Fire response syndromes of shrubs in grassy woodlands in the New England Tableland Bioregion

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Abstract: In fire-prone grassy woodlands, fire response and time to reach reproductive maturity are two traits that can be used to provide an indication of the minimum interval between fires needed to maintain biodiversity. This study examined the effects of fire intensity and adult size on shrub mortality together with the primary and secondary juvenile periods of shrub species in the New England Tableland (NET) Bioregion. Most shrub species resprouted via basal lignotubers following fire, irrespective of fire intensity and shrub size. The primary juvenile period of most species was found to be greater than four years and the secondary juvenile period for most resprouting species was less than four years. These results suggest that a minimal interval between fires of eight years may be needed to maintain shrub species in grassy woodlands in the NET Bioregion, and that repeated fires at intervals of less than 8 years should be avoided. The time taken for shrubs in the grassy woodlands of the NET Bioregion to reach reproductive maturity appears to be longer than conspecifics in other Bioregions. Caution is needed when using data collected from outside a Bioregion to determine minimum fire frequency thresholds.

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Introduction

Knowledge of how plant species respond to fire regimes is fundamental for management of biodiversity. In fire-prone communities, studies of the fate of the standing population, and of the time taken to reach reproductive maturity post-fire, are of two-fold importance. Firstly, when no quantitative data are available about the effects of different fire regimes on communities, species attributes can be used to predict qualitative changes in species composition (Noble & Slatyer 1980). Secondly, the continued study of factors affecting the post-fire survival of populations can be used to build on current models.

The fire response of an individual plant will either be death or survival and at a population level this dichotomy is often applied to describe species that survive fire (resprouters) and those killed by fire (obligate seeders). In reality, however, a continuum from 0–100% mortality of individuals within a population exists among species (Morrison 1995, Bond & Van Wilgen 1996, Morrison & Renwick 2000). Characteristics of a particular fire, distribution of size-classes and the physiological and anatomical features of a species will affect the percentage mortality of a population post-fire (Whelan 1995). Bond and Van Wilgen (1996) formalised size-specific post-fire survivorship into four survival curves. In summary, the first group (type I) acquires fire-tolerance quickly, and has little post-seedling mortality; the second group (type II) becomes increasingly fire-tolerant with increasing size; the third group (type III) attains fire-tolerance during juvenile stages, but loses fire-tolerance with age, and the final group (type IV) are those species that never attain fire-tolerance (obligate seeders). Knowledge of patterns of fire-tolerance and percentage mortality in different size-classes allows greater understanding of how species will react under different fire regimes, especially when communities are dominated by species that resprout.

The time taken to reach reproductive maturity following fire is important for both obligate seeders and resprouters, as it is directly related to generation length and will affect the capacity of a population to increase in size (Whelan 1995). The length of the primary juvenile period (the time taken to reach reproductive maturity from seed) is particularly important for obligate seeders as population decline or local extinction could potentially occur if the interval between fires is shorter than the time taken to reach reproductive maturity and to accumulate an adequate seedbank (Cary & Morrison 1995, Keith 1996). The time taken for resprouting individuals to flower is referred to as the secondary juvenile period. Population decline may occur if the time between fires is less than the secondary juvenile period of resprouters, particularly those species that do not generally display 100% post-fire survival (Keith 1996). Age at first reproduction has been found to vary among species within a community (Benson 1985, Bradstock & O'Connell 1988), between populations (Benson 1985) and between individuals within a population (Carthew 1993). Resprouting species generally take longer to flower from seed than obligate seeding species (Abbott 1985, Bell 2001). The secondary juvenile period of resprouters, however, tends to be shorter than the primary juvenile period for resprouters and obligate seeders (Zammit & Westoby 1987).

Knowledge of the fate of the standing population and the time to reach reproductive maturity after a fire event has increased steadily over the past decade for many community types in Australia. However, little is known about the fire ecology of woody plants in grassy woodlands in eastern Australia (see review by Clarke 2000). In particular there is a dearth of knowledge about the shrub species occurring in the cool temperate regions in the New England Tableland Bioregion of northern NSW (NET Bioregion). Some fire response and maturation observations from coastal grassy communities have been made but it is not known if it is appropriate to extrapolate data from conspecifics in different climates for use in fire management planning.

This study addresses four questions: (i) Which species resprout following fire and where does resprouting arise? (ii) Does plant size influence post-fire survival for those species that show some degree of resprouting? (iii) Does fire intensity affect mortality for those species that show some degree of resprouting? (iv) What is the length of the primary and secondary juvenile periods of shrub species in grassy woodlands?

Methods

Study area

The New England Tableland Bioregion (NET Bioregion) covers 3 004 080 ha., about 40% of which, native vegetation remains (National Land & Water Resources Audit 2001). About 7.5% of extant native vegetation is within conservation reserves (Benson 1999). Grassy woodlands once covered extensive areas of the NET Bioregion (Benson & Ashby 2000) but, have been extensively cleared for pastoralism. Remnant patches of grassy woodland occur in conservation reserves, travelling stock reserves, roadside reserves and on private land. Clarke (2003) demonstrated that under pastoralism, shrub abundances decline, although the herbaceous layer remains relatively intact.

Fire response studies were conducted in two grassy woodland conservation areas: Imbota Nature Reserve and Booroolong Nature Reserve. Imbota Nature Reserve (218 ha in size) is 10 km SE of Armidale (National Parks & Wildlife Service 2001). The average maximum temperature in January (summer) in Armidale is 27.1°C, while the average minimum temperature in July (winter) is 0.3°C. Average yearly rainfall is 790 mm. Areas at Imbota NR where experimental burns were conducted ranged from 1010–1040 m elevation. Experimental burns were conducted in areas with yellow podzolic soils and metasediment lithology on sites that were generally flat or with a slight to medium slope. The last recorded fire in Imbota NR was a small fire in 1969; no records exist for the fire history before this (National Parks & Wildlife Service 2001). Vegetation structure at Imbota NR ranges from woodland to low open forest with a sparse understorey of shrubs and a near-continuous herbaceous layer. The dominant tree species in the study sites were *Eucalyptus blakelyi*, *Eucalyptus bridgesiana*, *Eucalyptus caliginosa*, *Eucalyptus melliodora* and *Eucalyptus viminalis*. The dominant species in the herbaceous layer were *Poa sieberiana* var. *sieberiana* and *Themeda australis.*

Booroolong Nature Reserve (865 ha in size) is 30 km NW of Armidale (National Parks & Wildlife Service 2002). No specific data are available on the climate of Booroolong Nature Reserve, although the climate is similar to that of nearby Guyra, average maximum temperature in January (summer) is 24.6°C; average minimum temperature in July (winter) is 0.6°C, average yearly rainfall is 884 mm). Areas burnt in experimental fires ranged from 1290–1310 m elevation, on yellow podsolic soils, overlying a metasediment lithology. The areas were generally flat or had a slight to medium slope. No fires have been recorded at Booroolong NR for the past 20 years (National Parks & Wildlife Service 2002) and the area may not have been burnt for more than 50 years, based on the lack of fire scars. Vegetation structure at Booroolong NR ranges from woodland to open forest with a sparse to medium density of shrubs in the understorey and a dense herbaceous layer. The dominant tree species in the study sites were *Eucalyptus caliginosa, Eucalyptus dalrympleana* subsp. *heptantha, Eucalyptus laevopinea* and *Eucalyptus radiata. Poa sieberiana* var. *sieberiana* and *Themeda australis* were common in the herbaceous layer.

Fire response traits of shrub species

The fire response of shrub species was determined following three experimental burns at each Nature Reserve. Experimental burning occurred at Imbota NR in Spring 1999, and at Booroolong NR in Autumn 2000. Each burn site was approximately 50 × 50 m and had an average fine fuel load of approximately 8 tonnes/ ha. Before each fire, fine fuel (straw) was added to half the area of each burn site in order to increase the fuel loads to at least 16 tonnes/ ha so as to determine the effects of different fire intensities on plant mortality. Recording the intensity of fires is inherently difficult (Whight & Bradstock 1999) and intensity was not measured in the current study as the rate of spread could not be determined due to the way the fires were lit (along control lines and then burnt towards the centre). Kitchin (2001) used comparable fuel loads to that in the high fuel load areas of this study, and achieved fires of moderate intensity, indicating that moderate intensity and low intensity fires would have been expected in our high fuel load and low fuel load areas respectively.

Shrubs were tagged before each fire within each burn area, and in adjacent unburnt areas, and the size (measured as basal girth) of individuals was recorded. Three years after the fire individuals were assessed for evidence of resprouting, and the position of resprouting noted. Species were classified as obligate seeders when less than 30% of individuals survived 100% leaf scorch, and as resprouters when more than 70% of individuals survived 100% leaf scorch (Gill & Bradstock 1992).

Table 1. The post-fire response, method of resprouting of shrub species examined. For survival, numbers are the percentage survival (sample size). n.a. indicates that the life-history trait is not applicable as this species is an obligate seeder.

Species	Fire response	Survival %		Mode of resprouting
Acacia buxifolia subsp. *buxifolia*	resprouter	100	(6)	basal/lignotuber
Acacia dealbata	obligate seeder	0	(3)	n.a.
Acacia filicifolia	resprouter	78	(23)	suckers/epicormic
Acacia implexa	resprouter	100	(11)	suckers/basal
Acacia ulicifolia	obligate seeder	0	(9)	n.a.
Brachyloma daphnoides subsp. *glabrum*	resprouter	100	(4)	basal/lignotuber
Cassinia leptocephala	obligate seeder	0	(3)	n.a.
Cassinia quinquefaria	obligate seeder	21	(29)	n.a.
Cryptandra amara	resprouter	100	(5)	basal/lignotuber
Daviesia latifolia	resprouter	100	(2)	basal/lignotuber
Epacris microphylla	resprouter	100	(4)	basal/lignotuber
Hardenbergia violacea	resprouter	100	(10)	basal/lignotuber
Hibbertia acicularis	resprouter	100	(23)	basal/lignotuber
Hibbertia obtusifolia	resprouter	100	(47)	basal/lignotuber
Hovea heterophylla	resprouter	100	(3)	basal/lignotuber
Indigofera adesmiifolia	resprouter	100	(5)	basal/lignotuber
Indigofera australis	resprouter	100	(16)	basal/lignotuber
Jacksonia scoparia	resprouter	100	(5)	suckers
Leucopogon sp. nov	resprouter	100	(2)	basal/lignotuber
Leucopogon lanceolatus var. *lanceolatus*	resprouter	100	(7)	basal/lignotuber
Lissanthe strigosa subsp. *strigosa*	resprouter	100	(57)	basal/lignotuber
Lomatia silaifolia	resprouter	100	(5)	basal/lignotuber
Melichrus urceolatus	resprouter	100	(46)	basal/lignotuber
Monotoca scoparia	resprouter	100	(18)	basal/lignotuber
Olearia myrsinoides	resprouter	100	(15)	basal/lignotuber
Olearia sp. aff. *elliptica*	resprouter	70	(10)	basal/lignotuber
Olearia viscidula	resprouter	78	(33)	basal/lignotuber
Pimelea linifolia	resprouter	100	(3)	basal/lignotuber
Pultenaea microphylla	resprouter	100	(10)	basal/lignotuber
Pultenaea setulosai	resprouter	100	(12)	basal/lignotuber
Rhytidosporum diosmoides	resprouter	100	(3)	basal/lignotuber

Primary juvenile and secondary juvenile periods

Observations on primary and secondary juvenile periods were made in August 2002 and September 2003. Data for the primary juvenile period of species were collected from naturally recruiting populations and from seed sown in the field for another study. Shrubs were examined for evidence that they had reached reproductive maturity at a number of burn sites with different times-since-fire. At Imbota NR, three sites were 3 years post-fire, three sites were 2.5 years post-fire, three sites were 2 years post-fire and three sites were 1.5 years post-fire, when sampled in 2002. At Booroolong NR, three sites were 2.5 years post-fire, three sites were 2 years post-fire and three sites were 1.5 years post-fire when sampled in 2002.

Data analyses

Formal data analyses were only undertaken for species that displayed some variation in post-fire mortality. Plant mortality at the two different fire intensities was compared using analyses of deviance (with a binomial error structure) using GLMStat (Beath 2001). The relationship between plant mortality and plant size was investigated by assigning individuals to one of three size-classes based on stem diameter before fire (small: 0–10 cm, medium: 11–20 cm, and large: > 21 cm diameter) and analyses of deviance (with a binomial error structure) using GLMStat (Beath 2001).

Results

Post-fire response of species and location of dormant buds

Of 31 shrub species recorded (Table 1) 27 species classified as resprouters, including 24 species exhibiting 100% survival. Four species were classified as obligate seeders — *Acacia dealbata*, *Acacia ulicifolia*, *Cassinia leptocephala* and *Cassinia quinquefaria*. No mortality of individuals outside the burn areas was recorded.

All but three resprouting species resprouted exclusively from basal (lignotuberous) buds. *Jacksonia scoparia* and *Acacia implexa* resprouted via root suckers and *Acacia filicifolia* resprouted via root suckers and epicormic buds.

Achieving 100% leaf scorch of the mat-forming shrub *Pultenaea microphylla* proved difficult as the dense prostrate plant appears to be nearly fire resistant. With increased fuel loads, 100% leaf scorch was induced and resprouting from the lignotuber occurred.

Effects of fire intensity and plant size on mortality

Formal analysis was conducted on only those species that displayed variation in mortality — *Acacia filicifolia, Cassinia quinquefaria* and *Olearia viscidula* (*Olearia* sp. aff. *elliptica* did display some variation in mortality, but too few individuals were available to examine the effects of plant size

Table 2. The post-fire response time to flowering of shrub species examined. * Indicates that no data are available. n.a. indicates that the life-history trait is not applicable as this species is an obligate seeder

Species	Fire response	Primary juvenile period	Secondary juvenile period
Acacia buxifolia subsp. *buxifolia*	resprouter	*	Not flowering after 3.5 years
Acacia dealbata	obligate seeder	Not flowering after 4 years	n.a.
Acacia filicifolia	resprouter	Not flowering after 4 years	Not flowering after 4 years
Acacia implexa	resprouter	*	Not flowering after 4 years
Acacia ulicifolia	obligate seeder	3 years	n.a.
Brachyloma daphnoides subsp. *glabrum*	resprouter	*	2.5 years
Cassinia leptocephala	obligate seeder	Not flowering after 4 years	n.a.
Cassinia quinquefaria	obligate seeder	*	n.a.
Cryptandra amara	resprouter	*	3 years
Daviesia latifolia	resprouter	Not flowering after 4 years	Not flowering after 4 years
Epacris microphylla	resprouter	*	Not flowering after 3.5 years
Hakea eriantha	resprouter	Not flowering after 4 years	*
Hakea laevipes subsp. *graniticola*	resprouter	Not flowering after 4 years	*
Hardenbergia violacea	resprouter	4 years	3 years
Hibbertia acicularis	resprouter	*	3 years
Hibbertia obtusifolia	resprouter	*	Not flowering after 3 years
Hovea heterophylla	resprouter	*	2.5 years
Indigofera adesmiifolia	resprouter	*	Not flowering after 4 years
Indigofera australis	resprouter	4 years	1.5 years
Jacksonia scoparia	resprouter	*	Not flowering after 4 years
Leucopogon sp. nov	resprouter	*	< 3 years
Leucopogon lanceolatus var. *lanceolatus*	resprouter	Not flowering after 4 years	Not flowering after 3.5 years
Lissanthe strigosa subsp. *strigosa*	resprouter	*	< 1.5 years
Lomatia silaifolia	resprouter	*	Not flowering after 3.5 years
Melichrus urceolatus	resprouter	*	< 1.5 years
Monotoca scoparia	resprouter	*	< 1.5 years
Olearia myrsinoides	resprouter	*	< 1.5 years
Olearia sp. aff. *elliptica*	resprouter	Not flowering after 4 years	2 years
Olearia viscidula	resprouter	*	2 years
Pimelea linifolia	resprouter	*	3 years
Pultenaea microphylla	resprouter	*	3 years
Pultenaea setulosai	resprouter	*	3 years
Rhytidosporum diosmoides	resprouter	*	< 1.5 years

and fire intensity). Neither fire intensity nor plant size significantly affected mortality of *Acacia filicifolia* ($F_{1,4}$ = < 0.001, $P > 0.05$; $F_{3,3} = 2.29$, $P > 0.05$) or *Olearia viscidula* ($F_{1,4} = 0.123$, $P > 0.05$; $F_{2,3} = 1.77$, $P > 0.05$). For *Cassinia quinquefaria*, fire intensity did not significantly affect survival ($F_{1,4} = 6.67$, $P > 0.05$), but plant size did significantly affect mortality, with the smallest plants having greatest survivorship ($F_{3,5} = 14.02$, $P < 0.01$).

Primary and secondary juvenile periods of a selection of shrub species

Acacia ulicifolia (primary juvenile period 3 years), *Indigofera australis* (4 years) and *Hardenbergia violacea* (4 years) were the only species that had a primary juvenile period of four years or less (Table 2). Other species examined were not flowering and evidently have a primary juvenile period greater than four years though how long is unknown. Most resprouting species were found to have a secondary juvenile period of less than four years (Table 2).

Discussion

Fire response of species and the influence of fire intensity and plant size on mortality

The majority of species in this study was found to resprout after fire, with basal resprouting being the most common regeneration mode. Most resprouting species exhibited 100% survival, and neither fire intensity nor initial size of plants was found to influence mortality of most species. These results differ from previous studies where mortality within a species has been found to be influenced by fire intensity and plant size (e.g. Moreno & Oechel 1993, Morrison & Renwick 2000). Plant mortality within a species may increase with fire intensity, especially in the smallest size-classes (Morrison & Renwick 2000). The lack of a relationship between size and mortality may be due to all individuals being of roughly equivalent age or at least having had ample time to develop fire-tolerance. If germination events for shrub species generally occur after fire, then only a few individuals in the smallest size-classes would be expected in this study as fire is thought to have been excluded from both reserves for more than 30 years.

Few studies have examined the percentage post-fire survival of co-occurring species in Australian vegetation communities and of those, few have found such a preponderance of species with 100% post-fire survival (i.e. type I species as defined by Bond & Van Wilgen 1996). Hodgkinson (1998) examined shrub species in semi-arid woodlands of NSW and found survival ranged from 18–90%. Similarly, in open forests in the Sydney region, shrubs and small trees ranged from 0–83% survival under low intensity fires and 0–27% survival under high intensity fires (Morrison & Renwick 2000).

Our findings are consistent with a previous landscape scale study in the NET Bioregion (Clarke & Knox 2002) that found 81% of grassy woodland shrub species had a resprouting fire response. Clarke and Knox (2002) found grassy woodlands and wet heaths to have a higher proportion of resprouters than in shrubby forest communities. Various models were examined to account for these patterns although none was able to account for landscape scale differences in resprouting. An interesting feature of the mode of resprouting in our study was the prevalence of species with basal resprouting compared with epicormic shooting. Bellingham and Sparrow (2000) have suggested that such patterns are a result of selection under frequent intense disturbance. This theory needs to be tested by obtaining better information on the disturbance frequencies in grassy woodlands, although this may be difficult to reconstruct given the fragmented nature of grassy woodland in the present landscape.

Post-fire flowering

The primary juvenile period of most species was found to be greater than four years, conversely, the secondary juvenile period was generally found to be less than four years, results consistent with previous studies (e.g. Zammit & Westoby 1987).

There is limited but growing knowledge about the length of the primary juvenile period for Australian species, and the primary juvenile period of some of the species in the current study has been recorded elsewhere. The primary juvenile period of *Hardenbergia violacea* has been recorded as one year in the Sydney Region (Benson & McDougall 1996); in the current study, it was four years. Wark (1997) found the primary juvenile period of *Indigofera australis* to be two years in Victoria, but in the current study it appears to be more than four years. These differences may be related to climate, with the NET Bioregion experiencing a shorter growing season, and plants taking longer to reach reproductive maturity. This suggestion seems reasonable, as many obligate seeders within shrubby woodlands of the NET Bioregion have primary juvenile periods of greater than 5 years (Clarke, unpublished data). Caution is needed when using data about reproductive periods from different Bioregions.

Most of the shrubs in this study had a secondary juvenile period of less than four years and are similar to a range of shrub species within shrubby woodlands in the NET Bioregion (Clarke, unpublished data).

Management implications

Results from this study can be used to formulate a baseline for the minimum fire interval for grassy woodlands in the NET Bioregion. The primary juvenile period is a particularly important life-history attribute of obligate seeders, as population decline may occur if the interval between fires is shorter than the time taken to reach reproductive maturity. The primary juvenile period for most obligate seeders in this study was found to be greater than 4 years, suggesting that population decline will occur in the grassy woodlands if the interval between successive fires is less than 5 years. Keith et al. (2002) recommended that the minimum threshold in fire frequency should also include three reproductive seasons, in order to accumulate an adequate seedbank. The minimum threshold for these woodlands would therefore be a fire-free interval of 8 years. However the minimum threshold is likely to be greater than 8 years, as it is not known when the obligate seeders will reach reproductive maturity; continued monitoring in the future is necessary. The maximum fire-free period could not be determined from this study as data on the longevity of shrubs were not collected. However the very low densities of shrubs in remnant sites may reflect the exclusion of fire from some of these areas for more than 50 years. Hence the upper limit for exclusion of fire may be in the order of 20–40 years, for species which have fire-dependent germination cues.

One species, *Acacia filicifolia*, was found to have less than 100% post-fire survival, and a secondary juvenile period greater than 4 years. These results suggest that unless some inter-fire intervals are greater than the time taken for *Acacia filicifolia* to re-reach reproductive maturity (secondary juvenile period) then population decline might occur.

The historic fire regimes of grassy woodlands are poorly known and are difficult to reconstruct (Lunt 2002). There is a dearth of contemporary and historic data on fire regimes in the NET Bioregion. Benson and Ashby (2000) suggested that grassy woodlands of the NET Bioregion were subjected to relatively frequent burning by Aboriginal people, though, given the length of primary juvenile periods for obligate seeders in our study, a history of high fire frequency is unlikely for these places. In addition a field survey of the distribution and abundance of shrub species across the region showed that obligate seeding species were present in 60% of the sites (Knox, unpublished data) suggesting that inter-fire intervals were not generally shorter than 8 years.

For better management of shrub species in the remaining vestiges of the NET Bioregion grassy woodlands, further quantification of primary juvenile periods and fire responses for a broader range of species, including the rare and threatened taxa, is needed. Season of burn may also affect mortality in a population and this factor needs to be examined experimentally. Studies of the effects of fire regimes on other life history stages are also needed to develop a clear understanding of population dynamics of shrubs under different fire regimes. Finally, to test suggested minimal fire frequency thresholds in these woodlands, manipulative landscape studies of the effects of different fire regimes are needed.

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