

Effects of time since fire, topography and resprouting eucalypts on ephemeral understorey species composition, in semi-arid mallee communities in NSW.

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In 1985 and 1989, two studies examined the effects of time since fire, topography and resprouting eucalypts on the composition of understorey species in mallee vegetation at Yathong Nature Reserve, in semi-arid New South Wales. Emphasis was on ephemerals. Species richness was significantly higher at 2.5 years after fire. Species present five years after fire were a subset of those occurring earlier. Two-dimensional ordination based on ranked similarity measures of species and analysis of similarities indicated discrete time since fire groups. Short-lived species dominated early groups (≤ 2.5 years) i.e. *Haloragis odontocarpa*, *Convolvulus erubescens*, *Sclerolaena parviflora* and *Solanum coactiliferum*. All these species had disappeared at ≥ 5 years. The perennials *Triodia scariosa*, *Amphipogon caricinus* and *Halgania cyanea*, dominated at ≥ 5 years post-fire. Species composition was significantly affected by topographic position (upper, mid, lower dune) but not by mallee eucalypts (under canopy, in gap). Two-dimensional ordination based on ranked similarity measures of species and ANOSIM indicated that upper and lower topographic positions were significantly different. Most common species in upper topographic positions were *Haloragis odontocarpa*, *Bracteantha viscosa* and *Sclerolaena parviflora* and in the lower *Stipa scabra*, *Haloragis odontocarpa* and *Chenopodium* sp. Species richness was not significantly affected by topography or eucalypts ($17.45/10\text{m}^2 \pm 0.16$). The number of ephemeral species (10m^2) was higher in the lower topographic positions (7.87 ± 0.66) than the upper (4.88 ± 0.44). There was no significant effect of eucalypts on the number of ephemeral or perennial species.

Introduction

Although studies have examined the effects of factors such as time since fire and topography on perennial plant species in Australian semi-arid mallee communities (Cheal 1981, Hodgkinson & Griffin 1982, Maconochie 1982, Bradstock 1989, Hill 1989, Noble 1989a, 1989b, Wellington 1989, Bradstock & Cohn 2002, Noble & Grice 2002), comparatively little is known about the ephemeral grass and herb species with which they coexist. These species are difficult to study because they appear sporadically, which in part reflects their dependence on seasonal rainfall for germination, growth and reproduction (Holland 1968, Noble 1989b, Fox 1990).

A number of studies examining the effect of time since fire on ephemeral herb and grass species composition have either compared recently burnt and unburnt mallee stands (Zimmer 1940, Cheal 1981, Van der Moezel & Bell 1984), or, if a range of times since fire has been examined, then emphasis has been on biomass changes in the most dominant species (Noble 1989b). Whilst both types of studies agree on a decline in species richness with time since fire, resulting from the disappearance of short-lived herb and grass species, neither has provided detailed information on the changes in frequency of individual or suites of species over time.

In the semi-arid zone subtle changes in soil texture, water balance and nutritional status are known to determine the distribution of perennial species, resulting in a mosaic of mallee communities (Beadle 1981, Parsons 1981, Specht 1981, Bradstock & Cohn 2002). Within mallee dunefields of New South Wales, different vegetation patterns in swales and on dunes have been attributed to an interaction between topography, soil type and fire (Noble 1984). Although the broad distribution of mallee species in relation to topography and soil types is well documented (Bradstock 1989, Morcom & Westbrook 1990, Fox 1991, Scott 1992, Cohn 1995, Sivertsen & Metcalfe 1995, Porteners et al. 1997, Westbrooke et al. 1998), no study has concentrated on the small scale distribution of understorey ephemeral species in relation to those two factors. Work by Noble (1981, 1984) however suggests that the heavier soils of swales have a greater capacity to carry ephemeral species than the sandier soils of adjacent dunes.

Microhabitat diversity may also influence the distribution of herb and grass species. Mallee eucalypts develop pronounced soil hummocks at their bases, mostly from soil accretion (Noble 1989a). Since there is evidence that wind and water probably play a role in distributing seeds (Hodgkinson et al. 1980), the composition of herb and grass species may be different below eucalypts than in the gaps between them. A number of studies have found a relationship between species composition and distance from eucalypts (Story 1967, Hodgkinson et al. 1980, Harrington et al. 1981, Noble 1989b, Lunt 1990, Scanlan & Burrows 1990, Magcale-Macandog & Whalley 1991, Kirkpatrick 1997). Such trends, however, could be attributed to the influence of the overstorey in relation to radiation, temperature and competition for soil-moisture and nutrients (Kirkpatrick 1997). Such effects could be minimised directly after a fire when a reduction in competition from *Eucalyptus* spp. results from live tissue removal from the aerial growing parts and resprouting is in its infancy.

Our studies examine species richness and composition in the understorey; firstly in relation to a range of times since fire (up to 15 years), and secondly in relation to topographic position (lower slope, mid-slope, upper slope), the position of species in relation to resprouting eucalypts (in gap, under canopy), and their interactions.

Methods

The studies were undertaken in Yathong Nature Reserve, in central western New South Wales, approximately 130 km south of Cobar (32°35' S, 145°35' E). Sites were located in mallee on low east-west oriented dunes of deep red siliceous sands and in the swales on deep calcareous red earths and red texture-contrast soils (Lawrie &

Stanley 1980, Mabbutt et al. 1982, Soil Conservation Service 1984). The mallee was dominated in the overstorey by *Eucalyptus dumosa* and *Eucalyptus socialis* with an understorey of *Acacia rigens*, *Acacia wilhelmiana* and the hummock grass *Triodia scariosa* subsp. *scariosa*.

Most of the Nature Reserve lies between the 325 mm and 350 mm isohyets. Rainfall is characteristically non-seasonal, and variable annually (Leigh et al. 1989). At Cobar the mean minimum daily temperature in July is 4.1°C and the mean maximum daily temperature in January is 34.6°C. Evaporation is high, especially in non-winter months (Anon. 1968).

Taxonomy follows Harden (1990–1993). At the time of the survey the taxonomy of *Stipa variabilis* complex was in disarray. The complex has now been identified as four separate species namely *Austrostipa nitida*, *Austrostipa nodosa*, *Austrostipa drummondii* and *Austrostipa trichophylla*, which are considered annuals (Surrey Jacobs, pers. comm). Since our specimens were not available for a second examination, we have referred to this complex as *Austrostipa* spp.

Effects of time since fire

This study was undertaken in November 1989. We examined the frequency of occurrence of all species of grasses, herbs and seedlings of woody species at different times since fire. The chronosequence approach involved selecting sites with a range of times since last fire with uniform site characteristics. The five sampled sites were previously burnt in the summers of, respectively, 1974/75 and 1984/85, April of 1987, March of 1988 and 1989. The wildfires in 1974/75 and 1984/85 burnt extensive areas (> 10 000 ha) and the former burnt all study sites. The fires after 1985 were small-scale experimental burns varying in size from 50 ha in 1987, 20 ha in 1988 and 6 ha in 1989 (Bradstock et al. 1992, Cohn & Bradstock 2000). Within homogeneously burnt areas in each time since fire, 20 transects were selected within an area of approximately 1 km². Data were collected in 1 m² quadrats located along the transects, measuring 20 m in length. There were five quadrats per transect and within each, the presence of all plant species was recorded.

The chronosequence approach depended on uniformity of site characteristics. Departures from this included variation in the year/season of the last burn and previous fire intervals. Since the survival of post-fire seedlings are dependent on post-fire conditions, trends in our data may have been, in part, influenced by variations in rainfall and vertebrate grazing (Noble 1989a, 1989b, Cohn & Bradstock 2000). Former fire intervals ranged from 10 to 14 years, except for the 1974/75 fire, for which the previous interval was 'unknown'. Given that the known range of fire intervals was not large and that the decline in species richness for 1974/75 site were consistent with other similar studies in semi-arid mallee communities (Cheal 1981), concerns for this departure were considered minimal.

Effects of topography and eucalypts

This study was undertaken in December 1985 in an area previously burnt in the summer of 1984/85. It examined the effects of topography, eucalypt presence and their interactions on the composition of understorey species, especially ephemerals during ideal conditions i.e. in the first growing season after fire, following above average spring rainfall. On a transect placed from one swale to the next (i.e. bisecting a prominent dune; approx. 200 m long), plant species were recorded in 1 m² quadrats at specified topographic positions: swale, lower slope, mid-slope, dune crest and upper slope. At each topographic position, which occurred twice along the transect, 10 quadrats sampled under resprouting *Eucalyptus* spp. and a further 10 sampled in the gaps. A total of 200 quadrats were sampled. Data from the swale and lower slope were pooled and referred to as 'lower'; pooled data from the dune crest and upper slope were called 'upper'; mid-slope data was called 'mid'.

Statistical Analyses

Analyses of variance (ANOVA) used Tukey tests for post-hoc pairwise comparisons. To satisfy Cochran's test of homogeneity of variances, data were square root transformed. Where heterogeneity of variance could not be overcome through transformation, a more conservative level of significance ($P < 0.01$) was applied (Underwood 1981).

Effects of time since fire

The null hypothesis that the number of species (per transect i.e. 5 m²) did not vary with time since fire (0.75, 1.75, 2.5, 5, 15 years) was tested using a one-factor ANOVA. Pearson's correlation coefficient tested for a correlation between time since fire and the number of species.

The null hypothesis of no difference in the composition of plant species in different times since fire was tested. Presence/absence scores were modified to the frequency of each species (0 to 5) along each transect. The Bray Curtis association measure was used on the untransformed data to produce a similarity matrix. Ordination of the samples used non-metric, multi-dimension scaling (MDS) to graphically illustrate the ranked similarity matrix in two-dimensional space. One-way analyses of the ranked similarity of ordinated groups (ANOSIM: Analysis of similarities) used the statistic $R = (r_B - r_W) / (M/2)$, where r_W was the average rank of similarities within sites and r_B was the average rank of similarities from all pairs of replicates between sites; and $M = n(n-1)/2$, where n was the total number of samples (Clarke & Warwick 1994). The characterisation of sample groupings by species was computed using the average dissimilarity between all pairs of inter-group samples, reduced to contributions from each species.

Differences in the frequency of individual species (5 m²) were tested using ANOVA. One-factor ANOVAs examined the effect of time since fire on species which occurred in greater than 20% of the quadrats. Seedlings of perennial woody *Acacia* spp. were excluded, since emphasis was on grasses, herbs and sub-shrubs for which there was little information on their dynamics.

Effects of topography and eucalypts

The null hypotheses of no difference in species composition with respect to eucalypt position (in gap, under canopy) and topographic position (lower, mid, upper) were tested. Presence/absence scores were modified to frequency scores for each topographic position along each transect (10 m²), so each species had a score of between 0 and 10 (0 = not present in any quadrat, 1 = present in one quadrat etc). A similarity matrix based on the untransformed data and the Bray Curtis association measure formed the basis of analyses. Ordination of the samples used MDS. A two-way crossed (eucalypt position, topographic position) analysis of the ranked similarities tested the similarity of ordinated groups. Characterisation of the resultant group by species was computed using dissimilarity scores (see above).

Differences in the frequency of the 11 most common species (i.e. occurred in 50% of quadrats), species richness and the number of ephemeral and perennial taxa (10 m²) were tested. Orthogonal two-factor ANOVAs examined the effect of eucalypt (in gap, under canopy) and topographic positions (lower, mid, upper) on each. The lifecycles of eight taxa identified to genus were unknown, so they were excluded from analyses.

Results

Effects of time since fire

A total of 45 species were identified among all the transects sampled (total area of 500 m²). The number of species was inversely proportional to time since fire, i.e. 32, 24, 27, 16 and 8 species were found at respectively 0.75, 1.75, 2.5, 5 and 15 years post-fire, each within an area of 100 m² (Appendix 1). The mean number of species per transect (5 m²) was significantly affected by time since fire ($F = 76.7$, d.f. = 4,95, $P < 0.001$; $r = -0.835$, $P < 0.001$). The number was lower at 5 and 15 years after fire than from 0.75 to 2.5 years after fire (Fig. 1). Whilst there were no significant differences between 0.75, 1.75 and 2.5 years, the number of species was significantly higher at 5 years than 15 years after fire.

A two-dimensional ordination based on the ranked similarity measures (stress = 0.17) indicated discrete groups (Fig. 2). A global analysis based on species composition, showed significantly higher similarity along transects within the same time since fire than between different times since fire groups ($R = 0.776$, $P < 0.001$). Analyses of pairs of sample groups, which appeared close in the ordination, namely 5 (1985) and 15 (1974) years post-fire ($R = 0.489$, $P < 0.001$), 1.75 (1988) and 2.5 (1987) years post-fire ($R = 0.602$, $P < 0.001$), also showed significantly higher similarity within rather than between different times since fire.

The average within group similarity was lowest for 15 years post-fire, followed in order by 2.5, 5, 0.75 and 1.75 years (Table 1). Up to nine species characterised 90% of the average within group similarity for each time since fire. Up to seven plant species characterised 50% of the average dissimilarity between time since fire groups (Table 2). There was no gradual trend in the average dissimilarity between pairs of time since

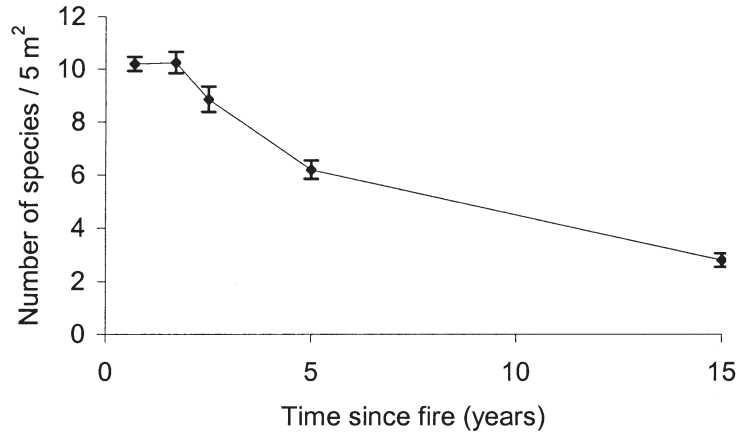


Fig. 1. Species richness (per transect: 5 m²) in different time since fire groups. Data are mean and standard error.

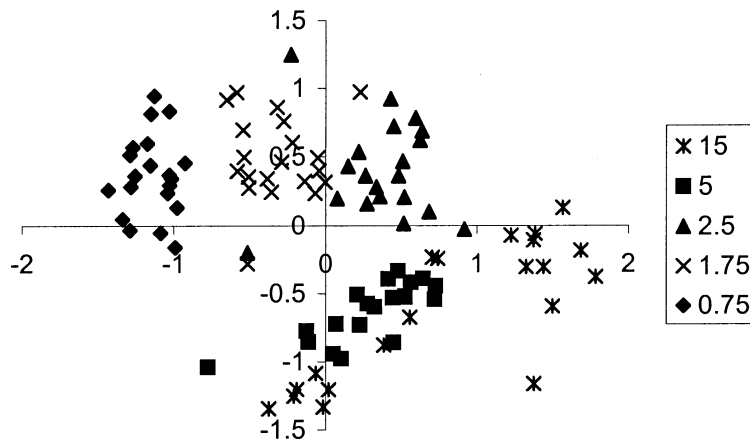


Fig. 2. Ordination plot (stress = 0.17) showing groups defined by cluster analysis. Each point represents a transect of 5 quadrats (5 m²) in time since last burnt (years).

Table 1. Species (ranked in order of importance) contributing to 90% of the similarities within each time since fire group.

Species	Average frequency (5 m ²)	Cumulative contribution to similarity (%)
0.75 years since fire		
	average similarity 58.20	
<i>Convolvulus erubescens</i>	4.80	37.63
<i>Haloragis odontocarpa</i>	3.55	61.15
<i>Triodia scariosa</i>	1.80	69.70
<i>Podolepis jaceoides</i>	1.05	75.11
<i>Psoralea eriantha</i>	1.10	80.26
<i>Goodenia willisiana</i>	1.25	84.71
<i>Poranthera microphylla</i>	1.15	89.05
1.75 years since fire		
	average similarity 55.81	
<i>Sclerolaena parviflora</i>	3.45	22.34
<i>Haloragis odontocarpa</i>	2.80	40.79
<i>Convolvulus erubescens</i>	2.20	51.86
<i>Solanum coactiliferum</i>	2.00	61.54
<i>Triodia scariosa</i>	1.85	69.95
<i>Amphipogon caricinus</i>	1.75	77.63
<i>Lomandra collina</i>	1.20	82.92
<i>Schoenus subaphyllus</i>	1.25	87.64
<i>Acacia wilhelmiana</i>	0.90	90.82
2.5 years since fire		
	average similarity 50.69	
<i>Amphipogon caricinus</i>	3.70	34.93
<i>Solanum coactiliferum</i>	2.50	52.84
<i>Haloragis odontocarpa</i>	1.60	64.88
<i>Triodia scariosa</i>	1.45	73.46
<i>Sclerolaena parviflora</i>	1.45	80.40
<i>Chenopodium desertorum</i>	1.00	86.18
<i>Vittadinia cuneata</i>	0.70	89.91
5 years since fire		
	average similarity 59.43	
<i>Halgania cyanea</i>	3.55	36.01
<i>Triodia scariosa</i>	2.95	63.40
<i>Amphipogon caricinus</i>	2.80	83.28
<i>Solanum coactiliferum</i>	1.00	90.21
15 years since fire		
	average similarity 40.26	
<i>Amphipogon caricinus</i>	2.35	63.08
<i>Triodia scariosa</i>	1.85	86.33

Table 2. Species (ranked in order of importance) contributing to 50% of the dissimilarities (dissim.) between pairs of time since fire (tsf) groups (5 m²).

Species	Tsf groups		Age diff. (years)	Mean dissim.	Meanfreq. tsf groups		Cum. contrib. to dissim. (%)
	1 (years)	2 (years)			1	2	
<i>Convolvulus erubescens</i>	0.75	1.75	1.00	61.95	4.80	2.20	10.19
<i>Sclerolaena parviflora</i>					0.95	3.45	20.11
<i>Amphipogon caricinus</i>					0.00	1.75	26.43
<i>Solanum coactiliferum</i>					0.65	2.00	32.74
<i>Triodia scariosa</i>					1.80	1.85	38.22
<i>Haloragis odontocarpa</i>					3.55	2.80	43.68
<i>Goodenia willisiana</i>					1.25	0.00	48.37
<i>Convolvulus erubescens</i>	0.75	2.5	1.75	78.66	4.80	0.10	16.07
<i>Amphipogon caricinus</i>					0.00	3.70	28.59
<i>Haloragis odontocarpa</i>					3.55	1.60	35.88
<i>Solanum coactiliferum</i>					0.65	2.50	42.94
<i>Sclerolaena parviflora</i>					0.95	1.45	47.71
<i>Convolvulus erubescens</i>	0.75	5	4.25	85.24	4.80	0.00	16.39
<i>Halgania cyanea</i>					0.00	3.55	28.41
<i>Haloragis odontocarpa</i>					3.55	0.05	40.20
<i>Amphipogon caricinus</i>					0.00	2.80	49.46
<i>Convolvulus erubescens</i>	0.75	15	14.25	92.94	4.80	0.00	19.52
<i>Haloragis odontocarpa</i>					3.55	0.00	33.71
<i>Amphipogon caricinus</i>					0.00	2.35	43.19
<i>Triodia scariosa</i>					1.80	1.85	50.96
<i>Amphipogon caricinus</i>	1.75	2.5	0.75	60.79	1.75	3.70	10.40
<i>Sclerolaena parviflora</i>					3.45	1.45	20.75
<i>Convolvulus erubescens</i>					2.20	0.10	29.86
<i>Solanum coactiliferum</i>					2.00	2.50	37.23
<i>Haloragis odontocarpa</i>					2.80	1.60	43.74
<i>Triodia scariosa</i>					1.85	1.45	49.96
<i>Sclerolaena parviflora</i>	1.75	5	3.25	74.36	3.45	0.00	13.05
<i>Halgania cyanea</i>					0.20	3.55	25.94
<i>Haloragis odontocarpa</i>					2.80	0.05	36.43
<i>Convolvulus erubescens</i>					2.20	0.00	44.74
<i>Sclerolaena parviflora</i>	1.75	15	13.25	82.12	3.45	0.00	15.24
<i>Haloragis odontocarpa</i>					2.80	0.00	27.74
<i>Convolvulus erubescens</i>					2.20	0.00	37.42
<i>Triodia scariosa</i>					1.85	1.85	46.25
<i>Halgania cyanea</i>	2.5	5	2.50	67.40	0.05	3.55	17.30
<i>Amphipogon caricinus</i>					3.70	2.80	27.11
<i>Triodia scariosa</i>					1.45	2.95	36.44
<i>Solanum coactiliferum</i>					2.50	1.00	45.58
<i>Solanum coactiliferum</i>	2.5	15	12.50	75.02	2.50	0.00	14.49
<i>Amphipogon caricinus</i>					3.70	2.35	26.87
<i>Triodia scariosa</i>					1.45	1.85	38.11
<i>Haloragis odontocarpa</i>					1.60	0.00	47.43
<i>Halgania cyanea</i>	5	15	12	67.21	3.55	0.20	25.44
<i>Triodia scariosa</i>					2.95	1.85	43.16

fire groups, based on their age differences. Dissimilarity was, however, highest between extremes in time since fire (0.75 and 15 years) and lowest between the closest (1.75 and 2.5, 0.75 and 1.75 years).

Ten of the most frequently occurring species (excluding seedlings of *Acacia* spp.) were tested for the effect of time since fire on their frequency of occurrence (Table 3). All species except *Triodia scariosa* and *Lomandra leucocephala* were significantly affected by time since fire. In seven significant cases, frequency was highest within five years of fire, dwindling to zero or near zero by 15 years after fire (Fig. 3). The frequencies of *Haloragis odontocarpa* and *Convolvulus erubescens* peaked quickly within 0.75 years of fire and had declined to near zero by five and 2.5 years respectively. *Sclerolaena parviflora* and *Solanum coactiliferum* peaked in frequency at respectively 1.75 and 2.5 years after fire and had declined to near zero by respectively five and 15 years after fire. *Halgania cyanea* peaked at five years after fire and was at low frequency 10 years later. *Podolepis jaceoides*, *Schoenus subaphyllus* and *Lomandra leucocephala* maintained relatively low frequencies throughout. Only *Triodia scariosa* and *Amphipogon caricinus* still had high frequencies at 15 years after fire. Whilst *Amphipogon caricinus* peaked at five years after fire, *Triodia scariosa* maintained a relatively high frequency throughout.

Effects of topography and eucalypts

A two-dimensional ordination based on the ranked similarity measures (stress = 0.08) indicated discrete plant species groups in relation to topographic position, confirmed by a two-way crossed ANOSIM ($R = 0.45$, $P < 0.001$; Fig. 4). Lower topographic sites differed significantly from upper topographic sites, but there were no significant differences between these sites and mid-slope sites. There was no significant effect of eucalypt canopy ($R = 0.22$, $P < 0.08$).

The average within group similarity was higher for the upper (61.67%) than the lower topographic positions (43.88%; Table 4). Ninety percent of the average within group similarity was characterised by nine in the upper and 13 species in the lower topographic positions. The percentage representation of ephemeral taxa was higher in the lower than the upper topographic positions.

The average dissimilarity between the upper and lower topographic groups was 69.41%. Thirteen plant species characterised 60% of this dissimilarity (Table 5): those more frequent in upper topographic positions included *Bracteantha viscosa*, *Amphipogon caricinus*, *Sclerolaena parviflora*, *Haloragis odontocarpa*, *Triodia scariosa* and an unknown species; those more frequent in lower topographic positions included *Hyalosperma semisterile*, *Rhyncharhena linearis*, *Austrostipa scabra*, *Chenopodium* sp., *Sclerolaena diacantha*, *Austrostipa* spp. and *Harmsiodoxa blennodioides*.

Of the 11 most frequently occurring species ($\geq 50\%$ of quadrats), nine were significantly affected by topographic position. Of these, two were also significantly affected by the position in relation to mallee eucalypts. Two species were not significantly affected by either factor (Table 6). Species more frequent in upper topographic positions concur with dissimilarity results, with the addition of *Halgania cyanea* (see above). *Austrostipa scabra* and *Harmsiodoxa blennodioides* were more frequent

Table 3. The effects of time since fire on species which occurred in greater than 20% of quadrats (excluding seedlings of perennial Acacia shrub spp.). Results are derived from one-way analyses of variance of the frequency of species (5 m²). Time since fire included 0.75, 1.75, 2.5, 5 and 15 years. Means are arranged in ascending order; underlining indicates no significant difference. Transformations of data include square root¹ and heteroscedastic data assessed at P < 0.01 were either untransformed² or square root transformed³ (P < 0.05 *, P < 0.01 **, P < 0.001***, not significant ns).

Species	Means					F _(4,95)	P
<i>Amhipogon caricinus</i>	0.75	1.75	15	<u>5</u>	2.5	19.6	***
<i>Convolvulus erubescens</i> ²	<u>15</u>	5	<u>2.5</u>	1.75	0.75	183	***
<i>Halgania cyanea</i> ¹	<u>0.75</u>	2.5	1.75	<u>15</u>	5	121	***
<i>Haloragis odontocarpa</i> ²	<u>15</u>	<u>5</u>	2.5	<u>1.75</u>	<u>0.75</u>	71.4	***
<i>Lomandra leucocephala</i>	<u>15</u>	1.75	<u>0.75</u>	<u>2.5</u>	<u>5</u>	1.0	ns
<i>Podolepis jaceoides</i> ³	<u>15</u>	<u>2.5</u>	<u>5</u>	1.75	0.75	12.7	***
<i>Schoenus subaphyllus</i> ¹	<u>0.75</u>	<u>2.5</u>	<u>15</u>	<u>5</u>	1.75	7.3	***
<i>Sclerolaena parviflora</i> ²	<u>15</u>	5	<u>0.75</u>	<u>2.5</u>	1.75	38.7	***
<i>Solanum coactiliferum</i> ¹	<u>15</u>	<u>0.75</u>	<u>5</u>	<u>1.75</u>	2.5	19.0	***
<i>Triodia scariosa</i> ²	<u>2.5</u>	<u>0.75</u>	1.75	15	<u>5</u>	3.0	ns

Table 4. Taxa (ranked in order of appearance) contributing to 90% similarities within the data set in lower and upper topographic positions (Lifecycle type taken from Harden (1990–3), S. Jacobs (pers. comm.): p = perennial, a = annual, slp = short lived perennial, ? = unknown).

Taxa	Mean freq. (10 m ⁻²)	Cumulative contribution to similarity (%)	Family	Lifecycle type
1/ Lower (average similarity 43.88)				
<i>Austrostipa scabra</i>	8.38	27.47	Poaceae	p
<i>Haloragis odontocarpa</i>	5.38	39.65	Haloragaceae	a
<i>Chenopodium</i> sp.	4.13	49.41	Chenopodiaceae	?
<i>Rhyncharrhena linearis</i>	4.00	56.48	Asclepidaceae	p
<i>Harmsiodoxa blennodioides</i>	3.50	63.08	Brassicaceae	a
<i>Hyalosperma semisterile</i>	4.00	68.86	Asteraceae	a
<i>Austrostipa</i> spp.	3.50	74.03	Poaceae	a
<i>Sclerolaena parviflora</i>	2.50	78.14	Chenopodiaceae	slp
<i>Sclerolaena diacantha</i>	3.25	82.19	Chenopodiaceae	p
<i>Rhodanthe floribunda</i>	2.12	84.80	Asteraceae	a
<i>Bracteantha viscosa</i>	2.00	86.77	Asteraceae	a
<i>Nicotiana velutina</i>	2.13	88.65	Solanaceae	a
<i>Vittadinia dissecta</i> var. <i>hirta</i>	1.50	90.40	Asteraceae	a/slp
2/ Upper (average similarity 61.67)				
<i>Haloragis odontocarpa</i>	9.50	22.86	Haloragaceae	a
<i>Bracteantha viscosa</i>	8.38	41.68	Asteraceae	a
<i>Sclerolaena parviflora</i>	7.38	56.34	Chenopodiaceae	slp
<i>Amhipogon caricinus</i>	6.00	66.13	Poaceae	p
<i>Austrostipa scabra</i>	5.25	74.21	Poaceae	p
Unknown sp. 9	4.00	80.07	Unknown	?
<i>Triodia scariosa</i>	3.38	85.10	Poaceae	p
<i>Halgania cyanea</i>	1.88	88.16	Boraginaceae	p
<i>Poranthera microphylla</i>	1.88	90.34	Euphorbiaceae	a

Table 5. Species (ranked in order of importance) contributing to 60% of the dissimilarities between lower and upper topographic groups.

Average dissimilarity between groups 69.41

Species	Mean frequency /10m ²		Cumulative contribution to dissimilarity (%)
	lower	upper	
<i>Bracteantha viscosa</i>	2.00	8.38	7.47
<i>Amphipogon caricinus</i>	1.00	6.00	13.58
<i>Sclerolaena parviflora</i>	2.50	7.38	19.46
<i>Haloragis odontocarpa</i>	5.38	9.50	24.36
<i>Hyalosperma semisterile</i>	4.00	0.13	28.98
<i>Rhyncharrhena linearis</i>	4.00	0.00	33.37
<i>Austrostipa scabra</i>	8.38	5.25	37.65
<i>Chenopodium</i> sp.	4.13	1.75	41.58
<i>Sclerolaena diacantha</i>	3.25	0.00	45.40
Unknown sp. 9	1.38	4.00	49.10
<i>Austrostipa</i> spp.	3.50	0.13	52.79
<i>Harmsiodoxa blennodioides</i>	3.50	0.25	56.45
<i>Triodia scariosa</i>	0.13	3.38	60.09

Table 6. Significant effects of topography (lower (l), mid (m), upper (u)) and position in relation to eucalypts (in gaps (g), under canopy (c)) on species which occurred in at least 50 % of quadrats. Results are derived from fully factorial two-way analyses of variance of the frequency of each species /10 m². Means are arranged in ascending order. Transformations of data include square root¹ and heteroscedastic data assessed at P < 0.01 were either untransformed² or square root transformed³ (P < 0.05*, P < 0.01, P < 0.001***, not significant ns).**

Species	Topography			Eucalypt		
	mean	F _(2,14)	P	mean	F _(1,14)	P
<i>Amphipogon caricinus</i>	l m u	9.0	**	-	-	ns
<i>Halgania cyanea</i>	l m u	4.4	*	-	-	ns
<i>Haloragis odontocarpa</i>	l m u	4.8	*	-	-	ns
<i>Harmsiodoxa blennodioides</i> ³	u l m	10.8	***	-	-	ns
<i>Bracteantha viscosa</i>	l m u	8.5	**	-	-	ns
<i>Sclerolaena parviflora</i>	l m u	9.3	**	c g	5.7	*
<i>Austrostipa scabra</i>	u l m	5.1	*	-	-	ns
<i>Triodia scariosa</i> ¹	l m u	9.1	**	-	-	ns
<i>Pseudognaphalium luteoalbum</i>	-	-	ns	-	-	ns
<i>Chenopodium</i> sp.	-	-	ns	-	-	ns
Unknown sp. 9	l m u	4.3	*	c g	7.9	*

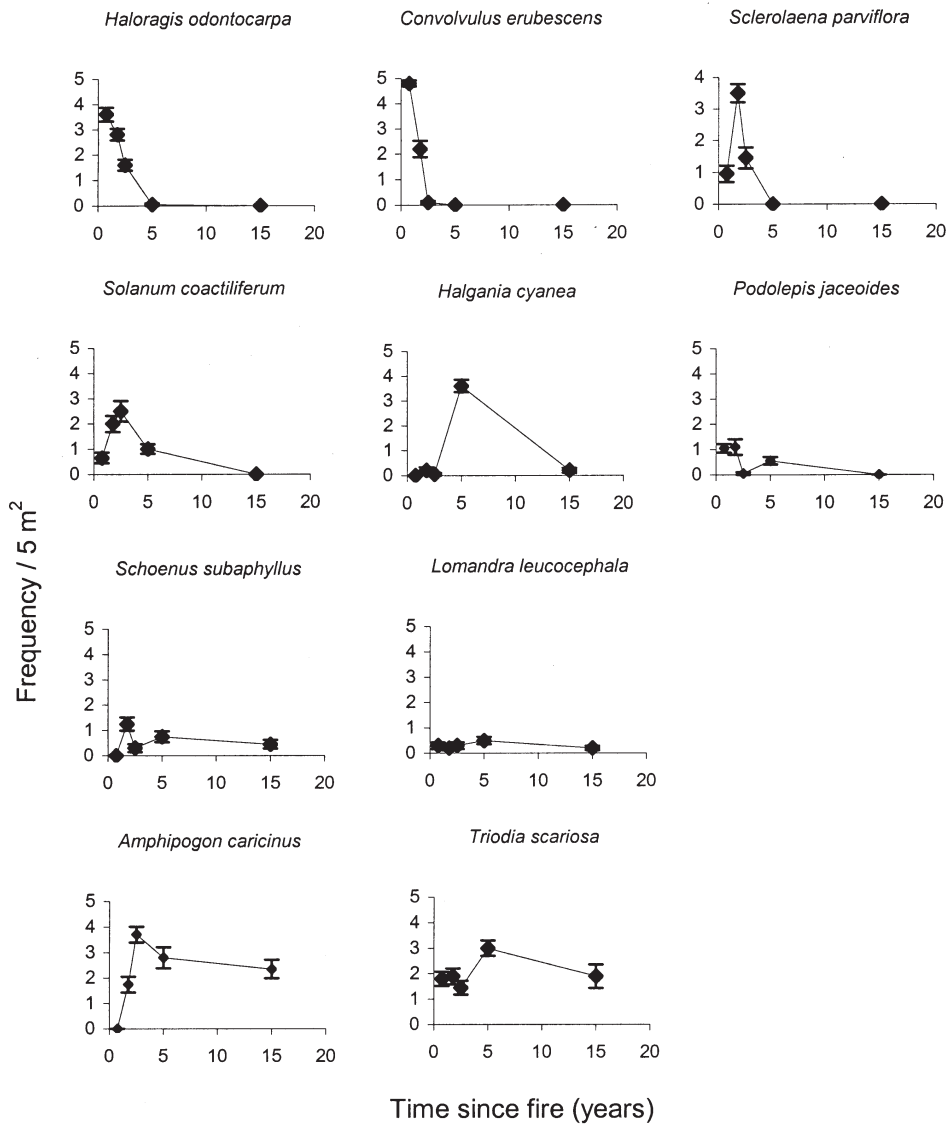


Fig. 3. Frequency of species (per transect: 5 m²) that occurred in greater than 20% of quadrats in response to time since fire. Data are mean and standard error.

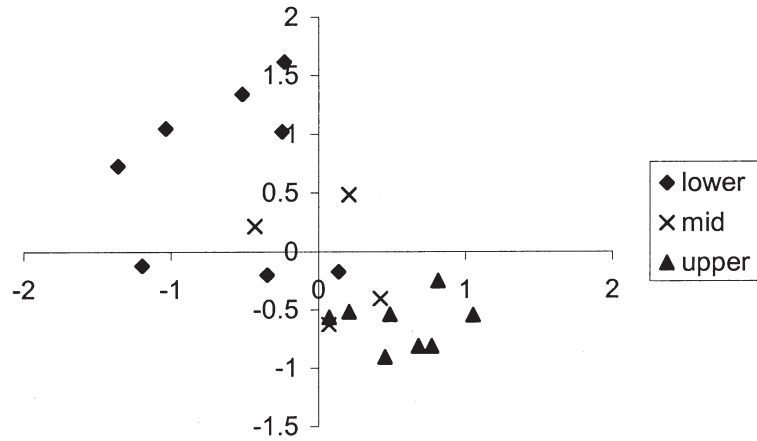


Fig. 4. Ordination plot (stress = 0.08) showing groups defined by cluster analysis. Each point represents 10 quadrats (10 m²) in the different topographic positions (lower slope, mid-slope, upper slope).

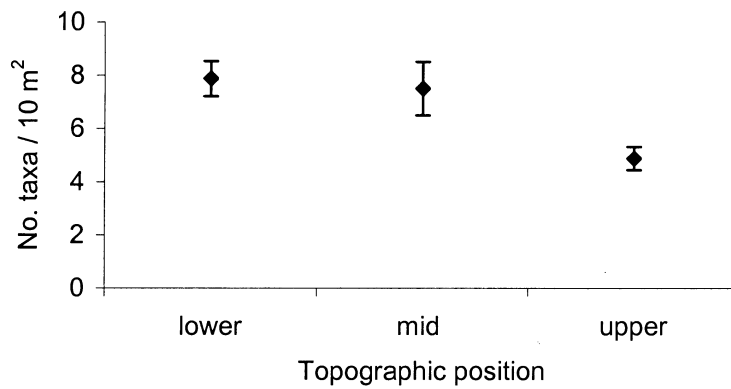


Fig. 5. Number of ephemeral taxa (10 m²) in different topographic positions (lower slope, mid-slope, upper slope). Data are mean and standard error.

in lower than upper topographic positions. *Sclerolaena parviflora* and an unidentified species occurred more frequently in the gaps than under the canopies of eucalypts. *Gnaphalium luteo-album* and *Chenopodium* sp. were not significantly affected by either factor or their interaction.

There were no significant effects of topography or eucalypt position on species richness per 10 m² ($P > 0.05$). The mean number of species for all the data pooled was 17.45 / 10 m² (+/- 0.16 s.e.). A total of 58 species were identified in the 200 quadrats sampled (200 m²).

There was a significant effect of topography on the number of ephemeral ($F = 6.6$, d.f. = 2, $P < 0.01$), but not perennial taxa ($P > 0.05$). The mean number of ephemeral taxa was higher in the lower than the upper topographic positions. Neither were significantly different from the mid-slope (Fig. 5). There was no significant effect of eucalypt position on the number of ephemeral or perennial taxa ($P > 0.05$).

Discussion

Effects of time since fire

The results from this study indicate a decline in the above ground richness of all understorey species with increasing time since fire. A flush of short-lived species up until 2.5 years after fire resulted in higher richness than five and more years after fire, which was dominated by perennials. The results confirm Bradstock's (1990) original observations that few ephemeral grasses and herbs existed five to seven years after fire. Trends in other mallee studies, which examined both total species (Zimmer 1940, Cheal 1981) and herbaceous species richness (Noble 1989b) with time since fire, are also comparable. Cheal (1981) found that total species richness in Victorian mallee dominated by *Eucalyptus foecunda* remained high up to four years after fire. A study by Holland (1968) in mallee near our study site also found that the life expectancy of field layer plants was between six months and five years.

Distinct suites of species defined different times after fire (Table 1). The most common short-lived species up to 2.5 years post-fire included *Haloragis odontocarpa* and *Convolvulus erubescens* which peaked in the first spring, followed by *Sclerolaena parviflora* in the second spring. All three species had either disappeared or were in very low numbers within five years of fire. *Solanum coactiliferum* peaked in the second / third springs and had disappeared 15 years after fire; in South Australian mallee it produces seeds within 2.4 years of fire (Morelli & Forward 1996). Other studies in semi-arid mallee in NSW have similarly observed the rapid growth and decline of *Haloragis odontocarpa* (Bradstock 1989), and *Sclerolaena parviflora* following fires, irrespective of the season of the burn (Noble 1989b). Noble (1989b) believed that the quick response of *Haloragis odontocarpa* to fire indicated an effect of scarification or charred wood, although his field observations also suggested its germination was stimulated by mechanical scarification.

In their respective studies, Noble (1989b) and Bradstock (1989) note the proliferation of the short-lived grasses *Stipa* spp. in the first year following fire. Since their presence is reliant on adequate rainfall (Noble 1989b, Noble & Vines 1993), their relative absence in our study may relate to the very low rainfall experienced in the spring at the start of the survey (1989), which received a monthly average of 7 mm. This was well below the long term spring monthly average of 27 mm (Cohn & Bradstock 2000).

Other relatively common species typifying early time since fire groups (≤ 2.5 years) included *Podolepis jaceoides*, *Psoralea eriantha*, *Goodenia willisiana*, *Poranthera microphylla*, *Lomandra collina* and *Vittadinia cuneata* (Table 1). All of these species had either disappeared or were rare five or more years after fire. A study by Cheal and Parkes 1989, found *Poranthera microphylla* as scattered individuals in the 'decades old mallee' dominated by *Callitris verrucosa*, suggesting that its seeds are not necessarily dependent on fire for germination.

Whilst the perennial grasses *Triodia scariosa* and *Amphipogon caricinus* were relatively common throughout most time since fire groups, they dominated along with *Halgania cyanea*, at five or more years after fire (Table 1). Their dominance coincided with a significant decline in species richness. Other studies have found that as the original dominants regain their post-fire structure and composition, a decline in richness and diversity occurs (Zimmer 1940, Noble et al. 1980, Cheal 1981). In hummock grasslands and woodlands, competition between *Triodia* spp. and other herbaceous species occurs as the former matures, leading to a decline in the initial number of species (Burbidge 1943, Allan & Griffin 1986, Noble 1989b, Allan & Baker 1990). Indeed, Noble (1989b) found a strong negative correlation between total herbage cover over time, with the combined cover of *Triodia* and mallee eucalypts.

The average similarity measure within each time since fire group was noticeably lowest at 15 years (40.26) than all other time since fire groups (50.69 to 59.43; Table 1). As the ephemerals 'died off' with increasing time since fire, one may have expected increasing homogeneity. It is possible that varying and subtle site factors or the hardiness of individual plants within a species to the same set of environmental conditions may have resulted in differential mortality for each species.

The highest mean dissimilarity measure between pairs of time since fire groups was between the most and the least recently burnt sites (Table 2). The species largely responsible were short-lived species *Convolvulus erubescens*, *Haloragis odontocarpa* and perennial grasses *Amphipogon caricinus* and *Triodia scariosa*. Whilst a study in *Triodia* spp. communities in central Australia found a similar trend in the dissimilarity measures between extremes in times since fire, it also found high variation in the dissimilarity measures between pairs of more recently burnt sites (Allan & Baker 1990). Allan and Baker (1990) believed this reflected the importance of rainfall in the early stages of post-fire recovery. Although our results do not show a high variation in dissimilarity between pairs of recently burnt sites, other studies in semi-arid mallee communities have recognised the influence of seasonal rainfall on the composition of ephemeral (Fox 1990) and perennial species, especially in the first growing season following fire (Noble 1989b, Cohn & Bradstock 2000).

For herbaceous 'fire species', which appear mainly after fire, reproduce and disappear until the next fire (e.g. *Haloragis odontocarpa*), the abundance and viability of the soil-stored seed is important (Van der Moezel & Bell 1984, Noble et al. 1986, Noble 1989a, 1989b). These species are described as obligate seed regenerators by McMahon (1984). It is believed that the abundance of these species is dependent on soil seed banks being 'topped up' by periodic fire (Noble et al. 1986, Noble 1989). Our results indicate a minimum fire interval of at least five years is needed to allow all herb and grass species recognised in this study, to grow and reproduce. Since the maximum number of above ground species was experienced within 2.5 years of fire, following a previous interval of 14 years, a maximum fire interval is estimated at 14 years. Similarly, in Victorian mallee dominated by *Eucalyptus incrassata*, Cheal (1981) found that fire ephemerals generally absent from vegetation 15 years or more post-fire, rapidly established from soil-stored seed. In mallee in NSW, Noble (1989a) found that *Haloragis odontocarpa* comprised of a proportionally higher biomass after a fire interval of 13 years (54% of biomass) rather than at least 50 years (4% of biomass).

Little is known about the lifecycles of the grasses and herbs in this study. While the appearances of seedlings of *Acacia* spp., *Haloragis odontocarpa* and possibly *Triodia scariosa* (Noble 1989b) were stimulated directly by the effects of fire, it is not known whether other species, which peaked in frequency soon after the fire, were similarly stimulated, or simply responded to a reduction in competition from perennial species. This was beyond the scope of this study.

Effects of topography and eucalypts

Given a well-defined dune system with corresponding soil texture differences, sandy soils on dune crests and heavier textured soils in swales, it was not surprising that this was reflected in species composition, with the mid-slope acting as a transition zone. Ephemeral species were more common in the lower than the upper topographic positions. At the microhabitat scale, species composition was not affected by eucalypt position.

A mixture of ephemeral, and perennial taxa from principally Asteraceae, Poaceae and Chenopodiaceae characterised the upper and lower topographic positions. Similarly, Fox's (1990) surveys of plant species, including ephemerals, in mallee in New South Wales, found that these families and Fabaceae predominated. In the lower topographic positions characteristic species included ephemerals *Harmsiodoxa blennodioides*, *Hyalosperma semisterile*, *Austrostipa* spp., and perennials *Austrostipa scabra*, *Rhyncharrhena linearis*, *Sclerolaena diacantha* and *Chenopodium* sp. In the upper slope and crest positions, ephemerals included *Haloragis odontocarpa*, *Bracteantha viscosa*, and perennials *Sclerolaena parviflora*, *Amphipogon caricinus* and *Triodia scariosa* (Table 5). Most of these species did not occur exclusively in one topographic position, but were simply more common in one.

A number of surveys and studies in mallee in southeastern Australia have found similar occurrences of some of these species i.e. *Sclerolaena diacantha* (Cheal & Parkes 1989, Porteners et al. 1997), *Triodia scariosa* (Bradstock 1989, Cheal & Parkes 1989, Morcom & Westbrooke 1990, Fox 1991, Scott 1992, Porteners et al. 1997), *Stipa scabra* complex (Cheal & Parkes 1989) and *Stipa variabilis* (= *Austrostipa* spp., Noble 1981,

1984). In mallee in South Australia and New South Wales, however, *Sclerolaena diacantha* has been found to occur in a variety of topographies and soil types (Forward 1996, Porteners et al. 1997). In their survey of mallee communities in north-western Victoria, Cheal and Parkes (1989) emphasised the dangers of extrapolating trends in the occurrence of species between sites which differ geographically and climatically.

The number of ephemeral species was significantly higher in the lower ($7.87/10\text{m}^2 \pm 0.66$ s.e.) than the upper topographic positions ($4.88/10\text{m}^2 \pm 0.44$ s.e.; Fig. 5). The preponderance of ephemerals in the soils of the lower topographic positions suggests that conditions are more favourable for their survival than the sandier soils of the upper topographic positions. Characteristics of the heavier soils, such as their lower porosity, proximity to the water table, and higher fertility would no doubt be an advantage to ephemerals which are characteristically shallow rooted and quick growing (Casson et al. 1984). Higher 'run-on' to the lower topographic positions would also assist survival. Cheal and Parkes (1989) similarly found that the distribution of mallee communities in Victoria was related to environmental features such as topography, elevation in relation to water table or depth to the under-lying sandstone.

Although our study found no effect of topography on species richness, a survey of mallee communities in south western New South Wales found species richness to be negatively correlated with topography, that is, higher in the swales (Fox 1984). In mallee in Western Australia, Van der Moezel and Bell (1989) found that soils with the lowest nutrient content i.e. sandy soils, had the highest species richness. The absence of a topographic effect in our study, may reflect its localised nature compared with the regional nature of these other studies. Greater variation in factors, such as, topography and soil type is more likely over larger areas and hence there is a higher potential for the distribution of species to influence species richness.

The presence of resprouting *Eucalyptus* spp. was found to have no significant effect on either the understorey species composition or richness. Common species, such as, ephemeral herbs/forbs *Bracteantha viscosa*, *Haloragis odontocarpa*, *Pseudognaphalium luteoalbum*, *Harmsiodoxa blennodioides*, perennial subshrub *Halgania cyanea*, perennial grasses *Amphipogon caricinus*, *Austrostipa scabra*, *Triodia scariosa* and *Chenopodium* sp., were just as likely to grow under eucalypts as in the gaps between them. An exception was *Sclerolaena parviflora*, which was found to be more common in the gaps. These results are contrary to observations by Noble (1989a) who found that after fire in the mallee, herbs rarely colonised eucalypt and *Triodia* mounds because of their hydrophobic properties. Most grew between the hummocks until eucalypt and triodia cover returned. It is possible, that the higher than average spring monthly rainfall prior to our study in 1985 (77 mm vs 27 mm long term spring monthly average; Cohn & Bradstock 2000), reduced any hydrophobic effect of the hummocks.

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Appendix 1. Average abundance of each species (5 m²) with time since fire. Data are taken from analyses of similarity (ANOSIM). Those species which occurred only once in a time since fire group are marked with an X and were not included in ANOSIM.

Species	Average abundance (5 m ²) at time since fire (years)				
	0.75	1.75	2.5	5	15
ASTERACEAE					
<i>Calotis cuneifolia</i>	-	-	0.6	0.5	-
<i>Chrysocephalum apiculatum</i>	-	-	0.3	-	-
<i>Rhodanthe floribunda</i>	-	X	0.3	-	-
<i>Olearia pimelioides</i>	-	X	0.1	-	-
<i>Podolepis arachnoidea</i>	-	0.7	X	-	-
<i>P. jaceoides</i>	1.1	1.1	0.7	0.6	-
<i>Vittadinia cuneata</i>	X	X	0.7	X	-
BORAGINACEAE					
<i>Halgania cyanea</i>	-	0.2	X	3.6	0.2
BRUNONIACEAE					
<i>Brunonia australis</i>	X	-	-	-	-
CAMPANULACEAE					
<i>Wahlenbergia</i> sp. 1	0.2	-	-	-	-
CARYOPHYLLACEAE					
<i>Spergularia rubra</i>	-	0.4	-	X	-
CHENOPODIACEAE					
<i>Chenopodium desertorum</i>	X	-	-	-	-
<i>Sclerolaena parviflora</i>	1.0	3.5	1.5	-	-
CONVOLVULACEAE					
<i>Convolvulus erubescens</i>	4.8	2.2	0.1	-	-
CYPERACEAE					
<i>Schoenus subaphyllus</i>	-	1.3	0.3	0.8	0.5
EUPHORBIACEAE					
<i>Poranthera microphylla</i>	1.2	-	X	-	-
FABACEAE					
<i>Acacia brachybotrya</i>	-	-	3.7	-	0.3
<i>A. rigens</i>	0.4	0.7	-	-	0.6
<i>A. wihelmiana</i>	0.6	0.9	0.8	0.4	X
<i>Eutaxia microphylla</i>	-	X	-	-	-
<i>Psoralea eriantha</i>	1.1	-	X	-	-
<i>Templetonia aculeata</i>	X	-	-	-	-
GOODENIACEAE					
<i>Goodenia cycloptera</i>	0.2	-	-	0.1	-
<i>G. willisiana</i>	1.3	-	-	-	-
<i>G.</i> sp. 1	0.3	-	X	-	-
<i>G.</i> sp. 2	X	-	-	-	-
<i>Scaevola aemula</i>	0.7	-	X	-	-
<i>S. depauperata</i>	0.2	-	0.3	X	-
<i>Velleia connata</i>	0.5	0.5	X	-	-

Species	Average abundance (5 m ²) at time since fire (years)				
	0.75	1.75	2.5	5	15
HALORAGACEAE					
<i>Haloragis odontocarpa</i>	3.6	2.8	1.6	X	-
LILIACEAE					
<i>Dianella revoluta</i>	X	X	-	-	-
LOMANDRACEAE					
<i>Lomandra effusa</i>	0.1	0.2	0.2	-	-
<i>L. collina</i>	-	1.2	-	-	-
<i>L. leucocephala</i>	0.3	0.2	0.3	0.5	0.2
MYRTACEAE					
<i>Eucalyptus</i> sp.	X	-	-	-	-
POACEAE					
<i>Amphipogon caricinus</i>	-	1.8	3.7	2.8	2.4
<i>Austrostipa nodosa</i>	-	-	0.3	0.1	-
<i>Triodia scariosa</i>	1.8	1.9	1.5	3.0	1.9
PROTEACEAE					
<i>Grevillea</i> sp.	X	-	-	-	-
SOLANACEAE					
<i>Nicotiana velutina</i>	0.1	-	-	-	-
<i>Solanum coactiliferum</i>	0.7	2.0	2.5	1.0	-
STACKHOUSIACEAE					
<i>Stackhousia monogyna</i>	0.3	X	-	-	-
THYMELACEAE					
<i>Pimelea simplex</i>	0.5	-	0.2	0.3	-
<i>Unknown</i> sp.1	0.1	-	-	-	-
<i>Unknown</i> sp.2	X	-	-	-	-
Number species with score	23	18	20	12	7
Number species with X	9	6	7	4	1
Total number	32	24	27	16	8