

Effects of different fire regimes on shrubs in grassy woodlands

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Abstract

The effects of different fire regimes on shrub species in grassy woodlands in the New England Tableland (NET) Bioregion were tested at three life stages; adults, seedling recruitment and reproduction. The adult stage was examined by testing the resprouting ability of 31 species after fires of differing intensity. Most shrub species resprouted via basal lignotubers following fire, irrespective of fire intensity and shrub size. Secondly, we examined the effects of different fire intensities and fire seasons on the recruitment (emergence and survival) of seedlings in a large manipulative field experiment. Fire season and fire intensity strongly influenced seedling emergence but to a lesser extent survival of seedlings. Furthermore, post-fire emergence was more strongly influenced by fire season than by fire intensity with spring fires resulting in the enhanced seedling emergence compared to those in autumn. Fires of moderate intensity also resulted in enhanced seedling emergence for species from the Fabaceae compared to fires of low intensity. Thirdly, we examined the length of time to reproduction (primary and secondary juvenile periods) of shrub species after fires. 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. Results from these three studies indicate that fires of moderate intensity, occurring in spring, result in greater seedling emergence. Finally, it appears 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 < 8 years should be avoided.

Introduction

Fire regimes affect the population dynamics of many plant species in fire-prone communities in Australia and elsewhere in the world. Moreover, fire has been found to be essential for some plant species to complete their life cycles. Few studies have examined the effects of fire regimes on plant species in temperate woodlands of Australia (Hobbs 2002), and no previous studies have examined the effects of fire regimes on plants in grassy woodlands and forests in the NET Bioregion.

Long-term manipulative studies of populations under different fire regimes are one means of determining the influence of fire regimes on the population dynamics of plants. Such studies require much time and resources, and hence few studies approach the study of plant populations in fire-prone environments in this manner. In contrast, short-term studies examining critical life events are often used to explain or predict the response of a population to different fire regimes (Whelan 1995). Critical life events that can be used to help predict the response of plants to different fire regimes include: (i) the response of adults to fire; (ii) post-fire emergence; (iii) the establishment and subsequent survivorship of seedlings after fire, and (iv) reproduction (Whelan 1995).

The study of the response of adults to fire are important as a broad dichotomy in the response of plant populations to fire exists between those species that generally die as a result of 100% leaf scorch (obligate seeders), and those that can survive fire (resprouters) (Gill and Bradstock 1992). Obligate seeders are dependant upon seed for their continued persistence at a site (Nieuwenhuis 1987). Seed may be stored in either the canopy in woody fruits ('serotinous' or 'bradysporous' seedbanks) or in the soil (soil-stored seedbanks) (Bradstock 1981). In reality, however, a continuum from 0-100% mortality of individuals within a population exists among species (Morrison 1995; Bond and Van Wilgen 1996; Morrison and 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).

Following fire, a pulse of seedling emergence is often observed in fire-prone communities (Gill 1981). The post-fire density of seedlings is potentially affected by a number of factors, including the seedbank size following fire, the proportion of seeds in the seedbank which have had their dormancy broken, and the suitability of post-fire conditions for seedling emergence. Fire intensity can affect the density of post-fire emergence of seedlings by influencing: (i) the percentage mortality of seedbanks during a fire; (ii) the proportion of seeds released from canopy-held seedbanks; (iii) the proportion of seeds in the seedbank which have their dormancy broken, and (iv) the suitability of the seedbed for germination. Fire season can potentially affect the density of post-fire emergence of seedlings due to factors influencing seedbank size and factors affecting germination, including effects of post-fire temperature and water regimes, and temperature thresholds of fires. Fire season may also be an important factor in influencing seedling survival, as mortality may be high during periods of water stress.

The time taken to reach reproductive maturity following fire is important 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 and 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 and 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 do obligate seeding species (Abbott 1985). The secondary juvenile period of resprouters, however, tends to be shorter than the primary juvenile period for resprouters and obligate seeders (Zammit and Westoby 1987).

We examined the effect of fires on three critical stages in the life of plants to make predictions about the effects of season, intensity and frequency on populations of shrubs in grassy woodlands on the New England Tablelands Bioregion. Firstly, we

examined processes influencing adult mortality by determining: (i) which species resprout following fire; (ii) whether plant size influences post-fire survival and (iii) whether fire intensity affects mortality. Secondly, we examined processes influencing post-fire seedling emergence and survival by determining whether: (i) fire intensity affects seedling emergence and survival, and (ii) fire season affects seedling emergence and survival. Thirdly, we measured the length of the primary and secondary juvenile periods of shrub species in grassy woodlands after fires.

Methods

Study area

The NET Bioregion extends over 3,004,080 ha. (National Land and Water Resources Audit 2001). About 40% of the native vegetation in the NET Bioregion remains (National Land and Water Resources Audit 2001), and 7.5% of extant vegetation is contained within conservation reserves (Benson 1999). Grassy woodlands once covered extensive areas of the NET Bioregion (Benson and Ashby 2000); however, they have been extensively cleared for pastoralism. All studies presented in this paper were conducted at Imbota Nature Reserve and Booroolong Nature Reserve.

Fire response traits

The fire response of shrub species was followed after three experimental burns at each Nature Reserve. Experimental burning occurred at Imbota Nature Reserve in Spring 1999 and at Booroolong Nature Reserve in Autumn 2000. Each burn site was approximately 50 x 50 m and had an average fine fuel load of approximately eight tonnes/ ha. Before each fire, fine fuel (straw) was added to half the area of each burn site to double the fuel loads and determine the effects of different fire intensities on plant mortality.

Shrubs were tagged before each fire within burn areas and in adjacent unburnt woodland. The size (measured as basal girth) of each individual was also recorded. Tagged plants were then followed for three years and examined for evidence of resprouting. When individuals were found to be alive post-fire, the position of resprouting was noted. Species were classified as obligate seeders when less than 30% of individuals survived 100% leaf scorch, and species were classified as resprouters when more than 70% of individuals survived 100% leaf scorch (Gill and Bradstock 1992).

Seedling emergence and survival: Effects of fire season and fire intensity

At each Nature Reserve, three experimental burns were conducted in two seasons (spring and autumn) in two consecutive years (Spring 1999, Autumn 2000, Spring 2000 and Autumn 2001). Each burn site was approximately 50 x 50 m and had an average fuel load of approximately 8 tonnes/ha. One of three burning treatments were applied (low intensity, moderate intensity and unburnt). In order to achieve moderate fire intensity, fine fuel (straw) was added to half the area of each burn site to increase the fuel loads to at least 16 tonnes/ha. Half the plots also received supplementary watering, to maintain water to above average rainfall, in order to discern the effects of post-fire temperature and post-fire rainfall.

Seed from shrub species with soil-stored seedbanks was sown one week prior to being burnt, while seed from species with serotinous seedbanks was surface sown two weeks post-fire. Seed from species with soil-stored seedbanks was sown into 20 cm

long furrows to a depth of 1 cm with one species per furrow. Post-fire seedling emergence and survival were monitored post-fire, weekly for the first three months, then fortnightly for the following three months and then at 38 weeks and 52 weeks.

Post-fire reproduction

Observations on the primary and secondary juvenile periods were made in August 2002 and September 2003. Shrubs were examined for evidence that they had reached reproductive maturity at a number of burn sites with different times-since-fire (given below). Data for the primary juvenile period of species were collected from naturally recruiting populations and from seed sown in the field. At Imbota Nature Reserve, 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 Nature Reserve, 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

Fire response traits

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).

Patterns in seedling emergence

The effects of site, fire season, fire intensity and water on emergence were examined using partly nested analyses of deviance (with a binomial error structure) using GLMStat (Beath 2001). Separate analyses were performed for each species, consisting of two crossed between-plot factors (sites and season) and two crossed within-plot factors (burning and watering). The dependant variable was the number of seedlings that emerged and the binomial denominator the average number of viable seeds sown (determined via viability tests). *Post hoc* comparisons were conducted using a Bonferroni correction.

Patterns in seedling survival

The effects of site, fire season, fire intensity and water on emergence were examined using partly nested analyses of deviance (with a binomial error structure) using GLMStat (Beath 2001). Separate analyses were performed for each species, consisting of two crossed between-plot factors (sites and season) and two crossed within-plot factors (burning and watering). The dependant variable was the number of seedlings that were alive at 52 weeks and the binomial denominator the number of seedlings that emerged in each plot. *Post hoc* comparisons were conducted using a Bonferroni correction.

Results

Response of adults to fire

The post-fire responses of 31 shrub species were recorded, with 27 species being classified as resprouters, of which 24 species exhibited 100% survival (Table 1). Four species were found to be obligate seeders (*Acacia dealbata*, *Acacia ulicifolia*,

Cassinia leptocephala, *Cassinia quinquefaria*). No mortality of individuals outside the burn areas was recorded.

All but three species that survived fire were found to resprout exclusively via basal (lignotuberous) buds. *Jacksonia scoparia* and *Acacia implexa* resprouted via root suckers and *Acacia filicifolia* resprouted via root suckers and epicormic buds.

Formal analysis was conducted on those species that displayed some variation in mortality (i.e. *Acacia filicifolia*, *Cassinia quinquefaria* and *Olearia viscidula*). Although *Olearia* sp. aff. *elliptica* did display some variation in mortality, too few individuals were available to examine the effects of plant size and fire intensity. Neither fire intensity nor plant size significantly affected the mortality of *Acacia filicifolia* ($P > 0.05$) and *Olearia viscidula* ($P > 0.05$). Plant size was found to significantly affect the mortality of *Cassinia quinquefaria* with the smallest plants having greatest survivorship ($P > 0.01$). Fire intensity did not significantly affect the survival of *C. quinquefaria* ($P > 0.05$).

Table 1 The post-fire response, method of resprouting and time to flowering of shrub species examined. * Indicates that no data are available. For stem survival, numbers are means (sample size). n.a. indicates that the life-history trait is not applicable as this species is an obligate seeder.

	Fire response	Survival (%)	Mode of resprouting	Primary juvenile period	Secondary juvenile period
<i>Acacia buxifolia</i> subsp. <i>buxifolia</i>	resprouter	100 (6)	basal/lignotuber	*	Not flowering after 3.5 years
<i>Acacia dealbata</i>	obligate seeder	0 (3)	n.a.	Not flowering after 4 years	n.a.
<i>Acacia filicifolia</i>	resprouter	78 (23)	suckers/epicormic	Not flowering after 4 years	Not flowering after 4 years
<i>Acacia implexa</i>	resprouter	100 (11)	suckers/basal	*	Not flowering after 4 years
<i>Acacia ulicifolia</i>	obligate seeder	0 (9)	n.a.	3 years	n.a.
<i>Brachyloma daphnoides</i> subsp. <i>glabrum</i>	resprouter	100 (4)	basal/lignotuber	*	2.5 years
<i>Cassinia leptocephala</i>	obligate seeder	0 (3)	n.a.	Not flowering after 4 years	n.a.
<i>Cassinia quinquefaria</i>	obligate seeder	21 (29)	n.a.	*	n.a.
<i>Cryptandra amara</i>	resprouter	100 (5)	basal/lignotuber	*	3 years
<i>Daviesia latifolia</i>	resprouter	100 (2)	basal/lignotuber	Not flowering after 4 years	Not flowering after 4 years
<i>Epacris microphylla</i>	resprouter	100 (4)	basal/lignotuber	*	Not flowering after 3.5 years
<i>Hakea eriantha</i>	obligate seeder	*		Not flowering after 4 years	*
<i>Hakea laevipes</i> subsp. <i>graniticola</i>	resprouter	*		Not flowering after 4 years	*
<i>Hardenbergia violacea</i>	resprouter	100 (10)	basal/lignotuber	4 years	3 years
<i>Hibbertia acicularis</i>	resprouter	100 (23)	basal/lignotuber	*	3 years
<i>Hibbertia obtusifolia</i>	resprouter	100 (47)	basal/lignotuber	*	Not flowering after 3 years
<i>Hovea heterophylla</i>	resprouter	100 (3)	basal/lignotuber	*	2.5 years
<i>Indigofera adesmiifolia</i>	resprouter	100 (5)	basal/lignotuber	*	Not flowering after 4 years
<i>Indigofera australis</i>	resprouter	100 (16)	basal/lignotuber	4 years	1.5 years
<i>Jacksonia scoparia</i>	resprouter	100 (5)	suckers	*	Not flowering after 4 years
<i>Leucopogon</i> sp. nov	resprouter	100 (2)	basal/lignotuber	*	< 3 years
<i>Leucopogon lanceolatus</i> var. <i>lanceolatus</i>	resprouter	100 (7)	basal/lignotuber	Not flowering after 4 years	Not flowering after 3.5 years
<i>Lissanthe strigosa</i> subsp. <i>strigosa</i>	resprouter	100 (57)	basal/lignotuber	*	< 1.5 years
<i>Lomatia silaifolia</i>	resprouter	100 (5)	basal/lignotuber	*	Not flowering after 3.5 years
<i>Melichrus urceolatus</i>	resprouter	100 (46)	basal/lignotuber	*	< 1.5 years
<i>Monotoca scoparia</i>	resprouter	100 (18)	basal/lignotuber	*	< 1.5 years
<i>Olearia myrsinoides</i>	resprouter	100 (15)	basal/lignotuber	*	< 1.5 years
<i>Olearia</i> sp. aff. <i>elliptica</i>	resprouter	70 (10)	basal/lignotuber	Not flowering after 4 years	2 years
<i>Olearia viscidula</i>	resprouter	78 (33)	basal/lignotuber	*	2 years
<i>Pimelea linifolia</i>	resprouter	100 (3)	basal/lignotuber	*	3 years
<i>Pultenaea microphylla</i>	resprouter	100 (10)	basal/lignotuber	*	3 years
<i>Pultenaea setulosai</i>	resprouter	100 (12)	basal/lignotuber	*	3 years
<i>Rhytidisporum diosmoides</i>	resprouter	100 (3)	basal/lignotuber	*	< 1.5 years

Seedling emergence: The effects of fire season and fire intensity

Seedling emergence of seven species (*A. dealbata*, *A. filicifolia*, *C. leptocephala*, *D. latifolia*, *H. eriantha*, *H. violacea*, *I. australis* and *O. sp. aff. elliptica*) was significantly ($P < 0.01$) affected by season (Tables 2, 3). For all species, seedling emergence was greatest following spring fires compared with autumn fires. There was a significant site x season interaction for *A. dealbata*. *A. dealbata* showed greater emergence in spring compared to autumn, but there less emergence in autumn at Imbota Nature Reserve, compared with Booroolong Nature Reserve, and more emergence in spring at Imbota Nature Reserve, compared with Booroolong Nature Reserve.

A significant season x burning interaction was found for *C. leptocephala*, where seedling emergence was low across all burn treatments following autumn burns, but in spring, there was greater overall emergence especially in the low fire intensity and moderate fire intensity plots. Furthermore, there was the previously described season x site x water interaction for *C. endlicheri*.

The burning treatment was found to significantly ($P < 0.01$) affect the emergence of six species (Tables 2, 3). Seedling emergence was greatest under moderate fire intensity, followed by low intensity and lowest in the unburnt area for three species, *A. dealbata*, *A. filicifolia* and *D. latifolia* (Table 3). *H. violacea* was found to have significantly ($P < 0.01$) greater emergence in the moderate fire intensity areas compared with the unburnt areas. Two species, *C. endlicheri* and *H. laevipes*, were found to have significantly ($P < 0.01$) greater emergence in the moderate and low intensity plots compared with the unburnt plots (Table 3).

As mentioned, there was a significant burning x season interaction for *C. leptocephala*. There was also a significant burning x water interaction for *O. sp. aff. elliptica* where watering enhanced emergence in low fire intensity plots, but not in moderate fire intensity and unburnt plots.

Watering interacted with another main effect for two species, *O. sp. aff. elliptica* and *C. endlicheri*. Watering enhanced emergence of *O. sp. aff. elliptica* in low intensity plots, but not in moderate intensity and unburnt plots.

A significant site x season x water interaction was found for *C. endlicheri* (Table 2). Seedling emergence occurred in only autumn burnt and watered plots at Booroolong Nature Reserve, but at Imbota Nature Reserve emergence occurred only in spring burnt plots.

The watering treatment significantly ($P < 0.01$) increased the emergence of seedlings of *O. sp. aff. elliptica* (Table 3). While emergence of seedlings for *C. endlicheri* was found to be significantly ($P < 0.01$) affected by water, there was a significant water x season interaction (Table 2). No seedlings emerged under the watering treatment in spring; however, in autumn, seedlings only emerged under the watering treatment.

Seedling survival: The effects of fire season and fire intensity

Season significantly affected the survival of *A. littoralis*, with survivorship being greater following autumn burns ($P < 0.01$) (Tables 4, 5). There was a significant season x water interaction for *A. dealbata*, where watering in the autumn resulted in

enhanced seedling survival compared with non-watered plots. The opposite pattern occurred in spring.

The burning treatment affected the post-fire survival seedlings of two species, *A. littoralis* and *I. australis* (Tables 4, 5). Seedlings of *A. littoralis* survived only in the moderate fire intensity plots. Seedlings of *I. australis* had significantly ($P < 0.01$) lower survivorship in unburnt rather than burnt plots (Table 5). The watering treatment did not significantly ($P > 0.01$) affect the survivorship of any species in this study (Table 4).

Post-fire reproduction

Acacia ulicifolia, *Indigofera australis* and *Hardenbergia violacea* were the only species that had a primary juvenile period of less than four years (Table 1). The eight other species examined had a primary juvenile period greater than four years. Most resprouting species had a secondary juvenile period of less than four years (Table 1).

Discussion

We examined the effect of fires on three critical stages in the life of plants and make predictions about the effects of season, intensity and frequency on populations of shrubs in grassy woodlands on the New England Tablelands Bioregion that are relevant to biodiversity management.

Firstly, we found that the majority of species in this study resprout following fire, with basal resprouting being the most common mode of regeneration. These results are consistent with those of Clarke and Knox (2002). 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 those of a number of previous studies where mortality within a species was influenced by fire intensity and plant size (e.g. Moreno and Oechel 1993; Morrison and Renwick 2000).

Secondly, we examined the effects of fire season and fire intensity on seedling emergence and survival and found them to influence the emergence and survival of the shrub species studied. Fire season had the strongest influence on seedling emergence, followed by fire intensity and patterns in abundance were more strongly influenced by seedling emergence rather than seedling survival. All species displayed greater seedling emergence following spring burns. Since the number of seeds sown before each fire was held constant, these seasonal effects are due to factors affecting seed germination and emergence rather than seasonal variation in seedbank size. Nevertheless some post-fire predation of serotinous species may have occurred before germination and hence some patterns may be an indirect result of seedbank size. In this study, supplementary watering was used to distinguish between the influence of post-fire water and post-fire temperature on seedling emergence. This watering did not increase seedling emergence of most species, and there were no meaningful season x water interactions which would have indicated that post-fire rainfall/water is the factor affecting recruitment in different seasons. These results suggest that post-fire temperature is a more important factor influencing seedling emergence in these woodlands than post-fire rainfall.

Table 2 Analyses of deviance on the effects of site, fire season, burning and watering on the cumulative seedling emergence of shrub species in grassy woodlands. ** indicates $P < 0.01$. n.s. indicates not significant.

		<i>A.dealbata</i>	<i>A.filicifolia</i>	<i>A.littoralis</i>	<i>C.endlicheri</i>	<i>C.leptocephala</i>	<i>D.latifolia</i>	<i>H.rianantha</i>	<i>H.laevipes</i>	<i>H.violacea</i>	<i>I.australis</i>	<i>O. sp. aff. elliptica</i>
Between-Plots	Sites	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.
	Season	**	**	n.s.	n.s.	n.s.	**	**	n.s.	**	**	**
	SeasonxSites	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Within-Plots	Burning	**	**	n.s.	**	n.s.	**	n.s.	**	**	n.s.	n.s.
	BurningxSites	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	BurningxSeason	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	BurningxSeasonxSites	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Water	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**
	SitesxWater	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**
	SeasonxWater	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	SeasonxSitesxWater	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	BurningxWater	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.	**
	BurningxSitesxWater	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	BurningxSeasonxWater	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	BurningxSeasonxWater	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	SitesxWater	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Table 3 Mean cumulative percentage emergence of seedlings. When treatments were found to not significantly affect the percentage emergence of seedlings, (and hence means do not differ from the overall mean) refer to the overall mean. Different letters beside means indicate a significant difference.

		<i>A. dealbata</i>	<i>A. filicifolia</i>	<i>A. littoralis</i>	<i>C. endlicheri</i>	<i>C. leptocephala</i>	<i>D. latifolia</i>	<i>H. rianantha</i>	<i>H. laevipes</i>	<i>H. violacea</i>	<i>I. australis</i>	<i>O. sp. aff. elliptica</i>
Site	Imbota								4.26			
	Booroolong								11.51			
Season	Spring	8.40	11.94				11.29	8.83		16.11	22.64	7.10
	Autumn	2.56	1.95				4.21	2.13		1.53	4.37	0.17
Burning	Moderate	10.00 ^a	12.59 ^a		0.79 ^a		12.97 ^a		8.61 ^a	10.39 ^a		
	Low	4.55 ^b	5.14 ^b		1.26 ^a		8.03 ^b		9.37 ^a	7.31 ^{ab}		
	Unburnt	0.64 ^c	0.97 ^c		0.00 ^b		0.73 ^c		4.13 ^b	5.64 ^b		
Watering	Water				1.24							3.90
	no water				0.13							2.38
Overall mean		5.06	6.18	3.20	0.61	1.50	7.30	5.00	7.36	7.44	12.14	3.24

Table 4 Analyses of deviance on the effects of site, fire season, burning and watering on the survival of shrub seedlings in grassy woodlands. n.a. indicates that analyses could not be carried out due to there being too few seedlings. ** indicates $P < 0.01$. n.s. indicates not significant.

		<i>A.dealbata</i>	<i>A.filicifolia</i>	<i>A.littoralis</i>	<i>C.endlicheri</i>	<i>C.leptocephala</i>	<i>D.latifolia</i>	<i>H.rianantha</i>	<i>H.laevipes</i>	<i>H.violacea</i>	<i>I.australis</i>	<i>O. sp. aff. elliptica</i>
Between-Plots	Sites	n.s.	**	n.s.	n.a.	n.a.	n.s.	n.s.	n.s.	**	n.s.	na
	Season	n.s.	n.s.	**			n.s.	n.s.	n.s.	n.s.	n.s.	
	SeasonxSites	n.s.	n.s.	n.s.			n.s.	n.s.	n.s.	n.s.	n.s.	
Within-Plots	Burning	n.s.	n.s.	**			n.s.	n.s.	n.s.	n.s.	**	
	BurningxSites	n.s.	n.s.	n.s.			n.s.	n.s.	n.s.	n.s.	n.s.	
	BurningxSeason	n.s.	n.s.	n.s.			n.s.	n.s.	n.s.	n.s.	n.s.	
	BurningxSeasonxSites	n.a.	n.s.	n.s.			n.s.	n.s.	n.s.	n.s.	n.s.	
	Water	n.s.	n.s.	n.s.			n.s.	n.s.	n.s.	n.s.	n.s.	
	SitesxWater	n.s.	n.s.	n.s.			n.s.	n.s.	n.s.	n.s.	n.s.	
	SeasonxWater	**	n.s.	n.s.			n.s.	n.s.	n.s.	n.s.	n.s.	
	SeasonxSitesxWater	n.s.	n.s.	n.s.			n.s.	n.s.	n.s.	n.s.	n.s.	
	BurningxWater	n.s.	n.s.	n.s.			n.s.	n.s.	n.s.	n.s.	n.s.	
	BurningxSitesxWater	n.s.	n.s.	n.s.			n.s.	n.s.	n.s.	n.s.	n.s.	
	BurningxSeasonxWater	n.s.	n.s.	n.s.			n.s.	n.s.	n.s.	n.s.	n.s.	
	BurningxSeasonxWater	n.s.	n.s.	n.s.			n.s.	n.s.	n.s.	n.s.	n.s.	
	BurningxSeasonxWater	n.a.	n.a.	n.a.			n.a.	n.s.	n.s.	n.a.	n.a.	
SitesxWater												

Table 5 Mean percentage survival of seedlings. When treatments were found to not significantly affect the percentage emergence of seedlings, (and hence means do not differ from the overall mean) refer to the overall mean. Different letters beside means indicate a significant difference.

		<i>A. dealbata</i>	<i>A. filicifolia</i>	<i>A. littoralis</i>	<i>C. endlicheri</i>	<i>C. leptocephala</i>	<i>D. latifolia</i>	<i>H. rianantha</i>	<i>H. laevipes</i>	<i>H. violacea</i>	<i>I. australis</i>	<i>O. sp. aff. elliptica</i>
Site	Imbota		14.80							37.75		
	Booroolong		35.27							69.9		
Season	Spring			0.00								
	Autumn			10.94								
Burn	Moderate			12.96 ^a							37.85 ^a	
	Low			0.00 ^b							34.27 ^a	
	Unburnt			0.00 ^b							17.75 ^b	
Water	Water											
	No water											
Mean survival of emerged seedlings		20.91	21.6	4.97	0.00	2.94	30.23	29.80	53.26	42.33	30.11	4.08

Greater seedling emergence occurred in the moderate intensity burn areas for species in the Fabaceae. These results support those of Clarke et al. (2000) who found that many shrub species from the Fabaceae, in grassy woodlands in the NET Bioregion, require heat for the breaking of seed dormancy. Enhanced seedling emergence of some species in areas with moderate fire intensity might be due to changes in the suitability of the seedbank.

Finally, we examined the time taken for species to reach reproductive maturity following fire. 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. These results are consistent with previous studies where the primary juvenile period has been found to be longer than the secondary juvenile period of co-occurring species (Zammit and Westoby 1987). These results show that the maturation rate for higher altitude woodland species are longer than coastal conspecifics (Knox 2003; Knox & Clarke in press).

Fire Management Implications

Whilst fire intensity had minimal influence on mortality of adults, and little influence on seedling survival, fire intensity had a profound affect on the emergence of species from the Fabaceae. These results suggest that fires of moderate intensity, or at least the avoidance of repeated burning at low fire intensity, are preferable in order to maintain population size of species with hard seedcoats within grassy woodlands.

Seedling emergence of shrubs was higher following spring fires, rather than autumn fires. Therefore, we suggest that fires occurring in spring are preferable, or at least repeated burning of areas in autumn should be avoided, as there was little seedling emergence of any species following autumn burns. Surprisingly, the season in which fires occurred had little influence on the subsequent survival of seedlings.

The 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. Given that the primary juvenile period for most obligate seeders in this study was found to be greater than 4 years, this suggests that population decline will occur for many obligate seeders 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 include three reproductive seasons in order to accumulate an adequate seedbank. Therefore, the minimum threshold for these woodlands would be a fire interval of 8 years. Clearly, the minimum threshold is likely to be greater than 8 years as it is not known when the obligate seeders will reach reproductive maturity, and so continued monitoring in the future is required.

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