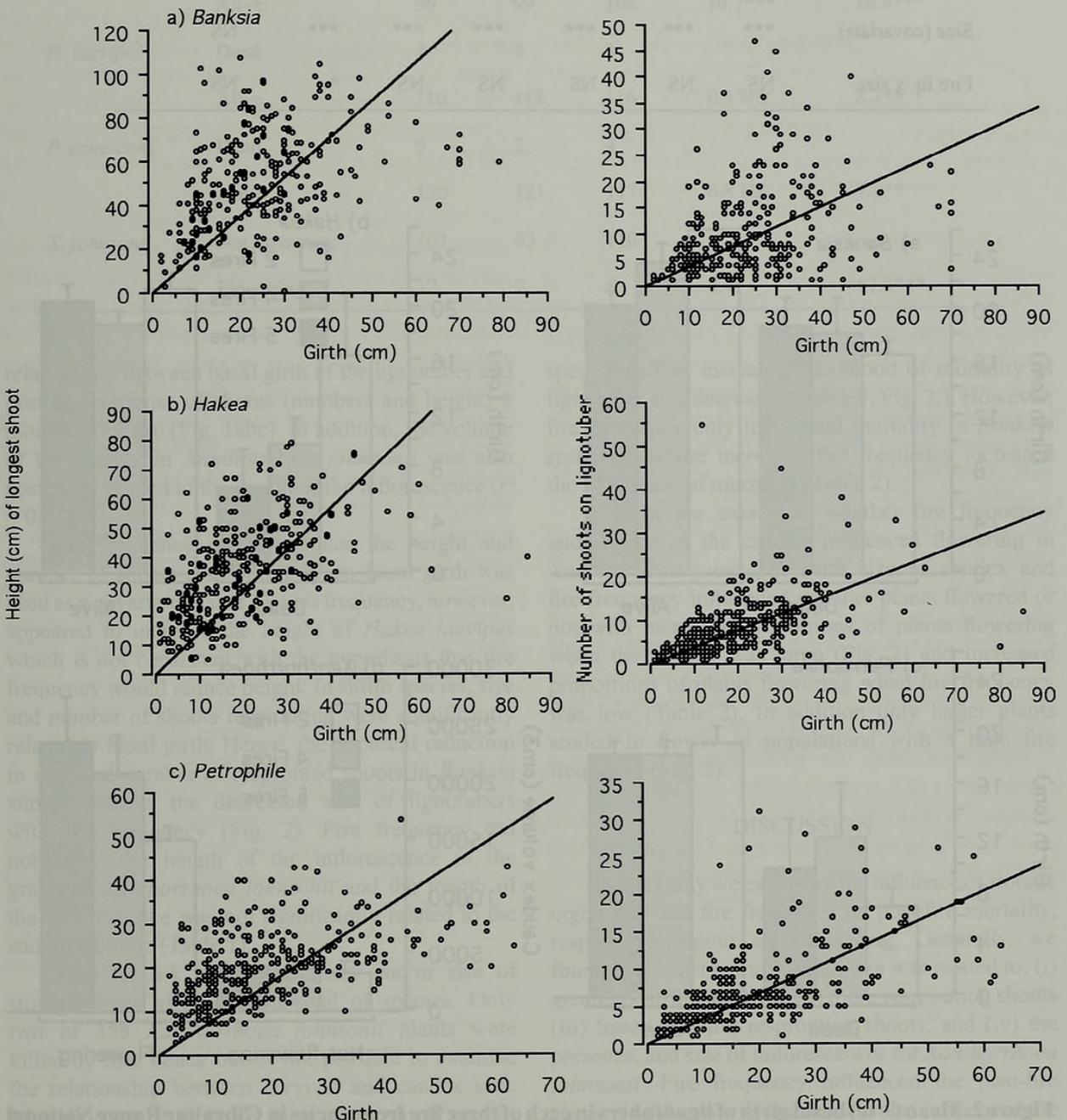


Figure 1. Regression of shoot height and number with lignotuber basal girth with 18 months after fire for a) *Banksia spinulosa*, $r^2 = 0.77, 0.59$; b) *Hakea laevipes*, $r^2 = 0.77, 0.70$; and c) *Petrophile canescens* $r^2 = 0.76, 0.77$, across all fire frequencies of fire at Gibraltar Range National Park.

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Table 1. Summary results for analysis of covariance for height (Ht) and numbers of shoots (Shoot) resprouted for *Banksia spinulosa*, *Hakea laevipes*, *Petrophile canescens* and length of inflorescence (Infl.) in *Xanthorrhoea johnsonii*. The size covariate for the three shrubs was basal girth and for the grasstree it was the caudex volume. * indicates $P < 0.05$, ** indicates $P < 0.01$, and * indicates $P < 0.001$**

Factors	<i>B. spinulosa</i>		<i>H. laevipes</i>		<i>P. canescens</i>		<i>X. johnsonii</i>
	Ht	Shoot	Ht	Shoot	Ht	Shoot	Infl.
Fire frequency	NS	NS	**	NS	NS	NS	NS
Size (covariate)	***	***	***	***	***	***	NS
Fire fq. x size	NS	NS	NS	NS	NS	*	NS

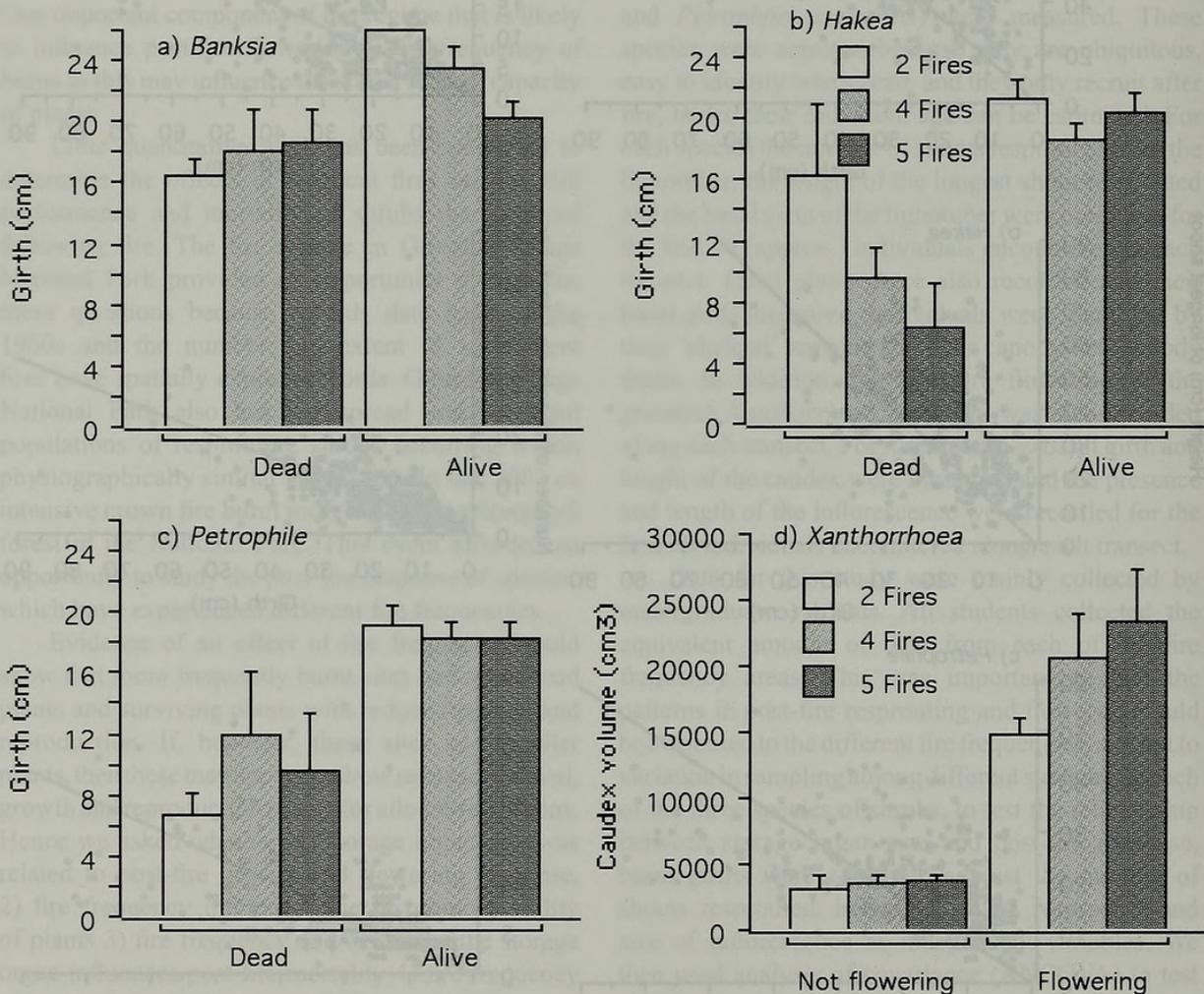


Figure 2. Mean (+ se) basal girth of lignotubers in each of three fire frequencies in Gibraltar Range National Park for a) *Banksia spinulosa*, b) *Hakea laevipes*, and c) *Petrophile canescens*. Mean volume of the caudex (+ se) for *Xanthorrhoea johnsonii* for each fire frequency where smaller plants flower in sites with less frequent fires.

Table 2. Number of plants recorded in each fire frequency category and the results of logistic regression for fire frequency and size of storage organ from likelihood ratio tests. * indicates $P < 0.05$, ** indicates $P < 0.01$, and * indicates $P < 0.001$**

Species	Logistic response variable	Fire frequency			Chi-squared Fire frequency	Chi-squared Basal girth/volume
		2	4	5		
<i>B. spinulosa</i>	Dead	10	21	24		
	Alive	96	99	108	10.7***	16.6***
<i>H. laevipes</i>	Dead	4	5	3		
	Alive	116	115	116	0.5 NS	8.7**
<i>P. canescens</i>	Dead	9	2	4		
	Alive	120	121	117	0.8 NS	7.9**
<i>X. johnsonii</i>	Not flowering	103	93	110		
	Flowering	17	7	8	8.4*	67.3***

relationship between basal girth of the lignotuber and post-fire response of shoots (numbers and height) 8 months after fire (Fig. 1abc). In addition, the volume of the caudex in *Xanthorrhoea johnsonii* was also positively related to the length of the inflorescence ($r^2 = 0.71$).

Fire frequency did not reduce the height and number of shoots resprouting when basal girth was used as a covariate (Table 1). Fire frequency, however, appeared to increase the height of *Hakea laevipes* which is not consistent with the hypothesis that fire frequency would reduce height. In shrub species, size and number of shoots resprouting were significantly related to basal girth. Hence, the apparent reduction in size and number of resprouted shoots in *Banksia* simply reflects the decreased size of lignotubers with fire frequency (Fig. 2). Fire frequency did not affect the length of the inflorescence in the grass tree *Xanthorrhoea johnsonii* and the length of the inflorescence was not significantly related to the caudex volume (Table 1).

Next we ask if fire frequency and/or size of storage organ affect the survival of species. Only two of 358 *Xanthorrhoea johnsonii* plants were killed by fire, hence it was not possible to examine the relationship between survival and caudex size. Mortality was sufficiently high in the shrub species to examine the effects of fire frequency and size on post-fire survival using logistic regression. All

species had an increased likelihood of mortality as lignotuber size decreased (Table 3, Fig. 2.). However, fire frequency only influenced mortality in *Banksia spinulosa* where increased fire frequency increased the likelihood of mortality (Table 2).

Finally, we examined whether fire frequency and/or size of the caudex influenced flowering in *Xanthorrhoea johnsonii*. Both size of caudex and fire frequency influenced whether plants flowered or not with increased proportions of plants flowering when the caudex was large (Fig. 2) and increased proportions of plants flowering when fire frequency was low (Table 2). In addition only larger plants tended to flower in populations with a high fire frequency (Fig. 2).

DISCUSSION

In this study we examined the influence of storage organ size and fire frequency on post-fire mortality, resprouting vigour and flowering. Generally, we found that larger storage organ size was related to: (i) greater post-fire survival, (ii) more resprouting shoots (iii) faster growing resprouting shoots, and (iv) the presence, and size of inflorescences for *Xanthorrhoea johnsonii*. Fire frequency influenced the post-fire survival of *Banksia spinulosa* and also influenced the presence of inflorescences of *Xanthorrhoea johnsonii* following fire (Table 2).

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Table 3. Summary of the results on the effect of fire frequency and size of storage organ on post-fire survival and resprouting of four species with canopy-held seed banks.

Species	Are storage organ size and post-fire growth response correlated?	Does increased fire frequency affect storage organ?	Does increased storage organ size affect post-fire survival?	Does increased fire frequency affect post-fire survival?
<i>Banksia spinulosa</i>	Yes +ive	Yes -ive	Yes +ive	Yes -ive
<i>Hakea laevipes</i>	Yes +ive	No evidence	Yes +ive	No evidence
<i>Petrophile canescens</i>	Yes +ive	No evidence	Yes +ive	No evidence
<i>Xanthorrhoea johnsonii</i>	Does storage organ size affect presence of inflorescence?	Does fire frequency affect size of inflorescence?	Does increased storage organ size affect post-fire survival?	Does fire frequency affect presence of inflorescence?
<i>Xanthorrhoea johnsonii</i>	Yes +ive	No evidence	No evidence	Yes -ive

Post-fire survival for the species studied ranged from 99% for *Xanthorrhoea johnsonii* to 82% for *Banksia spinulosa*, although we may have underestimated mortality if small dead plants were overlooked. For *Xanthorrhoea johnsonii*, individuals were found to survive fire irrespective of storage organ size. However, for the three shrubs, individuals with small storage organs were more likely to be killed by fire than those that had larger storage organs. This pattern is consistent with the idea that many species develop greater fire-tolerance as the storage organ increases in size and age (Morrison 1995; Keith 1996). This increased tolerance is likely to be a result of a larger dormant bud bank and more stored carbohydrate in less frequently burnt plants (Knox and Clarke 2005). We do, however, acknowledge that the sampling technique used might have underestimated the mortality of some populations if the fire intensity was great enough to incinerate fruits. This could have resulted in an under-sampling of dead individuals, as retained woody fruits were used to help identify individuals. There could have also been an underestimation of the mortality of pre-reproductive individuals, as there would not have been fruits present to identify the species. Clearly if this occurred then the percentage mortality of the populations would have been underestimated. While this may have influenced the recorded percentage mortality of the population, we feel that it would have little influence on our general findings.

When examining the relationship between the size of the storage organ and resprouting vigour we found that larger storage organ size was related to more resprouting shoots and faster growing

resprouting shoots. Although this pattern was not unexpected, we had hoped to be able to determine whether carbohydrate storage or number of dormant buds was the limiting factor when it came to the ability of individuals to resprout, but we did not detect any trends. Rather, it would appear that larger storage organs have more dormant buds available for resprouting and greater carbohydrate stores. Whether this greater resprouting vigour for individuals with larger storage organs translates to a greater reproductive output remains to be tested at this site, but other studies have shown a relationship between storage organ size and reproductive output (Auld 1987; Bowen and Pate 2004). Furthermore, there was clear evidence supporting this idea in the grasstree (*Xanthorrhoea johnsonii*) where the length of the inflorescence was positively correlated with the volume of the caudex. We also found that plants that lacked or had a short caudex did not flower in the first year following fire. This result contrasts with the findings of Lamont et al. (2000) who found that for a Western Australian grasstree, plant size was not positively related to the proportion of plants flowering.

Fire frequency did not affect the post-fire survival of *Hakea laevipes* or *Petrophile canescens*, but high fire frequency increased the mortality of *Banksia spinulosa*. Individuals of *Banksia spinulosa* in higher fire frequency sites were more likely to be killed by fire, were generally smaller in size when compared to less frequently burnt sites. Interestingly, we found no evidence that this increased mortality was a result of a depletion of the bud bank, as the number of shoots per plant did not differ among sites with different fire

frequencies. Similarly, we found no evidence that the mortality was directly related to a depletion of carbohydrate reserves, as the length of the longest resprout did not differ among sites with different fire frequencies. Rather, it appears that the cohort that recruited since the previous fire (1990) had not had an opportunity to reach fire tolerance and it was these individuals that contributed to the higher mortality in the more frequently burnt site. A synthesis of post-fire survival of juvenile resprouting species by Keith (1996) suggests that some Proteaceous shrubs (*Banksia oblongifolia*, *Telopea speciosissima*) develop the ability to resprout at around five years, but others (*Banksia serrata*, *Isopogon anemonifolius*) may take more than 10 years to develop a strong resprouting ability. Whether juvenile plants that recruit after fire are able to develop persistence in less than 10 years needs to be tested on seedlings that established after recent fires.

Xanthorrhoea johnsonii individuals were less likely to flower in the higher fire frequency site, but the length of the inflorescence was not affected by fire frequency. This is surprising given the large investment of resources in post-fire flush flowering in *Xanthorrhoea johnsonii*. The reduced flowering in the high fire frequency sites may be a result of previous fires depleting carbohydrate reserves. Knox and Morrison (2005) found a similar pattern for some resprouting shrubs where individuals in high fire frequency sites had lower reproductive output than in less frequently burnt sites. Interestingly, Taylor et al. (1998) found individuals of *Xanthorrhoea fulva* were more likely to flower in areas with high fire frequency than areas with less frequent fires. While this appears to contradict our findings, the intervals in that study were much shorter than those in the current study, and hence it is difficult to draw comparisons.

Previous studies that have examined the effects of fire frequency in dry sclerophyll vegetation have often found resprouters to decline in abundance under very short inter-fire intervals (e.g. Cary and Morrison 1995). In the current study, the shortest interval between fires was seven years and at this fire frequency two of the four species examined were adversely affected in the higher fire frequency sites. This is an important finding because the current Guidelines for Ecologically Sustainable Fire Management in NSW (Kenny et al. 2003) indicate that a lower minimum threshold between fires for dry sclerophyll shrub forest is seven years, and the results from this current study indicate that such an interval may be too short for these particular forests.

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