

Landscape patterns of woody plant response to crown fire: disturbance and productivity influence sprouting ability

PETER J. CLARKE*, KIRSTEN J. E. KNOX, KAREN E. WILLS and
MONICA CAMPBELL

Botany, School of Environmental Sciences and Natural Resources Management, University of New England,
Armidale, NSW 2351, Australia

Summary

1 The relationship between environment and the ability of plant species to resprout has been explored more in terms of disturbance frequency than of resource gradients, and has rarely been examined in non-Mediterranean landscapes.

2 The fire response of 296 non-eucalypt woody taxa was recorded in five habitats in the New England Tablelands (NET) Bioregion of eastern Australia: grassy woodlands, dry sclerophyll forests, rocky outcrops, wet heaths and wet sclerophyll forests. We then tested whether there was a dichotomy of response to crown fire, whether the proportion of resprouters differed among habitats, and if disturbance frequency or resource-productivity models could account for landscape patterns of resprouting.

3 There was a continuum of sprouting ability but most species could be classified as obligate seeders (killed by fire) or resprouters. Habitats differed in the proportion of resprouting species, with rocky outcrops having the lowest proportion and grassy forests and wet heaths the highest. This pattern was consistent at the congeneric and confamilial phylogenetic levels of comparison.

4 Resource/productivity models better explained landscape patterns of resprouting than disturbance frequency models. There was a strong positive relationship between resprouting and increasing soil fertility and moisture gradients. Species richness and obligate seeder richness increased with climate variability and landscape heterogeneity.

5 Landscape resprouting patterns were explained by a resource-competition model where resprouters are favoured because of their ability to persist in more competitive environments. Overall, we suggest that disturbance frequency has larger effects on species richness at the low end of the productivity gradient than at the high end.

Key-words: competition, disturbance, fire ecology, fire regime, obligate seeding, resprouting, reseeding, sclerophyll forest, vegetation dynamics

Journal of Ecology (2005) **93**, 544–555
doi: 10.1111/j.1365-2745.2005.00971.x

Introduction

Fire is a pivotal ecological factor that influences the functional response of woody plants in habitats prone to such disturbance (Whelan 1995; Bond & van Wilgen 1996). The growing realization that fire regimes can have profound effects on community dynamics (Bond & Midgley 2001) has led to intensive efforts to model the response of plants to fire (Vesk & Westoby 2004). In

particular, data on population responses of plants to crown fire is being sought to distinguish the effects of seed-based recruitment from that of persistence (resprouting) (Valiente-Banuet *et al.* 1998; Clarke & Knox 2002; Pausas *et al.* 2004; Vesk & Westoby 2004). A dichotomy exists between those taxa that are killed by fire and those that resprout following crown fire (Bradstock *et al.* 1998; Franklin *et al.* 2001; Bradstock & Kenny 2003), although Vesk & Westoby (2004) stress that there is actually a continuum of responses, and that population responses should therefore be used when developing models to explain resprouting ability.

Relationships between plant attributes and the habitats they occur in provide a basis for developing

Correspondence: Peter J. Clarke, Botany, School of Environmental Sciences and Natural Resources Management, University of New England, Armidale, NSW 2351, Australia (e-mail pclarke1@metz.une.edu.au).

functional classifications for predicting community dynamics (Noble & Gitay 1996; Pausas 1999). In particular, the relationship between specific response groups to productivity and disturbance gradients has been examined extensively for herbaceous species (e.g. McIntyre *et al.* 1995; Lavorel *et al.* 1997; Mabry *et al.* 2000; Verheyen *et al.* 2003). For woody species, the relationship between habitat and the ability of species to resprout has been explored in terms of disturbance frequency (Morrison *et al.* 1995) and disturbance intensity (Vesk & Westoby 2004), with less emphasis on productivity gradients (Lamont & Markey 1995; Bond & Midgley 2001; Clarke & Knox 2002; Vesk & Westoby 2004).

Contrasting the sprouting ability of species across disturbance and productivity gradients may also provide insights into how persistence traits have been selected (Bellingham & Sparrow 2000; Bond & Midgley 2001). Much of the theory for sprouting ability in relation to fire has developed from Mediterranean-type regions with limited phylogenetic control. From an evolutionary perspective, there is a growing emphasis on trait comparison in terms of phylogenetic independence although there are relatively few studies of fire response across diverse phylogenetic groups in non-Mediterranean-type regions.

The aim of this study was to compare the response of woody species (excluding *Eucalyptus*) to crown fire in five contrasting habitats and to test models that explain these patterns. Specifically, we examined whether the proportion of resprouting was significantly different among habitats and if these patterns were consistent among congeners and confamilial species across habitats. We then constructed a series of models from the literature to explain these patterns in relation to disturbance and productivity gradients and tested their predictions by examining the relationship between sprouting ability and covariation in gradients of disturbance and productivity.

Methods

STUDY REGION AND HABITATS

The study region is the New England Tablelands (NET) Bioregion of eastern Australia that falls within the Cfb (dry cool temperate) climate region (Thackway & Cresswell 1995) with an altitudinal range of 750–1500 m. Five major sclerophyllous habitats occur in the Bioregion: grassy eucalypt open forests and woodlands (grassy woodland), shrubby eucalypt open forests (dry sclerophyll forest), dry heathlands and heathy eucalypt scrub (rocky outcrop), heathlands and sedgeland (wet heath) and mesic tall eucalypt open forests (wet sclerophyll forest). These broad groups form distinct floristic associations that are related to climate gradients, lithology and local physiography (Benson & Ashby 2000). As a generalization, nutrient-poor siliceous soils provide habitats for scleromorphic shrub-dominated woodlands

and forests whilst the more clayey soils derived from metasediments and basalts support grassy woodlands and forests (Benson & Ashby 2000). Shrubs occur throughout the landscape but are less abundant and less species rich in the grassy woodlands. Wet heaths and sedgeland occur in areas of impeded drainage (Williams & Clarke 1997; Benson & Ashby 2000) whilst rocky outcrops support species-rich scrub and dry heath (Hunter & Clarke 1998). Although rainforest occurs adjacent to the wet sclerophyll forests in moister gullies in the higher rainfall area of the region, this habitat is rarely burnt and hence was excluded from the study.

GROWTH FORM AND FIRE RESPONSE TRAITS

The growth form traits of all woody species encountered in field sampling, excluding eucalypt trees, were determined from field observations, flora records and published records. Plant height, diaspore type, basal stem numbers and leaf type classes are shown in Table 1. Fire response records were created for 296 taxa after experimental burns (pre-fire tagging), hazard reduction exercises and wildfires that burnt 100% of crowns, and averaged for each species across all habitats. *Eucalyptus* species were excluded from the fire records because all resprout following fire in the NET Bioregion. Where possible, sprouting ability (i.e. whether they were killed or resprouted) was recorded for at least five individuals in at least two independent shrub populations. Hence, each species has a frequency between 0 and 1 for sprouting ability (*sensu* Vesk & Westoby 2004; Vesk *et al.* 2004; here termed resprouting) after crown-destroying fire. In a few species, allopatric populations responded differently to the same fire, with one having a high proportion of resprouters whilst another was uniformly killed. In such instances the populations were partitioned as different taxa rather than defining the overall species response as 0.5. The influence of water stress on the ability of plants to resprout was taken into account by recording resprouting ability after fire in differing seasons and years. However, records for the wet sclerophyll forests were obtained only in 2002 and 2003, when fires burnt for the first time in 50 years following a severe drought that affected most of eastern Australia.

The frequency of resprouting response in 11 classes from 100 to 0% was assessed across all species to determine if species could be classified into resprouters (70–100% class) or obligate seeders (0–30% class) (Gill & Bradstock 1992). In addition to data on resprouting, the position of resprouting and the type of seed bank was assessed for each species so they could be placed into one of the functional groups or fire syndromes of Gill & Bradstock (1992) (Table 2). Observations on pyrogenic flowering and post-fire induced emergence of seedlings were also made so that a more complete overview of fire-related syndromes could be made (Table 2).

Table 1 Summary table for growth form traits of 296 woody taxa occurring in 248 sample sites across five habitats in the New England Tableland Bioregion of eastern Australia. Note eucalypts not included

Attribute	Habitats					All habitats
	GW	DSF	RO	WH	WSF	
Plant height						
Prostrate/twining/suffruticose (< 10 cm)	4	10	4	10	7	21
Decumbent shrub (< 50 cm)	13	46	38	26	6	72
Shrub (50–200 cm)	28	92	70	33	26	138
Treelet (2–10 m)	7	14	8	2	39	56
Tree (> 10 m)	1	5	2	0	7	9
Total	53	167	122	71	85	296
Diaspore type						
Seed	37	126	98	61	31	203
Dry fruit	0	5	4	0	5	10
Fleshy fruit	16	36	20	10	49	83
Adult stem number						
Single	43	133	104	57	74	245
Multiple	10	34	18	14	11	51
Leaf type						
Sclerophyllous	37	126	93	65	22	183
Cladodinous	4	16	15	3	3	23
Coriaceous	4	9	4	0	13	24
Mesophyllous	8	16	10	3	47	66

GW, grassy woodland; DSF, dry sclerophyll forest; RO, rocky outcrop; WH, wet heath; WSF, wet sclerophyll forest.

Table 2 Summary table for fire-related syndromes in 296 woody taxa occurring in 248 sample sites across five habitats in the New England Tablelands Bioregion of eastern Australia. Regression and slope coefficients for total richness vs. resprouting for each habitat are given under fire response

Attribute	Habitats					All habitats
	GW	DSF	RO	WH	WSF	
Fire response (I–VII*)						
I. Killed, canopy-stored seedbank	0	1	7	2	0	7
II. Killed, soil-stored seed bank	10	53	55	7	17	90
IV. Resprouts via root suckers	7	10	3	1	8	16
V. Resprouts via basal stem	35	98	54	61	57	176
VI. Resprouts via stem bud bank	1	3	3	0	3	5
VII. Resprouts via terminal bud	0	2	0	0	0	2
Total	53	167	122	71	85	296
Fire response						
Killed (< 30% resprout)	8	45	55	11	18	89
Resprout (> 70% resprout)	38	100	53	55	63	179
Variable (30–70% killed)	7	22	26	5	4	28
r^2	0.97	0.97	0.93	0.99	0.99	0.93
Slope	0.85	0.75	0.41	0.93	0.87	0.72
Pyrogenic flowering						
Yes	2	5	0	1	1	5
No	51	162	122	70	84	291
Bradyspory						
Yes	3	23	17	2	5	36
No	50	144	105	50	80	260
Fire-induced germination						
Yes	41	122	100	47	69	189
No	12	45	22	24	23	107

*Roman numerals are classes used by Gill & Bradstock (1992). GW, grassy woodland; DSF, dry sclerophyll forest; RO, rocky outcrop; WH, wet heath; WSF, wet sclerophyll forest.

SITE SAMPLING AND ANALYSES OF
RESPROUTING

In each of the five habitats the occurrence of woody species was recorded in sample sites of 0.1 ha in which all woody taxa were recorded, including suffruticose and twinning species. All sample sites (248) were in areas that had not been burnt for at least 5 years and were in conservation reserves not grazed by stock for at least 10 years. Sample sites were allocated within habitats to sample across a wide geographical range (*c.* 50 km east–west and 100 km north–south) and stratified across major environmental variables of lithology and rainfall gradients (Table 3). Localized site environmental factors were measured *in situ* (Table 3) and climate variables for each site were derived from BIOCLIM climate modelling (Busby 1991). No direct measures of fire frequency were available for study sites but the likelihood of frequent fire can be estimated from fuel (cover, continuity), topography (slope) and climate variables. Fire frequency index was calculated from the product of mean maximum temperature, seasonality of moisture, understorey cover and slope.

The number of woody species, proportion of plants resprouting (total estimated sprouting ability in a site) and proportion of species resprouting (see classification above) in each habitat were compared using generalized linear models (Poisson error structure) based on the

presence of species in quadrats in that habitat. *A priori* habitat classification by vegetation physiognomy was confirmed with multivariate analyses (woody taxa only) showing separation of sites into clusters that corresponded to the five vegetation types. Analyses for the proportion of resprouting woody plants and proportion of resprouting species were repeated for species in genera and species in families occurring in at least three of the five habitats. This was done to assess if the patterns at species levels were independent of phylogenetic bias relating to clades being prominent in one or more habitats.

SPECIES TRAITS AND ENVIRONMENTAL
RELATIONSHIPS

Data matrices were constructed for floristic and environmental (Table 3) data prior to canonical correspondence analysis (CCA) (ter Braak & Prentice 1989; ter Braak & Smilauer 1998). In these analyses the degree of covariation between the environmental data and the floristic data was assessed and the significance of this was assessed using permutation tests. In addition, species richness of shrubs, resprouting proportions (total estimated sprouting ability in a site) and proportion of resprouting species were plotted as supplementary (passive) variables onto the CCA. This was done to test explicit models generated from the patterns of resprouting in the five habits in relation to theories on resprouting

Table 3 Environmental variables used for CCA and mean values for the five major habitat samples. All climate variables were modelled using BIOCLIM (Busby 1991). #Fire indices derived from environmental variables and climate variables; see Methods. *n* = number of sample sites in each habitat

Environmental variables	GW (<i>n</i> = 40)	DSF (<i>n</i> = 62)	RO (<i>n</i> = 35)	WH (<i>n</i> = 70)	WSF (<i>n</i> = 41)
Altitude (m)	1160	971	881	997	1033
Lithology					
Leucogranite	No	Yes	Yes	Yes	No
Porphyry	No	Yes	Yes	No	No
Metasediments	Yes	No	No	No	Yes
Basalt	Yes	No	No	No	No
Slope	3.8	5.1	4.5	0.8	5.6
Total nitrogen (%)	0.41	0.13	0.33	0.25	0.49
Total phosphorus (%)	0.077	0.016	0.032	0.012	0.049
Soil texture (index 1–5, clay–sand)	4.6	1.9	2.4	3.6	4.6
Time since fire (years)	29	12	24	15	24
Fine fuel cover (%)	7.7	28.0	22.3	76.5	59.7
Herbaceous over (%)	73.5	17.1	6.2	5.4	69.6
Canopy cover (%)	24.4	27.5	9.0	1.6	43.8
Ground fuel discontinuity (index 1–5)	1.37	2.45	4.51	1.07	1.14
Seasonality of temperature (annual cv)	1.66	1.73	1.74	1.61	1.56
Minimum temperature, coldest month (°C)	0.01	0.33	0.49	0.41	0.37
Precipitation seasonality (annual cv)	31.7	30.7	31.8	36.1	39.8
Precipitation (mm)	944	857	872	1032	1249
Annual radiation	17.8	18.0	18.0	17.6	16.9
Annual radiation seasonality (annual cv)	27.6	27.6	27.5	26.8	27.6
Mean annual moisture index	0.69	0.62	0.61	0.76	0.92
Mean annual moisture (annual cv)	18.5	22.0	22.7	15.6	10.2
Fire intensity index #	23.6	34.4	6.6	43.8	101.4
Fire frequency index #	33.5	56.8	25.7	36.4	25.5

GW, grassy woodland; DSF, dry sclerophyll forest; RO, rocky outcrop; WH, wet heath; WSF, wet sclerophyll forest; cv, coefficient of variation.

(see below). Analyses were repeated using congeners to test for congruence of patterns while controlling for phylogenetic bias, e.g. because rain forest shrubs are prominent in some wet sclerophyll forest sites.

MODELS

A set of explicit models and testable hypotheses were developed from the literature to explain patterns of resprouting among the five habitats (Table 4). The two paradigms used to explain selection for resprouting are elaborated in Clarke & Knox (2002): the first relates to frequency of disturbance (e.g. Morrison *et al.* 1995; Bond & Midgley 2001; Vesk & Westoby 2004) and the second to site productivity (e.g. Bellingham & Sparrow 2000; Pausas *et al.* 2004). The general null hypothesis, that proportion of resprouting is uniform through the landscape, was rejected in the habitat analyses. A subset of more explicit factors is proposed within each of the two general categories of explanation and specific models were developed as detailed in Table 4. Each has an explicit mechanism and a prediction that can be tested by CCA. Analyses were re-run for congener species to test if the outcome was robust with phylogenetic control.

Frequency of resprouting and frequency of resprouters was plotted onto the CCA and the direction and strength of the closest independent environmental variable was determined. For example, if fire frequency was proposed as an explanation for high levels of resprouting then this vector should be close to a plot of resprouting as a supplementary variable. Similarly, if soil fertility was proposed as an explanation for increased levels of resprouting in sites then soil P and soil N environmental vectors should correspond closely to a plot of resprouting as a supplementary variable. No attempt was made to examine the interactions of disturbance and productivity models due to the potentially large number of correlated models that could be generated.

Results

FLORISTICS

Data on the fire response of 296 taxa in 122 genera and 49 families were collected, of which 95 species occurred in more than one habitat. This represents about 80% of known woody taxa in the region. Grassy forest habitats had the lowest total number of woody taxa (53 spp.)

Table 4 Models explaining habitat differences in fire response of woody taxa occurring in five habitat types across the New England Bioregion in eastern Australia

Model	Mechanism	Model prediction	Tests	Results
<i>Disturbance models</i>				
(1) Fire frequency	Frequent fires inhibit seedling recruitment to maturity	Resprouting will be more frequent in landscapes with higher probabilities of frequent fire	CCA positive association of resprouting with fire frequency index/fuel discontinuity	Partial support
(2) Fire heterogeneity	Heterogeneous fires allow seedling recruitment to maturity	Resprouting will be more frequent in landscapes with higher probabilities of uniform fires	CCA positive association of resprouting with decreasing fuel continuity/landscape heterogeneity	Support
(3) Vertebrate herbivory	Increased herbivory inhibits seedling recruitment to maturity	Resprouting will be more frequent in landscapes with higher probabilities of herbivory	CCA positive association of resprouting with graminoid cover	No support
(4) Frost damage	Frost limits seedling recruitment to maturity	Resprouting will be more frequent in areas with coldest temperatures	CCA positive association of resprouting and minimum temperature of coldest month	No support
<i>Resource productivity models</i>				
(1) Soil fertility	Low soil fertility restricts growth of species that allocate resources in storage organs	Resprouting will be more frequent on soils that are more fertile	CCA positive association of resprouting with increasing soil nitrogen and phosphorus concentrations	Partial support
(2) Soil moisture	Soils that do not retain moisture close to the surface restrict growth of species that allocate resources in storage organs	Resprouting will be more frequent on soils that retain more moisture	CCA positive association of resprouting with decreasing soil texture/moisture index	Support
(3) Rainfall variability	More variable annual rainfall limits seedling recruitment to maturity	Resprouting will be more frequent in areas with more variable rainfall	CCA positive association of resprouting with CV rainfall	No support
(4) Habitat openness	Shade restricts seedling recruitment in post-fire environment	Resprouting will be more frequent in landscapes that have higher post-fire cover	CCA positive association of resprouting with increasing cover	Partial support
(5) Herbaceous competition	Competition from grasses restricts seedling recruitment in post-fire environment	Resprouting will be more frequent in landscapes that have higher herbaceous cover	CCA positive association of resprouting with graminoid cover	No support

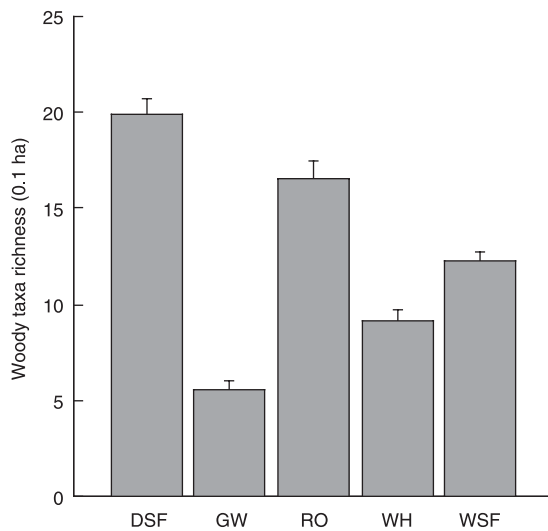


Fig. 1 Mean woody taxa richness (+ SE) (excluding eucalypts) among five habitats. DSF, dry sclerophyll forest; GW, grassy woodland; RO, rocky outcrops; WH, wet heath; WSF, wet sclerophyll forest. All pairwise contrasts are significantly different at $P < 0.001$.

whilst the dry sclerophyll forests had the highest woody species richness (167 spp.) followed by rocky outcrops (122 spp.) (Table 1). Scleromorphic shrubs in the families Fabaceae (74 spp.), Proteaceae (32 spp.), Epacridaceae (27 spp.), Myrtaceae (26 spp.) and Rutaceae (18 spp.) were represented in all habitats. Asteraceae shrub taxa (18 spp.) were, however, more common in the grassy landscape, whereas Proteaceae and Myrtaceae shrubs were species-rich in the DSF and heaths. Rutaceae and Lamiaceae taxa appear to be more species-rich in rocky outcrop habitats.

Shrubs and low shrubs were the most common woody plants throughout all habitats, although eucalypt trees were the dominant growth form in all habitats except the wet heaths. Non-eucalypt trees and small trees/shrubs (treelets) were more common in wet sclerophyll forests. Seed was the most common diaspore type in all habitats except the wet sclerophyll forest, where fleshy fruits were more common (Table 1). Single-stemmed growth forms were the most common in all habitats but were most prominent in rocky outcrops (Table 1).

SPECIES RICHNESS AND FIRE RESPONSE SYNDROMES

Species richness among habitats was significantly different ($F_{4,263} = 67.1$, $P < 0.0001$), including all pairwise habitat comparisons (Fig. 1). The highest species richness was in the dry sclerophyll forest sites followed by rocky outcrop, wet sclerophyll forest, wet heath and grassy forest sites (Fig. 1). These differences mean that only proportional data can be used for comparison between habitats for fire response traits as richness and resprouting richness were highly correlated ($r^2 = 0.93$), although the slopes of the relationships varied among habitats (Table 2).

The proportion of plants that resprouted varied between 0 and 100%, with less than 10% of species

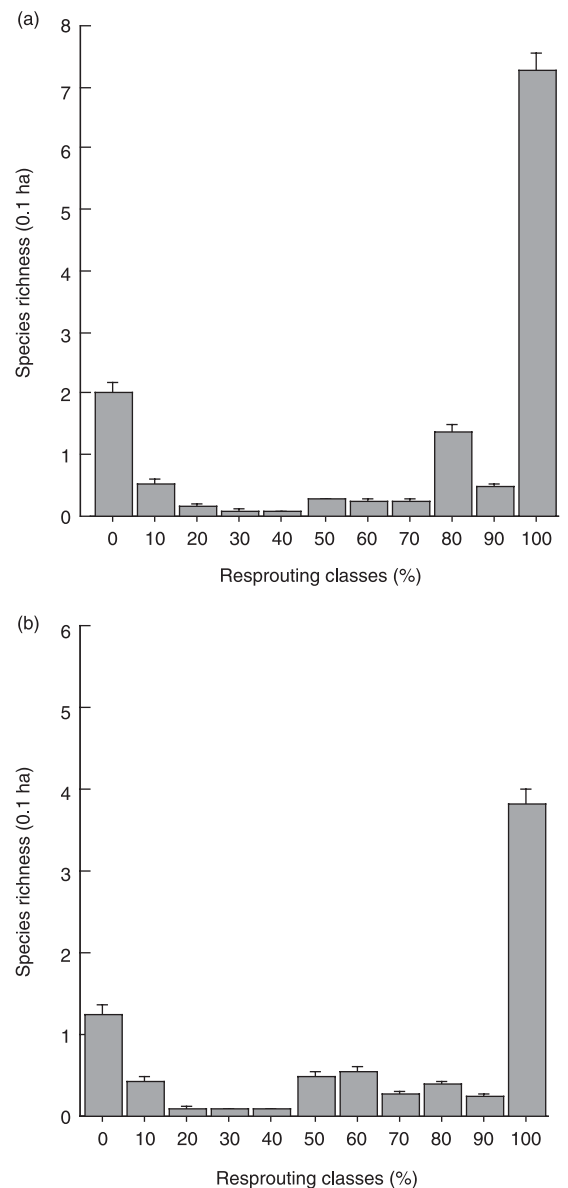


Fig. 2 Mean species richness (+ SE). (a) For each of eleven classes of resprouting for taxa encountered in 248 sample sites across all habitats. 100% indicates all individuals in a population resprouting and 0% no individuals in the population resprouting (i.e. obligate seeders). (b) For each of ten classes of resprouting for species in genera that were found in at least three of the five habitats across 248 sample sites.

showing variable responses (30–70% resprouts, 28 taxa) and the most frequent classes being 90–100% (142 taxa) and 0–10% (84 taxa) (Fig. 2a). The most common resprouting syndrome was from basal stem buds (176 spp.), followed by root suckers (16 spp.) and stem buds (5 spp.) (Table 2). For those species killed by fire, most had soil-stored seed banks (90 spp.) whilst only seven species killed by fire had canopy-stored seed banks (bradyspory) (Table 2). Pyrogenic flowering was uncommon, but bradyspory was more prominent, especially in the wet heath sites (Table 2). Fire-induced emergence of seedlings occurred in more than 60% of species and was particularly common for rocky outcrop species (Table 2).

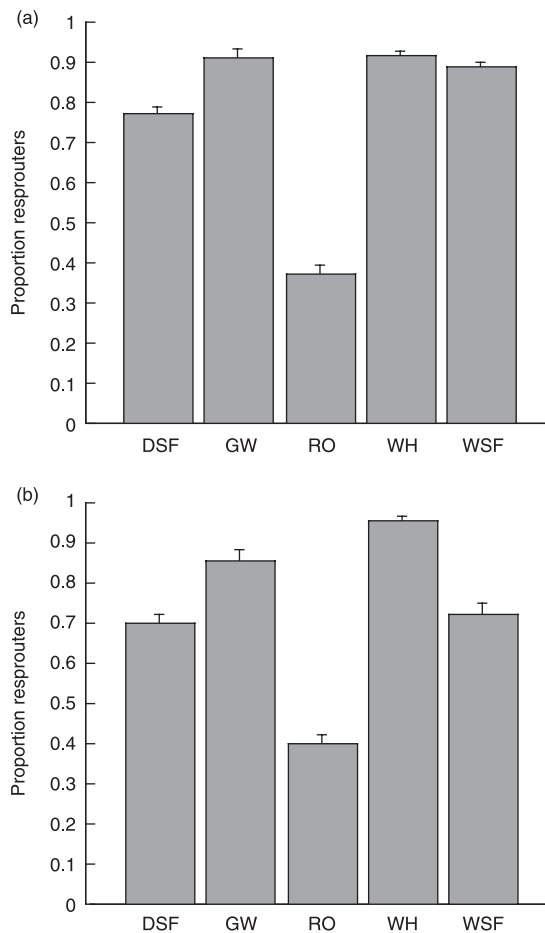


Fig. 3 Mean proportion of resprouting (population > 70%) for (a) all taxa found in sites across five habitats, (b) taxa in genera found in three or more habitats. DSF, dry sclerophyll forest; GW, grassy woodland; RO, rocky outcrop; WH, wet heath; WSF, wet sclerophyll forest. All pairwise contrasts significantly different, $P < 0.001$, except for GW vs. WH in (a).

The mean proportion of species resprouting (> 70% rule) in all sites was 0.80, whilst the total proportion of species in the data set was 0.60 resprouters, 0.30 obligate seeders and 0.10 variable (Table 2). Both the proportion of individuals that resprouted and the proportion of species classified as resprouters showed near identical patterns across habitats and hence only analyses of proportion of individuals resprouting will be presented. There were differences in the proportion of resprouting among habitats ($F_{4,243} = 123.1, P < 0.0001$), with the highest levels in grassy forests, followed by wet heath, wet sclerophyll forest, dry sclerophyll forest and rocky outcrops (Fig. 3a). Analysis of the proportion of individuals that resprout for congeners was also significant among habitats ($F_{4,243} = 97.1, P < 0.0001$), but a shift in the rank order (wet heaths > grassy forests > dry sclerophyll forests > wet sclerophyll forests > rocky outcrops; Fig. 3b) indicated an effect of phylogeny.

SITE ORDINATION AND ENVIRONMENTAL CORRESPONDENCE

Ordination of the sample sites using all woody taxa showed the distinct clustering of wet heath, wet sclero-

phyll forest and grassy woodlands, whilst rocky outcrop and dry sclerophyll forest sites had more overlap in composition. Constrained ordination using all woody plant taxa showed that the environmental variables were related to the first and second axes of a CCA (Table 5 and Fig. 4a). Overall, the highest marginal effects were associated with lithology factors followed by moisture index and cover; all factors were significant in a marginal effects model (Table 5). Although significant, factors associated with disturbance, such as fire, fuel continuity and minimum coldest temperature, were not ranked as high as factors associated with site productivity (Table 5 and Fig. 4a). Constrained ordination using only congeners produced a very similar biplot (Fig. 4b) and marginal effects were also very similar to the CCA with all species included.

Plots of the supplementary variables (frequency of resprouting, frequency of resprouters, obligate seeder richness and woody species richness) were strongly associated with several environmental variables (Fig. 4a,b). Species richness was negatively associated with increasing shrub cover, increasing annual precipitation and finer soil texture. Conversely, species richness and obligate seeding richness increased with fuel discontinuity, moisture and temperature seasonality. Both the frequency of resprouter species and proportion of resprouting were positively associated with soil texture, moisture index, annual precipitation and total cover in both full and congener species analyses (Fig. 4a,b).

MODELS

Fire frequency, temperature extremes and vertebrate herbivory (graminoid cover) did not correlate strongly with resprouting ability for the disturbance-based models (Fig. 4a,b and Table 4). However, fire heterogeneity (fuel discontinuity, slope) was strongly associated with decreasing proportions of resprouting (Fig. 4a,b and Table 4). Of the five resource (productivity)-based models, two were not supported by the CCA; neither rainfall variability nor graminoid cover was associated with resprouting (Fig. 4a,b and Table 4). The results for canopy openness were equivocal because shrub cover was positively associated with resprouting but tree cover was not. Two models, however, showed strong support, with both soil fertility / texture and soil moisture / texture showing strong association with increasing levels of resprouting (Fig. 4a,b and Table 4).

Discussion

A DICHOTOMY OF FIRE RESPONSE AT THE LANDSCAPE SCALE

Our results show that there is a continuum of response to crown fire in terms of the proportion of individuals that resprout from a large sample of 296 species. Nevertheless, the dichotomous classification of fire response of obligate seeders (< 30% resprout) and resprouters

Table 5 Result of ordinations by canonical correspondence analysis (CCA) for eigenvalues, species–environmental correlation coefficients and intraset correlations of environmental variables with the first two axes of CCA

	Axis 1	Axis 2	Marginal effects lambda	Conditional effects
Eigenvalues	0.84	0.65		
Correlation coefficients	0.97	0.93		
Gradient length	7.2	4.6		
Species environmental coefficients				
Altitude	0.23	0.15	0.34	0.18**
Leucogranite	–0.60	0.23	0.53	0.10**
Acid volcanics	–0.20	–0.09	0.32	0.28**
Metasediments	0.79	–0.14	0.67	0.67**
Basalt	0.21	–0.11	0.42	0.45**
Slope	0.09	–0.38	0.23	0.09 NS
Total nitrogen	0.35	–0.03	0.24	0.13**
Total phosphorus	0.32	–0.23	0.24	0.10*
Soil texture	0.60	0.27	0.49	0.11**
Time since fire	0.28	–0.13	0.31	0.19**
Shrub cover	0.32	0.70	0.51	0.49**
Graminoid cover	0.06	–0.27	0.37	0.18**
Canopy cover	0.62	–0.43	0.57	0.29**
Total cover	0.58	0.17	0.45	0.18**
Fuel discontinuity	–0.39	–0.44	0.49	0.32**
Seasonality of temperature	–0.62	–0.49	0.60	0.32**
Minimum temperature coldest month	–0.19	0.05	0.3	0.25**
Precipitation (mm)	0.69	0.28	0.55	0.17**
Annual radiation	–0.74	–0.27	0.61	0.26**
Annul radiation seasonality	0.06	–0.47	0.32	0.10**
Mean annual moisture index	0.71	0.36	0.62	0.23**
Mean annual moist seasonality	–0.68	–0.36	0.59	0.23**
Fire frequency index	–0.28	–0.15	0.28	0.14**

** $P < 0.01$; NS, not significant, Monte-Carlo permutation tests.

(> 70% resprout) is a useful generalization in the study region because less than 10% of all recorded species displayed a variable response to crown fire. This finding is consistent with the results of Vesk *et al.* (2004), who found that a dichotomy of ‘weak’ and ‘strong’ sprouters provided the best statistical fit to classification models.

Comparisons of the proportions of resprouting with regional floras are problematic because we have focused on woody taxa and about 10% of our species are classified as having a variable response. As a region, the proportion of resprouting (80% of woody species even when eucalypts, which are all resprouters are excluded) appears to be high compared with Mediterranean-type climate regions (Bell 2001; Vesk & Westoby 2004). Within plant families there also appears to be a much higher proportion of species that resprout compared with Mediterranean-type climate regions, e.g. 59 cf. 25% in Epacridaceae, 66 cf. 50% Proteaceae (Bell 2001). The general paucity of obligate seeders across this fire-prone landscape suggests that risks of post-fire recruitment are much higher in temperate sclerophyll communities, where there is no pronounced rainfall season, than in Mediterranean-type communities.

ARE PATTERNS OF RESPROUTING INDEPENDENT OF PHYLOGENY?

An important question arising from comparisons of resprouting among habitats was the degree to which

this pattern is a result of convergent traits among different phylogenetic lineages. Within genera and families with high species richness there was a mixture of resprouting responses that is consistent with the clade analyses of Vesk & Westoby (2004) showing that sprouting ability is a highly labile trait. Nevertheless, some phylogenetic bias was detected by comparing results for all species and for congeners. Most habitats revealed similar proportions of resprouting, although there was a marked decrease in the wet sclerophyll forest. This can be attributed to the large number of mesomorphic (mesophyllous leaf type) rainforest taxa found in the understorey of the wet sclerophyll forest (see Table 1), e.g. Lauraceae where most taxa resprout following disturbance (Vesk & Westoby 2004). The resprouting response of genera and families that are mostly restricted to the rainforest habitats may arise from selection from canopy disturbance by windthrow rather than fire.

DO HABITATS SHOW DIFFERENT FUNCTIONAL RESPONSES?

In all habitats there was a mixture of resprouting species and those killed by fire, although resprouters were more common. Both the proportion of resprouting species and the proportion of resprouting in our sites showed distinct differences among habitats, which is

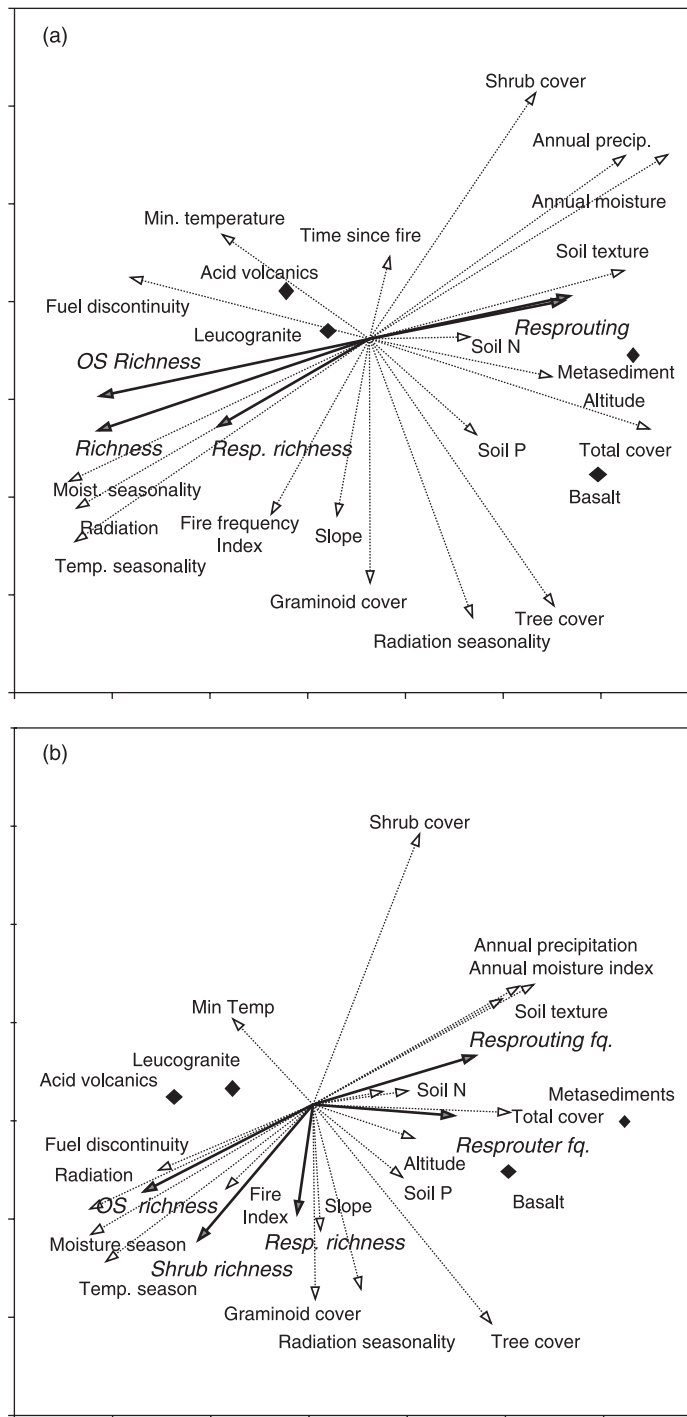


Fig. 4 Biplot diagrams of CCA ordinations for environmental variables, with supplementary variables as solid lines for (a) all woody taxa, (b) congener taxa. All plot axes are 1 by 1 units of ordination. Categorical variables shown as diamonds. Resprouting fq. variable is the proportion of individuals in a sample that resprout; resprouter fq. is the proportion of species classified as resprouters (> 70% resprout); OS variable is the proportion of species classified as obligate seeders (< 30% resprout).

consistent with previous regional studies where total numbers of resprouting species were compared among habitats (Clarke & Knox 2002; Clarke 2002a,b). Shrub species on rocky outcrops had a much lower proportion of resprouters than the other habitats, agreeing, in part, with Keeley (1977), Myerscough *et al.* (1995), Benwell (1998), Bell (2001) and Clarke (2002a,b) who found a higher proportion of obligate seeder shrubs in

more open habitats in chaparral and in dry heaths. Overall, most species resprout from basal stem tissue, which suggests that moderate frequencies of fire have been a selective force (Bellingham & Sparrow 2000). Higher levels of root suckering in the wet sclerophyll forest possibly reflect selection for site occupancy after disturbance events associated with treefall (Bellingham & Sparrow 2000).

WHICH MODELS BEST EXPLAIN LANDSCAPE
PATTERN OF SPROUTING?

Links between life-history traits and the selective regime of fire have focused on small-scale spatial patterns (e.g. Keeley 1977; Bond *et al.* 1988; Benwell 1998) and biogeographical patterns (e.g. Lamont & Markey 1995; Ojeda 1998) but rarely do they contrast habitat differences at a regional scale within a climatic region. Clarke & Knox (2002) generated two broad models that explain habitat differences in resprouting but had no explicit test for these models as they simply compared lists of species in different habitats. The explanatory models we have generated and tested are similar and involve disturbance frequency (see Bellingham & Sparrow 2000) or resource/productivity models elaborated in Table 4.

Disturbance frequency models have been invoked to explain patterns of resprouting both at local and landscape scales (Morrison *et al.* 1995; Bellingham & Sparrow 2000; Bell 2001; Clarke & Knox 2002; Clarke 2002a,b). We found little evidence to support these models across whole landscapes in our analyses using cold temperatures (frost disturbance), fire frequency index or graminoid cover (herbivory) as surrogate indices for disturbance frequency. This pattern was not consistent with the biogeographical model of Bellingham & Sparrow (2000), who predicted that increasing disturbance frequency in woody plants would strongly correlate with allocation to resprouting. At local scales, however, fire frequency appears to affect proportions of resprouters, especially on rocky outcrops, as there was a strong negative association of resprouting and fuel discontinuity in the CCA. This is related to the effect of isolation from fires (low frequency of fires) in rocky habitats as high fire frequency has been shown to eliminate obligate seeding species in dry sclerophyll forests (Morrison *et al.* 1995; Keith 1996; Clarke & Knox 2002; Clarke 2002a,b). Our data also show the highest proportion of bradysporous, obligate seeding, species in rocky outcrops, further supporting the local importance of disturbance frequency for species that cannot spread their recruitment risk via a dormant seed bank and are reliant on a long fire-free period to reach maturity. Overall, disturbance frequency appears to affect only the lower resource environments in our landscape and had little effect on resprouting in the more productive sites (grassy woodlands and wet sclerophyll forests) (Fig. 5). Better histories of disturbance and manipulative experiments are, however, required to test this model and the interactive effects of fire heterogeneity, frequency and intensity.

In environments with more variable climates, allocation to persistence (resprouting) may be favoured over seedling recruitment as the risks of seedling failure are higher (the 'environmental variance' model of Higgins *et al.* 2000; Bond & Midgley 2001). Evidence supporting this model comes from Mediterranean-type climates where resprouters in the genera *Banksia* and *Erica*

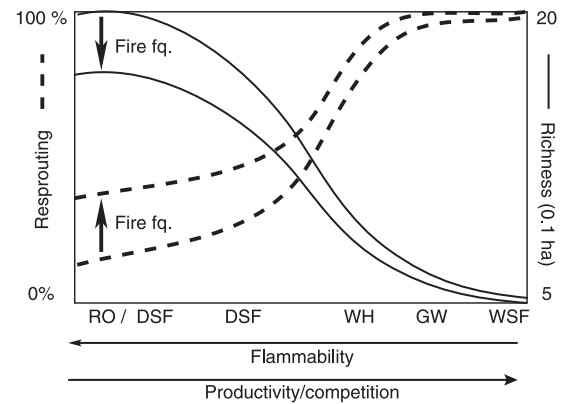


Fig. 5 Schematic model of the relationship between % of resprouting of woody taxa in a site (0 to 100%) and richness of woody taxa in a site (0.1 ha) in relation to the productivity and flammability gradient (products of climate, soil fertility, habitat heterogeneity) that represents the probability of a plant being burnt in a fire. The effect of fire frequency is greater on both attributes at the lower end of the productivity gradient, as shown by broader confidence limits. Position of broad community types may vary according to specific site variables. GW, grassy woodland; DSF, dry sclerophyll forest; RO, rocky outcrop; WH, wet heath; WSF, wet sclerophyll forest.

are more widespread than their obligate seeder congeners (Lamont & Markey 1995; Ojeda 1998). We found no evidence to support the environmental variance model using climate indices and, contrary to its predictions, we found that increased predictability in the annual moisture index was associated with increased proportions of resprouters. Our pattern is, however, consistent with landscape patterns in Western Australia and in California, where there is a decreasing proportion of resprouters in more arid environments (Bell 2001). In areas with more variable or lower rainfall, however, groundcover also decreases (see Fig. 4), hence competitive interactions with cover may also be important.

More open habitats may promote seeders through the availability of open spaces where competition from resprouters is less (Keeley 1977; Myerscough *et al.* 1995). In habitats with bare ground, post-fire gap sizes may be expected to be large and hence recruitment of seeders is enhanced (Carrington & Keeley 1999; Enright & Goldblum 1999). This model also explains why grassy forests and wet heaths have few obligate seeders, as these habitats have a ground stratum dominated by grasses or graminoids that tend to close gaps rapidly in the post-fire environment. Similarly, in the wet heaths and wet sclerophyll forests there is rapid post-fire shrub canopy closure favouring resprouter persistence over recruitment from seedlings. This model was supported by increasing shrub cover being correlated with resprouting and increased habitat openness (fuel discontinuity) with increased obligate seeder richness, but there was little support for the role of either ground layer or tree canopy cover.

A number of studies have found seeders to be more dominant on poorer soils, while resprouters appear to be more common on more fertile soils (e.g. Lamont &

Markey 1995; Wisheu *et al.* 2000). This pattern was partially supported by our analyses as total nitrogen levels in the soil tended to be associated with increasing levels of resprouting. However, the nutrient status of soils and their texture are not independent as the low nutrient lithosol and podsols (rock outcrops and shrubby forests) also have a sandy, well-drained texture. Conversely, the grassy forests, wet heath and wet sclerophyll forest soils have a higher nutrient status but have finer textured soils with greater moisture-holding capacity. Lamont & Markey (1995) proposed that nutrient status did not drive these patterns as such, but the physical properties of soils influenced competitive abilities by favouring shallow rooted resprouters on fine textured soils. These findings are consistent with our CCA analyses where finer textured soils were associated with increasing levels of resprouting. In their study, the poorly structured soils (deep sands) stored more accessible water than the more fertile soils (lateritic soils). Hence sandy soils will favour the growth of obligate seeders when moisture is limiting or variable and where disturbance frequencies are intermediate. Both soil depth and drought also influenced the resprouting ability of *Erica* species rather than frequency of fire (Lloret & Lopez-Soria 1993).

Finally, no attempt was made to examine the interactive effects of disturbance frequency and site productivity in the models. Such interactions are likely given the relationship between flammability and productivity but were not formally explored due the large number of potentially correlated variables and the use of indirect measures of disturbance rather than direct measures.

Conclusion

Our results suggest that soil texture, rainfall, nutrient status of the soils and fuel continuity interact to influence the ability of resprouters and obligate seeders to coexist (Fig. 5). Coexistence appears to be driven by competitive interactions across flammability gradients where resprouters become dominant in physiognomically dissimilar habitats (wet heath, grassy forests and wet sclerophyll forests). This can be explained by a resource-competition model where resprouting is favoured in environments having strong competition (high moisture index and/or fertile soils) irrespective of fire frequency (Fig. 5). In moist fertile soils, resprouters allocate to storage by reserve formation, whereas obligate seeders lack this ability (Bell 2001; Knox & Clarke 2005). Conversely, in habitats with moisture seasonality and well-drained soils of low fertility (dry sclerophyll forests and rocky outcrops) seedling recruitment is favoured because competition with surrounding vegetation is reduced. In low productivity environments frequent fires could eliminate obligate seeders if they did not have fire refugia. This explains why obligate seeding species are more common in rocky outcrops than in surrounding dry sclerophyll forests. We predict that disturbance

frequency has larger effects on species richness and obligate seeder richness at the low end of the productivity gradient than at the high end (Fig. 5). At the highest end of the productivity gradient fire frequency is lower and the influence of disturbance frequencies on obligate seeder abundances may be less. These interactive effects of disturbance and resource/productivity on recruitment success require testing in controlled manipulative experiments.

Acknowledgements

We thank the Armidale and Glen Innes offices of the New South Wales National Parks and Wildlife Service for their assistance in burning. We thank Peter Vesk, Peter Bellingham and William Bond for comments on the research. Financial support was provided to KJEK, KEW and MC by Australian Post-graduate Awards, NCW Beadle awards and by the NSW National Parks and Wildlife Service. Funding for PJC was provided by the University of New England. Lachlan Copeland, Catherine Nano and Ian Telford assisted with the collection, identification and nomenclature of the plant taxa.

References

- Bell, D.T. (2001) Ecological response syndromes in the flora of southwestern Western Australia: fire resprouters versus reseeders. *Botanical Review*, **67**, 417–440.
- Bellingham, P.J. & Sparrow, A.D. (2000) Resprouting as a life history strategy in woody plant communities. *Oikos*, **89**, 409–416.
- Benson, J.S. & Ashby, E.M. (2000) Vegetation of the Guyra 1: 100 000 map sheet New England Bioregion, New South Wales. *Cunninghamia*, **6**, 747–872.
- Benwell, A.S. (1998) Post-fire seedling recruitment in coastal heathland in relation to regeneration strategy and habitat. *Australian Journal of Botany*, **46**, 75–101.
- Bond, W.J. & Midgley, J.J. (2001) Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology and Evolution*, **16**, 45–51.
- Bond, W.J., Midgley, J.J. & Vlok, J. (1988) When is an island not an island? Insular effects and their causes in fynbos shrublands. *Oecologia*, **77**, 515–521.
- Bond, W.J. & van Wilgen, B.J.F. (1996) *Fire and Plants*. Chapman & Hall, London.
- ter Braak, C.J.F. & Prentice, I.C. (1989) A theory of gradient analysis. *Advanced Ecological Research*, **18**, 272–317.
- ter Braak, C.J.F. & Smilauer, P. (1998) *CANOCO 4.0. Reference Manual and Users Guide to Canoco for Windows*. Centre for Biometry, Wageningen, Netherlands.
- Bradstock, R.A., Bedward, M., Kenny, B.J. & Scott, J. (1998) Spatially-explicit simulation of the effect of prescribed burning on fire regime and plant extinctions in shrublands typical of south-eastern Australia. *Biological Conservation*, **86**, 83–95.
- Bradstock, R.A. & Kenny, B.J. (2003) An application of plant functional types to fire management in a conservation reserve in southeastern Australia. *Journal of Vegetation Science*, **14**, 345–354.
- Busby, J.R. (1991) Bioclim: a bioclimate analysis and prediction system. *Plant Protection Quarterly*, **6**, 6–9.
- Carrington, M.E. & Keeley, J.E. (1999) Comparison of post-fire establishment between communities in Mediterranean and non-Mediterranean climate ecosystems. *Journal of Ecology*, **87**, 1025–1036.

- Clarke, P.J. (2002a) Habitat insularity and fire response traits: evidence from a sclerophyll archipelago. *Oecologia*, **132**, 582–591.
- Clarke, P.J. (2002b) Habitat islands in fire prone vegetation: evidence for floristic and functional insularity in Australian vegetation. *Journal of Biogeography*, **29**, 677–684.
- Clarke, P.J. & Knox, K.J.E. (2002) Post-fire response of shrubs in the tablelands of eastern Australia: do existing models explain habitat differences? *Australian Journal of Botany*, **50**, 53–62.
- Enright, N.J. & Goldblum, D. (1999) Demography of a non-sprouting and resprouting *Hakea* species (Proteaceae) in fire-prone *Eucalyptus* woodlands of southeastern Australia in relation to stand age drought and disease. *Plant Ecology*, **144**, 71–82.
- Franklin, J., Syphard, A.D., Mladenoff, D.J., He, H.S., Simons, D.K., Martin, R.P. *et al.* (2001) Simulating the effects of different fire regimes on plant functional groups in Southern California. *Ecological Modelling*, **142**, 261–283.
- Gill, A.M. & Bradstock, R.A. (1992) A national register for the fire response of plant species. *Cunninghamia*, **2**, 653–660.
- Higgins, S.I., Pickett, S.T.A. & Bond, W.J. (2000) Predicting extinction risk for plants: environmental stochasticity can save declining populations. *Trends in Ecology and Evolution*, **15**, 516–520.
- Hunter, J.T. & Clarke, P.J. (1998) The vegetation of granitic outcrop communities on the New England batholith of eastern Australia. *Cunninghamia*, **5**, 547–618.
- Keeley, J.E. (1977) Seed production seed populations in soil and seedling production after fire for two congeneric pairs of sprouting and non-sprouting chaparral shrubs. *Ecology*, **58**, 820–829.
- Keith, D.A. (1996) Fire-driven extinction of plant populations: a synthesis of theory and review of the evidence from Australian vegetation. *Proceedings of the Linnean Society of New South Wales*, **116**, 37–78.
- Knox, K.J.E. & Clarke, P.J. (2005) Nutrient availability induces contrasting allocation and starch formation in resprouting and obligate seeding shrubs. *Functional Ecology*, in press.
- Lamont, B.B. & Markey, A. (1995) Biogeography of fire-killed and resprouting *Banksia* species in south-western Australia. *Australian Journal of Botany*, **43**, 283–303.
- Lavorel, S., McIntyre, S., Landsberg, J. & Forbes, T.D.A. (1997) Plant functional classifications; from general groups to specific groups based on response to disturbance. *Trends in Ecology and Evolution*, **12**, 474–478.
- Lloret, F. & Lopez-Soria, L. (1993) Resprouting of *Erica multiflora* after experimental fire treatments. *Journal of Vegetation Science*, **4**, 367–374.
- Mabry, C., Ackerly, D. & Gerhardt, F. (2000) Landscape and species-level distribution of morphological and life history traits in a temperate woodland flora. *Journal of Vegetation Science*, **11**, 213–224.
- McIntyre, S., Lavorel, S. & Tremont, R.M. (1995) Plant life-history attributes – their relationship to disturbance responses in herbaceous vegetation. *Journal of Ecology*, **83**, 31–44.
- Morrison, D.A., Cary, G.J., Pengelly, S.M., Ross, D.G., Mullins, B.J., Thomas, C.R. *et al.* (1995) Effects of fire frequency on plant species composition of sandstone communities in the Sydney region: inter-fire interval and time-since-fire. *Australian Journal of Ecology*, **20**, 239–247.
- Myerscough, P.J., Clarke, P.J. & Skelton, N. (1995) Plant coexistence in coastal heaths: floristic patterns and species attributes. *Australian Journal of Ecology*, **20**, 482–493.
- Noble, I.R. & Gitay, H. (1996) A functional classification for predicting the dynamics of landscapes. *Journal of Vegetation Science*, **7**, 329–336.
- Ojeda, F. (1998) Biogeography of seeder and resprouter *Erica* species in the Cape Floristic Region: where are the resprouters? *Biology Journal of the Linnean Society*, **63**, 331–347.
- Pausas, J.G. (1999) Mediterranean vegetation dynamics: modelling problems and functional types. *Plant Ecology*, **140**, 27–39.
- Pausas, J.G., Bradstock, R.A., Keith, D.A. & Keeley, J.E. (2004) Plant functional traits in relation to fire in crown-fire ecosystems. *Ecology*, **85**, 1085–1100.
- Thackway, R. & Cresswell, I. (1995) *An Interim Biogeographic Regionalisation for Australia: a Framework for Establishing the National System of Reserves*, Version 4.0. Australian Nature Conservation Agency, Canberra.
- Valiente-Banuet, A., Flores-Hernandez, N., Verdu, M. & Davila, P. (1998) The chaparral vegetation in Mexico under non-Mediterranean climate: the convergence and Madrean-Tethyan hypothesis reconsidered. *American Journal of Botany*, **85**, 1398–1408.
- Verheyen, K., Honnay, O., Motzkin, G., Hermy, M. & Forester, D.R. (2003) Response of forest plant species to land-use change: a life-history trait-based approach. *Journal of Ecology*, **91**, 563–577.
- Vesk, P.A., Warton, D.I. & Westoby, M. (2004) Sprouting by semi-arid plants: testing the dichotomy and predictive traits. *Oikos*, **107**, 72–89.
- Vesk, P.A. & Westoby, M. (2004) Global patterns of sprouting ability; can all plant species be divided into sprouters and non-sprouters? *Journal of Ecology*, **92**, 310–320.
- Whelan, R.J. (1995) *Ecology of Fire*. Cambridge University Press, Cambridge.
- Williams, P.R. & Clarke, P.J. (1997) Habitat segregation by serotinous shrubs in heaths: post-fire emergence and seedling survival. *Australian Journal of Botany*, **45**, 31–39.
- Wisheu, I.C., Rosenzweig, M.L., Olsvig-Whittaker, L. & Shmida, A. (2000) What makes nutrient-poor Mediterranean heathlands so rich in plant diversity? *Evolutionary Ecology Research*, **2**, 935–955.

Received 10 March 2004

revision accepted 10 November 2004

Handling Editor: Paul Adam