RESEARCH PAPER

Fire persistence traits of plants along a productivity and disturbance gradient in mediterranean shrublands of south-east Australia

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ABSTRACT

Aim To understand changes in fire persistence traits of plants along a latitudinal gradient, considering the interactions between productivity, community (fuel) structure and fire regime.

Location A gradient in the south of Australia (latitude 33–37° S; longitude 140–143° E), including: Little Desert National Park (VIC), Big Desert Wilderness Park (VIC), Murray-Sunset National Park (VIC), Danggali Conservation Park (SA) and Tarawi Nature Reserve (NSW).

Methods We selected four areas along a latitudinal gradient for which information on fire history and vegetation was available. Then, we tested to what extent the four selected areas have different climate and different fire regimes. Plant cover values of different life forms provided an indication of the plant community structure and flammability, and the proportion of species with different fire persistence traits (resprouting, seedbank persistence) informed us on the trait selection.

Results Precipitation decreases and temperature increases from south to north. Thus the selected sites represent a gradient from high productivity (low aridity) in the south to low productivity (high aridity) in the north. Fire statistics suggest that fire frequency parallels productivity. There is a tendency for life form dominance and community structure to shift in such a way that fuel connectivity is reduced towards the north. Resprouting species increase and obligate seeders decrease along the fire–productivity gradient.

Main conclusions Changes in plant traits are difficult to understand without simultaneous consideration of both the disturbance and the productivity gradients. In our study area, fire regime and productivity interact in such a way that decreases in productivity imply changes in fuel structure that produce a reduction in fire frequency. Resprouting species are better represented at the high fire–productivity part of the gradient, while obligate seeders are better represented at the opposite end of the gradient. The results also emphasize the importance of considering not only climate changes but also changes in fuel structure to predict future fire regimes.

Keywords

Aridity gradient, community flammability, fire regime, fuel connectivity, latitudinal gradient, mallee, resprouters, resprouting, seeders.

INTRODUCTION

Many plant species growing in mediterranean-type ecosystems possess traits that provide species persistence following disturbances such as fire and drought (Gill, 1981; Keeley, 1998; Bond & Midgely, 2001). These traits might have been acquired by an evolutionary adaptation and/or by ecological sorting processes (Herrera, 1992; Ackerly, 2003; Pausas *et al.*, 2006). The ability to recover vegetatively is recognized as a fundamental trait for persisting in fire-prone ecosystems worldwide (Noble & Slatyer, 1980; Gill, 1981; Kruger & Bigalke, 1984; Keeley, 1986; Bond & Midgely, 2001; Pausas *et al.*, 2004). While resprouting may be favoured under specific fire regimes (Keeley & Zedler, 1978; Kruger & Bigalke, 1984; Keeley, 1986; Hilbert, 1987; Pausas,

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1999; Loehle, 2000; Pausas *et al.*, 2004), it may also be linked to environmental conditions and consequent physiological constraints (Bellingham & Sparrow, 2000; Vesk *et al.*, 2004; Vesk & Westoby, 2004). Thus, many studies have questioned where species with resprouting capacity should dominate along a productivity/moisture gradient (Specht, 1981a; Lamont & Markey, 1995; Ojeda, 1998; Clarke *et al.*, 2005).

Productivity gradients may not only influence species composition (community assemblies) based on life history traits, but they may also directly affect fire regimes through inherent effects on the availability of biomass for burning. The relative influence of each mechanism (i.e. fire regime versus physiological effects) may therefore be inherently confounded and difficult to determine at points along a productivity gradient. Moreover, the inherent effects of productivity on disturbance regimes may be complex. For instance, in arid landscapes, fire frequency is often low because biomass is low even though environmental conditions conducive to fire (high temperatures, low humidity) are prevalent (e.g. Bond *et al.*, 2003). At the opposite end of the rainfall gradient, biomass and thus potential fuel may be high but environmental conditions (i.e. high fuel moisture) may be chronically unfavourable for fire, also resulting in low fire frequency. A range of possibilities exists between these extremes in terms of productivity (i.e. the capability of a site to accumulate biomass), as governed by factors such as soil and climate (e.g. rainfall), and their effect on fire regimes requires exploration. Therefore, it is important to describe the variations in fire regimes that may be associated with productivity gradients in order to better understand potential processes determining plant trait responses.

Such insights could provide an improved basis for comparisons between different studies spanning regions and continents. This is important because resprouters have other correlated functional traits, and these associated traits may differ across regions (Pausas, 2001; Pausas *et al.*, 2004, 2006) and lineages (Verdú, 2000; Pausas & Verdú, 2005), making worldwide comparisons difficult. For instance, many Australian woody resprouters also have a seedbank that persists after fire and thus they may resprout as well as produce offspring after a fire; in contrast, most woody resprouters in the Mediterranean Basin are obligate post-fire resprouters and no recruitment is produced after fire. These different associations between post-fire persistence traits can certainly change the fitness of the resprouters along disturbance gradients (Pausas *et al.*, 2004). Thus, consideration of both resprouting and seed persistence traits should improve the predictive value of the resprouting species along correlated productivity and disturbance gradients.

In the present study we evaluate the changes in two fire persistence traits, resprouting (persistence at individual level) and propagule (seed) persistence (persistence at population level), along a latitudinal gradient in southern Australia (see Methods for trait definitions). We first evaluate trends in productivity and fire regime along the geographical gradient based on climatic data and local fire reports. We then evaluate associated trends in plant life form abundance and dominance of post-fire persistence traits in the sclerophyllous shrublands (also called scrub-heath to mallee; Specht, 1981b) prevalent in this region. The relative homogeneity of southern Australian landscapes allows post-fire plant responses to be compared along a geographical gradient at a scale ranging over hundreds of kilometres, while keeping broad vegetation structure, evolutionary history, topography and lithology relatively fixed. Furthermore, this gradient study may offer insights into possible changes under climatic change.

We hypothesize that fire regime and productivity are linked and that the strong gradient produced by both variables should have implications for plant community assembly. Specifically, and because our study area has an overall dry climate (annual rainfall < 650 mm), we predict that productivity and fire frequency are positively related and linked to increasing fuel amount and connectivity. Thus, plant regeneration traits should not be randomly distributed along the geographical gradient but should follow a predictable trend along the combined fire–productivity gradient. Specifically, we predict that resprouters should be favoured in moister areas with high fire frequency because of the high frequency of strong post-fire competition inhibiting seedling regeneration and favouring the storage effect (Keeley, 1986; Iwasa & Kubo, 1997; Bellingham & Sparrow, 2000). Furthermore, species having both resprouting capacity and propagule-persistence capacity may be the most successful in environments with high fire frequency (Pausas *et al.*, 2004, 2006). We also test the effect of life form (woody vs. herbaceous species) because relatively frequent fire, relative to rates of growth and reproduction, may produce contrasting effects in woody long-lived species compared with herbaceous species.

METHODS

Study area

The study region encompassed an area through western Victoria, south-western New South Wales and central-eastern South Australia (latitude 33–37° S; longitude 140–143° E; Fig. 1). The landscapes within this region are flat to moderately undulating and of low elevation (*c.* 100 m above sea level). These subdued landscapes are dominated by a number of siliceous sand masses of aeolian origin perched on underlying calcareous sediments (Wasson, 1989). Most of these sand systems produce deep soils characterized by their quartzose nature, and vary from uniform sands to clayed sands, with a general absence of differentiation of horizons other than slight accumulation of organic matter in the topsoil. The sand masses within these landscapes currently contain relatively large expanses of natural vegetation, though fragmentation from clearing for agricultural use has occurred, most prominently in the southern and central part of the study area (Land Conservation Council, 1987). Vegetation associated with these sand masses is dominated by tall shrubs (Cheal *et al.*, 1979; Specht, 1981b; Cheal & Parkes, 1989; Sparrow, 1989; Forward & Robinson, 1996). The structure of these shrublands ranges from closed scrub in the south to open mallee shrublands in the north. Understoreys of these shrublands vary from sclerophyllous shrubs and sub-shrubs plus a minor component of herbaceous

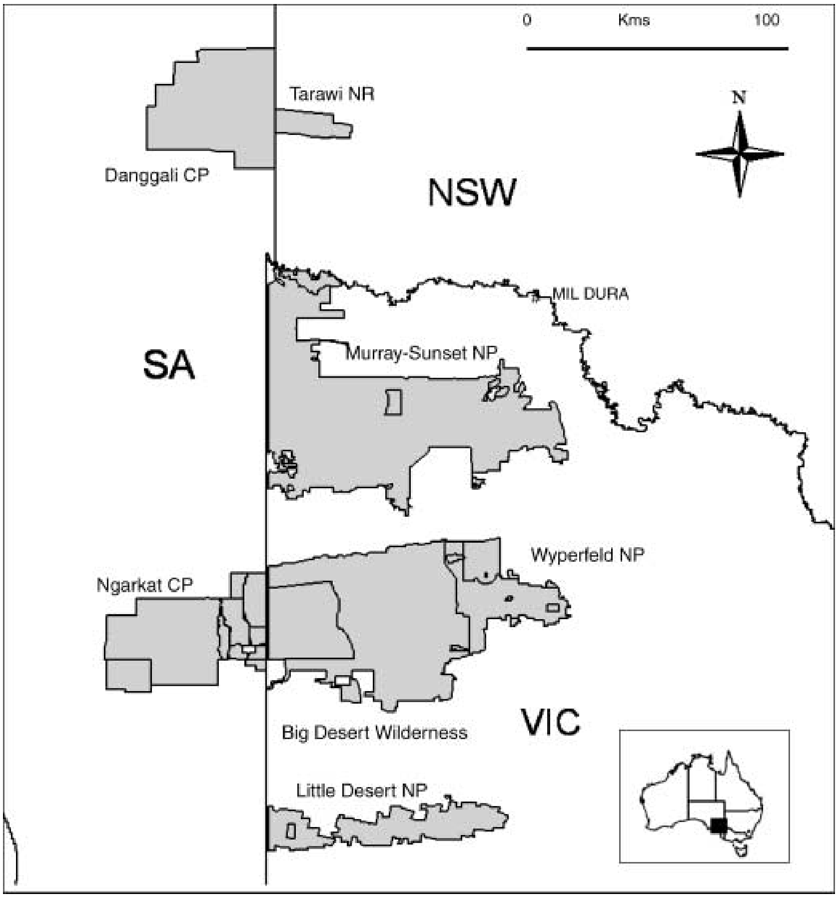

Figure 1 Location of the four study areas in the three Australian states (NSW, New South Wales; SA, South Australia; VIC, Victoria). From south to north, the study areas are abbreviated in the text as LD, BD, MS and DA.

species in the south to a more predominant mixture of sclerophyllous shrubs and hummock grasses in the north.

Fire is relatively common in these shrubland plant communities (Cheal *et al.*, 1979; Specht, 1981b; Hahs *et al.*, 1999; Bradstock & Cohn, 2002). In this region lightning ignitions are a predominant source of fire (Cheal *et al.*, 1979; Bradstock & Cohn, 2002) with a lesser input from human sources (planned and unplanned). The potential for large fires exists because of the relatively large areas occupied by these flammable shrublands.

Within this area, four specific areas (hereafter called LD, BD, MS and DA) were selected along a south–north gradient. From south to north these areas are (Fig. 1): LD, the Little Desert National Park (134,589 ha) located in western Victoria; BD, the Big Desert Wilderness Park (713,771 ha) located in north-western Victoria; MS, the Murray-Sunset National Park (805,001 ha) located in north Victoria; DA, the Danggali Conservation Park (523,230 ha) located in eastern South Australia, and the adjacent Tarawi Nature Reserve (33,620 ha) in the west of New South Wales. These represent the major tracts of remnant natural vegetation contained within public conservation reserves along the notional south–north gradient. Records of past fires were available for these public tenure lands, as were vegetation survey data for these and adjacent areas. While the sandy nature of the parent material is a feature of all these sites, some geomorphological differences exist among them. LD, BD and the south of MS are composed of siliceous irregular, transverse and parabolic dunes (Lowan dunes), while the north of MS and DA are mainly siliceous and clay aggregated short, narrow-crested linear dunes (Woorinen dunes; Wasson, 1989).

Climate

The study region lies broadly between the 650-mm and the 250-mm annual rainfall isohyet in the south and north, respectively (*Climatic Atlas of Australia*, Anon, 2000). The whole study area is located in the mediterranean climatic zone of Australia (defined by the Köppen climatic types Csa, Csb and Ksk), with an AET/PET ratio (moisture index) ranging from 0.8 to 0.3 (Specht, 1981b).

Long-term rainfall and temperature information was gathered for 17 stations spread throughout the study region (Table 1). These data were used to estimate the long-term mean and variability of rainfall and temperature for each meteorological station. The relationships between latitude and the climatic variables (precipitation, temperature and variability of precipitation) were assessed by linear regression with the 17 meteorological stations weighted by the number of years with data available at each station. We assume productivity to be positively related to increase in water availability (Rosenzweig, 1968), and in the study area this is related to increasing precipitation and decreasing temperature. Wang and Barrett (2001) provide a positive relationship between precipitation and productivity for the Australian continent, while Specht and Specht (1999) provide direct evidence

Table 1 List of the 17 meteorological stations used in this study, sorted by latitude (north to south), with their main characteristics: latitude, longitude, altitude and number of years with complete data for precipitation (*n* P) and temperature (*n* T)

	Name, state	Lat. (S)	Long. (E)	Altitude (m)	*n* P	*n* T
1	Danggali Conservation Park (Hypurna), SA	33°33′51″	140°55′47″	42	40	0
2	Lake Victoria Storage, NSW	34°02′23″	141°15′55″	43	80	58
3	Renmark, SA	34°10′16″	140°44′58″	20	112	41
4	Mildura Airport, VIC	34°13′50″	142°05′02″	50	56	56
5	Berri, SA	34°16′25″	140°35′34″	50	42	0
6	Loxton Research Centre, SA	34°26′20″	140°35′52″	30.1	18	17
7	Ouyen (Post Office), VIC	35°04′15″	142°18′52″	50.3	88	64
8	Walpeup Research, VIC	35°07′18″	142°00′08″	105	64	50
9	Murrayville, VIC	35°15′45″	141°10′42″	88	89	0
10	Lameroo, VIC	35°19′44″	140°31′03″	99	103	83
11	Rainbow Post Office, VIC	35°54′00″	142°00′00″	89.6	67	0
12	Beulah (Post Office), VIC	35°56′24″	142°25′08″	100	99	72
13	Jeparit, VIC	36°08′29″	141°59′11″	85	100	47
14	Serviceton North, VIC	36°12′47″	140°59′44″	122	30	0
15	Nhill, VIC	36°20′11″	141°38′07″	133	116	99
16	Horsham (Polkemmet), VIC	36°39′14″	142°06′13″	141	128	86
17	Longerenong, VIC	36°40′19″	142°17′56″	91	105	0

of a correlated gradient of rainfall, evaporation and net biomass (i.e. productivity) across the study gradient. Based on this evidence, productivity was assumed to decline with aridity along the study gradient.

Fire history

Data on area burned per annum in each of the study areas were obtained from archives of the relevant land management authorities (i.e. Victorian Department of Sustainability and Environment, Parks Victoria, New South Wales National Parks and Wildlife Service, South Australia Parks and Wildlife Service). The data include annual area burned for the periods from 1932 (MS), 1947 (BD), 1974 (DA) and 1976 (LD) to 2003. These data were used to estimate the annual mean area burnt and the fire cycle (the number of years required to burn over an area equal to each of the study areas; Johnson & Van Wagner, 1985). The fire cycle is computed as the temporal extent of the fire history data divided by the proportion of area burnt. Fire statistics were computed for the whole period available for each study area (above) and for the common period for the five study areas (i.e. 1976–2003).

Vegetation and plant functional traits

A list of species found in fire-prone shrubland types was compiled for each study area. Sources of information included published and unpublished surveys. Floristic data for LD, BD and SS were obtained from Cheal *et al.* (1979) and Cheal and Parkes (1989). For BD, the data came specifically from Wyperfeld National Park. Data for DA were a combination derived from surveys conducted within Dangalli Conservation Park (Forward & Robinson, 1996) and the adjacent Tarawi Nature Reserve (Westbrooke *et al.*, 1988). In addition to species lists for relevant shrubland communities, data on cover for various vegetation strata (e.g. overstorey shrubs, understorey shrubs, surface layer herbs and grasses) were compiled at each location from these sources. Thus the lists of species and associated life history traits (see below) represented a net regional overview for each study area. Cover data represented averages derived from multiple sample plots, and although they do not allow statistical comparisons they provide an indication of the community structure. Data were omitted from less flammable shrubland communities (e.g. chenopod-dominated shrublands) or non-shrubland communities (e.g. woodlands, grasslands), normally situated on soils of moderate fertility or heavier texture (Specht, 1981b) or special topographic features (e.g. saline depressions).

Various published and unpublished plant data bases (Gill & Bradstock, 1992; Bradstock & Kenny, 2003; Pausas *et al.*, 2004; D.A. Keith, pers. comm.; T.D. Auld, pers. comm.) were then used to determine the fire persistence traits (resprouting, propagule persistence) and life form of each species. For the statistical analysis, the species in which this information was unknown or variable between sources were omitted. Resprouting (R) is defined as the capacity of individuals to resprout after 100% scorch by fire (Gill, 1981). Propagule persistence (P) refers to the presence of traits allowing persistence of populations after fire in propagule form, i.e. seed or fruit, after 100% scorch by fire (i.e. having a persistent seedbank that allows post-fire recruitment) (for details see Pausas *et al.*, 2004). The species groups considered were defined by the binary combination of resprouting and propagule persistence. Thus we compare resprouters (R+) versus non-resprouters (R–), propagule persisters (i.e. species with seedbank, P+) versus non-propagule persisters (P–), and the four possible combinations of R and P: R+P– (obligate resprouters), R+P+ (facultative species), R–P+ (obligate seeders) and R–P– (see Pausas *et al.*, 2004 for more details). P+ species were further distinguished on

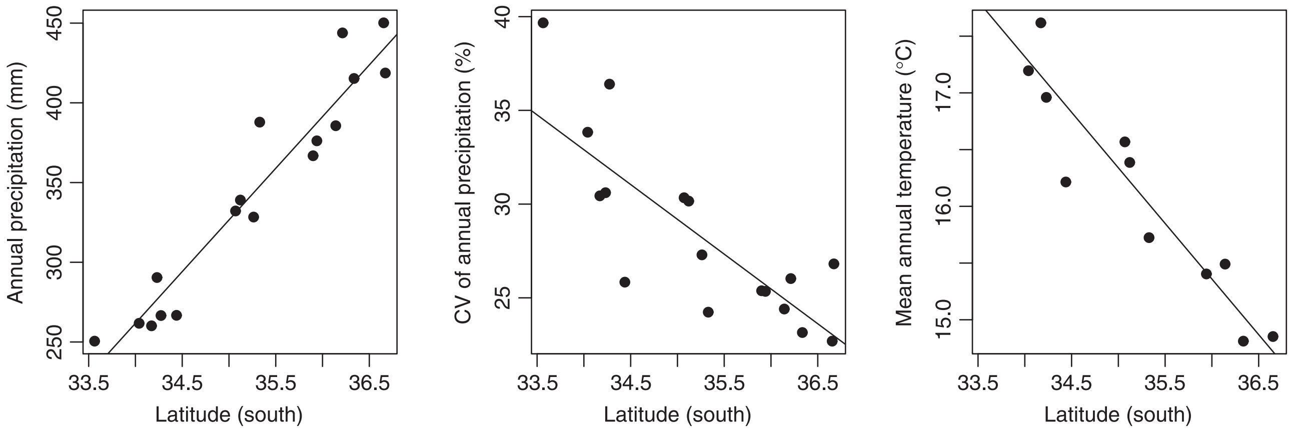

Figure 2 Relationship between climatic variables and latitude for the 17 meteorological stations in the study area. Total annual precipitation ($F_{1,15}$ = 185.5, P < 0.00001, R^2 = 0.925), coefficient of variation (CV, %) of annual precipitation ($F_{1,15}$ = 37.46, P < 0.00001; R^2 = 0.714) and mean annual temperature ($F_{1,9}$ = 112.4, P < 0.00001; R^2 = 0.926). Data are means and CV for the whole available period at each station (Table 1).

Table 2 Burnt area statistics for the four studied areas considering both the whole period available and the 28-year standardized period (1976–2003). Sites arranged from south (left) to north (right)

	Sites			
	LD	BD	MS	DA
Whole available period:				
Number of years	28	57	75	30
Proportion of fire years (%)	96	63	57	40
Mean area burnt (%/year)	3.39	2.33	0.80	0.48
Fire cycle (year)	29.5	43.0	125.0	206.6
Skewness	2.51	5.27	5.38	4.07
Kurtosis	7.29	29.91	32.52	16.79
Standardized period (1976–2003):				
Proportion of fire years (%)	96	89	79	39
Mean area burnt (%/year)	3.39	2.45	1.37	0.49
Fire cycle (year)	29.5	40.8	73.0	203.5
Skewness	2.51	3.48	4.01	3.93
Kurtosis	7.29	11.93	16.25	15.95

the basis of canopy retained or soil seed storages. Life forms considered were: mallee eucalypts, tall shrubs (0.5–3.5 m), low shrubs (< 0.5 m) and herbs. The chi-square test was used to test the association between the number of species in these groups and the four sites along the north–south gradient. If the association was significant, an inspection of the residuals was performed to investigate trends among sites.

RESULTS

Climate

Linear relationships between mean temperature, mean rainfall, rainfall variations and latitude were found (Fig. 2). From south to north, annual precipitation decreases and mean annual temperature increases. Monthly precipitation variability also shows a similar significant trend for all months (P values ranging from 0.017 to < 0.000001) except for December in which the trend was not significant (P = 0.20). Longitude was not related to any of the climatic variables. Because of the inverse trend in precipitation and temperature (Fig. 2), the latitudinal gradient is unambiguously related to water availability for plants (see also Specht & Specht, 1999). Thus, there is a clear trend towards decreasing productivity and increasing aridity from south to north. Between-year variability in annual precipitation increases towards the north (with aridity).

Fire history

LD is the area with the most fire years (highest fire frequency; fire occurs most years) compared with BD, MS and DA where fires occur in 63, 57 and 40% of the years, respectively (Table 2,

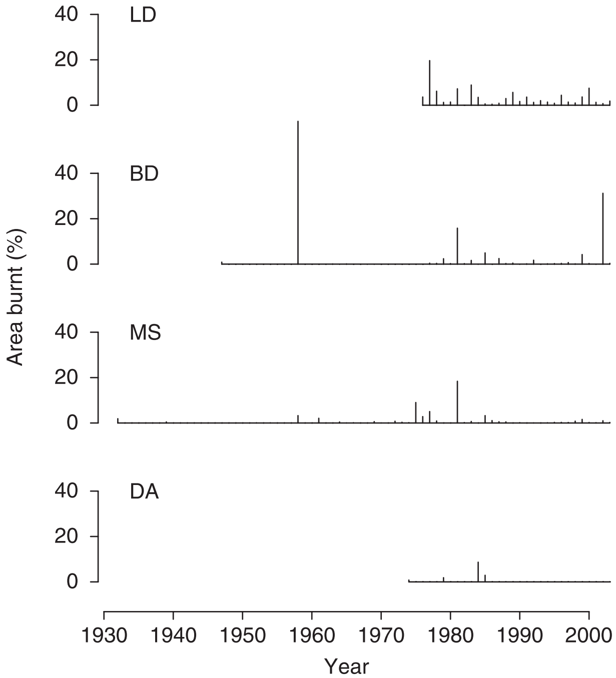

Figure 3 Fire history of the four studied areas (LD, BD, MS, DA), from south (top) to north (bottom), expressed as the annual proportion of area burnt. Note that periods with available data differ among sites (Table 2).

Fig. 3). Considering the average proportion of area burnt in each fire year, there is also a gradient from LD (3.4% of the area) to DA (0.5% of the area). LD has the shortest fire cycle (30 years), followed by BD; the MS fire cycle is about twice that of BD and half that of DA (Table 2). The annual area burnt shows a strongly left-skewed distribution on all sites (a few years with large areas burnt and many years with a small area burnt), but LD has the most evenly burnt area distribution (lowest skewness and kurtosis). Similar fire statistics are observed when considering only the common period through all sites (Table 2). Thus, there is a clear trend of increasing fire from north to south, that is, in parallel with productivity.

Vegetation and plant functional traits

There is a trend towards increasing mallee eucalypts overstorey cover and reducing shrub (both tall and low) and herb cover towards the north, with decreasing productivity and increasing aridity (Table 3). The proportion of species in each life form did not vary significantly among the four study areas (Tables 4 & 5). However, there was a significant decrease in the proportion of resprouter species with increasing aridity, from *c.* 60% (LD) to 26% (DA) (Tables 4 & 5). Both woody and non-woody resprouters decreased, while herbaceous non-resprouters increased along this gradient (Fig. 4a). There was no significant trend in the proportion of seeder species (P– vs. P+) nor in relation to seedbank types (none, canopy, soil) along the aridity gradient. There was, however, a significant trend in the combined fire response (R and P) along the gradient, where resprouters with seedbank (R+P+, facultative species) decreased while non-resprouters with seedbank (R–P+, seeders) increased with increasing aridity (Table 5, Fig. 4b).

Table 3 Average plant cover values (%) in the four areas studied. Sites arranged from south (left) to north (right)

	Sites			
	LD	BD	MS	DA
Mallees	12.5	29.1	40.8	30
Shrubs (0.5–3.5 m)	65.8	41.2	15.8	10
Low shrubs (< 0.5 m)	11.7	12.5	0	5
Herbs	35.4	22.2	22.1	12.5

Table 4 Number of species considered (i.e. with information on resprouting capacity), proportion of species with different life forms, proportion of resprouting species (for total and for woody species only) and the ratio of number of resprouting/non-resprouting species. Sites arranged from south (left) to north (right)

	Site			
	LD	BD	MS	DA
Total number of species	108	189	126	143
Life form:				
Mallees (%)	3.4	5.5	5.5	7.2
Shrubs (%)	42.4	34.7	33.3	33.6
Herbs (%)	54.2	59.7	61.2	59.2
Resprouters (%)	60.4	47.7	38.6	26.5
Woody resprouters (%)	33.3	24.3	19.2	13.5
Resprouters/non-resprouters	1.52	0.91	0.63	0.40

Table 5 Significance of the association between site (LD, BD, MS, DA) and the proportion of number of species with different plant characteristics. Significant associations are indicated in bold and plotted in Fig. 4

Variable (classes)	χ^2	d.f.	*P*
Life form (mallee, shrub, herb)	4.38	6	0.624
Resprouting (R–, R+)	28.15	3	< **0.0001**
for woody species only	10.66	3	**0.0136**
for herbaceous species only	16.54	3	**0.00088**
Seeding (P–, P+)	2.08	3	0.56
Fire response (R+P–, R+P+, R–P+, R–P–)	18.59	9	**0.028**
Seedbank (none, canopy, soil)	2.81	6	0.83

DISCUSSION

The four study sites selected along a south–north gradient represent a clear climatic gradient from the wettest and coolest in the south to the driest and hottest in the north, implying decreasing availability of water for plants from south to north.

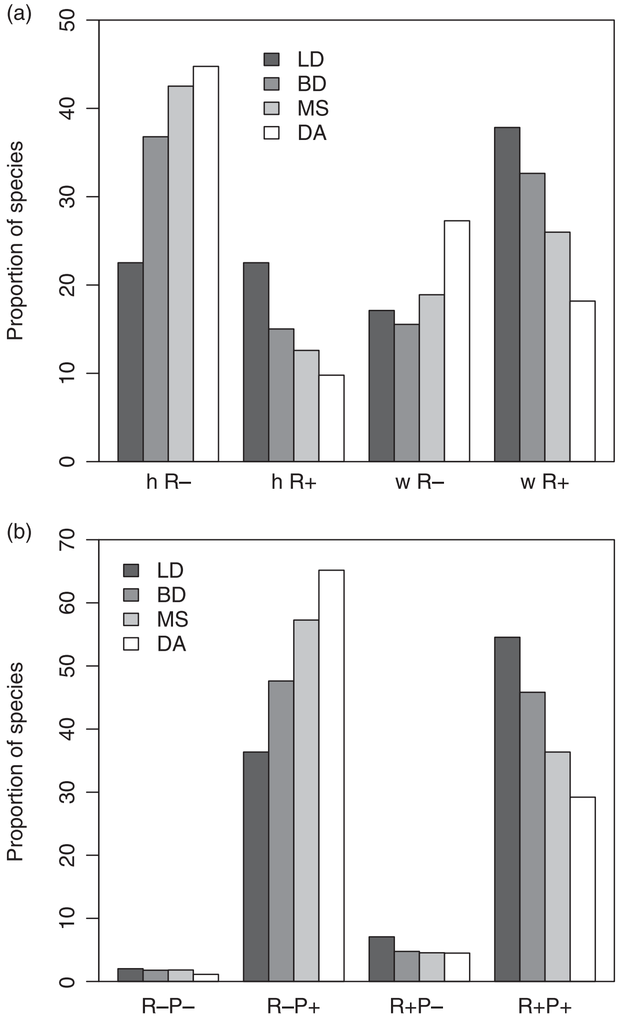

Figure 4 Proportion of species with different combinations of attributes on the four study sites. Sites are arranged from south (left, moister) to north (right, drier). h, herbaceous species; w, woody species; R+, resprouters; R–, non-resprouters; P+, with seedbank; P–, without seedbank. See Table 5 for level of significance.

Water availability is strongly related to productivity on a global scale (Rosenzweig, 1968) as well as within Australia (Specht & Specht, 1999). Furthermore, rainfall variability also increases with the aridity gradient, making rainfall less predictable and unreliable towards the northern arid zone. Although the fire history was limited (28–75 years), the decreasing productivity gradient (or increasing aridity gradient) matches well with a fire gradient, which ranges from high fire frequency and short fire cycle (*c.* 30 years) in the south to low fire frequency and long fire cycle (> 200 years) in the north (Table 6). That is, in our study area, drier areas have a lower fire frequency and longer fire cycle than wetter areas, and thus, productivity and fire frequency are positively related. These results suggest that within the vegetation type studied (heaths and mallee shrublands), fire regimes are determined by climatic conditions but mediated by the fuel loads and distribution. In these mediterranean conditions, higher moisture availability implies higher growth, higher fuel loads, higher fuel connectivity

Table 6 Climatic, fire and vegetation trends found along the south–north geographical gradient in southern Australia. Summary of the results obtained in Tables 2, 3, 4 and 5

South	Variable	North
	Climate:	
+	Annual precipitation	–
–	Mean annual temperature	+
–	Rainfall variability between years	+
+	Rainfall predictability	–
+	Productivity	–
–	Aridity	+
	Fire regime:	
+	Annual area burnt	–
+	Fire frequency	–
	Vegetation:	
+	Lower strata plant cover	–
–	Cover of mallee trees	+
–	Bare soil	+
+	Fuel continuity	–
+	Proportion of resprouting species	–
–	Proportion of obligate seeders (R–P+)	+

and thus higher fire hazard. The decreasing pattern of fire towards the north may be due to the decrease in the amount and connectivity of fuels, as observed by the structural changes in plant cover (Table 3). There is a reduction in the lower vegetation strata cover and a shift in cover upwards (fine fuel up the canopy) implying a reduction in horizontal fuel connectivity and an increase in bare soil towards the north. The average density and cover of mallee eucalypts are commonly insufficient for propagation of fire for many decades after fire (Bradstock & Cohn, 2002); they may even be insufficient for fire spread irrespective of time since fire (Cheal *et al.*, 1979).

Shifts in life form dominance (Table 3) may alter fuel structure and ecosystem flammability. Thus, although the flammability of plant tissues may be high (e.g. eucalypt and *Triodia* spp.), ecosystem (landscape) flammability is low in the drier mediterranean ecosystems of the northern part of the gradient due to reduced fuel connectivity. It fact, it has been suggested that in the northern mallee shrublands conditions conducive to large fires are governed by above average rainfall, through the stimulation of ephemeral grasses and herbs and the resultant increase in fine fuel connectivity (Noble, 1989).

This positive relationship between productivity and fire frequency should not be expected everywhere, however, because of the complex nonlinear relationship between fire regime and productivity (Fig. 5). In moister landscapes than our study area (e.g. other temperate communities) high precipitation and productivity may be related to higher moisture fuels and lower fire frequency, while low precipitation may be related to lower plant moisture and low decomposition rates, both of which could imply higher fire risk and frequency. Thus, under these moister conditions, an inverse relationship between productivity and fire frequency can be expected (Clarke & Knox, 2002; Clarke *et al.*,

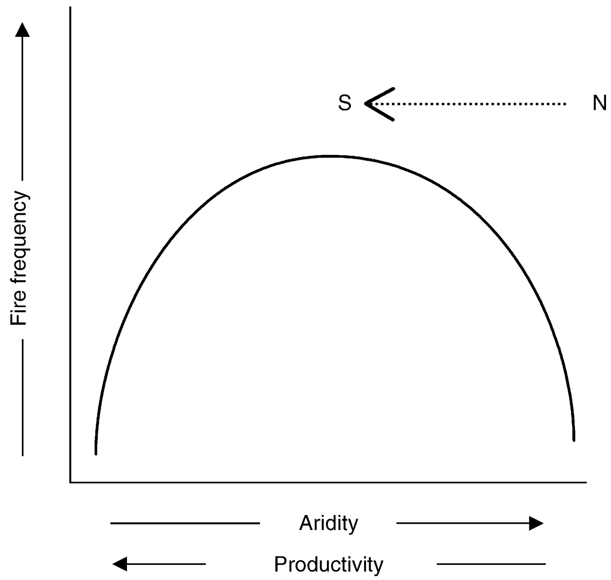

Figure 5 Hypothetical fire–productivity relationship. The dotted arrow indicates the range of conditions studied in the present paper, from north to south (the fire and productivity gradient). Because of the complex nonlinear relationship between fire regime and productivity, other studies in other portions of the productivity gradient are expected to find different results for fire persistence traits of plants.

2005). This different pattern has implications when studying post-fire plant traits along productivity gradients.

The proportion of resprouting species increases from DA (in the north) to LD (in the south) along the fire–productivity gradient (Fig. 4, Table 5). This is in agreement with Specht (1981a), who suggested a linear relationship between the proportion of resprouting species and the community cover (which in turn was directly related to moisture) for Australian shrublands. At a similar geographical scale, Ojeda (1998) suggested that the distribution of resprouting *Erica* species in the Cape Floristic Region was related to summer water availability (see also Smith *et al.*, 1992), and Lamont and Markey (1995) found that resprouting *Banksia* species in south-western Australia occurred in higher proportions in regions with higher average rainfall. At the local scale, more resprouters on moister sites (pole-facing slopes, deep or fissured soils) versus drier sites have been observed in many fire-prone ecosystems worldwide (Keeley, 1986; Keith, 1991; Benwell, 1998; Pausas *et al.*, 1999; Meentenmeyer *et al.*, 2001; Clarke & Knox, 2002). In most of these studies, changes in fire regime on contrasted productivity sites have not been evaluated. Our results unambiguously support a higher proportion of resprouters at the high end of the productivity–fire gradient, within the section of the gradient studied (Fig. 5). However, we cannot disaggregate the effect of each of the two variables, productivity and fire. Thus, our results can be explained by the advantage of resprouting in landscapes with high fire frequency and/or by the advantage of not relying on recruitment in highly competitive (moist) sites. High levels of moisture diminish the chance of successful post-fire recruitment through competitive effects of a resprouting overstorey, making resprouting a more successful strategy (resprouters as gap avoiders, *sensu* Keeley, 1998). In drier habitats more space may be available for post-fire seedling establishment and subsequent survival and growth of juveniles. Trends in productivity and fire recurrence may have complex effects on the total mix of functional types driven by competitive influences and, in turn, the functional type status of dominant species (Bond & Ladd, 2001; Tozer & Bradstock, 2003). Clarke *et al.* (2005) also found evidence supporting both productivity and fire hypotheses in a regional comparison of woody taxa in a moister area of Australia, and proposed a simple model that predicts that resprouting will respond to confounded gradients of productivity, flammability and fire frequency.

The presence of a seedbank (P– vs. P+) does not show any trend with the fire–productivity gradient (Table 5). However, when linked with resprouting capacity, a significant pattern emerges (Table 5, Fig. 4): the proportion of obligate seeder species (R–P+) decreases along the fire–productivity gradient (Fig. 4). Non-resprouting species with long-lived seedbanks capable of responding to multiple favourable germination events over time, and thus unlikely to be exhausted in a single germination episode, may be favoured in dry and unpredictable conditions (e.g. Jurado & Westoby, 1992; Auld, 1995). Such a seedbank trait may also allow species to persist under low-frequency fire regimes. The decrease in cover with aridity may provide space for seedling establishment (seeders as gap recruiters, *sensu* Keeley, 1998), unconstrained by the effects of overstorey cover. Thus, having a seedbank (P+) can be found in arid conditions as a strategy to cope with aridity, and in less arid, more fire-prone conditions, as a strategy to cope with fire. These possibilities make the changes in P+ along the fire–productivity gradient insignificant (Table 5) when not tested in conjunction with resprouting. They also make the seedbank trait very interesting from the ecological and evolutionary point of view. Discerning the effect of fire from the effect of drought in the sorting of persistence traits in mediterranean conditions is a challenge that requires further research. We also need to consider that some differences between herbaceous and woody species may be due to the fact that some non-resprouter herbaceous species are short-lived, i.e. they may complete their life cycle in the absence of fire. We would expect an increase in the frequency of canopy seedbanks with increasing productivity/fire probability (Enright *et al.*, 1998a,b) (i.e. a higher proportion of canopy seedbank in the south), while soil seedbanks may be favoured in dry conditions (north). Our results, however, indicated that there was no significant trend in seedbank type along the gradient (Table 5).

The relative influence of fire, aridity and competition on plant community composition may be difficult to disentangle. The alternative explanations place differing emphases on functional trait selection via the post-fire regeneration niche (chance of successful establishment) and thus the resultant degree of species reliance on persistence (the persistence niche; Bond & Midgely, 2001; Pausas *et al.*, 2004). Our results, however, do indicate that the effects of productivity and fire may be complementary in mediterranean ecosystems and perhaps synergistic rather than antagonistic. Compiling information for areas with different

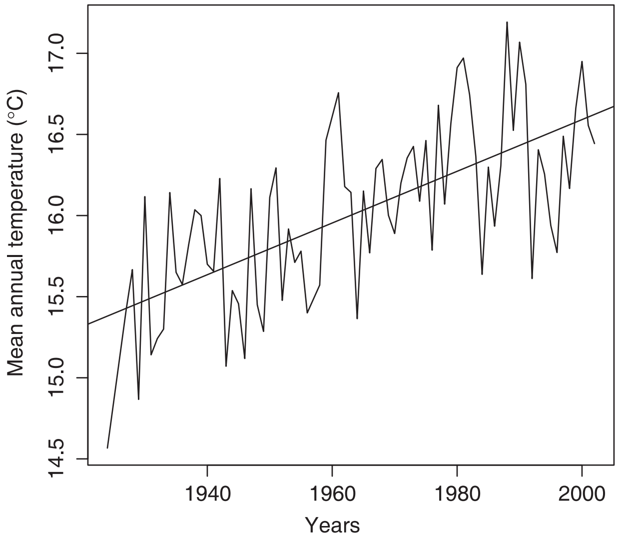

Figure 6 Changes in mean air temperature in the study area during the last eight decades. Data are the mean of the 11 meteorological stations with temperature data (Table 1). Years with data for fewer than six meteorological stations are not considered. The regression line is also shown ($F_{1,73} = 54.35$, $P < 0.00001$, weighted by the number of stations in each year).

productivity–fire relationships (different portions of the gradient in Fig. 5) may provide a clearer picture for understanding where the different plant traits are dominant and which selective pressures are more relevant. We believe that we cannot make general models on where different plant strategies should dominate along the productivity gradients without considering both fire regime and productivity simultaneously, because the relationship between these variables may vary among study areas.

Implications for climatic change research

Although total annual precipitation does not show any trend during the last decades (not shown), the observed increase in temperature (Fig. 6) implies a clear increase in aridity during the last century. The average temperature change observed during the last eight decades (*c.* 1.24 °C, Fig. 6) is within the range observed in the Australian continent (Collins, 2000), and it is equivalent to a displacement of about 1° latitude (*c.* 110 km) towards the north (Fig. 2). Climatic change predictions for Australia (CSIRO, 2001; Hughes, 2003) suggest that this change in temperature is going to be maintained in the future, although predictions about precipitation changes are uncertain. Overall increases in potential evaporation and aridity are clearly predicted. Thus, assuming no precipitation change, we would predict a future decrease in the mass and connectivity of fuels and a consequent decrease in fire frequency in the study area. Future fire scenarios predict an increase in the frequency of days exhibiting severe fire weather (Beer & Williams, 1995; Williams *et al.*, 2001); however, the spatial structure of fuel may limit the effects of this shift on fire regimes. The role of the spatial structure of fuels needs to be considered in developing predictions on changes to fire regimes. Further research is also needed to understand how changes in plant growth and competitive interactions due to elevated CO_2 levels would interact with the accumulation and connectivity of fuels.

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