Effects of fire intensity on plant species composition of sandstone communities in the Sydney region

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Abstract Fire intensity measures the heat output of a fire, and variation in fire intensity has been shown to have many effects on the demography of plant species, although the consequent effects on the floristic composition of communities have rarely been quantified. The effects of variation in fire intensity on the floristic composition of dry sclerophyll vegetation with different fire histories near Sydney was estimated. In particular, differences in species abundance of woodland and shrubland communities subjected to four fire-intensity classes: unburnt, low intensity ($<500 \, \text{kW m}^{-1}$), medium intensity ($500–2500 \, \text{kW m}^{-1}$) and high intensity ($>2500 \, \text{kW m}^{-1}$) were examined. The samples had a standardized previous fire frequency and season, thus minimizing the effects of other aspects of the fire regime. There was a clear effect of fire intensity on the relative abundances of the vascular plant species, with increasing intensity of the fire producing vegetation that was increasingly different from the unburnt vegetation. This pattern was repeated in both the woodland and shrubland vegetation types, suggesting that it was not an artefact of the experimental conditions. However, the effects of fire intensity on floristic composition were no greater than were the differences between these two similar vegetation types, with variation in fire intensity accounting for only approximately 10% of the floristic variation. Nevertheless, the effects of fire intensity on the abundance of individual species were consistent across taxonomic groups, with the monocotyledon and Fabaceae species being more abundant at higher than lower intensities, the Proteaceae and Rutaceae more abundant at intermediate intensities, and the Epacridaceae more abundant at lower rather than higher intensities. The number of fire-tolerant species increased with increasing fire intensity, and those fire-tolerant species present were most abundant in the areas burnt with medium intensity. The number of fire-sensitive species did not respond to fire intensity, and those species present were most abundant in the areas burnt with low intensity. This suggests that either fire-sensitive species respond poorly to higher fire intensities or fire-tolerant species respond poorly to lower fire intensities, perhaps because of differences in seed germination, seedling survival or competition among adults.

Key words: fire history, fire intensity, fire management, floristic composition, species abundance, species richness, species evenness.

INTRODUCTION

Fire is a common source of temporal and spatial change in plant species composition (Whelan 1995; Bond & van Wilgen 1996), especially in the dry sclerophyll communities of Australia. Fire regimes are usually considered to have three interrelated components that can affect plant community composition: fire frequency (how often the fires occur), season of occurrence (what times of the year they occur), and fire intensity (heat output of the fires) (Gill 1975). Most Australian work on plant–fire interactions at the community level has concentrated on the effects of fire frequency (see Morrison *et al.* 1995a), whereas the effects of fire season and intensity are relatively poorly understood.

Fire intensity is measured as kilowatts per metre of fire front (Luke & McArthur 1978; Cheney & Sullivan 1997), with extremes such as $60\,000 \, \text{kW m}^{-1}$ occurring

in forest wildfires in south-eastern Australia (Luke & McArthur 1978). Fire suppression becomes difficult at more than $2000 \, \text{kW m}^{-1}$ (Richmond 1981), and the upper limit for practical fire control is approximately $3500 \, \text{kW m}^{-1}$ (Gill *et al.* 1987). The normal limit for planned (prescribed) fires is approximately $500 \, \text{kW m}^{-1}$, whereas the lower limit for a self-propagating fire is about $150 \, \text{kW m}^{-1}$ (Luke & McArthur 1978; Cheney & Sullivan 1997). For the purposes of this paper, the following categories of approximate fire intensity are recognized:

1. Low intensity, $<500 \, \text{kW m}^{-1}$, flame height $<1 \, \text{m}$.
2. Medium intensity, $500–2500 \, \text{kW m}^{-1}$, flame height $1–3 \, \text{m}$.
3. High intensity, $>2500 \, \text{kW m}^{-1}$, flame height $>3 \, \text{m}$.

The floristic composition of a community after a fire is dependent on the preburn composition, but it can vary significantly from it (Keith 1996). Initial regrowth is usually by those species whose adult plants can survive fire (fire-tolerant species), whereas those

species whose adult plants do not normally survive fire (fire-sensitive species) tend to contribute more to the above-ground community later (Morrison *et al.* 1995a). The regrowth of vegetation is thus dependent on the degree to which the vegetation is scorched or consumed by the fire. Temporal or spatial variation in fire intensity therefore has the potential to change the floristic composition of a community by affecting the demography of the component species in ways that change their relative abundance (Keith 1996).

The effects of variation in fire intensity on the demography of plant species have been demonstrated to occur as a result of factors such as death or regrowth of adult plants (Purdie 1977a; Noble 1984; Auld 1986; Bradstock & Myerscough 1988; Moreno & Oechel 1993; Waldrop & Brose 1999; Williams *et al.* 1999; Morrison & Renwick 2000; Wardell-Johnson 2000), competitive interactions among surviving plants (Moser *et al.* 1996; Pelaez *et al.* 1997), death of the seed-bank (Bradstock & Bedward 1992; Bradstock *et al.* 1994), release of seeds from fruits (Bradstock & Myerscough 1981; Enright & Lamont 1989; Setterfield 1997; Waldrop & Brose 1999), breaking of seed dormancy (Barro & Poth 1988; Auld & O'Connell 1991; Hodgkinson 1991; Moreno & Oechel 1991; Bradstock & Auld 1995; Tyler 1995; Keeley & Fotheringham 1998; Odion & Davis 2000), suitability of the seed-bed for germination (Tomkins *et al.* 1991; Lamont *et al.* 1993; Rice 1993; Giovannini & Lucchesi 1997), and seedling survival (Purdie 1977b; Auld 1986; Moreno & Oechel 1992; Rice 1993; Segura *et al.* 1998).

Thus, the potential for effects of variation in fire intensity on floristic composition are quite considerable. However, mere recognition of these potential effects is insufficient, as they need to be tested by assessing their actual effects on plant communities as a whole. Unfortunately, such effects have rarely been examined (Peet 1971; Christensen & Kimber 1975 in south-western Australia; Dickinson & Kirkpatrick 1987 in Tasmania; Tellier *et al.* 1995 in Canada; Ewing & Engle 1988; Ducey *et al.* 1996 in the USA), and have only indirectly been demonstrated for the fire-prone vegetation of eastern Australia (Purdie & Slatyer 1976). In this paper I report on a quantitative study of some of the effects of spatial variation in fire intensity on the floristic composition of common plant communities of the Sydney region.

The study was purely descriptive (i.e. non-manipulative), relying entirely on the sampling of fortuitously available areas in the field with recent histories of different fire intensity. Such an experimental design is not ideal (see Gill 1977) but, given the practical difficulties of manipulating high fire intensities, large-scale manipulative field experiments for the study of fire intensity may be logistically impossible. Further-

more, interactions between the different aspects of a fire regime are complex. For example, fire intensity is influenced both by fire frequency, through the accumulation of fuel in the time between fires, and fire season, through prevailing weather conditions and soil moisture (Andersen *et al.* 1998). It is difficult to conduct an experiment that will untie these interdependencies without greatly simplifying the ecological situation. Finally, this study was concerned only with the above-ground component of plant species composition, as I did not quantify the soil-stored seed-bank for any species.

STUDY AREA AND METHODS

This work was carried out in dry sclerophyll communities of the Lambert Peninsula (151°16′W, 33°37′S) in Ku-ring-gai Chase National Park, a conservation reserve (approximately 15 000 ha) on the northern outskirts of Sydney. All samples were collected in winter and spring of 1995, from Hawkesbury Sandstone plateaus and ridgetops (approximately 150 m altitude), either in closed scrub/scrub–heath or in low woodland/low–open woodland. These two vegetation types occupy 42% of Ku-ring-gai Chase National Park (Thomas & Benson 1985), and are the most widespread natural vegetation types remaining in the Sydney region (Benson & Howell 1994).

Sample areas were chosen within an area burnt by a relatively large wildfire in early January 1994, which contained a mosaic of areas with a wide variety of prior histories of fires (Conroy 1996). Thus, all samples had a time-since-fire of 19–22 months, which should maximize the floristic diversity of the samples (Morrison *et al.* 1995a) and also avoid problems with identifying small seedlings. All samples were from areas that were last burnt by a wildfire in 1965, thus standardizing both the interfire interval (at 29 years) and the time-since-fire across all samples. This should reduce any interactive effects of fire frequency and fire intensity. Both wildfires (1965 and 1994) occurred in mid-summer, thus reducing any interactive effects of fire season and fire intensity.

Each sample was taken from a plant community that had clearly defined boundaries between areas with different fire histories (to ensure accuracy of sample placement), and had an understorey structure consistent with the recorded fire history (to ensure accuracy of the recorded fire regime). The fire history of each area was determined from the detailed fire-history records maintained by the NSW National Parks and Wildlife Service (Conroy 1996). Suitable replicate sampling areas were then chosen with respect to vegetation type, fire intensity during the 1994 fire, and ease of access. The sampling design thus assumed that the ranges of fire intensity, season and type (wildfire *vs*

prescribed burn) in the fires prior to 1994 were randomized across areas.

Within each of the two vegetation types (shrubland and woodland), two sample areas were located for each of the four fire-intensity classes: unburnt, low intensity, medium intensity and high intensity. The two replicate areas for each combination of vegetation type and fire intensity were separated by 1–2 km. The fire intensity at each area was estimated using a variety of methods based on the degree to which the combustible part of the vegetation canopy had been consumed by the 1994 fire, including crown scorch, height of fire scars and the size and composition of the remaining fuel load (Whight & Bradstock 2000). Basically, the fire-intensity classes were defined with respect to the above-ground parts of the vegetation layers as shown in Table 1 (cf. Peet 1971). In their study of the same fire, Whight & Bradstock (2000) estimated that the intensities in the 'high' category were of the order of 3000–3500 kW m^{-1} whereas those in the 'medium' category were approximately 1500 kW m^{-1}.

The abundance of each vascular plant species was estimated for each sample area by using the nested-quadrat technique of Outhred (1984). Each sample consisted of a pair of nested quadrats separated by 50–200 m (i.e. a total of 32 quadrats for this part of the experiment), with importance scores assigned to each species in each quadrat using seven square concentric (nested) subquadrats varying from 1 to 100 m^2. This technique produces abundance scores (on a scale of 1–14) that are functionally equivalent to frequencies (Morrison et al. 1995b), and thus are directly related to plant density (Bonham 1989). All species nomenclature follows Harden (1990, 1991, 1992, 1993).

To assess the possible effects of non-random patterns in the location of the areas with different fire intensities, floristic data were obtained from the same site but collected in spring 1991, prior to the 1994 wildfire. The data were collected as described in the preceding text, and from areas that had remained unburnt subsequent to the 1965 wildfire. The data from four quadrats at two locations were taken from Morrison et al. (1995a), with one sample location for the shrubland and one for the woodland.

Semi-strong hybrid multidimensional scaling (Belbin 1995) was used to investigate the patterns of plant species composition between the areas with different fire intensities and vegetation types. This multivariate ordination technique is a hybrid between metric and non-metric multidimensional scaling that attempts to combine the best features of each of the two techniques (Belbin 1991). A two-dimensional ordination was used, with the Bray–Curtis dissimilarity measure (Faith et al. 1987) and a cut point at dissimilarity = 0.9. The statistical significance of the differences in floristic composition between the areas with different fire intensities and vegetation types was assessed using analysis of similarities (Carr 1996). This is a multivariate Monte Carlo permutation test (Nicholas & Graves 1983; Clarke & Green 1988), which used the Bray–Curtis dissimilarity measure and a two-factor (vegetation type, fire intensity) orthogonal design. In addition, a redundancy analysis was performed, as described by Morrison et al. (1995a). This is a constrained ordination technique based on principal components analysis that, in a joint analysis of two data sets (e.g. floristic and environmental), assesses the degree to which they show covariation.

Each species was also recorded as fire-sensitive (>50% of the individuals usually killed by fire) or fire-tolerant (<50% adult mortality of a population subject to 100% leaf scorch; Gill 1975). For each sample, the floristic richness and evenness were calculated for each of these two species groups, with richness calculated as the total number of species present and evenness as the modified Hill's ratio (Ludwig & Reynolds 1988). The average frequency of these species groups was also calculated for each sample, as was the average frequency for those taxonomic groups for which several species were encountered (monocotyledons, Epacridaceae, Fabaceae, Myrtaceae, Proteaceae, Rutaceae). Each of these patterns was analysed by separate two-factor (vegetation type, fire intensity) orthogonal analyses of variance (Wilkinson 1991). All analyses of variance were tested for homoscedasticity using Bartlett's test (Wilkinson 1991).

As a heuristic technique to identify those species showing the largest response to fire intensity, the frequency data for each species were analysed by separate two-factor (vegetation type, fire intensity) orthogonal analyses of variance (Wilkinson 1991). This allowed the identification of those species for which either the intensity factor or the two-factor interaction was significant at $P < 0.01$ (to take into account the setwise error rate).

Table 1. Fire-intensity classes defined as per the above-ground parts of the vegetation layers

	Unburnt	Low	Medium	High
Herb/monocot/litter layer	Unscorched	Consumed	Consumed	Consumed
Small-shrub layer (<2m)	Unscorched	Scorched	Consumed	Consumed
Large-shrub/tree layer (>2m)	Unscorched	Unscorched	Scorched	Consumed

Scorched = dead but not consumed.

RESULTS

A total of 142 plant species were encountered in this study, with individual samples containing from 40 to 75 species per 200 m^2. Of these species, 83% occurred in the samples from the shrubland and 92% in the samples from the woodland, whereas 80% occurred in the unburnt samples, 73% in the samples burnt with low intensity, 73% in the samples burnt with medium intensity, and 80% in the samples burnt with high intensity. Of these species, 134 (94%) could be classified as either fire-sensitive (56 species) or fire-tolerant (78 species). The remainder either exhibited variable behaviour in different areas or were unknown.

The multidimensional scaling ordination of the samples showed a continuum in plant species composition (Fig. 1). The stress value (0.250) was rather high, indicating that there were other floristic patterns in the data that needed more than just two dimensions to be displayed properly. Furthermore, the redundancy analysis indicated that variation in fire intensity
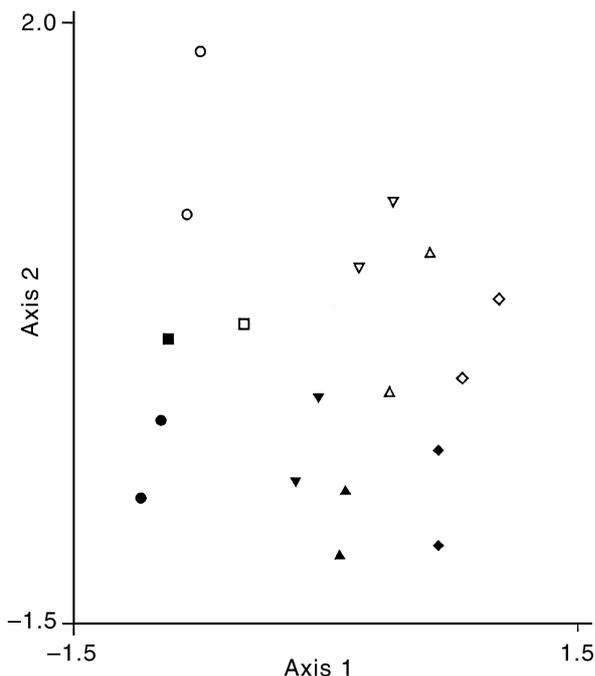

Fig. 1. Two-dimensional hybrid scaling ordination of the samples from the woodland (filled symbols) and shrubland (open symbols) areas of the Lambert Peninsula, Ku-ring-gai Chase National Park, that had been (●) unburnt or subjected to burning by a wildfire in 1994 at (▼) low, (▲) medium or (◆) high fire intensity, as well as (■) samples taken in unburnt vegetation prior to the 1994 fire. Each point represents one sample, and the relative position of the points on the graph indicates how similar the samples are to each other based on their floristic composition (points near each other are more similar than points further apart). The orientation and scale of the diagram are arbitrary. Stress = 0.250.

accounted for only approximately 9% of the floristic variation among the samples (i.e. the 'explained' variation), whereas the community differences accounted for approximately 11% of this variation.

However, there were two clear patterns in the multidimensional scaling ordination. First, there was a distinction in floristic composition between the shrubland and woodland areas irrespective of the fire intensity (basically variation along axis 2 of Fig. 1). Second, there was a consistent trend in floristic composition from unburnt vegetation through to vegetation burnt at low, medium and high fire intensity irrespective of the vegetation type (basically variation along axis 1 of Fig. 1). So, increasing intensity of the fire produced vegetation that was increasingly different from the unburnt vegetation. The spatial distribution of the points on the graph indicates that the effects of fire intensity on plant species composition were no greater than the differences between the two vegetation types. The samples taken prior to the 1994 wildfire had no obvious points of distinction from those samples taken in the unburnt area subsequent to the 1994 fire. Consequently, there was no evidence that the fire intensity classes were spatially distributed in a non-random way.

The analysis of similarities indicated that the floristic differences between the two vegetation types were statistically significant ($P = 0.011$, based on all 270 possible permutations), as were the differences between the fire intensities ($P = 0.003$, based on a sample of 5000 permutations).

Only the Myrtaceae species showed a statistically significant difference in average frequency between the two vegetation types ($P = 0.010$). This result was caused by the increased abundance of both tree species (e.g. *Eucalyptus gummifera, Eucalyptus haemastoma*) and some shrub species (*Darwinia fascicularis, Kunzea capitata, Leptospermum trinervium*) in the woodland areas. None of the groupings showed a significant interaction between vegetation type and fire intensity effects, and so the intensity patterns were similar in both vegetation types. Thus, the data could be pooled across the vegetation types for the analyses of fire intensity.

Most of the ecological and taxonomic groupings of the species showed statistically significant patterns of abundance in relation to fire intensity (Table 2). The average abundance of the species was greater in the burnt areas than in the unburnt areas. The fire-sensitive species were usually more abundant than the fire-tolerant species, with the fire-sensitive species being most abundant in the low-intensity areas and the fire-tolerant species most abundant in the medium-intensity areas. The Epacridaceae species were most abundant in the low-intensity areas, and much rarer in the high-intensity areas. The Proteaceae (notably *Banksia spinulosa, Grevillea speciosa, Petrophile pulchella*) and Rutaceae (notably *Philotheca salsolifolia*)

species were most abundant in the low- and medium-intensity areas, whereas the monocotyledons (notably *Caesia parviflora*, *Cyathochaeta diandra*, *Hypolaena fastigiata*, *Lepidosperma filiforme*, *Ptilothrix deusta*, *Thysanotus juncifolius*, *Xyris gracilis*) and the Fabaceae species (notably *Acacia myrtifolia*, *Dillwynia retorta*, *Gompholobium glabratum*, *Gompholobium grandiflorum*) were most abundant in the medium- and high-intensity areas. Other species showing significant differences in abundance were: *Mitrasacme polymorpha* (more abundant in low-intensity areas), *Scaevola ramosissima* (low- and medium-intensity), *Schizaea bifida* (medium-intensity) and *Bauera rubioides* (high-intensity), with *Pimelea linifolia* being more abundant in the burnt areas than in the unburnt areas.

The overall richness of the species increased with increasing fire intensity (Table 2), this being mainly due to the increasing richness of the fire-tolerant species. The evenness of the fire-sensitive species was greater in the burnt areas than in the unburnt areas.

DISCUSSION

There was a clear effect of fire intensity on the relative abundances of the vascular plant species among the samples, whereby increasing fire intensity produced vegetation that was increasingly different from the unburnt vegetation. This result was repeated in a consistent fashion in both the woodland and shrubland vegetation types, suggesting that the outcome was not an artefact of the experimental conditions. Furthermore, it is in agreement with the results of Purdie and

Slatyer (1976) for a forest community in south-eastern Australia. If this conclusion is a general one for other fire-prone sandstone communities of the Sydney region, it suggests that fire intensity is an important source of within-community variability in the relative abundances of the component plant species.

However, the effects of fire intensity on floristic composition were no greater than were the differences between the two (similar but distinct) vegetation types, and the high stress value of the multidimensional scaling ordination indicated that these two factors accounted for only part of the floristic patterns. This was confirmed by the redundancy analysis, which indicated that both the variation in the fire intensity and the community differences accounted for only approximately 10% of the floristic variation among the samples. This percentage is much less than the 55–60% of the floristic variation that has been reported to be accounted for in these communities by variation in fire frequency (Morrison *et al.* 1995a), although it is difficult to directly compare these numbers because of differences in the design of the experiments. Nevertheless, it seems reasonable to conclude that fire intensity apparently has a smaller effect than does fire frequency on the plant species composition.

In spite of this relatively small pattern, fire intensity produced consistent effects among the component species of the vegetation communities. For example, the effects of fire intensity on the abundance of individual species was consistent across taxonomic groups, with the monocotyledon and Fabaceae species being more abundant at higher than lower intensities, the Proteaceae and Rutaceae being more abundant at

Table 2. Mean frequency, richness and evenness of samples for various groupings of the plant species showing significant patterns in relation to the different fire intensities

Variate and species group	P	Unburnt	Low intensity	Medium intensity	High intensity
			Mean		
Average frequency					
All species	0.003	2.4	3.8	3.8	3.5
Fire-sensitive	0.020	2.9	4.9	4.1	4.0
Fire-tolerant	<0.001	2.0	3.2	3.6	3.3
Monocotyledons	<0.001	2.5	4.4	5.2	5.0
Epacridaceae	0.084	3.0	4.8	3.1	2.3
Fabaceae	0.010	2.9	4.7	5.1	5.0
Myrtaceae	0.260	NS	NS	NS	NS
Proteaceae	0.088	3.3	4.2	4.7	4.0
Rutaceae	0.082	1.8	3.0	2.9	1.8
Richness					
All species	0.006	54.3	63.3	69.0	71.0
Fire-sensitive	0.513	NS	NS	NS	NS
Fire-tolerant	0.001	27.2	35.0	38.3	36.8
Evenness					
All species	0.529	NS	NS	NS	NS
Fire-sensitive	0.001	0.99	1.04	1.03	1.03
Fire-tolerant	0.434	NS	NS	NS	NS

NS = not significant, and the probabilities (P) are from the analyses of variance (ANOVA).

intermediate intensities, and the Epacridaceae being more abundant at lower rather than higher intensities. Only the Myrtaceae species appeared to have no consistent patterns. These patterns presumably relate to the demographic characteristics of the species, as many species in the same taxonomic group often have similar life-history characteristics that have consequences for their demographic behaviour in response to fire regimes (Bradstock & Auld 1987; Pate 2000).

One of the most important demographic characteristics in relation to fire intensity is whether the species is fire-sensitive or fire-tolerant. The number of fire-tolerant species increased with increasing fire intensity, and those fire-tolerant species present were most abundant in the areas burnt with medium intensity. On the other hand, the number of fire-sensitive species was not affected by fire intensity, and those species present were most abundant in the areas burnt with low intensity. These results apparently support the fire-regime models proposed by Keeley and Zedler (1978) for Californian chaparral and Kruger and Bigalke (1984) for South African fynbos, which suggest that changes in the abundance of fire-sensitive and fire-tolerant species should be inversely related.

This result suggests that either the fire-sensitive species responded poorly to higher fire intensities or that the fire-tolerant species responded poorly to lower fire intensities. Distinguishing between these two possibilities would require a study of the demography of the species involved. However, a number of relevant considerations can be identified, based on those demographic features that seem to be most influenced by fire intensity (Keith 1996).

First, adults of fire-sensitive species are killed by 100% leaf scorch, which will occur at all fire intensities for those species with smaller individuals. Therefore, the main effect of fire intensity on the abundance of these species is likely to be via differences in seed and seedling survival, as these species all rely on a seed-bank to maintain themselves in the community. For example, high-intensity fires kill the seeds of some species but low-intensity fires do not (Bradstock *et al.* 1994), and medium-intensity fires lead to the germination of the seeds of some species whereas low-intensity fires do not. The influences of intensity on breaking of seed dormancy can be due to smoke composition (Keeley & Fotheringham 1998) or heat penetration of the soil (Auld & O'Connell 1991; Bradstock & Auld 1995; Odion & Davis 2000), although temperature is not directly related to intensity. It thus seems likely that fire-sensitive species will do poorly if subjected to high fire intensities.

Second, at least some of the adults of fire-tolerant species can survive 100% leaf scorch. However, adult survival in many of these species is related to fire intensity (Williams *et al.* 1999; Morrison & Renwick 2000), with higher intensities resulting in poorer survival. Furthermore, seeds of fire-tolerant species are often found to be less tolerant of increasing temperatures than are those of fire-sensitive species (Barro & Poth 1988; Moreno & Oechel 1991). These two observations suggest that fire-tolerant species might also do poorly if subjected to high-intensity fires. It thus seems likely that the relative success of fire-tolerant species at medium intensities may be due to decreased competition from the fire-sensitive species (Keith & Bradstock 1994; Bond & van Wilgen 1996).

I also observed that the evenness of the fire-sensitive species was less in the unburnt areas than in the burnt areas, indicating that the relative abundance of fewer of these species comes to dominate the community in the absence of fires. This is presumably a result of differences in longevity among the species, as many of the fire-sensitive species are relatively short-lived shrubs and subshrubs. These species rely on fire for the continuation of their contribution to the above-ground biomass, but may maintain their representation in the community via a soil-stored seed-bank.

The potential for variation in fire intensity is quite large, and this is of major importance in fire management. For instance, the intensity of a bushfire is the product of a series of physical characteristics, including the quantity of combustible fine fuel, the heat energy of the vegetation and the rate of forward spread of the fire front, the latter being determined by the wind speed, surface instability, slope and the combustion rate of the fine fuel (Richmond 1981). The combustion rate, in turn, is a product of the fuel characteristics, such as compaction, ventilation, component sizes and oil and moisture content, as well as weather conditions, such as long-term rainfall deficit, short-term drying conditions, surface temperature and humidity (Richmond 1981). Most of these factors are not directly related to the species composition of the vegetation, and so within-community variation in intensity is not greatly determined by the floristic variation itself. This means that there is unlikely to be much in the way of feedback interactions between species composition and fire intensity.

Current fire management practices in the fire-prone vegetation of the Sydney region are based mainly on the concept of hazard reduction via fuel reduction (Luke & McArthur 1978; Richmond 1981; Whelan & Muston 1991), which means that the fire regimes prescribed for a particular managed area are determined principally by the amount of fire fuel that has accumulated. It is thus fire intensity that is actively managed, rather than the other components of the fire regime. In practice, hazard-reduction burns in the Sydney region are carried out using low-intensity fires with an average frequency of approximately 5 years (Whelan & Muston 1991). The results presented here suggest that the repeated use of low-intensity rather than high-intensity fires for the management of

vegetation will not substantially alter biodiversity. However, it has been persistently reported that repeated use of a particular fire frequency reduces biodiversity (Gill & Bradstock 1995; Keith 1996), and thus this is presumably a more important issue for the potential extinction of biotas.

Finally, the sampling design used here was a descriptive one, as it relied entirely on the availability of areas with different fire intensities in the required vegetation types. It is not possible to perform a manipulative experiment using high-intensity fires as these are, by definition, beyond human control. Purdie and Slatyer (1976) used a before-after/control-impact (BACI) design, in which they sampled vegetation at three sites before and after a fire at both burnt and unburnt locations, but they achieved different fire intensities by having different prior fire regimes (and thus different fuel loads) at each site. This design thus confounds fire intensity with fire frequency (and to some extent fire season), so it is not necessarily a better design. Given that there is no prior knowledge about the locations of different intensities in a naturally occurring fire, and that artificial creation of high-intensity fires is either unethical or involves confounding other sources of variation, a BACI design will always be problematic.

There are a number of difficulties in interpreting a 'natural' experiment as described in this paper rather than a controlled manipulative one. Most notable is that variation in fire intensity may be related to some other factor that is also related to floristic variation, so that variation in fire intensity will be confounded with this other source of variation. It will then not be possible to disentangle their separate effects on floristic composition (if, indeed, they exist). It is thus possible that the effects attributed here to fire intensity are artefacts of the sampling design. Explicit attempts were made to reduce this possibility, although it cannot be eliminated entirely. First, the effects of other aspects of the fire regime were minimized by standardizing the fire season and the fire frequency throughout the areas sampled. Second, the potential effects of the spatial variation in the fire intensity were assessed by including data collected before the last fire, which were shown to be similar to those in unburnt areas after the fire.

Also, the precise fire intensity at the sample locations was not quantified, because the locations were not determined until after the fire had occurred. Consequently, only crude categories of intensity could be used (i.e. an ordinal rather than a ratio scale of measurement). These categories have a simple interpretation in relation to the effects of the fire on the individual plants (in terms of scorch and consumption of above-ground parts), and also in relation to fire management. However, it is possible that this design limitation may have distorted the patterns that were observed (Whight & Bradstock 2000), although the clarity of the patterns detected suggests that this is unlikely. More to the point, it is debatable whether the effects studied here can strictly be treated as the result of intensity in terms of heat output. Perhaps a better term would be fire 'severity', as discussed by Feller (1998).

In addition, whereas the present study replicated intensity classes in space, both within and between communities, it still involved only a single fire that is therefore unreplicated either in space or time. The results obtained here were very consistent, and the spatial variability associated with independent fires at the same time is likely to be no larger than that within a single fire (Whight & Bradstock 2000). So, it may be anticipated that similar outcomes would be obtained in the same vegetation types elsewhere within the Sydney region, and in other fires in other years, but no direct evidence for this is provided. In particular, only one fire frequency was studied here, with two fires several decades apart. Bond and van Wilgen (1996) suggest that fire intensity determines demographic changes at intermediate fire frequencies, rather than at short or long intervals and so it is possible that I might have detected a greater effect of fire intensity under other circumstances.

ACKNOWLEDGEMENTS

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