

Burnt to blazes: landscape fires, resilience and habitat interaction in frequently burnt coastal heath

Peter J. Myerscough^A and Peter J. Clarke^B

^AInstitute of Wildlife Research, School of Biological Sciences, The University of Sydney, Sydney, NSW 2006, Australia. Corresponding author. Email: pmyersco@bio.usyd.edu.au

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

Abstract. Four fires burned vegetation on a sand plain on a 4-km stretch of Pleistocene beach ridges between 1980–1981 and 1998. Fires of 1980–81 and 1991 burned the whole area. Those of 1994 and 1998 burned only parts of it. Cover of individual species and bare ground was scored on permanent plots at intervals between 1990 and 1996. Ordination and generalised linear model analysis of the data showed strong spatial variation between dry and wet heaths, four transects and plots within transects. This was strictly conserved through time, owing to the rapid regrowth of abundant resprouting species, most of which, after 1 year, showed little change in cover with increasing time-since-fire. Vegetation of the dry and wet heaths showed no detectable convergence or divergence in similarity with time-since-fire or variation of interval between fires. Changes with time-since-fire were found, and some change with the length of fire interval, owing to variation in cover of obligate-seeder species, which increased steadily with time up to 10 years since fire, and showed some decrease when fire interval decreased to 3.75 years. At 10 years since fire, obligate-seeder species reached ~25% of the totalled cover scores for all species, with 75% from resprouting species. Dry and wet heath were broadly similar in their general pattern of regrowth after fire, but in dry heath bare ground was more slowly covered than in wet heath, and wet heath had a higher cover of monocotyledons, especially restiads and sedges. Wet heath was more flammable than dry heath in the patchy fire of 1998. The heaths observed appeared highly resilient to recent fire regimes. Resprouting species always dominated their canopy; none of their obligate-seeding species formed a dominant overstorey canopy.

Introduction

Various aspects of landscape fires in Australia have been modelled by Bradstock *et al.* (1996, 1998), Marsden-Smedley and Catchpole (1995a, 1995b, 2001), Marsden-Smedley *et al.* (2001), Catchpole (2002) and McCarthy and Cary (2002). Regimes of fires across landscapes include components of fire frequency, fire intensity, fire season and type of fuel consumed (Gill 1975), as well as patchiness of areas burnt in it (Bradstock *et al.* 1998). After fire, vegetation in most sclerophyllous landscapes normally regrows and changes with time (Gill 1999). The number of vascular plant species in the cover of most communities rises soon after fire but then decreases through time (Gill 1999). With adequate rainfall for growth in the first 2 years after fire, seedlings are often abundant (e.g. Purdie 1977; Benwell 1998; Keith *et al.* 2002), and foliage from both seedlings and vegetative organs that survive fire begins to cover bare ground. As time-since-fire increases, cover of the leaf canopy usually increases towards a maximum and relative abundances of species change in it (e.g. Specht *et al.* 1958) and often species richness decreases (Gill 1999). In many habitats, the leaf canopy is dominated soon after fire by species with vegetative organs that survive fire and from which new shoots sprout after fire (resprouters). In some habitats, the canopy is later dominated by species that only regrow as seedlings after fire (obligate seeders). For instance, this may be so in some

heaths and related vegetation in the Sydney region where the tall-growing obligate-seeder shrub *Banksia ericifolia* is abundant (Siddiqi *et al.* 1976; Morris and Myerscough 1983, 1988; Nieuwenhuis 1987; Bradstock and O'Connell 1988; Keith and Bradstock 1994; Bradstock *et al.* 1997), and in other habitats, such as some wet sclerophyll forests where obligate-seeder trees such as *Eucalyptus regnans* F.Muell. come to dominate the leaf canopy (Ashton 1976). In dry sclerophyll forests, the leaf canopy does not switch from an early dominance by resprouters to later dominance by obligate seeders, although in most of them some increase in cover of obligate seeders relative to that of resprouters would be expected at some time after fire (Cary and Morrison 1995). Whether there is a switch in dominance of the leaf canopy from resprouters to obligate seeders with time-since-fire may depend on fire frequency.

Fires recurring at high frequency eliminate some populations of obligate-seeder species (Keith 1996), especially those whose seed bank is entirely held in fire-resistant fruit retained in the canopy of mature plants which are themselves killed by intense fire, though some of these plants may survive fires of low intensity (Morrison 1995; Morrison and Renwick 2000). After intense fire, populations of these obligate-seeder species with bradysporous fruits regenerate only from seeds released from the fire-resistant fruit which open after being heated during fire. Their populations are eliminated when successive fires occur

at intensities sufficient to kill the adult plants and at intervals less than the time taken for a seedling to become a seed-bearing mature plant, as Siddiqi *et al.* (1976) and Bradstock and O'Connell (1988) showed in some areas of the Sydney region.

In dry and wet heaths of the Pleistocene dune ridges of Myall lakes, obligate-seeder bradysporous species are almost entirely absent (Myerscough *et al.* 1995); however, they occur elsewhere in coastal shrublands in New South Wales on parts of Holocene beach ridges further south in the Fens embayment in Myall Lakes area (Clements 1988), in Keith's (2004) Sydney Coastal Heaths (Siddiqi *et al.* 1972, 1976) and in some types of heath described by Griffith *et al.* (2003) on the northern coast of New South Wales. Although the effects of high frequency of fire are often clear-cut in populations of bradysporous obligate-seeder plants, high fire frequency can also lower populations of obligate-seeder plants with seed banks in the soil (Cary and Morrison 1995; Keith 1995; Morrison *et al.* 1995; Bradstock *et al.* 1997) and severely deplete their seed banks (Meney *et al.* 1994; Auld and Scott 1997). Similarly, frequent fires with short intervals may result in the exhaustion of buds or carbohydrate reserves of resprouting species, resulting in loss of vigour, reduced reproduction or elevated mortality for those species (Bradstock and Myerscough 1988; Zammit 1988; Knox and Clarke 2006).

This study on heaths in the Myall Lakes area reports patterns in the vegetation in relation to four fires that occurred over a period of nearly two decades. Fox (1982, 1983), Fox and Fox (1987) and Monamy and Fox (2000) have shown how abundances of mammals in the area are related to fires and variation in habitat. Observations described here covered a distance of about 4 km and a range of habitat (Myerscough *et al.* 1995) on podsolised sand of low relief and nutrient status (Myerscough and Carolin 1986). The sand had been laid down as a plain of low beach ridges in the Pleistocene (Thom *et al.* 1992). Such Pleistocene sand plains form part of the coastal lowlands in northern New South Wales and southern Queensland, often termed 'wallum' (Coaldrake 1961; Griffith *et al.* 2003), although, as Griffith *et al.* (2003) pointed out, wallum is often used more narrowly to refer to the sand plains only. On sand plains, vegetation varies with depth to the water table. On the Pleistocene sand plain in the Eurunderee embayment of the Myall Lakes area, Carolin (1970) and Myerscough and Carolin (1986) showed that dry heath characteristically occurred on the crests of the ridges, wet heath on their slopes and swamp in the most waterlogged situations of their swales. The study by Myerscough *et al.* (1995, 1996) and Clarke *et al.* (1996) investigated mechanisms that may partition species between dry heath on the ridges and wet heath on the slopes. Dry heath of the ridges falls into Keith's (2004) class of Wallum Sand Heaths and wet heath of the slopes into his class of Coastal Heath Swamps. The work described in this paper used sites set up in dry and wet heaths by Myerscough *et al.* (1995). The terms dry heath and wet heath are retained here to refer, respectively, to each sort of heath and its habitat. Wet heath differs from dry heath in species composition and has a greater abundance of restiads and sedges. Because of this, after fire, its understorey can be expected to form a flammable fuel bed more quickly than that of dry heath. Consequently, fires may propagate more readily across the landscape on the slopes and swales than on the ridges.

Thus, to understand patterns of fire across the landscape, it is necessary to know how the vegetation of dry and wet heaths change after fire.

Frequency of fires and time since the last fire affect the species composition and structure of fire-prone vegetation. In this study, following marked quadrats through time and differing fire regimes, it was not only possible to follow changes of vegetation through time since the last fire but also to assess to some extent effects of differing fire frequencies on the vegetation at similar times since fire. We asked whether (1) changes after fire in dry heath are similar to those in wet heath, (2) fire frequency affects wet and dry heaths similarly, (3) the landscape is likely to burn uniformly on all occasions, or the spread of fire across it sometimes is dependent on habitat, and (4) the features and probable fire history of dry heath and wet heath observed in the Eurunderee Embayment are unique or are likely to occur elsewhere.

Beside addressing these questions, the study provided some preliminary data on the responses to fire of two species of bryophyte in the heaths, as well as extending data on the post-fire flowering of some angiosperms already published, in particular by Benson and McDougall (1995, 1997, 1998, 1999, 2001, 2002, 2005).

Materials and methods

Study area

The area studied was at Myall Lakes on the coast of New South Wales where the pattern of vegetation has previously been described (see Myerscough *et al.* 1995). It is in the Eurunderee embayment on the extensive sand plain of the Pleistocene beach ridge system, the differentiated Inner barrier system of Thom *et al.* (1992), known locally as the Moors. The Moors are somewhat sheltered from onshore winds by the much higher Holocene parabolic dunes of the Outer barrier, from which they are somewhat separated by the Inter-barrier lagoon system, but, inland, low-lying Pleistocene parabolic dunes link them to sandy parts of the shores of Myall and Boolambayte Lakes. Local tradition is that fires on the Moors are more frequent and often more intense than in the higher, more steeply sloping dunes of the Outer Barrier (Myerscough and Carolin 1986). Since the early 1970s the mining road built along the seaward edge of the Moors has allowed some control of fires running between most of the Moors and their most seaward parts. Heath covers much of the ridges and slopes of the Moors, although the ridges closer to the lake shores carry trees (see the vegetation map in Myerscough and Carolin 1986).

Sampling

The same four transects whose approximate locations are given in fig. 1 of Myerscough *et al.* (1995) were used in this study. The transects traverse ridges and swales of the Moors. Of the 24 plots of Myerscough *et al.* (1995), 16 were sampled in this study, eight on ridges and eight on slopes (Table 1). All six plots of the southernmost transect (T1) and all six plots of the northernmost transect (T4) were sampled. On each of the central transects (T2 and T3), only two plots were sampled; on each, the other four plots were used in experiments previously described (Clarke *et al.* 1996; Myerscough *et al.* 1996), and consequently, were

Table 1. Sample plot locations in relation to ridge position relative to coastline, habitat, time-since-fire (years) and fire frequency (FF)
DH, dry heaths; WH, wet heaths

Plot	Lat., long. (GDA) 32°S, 152°E	Transect	Ridge	Habitat	Time-since-fire (years)				FF
					1990	1994	1995	1996	
1	29.886'S ^A , 20.803'E	T1	Near	WH	10	3.7	1.1	2	2
2	29.811'S, 20.767'E	T1	Mid	WH	10	3.7	1.1	2	2
3	29.731'S, 20.704'E	T1	Far	WH	10	3.7	1.1	2	2
4	29.858'S ^A , 20.788'E	T1	Near	DH	10	3.7	1.1	2	2
5	29.766'S, 20.727'E	T1	Mid	DH	10	3.7	1.1	2	2
6	29.714'S, 20.695'E	T1	Far	DH	10	3.7	1.1	2	2
7	29.611'S ^A , 21.053'E	T2	Mid	WH	10	3.7	4.8	5.7	1
8	29.697'S, 21.126'E	T2	Near	DH	10	3.7	4.8	5.7	1
9	28.975'S ^A , 22.101'E	T3	Far	DH	10	3.7	4.8	5.7	1
10	29.014'S ^A , 22.136'E	T3	Far	WH	10	3.7	4.8	5.7	1
11	28.970'S, 22.944'E	T4	Near	WH	10	3.7	4.8	5.7	1
12	28.887'S ^A , 22.902'E	T4	Mid	WH	10	3.7	4.8	5.7	1
13	28.774'S, 22.910'E	T4	Far	WH	10	3.7	4.8	5.7	1
14	28.919'S, 22.936'E	T4	Near	DH	10	3.7	4.8	5.7	1
15	28.845'S, 22.922'E	T4	Mid	DH	10	3.7	4.8	5.7	1
16	28.762'S, 22.898'E	T4	Far	DH	10	3.7	4.8	5.7	1

^A30 × 5 m plot extends to left of marker post when facing inland; other plots extend to right of post.

disturbed by experimental manipulation and visitation. Each plot was 30 × 5 m, with longer side oriented along the slope or ridge. On each sampling occasion, in each plot, two 5 × 5 m quadrats were selected at random and grided at 0.5-m intervals. At each grid intersection, presence was recorded for each vascular-plant species touching a vertically placed pin, 5 mm in diameter, giving a cover score from the 100 points in the quadrat. A particular cover score might arise from contact with several small plants such as seedlings or with few large resprouting plants, but the data do not distinguish between these possibilities.

Data were collected in 1990, 1994, 1995 and 1996 as shown in Table 1. The data collected in 1990 are given in some detail in appendices 1 and 2 of Myerscough *et al.* (1995). In 1995 and 1996, but not in 1990 or 1994, data were collected from two species of ground-dwelling bryophytes on the plots.

The fire regime of the area during a period of some 16 years is indicated in Table 1. There was a wild fire across the Moors in 1981–1982 (NPWS data) and another on 8 January 1991. After the data had been collected in 1994, a wild fire on 2 or 3 October 1994 burned all plots on T1 but no other plots. There was a wild fire on 1 January 1998 that burned all plots on T2, nearly all on T4, but only some plots on T3 and T1, leaving some of them partially burnt, and others unburnt. Notes were made of the appearance of the vegetation on the plots a few days after the fires in 1991, 1994 and 1998, and, at intervals through 1991, of the first flowering after fire of some species and the sporulation of a ground-dwelling species of liverwort. Nomenclature of vascular plants follows that of Harden (1990, 1992, 1993, 2002).

Data structure

Various aspects of change in the vegetation after fire were observed as follows. The first occasion of sampling in October 1990 provided an estimate of the condition of the vegetation 10 years after fire, and the second, in September 1994, 3.7 years after fire. The third occasion in November 1995 provided an

estimate of the state of the vegetation 1.1 years after fire on plots of T1, and 4.8 years after fire on plots sampled on T2, T3 and T4. The fourth occasion in October 1996 provided an estimate of the state of the vegetation 2 years after fire on plots of T1, and 5.7 years after fire on plots sampled on T2, T3 and T4 (Table 1).

The data were used to estimate, separately for slopes and ridges, general patterns of change in the heaths through time following fires. The estimates were based on two assumptions. The first assumption was that the fires of 1981–82 and those of January 1991 and of October 1994 on plots of T1 were similar in their effects on the vegetation, and the second assumption that regrowth of the vegetation after a fire was relatively independent of the length of intervals between successive fires. Furthermore, we expected that data from plots on T1 would be similar to those from the plots sampled on T2 and T3 and plots of T4 when sampled in October 1990 and September 1994, when all plots shared a common immediate post-fire history.

Analyses of time-since-fire

Patterns of floristic similarity among data collected from the quadrats in relation to time-since-fire were explored through constrained ordination with canonical correspondence analyses (CCA), using CANOCO (ter Braak and Smilauer 2002). This multivariate approach models the relative abundance of species and employs a method of ordination in which the axes are constrained to be linear combinations of environmental variables. It focuses on β -diversity, or dissimilarity among sites, and assumes a unimodal response model. We used CCA over RDA after first checking the gradient length in the ordination. The derived synthetic gradients (ordination axes) maximise the niche separation of species by using species centroids (weighted averages) as an estimate of the species optimum (ter Braak and Verdonschot 1995). The statistical significance of the relationship between environmental data and sites was determined by a Monte Carlo permutation

test, with 199 permutations. To compare the floristic change with time-since-fire and spatial variation relating to transects, ridges and heath types, a matrix of species and sites was constructed for all sample sites in each of the four sample times. A corresponding matrix of all sites and time-since-fire (1.1, 2, 3.7, 4.8, 5.7 and 10 years), transect number (T1, T2, T3, T4), ridge position relative to position from the coast (near, mid, far) and heath type (wet heath, dry heath) was constructed and used in the CCA. In addition, a matrix of community characteristics was also constructed, consisting of sites and various community indices (species richness, number and cover of obligate seeders, numbers of resprouters, bare ground, shrubs and monocots). This matrix was used to plot onto the constrained ordination 'passive' variables to visualise the direction and strength of these variables, which were subsequently explored more formally with generalised linear models (GLM).

Two-way factorial GLMs were used to test for the fixed effects of habitat (wet and dry heath) and time-since-fire (1.1, 2, 3.7, 4.8, 5.7 and 10 years) and their interactions on the variation in community variables and a range of common species. Where the response variable was the number of species, a Poisson error with a log-link function was used, whereas for abundance data a normal error structure with an identity link function was used because the cover values were not constrained between 0 and 100.

Analyses of fire frequency

Constrained ordination (CANOCO) was also used to explore floristic change following consecutive fires. In this analysis, a subset of plots was used to control for the effect of time-since-fire and frequency of fire since sampling began. Hence, data from 1994 (3.7 years after fire) were compared with data collected in 1996 for Transects 1 and 4. Transect 1 was burnt soon after it was sampled in 1994. In 1996, Transects 1 and 4 thus differed in both the number of fires since 1990 (T1, two fires; T4, one fire) and time since the last fire (T1, 2 years; T4, 5.7 years). A CCA ordination was used to examine variation in the floristic data in relation to these differences in fire history. In this analysis, the ordination was constrained; second fire in 1994 (impact) v. no second fire (control) as well as the spatial effects of transects (T1, T4) and ridge position (near, mid, far) and heath type (wet heath, dry heath). Again, a range of community indices was used as passive variables to examine general functional group trends in the ordination.

Two-way factorial GLMs were used to test for the fixed effects of habitat (wet and dry heath) and fire (1994 before control, before fire, 1996 after control, after fire) and their interactions on the variation in community variables and a range of common species. Where the response variable was the number of species, a Poisson error with a log-link function was used, whereas for abundance data, a normal error structure with an identity link function was used.

Results

Fires

The three fires that occurred between January 1991 and January 1998 varied in their extent, patchiness and intensity.

The fire of January 1991 was clearly the most extensive and intense. All foliage and litter were consumed. Even the woody capsules of *Leptospermum liversidgei* and *L. juniperinum* were mostly consumed, but many infructescences of *Banksia aemula* and *B. oblongifolia*, although severely singed, released viable seeds. The fire of October 1994 burnt only T1. The fire of January 1998 was the most patchy and apparently least intense. On T3, heath was burnt in plots on the slopes, but mostly not in those on the ridges, and on areas burnt some of the foliage was only lightly singed. Similarly, in areas burnt on T1 and T4, foliage had been incompletely consumed. On T2, the fire had been more intense, with foliage almost completely consumed on all plots.

Flowering after fire

The first plants in flower were observed in February, 37 days after the fire on 8 January 1991 (Appendix 1). All plants observed to have flowered within 1 year of the fire were resprouters, except for *Hibbertia fasciculata* (Appendix 1). Other resprouting species flowered later but usually in 1992; for instance, *Banksia aemula* and *B. oblongifolia* flowered early in the year. On T1, 60 days after the fire on 2 or 3 October 1994, *Blandfordia grandiflora*, *Drosera binata*, *Sowerbaea juncea*, *Stylidium debile*, *S. graminifolium* and *Villarsia exaltata* were observed to be in flower; *Villarsia exaltata* does not occur on the slopes or ridges but in swampy depressions in lowermost situations between ridges. Spring-flowering species of obligate seeders *Dillwynia floribunda* and *Epacris obtusifolia* were seen in flower 3.7 years after the 1991 fire.

Effects of time-since-fire

In the ordination (Fig. 1), the first two axes accounted for 26% of the total floristic variation and 86% of the floristic–environmental relation. Floristic patterns varied with time-since-fire both in the wet-heath and dry-heath plots and followed similar trajectories in the four transects across the Pleistocene beach system (Fig. 1a, b). Both transects and heath-type centroids were separated by greater distance than the effect of time-since-fire. However, plots that had not been burnt for 10 years were distant from those sites more recently burnt, irrespective of heath type or transect position. The trajectories of community characteristics (cover and species richness of functional groups) varied in both space and time, but most were not aligned with ordination axes, suggesting interactive effects of habitat and time-since-fire (Fig. 1b). For example, bare ground decreased with time-since-fire more in the wet-heath plots than the dry-heath plots. The significance of trajectories plotted as 'passive' variables in the constrained ordinations were resolved by quantitative analyses with GLMs.

Trends in community characteristics, fire responses and species abundances were further explored in univariate analyses where the effect of fire frequency was removed as a confounding factor in the analyses and variation among plots (transects and ridges) was examined explicitly in the models. Initial models showed that despite the overall floristic variation present among transects, there were no significant transect effects for individual attributes and this factor was removed from the model. Overall, there were stronger effects of habitats than time-since-fire and generally time-since-fire effects were consistent among habitats,

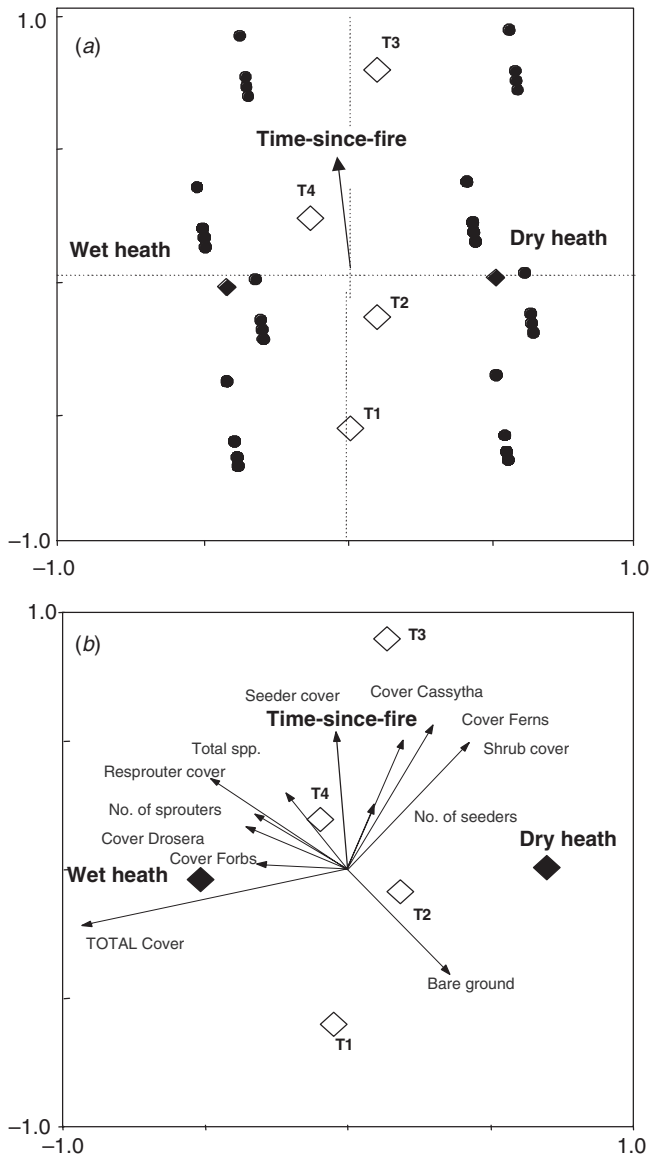


Fig. 1. Ordination (CCA) of plots, showing the effect of time-since-fire on (a) the community composition in each site, and (b) the covariation in cover and functional groups. Transect (T1–T4) centroids are well spaced as are the wet-heath and dry-heath centroids.

with the exceptions of the number of obligate seeders and the abundance of *Cassytha* (Table 2).

Exposed bare ground rapidly decreased with time-since-fire from 20 to 2% in 10 years and wet heath consistently had less bare ground than dry heath as the resprouting leaf canopies responded quickly after fire (Table 2). Leaf canopies of plots are dominated by resprouting species, especially in the early stages after fire. In both habitats, resprouters initially accounted for 97% 1 year after fire, but, after 10 years, decreased to ~75% of the summed cover values of all (Table 2). Conversely, obligate seeders took up less than 5% of summed cover scores 2 years after fire, reaching ~25% 10 years after fire (Table 2). As might be expected, the number of species of obligate seeders contacted rose with time-since-fire from ~2 to 8, but the number of resprouters contacted

varied little with time (Table 2). Similarly, in the cover of more abundant species, there was less variation in time for resprouting species than for obligate-seeding species (Table 2). Maximum scores are reached at various times since fire in resprouting species, but in obligate-seeding species these are mostly reached at the longest interval (10 years), particularly in the dry heath (Table 2). For example, *Epacris pulchella* and *Dillwynia floribunda* were rarely encountered in the first few years after fire, despite massive seedling recruitment. However, with time their cover increased up to 5%, but rarely do obligate-seeding shrubs exceed 10% cover. Conversely, resprouting shrubs have much higher cover and in some dominant species, such as *Banksia oblongifolia*, decrease in time. Generally, monocots are the dominant resprouters, especially in the wet heaths, where *Xanthorrhoea fulva* and *Lepyrodia interrupta* dominate across all plots and times. Summed across all monocots, their cover is greater in the wet heaths than in the dry heath and over time they decrease from ~40 to 30% of summed cover scores over 10 years.

Moss *Campylopus clavatus* (R.Br.) Wils. and liverwort *Goebelobryum unguiculatum* (Hook. f. et Taylor) Grolle occur patchily with low cover (*C. clavatus* <5%, *G. unguiculatum* <2%) in both habitats. In June, 6 months after the fire on 8 January 1991, liverwort sporophytes were observed to have emerged from soil in the absence of any green parts of the plants on the surface.

Effects of a short fire interval

In the ordination shown in Fig. 2, the first two axes account for 24% of the total floristic variation and 56% of the floristic–environmental relation. The effects of fire intervals are potentially confounded by large spatial differences in the composition of wet and dry heaths among ridges and transects across the Pleistocene sand plain as shown in the time-since-fire constrained ordination. In an attempt to examine fire–frequency effects, only plots from T1 and T4 were used in the constrained ordination. As expected, plots from T1 and T4 showed large floristic differences throughout time (Fig. 2) and these were present in 1994, 3.5 years after fire (Fig. 2). However, the floristic differences, exposed bare ground and proportions of obligate seeder cover and shrub cover in total cover scores in 1996 markedly diverged between the transects. It is possible that this divergence is simply related to the difference in time-since-fire between the transects in 1996, although the divergence appears to be somewhat greater than would have been expected from that source alone.

The general trends detected in the constrained ordination were more formally examined in the GLM analyses which tested the effects of habitat and its interaction with fire interval (Table 3). The proportion of the summed cover scores of all species attributed to resprouters, resprouter richness and individual resprouter species did not show any significant change in T1 after a short fire interval (Table 3). In contrast, the summed cover, richness and cover of individual species for obligate seeders all decreased after a short fire interval in comparison to T4 which remained unburnt. These differences are unlikely to be artefacts of cover detection as time-since-fire is similar in the before and after comparisons.

Table 2. Summary results for two-factor generalised linear model (GLM), habitat mean values and time-since-fire (TSF, years) mean values for dominant functional groups and cover (%) for most abundant taxa in dry heaths (DH) and wet heaths (WH) at Myall Lakes
 OS, obligate seeders; RS, resprouters; NT, no test; * $P < 0.05$; ** $P < 0.001$; *** $P < 0.0001$; n.s., not significant

Variable	GLM sequential model			Habitat		Time-since-fire in years					
	Habitat	TSF	H × TSF	DH	WH	1.1 TSF	2.0 TSF	3.7 TSF	4.8 TSF	5.7 TSF	10 TSF
Cover bare ground (%)	***	***	n.s.	9.5	4.5	20.1	12.0	7.8	5.7	4.0	2.1
%summed cover score											
Resprouters	n.s.	***	n.s.	–	–	97.1	95.0	88.5	84.5	80.3	75.1
Obligate seeders	n.s.	***	n.s.	–	–	2.91	5.0	10.2	15.1	18.2	26.1
Monocots	***	***	n.s.	19.5	48.6	39.6	41.2	38.5	30.9	27.0	31.4
Obligate seeder richness	***	n.s.	***								
DH				–	–	2.2	2.8	5.4	7.3	9.7	8.7
WH				–	–	1.5	4.0	6.7	6.7	5.5	7.5
Resprouter richness	*	n.s.	n.s.	16.6	18.8	15.9	18.2	17.6	19.0	20.2	18.0
Total richness	**	***	***								
DH				–	–	14.6	18.8	22.2	25.0	28.8	25.7
WH				–	–	20.8	24.3	24.9	26.3	24.7	25.4
<i>Kunzea capitata</i> (OS)	*	*	n.s.	5.8	3.1	0	0	0.4	1.2	5.1	3.8
<i>Cassylia glabella</i> (OS)	**	n.s.	***								
DH				–	–	0	0	8.0	0.8	0.8	0.3
WH				–	–	0	0	1.8	0.5	0.3	4.5
<i>Darwinia leptantha</i> (OS)	***	***	n.s.	0.5	6.3	0	0.1	3.1	4.8	5.3	4.1
<i>Dillwynia floribunda</i> (OS)	***	***	n.s.	1.4	6.9	0.1	0.7	2.9	4.4	7.6	5.9
<i>Dillwynia retorta</i> (OS)	NT	*	NT	3.1	0	0	0.1	0.3	0.6	1.3	4.6
<i>Epacris obtusifolia</i> (OS)	***	***	n.s.	0.6	6.4	0.9	0.5	1.5	2.4	3.6	8.2
<i>Epacris pulchella</i> (OS)	***	*	n.s.	4.0	0.1	0	0	0.7	2.0	3.1	4.1
<i>Banksia aemula</i> (RS)	***	n.s.	n.s.	30.5	2.1	–	–	–	–	–	–
<i>Banksia oblongifolia</i> (RS)	***	*	n.s.	11.7	0.8	8.2	11.2	12.6	16.2	13.0	8.5
<i>Melaleuca nodosa</i> (RS)	***	n.s.	n.s.	20.1	1.2	–	–	–	–	–	–
<i>Hypolaena fastigata</i> (RS)	***	*	n.s.	14.5	2.9	7.5	12.0	11.3	7.7	8.4	6.2
<i>Lepyrodia interrupta</i> (RS)	***	*	n.s.	5.0	32.4	8.4	18.0	23.4	13.9	13.0	24.7
<i>Xanthorrhoea fulva</i> (RS)	***	n.s.	n.s.	2.8	28.9	–	–	–	–	–	–

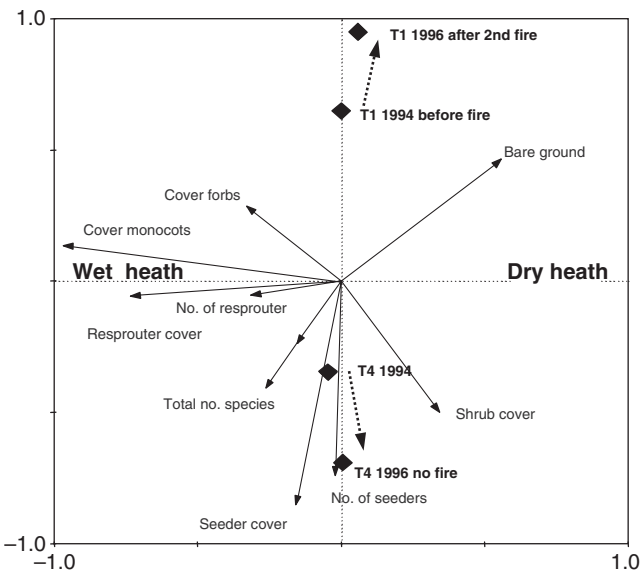


Fig. 2. Ordination (CCA) of plots, showing the effect of time and fire frequency on the community composition in each transect and the covariation in cover and functional groups. Transect (T1–T4).

The only bradysporous obligate-seeding species in the system, *Petrophile pulchella*, was recorded from both habitats

and in T1 and T4, but with very low cover and occurrence in quadrats; the highest cover recorded in any one quadrat was 2% in a quadrat on a ridge in T1, 10 years after fire. In March 2004, no individuals of *Petrophile pulchella* could be found in any of the plots on T1, but were found a short distance to the north-west of the dry-heath plot on the far ridge of T1 on the unburnt side of the boundary of the fire in October 1994.

Discussion

Spatial and time-since-fire variation

Spatial variation in the vegetation of the coastal heaths studied was strongly conserved over several years that included an intense fire. Changes of vegetation after one and more years since fire followed similar trajectories in dry and wet heaths in all four transects studied. There was no evidence that the vegetation of dry and wet heaths, or individual transects, converged or diverged in similarity with increasing time-since-fire (Fig. 1, Table 2).

The preservation of distinct features of the vegetation of the heaths through time in relation to habitat, and other spatial components of their environment, was due to the dominance in their canopies of certain species of resprouting plants that characterised each type of heath. After 1 year from fire, the cover of these species either changed little with increasing time-since-fire, slightly decreased, or showed no consistent increase. In contrast, species that regenerate only from seed after fire

Table 3. Summary results for two-factor generalised linear model (GLM), habitat mean values and fire frequency (FF) mean values for dominant functional groups and cover (%) for most abundant taxa in dry heaths (DH) and wet heaths (WH) at Myall Lakes
OS, obligate seeder; RS, resprouter; NT, no test; * $P < 0.05$; ** $P < 0.001$; *** $P < 0.0001$; n.s., not significant

Variable	GLM model			Habitat		Fire status			
	Habitat	FF	H × FF	DH	WH	T1 before	T1 after fire	T4 before	T4 after no fire
Cover bare ground (%)	***	**	n.s.	11.0	4.9	9.0	12.0	6.6	4.4
%Summed cover scores									
Resprouters	n.s.	***	n.s.	–	–	92.1	95.0	87.4	81.7
Obligate seeders	n.s.	***	***						
DH				–	–	4.8	4.5	15.1	20.8
WH				–	–	11.0	5.5	10.0	15.6
Monocots	***	n.s.	n.s.	23.1	55.1	–	–	–	–
Obligate seeder richness	n.s.	***	n.s.	–	–	5.8	3.4	6.3	7.6
Resprouter richness	n.s.	n.s.	n.s.	–	–	–	–	–	–
Total richness	n.s.	**	**						
DH				–	–	21.8	18.3	22.7	28.8
WH				–	–	25.1	24.3	24.6	24.6
<i>Kunzea capitata</i> (OS)	**	n.s.	n.s.	2.2	0.3	–	–	–	–
<i>Cassylia glabella</i> (OS)	***	***	n.s.	4.2	1.0	1.2	0.0	8.7	0.6
<i>Darwinia leptantha</i> (OS)	***	***	n.s.	0.2	5.1	2.2	0.1	4.1	4.1
<i>Dillwynia floribunda</i> (OS)	***	**	*						
DH				–	–	0.5	0.0	1.2	5.0
WH				–	–	5.0	1.5	2.8	7.0
<i>Dillwynia retorta</i> (OS)	NT	**	n.s.	–	–	0.7	0.1	0.2	1.8
<i>Epacris obtusifolia</i> (OS)	***	**	n.s.	0.4	3.8	2.1	0.5	1.6	4.2
<i>Epacris pulchella</i> (OS)	n.s.	*	n.s.	–	–	0.5	0.0	0.3	2.3
<i>Banksia aemula</i> (RS)	***	n.s.	n.s.	33.2	0.2	–	–	–	–
<i>Banksia oblongifolia</i> (RS)	***	n.s.	n.s.	1.3	24.1	–	–	–	–
<i>Melaleuca nodosa</i> (RS)	***	n.s.	n.s.	14.7	0.5	–	–	–	–
<i>Hypolaena fastigata</i> (RS)	***	n.s.	n.s.	16.4	3.4	–	–	–	–
<i>Lepyrodia interrupta</i> (RS)	***	n.s.	n.s.	5.5	36.1	–	–	–	–
<i>Xanthorrhoea fulva</i> (RS)	***	n.s.	n.s.	3.7	36.3	–	–	–	–

(obligate seeders), although also characteristic of each type of heath, consistently increased in cover with time-since-fire. Thus, there are two groups of plants differing in the ways they responded with time-since-fire; the resprouters with little or no consistent change and the obligate seeders whose cover increased steadily up to 10 years since fire. The stable differentiation between dry and wet heaths through time largely depended on the resprouters, whereas the evident consistent changes with time-since-fire largely depended in these heaths on the obligate seeders (Fig. 1, Table 2).

In these heaths, the distinction between obligate seeders and resprouters was clear-cut, especially after the intense fire of January 1991. The species of resprouters with high cover, i.e. those indicated in Table 2, each appeared to have mature plants with high rates of survival through fire. Species of resprouting plants with lower survival through fire, and usually higher numbers of seedlings after fire, certainly occur in similar heaths elsewhere on the northern coast of New South Wales (Benwell 1998), but none of these had particularly high abundance in dry or wet heaths of the study area.

The dry and wet heaths were similar in the general trajectory of change they followed with time-since-fire. By 10 years after fire they had similar species richness. Their canopies were both dominated by resprouting species, and, in each, species of obligate seeders achieved only ~25% of the summed total cover scores of all species after 10 years. In neither dry nor wet heath did the canopy of obligate seeders significantly shade the

canopy of resprouting species, such as seen in heaths that come to be dominated by *B. ericifolia* (Siddiqi *et al.* 1976; Morris and Myerscough 1988; Keith and Bradstock 1994). Wet heaths had a higher proportion of monocotyledons in their cover than did dry heaths. Dry heaths had more bare ground than wet heaths, with the bare ground more rapidly covered by a leaf canopy in wet heath after fire than in dry heath.

The lower species richness of dry heath than of wet heath in the early years of time-since-fire (Table 2) may be related to the slower growth of leaf canopy in dry heath and the method of recording of species by contact with a pin. Had species richness been recorded by direct observation of the presence/absence of species, dry and wet heaths may have differed less in species richness in early years of time-since-fire. Also, direct observation of the presence of species as plants 1 year after fire would probably have shown little change in species richness with time as most of the seedling recruitment, particularly of obligate-seeding species, appears to occur in these coastal heaths within the first year after fire (Myerscough *et al.* 1995; Benwell 1998).

The changes observed with time-since-fire may have been different under drier conditions. Had conditions been drier, or observations been made less than 1 year after fire, changing cover of resprouting species may have contributed more significantly to changes observed with-time-since fire. In their observations of wet heath after the fire in October 1994 in the same general area as our plots, Monamy and Fox (2000) noted the rapidity

with which cover of vegetation returned and increased after the fire, and relate this in part to high rainfall shortly after the fire.

Part of the spatial variation observed in the heaths in our study was among transects. As is evident in Fig. 1, and seen in a fuller set of data collected in 1990 (Myerscough *et al.* 1995), no consistent SW–NE trend was apparent in the vegetation of the heaths on the sands of this Pleistocene beach system. The basis of this variation evident among transects may be in local factors and the haphazard way in which individual plots were selected in dry and wet heaths within transects.

Variation of fire interval

Even though effects of a short time interval between fires cannot be completely separated from changes with time-since-fire, there is evidence that cover of obligate-seeding species was decreased by a short interval, whereas no effect on the cover of resprouting species was detected (Fig. 2, Table 3). The fire of October 1994 on T1 was only 3 years and 9 months after the previous fire. Probably, most of the cover of obligate seeders recorded in T1 in November 1996 would have been from seedlings that originated from seed remaining dormant in the soil through the fire of January 1991 but that germinated after the fire in October 1994. Few seeds are likely to have been matured and shed into the soil from obligate seeders in the 3 years and 9 months between the fires.

Design of observations

These observations of patterns of regrowth of vegetation through time, made on spatially replicated plots, used a mixture of direct observations through time and observations on plots differing in space and time-since-fire. Changes since fire may be directly observed through time (Whelan 1995), but many studies seek to establish patterns of changes through time in vegetation by using plots burned at different times but observed at the same time, the space-for-time design, as in Morrison *et al.* (1995), Watson and Wardell-Johnson (2004) and others. The assumption that plots differing in space would be similar in vegetation at similar times-since-fire could be examined in this study. This was because all plots were examined at two common times-since-fire in 1990 and in 1994, allowing direct assessment of similarity in their vegetation. Floristic differences among transects and the ridge–swale systems were remarkably aligned through time. This consistency through time applied to both wet- and dry-heath plots, which showed the same trajectory with increasing time-since-fire. Our findings are important in the context of space-for-time analyses of time-since-fire effects because those often assume floristic similarity across uniform landscapes. Clearly, our transects differed significantly in their floristic composition despite their visual uniformity in structure and species dominance. Hence, if the chronological sequences differed among transects, spatial and temporal floristic patterns would have been confounded. Such chronosequences are common in analyses of time-since-fire studies, with relatively few sequential studies being reported (Gill 1999).

The apparent robustness of this hybrid method of establishing patterns of regrowth through time-since-fire almost certainly rests on the dominance of resprouting species in the vegetation of both ridges and slopes. Obligate seeders were not seen to

dominate the canopy at any time, as they have, for instance, in certain shrublands with *B. ericifolia* some years after fire in the Sydney region (Siddiqi *et al.* 1976; Morris and Myerscough 1983, 1988; Bradstock and O'Connell 1988; Keith and Bradstock 1994) or heath in South Australia with *B. ornata* (Specht *et al.* 1958). Obligate seeders with bradysporous seed banks are also important in understoreys of some dry sclerophyll forests in the Sydney region, and are critically affected by short intervals between fires (Cary and Morrison 1995; Morrison *et al.* 1995). Had such potentially canopy-dominating obligate seeders been present in the system then this hybrid method of establishing general patterns of regrowth after fire would have failed, simply because it ignores the dynamics of seed banks. This is especially so with bradysporous seed banks, such as those of *B. ericifolia* and *B. ornata*, which are normally entirely exhausted after fire, and require some years before they are replaced. In such species, if no seed is present before a fire, they can only continue in a habitat if seed arrives by dispersal from elsewhere. All obligate-seeding species, except one, in the study area have soil seed banks, which may have a carry-over of viable seed from one fire to the next.

Attributes of species

It is not immediately obvious why there were no tall-growing potentially canopy-dominating obligate-seeding plants in the heaths we studied. It is possible that such an absence is common, or even perhaps general, for similarly highly leached infertile Pleistocene beach sands along the coast of New South Wales and southern Queensland. If so, this would make the search for an explanation more general, with interesting comparisons to be made with shrublands on Holocene stabilised beach sands, some of which do have canopy-dominating bradysporous obligate-seeding plants, as in the Fens Embayment further south in Myall Lakes National Park and in Crowdy Bay National Park. Infertility of sands bearing heath does not preclude the occurrence of *B. ornata*, a canopy-dominating bradysporous obligate-seeding species, on the Ninety-mile Plain in South Australia, nor does the occurrence of extensive areas of highly flammable sedges and restiads preclude the occurrence of *B. ericifolia*, another such species, on the Barren Grounds (Burrough *et al.* 1977) or in the catchment of O'Hares Creek (Keith 1994), south of Sydney. In the absence of more general evidence, frequency of fires across the heaths we studied may be a sufficient explanation for lack of tall-growing canopy-dominating obligate-seeding species, but this requires the survival of a bradysporous obligate-seeding species in these heaths to be explained.

There is no evidence that *Petrophile pulchella* survives through very short intervals between successive fires in these heaths. It was found on T1 when surveyed in 1990, 10 years after fire, but was not recorded again in T1 after the fire in October 1994, which occurred 3.7 years after the fire in January 1991. There is, thus, no need to invoke the hypothesis of Myerscough *et al.* (2000) that some of its achenes remain dormant within the soil. Rather, it appears that intervals between fires that burn this whole area of the heathland may never be less than the minimum required for seedlings to become reproductive and bear ripe achenes. If, as seems to have occurred on the plots of T1 after the fire in October 1994, populations become locally

extinct, they may be re-established after fire by wind-dispersal from surrounding areas. Following the fire in January 1991, when the whole of the area of heath studied was burned, many strong willy-willies were observed that scooped up fragments from the soil surface and redistributed them over wide areas. Achenes of *P. pulchella* and winged seeds of *Banksia* are likely to be distributed over wide areas in this fashion following such intense fires that burn large areas of heath.

With the exception of *P. pulchella*, seed banks of obligate-seeding species in the heaths studied are in the soil, and must vary in their abundance with time-since-fire. Understanding how populations of obligate seeders react to various intervals between fires obviously depends on knowing how the seed banks build up between fires, and how seedlings recruit from them after fire and the extent to which seeds remain viable and dormant through fires. For *Dillwynia floribunda*, Myerscough *et al.* (1996) showed that addition of seeds, treated to break their dormancy, to quadrats shortly after the fire of January 1991 did not greatly increase recruitment of seedlings in wet heath. This showed that, after 10 years since the previous fire, there were relatively high numbers of seeds in the natural seed bank and that many of these were rendered non-dormant, ready to germinate, by the fire of January 1991. Apart from this, little is directly known of the soil seed banks of obligate-seeding species in the heaths studied.

Resprouting species, as a group, very quickly formed the dominant cover in the heaths after fire. The cover of some species of resprouters showed little change with time-since-fire, but the cover of two species of resprouters, *B. oblongifolia* largely in wet heath and *Hypolaena fastigata* principally in dry heath, increased to a maximum and then decreased with increasing time-since-fire (Table 2). Auld (1987) found a similar pattern to occur in the canopy of *Angophora hispida*. Whether this pattern is related to environmental constraints or constraints intrinsic to the plants is unknown. Some reduction of the capacity to resprout might have been expected under a high fire frequency from the work of Zammit (1988) and Knox and Clarke (2006), but there was no evidence that the short fire interval of 3 years and 9 months reduced the cover of any of the more abundant resprouting species in either wet or dry heaths (Table 3).

The two species of bryophytes found in the heaths appear to be resprouters in that they seem to persist in the vegetative state through fire, from living tissue sufficiently deeply buried in the soil for survival. Furthermore, the liverwort sporophytes seem to have emerged from the soil in mid-winter, 6 months after an intense fire, although not conclusively identified at the time, almost certainly belong to *Goebelobryum unguiculatum*. This was the only species of liverwort found on the plots, and it is unlikely that a subterranean saprophytic liverwort exists in the area. According to Allison and Child (1975), the marsupium of *G. unguiculatum* is terminal on the stem, long cylindrical and more or less coated with rhizoids. Were the marsupia to be sufficiently deeply buried in the soil they would afford the developing sporophytes they enclose the means of surviving fire and sustenance during their emergence after the fire. It is unclear whether the sporulation was a direct response to fire, or whether the liverwort normally sporulates profusely in winter. Mechanisms of survival and reproduction in relation to fire require further study in both species of bryophyte. Also it is

not clear whether 'resprouting' bryophytes occur extensively in other intensely burnt systems.

Flowering followed very quickly after intense fire in several species. This was especially so for *Chorizandra sphaerocephala*, *Drosera binata* and *Stylidium debile*, where flowering was observed in a little over a month after intense fire in mid-summer. *D. binata* is known to have flowered within a month of intense fire in Ku-ring-gai Chase (Benson and McDougall 1995). Other data recorded in Appendix 1 modify or add to some of those recorded for these species in the Sydney region by Benson and McDougall (1995, 1997, 1998, 1999, 2001, 2002); for instance, *S. debile* is in the Myall Lakes area a resprouter with flowering stimulated by fire (cf. Benson and McDougall 2001). The timing of flowering of some of the species observed differed according to the season of occurrence of fires. For instance, after the fire of 8 January 1991, flowering of *Blandfordia grandiflora* and *Xanthorrhoea fulva* was seen some 300 days after that fire, but only 60 days after fire on 2 or 3 October 1994. This suggests that flowering of such species, although triggered by fire, is restricted to certain seasons, as in the cases for *B. grandiflora* (Benson and McDougall 2002) and *X. fulva* (Benson and McDougall 2005). In *X. fulva*, Taylor *et al.* (1998) found that in these heaths summer fires stimulated greater number of plants to flower than spring fires.

Landscape flammability and heath type

The fire history of the area covered two decades. The first started in the early 1980s with a fire that burnt the whole area, and finished with another in January 1991 that did the same. During the second decade, after the fire in January 1991, there were two fires, neither of which burnt the whole area, and each of which was of lower intensity than the fire of January 1991. Some parts were burnt, at least partially, by fires in both 1994 and 1998, others by only the 1998, and a few by neither of them. Thus, time between successive fires in the 1990s varied from 3.7 years for ridges of T1, and 3.25 years for some areas of wet heath on T1, to not having been burnt since the fire of January 1991 at least until October 2006 for areas of dry heath on T3. Fires observed in the system have thus varied in frequency, intensity and patchiness. In short, this apparently simple landscape with its subdued topographic variation and its uniform parent material of old beach sand has recently had a complex fire regime. In it, fire and heath type have interacted. This was evident in the incidence of some fires, in which wet heath burnt more readily than dry heath, and in patterns of regrowth after fire, in which exposed bare ground was more quickly covered in wet heath than in dry heath.

In both dry and wet heath, resprouting species were dominant. Regrowth in wet heath was not only faster than in dry heath but also more dominated by monocots. In wet heath, photosynthetic surfaces of the monocots regrew from the soil surface, and quickly formed a bed of finely divided fuel concentrated just above the soil surface. Wet heaths thus showed many of the characteristics of the highly flammable buttongrass moorland described by Marsden-Smedley and Catchpole (1995a, 1995b, 2001). In contrast, in dry heath, more of the canopy regrew from fire-resistant stems, and would not so quickly recreate a bed of fine fuel at the soil surface. Even the grass tree of the dry

heath, *Xanthorrhoea glauca*, has an emergent caudex that forms a small trunk, whereas in the wet heath the caudex of *X. fulva* is largely buried, so its new leaves are formed at or near the ground surface. Thus, the faster regrowth and the nature and position of that regrowth are likely to render wet heath more quickly susceptible to fire than dry heath. This may explain why, in one episode of fire, wet heath was seen to have burned whereas in the same general area dry heath had not.

Resilience of the system

The heaths studied showed marked resilience to various regimes of fire. The heaths are part of catenary sequences of vegetation that cover the Pleistocene beach system, termed the differentiated inner barrier by Myerscough and Carolin (1986) in their naming of Eurunderee land systems. It is likely that similar resilience to various fire regimes extends to adjoining Pleistocene sand systems in the Eurunderee area. Their vegetation has been subject to similar fire history and is also largely dominated by resprouting species.

The heaths show no susceptibility to destruction through ground fire, as may occur in Tasmanian moorlands (Brown *et al.* 2002). Peat in the wet heaths studied here and in the intervening swamps, does not appear to accumulate to such a depth that underground organs of resprouting species and seed banks of obligate-seeding species occur entirely within it. They are mostly within non-combustible soil horizons, which are at least partially sandy. The heaths, thus, appear to be highly resilient under fire regimes to which they have been, and probably will continue to be, subject.

They also have shown little evidence of die-back or invasion by weeds or locally occurring, tall-growing obligate seeders such as *Leptospermum laevigatum*, which Burrell (1981) found invaded coastal heaths in Victoria. This is despite a rock and gravel road having been laid across part of the system in the 1970s to facilitate transport of rutile mined from sands further seaward and towards Seal Rocks. The effects of the road appear to be confined to its immediate vicinity, in particular the well grown trees, mostly *Melaleuca quinquenervia*, that grow at its edges. Monamy and Fox (2000), however, thought that the regrowth of vegetation on one of their plots had possibly been sped up by an input of nutrients in drainage water it had received from the road.

The system of which the heaths studied are part has an origin going back some 125 000 years (Thom *et al.* 1992). Its present vegetation, largely differentiated in relation to depth to water table into dry heath, wet heath and swamp (Carolin 1970; Myerscough and Carolin 1986), probably has a continuous history back to the origin of the beach sand system itself. The differentiation of the heaths into wet and dry heaths is highly stable through the time span of recently observed fire regimes, as this study has shown. This differentiation can obviously be destroyed by major disturbance such as mining of the sands carrying the heaths. The whole system itself would be destroyed if the sea rose much above its present levels. Meanwhile, under present conditions and watertable levels, the system appears to be highly resilient, particularly to regimes of fire similar to those it has recently experienced. Its vegetation, dominated by long-lived resprouters in which obligate seeders nearly all have soil

seed banks and never form an overtopping leaf canopy, is what would be expected from a fire history that included some very short intervals between fires.

Acknowledgements

The start of the work was supported by an ARC Small Grant 1990–1992 to one of us (PJM). The following are thanked: Nicholas Skelton with whom the work was started and the 1990 data were collected; Neil Tridgell for great help in the field 1994–1996; Elizabeth Brown of the National Herbarium, Sydney, for confirming our identification of the bryophytes; Dylan Kendall of the Hunter Region of the NSW National Parks and Wildlife Service for information on the 1980–1981 fire and helpful discussion on fire in sedgeland; and two anonymous referees for their constructive comments on the manuscript. The work was conducted under a Scientific Licence from the Director-General of the NSW National Parks and Wildlife Service.

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Manuscript received 6 June 2006, accepted 6 November 2006

Appendix 1. Species flowering within the first year after high-intensity fire on 8 January 1991

Time of observation (days after fire)	Species seen to flower for first time after fire
37	<i>Chorizandra sphaerocephala</i> , <i>Drosera binata</i> , <i>Stylidium debile</i>
51	<i>Comesperma defoliatum</i> , <i>Melaleuca thymifolia</i> , <i>Panicum simile</i> , <i>Stylidium graminifolium</i> , <i>Villarsia exaltata</i> , <i>Xyris</i> sp.
98	<i>Callistemon citrinus</i> , <i>Thysanotus</i> sp.
137	<i>Adastraea salicifolia</i> , <i>Trachymene incisa</i>
155	<i>Baeckea diosmifolia</i>
173	<i>Ricinocarpos pinifolius</i> , <i>Sowerbaea juncea</i>
222	<i>Boronia pinnata</i> , <i>Chloanthes stoechadis</i> , <i>Glossodia major</i> , <i>Hibbertia fasciculata</i> ^A
307	<i>Blandfordia grandiflora</i> , <i>Haemodorum corymbosum</i> , <i>H. planifolium</i> , <i>Leptospermum trinervium</i> , <i>Melaleuca nodosa</i> , <i>Philotheca salsolifolia</i> , <i>Pimelea linifolia</i> , <i>Stypandra glauca</i>
360	<i>Leptospermum juniperinum</i> , <i>L. liversidgei</i> , <i>Platysace lanceolata</i>

^AAn obligate-seeding sp.; the rest of the spp. are resprouting.