Effects of fire regime (recency, interval and season) on spinifex (*Triodia* spp.) dominated sandridge communities in the Western Desert of Australia

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Abstract

Between 2000 and 2002, central Australia experienced the largest fire season in three decades when c. 500 000 km^2 burned. The effects that these and preceding wildfires in the 1980s had on spinifex (*Triodia* spp.) sandridge plant communities were examined at 38 sites in central Australia. We used both multivariate and univariate techniques to assess floristic differences between sites of contrasting time-since-fire, fire season and fire interval. Time-since-fire had a consistent floristic influence across the landscape, with high abundances of ephemeral grasses and forbs soon after fire but decreasing long after fire across a range of spatial scales. Fire season had little effect on most functional groups of plants, although seedlings of woody species were significantly more abundant following summer compared to 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, and herbaceous clonal species, and a reduced species richness was also evident. 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. This study highlighted the relative stability of spinifex vegetation types in the face of landscape-scale pyric perturbation, but emphasised that localised shifts in plant community composition and structure may occur under certain fire regimes.

Introduction

Vegetation processes in Australia's vast sandridge deserts are driven by interactions between three primary structuring factors: unreliable 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, Phillips *et al.* 2003). These conflagrations constituted the most extensive 'fire event' in inland Australia since the mid-1970s, burning more than 500 000 km^2 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 are much shorter than 'typical' fire interval ranges for spinifex systems, of between 8 and 30 years (Allan and Griffin 1986; Allan and Southgate 2001; Gill 2000; Noble 1993).

This 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, Phillips *et al.* 2003, McConnel S. 2002, pers.comm.,13 February). Additionally, previous examinations of LANDSAT satellite imagery suggested that similar events had 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 central Australia (Allan and Southgate 2001; Griffin, Price *et al.* 1983).

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 (Allan and Baker 1990; Burbidge 1943; Griffin, Morton *et al.* 1990; Suijdendorp 1981; Zimmer 1940). 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, the ground layer generally becomes dominated by a single

species of the highly competitive grass genus *Triodia*, while the overstory becomes dominated by a small number of longer-lived woody species (Allan and Southgate 2001; Griffin, Morton *et al.* 1990; Noble 1998).

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 (*Eucalyptus – Triodia* spp.) associations it has been demonstrated that resprouting woody plants can be negatively affected by variation in the seasonality and interval of fire (Hodgkinson 1986; Noble 1989; Noble 1998). These studies suggest that the season of fire influences resprouting both 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 from other non-spinifex habitats have also indicated that fire season can affect recruitment dynamics by interacting with the fruiting and flowering phenologies of shrubs and trees (Williams, Congdon *et al.* 2005). Short fire intervals have been shown to reduce the resprouting ability of woody species through the depletion of stored carbohydrate reserves (Bowen and Pate 1993; Bowen and Pate 2004; Zammit 1988).

This study seeks to address concerns about the effects of fire regime on spinifex sandridge vegetation by examining the ecological effects of the 1980s and 2000-02 fire events in the Haasts Bluff Aboriginal reserve, west of Alice Springs. 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 1979-2003 (Wright unpublished). Specifically, we tested whether 1) time-since-fire had an overriding influence on species composition irrespective of other fire regime components; 2) summer compared to winter fires reduced the abundance of woody vegetation; and 3) whether short fire intervals, both recently and in the 1980s, reduced woody species abundance but had little effect on herbaceous species.

Methods

Study area

The southern portion of the Haasts Bluff reserve is dominated by a complex system of erratically oriented sand ridges, while in the north it is characterised by more regular parallel ridges, which grade into a large flat sandplain in the north east. Mountain ranges also occur over large areas, with the western most extension of the MacDonnell Ranges running from east to west through the centre of the study area, and smaller outcrops of sandstone, limestone and dolomite also occurring sporadically throughout the region (Perry, Litchfield *et al.* 1962). Vegetation sampling occurred at sites in the southern sandridge complex (Fig. 1), where soils were composed of deep, red siliceous sands that were highly infertile and possessed little development of organic layers. No sampling occurred in areas where floodout/drainage line/range influences on vegetation were suspected.

Overstorey vegetation of the sandridges was generally composed of tree species such as *Allocasuarina decaisneana*, *Brachychiton gregorii*, *Eucalyptus gamophylla* and *E. oxymitra*. Shrub layers consisted of species belonging to the genera *Acacia*, *Eremophila*, *Gyrostemon* and *Senna*. Ground layers were normally dominated either by moribund *Triodia* hummocks or by shorter lived grasses and forb species (with the relative proportions of these growth forms 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 100m up to several kilometres.

Sampling design

Vegetation was sampled from 38 sites between May and 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 (Figs 1 and 2). Time-since-fire (examined across sites of 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 1982-85). Fire interval was also examined in a separate analysis, in which sites that had been burned once during the 2000-02 fire

event were compared to sites that had been burned twice during this period (Figs 1 and 2). For this 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 spring/summer (September 2001-March 2002) compared to sites burned in autumn/winter (April 2002-August 2002). These sites were stratified across sites that had or had not been burned by a short interval fire 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 1979-2003. 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 well balanced (Fig. 2). Within each site, three replicate plots were surveyed, resulting in 124 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 at least 1 km distant from other replicates.

Sampling

At each plot vegetation was surveyed using the compound quadrat technique of Morrisson *et al.* (1995). This procedure involved the use of a compound quadrat comprised of 10 sub-quadrats, in which areas of sub-quadrats were delineated by concentric 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^2. 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 used a separate sampling technique to estimate woody abundance. An additional quadrat of area of 2044 m^2 was constructed by extending the corners of the nested quadrat a further 20 m. In this extended quadrat, counts were made of all standing adult vegetation of all tree and shrub species. 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 or not.

Environmental variables measured *in situ* were geographic location (with precise AMG coordinates), soil cover and crust cover. At each site two soil samples were also collected; one from the surface and one from 1 m below the surface. These samples were analyzed for pH, electrical conductivity, soil colour, clay content and gravel content. Soil pH and electrical conductivity were measured using a Cyberscan 520™ according to the methods described by Smiley and Cook (1972). Soil colours for the various samples were determined using a Munsell soil colour chart. Clay and gravel contents were determined by agitating soil samples in a slurry with deionized water in test tubes for one hour. They were then allowed to settle for 24 hours and the relative proportions of clay and gravel were recorded. A series of soil variables was also acquired for each of the 124 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 three naturally occurring elements in the soil and rocks: potassium (ARAK–radiometric potassium count), thorium (ARTH–radiometric thorium count) and uranium (ARAU–radiometric uranium 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 x fire interval (1980-85) analysis, a season analysis and a recent fire interval (2000-02) analysis. In order to conduct these analyses, a series of floristic, environmental, fire history and supplementary data matrices was first constructed in Microsoft Excel ™. The floristic and environmental matrices comprised the species abundance and environmental information that had been recorded at each plot. The fire history matrices comprised information relating to the fire regimes that had been experienced at each plot (time-since-fire, fire interval and fire season). The supplementary data matrices comprised species abundance data for seven functional fire response groups and life-history stages: woody resprouters, woody obligate seeders, seedlings of woody serotinous species, seedlings of non-serotinous woody species, fire promoted ephemerals, clonal forbs and *Triodia* species (Appendix 4.1).

Constrained ordination analyses were calculated on the three groups using the CANOCO for Windows 4.5 software package (ter Braak and Smilauer 2002). Species abundance matrices were initially ordinated using 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 were in the range of 2–3 for all data sets, it was decided that the data would be ordinated using 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 (Hallgren, Palmer *et al.* 1999; Leps and Pysek 1991). Parameters for the RDA analyses were set as follows: scaling was focused on inter-sample distances and species data were transformed using a log transformation (10*y+1; where y was the species frequency score). Sample data were not centered or standardised, while 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 group, 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 variables on species abundances and focused the solution of the RDA on the fire variables (Fig. 3, 5 and 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 using the results of the axes (Fig. 4, 6 and 8).

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

Univariate analyses

The effects of time-since-fire, fire interval and fire season on the abundance of the seven functional groups were analysed using general linear models (Quinn and Keough 2002). These analyses used a Poisson error structure with a log link function and orthogonal combinations of treatments. When 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 shows 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 percent (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 1). Those groups that were significantly affected by time-since-fire and demonstrated higher abundance with short-time-since fire included dead obligate seeders, dead resprouters, 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 alive obligate seeders and mature *Triodia* hummocks. Two groups, pre-fire abundance of resprouters and alive resprouters, showed significantly higher abundances at sites that had experienced a short fire interval during the early 1980s. Another two groups, alive 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, while 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 alive resprouters was also difficult to interpret and may simply represent a sampling artifact.

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 using the GLM analyses (Table 2) (Fig. 6). Seedlings of serotinous and non-serotinous woody species were both significantly affected at the $P<0.01$ level, with the frequency of seedlings in these group being much higher following summer compared to winter fires. Clonal forbs appeared to be negatively affected by summer burns and were significantly more abundant at sites burned during winter months ($P < 0.01$). The abundance of alive resprouters was less at sites burned during summer months, although this result was deemed unlikely to be an effect of the burn season. Instead, it was most likely a sampling artifact, with pre-burn abundances of resprouters being significantly higher at sites burned in winter.

Fire interval 2000-2003

The occurrence of a recent short fire interval (2000-2003) was found to exert a stronger influence on floristic composition than 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 and 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 3) (Fig.8). Generalised linear models also revealed that the abundance of dead resprouters was less at sites that had been burned with a short fire interval (Table 3). However, this may be deemed a sampling artifact after examining the raw data, as the pre-fire abundance of resprouters (the sum of dead and alive resprouters) was simply by chance higher at sites that did not receive a short fire interval. Groups that were unaffected by recent fire interval were woody 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 sandridge country. During the early stages of post-fire succession, species richness at all spatial scales 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 (Beadle 1981; Burbidge 1943; Griffin 1990; Griffin, Morton *et al.* 1990; Jacobs 1992; Suijdendorp 1981; Zimmer 1940). 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 (Bradstock, Auld *et al.* 1992; Hodgkinson and Oxley 1990; Ross 1976), or the release of water or light resources as the result of the removal of standing vegetation (Wellington 1989; Wellington and Noble 1985). 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 occur almost solely in country that has been burned recently (Burbidge 1943; Cohn and Bradstock 2000; Noble 1993; Wellington 1989; Wellington and Noble 1985). Several reasons have been put forward to explain this phenomenon: the mechanical impedance of seedling growth by extant vegetation in unburned country, the capturing of resources by perennial vegetation in unburned areas, and satiation of seed predators in burned country by fire-induced release of seed from woody fruits. The presence of seedlings of serotinous species in our study indicates that despite the presence of high densities of granivorous birds, rodents and ants in the Haasts Bluff region (Gunawardene and Majer 2005, Ikuntji-Mt. Winter fauna survey, unpublished data), serotinous plants are still able to maintain seed banks in both burned and unburned country. In burned country, the presence of seed is adequately explained by

the predator satiation hypothesis, with massive pulses of seed input occurring when fires cause synchronised drying of woody fruits. In unburned country, however, it is suggested that soil seed banks are maintained by a constant, albeit more gradual supply of seed from the canopy-stored seed bank, as capsules release seed in response to drying by ambient heat.

Fire interval

An unexpected finding from our study was the lack of recent fire interval (2000-02) effects on 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; Cary and Morrison 1995; Morrison and Renwick 2000; Noble 1998; Watson and Wardell-Johnson 2004). It does, however, support Bowen and Pate's (1993) premise that some Australian resprouters are resilient to shortly spaced perturbations because of their ability to recover carbohydrate reserves rapidly. Field experiments on common arid *Acacias* in the Haasts Bluff region support this view, with *A. aneura*, *A. kempeana*, *A. maitlandii* and *A. melleodora* all being found to be capable of repeatedly resprouting under certain seasonal conditions (Wright and Clarke in press). Paradoxically, the abundance of resprouters was higher in 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 the study area. Firstly, many of these plants are capable of resprouting during juvenile growth phases (Wright and Clarke in press). Consequently, closely spaced follow-up fires do not necessarily eliminate recruits that establish after initial fires; this in contrast to interval effects observed in other Australian systems (Gill and McCarthy 1998; Morrison, Cary *et al.* 1995). Secondly, many of these species possess short secondary juvenile periods, so their resprouted shoots are capable of rapid seed production soon after initial fires (Wright and Clarke unpublished data). This prepares populations for the possibility of closely spaced follow-up fires by 'topping up' seed bank reserves that would otherwise have been depleted by post-fire recruitment events. The prevalence of these two physiological traits among sandridge 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 toward 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 (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 (Rice and Westoby 1999; Westoby, Rice *et al.* 1988). The observed effect is explained by the slow-growing trait of *Triodia* spp. which require 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 that would have been depleted following initial recruitment events (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 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 by reaching reproductive maturity quickly and replenishing seed banks that become reduced following post-fire recruitment (Lunt and Morgan 1999; Morgan 1998; Morgan 1999). Several factors may explain our contradictory pattern, including seed bank depletion following the initial fire (possibly caused by seed predation or seed 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/or 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, with sites burned with and without a 1980s short fire interval showing no significant differences when sampled in 2003. Once again, this indicates that the observed interval effects on these species are not long-lived, with populations probably recovering 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 seeding vegetation. Once again, this result contrasts with the findings of previous research from other semi-arid (Vlok and Yeaton 2000; Zedler, Gautier *et al.* 1983) and mesic systems (Cary and Morrison 1995; Morrison and Renwick 2000; Nieuwenhuis 1987; Russel-Smith, Ryan *et al.* 1998). 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), or that their seed banks are persistent and are not exhausted following an initial fire. 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 the 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 adult numbers remain relatively static following fire (owing to their ability to recover vegetatively) and their populations can be significantly augmented by the recruitment of seedlings. 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, Lloret *et al.* 1991; Francisco and Lopez-Soria 1993; Moreno and Oechel 1991; Morrison 1995; Vesk, Warton *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 (Auld 1990; Bell, Plummer *et al.* 1993; Knox and Clarke 2005; Noble 1989; Wellington 1989). 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, while a period of over 12 months elapsed between the winter 2002 burns and the next good rains – see Figure 2). Thus, seed predators had a much longer period at winter-burned plots with which 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, Congdon *et al.* 2004; Williams, Congdon *et al.* 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, Nelson *et al.* 1993; Friedel, Nelson *et al.* 1994). Hence, for such plants there are more seeds available to be cued by spring and summer burns because seed bank abundances peak in these months following seed shed, but become significantly reduced by winter-time due to 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 think that this is 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 demonstrate the potential for fire regimes to cause shifts in the mix of woody versus 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.

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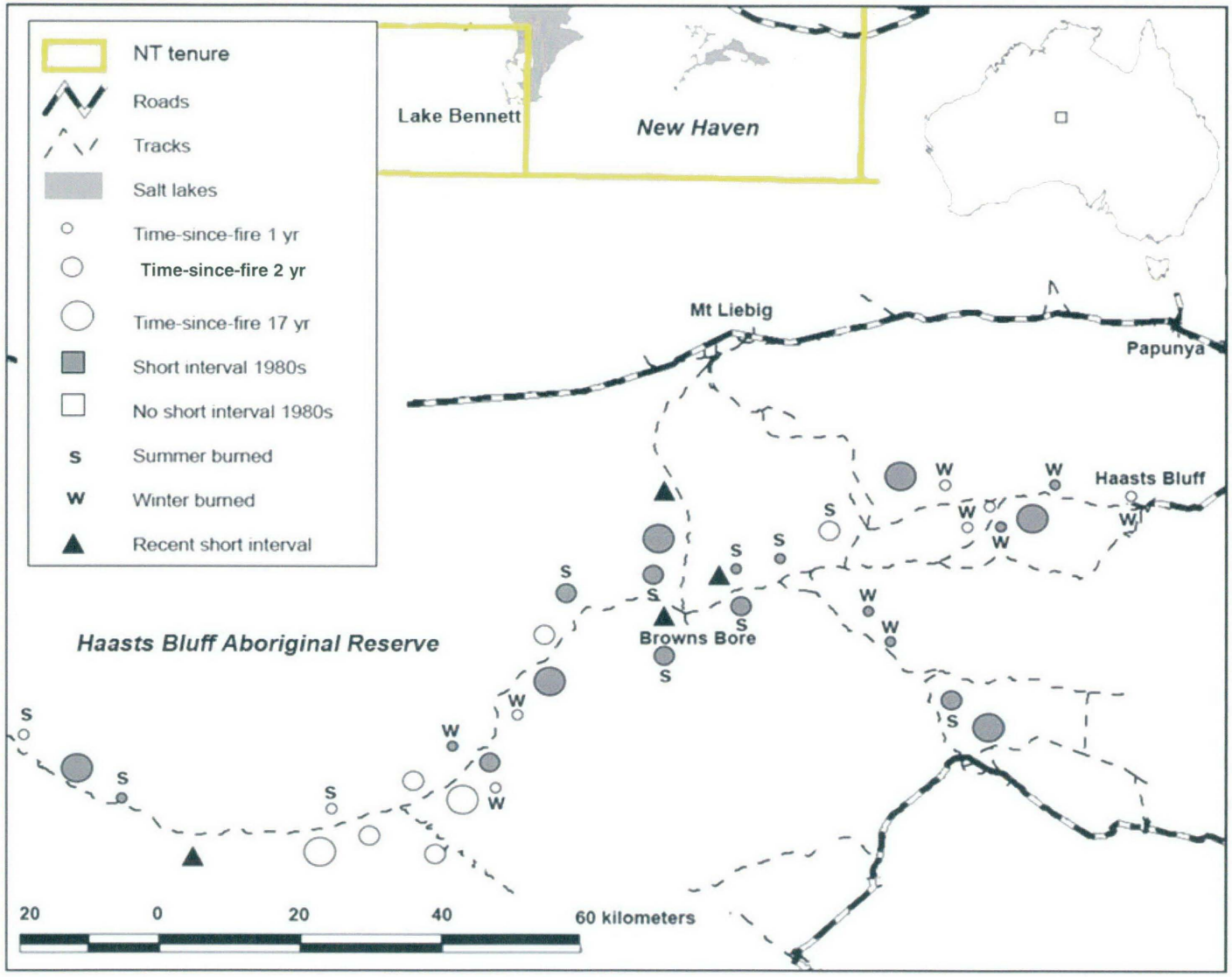
Figure 1. Location of sample sites within the Haasts Bluff reserve.



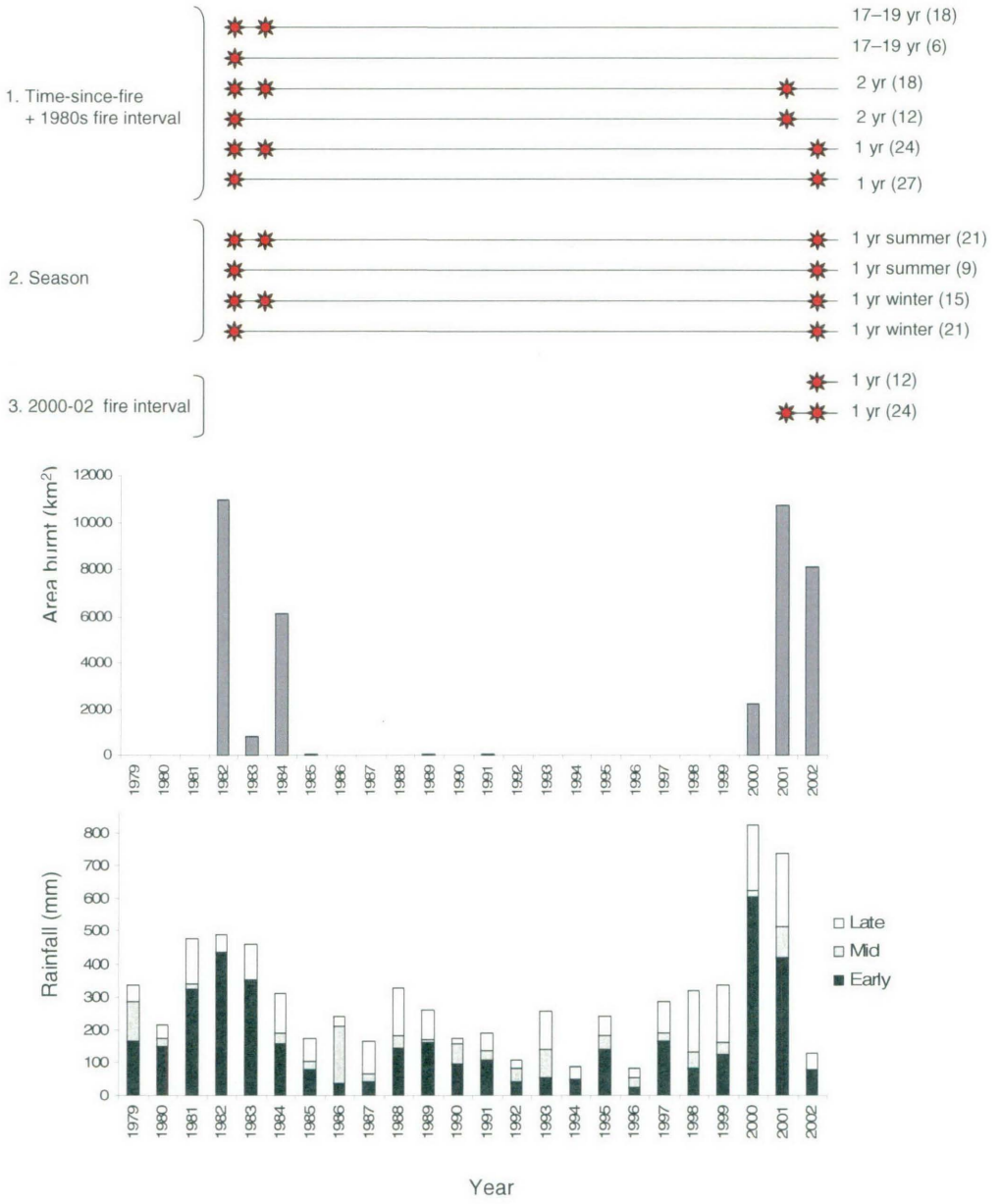


Figure 2. Upper diagram depicts fire sequences involved in the three series of fire history analyses, with length of each bar representing time-since-fire and stars indicating fire occurrence. Upper bar chart shows area burned by year in Haasts Bluff study area from 1982–2002. The lower bar chart indicates the mean annual rainfall recorded from Derwent, Newhaven and Glen Helen pastoral stations and of the Mereenie gas fields. These locations are situated adjacent to the study area's northern, eastern and south eastern boundaries, and the average of their annual rainfalls was considered a reliable indicator for general rain that had occurred within the study area.

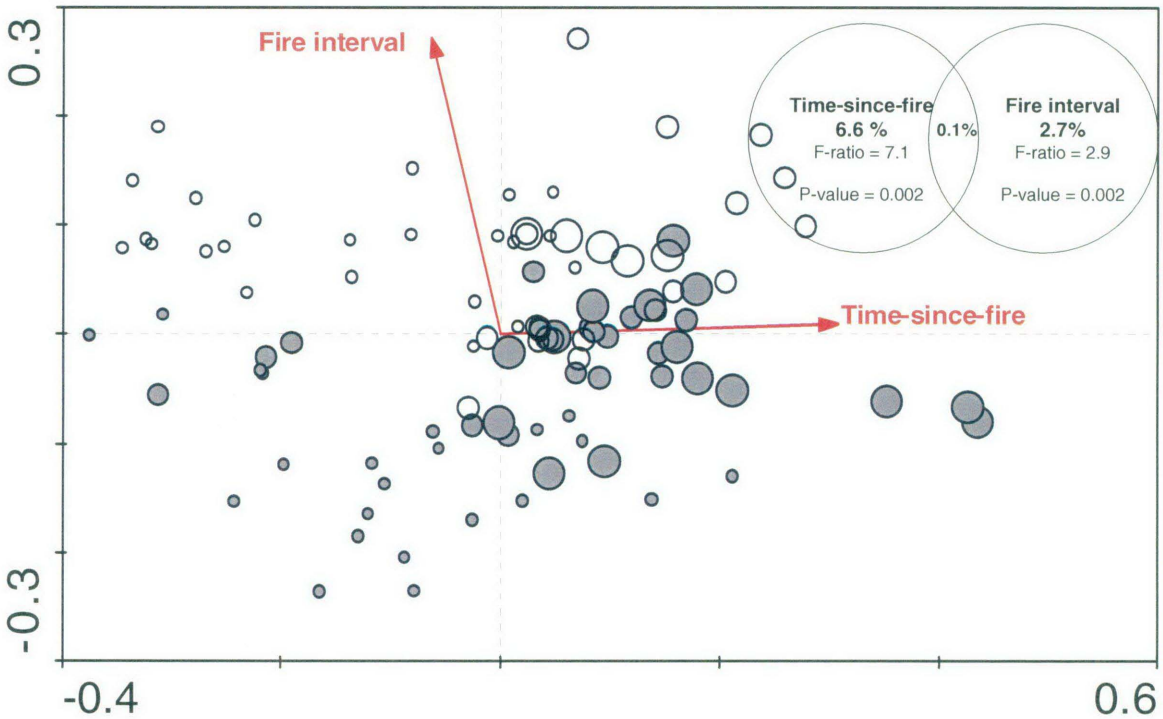


Figure 3. Ordination (RDA) biplot of sites with time-since-fire and fire interval as environmental variables. Sites that experienced long fire intervals are shaded, while sites that experienced a fire interval of 2 years are unshaded. Symbol size corresponds to the time since last fire, with sites sampled at 1 yr since fire being smallest circles, sites sampled at 2 yr since fire with middle sized circles and sites sampled at 17-18 yr since fire with large circles. Variance partitioning is inserted as a Venn diagram.

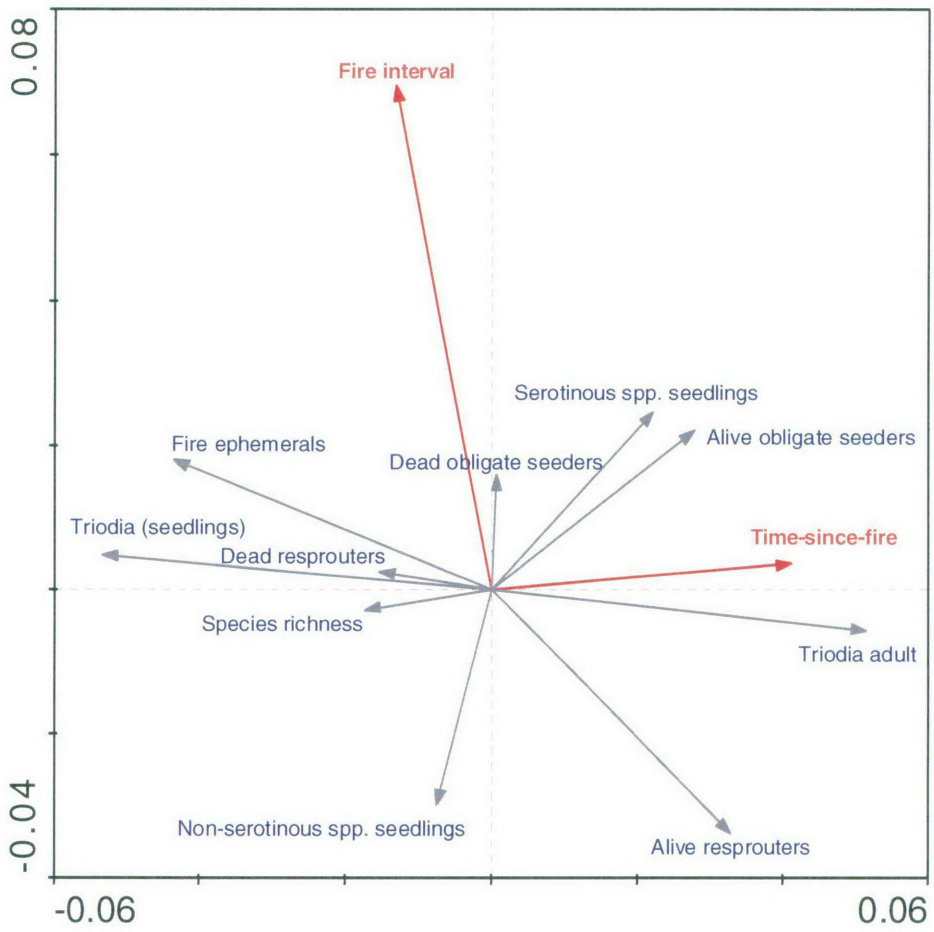


Figure 4. Ordination with significant (in GLM analysis) supplementary growth form variables imposed on time-since-fire by fire interval environmental variables. Only those variables found to be significant in the GLM analysis are included in the bi-plot.

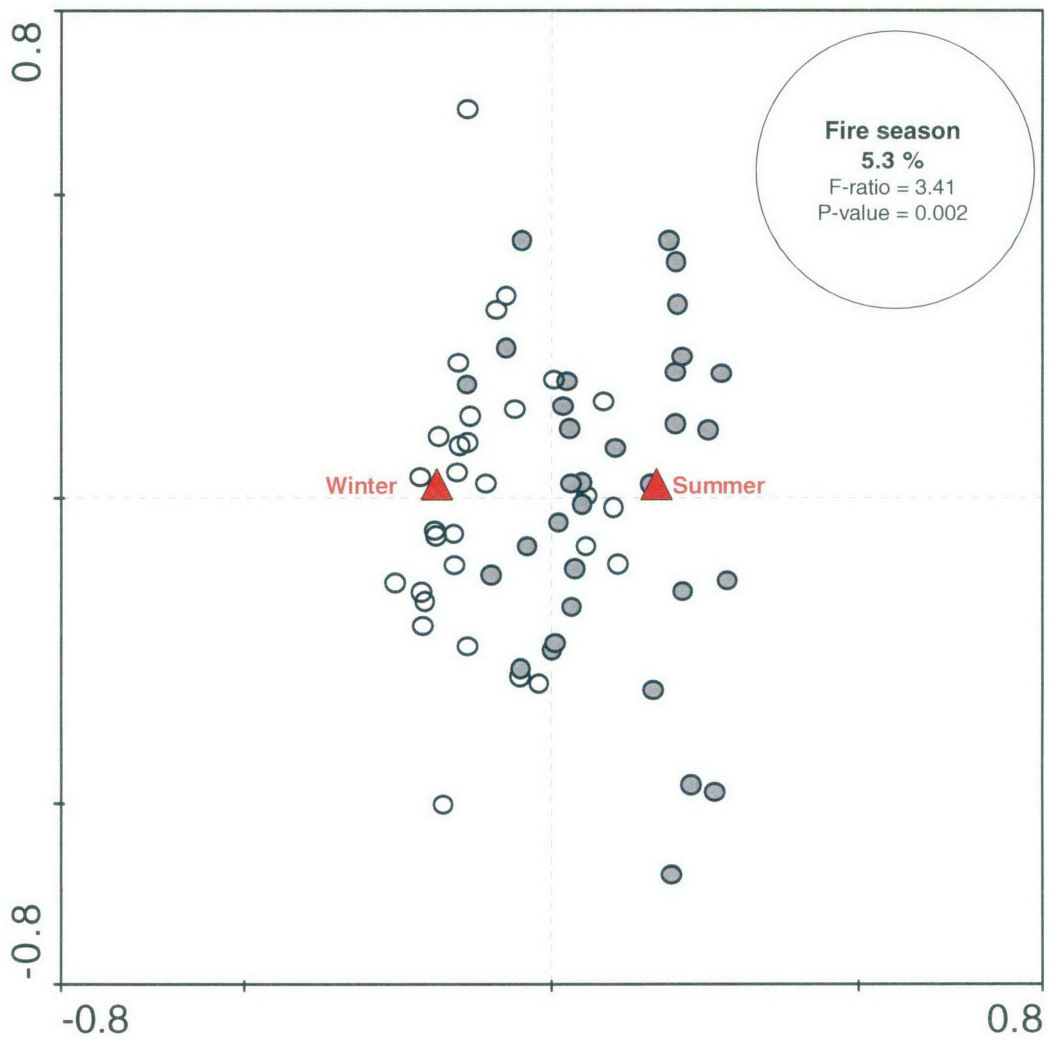


Figure 5. Ordination (RDA) of sites in relation to fire season. Sites that experienced fire between Oct. 2001 and Mar. 2002 (summer) are shaded while sites that experienced fire between Apr. 2002 and Sept. 2002 (winter) are unshaded. Results of variance partitioning are inserted in Venn diagram.

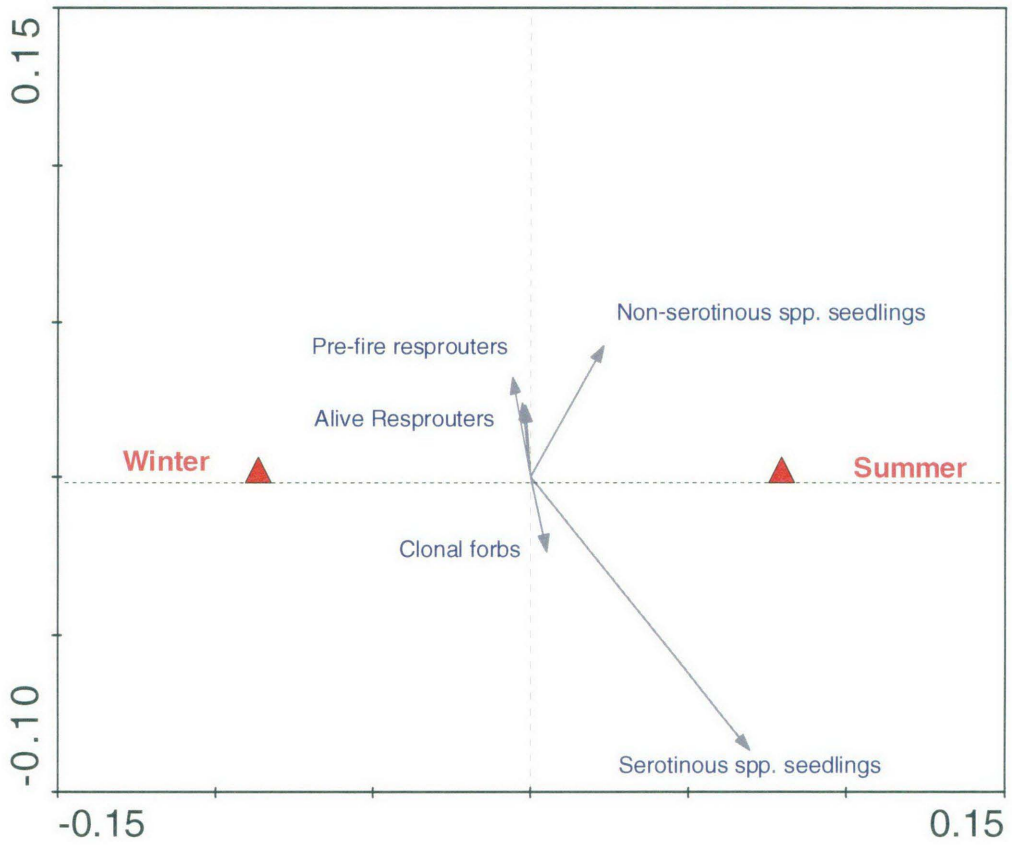


Figure 6. Ordination with supplementary growth form variables imposed on season RDA ordination diagram. Only those variables found to be significant in the GLM analysis are included in the bi-plot.

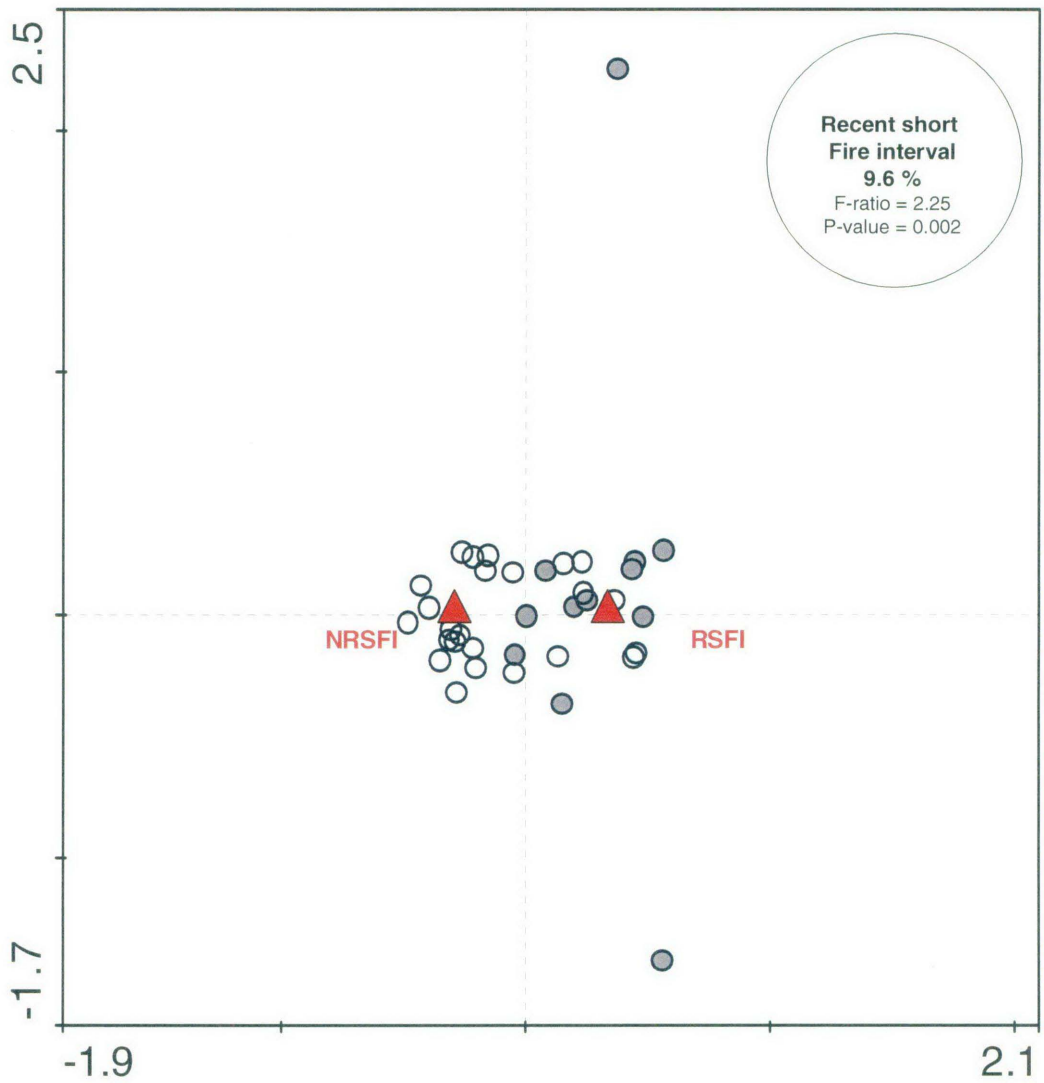


Figure 7. Ordination (RDA) of sites in relation to recent short fire interval. Sites that experienced a short fire interval between 2000-03 are shaded, while sites that did not receive a short fire interval during this period are unshaded. Results of variance partitioning are inserted in Venn diagram.

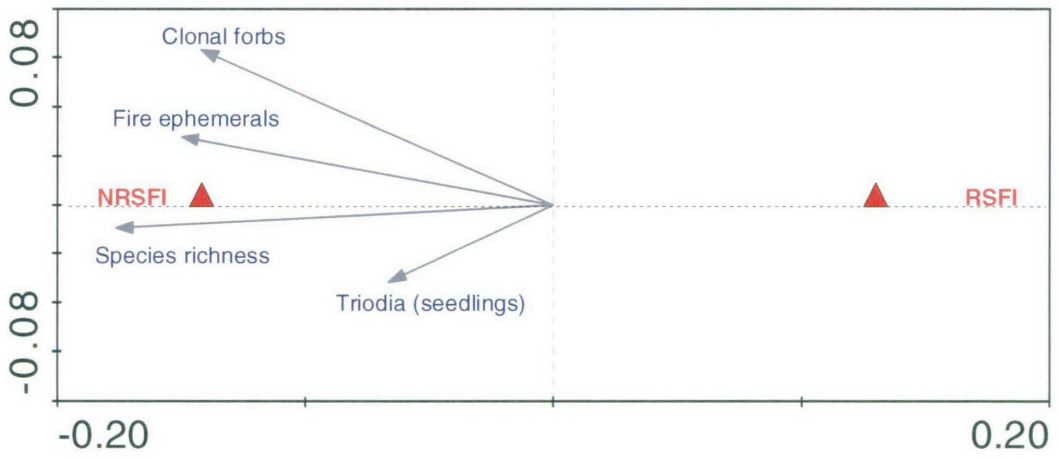


Figure 8. Ordination with supplementary growth form variables imposed on results of recent fire interval RDA analysis. Only those variables found to be significant in the GLM analysis are included in the bi-plot.

Table 1. 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 1982-85.

	GLM sequential model			Time since fire			Fire interval	
Factor	TSF	FI	TSFxFI	1 yr	2y	17y	SFI	NSFI
Alive obligate seeders	*	ns	ns	0	0	2	-	-
Dead obligate seeders	**	ns	ns	2	1	0	-	-
Alive resprouters	*	*	**	98	64	120	109	75
			SFI	110	59	149		
			NSFI	87	70	32		
Dead resprouters	**	ns	ns	14	11	3	-	-
Serotinous spp. seedlings	ns	*	***	-	-	-	-	-
Non-serotinous spp. seedlings	ns	*	ns	-	-	-	-	-
Fire ephemerals	***	ns	ns	37	39	16	-	-
Clonal forbs	ns	ns	ns	-	-	-	-	-
Triodia spp. (adult)	***	ns	ns	1	1	9	-	-
Triodia spp. (seedlings)	***	ns	*	8	7	1	-	-
			SFI	8	6	2		
			NSFI	8	8	0		
Species richness	***	ns	ns	27	26	23	-	-

#, $P < 0.1$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, not significant

Table 2. Summary of results for one factor generalised linear models (GLM) for functional groups according to whether sites were burned between October 2001-March 2002 (summer burns), or between April 2002-September 2002 (Winter burns).

	GLM model	Season	
Factor	Season	Summer	Winter
Alive obligate seeders	ns	-	-
Dead obligate seeders	ns	-	-
Alive resprouters	*	71	100
Dead resprouters	ns	-	-
Serotinous spp. seedlings	**	2	<1
Non-serotinous spp. seedlings	**	3	1
Fire ephemerals	ns	-	-
Clonal forbs	**	16	21
Triodia spp. (adult)	ns	-	-
Triodia spp. (seedlings)	ns	-	-
Species richness	ns	-	-

#, $P < 0.1$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, not significant

Table 3. 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.

	GLM model	Fire interval	
Factor	Fire interval	Recent SFI	No recent SFI
Alive obligate seeders	ns	-	-
Dead obligate seeders	ns	-	-
Alive resprouters	ns	-	-
Dead resprouters	*	3	14
Serotinous spp. seedlings	ns	-	-
Non-serotinous spp. seedlings	ns	-	-
Fire ephemerals	**	23	36
Clonal forbs	***	8	19
Triodia spp. (adult)	ns	-	-
Triodia spp. (seedlings)	***	4	8
Species richness	***	21	27

#, $P<0.1$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, not significant

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