

Fire season and intensity affect shrub recruitment in temperate sclerophyllous woodlands

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Received: 5 August 2005 / Accepted: 31 May 2006 / Published online: 18 July 2006
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Abstract The season in which a fire occurs may regulate plant seedling recruitment because of: (1) the interaction of season and intensity of fire and the temperature requirements for seed release, germination and growth; (2) post-fire rainfall and temperature patterns affecting germination; (3) the interaction of post-fire germination conditions and competition from surrounding vegetation; and (4) the interaction of post-fire germination conditions and seed predators and/or seedling herbivores. This study examined the effects of different fire intensities and fire seasons on the emergence and survival of shrubs representing a range of fire response syndromes from a summer rainfall cool climate region. Replicated experimental burns were conducted in two seasons (spring and autumn) in 2 consecutive years and fuel loads were increased to examine the effects of fire intensity (low intensity and moderate intensity). Post-fire watering treatments partitioned the effects of seasonal temperature from soil moisture. Higher intensity fires resulted in enhanced seedling emergence for hard-seeded species but rarely influenced survival. Spring fires enhanced seedling emergence across all functional groups. Reduced

autumn recruitment was related to seasonal temperature inhibiting germination rather than a lack of soil moisture or competition. In Mediterranean-type climate regions, seedling emergence has been related to post-fire rainfall and exposure of seeds to seed predators. We think a similar model may operate in temperate summer rainfall regions where cold-induced dormancy over winter exposes seeds to predators for a longer time and subsequently results in recruitment failure. Our results support the theory that the effect of fire season is more predictable where there are strong seasonal patterns in climate. In this study seasonal temperature rather than rainfall appears to be more influential.

Keywords Fire regime · Seedling emergence · Seedling survival · Grassy woodlands

Introduction

Fire is a recurring event in the world's fire-prone formations and has the capacity to change the composition of vegetation (Bond et al. 2005). In particular, the composition of fire-prone sclerophyll ecosystems of the southern hemisphere is known to be strongly influenced by fire regimes (frequency, intensity and season) (Bond and van Wilgen 1996; Bradstock et al. 2002). While the effects of fire frequency on plant populations are well known, comparatively few studies have examined the effects of fire season and fire intensity in replicated experiments. This is particularly true of the fire-prone forest and woodland communities in non-Mediterranean climates where both fire intensity and season are variable (Bradstock et al. 2002).

Communicated by Fernando Valladares

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Fire intensity potentially influences plant population dynamics by affecting not only adult persistence (Vesk and Westoby 2004), but also post-fire seedling emergence and survival. Fire intensity regulates the dormant proportions of seed banks for species with heat-related germination cues (Auld 1986; Bell et al. 1987a, b; Bond and Van Wilgen 1996), and influences seed release of species with canopy-held seed banks (Bradstock and Myerscough 1981; Zammit and Westoby 1987; Enright and Lamont 1989; Bradstock et al. 1994; Setterfield 1997). Fire intensity also affects the amount of standing vegetation that is consumed by a fire, thereby influencing the degree to which post-fire competition from persisting vegetation affects seedling mortality (Bond 1984).

Fuel accumulation, flammability, and ignition are all influenced by climatic and weather conditions and hence determine the season in which a fire occurs. In turn, fire season may regulate seedling recruitment because of: (1) the interaction of season and intensity of fire and the temperature requirements for seed release, germination and growth; (2) post-fire rainfall and temperature patterns affecting germination; (3) the interaction of post-fire germination conditions and competition from surrounding vegetation; and (4) the interaction of post-fire germination conditions and seed predators and/or seedling herbivores. The first two hypotheses relate to abiotic thresholds, whilst the third and fourth involve the interaction of these thresholds with biotic forces causing seedling attrition.

Post-fire recruitment of sclerophyllous shrub species is often mediated by rainfall patterns and temperature, both of which vary with season (e.g. Clark 1988; Hodgkinson 1991; Bradstock and Bedward 1992). Hence, there has been some focus on the effect of season of burn in winter-dominated rainfall regions (Bond 1984; Bell et al. 1987a, b; Cowling and Lamont 1987; Hobbs and Atkins 1990; Grant and Loneragan 1999) but few in uniform (Clark 1988; Whelan and York 1998) or in temperate summer rainfall regions. More critically, no experiments have attempted to discriminate the effects of post-fire temperature from post-fire rainfall; hence, little is known about the applicability of these studies to areas with summer-dominated rainfall.

While the experimental designs of most studies examining the effects of fire season on seedling emergence and survival have included spatial replication (but see Cowling and Lamont 1987; Hobbs and Atkins 1990), most have lacked temporal replication (Cowling and Lamont 1987; Hodgkinson 1991; Grant et al. 1997; but see Whelan and York 1998; Liu et al. 2005). Clearly, to confidently conclude that patterns in seedling

emergence and survival are due to seasonal effects, replication of fire season across years is required. Another inherent challenge in examining the effects of fire season is the potential interaction of season and fire intensity affecting both abiotic and biotic thresholds. Fire season may influence the moisture content of fuels and therefore influence the intensity of a fire (Grant et al. 1997). Similarly, fire season may influence heat penetration into soil due to differing soil moisture contents of the soil (Hodgkinson 1991).

One means of distinguishing between seasonal effects, and those due to the interaction between fire season and fire intensity, is to include both factors in the design of a replicated field experiment and to initially saturate the seed bank. Therefore, our study examined the effects of fire intensity and fire season on the recruitment of shrubs, with a range of fire response syndromes, in eucalypt-dominated grassy woodlands. We first tested whether fire affected seedling emergence in contrast to unburnt ground. We next tested whether: (1) fire intensity or fire season more strongly influenced seedling emergence and survival; (2) there were synergistic effects of fire season and intensity on seedling emergence and survival; and (3) effects of fire season were related to post-fire temperature or moisture thresholds. To test whether seasonal temperature, rather than a lack of soil moisture, inhibited emergence additional laboratory germination experiments were implemented.

Materials and methods

Study region

The study region is the New England Tableland (NET) Bioregion of eastern Australia that falls within the Cfb (dry cool temperate) summer rainfall climate region with an altitudinal range of 750–1,500 m. Five major sclerophyllous vegetation types occur in the Bioregion; grassy woodlands, dry sclerophyll forests, rocky outcrops, wet heaths and wet sclerophyll forests. These broad groups form distinct floristic associations that are related to climate gradients, lithology and local physiography rather than fire history (Benson and Ashby 2000). As a generalization, nutrient-poor siliceous soils provide habitats for scleromorphic shrub-dominated woodlands and forests whilst the more clayey soils derived from metasediments and basalts support grassy woodlands and forests (Benson and Ashby 2000), which are the focus of our experiments.

Two nature reserves representative of eucalypt-dominated tableland grassy woodlands in the Bioregion

were selected as experimental study sites. The lower altitude site (Imbota Nature Reserve) at ca. 1,020 m has an average maximum temperature in January (summer) of 27.1°C, while the average minimum temperature in July (winter) is 0.3°C, with an average yearly rainfall of 790 mm. The higher altitude experimental site (Booroolong Nature Reserve) at ca. 1,300 m has an average maximum temperature in January of 24.6°C with an average minimum temperature in July of -0.6°C, and an average yearly rainfall of 884 mm. Both experimental sites have metasediment lithology with yellow podzolic soils and were in areas that were generally of slight slope. Weather patterns during the course of this study were similar to those of long-term climate averages.

Prior to this study neither of the nature reserves had been burnt for at least 30 years. There is little knowledge of the pre-European fire regime of the NET bioregion, but it would appear that fragmentation of the landscape has led to a reduction in fire frequency.

Species selection

We selected a range of shrub species representative of woody lineages commonly found in temperate grassy woodlands (i.e. Fabaceae, Ericaceae, Asteraceae and Proteaceae; see Clarke and Knox 2002) (see Table 1). These represent a wide range of seed and adult plant-persistence traits including resprouters and obligate seeder (killed by fire) species with different allocation patterns (Knox and Clarke 2005) and those with soil-stored and canopy-held seed banks (Table 1). A total of 13 species was selected to examine the effects of different fire regimes on the emergence and survival of

shrubs in the grassy woodlands. All species, with the exception of *Lissanthe strigosa* and *Melichrus urceolatus* were found to emerge in the field. Following the spring 1999 fires, it was decided to discontinue examining *L. strigosa* and *M. urceolatus* due to the lack of emergence and the time required for collecting seed.

Field experiment

The experimental design of this study is a fully replicated partly nested model (Quinn and Keough 2002). At each nature reserve, three experimental sites were established in two seasons (spring and autumn) in 2 consecutive years (spring 1999, autumn 2000, spring 2000 and autumn 2001). One of three burning treatments was applied (low intensity, moderate intensity and unburnt). In order to achieve a 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 t/ha. Each burn site was approximately 50 × 50 m and had an average fine fuel load of approximately 8 t/ha. Two watering regimes were also applied (supplementary water and no supplementary water). Supplementary water was applied in order to partition the effects of post-fire temperature from that of post-fire rainfall. Plots that received supplementary watering included a buffer zone to make the plot areas watered 1 m². Watered plots received supplementary water to achieve a total of 25 mm water/week (rainfall plus supplementary water). When rainfall was greater than 25 mm for the week, no additional water was added to the plots. The figure of 25 mm/week derives from a calculation based on total rainfall for the wettest month. The median rainfall of the wettest month is

Table 1 Life history traits of shrub species used to examine the effects of different fire regimes in field and laboratory experiments. *HS* Hard-seededness, *FE* field experiment, *LG*

laboratory germination, *SG* soil germination, *R+* resprouters, *R-* obligate seeders, *P+* persistent seed bank, *P-* non-persistent seed bank

Family	Species	Experiments	Seed mass (mg)	Adult fire response	Storage of seedbank	Innate Dormancy	Persistence groups ^a	Mean seed viability
Asteraceae	<i>Cassinia leptcephala</i>	FE, LG, SG	0.09	Killed	None	None	R-P-	60.9
	<i>Olearia</i> sp. aff. <i>elliptica</i>	FE, LG	0.45	Resprouts	None	None	R+P-	82.5
Casurinaceae	<i>Allocasuarina littoralis</i>	FE, LG	2.59	Resprouts	Canopy	None	R+P+	70.6
Cupressaceae	<i>Callitris endlicheri</i>	FE, LG	3.80	Killed	Canopy	None	R-P+	20.9
Ericaceae	<i>Lissanthe strigosa</i>	FE	8.96	Resprouts	Soil	Yes	R+P+	-
	<i>Melichrus urceolatus</i>	FE	4.52	Resprouts	Soil	Yes	R+P+	-
Fabaceae	<i>Acacia dealbata</i>	FE, LG	13.83	Killed	Soil	Yes (HS)	R-P+	73.4
	<i>Acacia filicifolia</i>	FE, LG, SG	12.40	Resprouts	Soil	Yes (HS)	R+P+	67.8
	<i>Daviesia latifolia</i>	FE, LG	7.05	Variable	Soil	Yes (HS)	R+P+	84.6
	<i>Hardenbergia violacea</i>	FE, LG	39.64	Resprouts	Soil	Yes (HS)	R+P+	74.4
	<i>Indigofera australis</i>	FE, LG	6.14	Resprouts	Soil	Yes (HS)	R+P+	82.2
Proteaceae	<i>Hakea eriantha</i>	FE, LG, SG	18.25	Variable	Canopy	None	R+P+	100
	<i>Hakea laevipes</i>	FE, LG, SG	20.1	Resprouts	Canopy	None	R+P+	99.9

^aPersistence groups of Pausas et al. (2004)

91 mm, therefore, 100 mm water/ month is approximately 10% greater than the median rainfall of the wettest month. Rainfall was assessed weekly for a local (Armidale) rain station (Australian Bureau of Meteorology 1999–2002). There were three replicates of each treatment. Unfortunately, due to the spring of 1999 being very wet, the experimental burns at Booroolong Nature Reserve could not be conducted and hence an unbalanced design resulted. There were 378 plots in total.

Seed from shrub species with soil-stored seedbanks was sown 1 week prior to being burnt, while seed from species with serotinous seedbanks was surface sown 2 weeks post-fire (Tables 1, 2). Twenty seeds of each species were sown in each plot with the exception of the Asteraceae species where ten seeds were sown. Seed for species with soil-stored seedbanks were sown into 20-cm-long furrows to a depth of 1 cm, one species per furrow. Species with serotinous seedbanks were surface sown in rows. Seeds were sown in rows in order to minimise mistaking naturally recruiting seedlings for those that were artificially sown. Nevertheless, if there was natural recruitment it would not alter our conclusions as recruitment would be randomised across treatments. Seed viability was determined before each burn (Table 2). A total of 77,760 seeds were sown in the experiment. Post-fire seedling emergence and survival were monitored at weekly intervals for the first 3 months, then fortnightly for the following 3 months and then at 38 and 52 weeks.

Laboratory experiments

The first laboratory experiment tested the germination of all species used in the field under two temperature regimes representing spring–summer conditions and autumn–winter conditions with respective mean diurnal regimes of 15/25°C and 0/15°C with the same day length. Three replicates each of ten seeds of each species (Table 1) were placed on germination trays on moistened germination pads and germination was recorded when the radicle had emerged from the seed coat. All hard-seeded species had their innate dormancy broken by heating them to 80°C for 10 min to rupture their seed coats. Germinations were monitored for 28 days.

A second germination experiment examined seedling emergence from seeds buried in soil and exposed to factorial combinations of temperature and moisture. Ten seeds of each of four species (Table 1) were sown to a depth of 1 cm in containers (10 × 15 × 5 cm³) packed with soil to match field bulk density. Three water treatments were applied; emulation of summer

rainfall (3 wet days per week), above average rainfall (6 wet days per week) and winter rainfall (1 wet day per week). A wet day involved wetting of soil to field capacity. Three replicate containers of each treatment were placed into germination cabinets for each of two temperature regimes; summer (15/25°C) and winter (5/15°C). All hard-seeded species had their innate dormancy broken by scarification of the seedcoat with a razor blade. Emergences were monitored for 28 days.

Data analyses

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 generalized linear models (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 variables were: (1) the number of seedlings that emerged and the binomial denominator the average number of viable seeds sown (determined via viability tests), and (2) 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. In the germination experiments, number of germinations or emergences after 28 days were analysed in GLM using a binomial error structure with the binomial denominator adjusted for the number of viable seeds sown.

Results

Seedling emergence

Seedling emergence generally occurred in those areas where seeds were sown and few seedlings were observed to emerge from natural seedbanks. The highest number of seedlings observed to emerge was from the hard-seeded legume group, whilst the lowest was generally from the serotinous species (Table 2) and no seedlings were observed to emerge from seeds of the two epacrids. The response to treatments varied among species, and whilst complex interactive effects were detected in a few species, most responded to treatments in a consistent way in time and space. Season of fire and intensity of fire were prominent in affecting number of seeds to emerge whilst watering and site factors were less so (Table 2, Figs. 1, 2). Resprouting species with persistent seed banks showed the strongest response to season and fire (Figs. 1, 2).

Table 2 Mean cumulative percentage emergence of seedlings where there were significant effects of treatments. When treatments did not significantly affect emergence of seedlings (and hence means do not differ from the overall mean) the overall mean is presented. Different letters indicate a significant difference where there were more than two levels in a treatment

	<i>A. dealbata</i>	<i>A. filicifolia</i>	<i>A. littoralis</i>	<i>C. endlicheri</i>	<i>C. leptoccephala</i>	<i>D. latifolia</i>	<i>H. eriantha</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			12.97 a		8.61 a	10.39 a		
	Low	4.55 b	5.14 b		0.79 a	8.03 b		9.37 a	7.31 a, b		
	Unburnt	0.64 c	0.97 c		1.26 a	0.73 c		4.13 b	5.64 b		
Watering	Water				0.00 b						3.90
	No water				1.24						2.38
Overall mean		5.06	6.18	3.20	0.61	7.30	5.00	7.36	7.44	12.14	3.24

Effects of season and site on seedling emergence

Seedling emergence of seven species (*Acacia dealbata*, *Acacia filicifolia*, *Daviesia latifolia*, *Hakea eriantha*, *Hardenbergia violacea*, *Indigofera australis* and *Olearia sp. aff. elliptica*) was significantly ($P < 0.01$) affected by season of fire (Table 2). For all of these species seedling emergence was enhanced following spring fires compared with autumn fires (Table 2; Fig. 2). A significant site \times season interaction was found for one species, *A. dealbata*, with seasonal effects being stronger at Imbota Nature Reserve than at Booroolong Nature Reserve. Similarly, one serotinous species (*Hakea laevipes*) had consistently more emergence at Imbota Nature Reserve in all seasons (Tables 2). The daisy shrub, *C. leptoccephala*, had a significant season \times burning interaction 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. A complex site \times season \times water interaction was found for the fire-killed serotinous tree, *Callitris endlicheri* where a few seedlings emerged following the autumn burn in watered plots at Booroolong Nature Reserve, whereas emergence only occurred following spring burns in Imbota Nature Reserve. Site was found to significantly ($P < 0.01$) interact with other main factors for four other species. The significant site \times water interaction for the daisy shrub (*O. sp. aff. elliptica*) was due to watering-enhanced emergence at the Imbota Nature Reserve, but not at Booroolong Nature Reserve.

Effects of fire intensity and watering on seedling emergence

The burning treatment was found to significantly ($P < 0.01$) affect the emergence of six species (Table 2, Fig. 1). Seedling emergence was greatest under moderate fire intensity, followed by low intensity and lowest in the unburnt area for three legume species with hard seed coats (*A. dealbata*, *A. filicifolia* and *D. latifolia*) (Table 2). In addition, the twinning legume, *H. violacea*, was found to have significantly ($P < 0.01$) greater emergence in the moderate fire intensity areas compared with the unburnt areas. Two serotinous species, *C. endlicheri* and *H. laevipes*, were found to have significantly ($P < 0.01$) greater emergence following moderate and low intensity fires compared with unburnt areas that had seed sown into them (Table 2). Watering had no consistent effect on the emergence of seedlings with only one daisy shrub, *O. sp. aff. elliptica*,

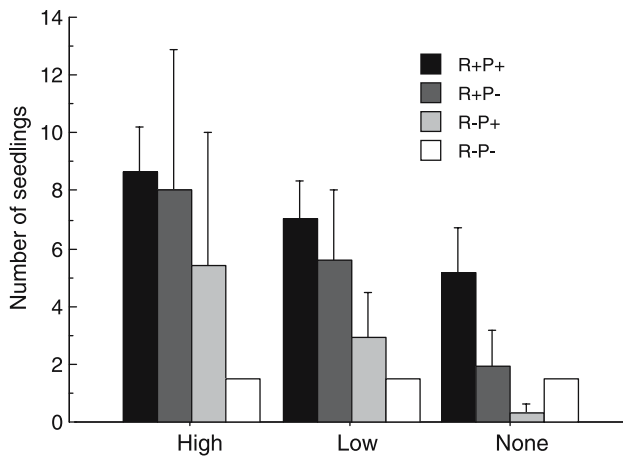


Fig. 1 Mean (+ SE) number of seedlings emerging for each fire intensity treatment pooled across all other treatments. *R+* Resprouters, *R-* obligate seeders, *P+* persistent seed bank, *P-* non-persistent seed bank (see Table 1 for persistence groups)

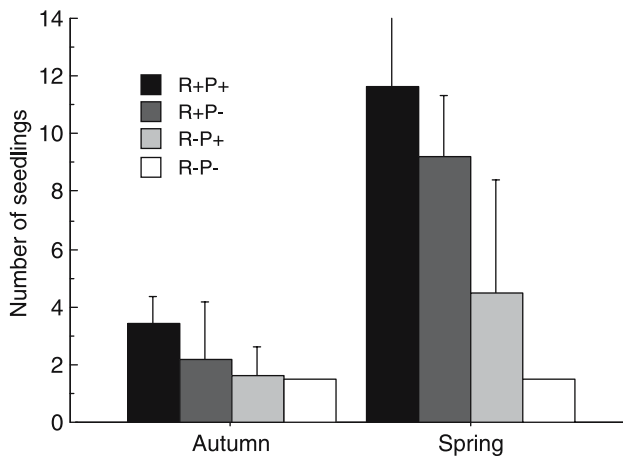


Fig. 2 Mean (+ SE) number of seedlings emerging for each fire season treatment pooled across all other treatments. See Table 1 for persistence groups. For abbreviations, see Fig. 1

having enhanced emergence in low intensity plots, but not in moderate intensity and unburnt plots.

Survival of seedlings

The serotinous species *H. laevipes*, *C. endlicheri* had the highest (53%) and lowest (0%) proportion of seedlings surviving, respectively, whilst the hard-seeded legumes consistently had greater than 20% seedling survival (Table 3). Furthermore, the percentage survival of emerged seedlings for the two daisy shrubs (*C. leptoccephala*, and *O. sp. aff. elliptica*) was below 5% (Table 3). Season of fire, fire intensity and site did not consistently affect seedling survival among species, nor did watering affect seedling survival. Season of fire

Table 3 Mean percentage survival of seedlings as a percentage of emerged seedlings and as a percentage of viable seeds sown and treatment effects^a

	<i>A. dealbata</i>	<i>A. filicifolia</i>	<i>A. littoralis</i>	<i>C. endlicheri</i>	<i>C. leptoccephala</i>	<i>D. latifolia</i>	<i>H. eriantha</i>	<i>H. laevipes</i>	<i>H. violacea</i>	<i>I. australis</i>	<i>O. sp. aff. elliptica</i>
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
Mean survival of viable seeds	1.06	1.34	0.16	0.00	0.04	2.21	2.20	3.96	2.12	3.66	0.13

^aSite: *A. filicifolia*—Imbota Nature Reserve (NR) 14.80%, Booroolong NR 35.27%; *H. violacea*—Imbota NR 37.75%, Booroolong NR 69.90%. Season: *A. littoralis*—spring 0.00%, autumn 10.94%. Burning: *A. littoralis*—moderate 12.96%, low 0.00%, unburnt 0.00%; *I. australis*—moderate 37.85%, low 34.27%, unburnt 17.75%

significantly ($P < 0.01$) affected survival of one species (*A. littoralis*) with survivorship being greater following autumn burns (11%) compared to no seedlings surviving spring burns. There was a significant season \times water interaction for *A. dealbata*, where watering in the autumn resulted in enhanced seedling survival compared with non-watered plots, whilst the opposite pattern occurred in spring. The burning treatment affected the post-fire survival seedlings of two species (*A. littoralis* and *I. australis*) with significantly lower survival in unburnt plots. Site significantly ($P < 0.01$) affected the survival of two species (*A. filicifolia* and *H. violacea*) where both had greater survivorship at Booroolong Nature Reserve than at Imbota Nature Reserve.

Laboratory germinations and emergence

Numbers of seeds germinating after 28 days were significantly greater in the summer temperature regime compared with the winter regime and the response to temperature was similar across the range of functional types (Table 4). Several species failed to germinate at all under winter temperatures even when their seed coats had been ruptured and they appeared imbibed. Seedling emergences in the second experiment were also strongly temperature dependent with no seedling emergences of serotinous species under the winter-wet conditions (Table 4). Moisture conditions also strongly regulated emergence under summer temperatures with no seedling emergences with 1 day/week watering.

Discussion

Fire regimes influenced the pattern of post-fire recruitment of all shrub species in the grassy woodlands studied. In summary we found:

1. Fire enhanced the recruitment of most species regardless of functional groups.
2. Higher fire intensity increased post-fire emergences of most species, particularly those species with hard seed coats, but had little influence on post-fire survival of seedlings.
3. Fire season affected seedling emergence of most species, with enhancement following spring fires, but had little influence on seedling survival.
4. The season effect was related to soil temperature rather than moisture deficits.

Nevertheless, while these generalisations can be made not all species responded in this manner and there was some interspecific variation in response.

Effects of burning on emergence

Fires have not occurred in these woodlands for more than 30 years and while the pre-European burning regime of these areas is not known, it is almost certain that fire would have occurred more frequently than they do currently (Benson and Ashby 2000). Burning the woodlands resulted in increased emergence of seedlings across a broad spectrum of persistence syndromes and recruitment was not inhibited by fire for any species. This suggests that fire is an important regulator of shrub populations in temperate eucalypt woodlands but the intensity and season of fire further mediate recruitment patterns. The enhanced emergence of seedlings at burnt sites reflects both fire-related germination cues and/or fire altering the site conditions (regeneration niche). In our study the dormancy of hard-seeded species (*Acacia*, *Davesia*, *Hardenbergia*) was not artificially broken prior to sowing and subsequently fire enhanced seedling emergence. This pattern is attributed to heat breaking

Table 4 Mean proportion of germinations and emergences from laboratory germination experiments

Family	Species	Experiment 1			Experiment 2			
		Summer	Winter	χ^2, P	Summer wet	Summer moist	Winter wet	Winter moist
Asteraceae	<i>C. leptcephala</i>	0.10	0		0	0	0	0
	<i>O. sp. aff. elliptica</i>	0.16	0		0	0	0	0
Casurinaceae	<i>A. littoralis</i>	0.16	0		–	–	–	–
Cupressaceae	<i>C. endlicheri</i>	0.10	0		–	–	–	–
Fabaceae	<i>A. dealbata</i>	0.20	0.03	3.7, $P < 0.05$	0.60	0.32	0.25	0.20
	<i>A. filicifolia</i>	0.33	0		0.64	0.24	0.41	0.38
	<i>D. latifolia</i>	0.37	0		–	–	–	–
	<i>H. violacea</i>	0.53	0.10	5.4, $P < 0.01$	–	–	–	–
	<i>I. australis</i>	0.47	0		–	–	–	–
Proteaceae	<i>H. eriantha</i>	0.83	0		0.85	0.15	0	0
	<i>H. laevipes</i>	0.90	0.33	12.6, $P < 0.01$	0.80	0.10	0	0

seed dormancy rather than changing site conditions, because the study by Clarke and Davison (2001) showed no difference in recruitment between burnt and unburnt treatments for hard-seeded species with their dormancy broken prior to dispersal. Conversely, two serotinous species (*Callitris* and *Hakea*) had enhanced recruitment when sown into burnt ground, which is a similar result to that found by Clarke and Davison (2001) where non-soil-stored seeded species (*Cassinia* and *Xanthorrhoea*) were sown into burnt ground. These patterns suggest the reduced competition in the post-fire environment enhances seedling emergence for those species that disperse into burnt ground (Keeley and Zedler 1978).

Effects of fire intensity on seedling emergence and survival

Fire intensity not only affects survival of standing plants but regulates seed bank release and dormancy (Auld 1986; Bradstock et al. 1994). In a related study, Knox and Clarke (2004) found that fire intensity did not affect adult survival for our study species but in this study it strongly affected seedling emergence of hard-seeded species. Dry heat is known to break seed dormancy in fire-prone ecosystems throughout the world (Keeley and Bond 1997) and in our study region (Auld 1996; Clarke et al. 2000). Pre-germination heat shock has also been shown to increase initial growth rates of seedlings in hard-seeded species (Hanley et al. 2001). Hence, fire intensity was expected to strongly influence the emergence of hard-seeded legume species and limit their recruitment to the post-fire period. With the passage of fires, four legume species showed enhanced emergence with the more intense fire and lowest emergence in the unburnt treatments. More varied responses would be expected from seeds naturally distributed in the soil profile because we sowed seeds to a uniform depth. Hence seeds closer to the surface may have been killed by the more intense fire and those distributed more than 4 cm deep may not have their dormancy broken (Auld 1996). No intensity by season interactions were detected, suggesting that post-fire soil heating on burnt ground via insolation (independent of soil temperatures generated by fires) did not affect seedling emergence. However, soil heating after summer wildfires may be sufficient to promote germination of hard-seeded species if they are intense enough to remove the forest canopy (Auld and Bradstock 1996). Moderate fire intensity also increased the survival of one species (*Allocasuarina*) suggesting fire intensity may reduce competition from standing

vegetation, resulting in the greater survivorship of seedlings.

Fire intensity did not affect seedling emergence of any serotinous species; this was expected because this study did not examine the influence of fire intensity on post-fire seedbank size of serotinous species. Previous studies have shown that fire intensity can affect seedling emergence of serotinous species by influencing the mortality of seeds in the canopy (Bradstock et al. 1994) and the release of seeds from the canopy (Bradstock and Myerscough 1981; Zammit and Westoby 1987; Enright and Lamont 1989; Setterfield 1997).

Effects of season on seedling emergence and survival

Fire season was found to affect the emergence of seedlings for eight of the species sown, all of which displayed greater seedling emergence following spring burns. Since the number of seeds sown was held constant, these seasonal effects were due to factors affecting seed germination and emergence rather than seasonal variation in seed bank size. The seasonal effect, however, contrasts with research in Mediterranean-type climates that found seedling emergence to be greatest following autumn burns (Bond 1984; Bond et al. 1984; Bell et al. 1987a, b; Cowling and Lamont 1987; Hobbs and Atkins 1990; Midgley 1989; Grant and Loneragan 1999). Our seasonal pattern also contrasts with those in subtropical climates where winter (dry season) burns result in enhanced plant recruitment (Spier and Snyder 1998; Liu et al. 2005).

Several hypotheses have been suggested to explain why fire season may affect post-fire germination and emergence in seasonal climates. The explanations are the: (1) dormancy threshold hypothesis, (2) post-fire resource hypothesis, and (3) post-fire competition/predation hypothesis. Several post-fire studies have noted seedling emergence was lowest when burning occurred in the cool season and suggested that this may not be a response to season per se but to soil heat penetration (e.g. Hodgkinson 1991). Thus in the cool season, when the soil retains more moisture, the passage of fire may not heat the soil enough to break the dormancy of seeds requiring heat shock. If such a process were influencing seedling emergence in our study, a significant burning \times season interaction would have been detected for hard-seeded species, which was not the case in our study.

The post-fire resource hypothesis suggests that seedling emergence will be greatest under conditions that favour the successful germination, emergence and survival of seedlings. Bradstock and Bedward (1992)

modelled this effect in eastern Australia and found that summer/autumn fires should be most favourable for seedling survival because of rainfall patterns. In our study, we used supplementary watering as a treatment to distinguish between the influence of post-fire water availability and post-fire temperature on seedling emergence. Supplementary watering did not, however, increase seedling emergence of most species, and there were no meaningful season \times water interactions which would have indicated that post-fire rainfall is the factor affecting recruitment in different seasons. Hence, our field experiment results suggest that post-fire soil temperature plays an important role in seedling emergence as it does in the genus *Leucopogon* (Ooi et al. 2004). This is supported by our laboratory experiments that showed germination of all species was inhibited by cold temperatures. Curiously, season of emergence did not influence the survival of seedlings for most species studied and the watering treatment did not enhance emergence or survival. This result is surprising since desiccation might be expected to be one of the main factors contributing to seedling mortality (Clarke and Davison 2001).

In the winter rainfall regions of South Africa and in south-western Australia seedling emergence of serotinous Proteaceae species has been explained by interaction of post-fire germination resources and seed predators and/or seedling herbivores (Bond 1984; Bell et al. 1987a, b; Midgley 1989). In these circumstances summer-dormant seeds are removed by seed predators prior to autumn/winter rainfall. Hence, late season fires that release seeds favour recruitment because there is less attrition due to seed predators. We think a similar model may operate in temperate summer rainfall regions where cold-induced dormancy over dry winters exposes canopy-released seed to predators over winter. This explains why seeds sown in autumn did not germinate in the subsequent summer when soil temperatures were high enough. Ants are known to remove seeds of all species we used and experiments have shown that they influence seedling emergence of both serotinous and soil-stored seeds (Clarke and Davison 2001). Hence we think the predator-mediated attrition model of Bond (1984) may be applicable. This model could also operate for soil-stored seeds where imbibed seeds are more vulnerable to predation and decay over winter, but this requires further examination.

Conclusions

We found strong evidence that fire regimes influence seedling emergence of shrubs in temperate (summer-

wet) woodlands. Fire intensity regulates recruitment patterns directly through abiotic thresholds by breaking dormancy and possibly through control of competition as a biotic threshold. In contrast to that found for Mediterranean-type climates, spring fires resulted in higher recruitment than autumn fires. This may be explained through a combination of abiotic thresholds and biotic interactions where post-fire temperatures inhibit germination and expose seeds to predation and/or seed decay prior to summer when temperature and rainfall are conducive to germination. Thus, higher intensity spring fires that release seeds from canopies, break dormancy and reduce competition are likely to result in enhanced shrub recruitment in these temperate woodlands.

Acknowledgements We thank the New South Wales National Parks and Wildlife Service (NSW NPWS) for their assistance with this research. Financial support was provided for K. J. E. K. by an Australian Postgraduate Award, an NCW Beadle award and NSW NPWS. The staff and students of Botany at the University of New England helped in various ways. Comments from reviewers and editors were helpful for revision of this article. All experiments comply with Australian law. We thank Wal Whalley for valuable input. We thank Mike Ramsey for advice on GLIMStat.

References

- Auld TD (1986) Population dynamics of the shrub *Acacia suaveolens* (Sm.) Willd: fire and the transition to seedlings. *Aust J Ecol* 11:373–385
- Auld TD (1996) Ecology of the Fabaceae in the Sydney region: fire, ants and the soil seedbank. *Cunninghamia* 4:531–553
- Auld TD, Bradstock RA (1996) Soil temperatures after the passage of fire: do they influence the germination of buried seed? *Aust J Bot* 21:106–109
- Beath KJ (2001) GLMStat user manual, version 5.5. Sydney
- Bell DT, van der Moezel PG, Delfs JC, Loneragan WA (1987a) Northern sandplain Kwongan: effects of fire on *Hakea obliqua* and *Beaufortia elegans* population structure. *J R Soc West Aust* 69:139–143
- Bell DT, Vlahos S, Watson LE (1987b) Stimulation of seed germination of understorey species of the northern Jarrah forest of Western Australia. *Aust J Bot* 35:593–599
- Benson JS, Ashby EM (2000) Vegetation of the Guyra 1: 100 000 map sheet New England Bioregion, New South Wales. *Cunninghamia* 6:747–872
- Bond WJ (1984) Fire survival of Cape Proteaceae—Influence of fire season and seed predators. *Vegetatio* 56:65–74
- Bond WJ, van Wilgen BJF (1996) Fire and plants. Chapman & Hall, London
- Bond WJ, Vlock J, Viviers M (1984) Variation in seedling recruitment of cape Proteaceae after fire. *J Ecol* 72:209–221
- Bond WJ, Woodward FI, Midgley GF (2005) The global distribution of ecosystems in a world without fire. *New Phytol* 165:525–538
- Bradstock RA, Bedward M (1992) Simulation of the effects of season of fire on post-fire seedling emergence of two *Banksia* species based on long-term rainfall records. *Aust J Bot* 40:75–88

- Bradstock RA, Gill AM, Hastings SM, Moore PHR (1994) Survival of serotinous seedbanks during bushfires: comparative studies of *Hakea* species from southeastern Australia. *Aust J Ecol* 19:276–282
- Bradstock RA, Myerscough PJ (1981) Fire effects on seed release and the emergence and establishment of seedlings in *Banksia ericifolia* Lf. *Aust J Bot* 29:521–531
- Bradstock RA, Williams JE, Gill MA (2002) Flammable Australia: the fire regimes and biodiversity of a continent. Cambridge University Press, Cambridge
- Clark SS (1988) Effects of hazard-reduction burning on populations of understorey plant species on Hawkesbury Sandstone. *Aust J Ecol* 13: 473–484
- Clarke PJ, Davison EA (2001) Experiments on the mechanism of tree and shrub establishment in temperate grassy woodlands: seedling emergence. *Aust Ecol* 26: 400–412
- Clarke PJ, Davison EA, Fulloon L (2000) Germination and dormancy of grassy woodland and forest species: effects of smoke, heat, darkness and cold. *Aust J Bot* 48:687–700
- Clarke PJ, Knox KJE (2002) Post-fire response of shrubs in the tablelands of eastern Australia: do existing models explain habitat differences? *Aust J Bot* 50:53–62
- Cowling RM, Lamont BB (1987) Post-fire recruitment of four co-occurring *Banksia* species. *J Appl Ecol* 24:645–658
- Enright NJ, Lamont BB (1989) Seed banks, fire season, safe sites and seedling recruitment in five co-occurring *Banksia* species. *J Ecol* 77:1111–1122
- Grant CD, Loneragan WA (1999) The effects of burning on the understorey composition of 11–13 year-old rehabilitated bauxite mines in Western Australia—vegetation characteristics. *Plant Ecol* 145:291–305
- Grant CD, Loneragan WA, Koch J, Bell DT (1997) Fuel characteristics, vegetation structure and fire behaviour of 11–15 year-old rehabilitated bauxite mines in Western Australia. *Aust For* 60:147–157
- Hanley ME, Fenner M, Ne'eman G (2001) Pregermination heat shock and seedling growth of fire-following Fabaceae from four Mediterranean-climate regions. *Acta Oecol Int J Ecol* 22:315–320
- Hobbs R, Atkins L (1990) Fire-related dynamics of a *Banksia* woodland in south-western Australia. *Aust J Bot* 38:97–110
- Hodgkinson KC (1991) Shrub recruitment response to intensity and season of fire in semi-arid woodland. *J Appl Ecol* 115:64–72
- Keeley JE, Bond WJ (1997) Convergent seed germination in South African fynbos and Californian chaparral. *Ecology* 133:153–167
- Keeley JE, Zedler PH (1978) Reproduction of chaparral shrubs after fire: a comparison of sprouting and seedling strategies. *Am Midl Nat* 99:142–161
- Knox KJE, Clarke PJ (2004) Fire response syndromes of shrubs in grassy woodlands in the New England Tableland Bioregion. *Cunninghamia* 8: 348–353
- Knox KJE, Clarke PJ (2005) Nutrient availability induces contrasting allocation and starch formation in resprouting and obligate seeding shrubs. *Funct Ecol* 19: 690–698
- Liu H, Menges ES, Quintana-Ascencio PF (2005) Population viability analyses of *Chamaecrista keyensis*: effects of fire season and frequency. *Ecol Appl* 15:210–221
- Midgley JJ (1989) Season of burn of serotinous fynbos Proteaceae: a critical review and further data. *S Afr J Bot* 55:65–170
- Ooi MKJ, Auld TD, Whelan RJ (2004) Delayed post-fire seedling emergence linked to season: a case study with *Leucopogon* species (Epacridaceae). *Plant Ecol* 174:183–196
- Pausas JG, Bradstock RA, Keith DA, Keeley JE, GCTE Fire Network (2004) Plant functional traits in relation to fire in crown-fire ecosystems. *Ecology* 85:1085–1100
- Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge
- Setterfield SA (1997) The impact of experimental fire regimes on seed production in two tropical eucalypt species in northern Australia. *Aust J Ecol* 22:279–287
- Spier LP, Snyder JR (1998) Effects of wet and dry season fires on *Jacquemontia curtisii*, a south Florida pine forest endemic. *Nat Areas J* 18:350–357
- Vesk PA, Westoby M (2004) Global patterns of sprouting ability; can all plant species be divided into sprouters and non-sprouters? *J Ecol* 92:310–320
- Whelan RJ, York J (1998) Post-fire germination of *Hakea sericea* and *Petrophile sessilis* after spring burns. *Aust J Bot* 46:367–376
- Zammit C, Westoby M (1987) Seedling recruitment strategies in obligate-seeding and resprouting *Banksia* shrubs. *Ecology* 68:1984–1992