

# Fire regime (recency, interval and season) changes the composition of spinifex (*Triodia* spp.)-dominated desert dunes

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**Abstract.** Between 2000 and 2002, central Australia experienced the largest fire season in three decades when ~500 000 km<sup>2</sup> burned. The effects of these and preceding wildfires in the 1980s on spinifex (*Triodia* spp.) sand-ridge plant communities were examined at 38 sites in central Australia. We used both multivariate and univariate techniques to assess floristic differences among sites of contrasting time-since-fire, fire season and fire interval. Time-since-fire had a consistent floristic influence across the landscape, with increased abundances of ephemeral grasses and forbs and *Triodia* seedlings, and species richness soon after fire but decreasing long after fire. Fire season had little effect on most functional groups of plants, although seedlings of woody species were significantly more abundant following summer than winter fires. Likewise, recent short fire intervals appeared to have little impact on the population dynamics of most functional groups, although some transient effects were observed on abundances of ephemeral forbs, *Triodia* seedlings and herbaceous clonal species. Long-term woody species abundances appeared to be affected by short fire intervals in the 1980s when repeated fires seemed to stimulate recruitment of some resprouting species. The present study highlighted the relative stability of spinifex vegetation types in the face of landscape-scale pyric perturbation, but emphasised that localised shifts in the composition and structure of the plant community may occur under certain fire regimes.

## Introduction

Vegetation processes in Australia's vast sand-ridge deserts are driven by interactions between the following three primary structuring factors: variable and intermittently pulsed rainfall, highly sorted and infertile soils and fire (Ross 1969; Stafford-Smith and Morton 1990). Of these factors, fire has received the most attention recently, with the flammability of spinifex deserts highlighted when wildfires swept across central Australia in the summers of 2001 and 2002 (Allan *et al.* 2003). These conflagrations constituted the most extensive 'fire event' in inland Australia since the mid-1970s, burning more than 500 000 km<sup>2</sup> in the Northern Territory arid zone alone. Furthermore, significant portions of the landscape were burned twice within the space of only 2–3 years, exposing plant communities to fire-return intervals that were much shorter than 'typical' fire-interval ranges for spinifex systems, of between 8 and 30 years (Allan and Griffin 1986; Noble 1993; Gill 2000; Allan and Southgate 2001).

The 2001–2002 fire event was widely perceived to have been an 'environmental disaster', with the short intervals and extreme temperature intensities produced by the summer burns believed to have resulted in collapses in both plant and animal populations (Allan *et al.* 2003; S. McConnell, pers. comm.). Additionally, previous examinations of LANDSAT satellite imagery suggested that similar events had also occurred in the early 1980s and mid-1970s, indicating that periodic, summer-driven fire events have now become a characteristic of

the contemporary fire regime of the central Australia (Griffin *et al.* 1983; Allan and Southgate 2001).

Despite the scale and potentially catastrophic nature of these fire events, there remains a dearth of fire-related research in spinifex-dominated vegetation types. Investigations into potentially important interactions between fire and other structuring factors such as rainfall and soil fertility have been minimal, and most research has instead focused on changes in species composition with time-since-fire (Zimmer 1940; Burbidge 1943; Suijendorp 1981; Allan and Baker 1990; Griffin 1990). These studies have shown that species richness and diversity increase in spinifex communities during early stages of pyric succession, with recently burned vegetation normally characterised by high richness of resprouting perennials, short-lived grasses and ephemeral forbs. During later stages of succession, ground layers generally becomes dominated by a single species of the highly competitive grass genus *Triodia* R.Br., whereas the overstorey becomes dominated by a small number of longer-lived woody species (Griffin 1990; Noble 1998; Allan and Southgate 2001).

How the interactive effects of fire season and interval drive vegetation dynamics in central Australian spinifex grasslands is poorly understood. In more Mediterranean mallee-hummock grassland associations, it has been demonstrated that resprouting woody plants can be affected by variation in the seasonality and interval of fire (Hodgkinson 1986; Noble 1989a, 1998). These studies suggest that the season of fire influences resprouting

through its interaction with temporal changes in the physiology of plants, and through its interaction with post-fire environmental conditions such as rainfall and air temperature. Studies on four common central Australian *Acacia* species (*A. aneura*, *A. kempeana*, *A. maitlandii* and *A. melleodora*) have also suggested that higher soil temperatures during summer fire can increase the mortality rates of resprouting shrubs burned during this season (Wright and Clarke 2007). Studies from other non-spinifex habitats have also indicated that fire season can affect seedling-recruitment dynamics by interacting with the fruiting and flowering phenologies of shrubs and trees (Williams *et al.* 2005). Short fire intervals have been shown to reduce the resprouting vigour of woody species through the depletion of stored carbohydrate reserves (Zammit 1988; Bowen and Pate 1993, 2004).

The present study seeks to address concerns about the effects of fire regime on spinifex sand-ridge vegetation by examining the ecological effects of the 1980s and 2000–2002 fire events in the Haasts Bluff Aboriginal Reserve, west of Alice Springs, Australia. We used a stratified random sampling approach where natural combinations of fire recency, interval and season were sampled across replicated patches in space. The baseline fire-history data for the sampling was derived from an analysis of fire regimes in the Haasts Bluff Reserve from 1979 to 2003 (B. R. Wright, unpubl. data). Specifically, we tested (1) whether the abundance of annual and other short-lived growth forms was highest at sites with short time-since-fire, (2) whether mortality rates of burned woody vegetation were higher after summer than winter fires and (3) whether short fire intervals, both recently and in the 1980s, reduced woody-species abundance but had little effect on herbaceous species.

## Materials and methods

### Study area

The southern portion of the Haasts Bluff Reserve, Alice Springs, Australia, is dominated by a complex system of erratically oriented sand ridges, whereas in the north, the ridges run virtually parallel and grade into a large, flat sandplain in the north-east. Mountain ranges also occur over vast areas, with the westernmost extension of the Macdonnell Ranges running from east to west through the centre of the study area. Small outcrops of sandstone, limestone and dolomite also occur sporadically throughout the region (Perry *et al.* 1962). The climate of the study area is characterised by high seasonal and diurnal fluctuations in temperature and solar radiation. Temperatures in summer can reach 50°C, whereas in winter, night-time temperatures regularly drop below freezing point. Rainfall in the region is always unpredictable and droughts are common. Summer thunderstorms contribute up to 70% of annual rainfall, and in Alice Springs, the 100-year mean annual rainfall is 271 mm (Griffin *et al.* 1983).

Vegetation sampling occurred at sites in the southern sand-ridge complex (below the Papunya Mt Liebig Road; Fig. 1), where soils were composed of deep and highly infertile red siliceous sands. No sampling occurred in areas where floodout/drainage line/range influences on vegetation were suspected. Overstorey vegetation of the sand ridges was generally composed of tree species such as *Allocasuarina*

*decaisneana* (F.Muell.) L.A.S.Johnson, *Brachychiton gregorii* F.Muell., *Eucalyptus gamophylla* F.Muell. and *E. oxymitra* Blakely. Shrub layers consisted of species belonging to the genera *Acacia* Mill., *Eremophila* R.Br., *Gyrostemon* Desf. and *Senna* Mill. Ground layers were normally dominated either by moribund *Triodia* hummocks or by shorter-lived grasses and forb species (with the relative proportions of these being primarily dependent on the recency of fire). All vegetation sampling took place within inter-ridge flats, thereby avoiding the structurally separate vegetation types that occur on dune slopes and crests. These flats ranged in breadth from 100 m up to several kilometres.

### Sampling design

Vegetation was sampled from 38 sites during the winter and spring months of May–October 2003. Sites were stratified across three fire-history analyses, each of which was based on a subset of some combination of time-since-fire, fire interval and fire season (Fig. 2). Time-since-fire (examined across sites 1, 2 and 17 years since fire) was stratified across sites that had or had not been burned by a short fire interval during the 1980s fire event (burned once only, or twice during the event period 1982–1985). A recent short fire interval was also examined in a separate analysis, in which sites that had been burned once during the 2000–2002 fire event were compared with sites that had been burned twice during this period (Fig. 2). For the recent interval analysis, the 1980s fire history was kept constant at all sites (burned twice during the 1980s event). Fire season was examined across sites that were burned during summer/spring (September 2001–March 2002) compared with sites burned in autumn/winter (April–August 2002). These sites were stratified across sites that had not been burned by a short interval during the 1980s event. This stratification was not directly examined in the season analyses, but served to increase the number of summer and winter replicates that could be examined (with the effects of the 1980s interval being co-varied out in the multivariate analyses—see below).

Site locations were based on data from the Haasts Bluff fire-history study. This study had used automated and non-automated fire mapping techniques to map fire scars from LANDSAT TM and MSS satellite imagery of the Haasts Bluff region from 1979 to 2003. Site selection was governed primarily by fire history and habitat suitability, although vehicle accessibility was also a constraint. For this reason, all sites had to lie within close proximity to roads and tracks. Consequently, some of the stratifications across the three fire-history groupings were not ideally balanced (Fig. 2). Within each site, three replicate plots were surveyed, resulting in 114 plots in total. Locations for these plots were selected remotely in ARCVIEW from series of randomly generated points within each of the designated site areas. The distance between plots was governed by the size of the fire-history patches, but each replicate was spaced a minimum of 1 km distant from other replicates.

### Sampling

At each plot, vegetation was surveyed by the nested quadrat technique of Morrison *et al.* (1995b). This procedure involved the use of a compound quadrat composed of 10 sub-quadrats, in which areas of sub-quadrats were delineated by concentric

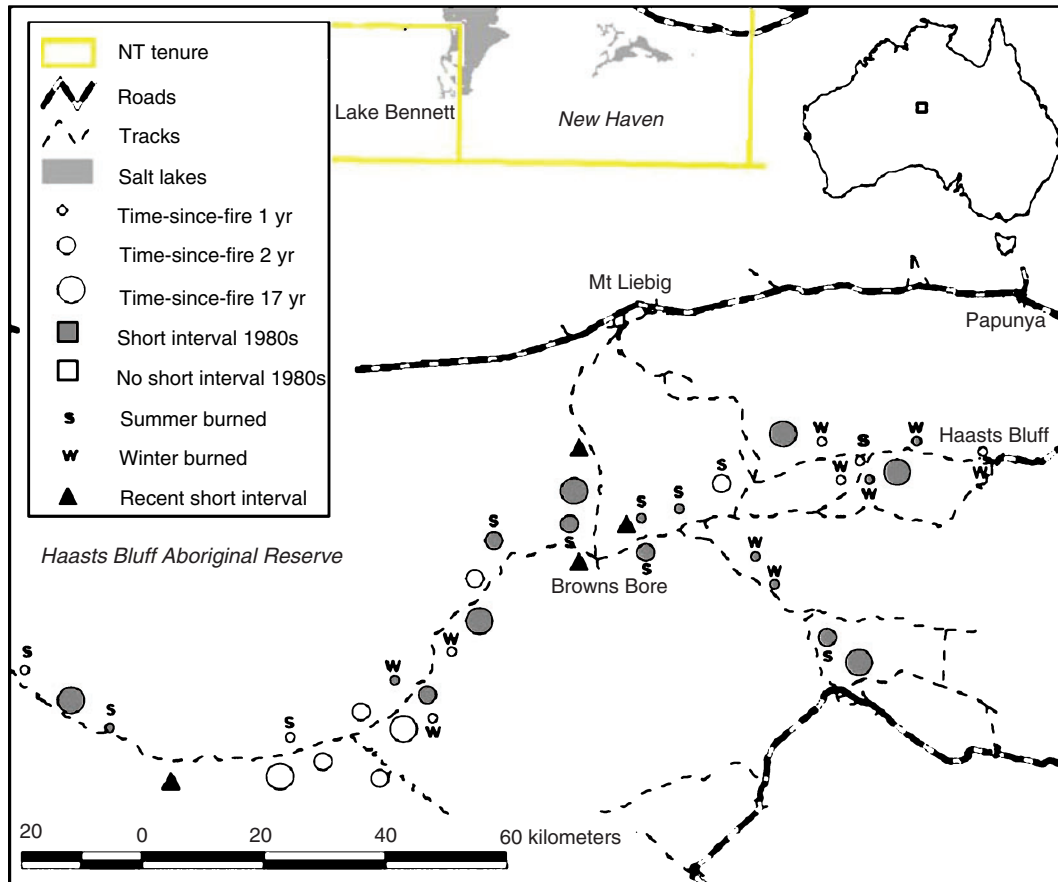


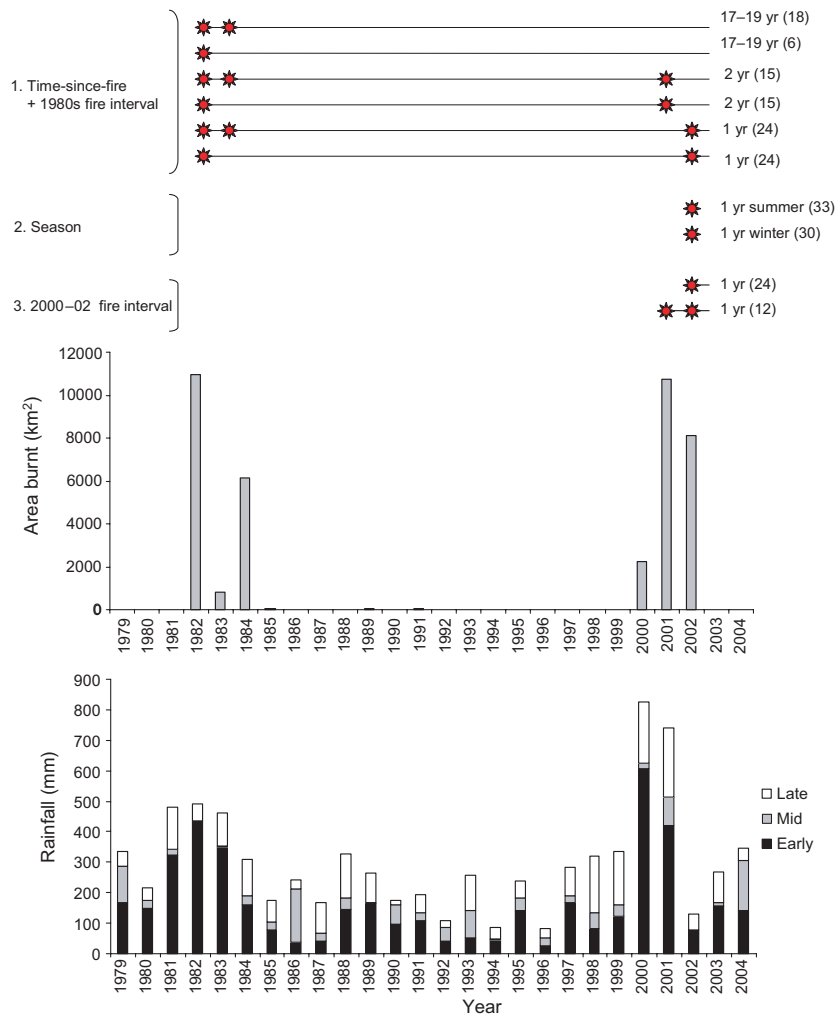
Fig. 1. Location of sample sites within the Haasts Bluff reserve in central Australia.

squares, the corners of which were defined by marks on tape measures that lead outwards from a centrally located metal picket. The cumulative areas of the sub-quadrats were 2, 4, 8, 16, 32, 64, 128, 256, 512 and 1024 m<sup>2</sup>. Vegetation in the sub-quadrats was surveyed progressively from smallest to largest, and 'frequency scores' were calculated for each species by summing the number of sub-quadrats in which individuals occurred. While recording the presence of plant species, it was also noted whether the plants were alive or dead, whether they were in a state of post-fire recovery (i.e. resprouting from above- or below-ground vegetative tissue), or whether they were in an adult or juvenile life stage. Voucher specimens of all species were collected and submitted to the Northern Territory Herbarium, Alice Springs.

Because of the sparseness of woody vegetation, we also used an additional sampling technique to estimate woody abundance. At each site, an extra quadrat of area 2044 m<sup>2</sup> was constructed by extending the corners of the nested quadrat a further 20 m. Counts were made of all standing adult vegetation of all tree and shrub species within this extended quadrat. Once again, notes were made regarding whether or not the plants were alive or dead, or whether they were in a state of post-fire recovery.

A series of environmental variables were also collected and used as co-variables in subsequent multivariate analyses to partial out effects related to environmental variation across the

large study area. At each site, two soil samples were collected, one from the surface and one from 1 m below the surface. These samples were analysed for pH, electrical conductivity, soil colour, clay content and gravel content. Soil pH and electrical conductivity were measured with a Cyberscan 520 (Eutech Instruments) according to the methods described by Smiley and Cook (1972). Soil colours for the various samples were determined by the use of a Munsell soil colour chart. Clay and gravel contents were determined by agitating soil samples in a slurry with de-ionised water in test tubes for 1 h. They were then allowed to settle for 24 h and the relative proportions of clay and gravel were recorded. A series of soil variables was also acquired for each of the 114 plots from a database of airborne gamma-ray survey data from the Northern Territory Department of Mines and Energy. These variables contained data relating to the magnetic intensity of regolith just below the soil surface (TMI, total magnetic intensity; STMI, adjusted magnetic intensity), as well as data relating to the elevation of the earth's surface as derived from the difference between aircraft height above sea level and ground clearance (DTM, digital terrain model). Radiometric data were also acquired, which measured the natural gamma radiation emitted by the following three naturally occurring elements in the soil and rocks: potassium (ARAK, radiometric potassium count), thorium (ARTH, radiometric thorium count) and uranium (ARAU, radiometric uranium



**Fig. 2.** Upper diagram depicts fire sequences involved in the three series of fire-history analyses, with the length of each bar representing time-since-fire and stars indicating fire occurrence. Numbers in parenthesis indicate number of plots used in each fire-history analysis. Upper bar chart shows area burnt by year in Haasts Bluff study area from 1982 to 2002, Alice Spring, Australia. The lower bar chart indicates the annual rainfall for the study area (calculated as the mean from Derwent, Newhaven and Glenn Helen pastoral stations and the Mereenie gas fields).

count). These radiometric data provided insight into soil and rock characteristics across the landscape and indicated where potential between-site variation may exist in underlying regolith materials.

#### Multivariate analyses

Three series of data analyses were structured to test the effects of the various components of fire regime on vegetation composition: a time-since-fire by fire-interval (1980–1985) analysis, a season analysis and a recent-fire interval (2000–2002) analysis. In order to conduct these analyses, series of floristic, environmental, fire-history and supplementary data matrices were first constructed in Microsoft Excel. The floristic data matrices comprised the 'frequency score' data that had been obtained from the nested quadrats during the vegetation survey. The environmental matrices contained soil and remotely sensed radiometric data that had been obtained at each plot. The fire-history matrices comprised information relating to previous

seasons of fire, interval and time-since-fire at each plot (this data had been previously obtained during a remote-sensing study of fire regimes in the Haasts Bluff reserve from 1979 to 2003). The supplementary data matrices comprised species abundance data for the following eight functional fire response groups: woody resprouters, woody obligate seeders, seedlings of woody serotinous species, seedlings of non-serotinous woody species, fire ephemerals (short-lived species that proliferate only after fire), clonal forbs, *Triodia* hummocks and *Triodia* seedlings (Table 1, Appendix 1).

Constrained ordination analyses were calculated on the three groups with the CANOCO for Windows 4.5 software package (ter Braak and Smilauer 2002). Species-abundance matrices were initially ordinated by detrended correspondence analysis (DCA). This provided an estimate of the heterogeneity of the species data, and allowed the determination of whether to use linear or unimodal methods for the constrained ordinations (Leps and Smilauer 2003). As the lengths of the DCA gradients

**Table 1. Data types used for each functional fire-response group in redundancy analysis (RDA) and generalised linear model (GLM) analyses**

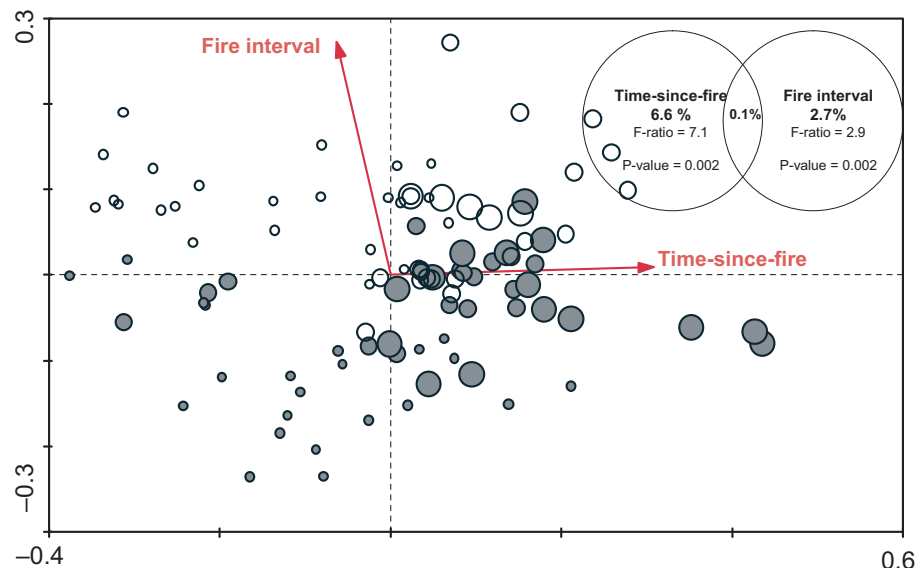
Functional fire-response group	Data used		
	Floristic matrices (RDA)	Supplementary matrices (RDA)	GLM analyses
Fire ephemerals	Frequency score	Frequency score	Frequency score
Clonal forbs	Frequency score	Frequency score	Frequency score
Seedlings (serotinous spp.)	Frequency score	Frequency score	Frequency score
Seedlings (non-serotinous spp.)	Frequency score	Frequency score	Frequency score
<i>Triodia</i> spp. hummocks	Frequency score	Frequency score	Frequency score
<i>Triodia</i> spp. seedlings	Frequency score	Frequency score	Frequency score
Resprouters	Frequency score	Count	Count
Obligate seeders	Frequency score	Count	Count

were in the range of 2–3 for all datasets, it was decided that the data would be ordinated by the linear ordination technique of redundancy analysis (RDA). RDA is a constrained version of principal components analysis that reveals gradients of variability in species composition that can be explained by measured environmental variables (Pysek and Leps 1991; Hallgren *et al.* 1999). Parameters for the RDA analyses were set as follows: scaling was focused on inter-sample distances and species data were transformed by using a log-transformation ( $\log(y+1)$ ). Sample data were not centred or standardised, whereas species data were centred only.

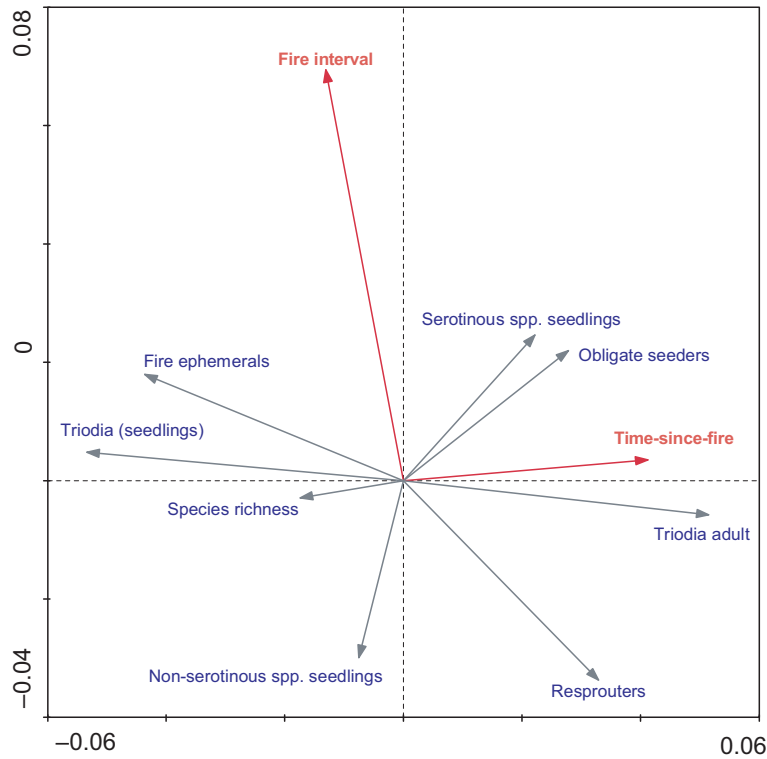
Forward selection was used on all RDA analyses, as many of the environmental variables co-varied (shared the same information). In this procedure, a Monte Carlo permutation test (499 permutations under a reduced model) ranked each environmental variable by the amount of species variability attributable to that variable alone (the marginal effect). These variables were then tested for their effect on species composition that was additional to the effect of variables already selected

(the conditional effect). The environmental variables were then ranked in order of their conditional ‘importance’ and those variables that accounted for a significant proportion of the species variation ( $P < 0.05$ ) were selected for new RDA analyses. This resulted in simpler, more interpretable models.

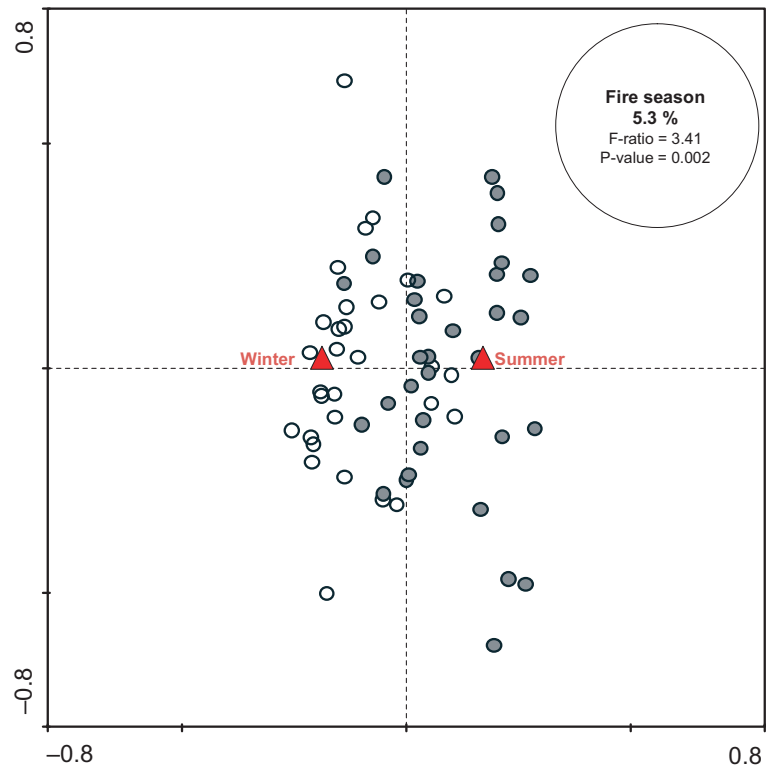
In the final RDA analysis for each fire-regime component, those environmental variables that qualified for inclusion were used as co-variables and the fire variables were entered as the primary variables of interest. This partitioned out the effects of the measured environmental and remotely sensed radiometric variables on species abundances and focused the solution of the RDA on the fire variables (Figs 3, 5, 7). Supplementary matrices were not used directly in these RDA analyses, but were instead projected passively onto the axes of the constrained ordination diagrams. In this way, the plotted variables of the supplementary matrices did not contribute to the calculation of the constrained ordination axes, but their meaning could be interpreted by using the results of the axes (Figs 4, 6, 8).



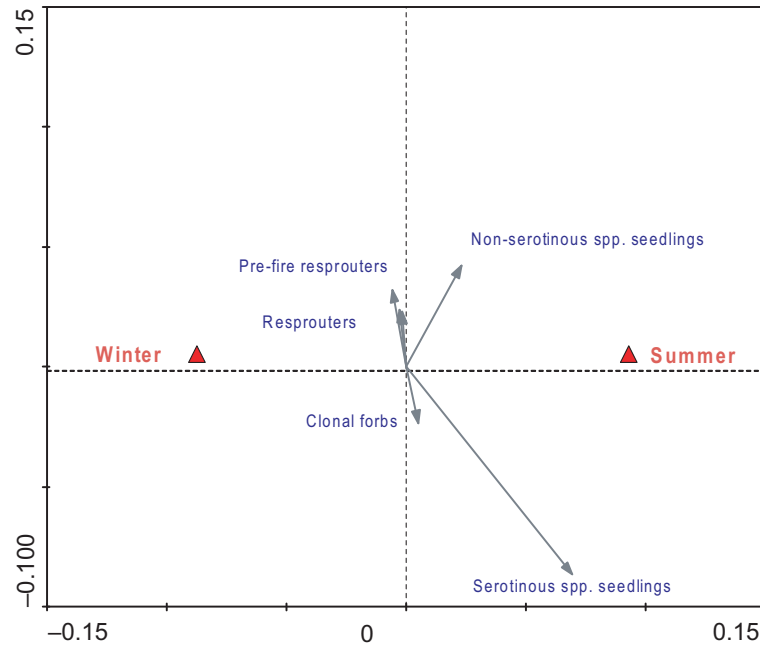
**Fig. 3.** Ordination (redundancy analysis, RDA) biplot of sites with time-since-fire and fire interval as environmental variables. Sites that experienced long fire intervals are shaded, whereas sites that experienced a short fire interval are unshaded. Symbol size corresponds to the time-since-last fire, with the smallest circles indicating sites sampled 1 year after fire, middle-sized circles indicating sites sampled 2 years after fire and large circles indicating sites sampled 17–18 years after fire. Results of a variance partitioning are inserted in a Venn diagram.



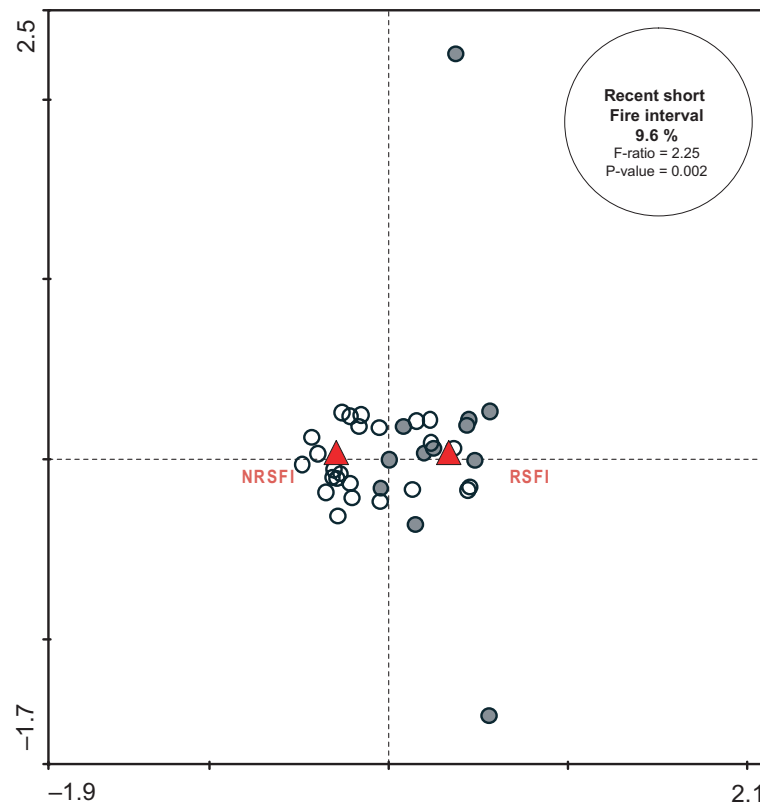
**Fig. 4.** Ordination with significant (in generalised linear model (GLM) analysis) supplementary growth-form variables imposed on time-since-fire by fire-interval environmental variables. Only those variables found to be significant in the GLM analysis are included in the bi-plot.



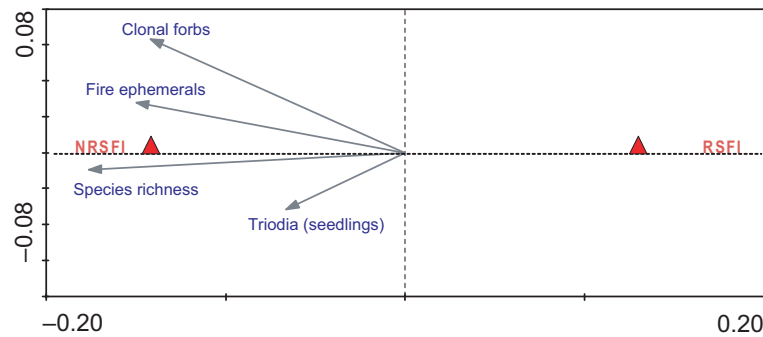
**Fig. 5.** Ordination (redundancy analysis, RDA) of sites in relation to fire season. Sites that experienced fire between October 2001 and March 2002 (summer) are shaded, whereas sites that experienced fire between April and September 2002 (winter) are unshaded. Results of variance partitioning are inserted in a Venn diagram.



**Fig. 6.** Ordination with supplementary growth-form variables imposed on season redundancy analysis (RDA) ordination diagram. Only those variables found to be significant in the generalised linear model (GLM) analysis are included in the bi-plot.



**Fig. 7.** Ordination (redundancy analysis, RDA) of sites in relation to recent short fire interval. Sites that experienced a short fire interval in 2000–2003 are shaded, whereas sites that did not receive a short fire interval during this period are unshaded. Results of variance partitioning are inserted in a Venn diagram. NRSFI indicates no recent short fire interval, SFI indicates a recent short fire interval.



**Fig. 8.** Ordination with supplementary growth form variables imposed on results of recent fire interval redundancy analysis (RDA) analysis. Only those variables found to be significant in the generalised linear model (GLM) analysis are included in the bi-plot. NRSFI indicates no recent short fire interval, SFI indicates a recent short fire interval.

As the principal focus of the multivariate analyses was to investigate the influence of fire regime (time-since-fire, fire interval and season), we also examined the effects that these variables contributed individually, by using variance partitioning (Leps and Smilauer 2003). In this procedure, the variables of interest were entered as environmental variables in an RDA analysis and the statistical significance of the variables was tested with Monte Carlo permutation tests (499 permutations under a reduced model). Where the analysis contained two fire variables (as in the time-since-fire by fire interval analysis), the independent contributions of each variable and the residual variation explained by both variables were presented in Venn diagrams (Leps and Smilauer 2003).

#### Univariate analyses

The effects of time-since-fire, fire interval and fire season on the abundance of the eight functional groups were analysed by using general linear models (Quinn and Keough 2002). For these analyses, count data from the extended quadrats were used for the woody-resprouter and woody-obligate seeder functional groups, whereas 'frequency score' data were used for the remaining six groups (Table 1). All analyses used a Poisson error structure with a log link function and orthogonal combinations of treatments. Where more than one factor was present in a particular model, orthogonal combinations were sequentially deleted when they were not significant. Plots of residuals were examined initially to detect any non-linear trends.

## Results

### Time-since-fire and fire interval 1982–1985

The constrained ordination of sample sites showed clear trends with both 1980s fire interval and time-since-fire (Fig. 3). Both time-since-fire and fire interval together explained 9.4% of the floristic variation. Of this variation, 6.6% was attributable to time-since-fire ( $F = 7.1$ ,  $P = 0.002$ ) and 2.7% was attributable to the occurrence of a short fire interval during the early 1980s ( $F = 2.9$ ,  $P = 0.002$ ). Less than one per cent (0.1%) of variation explained by the two variables together could not be attributable to either with certainty.

Numerous associations could be discerned when fire regime and species functional groups were plotted passively against

the results of the RDA (Fig. 4) and then explored more formally in the GLM analyses (Table 2). Groups that were significantly affected by time-since-fire and demonstrated higher abundance with short time-since-fire included fire ephemerals, *Triodia* spp. seedlings and species richness. Groups that were significantly affected by time-since-fire but whose abundance increased with longer time-since-fire included live obligate seeders and mature *Triodia* hummocks. Resprouters showed significantly higher abundances at sites that had experienced a short fire interval during the early 1980s. Another two groups, resprouters and *Triodia* seedlings, showed significant interactions between time-since-fire and fire interval. For *Triodia* seedlings, it appeared that abundances at sites burned with a short fire interval decreased gradually with increasing time-since-fire, whereas the decrease in abundance was much more rapid at sites not burned with a short fire interval. The interaction between time-since-fire and interval for resprouters was also difficult to interpret and may simply represent a sampling artefact.

### Season

Despite the relatively large amount of explainable variation that was attributable to fire season (5.3%) (Fig. 5), few of the supplementary variables showed a significant response when tested by the GLM analyses (Table 3; Fig. 6). Seedlings of serotinous and non-serotinous woody species were both strongly affected ( $P < 0.01$ ) by burn season, with the frequency of seedlings in these groups being much higher following summer than winter fires. Clonal forbs appeared to be negatively affected by summer burns, being significantly more abundant at sites burned during winter months ( $P < 0.01$ ). The abundance of resprouters was less at sites burned during summer months, although this result was deemed unlikely to have been an effect of burn season. Instead, it was possibly a sampling artefact, reflecting the broad-scale heterogeneity of plant densities across the study area. Consultation of the raw data revealed an outlier among the winter data, with an average of 254 woody plants before burning at one of the winter-burned sites (calculated by summing both alive and dead plants). This was in contrast to the grand mean of 89 from the remaining summer and winter sites.

**Table 2. Summary of results for two-factor generalised linear model (GLM) for functional groups according to whether sites were burned 1, 2 or 17 years ago, and whether these sites were burned with or without a short fire interval between 1982 and 1985**

Units of 'obligate seeders' and 'resprouters' are mean counts, units of other groups are mean 'frequency scores'. TSF = time-since-fire, FI = fire interval (1980s), SFI = a short fire interval occurred during the 1980s, NSFI = no short fire interval occurred during the 1980s.

\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ; n.s., not significant

Functional fire-response group	GLM sequential model			Time-since-fire (years)			Fire interval	
	TSF	FI	TSF × FI	1	2	17	SFI	NSFI
Obligate seeders	*	n.s.	n.s.	0	0	2	–	–
Resprouters	*	*	**	98	64	120	109	75
			SFI	110	59	149		
			NSFI	87	70	32		
Serotinous spp. seedlings	n.s.	*	***	–	–	–	–	–
Non-serotinous spp. seedlings	n.s.	*	n.s.	–	–	–	–	–
Fire ephemerals	***	n.s.	n.s.	37	39	16	–	–
Clonal forbs	n.s.	n.s.	n.s.	–	–	–	–	–
<i>Triodia</i> spp. (adult)	***	n.s.	n.s.	1	1	9	–	–
<i>Triodia</i> spp. (seedlings)	***	n.s.	*	8	7	1	–	–
			SFI	8	6	2		
			NSFI	8	8	0		
Species richness	***	n.s.	n.s.	27	26	23	–	–

**Table 3. Summary of results for one-factor generalised linear models (GLM) for functional groups according to whether sites were burned between October 2001 and March 2002 (summer burns), or between April and September 2002 (winter burns)**

Units of 'obligate seeders' and 'resprouters' are mean counts, units of other groups are mean 'frequency scores'. \* $P < 0.05$ ; \*\* $P < 0.01$ ; n.s., not significant

Functional fire-response group	GLM model Season	Season	
		Summer	Winter
Obligate seeders	n.s.	–	–
Resprouters	*	71	100
Serotinous spp. seedlings	**	2	<1
Non-serotinous spp. seedlings	**	3	1
Fire ephemerals	n.s.	–	–
Clonal forbs	**	16	21
<i>Triodia</i> spp. (adult)	n.s.	–	–
<i>Triodia</i> spp. (seedlings)	n.s.	–	–
Species richness	n.s.	–	–

**Table 4. Summary of results for one-factor generalised linear models (GLM) for functional groups according to whether sites have or have not experienced a recent short fire interval between 2000 and 2003**

RSFI = a recent short fire interval, NRSFI = no recent short fire-interval. Units of 'obligate seeders' and 'resprouters' are mean counts, units of other groups are mean 'frequency scores'. \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ; n.s., not significant

Functional fire-response group	GLM model Fire interval	Fire interval	
		RSFI	NRSFI
Obligate seeders	n.s.	–	–
Resprouters	n.s.	–	–
Serotinous spp. seedlings	n.s.	–	–
Non-serotinous spp. seedlings	n.s.	–	–
Fire ephemerals	**	23	36
Clonal forbs	***	8	19
<i>Triodia</i> spp. (adult)	n.s.	–	–
<i>Triodia</i> spp. (seedlings)	***	4	8
Species richness	***	21	27

### Fire interval 2000–2003

The occurrence of a recent short fire interval (2000–2003) exerted a stronger influence on floristic composition than did the occurrence of a temporally distant short fire interval (1982–1985), explaining 9.6% of species variation ( $F = 2.25$ ,  $P = 0.002$ ) (Figs 7, 8). Functional groups that were significantly less abundant at sites that had a short fire interval included fire ephemerals, clonal plants, *Triodia* seedlings and species richness (Table 4). Groups that were unaffected by recent fire interval were obligate seeders, seedlings of serotinous and non-serotinous woody species, and mature *Triodia* hummocks (Table 4).

## Discussion

### Time-since-fire

As expected, time-since-fire proved to be a strong determinant of floristic composition in spinifex sand-ridge country. During the early stages of post-fire succession, species richness increased markedly. This early flush of vegetation was reflected by increases in abundance of fire ephemerals and spinifex seedlings, and largely mirrored observations from other literature on fire and spinifex communities (Zimmer 1940; Burbidge 1943; Beadle 1981; Suijendorp 1981; Allan and Baker 1990; Griffin *et al.* 1990; Jacobs 1992). However, the mechanisms that triggered this fire-stimulated flush of new growth are largely

unknown. Possible factors that may have encouraged the growth of these 'fire promoted' species include the release from dormancy by the effects of smoke or heat during fire (Ross 1976; Hodgkinson and Oxley 1990; Bradstock *et al.* 1992), or the release of water or light resources as the result of the removal of standing vegetation (Wellington and Noble 1985; Wellington 1989). This last factor would be especially applicable for *Triodia* spp. as seeds of these species are generally not known to possess long-term dormancy or heat requirements for release from dormancy (Rice and Westoby 1999).

Our study also found that seedling numbers of serotinous woody species did not fluctuate with time-since-fire. Previous fire studies on spinifex vegetation have found that seedlings of serotinous woody species were absent in country that had not been burned recently (Burbidge 1943; Wellington and Noble 1985; Wellington 1989; Noble 1993; Cohn and Bradstock 2000). Authors of these papers put forward several reasons to explain this phenomenon, including the mechanical impedance of seedling growth by extant vegetation in long-unburned country, the capturing of resources by perennial vegetation in long-unburned areas and rapid removal of seed by granivorous birds, rodents and ants. The presence of seedlings of serotinous species at burned and unburned sites in our study indicated that despite the presence of high densities of seed harvesting/predating fauna (Gunawardene and Majer 2005, Ikuntji—Mount Winter fauna survey, unpubl. data), serotinous plants were still able to maintain seed banks in both burned and long-unburned country. In burned country, the presence of seed was adequately explained by the predator-satiation hypothesis, with massive pulses of seed input occurring when fires caused synchronised drying of woody fruits. In long-unburned country, however, it is suggested that soil seed banks were maintained by a constant, albeit more gradual supply of seed from the canopy-stored seed bank, as capsules released seed in response to drying by ambient heat.

#### *Fire interval*

An unexpected finding from our study was the lack of recent fire-interval (2000–2002) effects on the resprouting woody species. This finding differs from much of the literature concerning the impacts of fire interval on vegetation in Australian ecosystems, nearly all of which have demonstrated negative effects of short fire intervals on resprouting vegetation (Auld 1986; Nieuwenhuis 1987; Zammit 1988; Morrison *et al.* 1995a; Noble 1998; Morrison and Renwick 2000; Watson and Wardell-Johnson 2004). It does, however, support the premise that some Australian resprouters are resilient to shortly spaced perturbations because of their ability to recover carbohydrate reserves rapidly (Bowen and Pate 1993). Our findings also support those of Cruz *et al.* (2003), who found that plant mortality following successive fires was unlikely to occur as the result of depleted carbohydrate reserves, because carbohydrate levels needed to sustain resprouting episodes were only a small fraction of the storage capacities of Mediterranean plants.

Paradoxically, the abundance of resprouters was higher at sites burned with a short fire interval during the 1980s than at sites that were not. This result may be explained by the

frequent presence of two particular physiological adaptations among resprouters in our study area. First, many of these plants are capable of resprouting during juvenile growth phases (Wright and Clarke 2007). Consequently, closely spaced follow-up fires did not necessarily eliminate recruits that establish after initial fires; in contrast to interval effects observed in other Australian systems (Morrison *et al.* 1995a; Gill and McCarthy 1998). Second, many of these species possess short secondary juvenile periods, so their resprouted shoots were capable of rapid seed production soon after initial fires (B. R. Wright and P. J. Clarke, unpubl. data). This prepared populations for the possibility of closely spaced follow-up fires by 'topping up' seed-bank reserves that would otherwise be depleted by post-fire recruitment events. The prevalence of these two physiological traits among sand-ridge vegetation (as well as the common occurrence of fire-cued seeds, and the almost ubiquitous presence of resprouting as a fire response across the flora) illustrates the resilience of these communities to fire, and points towards a long evolutionary history of both short- and long-interval fires in these ecosystems. Additionally, higher abundances of resprouters after the short-interval 1980s fires may reflect an effect resulting from a release from competition after fire, as repeated fires would have reduced *Triodia* competition on shrub recruits (see below).

Seedling abundances of *Triodia* were strongly reduced by the occurrence of recent short fire intervals. This finding has important ramifications, given that the *Triodia* species in our study area are generally obligate seeders and are almost entirely dependent on recruitment from soil seed banks for persistence after fire (Westoby *et al.* 1988; Rice and Westoby 1999). The observed effect is explained by the slow-growing nature of *Triodia* which requires long periods after fire to allow hummocks to mature sufficiently to produce dense seed crops. Thus, when the initial post-fire seedling cohort was killed by follow-up fires, there had not been sufficient time for the vegetation to replenish seed banks after the initial post-fire recruitment event (Rice and Westoby 1999).

Despite the observed decline in *Triodia* following the recent short fire intervals, the long-term effects of short fire intervals on *Triodia* populations were minimal, with no significant differences in abundance of mature hummocks between sites that had or had not been burned with a short fire interval during the 1980s. This indicates that fire-interval effects on *Triodia* species are transitory and that, over long periods of time, the standing vegetation is able to recover either from sparse residual seed banks or perhaps *via* dispersal from long-unburned patches.

Another outcome of interest was the negative effect of proximate closely spaced fire intervals on populations of fire-ephemeral species. This result was also unexpected, as theory predicts that short-lived species should be tolerant of short intervals, as these species reach reproductive maturity quickly and should rapidly replenish seed banks that become reduced following post-fire recruitment events (Morgan 1998; Lunt and Morgan 1999; Morgan 1999). Several factors may explain our contradictory pattern, including seed-bank depletion following the initial fire (possibly caused by seed predation or deterioration), inappropriate season of fire to cue seeds (certain species may require the deep soil heat penetration of

summer fires to break seed dormancies), and insufficient or inappropriate season of post-fire rain for germination. As with *Triodia*, however, the observed effects of short fire intervals appeared to be transitory, and no interval effects were evident at sites burned with a short interval during the 1980s. Once again, this probably indicates that populations had recovered over time either from residual seed banks and/or *via* dispersal from spatially distant seed sources.

Another unexpected finding from our study was the absence of any fire-interval effect on woody obligate seeders. Once again, this result contrasts with the findings of previous research from other semi-arid (Zedler *et al.* 1983; Vlok and Yeaton 2000) and mesic systems (Nieuwenhuis 1987; Morrison *et al.* 1995a; Russell-Smith *et al.* 1998; Morrison and Renwick 2000). Such a result may indicate that the majority of obligate-seeding species in the Haasts Bluff study area reach their primary juvenile period quickly after fire (and replenish their seed banks before follow-up fires occur). Alternatively, the failure to find a significant result may simply reflect the very low numbers and abundance of obligate-seeding species in these landscapes, with many obligate seeders being confined to dune crests (which were not sampled in our survey).

#### Fire season

The abundance of seedlings of both serotinous and non-serotinous woody species was found to be significantly higher following summer fires. This finding suggests that summer fires have the potential to increase the abundance of woody resprouters, as populations can be significantly augmented by the recruitment of seedlings after summer fires, and adult numbers remain relatively static following fire (owing to their ability to recover vegetatively). Such a prediction should be treated cautiously, however, as the survivability of adult shrubs and trees following fire is also contingent on a large number of other factors, such as pre- and post-fire soil moisture, environmental conditions after fire, and the inherent resilience of particular species to fire damage (Canadell *et al.* 1991; Moreno and Oechel 1991; Lloret and Lopez-Soria 1993; Morrison 1995; Veski *et al.* 2004). Also, the actual survival of seedlings into adulthood following summer fire would depend on many variables, including the occurrence of post-fire rain, the degree of herbivory and post-fire environmental conditions (Noble 1989b; Wellington 1989; Auld 1990; Bell *et al.* 1993; Knox and Clarke 2006). Nevertheless, these results point to the possibility of landscape-scale shifts in woodiness, driven simply by the interaction between fire season and post-fire conditions.

Why the abundance of woody seedlings was higher following summer fire is uncertain and could have been the result of numerous factors. For the serotinous species, winter fires may not have been intense enough to release sufficient seed from their woody fruits to satiate seed predators. Alternatively, the period of time that elapsed between canopy seed release and good post-fire rains was much shorter for the summer burns than for winter burns (good rains fell shortly after the summer fires in late 2001 and early 2002, whereas a period of >12 months elapsed between the winter 2002 burns and the next good rains—see Fig. 2). Thus, seed predators had a much longer period at

winter-burned plots to consume/harvest the fire-induced seed 'pulse' before germinating rains finally fell.

For non-serotinous species with soil-stored seed banks, higher soil temperatures during summer fires may have promoted more germination by providing greater dormancy-breaking stimuli to hard-seeded species (Williams *et al.* 2004, 2005). The increased number of seedlings of non-serotinous species after summer fire could also be explained by an interaction between high levels of seed predation and the relatively consistent spring/summer flowering and fruiting patterns in these taxa (Friedel *et al.* 1993, 1994). Hence, for such plants, there were more seeds available to be cued by spring and summer burns because seed bank abundances peak in these months following seed shed, but became significantly reduced by winter because of high rates of seed predation.

#### Conclusion

We have shown that all components of the fire regime can influence the floristic composition of spinifex-dominated vegetation. Time-since-fire was found to regulate the abundance of ephemeral grasses and forbs and we believe that this was primarily driven by the breaking of dormancies by fire-related cues such as heat and/or smoke. By contrast, the results of both the fire-season and the fire-interval analyses largely refuted our initial ideas. Recent short fire intervals had surprisingly little impact on community woody composition and caused relatively little change in structure. Conversely, proximate short fire intervals reduced the abundance of *Triodia* spp. seedlings and fire-ephemeral species, although these effects were transient and could not be detected at sites that had experienced a short fire interval during the early 1980s. A more lasting effect was seen in the increased abundance of resprouting woody species after repeated events in the 1980s, which resulted from enhanced recruitment, possibly as a result of decreased *Triodia* competition. Fire season had little effect on most functional groups, although an important finding was that summer fires increased the abundance of seedlings of woody species. Thus, the combined results of both fire interval and fire season demonstrated the potential for fire regimes to cause shifts in the mix of woody *v.* herbaceous species under long-term fire and climate events. Rather than thinning woody vegetation, we think sequences of fire can cause thickening of the woody component through fire-cued germination and release from competition. Overall, we have shown that spinifex communities in the western deserts of Australia are relatively resilient to fire-induced change at the landscape scale but emphasise that, under certain circumstances, fire regimes can act as strong drivers of compositional change.

#### Acknowledgements

This study was funded by an Australian Post graduate Award (APA) scholarship and an NCW Beadle award to BRW. We thank Cathy Nano and Richard Willis for their comments on the draft manuscript and Dave Albrecht, Grant Allen and Peter Latz for their knowledge and support. Appreciation is also extended to the Haasts Bluff community for their support, and special thanks go to Herbert Multa, Derek Dixon, Alice Nampitjimpa, Kumenjai Dixon and Jacob Hayes for their company and assistance over the many months of fieldwork undertaken in this project.

The Northern Territory Central Lands Council, the Jugadai family and Douglas Multa, are also thanked for their permission to conduct research on Aboriginal freehold land.

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**Appendix 1. Abundances of species used in supplementary data matrices for redundancy analysis (RDA) and generalised liner model (GLM) analyses**

Species with \* indicate mean count data across sites, all other species are mean 'frequency score' data across sites. Functional fire-response groups: FE, fire ephemera; CF, clonal forb; R, resprouter; OS, obligate seeder; Se, serotinous tree; T, *Triodia* species. Growth form categories: F, forb; G, grass; S, shrub; T, tree. Fire interval (1980s) categories are: SFI, short fire interval during the 1980s; NSFI, no short fire interval during the 1980s. Recent fire interval (2000–2002) categories: RSFI, recent short-fire-interval; NRSFI, no recent-short-fire-interval. Season categories: sum., summer; wint., winter

Species	Fire response	Growth form	Time-since-fire (years)			Fire interval (1980s)		Fire interval (2000–2002)		Season	
			1	2	17	SFI	NSFI	RSFI	NRSFI	Sum.	Wint.
Apocynaceae subfam. Asclepiadoideae											
<i>Marsdenia australis</i> (R.Br.) Druce	FE	F	0.90	0.17	0.29	0.53	0.58	0.00	0.88	0.00	1.28
Asteraceae											
<i>Brachyscome ciliaris</i> (Labill.) Less.	FE	F	0.35	1.30	0.00	0.86	0.17	0.67	0.67	0.40	0.33
<i>Minuria tridens</i> (D.A.Cooke)	FE	F	0.16	0.00	0.00	0.02	0.15	0.00	0.04	0.00	0.22
Lander											
Boraginaceae											
<i>Halgania erecta</i> Ewart & B.Rees	CF	F	0.63	0.27	0.42	0.49	0.46	0.00	0.79	0.87	0.53
<i>Trichodesma zeylanicum</i> (Burm. f.) R.Br.	FE	F	0.02	0.10	0.00	0.02	0.06	0.00	0.00	0.00	0.03
Casuarinaceae											
<i>Allocasuarina decaisneana</i> (F.Muell.) L.A.S.Johnson*	R	T	3.37	8.77	1.83	6.11	2.73	10.17	4.38	6.13	2.22
<i>A. decaisneana</i> (seedlings)*	R	T	11.61	10.77	2.38	9.37	9.13	9.58	14.46	19.53	8.31
Convolvulaceae											
<i>Bonamia erecta</i> R.W.Johnson	CF	F	8.35	5.33	4.71	6.32	7.06	1.83	7.96	8.20	8.42
<i>Evolvulus alsinoides</i> L.	FE	F	0.47	0.40	0.00	0.25	0.46	0.75	0.08	0.07	0.64
Euphorbiaceae											
<i>Euphorbia drummondii</i> Boiss.	FE	F	0.49	0.00	0.00	0.14	0.35	0.00	0.33	0.07	0.67
<i>E. tannensis</i> Spreng. var. <i>eremophila</i> (A.Cunn) Hassal	FE	F	1.94	0.43	0.04	0.84	1.35	0.67	1.54	1.40	2.17
<i>E. wheeleri</i> Baill.	FE	F	1.22	0.33	0.00	0.51	0.90	0.00	0.96	2.40	0.72
Fabaceae subfam. Faboideae											
<i>Crotalaria eremaea</i> F.Muell.	FE	F	0.10	0.00	0.00	0.09	0.00	0.00	0.21	0.00	0.14
<i>Indigofera psammophila</i> P.G.Wilson	FE	F	0.55	0.00	0.13	0.44	0.13	0.17	0.92	0.00	0.78
<i>Leptosema chambersii</i> F.Muell	CF	F	6.82	6.77	5.50	6.49	6.52	2.67	6.83	3.93	8.03
Fabaceae subfam. Mimosoideae											
<i>Acacia aneura</i> F.Muell. ex Benth.*	OS	T	0.33	0.10	0.58	0.25	0.42	0.08	0.17	0.00	0.47
<i>A. aneura</i> (seedlings)	OS	T	0.00	0.00	0.04	0.02	0.00	0.00	0.00	0.00	0.00
<i>A. coriacea</i> DC.*	R	T	0.53	0.20	0.00	0.12	0.54	0.00	0.29	0.00	0.75
<i>A. coriacea</i> (seedlings)	R	T	0.00	0.07	0.00	0.00	0.04	0.00	0.00	0.00	0.00
<i>A. estrophialata</i> F.Muell.*	R	T	0.02	0.50	0.25	0.39	0.00	0.00	0.04	0.00	0.03
<i>A. estrophialata</i> (seedlings)	R	T	0.06	0.10	0.13	0.05	0.13	0.00	0.00	0.00	0.08
<i>A. kempeana</i> F.Muell.*	R	S	5.12	2.33	8.83	6.09	4.08	0.67	4.33	6.73	4.44
<i>A. kempeana</i> (seedlings)	R	S	0.14	0.03	0.21	0.16	0.08	0.00	0.21	0.33	0.06
<i>A. ligulata</i> A.Cunn. ex Benth.*	R	S	0.63	1.17	11.25	5.25	0.79	1.83	0.33	0.73	0.58
<i>A. ligulata</i> (seedlings)	R	S	0.00	0.23	0.25	0.12	0.13	0.00	0.00	0.00	0.00
<i>A. maitlandii</i> F.Muell.*	R	S	31.12	14.63	22.46	30.82	16.83	9.92	43.54	37.67	28.39
<i>A. maitlandii</i> (seedlings)	R	S	1.02	1.07	0.17	0.86	0.81	1.25	1.50	2.40	0.44
<i>A. melleodora</i> Pedley*	R	S	20.82	4.80	27.46	23.95	10.42	3.08	28.08	12.80	24.17
<i>A. melleodora</i> (seedlings)	R	S	0.71	0.20	0.54	0.68	0.33	0.17	1.08	1.53	0.36
<i>A. murrayana</i> F.Muell. ex Benth. \*	R	S	1.82	3.77	2.83	3.46	1.60	16.67	0.71	1.07	2.14
<i>A. murrayana</i> (seedlings)*	R	S	0.10	0.33	0.50	0.47	0.00	0.00	0.21	0.07	0.11
<i>A. victorae</i> Benth.*	R	S	0.00	0.00	0.00	0.00	0.00	1.75	0.00	0.00	0.00
Fabaceae subfam. Caesalpinoideae											
<i>Senna</i> form taxon ' <i>helmsii</i> ' (Symon) Randell (seedlings)	R	S	0.02	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.03
<i>Senna</i> form taxon ' <i>petiolaris</i> ' Randell (seedlings)	R	S	0.16	0.00	0.00	0.14	0.00	0.00	0.33	0.13	0.17
<i>Senna</i> form taxon ' <i>sturtii</i> ' (R.Br.) (seedlings)	R	S	0.02	0.00	0.00	0.02	0.00	0.00	0.04	0.00	0.03
<i>Senna</i> form taxon ' <i>filifolia</i> ' Randell (seedlings)	R	S	0.10	0.00	0.00	0.07	0.02	0.00	0.17	0.00	0.14

## Appendix 1. (continued)

Species	Fire response	Growth form	Time-since-fire (years)			Fire interval (1980s)		Fire interval (2000–2002)		Season	
			1	2	17	SFI	NSFI	RSFI	NRSFI	Sum.	Wint.
Goodeniaceae											
<i>Brunonia australis</i> Sm.	FE	F	0.92	0.87	0.29	0.56	1.00	0.00	1.08	1.00	0.89
<i>Goodenia larapinta</i> Tate	FE	F	0.16	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.22
<i>G. triodiophila</i> Carolin	FE	F	0.10	0.43	0.00	0.18	0.17	0.00	0.21	0.27	0.03
Gyrostemonaceae											
<i>Codonocarpus cotinifolius</i> F.Muell.*	R	S	0.12	0.03	0.00	0.02	0.13	0.08	0.04	0.27	0.06
<i>Gyrostemon tepperi</i> (F.Muell. ex H.Walter) A.S.George*	R	S	3.02	4.37	1.17	0.70	5.69	0.08	0.88	5.67	1.92
Malvaceae subfam. Byttnerioideae											
<i>Keraudrenia integrifolia</i> Steud	CF	F	0.16	0.13	0.38	0.28	0.10	0.00	0.29	0.00	0.22
<i>Rulingea loxophylla</i> F. Muell.	CF	F	1.31	0.50	0.21	0.63	1.06	0.83	1.42	0.47	1.67
Malvaceae subfam. Malvoideae											
<i>Hibiscus sturtii</i> Hook	FE	F	0.00	0.23	0.00	0.11	0.02	0.00	0.00	0.00	0.00
<i>Sida</i> sp. A86753 pindans (B.G.Thompson 3398)	FE	F	4.57	4.80	0.25	2.95	4.48	0.50	4.38	5.73	4.08
<i>Sida</i> sp. Rabbit Flat (B.J.Carter 626)	FE	F	0.55	0.07	0.00	0.30	0.27	0.58	0.71	0.27	0.67
<i>Sida</i> sp. Wakaya Desert (P.K.Latz 11894)	FE	F	0.24	0.30	0.08	0.18	0.27	0.50	0.21	0.00	0.33
<i>Sida</i> sp. Western sand dunes (P.K.Latz 11980)	FE	F	0.02	0.00	0.00	0.00	0.02	0.00	0.00	0.07	0.00
Malvaceae subfam. Sterculioideae											
<i>Brachychiton gregorii</i> F.Muell.*	R	T	0.94	0.00	1.67	1.21	0.40	0.00	1.21	0.27	1.22
<i>B. gregorii</i> (seedlings)	R	T	0.00	0.03	0.04	0.04	0.00	0.00	0.00	0.00	0.00
Myrtaceae											
<i>Eucalyptus gamophylla</i> F.Muell.*	R, Se	T	14.90	3.73	24.08	17.35	9.60	0.08	16.50	0.27	21.00
<i>E. gamophylla</i> (seedlings)	R, Se	T	0.04	0.33	0.04	0.04	0.23	0.00	0.00	0.00	0.06
<i>E. oxymytra</i> Blakely*	R, Se	T	10.51	0.00	6.08	8.35	4.29	0.00	13.75	1.80	14.14
<i>Melaleuca uncinata</i> R.Br.*	R, Se	S	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00
Poaceae											
<i>Aristida holathera</i> Domin.	FE	G	9.31	9.83	8.67	9.02	9.67	9.67	8.92	9.07	9.42
<i>Eragrostis eriopoda</i> Benth.	FE	G	3.16	5.27	1.21	3.11	3.56	4.08	3.17	4.20	2.72
<i>Eriachne helmsii</i> (Domin) W.Hartley	FE	G	2.98	4.27	2.00	2.89	3.40	3.33	2.63	4.73	2.25
<i>Panicum effusum</i> R.Br.	FE	G	0.80	0.73	0.29	0.58	0.77	1.67	0.79	0.33	1.00
<i>Paspalidium reflexum</i> R.D.Webster	FE	G	0.78	0.20	0.25	0.51	0.48	0.17	0.83	0.13	1.06
<i>Triodia basedowii</i> E.Pritz. (hummocks)	T	G	0.12	0.00	0.92	0.49	0.00	0.00	0.25	0.40	0.00
<i>T. basedowii</i> (seedlings)	T	G	0.22	0.00	0.33	0.32	0.02	0.00	0.42	0.67	0.03
<i>T. schinzii</i> (Henrard) Lazarides (hummocks)	T	G	0.49	0.57	8.08	2.89	1.48	0.67	0.42	0.60	0.44
<i>T. schinzii</i> (seedlings)	T	G	7.80	6.87	1.13	5.19	6.98	4.75	7.58	7.47	7.94
<i>Yakirra australiensis</i> (Domin) Lazarides & R.D.Webster	T	G	4.12	3.07	0.00	2.51	3.31	2.50	4.08	2.00	5.00
Proteaceae											
<i>Grevillea eriostachya</i> Lindl.*	R	S	7.65	5.73	0.08	1.33	10.17	0.00	1.08	2.20	9.92
<i>G. eriostachya</i> (seedlings)	R	S	0.04	0.07	0.00	0.00	0.08	0.00	0.00	0.00	0.06
<i>G. juncifolia</i> Hook.*	R	S	8.67	15.70	13.58	11.39	12.29	8.58	10.92	9.07	8.50
<i>G. juncifolia</i> (seedlings)	R	S	0.00	0.17	0.00	0.04	0.06	0.17	0.00	0.00	0.00
<i>G. stenobotrya</i> F.Muell.*	OS	S	0.00	0.00	0.67	0.26	0.02	0.00	0.00	0.00	0.00
<i>Hakea divaricata</i> L.A.S.Johnson*	R, Se	T	0.04	0.27	0.04	0.19	0.00	1.33	0.08	0.07	0.03
<i>H. divaricata</i> (seedlings)	R, Se	T	0.00	0.13	0.00	0.07	0.00	0.08	0.00	0.00	0.00
Rubiaceae											
<i>Psyrax latifolia</i> (F.Muell. ex Benth.) S.T.Reynolds	R	S	0.04	0.00	0.00	0.02	0.02	0.00	0.04	0.00	0.06
Santalaceae											
<i>Santalum lanceolatum</i> R.Br*	R	S	0.22	0.00	0.00	0.00	0.23	0.00	0.00	0.00	0.31
<i>S. lanceolatum</i> (seedlings)	R	S	0.00	0.00	0.04	0.02	0.00	0.00	0.00	0.00	0.00

**Appendix 1.** (continued)

Species	Fire response	Growth form	Time-since-fire (years)			Fire interval (1980s)		Fire interval (2000–2002)		Season	
			1	2	17	SFI	NSFI	RSFI	NRSFI	Sum.	Wint.
<b>Sapindaceae</b>											
<i>Atalaya hemiglauca</i> F.Muell. ex Benth.*	R	T	0.00	0.00	0.00	0.00	0.00	1.25	0.00	0.00	0.00
<i>A. hemiglauca</i> (seedlings)	R	T	0.00	0.03	0.00	0.02	0.00	0.00	0.00	0.00	0.00
<i>Dodonea viscosa</i> L. var. <i>angustissima</i> D.C.*	R	S	0.04	0.00	0.58	0.28	0.00	0.00	0.08	0.07	0.03
<b>Solanaceae</b>											
<i>Nicotiana rosulata</i> ssp. <i>Ingulba</i> (S. Moore) Domin.	FE	F	0.04	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.06
<i>Solanum centrale</i> J.M.Black	FE	F	1.06	1.53	0.17	1.23	0.71	0.08	1.67	0.60	1.25
<i>S. coacteliferum</i> J.M.Black	FE	F	0.59	0.37	2.00	1.18	0.46	2.08	0.46	0.47	0.64
<b>Zygophyllaceae</b>											
<i>Tribulopsis angustifolia</i> R.Br	FE	F	0.12	0.17	0.00	0.09	0.13	0.25	0.21	0.07	0.14