CALMScience Supplement 4: 199-206 (1995)

Mosaics in Sydney healthland vegetation: the roles of fire, competition and soils

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ABSTRACT

Sydney's coastal sandstone plateaux support a heathland mosaic that includes thicket of tall dense shrubs and heath with a diverse complement of small shrubs, forbs and graminoids. Thicket dominants are infrequent or absent in heath, while smaller plants that typify heath are less frequent and less diverse in thicket. Examination of a sequence of aerial photographs spanning 50 years showed that the mosaic was dynamic over time and that changes in the distribution and abundance of the two structural forms are related to fires. Comparative studies of *Banksia oblongifolia*, a species of understorey shrub, have shown that its fruit production is reduced when in the presence of mature thicket dominants. This species, and numerous others with similar life-cycle attributes, is less abundant in thicket than in open-heath, suggesting that competition from thicket dominants may be an important factor influencing community composition. Manipulative experiments to test this hypothesis are in progress. Analyses of soil chemistry showed some variability between sites within the mosaic. There was evidence that some aspects of soil chemistry are dynamic through time in response to temporal changes in vegetation.

Fire management of mosaics must take cognisance of complex interactions that control spatial and temporal variation. If full diversity is to be conserved, a variable fire regime must be implemented that is responsive to the existing state of the system and its rate and direction of change.

INTRODUCTION

Ecosystems are traditionally depicted as a web made up of interactive components. Agricultural systems may be managed by manipulating any of these components, but in natural systems interactions, complexity and cost dictate that fire is the principal management tool. We want to manipulate natural systems through fire management to conserve biodiversity and to protect life and property. Socio-political pressures often lead managers to consider regular pre-defined fire regimes directed principally at fuel management, or regimes designed with the intention to protect one or a few species perceived to be important because of rarity or socio-economic value. This paper evaluates the effectiveness of such management strategies in the maintenance of full biodiversity by examining patterns and dynamics in heathland mosaics near Sydney.

Study Area and Methods

Heathlands on Sydney's coastal sandstone plateaux comprise mosaics of dense shrub thicket and open heath/sedgeland. Thicket (Banksia Thicket of Keith and Myerscough 1993) is dominated by an overstorey of tall serotinous obligate seeding shrubs (e.g. *Banksia ericifolia*) with an understorey of smaller shrubs (e.g. *Pimelea linifolia*), graminoids (e.g. *Lepidosperma neesii*) and forbs (e.g. *Goodenia dimorpha* var. *angustifolia*). Open heath (Restioid Heath of Keith and Myerscough 1993) is without overstorey, but has a more diverse array of small shrubs, graminoids and forbs than thicket. The study area is 350 ha of heathland west of Jibbon Hill (34° 09'S, 151° 09'E) in Royal National Park.

Fires and the two vegetation types were mapped over a period of 50 years using a sequence of aerial photographs. The maps were digitized and incorporated into a geographic information system (GIS) based on 25 m grid cells, allowing the distribution of thicket to be compared between times and related to the occurrence of fires. Field studies on plant populations and soils were carried out after a fire in 1988. Samples were located along transects in each of open heath and several structural variants of thicket characterized by differences in height and density of dominant plants (Keith and Bradstock 1994).

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RESULTS

Fire

Management of the mosaics centres on whether they are static and related to physical environmental factors or spatially dynamic in response to temporal events such as fire. Figure 1 clearly shows that spatial patterns are dynamic. There was no evidence of thicket in the area prior to 1960 (maps not shown). The extent of thicket increased at the expense of heath from 1960 through to the mid 1970s, when a major reduction occurred. Thicket again increased from the late 1970s until 1988. After 1988 another major reduction in thicket occurred (map not shown).

Dynamics of the mosaic are related to fire (Fig. 2). The overstorey of thicket was destroyed by fire (at least temporarily). In the absence of fire, the extent of thicket increased. The gradual, rather than sudden post-fire expansion was not due to continuous seedling recruitment in the years after fire. Rather, it reflects spatially variable growth rates that cause thicket dominants to become visible on aerial photographs at different times since fire.

Banksia ericifolia is the major overstorey species in thicket. The population model developed for *B. ericifolia* by Bradstock and O'Connell (1988) is applicable to other overstorey species (*Hakea teretifolia* and *Allocasuarina distyla*) because these have similar life histories. The model identifies fire frequency and seedling establishment as the major factors controlling population density. If fires recur at less than a critical interval, then overstorey populations will decline. The length of the critical interval varies between six and 13 years depending on the level of seedling establishment, which is a function of post-fire rainfall and site quality (Bradstock and O'Connell 1988).

The model predictions were examined at landscape scale by analysing the history of fire, fate of thicket and rainfall records between 1972 and 1988. In the interval between 1972 and 1988, three fires burnt various parts of the study area, hence there were eight possible fire histories (Fig. 3). Four of these (BBB, BNB, NNB and NNN) were spatially restricted and therefore not analysed. Two of the remaining fire histories (BNN and NBN) had one fire between 1972 and 1988 and two (BBN and NBB) had two fires. The penultimate fire intervals for BBN and NBB were 2.5 years and 4 years, respectively (i.e. less than the critical interval of Bradstock and O'Connell 1988). BNN and NBN had penultimate fire intervals of at least 10 and 12 years, respectively (i.e. more than the critical interval unless seedling establishment was minimal). In the two years after fire, annual rainfall was highest after the 1974 fire, lowest after the 1980 fire and intermediate after the 1976 fire (Fig. 4).

At both 1972 and 1988, the minimum post-fire age of any grid cell was 8 years. It was assumed that grid cells in which no overstorey was visible on aerial photographs flown in 1972 and 1988 did not contain overstorey in an immature (hence undetectable) state. Grid cells that contained overstorey in 1972, but not in 1988 were recorded as overstorey extinctions.

The proportion of overstorey extinctions was greater in grid cells subject to short fire intervals (BBN and NBB) than in grid cells subject to fire intervals as long or longer than the critical interval (BNN and NBN) (Fig. 5, $P<0.001$). The effect of post-fire rainfall was examined by comparing BBN with NBB and BNN with NBN. In each case, where rainfall after the last fire was lowest (NBB and NBN, respectively) there was a higher proportion of extinctions (Fig. 5). The differences in frequencies of patch extinctions observed in relation to fire frequency and post-fire rainfall suggest that Bradstock and O'Connell's (1988) population model is applicable at landscape scales.

The results showed that a single short fire interval is not sufficient to drive overstorey to widespread extinction. In BBN, the short fire interval did not cause overstorey extinction in all grid cells (even though recruits after the 1974 fire could not have produced seed before being killed by the 1976 fire). This was possibly because: (i) a small residual seed bank may be retained in cones of dead plants, allowing an opportunity for recruitment after a second fire (Bradstock, unpublished); and (ii) seeds may be dispersed from nearby patches that did not experience a short fire interval.

Competition

Richness of understorey species, particularly shrubs, varies inversely with overstorey density (Fig. 6). This relationship has been observed in other heathlands and has been put forward as evidence that overstorey adversely affects understorey through competition (e.g. Specht and Specht 1989; Cowling and Gxaba 1990). The mechanism of such an interaction is that dense overstories deprive understorey plants of resources, reducing their survival and reproduction, and eventually cause elimination (Keith and Bradstock 1994). The process is interrupted by fire which removes overstorey, either temporarily until it regains dominance, or, in the case of frequent fire, overstorey cover may be reduced or eliminated for one or more fire intervals.

Understorey species vary in their response to overstorey competition. This was examined by defining functional groups of species based on their life-history attributes. One group consists of serotinous resprouters (e.g. *Banksia oblongifolia*), while a second group includes obligate seeders with longer lived soil seed banks (e.g. *Acacia suaveolens*). Observations on population densities suggest that all eight species surveyed in the resprouting group were adversely affected by various overstorey types (Table 1). In contrast, only one of eleven species in the obligate seeder group had the same response, while the remainder were either unaffected by overstorey or responded in a way that could not readily be ascribed to competitive effects.

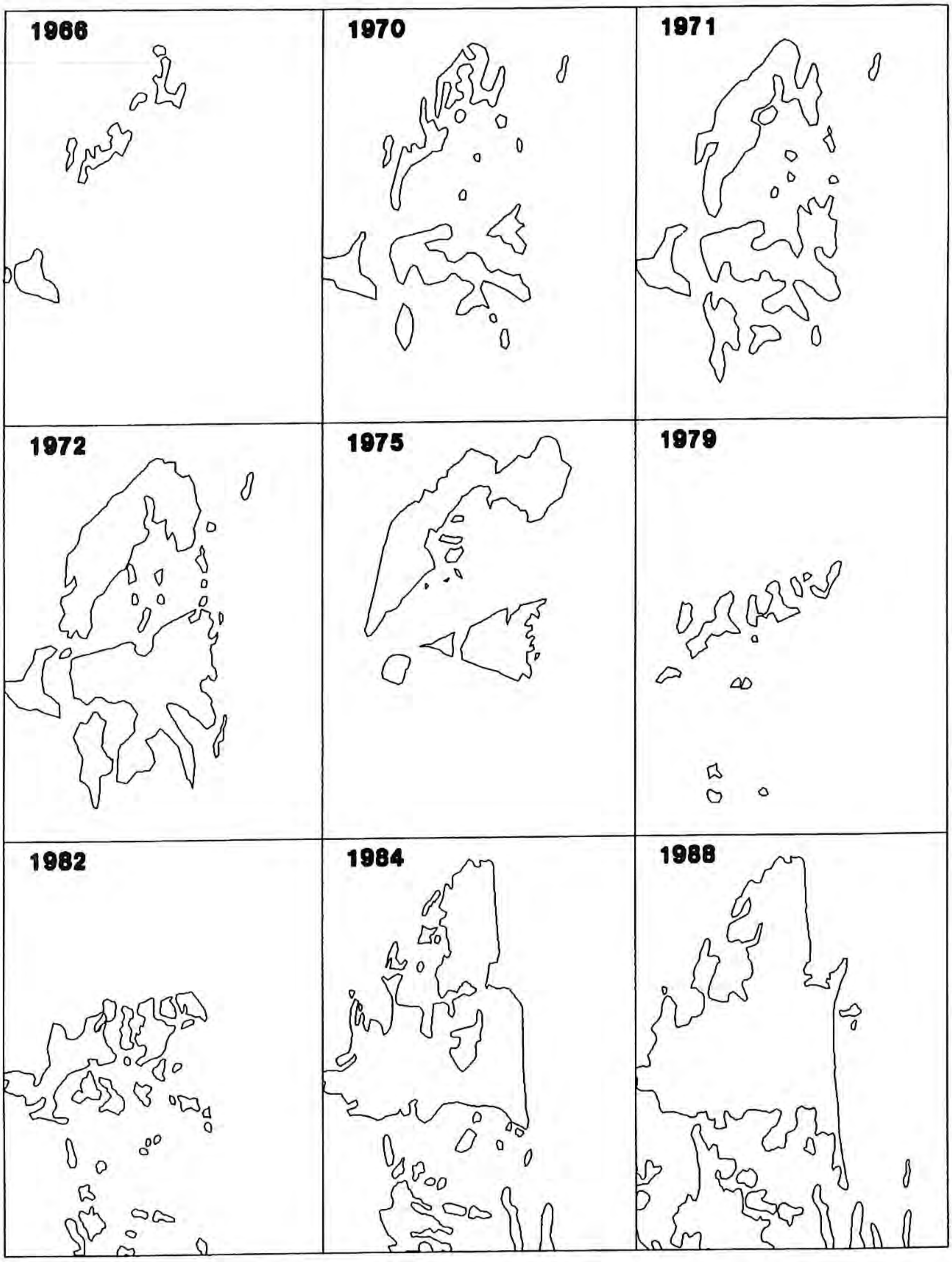


Figure 1. Series of maps showing changes in the distribution of thicket 1966-1988. The remaining area in each map is open heath.

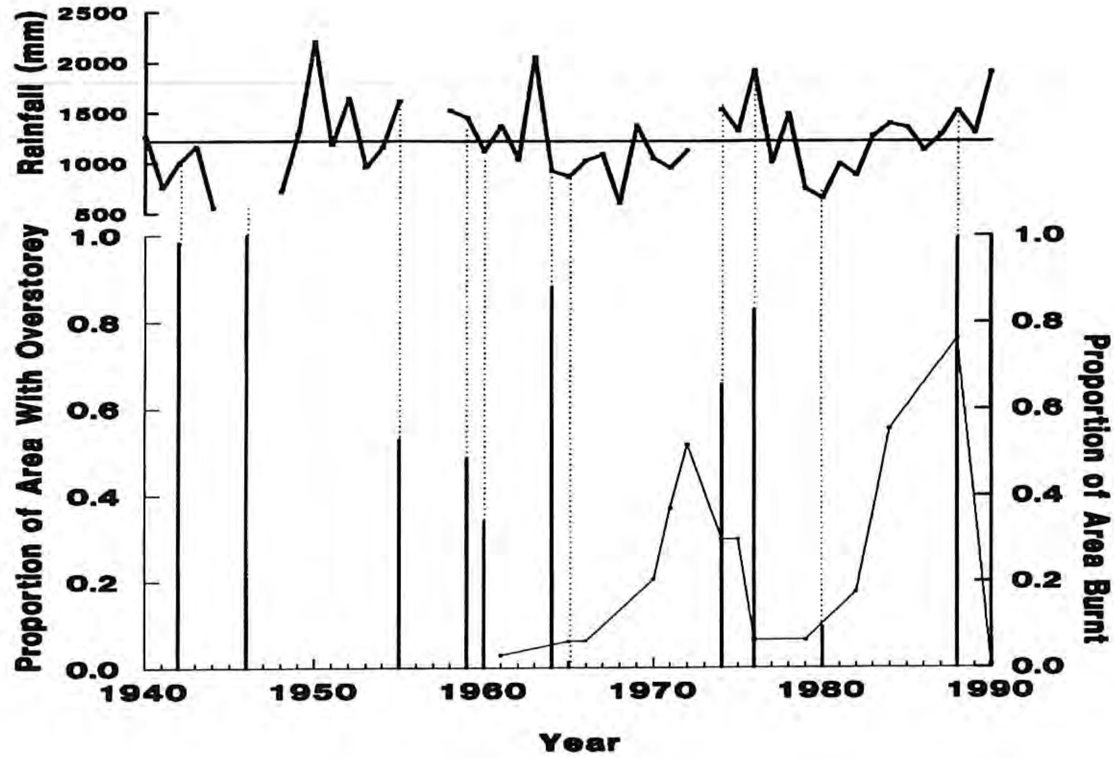
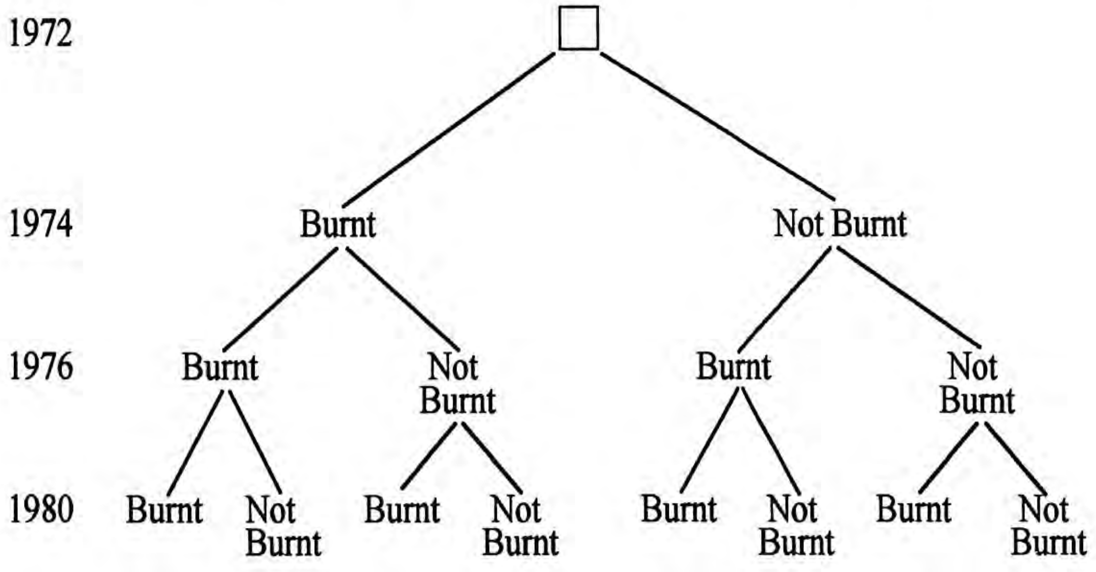


Figure 2. The extent of thicket (thin line) and fires (unbroken vertical lines) for the period 1940-1990. Increases in overstorey coincide with intervals of more than 10 years between major fires. Declines in overstorey coincide with major fires in 1974-1976 and 1988. Top graph shows variation in annual rainfall, horizontal line represents mean.



	(BBB)	(BBN)	(BNB)	(BNN)	(NBB)	(NBN)	(NNB)	(NNN)
Cells	7	265	3	92	39	154	0	2

Figure 3. Tree diagram showing eight possible fire histories between 1972 and 1988 and their extent (number of grid cells burnt).

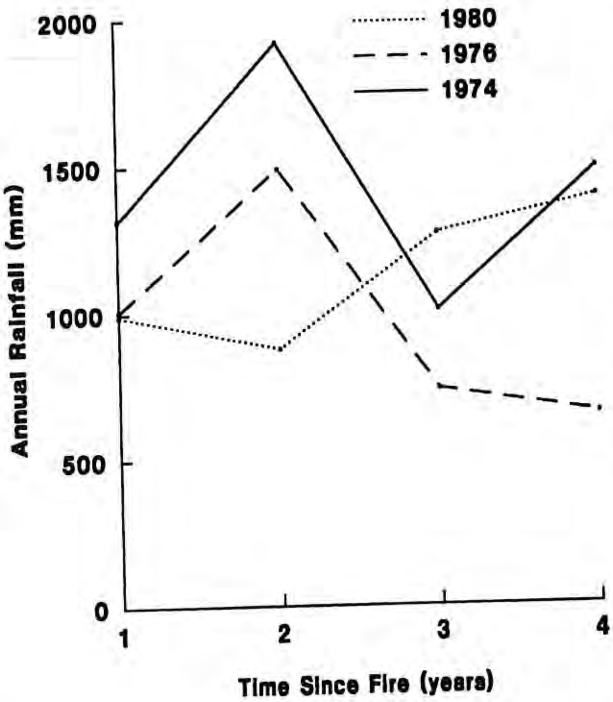


Figure 4. Annual rainfall after fires in 1974, 1976 and 1980.

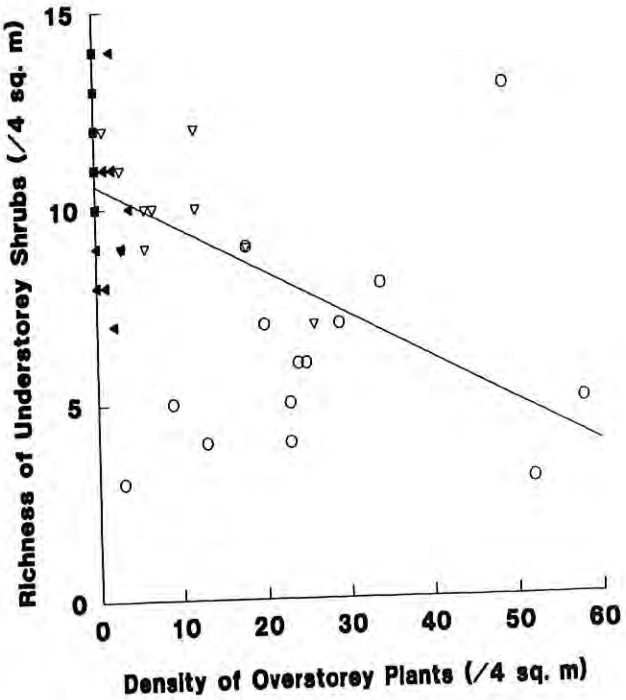


Figure 6. Relationship between overstorey density and richness of understorey shrub species, $R^2=0.27$, $P<0.001$ (after Keith and Bradstock 1994).

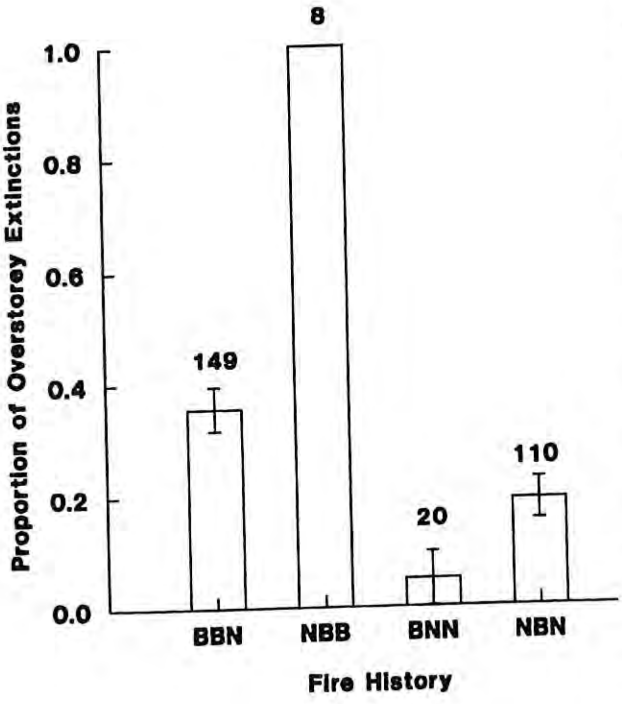


Figure 5. Proportion of overstorey extinctions under four fire histories. Numbers are total grid cells with overstorey in 1972 for each fire history. Error bars show standard errors.

TABLE 1

Differences in density of post-fire populations in two groups of understorey shrubs: serotinous resprouters and obligate seeders with soil seed banks. Overstorey types: A- absent; O- open; S- short; T- tall.

SEROTINOUS RESPROUTERS	
Allocasuarina nana	A>S O T
Banksia oblongifolia	A>O>S>T
Callistemon linearis	A O S T
Hakea dactyloides	A>S O T
Isopogon anemonifolius	A>O S T
Lambertia formosa	A>S O T
Leptospermum continentale	A>O>S T
Melaleuca nodosa	A>T O S
OBLIGATE SEEDERS WITH SOIL SEED BANK	
Acacia suaveolens	ns
Cryptandra ericoides	T>S O A
Dillwynia floribunda	O>T>S A
Epacris microphylla	O A>T>S
Eriostemon buxifolius	ns
Gompholobium glabratum	T A>O S
Leucopogon microphyllus	O>T S A
Mirbelia rubiifolia	A>O S T
Persoonia lanceolata	ns
Pimelea linifolia	O>A S>T
Xanthosia tridentata	ns

Differences between the two functional groups relate to their ability to exploit a post-fire window of reduced overstorey competition (Keith and Bradstock 1994). In the obligate seeder group, post-fire recruits mature rapidly and establish a long-lived seed bank before overstorey species regain their dominance and exert competitive effects. Post-fire recruits of resprouters are unable to reproduce within the window due to their slower growth and maturation. Beneath overstorey, they may suffer increased mortality and/or reduced fruit production. If recruitment fails to compensate for adult deaths, populations will decline.

Observations on *B. oblongifolia*, a serotinous resprouting understorey shrub, support this model. Its fruit production was reduced beneath or in the vicinity of various overstorey types (Fig. 7, P<0.0001), an effect that was translated into reduced recruitment in the next fire interval (P<0.05).

Soils

Soil properties vary spatially and temporally between vegetation types within the mosaic. Levels of topsoil nutrients are generally higher under various types of overstorey than in open heath (Fig. 8). Topsoil nutrients also increase in the early post-fire years, although organic matter decreases. There is evidence from a manipulative experiment that soil properties vary through time in relation to changes in overstorey. After fire, exchangeable cations accumulate in topsoil more rapidly where overstorey plants were retained than where regenerating overstorey was removed (Fig. 9, P<0.01). However, changes in organic matter content and some other soil properties occurred at a similar rate in treatment and control plots (Fig. 9, P>0.05).

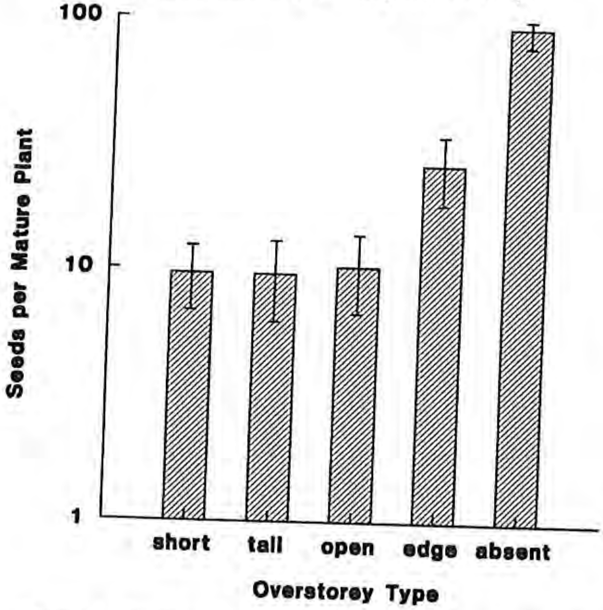


Figure 7. Fruit production of Banksia oblongifolia *in the presence of various overstorey types: short, tall and open are structural variants of thicket; absent is open-heath with no overstorey dominants; edge is boundary area between thicket and open heath (after Keith and Bradstock 1994).*

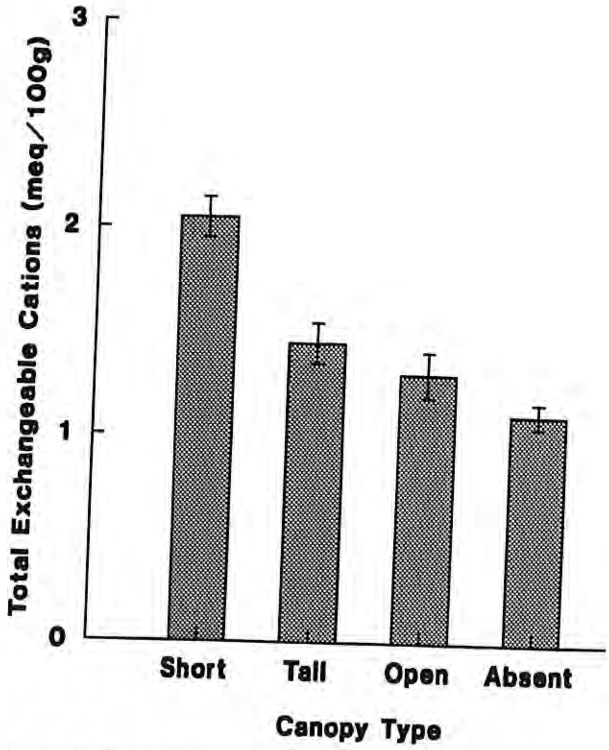


Figure 8. Total exchangeable cations in top soil (0-7 cm depth) beneath various overstorey types.

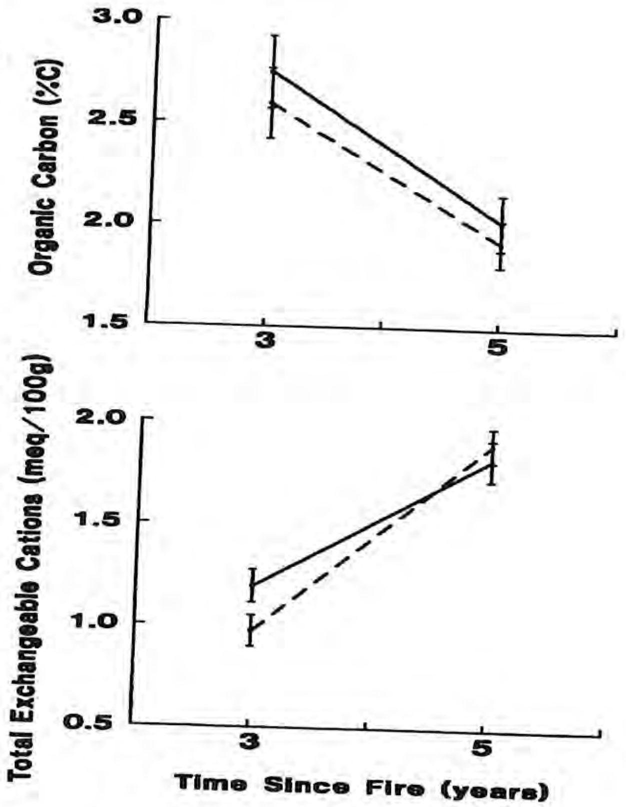


Figure 9. Rates of change with time since fire in organic carbon and total exchangeable cations of topsoil beneath a developing overstorey (broken line) and at sites from which seedlings of overstorey species were experimentally removed.

DISCUSSION AND CONCLUSIONS

Heathland mosaics are interactive and dynamic systems. The properties that characterize mosaics: spatial heterogeneity; temporal dynamics; and interactive processes, are inherent in all natural systems and are the ultimate means of sustaining their biodiversity. Mosaics should therefore be considered the norm of natural systems, rather than the exception. Management of these systems for conservation of their biota must focus on fire as the major component amenable to practical manipulation. Direct management of other components is either prohibitively expensive or untenable because of logistic limitations or a lack of knowledge of likely responses.

Fire management of heathland mosaics for conservation should aim to promote coexistence by avoiding at least two mechanisms of extinction: elimination of plants by frequent fire; and competitive elimination of understorey plants by overstorey over a series of long fire intervals. While mechanisms of animal extinction need to be identified and avoided in management, maintenance of structural and floristic diversity of vegetation may be the first step toward animal conservation.

A range of fire management options are available for conservation of heathland mosaics, for example (i) repeated application of frequent fires; (ii) repeated application of fires at intermediate intervals; (iii) a compartmental strategy where different fire regimes are applied to different patches; or (iv) a flexible strategy that seeks to implement reversible changes. Strategy (i) will cause decline and eventual extinction of overstorey species (and some understorey species), decline of dependent fauna (e.g. nectar feeding mammals and birds) and decline in certain soil resources. Strategy (ii) may avoid these effects and has some theoretical basis in the intermediate disturbance hypothesis of maximum diversity (Connell 1978), but will nonetheless cause decline and eventual loss of some understorey through overstorey competition. Strategies that are devised for management of single species or groups of species are of a kind exemplified by (i) and (ii): they identify a pre-defined schedule of fires that are perceived to be favourable or unfavourable to target species. These strategies will ultimately fail to meet broader conservation goals because they are 'blind' to dynamic interactions between components of the system that maintain its overall diversity.

Strategy (iii) is an attempt to resolve apparent conflicts in requirements of different species, by assigning them to specially managed patches. However, this static view of a mosaic is also unlikely to succeed because it ignores the temporal dimension of interactions and the vagaries of unplanned fires. The most appropriate strategy is a flexible one (iv) that is responsive to the existing state of the system and its direction and rate of change. Such a strategy is likely to result in a fire regime that is variable in space and time. The goal is to ensure that changes are reversible, rather than seeking to prevent change. Long or short fire intervals may need to be implemented over part of a mosaic from time to time to avoid spatially extensive extinctions. For example, a single short fire interval may release understorey species from suppression and is apparently insufficient to drive obligate-seeding overstorey species to extinction. Although the latter may decline, they may recover if subsequent fire intervals are long and the area affected by the short interval was not overly extensive.

Both strategies (iii) and (iv) must explicitly consider the scale fire mosaics. Mosaics are often put forward as a panacea for fauna conservation, but may fail if implemented at too fine a scale. Minimum viable habitat patch sizes and the concentration of predators on small patches may set a lower limit on the scale at which mosaics benefit biodiversity.

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