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ERRATA

- p 6 para 3, line 3: insert "in terms of long-term survival" after "lower susceptibility"
- p 12: add at end of first sentence in para 2 "Sand heathland is here defined as heath vegetation that occurs on sandy substrates."
- p 17 para 2, line 1: insert "(Parks Victoria 1998)" after "management aims for the Park"
- p 27 para 2, line 8: insert "of oven-dry soil" after "saturation capacity"
- p 28 para 1, line 11: insert "(Munsell soil colour charts)" after "soil colour"
- p 28: add at end of para 1 "In addition, soil samples were taken from the B₂ horizon at BS-0.5 and T2-27, to determine whether any differences occurred in soil properties between horizons at these sites."
- p 30-33, 37-38: replace "O1", "O2", "A1", "A2", "A3", "B1" and "B2" with "O₁", "O₂", "A₁", "A₂", "A₃", "B₁" and "B₂"
- p 30 para 3, line 1-2: "grey to dark greyish brown" for "grey-brown to brown"
- p 30 para 3, line 9: "a slightly darker grey" for "grey-brown"
- p 30 para 4, line 2: "grey to a light brown/reddish grey colour" for "white to an orange hue"
- p 40: add at end of fourth sentence in para 2 "This site was considered to be representative of other sites within the heath."
- p 47 line 1: equation should read " $S_{MM} = S_{max} n_{sat} / (B + n_{sat})$ "
- p 47 line 2: insert " S_{MM} is the estimate of site species richness based on extrapolation of the Michaelis-Menten equation," after "where"
- p 47 line 8: equation should read " $S_{Jack1} = S_{obs} + L(n - 1/n)$ "
- p 47 line 9: insert " S_{Jack1} is the first-order jackknife estimate of site species richness," after "where"
- p 49 para 2, line 4: "is considered" for "has been well-argued as being"
- p 50 para 2, line 4: equation should read " $J' = H'(\text{observed}) / \log_2(S)$ "
- p 50 para 2, line 10: equation should read " $H' = - \sum_i p_i (\log_2 p_i)$ "
- p 79 figure caption, line 2: equation should read " $S_{MM} = S_{max} n_{sat} / (B + n_{sat})$ "
- p 116 para 2, line 5: equation should read " $Y = aX^b$ "
- p 116 para 2, line 6: "x" for "b" and "b" for "x"
- p 129 figure caption, line 2: equation should read " $Y = aX^b$ "
- p 150 table heading, line 1: "the seven sites" for "every site"
- p 164: comment at end of second last sentence in para 2 "Seed germination relates to the percentage of individuals in post-fire stands that germinated from seed."
- p 198 para 3, line 2: insert "there is strong evidence to suggest that" after "First,"
- p 205 para 8, line 1: "Pickctt, S.T.A." for "S.T.A., P."

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Succession in sand heathland at Loch Sport, Victoria:
changes in vegetation, soil seed banks and species traits

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ABSTRACT

In the sandy, nutrient-poor heathlands of south-east Australia, fire and its related effects act as the trigger promoting mass regeneration of many species. In a sense, fire resets the successional clock. However, the manner in which succession proceeds is dependent on the various components of the fire regime (frequency, season, intensity and type of fire). This study investigated vegetation succession in the heathlands of the Gippsland Lakes Coastal Park in south-east Australia and specifically examined three issues: (a) the pattern of change in the heath with time since fire, (b) the effect of sampling grain on these patterns, and (c) whether species present at different times since fire differed in their regeneration biology.

Species richness (total and mean), evenness (J) and diversity (H) were all found to decrease significantly with time since fire (13 different ages up to 27 years post-fire). In addition, species composition differed significantly according to site age. However, relationships between these parameters and site age were often found to be scale-dependant, i.e. a trend was evident at one sampling grain but absent at another. Furthermore, community heterogeneity was unrelated to time since fire.

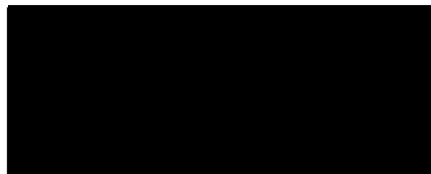
The species richness and seedling density of the germinable soil seed bank were both unrelated to site age. However, species composition of the soil seed bank differed significantly among age classes, with the greatest difference existing between young (0-6 years since fire) and old (23-27 years since fire) sites. There was no trend in the similarity between the extant vegetation and composition of the germinable soil seed bank with increasing time since fire.

Species occurring only in the vegetation of young sites were characterised by their intolerance to establishing in the presence of adult ~~competition~~^{an}, and the unassisted mode of dispersal^(e.g. gravity). Species occurring solely in old sites were characterised by their longevity, tolerance to establishing in the presence of adults ~~competitors~~, wind-dispersal and obligate resprouting. Species that occurred across young, intermediate and old-aged sites were characterised by their longevity, intermediate propagule size, tolerance to establishing in the presence of adult ~~competition~~ and their shrub life-form.

Succession in the heath appeared to correspond well with Egler's 'Initial floristic composition' model. However, even though the heath appears to fit this model of succession, the effect of different fire regimes is largely unknown and can only be inferred. This study has highlighted the importance and effect that spatial scale (sampling grain) may have on the interpretation of ecological data in heathlands.

DECLARATION

To the best of my knowledge, this thesis contains no material that has been accepted for the award of any other degree or diploma in any university or other institution, and does not contain any material previously published or written by another person, except where due reference has been made in the text.



Timothy Jarrod Wills

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CHAPTER 1

INTRODUCTION

WORLD PERSPECTIVE ON HEATHLANDS

Heathlands are found across a broad climatic spectrum, ranging from the tropics to the subarctic and from lowland to alpine regions (Specht 1979a). Throughout the world, heathlands are characterised by (a) their evergreen, sclerophyllous ^{vegetation} nature, (b) the presence of one or more of the heath families, Diapensiaceae, Empetraceae, Epacridaceae, Ericaceae, Grubbiaceae, Prionotaceae and Vacciniaceae, and (c) their restriction to highly infertile soils (Specht 1979a; Groves 1981). True heathlands are devoid of emergent trees and tall shrubs, and are characterised by a dense to mid-dense assemblage of evergreen, sclerophyllous shrubs and subshrubs less than 2 m in height, with seasonal geophytes, grasses and herbs also present, although usually in smaller numbers (Specht 1979a; Specht 1979b).

The Australian heathland flora is considered to be very similar in physiognomy, morphology and physiology to the vegetation of other Mediterranean-type climates of the world, namely, the *maquis (macchia)* and *garigue* around the Mediterranean Sea, the *chaparral* of California, and the *matorral* of Chile (Schimper 1903 in Specht 1979b). However, Australian heathlands are most closely allied with the South African *fynbos* (Specht 1994).

SOUTHERN AUSTRALIAN LOWLAND HEATHLANDS

Climate and soils

Australian heathlands exist across a broad climatic spectrum, ranging from the monsoonal tropics in the north, to the more temperate climate of southern Australia, with the arid expanse of central Australia appearing to be the only climatic zone where heath is largely absent (Specht 1979b; Specht 1994). Heathlands are also found extensively along an elevational gradient from coastal areas to the alpine regions of the eastern seaboard (Specht 1979b).

Within this broad climatic and distributional range, heathlands in the lowland areas of south-east Australia are restricted to environments characterised by soils of extremely low nutrient availability (Specht & Moll 1983; Adams *et al.* 1994; Cheal 1996). In fact, the levels of available soil nutrients, particularly phosphorus, are thought to be the major determinants influencing heathland distribution (Beadle 1954; Beadle 1962; Specht 1979b). South-eastern Australian lowland heathlands develop on a wide range of soils, including (a) windblown sands, (b) soils derived from sandstone, quartzite or granite parent material, (c) highly leached soils such as podzols and lateritic podzols, and (d) peat (Specht 1994). Furthermore, these heathlands are often broadly subdivided into wet heathlands (poorly drained or seasonally waterlogged) and dry heathlands (seasonally droughty) depending on substrate permeability (Groves & Specht 1965; Specht 1979b).

Species richness, structure and composition

Fire is the usual form of landscape-scale disturbance in south-eastern Australian heathlands, with species richness commonly peaking in the first few years following fire (Specht *et al.* 1958; McMahon 1984b; Wark 1996). This trend is exhibited in both dry and wet heathlands, however, dry heathlands are usually more species-rich (Specht 1979b). Species richness is also generally greater in heathlands where emergent trees or dominant overstorey shrubs are absent, as their cover tends to exclude species in the lower strata (Specht & Morgan 1981; Specht & Specht 1989). Similar patterns have also been recorded in South African fynbos (Cowling & Gxaba 1990).

Generally, heathlands may be structurally divided into three broad strata (Specht 1979b; Specht 1994). The upper stratum comprises deep-rooted nanophanerophytes (up to 2 m tall) with relatively broad, sclerophyllous leaves. The mid-stratum is characterised by relatively shallow-rooted nanophanerophytes (0.5-1.5 m tall) with narrow semi-sclerophyllous leaves. Finally, the ground stratum comprises a mixture of sclerophyllous hemicryptophytes and shallow-rooted chamaephytes with small, densely packed leaves (Specht 1994).

True heathlands (in the structural sense of the word) are found in most areas of Australia, but are generally restricted to relatively small patches in the midst of taller scrubs, woodlands and forests that occur on soils with slightly greater nutrient

availabilities (Specht 1979b). As environmental conditions become increasingly favourable, and/or time since disturbance (usually fire) increases, the heath elements often become overtopped by taller shrubs and trees, mainly of the genera *Banksia*, *Allocasuarina* and *Eucalyptus* (Specht 1994).

Temperate heathlands of south-east Australia are dominated by the dicotyledonous families, Fabaceae (13 genera), Myrtaceae (11 genera), Epacridaceae (eight genera) and Proteaceae (eight genera), the monocotyledonous families, Orchidaceae (13 genera), Cyperaceae (seven genera) and Poaceae (seven genera), and Pteridophytes (nine genera) (Specht 1994). Generally, these heathlands are characterised by an abundance of shrubs, with sedges and similar sclerophyllous monocots common, while grasses and ephemeral herbs are noticeably rare (Specht 1994; Cheal 1996).

THE IMPORTANCE, INFLUENCE AND EFFECT OF FIRE IN HEATHLANDS

Fire as a form of disturbance

Fire is undoubtedly the principle^{al} form of landscape-scale disturbance in south-eastern Australian lowland heathlands, predominantly owing to the characteristically dense vegetation, the tendency for dead foliage to remain on some species, the relatively slow rates of litter decomposition and the large proportion of sclerophyllous species possessing high concentrations of volatile oils and resins in their leaves (Specht 1979a; Specht 1981b; Keith *et al.* 2002). These factors, together with the hot and dry weather conditions experienced each summer, render south-eastern Australian lowland heathlands highly susceptible to fire (Gill & Groves 1981).

Although fire is often seen as a catastrophic disturbance in these heathlands, many species are dependent on fire for their continued regeneration and persistence, whether by seed or resprouting (Whelan 1995). In fact, fire is literally the event that acts to 'restart' the successional process. Following fire, resource competition is thought to dramatically decrease as a result of reduced overstorey cover and an associated increase in light availability (Specht & Specht 1989; Keith & Bradstock 1994; Keith 1995). In addition, soil nutrient availability has been shown to increase in the immediate post-fire environment, owing to the mineralisation of organically-bound nutrients during fire (the 'ash-bed' effect) (Specht 1979b; Warcup 1980; Humphreys & Craig 1981). Changes in

soil temperature regimes (Auld & Bradstock 1996), a reduction in seed predation (O'Dowd & Gill 1983; Bond *et al.* 1984; Bradstock 1991) and lower levels of root pathogens (Specht 1979b) and allelopathic chemicals in foliar and litter leachates (del Moral *et al.* 1978; Gill & Groves 1981; Keeley *et al.* 1985) may also be associated with the immediate post-fire environment. In combination, these factors facilitate an environment conducive to plant regeneration, compared with unburnt heath, where regeneration is uncommon (Specht *et al.* 1958; Meney *et al.* 1994; Benwell 1998).

Fire regime

The continued persistence and success of plant species at any given site is dependent upon the local fire regime, which consists of four components: the type, intensity, season and frequency of fire (Gill 1975; Gill 1981a). Because every species responds differently to a given fire regime, variation in each of these components may result in significant differences in vegetation species composition, richness and diversity at a given site (Bond & van Wilgen 1996).

Fire type is the component of the fire regime that distinguishes between above- and below-ground fire (Gill & Groves 1981). Most fires occur above-ground, however, in areas where a peat or humus layer is present in the substrate, fires may burn below-ground for substantial amounts of time (Gill & Groves 1981; Gill 1993). Fire intensity may be measured in terms of fire temperature, the rate of spread of a fire, soil heating during the passage of fire, and levels of plant scorch (Byram 1959; Gill & Groves 1981; Bradstock & Auld 1995; Auld & Tozer 1999). Fire intensity is influenced by a number of factors, including fuel load, fuel moisture, slope, temperature, humidity and wind speed (Gill & Groves 1981), and it may have significant impacts on species composition and abundance (Moreno & Oechel 1991; Rice 1993; Segura *et al.* 1998). The season of fire is another component of the fire regime influencing species survival and persistence, and is often related to fire intensity (Bond 1980; Le Maitre 1987; Enright & Lamont 1989). Finally, fire frequencies have the potential to substantially affect the composition and relative abundance of species within heathlands. This is mainly due to their influence on whether species have the opportunity to reach reproductive maturity and produce sufficient seed to re-establish themselves (Cary & Morrison 1995; Morrison *et al.* 1995; Bradstock *et al.* 1997).

Post-fire species regeneration

The response of plants to fire is an important facet of community dynamics in heathlands, influencing the speed at which species regenerate and gain biomass after fire (Specht 1981b; Bellingham & Sparrow 2000; Bond & Midgley 2001), the time to reach reproductive maturity (Benson 1985) and the capacity for species to tolerate different disturbance (fire) regimes (Gill & Groves 1981; Bell *et al.* 1984; Keith 1996; Gill & McCarthy 1998). In a seminal paper by Naveh (1975), three modes of fire-response were recognised: obligate seed regeneration (OS) (recovery only from seed), facultative resprouting (FR) (recovery from seeds and vegetative resprouts) and obligate resprouting (OR) (recovery only from resprouts). However, despite the prevalence of resprouting in many mediterranean-type systems, the importance of persistence (via sprouting) has often been overlooked in favour of seed-based recruitment models of succession and diversity (Bond & Midgley 2001).

Recruitment from seed

For species killed by fire, regeneration from seed is the only means of persistence, and occurs via three sources (Gill 1981a; Gill 1981b). First, some species store seed on the plant in protective woody fruits (serotiny/bradyspory) that are predominantly triggered to open and release seed at the time of fire, immediately after fire, or upon death of the branch bearing the woody fruits (Specht 1979b; Gill 1981a; Bell *et al.* 1984; Lamont *et al.* 1991; Whelan *et al.* 1998). Second, many species store seed in the soil that is triggered to germinate by soil heating, the leaching of smoke by-products, or other mechanisms associated with fire (Gill 1981a; Bell 1999). Finally, some fire-sensitive (fire-killed) species have no seed store in the burnt area; instead, they rely on post-fire seed dispersal into the system (e.g. bird-dispersed, parasitic mistletoe species such as *Amyema* spp.) (Gill 1981a).

Although fire-cued seed germination allows species to take advantage of the benefits provided by the immediate post-fire environment (e.g. high light and nutrient availability, and low competition levels), there are a number of risks involved for obligate seed regenerators. These risks are predominantly related to species characteristics such as the juvenile period, seed longevity, plant longevity, and the ability of plants to regenerate in the presence of adult competition during the inter-fire

period (Noble & Slatyer 1980). Depending on the traits of individual species, variation in components of the fire regime may facilitate local species extinctions (Keith 1996; Midgley 1996; Bond 1997). For example, high frequency fire regimes may lead to the local elimination of obligate seed regenerating species with juvenile periods greater than the time elapsed between fires, as they may have insufficient time to reach reproductive maturity, and are therefore unable to set enough viable seed to germinate successfully in the interval between fires (Noble & Slatyer 1980; van Wilgen 1981; Zedler *et al.* 1983; McMahon 1984a; Cary & Morrison 1995; Morrison *et al.* 1995; Bradstock *et al.* 1996; Keith 1996; Gill & McCarthy 1998). Conversely, low fire frequencies (long intervals between fires) may lead to the extinction of relatively short-lived species with transient or weakly persistent soil seed banks that depend on fire and its associated effects for regeneration (Keith 1996). Therefore, obligate seed regeneration may be a high-risk strategy for certain species if fire does not occur within a particular window of time. However, for most other species, it is a highly effective mode of regeneration that maintains genetic variability within populations and allows dispersal.

Vegetative regeneration

Obligate resprouters are defined as those plants that survive fire when reproductively mature individuals are subject to 100% leaf scorch (Gill 1981a; Gill 1981b). Although the above-ground parts of these plants may be destroyed by fire, they readily resprout from rhizomes, lignotubers, corms or bulbs protected in the soil (Specht 1979b; Gill 1981a). In addition, some tree species resprout from epicormic buds along the stem (e.g. *Eucalyptus* spp.) (Specht 1979b), while other species resprout from undamaged active aerial pre-fire buds (e.g. *Xanthorrhoea australis*) (Gill 1981b). Resprouting is generally the dominant mode of post-fire recovery in Australian heathlands and shrublands, with 65% to 80% of species possessing the ability to resprout, either obligately or facultatively (Specht *et al.* 1958; Siddiqi *et al.* 1976; Russell & Parsons 1978; Bell *et al.* 1984; McMahon 1984b; van der Moezel *et al.* 1987; Wark *et al.* 1987; Molnar *et al.* 1989; Benwell 1998).

The main advantage of obligate resprouters compared with obligate seed regenerators lies in their relatively shorter time interval to reproductive maturity (McMahon 1984b; Keeley 1986), their generally lower susceptibility to high fire frequencies (Specht *et al.* 1958; Siddiqi *et al.* 1976; McMahon 1984a; Bradstock 1990; Morrison *et al.* 1995;

Bradstock *et al.* 1997) and their ability to establish immediately after fire and add biomass to the system more quickly than seeders (Specht 1979b; Bellingham & Sparrow 2000). Furthermore, even though obligate resprouters by definition regenerate solely by resprouting, most still germinate from seed at some stage (albeit a lot less efficiently than obligate seeders), depending on the disturbance intensity and post-disturbance environmental conditions (Midgley 1996). This tendency effectively acts as a form of 'bet-hedging', allowing obligate resprouters to germinate by seed occasionally, thus conserving genetic diversity in the population (Bond & Midgley 2001).

Unfortunately for researchers, categorising species into obligate seed regenerators and obligate resprouters is a difficult task, because many species exhibit both modes of regeneration, depending on the disturbance intensity and the genetic variant at a particular site (Bellingham & Sparrow 2000; Bond & Midgley 2001). In actuality, levels of resprouting and seeding ^{may} vary continuously along gradients of disturbance intensity, both within and between species (Midgley 1996; Bellingham & Sparrow 2000). Because of the tendency for species to display both traits, Naveh (1975) introduced the term 'facultative resprouters', to describe those species that recover from both seed and vegetative resprouts. Facultative resprouters possess an advantage over obligate seeders and resprouters in that they may act as ^{both} either seeders or resprouters depending on site conditions, and disturbance severity and frequency.

Fire management and optimal fire regimes

One of the major challenges currently facing heathland management is the establishment of ecologically sound fire regimes (State of Victoria 1997). This is a complex task, owing to a range of factors including the following: (a) the need to protect life and property (from catastrophic fire), through fuel reduction burning and fire suppression activities (State of Victoria 1995; Benwell 1998; Gill 1999); (b) the desire to enhance population viability of rare or threatened plant populations (Benwell 1998); (c) the desire to maintain species diversity (van Wilgen *et al.* 1994; Bradstock *et al.* 1995; Gill 1999); and (d) the need to manipulate habitat for particular animal species (Meredith & Isles 1980; Day *et al.* 1999). In addition, management agencies must have a clear vision of the fire regimes they propose to implement for a given area. For example, do they propose to reintroduce pre-European fire regimes and restore ecosystems to pre-

settlement conditions, or do they apply fire regimes in relation to current circumstances and management priorities (Gill & McCarthy 1998)?

Many researchers have made recommendations regarding optimal fire regimes in heathlands, with most suggesting that fire frequencies every 8-15 years are required to maintain species diversity, based on species reproductive and life-history traits (Russell & Parsons 1978; Gill & Groves 1981; van der Moezel *et al.* 1987; McFarland 1988). In heathlands dominated by *Banksia ornata*, fire frequencies need to be even longer (i.e. 16 years or greater) for the obligate seeder, *B. ornata*, to successfully re-establish and replace itself (Gill & McMahon 1986). Research is also beginning to reveal that fires in the 'naturally-occurring' fire season (summer/autumn) of Mediterranean-type systems promote more effective seed germination than fires lit for fuel reduction purposes during spring, when fuel moisture levels are usually greater (Bond 1980; Le Maitre 1987; Enright & Lamont 1989). In addition, other studies recommend burning heathlands in a mosaic pattern (van der Moezel *et al.* 1987; McFarland 1988), in order to create habitat heterogeneity and maintain variability in population structures.

THE IMPORTANCE OF SPATIAL SCALE

The concepts of spatial and temporal scaling are integral to any discussion focussing on pattern and process in vegetation, as pattern and process are likely to be scale-dependent, i.e. they are likely to vary at different spatial and temporal scales (Allen & Starr 1982; Reed *et al.* 1993; MacNally & Quinn 1998). For instance, a range of factors may drive vegetation parameters such as species richness, composition, community heterogeneity and structure. At the landscape/regional scale, environmental factors such as biogeography, geology, climate and topography probably drive these parameters more so than biotic factors. Conversely, at the local level, soils, microtopography, drainage, fire regime, light availability, competition, mutualistic interactions, herbivory, plant regeneration strategies, dispersal characteristics and seed bank composition all combine to determine the make-up of the community and how it functions (Armesto *et al.* 1991; Huston 1994).

Although scale-dependence is likely in natural systems, choosing an appropriate spatial scale to study is often difficult, owing to the fact that the scale at which we interpret pattern and process may be totally different from the way in which organisms such as

plants respond to their environment (Levin 1992). Therefore, in some cases, a multi-scale approach may be the most appropriate way in which to study natural systems (Walker *et al.* 1972; Levin 1988; Þórhallsdóttir 1990; Gardner 1998). Despite the intuitive benefits of the multi-scale approach, very little work has been undertaken examining the effect of observational spatial scale in Australian heathland systems, although studies by Brown & Hopkins (1983) and Keith & Myerscough (1993) are exceptions.

HEATHLAND VEGETATION SUCCESSION

Ecological succession describes the process of change in plant species composition and abundance over time at a given site, in response to disturbance. Various models and mechanisms of succession have been proposed, tested and debated over the past century, however, three main theories appear to dominate the ecological literature (Clements 1916; Gleason 1926; Clements 1936; Egler 1954; Drury & Nisbet 1973; Connell & Slatyer 1977; Noble & Slatyer 1980; Pickett *et al.* 1987; McCook 1994).

The first theory, proposed by Clements (1916), assumes that different groups of species sequentially invade a site following disturbance, with each group of species modifying the environment to a degree, making it less favourable to themselves and more favourable to their potential successors. This concept of succession has since become known as either *relay floristics* (Egler 1954) or *facilitation* (Connell & Slatyer 1977). In contrast, Egler (1954) proposed the *initial floristic composition* model of succession, where vegetation development (succession) proceeds from the initial flora present following disturbance. Changes in species dominance are primarily due to the differential growth rates of the species present on site at the time of disturbance (Egler 1954), and the loss of species through natural mortality, rather than the result of species invasions. However, although initial floristic composition theoretically accounts for the majority of species on site, Egler (1954) considered that relay floristics may still account for the presence of some species through later invasion. Initial floristic composition is analogous to the *inhibition* model of Connell & Slatyer (1977), where 'later' species cannot grow to maturity because they are inhibited by the presence of species that established quickly after disturbance. A key feature of this model is that species are 'lost' from the system as a function of lifespan, rather than competition. Finally, the *tolerance* model described by Connell & Slatyer (1977), outlines a successional

sequence where species colonising outside of the immediate post-disturbance period are successful, irrespective of whether other species have preceded them. A key feature of this model is that species are eliminated via competition.

Australian heathlands are generally thought to adhere to the initial floristic composition model of succession (Russell & Parsons 1978; Groves & Specht 1981; Bell *et al.* 1984; Wark 1996), which is equivalent to the term *autosuccession*, described by Hanes (1971). Owing to the general lack of invading species, Groves & Specht (1981) and Specht (1994) regard most Australian heathlands as edaphic climaxes, with any structural changes probably due to human modifications to the environment. However, Gill & Groves (1981) suggest that this may not always be the case, with heathland being seral to woodlands or tall shrub thickets in some instances. Numerous studies confirm this viewpoint (e.g. Burrell 1981; Brown & Podger 1982; McMahon 1984b; Bennett 1994; Cheal 1996; McMahon *et al.* 1996; Cheal 2000). In addition, relatively high fire frequencies may cause a change in dominance (and possibly composition) in sedgeland-heath communities (the ecological drift hypothesis of Jackson 1968), with heath elements eliminated or substantially reduced, while sedges increase in abundance (Jackson 1968; Bowman & Jackson 1981; Bradstock *et al.* 1997). The opposite may occur with long inter-fire periods (Jackson 1968).

THE CHRONOSEQUENCE APPROACH

There are two main approaches for assessing successional dynamics in vegetation, permanent plot studies and chronosequences. Owing to practical limitations, long-term (greater than 15-20 years) permanent plot studies are rare (Foster & Tilman 2000), especially in Australia, although the study examining vegetation dynamics in relation to grazing at Koonamore, South Australia, is an exception (Crisp 1978). Instead, the common practice for examining vegetation dynamics over large temporal scales (often over 100 years) is to adopt the chronosequence approach (space-for-time substitution) (Pickett 1989), where a series of samples of varying time since disturbance are used in an attempt to identify or infer temporal trends in the vegetation.

Many studies have been conducted in a range of ecosystems throughout the world using the chronosequence approach. Some of these studies have concentrated on examining primary successional sequences (Reiners *et al.* 1971; de Kovel *et al.* 2000), while others

have concentrated on secondary succession following disturbance such as fire (Specht *et al.* 1958; Shafi & Yarranton 1973a; Shafi & Yarranton 1973b; Russell & Parsons 1978; Brown & Podger 1982; van Wilgen 1982; McMahon 1984b; Hoffman *et al.* 1987; McFarland 1988; Zammit & Zedler 1988; Ough & Ross 1992; Ne'eman & Izhaki 1999), clearfell logging (Ough & Ross 1992), or agricultural abandonment (Christensen & Peet 1984; Inouye *et al.* 1987; Bakker *et al.* 1996; Dalling & Denslow 1998; Bekker *et al.* 2000; Foster & Tilman 2000). These studies have been undertaken for a variety of purposes, namely, to study vegetation succession (Reiners *et al.* 1971; Brown & Podger 1982; Christensen & Peet 1984; Hoffman *et al.* 1987; Inouye *et al.* 1987; de Kovel *et al.* 2000; Foster & Tilman 2000), changes in species composition, richness and diversity (Specht *et al.* 1958; Reiners *et al.* 1971; Shafi & Yarranton 1973a; Russell & Parsons 1978; McMahon 1984b; Hoffman *et al.* 1987; Inouye *et al.* 1987; McFarland 1988), soil seed banks (Zammit & Zedler 1988; Bakker *et al.* 1996; Dalling & Denslow 1998; Ne'eman & Izhaki 1999; Bekker *et al.* 2000), soil nutrients (Specht *et al.* 1958; Inouye *et al.* 1987; Enright *et al.* 1994; de Kovel *et al.* 2000), vegetation heterogeneity (Shafi & Yarranton 1973b), biomass (Specht *et al.* 1958; van Wilgen 1982) and stand structure (Specht *et al.* 1958; McMahon 1984b; McFarland 1988; Denslow & Guzman 2000) with increasing time since disturbance.

In a study examining the advantages and disadvantages of chronosequences, Pickett (1989) concluded that space-for-time substitution was limiting because it had an averaging effect, somewhat disguising the short-term dynamics of the system in question. In contrast, Foster & Tilman (2000) saw this averaging effect as an advantage, as chronosequences "could reveal broad successional trends by averaging across site-to-site differences in species composition that occur because of differences in environmental conditions and site history." Milberg (1995) had other concerns regarding the use of chronosequences, namely, the fact that site selection for many successional studies is made on the basis of the researcher's preconceived idea of what the vegetation should look like at a given successional stage. Often, this preconceived idea assumes the species-replacement (relay floristics) view of succession (Clements 1936), which is frequently not the case in nature, particularly in Australian heathlands (Purdie & Slatyer 1976). Therefore, according to Milberg (1995), this approach may lead to potentially erroneous findings.

Chronosequence studies are potentially useful because they may indicate change in various community parameters with increasing time since disturbance, which for the purpose of this study, is fire. They may also be used to generate hypotheses about patterns and mechanisms (Pickett 1989). However, the mechanisms underlying the observed patterns can only be understood through experimentation, and/or long-term monitoring studies. In addition, there are some very important assumptions that must be recognised and addressed for a chronosequence study to be useful and worthwhile. First, environmental factors such as climate, geomorphology and soils are assumed to be similar or relatively unvarying among sites (Pickett 1989; Denslow & Guzman 2000). Second, all sites are assumed to have had the same initial pre-fire conditions. This involves the assumption that past fire history is the same, or at least randomised across sites (Morrison *et al.* 1995). If both of the above assumptions are met, any trends among sites are assumed to be due to the time elapsed since fire, rather than environmental differences. One of the inherent dangers in using the chronosequence approach is that unknown historical and/or site factors may explain a portion of the variation among sites (Pickett 1989). However, if the above criteria are met, and trends are evident along the chronosequence, then the chance that inherent site differences are causing the trends is minimised, and the likelihood that time since fire may be a determining factor is enhanced.

AIMS, SIGNIFICANCE AND OVERVIEW OF THE STUDY

This study uses the chronosequence approach to investigate vegetation succession in the sand heathlands of the Gippsland Lakes Coastal Park, near the township of Loch Sport, in eastern Victoria, Australia. The study area has a relatively detailed fire history and consists of an extensive heathland (c. 3,500 ha) with multiple post-fire age classes. Environmental factors such as climate, geomorphology and topography are remarkably similar throughout the study area, implying that the study area seemingly meets the fundamental assumption of the chronosequence design (Pickett 1989).

The general aims of this study are to:

- (1) determine the pattern of vegetation change in the Loch Sport sand heathland in relation to time since fire, in terms of

- (a) above-ground (extant vegetation) species richness, evenness, diversity, composition, community heterogeneity, community structure and life-form richness, and
 - (b) below-ground (soil seed bank) species richness, seed density and composition;
- (2) determine the effect of spatial scale (sampling grain) on vegetation species richness, evenness, diversity, composition and community heterogeneity, with changing time since fire; and
 - (3) determine whether species present at different successional stages differ in their regeneration biology.

Numerous studies have examined the successional response of heath-type vegetation communities to fire, with most of these studies including basic community descriptors such as species richness and composition (e.g. Russell & Parsons 1978; Cheal 2000). Some studies have also determined species diversity, community structure and life-form diversity (e.g. Specht *et al.* 1958; Hanes 1971; McMahon 1984b; Hoffman *et al.* 1987; McFarland 1988; Enright *et al.* 1994; Wark 1996). However, none appear to have examined community heterogeneity through a successional sequence. This study attempts to examine all of the aforementioned vegetation parameters and determine the effect of multiple sampling grains upon each of these (a first for any successional study in Australian heathlands). In addition, soil seed banks and the biological traits of each species will be assessed in relation to time since fire, to gain a more complete understanding of regeneration dynamics and successional processes in south-eastern Australian heathlands.

Soil seed bank studies are an effective means by which absolute species richness at a site can be estimated (Valbuena & Traubald 2001), rather than simply above-ground richness, which is the parameter most often used to determine species richness of heathlands. Soil seed bank studies can also indicate whether short-lived or post-fire ephemeral species are present in the heathland soil, waiting for fire to break seed dormancy and induce germination. Despite the value of these studies, little work has been undertaken to document the soil seed banks of south-eastern Australian heathlands, although studies by Carroll & Ashton (1965) and Molnar *et al.* (1989) are exceptions.

In Chapter 2, the study area is described, with a particular focus on environmental variables, conservation and fire history, and the methods used in selecting study sites. Chapter 3 focuses on soils and encompasses two main themes: (a) a description of the study site soils, and (b) validation of the chronosequence design. The vegetation of the study area is described in Chapter 4, with the effect of time since fire on species richness, evenness, diversity, composition, life-form diversity, community heterogeneity and structure determined. Chapter 5 examines the effect of spatial scale, in particular, sampling grain, on the vegetation parameters measured in Chapter 4. The effect of sampling grain on trends in vegetation parameters with time since fire is also assessed. Chapters 6 and 7 focus on the soil seed bank. Chapter 6 is a pilot study determining optimal experimental procedures and treatments to promote seed germination, while Chapter 7 examines the effect of time since fire on the species richness, density and composition of the soil seed bank, and the similarity between the soil seed bank and the extant vegetation. In Chapter 8, the biological and ecological characteristics of each species, which influence how a species regenerates and subsequently survives after disturbance (fire) are examined, to determine whether species that occur only in early successional stages possess different traits to those occurring in late successional stages. Finally, Chapter 9 attempts to synthesise all of the previous chapters and discusses the findings in terms of vegetation succession theory.

CHAPTER 2

STUDY AREA AND SITE DESCRIPTIONS

The study area is situated approximately 230 km east-south-east of Melbourne, in Victoria, south-east Australia (Figure 2.1), and comprises approximately 3500 ha of sand heathland, located predominantly within the 17600 ha Gippsland Lakes Coastal Park. The study area is located between the townships of Golden Beach and Loch Sport, and is surrounded by Lake Victoria in the north, Lake Wellington to the north-west and Lake Reeve in the south, forming part of what is collectively known as the Gippsland Lakes. These waterbodies encompass a broad range of conditions ranging from the brackish to hypersaline swamps and lagoons of Lake Reeve, to the fresh to saline waters of Lake Wellington and Lake Victoria (Harris 1976). Immediately adjacent to Lake Reeve is the coastal barrier system and the 90 Mile Beach (Harris 1975).

CLIMATE

The closest weather station to the study area is the East Sale Airport, which is 22 km west-north-west from the south-west extremity of the study area. The climate here is typically mediterranean, with warm summers (mean maximum and minimum temperatures of the warmest month are 25.2°C and 12.7°C respectively) and cool to mild winters (13.7°C and 3.2°C respectively). The mean annual rainfall of 616 mm is spread evenly throughout the year with a small peak in late spring (63 mm per month in November). Climate averages are based on 57 years of data (Bureau of Meteorology 2000) and are considered to be representative of the study area.

GEOMORPHOLOGY

The study area is largely composed of a level sandplain, with a small area of stabilised dunefields toward the eastern end. The sandplain and associated dunes are thought to have originated from siliceous beach and dune ridge barrier deposits, laid down when sea level was higher than present (Geological Survey of Victoria 1967; Jenkin 1968; Harris 1976). Elevation is constant at approximately 5-10 m above sea level (a.s.l.),

apart from the dunes, which reach heights up to 20 m a.s.l. There is no stream channel development within the study area.

SOILS

Soils of the study area consist of deep, uniform, well-drained, siliceous sands that are highly acidic. Profile development is poor, with grey-brown sands found at the surface, whitish-grey to white sands below, and orange sands deeper down the profile. Owing to the well-drained and highly leached nature of the soil profile, nutrient levels and organic matter content in the soil are extremely low. A detailed analysis of soils is given in Chapter 3.

VEGETATION

Across most of the broad study area, there is a clear transition between vegetation types along a gradient of soil moisture, fertility and salinity. The predominant vegetation type of the study area is heath found on sandy substrates. Within this 'sand heath', the shrub, *Leptospermum myrsinoides* is the dominant species, with *Monotoca scoparia*, *Banksia marginata*, *Allocasuarina misera*, *Epacris impressa* and *Caustis pentandra* also abundant in the mid-stratum. *Hypolaena fastigiata* dominates the ground stratum, while the tree, *Banksia serrata*, and the 'mallee-form' eucalypts, *Eucalyptus* aff. *willisii* (Gippsland Lakes) and *E. viminalis* ssp. *pryoriana*, are emergent and scattered throughout. On soils of relatively greater moisture availability and higher fertility, the sand heath gives way to a herb-rich woodland. This community is characterised by an abundance of forbs, grasses and orchids, with *E. viminalis* ssp. *pryoriana*, *E. radiata*, *B. serrata* and *Acacia mearnsii* dominant in the overstorey, and *Pteridium esculentum* and *A. longifolia* var. *sophorae* common in the midstorey (Davies & Oates 2001). Moving closer to the lakes, the woodland community is frequently bounded by a dense *Melaleuca ericifolia* scrub, with a halophytic ground layer of graminoids and herbs (Davies & Oates 2001). Finally, coastal saltmarsh is abundant on the more saline margins of Lake Reeve (Davies & Oates 2001).

CONSERVATION MANAGEMENT

The Gippsland Lakes Coastal Park was proclaimed in 1979 and is reserved under Schedule 3 of the National Parks Act (Parks Victoria 1998). Parks Victoria manages the majority of the Park for both conservation and recreation purposes, however, the section between Beacon Swamp Track and Tip Track is managed solely for conservation (Parks Victoria 1998). Wellington Shire Council also manages a small portion of the eastern and western extremities of the study area.

The relevant conservation management aims for the Park are to:

- Protect and conserve the natural environment
- Allow natural environmental processes to continue with a minimum of interference
- Maintain biodiversity
- Conserve native plant communities
- Improve knowledge of the Parks' native vegetation and its management requirements
- Actively manage significant flora species where required
- Provide special protection and undertake specific management for threatened fauna and communities where appropriate (Parks Victoria 1998)

FIRE HISTORY AND MANAGEMENT

Prior to European settlement in Australia, Aborigines burned much of the landscape regularly for a variety of reasons, such as optimising the local abundance of food plants, providing favourable habitats for animals they hunted, signalling, and clearing vegetation to facilitate travel (Bowman 1998). Fire regimes are predominantly thought to have altered from a relatively high frequency, low intensity regime maintained by the Aborigines, to a low frequency, high intensity regime caused by the accumulation of fuel associated with active fire suppression following European settlement (Burrows *et al.* 1995; Bowman 1998; Ward *et al.* 2001). Conversely, Gell *et al.* (1993) found evidence for a marked increase in fire frequency in East Gippsland, Victoria, following European settlement. This was then followed by a much lower fire frequency associated with fire suppression policies implemented after the massive fires of 1939 that burnt large areas of Victoria. Despite the contradictory nature of these studies, one certainty is that evidence regarding the pre- and post-European fire history of the study area is

largely unknown, and any attempt to infer fire history without the proper techniques is fraught with danger.

Wildfire is a significant and constant threat in the study area, with government policy directing that all fires on, or threatening public land, be brought under control (State of Victoria 1995). In order to minimise the risk of wildfire, prescribed burning for fuel reduction purposes has been undertaken by the Department of Natural Resources and Environment (DNRE) and the Country Fire Authority (CFA) within the study area since at least 1981. Fire history mapping of wildfires and prescribed fires was commenced in 1981 by DNRE, however, prior to this, there are no detailed fire records for the study area.

Due to wildfire and prescribed burning over the past few decades, a mosaic of post-fire age classes exist across the study area. In 1980, a wildfire burnt approximately 290 ha, while in 1983, another large wildfire burnt approximately half of the study area (c. 1830 ha). The ensuing 14 years saw a lack of large wildfires, however, in 1999, a prescribed burn 'escaped' from control lines and burnt approximately 100 ha. Two large prescribed burns were conducted in 1997 and 2000, burning approximately 560 and 330 ha of heathland respectively. Apart from the fires listed above, all other fires within the heathland over the past 20 years have been approximately 32 ha, or smaller.

Fire is pivotal to the success of conservation efforts in the study area. Currently, there are two main foci of burning in the study area. Firstly, there is the asset protection advantage provided by fuel reduction burning near the township of Loch Sport (between Tip Track and the Loch Sport golf course). Secondly, there is an ecological focus across most of the study area aimed at maintaining suitable habitat for the New Holland Mouse (*Pseudomys novaehollandiae*) (G. Hollis pers. comm.), which is critically endangered in Victoria (Parks Victoria 1998). This burning program also has the joint management benefit of reducing fuel loads and consequently, the potential intensity of wildfires (State of Victoria 1995). Despite the conservation focus across much of the study area, the burning program is heavily biased toward conservation of the New Holland Mouse, whilst the fire-related requirements for the survival of individual plant species have yet to be addressed and incorporated into prescribed burning programs.

Presently, approximately half of the sand heathland within the study area is over 20 years of age. Owing to the New Holland Mouse's preference for early successional or regenerating heath two to nine years old (Hollis 1996), Park management aims to implement a burning program that will reduce the amount of vegetation contained within older age classes, therefore enlarging the area of suitable Mouse habitat (L. Jeremiah pers. comm.). Park management is currently in the process of implementing an ecological burning program, where the aim is to burn three discrete blocks spread between the Gippsland Lakes Coastal Park and the nearby Lakes National Park each year (B. Houghton pers. comm.).

STUDY SITE SELECTION AND ESTABLISHMENT

Fifteen study sites were chosen according to three selection criteria. First, sites had to be on sandy soils and comprise 'heath' vegetation, or a potentially related successional stage. Specht (1970) defined heath as vegetation less than 2 m in height, with a projective foliage cover of the tallest stratum greater than 30%. Scattered, emergent trees are allowable under this definition of heath (Specht 1970). All sites were classified as heath, according to Specht's definition, except SS-26 and T2-27, which possessed an average vegetation height (excluding emergent trees) of 2.3 m and 3.4 m respectively, placing them in the 'scrub' classification of Specht (1970). Second, sites were required to be at least 4 ha in size, in order to gain a comprehensive overview of community composition, richness and heterogeneity for a particular post-fire age. However, five of the study sites were smaller than 4 ha, owing to (a) inaccuracies in establishing site boundaries due to navigational difficulties in extremely dense vegetation (WT-16 and T2-27), (b) the approximately linear shape of fire patches that were narrower than originally thought (SS-6 and TT-9), and (c) the presence of a more mesic, non-heathland vegetation type at the base of a dune (WT-2.5). Finally, each site had to be of a different post-fire age (time since fire) to allow comparisons to be made among ages. The major characteristics of the study sites are given in Table 2.1.

It is clear from Figure 2.2 that most of the recently burnt (relatively young) sites are situated at the north-east end of the study area, largely due to the greater incidence of prescribed burning near the township of Loch Sport. A range of young and old sites randomly dispersed throughout the study area would have been optimal from a design

perspective, so as not to confound site location with time since fire, however, such a distribution of ages was unavailable. In addition, a broader range of ages would have added depth to the study. However, within the study area, there was no evidence of heath older than 27 years, or a related late successional stage comprising scrub or heathy woodland vegetation. The only woodland in the study area was confined to the lake-side margins of the heath, and occasional depressions, which appear to be slightly more nutrient-rich and mesic than the adjoining heath – factors that do not suit the assumptions of the chronosequence approach.

Apart from the 15 study sites there is only one other patch (*c.* 350 ha at Track 3), burnt between *c.* 1974 and March 1976, that I am aware of that meets the site selection criteria. Other fire patches were located, such as those along Lakeside Track, however, these were thin strips less than 70 m wide, and were often not heath vegetation. In addition, fires occurred in 1986, 1989 and 1992, between Tip Track and the Loch Sport golf course, however, these fire patches were not sampled, owing to inadequate patch size, inappropriate vegetation type, and/or fire boundaries being overridden by more recent fires (which were subsequently sampled). Furthermore, a number of patches pre-dating DNRE fire history mapping were located, with four of these chosen as study sites (GP-23, T4-25, SS-26 and T2-27). Apart from the patch mentioned earlier, the likelihood of finding any further 'old' sites is very low, as the vegetation adjacent to every track within the study area was checked for this purpose.

Once a fire patch was deemed suitable to study, a 4 ha study site was randomly chosen within the patch, with the only condition being that one of its boundaries was within 50 m of a track, for ease of access. For this study, each 4 ha site is considered to be representative of a particular post-fire age. Obviously, study sites situated in small fire patches will depict the effects of that particular burn on the vegetation more accurately than a single site located in a large fire patch, owing to the similarity between fire patch size and the size of the study site. However, in this study, I am examining variation in parameters within and between 4 ha sites only, so as not to confound age with patch area.

It should be noted here that WT-16 and SS-16 were burnt by the same fire in 1983. Although DNRE mapping indicated that these sites were the same post-fire age, visual

inspection suggested that this may not be the case, with SS-16 appearing to be notably stunted in stature, compared to WT-16. However, after dating the site using the *Banksia marginata* node count method and aerial photographs (Appendix 1), it was found to correspond with the mapped age. Therefore, to avoid the problem of pseudoreplication, data from these sites were merged and the mean values used in all analyses.

DETERMINING SITE AGE

The ages of the fifteen sand heathland patches were identified using a range of methods. First, DNRE fire history maps were used to date sites burnt from 1981 onwards. Second, an ex-ranger at the Gippsland Lakes Coastal Park gave the year of the last fire at one site pre-dating DNRE mapping (R. Cumow pers. comm.). Finally, the *Banksia* node count method, which has previously been used to determine *Banksia* and/or heathland age (Specht *et al.* 1958; Lamont 1985; Cowling *et al.* 1987; Witkowski *et al.* 1991; Witkowski *et al.* 1992; Marsden-Smedley *et al.* 1999), was used to estimate the age of the four other sites burnt before 1981, in conjunction with aerial photograph interpretation and consultation with old newspapers. Field checks at each site confirmed the accuracy of DNRE fire history mapping and the legitimacy of the *Banksia* dating method (refer to Appendix 1 for a detailed description of the verification procedure).

SITE ENVIRONMENTAL VARIABLES

Thirteen of the 15 study sites occur on a flat sandplain, lying approximately 10 m a.s.l (Table 2.1), whilst SS-5 and WT-2.5 occur on a stabilised dunefield that reaches heights up to 20 m. SS-5 comprises land covering a dune crest, dune slopes and a depression, with gently inclined slopes up to 5°, and an aspect ranging predominantly from 140° to 360°. WT-2.5 incorporates a dune crest and slopes, with gently inclined slopes up to 5°, and an aspect ranging predominantly from 0° to 50°. It should also be noted that SS-6 is at the immediate base of the dunefield where SS-5 and WT-2.5 are located.

Table 2.1 Site location, fire history and environmental information. Prescribed fire is defined as any fire ignited by management authorities for fuel reduction or ecological purposes. Wildfire is defined as any fire outside the realms of prescribed fire, including prescribed fires that escape control lines. Landforms follow McDonald *et al.* (1990).

Site code	Location	Site dimensions	Site area (ha)	Previous fires	Type of fire	Size of fire (ha)	Fire coverage (%) (estimate)	Vegetation sampling date	Site age (years)	Landform	Elevation (m a.s.l.)	Slope (degrees)	Aspect (degrees)
BS-0.5	Beacon Swamp Track	200 × 200 m	4	1999 (Mar) < 1970	Wildfire ³	100	99	13/10/99 – 15/10/99	0.5	Sandplain	10	0	-
BS-1.5	Beacon Swamp Track	200 × 200 m	4	1997 (Apr) 1983 (Mar)	Prescribed ⁴	560	99	08/12/98 – 11/12/98	1.5	Sandplain	10	0	-
WT-2.5	Waverley Track	200 × 145 m	2.9	1997 (Mar) 1989	Prescribed ⁵	9	98	25/10/99 – 27/10/99	2.5	Dunefield	10-20	0-5	0-50
SS-5	Seacombe – Sperm Whale Head Road	200 × 200 m	4	1994 (Mar) 1986 ¹	Prescribed	13	99	10/05/99 – 12/05/99	5	Dunefield	10-20	0-5	140-360
SS-6	Seacombe – Sperm Whale Head Road	270 × 130 m	3.5	1993 (Apr) < 1981	Prescribed	15	99	15/02/99 – 17/02/99	6	Sandplain	10	0	-
TI-7	Track 1	200 × 200 m	4	1992 (Apr) < 1976	Wildfire	5	98	18/02/99 – 17/03/99	7	Sandplain	10	0	-
TT-9	Trig Track	200 × 150 m	2.6	1990 (Mar) 1980 ²	Prescribed	32	99	02/02/99 – 04/02/99	9	Sandplain	10	0	-
T4-14	Track 4	200 × 200 m	4	1984 (Oct) < 1976	Wildfire ⁶	16	-	21/01/99 – 02/02/99	14	Sandplain	10	0	-
WT-16	Waverley Track	200 × 200 m	3.3	1983 (Mar) < 1970	Wildfire	1830	-	18/01/99 – 21/01/99	16	Sandplain	10	0	-
SS-16	Seacombe – Sperm Whale Head Road	200 × 200 m	4	1983 (Mar) < 1976	Wildfire	1830	99	17/09/99 – 13/10/99	16	Sandplain	10	0	-
UT-19	Unnamed track	200 × 200 m	4	1980 ² < 1976	Wildfire	290	> 96 ⁸	14/09/99 – 16/09/99	19	Sandplain	10	0	-
GP-23	Gas pipeline easement	200 × 200 m	4	1976 ⁷	Wildfire	350 ⁷	-	18/03/99 – 20/03/99	23 ⁹ (23-26)	Sandplain	10	0	-
T4-25	Track 4	200 × 200 m	4	1974 ⁷	Wildfire	-	-	13/05/99 – 15/05/99	25 ⁹ (25-28)	Sandplain	10	0	-

Table 2.1 (continued) Site location, fire history and environmental information. Prescribed fire is defined as any fire ignited by management authorities for fuel reduction or ecological purposes. Wildfire is defined as any fire outside the realms of prescribed fire, including prescribed fires that escape control lines. Landforms follow McDonald *et al.* (1990).

Site code	Location	Site dimensions	Site area (ha)	Previous fires	Type of fire	Size of fire (ha)	Fire coverage (%) (estimate)	Vegetation sampling date	Site age (years)	Landform	Elevation (m a.s.l.)	Slope (degrees)	Aspect (degrees)
SS-26	Seacombe - Sperm Whale Head Road	200 x 200 m	3.8	1974*	Wildfire	-	-	22/11/99 - 24/11/99	26 [†] (26-35)	Sandplain	10	0	-
T2-27	Trnek 2	200 x 200 m	4	1973*	Wildfire	-	-	02/10/00 - 04/10/00	27 [†] (26-28)	Sandplain	10	0	-

* 'Previous fires' and 'Site age' based on *Banksia marginata* node counts and aerial photograph interpretation (refer to Appendix 1 for methodology). Potential age range (margin of error) indicated within brackets.

1 Site was possibly burnt previously in 1986, however mapping resolution makes this difficult to determine.

2 Ross Curnow (former Gippsland Lakes Coastal Park ranger) (pers. comm.)

3 Wildfire that commenced after escaping from prescribed burn control lines (T. Wills pers. obs.).

4 Prescribed burn conducted by the Department of Natural Resources and Environment (DNRE). Very intense fire, with flame height up to 30 m (B. Houghton pers. comm.).

5 Prescribed burn. Hot fire, with flame height up to 3-10 m. Approximately 98% burn coverage (B. Houghton pers. comm.).

6 Wildfire that commenced after escaping from a private property burn off. Low intensity fire, spotting up to 50 m ahead, with a slow rate of spread. Fire is likely to have been patchy, with some areas unburnt (B. Houghton pers. comm.).

7 Size of fire based on aerial photograph interpretation.

8 Fire coverage greater than 96% based on *Banksia marginata* node counts, which indicate that less than 4% of individuals are older than approximately 25 years.

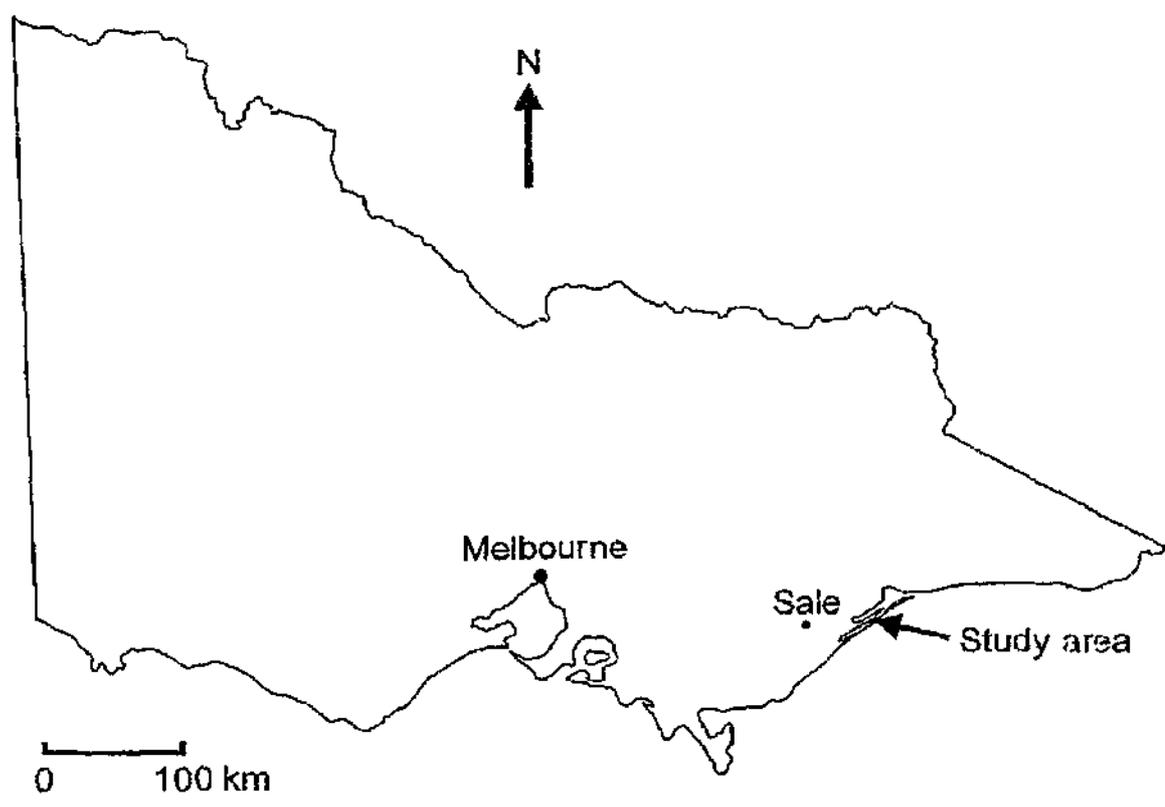


Figure 2.1 Map of Victoria showing the study area location.

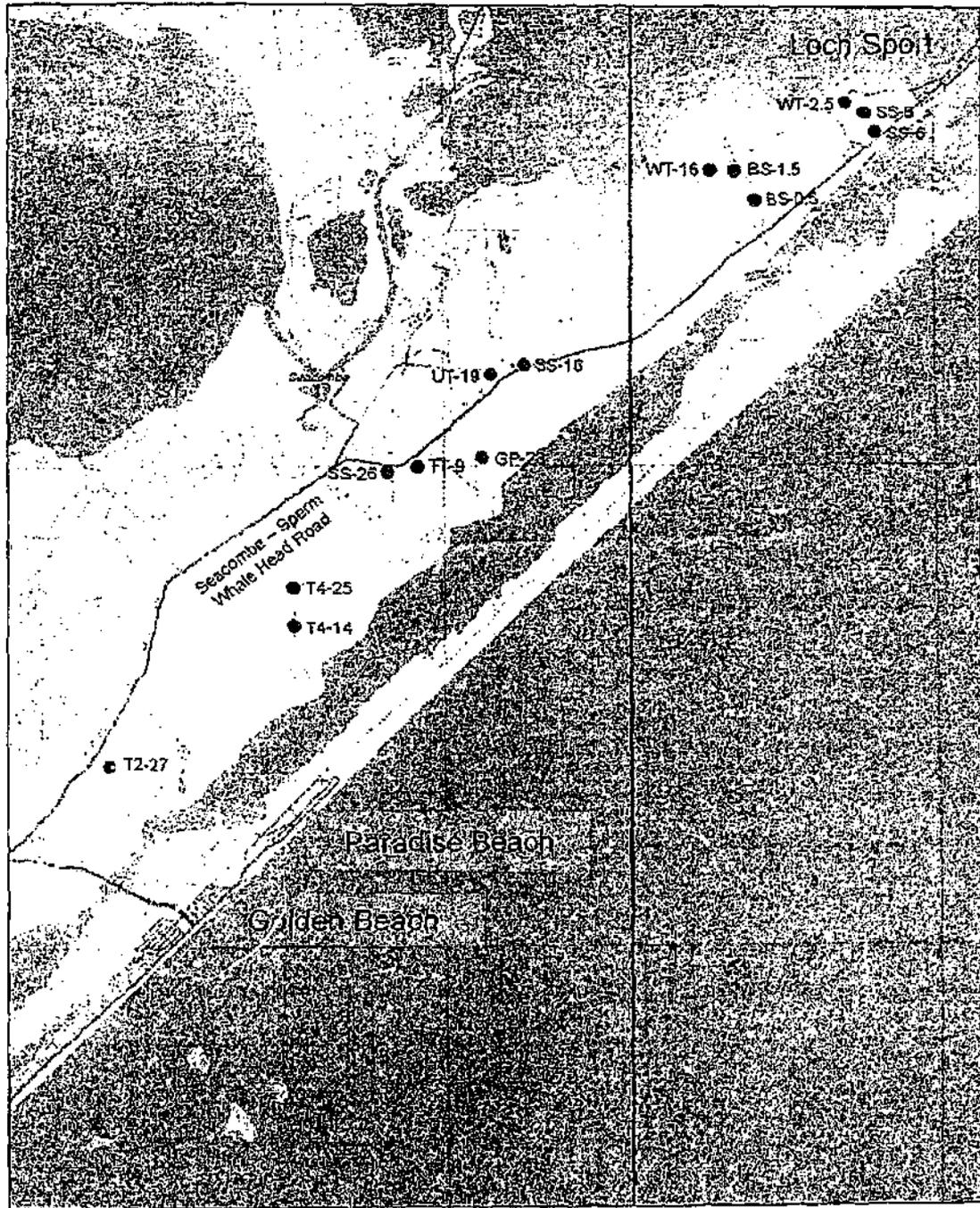


Figure 2.2 Locations of the 14 study sites.

CHAPTER 3

SOILS AND VALIDATION OF THE CHRONOSEQUENCE APPROACH

INTRODUCTION

Soil is vital for plant growth and survival, with properties such as water-holding capacity, acidity, nutrient availability, exchangeable cations and organic content combining to influence species distributions and local species composition and structure (Beadle 1954; Gill 1994). On a global scale, Australian soils are generally recognised as possessing very low nutrient levels, with heathland soils regarded as some of the most nutrient-poor in relation to other vegetation communities (Beadle 1962; Specht 1979a; Groves 1983; Specht 1994).

Soils are very complex and variable in time (Stock & Lewis 1986; Gross *et al.* 1995; Farley & Fitter 1999; de Kovel *et al.* 2000) and space (both horizontally and vertically) (Stock & Lewis 1986; Stark 1994; Gross *et al.* 1995; Farley & Fitter 1999). For example, soil nutrients^{availability} may vary temporally, with the time of year (Stock & Lewis 1986; Farley & Fitter 1999), the successional stage (age) of the vegetation (Enright *et al.* 1994; de Kovel *et al.* 2000), or the age of the parent material (Spain *et al.* 1983). One well-known fire-related effect of successional age on soil fertility is the 'ash-bed effect' (Specht *et al.* 1958; Specht 1979b; Humphreys & Craig 1981), where nutrient availability increases immediately after fire, owing to the mineralisation of organically-bound nutrients (Adams *et al.* 1994). However, nutrient levels quickly return to near pre-fire levels, usually within one year (Stock & Lewis 1986; Adams *et al.* 1994; Marafa & Chau 1999).

Despite the evidence for surface soil properties changing with time since fire, there are limited data on the effect of successional age on soils at greater depths, however, the study by Specht *et al.* (1958) is an exception. Specht and his co-workers found that levels of total C, N and P, and a range of trace elements decreased in concentration with depth (0-75 cm) in the A horizon of the soil profile, although there was evidence at one site for an increase in nutrients in the B horizon. Although no statistical tests were

undertaken, nutrient concentrations of surface samples appeared to vary substantially with time since fire, while samples taken from 30-75 cm were consistently very similar across a range of four post-fire ages to 25 years (Specht *et al.* 1958).

As this present study is based on the chronosequence approach, it is very important that each site be as similar as possible in terms of substrate. Owing to the geological and topographical uniformity of the study area, soils at depth were expected to be similar, regardless of time since fire. Conversely, properties of surface soils were expected to change more readily with time since fire because of the influence of the extant vegetation. Therefore, in an attempt to validate the chronosequence design, this study used deep soil samples to determine the degree of similarity among sites. The soil properties examined in this study are saturation capacity, loss-on-ignition, total N, available P and pH, and are chosen to reflect a range of soil properties important for plant growth and survival, including nutrient availability, organic matter content, water-holding capacity and acidity.

The study aims to:

1. describe the soils of the study area; and
2. justify the chronosequence design of the project in terms of soil properties from deep samples across the study sites.

METHODS

Soil field sampling

Soil was sampled from three randomly located points at all 15 study sites. At each random point, a combined surface sample (0-10 cm) and a deep sample (50-60 cm) were extracted using a 75 mm diameter sand auger, and the soil profile was described. Surface samples were combined from two surface cores (0-10 cm) extracted from the north and south points of a circle with a 1 m radius surrounding the random point. Surface litter was removed from the sample. Deep samples were taken beside the 'north' surface sample. Owing to the sandiness of the soil, the auger failed to extract approximately half of the deep samples (50-60 cm), therefore, these samples were taken by hand from the auger hole and may have been slightly contaminated by soil closer to the surface during the extraction process. Soil profiles were described to a depth of at least 55 cm at each point using the deep core, with horizon depths, soil colour, field texture and primary profile form noted (Northcote 1974). Profile descriptions below this depth^(down to 1.85 m) were made where possible (BS-0.5 and T2-27), and soil samples taken, to gain a broader understanding of soil profile composition.

Soil sampling was undertaken for all sites between late November and mid-December 1999, except T2-27, which was sampled in early October 2000. Following collection, soils were air-dried and stored in sealed plastic bags at room temperature until physical and chemical analyses were undertaken.

Soil laboratory analyses

Prior to conducting soil analyses, samples were reduced to a 2 mm fraction by sieving, and divided into the required weights using a Rotary Sample Divider, fed by a Vibratory Feeder. A Planetary Micro Mill (*Pulverisette-7*) was used to grind samples to 0.2 mm for use in determining total nitrogen.

Saturation capacity was calculated as the maximum amount of water a given amount of oven-dry soil could hold, following the procedure of Dewis & Freitas (1970) cited in Grimshaw (1989). pH was measured in a 1:5 (w:v) mixture of air-dry soil and distilled water (Grimshaw 1989). Percentage organic matter was estimated by loss-on-ignition at 550°C for two hours, using c. 5 g samples of air-dry soil (Grimshaw 1989). Available

phosphorus was measured on air-dry soil using the Bray and Kurtz No. 2 method (Bray & Kurtz 1945; Rayment & Higginson 1992). Total nitrogen content was determined on a 0.2 mm air-dry soil fraction using a Leco CHN-2000 analyser.

Data analyses

For the purposes of all analyses, values for WT-16 and SS-16 were combined and averaged, as these sites were both burnt by the same fire in 1983. This reduced the number of data points in all analyses to 14. Linear regression was used to examine the relationship between the mean of each soil parameter and time since fire. Pearson correlations were used to determine the degree of correlation between each soil parameter. No adjustments were made for multiple pairwise comparisons, following the reasoning of Stewart-Oaten (1995). Paired *t*-tests were used to determine whether there were differences between surface (0-10 cm) and deep (50-60 cm) samples for each soil parameter. Data were \log_{10} or $\log_{10}(x + 1)$ transformed to improve homogeneity of variances when required. Data were also analysed after removing TI-7, as this site did not meet the assumptions of the chronosequence design. The rationale for this is outlined in the *Discussion*. A critical value of $\alpha = 0.05$ was used in all hypothesis testing.

RESULTS

Soil profiles

Soil profiles displayed considerable similarity across the study area, and are described in Table 3.1. In terms of soil texture, all profiles were highly uniform, *sensu* Northcote (1974), with the greatest difference being the transition from sand/loamy sand to sand at BS-0.5, WT-2.5, T1-7, TT-9 and T4-25 (Table 3.1). There is evidence for texture uniformity occurring as deep as 1.85 m below the surface (T2-27) (Table 3.1).

In terms of horizontal differentiation, a number of zones were commonly noted. First, most sites (except two burnt recently) had a thin O1 horizon, usually less than 0.5 cm deep, comprising undecomposed organic matter such as leaves and twigs (Table 3.1). As expected, the greatest accumulation of matter in this horizon occurred in the two oldest study sites, SS-26 and T2-27.

Beneath the O1 horizon was the A1 mineral horizon, characterised by grey-brown to brown sands and loamy sands to a depth of *c.* 30 cm (Table 3.1). There was also some accumulation of humified organic matter, giving this horizon a darker colour than underlying horizons. In addition, the upper 2 cm of the A1 horizon contained a layer of dense mycorrhizal roots, particularly at the older sites. In contrast, the A2 horizon was characterised by ~~white-grey to white~~ sands from *c.* 30 cm to *c.* 70 cm below the soil surface. However, the depth of this horizon varied considerably, terminating at 45 cm at SS-5 and 155 cm at T2-27 (Table 3.1). The A2 horizon at T1-7 was noticeably different from all other sites in that sand colour was grey-brown.

The B2 horizon commenced at a depth of *c.* 70 cm (although closer to the surface at some sites), where the sand changed from a white to an orange hue (Table 3.1). Sands within the B1 horizon commonly formed aggregations up to 1 cm across, with a thin hardpan evident at two sites (BS-1.5 and SS-5). It should be noted that the B horizon is considerably closer to the surface at the dune field sites (WT-2.5 and SS-5) compared with the 13 sandplain sites (Table 3.1).

Soil analyses

All surface (0-10 cm deep) samples were taken from the A1 horizon. Deep (50-60 cm depth) samples were all taken from ~~white-grey to white~~ sand in the A2 horizon, except

~~T1-7 (all cores in grey-brown sand)~~, SS-5 (all cores in orange-brown sand, B1 horizon), and WT-2.5 (one core in orange-brown sand, B1 horizon). One core from SS-5 and WT-2.5 was taken from a depth of 45-50 cm owing to auger failure in the sandy soil.

Saturation capacity differed markedly between surface and deep cores, with most surface soils ranging from 40-70%, while deep soils were mainly between 25-30% (Figure 3.1a). Cores from the B2 horizon (BS-0.5: 70-80cm deep, T2-27: 150-180 cm deep) had a saturation capacity of 28-32%. Saturation capacity at 0-10 cm was significantly greater with increasing time since fire (\log_{10} transformed data, $F = 10.9$, $p = 0.006$), however, the oldest site (T2-27) was an outlier (Figure 3.1a). When T2-27 was removed from the analysis results were unchanged ($F = 7.04$, $p = 0.022$). When analysed without T1-7, similar results were obtained (\log_{10} transformed data, $F = 13.1$, $p = 0.004$). Saturation capacity at 50-60 cm did not differ significantly with time since fire ($F = 0.68$, $p = 0.425$), however, T2-27 was an outlier (Figure 3.1a). Conclusions were unchanged after removing T2-27 from the analysis and after removing T1-7. It should be noted that surface soils were extremely water-repellent.

Loss-on-ignition ranged between 4% and 11% for surface soils, 0.5-3% for deep samples, and 1-3% for sand from the B2 horizon at BS-0.5 and T2-27 (Figure 3.1b). Loss-on-ignition for surface samples was significantly greater as site age increased (\log_{10} transformed data, $F = 6.92$, $p = 0.022$), although T2-27 was an outlier (Figure 3.1b). After removing T2-27, loss-on-ignition was no longer significantly different (\log_{10} transformed data, $F = 3.36$, $p = 0.094$). However, when analysed without T1-7, there was again a significant positive relationship (\log_{10} transformed data, $F = 10.8$, $p = 0.007$). Loss-on-ignition at 50-60 cm was not significantly different with time since fire (\log_{10} transformed data, $F = 0.08$, $p = 0.779$) (Figure 3.1b). Conclusions were unchanged after removing T1-7 from the analysis.

Total nitrogen differed substantially between surface soils (0.08-0.25%), deep samples (0-0.04%), and the B horizon at BS-0.5 and T2-27 (0.02-0.04%) (Figure 3.1c). Total N in surface soils did not differ significantly with time since fire (\log_{10} transformed data, $F = 3.00$, $p = 0.109$), however, T2-27 was an outlier (Figure 3.1c). Results were unchanged after the outlier was removed ($F = 0.62$, $p = 0.448$), and when the data were analysed without T1-7 (\log_{10} transformed data, $F = 4.69$, $p = 0.053$). Total nitrogen for

deep samples, was also not significantly different ($F = 0.03$, $p = 0.865$). Conclusions did not differ after removing T1-7 from the analysis.

Available phosphorus was greater at the surface, with most samples ranging from $1.4 \mu\text{g g}^{-1}$ to $4.2 \mu\text{g g}^{-1}$, except T1-7, which was substantially higher at $7.7 \mu\text{g g}^{-1}$ (Figure 3.1d). Deep samples were lower in available P and ranged from $0.4 \mu\text{g g}^{-1}$ to $1.2 \mu\text{g g}^{-1}$, although T1-7 was again an exception at $1.8 \mu\text{g g}^{-1}$ (Figure 3.1d). Available P in the B2 horizon ranged from 0.7 - $1.1 \mu\text{g g}^{-1}$ at BS-0.5 and T2-27. For surface samples, available P did not differ significantly with time since fire (\log_{10} transformed data, $F = 0.02$, $p = 0.906$), however, T1-7 was an outlier (Figure 3.1d). Results did not alter after removing the outlier (\log_{10} transformed data, $F = 0.95$, $p = 0.350$). Deep samples were also not significantly related to site age (\log_{10} transformed data, $F = 1.48$, $p = 0.247$) (Figure 3.1d). Conclusions were the same when T1-7 was removed from the analysis.

Soil pH was lower at the surface, ranging from 3.7 to 4.4, compared to deep samples, which ranged from 4.2 to 4.7, and samples in the B2 horizon at BS-0.5 and T2-27 (4.7 to 5.0) (Figure 3.1e). pH decreased significantly for both surface and deep samples as site age increased (0-10 cm: $F = 35.7$, $p < 0.001$; 50-60 cm: $F = 9.69$, $p = 0.009$) (Figure 3.1e). When analysed without T1-7, conclusions for surface and deep samples were unchanged.

Pearson correlation coefficients indicated that more soil parameters were correlated for surface soils than in deep samples, when analysed with and without T1-7 (Table 3.2). For surface soils ($n = 14$), six of the 10 pairwise comparisons were significantly correlated, with total N, loss-on-ignition and saturation capacity showing the strongest correlation (Table 3.2a). Deep samples ($n = 14$) showed lower levels of correlation, with only two pairwise comparisons significantly correlated (loss-on-ignition with both available P and N) (Table 3.2b). When T1-7 was excluded from the analysis for surface samples, all pairwise comparisons were significantly correlated except available P and pH (Table 3.2c). The exclusion of T1-7 did not affect the results for deep samples.

Paired *t*-tests indicate that there are significant differences between surface and deep samples for each of the five soil parameters, with and without T1-7 in the analysis (Table 3.3).

DISCUSSION

Generally speaking, the soils of the study area are deep, uniform, strongly-leached, nutrient-poor, acidic sands. However, before any argument is presented to justify the chronosequence design, it is important to examine individual sites to determine whether they meet the chronosequence assumptions, outlined in Chapter 1. After examining the data for outliers and unusually high or low readings, two sites appeared distinctive, namely T1-7 and T2-27.

T1-7 is an anomaly in the data set for a number of reasons. First, sand in the A2 horizon was ~~grey-brown in colour~~ ^{a darker grey}, compared with the ~~white-grey~~ colour of all other sites, which suggests that T1-7 contained more organic matter. This was confirmed by loss-on-ignition results, indicating that T1-7 had the third highest organic matter content.¹ Second, available P in deep samples at T1-7 was 47% greater than the next highest site, and 137% greater than the mean of all sites, excluding T1-7. Furthermore, available P at T1-7 was an outlier in the surface soil, being 85% higher than the next site, and 241% greater than the mean of all sites, excluding T1-7. Considering that soil P is largely recognised as the most crucial nutrient affecting plant growth in Australian heathlands (Groves 1983), plant growth and species composition at T1-7 may be substantially different, compared to other sites. Finally, deep samples at every site had a higher pH than surface samples, however, the opposite occurred at T1-7. Owing to these anomalies, T1-7 does not meet all assumptions of the chronosequence design, and consequently, is excluded from the study and all further analyses.

In addition, T2-27 was an outlier in saturation capacity (surface and deep samples) and loss-on-ignition (surface sample). The greater saturation capacity and loss-on-ignition in surface soil at T2-27 is predominantly due to the greater density of mycorrhizal roots present, which markedly increases the amount of organic matter (loss-on-ignition) and the amount of water absorbed, thus increasing saturation capacity. Saturation capacity at depth was lower at T2-27, indicating that the soil was slightly sandier, having less

¹ Soils from the two sites possessing greater organic matter were taken from the B horizon. Deep samples from 70-80 cm at BS-0.5 and 150-180 cm at T2-27 suggest that the B horizon contains more organic matter than the overlying A2 horizon. Therefore, results from the two sites yielding greater loss-on-ignition are possibly inflated when compared with other sites where samples have been taken from the A2 horizon, implying that T1-7 may have the highest loss-on-ignition for soils in the A2 horizon.

fine particles than the other sites. However, these soil characteristics do not warrant exclusion of T2-27 from the study.

The two sites situated on the dunefield (WT-2.5 and SS-5) also differed from other sites in that they were not ~~found~~^{present} on the sandplain, however, no outliers in soil parameters were found at these sites, indicating that soil properties are similar to those of sandplain sites.

After careful examination of the data and the elimination of T1-7 from the data set, it appears that the assumptions of the chronosequence are met on two fronts, with respect to soil properties. First, the chronosequence appears to be validated by the uniformity and consistency of the soil profiles among sites. Second, the results of laboratory analyses indicate that soils at depth (50-60 cm) are remarkably similar across the entire study area. Because deep soil samples are likely to be less affected by time since fire and vegetation growth, the consistency among sites again suggests that the chronosequence is validated. In fact, it is extremely difficult to find a chronosequence study of at least 13 different-aged sites anywhere in the literature that are so uniform in terms of topography, elevation, geomorphology and soils. Therefore, I am confident that the chronosequence used in this study represents an effective substitution of space for time (Pickett 1989). However, it should be noted that fire history has not been controlled for in this study.

The soils of the study sites are similar to other heathlands on sand in south-east Australia, where soils are nutrient-poor and acidic (Specht *et al.* 1958; Parsons 1966; Groves 1981; Wark *et al.* 1987; Adams *et al.* 1994). In this study, soil properties also differ significantly between the surface 10 cm and 50-60 cm, with nutrient and organic matter levels decreasing with depth; a finding supported by other studies (Specht *et al.* 1958; Parsons 1966; Stock & Lewis 1986; Adams *et al.* 1989; Read 2001). However, despite the common finding that nutrient levels decrease with depth, Specht *et al.* (1958) reported an increase in C, N, P and other trace elements in the B horizon. In their review of organic matter in Australian soils, Spain *et al.* (1983) also reported that small increases in organic matter in subsoils below the bleached A horizon were not uncommon. The limited evidence from the B horizon of two sites in this study also suggests that the B horizon may be a zone of slightly higher nutrient accumulation.

In this study, levels of available P for surface soils are 1.4-4.2 $\mu\text{g P g}^{-1}$, a figure comparable to other south-eastern Australian heathlands, which range between 0.3 and 2.4 $\mu\text{g P g}^{-1}$ (Wark *et al.* 1987; Adams *et al.* 1994; Bennett 1994; Hahs *et al.* 1999). However, higher levels have been recorded, with Siddiqi *et al.* (1972) and Enright *et al.* (1994) reporting mean levels of *c.* 7.5 and 18 $\mu\text{g P g}^{-1}$ respectively. Total N in surface soils (0.08-0.25%) was also similar to other sand heathlands, which contained 0.06-0.19% N (Siddiqi *et al.* 1972; Wark *et al.* 1987; Adams *et al.* 1994) but Specht *et al.* (1958) reported lower levels (0.02-0.04%). At depth (50-60 cm), total N was very low, ranging from 0-0.04%, which is similar to deep samples taken by Specht *et al.* (1958) (0-0.01%) in south-eastern Australian heath and Stock & Lewis (1986) (0.01%) in South African fynbos. Therefore, N and P appear to be similar to many other heathlands, particularly those within south-east Australia. However, caution should be exercised when making comparisons between studies because of the different methods used in extracting and measuring soil nutrients.

Surface soils were very acidic and ranged between a pH of 3.7 and 4.4. This appears to be more acidic than other south-eastern Australian heathlands, which range from 4.5-6.4 (Raupach 1951 in Specht & Rayson 1957; Parsons 1966; Siddiqi *et al.* 1972; Wark *et al.* 1987; Adams *et al.* 1994; Enright *et al.* 1994; Hahs *et al.* 1999). As depth increased, sands also became less acidic, a trend also reported by Raupach (1951) in Specht *et al.* (1958) for the Makin sand in south-east Australia.

Generally, the properties of surface soils were highly correlated (nine out of 10 combinations), however, those of deep samples were not, with only loss-on-ignition correlated with available P and N. The reason that many surface soil properties were strongly correlated is probably due to the major influence of organic matter in the A horizon, which is usually strongly associated with loss-on-ignition and N.

Some soil properties were distinctly correlated with time since fire, particularly in the surface soils, where saturation capacity and loss-on-ignition increased significantly, and pH decreased significantly with increasing site age. At 50-60 cm depth, only pH varied significantly with increasing time since fire, with all other soil properties showing no difference. The lack of a consistent trend in deep soils suggests that the effects of fire are generally confined to surface soils. Specht *et al.* (1958) found a similar result in a south-eastern Australian heathland, where the time since fire markedly affected a range

of soil nutrients and exchangeable cations in the surface soil (0-15 cm), with the general trend being for nutrients to increase in concentration with increasing time since fire. However, soil properties at depth (30-75 cm) did not differ with changing site age (Specht *et al.* 1958). Adams *et al.* (1994) also reported similar results (but over a much finer scale) for heathlands at Wilson's Promontory, where the effects of fire (including repeated fires), on C, N and P were confined to the surface 2 cm, while soils from a depth of 2-7 cm showed no significant variation with time since fire. Furthermore, the time elapsed since fire has also been shown to contribute to increased acidity and total N for surface soils during primary succession on inland sand drifts in the Netherlands (de Kovel *et al.* 2000). However, Enright (1994) reported no trend in soil exchangeable cations and pH with site age for surface soils 0-5 cm deep.

Although some surface soil properties were shown to change with increasing time since fire, this study provided no evidence for an 'ash-bed' effect, created through the mineralisation of nutrients during fire. However, the youngest site studied was sampled eight months after fire, and any post-fire flush of nutrients may have already been leached through the soil profile, or taken up by plants, by this stage in time.

Table 3.1 Soil profile horizons, depth, Munsell field colour and field texture for each study site. All cores were taken to a depth of 55-90 cm, as soil texture prevented deeper cores being taken. T2-27 was the only site where cores were taken deeper than 90 cm.

Site	Site age (years)	Primary Profile Form	Horizon: depth (cm), field colour, field texture						
			O1	O2	A1	A2	A3	B1	B2
BS-0.5	0.5	U	-	-	0-35, grey, S/LS	35-60, grey, S	-	-	60-90+, light brown, S ²
BS-1.5	1.5	U	0-0.2	-	0-20, grey, S	20-75, grey, S	-	75-85+, brown, S ¹	
WT-2.5	2.5	U	-	-	0-25, grey, S/LS	25-40(-60), brown, S	-	(40-)60+, brown, S	
SS-5	5	U	0-0.2	-	0-30, grey, S	30-45, brown, S	-	45-65, brown, S ¹	65-75+, light brown, S
SS-6	6	U	0-0.5	-	0-30, grey, S	30-60+, grey, S			
T1-7	7	U	0-0.3	-	0-20, greyish brown, S/LS	20-55+, grey, S			
TT-9	9	U	0-0.5	-	0-30, grey, LS	30-90+, grey, S			
T4-14	14	U	0-0.4	-	0-25, grey, S	25-55+, grey, S			
WT-16	16	U	0-0.3	-	0-30, grey, S	30-60+, grey, S			
SS-16	16	U	0-0.2	-	0-30, grey, S	30-65+, grey, S			
UT-19	19	U	0-0.3	-	0-30, grey, S	30-65+, grey, S			
GP-23	23 (23-26)	U	0-0.4	-	0-30, grey, S	30-70+, grey, S			
T4-25	25 (25-28)	U	0-0.4	-	0-25(-45), grey, S/LS	(25-)45-55+, grey, S			
SS-26	26 (26-35)	U	0-1.3	-	0-30(-55), dark greyish brown, S	(30-)55+, grey, S			
T2-27	27 (26-28)	U	0-1.0	1-1.5	0-45, grey, S	45-155, grey, S	155-165, reddish grey, S	-	165-185+, brown / light brown, S

Table 3.1 (continued) Soil profile horizons, depth, field colour and field texture for each study site. All cores were taken to a depth of 55-90 cm, as soil texture prevented deeper cores being taken. T2-27 was the only site where cores were taken deeper than 90 cm.

Horizon descriptions (McDonald *et al.* 1990):

- O1 Undecomposed organic debris (leaves, twigs, etc).
- O2 Decomposing organic debris.
- A1 Mineral horizon near the surface with some accumulation of humified organic matter. Usually darker in colour than underlying horizons and containing the greatest levels of biological activity.
- A2 Mineral horizon having less organic matter, sesquioxides and/or silicate clay than adjacent horizons, and usually paler in colour than A1.
- A3 Transitional between A and B, and dominated by properties of A1 or A2.
- B1 Transitional between A and B, and dominated by properties of B2.
- B2 Horizon characterised by an illuvial, residual or other concentration of silicate clay, iron, aluminium, or humus; and/or different structure, consistency, or stronger colour development than A horizons.
- U Uniform soil profile: dominated by the mineral fraction with small, if any texture differences throughout the profile (Northcote 1974).
- S Sand
- LS Loamy sand
- ¹ Hardpan (sand aggregations appearing richer in iron)
- ² Gravel (coarse, stony fragments up to 20 mm diameter) at 85 cm

Table 3.2 Pearson correlation (r) matrix of soil parameters. An asterisk indicates a significant pairwise correlation: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

(a) 0-10 cm depth, $n = 14$

	Saturation capacity	Loss-on- ignition	Total N	Available P
Loss-on-ignition	0.98 ***			
Total N	0.92 ***	0.97 ***		
Available P	0.39	0.53	0.59 *	
pH	-0.68 **	-0.55 *	-0.43	0.22

(b) 50-60 cm depth, $n = 14$

	Saturation capacity	Loss-on- ignition	Total N	Available P
Loss-on-ignition	0.51			
Total N	0.23	0.88 ***		
Available P	0.28	0.62 *	0.43	
pH	0.33	0.22	0.11	-0.11

Table 3.2 (continued) Pearson correlation (r) matrix of soil parameters. An asterisk indicates a significant pairwise correlation: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

(c) 0-10 cm depth, $n = 13$ (T1-7 excluded from analysis)

	Saturation capacity	Loss-on- ignition	Total N	Available P
Loss-on-ignition	0.99 ***			
Total N	0.93 ***	0.97 ***		
Available P	0.70 **	0.76 **	0.82 **	
pH	-0.80 **	-0.72 **	-0.62 *	-0.37

(d) 50-60 cm depth, $n = 13$ (T1-7 excluded from analysis)

	Saturation capacity	Loss-on- ignition	Total N	Available P
Loss-on-ignition	0.54			
Total N	0.24	0.88 ***		
Available P	0.45	0.63 *	0.45	
pH	0.35	0.36	0.18	0.22

Table 3.3 Paired *t*-test results for differences between surface (0-10 cm) and deep (50-60 cm) soil samples for each soil parameter.

Soil parameter	All sites (<i>n</i> = 14)		T1-7 excluded (<i>n</i> = 13)	
	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>
Saturation capacity	6.08	<0.001	5.56	<0.001
Loss-on-ignition	6.13	<0.001	5.60	<0.001
Total N	7.77	<0.001	7.18	<0.001
Available P	4.79	<0.001	6.59	<0.001
pH	-7.23	<0.001	-12.50	<0.001

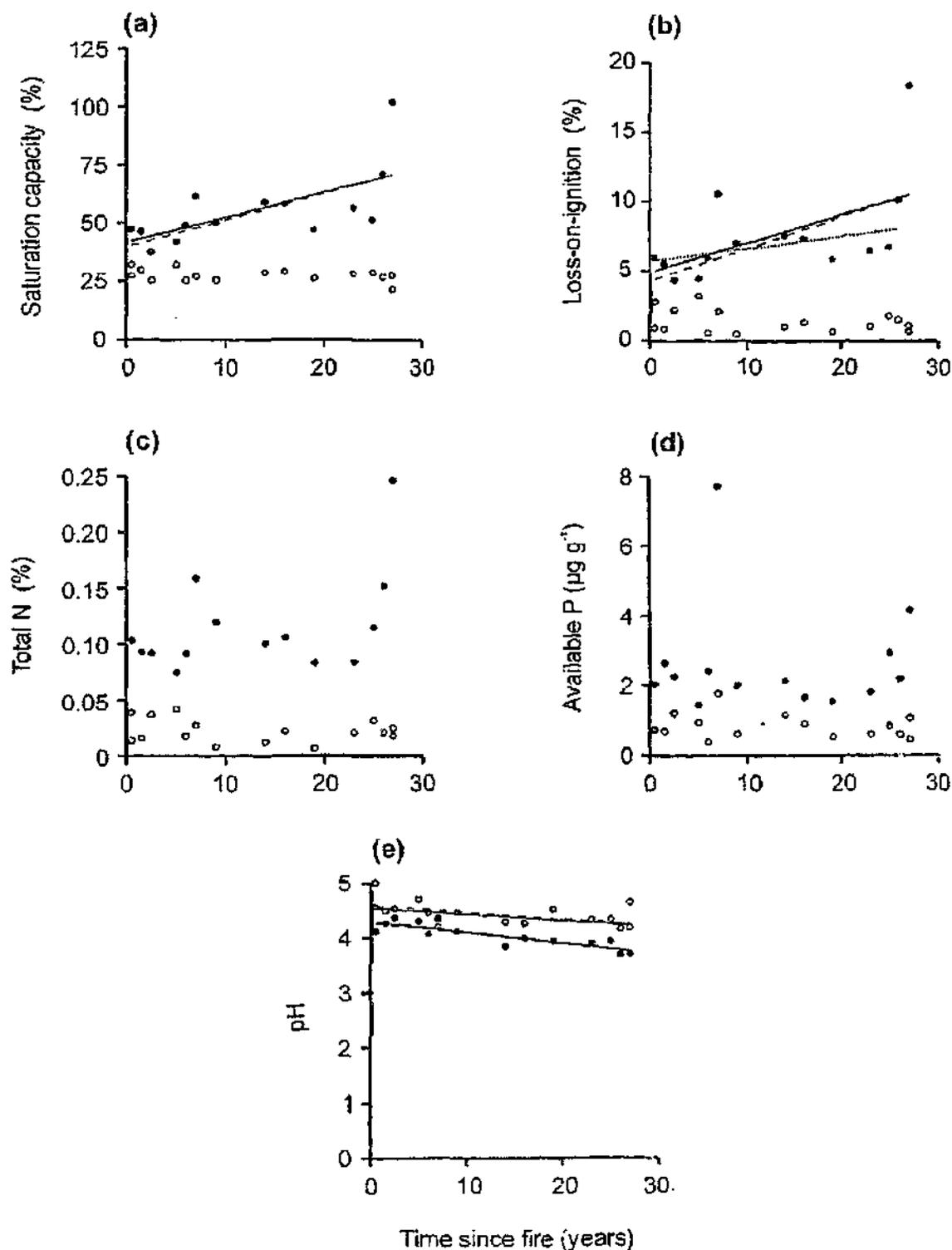


Figure 3.1 Mean values of soil parameters with increasing site age: (a) Saturation capacity; (b) Loss-on-ignition; (c) Total nitrogen; (d) Available phosphorus; (e) pH. Linear regression lines of best fit are displayed where soil parameters differ significantly with time since fire. Dashed lines indicate line of best fit after an outlier from linear regression has been removed; dotted line indicates line of best fit after removing T1. ●, 0-10 cm; ○, 50-60 cm; ◇, 70+ cm.

CHAPTER 4

VEGETATION

INTRODUCTION

Australian heathlands are generally thought to adhere to the 'initial floristic composition' model of succession (Egler 1954), where any given species assemblage is basically a subset of the initial composition following post-disturbance recruitment (Russell & Parsons 1978; Groves & Specht 1981; McFarland 1988). This initial post-fire composition may be markedly affected by the fire regime, which is composed of the season, intensity, frequency and type of fire (Gill 1975). Furthermore, the time elapsed since the last fire may substantially affect the species composition, richness, diversity, evenness, heterogeneity and structure of heathlands, depending on post-fire conditions (Lamont *et al.* 1993) and the reproductive and life-history characteristics of individual species.

As time since fire increases, heathlands can be said to experience four phases of development: the pioneer, building, mature and degenerate phases (Barclay-Estrup & Gimingham 1969). The pioneer stage encompasses the first few years after fire, and is often characterised by the presence of short-lived, post-fire ephemeral species (McMahon 1984b; Enright *et al.* 1994; Wark 1996). Following the pioneer phase, the heath undergoes a building phase, where most species increase their projected cover, until the total cover plateaus upon reaching the mature phase (Specht *et al.* 1958; Russell & Parsons 1978; Wark 1996). Finally, the heath may enter a degenerate phase where many species begin to senesce, and the heath elements become overtopped by taller shrubs and scattered trees, mainly of the genera *Banksia*, *Allocasuarina* and *Eucalyptus* (Gill & Groves 1981; Specht 1994).

Relatively few studies have used statistical techniques to examine the effect of time since fire on community composition in south-eastern Australian heathlands. Some exceptions are Posamentier *et al.* (1981) and Enright *et al.* (1994), who have shown species composition to change with increasing time since fire. However, Russell & Parsons (1978) found that sites geographically closer together were more similar than

sites of similar age, suggesting that the environment, rather than time since fire, was playing a more influential role in determining species composition. Species richness is also commonly associated with changes in species composition, and usually peaks in the first few years after fire. After this 'pioneer' phase, richness progressively declines, however, various studies have indicated different levels of decline, and shifts in species dominance, with increasing time since fire (Specht *et al.* 1958; Russell & Parsons 1978; Posamentier *et al.* 1981; McMahon 1984b; Enright *et al.* 1994; Wark 1996).

In addition to the composition, richness and physical structure of the vegetation, an important facet of ecology is the spatial structuring, or heterogeneity, of the vegetation. Christensen (1997) states that heterogeneity, complexity and diversity are critical elements to sustained ecosystem function. Environmental patchiness creates heterogeneity in resource availability, which provides an array of opportunities for colonisation and survival, thereby accomplishing one of the major objectives of conservation biology - fostering species diversity (Ewel 1997). Armesto *et al.* (1991) reviewed patterns of heterogeneity during oldfield succession and consistently found that community heterogeneity changed over time. Despite the growing interest in heterogeneity over the past 15-25 years (Wiens 1997), there have been no studies in Australia to my knowledge that address the issue of spatial heterogeneity in heathlands, let alone, the effects of time since fire on this parameter. This study aims to help fill this gap.

The central aim of this study is to determine the effects of time since fire on species composition, richness, diversity, evenness, life-form richness, community heterogeneity and structure in the heathlands of the Gippsland Lakes Coastal Park.

Associated with these aims are a number of predictions:

- (1) Vegetation will follow the 'Initial Floristic Composition' model of succession (Egler 1954), with no new species recruited after the initial post-fire recruitment pulse lasting 1-2 years, and composition in older heaths consisting of a subset of the initial composition following fire. Species that are long-lived, and/or can regenerate in the absence of fire, are also predicted to become dominant in older heaths.

- (2) Species richness, evenness (J) and diversity (H) are all predicted to peak c. 1-2 years after fire, then gradually decrease with increasing time since fire.
- (3) Life-form richness will peak as species richness peaks, then gradually decline as post-fire colonisers and relatively short-lived species die out.
- (4) Community heterogeneity will be greatest in the period of species establishment in the immediate 1-2 years following fire, and lowest as the heath ages and species die out or become competitively excluded.
- (5) Vegetation structure is predicted to change with increasing time since fire, with projected foliage cover greatest in the lower height classes of young heath and the upper height classes of older heath.

METHODS

Field sampling

Within each fire patch, a random point was generated which delineated the south-west point of the study site, the only constraint being that site boundaries were within 50 m of an access road or track. Site boundaries were then defined by taking a compass bearing east for 200 m, then north, west and south for the same distance. Random coordinates (south-west point) for quadrat locations were then generated.

In order to meet the aims of the study, an appropriate spatial scale (grain), *sensu* Allen & Starr (1982) needed to be determined prior to conducting the major component of the study. Therefore, five spatial grains were sampled, with each increasing by an order of magnitude (except for the 900 m² grain, which was close to an order of magnitude greater than the 100 m² grain). The spatial grains examined were 1 m², 10 m², 100 m², 900 m² and 1 ha. The number of random quadrats required to effectively sample the species richness at a site for each grain was then determined by examining species accumulation curves at BS-1.5, which was the first site sampled. Because the shape of the species accumulation curve is sensitive to the order in which quadrats are sampled (Palmer 1990a; Colwell & Coddington 1994; Inouye 1998), mean values of 1000 random quadrat sequences were used to plot curves for each sampling grain. Using this method, site species richness appeared to plateau substantially after ten 10 m² quadrats, seven 100 m² quadrats, or three 900 m² quadrats. At the 1 m² grain, species richness began to plateau after 20 quadrats, however, the curve was not as flat as the other three sampling grains (Figure 4.1).

In order to estimate sampling efficiency at each spatial scale, three estimates of total site species richness were made. First, total observed richness for the entire site, $S_{obs(TOT)}$, was derived from quadrat sampling over three days and at least one return visit in spring, to search for annuals and/or geophytes that may not have been found in the original survey. Second, species accumulation curves were extrapolated to 4 ha using the asymptotic, two-parameter hyperbola, known as the Michaelis-Menten equation:

$$S_{MM} = (S_{max} * n_{sat}) / (B + n_{sat})$$

where S_{max} , the asymptote, is a fitted constant, estimating true richness for the site, B is a fitted constant, and n_{sat} is the number of quadrats required to saturate the site for a given sampling scale (Colwell & Coddington 1994; Inouye 1998). An asymptotic curve was used, because (a) site richness was expected to be finite, owing to the finite sample area, and (b) the curves fitted the data extremely well. Third, the first-order jackknife estimate was used:

$$S_{Jack1} = S_{obs} + L (n-1 / n)$$

where S_{obs} is the observed number of species in the sampled quadrats (at a given scale), L is the number of species present in only one quadrat, and n is the number of quadrats sampled. The first-order jackknife estimate takes into account the number of 'singletons' (species occurring in only one quadrat), with higher proportions of singletons yielding higher estimates of species richness (Heltshe & Forrester 1983; Palmer 1990a).

The total observed species richness proved to be the most appropriate of the three estimators of actual site richness at BS-1.5, as it consistently yielded the greatest number of species for each grain sampled. Extrapolation using the Michaelis-Menten equation, and estimation using the first-order jackknife both yielded consistently lower estimates than $S_{obs(TOT)}$ for each sampling grain, except 900 m², where all three estimators gave the same value (Table 4.1). The lower estimates of the first-order jackknife are probably due to the low proportion of singletons, which suggests that the vegetation is quite homogeneous. The estimates of both equations imply that they were inadequate estimators of species richness, since they were lower than $S_{obs(TOT)}$ (Palmer 1990a). $S_{obs(TOT)}$ may in fact have been very close to the actual richness^{at the site}. Although the Michaelis-Menten equation and the first-order jackknife are commonly used estimators of species richness, the appropriateness of each model may vary according to the spatial heterogeneity of the vegetation (Colwell & Coddington 1994) and the sampling scale employed (Palmer 1990a). Therefore, owing to the results given in Table 4.1, $S_{obs(TOT)}$ will be used to determine sampling efficiency, since it was the most effective estimator of site species richness at BS-1.5, the first site sampled in this study.

Using $S_{obs(TOT)}$ as the estimator of site richness, twenty 1 m² quadrats estimated 81% of total site richness, ten 10 m² quadrats estimated 83% of site richness, seven 100 m² quadrats estimated 86% of site richness and three 900 m² quadrats estimated 93% of site richness (Table 4.2).

Choosing an appropriate scale to study is often a difficult task, as there is rarely, if ever, a 'correct' scale to study a given pattern or process (Levin 1988; Gardner 1998). However, for the purpose of this chapter, vegetation description and analyses will focus on a single spatial scale (grain), 100 m², while the effects of scale on vegetation parameters will be examined in Chapter 5. The 100 m² grain was chosen because the inflection point on the plot of mean species richness per quadrat for each grain (averaged across all sites) was between 10 m² and 100 m² (Figure 4.2), a similar result to that obtained by Cheal (2000) for a south-eastern Australian semi-arid heathland. At quadrat sizes below 100 m², the relationship between species richness and area increased rapidly, while the rate of increase of species added per unit area over 100 m² was very low. Specht (1979b), Specht & Specht (1989) and Keith & Myerscough (1993) provide a summary of species-area relationships in Australian heath-type vegetation.

At each quadrat, every species with living material projecting vertically over the quadrat was recorded and given a cover-abundance value, even if it was rooted outside the quadrat. Cover values were assigned from one of 12 classes: <1%, 1-5%, 6-10%, and thereafter in 10% intervals up to 100%. Total species cover abundance within five height classes (0-0.1 m, 0.2-0.3 m, 0.4-1.0 m, 1.1-2.5 m and 2.6-8.0 m) was estimated to provide a measure of community structure. The cover of bare ground, litter, bryophytes and lichens was also estimated at each quadrat.

Sites that were surveyed in summer and autumn were rechecked at least once in spring to determine whether any annuals or ephemerals were present that may have been overlooked in the original survey. In addition, GP-23 was re-surveyed with a further seven random 100 m² quadrats in December 2000, following a large (330 ha) prescribed fire in May 2000.

Nomenclature follows Ross (2000), apart from the updated treatment of *Boronia anemonifolia* by Neish & Duretto (2000). *Lomandra longifolia* and *Drosera peltata*

were not segregated to subspecies level because suitable material was not always present.

Data analysis

The mid-point (% cover) of each cover class was used for all analyses. Non-metric Multidimensional Scaling (NMDS) using the Bray-Curtis similarity index was employed to ordinate quadrat data using the PRIMER statistical package (Clarke & Gorley 2001). NMDS, using Bray-Curtis dissimilarities has been well-argued as being one of the most robust and appropriate ordination methods available for vegetation data (Faith *et al.* 1987; Minchin 1987; Clarke & Warwick 1994). Quadrat data for each site were ordinated using cover-abundance data, standardised cover data and presence/absence data, as these different measures are useful to gain a comprehensive overview of species patterns (Allen & Wyleto 1983). Standardisation was achieved by dividing each entry by the total abundance in that sample and multiplying by 100. In addition to the three forms of data just mentioned, ordination plots were derived for the means of the seven quadrats at each site, grouping sites into young (0-6 years old, $n = 5$), intermediate (9-19 years, $n = 5$) and old (23-27 years, $n = 4$) age classes, enabling easier interpretation of ^{coarser} larger-scale patterns. The young age class was designed to incorporate any post-fire ephemerals that may be present, while the old age class was designed (within the confines of the age range available) to be representative of sites where species senescence had already begun. All ordinations were plotted in two dimensions, with the plane of maximum variation represented on the x -axis, as recommended by Clarke & Warwick (1994).

The difference in species composition for the three abundance measures, first, among sites, and second, among age classes, was tested by Analysis of Similarity (ANOSIM), using PRIMER. ANOSIM works by testing for global differences between groups of samples, specified *a priori*, and then by analysing all pairwise comparisons (Clarke & Gorley 2001). Pairwise comparisons between every site (91 possible comparisons) were of no great interest, therefore, they are not reported here. However, pairwise comparisons between young, intermediate and old sites are reported, with no adjustments made for multiple comparisons, following the reasoning of Stewart-Oaten (1995). The contribution of each species to the similarity within groups was also calculated using the Similarity Percentages (SIMPER) routine in PRIMER.

Spatial autocorrelation between sites was assessed to determine whether sites were truly independent replicates that were unaffected by the species assemblage in surrounding sites (Legendre 1993). Autocorrelation was assessed using a one-tailed Mantel test (Mantel 1967; Legendre & Legendre 1998), which is designed to determine whether sites that are physically close to one another are more similar in terms of species composition than sites that are further apart. The test works by comparing the ranks of two independent distance matrices, in this case, ecological distances measured using Bray-Curtis dissimilarities, and geographic distances measured in kilometres, to determine whether a significant relationship exists between the two.

Species richness (S) was defined as the total number of species at a given quadrat, group of quadrats, or site. A measure of the evenness (J) of species cover-abundances was calculated using Pielou's evenness index:

$$J' = H' (\text{observed}) / \log_2(S)$$

where S = total number of species (Pielou 1966). J ranges from zero (all species possess different cover-abundances) to one (communities or sampling units where all species possess the same cover). Species diversity (H) takes into account both the total number of species (S) and their relative frequency or abundance (J), and was measured in terms of species cover-abundance using the Shannon-Wiener index:

$$H' = - \sum_i p_i (\log_2 p_i)$$

where p_i is the proportion of the total count arising from the i th species (Peet 1974). Life-form richness was determined by dividing each species into seven morphological classes: trees, shrubs, subshrubs, graminoids (sedges/rushes/grasses), forbs/geophytes, twiners and parasitic mistletoes, according to categorisations given by Walsh & Entwisle (1994), Walsh & Entwisle (1996) and Walsh & Entwisle (1999).

Community heterogeneity (CH) was measured using the Similarity Percentages (SIMPER) procedure in PRIMER, which determines the Bray-Curtis similarity in composition between each sampling unit and then averages pairwise similarities to give an inverse measure of dissimilarity (Clarke & Gorley 2001), or heterogeneity. This method has previously been used in oldfields and tallgrass prairie vegetation by Muraoka *et al.* (1984), Inouye *et al.* (1987) and Collins (1992). The average similarity

between pairs of plots should be lower as communities become more internally heterogeneous (Armesto *et al.* 1991). Community heterogeneity was analysed using cover data, standardised cover data and presence/absence data.

The effect of time since fire on species richness (total and mean), diversity (H), evenness (J), life-form richness, community heterogeneity (mean Bray-Curtis dissimilarity within a site), structure and bryophyte and lichen cover was assessed using linear regression. In addition, structural data displaying non-linear trends, litter cover, and bare ground cover were fitted with the LOWESS smoothing function for descriptive purposes. The LOWESS function estimates y based on the weighted average of nearby y values, with the local amount of flex (tension) adjusted on a scale of 0-1 (Anon. 2000). Pearson correlations were used to determine the degree of correlation between selected vegetation parameters. All data were square-root, \log_{10} , or $\log_{10}(x + 1)$ transformed to improve normality and homogeneity of variances when required. A critical value of $\alpha = 0.05$ was used in all hypothesis testing. Pairwise comparisons in correlation matrices were not adjusted for multiple comparisons, following the reasoning of Stewart-Oaten (1995). All regression and correlation analyses were carried out using the SYSTAT statistical software package (Anon. 2000).

RESULTS

Species composition

During the study, 94 species from 31 families and 66 genera were recorded across all sampling grains (Appendix 2). In terms of species richness, the dominant families were Orchidaceae (11 species), Myrtaceae (8), Fabaceae (7), Poaceae (7), Epacridaceae (6), Casuarinaceae (5), Xanthorrhoeaceae (5), Cyperaceae (4), Dilleniaceae (4) and Proteaceae (4). Twenty species were recorded at every study site (Table 4.3), with five of these belonging to Epacridaceae and four to Fabaceae. Of these 20 ubiquitous species, 14 were shrubs, two were trees, two were subshrubs and two were sedges. Twenty-four species were only recorded at one study site (Table 4.3), with eleven of these belonging to either Orchidaceae (6) or Poaceae (5). Of these 24 species, 16 were herbs (forb/geophyte and sedge/rush/grass) and six were shrubs, with 12 of these species found in young sites (0-6 years since fire) (seven herbs) and 12 found in old sites (23-27 years since fire) (nine herbs) (Table 4.3). All species recorded were native, except for four very localised and uncommon herbaceous weeds, each occurring at only one or two sites.

Focussing on the 100 m² grain, the heath was dominated by the shrub *Leptospermum myrsinoides*, which had a mean cover of $29 \pm 2\%$ in all sites nine years and older (Table 4.4). Sub-dominants of the shrub layer were *Monotoca scoparia*, with a mean cover of $6 \pm 1\%$ in sites nine years and older, *Banksia marginata* ($5 \pm 1\%$), *Epacris impressa* ($2 \pm 1\%$) and *Allocasuarina misera* ($3 \pm 1\%$). Other shrubs common to at least 13 of the 14 sites were *Acacia oxycedrus*, *Bossiaea cinerea*, *B. heterophylla*, *Brachyloma daphnoides*, *Dillwynia glaberrima*, *D. sericea*, *Hibbertia fasciculata* var. *prostrata*, *H. virgata*, *Leucopogon ericoides* and *L. virgatus* var. *virgatus* (Table 4.4). *Astroloma pinifolium*, *Calytrix tetragona*, *Thryptomene micrantha* and *Xanthorrhoea australis* were locally common and abundant (up to 5% cover), however they were only found at certain sites. The heathland was overtopped to varying degrees by scattered *Banksia serrata* ($6.6 \pm 2.2\%$) trees up to 8 m, and the 'mallee-form' eucalypt, *Eucalyptus* aff. *willisii* (Gippsland Lakes) ($3.7 \pm 0.4\%$), to 5 m. The rush, *Hypolaena fastigiata* ($7.0 \pm 2.0\%$) and the sedge, *Caustis pentandra* ($4.5 \pm 0.9\%$) dominated the ground layer, while other herbaceous species were very uncommon and/or had extremely low cover-abundances.

NMDS suggests a number of interesting relationships among the study sites. Cover data indicate that the youngest site, BS-0.5, was substantially different in species composition from all other sites, while the next three youngest sites, BS-1.5, WT-2.5 and SS-5 were also separate from the main group, which comprised the remaining 10 sites (Figure 4.3a). Following standardisation of the data, BS-0.5 remains distinctly separate, with SS-5 and WT-2.5 on the fringes of the main group (Figure 4.3b). Analysis of presence/absence data suggests that BS-0.5 and T2-27, the youngest and oldest sites respectively, are substantially different from the main group, with each at opposite ends of the axis of maximum variation (Figure 4.3c). The second oldest site, SS-26, is closest to T2-27, and forms a group on the edge of the main group, while WT-2.5 and SS-5 also form a distinct group (Figure 4.3c). Species composition differed significantly among sites, using cover (ANOSIM: $R = 0.83$, $p < 0.001$), standardised cover (ANOSIM: $R = 0.80$, $p < 0.001$) and presence/absence (ANOSIM: $R = 0.80$, $p < 0.001$) data. The effect of low frequency species was assessed for presence/absence data by removing any species restricted to a single quadrat (seven species in total). This produced no discernible change in the NMDS plot, and ANOSIM conclusions were unchanged.

Sites were ~~highly negatively~~ ^{positively} autocorrelated, with the standardised Mantel test statistic ($r_M = 0.495$) lying well ~~below~~ ^{outside} the 5% confidence level of 0.192, implying that sites geographically closer together were more similar in terms of species composition.

When sites were grouped into young (0-6 years old), intermediate (9-19 years) and old (23-27 years) age classes, NMDS of untransformed cover data suggests that old and intermediate-aged sites were grouped together, while young sites were grouped separately but covered a much broader area in multidimensional space (Figure 4.4a). The oldest of the young sites (SS-6) was grouped with the cluster of intermediate sites. A similar result was obtained using standardised data, with the intermediate and old sites largely inseparable (Figure 4.4b). Presence/absence data differed from the previous two NMDS plots in that there was no clear separation of young, from intermediate and old sites. However, there was a general trend from young, to intermediate, to old sites along the axis of maximum variation, with the oldest site (T2-27) substantially different from all other sites (Figure 4.4c). Using axis scores from the NMDS ordination of the mean of the seven 100 m² quadrats at each site, time since fire was found to be

significantly correlated with the axis of maximum variation (axis 1) for cover data ($R = -0.71$, $p = 0.004$), standardised cover data ($R = -0.72$, $p = 0.003$) and presence/absence data ($R = 0.61$, $p = 0.020$). Species composition differed significantly among age classes using untransformed (ANOSIM: $R = 0.31$, $p = 0.004$) and standardised (ANOSIM: $R = 0.23$, $p = 0.022$) data, while presence/absence data was not significantly different (ANOSIM: $R = 0.14$, $p = 0.074$). Pairwise comparisons indicated that young and intermediate-aged sites were significantly different in composition for cover and standardised cover data (cover: $R = 0.50$, $p = 0.008$; standardised cover: $R = 0.45$, $p = 0.008$), while young and old sites were significantly different for cover data ($R = 0.33$, $p = 0.024$). All other pairwise comparisons were non-significant.

The percentage contribution of dominant species to the average similarity within a site was calculated using the SIMPER routine in PRIMER, and is given in Table 4.5. *Leptospermum myrsinoides* is clearly the dominant species, contributing the most toward overall within-site similarity at every site, except BS-0.5. Other species that contributed substantially (at least 5%) to overall similarity within sites were *Monotoca scoparia* (10 sites), *Hypolaena fastigiata* (8 sites), *Banksia serrata* (6 sites), *B. marginata* (5 sites) and *Xanthorrhoea australis* (4 sites).

Species richness

Both total and mean species richness decreased significantly as site age increased. Total richness for the seven 100 m² quadrats at each site ranged between 26 at the oldest site (T2-27) and 43 at the youngest site (BS-0.5), indicating a gross decline of 40% for total richness, or a decrease of 19% derived by linear regression ($y = -0.276x + 39.508$) (Figure 4.5a). Mean richness ranged between 15.1 at T2-27 and 28.4 at BS-1.5, indicating a gross decline of 47%, or a decrease of 22% using linear regression ($y = -0.227x + 28.092$) (Figure 4.5b). T2-27 was an outlier for mean richness, however, when removed from the analysis, the result was still significantly different. Total and mean richness were both significantly negatively correlated with mean tree cover (total: $r = -0.60$, $p = 0.032$; mean: $r = -0.71$, $p = 0.007$).

Species diversity and evenness

Mean species diversity (H) decreased significantly with increasing time since fire, ranging from a high of 4.7 at the youngest site (BS-0.5) to a low of 2.4 at the oldest site (T2-27) (Figure 4.6a). Evenness (J) displayed a similar trend, decreasing significantly with time since fire, and ranging from a peak of 0.98 at the youngest site (BS-0.5) to a low of 0.62 at the oldest site (T2-27) (Figure 4.6b). The youngest site was a strong outlier but when removed from the data set, the result was still significant.

Life-form richness

Total life-form richness across all sites was dominated by shrubs (44% of species), followed by forbs/geophytes (24%) and graminoids (sedges/rushes/grasses) (17%). Subshrubs (6% of species), trees (4%), twiners (3%) and parasites (1%) made up a minor component of the vegetation in terms of the richness of life-forms. Total richness of life-forms at the 100 m² scale did not differ significantly with time since fire, with all sites possessing between five and seven of the seven defined life-forms (Table 4.6). Shrubs were by far the dominant life-form, with each quadrat possessing 15.6-19.4 shrub species on average, however, T2-27 was substantially lower in richness than all other sites, with a mean of 9.6 shrubs. The next most dominant life-forms were graminoids, with a mean of 1.9-3.9 species, and subshrubs (1.5-3.9 species), which was the only life-form to differ with time since fire, decreasing significantly; all other life-forms exhibited no significant difference in richness with time since fire. Trees ranged from 1.6-2.4 species per quadrat, while all other life-forms were predominantly less than one species per quadrat, with the exception of forbs/geophytes at one site, BS-0.5.

Community heterogeneity

Community heterogeneity appeared to show no trend and did not differ significantly with increasing time since fire, regardless of whether data were transformed or standardised, using linear or non-linear regression (Table 4.7). Values ranged from 24-37% for cover data, 26-38% for standardised cover data, and 11-27% for presence/absence data (Figure 4.7). Following removal of low frequency species (those restricted to one quadrat), mean dissimilarity differed by less than 1% in comparison to the full data set.

Correlations between selected vegetation parameters

Pearson correlation coefficients indicated that species richness (mean and total), J and H were all positively correlated (Table 4.8). Community heterogeneity (presence/absence data) was not correlated with any of the parameters tested, except mean species richness, with which it was negatively correlated (Table 4.8).

Community structure

Mean total vegetation cover increased rapidly until reaching *c.* 70% cover 6-9 years after fire (Figure 4.8). Following the initial increase, cover plateaued at 75-85% until *c.* 25 years, after which, it appeared to sharply decline. Mean cover in each height class also displayed distinct trends, with two patterns emerging. In the 0-0.1 m, 0.2-0.3 m and 0.4-1.0 m height classes, cover increased quickly until reaching a peak 9-16 years post-fire (Figure 4.9a,b,c). The maximum cover recorded at the ground layer (0-0.1 m) was 44%; this increased to 58% in the 0.2-0.3 m height class, and 72% in the 0.4-1.0 m height class. Following the peak at 'intermediate' ages, cover declined at a similar rate to which it initially increased. In the 1.1-2.5 m and 2.6-8.0 m height classes, there was a significant positive linear relationship between cover and time since fire, with young sites virtually devoid of cover in these height classes, and older sites reaching covers of 26-38% (1.1-2.5 m) and 4-28% (2.6-8.0 m) (Figure 4.9d,e). Mean height of the upper stratum of the heath (excluding emergent *Banksia serrata* and *Eucalyptus* spp.) was below 2.0 m at all sites, except SS-26 and T2-27, where it was 2.3 ± 0.1 m and 3.4 ± 0.1 m respectively. Mean tree cover (square-root transformed) did not increase significantly with time since fire ($F = 2.63$, $p = 0.133$).

Litter, bare ground, bryophyte and lichen cover

Mean cover of bare ground was greatest in the first 2.5 years following fire, with values ranging from 60-66% (Figure 4.10). Following this time, bare ground cover decreased ^{markedly} dramatically until it reached a constant level of 1-3% from 14 to 27 years after fire. Mean litter cover (incorporating charred material, leaves and twigs smaller than 5 mm diameter) increased steadily following fire, until it began to plateau at a cover of 90-95% 19 years after fire (Figure 4.10).

Mean cover of bryophytes and lichens increased significantly with time since fire, from zero cover at the youngest three sites, to a maximum of $3 \pm 1\%$ cover at the oldest site (linear regression, square-root transformed data: $F = 7.68, p = 0.018$).

Vegetation change following fire at GP-23

Species composition was significantly different between pre- (23 year old) and post-fire (0.5 year old) quadrats at GP-23, using species presence/absence data (ANOSIM: $R = 0.49, p = 0.001$). NMDS confirmed this result, indicating that the two groups had minimal overlap (Figure 4.11), with the seven pre-fire (23 year old) quadrats grouped tightly together (mean similarity: 82%), while the post-fire (0.5 year old) quadrats were grouped further apart, and were more dissimilar (mean similarity: 76%) in terms of composition. Interestingly, the mean dissimilarity between pre- and post-fire vegetation was 26%, a level of dissimilarity that was greater than that between GP-23 and five of the six sites located within 5 km of GP-23. Eight extra species were recorded post-fire, after 33 species were found in the original survey of seven 100 m² quadrats. This represents an increase of 24% following fire, however, four species recorded in the original survey were not found after fire. Of the new species found, a number were herbaceous species, including *Cassytha glabella*, *Drosera peltata*, *Gonocarpus tetragynus* and *Thelionema* sp.

DISCUSSION

Species composition changed notably as time since fire increased. However, sites that were situated closer together were found to be significantly ^{positively} ~~negatively~~ autocorrelated in terms of species composition, i.e. sites closer together were compositionally more similar. Nevertheless, this does not preclude fire from being the determining factor. Since the youngest sites were all grouped geographically close together at the eastern end of the study area, it is difficult to separate the effects of time since fire from the effects of site proximity. A random distribution of site ages throughout the study area would have potentially alleviated this design problem but such a distribution was not present. Although sites that were closer together were more similar, there is evidence that time since fire is the more important factor, because the mean dissimilarity between pre-fire (23 years old) and post-fire (0.5 years) composition at GP-23 was greater than that between GP-23 and five of the six sites located within 5 km of GP-23. Therefore, there is no basis for excluding sites due to spatial autocorrelation. However, the results do need to be interpreted with this in mind.

The vegetation comprised many genera common to other south-eastern Australian heathlands, with Coaldrake (1951), Specht *et al.* (1958), Russell & Parsons (1978), McMahon (1984b), Enright *et al.* (1994), Myerscough *et al.* (1995) and Wark (1996) all reporting similar dominants (e.g. *Allocasuarina* spp., *Banksia* spp., *Leptospermum* spp. and *Xanthorrhoea* spp.). Shrubs were clearly the dominant life-form in terms of richness, total cover and percentage contribution to the average similarity within sites, with *Leptospermum myrsinoides* consistently dominating the shrub layer, and *Monotoca scoparia* and *Banksia marginata* sub-dominant. Although forbs/geophytes accounted for 24% of all species in the heathland, their contribution to total cover was very low, with no species contributing more than 5% to the average similarity within a site. The frequency of forbs/geophytes was also very low, with 70% restricted to only one or two sites. Conversely, shrubs were very frequent, with 56% of recorded species present on at least 10 of the 14 sites. These findings are similar to those of Russell & Parsons (1978). The other relatively dominant life-form in terms of species richness were the graminoids, dominated by *Hypolaena fastigiata* and *Caustis pentandra*, however, as with the forbs/geophytes, frequency was low, with only 19% of species in this category present in more than half of the study sites. In terms of overall species richness, trees

contributed little, however, the tree layer was nonetheless important, with *Banksia serrata* dominating, in association with *Eucalyptus* aff. *willisii* (Gippsland Lakes). Cover of non-vascular plants increased significantly with time since fire, however, it was never a significant component of the vegetation in terms of cover, compared with other studies which have found bryophytes and lichens to be considerably more abundant following fire (Wark 1996; Esposito *et al.* 1999).

The composition of the heath changed significantly with increasing time since fire, however, the degree of variation was dependent on whether data were standardised, transformed, or split into age classes of young, intermediate and old. NMDS indicates that BS-0.5 was substantially different from all other sites, even when data were standardised and transformed. This suggests that differences in BS-0.5 compared to other sites were due to species composition rather than any influence of the low plant cover in the regenerating heath. The next three youngest sites, BS-1.5, WT-2.5 and SS-5, were grouped separately (to a degree) from the main group, while the main group comprised the remaining 10 sites. The main group appears to be reasonably similar in composition and cover, despite the fact that most pairwise comparisons are at least 'well separated' (Clarke & Gorley 2001). The presence/absence transformation separates sites even further, particularly at the older end of the age spectrum, and suggests that the axis of maximum variation is representing time since fire, since the two oldest sites are at one end and the two youngest sites at the opposite end of the axis, with the remaining sites grouped in between.

Coarse-scale trends were similar when sites were grouped into age classes, with intermediate and old-aged sites grouped together and young sites largely separate for untransformed, standardised and presence/absence data. However, the oldest of the young sites, SS-6, was closer to the intermediate and old sites, suggesting that after six years composition was more similar to older sites, owing largely to the general absence of post-fire ephemerals (Table 4.3). This response appears to be similar to other studies, where vegetation cover was levelling off, and/or post-fire ephemerals had disappeared after *c.* 6 years (Spoccht *et al.* 1958; McMahon 1984b).

The results of ANOSIM were notable in that species composition differed among age classes using cover and standardised cover data but not with presence/absence data, *i.e.* they differed only in abundance and relative abundance. However, the age class into

which each site was placed may have affected the findings of this study. For example, the young age class may have been too broad, encompassing a six year old site (SS-6), where any post-fire ephemerals characteristic of young sites may have already disappeared.

Despite the lack of a significant difference among age classes with presence/absence data, there was a significant correlation between the mean position of the seven quadrats at each site (along the axis of maximum variation on the NMDS) with time since fire. This suggests that species composition is changing with time since fire. Many studies in Australian heathlands (Specht *et al.* 1958; Posamentier *et al.* 1981; McMahon 1984b; McFarland 1988; Enright *et al.* 1994; Wark 1996), South African fynbos (Hoffman *et al.* 1987) and Californian chaparral (Hanes 1971) suggest that vegetation composition changes with time since fire, with the findings of Russell & Parsons (1978) an exception to the general rule. However, where compositional change is evident, the exact 'level' of difference among sites is difficult to determine for two reasons. First, many of the aforementioned studies use the chronosequence approach, which considerably increases the likelihood of additional 'noise' in the data set, owing to inherent site to site variation. Consequently, this makes the determination of change more difficult and less precise, compared to a permanent plot study. Second, many studies (including all of the above studies) do not undertake statistical tests to determine whether significant differences exist in composition among sites. Instead, compositional changes are reported in a descriptive manner, in part because some tests were unavailable when these studies were carried out. However, if changes in vegetation composition with time since fire had been statistically analysed in these studies, the conclusions reached may have been different.

It is interesting to note that of the 26% of species that were restricted to a single site, half were found in sites at least 23 years old. This is an intriguing finding, in that the majority of species restricted to a particular site were predicted to be post-fire ephemerals, occurring predominantly in recently burnt sites (e.g. younger than five years old), as found by Bell *et al.* (1984), McMahon (1984b), Enright *et al.* (1994) and Wark (1996) in different Australian heathlands. Furthermore, the fact that herbaceous species comprised a greater proportion of the 'restricted' species in old sites compared to young sites was also unexpected. These unexpected results may be due to a number of factors.

First, the similar proportion of species restricted to young versus old sites may be due to the lack of genuine post-fire ephemeral species, defined here as species that appear soon after the occurrence of fire, have short life cycles and depend on fire for their occurrence (Gill 1981b). Second, some post-fire ephemerals may be present but at more than one site. Third, some species may be inherently rare in the study area, and therefore be site-specific. Species likely to be site-specific rather than ephemeral are woody species such as *Baeckea ramosissima* ssp. *prostrata*, *Bossiaea obcordata*, *Hibbertia riparia* and *Eucalyptus viminalis* ssp. *pyoriana* X *Eucalyptus cephalocarpa* in the young sites, and *Allocasuarina littoralis*, *Persoonia juniperina* and *Boronia anemonifolia* ssp. *anemonifolia* in the old sites. Finally, the relatively high number of restricted herbaceous species in old sites may be due to recruitment from soil-stored seed, or bulbs, corms and tubers as the understorey begins to 'open up' with increasing age (Specht *et al.* 1958; Patric & Hanes 1964; Keeley 1992b).

It is difficult to ascribe the status of 'post-fire ephemeral' to a species, particularly when it is recorded at only one or two sites, as there is no way of determining, apart from establishing permanent monitoring plots, whether the species is simply site-specific. Even so, 17 of the 94 species recorded in this study were restricted to the youngest four sites, all burnt 0.5-5 years prior to sampling. Of these 17 species, eight were forbs/geophytes, four were graminoids, four were shrubs and one was a subshrub. Owing to the potential life-span of the shrubs, they are not considered here as post-fire ephemerals; instead, they are most likely site-specific species that are rare within the study area. In addition, two of the species were exotic weeds that were probably opportunistic colonisers of disturbed ground, rather than true post-fire ephemerals, while one species was a seasonal geophyte that avoided fire. Therefore, 10 species, nine of which are herbaceous, are considered to be potential post-fire ephemerals in the context of this study. They are *Anisopogon avenaceus* (graminoid), *Caesia parviflora* (forb/geophyte), *Carpobrotus rossii* (forb/geophyte), *Crassula sieberiana* (forb/geophyte), *Euchiton sphaericus* (forb/geophyte), *Isolepis marginata* (graminoid), *Laxmannia orientalis* (forb/geophyte), *Rhynchospora procumbens* (subshrub), *Schoenus imberbis* (graminoid) and *Thelionema* sp. (forb/geophyte). Without having detailed information regarding the biology of each of these species, it is difficult to categorically state that all are true post-fire ephemerals as defined in the previous paragraph. However, most of these species appear to be fire-sensitive and regenerate by

seed rather than resprouting, which is a characteristic of fire ephemerals (Bell *et al.* 1984). This will be discussed in more detail in Chapters 7 and 8.

Species richness in heathlands is usually reported (and generally accepted) to reach a peak in the first few years following fire (Campbell & van der Meulen 1980), and then decrease as time since fire increases. For example, Specht *et al.* (1958) found that total species richness in dry heathland declined by 44% in the 25 years after fire, McMahon (1984b) found a 36% decrease in total richness in a semi-arid heathland up to 20 years post-fire, and Wark (1996) reported a 33% decrease from one to ten years after fire in coastal heathland, while Russell & Parsons (1978) found no obvious decline in wet heathland total richness for at least 10 years after fire, followed by a 22% decrease up to 21 years post-fire. Conversely, Cheal (2000) found that mean richness increased by 13% over a 14 year period in plots that were burnt 33 years earlier, and 33% over the same 14 year period in plots burnt eight years earlier in semi-arid heathland. The results of this study are most similar to the first two of the aforementioned studies. However, the degree of decline in richness varies, depending on (a) whether total or mean richness is used, and (b) whether the regression slope is used, or the difference between the most species-rich and most species-poor site is used to calculate the degree of change. Using the difference between the most species-rich and poor sites, total richness declined by 40% over 27 years, after reaching a peak 0.5 years after fire. This is highly comparable with the studies of Specht *et al.* (1958) and McMahon (1984b) in *Banksia ornata* dominated heathlands, in terms of both the decline in species richness and the time scale over which this decline occurred. However, when the regression equation is used, the magnitude of the decrease in richness is approximately halved. This may actually be a more suitable method of estimating change in richness for chronosequence studies, owing to the inherent variability in richness between sites, irrespective of time since fire.

In addition to time since fire, tree cover was also a significant correlate of species richness, with mean and total richness both significantly negatively correlated with mean tree cover, even though tree cover was not correlated with time since fire. This suggests that tree cover has an independent effect from time since fire that accelerates the decline in species richness. Potential sources of this 'tree cover effect' are chemical inhibition (allelopathy) via foliar and/or litter leachates (del Moral *et al.* 1978; Gill & Groves 1981; Hobbs 1984; Keeley *et al.* 1985; May & Ash 1990; Vila & Sardans 1999)

and increased competition for light as a result of canopy shading (Specht & Specht 1989; Vila & Sardans 1999).

Species evenness (J) in terms of projected cover was greatest at the youngest site as expected, owing to the low cover of all species following the recent fire. Evenness decreased significantly, albeit gradually, until reaching its lowest point 27 years after fire, where the cover of each species was the most variable ('uneven'). Morrison *et al.* (1995) also reported a decline in evenness (modified Hill's ratio) for fire-tolerant species in dry sclerophyll communities near Sydney with increasing time since fire, however, I am unaware of any studies that have calculated evenness in Australian heathlands. Species diversity (H) is a product of the species richness (number of species) at a site and the evenness (J) of the cover of each species. Therefore, the significant decrease in diversity with increasing time since fire is not surprising, given that species richness and evenness were both found to decrease significantly with time since fire. A similar result was found in North American boreal forest burnt up to 44 years prior to sampling, where richness, evenness (V , Hurlbert 1971) and diversity (H) all decreased along a chronosequence of increasing time since fire, although there was variability between sites during the succession (Shafi & Yarranton 1973a). Campbell (1980) also found that young (four year old) fynbos was more diverse (H) than older (36 year old) fynbos, however, Kruger (1983) indicates that fynbos diversity may increase again later in succession as older shrubs senesce, creating gaps and opportunities for understorey species to regenerate. Unfortunately, the temporal scale of this study is limited to 27 years post-fire, owing to a lack of older sites in the study area; therefore, it is difficult to predict future trends in diversity with increasing fire-free periods. However, because diversity is strongly correlated with both total and mean species richness, it should mirror any change in richness further than 27 years, which is likely to be a decrease with increasing time since fire.

According to models of community structure, species richness and/or diversity are predicted to be greater where environmental heterogeneity is greater, owing to the increased availability of resource niches and the subsequent opportunity for more species to colonise these niches (Tilman 1982; Shmida & Wilson 1985; Burnett *et al.* 1998; Nichols *et al.* 1998; Huston 1999). If this relationship holds true, the variability (heterogeneity) expressed as the mean Bray-Curtis dissimilarity in composition among

sampling points (quadrats) is also predicted to be greater where environmental heterogeneity is large between any two points. Therefore, one would expect species richness, diversity and community heterogeneity to be positively correlated, if all were related in a similar manner to environmental heterogeneity. However, owing to the relatively uniform nature of the soil at the 100 m² grain across the study area, differences in community heterogeneity between sites are likely to be also influenced by variance in fire regimes, interspecific competition, species dispersal characteristics and reproductive strategies.

In a review of spatial heterogeneity during oldfield succession, Armesto *et al.* (1991) consistently found that community heterogeneity changed over time, with many studies suggesting that there are cycles of community heterogeneity that tend to be more pronounced during early rather than late succession. As a consequence of this, Armesto *et al.* (1991) proposed a theoretical model of community heterogeneity based on disturbance characteristics, life history and autecology of species through succession. The structural essence of the model is that high and low periods of spatial heterogeneity in community composition alternate through succession. The functional essence of the model is that periods of high community heterogeneity represent periods of species invasion and establishment, whereas periods of low heterogeneity represent periods of species exclusion. Therefore, in accordance with the model of Armesto *et al.* (1991), sand heath community heterogeneity was predicted to be greatest in the period of species establishment in the immediate years following disturbance (fire), and lowest as the heath aged and species died out or became competitively excluded. Although there was a peak in species richness and diversity in the first 2.5 years following fire, no such peak was observed for community heterogeneity. Furthermore, even though a significant decrease in species richness (total and mean) and diversity with time since fire was found in this study, no comparable trend was observed for community heterogeneity, which concurs with results obtained by Facelli *et al.* (1987) for a South American grassland succession. However, community heterogeneity (presence/absence data) was significantly negatively correlated with mean species richness. This finding is highly contrary to most other studies that have examined the relationship between richness, diversity and community heterogeneity. For example, Whittaker & Levin (1977), Inouye *et al.* (1987) and Collins (1992) all found that species richness and/or

diversity were significantly positively correlated with community heterogeneity, although Collins (1992) did note that heterogeneity is likely to be scale dependent.

The absence of a trend in community heterogeneity, and the negative correlation with mean species richness in this study, have two possible explanations. First, although quadrats at younger sites contained more species on average than older sites, it does not imply that their mean dissimilarity should automatically be greater than that of older sites containing fewer species. For instance, young sites may exhibit high mean richness but low community heterogeneity if each sampling unit contains a similar suite of species (and environmental heterogeneity is similar between sampling units). Conversely, an old site may exhibit low mean richness but greater heterogeneity, as species become competitively excluded and potentially more patchily distributed across the site. An alternative explanation is that species colonisation and invasion may be influencing community heterogeneity at older sites. However, the extent of this is considerably lower than in the North American oldfields in which the model was derived, where waves of invasion and extinction are common during secondary succession (Shafi & Yarranton 1973b; Armesto & Pickett 1985). In terms of the model derived by Armesto *et al.* (1991), there is no evidence of cycles of heterogeneity in the Loch Sport sand heathlands, as any site to site variation in heterogeneity is most likely attributable to inherent site variability, rather than specific waves of invasion or colonisation. Invasion may potentially occur, given a long enough fire-free period, however, extended fire-free periods are rare in this system. If an effect of colonisation or invasion does exist, it would only occur in sites 23 years or older, as species establishment from seed was uncommon in younger sites apart from the immediate post-fire environment, and 'invasion' was restricted to the bird-dispersed mistletoe, *Amyema pendula* ssp. *pendula*, and a small number of highly uncommon herbaceous weeds, often confined to abandoned fire control lines.

As expected from other studies, the structure of the heath changed markedly with increasing time since fire. Initially, in the first six years after fire, total cover increased dramatically to c. 70%, and was largely influenced by a dense cover of shrubs and graminoids in the 0-0.1, 0.2-0.3 and 0.4-1.0 m height classes. This is consistent with the findings of Specht *et al.* (1958), Bell *et al.* (1984) and Wark (1996) for South Australian heath, Western Australian kwongan (scrub-heath vegetation) and Victorian coastal heath

respectively, where it took 5-10 years to reach *c.* maximum cover of 70-92%. During this time, the cover of bare ground decreased ^{markedly} ~~dramatically~~, while litter cover increased in a similar manner, although litter cover was initially relatively high, owing to charred plant remains in young sites. As the time since fire increased to 14 years, cover in the five height classes continued to increase, in what could be described as the building phase. Following the building phase, the heath experienced a mature phase, where total cover remained constant at *c.* 75-85% until 25 years after fire, and decreased to *c.* 50% 27 years after fire. During this time, many shrubs continued to grow in stature and trees regained pre-fire cover levels, while the cover in height classes below 1.0 m declined substantially, a similar trend to that reported by Meredith & Isles (1980). This decline in understorey cover is predominantly due to the increased cover of shrubs and emergent trees in the 1.1-2.5 and 2.6-8.0 m layer (Specht & Specht 1989), which reduces light availability to the strata below. As a consequence of this, many shrubs shed foliage from the lower strata and allocate a greater proportion of photosynthetic tissue to the upper shrub stratum, where light availability is greater. Although total cover decreased by *c.* 25% from 25-27 years after fire, this is not evidence of a degenerate phase *sensu* Barclay-Estrup & Gimingham (1969), as there is no clear evidence for mass senescence of different species. Groves & Specht (1981) actually suggest that the degenerate phase is uncommon in Australian heathlands, most likely as a result of inter-fire intervals being too short to allow the vegetation to reach this stage.

In a chronosequence spanning 60 years, McMahon (1984b) found that heath structure began to change markedly *c.* 20 years following fire, with two of the four dominant shrub species (*Allocasuarina* spp.) beginning to senesce and decline in cover. In response to the resultant canopy openings and increased light availability, the cover of rhizomatous monocotyledons then increased substantially. In this study, no such trend was observed, with no widespread senescence of dominant shrub species, and no noticeable increase in the total cover of ground layer species.

In addition to the time elapsed since fire, community structure may be influenced by water and nutrient availability (Specht 1979b). The most pertinent example of this occurs in the two 16 year old sites that were sampled from within the same fire patch, although they were 5.3 km apart. The shrub layer at SS-16 (mean height: 1.1 m) was noticeably shorter than WT-16 (mean height: *c.* 1.5 m), while the eucalypts at SS-16

were the most stunted of any of the sites in the entire study area, possessing a mean height of *c.* 3.5 m. In addition, total cover was very similar at both sites, however, the cover in each height class was ~~dramatically~~ ^{markedly} different, with the heath at WT-16 much more dense than SS-16. The structural discrepancy between the two sites may be due to the lower available P, total N, organic matter and reduced saturation capacity at SS-16 compared with WT-16. However, due to the general uniformity of the study area in terms of soil characteristics, this is seen as a secondary influence to that of time since fire.

Table 4.1 Species richness estimators for BS-1.5. n = number of quadrats sampled; S_{obs} = number of species observed in the sampled quadrats; $S_{obs(TOT)}$ = total observed species richness at the site; L = number of species present in only one quadrat; S_{Jack1} = first-order jackknife estimate of site species richness; S_{MM} = estimate of site species richness based on extrapolation of Michaelis-Menten equation; R^2 = goodness of fit for the Michaelis-Menten equation.

Scale (m ²)	n	S_{obs}	$S_{obs(TOT)}$	L	S_{Jack1}	S_{MM}	R^2
900	3	39	42	4	42	42	1.00
100	7	36	42	3	39	37	1.00
10	10	35	42	4	39	37	1.00
1	20	34	42	5	39	-	-

Table 4.2 Levels of saturation ($S_{obs} / S_{obs(TOT)}$) observed for each sampling grain at every site. 1 m²: 20 quadrats per site; 10 m²: 10 quadrats per site; 100 m²: 7 quadrats per site; 900 m²: 3 quadrats per site; 1 ha: 1 quadrat per site.

Site	Sampling grain				
	1 m ²	10 m ²	100 m ²	900 m ²	1 ha
BS-0.5	0.62	0.75	0.81	0.83	0.79
BS-1.5	0.81	0.83	0.86	0.93	0.90
WT-2.5	0.53	0.70	0.79	0.89	0.77
SS-5	0.75	0.82	0.75	0.78	0.75
SS-6	0.64	0.68	0.84	0.82	0.86
TT-9	0.80	0.78	0.85	0.90	0.88
T4-14	0.63	0.65	0.85	0.83	0.85
WT-16 / SS-16	0.74	0.86	0.84	0.87	0.87
UT-19	0.63	0.83	0.83	0.83	0.83
GP-23	0.65	0.78	0.83	0.83	0.88
T4-25	0.67	0.71	0.88	0.88	0.86
SS-26	0.65	0.75	0.80	0.90	0.83
T2-27	0.58	0.58	0.60	0.79	0.67

Table 4.4 Frequency (F) (maximum = 7) and mean cover (C) (± 1 SE) of each species found at the 100 m² sampling grain.

Species	BS-0.5		BS-1.5		WT-2.5		SS-5		SS-6		TT-9		T4-14		WT-16		SS-16		UT-19		GP-23		T4-25		SS-26		T2-27			
	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C		
<i>Acacia longifolia</i> var. <i>longifolia</i>	0	0	0	0	0	0	1	0.1 \pm 0.1	3	0.6 \pm 0.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Acacia oxycedrus</i>	7	0.5 \pm 0	7	0.5 \pm 0	3	0.2 \pm 0.1	3	0.2 \pm 0.1	5	1.1 \pm 0.5	7	2.6 \pm 0.4	7	1.2 \pm 0.5	7	1.6 \pm 0.5	7	1.9 \pm 0.5	7	1.2 \pm 0.5	3	0.2 \pm 0.1	7	1.2 \pm 0.5	7	0.5 \pm 0	0	0		
<i>Allocasuarina misera</i>	0	0	1	0.1 \pm 0.1	6	0.4 \pm 0.1	6	2.9 \pm 0.9	5	0.7 \pm 0.4	7	4.3 \pm 0.8	3	1.9 \pm 1.1	7	1.6 \pm 0.5	6	3.5 \pm 1.1	6	2.2 \pm 0.5	7	6.4 \pm 2.2	6	1.9 \pm 0.5	6	1.9 \pm 0.5	0	0		
<i>Allocasuarina paludosa</i>	0	0	4	0.3 \pm 0.1	2	0.1 \pm 0.1	3	0.2 \pm 0.1	1	0.4 \pm 0.4	1	0.4 \pm 0.4	0	0	2	0.5 \pm 0.1	6	2.1 \pm 1.0	6	1.5 \pm 0.5	2	0.5 \pm 0.4	1	0.1 \pm 0.1	1	0.4 \pm 0.4	0	0		
<i>Allocasuarina paradoxa</i>	0	0	0	0	0	0	0	0	0	0	1	0.1 \pm 0.1	0	0	0	0	0	0	1	0.1 \pm 0.1	0	0	0	0	0	0	0	0	0	
<i>Allocasuarina</i> sp.	6	0.4 \pm 0.1	0	0	0	0	0	0	1	0.4 \pm 0.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Amperea xiphioides</i> var. <i>xiphioides</i>	6	0.4 \pm 0.1	7	0.5 \pm 0	5	0.4 \pm 0.1	6	0.4 \pm 0.1	6	0.4 \pm 0.1	6	0.4 \pm 0.1	5	0.4 \pm 0.1	5	0.4 \pm 0.1	3	0.2 \pm 0.1	4	0.3 \pm 0.1	6	0.4 \pm 0.1	4	0.3 \pm 0.1	7	0.5 \pm 0	5	0.4 \pm 0.1		
<i>Amymma pendula</i> ssp. <i>pendula</i>	0	0	0	0	0	0	1	0.1 \pm 0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Antisopogon avenaceus</i>	1	0.1 \pm 0.1	0	0	0	0	1	0.1 \pm 0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Aotus ericoides</i>	0	0	0	0	0	0	0	0	0	0	1	0.1 \pm 0.1	0	0	0	0	0	0	1	0.1 \pm 0.1	0	0	0	0	0	0	0	0	0	0
<i>Astroloma pinifolium</i>	0	0	0	0	5	0.4 \pm 0.1	4	0.3 \pm 0.1	2	0.1 \pm 0.1	3	0.2 \pm 0.1	2	0.5 \pm 0.4	7	2.6 \pm 2.1	0	0	0	0	0	0	0	3	0.6 \pm 0.4	6	4.1 \pm 1.3	7	5.6 \pm 0.9	
<i>Banksia marginata</i>	6	0.4 \pm 0.1	7	0.9 \pm 0.4	5	1.1 \pm 0.5	7	2.3 \pm 0.5	7	3.0 \pm 0.6	7	13.0 \pm 3.5	7	2.9 \pm 0.9	7	11.0 \pm 4.5	7	4.9 \pm 0.9	7	3.3 \pm 0.8	7	4.9 \pm 0.9	7	4.6 \pm 1.9	7	1.9 \pm 0.5	2	0.5 \pm 0.4		
<i>Banksia serrata</i>	5	0.4 \pm 0.1	7	1.9 \pm 0.5	7	3.3 \pm 0.8	7	3.9 \pm 1.0	7	10.1 \pm 1.8	4	1.1 \pm 0.6	7	16.9 \pm 5.6	7	2.6 \pm 0.9	6	1.5 \pm 0.5	5	4.9 \pm 2.6	6	2.9 \pm 0.9	5	2.1 \pm 1.0	6	9.8 \pm 3.4	7	17.6 \pm 3.8		
<i>Bassia cinerea</i>	7	0.5 \pm 0	7	0.9 \pm 0.4	5	0.4 \pm 0.1	2	0.1 \pm 0.1	7	2.6 \pm 0.4	5	1.7 \pm 0.5	7	1.9 \pm 0.5	7	0.9 \pm 0.4	7	2.2 \pm 1.0	7	4.3 \pm 2.0	7	0.9 \pm 0.4	7	2.3 \pm 0.5	7	0.9 \pm 0.4	5	0.4 \pm 0.1		
<i>Bassia heterophylla</i>	7	0.5 \pm 0	7	0.5 \pm 0	7	0.9 \pm 0.4	7	3.0 \pm 0.6	6	3.2 \pm 0.8	2	0.1 \pm 0.1	7	0.5 \pm 0	7	0.5 \pm 0	7	1.2 \pm 0.5	7	0.5 \pm 0	7	1.9 \pm 0.5	7	1.2 \pm 0.5	0	0	1	0.1 \pm 0.1		
<i>Brachyotum daphnoides</i>	1	0.1 \pm 0.1	1	0.1 \pm 0.1	6	1.1 \pm 0.5	5	0.7 \pm 0.4	4	0.6 \pm 0.4	6	0.8 \pm 0.4	4	1.0 \pm 0.5	2	0.1 \pm 0.1	5	0.7 \pm 0.4	5	0.7 \pm 0.4	7	3.0 \pm 0.6	5	1.7 \pm 1.0	7	1.9 \pm 0.5	2	0.1 \pm 0.1		
<i>Caladenia carnea</i> var. <i>carnea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.1 \pm 0.1		
<i>Calceana major</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.1 \pm 0.1		
<i>Calochilus robertsonii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Calochilus</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.1 \pm 0.1		
<i>Calyrix tetragona</i>	0	0	0	0	6	0.8 \pm 0.4	7	6.6 \pm 1.6	1	0.1 \pm 0.1	7	8.8 \pm 3.2	2	0.1 \pm 0.1	0	0	0	0	1	0.1 \pm 0.1	0	0	0	0	7	2.5 \pm 1.3	5	0.4 \pm 0.1		
<i>Cassytha globella</i>	7	0.5 \pm 0	0	0	2	0.1 \pm 0.1	2	0.1 \pm 0.1	0	0	1	0.1 \pm 0.1	0	0	0	0	0	0	0	0	0	0	0	3	0.2 \pm 0.1	0	0	1	0.1 \pm 0.1	
<i>Cassytha melantha</i>	0	0	0	0	0	0	0	0	0	0	2	0.1 \pm 0.1	0	0	0	0	1	0.1 \pm 0.1	0	0	0	0	0	0	0	0	0	0	0	
<i>Cassytha pubescens</i>	0	0	0	0	0	0	0	0	0	0	4	0.3 \pm 0.1	1	0.1 \pm 0.1	6	0.4 \pm 0.1	5	0.4 \pm 0.1	3	0.2 \pm 0.1	2	0.1 \pm 0.1	1	0.1 \pm 0.1	4	0.3 \pm 0.1	0	0	0	
<i>Cleistis pentandra</i>	7	0.5 \pm 0	7	0.5 \pm 0	7	0.5 \pm 0	7	0.5 \pm 0	1	0.1 \pm 0.1	7	3.6 \pm 0.6	6	4.5 \pm 1.1	7	5.6 \pm 0.9	7	5.6 \pm 0.9	6	4.9 \pm 2.1	6	1.1 \pm 0.5	6	2.2 \pm 0.5	7	10.1 \pm 1.8	7	2.6 \pm 0.9		
<i>Conesperma calymega</i>	0	0	6	0.4 \pm 0.1	4	0.3 \pm 0.1	0	0	0	0	1	0.1 \pm 0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
* <i>Coryza</i> sp.	4	0.3 \pm 0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Correa reflexa</i> var. <i>speciosa</i>	4	0.5 \pm 0.1	1	0.1 \pm 0.1	0	0	0	0	0	0	0	0	0	0	4	0.3 \pm 0.1	7	0.5 \pm 0	2	0.1 \pm 0.1	2	0.1 \pm 0.1	2	0.1 \pm 0.1	3	0.2 \pm 0.1	0	0	0	
<i>Crassula siebertiana</i>	0	0	0	0	1	0.1 \pm 0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Dampiera stricta</i>	7	0.5 \pm 0	7	0.5 \pm 0	1	0.1 \pm 0.1	3	0.2 \pm 0.1	6	0.4 \pm 0.1	4	0.5 \pm 0.1	2	0.1 \pm 0.1	6	0.4 \pm 0.1	7	0.5 \pm 0	5	0.4 \pm 0.1	4	0.3 \pm 0.1	7	0.9 \pm 0.4	6	0.4 \pm 0.1	0	0	0	0
<i>Dillwynia globerrima</i>	6	0.4 \pm 0.1	7	0.5 \pm 0	2	0.1 \pm 0.1	2	0.1 \pm 0.1	5	0.7 \pm 0.4	7	0.9 \pm 0.4	4	0.3 \pm 0.1	7	1.2 \pm 0.5	7	1.2 \pm 0.5	7	0.5 \pm 0	7	0.5 \pm 0	5	0.4 \pm 0.1	3	0.2 \pm 0.1	5	0.4 \pm 0.1		
<i>Dillwynia stricta</i>	1	0.1 \pm 0.1	7	0.5 \pm 0	7	0.5 \pm 0	6	0.4 \pm 0.1	6	0.4 \pm 0.1	7	0.5 \pm 0	7	0.5 \pm 0	2	0.1 \pm 0.1	5	0.4 \pm 0.1	3	0.2 \pm 0.1	7	0.5 \pm 0	4	0.3 \pm 0.1	0	0	0	0	0	0

Table 4.4 (continued) Frequency (F) (maximum = 7) and mean cover (C) (± 1 SE) of each species found at the 100 m² sampling grain.

Species	BS-0.5		BS-1.5		WT-2.5		SS-5		SS-6		TT-9		T4-14		WT-16		SS-16		UT-19		GP-23		T4-25		SS-26		T2-27			
	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C		
<i>Drosera peltata</i>	1	0.1 \pm 0.1	0	0	1	0.1 \pm 0.1	4	0.3 \pm 0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Epacris impressa</i>	3	0.2 \pm 0.1	7	0.9 \pm 0.4	5	0.4 \pm 0.1	6	0.4 \pm 0.1	7	1.2 \pm 0.5	7	3.6 \pm 0.6	7	1.2 \pm 0.5	7	2.3 \pm 0.5	7	4.9 \pm 0.9	7	3.6 \pm 0.6	7	3.0 \pm 0	7	4.3 \pm 0.8	7	1.6 \pm 0.5	7	0.9 \pm 0.4		
<i>Eucalyptus</i> aff. <i>willistii</i> (Gippsland Lakes)	7	0.5 \pm 0	6	4.9 \pm 1.9	5	3.4 \pm 1.2	7	4.4 \pm 1.8	5	4.8 \pm 2.1	5	2.1 \pm 1.0	7	5.3 \pm 2.0	7	4.6 \pm 1.9	7	3.2 \pm 1.2	7	3.2 \pm 1.2	6	2.9 \pm 0.9	6	4.9 \pm 1.9	6	3.2 \pm 0.8	7	4.2 \pm 1.2		
<i>Eucalyptus viminalis</i> ssp. <i>pyroriana</i>	1	0.1 \pm 0.1	2	2.1 \pm 1.4	0	0	0	0	1	3.4 \pm 0.4	3	0.2 \pm 0.1	0	0	0	0	2	0.1 \pm 0.1	5	3.1 \pm 1.2	5	1.4 \pm 0.6	0	0	1	0.1 \pm 0.1	0	0		
<i>Gompholobium huegelii</i>	2	0.1 \pm 0.1	3	0.2 \pm 0.1	2	0.1 \pm 0.1	0	0	0	0	7	0.5 \pm 0	2	0.1 \pm 0.1	7	0.5 \pm 0	7	0.5 \pm 0	3	0.2 \pm 0.1	5	0.4 \pm 0.1	7	0.5 \pm 0	4	0.3 \pm 0.1	0	0		
<i>Gonocarpus tetragynus</i>	7	0.5 \pm 0	3	0.6 \pm 0.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.1 \pm 0.1	0	0	0	0	0	0	0	0	0	
<i>Hibbertia acicularis</i>	7	0.5 \pm 0	7	0.5 \pm 0	6	0.4 \pm 0.1	5	0.4 \pm 0.1	7	0.5 \pm 0	7	0.5 \pm 0	5	0.4 \pm 0.1	0	0	7	0.5 \pm 0	7	0.5 \pm 0	7	0.5 \pm 0	7	0.5 \pm 0	7	0.5 \pm 0	4	0.3 \pm 0.1	0	0
<i>Hibbertia fasciculata</i> var. <i>prostrata</i>	0	0	7	0.5 \pm 0	7	0.5 \pm 0	7	0.9 \pm 0.4	7	0.5 \pm 0	7	0.5 \pm 0	4	0.3 \pm 0.1	7	0.5 \pm 0	7	0.5 \pm 0	7	0.5 \pm 0	4	0.3 \pm 0.1	5	0.4 \pm 0.1	4	0.3 \pm 0.1	2	0.1 \pm 0.1	0	0
<i>Hibbertia virgata</i>	7	0.5 \pm 0	7	0.9 \pm 0.4	7	0.5 \pm 0	7	0.5 \pm 0	6	0.4 \pm 0.1	7	0.5 \pm 0	7	0.5 \pm 0	7	0.5 \pm 0	7	0.5 \pm 0	7	0.5 \pm 0	7	0.5 \pm 0	7	0.5 \pm 0	7	0.5 \pm 0	5	0.4 \pm 0.1	0	0
* <i>Hypochoeris radicata</i>	2	0.1 \pm 0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hypolaena fastigiata</i>	7	0.5 \pm 0	7	3.0 \pm 0	7	0.5 \pm 0	7	9.6 \pm 1.4	7	7.3 \pm 1.5	7	12.1 \pm 2.5	7	1.9 \pm 1.0	7	0.5 \pm 0	7	8.6 \pm 1.1	7	11.8 \pm 1.5	7	13.6 \pm 3.1	7	13.3 \pm 1.7	2	1.1 \pm 1.1	0	0	0	0
<i>Isoetes marginata</i>	1	0.1 \pm 0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lacmannia orientalis</i>	0	0	0	0	0	0	1	0.1 \pm 0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Leptosperma concavum</i>	1	0.1 \pm 0.1	0	0	0	0	2	0.5 \pm 0.4	1	0.1 \pm 0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Leptospermum continentale</i>	1	0.1 \pm 0.1	5	0.4 \pm 0.1	1	0.1 \pm 0.1	0	0	7	2.2 \pm 1.0	0	0	1	0.1 \pm 0.1	5	1.1 \pm 0.5	5	0.4 \pm 0.1	4	0.3 \pm 0.1	2	0.1 \pm 0.1	0	0	0	0	2	0.1 \pm 0.1	0	0
<i>Leptospermum myrsinoides</i>	7	0.5 \pm 0	7	10.7 \pm 1.5	7	8.6 \pm 1.1	7	9.6 \pm 1.4	7	22.1 \pm 1.8	7	29.3 \pm 2.0	7	40.7 \pm 2.0	7	29.5 \pm 2.0	7	22.1 \pm 1.8	7	30.7 \pm 2.0	7	25.0 \pm 2.2	7	26.4 \pm 1.4	7	26.4 \pm 5.1	7	26.4 \pm 1.4	7	26.4 \pm 1.4
<i>Leucopogon ericoides</i>	4	0.3 \pm 0.1	6	0.4 \pm 0.1	7	0.5 \pm 0	7	2.3 \pm 0.5	7	1.9 \pm 0.5	7	1.2 \pm 0.5	6	0.8 \pm 0.4	7	0.5 \pm 0	7	1.9 \pm 0.5	7	0.5 \pm 0	4	0.3 \pm 0.1	5	0.4 \pm 0.1	6	0.4 \pm 0.1	5	0.4 \pm 0.1	5	0.4 \pm 0.1
<i>Leucopogon virgatus</i> var. <i>virgatus</i>	7	0.5 \pm 0	7	0.5 \pm 0	7	0.5 \pm 0	7	0.5 \pm 0	7	0.5 \pm 0	7	0.9 \pm 0.4	7	0.5 \pm 0	5	0.4 \pm 0.1	4	0.3 \pm 0.1												
<i>Lomandra filiformis</i> ssp. <i>filiformis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.1 \pm 0.1	0	0	0	0	2	0.1 \pm 0.1	0	0	0	0	0	0
<i>Lumandra glauca</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0.8 \pm 0.4	5	0.7 \pm 0.4	0	0	0	0	0	0	2	0.1 \pm 0.1	0	0
<i>Lomandra longifolia</i>	5	0.4 \pm 0.1	0	0	0	0	0	0	7	2.3 \pm 0.5	7	0.9 \pm 0.4	6	0.4 \pm 0.1	1	0.1 \pm 0.1	3	0.2 \pm 0.1	7	0.5 \pm 0	7	0.5 \pm 0	5	0.4 \pm 0.1	5	0.4 \pm 0.1	4	0.3 \pm 0.1	0	0
<i>Munatoca scaparia</i>	7	0.5 \pm 0	7	3.0 \pm 0	7	2.6 \pm 0.4	7	3.0 \pm 0	7	9.6 \pm 1.4	7	7.1 \pm 2.1	7	7.1 \pm 2.1	7	1.2 \pm 0.5	7	4.3 \pm 0.8	7	7.3 \pm 1.5	7	9.6 \pm 1.4	7	11.8 \pm 1.5	7	4.4 \pm 1.8	7	1.9 \pm 0.5	0	0
<i>Pimelea limifolia</i> ssp. <i>limifolia</i>	6	0.4 \pm 0.1	3	0.2 \pm 0.1	0	0	2	0.1 \pm 0.1	0	0	0	0	0	0	0	0	2	0.1 \pm 0.1	0	0	0	0	2	0.1 \pm 0.1	0	0	0	0	0	0
<i>Platyace ericoides</i>	5	0.4 \pm 0.1	7	0.5 \pm 0	6	0.4 \pm 0.1	7	0.5 \pm 0	7	1.9 \pm 0.5	1	0.1 \pm 0.1	2	0.1 \pm 0.1	0	0	0	0	2	0.1 \pm 0.1	1	0.1 \pm 0.1	4	0.3 \pm 0.1	3	0.2 \pm 0.1	0	0	0	0
Poaceae sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.1 \pm 0.1	0	0	0	0	0	0
<i>Poa sieberiana</i> var. <i>sieberiana</i>	0	0	0	0	0	0	0	0	2	0.1 \pm 0.1	0	0	0	0	0	0	1	0.1 \pm 0.1	1	0.1 \pm 0.1	2	0.1 \pm 0.1	0	0	0	0	0	0	0	0
<i>Pteridium esculentum</i>	0	0	0	0	0	0	6	5.9 \pm 2.5	0	0	4	2.7 \pm 2.1	0	0	0	0	0	0	0	0	0	0	4	0.6 \pm 0.4	4	0.6 \pm 0.4	6	1.5 \pm 0.5	0	0
<i>Pterostylis parviflora</i>	0	0	0	0	0	0	2	0.1 \pm 0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pterostylis</i> sp.	0	0	0	0	0	0	2	0.1 \pm 0.1	0	0	0	0	0	0	0	0	3	0.2 \pm 0.1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pyrochlis nigricans</i>	5	0.4 \pm 0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0.5 \pm 0	2	0.1 \pm 0.1	0	0	2	0.7 \pm 0.1	0	0	1	0.1 \pm 0.1	0	0
<i>Ricinocarpos pinifolius</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0.3 \pm 0.1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Schoenus imberbis</i>	0	0	0	0	6	0.4 \pm 0.1	5	0.4 \pm 0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Stylidium</i> sp. 2	3	0.2 \pm 0.1	4	0.3 \pm 0.1	3	0.2 \pm 0.1	0	0	4	0.3 \pm 0.1	0	0	0	0	0	0	4	0.3 \pm 0.1	4	0.3 \pm 0.1	2	0.1 \pm 0.1	0	0	0	0	0	0	0	0

Table 4.4 (continued) Frequency (F) (maximum = 7) and mean cover (C) (± 1 SE) of each species found at the 100 m² sampling grain.

Species	BS-0.5		BS-1.5		WT-2.5		SS-5		SS-6		TT-9		T4-14		WT-16		SS-16		VT-19		GP-23		T4-25		SS-26		T2-27	
	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C
<i>Tetrabecca pilosa</i> ssp. <i>latifolia</i>	5	0.4 \pm 0.1	2	0.1 \pm 0.1	0	0	0	0	1	0.1 \pm 0.1	0	0	0	0	0	0	2	0.1 \pm 0.1	1	0.1 \pm 0.1	0	0	0	0	0	0	0	0
<i>Thelionema</i> sp.	1	0.1 \pm 0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tryptanene micrantha</i>	0	0	7	0.5 \pm 0	7	0.9 \pm 0.4	7	9.4 \pm 2.1	1	0.1 \pm 0.1	0	0	4	4.1 \pm 3.5	3	0.2 \pm 0.1	0	0	0	0	0	0	0	0	5	11.6 \pm 4.8	0	0
<i>Xanthorrhoea australis</i>	5	1.4 \pm 0.6	7	3.0 \pm 0	7	5.6 \pm 0.9	7	5.6 \pm 1.8	0	0	0	0	0	0	5	1.4 \pm 0.6	3	1.3 \pm 0.6	0	0	0	0	0	0	0	0	0	0
<i>Xanthorrhoea minor</i> ssp. <i>lutea</i>	5	0.4 \pm 0.1	5	0.4 \pm 0.1	7	0.5 \pm 0	2	0.1 \pm 0.1	0	0	0	0	0	0	1	0.1 \pm 0.1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Xanthoxia pilosa</i>	0	0	0	0	0	0	0	0	0	0	0	0	3	0.2 \pm 0.1	0	0	0	0	0	0	0	0	0	0	1	0.1 \pm 0.1	0	0
<i>Zuera veronica</i>	3	0.2 \pm 0.1	0	0	0	0	2	0.1 \pm 0.1	0	0	0	0	2	0.1 \pm 0.1	0	0	0	0	0	0	0	0	0	0	1	0.1 \pm 0.1	0	0

Table 4.5 Percentage contribution of species to average similarity within a site at the 100 m² scale, using untransformed cover data. Species were only included if they contributed greater than 5% to average similarity within a site. S: shrub; Gr: graminoid; Tr: tree.

Species	Life-form	BS-0.5	BS-1.5	WT-2.5	SS-5	SS-6	TT-9	T4-14	WT-16	SS-16	UT-19	GP-23	T4-25	SS-26	T2-27
<i>Allocasuarina misera</i>	S											6			
<i>Astroloma pinifolium</i>	S														9
<i>Banksia marginata</i>	S					5	12		9	7		6			
<i>Banksia serrata</i>	Tr			8	5	12		13						9	25
<i>Bossiaea heterophylla</i>	S				6										
<i>Calytrix tetragona</i>	S				9		6								
<i>Caustis pentandra</i>	Gr								8	8				15	
<i>Epacris impressa</i>	S									6					
<i>Eucalyptus</i> aff. <i>wiltisii</i> (Gippsland Lakes)	Tr		8	6											
<i>Hypolaena fastigiata</i>	Gr		10		16	9	12			13	15	15	17		
<i>Leptospermum myrsinoides</i>	S		27	28	16	32	38	58	54	34	44	36	36	42	52
<i>Monotoca scoparia</i>	S		10	8	6	13	6	6		6	8	13	14		
<i>Thryptomene micrantha</i>	S				12									6	
<i>Xanthorrhoea australis</i>	S	5.0	10	16	6										

Table 4.6 Mean quadrat species richness in each life-form class at the 100 m² spatial scale. ^S Square-root transformation; ^L Log₁₀ transformation.

Site	Site age (years)	Total life-form richness (100 m ²)	Tree	Shrub	Subshrub	Graminoid	Forb / Geophyte	Twiner	Parasite
BS-0.5	0.5	6.0	1.9	15.6	2.6	3.9	3.3	1.0	0.0
BS-1.5	1.5	5.0	2.1	18.7	3.9	2.7	1.0	0.0	0.0
WT-2.5	2.5	6.0	1.7	17.7	2.3	3.9	0.7	0.3	0.0
SS-5	5	7.0	2.0	17.7	2.3	3.4	1.3	0.3	0.1
SS-6	6	5.0	1.9	17.6	2.7	2.6	0.6	0.0	0.0
TT-9	9	5.0	1.7	7.6	1.7	3.0	0.0	1.0	0.0
T4-14	14	5.0	2.0	16.3	1.7	2.7	0.0	0.1	0.0
WT-16/SS-16	16	5.5	2.1	19.4	1.5	2.9	1.0	0.9	0.0
IT-19	19	6.0	2.4	18.0	1.6	3.7	1.1	0.4	0.0
GP-23	23	6.0	2.4	15.6	1.6	3.3	0.3	0.3	0.0
T4-25	25	6.0	1.6	18.3	2.3	2.9	0.3	0.6	0.0
SS-26	26	6.0	1.9	15.9	2.3	2.0	0.1	0.6	0.0
T2-27	27	6.0	2.0	9.6	0.7	1.9	0.9	0.1	0.0
<i>R</i> ²		0.04 ^S	0.03	0.18	0.41 ^S	0.30 ^L	0.15 ^S	0.00	0.07
<i>F</i>		0.48	0.38	2.44	7.68	4.76	1.92	0.00	0.77
<i>p</i>		0.504	0.551	0.147	0.018	0.052	0.194	0.989	0.400

Table 4.7 Effect of time since fire on community heterogeneity, using linear and quadratic regression. ^S Square-root transformation; ^L Log₁₀ transformation. Quadratic equation: $y = a + bx + cx^2$.

Abundance measure	Linear regression			Quadratic regression		
	R^2	F	p	R^2	F	p
Cover ^S	0.06	0.70	0.421	0.27	1.85	0.207
Standardised cover ^L	0.02	0.26	0.618	0.14	0.80	0.475
Presence/absence	0.21	2.91	0.116	0.38	3.12	0.089

Table 4.8 Pearson correlation (r) matrix of vegetation parameters. S : Species richness; J : Pielou's evenness; H : Shannon-Weiner diversity; CH : Community heterogeneity. ^s Square-root transformation. Asterisks indicate significant pairwise correlations: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Vegetation parameter	S (mean)	S (total)	J^s	H^s
S (total)	0.87 ***			
J^s	0.64 *	0.74 **		
H^s	0.80 **	0.84 ***	0.97 ***	
CH (presence/absence data)	-0.72 **	-0.32	-0.22	-0.39

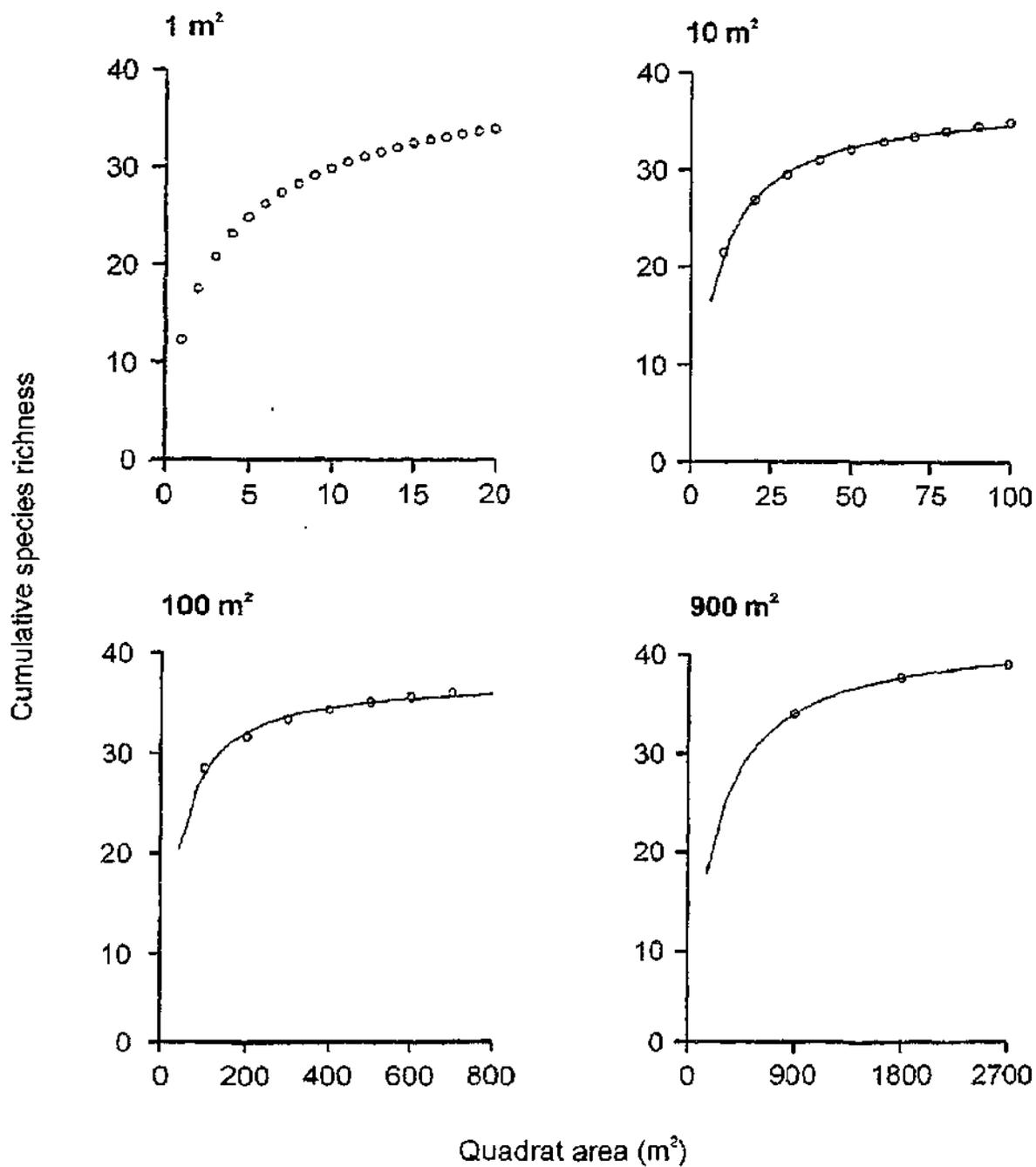


Figure 4.1 Species accumulation curves for the four spatial grains sampled at BS-1.5. Data are fitted with the Michaelis-Menten equation, $y = (a*x) / (b+x)$.

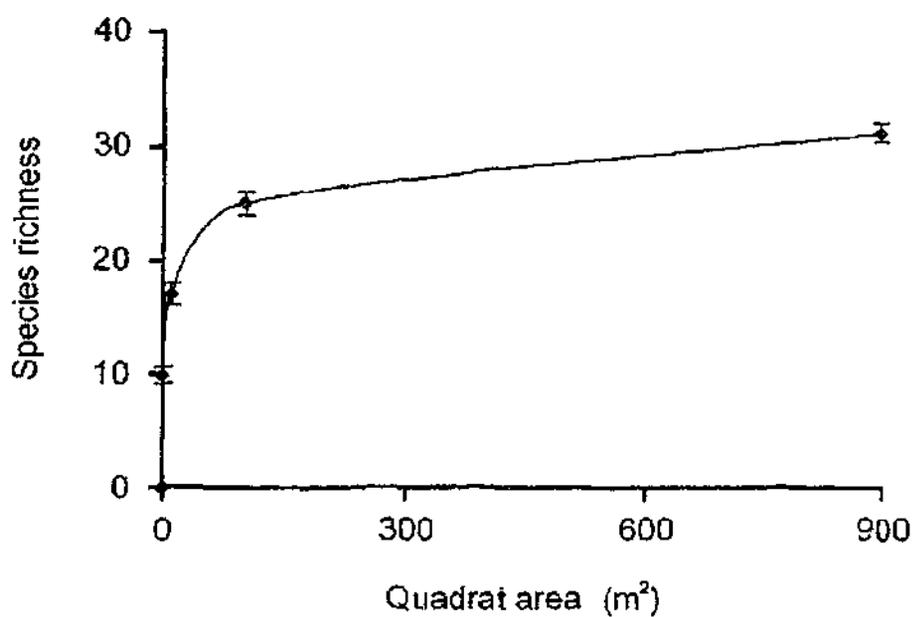
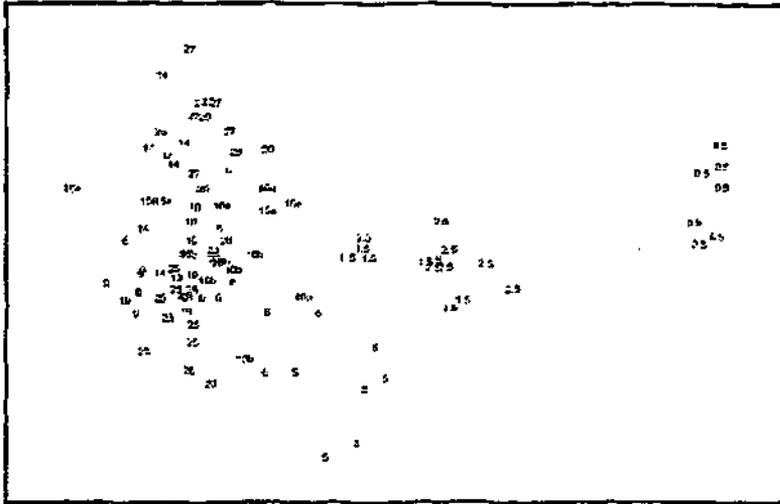
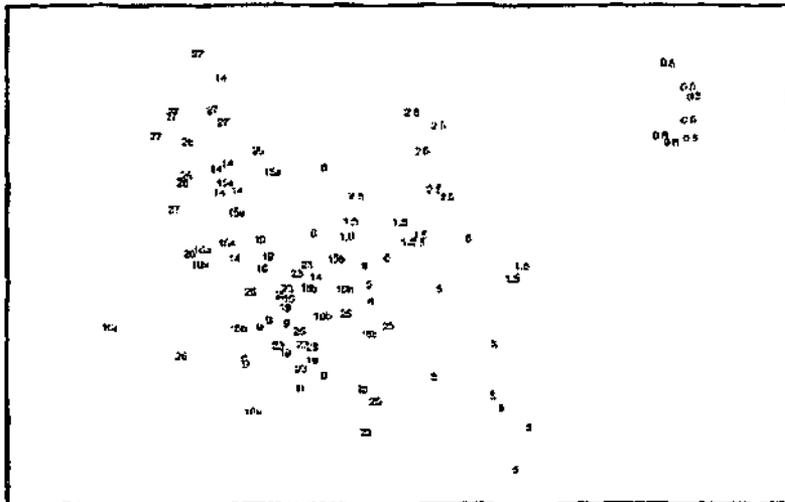


Figure 4.2 Species-area curve showing mean quadrat species richness (± 1 SE), averaged across all sites.

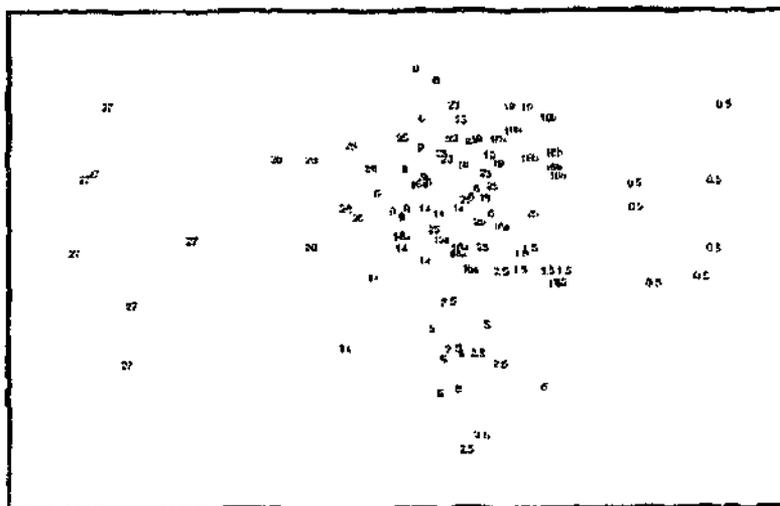
(a) Untransformed cover data; stress = 0.15



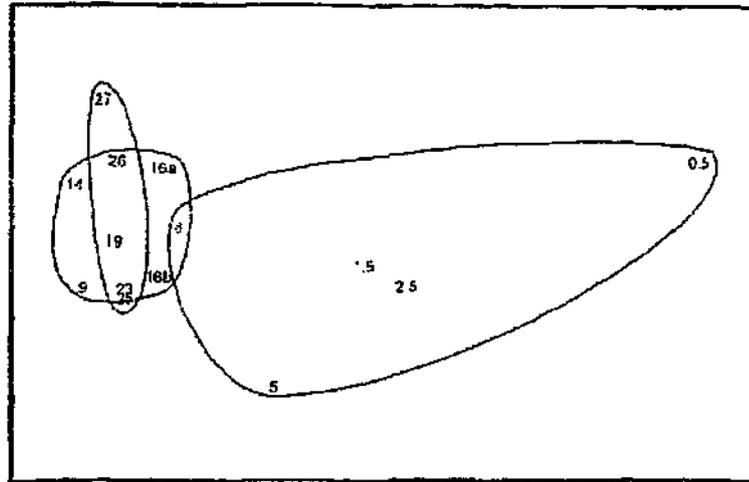
(b) Standardised cover data; stress = 0.18



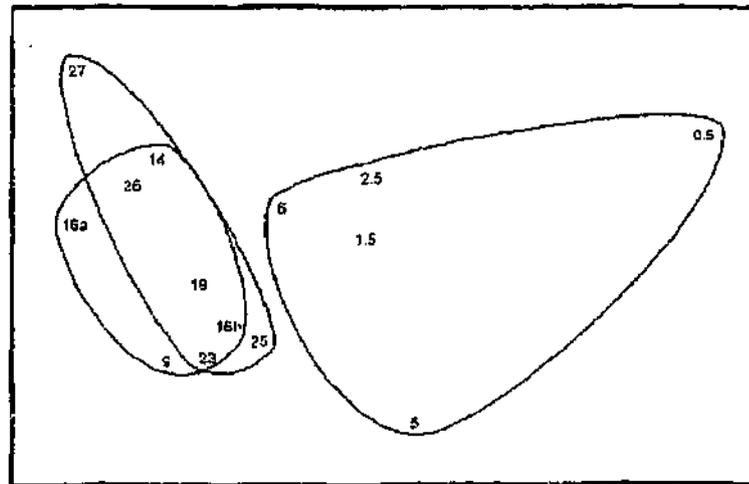
(c) Presence/absence data; stress = 0.20

Figure 4.3 Ordination by NMDS of all quadrats at the 100 m² scale.

(a) Untransformed cover data; stress = 0.08



(b) Standardised cover data; stress = 0.10



(c) Presence/absence data; stress = 0.11

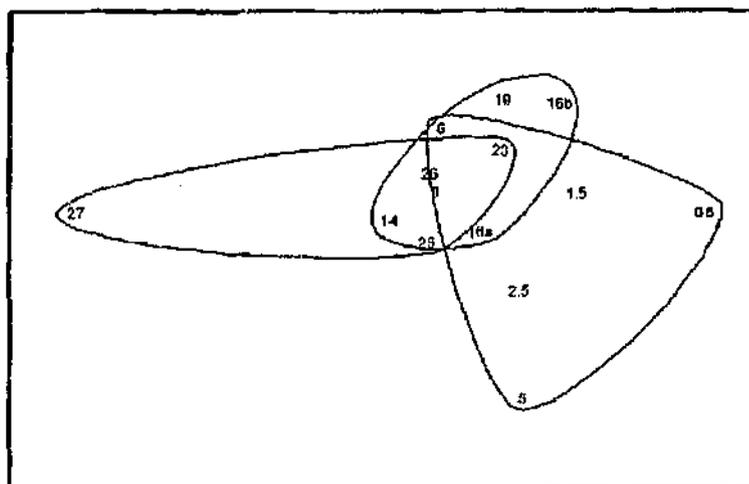


Figure 4.4 Ordination by NMDS of mean quadrat data points at the 100 m² scale. Sites are grouped into young (0-6 years), intermediate (9-19 years) and old (23-27 years) age classes.

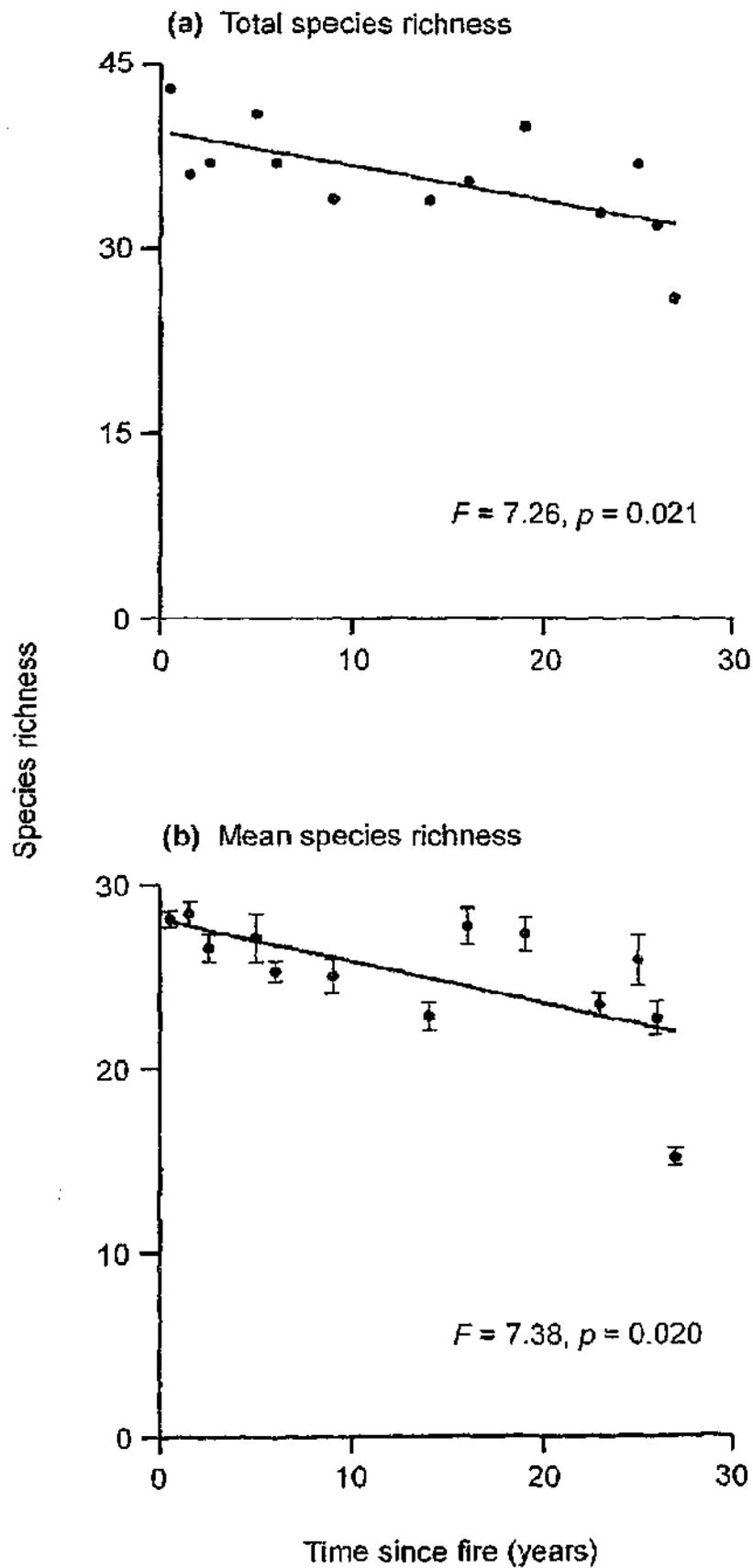


Figure 4.5 Relationship between species richness and time since fire at the 100 m² grain. (a) Total species richness; (b) Mean species richness (± 1 SE).

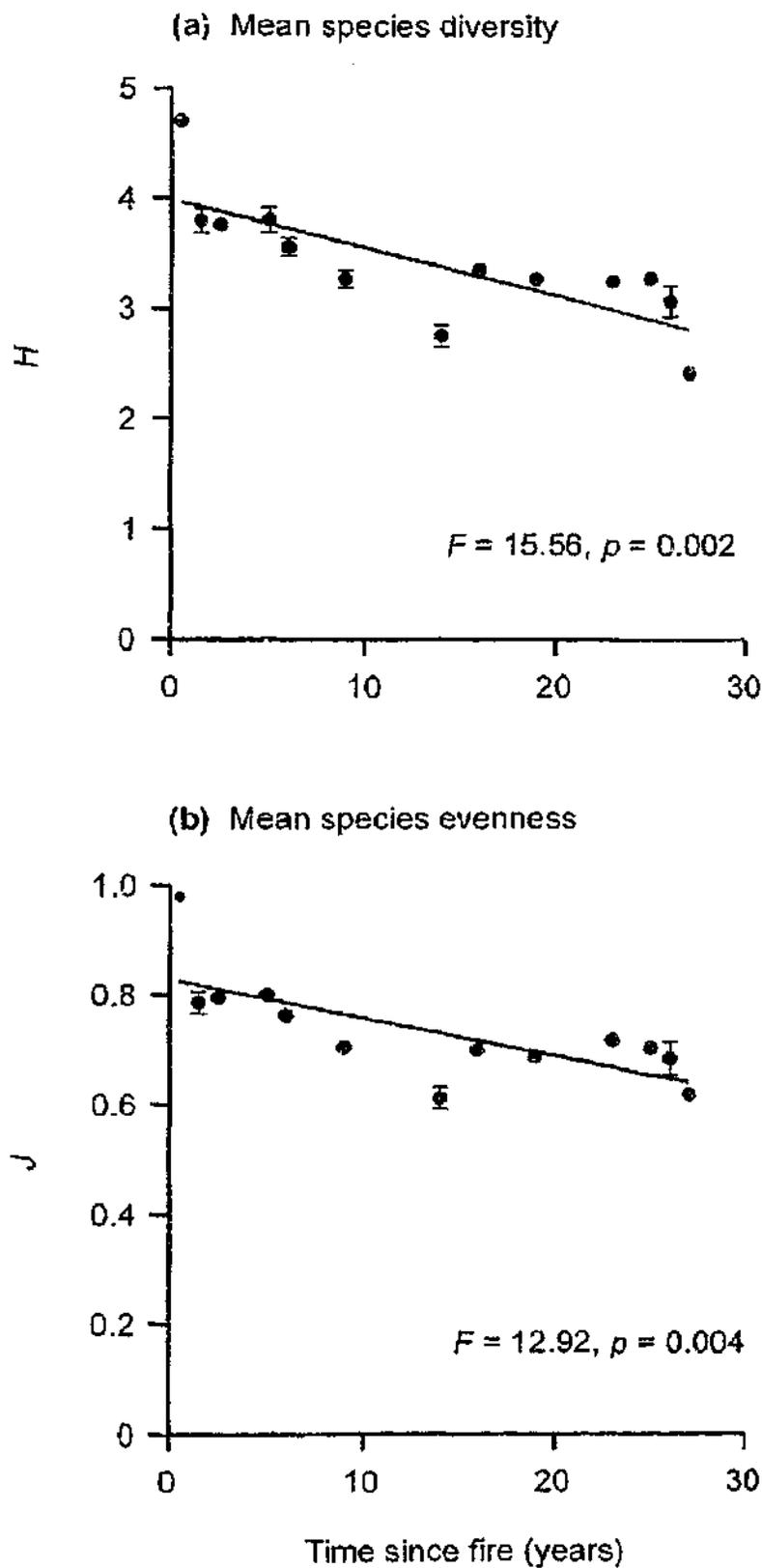


Figure 4.6 Relationship between: (a) mean species diversity (H) (± 1 SE), and (b) mean species evenness (J) (± 1 SE), with time since fire at the 100 m^2 grain. Data points with no SE bars indicate that SE is zero, or less than the size of the symbol. Data have been square-root transformed for statistical analysis.

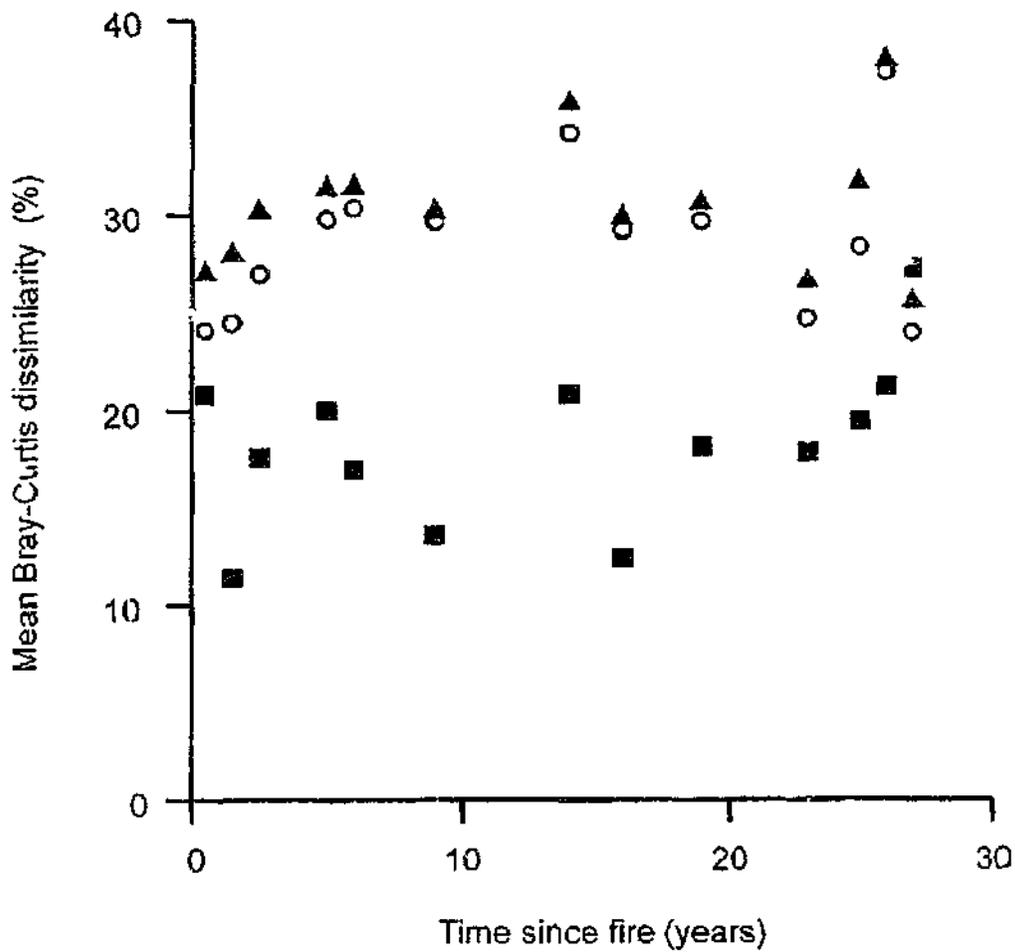


Figure 4.7 Relationship between community heterogeneity (mean Bray-Curtis dissimilarity) and time since fire at the 100 m² grain. ○ cover data; ▲ standardised cover data; ■ presence/absence data.

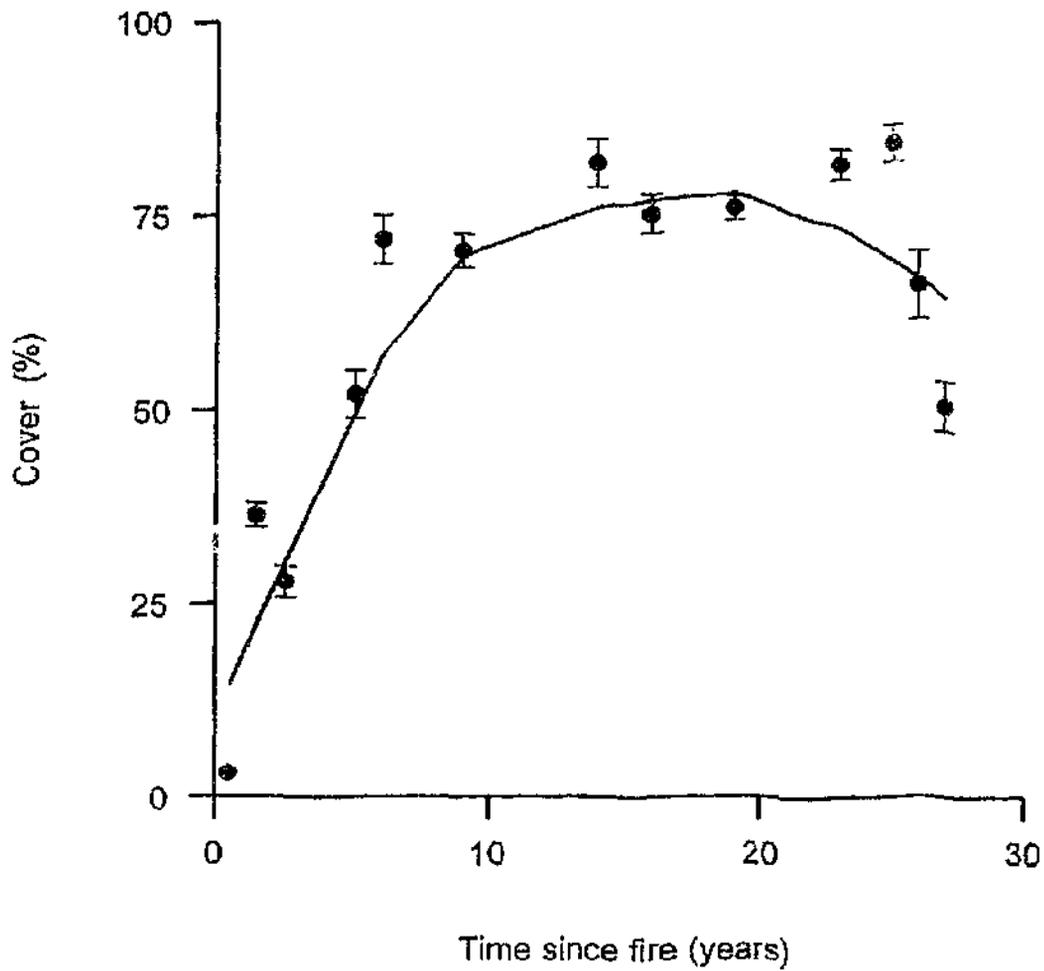


Figure 4.8 Mean total vegetation cover (± 1 SE) at the 100 m² scale, with LOWESS smoothing function fitted to the data (tension: 0.6).

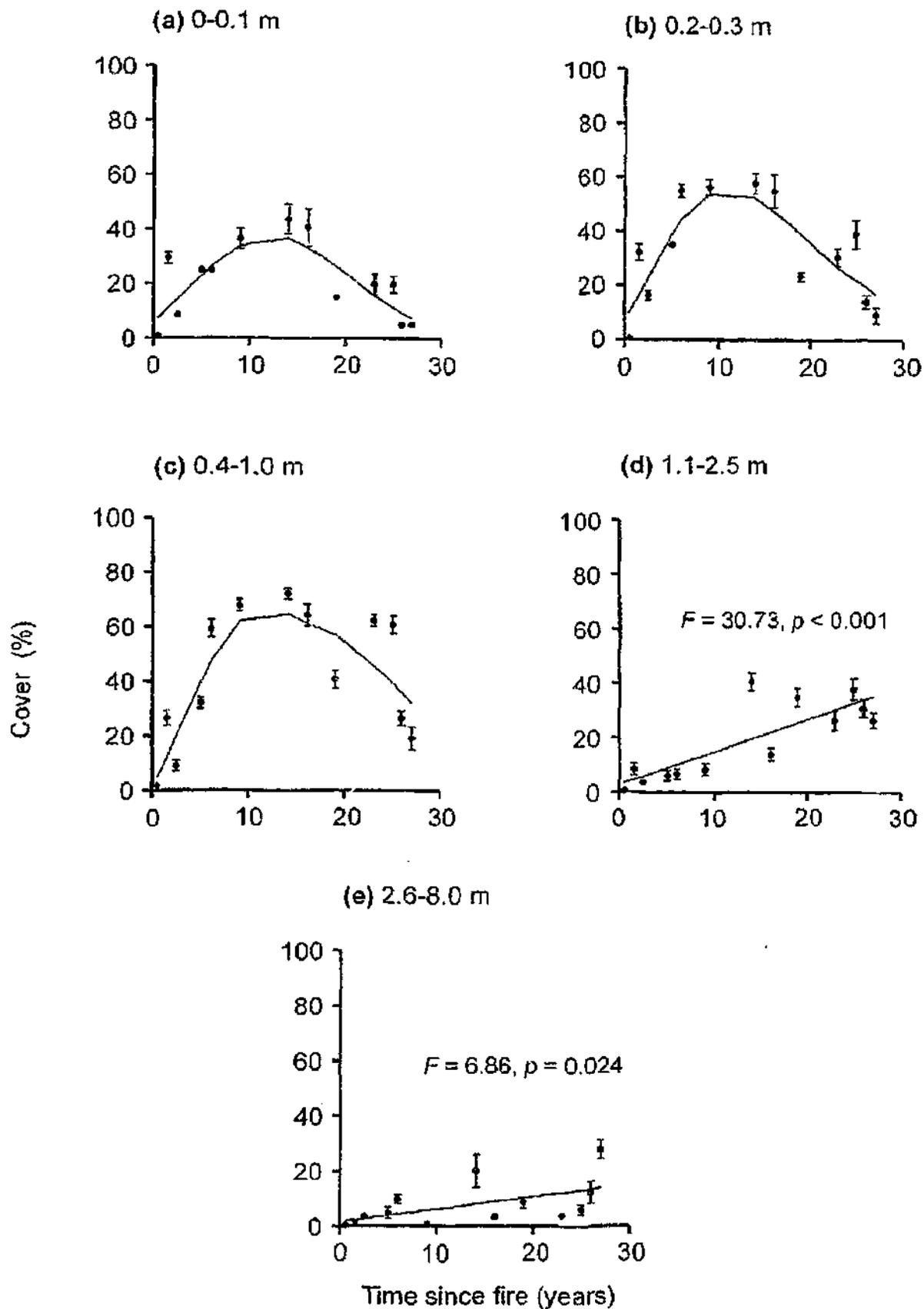


Figure 4.9 Mean vegetation cover (± 1 SE) for each height class at the 100 m² scale, with LOWESS smoothing function fitted to the data (tension: 0.6) on (a) - (c), and linear regression line of best fit on (d) and (e). Data points with no SE bars indicate that SE is zero, or less than the size of the symbol. Data for (d) and (e) were square-root transformed for the statistical test.

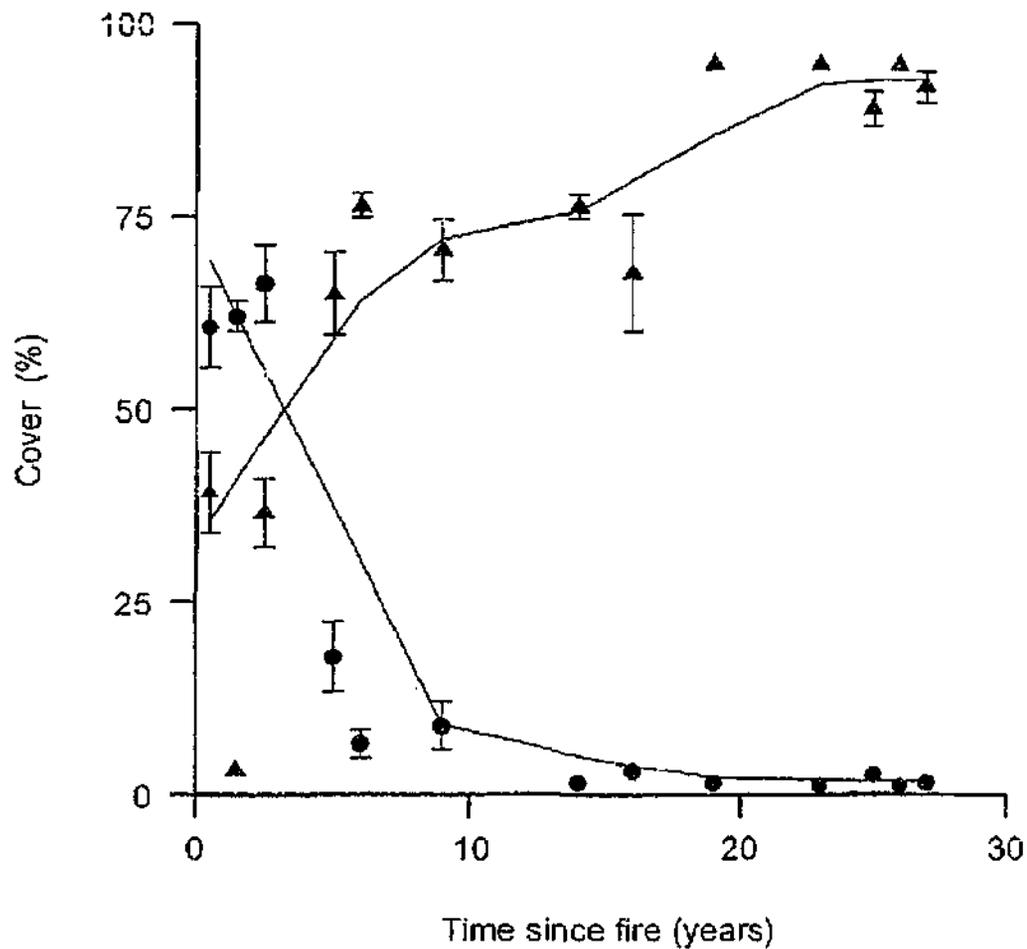


Figure 4.10 Mean litter (\blacktriangle) and bare ground (\bullet) cover (± 1 SE) at the 100 m² scale, with LOWESS smoothing function fitted to the data (tension: 0.6). Data points with no SE bars indicate that SE is zero, or less than the size of the symbol.

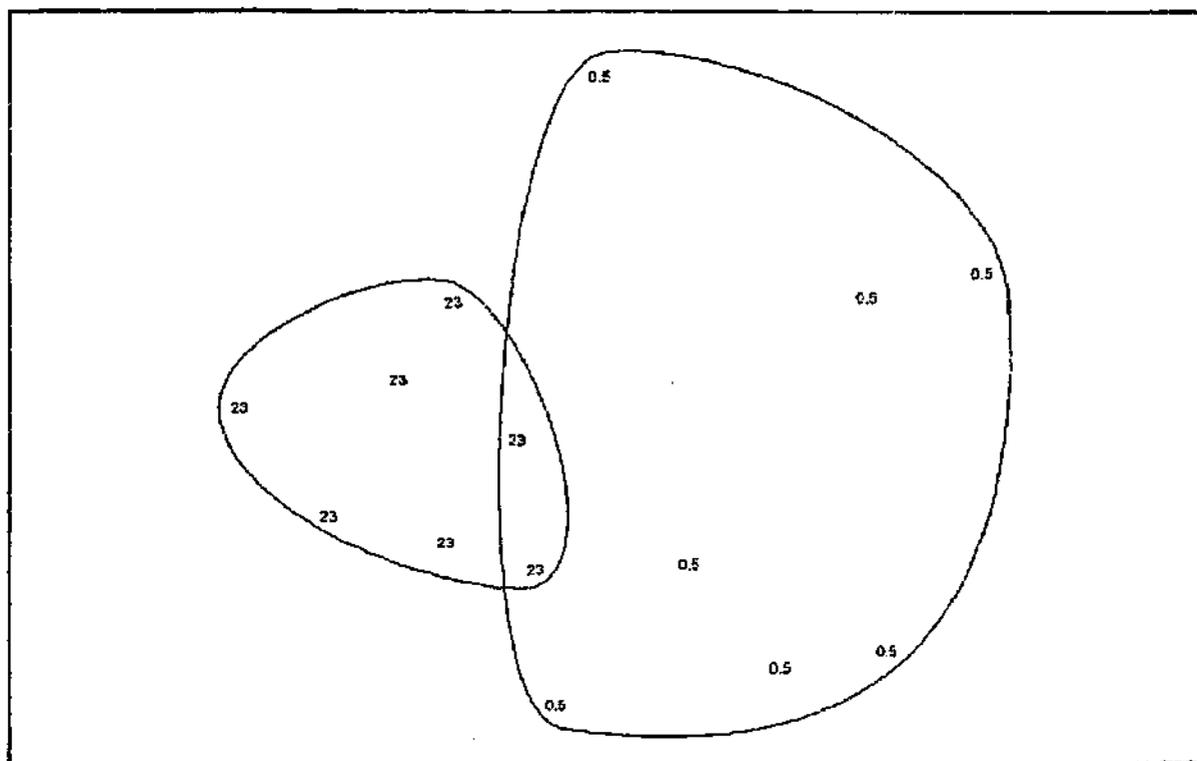


Figure 4.11 NMDS ordination at GP (stress = 0.16), using species presence/absence data pre- (23 year old) and post-fire (0.5 year old) at the 100 m² scale.

CHAPTER 5

INFLUENCE OF SAMPLING GRAIN ON VEGETATION PARAMETERS

INTRODUCTION

In recent decades, the issue of scale in natural communities has been recognised as a major issue in ecology (Allen & Starr 1982; Levin 1992; Gardner 1998; MacNally & Quinn 1998; Scheiner *et al.* 2000). Many ecological patterns and processes have been shown to be spatially and/or temporally scale-dependent (Allen & Starr 1982; Reed *et al.* 1993; MacNally & Quinn 1998). For example, landscape-scale processes such as climate, geomorphology (Nichols *et al.* 1998) and fire (Williams *et al.* 1994) all combine to influence species distributions. However, at a smaller scale, features such as environmental microheterogeneity (Weir & Wilson 1987; Vivian-Smith 1997; Kleb & Wilson 1999), fire intensity (Rice 1993; Williams *et al.* 1994), interspecific competition (Keith & Bradstock 1994; Vila & Sardans 1999) and species dispersal mechanisms (Reed *et al.* 2000) also interact to substantially affect local species composition and abundance. Despite the growing literature, we still have much to learn regarding the scale(s) at which different biological processes operate, the scale(s) at which different organisms live and interact, and the scaling of different communities. Often, we perceive patterns and processes at particular spatial and temporal scales based on our world-view, however, the manner in which other organisms perceive the world may be totally different (Levin 1992). Furthermore, *"as one moves to finer and finer scales of observation, systems become more and more variable over time and space, and the degree of variability changes as a function of the spatial and temporal scales of observation"* (Levin 1988).

Central to an understanding of spatial scale are the concepts of sampling *grain*, *extent* and *intensity*. The grain of a study is the size of the sampling or experimental units (e.g. quadrat size) (Allen & Starr 1982), or the lower limit of resolution (Reed *et al.* 1993). Extent refers to the size of the area over which the individual samples are distributed (Reed *et al.* 1993) (e.g. 4 ha sites in this study). Finally, intensity refers to the total area

sampled (Reed *et al.* 1993) (e.g. c. 3500 ha in this study). Furthermore, the number of sampling units used and the shape of these sampling units are also important factors to consider when designing and comparing studies (Palmer & White 1994).

Prior to any ecological study, a sampling grain (or multiple grains) should be chosen that is appropriate to the question being asked (Dutilleul 1993; MacNally & Quinn 1998), otherwise, difficulties can arise in making ecologically meaningful interpretations of the data. Despite the importance of sampling grain, it is frequently chosen on the basis of current practice or precedent, without carefully considering the ecological processes or organisms being studied (MacNally & Quinn 1998). For instance, heathland studies in Australia usually employ sampling grains ranging from 1-100 m² (Specht & Rayson 1957; McMahon 1984b; Wark *et al.* 1987; Enright *et al.* 1994; Myerscough *et al.* 1995; Bradstock *et al.* 1997; Cheal 2000), and sometimes up to 800 m² (Posamentier *et al.* 1981). However, the majority of these studies do not explain the reason for choosing a particular sampling grain. As there appears to be no single 'correct' scale in which to investigate a given community (Palmer 1990b; Levin 1992), a multi-scale approach may often yield more information and be more appropriate (Walker *et al.* 1972; Levin 1988; Thórhallsdóttir 1990; Gardner 1998).

This study aims to determine the effect of sampling grain on:

- (1) heathland species composition, richness, diversity, evenness and community heterogeneity; and
- (2) trends in these vegetation parameters with increasing time since fire.

The study is significant in that it is the only study that I know of that examines trends in vegetation parameters with time since fire across multiple spatial scales in Australian heathlands.

METHODS

The field sampling methods follow those outlined in Chapter 4. In addition to the five spatial grains sampled (1 m^2 , 10 m^2 , 100 m^2 , 900 m^2 and 1 ha), a sixth scale, that of the entire site (4 ha), is included in analyses where possible. All data analyses follow those outlined in Chapter 4, except those outlined below.

Species composition is only analysed using the mean values averaged across a site, rather than individual data points (quadrats). Results from Chapter 4 suggest that the mean values are a reasonable approximation of the actual data points in multidimensional space (see Figure 4.3 and Figure 4.4). Furthermore, they allow for a simpler set of pairwise comparisons, grouping sites into young, intermediate and old age classes, rather than attempting to deal with the 91 pairwise comparisons among individual sites.

RESULTS

Species composition

For all six sampling grains studied, NMDS of cover data generally grouped old (23-27 years old) and intermediate (9-19 years old)-aged sites closely together, while young sites were grouped separately but covered a much broader area in multidimensional space (Figure 5.1a-f). BS-0.5 was distinctly different from all other sites for each grain, but most notably at the 1 m² and 10 m² grains, where all other sites were grouped tightly together. The next three youngest sites, BS-1.5, WT-2.5 and SS-5, were also grouped separately, while the remaining 10 sites that were six years or older at the time of sampling were grouped together. The oldest site, T2-27, appeared to become more distant from the main group as grain increased, particularly at the 1 ha and 4 ha grains. Following standardisation of the cover data, general patterns were similar. However, the pattern at the 1 m² and 10 m² grains changed markedly, representing each site in two-dimensional space in a similar manner to the other grains (Figure 5.2a-f). As with the unstandardised cover data, young sites were generally grouped separately from the rest. However, there were small variations in the degree of overlap between young and intermediate/old sites, particularly with SS-6. Finally, transformation of the data to presence/absence caused the most noticeable difference in how sites were grouped in two-dimensional space (Figure 5.3a-f). The oldest site, T2-27, was separated much more distinctly from all other sites, across all grains, than it was for either the cover or standardised cover data. This was particularly evident at the 1 ha grain (Figure 5.3e). Young sites (0-6 years old) were also grouped separately, with the exception of SS-6, which was sometimes associated with the main group. All other sites were grouped relatively close together.

ANOSIM indicated that species composition differed significantly among age classes for cover, standardised cover and presence/absence data at all sampling grains, except 100 m² (presence/absence) and 1 m² (all three abundance measures) (Table 5.1). Pairwise comparisons indicated that young and intermediate sites were significantly different for cover, standardised cover and presence/absence data at all sampling grains, except 100 m² (presence/absence) and 1 m² (all three abundance measures) (Table 5.1). In addition, composition differed significantly between young and old sites for the 4 ha,

1 ha and 900 m² grains, for cover and presence/absence data, and 100 m² for cover data (Table 5.1). Composition did not differ between intermediate and old sites.

Species richness

Species richness was markedly influenced by sampling grain in two ways. First, as sampling grain increased, species richness generally increased, as expected (Figure 5.4). This was true at every site for mean richness. However, total richness was not always greater as sampling grain increased, because of the different number of quadrats sampled at each grain, and the different levels of saturation associated with this sampling regime (Figure 4.1, Table 4.2). Second, species richness (total and mean) decreased significantly with increasing time since fire for some sampling grains but not for others (Figure 5.4, Table 5.2).

Total site species richness decreased significantly with increasing time since fire for the 100 m², 900 m² and 1 ha grains (Table 5.2a). However, there was no significant change for the two smallest grains sampled, 1 m² and 10 m², and the largest grain, which was the entire site (4 ha). Mean species richness displayed a similar trend, with the 10 m², 100 m² and 900 m² grains indicating a significant decrease in richness with time since fire, while at the 1 m² grain there was no such difference (Table 5.2b).

Species evenness and diversity

Unlike species richness, evenness (J) displayed no consistent pattern (e.g. a clear trend toward higher or lower evenness with increasing grain) among sampling grains (Figure 5.5a). In terms of the line of best fit derived via linear regression, there was a greater discrepancy among grains at young sites compared to older sites, where evenness appears to be converging, irrespective of grain (Figure 5.5a). J decreased significantly with increasing time since fire for all grains except 1 m² (Table 5.3).

Species diversity (H) responded to sampling grain in a similar manner to richness. First, H increased from the smallest to the largest grain in an approximately parallel fashion, although mean diversity at the 900 m² grain was usually slightly more than the 1 ha grain (Figure 5.5b). Second, H decreased significantly with increasing time since fire for all six grains (Table 5.4).

Community heterogeneity

Community heterogeneity (mean Bray-Curtis dissimilarity) decreased markedly with increasing grain, for both cover and presence/absence data, although WT-2.5 and BS-0.5 were exceptions to this general pattern (Figure 5.6). Using cover data, community heterogeneity averaged across all sites decreased from a peak of $61 \pm 3\%$ at the 1 m^2 grain, to $45 \pm 2\%$ (10 m^2), $29 \pm 1\%$ (100 m^2) and $18 \pm 2\%$ at the 900 m^2 sampling grain. Similarly, using presence/absence data, heterogeneity decreased from a peak of $44 \pm 2\%$ at the 1 m^2 grain, to $31 \pm 2\%$ (10 m^2), $18 \pm 1\%$ (100 m^2) and $14 \pm 1\%$ at the 900 m^2 grain. Heterogeneity for both cover and presence/absence data did not display a linear trend with time since fire for any of the four grains sampled (Table 5.5). However, the quadratic equation appeared to fit the data much better than linear regression, with cover data at the 10 m^2 grain significantly related to time since fire in the form of a positive quadratic equation ($y = 52.13 - 2.12x + 0.08x^2$). In addition, R^2 values were substantially higher for the quadratic regression compared with linear regression. Generally speaking, at the 1 m^2 and 10 m^2 grains for cover and presence/absence data, heterogeneity appeared to be relatively high initially following fire, after which it decreased until *c.* 15 years after fire, and subsequently increased to reach immediate post-fire levels 26-27 years after fire (Figure 5.6). For presence/absence data, the pattern at the 100 m^2 and 900 m^2 grains is similar to that mentioned above, while cover data suggest no trend at the 900 m^2 grain, and a slightly inverse trend at the 100 m^2 grain (Figure 5.6). However, the results should be interpreted with caution, owing to the variability of the data set.

DISCUSSION

Spatial scale, in the form of sampling grain, was found to influence various vegetation parameters and in some instances, significantly affect their relationship with time since fire. There was a distinct trend toward higher mean species richness as sampling grain increased, which is an almost universal finding in studies worldwide (Colwell & Coddington 1994; Palmer & White 1994), which Lomolino (2000) describes as the closest thing to a rule in ecology. However, total richness did not always display this trend, predominantly owing to the fact that as grain increased, sample number decreased, subsequently^{potentially} affecting total richness values at each scale.

Species richness was found to decrease significantly with increasing time since fire. In the context of Australian heathlands, this is not surprising, given the number of studies that have reported this trend (e.g. Specht *et al.* 1958; McMahon 1984b; Wark 1996). However, this study is unique in that mean richness was shown to decrease^{with time} at three of the four sampling grains, while total richness decreased^{with time} at only three of the six grains, i.e. the decline in richness with time since fire is dependent upon sampling grain. In a dry European heathland, Chytrý *et al.* (2001) found that richness changed with time since experimental disturbance in a similar manner across three different spatial scales, 0.1 m², 1 m² and 9 m², however, the timing of the peak in richness was scale dependent. These findings have major implications for studies investigating the effect of time since disturbance (e.g. fire) on species richness, as they provide evidence that the effect of time since disturbance is scale dependent (Palmer & White 1994). This also suggests that studies reporting a change in richness over time should only be interpreted at the grain sampled, and not extrapolated to larger spatial scales (Walker *et al.* 1972; Palmer 1990b; Carpenter 1996), as is commonly the case (MacNally & Quinn 1998).

The lack of a decrease in total and mean richness with time since fire at the 1 m² grain is intriguing, given the trends observed at larger grains. For instance, greater numbers of species are expected to be packed into an area of 1 m² in the immediate years following fire, owing to the promotive effect of fire on germination (Gill & Groves 1981; Tyler 1995), the relatively small size of each individual (Rice & Westoby 1983; Crawley & Harral 2001) and the reduced levels of resource competition in the initial years after fire (Grime 1977; Clarke *et al.* 1996; Vila & Sardans 1999). As time since fire increases, individuals grow in size to the point where trees (*Banksia serrata* and *Eucalyptus* spp.)

and large shrubs (e.g. *Allocasuarina* spp., *Banksia marginata* and *Leptospermum* spp.) may cover an area greater than the grain size (1 m^2), competition for resources increases (Vila & Sardans 1999), and weaker plants or shorter-lived species are expected to die out, resulting in reduced species richness (Specht & Specht 1989; Keith 1995). Despite this prediction, such a trend in species richness was not evident at the 1 m^2 grain in this study. There are two possible reasons for this. First, there was a dearth of post-fire ephemeral species present at the 1 m^2 grain (only four of the 10 species that were recognised as potential post-fire ephemerals in Chapter 4), therefore, reducing any potential decrease in richness due to these species from the outset. Second, in the immediate post-fire environment, higher seedling densities do not necessarily equate with higher species richness; instead, there may simply have been a greater number of individuals of only a few species.

In addition to the absence of a decrease in total and mean richness at the 1 m^2 grain, and total richness at the 10 m^2 grain, there was also no significant decrease in total richness with time since fire at the scale of the entire site (4 ha). This is surprising in the context of other heathland studies, however, it may be explained by the degree of patchiness in species distributions. For example, species frequencies are hypothesised to reach their respective maxima for a given grain approximately 1-2 years following fire, when all seed promoted to germinate by fire has emerged (Keith & Bradstock 1994). Thereafter, as populations increase in age and become increasingly subject to competition from surrounding plants (Grime 1977), many species begin to 'thin out' via density-dependent mortality (Begon *et al.* 1990) and/or old age, to the point where richness displays a decrease with time since fire at the intermediate grains assessed in this study. Despite this 'thinning' effect, after 27 years of post-fire vegetation development, many species may still be present at a site, but at a much lower frequency, thus maintaining species richness and preventing a decrease in richness with time since fire. Furthermore, different determinants of species richness may operate at different spatial scales (Palmer 1990b; Crawley & Harral 2001). This is a phenomenon that may be occurring in the heathlands of this study, with the potential scale-dependent determinants of species richness being past fire regimes, patchiness in fire intensity, environmental heterogeneity and variability in distance to propagule sources.

According to Kwiatkowska & Symonides (1986) and Kvålseth (1991), species evenness (J) is predicted to alter with sampling grain, with the most basic model predicting this change to be an increase in J as spatial grain increases (Wilson *et al.* 1999). Despite this prediction, Wilson *et al.* (1999) found the opposite, Kwiatkowska & Symonides (1986) found no pattern in plots ranging from 1-64 m², while this study also found no clear pattern, although there was a general trend for J to increase with increasing grain (although the 1 ha grain was an anomaly). This suggests that at larger grains, species cover-abundances were generally more even, pointing to the relatively uniform nature of the heathland. In addition, J decreased with increasing time since fire for all grains except 1 m², indicating that species cover-abundances were becoming more variable as time since fire increased. This pattern is probably attributable to a combination of variability in individual plant size, species frequencies, and growth and mortality rates. In terms of the total variability among grains, J appears to be more variable at young sites compared with older sites, where J values are very similar among grains. For example, the total spread of J values from the 1 m² to the 1 ha grain at T2-27 was only 0.63-0.67. This suggests that J is beginning to converge across spatial grains as time since fire increases.

In a similar manner to mean species richness, diversity (H) increased as sampling grain increased, although the 1 ha grain was slightly less diverse than the 900 m² grain. The overall trend of increased diversity with area was expected, as H is a direct by-product of species richness and J . The decline in H with time since fire appeared to be independent of scale, as all six grains decreased significantly with increasing time since fire, indicating that this was a universal trend when sampling at any grain between 1 m² and 4 ha.

As with richness, changes in species composition among young, intermediate and old sites were dependent on sampling grain, with all grains exhibiting significant differences in composition, apart from the 1 m² grain (cover, standardised cover and presence/absence data) and the 100 m² grain (presence/absence data). This again indicates the importance of sampling at multiple spatial scales, as the grain chosen to study (100 m²) based on a species-area curve in Chapter 4, yielded a non-significant difference, while four of the other five grains were significantly different. Prior to the study, young and old sites were postulated to be the most dissimilar in terms of species

composition, owing to species senescence over time, however, pairwise comparisons indicated that young and intermediate sites were more often significantly different across a range of grains and abundance measures (Table 5.1).

The importance of scale in determining the level of heterogeneity within a given site remains when the focus shifts from composition to changes in community heterogeneity with time since fire. For instance, at one scale, landscapes may appear quite heterogeneous, however, at another scale, they may seem homogeneous, thus making spatial scale essential in definitions of landscape heterogeneity and diversity (Meentemeyer & Box 1987). Despite the recognised importance of scale, studies determining its effects on plant community heterogeneity are uncommon (Steinberg & Kareiva 1997). In this study, the level of community heterogeneity decreased markedly as spatial grain increased, to the point where heterogeneity among quadrats at the 900 m² grain was quite low. This pattern is predominantly due to the fact that larger samples are more likely to include a greater subset of species from a given community, thus, increasing the level of similarity among quadrats, compared with smaller quadrats (Collins 1992). Comparisons with other Australian communities are unable to be made, owing to the paucity of data on community heterogeneity in Australia, however, the heathland in this study appears to be relatively homogeneous in composition within sites, especially at the 900 m² grain.

In two of the few exceptions examining heterogeneity in terms of compositional dissimilarity, Collins (1989) and Collins (1992) found that community heterogeneity on annually burned grasslands was significantly lower than on unburned or once-burned grasslands, suggesting that higher fire frequency reduced heterogeneity. However, Collins (1992) found this effect to be scale-dependant, with community heterogeneity on an annually burned grassland significantly lower than unburned (control) grassland at a small scale (10 m²), but not at a larger scale (200 m²). Evidence for scaling effects on the relationship between heterogeneity and fire (in this case, time since fire) were also found in this study, with a positive quadratic relationship appearing to exist between community heterogeneity and time since fire for some scales. Although these relationships were rarely statistically significant, some observations may be made. Generally, heterogeneity was high (relatively speaking in the context of this study) in the early post-fire years, owing to a combination of relatively high species diversity and the

potential presence of post-fire ephemerals. This can be seen as the period of high heterogeneity associated with species establishment, as proposed in the cyclic heterogeneity model of Armesto *et al.* (1991). As time progresses to an intermediate heath age, post-fire ephemerals and short-lived species die out, while most other species remain alive, resulting in decreased heterogeneity. In this study, it is unclear to what degree species loss is due to the shortening of plant lifespans caused by competition, where species can no longer compete under changing site conditions, compared with inherent plant lifespan constraints. Finally, as time since fire increases further to the oldest age sampled in this study (27 years), heterogeneity appears to increase, even though species richness is decreasing. This phase is hypothesised by Armesto *et al.* (1991) to signify species invasions, however, the incidence of invasion, or even recruitment for that matter, is very low in the older sites of this study. Therefore, a possible explanation for this pattern is that as some species begin to die out at a given sampling grain, whether through old age or competitive exclusion, their distribution becomes patchier, thus increasing the mean dissimilarity between any two quadrats. Given the relatively short age-span of this study, it would be pre-emptive to suggest that cycles of heterogeneity exist within the heathland, *sensu* Armesto *et al.* (1991), however, there is evidence to suggest that this may be the case. Further monitoring and sampling of sites as they increase in age may shed more light on this situation.

Overall, sampling grain was shown to have a major effect on

- (a) species composition, and levels of species richness, evenness, diversity and community heterogeneity, and
- (b) the significance of trends in some of these vegetation parameters with increasing time since fire.

If this study had simply presented the results of Chapter 4 without analysing for the effect of different sampling grains, conclusions would have been markedly different and would have led to a distorted image of the system (Levin 1988). In particular, this study gives further weight to the view that multiple sampling grains are essential to comprehensively understand pattern and process in communities.

Table 5.1 ANOSIM results (R values) for cover (c), standardised cover (sc) and presence/absence (pa) data for mean data points at each site for the six sampling grains. Y: young sites (0-6 years since fire); I: intermediate sites (9-19 years since fire); O: old sites (23-27 years since fire). An asterisk indicates statistical significance: * $p < 0.05$; ** $p < 0.01$. No p -values were < 0.001 .

Sampling grain	Abundance measure	Global test	Pairwise comparisons		
			Y-I	Y-O	I-O
4 ha	c	0.31 **	0.48 **	0.46 *	0.18
4 ha	sc	0.22 *	0.37 **	0.23	0.13
4 ha	pa	0.29 **	0.53 **	0.37 *	0.08
1 ha	c	0.31 **	0.49 **	0.43 *	0.15
1 ha	sc	0.21 *	0.36 **	0.21	0.09
1 ha	pa	0.24 **	0.47 **	0.23 *	0.00
900 m ²	c	0.25 **	0.44 *	0.45 *	-0.07
900 m ²	sc	0.19 *	0.35 **	0.26	-0.06
900 m ²	pa	0.25 **	0.42 *	0.33 *	-0.02
100 m ²	c	0.31 **	0.50 **	0.33 *	0.08
100 m ²	sc	0.23 *	0.45 **	0.19	0.00
100 m ²	pa	0.11	0.26	0.27	-0.14
10 m ²	c	0.29 **	0.39 *	0.24	0.24
10 m ²	sc	0.29 **	0.40 **	0.28	0.23
10 m ²	pa	0.20 *	0.40 *	0.13	0.08
1 m ²	c	0.16	0.34	0.01	0.03
1 m ²	sc	0.03	0.08	0.06	-0.08
1 m ²	pa	0.13	0.27	0.14	0.02

Table 5.2 Results of linear regression of species richness in relation to increasing time since fire. ^S Square-root transformation; ^L Log₁₀ transformation.

(a) Total richness

Sampling grain (m ²)	<i>R</i> ²	<i>F</i>	<i>p</i>
1	0.29	4.42	0.059
10 ^L	0.26	3.83	0.076
100	0.40	7.26	0.021
900	0.43	8.26	0.015
10000	0.43	8.38	0.015
40000	0.27	4.07	0.069

(b) Mean richness

Sampling grain (m ²)	<i>R</i> ²	<i>F</i>	<i>p</i>
1	0.23	3.37	0.094
10 ^S	0.42	7.83	0.017
100	0.40	7.38	0.020
900	0.33	5.32	0.041

Table 5.3 Results of linear regression of species evenness (J) in relation to increasing time since fire. ^S Square-root transformation; ^L Log₁₀ transformation.

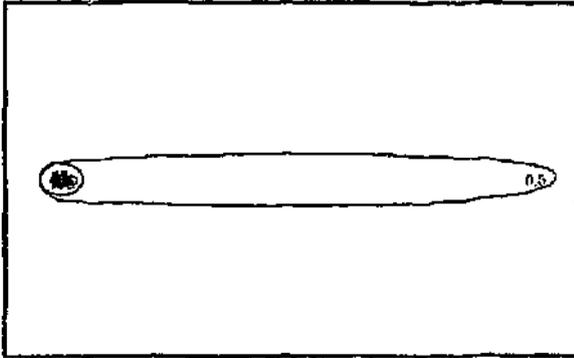
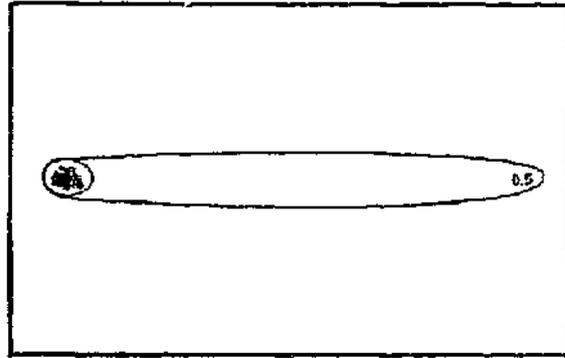
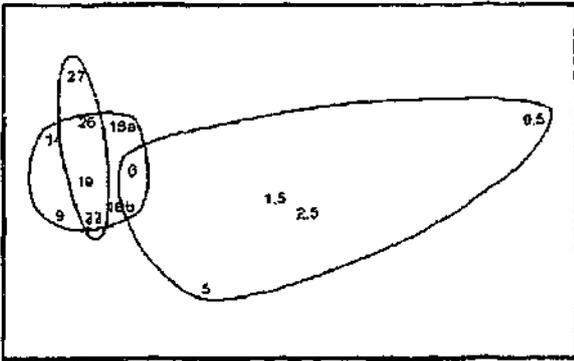
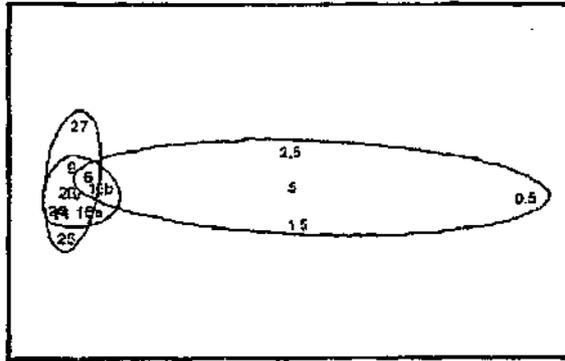
Sampling grain (m ²)	R^2	F	p
1 ^L	0.12	1.53	0.243
10 ^L	0.37	6.40	0.028
100 ^S	0.55	13.5	0.004
900 ^L	0.65	20.4	0.001
10000 ^L	0.49	10.6	0.008
40000 ^L	0.57	14.6	0.003

Table 5.4 Results of linear regression of species diversity (H) in relation to increasing time since fire. ^S Square-root transformation; ^L Log₁₀ transformation.

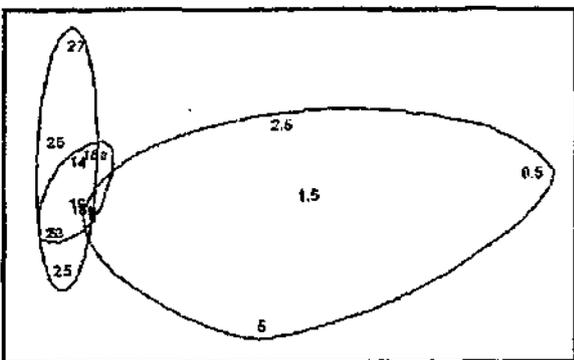
Sampling grain (m ²)	R^2	F	p
1 ^L	0.32	5.11	0.045
10 ^S	0.51	11.4	0.006
100 ^S	0.59	15.5	0.002
900 ^S	0.62	18.1	0.001
10000 ^L	0.53	12.4	0.005
40000 ^L	0.57	14.4	0.003

Table 5.5 Results of linear and quadratic regression of community heterogeneity in relation to increasing time since fire. c: cover data; pa: presence/absence data. ^s Square-root transformation; ^L Log₁₀ transformation. Quadratic equation: $y = a + bx + cx^2$.

Sampling grain (m ²)	Abundance measure	Linear regression			Non-linear regression		
		<i>R</i> ²	<i>F</i>	<i>p</i>	<i>R</i> ²	<i>F</i>	<i>p</i>
1	c	0.07	0.79	0.393	0.24	1.61	0.249
1	pa	0.07	0.85	0.376	0.39	3.25	0.082
10	c	0.01	0.07	0.791	0.52	5.39	0.026
10 ^L	pa	0.07	0.78	0.397	0.41	3.51	0.070
100 ^s	c	0.06	0.70	0.421	0.27	1.85	0.207
100	pa	0.21	2.91	0.116	0.38	3.12	0.089
900 ^L	c	0.01	0.10	0.759	0.03	0.13	0.881
900 ^L	pa	0.04	0.41	0.534	0.23	1.50	0.269

(a) 1 m²; stress = 0.01(b) 10 m²; stress = 0.01(c) 100 m²; stress = 0.08(d) 900 m²; stress = 0.06

(e) 1 ha; stress = 0.05



(f) 4 ha; stress = 0.05

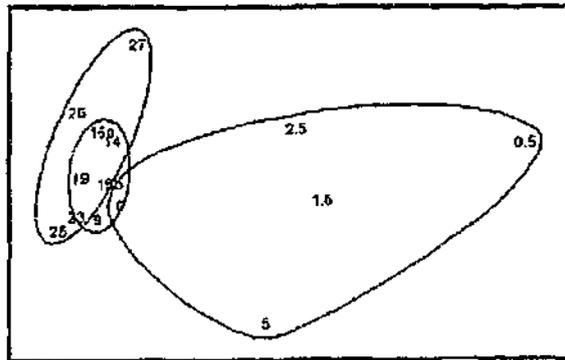
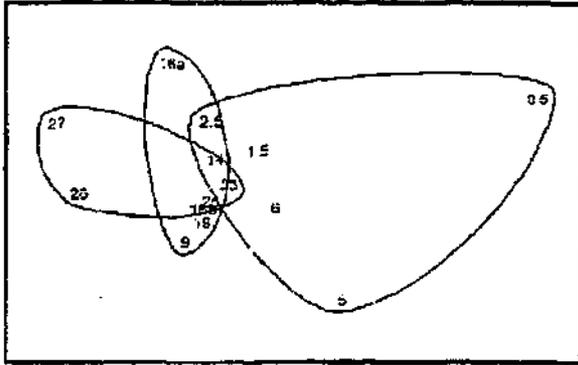
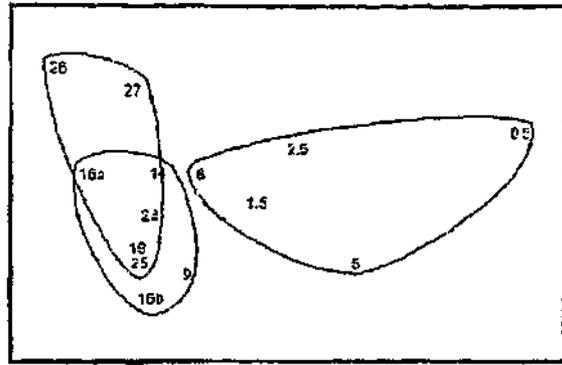
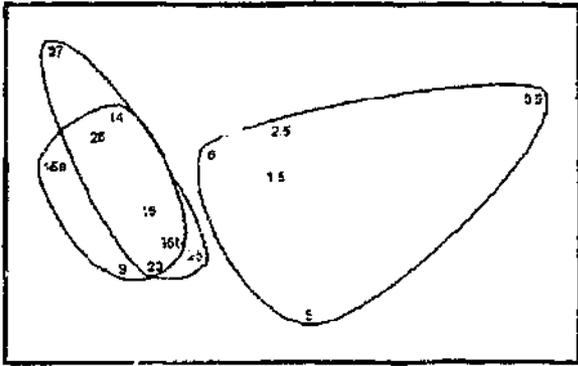
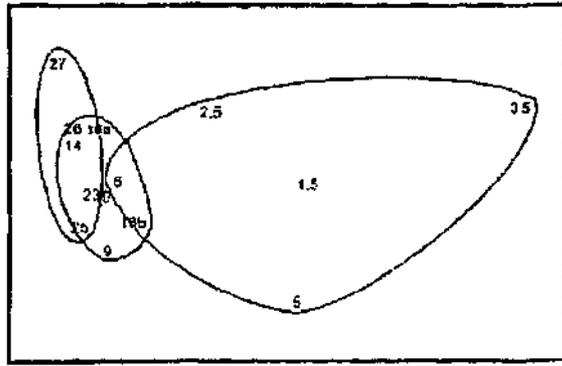
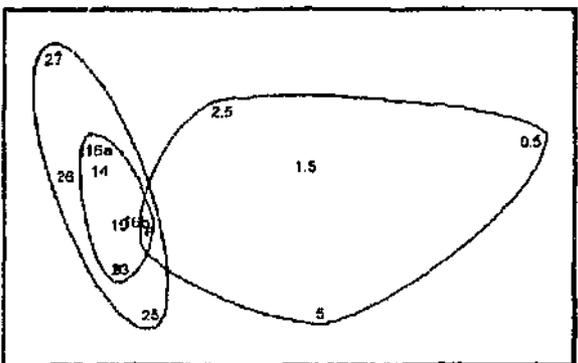


Figure 5.1 Ordination by NMDS (cover data) of mean data points at each site, for the six sampling grains. Sites are grouped into young (0-6 years), intermediate (9-19 years) and old (23-27 years) age classes.

(a) 1 m²; stress = 0.10(b) 10 m²; stress = 0.12(c) 100 m²; stress = 0.10(d) 900 m²; stress = 0.06

(e) 1 ha; stress = 0.06



(f) 4 ha; stress = 0.05

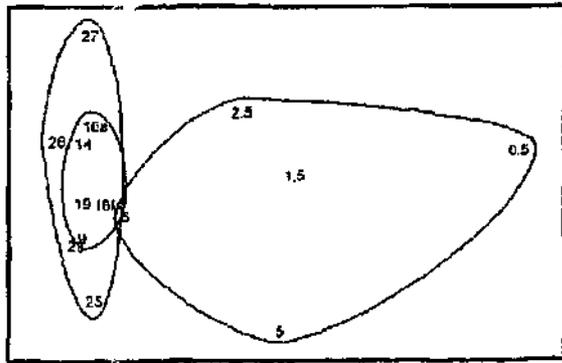
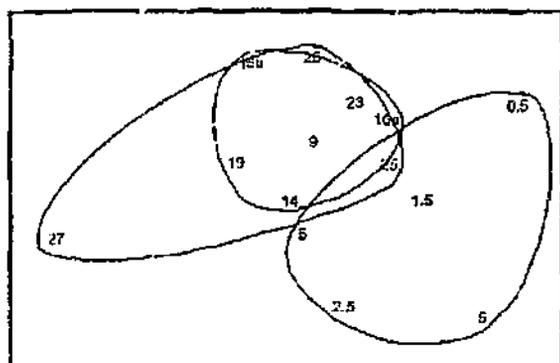
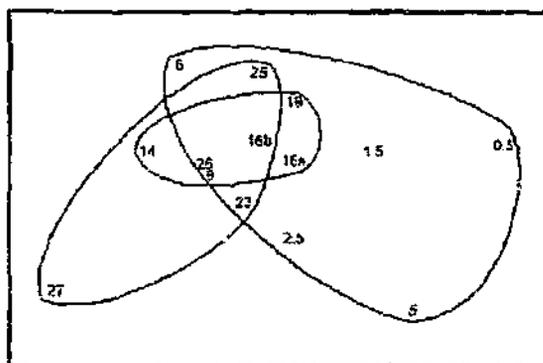
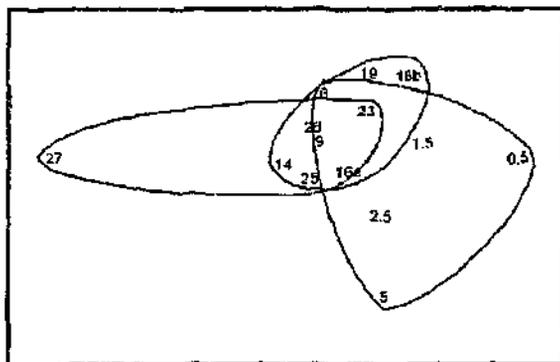
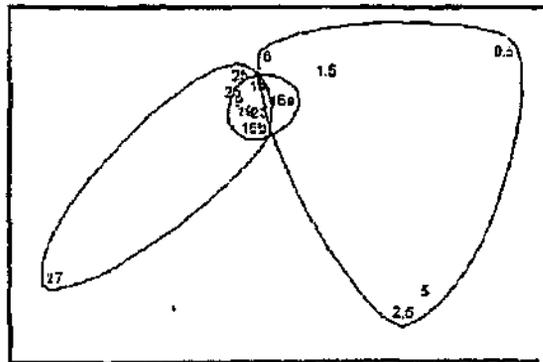
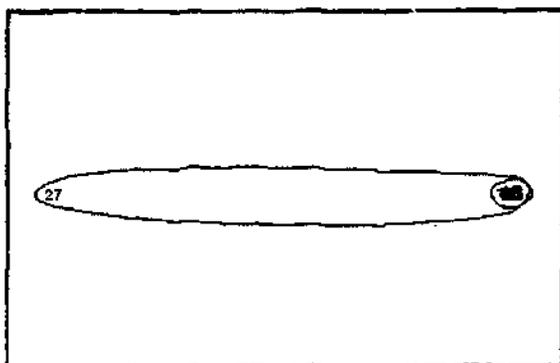


Figure 5.2 Ordination by NMDS (standardised cover data) of mean data points at each site, for the six sampling grains. Sites are grouped into young (0-6 years), intermediate (9-19 years) and old (23-27 years) age classes.

(a) 1 m²; stress = 0.14(b) 10 m²; stress = 0.13(c) 100 m²; stress = 0.11(d) 900 m²; stress = 0.09

(e) 1 ha; stress = 0.01



(f) 4 ha; stress = 0.11

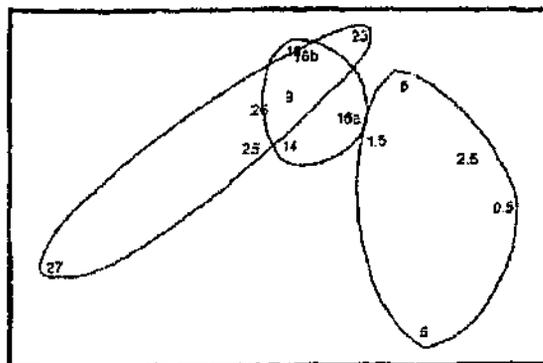


Figure 5.3 Ordination by NMDS (presence/absence data) of mean data points at each site, for the six sampling grains. Sites are grouped into young (0-6 years), intermediate (9-19 years) and old (23-27 years) age classes.

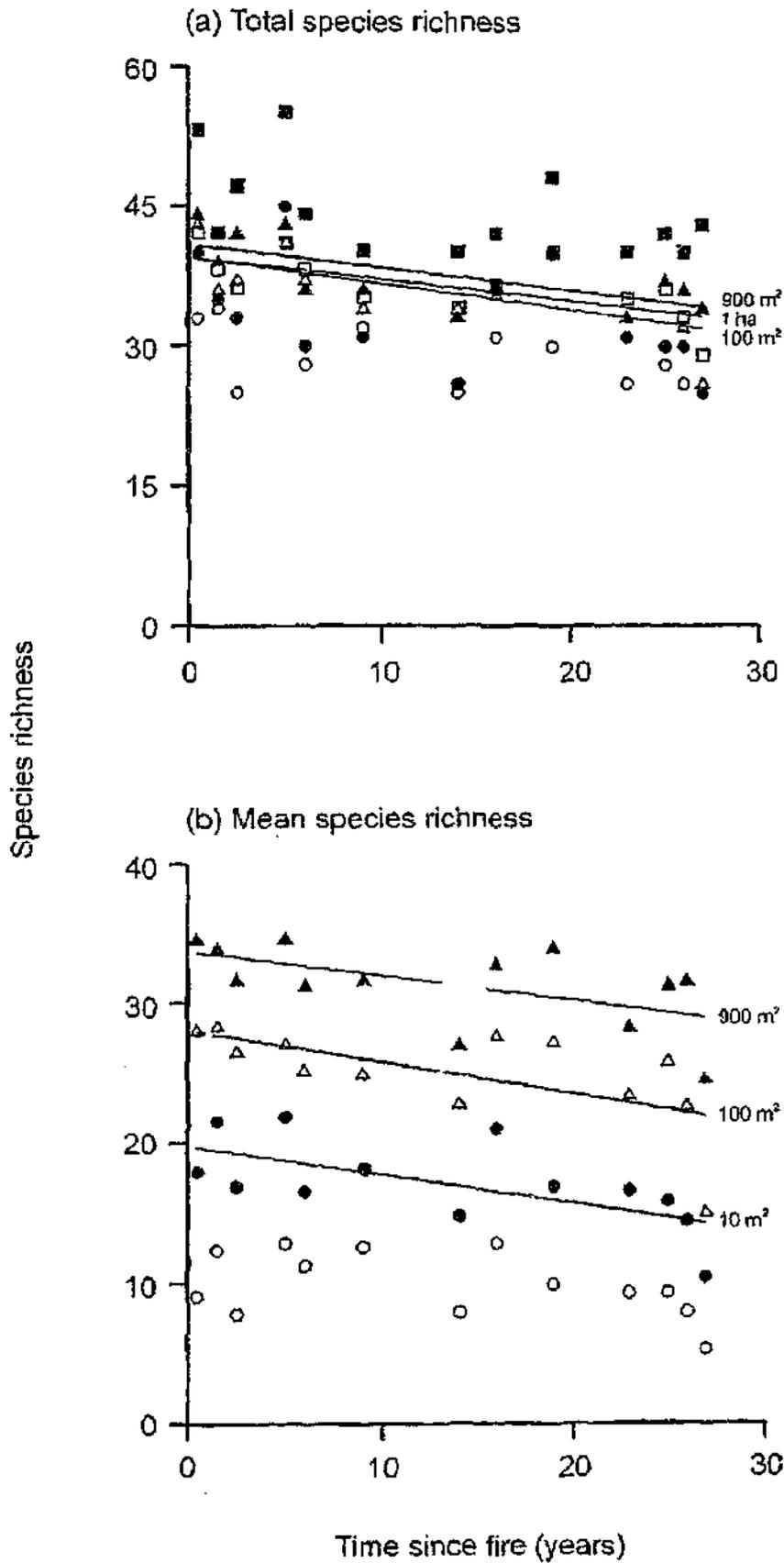


Figure 5.4 Total and mean species richness in relation to time since fire and sampling grain. \circ 1 m²; \bullet 10 m²; \triangle 100 m²; \blacktriangle 900 m²; \square 1 ha; \blacksquare 4 ha. Data have been square-root or \log_{10} transformed where appropriate to derive the line of best fit by linear regression.

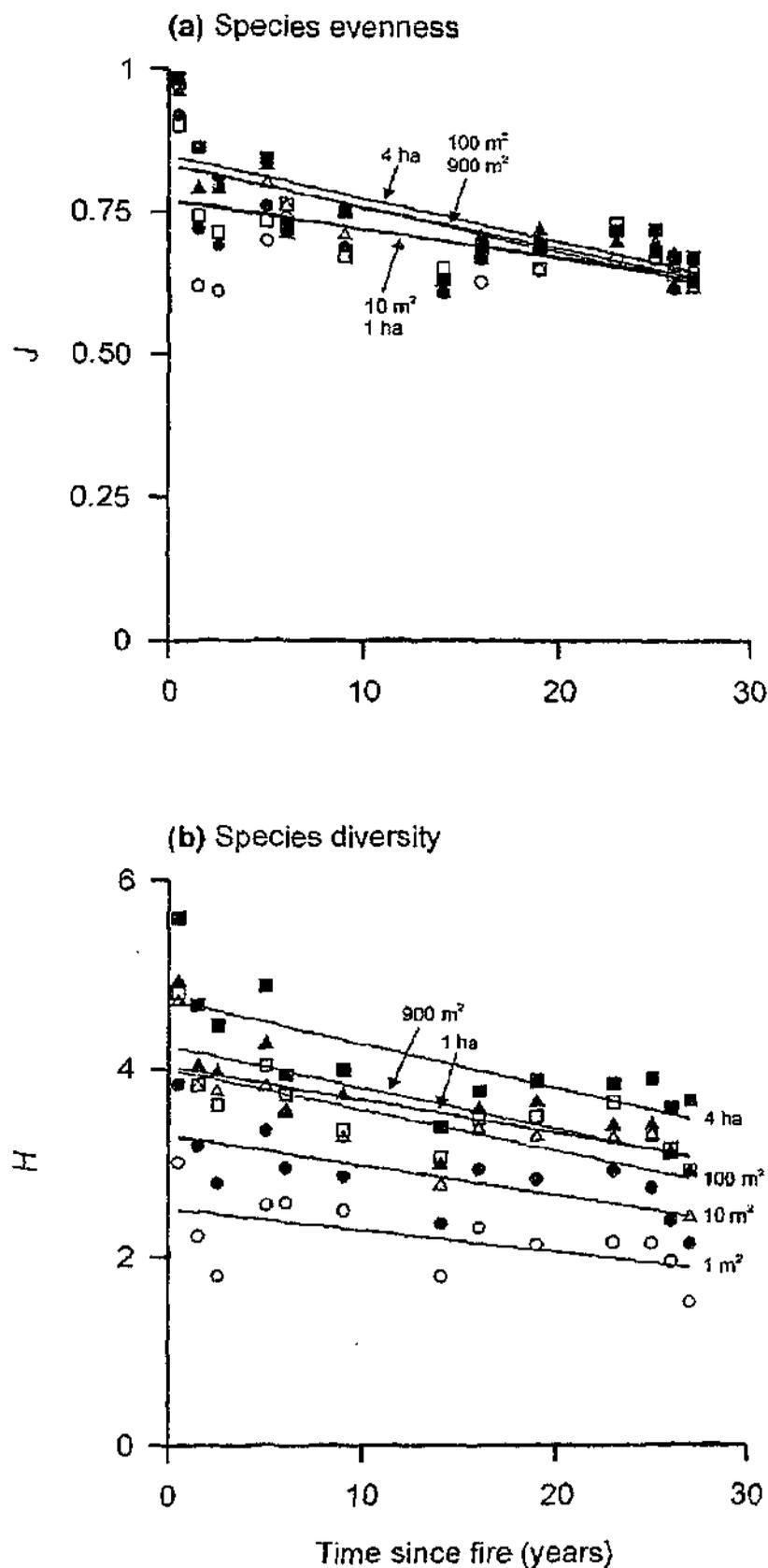


Figure 5.5 Relationship between: (a) mean species evenness (J), and (b) mean species diversity (H) with time since fire across all sampling grains. \circ 1 m²; \bullet 10 m²; Δ 100 m²; \blacktriangle 900 m²; \square 1 ha; \blacksquare 4 ha. Data have been square-root or \log_{10} transformed where appropriate to derive the line of best fit by linear regression.

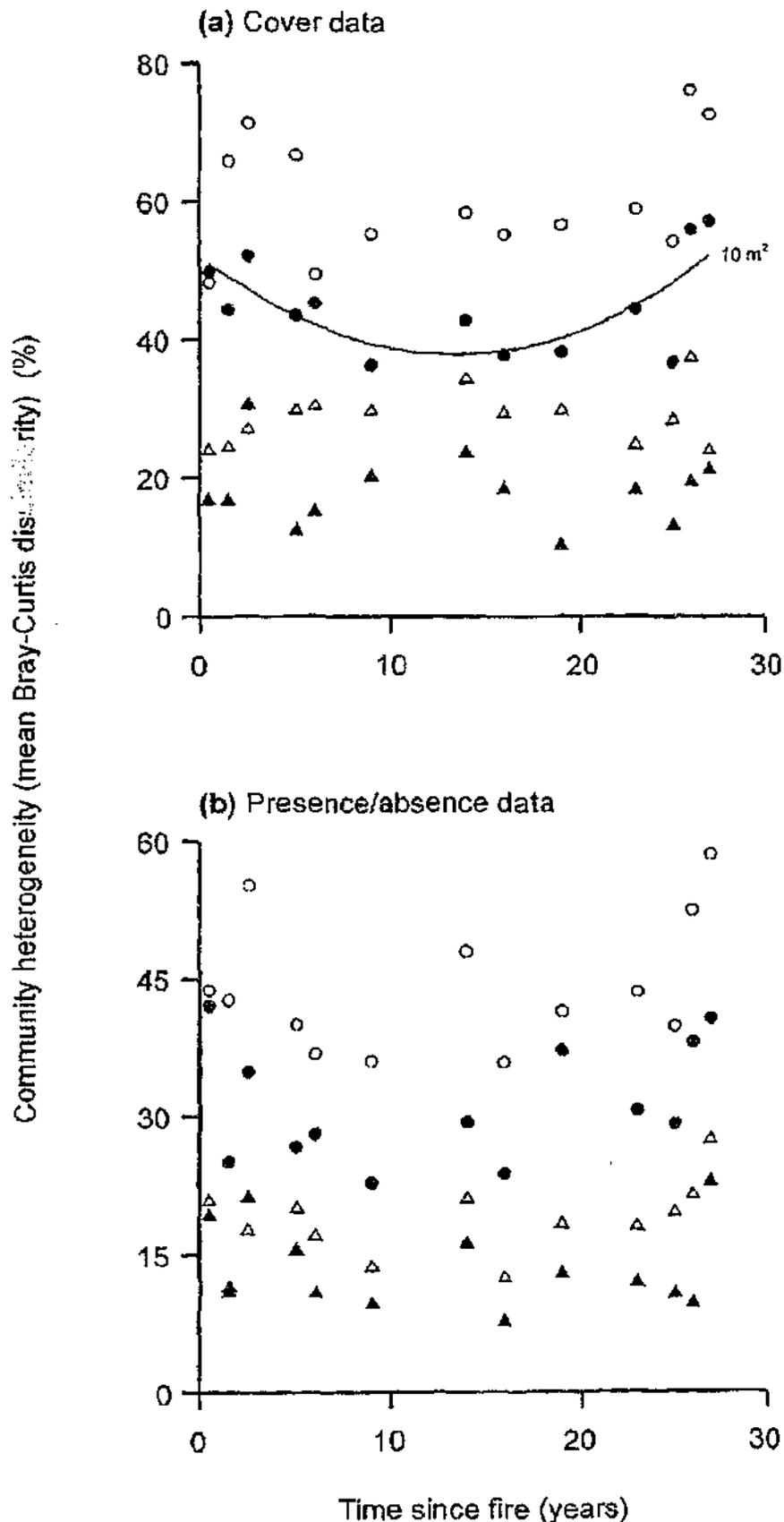


Figure 5.6 Relationship between community heterogeneity and time since fire among sampling grains: (a) cover data, (b) presence/absence data. \circ 1 m²; \bullet 10 m²; \triangle 100 m²; \blacktriangle 900 m². Data have been square-root or log₁₀ transformed where appropriate to derive the line of best fit by quadratic regression.

CHAPTER 6

SOIL SEED BANK PILOT STUDY

INTRODUCTION

Fire plays an integral role in maintaining species diversity in mediterranean-type systems, with many species dependant on it for regeneration. Following fire, resource competition is thought to ~~dramatically~~ ^{markedly} decrease as a result of reduced overstorey cover and increased availability of light and soil nutrients (Specht 1979b; Warcup 1980). Changes in soil temperature regimes (Auld & Bradstock 1996), a reduction in seed predation (Bond *et al.* 1984; Bradstock 1991) and lower levels of allelopathic chemicals (Keeley *et al.* 1985) may also be associated with the post-fire environment. This environment promotes mass regeneration, with species regenerating from soil or canopy-stored seed (obligate seed regenerators), by resprouting from lignotubers, rootstocks, rhizomes, bulbs, tubers and epicormic buds (obligate resprouters), or from a combination of both (facultative resprouters) (Purdie & Slatyer 1976).

Many seed regenerators only germinate after fire, or else in very low numbers during the inter-fire period (Specht *et al.* 1958; Russell & Parsons 1978; Wark 1996; Benwell 1998). This phenomenon is commonly regulated by seed dormancy, which may occur by physiological, morphological, physical or chemical means (Baskin & Baskin 1998). The prevalence of seed dormancy in mediterranean-type systems, means that knowledge of the mechanisms that break dormancy and induce germination is essential to understand vegetation regeneration dynamics.

Various fire-related agents have been shown to promote germination of soil-stored seed in a range of species in mediterranean-type systems. These include heat (Warcup 1980; Vlahos & Bell 1986; Enright *et al.* 1997; Read *et al.* 2000), smoke (Dixon *et al.* 1995; Enright *et al.* 1997; Marsden-Smedley *et al.* 1997; Roche *et al.* 1998), charred wood (Keeley *et al.* 1985) and different combinations of these (Marsden-Smedley *et al.* 1997). Ash (Enright *et al.* 1997; Marsden-Smedley *et al.* 1997) and stratification (Carroll & Ashton 1965; Marsden-Smedley *et al.* 1997) have also been used to promote germination; however, their promotive value is generally low in comparison to heat and

smoke treatments. Most studies indicate that smoke and heat are consistently the most successful agents for breaking seed dormancy and promoting germination in mediterranean-type systems.

Knowledge of the composition of soil seed banks is important from a conservation management perspective, particularly with regard to the fire-prone heathlands of south-east Australia, where burning for management purposes is common practice (Avis 1993; Friend *et al.* 1999). In these dense, sclerophyllous and highly flammable heathlands, fire is essential to promote recruitment of many species, particularly obligate seed regenerators (Specht 1979a; Benwell 1998). Despite the growing soil seed bank literature, little work has been undertaken in south-eastern Australian heathlands, particularly with regard to the effects of fire-related products such as heat (see Molnar *et al.* 1989) and smoke on germination of soil-stored seed. If future studies are to be accurate in determining the species composition, richness and density of the soil seed bank, then the optimal methods for breaking seed dormancy and inducing germination need to be known.

This pilot study aims to determine:

- (1) the effects of smoked water and heat on species richness, composition and density of seedlings emerging from the soil seed bank;
- (2) the number of soil cores needed to adequately estimate species richness and composition of the soil seed bank at a 4 ha site;
- (3) species emergence rates, to indicate appropriate experimental time-spans for future soil seed bank studies; and
- (4) the compositional similarity between the soil seed bank and the extant vegetation

METHODS

Experimental procedure

A relatively large number of small samples is generally more suitable than a small number of large samples in soil seed bank studies (Benoit *et al.* 1989; Thompson *et al.* 1997). Therefore, 36 randomly located soil cores (8 cm diameter, 5 cm depth) were extracted at each of four random 100 m² quadrats in a mature heath (GP-23), giving 144 cores over the 4 ha site (total surface area of cores sampled: 0.724 m²; total volume: 0.036 m³). This is comparable to other studies, which sampled 0.557 m² (0.056 m³) of soil in heath (Carroll & Ashton 1965), 0.018 m² (0.002 m³) in heath (Molnar *et al.* 1989), 1.000 m² (0.050 m³) in heathy woodland (Enright *et al.* 1997), and 0.456 m² (0.046 m³) in heathy forest (Marsden-Smedley *et al.* 1997). Surface litter was included as it is a potentially important seed source, especially in relatively old heath, with almost 100% litter cover.

Sampling was undertaken on 21 March 1999, after most species had finished fruiting and released their seed. This allowed comparison with other studies of south-eastern Australian soil seed bank where soil was collected during March (Carroll & Ashton 1965; Enright *et al.* 1997; Marsden-Smedley *et al.* 1997).

The seedling emergence technique was used to estimate species composition, richness and density of the soil seed bank (Simpson *et al.* 1989). In order to maximise germination and obtain the best estimate of composition, richness and density, cores were exposed to three contrasting treatments. Of the 36 cores from each quadrat, 12 random cores were treated with heat, 12 with smoked water and 12 were left untreated (control), giving 48 cores in each treatment.

Various Australian studies across a range of vegetation types have promoted seed germination by treating soil with dry heat at temperatures ranging from 80°C to 120°C for 20-30 min (Vlahos & Bell 1986; Enright *et al.* 1997; Marsden-Smedley *et al.* 1997; Smith *et al.* 2000). Studies on south-eastern Australian legume species and South African fynbos species have also found substantial variation in emergent seedling densities in response to different combinations of heating (40-120°C) and exposure period (0-120 min), indicating that individual species may possess markedly different temperature optima for breaking seed dormancy (Auld & O'Connell 1991; Musil 1991).

As a result of these findings, a temperature of *c.* 100°C was considered appropriate to break dormancy in most species without killing the seed. Therefore, heat was applied prior to potting, with 12 random cores from each quadrat spread on trays to a thickness of 1.0-1.5 cm and heated in ovens set at 100°C for 15 min. Cores were randomised across three ovens. The actual temperatures inside the ovens varied between 80°C and 100°C, owing to temperature losses when oven doors were opened.

The smoke treatment was applied with *Regen 2000 SMOKEMASTER* smoked water, derived by burning predominantly *Eucalyptus* spp. (including some *Pinus* sp.) sawdust waste and percolating the smoke through water. Four *c.* 5 ml applications of undiluted smoked water were lightly sprayed over each potted soil core at 1 week intervals, commencing 1 week after potting, providing a total of 22 ml of smoked water per core. Watering was minimised in the days following treatment to avoid leaching the active agents from the soil. Although the application of smoked water to each core was independent in time, the smoked water used originated from the same batch; therefore, the experimental treatment is not truly replicated (Morrison & Morris 2000). The remaining 12 cores from each quadrat were left untreated to act as controls.

Before cores were potted, coarse litter was removed from each sample. Each core was then spread to a depth of 1 cm, over 2.5 cm of sterilised river sand in two punnets. All cores were potted within two days of collection and randomly placed on benches within a large, fine-mesh enclosure, open to sunlight, rain and wind, while excluding external wind-borne seed and minimising seedling herbivores. To determine whether extraneous seed was present in the sand, or dispersed into the punnets once the experiment had commenced, 20 punnets containing sterilised river sand with no soil were established. Monitoring indicated that no extraneous seeds were likely to have been present.

Punnets were watered as required. Mean monthly maximum and minimum temperatures in the enclosure ranged from a low of 14.9°C and 6.1°C, respectively, in June 1999 to a high of 32.9°C and 15.6°C, respectively, in February 2000. Seedlings were recorded on a weekly basis for the first 3 months and then on a fortnightly basis. The experiment concluded when no germination occurred over a 5 week period, which was after 11 months.

Species composition of the standing vegetation at the study site was sampled several days before collection of soil cores, as part of the study examining vegetation pattern at different spatial grains (Chapter 5). The samples comprised 41 quadrats from five spatial grains (1 m² sampling grain: 20 quadrats; 10 m²: 10 quadrats; 100 m²: seven quadrats; 900 m²: three quadrats; 1 ha: one quadrat), together with general reconnaissance across the site. The four 100 m² quadrats used for sampling the soil seed bank were not the same quadrats as those sampled during the vegetation survey. Nomenclature follows Ross (2000).

Data analysis

Species-area curves for each of the three treatments, grouping quadrats together, were generated from a random accumulation curve with 100 random starts. A two-parameter power function by the least squares Gauss-Newton method was then applied to estimate species richness, according to the equation

$$y = ab^x$$

where y is species richness, b is area and a and x are estimated parameters.

Species richness and density data were analysed with a randomised block ANOVA, with quadrat acting as the blocking variable and the three germination treatments blocked within each of the four quadrats. The 12 cores in each treatment-quadrat combination were combined to give one value, as individual cores were too variable to act as effective replicates. Tukey's post-hoc tests were used to examine unplanned pairwise comparisons of treatments. The assumptions of ANOVA were checked, with log₁₀, or square-root transformations used when required. A critical value of $\alpha = 0.05$ was used in all hypothesis testing.

Non-metric Multidimensional Scaling (NMDS) was used to ordinate quadrat data, using the Bray-Curtis similarity index. Differences in species composition among treatments were tested by two-way unreplicated Analysis of Similarity (ANOSIM2), and mean similarity between treatments was calculated by the Similarity Percentage (SIMPER) procedure in PRIMER (Plymouth Marine Laboratory 1994). Compositional similarity between the soil seed bank and the standing vegetation of the entire site was calculated

by using both Bray-Curtis and Jaccard similarity indices (Kent & Coker 1992), to enable comparison with other studies.

RESULTS

Species richness, composition and density

Species-area curves for each treatment indicate that species richness increased with core number (sample area), although it did not reach saturation (Figure 6.1). The power function fitted the species-area curves extremely well (Figure 6.1), with $R^2 > 0.99$ for each treatment.

The germinable soil seed bank comprised 20 identifiable taxa, from 17 genera and 12 families, all of which were native (Table 6.1). A small percentage of seedlings could not be identified (1%), or were only identified to genus or family level because of premature death (2%). *Dillwynia glaberrima* and *D. sericea* were grouped together, because of the death of most seedlings before identification to species level was possible.

Sixteen of the 20 species were recorded in the heat-treated soil, 11 in the smoke treatment and nine in the control (Table 6.1). Mean richness per quadrat of the germinable soil seed bank differed significantly among treatments ($F = 15.05$, $p = 0.005$), with richness of heat-treated soil significantly greater than both smoked and control soils, while no significant difference occurred between smoked and control soils (Figure 6.2). There was no significant quadrat (blocking) effect ($F = 3.77$, $p = 0.078$). Ten species were restricted to a specific treatment (six in the heat treatment, three in the control and one in the smoke treatment) (Table 6.1), with each of these recorded only once or twice. When species present in only one treatment-quadrat combination were excluded from the analysis, there was still a significant treatment effect on the mean number of species germinating from the soil seed bank ($F = 34.26$, $p = 0.001$) and no significant block effect ($F = 4.63$, $p = 0.053$). A total of 30% of species present within the soil seed bank was recorded in all treatments (Table 6.1).

Species composition based on density data differed significantly among treatments (ANOSIM2: $R = 1.00$, $p = 0.006$), while presence/absence data yielded non-significant results ($R = 0.08$, $p = 0.317$). Conclusions were unchanged when species present in only one treatment-quadrat combination were excluded from the analysis. Although there was no test for pairwise comparisons, two-dimensional NMDS of density data suggests that control and heat-treated quadrats were most dissimilar, with smoke quadrats

intermediate (Figure 6.3). Mean similarity between treatments was lowest between control and heat-treated soils, with density data consistently more dissimilar than presence/absence data (Table 6.2).

In total, 1769 seedlings were recorded, with heat, smoke and control treatments yielding 276 ± 54 , 137 ± 26 and 29 ± 5 seedlings per quadrat (0.060 m^2), respectively. Mean seedling density per quadrat was significantly different between all treatments ($F = 93.34$, $p < 0.001$) (Figure 6.4). Highest seedling density was recorded in the heat treatment, 10 times higher than the control, with seedling density in the smoke treatment five times higher than controls. There was a significant quadrat (block) effect ($F = 7.53$, $p = 0.019$), indicating patchiness in seed density across the site. *Epacris impressa* was by far the most common species (71% of all seedlings), followed by *Leptospermum myrsinoides* (15%). Six of the 20 taxa (*E. impressa*, *Leptospermum myrsinoides*, *Leucopogon ericoides*, *Hypolaena fastigiata*, *Bossiaea heterophylla* and *Dillwynia* spp.) comprised 98% of the seedlings. The total density for heat-treated soil was $4575 \text{ seedlings m}^{-2}$, with 2271 and $485 \text{ seedlings m}^{-2}$ recorded in the smoke and control treatments, respectively.

Mean seedling densities of five taxa, *Dillwynia* spp., *E. impressa*, *H. fastigiata*, *Leptospermum myrsinoides* and *Leucopogon ericoides*, were significantly different among treatments (Table 6.3). Smoked water yielded significantly greater seedling densities than the control in three species (*E. impressa*, *H. fastigiata* and *Leptospermum myrsinoides*), while seedling densities of heated soil were significantly greater than the control in all of the five species (Table 6.3).

Rate of emergence

All 20 species present within the germinable soil seed bank germinated within 164 days (Figure 6.5a). A steady number of new species emerged for approximately the first 90 days, after which the rate of emergence declined until 164 days, with no new species emerging over the final 173 days of the trial (Figure 6.5a). The rate of species emergence was very similar between the heat and smoke treatments, while the control soils had a slightly delayed emergence (Figure 6.5b). Shrubs (nine species) and sedges/rushes (three species) dominated the early stages of emergence.

Cumulative seedling density for each treatment followed a sigmoidal distribution, where

the rate of increase peaked after 66 days for the smoke and heat treatments and after 80 days for controls, after which it quickly plateaued (Figure 6.6a). In the heat-treated soil, 90% of seedlings germinated after 94 days; in the smoked soil, 90% of seedlings germinated after 122 days; while 90% germination occurred after 150 days in control soils (Figure 6.6b). Of the six species present in every treatment, seedlings within control trays never emerged before seedlings in heat- or smoke-treated soil.

Similarity between soil seed bank and vegetation

Fifteen of the 20 species (75%) present in the germinable soil seed bank were present on site in the vegetation, while five (25%) were only found in the soil seed bank (Table 6.1). Of the five, all were herbaceous, including two forbs (*Drosera peltata* and *Euchiton* sp.), two geophytes (*Pyrorchis nigricans* and Orchidaceae sp.) and one herbaceous twiner (*Cassytha glabella*). The Bray-Curtis similarity between the soil seed bank and the vegetation was 50%, while the Jaccard similarity was 20%.

DISCUSSION

More than half of the species found in the germinable soil seed bank required a heat or smoke stimulus to promote germination. In terms of both total and mean species richness and seedling density of the germinable soil seed bank, heat was the most successful treatment for promoting seed germination, followed by smoked water, then controls. However, variability in the intensity, concentration and duration of treatments may result in differences in relative germination (Warcup 1980; Auld & O'Connell 1991; Musil 1991; Baldwin *et al.* 1994; Roche *et al.* 1997b). Therefore, the results of this study are applicable only to the particular heat and smoke treatments used, not to heat and smoke *per se*.

Five species differed significantly in seedling density between treatments, with all greater in either smoke- and/or heat-treated soil than in controls. Heat-treated soil also had more unique species than smoked and control soils, a result also found by Enright *et al.* (1997) in a Victorian heathy woodland. Even though certain species only germinated in one treatment, this does not imply that they are constrained to that treatment, as the species may be inherently rare in the soil seed bank. However, the greater number of species unique to heat-treated soil, compared to smoked and control soils, and the lack of any effect on mean germinable species richness or composition created by the removal of species restricted to a single treatment-quadrat combination, suggests a treatment effect rather than a sampling artefact. There was little evidence of heat or smoke treatments inhibiting germination in any species, consistent with the studies of Enright *et al.* (1997) and Marsden-Smedley *et al.* (1997). However, in other communities (e.g. grassy woodland and forest), heat and smoke may actually inhibit germination (Clarke *et al.* 2000).

Species that required a heat or smoke stimulus for germination are highly likely to germinate from seed following fire. However, they may die out during the sustained absence of fire if their requirements for seedling establishment are not met and if dormancy does not change over time (Auld *et al.* 2000). In contrast, species that did not require a heat or smoke stimulus may be more likely to increase in abundance during the prolonged absence of fire. However, unknown mechanisms (e.g. soil disturbance, exposure to light) associated with the control treatment may have broken seed dormancy and triggered germination. Furthermore, survival of inter-fire seedlings under field

conditions might be low because of factors such as canopy shading, dense leaf litter and associated allelopathic chemicals (Keeley *et al.* 1985), soil pathogens and herbivores. Following the initial post-fire flush of germination, seedlings in the study area are very uncommon, potentially because of either of the above explanations.

Use of heat and smoke treatments gave a more reliable estimate of the species richness and density of the soil seed bank in this community than untreated soil. The density of seedlings in untreated soil (485 m^{-2}) is comparable with that found by Carroll and Ashton (1965) in the top 5 cm of soil in heath (388 m^{-2}), and Enright *et al.* (1997) in heathy woodland (605 m^{-2}). However, the heat-treated soil gave the highest, and therefore most reliable estimate of viable seed densities (4575 m^{-2}). This compares with Enright *et al.* (1997), who found wet heat to be the optimal treatment (1080 m^{-2}), and Marsden-Smedley *et al.* (1997), who found total native seed density in heathy forest to be $4212 \text{ seeds m}^{-2}$ (average of all treatments for the top 5 cm of the soil). The actual richness and density of the soil seed bank may be even greater than that found in this study, given that dormancy may not have been broken in some seeds. The accuracy of results may have increased if soil sieving and tests for seed viability were undertaken (Baskin & Baskin 1998).

Studies in Australian heath and forest suggest similarity between the germinable soil seed bank and the existing vegetation is of the order of 11-38% (Vlahos & Bell 1986; Molnar *et al.* 1989; Marsden-Smedley *et al.* 1997). However, comparisons with this study (Jaccard index, 20%, and Bray-Curtis index, 50% similarity) are difficult because the similarity index used is often not stated. The discrepancy between composition of the soil seed bank and the extant vegetation in this and other studies may be due to a number of factors. First, certain species may have been absent from the soil at the time of sampling, for either of the following two reasons: (a) species possessed transient seed banks, i.e. they were persistent for less than one year, due to seed senescence or germination prior to sampling; or (b) species were serotinous and stored seed in the canopy, releasing little seed between fires (e.g. *Allocasuarina* spp., *Eucalyptus* spp., *Banksia* spp. and *Leptospermum continentale*). Second, dormancy in some species (e.g. hard-seeded species in the Fabaceae and Mimosaceae) may not have been broken by the treatments applied. Third, sampling intensity may have been insufficient to record species with patchy distributions. Fourth, predators, particularly ants, may have

depleted the seed bank of some species (Andersen & Ashton 1985). Fifth, seed production and/or viability may be inherently low in some species, particularly resprouters (Bell *et al.* 1987), as they are predicted to allocate more resources to root biomass at the expense of seed production (Bond & Midgley 2001). Finally, some species may be short-lived relative to the time elapsed since the last fire, yet have strongly persistent soil seed banks or highly effective dispersal capabilities.

Species-area curves reached 90% of the sampled species numbers by using 69-73% of cores, in comparison to Gross (1990), who found 80% of samples were required to assess 90% of species in the germinable seed bank. Although sampling of the extant vegetation reached saturation, the number of species recorded in the soil seed bank was still increasing, most likely because of differences in the extent and intensity of sampling. Extrapolation of the species-area curves by using the power function estimated that species richness of the germinable soil seed bank would increase by 28-36% if sampling intensity was doubled. Although the power function fitted the data well, it is a curve displaying continuous increase and is therefore likely to yield an overestimate of richness. A curve reaching an asymptote would be more useful for extrapolation, but none was found to fit the data satisfactorily. Despite inaccuracies in extrapolating from the data, Figure 6.1 does suggest that not all species present in the soil seed bank were sampled. Assuming that the soil-stored seed of most species follows a Poisson distribution, the minimum detectable density of seeds with a 95% confidence level is 12 m⁻² (for each treatment), according to the formula of Thompson *et al.* (1997). Species with seed abundances below this level and/or with very clumped distributions, were likely to be overlooked by this sampling regime. Six months appears to be an adequate time period to conduct soil seed bank studies in this vegetation; a shorter period means there is a risk of not recording species with delayed germination responses.

The study further reinforces the importance of treating soil with heat, and to a lesser extent smoke, prior to conducting soil seed bank germination trials in fire-prone systems to obtain an accurate estimate of the soil seed bank. Although smoke appears to be secondary in importance to heat in breaking seed dormancy, this may be a result of (a) the type of smoke used in this study, i.e. a commercial product, rather than smoke, or smoked water, derived from combustion of species found on site (Dixon *et al.* 1995;

Roche *et al.* 1997b) or (b) the concentration of the smoke product used (Lloyd *et al.* 2000). However, after testing germination responses to smoke derived from 27 grassland species, Baxter *et al.* (1995) found that smoke from 26 of the 27 species promoted various levels of germination in *Themeda triandra*, but no species produced smoke detrimental to *Themeda* germination. These findings, together with those of Baldwin *et al.* (1994), suggest the active ingredient in smoke is present across a range of species. In addition, germination of selected heath species has been shown to increase when treatments such as heat and smoke are combined (Keith 1997; Gilmour *et al.* 2000; Kenny 2000; Morris 2000), but this was not examined in the current study.

This study indicates that when the above-ground (vegetation) and below-ground (soil seed bank) components of the flora are taken into account, the total species richness at a given site is higher than that apparent solely in the extant vegetation. This is important from a conservation management perspective, as seed bank studies can indicate the potential success of fire in promoting germination of soil-stored seed and thus species diversity, and in rehabilitating systems degraded by human impact or weed invasions.

In this study, one site of a single age was used to determine similarity in species composition between the vegetation and the soil seed bank. It is inappropriate at this stage to extrapolate these results to other sand heaths. In particular, the post-fire age of a site may influence the composition of the soil seed bank in two main ways. First, time since fire will influence the presence of species above-ground, and consequently, the input of seed into the soil seed bank, as well as influencing the build-up of seed dispersed into the system. Second, time since fire may affect the seed bank indirectly by influencing trends in reproductive characteristics of the vegetation. For example, in some systems, early successional plants tend to produce dormant seeds, whereas the seeds of late successional plants tend to lose viability quickly (Bazzaz 1979). The effects of post-fire age upon the composition, richness and density of the soil seed bank will be examined in Chapter 7.

Table 6.1 Species present in the vegetation and/or the soil seed bank. C, control; S, smoke; H, heat. An asterisk indicates presence in the vegetation.

Family and species	Life-form	Soil seed bank	Vegetation
FERNS AND ALLIED PLANTS			
DENNSTAEDTIACEAE			
<i>Pteridium esculentum</i>	Fern		*
MONOCOTYLEDONS			
CYPERACEAE			
<i>Caustis pentandra</i>	Sedge/Rush	SH	*
<i>Lepidosperma concavum</i>	Sedge/Rush	H	*
ORCHIDACEAE			
Orchidaceae sp.	Geophyte	C	
<i>Pyrorchis nigricans</i>	Geophyte	H	
POACEAE			
<i>Austrodanthonia geniculata</i>	Grass		*
Poaceae sp.	Grass		*
<i>Poa sieberiana</i> var. <i>sieberiana</i>	Grass		*
RESTIONACEAE			
<i>Hypolaena fastigiata</i>	Sedge/Rush	CSH	*
XANTHORRHOEACEAE			
<i>Lomandra longifolia</i>	Sedge/Rush		*
<i>Xanthorrhoea australis</i>	Grass tree		*
<i>Xanthorrhoea minor</i> ssp. <i>lutea</i>	Grass tree		*
DICOTYLEDONS			
APIACEAE			
<i>Platysace ericoides</i>	Subshrub	SH	*
ASTERACEAE			
<i>Euchiton</i> sp.	Forb	H	
CASUARINACEAE			
<i>Allocasuarina misera</i>	Shrub		*
<i>Allocasuarina paludosa</i>	Shrub		*
DILLENACEAE			
<i>Hibbertia acicularis</i>	Shrub	C	*
<i>Hibbertia fasciculata</i> var. <i>prostrata</i>	Shrub		*
<i>Hibbertia virgata</i>	Shrub	H	*
DROSERACEAE			
<i>Drosera peltata</i>	Forb	CSH	

Table 6.1 (continued) Species present in the vegetation and/or the soil seed bank. C, control; S, smoke; H, heat. An asterisk indicates presence in the vegetation.

Family and species	Life-form	Soil seed bank	Vegetation
EPACRIDACEAE			
<i>Astroloma pinifolium</i>	Shrub		*
<i>Brachyloma daphnoides</i>	Shrub		*
<i>Epacris impressa</i>	Shrub	CSH	*
<i>Leucopogon ericoides</i>	Shrub	CSH	*
<i>Leucopogon virgatus</i> var. <i>virgatus</i>	Shrub	S	*
<i>Monotoca scoparia</i>	Shrub		*
EUPHORBIACEAE			
<i>Amperea xiphoclada</i> var. <i>xiphoclada</i>	Subshrub		*
FABACEAE			
<i>Bossiaea cinerea</i>	Shrub	SH	*
<i>Bossiaea heterophylla</i>	Shrub	CSH	*
<i>Dillwynia</i> spp. (<i>glaberrima</i> / <i>sericea</i>)	Shrub	SH	*
<i>Gompholobium huegelii</i>	Shrub		*
GOODENIACEAE			
<i>Dampiera stricta</i>	Subshrub	H	*
LAURACEAE			
<i>Cassytha glabella</i>	Twiner	H	
<i>Cassytha pubescens</i>	Twiner		*
MIMOSACEAE			
<i>Acacia oxycedrus</i>	Shrub		*
MYRTACEAE			
<i>Calytrix tetragona</i>	Shrub	C	*
<i>Eucalyptus</i> aff. <i>willisii</i> (Gippsland Lakes)	Tree (mallee)		*
<i>Eucalyptus viminalis</i> ssp. <i>pryoriana</i>	Tree (mallee)		*
<i>Leptospermum continentale</i>	Shrub		*
<i>Leptospermum myrsinoides</i>	Shrub	CSH	*
PROTEACEAE			
<i>Banksia marginata</i>	Shrub		*
<i>Banksia serrata</i>	Tree		*
RUTACEAE			
<i>Correa reflexa</i> var. <i>speciosa</i>	Shrub		*
STYLIDIACEAE			
<i>Stylidium</i> sp. 2	Forb		*
TREMANDRACEAE			
<i>Teiratheca pilosa</i> ssp. <i>latifolia</i>	Shrub		*

Table 6.2 Mean Bray-Curtis similarity between treatments, from presence/absence and density data.

Form of quadrat data	Mean similarity between treatments (%)		
	Control and Smoke	Control and Heat	Smoke and Heat
Species presence/absence	66	54	71
Species density	33	20	58

Table 6.3 Mean density of seedlings recorded in the germinable soil seed bank for each treatment.

The results of randomised block ANOVA of mean seedling density among treatments are presented. Species are only included if more than five seedlings in total were recorded. Mean density values represent the number of seedlings per surface area of the 12 cores (0.060 m²) sampled in each quadrat. Shared lower-case alphabet letters indicate no significant difference by Tukey's post-hoc comparisons. ^S Square-root transformation; ^L Log₁₀ transformation; ^{L1} Log₁₀ (x + 1) transformation. ^{ns}, not significant; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Species	F_{Treat}	Control	Smoke	Heat	Total
<i>Bossiaea heterophylla</i>	0.57 ^{ns}	2.5 ± 1.2	2.8 ± 0.3	3.8 ± 1.1	36
<i>Dillwynia</i> spp. ^{L1}	14.4**	0 ^a	0.3 ± 0.3 ^a	8.5 ± 3.3	35
<i>Epacris impressa</i> ^{L1}	263***	11 ± 3	94 ± 26	209 ± 52	1257
<i>Hypolaenu fastigiata</i> ^{L1}	26.3**	0.3 ± 0.3	3.8 ± 1.3	9.0 ± 1.9	52
<i>Leptospermum myrsinoides</i> ^{L1}	35.7***	11 ± 3	29 ± 6 ^a	28 ± 5 ^a	273
<i>Leucopogon ericoides</i> ^S	5.49*	2.3 ± 1.1 ^a	4.3 ± 1.7 ^{ab}	12.0 ± 2.9 ^b	74
Unidentified seedlings	1.00 ^{ns}	1.0 ± 0.4	1.8 ± 0.5	1.3 ± 0.3	16

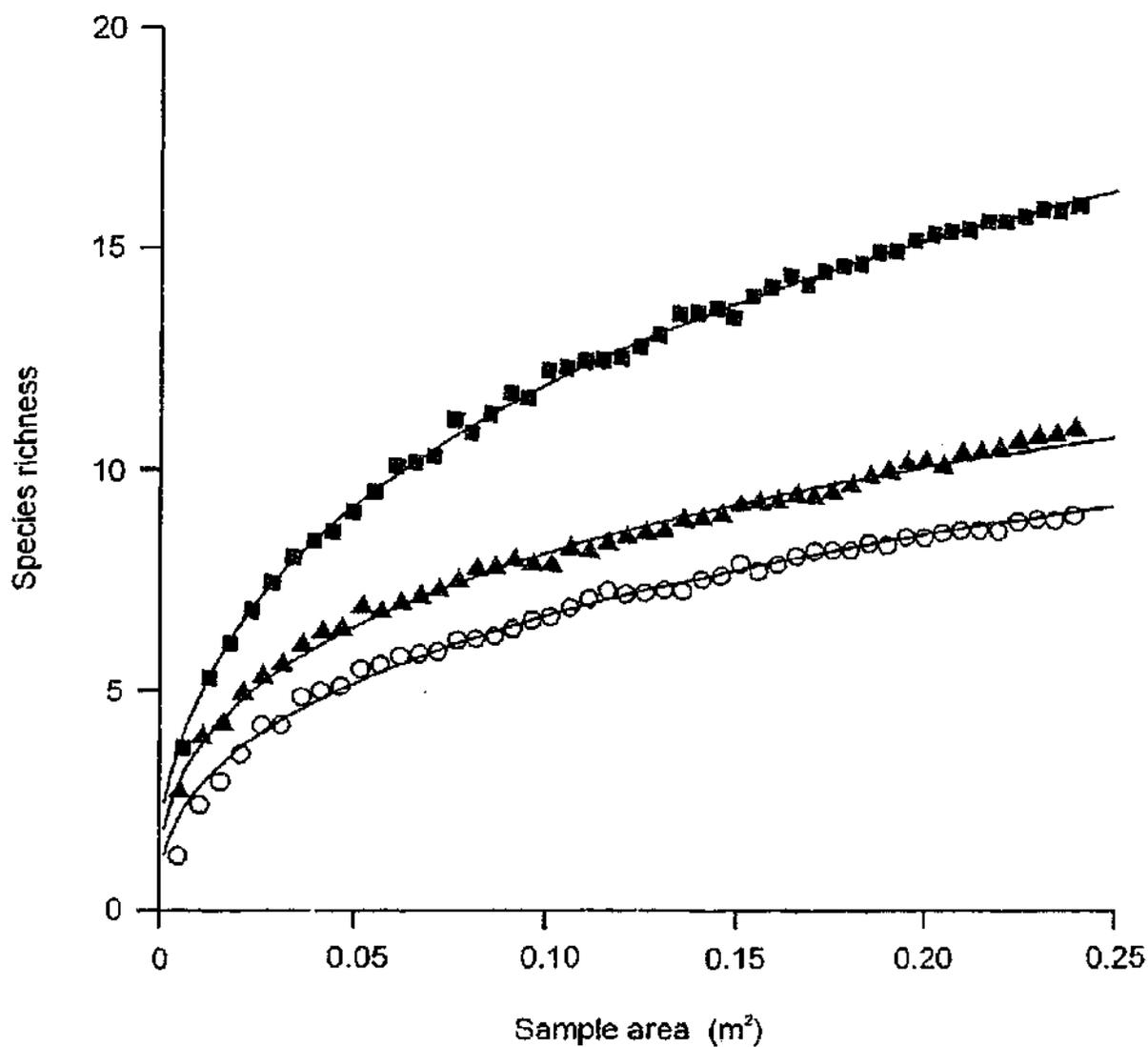


Figure 6.1 Species-area relationships for each treatment (O, control; ▲, smoke; ■, heat) determined by the power function $y = ab^x$. Individual points represent the mean value derived from 100 random accumulation curves.

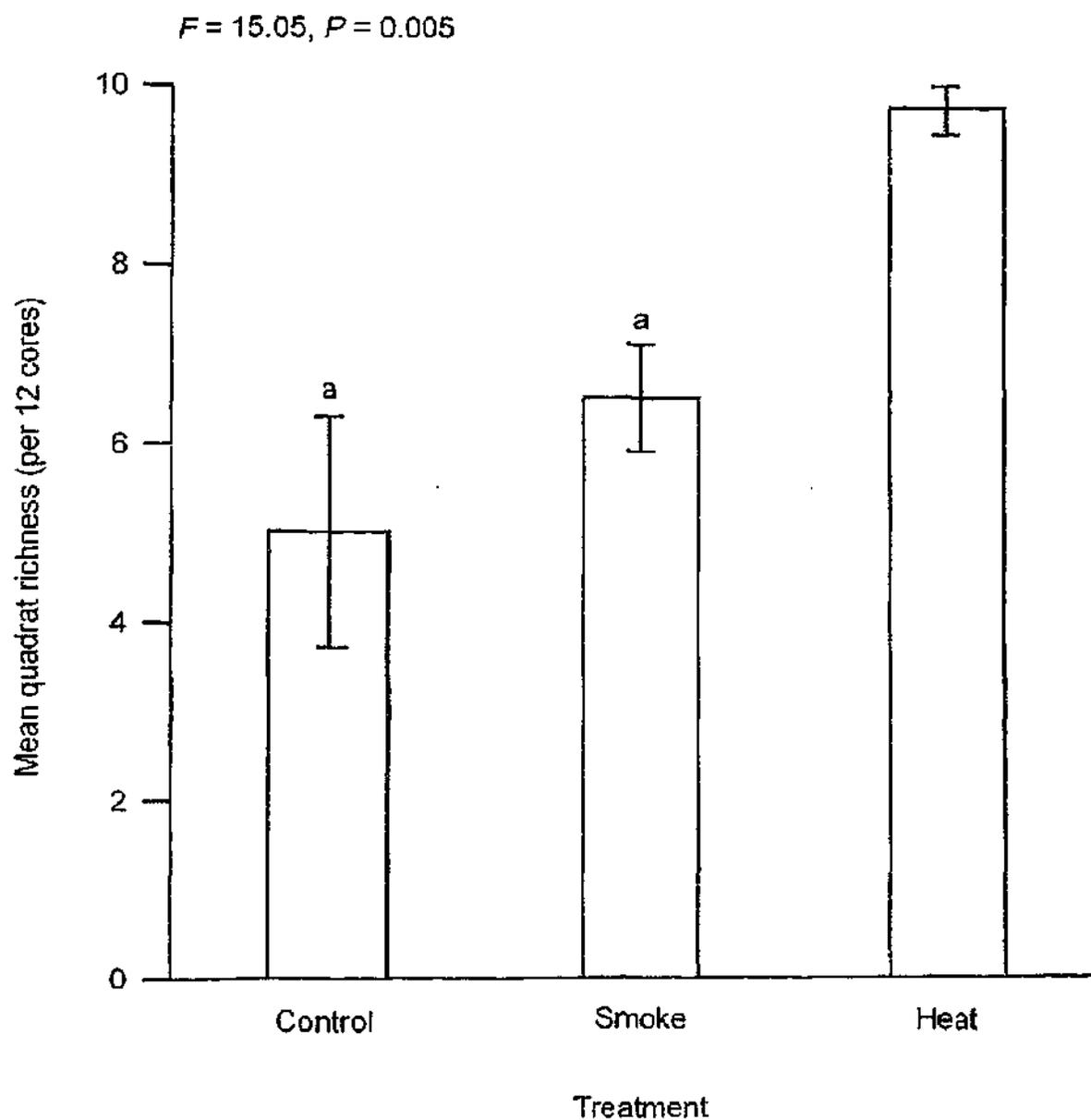


Figure 6.2 Mean species richness of the germinable soil seed bank for quadrats (\pm SE) in each treatment. The results of one-way ANOVA of square-root transformed data are given. Shared alphabet letters indicate no significant difference among treatments according to Tukey's *post-hoc* comparisons.

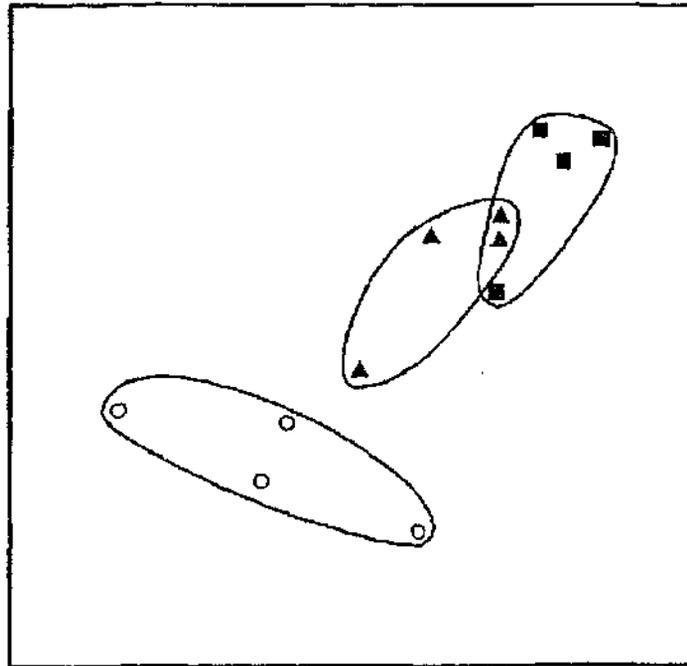


Figure 6.3 Ordination by NMSD of quadrats in each treatment (density data) (O, control; ▲, smoke; ■, heat). Minimum two-dimensional stress = 0.03.

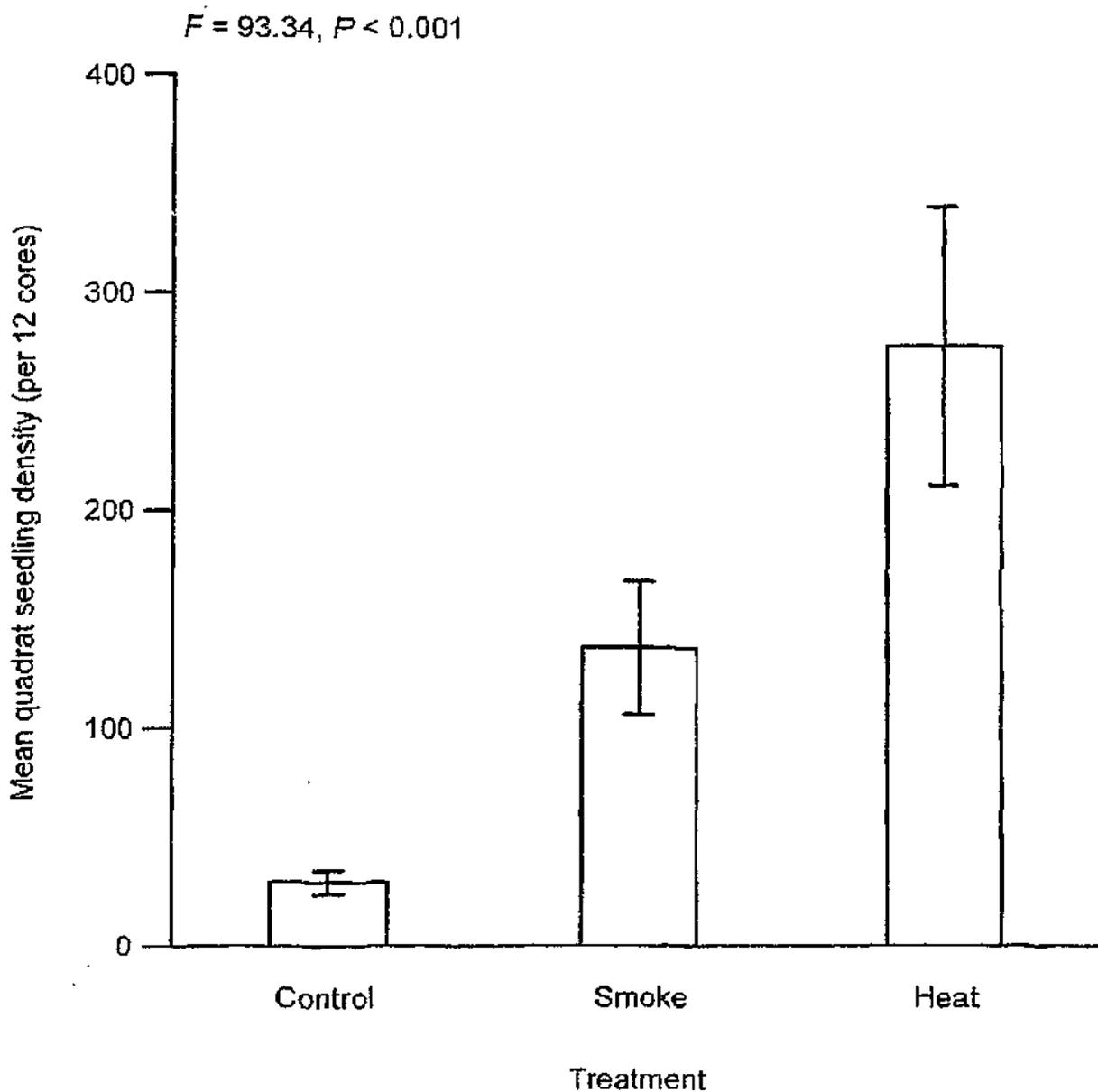


Fig 6.4. Mean seedling density of quadrats (\pm s.e.) for each treatment. The results of one-way ANOVA of \log_{10} -transformed data are given. Post-hoc Tukey's tests indicate significant differences among all treatments.

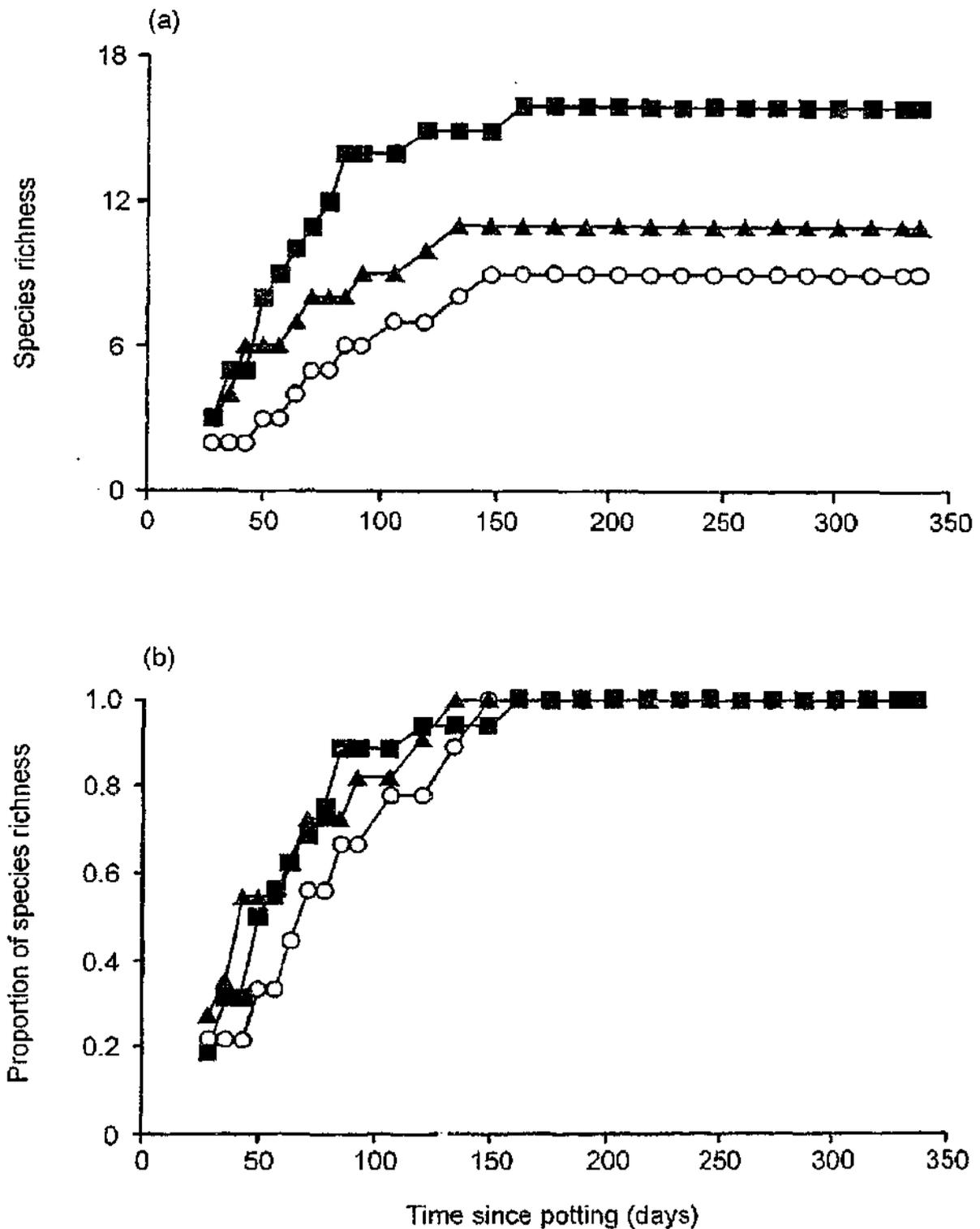


Figure 6.5 Cumulative species richness of the germinable soil seed bank for each treatment (O, control; ▲, smoke; ■, heat). (a) Species richness for each treatment; (b) proportion of species richness for each treatment.

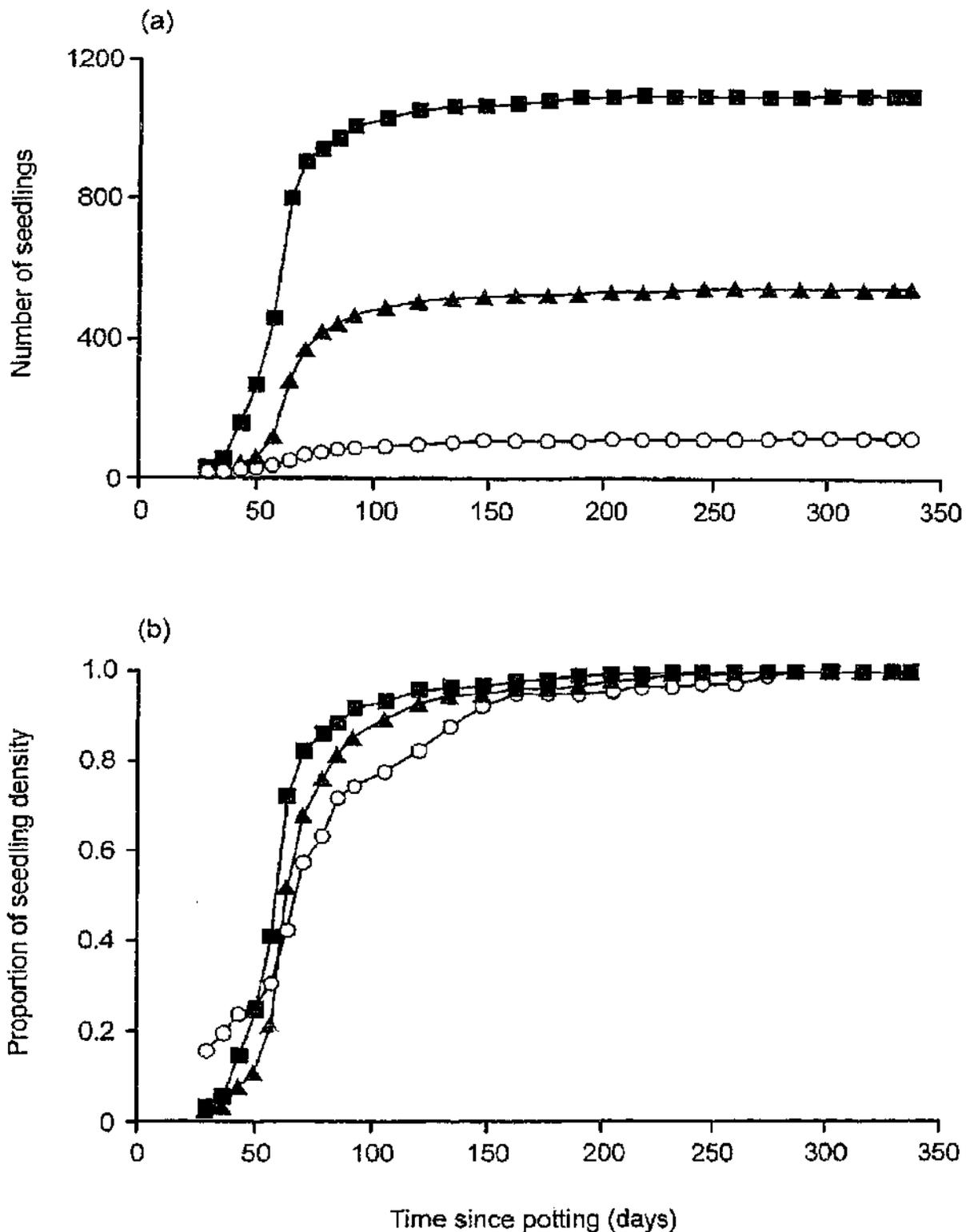


Figure 6.6 Cumulative seedling density of the soil seed bank for each treatment (O, control; ▲, smoke; ■, heat). (a) Number of seedlings for each treatment; (b) proportion of seedling density for each treatment.

CHAPTER 7

SOIL SEED BANK: CHANGES WITH TIME SINCE FIRE

INTRODUCTION

Pattern and change in the composition of soil seed banks over successional time has been well documented, with Milberg (1995) citing 25 papers over the 100 year period from 1893 to 1993 that specifically address this topic using the chronosequence approach. Since Milberg's study, the theme has been continued by Bakker (1996), Dalling (1998), Ne'eman (1999) and Bekker (2000). Although a wealth of information has been gathered regarding changes in soil seed bank composition, richness and density over successional time, only a small number of studies have been conducted in heath or shrub-dominated vegetation (Zammit & Zedler 1988; Zammit & Zedler 1994; Mitchell *et al.* 1998), with none of these being in Australian systems.

A general finding of soil seed bank studies is that species richness and density usually decrease or remain relatively unchanged as time since disturbance (or abandonment) increases (Granström 1988; Roberts & Vankat 1991; Milberg 1995; Bakker *et al.* 1996; Dalling & Denslow 1998; Ne'eman & Izhaki 1999), however, this pattern may not be universal (Bekker *et al.* 1999). Because the great majority of studies examining soil seed bank successions are from the Northern Hemisphere, the general trends reported may not be widely applicable to the fire-prone, nutrient-poor, mediterranean-type heathlands of Australia, South Africa and California, which usually adhere to the initial floristic composition model of succession (Hanes 1971; Groves & Specht 1981; Kruger 1983).

In this study, soil seed banks were investigated at seven sites of varying time since fire. The aims of the study were to determine:

- (1) the role of the soil seed bank in vegetation succession; and
- (2) whether differences occurred among young, intermediate and old-aged sites in compositional similarity between the soil seed bank and the extant vegetation

A number of predictions were made relating to the effects of time since fire on the soil seed bank:

- (1) Overall species richness of the soil seed bank was predicted to increase and then decrease with time since fire. This prediction is based on the assumption that richness will be relatively low in the first few years after fire, as most soil-stored seed should be either killed, or stimulated to germinate by the fire event, and seed production will be low as most species will still be reproductively immature. As species begin to reach reproductive maturity, seed input to the soil increases, and consequently, richness is predicted to increase. As species with transient (short-lived) seed banks either die out, or become competitively excluded, seed bank richness is then predicted to gradually decline with time since fire.
- (2) Total density of soil-stored seed was predicted to increase and then decrease with time since fire, as suggested by Whelan (2002). An initial increase was predicted, as the number of reproductively mature species and the number of years they have been reproductively mature increases. The increasing number of years a species has been reproductively mature is particularly important as this hypothetically facilitates increased soil seed densities, especially in species with long-lived (persistent) soil seed banks, which appear to be relatively common in heathlands (Keeley 1995). As total vegetative cover begins to decrease *c.* 25 years after fire (refer to Chapter 4), total soil seed bank density is also predicted to decline (although the delay may lag somewhat), given the potentially reduced seed source.
- (3) Species composition of the soil seed bank is predicted to differ between young (0-6 years), intermediate (9-19 years) and old (23-27 years) sites. However, there may be less variation in the below-ground (soil seed bank) component of the vegetation, as viable seeds may remain in the soil well past the lifespan of the parent plants.

METHODS

Experimental procedure

Seven of the 14 sites used in the vegetation study (Chapters 4 and 5) were used to sample the soil seed bank across a range of ages since the last fire. Milberg (1995) raised a number of concerns regarding the validity and appropriateness of using chronosequences to study soil seed banks. The validity of the chronosequence in this study has already been assessed as far as possible in Chapter 3, with the uniformity of climate, topography, soil profiles, and soil saturation capacity and nutrients at depth, suggesting that the basic assumptions of the chronosequence have been met. For the purposes of this study, site fire histories are unknown and assumed to be random. To obtain a representative range of site ages, two sites were randomly chosen from within each of the three age classes (young, 0-6 years since fire; intermediate, 9-19 years since fire; old, 23-27 years since fire) determined in Chapter 4, with an extra site randomly selected from the 'old' age class. The sites/ages chosen were as follows: young, BS-1.5 (three years since fire) and SS-5 (six years since fire); intermediate, TT-9 (10 years since fire) and SS-16 (17 years since fire); old, GP-23 (24 years since fire), T4-25 (26 years since fire) and SS-26 (26 years since fire). Site ages were older than the coded age for each site because soil seed bank sampling was conducted up to 18 months after the vegetation had been sampled at all sites. Site ages given throughout the remainder of this chapter are the actual ages of the site at the time of soil seed bank sampling, rather than the age at the time of vegetation sampling.

At each of the seven sites, 88 random soil cores were taken to a depth of 5 cm using an 8 cm diameter section of plastic tubing (total surface area of cores sampled per site: 0.442 m²; total volume per site: 0.022 m³). Surface litter was included, as it is a potentially important source of seed. The number of cores per site was set at 88 (compared with 144 in the pilot study) for a number of reasons. First, the pilot study (Chapter 6) indicated that the smoked water treatment added no information in terms of species richness, apart from one species that only had one seedling present. This indicates that 96 cores (comprised of the control and heat treatments), instead of 144, would have yielded a species richness of only one less. Therefore, the smoke treatment was not used in this study. Secondly, the 88 cores sampled at each site in this study were fully randomised, whereas the cores sampled in the pilot study were blocked

within four 100 m² quadrats. By fully randomising sampling in this manner, a more complete coverage of each study site is obtained, thus increasing the likelihood of sampling species with highly clustered distributions (Bigwood & Inouye 1988), and subsequently obtaining the most accurate estimate possible of soil seed bank richness. Therefore, 88 fully randomised cores per site were likely to yield as much information, and possibly more, compared with the 144 cores used in the pilot study (Chapter 6).

Sampling was undertaken on March 20-22, 2000 (early autumn) after most species had finished fruiting and had set seed. This also allowed for comparison of results with the pilot study, and other south-eastern Australian soil seed bank studies where soil was collected during March (Carroll & Ashton 1965; Enright *et al.* 1997; Marsden-Smedley *et al.* 1997).

For this study, heat and control treatments were used. The smoked water treatment used in Chapter 6 was not used, given that only one of the 21 species identified in the pilot study occurred solely in the smoked water treatment, while six occurred solely in the heat-treated soil and three were restricted to controls. Therefore, to promote maximum germination of individual species, efforts were concentrated on the heat and control treatments. Heat treatment was undertaken only a few days after soil collection and prior to potting, with 44 randomly selected cores from each site spread on oven trays to a thickness of approximately 1 cm and heated in ovens set at 80°C for 15 minutes. Cores were randomised across three ovens. The remaining 44 cores from each site were left untreated to act as controls and also determine which species possessed non-dormant (transient) seed.

Following soil collection and the heat treatment, coarse litter (twigs and large leaves) was removed from each sample. Four cores from each site-treatment combination were then combined and spread to a depth of 1 cm, over 2.5 cm of sterilised river sand in germination trays. This gave 11 trays per site for each treatment. All cores were 'potted' on March 25, 2000 and randomly positioned on benches within a large, fine-mesh enclosure, open to sunlight, precipitation and wind, while excluding external wind-borne seed and minimising seedling herbivores. To determine whether any extraneous seed was initially present, or being dispersed into the punnets once the experiment had commenced, twenty punnets containing sterilised river sand with no study site soil were established and monitored regularly. Monitoring indicated that

extraneous seed did germinate during the course of the experiment, however, these species were easy to identify and were subsequently removed.

The experiment ran for 409 days. Mean monthly maximum and minimum temperatures in the germination enclosure were 23.9°C and 12.1°C respectively at the commencement of the experiment in March/April 2000. Temperatures dropped to a low of 8.8-15.9°C in May 2000, and subsequently peaked in February 2001 (16.8-30.5°C). The absolute maximum and minimum temperatures recorded during the study were 41.9°C and 3.1°C respectively. Watering was controlled using an electronically timed mist-sprayer watering system. Seedlings were recorded on a weekly basis for the first three months of the germination trial and thereafter on a fortnightly basis. Seedlings that were difficult to identify were removed from the germination trays, and subsequently 'grown on' in more fertile soil until they became identifiable. Nomenclature follows Ross (2000).

Data analysis

Non-metric Multidimensional Scaling (NMDS) was used to ordinate site data for density, standardised density and presence/absence data, using the Bray-Curtis similarity index. The methods used follow those outlined in Chapter 4, however, all cores from a given site were combined for the analysis, to enable differences in composition among the three age classes to be assessed. Differences in species composition among age classes were tested by one-way Analysis of Similarity (ANOSIM), and mean similarity between treatments was calculated using the Similarity Percentage (SIMPER) procedure in PRIMER (Clarke & Gorley 2001).

Total species richness and seedling density data were analysed using linear and quadratic regression, with square-root and \log_{10} transformations used to improve normality and homogeneity of variances where appropriate. Two-sample *t*-tests were used to determine the effect of treatment (control vs heat) on seedling density and species richness of the soil seed bank at each site. Paired *t*-tests were used to determine the effect of treatment (control vs heat) on seedling density for each species, using sites as replicates. No data transformations were necessary. A critical value of $\alpha = 0.05$ was used for all hypothesis testing.

Compositional similarity between the soil seed bank and the vegetation was calculated using both Bray-Curtis and Jaccard similarity indices (Kent & Coker 1992), to enable comparison with other studies. Pearson correlation was then used to determine whether there was a significant relationship between these similarity indices and time since fire.

All analyses were conducted using the site age at the time of sampling the soil seed bank.

RESULTS

Species richness, density and composition

The germinable soil seed bank comprised 34 identifiable taxa, from 31 genera and 20 families, all of which were native (Table 7.1). A small percentage of seedlings were unable to be identified (<1%), or were only identified to genus, owing to premature death (2%). *Dillwynia glaberrima* and *D. sericea* were grouped together, owing to the death of most seedlings before identification to species level was possible. Most (>99%) of the recorded seedlings germinated within the first 200 days of the germination trial, which lasted for 409 days in total. A very small number (<0.1%) of freshly emerged seedlings were recorded on the final sampling date.

Total species richness of the germinable soil seed bank at each site ranged from 13-22 species, however, it did not differ significantly with increasing time since fire, using either linear (\log_{10} transformed data: $F = 1.33$, $p = 0.301$) or quadratic regression (\log_{10} transformed data: $F = 1.67$, $p = 0.297$) (Figure 7.1). Similarly, mean species richness of the germinable soil seed bank for each tray did not differ significantly with time since fire, using either linear (\log_{10} transformed data: $F = 2.11$, $p = 0.206$) or quadratic regression (\log_{10} transformed data: $F = 1.05$, $p = 0.431$) (Figure 7.2). Mean species richness appeared to be slightly higher in heat-treated soils compared with controls at each site, however, this difference was only significant at SS-26 ($t = -2.28$, $p = 0.046$) (Figure 7.2).

Overall, *Epacris impressa* accounted for 79% of all seedlings, with *Leucopogon ericoides* (4%), *Leptospermum myrsinoides* (4%) and *Calytrix tetragona* (3%) accounting for a further 11% of seedlings in the germinable soil seed bank (Table 7.1). The remaining 30 taxa in the germinable soil seed bank comprised 10% of all seedlings. Total seedling density did not differ significantly with time since fire, using both linear (\log_{10} transformed data: $F = 0.75$, $p = 0.426$) and quadratic regression equations (\log_{10} transformed data: $F = 0.51$, $p = 0.637$) (Figure 7.3). The data were re-analysed after removing the dominant species (*E. impressa*) from the analysis. Subsequent re-analysis indicated that the high densities of *E. impressa* seedlings did not affect the regression conclusions. Using linear regression, *Leptospermum myrsinoides* was the only species

that increased significantly in seedling density with increasing time since fire (square-root transformed data: $F = 11.9, p = 0.018$).

Seedling densities of heat-treated soil yielded 2005 ± 932 seedlings m^{-2} for young sites ($n = 2$), 5213 ± 1154 seedlings m^{-2} for intermediate-aged sites ($n = 2$) and 3713 ± 419 seedlings m^{-2} for old sites ($n = 3$). Control soil yielded 1109 ± 330 seedlings m^{-2} for young sites ($n = 2$), 1538 ± 77 seedlings m^{-2} for intermediate-aged sites ($n = 2$) and 1379 ± 151 seedlings m^{-2} for old sites ($n = 3$). Mean seedling density was significantly greater in heat-treated soils compared with controls for all sites except SS-5 (Figure 7.4).

Ordination by NMDS using density data suggests that six of the seven sites were very similar, with SS-5 markedly different from all other sites (Figure 7.5). Following standardisation, young and intermediate sites remained in relatively the same positions on the ordination plot, while old sites were grouped separately from the rest (Figure 7.5). When presence/absence data were used, young, intermediate and old sites were all grouped separately from each other (Figure 7.5). Species composition among age classes differed significantly using species presence/absence data ($R = 0.55, p = 0.029$), however, density data ($R = 0.15, p = 0.267$) and standardised density data ($R = 0.15, p = 0.200$) yielded no significant differences among age classes. Conclusions were unchanged when the seven species found at only one site were excluded from the analysis. Furthermore, the removal of *Epacris impressa* from the analyses had no effect on conclusions. Pairwise comparisons were unable to be assessed at the 0.05 significance level, as there were only 10 possible permutations. However, Clarke (1994) and Clarke (2001) suggest that pairwise R values are more useful than p values, since they give an absolute measure of the degree of separation between two age classes, on a scale of zero (indistinguishable) to one (all similarities within age classes are less than any similarity between age classes). Using this scale, $R > 0.75$ suggests that age classes are well separated, $R = 0.5-0.75$ suggests that groups are overlapping but clearly different, while $R < 0.25$ implies that groups are barely separable (Clarke & Gorley 2001). Based on these guidelines, young and old sites are well separated ($R = 0.83$), intermediate and old sites are overlapping but clearly different ($R = 0.50$), while young and intermediate sites are not separable ($R < 0.01$) using presence/absence data.

Similarity between soil seed bank and vegetation

The Jaccard similarity between the composition of the soil seed bank and the extant vegetation ranged from a low of 16% at the youngest site to a high of 22% at the oldest site studied (Figure 7.6). Bray-Curtis similarities exhibited a similar trend and ranged from 37-58% (Figure 7.6). There was no significant relationship between either of the similarity indices and time since fire, although visually there appears to be a trend toward greater similarity between the soil seed bank and the extant vegetation as time since fire increases (Figure 7.6).

All taxa found in the soil seed bank over the seven sites studied were present as extant vegetation in at least one of the 14 study sites. However, 11 of the 34 taxa were found in the soil seed bank at a particular site but not in the extant vegetation at that site (Table 7.2). Of these 11 species, eight (73%) were herbaceous, two were shrubs and one was a subshrub (Table 7.2). These species effectively increased the estimate of total species richness (above and below-ground) at these sites by between 2% and 13%, depending on the site (young sites, 6% increase; intermediate sites, 9% increase; old sites, 8% increase). However, they had no effect on the significance of the relationship between species richness and time since fire. In other words, for the seven sites examined in this study, total species richness of the vegetation did not differ significantly with time since fire (\log_{10} transformed data: $F = 1.61, p = 0.261$). Similarly, when the additional species found in the soil seed bank were added to the total species richness of the vegetation, there was no significant difference in richness in relation to time since fire (\log_{10} transformed data: $F = 2.10, p = 0.207$).

DISCUSSION

Species richness and seedling density of the germinable soil seed bank were not significantly correlated with time since disturbance (fire), which concurs with other studies undertaken in a range of systems and disturbance types (Zammit & Zedler 1994; Milberg 1995; Dalling & Denslow 1998). However, this finding is contrary to predictions made in the *Introduction*. Although the youngest site (BS-1.5) followed predictions by having the lowest recorded number of species in the germinable soil seed bank, a significant trend of increasing richness initially after fire, followed by a decrease some years later was not recorded. In the context of other studies that have examined soil seed bank chronosequences, the seven sites sampled here constitute a comparatively large sample size (Granström 1988; Zammit & Zedler 1988; Roberts & Vankat 1991; Zammit & Zedler 1994; Milberg 1995; Dalling & Denslow 1998; Bekker *et al.* 1999; Ne'eman & Izhaki 1999; Bekker *et al.* 2000; Izhaki *et al.* 2000). However, it is still a relatively low number of points for a regression analysis. Therefore, any trend in species richness may not have been detected, owing to the low sample size and the presence of 'noisy' data points that have the potential to markedly affect results. Another possible reason for the lack of a trend with time since fire is that the time scale studied (26 years) was not large enough to detect any potential decline in richness and seedling density (Milberg 1995). Given that there are no comparable studies in Australian heath, it is uncertain when species richness and density of the germinable soil seed bank would begin to decline (if at all). In comparison to forest chronosequences, the time span used in this study is short, however, in south-eastern Australian heathlands it is very difficult to obtain sites older than 25 years (Specht *et al.* 1958; Siddiqi *et al.* 1976; Russell & Parsons 1978; Wark *et al.* 1987; Enright *et al.* 1994), simply because current fire frequencies inhibit the vegetation from reaching ages much older than this (Cheal 2000).

Heat-treated soil consistently yielded higher germination levels than controls at six of the seven study sites. The seedling density of heat-treated soil from the pilot study at GP-23 was comparable with that obtained from GP-23 in this study and values from other heat-treated soil in Australian heathlands (Enright *et al.* 1997; Marsden-Smedley *et al.* 1997) mentioned in Chapter 6. However, in this study seedling densities in control soils were substantially higher at GP-23 (1148 m⁻²) compared to the pilot study

(485 m⁻²). In the pilot study, seedling densities in heat-treated soil were almost 10 times greater than those in the controls (see Chapter 6), however, in this study they were only c. three times greater, even though densities in heat-treated soil were relatively comparable. Therefore, the reduced effect of the heat-treatment in this study appears to have arisen not from a deficiency in the heat treatment, but from a relative increase in the germination of seed from control soils. This phenomenon may have been caused by a number of factors, including increased seed density and viability in the season's seed crop (particularly in *E. impressa*), better climatic conditions during the germination trial for breaking dormancy and inducing germination, and a more regular and consistent watering regime. The reduced effect of the heat treatment relative to controls was also apparent for mean richness estimates of the germinable soil seed bank, with only one site, SS-26, reporting a significant increase in richness for heat-treated soils relative to controls. However, it should be noted that all other sites did show a non-significant trend toward greater mean richness in heat-treated soils.

Overall, the heat treatment did improve estimates of species richness and seedling density of the germinable soil seed bank, but not as much as at GP-23 in the pilot study. As mentioned in Chapter 6, and shown in numerous studies (Warcup 1980; Auld & O'Connell 1991; Musil 1991; Baldwin *et al.* 1994; Roche *et al.* 1997b), estimates of seed densities and richness are dependent on the intensity and duration of the treatments used to break dormancy and induce germination. Furthermore, Bradstock (1995) indicate that soil temperatures during the passage of fire may have a substantial effect on species germination. Therefore, the results of this study are only applicable to the particular heat treatment used, not to heat *per se*. Estimates of soil seed bank species richness, density and composition are also dependent on a range of other factors, including seed longevity (Auld *et al.* 2000), dormancy (Baskin & Baskin 1989; Bell 1999), seed production and viability (Auld 1986; Bell *et al.* 1987), seed predation (Andersen & Ashton 1985; Louda 1989; Clarke *et al.* 1996), seed bank heterogeneity (Thompson 1986; Ne'eman & Izhaki 1999), seasonal variation in seed banks (Thompson & Grime 1979; Grant & Koch 1997; Ward *et al.* 1997) and sampling intensity (Dessaint *et al.* 1996).

In this study, the minimum detectable density of soil-stored seed with a 95% confidence level and assuming a Poisson distribution, was 14 seeds m⁻² (per treatment), according

to the formula of Thompson (1997), given in Chapter 6. Species with seed abundances below this level, and/or with very clumped distributions, were likely to be overlooked using the sampling regime employed in this study.

In Californian chaparral, Zammit (1988) found that total seed density increased significantly with time since fire, however, the increase was entirely due to seed accumulation of the dominant shrub, *Adenostoma fasciculatum*, in the soil. Furthermore, some species increased in density with increasing time since fire, while others decreased (Zammit & Zedler 1988). In this study, *Epacris impressa* was by far the most abundant species in the germinable soil seed bank (as in the pilot study), comprising $79 \pm 10\%$ of all seedlings. Findings such as these are common in the heathland seed bank literature, where a single species (e.g. *Calluna vulgaris* in Europe and *Adenostoma fasciculatum* in California) dominates the germinable soil seed bank (Granström 1988; Zammit & Zedler 1988; Mitchell *et al.* 1998). However, these species are also usually dominant in terms of above-ground vegetative cover in their respective environments, unlike *E. impressa* in this study, which had a mean vegetative cover of only $2 \pm 0\%$. In contrast, the dominant shrub at every site, *Leptospermum myrsinoides*, comprised $4 \pm 1\%$ of all seedlings emerging from the soil seed bank, while its mean vegetative cover across all sites was $22 \pm 3\%$. This was the only species to increase in seedling density with increasing time since fire. This suggests that *L. myrsinoides* will recruit more seedlings following fire after long fire-free periods, increasing plant density and therefore, facilitating even greater dominance of the heath. Furthermore, the ability of *L. myrsinoides* to regenerate from basal sprouts enables this species to maintain and increase its dominance under relatively long fire intervals.

Most species present in the extant vegetation in the study area were not recorded (63%) or were in very low abundances (i.e. $<1\%$ of all seedlings recorded) in the soil seed bank (29%), a finding also commonly reported elsewhere in the literature (Zammit & Zedler 1988; Dalling & Denslow 1998; Morgan 1998). This may reflect both actual seed abundances at the time of sampling, and the inability of the heat treatment to break seed dormancy and induce germination in certain species.

Species composition of the germinable soil seed bank differed significantly among age classes (presence/absence data), with the greatest compositional difference existing between young and old sites. This finding is not unusual, given that the soil seed banks

of many species may become exhausted or severely depleted following fire, consequently exerting a negative influence on estimates of germinable species richness of the soil seed bank at young sites.

It was predicted that seeds of post-fire ephemeral and short-lived species would be relatively abundant in the soil seed bank, as germination from seed would be their only means of re-establishing after fire unless seed was dispersed into the site. Instead, the seven most common species in the germinable soil seed bank were long-lived (> 25 years) shrubs. Seeds of post-fire ephemeral and short-lived species were extremely uncommon in the soil seed bank, with only three of the 11 post-fire ephemeral species, *Euchiton sphaericus*, *Isolepis marginata* and *Laxmannia orientalis*, germinating from soil-stored seed in this study. This is consistent with the uncommon nature of post-fire ephemeral and short-lived species in the above-ground component of the vegetation.

The similarity between the composition of the germinable soil seed bank and the extant vegetation was not significantly related to time since fire, using both the Jaccard and Bray-Curtis similarity indices, however, there was a general trend toward greater similarity with increasing time since fire. Studies in tropical forest (Dalling & Denslow 1998), Mediterranean pine forest (Ne'eman & Izhaki 1999), Dutch dune slacks (Bekker *et al.* 1999) and hayfield successions (Bekker *et al.* 2000) also suggest that similarities between the soil seed bank and the extant vegetation are not significantly related to site age, whether it be time since the last fire or agricultural abandonment. I could find no evidence in the literature for a significant relationship between time since disturbance and the similarity between the soil seed bank and the extant vegetation. This does not necessarily imply that there is no relationship. However, owing to the (a) low number of sites used in most studies (usually less than six), (b) the heterogeneity of soil seed banks (Thompson 1986; Ne'eman & Izhaki 1999), and (c) the inherent variability between sites in a chronosequence (Pickett 1989), it would be surprising to find a significant trend in the literature.

Similarities between the germinable soil seed bank and the extant vegetation were difficult to compare with other heathland studies, owing to the different methods of calculating similarity in each of the studies. However, comparisons were able to be made between the two sampling years at GP-23, with both Jaccard and Bray-Curtis similarity indices indicating similar values between the two years (Bray-Curtis,

50→46%; Jaccard, 20→19%). However, when the composition of the germinable soil seed bank at GP-23 is compared over the two years, differences in composition of the germinable soil seed bank are evident, with seven taxa recorded from this study that were not recorded during the pilot study. This is a substantial figure given that there were only 20 species recorded from the germinable soil seed bank during the pilot study (see Chapter 6), and suggests that sampling over multiple seasons may substantially increase the accuracy of soil seed bank density and richness estimates. However, the extra species recorded may simply be a result of sampling extra cores.

Species found in the soil seed bank that are not present in the extant vegetation are important in that they give an insight into what may germinate in the post-fire environment. In addition, the identification of these species may enable more complete estimates of site species richness to be made, as shown by the 13% increase in site richness at GP-23. More intensive sampling of the soil seed bank is likely to yield even higher estimates of total site species richness (above and below-ground richness combined). In this study, 11 such species were recorded, with eight of these being herbaceous species. This is a high proportion of herbaceous species relative to shrub species when compared with the extant vegetation across all sites, which is dominated by shrubs (see Chapter 4). It is also interesting to note that seven of the 11 species (63%) found in the soil seed bank but not in the extant vegetation at a given site were obligate seeders (species that regenerate solely by seed), compared to 34% across the entire study area (see Chapter 8). A further three species were facultative resprouters (species that may regenerate either by seed or resprouting), while only one of the 11 was an obligate resprouter.

In conclusion, this study found no change in the richness and density of the germinable soil seed bank with increasing time since fire. Furthermore, the significance of the relationship between total species richness and time since fire was unaffected by the inclusion of additional species that were present only in the soil seed bank. However, species composition was significantly different among age classes, using presence/absence data. Heat treatment of soils promoted seed germination, increasing the density of seedlings emerging from the soil seed bank but generally having no significant effect on germinable richness of the soil seed bank. In addition, no trend was

observed in similarity between the extant vegetation and the soil seed bank with time since fire.

Table 7.1 Total density of seedlings recorded in the germinable soil seed bank for each treatment at every site. FG: forb/geophyte; Gr: graminoid; S: shrub; Ss: subshrub; Tw: twiner. C: control treatment; H: heat treatment. MR: mode of regeneration; OS: obligate seeder; OR: obligate resprouter; FR: facultative resprouter. See Chapter 8 for a description of the methodology used in determining the mode of regeneration.

Time since fire (years)	Life-form	MR	BS-1.5		SS-5		TT-9		SS-16		GP-23		T4-25		SS-26		Total
			3	6	10	17	24	26	26								
Treatment			C	H	C	H	C	H	C	H	C	H	C	H	C	H	
<i>Acacia oxycedrus</i>	S	OS	0	0	0	1	0	0	1	0	0	2	0	0	0	1	5
<i>Allocasuarina</i> sp.	S	FR	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
<i>Amperea xiphoclada</i> var. <i>xiphoclada</i>	Ss	FR	0	0	0	0	0	0	1	0	0	1	0	0	2	1	5
<i>Astroloma pinifolium</i>	S	OS	0	0	1	2	0	0	0	0	2	0	3	0	23	31	62
<i>Bossiaea cinerea</i>	S	FR	0	0	0	0	0	0	0	1	0	0	0	0	1	3	5
<i>Bossiaea heterophylla</i>	S	FR	2	6	8	28	3	0	3	10	5	18	5	52	0	1	141
<i>Caleana major</i>	FG	OR	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
<i>Calytrix tetragona</i>	S	OS	0	1	26	40	20	5	0	2	0	9	1	0	46	44	194
<i>Cassytha glabella</i>	Tw	OS	0	0	0	0	0	0	0	0	0	1	0	1	0	0	2
<i>Caustis pentandra</i>	Gr	OS	1	0	1	0	0	0	0	1	0	0	0	0	2	0	5
<i>Dampiera stricta</i>	Ss	FR	0	0	0	3	1	0	2	1	0	0	0	1	0	1	9
<i>Dillwynia</i> spp.	S	FR	0	10	0	7	1	29	3	25	0	4	1	17	0	15	112

Table 7.1 (continued) Total density of seedlings recorded in the germinable soil seed bank for each treatment at every site. FG: forb/geophyte; Gr: graminoid; S: shrub; Ss: subshrub; Tw: twiner. C: control treatment; H: heat treatment. MR: mode of regeneration; OS: obligate seeder; OR: obligate resprouter; FR: facultative resprouter. See Chapter 8 for a description of the methodology used in determining the mode of regeneration.

Time since fire (years)	Life-form	MR	BS-1.5		SS-5		TT-9		SS-16		GP-23		T4-25		SS-26		Total
			3	6	6	10	17	24	26	26							
Treatment			C	H	C	H	C	H	C	H	C	H	C	H	C	H	
<i>Drosera peltata</i>	FG	FR	2	1	19	7	0	0	0	0	1	0	0	0	0	0	30
<i>Epacris impressa</i>	S	FR	295	615	36	42	253	1296	283	804	146	567	212	792	182	599	6122
<i>Euchiton sphaericus</i>	FG	OS	1	0	1	2	0	0	0	0	0	0	0	0	0	0	4
<i>Genoplesium sp. aff. rufum</i>	FG	OR	0	0	0	2	0	0	0	0	0	0	0	0	0	0	2
<i>Gompholobium huegelii</i>	S	FR	0	0	0	0	0	0	1	8	0	1	0	1	0	1	12
<i>Gonocarpus tetragynus</i>	FG	OS	1	0	0	0	11	17	0	2	0	0	12	9	23	36	111
<i>Hibbertia acicularis</i>	S	FR	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
<i>Hibbertia virgata</i>	S	FR	0	0	0	2	0	0	0	2	0	0	0	0	0	0	4
<i>Hypolaena fastigiata</i>	Gr	OR	1	1	0	3	1	16	0	2	9	7	4	5	0	1	50
<i>Isolepis marginata</i>	Gr	OS	0	0	0	3	0	1	0	0	0	0	2	0	1	0	7
<i>Laxmannia orientalis</i>	FG	OS	0	0	5	9	0	4	0	0	1	7	0	0	0	0	26
<i>Leptospermum myrsinoides</i>	S	FR	6	2	8	13	21	10	15	7	66	37	28	41	24	24	302
<i>Leucopogon ericoides</i>	S	OS	5	6	23	37	34	24	5	24	15	27	13	19	38	57	327

Table 7.1 (continued) Total density of seedlings recorded in the germinable soil seed bank for each treatment at every site. FG: forb/geophyte; Gr: graminoid; S: shrub; Ss: subshrub; Tw: twiner. C: control treatment; H: heat treatment. MR: mode of regeneration; OS: obligate seeder; OR: obligate resprouter; FR: facultative resprouter. See Chapter 8 for a description of the methodology used in determining the mode of regeneration.

Time since fire (years)	Life-form	MR	BS-1.5		SS-5		TT-9		SS-16		GP-23		T4-25		SS-26		Total	
			3		6		10		17		24		26		26			
			C	H	C	H	C	H	C	H	C	H	C	H	C	H		
	<i>Leucopogon virgatus</i> var. <i>virgatus</i>	S	OR	0	0	0	4	0	1	1	0	0	0	0	0	0	0	6
	<i>Lomandra glauca</i>	Gr	FR	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
	<i>Monotoca scoparia</i>	S	FR	0	0	0	0	0	0	0	0	0	0	0	0	2	1	3
	<i>Pimelea linifolia</i> ssp. <i>linifolia</i>	S	OS	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
	<i>Platysace ericoides</i>	S	OS	0	0	0	0	0	0	1	5	0	0	0	1	0	0	7
	<i>Poa siebertana</i> var. <i>sieberiana</i>	Gr	FR	0	0	0	0	10	0	3	1	3	2	0	0	0	0	19
	<i>Pyrorchis nigricans</i>	FG	FR	0	1	0	0	0	2	1	0	2	1	0	0	0	0	7
	<i>Thryptomene micrantha</i>	S	OS	4	2	43	30	1	0	0	0	0	0	31	5	1	3	120
	<i>Xanthosia pilosa</i>	Ss	FR	0	0	0	0	0	0	0	0	1	0	0	5	1	0	7
	Unidentified seedlings			0	4	1	2	1	2	1	1	2	4	1	1	1	4	25

Table 7.2 Species found in the germinable soil seed bank but not in the extant vegetation at a given site. LF: life-form; FG: forb/geophyte; Gr: graminoid; S: shrub; Ss: subshrub; Tw: twiner. LH: life-history; a: annual; p: perennial. MR: mode of regeneration; OS: obligate seeder; OR: obligate resprouter; FR: facultative resprouter. See Chapter 8 for a description of the methodology used in determining the mode of regeneration.

Species	LF	LH	MR	Site							
				BS-1.5	SS-5	TI-9	SS-16	GP-23	TA-25	SS-26	
<i>Caleana major</i>	FG	p	OR				+				
<i>Calytrix tetragona</i>	S	p	OS				+				
<i>Cassytha glabella</i>	Tw	p	OS					+			
<i>Drosera peltata</i>	FG	p	FR	+					+		
<i>Euchiton sphaericus</i>	FG	a	OS	+	+						
<i>Gonocarpus tetragynus</i>	FG	p	OS			+	+				
<i>Isolepis marginata</i>	Gr	a	OS		+	+				+	+
<i>Lacmannia orientalis</i>	FG	p	OS			+		+			
<i>Pyrorchis nigricans</i>	FG	p	FR	+				+			
<i>Thryptomene micrantha</i>	S	p	OS			+					+
<i>Xanthosia pilosa</i>	Ss	p	FR					+			+

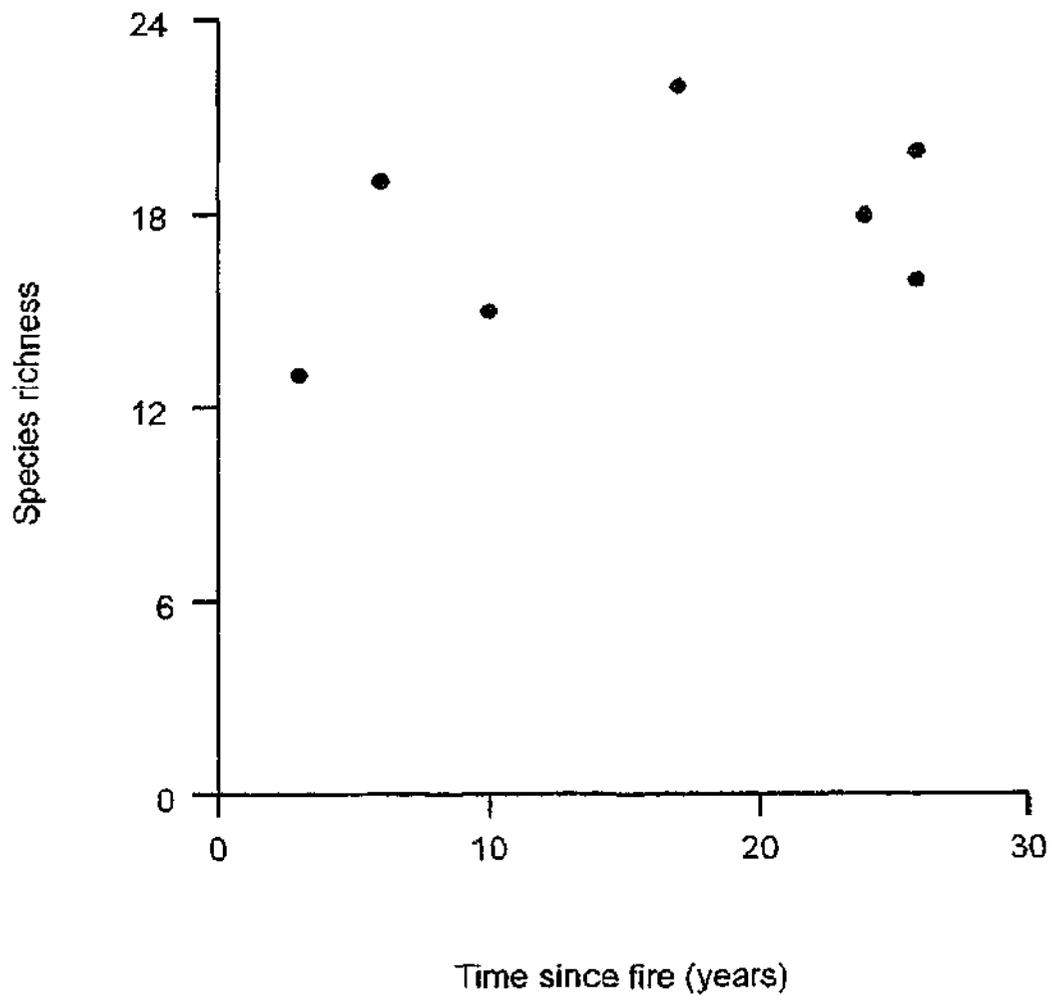


Figure 7.1 Relationship between total germinable species richness of the soil seed bank at each study site and time since fire.

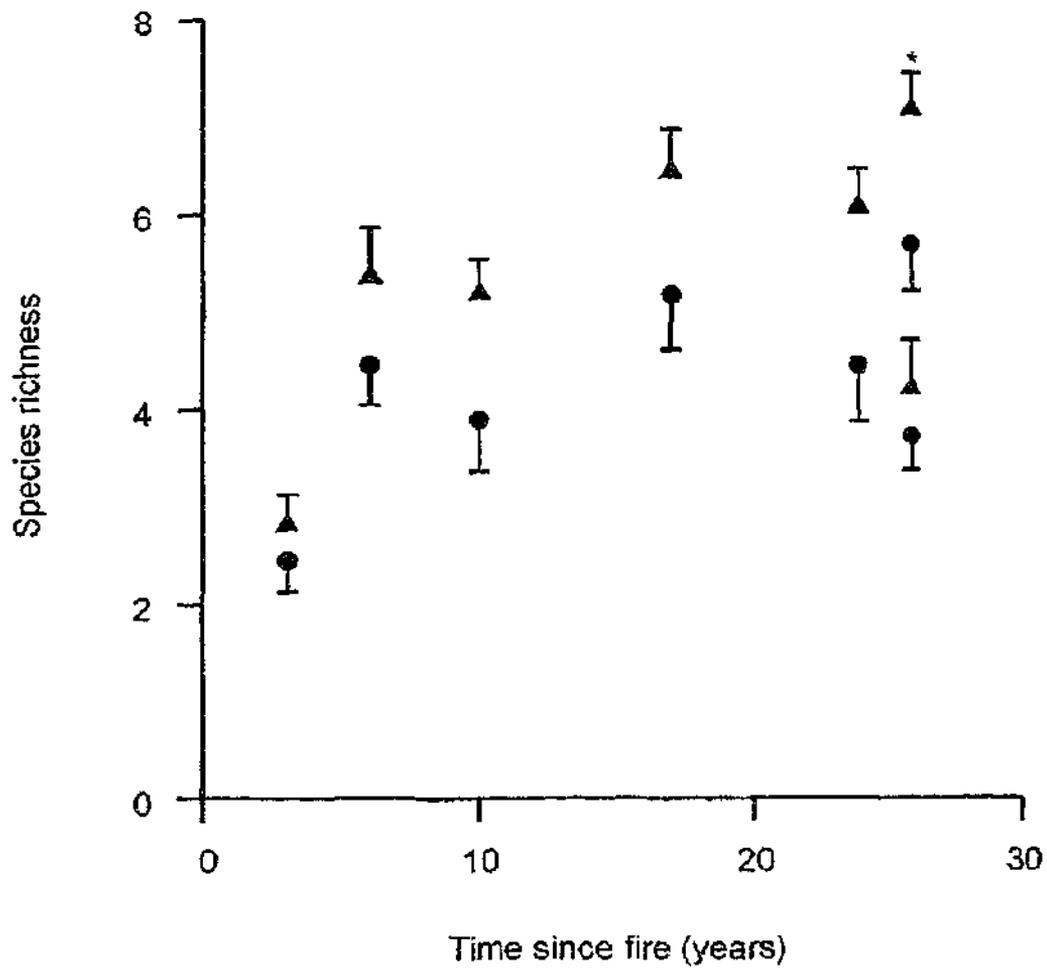


Figure 7.2 Mean germinable species richness (± 1 SE) per germination tray (four soil cores: 0.060 m^2) in relation to time since fire. ●, control; ▲, heat. An asterisk indicates significant differences between control and heat treatments: * $p < 0.05$.

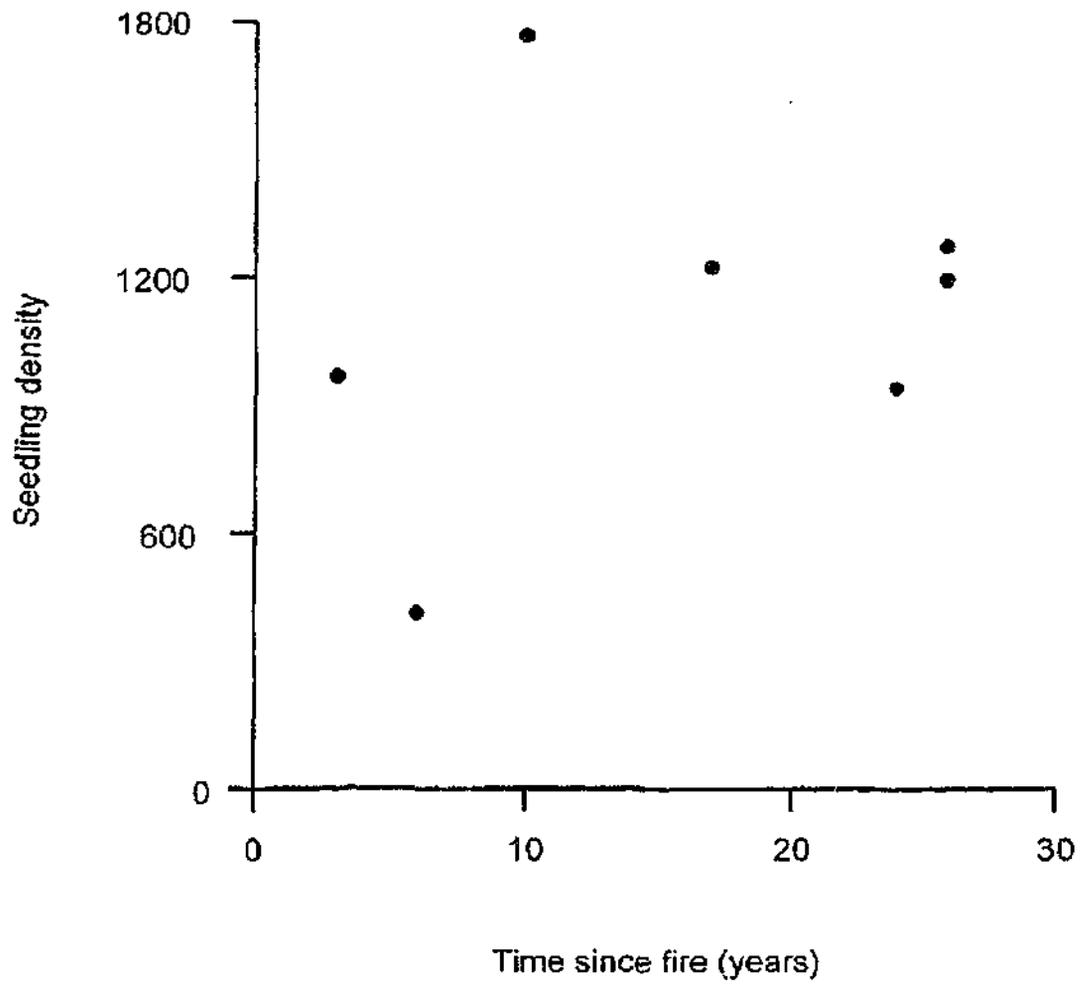


Figure 7.3 Relationship between total germinable seedling density of the soil seed bank at each study site and time since fire.

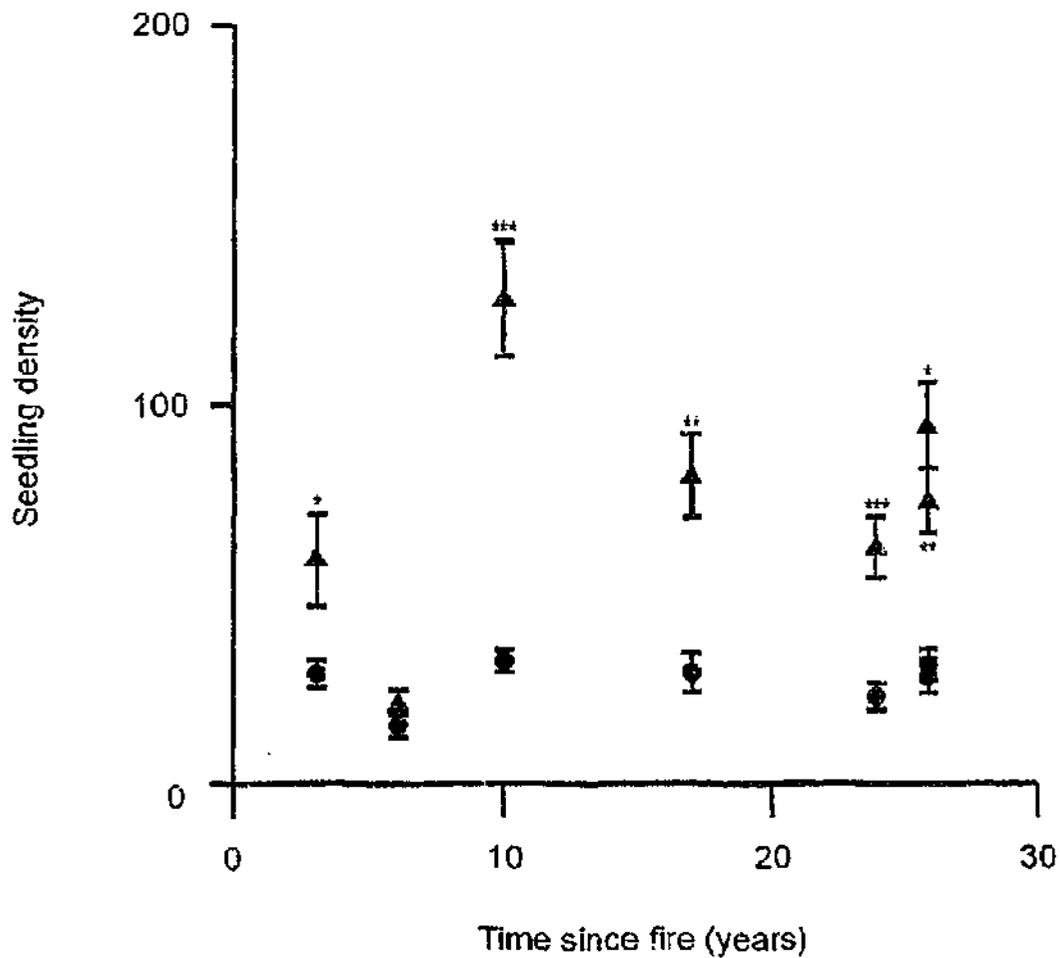
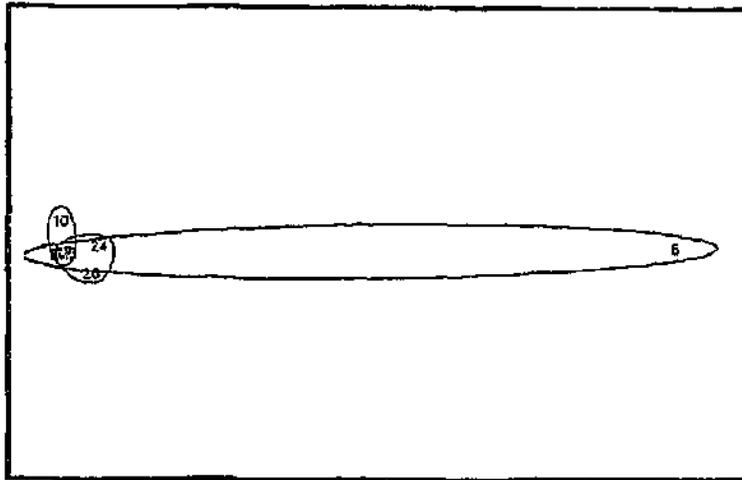
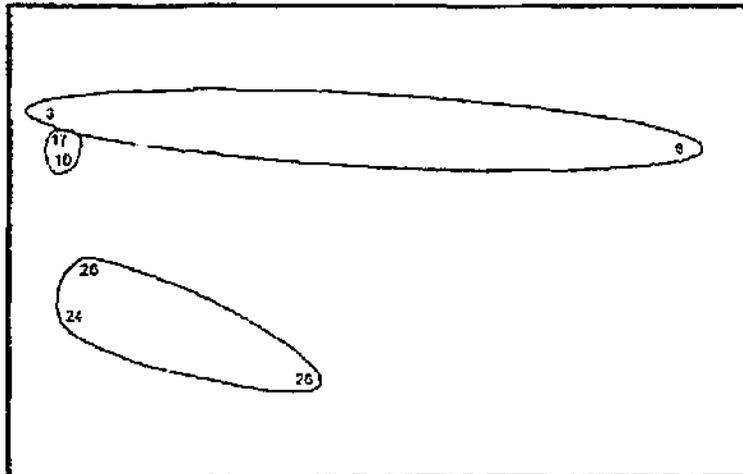


Figure 7.4 Mean germinable seedling density (± 1 SE) per germination tray (four soil cores: 0.060 m^2) in relation to time since fire. ●, control; ▲, heat. An asterisk indicates significant differences between control and heat treatments: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

(a) Density data; stress = 0.01



(b) Standardised density data; stress <math>< 0.1</math>



(c) Presence/absence data; stress = 0.09

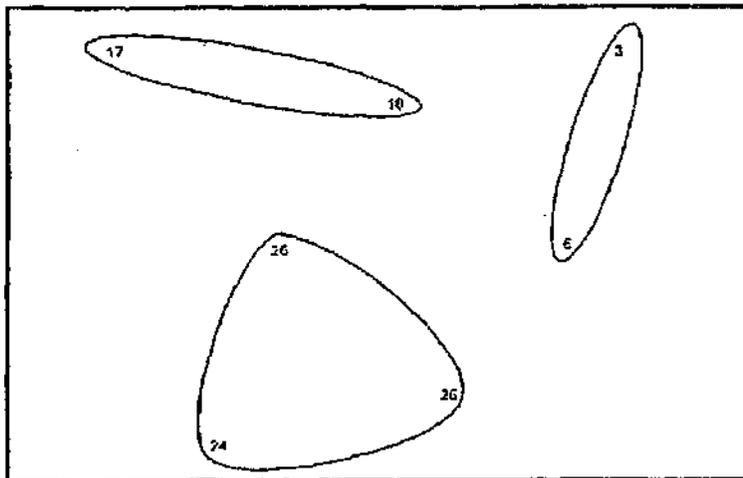


Figure 7.5 Ordination by NMDS of soil seed bank data at each site. Sites are grouped into young (0-6 years), intermediate (9-19 years) and old (23-27 years) age classes.

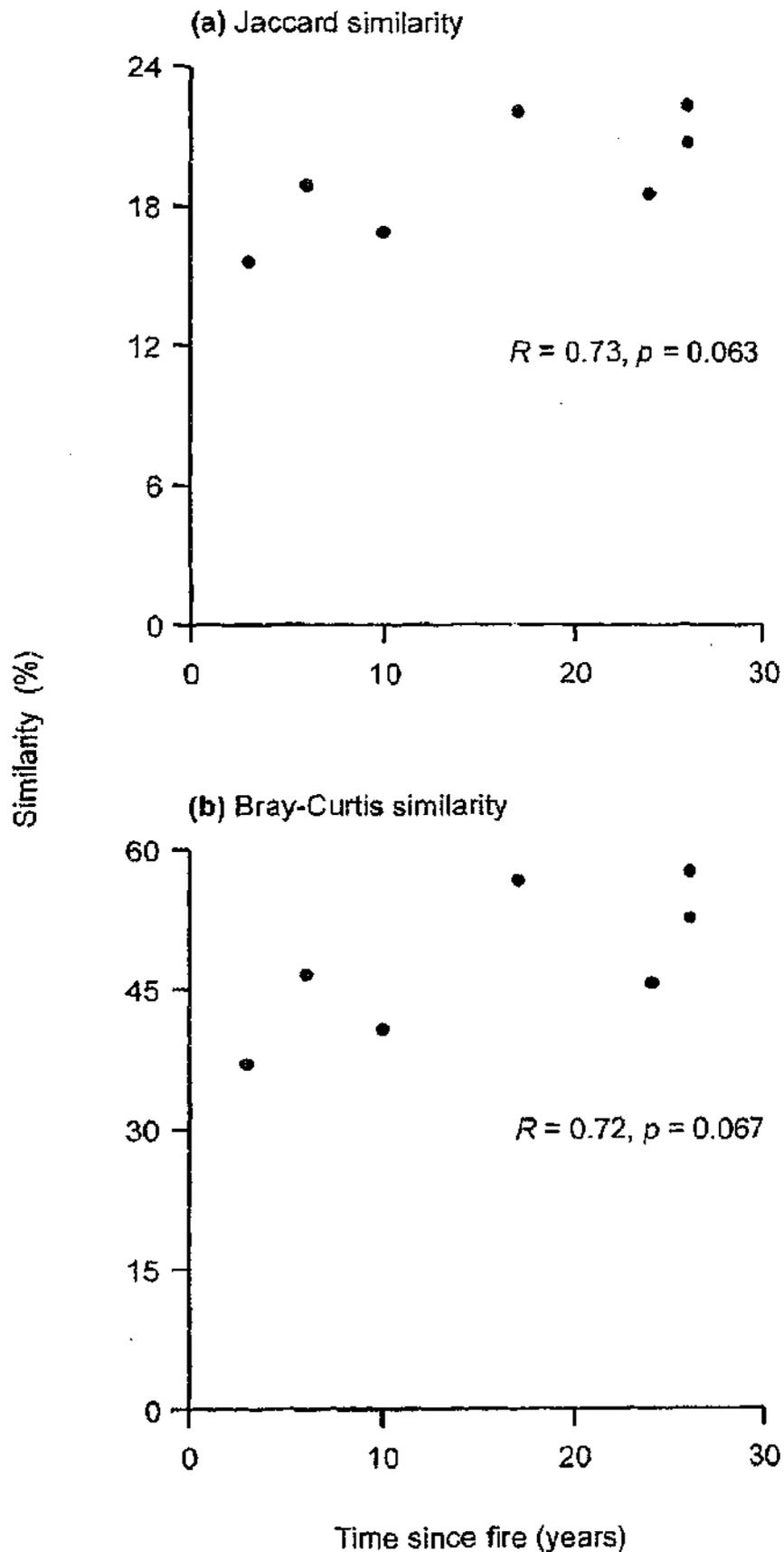


Figure 7.6 Similarity between composition of the extant vegetation and the soil seed bank at each study site in relation to time since fire. (a) Jaccard similarity; (b) Bray-Curtis

CHAPTER 8

RELATIONSHIP BETWEEN SPECIES TRAITS AND SITE AGE

INTRODUCTION

Plant communities have traditionally been classified using a binary system (species presence/absence), or a system based on species cover-abundance or density (e.g. Chapters 4 and 5). These methods of classification have historically proved very useful for analysing the similarities and differences in composition among plant communities. However, when the aim is to make ecological comparisons between compositionally distinct floras (e.g. between South African fynbos and Australian heath), a more general non-taxonomic approach is required.

In response to the need to predict the broad effects of changing climate and disturbance regimes on ecosystem dynamics, strong interest has arisen regarding the classification of vegetation on the basis of functional types (groups), as an alternative to vegetation classification based on species composition (McIntyre *et al.* 1995; Gitay & Noble 1997; Lavorel *et al.* 1997; McIntyre *et al.* 1999a; Weiher *et al.* 1999). For the purposes of this study, plant functional groups are defined as non-phylogenetic groupings of species that respond similarly to a set of environmental factors, based on a set of common biological traits (Gitay & Noble 1997; Lavorel *et al.* 1997). Functional groups have already been used to predict and compare the response of vegetation to different disturbance types and intensities such as grazing (Trémont 1994; McIntyre *et al.* 1995; Lunt 1997; Hadar *et al.* 1999) and soil disturbance (McIntyre *et al.* 1995; Hadar *et al.* 1999; Kleyer 1999; Lavorel *et al.* 1999).

Functional and morphological traits of individual species are important, as they influence how species disperse, establish and persist after disturbances such as fire (Trémont 1994; Weiher *et al.* 1999). If an understanding can be gained of the particular traits of each species within a given area or community, then more detailed predictions relating to regeneration dynamics and community processes may be possible. Many studies in mediterranean-type shrubland ecosystems have examined the changing

patterns in species composition and thus, morphological traits, along environmental gradients (Montalvo *et al.* 1991). However, few studies have examined species traits across an entire plant community in relation to post-disturbance successional sequences, (e.g. Gomez Sal *et al.* 1986).

This study attempts to understand elements of the biology of post-fire vegetation succession, and asks two main questions:

- (1) How does the frequency of particular plant traits change with time since fire?
- (2) Do species present at different successional stages differ in their regeneration biology?

To answer these questions, 13 life-history, morphological and regenerative plant traits were chosen on the basis of their potential ecological importance and influence on community composition and dynamics (Table 8.1). The list of traits is by no means exhaustive, however, it gives a broad overview of characteristics that should intuitively be important in heathland systems.

METHODS

Plant traits

The 13 plant traits were each divided into two to five categories (Table 8.1), with one category per trait ascribed to each of the 94 species found during the vegetation study (Chapter 4 and 5). Where possible, traits were recorded in the field or measured in the laboratory. Otherwise, the 'Flora of Victoria' (Walsh & Entwisle 1994; Walsh & Entwisle 1996; Walsh & Entwisle 1999) or other relevant literature was consulted.

1. Life-history

Plant life-history was divided into two categories: annual and perennial species. Data were sourced from Walsh (1994), Walsh (1996) and Walsh (1999).

2. Juvenile period

The juvenile period indicates the absolute minimum time span between two fires for a species to reach reproductive maturity and set seed. Gill (1975) divided juvenile period into primary and secondary classes, with primary juvenile period indicating the time required for post-fire seedlings to flower, and secondary juvenile period denoting the time for resprouting individuals to recover from complete leaf death and recommence flowering. For the purposes of this study, juvenile period was divided into three categories: 0-2 years, 3-4 years and 5-6 years from the time of fire. However primary and secondary juvenile periods were not differentiated, owing to difficulties in determining whether individuals had regenerated by seed or sprouts, particularly in sites burnt more than three years prior to sampling.

Data were collected in the field during the course of the vegetation study. Juvenile period was assigned based on the youngest flowering or fruiting specimen observed. Juvenile period for species that were not recorded flowering or fruiting, or species that were only recorded in intermediate- and old-aged sites, was assigned based on data from the literature. Where this was not possible, an estimate of juvenile period was made based on knowledge of plant life-history and life-form.

3. Plant longevity

Plant longevity is a trait that is especially important to obligate seeders with relatively short lifespans or short-lived seed banks. Longevity was divided into four categories: 0-1 years, 2-6 years, 7-22 years and >23 years, and it was assumed that all plants regenerated in the first year following fire. Data were sourced from sites sampled in the vegetation study and the literature. Plant longevity for obligate resprouters and geophytes was taken as the maximum site age a given species was found at, even though individual rootstocks may survive many successive fires. Some plant longevities were estimated if a species was restricted to relatively young sites and would clearly live longer than the maximum age recorded during this study.

4. Life-form

Plant life-form may influence the competitive ability of species and thus, their ability to persist at a given site. Life-form was divided into five morphological categories: tree, shrub, twiner, forb/geophyte and graminoid. The additional categories of subshrub and parasitic mistletoe that were used in Chapter 4 were merged into the shrub category, so that the number of categories for the life-form trait were not so great as to unduly bias the trait when analysed with all other traits. All life-form data were obtained from Walsh (1994), Walsh (1996) and Walsh (1999).

5. Maximum plant height

Plant height is viewed as a strong indicator of competitive ability (Gaudet & Keddy 1988; Westoby 1998; Weiher *et al.* 1999). It may also reflect carbon immobilisation in support tissue, which is possibly an important indicator of soil water and nutrient supply (Tilman 1988). Maximum plant height was divided into four categories: 0-0.3 m, 0.4-1.0 m, 1.1-2.5 m and 2.6-8.0 m, according to field observations and the heights given in Walsh (1994), Walsh (1996) and Walsh (1999).

6. Mode of regeneration

Mode of regeneration following disturbance may strongly influence the potential for individual species to achieve local dominance following fire (Purdie & Slatyer 1976). It may also have a significant bearing on the continued persistence of a species, particularly when subject to either high or low frequency fire regimes (Keith 1996).

Mode of regeneration for each species was assessed by either examining or excavating plants in the field and/or consultation with the National Fire Response Register, a database established by Gill (1992). Field data were collected from nine of the 14 study sites during the vegetation study, with a maximum of 20 individuals of each species sampled from each site. Sampling was conducted randomly within the 10 m², 100 m² and 900 m² quadrats used for the vegetation study (Chapters 4 and 5). A maximum of two individuals per species was sampled from a single quadrat, to avoid the effects of population 'clumping', where a given species may exhibit different modes of regeneration depending on the local environment and genetic variant of the species (Williams *et al.* 1994; Kruger & Midgley 2001). For uncommon species, more than two individuals may have been sampled from a quadrat, while for very uncommon species, samples were taken from wherever an individual was located. For many species, 20 samples were not taken at each site, owing to plant rarity.

Two fire response classifications were used for this study. The first divided species into six categories and was largely based on the classification of Gill (1993) (Table 8.2). The categories were: fire avoiders (e.g. geophytes), fire ephemerals (species with fire-induced seed germination that complete their life cycle in the first few years after fire) (Bell *et al.* 1984), annuals, obligate seeders (species that regenerate solely by seed), obligate resprouters (species that predominantly resprout following disturbance) and facultative resprouters (species that exhibit vegetative and seed regeneration). This classification was used for examining the effect of site age on species fire response. The second classification used a simplified approach, dividing species into three categories: obligate seeders (>91% seed germination), obligate resprouters (0-10% seed germination) and facultative resprouters (11-90% seed germination). This classification was used for (a) examining the effect of site age on species fire response, and (b) the ordination of species traits, which will be explained in the *Data analysis* section.

7. Conditions for establishment

Conditions for establishment were defined by Noble (1980) as a component of the 'Vital Attributes' scheme. They are divided into three categories: (1) *tolerant* species are those species that are able to establish and grow immediately after disturbance and in the inter-fire period when resource competition is greater; (2) *intolerant* species can only establish and grow in the immediate post-fire environment where competition is largely

removed; while (3) some species require certain pre-conditions associated with an older community to be met prior to establishment (Noble & Slatyer 1980).

Data were gathered from intermediate- and old-aged sites during the vegetation study. Wherever a species was observed regenerating outside of the first five years following fire, it was classified as *tolerant*. All other species that did not require obvious pre-conditions to be met before establishment were classified *intolerant*.

8. Flowering season

Season of flowering is an approximate indicator of fruiting and therefore, subsequent seed production. This has major relevance to species in fire-prone heathlands, where the season of fire may substantially influence opportunities for seed-based regeneration, particularly in species with short-lived (transient) seed banks (Le Maitre 1987; Enright & Lamont 1989; McIntyre *et al.* 1999b). Flowering season was divided into four categories for this study: summer, autumn, winter and spring. All data were obtained from Walsh (1994), Walsh (1996) and Walsh (1999). If the flowering period spanned at least two months of a season, then it was included as flowering in that season (flowering recorded in only one month of a season was not included). If species flowered over more than one season, then they were recorded for all seasons in which they flowered.

9. Fruit type

The fruit type of species is important as it has implications for both seed dispersal and protection. Fruit type was classified into three categories in this study: (1) dry *dehiscent* fruits (follicles, legumes and capsules) are those that release seeds by opening in a regular manner, either by pores or splits; (2) dry *indehiscent* fruits (schizocarps, nuts, achenes and samaras) release seed by decaying or breaking up in an irregular manner; while (3) *fleshy* fruits contain seed(s) inside a fleshy mesocarp (Duigan 1992). Data were sourced from Ralph (1994), Walsh (1994), Walsh (1996) and Walsh (1999).

10. Propagule size (maximum length)

Seed mass is thought to generally correlate with mode of dispersal, plant height and growth form (Westoby *et al.* 1996). In addition, seed mass or shape has been generally thought to correspond with persistence in the soil (Thompson *et al.* 1993; Bekker *et al.* 1998; Funes *et al.* 1999). However, recent studies suggest that this may not be the case

in some Australian (Westoby *et al.* 1996; Leishman & Westoby 1998) and New Zealand (Moles *et al.* 2000) systems. For this study, propagule size was measured in terms of maximum length (Osunkoya 1996), with three seed length categories used: 0-1 mm, 2-7 mm and >8 mm. Mean values were obtained after randomly collecting 10-20 seeds from different plants for as many species as possible, and measuring seeds with a set of callipers. If seed was unable to be collected, seed size was either obtained from Walsh (1994), Walsh (1996) and Walsh (1999), or estimated based on personal knowledge of species biology.

11. Serotiny

Serotiny relates to the retention of seeds within closed, woody fruits or cones in the plant canopy for more than one year (Lamont *et al.* 1991; Enright *et al.* 1998). The ecological significance of serotiny lies in the fact that the large majority of seed is stored in the canopy until fire usually triggers mass release, satiating seed predators, and giving seedlings the best possible opportunity to establish and grow in the relatively high nutrient, reduced competition, post-fire environment (Gill 1981a; O'Dowd & Gill 1983; Enright *et al.* 1998). However, the woody fruits and cones may be equally important as a means of offering protection from seed predators (Bell *et al.* 1984). Serotiny was simply categorised into presence and absence in this study, based on field observations of all species present in the heath.

12. Seed dormancy

Seed dormancy is a common trait in mediterranean-type ecosystems (Keeley 1991; Bell *et al.* 1993; Keeley 1995), and is defined by Baskin (1989) as seed "that will not germinate under any set of normal environmental conditions". Seed dormancy has the potential to influence the continued persistence of species at a given site, following the death of all extant individuals (Keeley 1995; Auld *et al.* 2000). Dormancy was divided into two categories: (1) species with *persistent* seed banks (some seeds live longer than one year in the soil), and (2) species with *transient* seed banks (no seed persists for more than one year) (Baskin & Baskin 1989). Data were sourced from the literature, and Chapters 6 and 7, with species germinating in significantly greater numbers in smoke- or heat-treated soil, or species that emerged after more than 12 months in the soil (Chapter 7) classified as possessing dormant seed. Owing to the lack of data on the longevity of

soil seed banks (Parker & Kelly 1989; Keith 1996; Auld *et al.* 2000), dormancy was assessed for only 50% of species. Therefore, the effect of site age on the frequency of species possessing dormant seed was only assessed for half of the species present in the heath.

13. Mode of dispersal

Mode of seed dispersal is ecologically important as it suggests the potential distance a seed may disperse once emitted from the parent plant (Hoffmann & Armesto 1995). In addition, mode of dispersal may also influence the success of seedling establishment (Berg 1981; Keeley 1995).

Mode of dispersal was inferred from propagule morphology; a method commonly used in other studies, (e.g. van der Pijl 1982; Hoffmann & Armesto 1995). Five categories of seed dispersal were recognised: (1) *unassisted* (seed lacking specialised dispersal mechanisms); (2) *anemochory* (seed of extremely light weight, or with wings, plumes or pappus adapted for wind dispersal); (3) *ballistichory* (seed propelled by explosive fruit dehiscence); (4) *myrmecochory* (seed possessing ant-attracting appendage termed an elaiosome); and (5) *zoochory* (seed with obvious barbs or spines for attachment to animal fur or feathers, or fleshy fruits suited for animal ingestion) (Berg 1975; van der Pijl 1982; Hoffmann & Armesto 1995). Mode of dispersal was determined from the extensive literature and personal observations of seed and fruit morphology. Most species have a clear morphological feature, suggesting a particular dispersal mechanism. However, certain species possessed more than one obvious feature and were thus recorded in both dispersal categories.

Data analysis

Data for each trait were organised into Model 1 two-way contingency tables, with each cell representing the number of species present in a given 'age class-plant trait variable' combination. Owing to the uneven number of sites sampled in each age class, one young site and one intermediate-aged site were excluded, so as not to unduly bias species counts in these age classes. The oldest of the young sites (SS-6) was removed, while one of the sites burnt 16 years prior to sampling was also randomly chosen to be removed (SS-16), giving four sites in each of the three age classes (young: 0-6 years; intermediate: 9-19 years; old: 23-27 years). *G*-tests of independence using Model 1

two-way contingency tables, were conducted to determine the significance of the effect of age class for each of the 13 plant traits (Sokal & Rohlf 1995). The *G*-test of independence works by testing the goodness of fit of the observed cell frequencies to their expected frequencies, and tests the null hypothesis that site age class and plant trait are independent of one another (Sokal & Rohlf 1995). All traits were categorical (after conversion of continuous traits), to enable ease of comparison and analysis (Diaz *et al.* 1999).

To determine whether species present at different successional stages differ in their biology, a matrix of all 94 species by the 13 traits was established. Each of the 13 traits was divided into two to five binary options, giving a matrix of 94 species by 43 trait categories. The matrix was subsequently reduced to 41 categories by eliminating the seed dormancy trait, which had insufficient data to be included in the analysis. Furthermore, the number of species was reduced to 75, by only keeping those species that were restricted to young sites, old sites, or a combination of young, intermediate and old-aged sites. Species restricted to intermediate-aged sites or any other combination of sites were not used in the analysis.

Non-metric Multidimensional Scaling (NMDS) using the Bray-Curtis similarity index was employed to plot species similarities based on the full set of character traits, using PRIMER 5.2 (Clarke & Gorley 2001). In addition, hierarchical agglomerative clustering using the group average linkage was employed to identify species clusters (Clarke & Warwick 1994). This complementary method was used because of the high stress of the NMDS plot. Groups (clusters) were then superimposed on the ordination plot to check the accuracy of the ordination procedure, as recommended by Clarke (1994).

The difference in species attributes among the three age categories (species only occurring in young sites; species only occurring in old sites; species found across young/intermediate/old sites) was tested by Analysis of Similarity (ANOSIM), using PRIMER 5.2. Pairwise comparisons between age groupings are reported, with no adjustments made for multiple comparisons, following the reasoning of Stewart-Oaten (1995). In addition, the contribution of each species to the similarity within groups and dissimilarity between groups was calculated using the Similarity Percentages (SIMPER) routine (Clarke & Warwick 1994).

RESULTS

Overall, plant traits differed little among site age classes, with only three traits, life-history, plant longevity and mode of regeneration (six categories), associating significantly with site age (Table 8.3). The biological traits for each species are given in Table 8.4.

The heathland is dominated by perennial species (93% of all species) in all age classes (Table 8.5a). Life-history was significantly associated with age class, with the standardised residuals suggesting that the lack of independence was predominantly due to the greater number of annuals than expected in young sites. Most species (73%) possessed juvenile periods of two years or less, with a further 23% of species reaching reproductive maturity by four years after fire (Table 8.5b). All species in the heathland are able to reach maturity by six years following fire. However, it should be noted that primary and secondary juvenile periods have not been differentiated here. For instance, based on field evidence, the juvenile period for *Banksia serrata* in this study was three years, however, the primary juvenile period may actually be up to nine years (Benson 1985). Plant longevity was also significantly associated with age class, with standardised residuals suggesting that at young sites, more species were present than expected in the three shortest longevity categories (0-1 years, 2-6 years and 7-22 years) (Table 8.5c). Overall, 76% of all species were present in the longest-lived category (23+ years), while a combined total of only 14% of species were present in the two shortest-lived categories (0-1 years and 2-6 years) (Table 8.5c).

Shrubs dominated the life-form trait (51% of all species), while forbs/geophytes (24%) and graminoids (17%) were also relatively abundant life-forms (Table 8.5d). Trees (4% of all species) and twirners (3%) were poorly represented life-forms. In terms of maximum plant height, more species were present in the 0.4-1.0 m category (37% of all species) than any other category (Table 8.5e). The number of species in each of the other three categories was very evenly distributed, ranging from 19-23%.

Mode of regeneration was not significantly associated with age class, using the three category classification of Naveh (1975). Species were very evenly spread between obligate seeders (34% of all species) and obligate resprouters (29%), while those exhibiting both modes of regeneration (facultative resprouters) accounted for 37% of

species in the heathland (Table 8.5f). Using the six category classification based on Gill (1993), mode of regeneration was significantly associated with age class. Standardised residuals suggest that the lack of independence is primarily due to (in decreasing order of importance) more post-fire ephemerals in young sites, more fire avoiders in old sites and a greater number of obligate resprouters than expected in intermediate-aged sites (Table 8.5g). Under the six-category classification, facultative resprouting was the dominant fire response (30% of all species), while obligate seeders (24%) and obligate resprouters (18%) were the next most important responses in terms of species numbers (Table 8.5g). Fire avoiders (13% of all species), post-fire ephemerals (11%) and annuals (4%) comprised the remainder of species in the heathland.

Conditions for establishment were not significantly associated with age class. However, old sites possessed twice as many tolerant species compared to intolerant, while young sites possessed exactly the same amount of tolerant and intolerant species (Table 8.5h). Overall, the heathland was dominated by species intolerant of establishing in the presence of adult competition (65% of all species), while 34% of species were tolerant (Table 8.5h). Only one species, the parasitic mistletoe *Amyema pendula* ssp. *pendula*, required certain pre-conditions to be met before establishment – namely, the availability of branches within *Eucalyptus* spp. crowns where bird-dispersed seed could have opportunity to lodge (Gill 1993).

Spring was the dominant flowering season, with 87% of species flowering at this time of year, followed by summer (40% of all species) and autumn and winter (both 24%) (Table 8.5i). The total percentages add to more than 100% because some species were recorded flowering in more than one season.

Fruit type was dominated by the dry dehiscence attribute (62% of all species), while the number of species with dry indehiscent (26%) or fleshy fruits (12%) was considerably less (Table 8.5j). The maximum length of dispersal propagules was generally between 1-7 mm (68% of all species), while 19% of species possessed small propagules less than 1 mm in length, and 13% possessed relatively large propagules greater than 7 mm in length (Table 8.5k). Virtually all species possessed propagules with a length no more than four times greater than the seed width. Serotiny was relatively uncommon, with 12% of species storing seed in woody fruits within the plant canopy (Table 8.5l).

Many species appear to possess persistent seed banks (41 out of the 47 species with available information in the literature), while species with only transient seed seem to be uncommon (6 species) (Table 8.5m). However, this may be due to an unforeseen bias in the literature toward reporting evidence of dormancy/persistence in seeds, rather than transience.

Mode of dispersal was dominated by three main strategies: anemochory (37% of all species), unassisted (32%) and myrmecochory (29%) (Table 8.5n). Zoochory (15%) and ballistichory (3%) were notably more uncommon. The total percentages add to more than 100% because some species possessed more than one recognised mode of dispersal.

The ordination of species according to the 41 plant attributes resulted in a plot that possessed a stress level of 0.23, which is considered to be too high for a two-dimensional picture to be considered reliable (Clarke & Warwick 1994) (Fig 8.1). Therefore, groups derived through an hierarchical agglomerative cluster analysis using the group average linkage were superimposed onto the ordination plot, to check the reliability of the plot (Clarke & Warwick 1994). At the 55% similarity level, seven species groups were formed by the cluster analysis, with five of these functional groups corresponding extremely well with groupings on the ordination plot (Fig 8.1). However, two small groups of two and three species derived from the cluster analysis did not correspond with the ordination. Despite this, the ordination was considered to be reasonably reliable, as 70 of the 75 species were grouped similarly in both analyses.

The first functional group comprised six species that were all annuals (Fig 8.1). The group was characterised by obligate seeding, short-lived forbs/geophytes and graminoids that were intolerant to establishing in the presence of adult competition. The mode of dispersal of these species was either unassisted or by wind. The second group was composed of nine species, with eight being perennial, geophytic orchids, while one was a fern (Fig 8.1). This functional group was characterised by obligate resprouting species with short juvenile periods (<2 years), long plant longevities (>23 years), dehiscent fruits and tiny, wind-dispersed propagules. The third functional group comprised 16 species and was dominated by perennial forbs/geophytes and graminoids, although there were two shrubs present (Fig 8.1). For this group, juvenile periods were short, propagule sizes were intermediate (1-7 mm length) and the mode of dispersal was

unassisted in all species except one. The largest functional group comprised 31 species and was dominated by long-lived (>23 years) shrubs (one twiner was present), possessing dehiscent or fleshy fruits, intermediate to large propagules and predominantly ant- and vertebrate-dispersed seed (Fig 8.1). Finally, the fifth functional group comprised eight serotinous shrub or tree species (Fig 8.1). These species were generally long-lived facultative or obligate resprouters that were tall in stature and dispersed by wind or gravity (unassisted). The remaining five species were classified into two groups of negligible biological significance, which did not correspond well with groupings on the ordination plot.

Of the five functional groups indicated by cluster analysis, three appeared to relate reasonably well to species groupings based on age class. Functional group 1 closely coincided with species restricted to young sites, while functional groups 4 and 5 were predominantly composed of species present across all three age classes (Fig 8.1). In contrast, functional groups 2 and 3 were characterised by species that occur across a wide range of site ages.

ANOSIM indicates that there is a significant difference in plant attributes among species occurring in young, old and young/intermediate/old sites ($R = 0.34, p < 0.001$). Pairwise comparisons suggest significant differences between all three comparisons (young-old: $R = 0.14, p = 0.040$; young-young/intermediate/old: $R = 0.42, p < 0.001$; old-young/intermediate/old: $R = 0.24, p = 0.007$). However, Clarke (1994) note that significant results may be obtained even if R is low when the number of replicates is high. In this case, R values can be a more useful indicator of the significance of pairwise comparisons than derived p values (Clarke & Warwick 1994; Clarke & Gorley 2001). Using the definition of Clarke (2001), which states that groups with a pairwise comparison of $R < 0.25$ are barely separable, there is virtually no difference in plant attributes between species occurring in young versus old sites, and old versus young/intermediate/old sites. The difference between species occurring in young versus young/intermediate/old sites is relatively more substantial but there is still a considerable degree of overlap.

Using the SIMPER routine in PRIMER, and a 5% cut-off level signifying species making a substantial contribution to total variation within an age category (i.e. species occurring only in young, old, or young/intermediate/old sites), five attributes were found

to be effectively redundant. The five attributes were life-history (perennial), juvenile period (0-2 years), flowering season (spring), fruit type (dehiscent) and serotiny (absence). Species restricted to young sites were primarily characterised by their intolerance to establishing in the presence of adult competition (contribution of 14% to within-'age class' similarity). In addition, the unassisted mode of dispersal contributed 5% to within-'age class' similarity. Species occurring solely in old sites were characterised by their high (>23 years) plant longevity (12%), tolerance to establishing in the presence of adult competitors (7%), wind-dispersal (7%) and obligate resprouting (5%). Finally, species that occurred across all age classes were characterised by their long plant longevity (13%), intermediate (1-7 mm length) propagule size (10%), tolerance to establishing in the presence of adult competition (7%) and shrub life-form (7%).

Plant attributes contributing most to the dissimilarity between species restricted to young sites versus species occurring in all age classes were plant longevity (> 23 years) (substantially greater in species present in all age classes), and conditions for establishment (more intolerant species in the young group), which are both predictable outcomes.

DISCUSSION

The purpose of this study was to determine (1) how the frequency of particular plant traits changed with time since fire, and (2) whether species present at different times since fire are distinctive in terms of their regeneration biology.

In response to the first aim, the frequency of species categories in the first 27 years after fire differed little with time since fire, with only three of the 14 character traits, life-history, plant longevity and mode of regeneration (six-categories) differing significantly in frequency among young, intermediate and old-aged sites. The overall lack of trends with time since fire may be due to a number of reasons. First, there may have indeed been no change in the frequency of different plant attributes with increasing time since fire. Second, any change in species composition with increasing time since fire may not have been great enough to influence the frequency of plant categories recorded. Finally, the chronosequence may have been too short to effectively determine whether there was a trend with increasing site age.

Two of the three traits that were significantly associated with site age were related to plant life-span (life-history and plant longevity), with a greater number of annual or short-lived species found than expected in young sites, compared with intermediate and old-aged sites. This trend is not uncommon and has been observed to varying degrees in Australian heath (Specht *et al.* 1958; Bell *et al.* 1984; Wark *et al.* 1987; Gill 1993), Californian chaparral (Keeley 1991) and the Mediterranean region (Ojeda *et al.* 1996). It suggests that plant life-span is an important trait influencing post-fire vegetation succession and dynamics, although the successional development is also influenced by seed dormancy and longevity in the soil, and the ability of species to regenerate and reach reproductive maturity in the presence of adult competition.

Mode of regeneration (six categories) was the only other trait found to be associated with site age, even though the mode of regeneration (three categories), which is simply a broader categorisation, was not related to time since fire. The significance of the more detailed classification of mode of regeneration is probably due to the incorporation of aspects of plant life-span, such as annuals and post-fire ephemerals (Table 8.2), thus reiterating the importance of life-history and plant longevity as descriptive traits. The greater frequency of 'fire avoiders' than expected in old sites appears to have arisen

from the presence of an unusually high number of geophytic orchids (eight) at T2-27. However, it is uncertain whether this is a site-specific phenomenon, or the representation of a trend toward greater establishment of fire-avoiders in old heath as the understorey begins to open-up and total vegetative cover decreases (refer to Chapter 4).

The heathland sampled in this study was relatively similar to other Australian heathlands in terms of the overall percentage of species possessing the ability to sprout, with 66% of all species either obligately or facultatively resprouting. This figure is at the low end of the spectrum in relation to other Australian heathlands, where 65-80% of species possess the ability to obligately or facultatively resprout (Specht *et al.* 1958; Siddiqi *et al.* 1976; Russell & Parsons 1978; Bell *et al.* 1984; McMahon 1984b; van der Moezel *et al.* 1987; Wark *et al.* 1987; Molnar *et al.* 1989; Benwell 1998; Clarke & Knox 2002). It should be noted that some species showed a range of responses, with common species such as *Banksia serrata*, *Epacris impressa* and *Hibbertia virgata* all displaying increased frequency of seeding at some sites and increased frequency of resprouting at others. This is a response commonly reported in heath-type vegetation (Bell *et al.* 1984; Whelan *et al.* 2002). This continuum of responses to disturbance may be due to differences in fire regimes (particularly the severity of fire), genetic variation between populations and the developmental stage of different species at the time of disturbance (Gill 1981a; Midgley 1996; Bellingham & Sparrow 2000; Bond & Midgley 2001; Kruger & Midgley 2001; Whelan *et al.* 2002).

Bellingham^λ & Sparrow (2000) recently devised a model to predict allocation to resprouting (versus seeding) in relation to disturbance severity and frequency. In brief, the model predicts that at high disturbance severity, seed regeneration will be more important at low and high disturbance frequencies, while resprouting will be dominant at intermediate disturbance frequencies. The model also predicts that resprouters will dominate at low disturbance severities, irrespective of disturbance frequency (Bellingham & Sparrow 2000). It is evident from this model that subtle differences in disturbance frequency and severity have the potential to affect both the mode of regeneration of individual species, and the presence or absence of different species. However, the direct effect of disturbance severity and frequency on mode of regeneration was not quantified in this study.

NMDS did not clearly group post-fire ephemerals or early successional species separately from long-lived or late successional species. However, when groupings from the 55% similarity level of the cluster analysis were superimposed onto the ordination plot, five functional groups based mainly on life-history and life-form were identified, with three of these groups corresponding well with a given age class. The first functional group was composed of annuals that were predominantly found in young sites; the fourth functional group was dominated by long-lived shrubs, which were found across the range of young, intermediate and old-aged sites; while the fifth group comprised serotinous trees and shrubs that occurred across all age classes. The other two groups did not correspond well with a particular age class. One (functional group 2) was dominated by orchids, while the other (functional group 3) was dominated by perennial forbs/geophytes and graminoids, including a number of post-fire ephemeral species. Therefore, it appears that species are grouped more decisively based on life-history and life-form attributes, rather than site age. McIntyre (1995) also found that life-form was the most useful trait for characterising responses to various disturbance types.

Conditions for establishment appears to be an important trait for all age classes, with species that only occur in young sites intolerant to establishing in the presence of adult competition, while species occurring only in old sites, or all age classes, were generally tolerant to establishing in older heath. In a study of calcareous grassland species, Leishman (1999) showed that the establishment ability of a species was context-dependent. That is, post-emergence growth and survival was dependent on neighbouring species. This is also likely to be the case in heathlands, with toxic foliar and litter leachates (del Moral *et al.* 1978), and canopy shading (Specht & Specht 1989; Cowling & Gxaba 1990) possibly affecting the inter-fire establishment ability of neighbouring species possessing soil-stored propagules. Even if a species establishes in the presence of adult competition it may not persist to reach sexual maturity. In this study, the generally uniform population age structures of most species suggests a single regeneration pulse in the year following fire. Therefore, many seedlings or sprouts classified in this study as tolerant may actually fail to reach maturity in the heathland, and would be classified as intolerant in the strict sense of the definition given by Noble (1980). In contrast, future canopy senescence may facilitate opportunities for species

not recorded as tolerant in this study to germinate and sprout due to increased light availability.

The tendency for species restricted to young sites to possess no obvious adaptations for dispersal may be due to the longevity of their seeds. For instance, eight of the ten potential post-fire ephemerals present have no adaptation for long-distance dispersal into a recently burnt site. Therefore, they must possess dormant seed that is stored in the soil for many years if they are to persist until the next fire (Keeley 1991). However, the other two post-fire ephemerals have obvious appendages designed for wind (pappus) and animal (barb) dispersal into a site following fire. For these species, the amount of time seed may be stored in the soil is probably not as important. Species occurring solely in old sites were characterised by wind-dispersed seed. However, this is probably an artefact of the relatively large number of wind-dispersed orchids possessing minute seeds in this age class.

It is interesting to note that most of the long-lived shrubs that occurred in all age classes (functional group 4) were either myrmecochorous or zoochorous. Many species in Australian heathlands possess seeds or fruits with ant-attracting appendages or nutritious food bodies called elaiosomes (Berg 1975; Rice & Westoby 1981; Handel & Beattie 1990). Ants readily collect these seeds, utilise the elaiosome, and deposit the propagule underground in ant nests or in 'safe' sites, where they are protected from excessive heat at the soil surface during fires (Berg 1981; Auld & Denham 1999). In addition, seed burial by myrmecochorous ants is likely to aid in decreasing the occurrence of seed predation (Auld & Denham 1999). Therefore, myrmecochory may be of great importance in facilitating the germination and subsequent persistence of many of the shrub species in the heathland.

The mode of regeneration contributed little to the overall variation within species occurring only in young sites, and species found in all age classes. In contrast, species that were restricted to old sites were characterised by obligate resprouting, which is probably due to a combination of (a) the disproportionate abundance of resprouting orchids in this age class, and (b) the reduced number of obligate seeders, owing to the absence of post-fire ephemerals and short-lived species. The low tendency for any of the mode of regeneration categories to contribute substantially (e.g. >5%) to overall variation within species restricted to young sites and species occurring in all age classes

is predominantly due to the even distribution of obligate seeders, obligate resprouters and facultative resprouters among age classes.

In a study on grazed pastures in Spain, Gomez Sal (1986) found that time since disturbance (ploughing) had a substantial effect on the occurrence of species morphological attributes present at a site. However, I know of no other studies examining differences in plant biological and ecological traits in relation to post-fire succession. The univariate analyses conducted in this study indicated that three plant traits, life-history, plant longevity and mode of regeneration (six categories), differed significantly in frequency among age classes. Multivariate analyses also identified five major functional groups, three of which were related to site age: (a) annuals occurring predominantly in young sites, (b) long-lived shrubs occurring in all age classes and (c) long-lived serotinous trees and shrubs occurring in all age classes. Two other functional groups comprising forbs/geophytes and graminoids were not related to site age. Overall, there is strong evidence that species restricted to young sites possess a different suite of attributes from species restricted to relatively old sites, however, a degree of overlap does exist among species. A greater range of site ages would possibly yield even more conclusive results.

Table 8.1 Biological traits and the associated categories assessed for each species.

Species trait	Code	Categories
Life-history	A	Annual
	P	Perennial
Juvenile period	1	0-2 years
	2	3-4 years
	3	5-6 years
Plant longevity	1	0-1 years
	2	2-6 years
	3	7-22 years
	4	23+ years
Life-form	Tr	Tree
	S	Shrub
	Tw	Twiner
	FG	Forb/geophyte
	Gr	Graminoid
Maximum plant height	1	0-0.3 m
	2	0.4-1.0 m
	3	1.1-2.5 m
	4	2.6-8.0 m
Mode of regeneration	OS	Obligate seeder
	OR	Obligate resprouter
	FR	Facultative resprouter
Conditions for establishment	T	Tolerant
	I	Intolerant
	R	Requires some pre-condition to be met before establishment
Flowering season	Su	Summer
	A	Autumn
	W	Winter
	Sp	Spring
Fruit type	D	Dehiscent
	I	Indehiscent
	F	Fleshy
Propagule size (maximum length)	1	<1 mm
	2	1-7 mm
	3	>7 mm
Serotiny	Y	Yes
	N	No
Seed dormancy	P	Persistent
	T	Transient
Mode of dispersal	U	Unassisted (Gravity)
	A	Anemochory (Wind)
	B	Ballistichory (Explosive)
	M	Myrmecochory (Ant)
	Z	Zoochory (Animal)

Table 8.2. Key to the classification of plant species in relation to fire responses (mode of regeneration) (reproduced from Gill (1993))

-
- 1 (a) Plants in vegetative state not exposed to fires
 - 2 (a) Seeds or spores or other dormant propagules in soil are not exposed to fires
(**fire avoiders**)
 - 2 (b) Seeds or spores or other dormant propagules in soil are exposed to fires
 - 3 (a) life cycle associated with fire occurrence (**fire ephemerals**)
 - 3 (b) life cycle usually 'independent' of fire occurrence (e.g. some **annuals**)
 - 1 (b) Plants in vegetative state exposed to fires
 - 4 (a) **Annuals**
 - 4 (b) **Perennials**
 - 5 (a) Reproductive plants subject to 100% leaf scorch die (non-sprouters or seeders)
 - 6 (a) seed storage on plant (scrotinous seeders) (I)
 - 6 (b) seed storage in soil (II)
 - 6 (c) no seed storage in burnt area (III)
 - 5 (b) Reproductive plants subject to 100% leaf scorch survive (**sprouters**)
 - 7 (a) subterranean regenerative buds present (or induced)
 - 8 (a) recovery from root suckers, or horizontal rhizomes (IV)
 - 8 (b) recovery from basal stem sprouts (V)
 - 7 (b) aerial regenerative buds present
 - 9 (a) epicormic buds grow out (VI)
 - 9 (b) large pre-fire apical buds continue growth (VII)

Categories I-VII are based on the methods of regeneration of a population of plants after a single fire has killed all the leaves of the reproductively mature plants. The key can apply to herbaceous perennials, but categories I and VI apply only to woody plants.

Table 8.3 Effect of time since fire on the frequency of plant traits. An asterisk indicates a significant association between age class and categories within plant traits: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Plant trait	G	df
Life-history	7.34 *	2
Juvenile period	0.87	4
Plant longevity	25.5 ***	6
Life-form	5.95	8
Maximum plant height	4.37	6
Mode of regeneration (6 categories)	28.8 **	10
Mode of regeneration (3 categories)	2.09	4
Conditions for establishment	4.94	4
Flowering season	0.20	6
Fruit type	1.37	4
Propagule size (maximum length)	4.62	4
Serotiny	0.11	2
Seed dormancy	0.45	2
Mode of dispersal	2.87	8

Table 8.4. Biological traits and categories for all species recorded during the study. All data are from this study, except where noted as a superscript. *Life-history*, A: annual; P: perennial. *Juvenile period (years)* followed by code in brackets, 1: 0-2; 2: 3-4; 3: 5-6. *Plant longevity (years)* followed by code in brackets, 1: 0-1; 2: 2-6; 3: 7-22; 4: >23. *Life-form*, Tr: tree; S: shrub; Tw: twiner; FG: forb/geophyte; Gr: graminoid. *Maximum plant height (m)* followed by code in brackets, 1: 0-0.3; 2: 0.4-1.0; 3: 1.1-2.5; 4: 2.6-8.0. # indicates where maximum height given in Walsh (1994), Walsh (1996) and Walsh (1999) has been adjusted upwards based on data from this study. *Mode of regeneration*, OS: obligate seeder; OR: obligate resprouter; FR: facultative resprouter. ^a based on data collected during this study >20 replicate plants; ^b based on data collected during this study (<20 replicate plants); ^c based on records of studies contained within the National Fire Response Register established by Gill (1992); ^d based on data collected during this study (<20 replicate plants) and records of studies contained within the National Fire Response Register; ^e based on general knowledge of species biology. *Conditions for establishment*, T: tolerant; I: intolerant; R: requires pre-conditions to be met before establishment. *Flowering season*, Su: summer; A: autumn; W: winter; Sp: spring; All: all seasons. *Fruit type*, D: dehiscent; I: indehiscent; F: fleshy. *Propagule size (maximum length in mm)* followed by code in brackets, 1: <1 mm; 2: 1-7 mm; 3: >7 mm. *Serotiny*, Y: yes; N: no. *Seed dormancy*, P: persistent (seed may remain viable in soil > 12 months); T: transient (seed lives < 12 months in soil). ^f seedling density significantly greater in smoke or heat-treated soil (Ch. 6 and 7), or seedling emergence after more than 12 months in the soil (Ch. 7). *Mode of dispersal*, U: unassisted; A: anemochory; B: ballistichory; M: myrmecochory; Z: zoochory. + indicates a gap in the data that I have filled in, and/or species for which age estimates have been increased based on life-history and life-form data. * indicates introduced species.

Species	Life-history ²⁷	Juvenile period (yrs)	Plant longevity (yrs)	Life-form ²⁷	Maximum plant height (m) ²⁷	Mode of regeneration	Conditions for establishment	Flowering season ²⁷	Fruit type	Propagule size (max. length, mm)	Serotiny	Seed dormancy	Mode of dispersal
<i>Acacia longifolia</i> var. <i>longifolia</i>	P	2 (1) ¹⁰	50 (4) ²⁸	S	1.5-10 (4)	OS ^a	I	W	D ^{21,27}	7-8 (3)	N	P ^{5,11,21,28}	M ²² , Z ⁶
<i>Acacia oxycedrus</i>	P	3 (2)	27 (4)	S	1.0-10 (4)	OS ^a	T	W, Sp	D ^{21,27}	5-6 (2)	N	P ²³	M ²²
<i>Acacia suaveolens</i>	P	1 (1) ³	25 (4) ^{3,10,20}	S	1.0-3.0 (4)	OS ^d	I	A, W, Sp	D ^{21,27}	7-9 (3)	N	P ^{2,5,8}	M ^{1,21}
* <i>Aira coryphyllea</i>	A	1 (1)	1 (1)	Gr	<0.4 (2)	OS ^d	T	Sp	I	2-4 (2) ²⁷	N		U
<i>Allocasuarina littoralis</i>	P	3 (2) ⁹	50 (4) ⁹	S	5.0-15 (4)	FR ^c	T ⁹	All	I ²⁷	4-10 (3) ²⁷	Y		A ²⁹
<i>Allocasuarina nitida</i>	P	3 (2)	26 (4)	S	0.5-2.5 (3) ⁹	FR ^c	I	All	I ²⁷	4-6 (2) ²⁷	Y		A ¹⁶
<i>Allocasuarina paludosa</i>	P	5 (3)	60 (4) ^{2,9}	S	0.3-3.0 (4)	FR ^c	T ²⁵	All	I ²⁷	3-5 (2) ²⁷	Y		A ⁹
<i>Allocasuarina parviflora</i>	P	5 (3)	19 (3)	S	0.5-2.0 (3)	FR ^c	I	All	I ²⁷	4-8 (2) ²⁷	Y		A ¹⁶
<i>Allocasuarina</i> sp.	P	2 (1)	25 (4)	S	<2.5 (3) ⁹	FR ^a	I	All	I ²⁷	4-6 (2)	Y	P ^f	A ¹⁶
<i>Amphipogon xiphocladus</i> var. <i>xiphocladus</i>	P	1 (1)	27 (4)	S	0.2-0.9 (2)	FR ^a	T	Sp	D ²⁷	2 (2)	N		M ¹³
<i>Amphipogon pendula</i> ssp. <i>pendula</i>	P	2 (1)+	27 (4)	S	1.5-5.0 (4) ⁹	OS ^c	R	All	F ²⁷	(2)	N		Z ^{10,21}
<i>Anisopogon avenaceus</i>	P	2 (1)	6 (2)	Gr	<1.3 (3)	FR ^d	I	Sp	I ²¹	(3)	N	P ⁷	A, Z ⁷
<i>Aotus ericoides</i>	P	3 (2) ⁶	60 (4) ¹⁰	S	<2.0 (3)	OR ^a	I	Sp	D ^{21,27}	3 (2) ²⁷	N	P ^{5,8,23}	M ²⁹
<i>Astiloma pinifolium</i>	P	3 (2)	27 (4)	S	0.2-1.0 (2)	OS ^a	T	Sp	F ^{21,27}	5-6 (2)	N		Z
<i>Austrodanthonia gracilicoma</i>	P	2 (1)+	23 (4)	Gr	<0.6 (2)	OR ^c	I	Sp	I ²¹	3-4 (2) ²⁷	N		A, Z
<i>Baccharis ramossissima</i> ssp. <i>prostrata</i>	P	3 (2)+	21 (3) ²⁶	S	0.1-0.2 (1)	OS ^d	I	W, Sp, Su	D ²⁷	(1) ²⁷	N		A ¹⁶ , M ¹
<i>Banksia marginata</i>	P	3 (2)	50 (4) ²⁵	S	<12 (4)	FR ^a	T	A, W	D ^{21,27}	5-8 (3) ²⁷	Y	T	A ^{12,21}
<i>Banksia serrata</i>	P	3 (2)	100 (4) ¹²	Tr	<16 (4)	FR ^a	T	Su, A	D ^{21,27}	10-12 (3) ²⁷	Y		A ^{12,21}
<i>Boronia anemonifolia</i> ssp. <i>anemonifolia</i>	P	3 (2)+	26 (4)	S	<2.5 (3)	OS ^c	I	Sp	D ²⁷	3 (2) ²⁷	N	P ²³	M ¹³ , B ²⁷
<i>Bassia cinerea</i>	P	2 (1)	27 (4)	S	<1.5 (3)	FR ^b	T	Sp	D ^{21,27}	2-4 (2)	N	P ²¹	M ¹³
<i>Bassia heterophylla</i>	P	2 (1)	27 (4)	S	<1.0 (2)	FR ^a	T	A	D ^{21,27}	3-4 (2)	N	P ^{5,8,23}	M ^{13,21}
<i>Bassia obcordata</i>	P	2 (1) ¹⁰	15 (3)+	S	<1.5 (3)	OR ^c	I	Sp	D ^{21,27}	2-3 (2)	N	P ^{5,12,21}	M ¹³
<i>Brachylaena daphnoides</i>	P	2 (1)	27 (4)	S	<2.0 (3)	OR ^a	I	Sp	F ²⁷	2 (2)	N		M ¹³ , Z ²⁹
<i>Cassia parviflora</i>	P	1 (1)+	10 (3) ²⁶	FG	<0.8 (2)	OR ^d	I	Sp	D ²⁷	1-2 (2) ²⁷	N		U
<i>Caladenia alata</i>	P	1 (1)+	27 (4)	FG	0.1-0.2 (1)	OR ^c	T	Sp	D ²⁷	(1) ²⁷	N		A
<i>Caladenia carneae</i> var. <i>carneae</i>	P	1 (1)+	27 (4)	FG	0.1-0.3 (1)	OR ^c	T	Sp	D ²⁷	(1) ²⁷	N		A
<i>Caladenia</i> sp.	P	1 (1)+	25 (4)	FG	<0.3 (1) ⁹	OR ^c	T	Sp	D ²⁷	(1) ²⁷	N		A
<i>Caleana major</i>	P	1 (1)+	27 (4)	FG	0.2-0.4 (2)	OR ^c	T	Sp, Su	D ²⁷	(1) ²⁷	N		A

Table 8.4. (continued) Biological traits and categories for all species recorded during the study.

Species	Life-history ³⁷	Juvenile period (yrs)	Plant longevity (yrs)	Life-form ³⁷	Maximum plant height (m) ³⁷	Mode of regeneration	Conditions for establishment	Flowering season ³⁷	Fruit type	Propagule size (max. length, mm)	Serotiny	Seed dormancy	Mode of dispersal
<i>Calochilus robertsonii</i>	P	1 (1)+	26 (4)	FG	0.2-0.5 (2)	OR ^a	T	Sp	D ^{13,37}	<1 (1)	N		A
<i>Calochilus</i> sp.	P	1 (1)+	27 (4)	FG	<0.4 (2) ^f	OR ^a	T	Sp	D ^{13,37}	(1) ³⁵	N		A
<i>Calystix tetragona</i>	P	3 (2)	27 (4)	S	0.5-3.0 (4)	OS ^a	T	Sp, Su	D ³¹	(2)	N	p ²⁵	A, Z
<i>Carpobrotus rossii</i>	P	2 (1)+	3 (2)	FG	<0.2 (1) ^f	OS ^c	I	All	D ³⁷	1-2 (2) ³⁷	N		U
<i>Cassytha glabella</i>	P	3 (2)	27 (4)	Tw	<3.0 (4) ^f	OS ^a	T	W, Sp	F ^{31,37}	3-5 (2) ³⁷	N		Z ²⁰
<i>Cassytha melantha</i>	P	4 (2)+	26 (4)	Tw	<4.0 (4) ^f	OS ^c	I	W, Sp	F ^{31,37}	3-7 (2)	N		Z
<i>Cassytha pubescens</i>	P	4 (2)+	27 (4)	Tw	<3.5 (4) ^f	OS ^c	I	Su	F ^{31,37}	4-5 (2)	N		Z ²⁰
<i>Causilis pentandra</i>	P	3 (2)+	27 (4)	Gr	<1.4 (3) ^f	OS ^a	T	Sp, Su	I ^{31,37}	4 (2)	N		U
<i>Coccoloba calymega</i>	P	2 (1)	9 (3)	S	<0.6 (2)	FR ^b	I	Sp, Su	D ³⁷	2 (2)	N	p ²⁵	A
* <i>Conyza</i> sp.	A	1 (1)	1 (1)	FG	<2.0 (3)	OS ^a	I	Sp, Su, A	I ³⁷	1-2 (2) ³⁷	N		A
<i>Correa reflexa</i> var. <i>speciosa</i>	P	2 (1)	26 (4)	S	<1.0 (2)	FR ^a	T	A, W, Sp	D ³⁷	2-4 (2) ³¹	N	p ¹⁵	B ³²
<i>Crassula sieberiana</i>	A	1 (1)	1 (1)	FG	<0.1 (1) ^f	OS ^a	I	Sp	D ³⁷	<1 (1)	N	p ²⁷	U
<i>Dampiera stricta</i>	P	1 (1)	26 (4)	S	<0.9 (2)	FR ^a	T	Sp, Su	I ³⁷	4-5 (2) ³⁷	N	p ^f	U
<i>Dillwynia glaberrima</i>	P	2 (1)	27 (4)	S	0.5-2.0 (3)	FR ^a	T	Sp, Su	D ^{31,37}	3 (2)	N	p ¹⁹	M ¹³
<i>Dillwynia sericea</i>	P	3 (2)	27 (4)	S	0.5-1.0 (2)	OS ^a	T	Sp	D ^{31,37}	(2)	N	p ^f	M ^{13,39}
<i>Drosera peltata</i>	P	1 (1)	25 (4)	FG	0.1-0.5 (2)	FR ^d	T	Sp, Su	D ³⁷	<1 (1) ¹⁷	N		U
<i>Epacris impressa</i>	P	1 (1)	27 (4)	S	<2.0 (3)	FR ^a	T	A, W, Sp	D ³⁷	(2)+	N	p ^{19,24,27}	A ¹⁶
<i>Eucalyptus</i> aff. <i>willisii</i> (Gippsland Lakes)	P	3 (2)	100 (4)+	Tr	<15 (4)	OR ^a	I	Sp	D ³¹	1 (2)	Y	T	U, A ¹⁶
<i>Eucalyptus viminalis</i> ssp. <i>pyramida</i>	P	6 (3)	100 (4)+	Tr	<15 (4)	OR ^a	I	Su	D ³¹	1-2 (2)	Y	T	U, A ¹⁶
<i>Eucalyptus viminalis</i> ssp. <i>pyramida</i> X	P	6 (3)	100 (4)+	Tr	<15 (4) ^f	OR ^c	I	Su, A	D	(2) ³²	Y	T	U, A ¹⁶
<i>Eucalyptus cephalocarpa</i>													
<i>Euchiton sphaericus</i>	A	1 (1)	1 (1)	FG	<1.0 (2)	OS ^d	I	Sp	I ³⁷	<1 (1) ³⁷	N	p ^f	A
<i>Genoplesium</i> sp. aff. <i>rujum</i>	P	1 (1)+	27 (4)	FG	0.1-0.3 (1)	OR ^c	T	Su, A	D ³⁷	<1 (1) ³⁷	N		A
<i>Glossodia major</i>	P	1 (1)+	27 (4)	FG	0.1-0.3 (1)	FR ^c	T	Sp	D ³⁷	<1 (1) ³⁷	N		A
<i>Gompholobium huegelii</i>	P	2 (1)	26 (4)	S	<1.0 (2)	FR ^a	I	Sp, Su, A	D ^{31,37}	2 (2)	N	p ²⁵	M
<i>Gonocarpus tetragynus</i>	P	1 (1)	2 (2)	FG	0.1-0.3 (1)	OS ^a	T	Sp, Su	I ³⁷	1 (2) ³⁷	N	p ²⁵	U
<i>Grevillea chrysaphaea</i>	P	3 (2)+	20 (3)+	S	0.3-2.5 (3)	OS ^b	I	W, Sp	D ^{31,37}	7-12 (3) ³¹	N	p ²⁵	U, A ¹⁶
<i>Hibbertia acicularis</i>	P	2 (1)	27 (4)	S	<0.6 (2) ^f	FR ^a	I	Sp	D ^{31,37}	2-3 (2)	N	p ²⁵	M
<i>Hibbertia fasciculata</i> var. <i>prostrata</i>	P	2 (1)	27 (4)	S	<0.6 (2) ^f	OS ^a	T	Sp	D ^{31,37}	(2) ³⁷	N	p ²⁵	M
<i>Hibbertia riparia</i>	P	3 (2)+	60 (4) ⁹	S	<1.2 (3)	OR ^c	I	Sp	D ^{31,37}	(2) ³⁷	N	p ²⁵	M ³⁹
<i>Hibbertia virgata</i>	P	2 (1)	27 (4)	S	<1.5 (3)	FR ^a	T	Sp	D ^{31,37}	2 (2)	N	p ²⁵	M
* <i>Hypochaeris radicata</i>	P	1 (1)+	2 (2)	FG	0.1-0.8 (2)	FR ^d	T	Sp	I ³⁷	8-17 (3) ³⁷	N	p ²⁴	A ¹¹
<i>Hypolaena fastigata</i>	P	2 (1)	60 (4) ²⁰	Gr	0.2-0.6 (2) ^f	OR ^a	T	Sp	I ³⁷	(2)	N	p ^f	U
<i>Isotria medeoloides</i>	A	1 (1)	1 (1)	Gr	<0.1 (1)	OS ^a	I	Sp	I ³⁷	1 (1)	N	p ^{19,24}	U
<i>Laxmannia orientalis</i>	P	2 (1)	5 (2)	FG	<0.2 (1)	OS ^c	I	Sp	D ³⁷	2-3 (2) ³⁷	N	p ²⁵	U
<i>Lepidosperma canarum</i>	P	2 (1)+	16 (3)	Gr	0.2-0.6 (2)	FR ^a	I	Sp, Su	I ^{31,37}	3-4 (2) ³⁷	N		M ¹³
<i>Leptospermum continentale</i>	P	2 (1)	60 (4) ¹¹	S	<2.5 (3) ^f	OR ^a	I	Sp, Su	D ^{31,37}	2 (2)	Y	T	A ^{16,18} , M ¹
<i>Leptospermum myrsinoides</i>	P	2 (1)	60 (4) ¹³	S	<4.0 (4) ^f	FR ^a	T	Sp	D ^{31,37}	2 (2)	N	p ¹⁹	A ^{16,19} , M ¹
<i>Leucopogon ericoides</i>	P	2 (1)	27 (4)	S	0.3-2.0 (3)	OS ^a	T	Sp	F ^{31,37}	(2)+	N	p ^f	Z
<i>Leucopogon virgatus</i> var. <i>virgatus</i>	P	2 (1)	27 (4)	S	<0.6 (2) ^f	OR ^a	I	W, Sp	F ^{31,37}	(2)+	N		M ¹⁴ , Z
<i>Lomandra filiformis</i> ssp. <i>filiformis</i>	P	2 (1)+	25 (4)	Gr	0.1-0.4 (2)	OR ^c	I	Sp	D ^{31,37}	(2)	N		U
<i>Lomandra glauca</i>	P	2 (1)+	27 (4)	Gr	0.2-0.3 (1)	FR ^d	I	Sp	D ^{31,37}	(2)	N		U
<i>Lomandra longifolia</i>	P	1 (1)	27 (4)	Gr	0.3-1.0 (2)	OR ^a	I	Sp, Su	D ^{31,37}	2-5 (2)	N		U
<i>Monotoca scoparia</i>	P	2 (1)	27 (4)	S	<2.0 (3)	FR ^a	I	Su, A, W	F ³⁷	1-2 (2)	N		M ^{14,17} , Z ³⁹
<i>Persoonia juniperina</i>	P	3 (2)+	25 (4)	S	<2.0 (3)	FR ^c	I	Su	F ³⁷	7-8 (2)	N		Z

Table 8.4. (continued) Biological traits and categories for all species recorded during the study.

Species	Life-history ²⁷	Juvenile period (yrs)	Plant longevity (yrs)	Life-form ³⁷	Maximum plant height (m) ²⁷	Mode of regeneration	Conditions for establishment	Flowering season ³⁷	Fruit type	Propagule size (max. length, mm)	Serotiny	Seed dormancy	Mode of dispersal
<i>Pimelea linifolia</i> ssp. <i>linifolia</i>	P	2 (1)	26 (4)	S	<1.5 (3)	OS ^a	I	W, Sp, Su	F ¹¹	(2)+	N	P ^{12,13}	U
<i>Platysace ericoides</i>	P	2 (1)	27 (4)	S	<0.8 (2) ⁹	OS ^a	T	Sp	I ³⁷	(2)	N	P ²¹	U
<i>Poaceae</i> sp.	P	2 (3)+	23 (4)	Gr	<0.3 (1) ⁹	OS ^b	I	?	I	(2)+	N		U
<i>Poaceae</i> sp. 2	P	2 (1)+	27 (4)	Gr	<0.3 (1) ⁹	?	I	?	I	(2)+	N		U
<i>Poa sieberiana</i> var. <i>sieberiana</i>	P	2 (1)+	23 (4)	Gr	<0.8 (2)	FR ^d	I	Sp, Su	I ³¹	2-3 (2) ³⁷	N		U
<i>Preridium esculentum</i>	P	2 (1)+	27 (4)	S	0.3-2.5 (3)	OR ^a	I	Sp+	I+	(1)	N		A
<i>Pterostylis parviflora</i>	P	1 (1)+	27 (4)+	FG	0.1-0.2 (1)	OR ^a	I	A	D ³⁹	<1 (1) ³⁷	N		A
<i>Pterostylis</i> sp.	P	1 (1)+	27 (4)	FG	<0.1 (1) ⁹	OR ^a	T	A	D ³⁷	<1 (1) ³⁷	N		A
<i>Pyrrhichis nigricans</i>	P	1 (1)	27 (4)	FG	0.1-0.2 (1)	FR ^d	T	Sp	D ³⁷	<1 (1) ³⁷	N		A
<i>Rhizidoporum procumbens</i>	P	3 (2)+	15 (3)+	S	<0.4 (2)	OS ^b	I	Sp	D ³⁷	2 (2) ³⁷	N	P ²⁷	U
<i>Ricinocarpos platifolius</i>	P	2 (1) ⁹	19 (3)	S	1.0-3.0 (4)	FR ^d	I	W, Sp	D ³⁷	6-10 (3) ³⁷	N		M ^{13,14}
<i>Schoenus imbricatus</i>	P	2 (1)	15 (3)+	Gr	0.1-0.4 (2)	FR ^d	I	Sp, Su	I ³⁷	(2)	N		U
<i>Stylidium</i> sp. 2	P	1 (1)	23 (4)	FG	0.2-1.0 (2)	FR ^d	I	Sp, Su	D ^{31,37}	1 (2)	N	P ²¹	U
<i>Tetraloche pilosa</i> ssp. <i>latifolia</i>	P	2 (1)	23 (4)	S	<0.6 (2)	OR ^a	I	Sp	D ³⁷	3 (2) ³⁷	N	P ²²	M ^{13,14}
<i>Thelionema</i> sp.	P	1 (1)+	5 (2)+	FG	<0.9 (2)	FR ^d	I	Sp, Su	D ³⁷	3-4 (2) ³⁷	N		U
<i>Thyridomene micrantha</i>	P	2 (1)	25 (4)	S	0.5-3.0 (4) ⁹	OS ^a	T	Sp	D ³⁷	(2)	N	P ¹	A
* <i>Vulpia bromoides</i>	A	1 (1)	1 (1)	Gr	<0.5 (2)	OS ^d	I	Sp, Su	I	5-9 (3) ³⁷	N	P ^{27,33}	U
<i>Wahlenbergia gracilenta</i>	A	1 (1)	1 (1)	FG	<0.3 (1) ⁹	OS ^d	T	Sp	D ^{31,37}	(1)	N	P ¹⁹	U
<i>Xanthorrhoea australis</i>	P	1 (1)	100 (4) ¹⁷	S	<3.0 (4)	OR ^a	I	W, Sp	D ^{31,37}	7-9 (3)	N		M ¹
<i>Xanthorrhoea minor</i> ssp. <i>lutea</i>	P	1 (1)+	23 (4)	Gr	<1.0 (2) ⁹	OR ^a	I	Sp, Su, A	D ^{31,37}	(2)	N		U
<i>Xanthosia pilosa</i>	P	2 (1)+	27 (4)	S	<0.7 (2)	FR ^a	T	Sp, Su, A	I ³⁷	2-3 (2) ³⁷	N		M ^{13,14}
<i>Zieria veronicaea</i>	P	3 (2)	27 (4)	S	<0.6 (2)	OS ^a	T	Sp	D ³⁷	3 (2)	N	P ²¹	B ³⁷

Data sources: ¹ (Andersen & Ashton 1985); ² (Auld 1986); ³ (Auld & Myerscough 1986); ⁴ (Auld 1987); ⁵ (Auld & O'Connell 1991); ⁶ (Auld 1996); ⁷ (Auld *et al.* 2000); ⁸ (Bell 1999); ⁹ (Benson & McDougall 1995); ¹⁰ (Benson & McDougall 1996); ¹¹ (Benson & McDougall 1998); ¹² (Benson & McDougall 2000); ¹³ (Berg 1975); ¹⁴ (Berg 1981); ¹⁵ (Blombery & Maloney 1994); ¹⁶ (Clifford & Drake 1981); ¹⁷ (Curtis 1998); ¹⁸ (Duigan 1992); ¹⁹ (Enright & Kintrop 2001); ²⁰ (French & Westoby 1996); ²¹ (Gill 1993); ²² (Hammill *et al.* 1998); ²³ (Keith 1996); ²⁴ (Kintrop & Enright 1999); ²⁵ (Kruger 1983); ²⁶ (Ladd 1988); ²⁷ (Marsden-Smedley *et al.* 1997); ²⁸ (McCarthy & Tolhurst 1997); ²⁹ (McMahon 1984b); ³⁰ (Morrison *et al.* 1983); ³¹ (Ralph 1994); ³² (Rice & Westoby 1981); ³³ (Roberts 1986a); ³⁴ (Roberts 1986b); ³⁵ (Roche *et al.* 1997a); ³⁶ (Russell & Parsons 1978); ³⁷ (Walsh & Entwisle 1994; Walsh & Entwisle 1996; Walsh & Entwisle 1999); ³⁸ (Weiss 1984); ³⁹ (Westoby *et al.* 1990).

Table 8.5 Number of species found in every category of each plant trait in relation to site age (young: 0-6 years; intermediate: 9-19 years; old: 23-27 years).**a. Life-history, $n = 94$**

Site age	Life-history	
	Annual	Perennial
Young	6	67
Intermediate	0	56
Old	2	63

b. Juvenile period, $n = 94$

Site age	Juvenile period (years)		
	0-2	3-4	5-6
Young	55	16	4
Intermediate	41	14	3
Old	49	16	2

c. Plant longevity, $n = 94$

Site age	Plant longevity (years)			
	0-1	2-6	7-22	23+
Young	6	6	9	54
Intermediate	0	2	4	52
Old	2	1	0	64

d. Life-form, $n = 94$

Site age	Life-form				
	Tree	Shrub	Twiner	Forb/geophyte	Graminoid
Young	4	43	1	17	10
Intermediate	3	38	3	6	8
Old	3	37	3	13	11

e. Maximum plant height, $n = 94$

Site age	Maximum plant height (m)			
	0-0.3	0.4-1.0	1.1-2.5	2.6-8.0
Young	12	28	19	14
Intermediate	4	23	14	15
Old	12	25	15	15

Table 8.5 (continued) Number of species found in every category of each plant trait in relation to site age (young: 0-6 years; intermediate: 9-19 years; old: 23-27 years).f. Mode of regeneration (3 categories), $n = 94$

Site age	Mode of regeneration		
	OS	OR	FR
Young	27	17	29
Intermediate	16	15	25
Old	20	21	25

g. Mode of regeneration (6 categories), $n = 93$

Site age	Mode of regeneration					
	OS	OR	FR	Fire avoider	Fire ephemeral	Annual
Young	18	21	15	6	10	3
Intermediate	16	25	12	3	0	0
Old	18	23	13	10	0	2

h. Conditions for establishment, $n = 94$

Site age	Conditions for establishment		
	Tolerant	Intolerant	Require pre-conditions
Young	37	37	1
Intermediate	35	22	1
Old	44	22	1

i. Flowering season, $n = 92$

Site age	Flowering season			
	Summer	Autumn	Winter	Spring
Young	31	20	19	64
Intermediate	23	15	16	50
Old	25	16	15	55

j. Fruit type, $n = 94$

Site age	Fruit type		
	Dehiscent	Indehiscent	Fleshy
Young	48	18	8
Intermediate	35	12	10
Old	40	15	11

k. Propagule size (maximum length), $n = 94$

Site age	Propagule size (maximum length, mm)		
	0-1	2-7	8+
Young	12	54	9
Intermediate	4	48	6
Old	12	50	5

l. Serotiny, $n = 94$

Site age	Serotiny	
	Yes	No
Young	10	65
Intermediate	8	50
Old	9	58

m. Seed dormancy, $n = 47$

Site age	Seed dormancy	
	Persistent	Transient
Young	40	6
Intermediate	27	5
Old	26	5

n. Mode of dispersal, $n = 94$

Site age	Mode of dispersal				
	Unassisted	Anemochory	Ballistichory	Myrmecochory	Zoochory
Young	25	27	2	24	9
Intermediate	14	18	2	22	10
Old	18	25	3	19	12

Table 8.6 Key to species codings used in Figure 8.1.

Species code	Species
ACLO	<i>Acacia longifolia</i> var. <i>longifolia</i>
ACOX	<i>Acacia oxycedrus</i>
AICA	<i>Aira caryophyllea</i>
ALLI	<i>Allocasuarina littoralis</i>
ALMI	<i>Allocasuarina misera</i>
ALPA	<i>Allocasuarina paludosa</i>
AMXI	<i>Amperea xiphoclada</i> var. <i>xiphoclada</i>
AMPE	<i>Amyema pendula</i> ssp. <i>pendula</i>
ANAV	<i>Anisopogon avenaceus</i>
ASPI	<i>Astroloma pinifolium</i>
AUGE	<i>Austrodanthonia geniculata</i>
BARA	<i>Baeckea ramosissima</i> ssp. <i>prostrata</i>
BAMA	<i>Banksia marginata</i>
BASE	<i>Banksia serrata</i>
BOAN	<i>Boronia anemonifolia</i> ssp. <i>anemonifolia</i>
BOCI	<i>Bossiaea cinerea</i>
BOHE	<i>Bossiaea heterophylla</i>
BOOB	<i>Bossiaea obcordata</i>
BRDA	<i>Brachyloma daphnoides</i>
CAPA	<i>Caesia parviflora</i>
CAAL	<i>Caladenia alata</i>
CACA	<i>Caladenia carnea</i> var. <i>carnea</i>
CAIA	<i>Caladenia</i> sp.
CAMA	<i>Caleana major</i>
CALO	<i>Calochilus</i> sp.
CATE	<i>Calytrix tetragona</i>
CARO	<i>Carpobrotus rossii</i>
CAGL	<i>Cassytha glabella</i>
CAPE	<i>Caustis pentandra</i>
COSP	<i>Conyza</i> sp.
CORE	<i>Correa reflexa</i> var. <i>speciosa</i>
CRSI	<i>Crassula sieberiana</i>
DAST	<i>Dampiera stricta</i>
DIGL	<i>Dillwynia glaberrima</i>
DISE	<i>Dillwynia sericea</i>
DRPE	<i>Drosera peltata</i>
EPIM	<i>Epacris impressa</i>
EUWI	<i>Eucalyptus</i> aff. <i>willisii</i> (Gippsland Lakes)
EUVI	<i>Eucalyptus viminalis</i> ssp. <i>pryoriana</i>
EUVX	<i>Eucalyptus viminalis</i> ssp. <i>pryoriana</i> X <i>Eucalyptus cephalocarpa</i>
EUSP	<i>Euchiton sphaericus</i>
GOHU	<i>Gompholobium huegelii</i>
GOTE	<i>Gonocarpus tetragynus</i>
GRCH	<i>Grevillea chrysophaea</i>
HIAC	<i>Hibbertia acicularis</i>
HIFA	<i>Hibbertia fasciculata</i> var. <i>prostrata</i>

Table 8.6 (continued) Key to species codings used in Figure 8.1.

Species code	Species
HIRI	<i>Hibbertia riparia</i>
HIVI	<i>Hibbertia virgata</i>
HYFA	<i>Hypolaena fastigiata</i>
ISMA	<i>Isolepis marginata</i>
LAOR	<i>Laxmannia orientalis</i>
LECO	<i>Leptospermum continentale</i>
LEMY	<i>Leptospermum myrsinoides</i>
LEER	<i>Leucopogon ericoides</i>
LEVI	<i>Leucopogon virgatus</i> var. <i>virgatus</i>
LOLO	<i>Lomandra longifolia</i>
MOSC	<i>Monotoca scoparia</i>
PEJU	<i>Persoonia juniperina</i>
PILI	<i>Pimelea linifolia</i> ssp. <i>linifolia</i>
PLER	<i>Platysace ericoides</i>
POSI	<i>Poa sieberiana</i> var. <i>sieberiana</i>
PTES	<i>Pteridium esculentum</i>
PTPA	<i>Pterostylis parviflora</i>
PTSP	<i>Pterostylis</i> sp.
PYNI	<i>Pyrorchis nigricans</i>
RHPR	<i>Rhizidiosporum procumbens</i>
SCIM	<i>Schoenus imberbis</i>
STSP	<i>Stylidium</i> sp. 2
TEPI	<i>Tetratheca pilosa</i> ssp. <i>latifolia</i>
THSP	<i>Thelionema</i> sp.
THMI	<i>Thryptomene micrantha</i>
VUBR	<i>Vulpia bromoides</i>
XAAU	<i>Xanthorrhoea australis</i>
XAMI	<i>Xanthorrhoea minor</i> ssp. <i>lutea</i>
ZIVE	<i>Zieria veronicea</i>

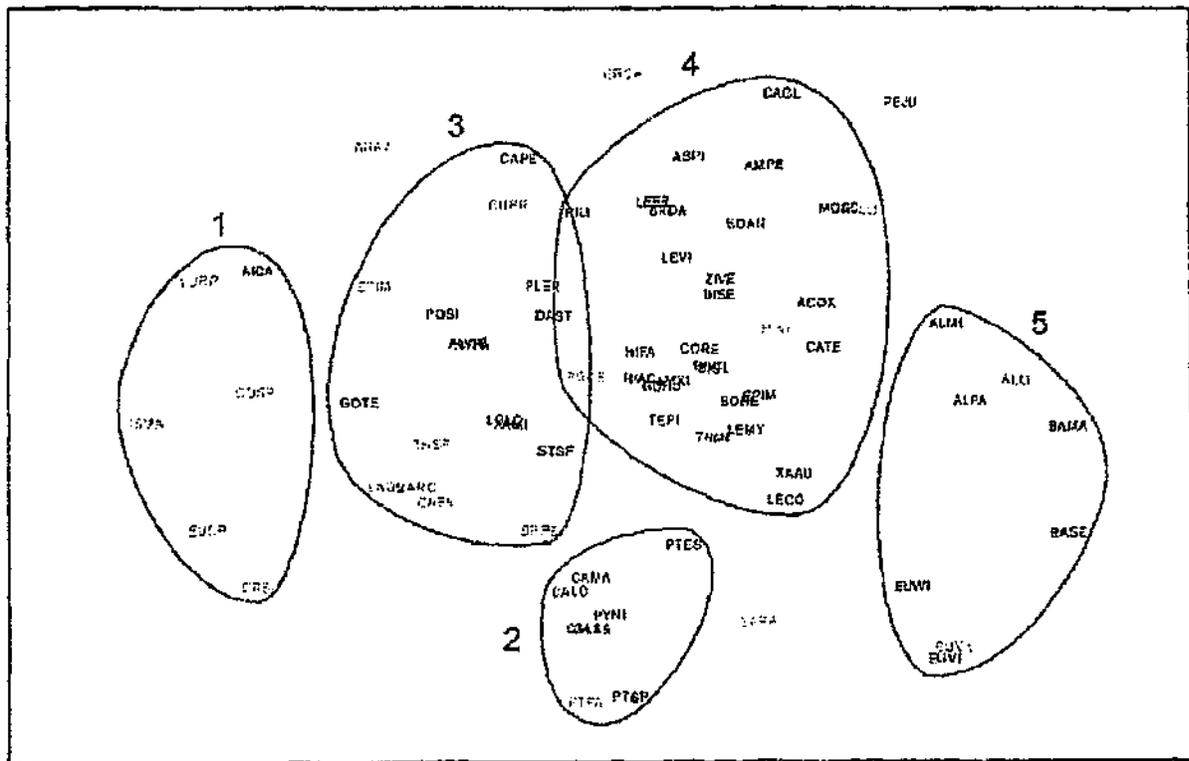


Figure 8.1 NMDS ordination of species according to plant attributes (stress = 0.23). Numbered groupings derived using the 55% similarity level from an hierarchical agglomerative clustering analyses (group average linkage). Species only occurring in young sites are coded red; species only occurring in old sites are coded green; species occurring in young, intermediate and old-aged sites are coded black. Refer to Table 8.6 for key to species coding.

CHAPTER 9

GENERAL DISCUSSION

This study has documented the post-fire succession in a sandy, lowland heathland in south-east Australia, in terms of both the vegetation and the soil seed bank. In addition, the biological traits of each species have been assessed to determine the characteristics of early successional versus late successional species. These traits influence the dispersal, establishment and persistence capabilities of individual species through successional time.

The results of this study are significant on a number of fronts. First, this is the most comprehensive chronosequence study of Australian heathlands, in terms of the number of post-fire ages sampled (13), and the attention paid to validating the design using environmental data, soil profiles, and soil chemical and physical analyses. Second, in addition to standard vegetation parameters such as species richness, diversity and composition that are often assessed in heathlands, community heterogeneity, vertical structure and evenness were quantified to gain a broader overview of how the heath was changing with successional age. These three characteristics have rarely been quantified in Australian heathlands, although some studies have examined vegetation structure but in a different manner (e.g. Specht *et al.* 1958; McMahon 1984b; McFarland 1988; Wark 1996). Third, six spatial grains, ranging from 1 m² to 4 ha, were sampled across all post-fire ages to determine the effect of sampling grain on trends in vegetation parameters with time since fire. There are only two other studies that I know of that have sampled multiple spatial scales in Australian heath-type vegetation: Brown (1983) in Western Australian kwongan, and Keith (1993) in upland swamp (sedge-heath) vegetation near Sydney. Neither of these studies covered the same breadth of spatial grains as this study. Fourth, this is the first study in Australian heathlands to examine the species composition, richness and seedling density of the soil seed bank in relation to time since fire. Finally, a range of important biological traits were assessed for each species in the heathland, to determine whether early successional species possessed a different set of traits from late successional or long-lived species, an analysis that has not been carried out in Australian heathlands before.

KEY FINDINGS

The main findings of the study are as follows:

Vegetation

- Species richness (total and mean) usually decreased significantly with increasing time since fire, however, both relationships were scale-dependent
- Species evenness (J) usually decreased significantly with increasing time since fire, however, the relationship was scale-dependent
- Species diversity (H) decreased significantly with increasing time since fire across all spatial grains
- Species composition usually differed significantly with time since fire, however, the relationship was scale-dependent
- Community heterogeneity did not usually differ significantly with increasing time since fire
- Overall vegetation cover increased rapidly until six to nine years after fire, after which it plateaued, then declined sharply at c. 25 years post-fire
- Total cover in each height class differed according to post-fire age, with vegetation in the 0-0.1 m, 0.2-0.3 m and 0.4-1.0 m height classes increasing and then decreasing with time since fire, and vegetation in the 1.1-2.5 m and 2.6-8.0 m height classes displaying a significant increase with time since fire
- Life-form richness was dominated by shrubs, however, graminoids were the only life-form to differ (decrease) significantly with time since fire

Soil seed bank

- Germinable species richness did not differ significantly with increasing time since fire
- Germinable seedling density did not differ significantly with increasing time since fire

- Germinable species composition differed significantly among age classes (presence/absence data), with the greatest difference existing between young and old sites
- The composition of the vegetation and the germinable soil seed bank did not differ significantly with increasing time since fire, however, there was a trend toward greater similarity with time since fire

Plant traits

- Five functional groups were identified: (1) annuals occurring in young sites, (2) geophytic orchids, (3) perennial forbs/geophytes and graminoids, (4) shrubs occurring in all age classes, and (5) serotinous trees and shrubs occurring across all age classes.
- Species occurring only in young sites were characterised by their intolerance to establishing in the presence of adult competition, and the unassisted mode of dispersal. Species occurring solely in old sites were characterised by their longevity, tolerance to establishing in the presence of adult competitors, wind-dispersal and obligate resprouting. Species that occurred in young, intermediate and old-aged sites were characterised by their longevity, intermediate propagule size, tolerance to establishing in the presence of adult competition and shrub life-form.

LIMITATIONS OF THE STUDY

This study has two main limitations that may influence the conclusions. First, the study sites could not be controlled for variability in fire regimes, since these were unknown. Consequently, for the purpose of this study, fire frequency, season and intensity were each assumed to be random among sites. However, this may not have always been the case. Second, results pertaining to trends with time since fire may have been influenced by the significant ^{positive} autocorrelation in terms of species composition that existed among sites. However, although sites that were closer together were compositionally more similar, this pattern may still be controlled by time since fire, given that recently burnt sites occurred close together. Furthermore, evidence is presented in Chapter 4 suggesting that time since fire has a greater influence on species composition than the distance between sites.

VEGETATION SUCCESSION IN THE SAND HEATHLAND

Regeneration strategy

Fire acts as the trigger that 'resets' the successional clock in the sandy heathlands of the Gippsland Lakes area in eastern Victoria. Heat from the fire, chemicals in smoke leached through the soil, and other fire-related by-products, act to break dormancy and induce germination in a range of obligate seeders and facultative resprouters (and a few obligate resprouters) that store seed in the soil. Evidence from the soil seed bank study (Chapters 6 and 7) and field observations suggest that all species regenerate within the first year following fire, a phenomenon commonly reported elsewhere (Bell *et al.* 1984; Benwell 1998) and consistent with the Initial Floristic Composition model of succession (Egler 1954). In addition, heat also acts to trigger mass seed release from canopy-stored fruits in serotinous species (Lamont *et al.* 1991; Enright *et al.* 1998), although seeds may be gradually released in the inter-fire period as dehiscence occurs upon dehydration of the woody fruit (Gill & Groves 1981). In contrast to seed germination, fire induces many species to resprout, either facultatively or obligately, from underground lignotubers, rootstocks, rhizomes, bulbs and tubers, and epicormic buds located on tree trunks (Specht 1979b; Gill 1981a). In this study, the number of species categorised in each of the three modes of regeneration was very similar, suggesting that no one strategy dominated in the heath. Although the mode of regeneration is generally viewed as a highly important factor influencing the establishment and continued survival of species, it appears to be unrelated to the occurrence of species in particular age classes (young, old, young/intermediate/old) in this study.

Seed dispersal

The mode by which species disperse propagules is another important factor influencing the dynamics of the heathland. Approximately half of the species in the heath appear to have a maximum dispersal distance of *c.* 15 m (Berg 1981; Westoby *et al.* 1982), as their mode of dispersal is either unassisted, ballistic or by ants. Such a distance appears to be quite small, however, it is still large enough for species to gradually increase their range, given that they are able to establish and persist successfully. The unassisted mode of dispersal may be beneficial for both seeders and sprouters. Seeders will deposit seed (usually persistent) immediately below the parent plant, which will presumably

germinate following fire. The resultant high seedling density should ensure that the patch is re-occupied by the same species as the heath increases in age. Conversely, obligate resprouters may not require an elaborate dispersal mechanism, as they rarely regenerate from seed. Almost 30% of species in the heath were adapted for ant-dispersal, with the primary benefit of this being seed burial, which reduces post-dispersal seed predation and helps shield the seed from death-inducing temperatures at the surface during fire (Berg 1981; Keeley 1995).

Half of the species in the heath were adapted for long-distance dispersal by either wind or animal (via ingestion or external adhesion). However, it is difficult to ascertain whether in fact species were dispersing into the heath following fire and if so, what proportion of propagules were dispersed in this way (as opposed to simply dropping to the ground beneath the parent plant) and what distances were involved. Clearly, these species have a greater chance of increasing their geographical range in a relatively quick manner compared with species that are dispersed over short distances. However, Keith (2002) and Whelan (2002) indicate that long-distance dispersal and subsequent colonisation from outside of burnt areas is uncommon in fire-prone Australian vegetation, particularly heathlands. Following fire, the reduction or virtual elimination of all live plant cover allows for greater wind speeds in burnt areas, ensuring more effective wind dispersal of canopy-stored seed released in the months after fire (Whelan 1986; Hammit *et al.* 1998). However, the bird-dispersed parasitic mistletoe, *Amyema pendula* ssp. *pendula* was the only species known to be totally reliant on seed dispersal into a site following fire, as any seed present at the time of fire would probably be consumed. In addition, there may be no suitable substrates (eucalypt branches) for the seed to lodge on following the passage of fire.

Post-fire environment

In addition to its promotive effect on seed germination and regeneration via resprouting, fire creates an environment that is favourable for the establishment of many species. This post-fire environment is characterised by greater light availability (Specht & Specht 1989; Keith & Bradstock 1994), increased nutrient availability in the first year after fire (Specht 1979b; Humphreys & Craig 1981; Adams *et al.* 1994), reduced resource competition (Specht & Specht 1989; Keith & Bradstock 1994), reduced herbivory (away from the fire boundary) (Whelan 1986; Tyler 1995) and the potential elimination

(through combustion) of root pathogens (Specht 1979b) and phytotoxins that are inhibitory to seedling establishment and plant growth (Gill & Groves 1981; Hobbs 1984; Keeley *et al.* 1985; Reigosa *et al.* 1999). The mass release of seed from serotinous species following fire also acts to satiate seed predators and seedling herbivores, giving the best possible opportunity for seeds to germinate and establish (O'Dowd & Gill 1983). Despite the obvious benefits of the post-fire environment, increased soil heating due to a decrease in plant cover (Odion & Davis 2000), reduced water retention as a result of litter layer combustion (Moreno & Oechel 1992) and the potential for serious droughts (Whelan 1986), may impact negatively upon seed germination and seedling survival.

Post-fire ephemerals

In the first few years following fire, a number of ephemeral species are present in the heath, however, it is unknown whether these species are actually true post-fire ephemerals that are dependent on fire for germination, or simply effective colonisers of disturbed ground. The majority of the potentially post-fire ephemeral species recorded in this study are herbaceous, short in stature, spring flowering, obligate seeders that possess persistent soil seed banks, an unassisted mode of dispersal and are intolerant to establishing in the presence of adult competition. The nature of seed dispersal in these species, together with information in the literature relating to seed dormancy, suggests that eight of the 10 post-fire ephemerals recorded in this study possess a highly dormant seed fraction that is very long-lived. This finding supports the hypothesis of Whelan (1986) that short-lived species in frequently burnt areas will possess long-lived seeds, rather than adaptations for long-distance dispersal. In contrast, two of the species, *Anisopogon avenaceus* and *Euchiton sphaericus*, appear to be adapted for long-distance dispersal and may re-colonise burnt sites, rather than persisting in the soil for extended time periods.

Although post-fire ephemerals comprised 11% of the species recorded across the entire study area, they were extremely uncommon, possessing less than 0.1% of the total vegetative cover in recently burnt sites. This concurs with some other Australian heathlands, which appear to have a low incidence of post-fire ephemerals (Russell & Parsons 1978; Specht 1994; Cheal 1996). However, heathlands in the Grampians and at Anglesea in western Victoria differ in that they possess a large number of post-fire

ephemerals. Enright (1994) found that sand heathland sites under two years of age were clearly different in composition to sites burnt 3-24 years ago, mainly owing to the presence of 19 fire ephemeral species. Furthermore, Wark (1996) found that 25% of species recorded in the first year following fire in coastal heathland were not present in quadrats sampled three years after fire, implying a substantial change in community composition with successional age.

Changes in species richness, diversity, evenness, composition, community heterogeneity and structure

Species richness and diversity peaked in the first year following fire and gradually decreased as time since fire increased, however, the decrease in richness was dependent upon the grain sampled. For example, at the 100 m², 900 m² and 1 ha grains, total richness decreased significantly with time since fire, however, at the 4 ha (site) scale no trend was observed. The scale-dependence of this relationship suggests that the distribution of some species was becoming increasingly patchy with time since fire as individuals began to die off, to the point where they were becoming absent from smaller grains but still present at the scale of the entire site. Whether this increasing patchiness is reflected in the composition and density of the soil seed bank is uncertain, owing to the paucity of data on the longevity of species soil seed banks (Auld *et al.* 2000). However, any increase in the patchiness of above-ground species distributions should be followed by a lag in soil seed bank patchiness, as most species (87% of those with available data) possess persistent seed. This finding has important implications for heathland management, as observed trends are clearly scale-dependent. Therefore, managers need to be wary of extrapolating up or down from studies conducted at a single spatial scale, as this may lead to misleading information on changes in heath richness with successional time.

As time since fire increased, total vegetative cover increased rapidly to *c.* 70% after 6-9 years in what may be described as the building phase (Barclay-Estrup & Gimingham 1969). By this stage, all post-fire ephemerals had died out, and all species had reached reproductive maturity and were producing seed. After this initial growth phase, the heath entered the 'mature' phase, where total cover stabilised at *c.* 75-85% until 25 years after fire. During this stage, total cover in each of the lower height classes (<1 m) reached a maximum and then began to decrease. The decrease was most likely due to

increased competition for light, which resulted in a greater amount of photosynthetic tissue being allocated to the upper height classes (at the expense of the lower) as the heath aged. The decrease was not due to senescence of ground layer species, as their contribution to total cover was relatively minor. Conversely, cover in the upper height classes (>1 m) displayed a continual increase, owing to the growth of large shrubs and trees such as *Allocasuarina* spp., *Banksia* spp., *Eucalyptus* spp., *Leptospermum myrsinoides* and *Monotoca scoparia*.

Leptospermum myrsinoides is clearly the dominant species throughout the heath in terms of total vegetative cover, which ranges from 34-54% in intermediate and old-aged sites. It quickly dominates the heath, reaching a cover of 27% only 18 months after fire, largely due to prolific resprouting from underground basal buds. In addition, *L. myrsinoides* establishes in large numbers from the soil seed bank, and is the only species to record an increase in germinable seedling density with increasing time since fire. This is probably due to increased seed production from larger individuals in older heath, plus the long-term storage of persistent seed in the soil, as *L. myrsinoides* seed was found to respond extremely well to smoke and heat treatments. These characteristics of *L. myrsinoides*, in addition to its comparatively fast growth rate, relatively long lifespan, tall stature, and dispersal by both wind (long distances) and ants (germination benefits associated with seed burial) suggest that as the heath increases in age, dominance may become even more pronounced.

Influence of overstorey species

The decrease in species richness at certain spatial scales with time since fire may have been caused by a number of factors, possibly acting together. First, the loss of post-fire ephemerals probably contributed to the initial decline in species richness. Second, the increase in overstorey cover with time since fire and the subsequent reduction in light availability to understorey species, as suggested by Specht (1989) and Cowling (1990), may have led to the death of shade-intolerant understorey species. Evidence to support this assertion is found in the significant decrease in subshrub richness with time since fire.

Finally, resource competition for scarce water and nutrients, and the potential allelopathic effects of certain species may exclude others from the heath (Vila &

Sardans 1999). For example, in areas of coastal heath dominated by *Eucalyptus Baxteri*, del Moral (1978) showed that the zone of plant suppression beneath the canopy was due to the allelopathic ability of the eucalypt. A similar pattern appears to be evident in the heath examined in this study, where a zone of suppression exists immediately surrounding the base of eucalypts. However, the cause of this suppression is unknown. Certain species such as *Amperea xiphoclada*, *Bossiaea cinerea*, *Correa reflexa* var. *reflexa*, *Dampiera stricta*, *Lomandra longifolia* and *Poa sieberiana* var. *sieberiana* appear to be unaffected and may actually thrive in this environment, a finding also reported by del Moral (1978). As time since fire increases, this phenomenon appears to intensify, resulting in the creation of local patches of mallee-form eucalypts with a species-poor understorey. However, the number of these patches within the heath is not predicted to increase, owing to the obligate resprouting nature of the eucalypts and the extreme lack of recruitment observed during the study across a number of recently burnt sites.

A similar effect also occurs beneath the dense canopy of *Banksia serrata* individuals, the tallest species in the heath. During the inter-fire period, juvenile plants and root suckers commonly establish around the base of mature individuals, assisting in the formation of dense (>80% foliage cover) *B. serrata* groves, with an extremely depauperate understorey. Where allelopathy may have been a factor influencing species composition beneath the eucalypts, shading appears to be the major factor excluding species from beneath *B. serrata* individuals. In addition, the dense (100% cover) and thick (up to 10 cm deep) litter layer probably acts as a highly effective barrier preventing seed of other species from dispersing onto the soil beneath the canopy (Facelli & Pickett 1991). Consequently, seedling density is low immediately beneath *B. serrata* individuals, even in the immediate post-fire environment. Thus, as the interval between fires increases, there is anecdotal evidence to suggest that *B. serrata* actively excludes species from beneath its canopy and increases its range by establishing new seedlings outside of the existing canopy.

Recruitment between fires

Recruitment outside of the initial 'window of opportunity' in the first year after fire is relatively uncommon in the heathland. Although c. one third of all species were observed to be tolerant to establishing in the presence of adult competition, there was

little evidence to suggest that individuals arising after the initial post-fire period reached reproductive maturity, apart from *B. serrata* (seedlings and basal sprouts), *B. marginata* (occasional root suckers) and a number of herbaceous species (particularly geophytic orchids). Whelan (1998) also reported recruitment during the inter-fire period for *B. serrata*, however, the degree of recruitment during this time varied substantially among populations and habitats. The lack of recruitment in mature vegetation found in this study is not uncommon in Australian heath, with Specht (1958), Russell (1978), Wark (1996) and Keith (2002) all reporting similar results. However, Cheal (2000) reported an increase in establishment and species richness in semi-arid heath with increasing time since fire. In the Californian chaparral, seedling recruitment does occur in older stands (Patric & Hanes 1964), however, this is minimal and there is little evidence that saplings reach the canopy (Keeley 1992a; Keeley 1992b). Instead, resprouting appears to be the dominant mode of regeneration in senescent chaparral (Keeley 1992b). As the chronosequence in this study spanned 27 years, it is not possible to determine whether recruitment will increase in older vegetation as the heath begins to die back and light-availability subsequently increases, or whether the heavy build up of litter, with its associated allelopathic substances (Facelli & Pickett 1991), would inhibit seed germination and seedling growth.

Vegetation succession

Many studies in Australian heath suggest that succession follows the 'Initial floristic composition' model of vegetation development (Russell & Parsons 1978; Groves & Specht 1981; Bell *et al.* 1984; McFarland 1988; Wark 1996), where species present later in the succession are a subset of those present initially after disturbance (Egler 1954). In this model, changes in species dominance are essentially due to the varying growth rates and plant longevities of the species present at the time of disturbance, rather than the invasion of new species (Egler 1954). However, there is substantial evidence indicating that some Australian heathlands are invaded by different species after the initial post-fire period. For example, *Leptospermum laevigatum*, *Kunzea ambigua* and *Acacia longifolia* var. *sophorae* have been shown to invade coastal heathlands and form dense thickets across a range of sites in Victoria, probably owing to fire regimes that have been altered following European settlement (Parsons 1966; Burrell 1981; Molnar *et al.* 1989; Offor 1990; Bennett 1994; McMahon *et al.* 1996). McMahon (1996) also suggest

that invasions by species such as these may substantially alter species composition of these heathlands, as species are excluded and soil seed banks become increasingly unviable with successional time. Semi-arid heathlands in south-east Australia are also subject to invasion by *Callitris* spp. following death of the *Banksia ornata* dominated overstorey through old age or frost damage (McMahon 1984b; Cheal 1996; Cheal 2000). This led Cheal (1996) to conclude that the *B. ornata* heathlands do not reach a climax (unchanging) state. Plant dieback, especially due to the root pathogen, *Phytophthora cinnamomi*, may also substantially alter the composition and relative dominance of different species in heath communities (Kennedy & Weste 1986; Weste & Kennedy 1997).

Unlike some of the heathlands just mentioned, this study provided no evidence to suggest that species were invading the heath at any of the study sites. This apparent lack of invasive species may be due to the inability of such species to tolerate the extremely low nutrient availability of the sandy soils within the study area. Alternatively, fire regimes within the study area may not have been altered as much as those in other areas. Finally, the heathlands at Wilson's Promontory are much more fragmented and dissected than the heath examined in this study. Therefore, there may be greater 'edge effects' in the Wilson's Promontory heathlands, rendering them more susceptible to invasion by species in neighbouring plant communities. Owing to the lack of invasion in the heath examined in this study, succession appeared to correspond well with Egler's 'Initial floristic composition' model, although the mechanism(s) by which species inhibit invasion is poorly known. Even though the heath fits the Initial floristic composition model of succession, there is still considerable scope for the composition and structure of the heath to change in accordance with different fire regimes, with fire frequency likely to have the greatest effect on heath composition and structure (Cary & Morrison 1995; Morrison *et al.* 1995; Bradstock *et al.* 1997).

As time since fire increased, the height of the shrub stratum increased to the point where the heath became a scrub after *c.* 25 years, in the strict sense of the definition given by Specht (1970). Furthermore, as the inter-fire period increases, the likelihood of *B. serrata* recruitment increases, and the potential for this species to become more dominant is enhanced. Under such conditions, there is a possibility that the heath could gradually convert in structure to heathy woodland, given sufficient time, although this

study reported no significant trend of increasing tree cover with time since fire. Under the prolonged absence of fire in the heath, some obligate seeders would undoubtedly become locally extinct, as they require fire for new seedlings to establish before the persistent fraction of the soil seed bank is depleted. Conversely, high frequency fire regimes may impact on the composition and structure of the heath substantially, by eliminating some fire-sensitive (obligate seeder) shrub species (McMahon 1984a; Bradstock & Myerscough 1988; Cary & Morrison 1995; Morrison *et al.* 1995; Bradstock *et al.* 1997), increasing the abundance of resprouting species (Nieuwenhuis 1987), and possibly converting the heath to a more sedge-dominated system (Groves & Specht 1981; Bradstock *et al.* 1997).

MANAGEMENT IMPLICATIONS

In the mediterranean-type ecosystems of the world, fire is commonly used as a major ecological tool in vegetation management, with managers often facing the conflict of biodiversity conservation (Gill 1977) versus the protection of human life and resources (State of Victoria 1995). Even when the aims of fire management are for ecological purposes (compared with the protection of life and property), the specific management goals may be very different, and may include biodiversity conservation (van Wilgen *et al.* 1994), habitat manipulation for animal conservation (Meredith & Isles 1980; Day *et al.* 1999), land rehabilitation (Smith *et al.* 2000) and management of weed infestations (McMahon *et al.* 1996; Downey 1999). According to land managers, the heathland examined during this study has two main foci of burning: (a) fuel reduction for protection of human life and resources, and (b) maintenance of optimal habitat for the New Holland Mouse (*Pseudomys novaehollandiae*) (G. Hollis and L. Jeremiah pers. comm.). However, there is no fire management plan for biodiversity and plant community conservation, despite these being specific goals of park management (Parks Victoria 1998).

Implicit in any fire management plan is the concept of fire regime (Gill 1975). It appears that most studies in heathlands recommend fire frequencies in the order of every 8-15 years, in order to maintain species diversity (Russell & Parsons 1978; Gill & Groves 1981; van der Moezel *et al.* 1987; McFarland 1988). Fire intervals shorter than this may lead to the extinction of some of the dominant obligate seeding shrubs with long maturation periods (Keith 1996), while extended fire-free periods may lead to the

gradual local extinction of other species, as they have no opportunity to regenerate. However, Cary (1995), Morrison (1995) and Gill (1998) illustrate that variable fire frequencies should have a greater effect on maintaining species diversity than burning at regular intervals, which may ultimately result in reduced diversity as the same species would always be favoured by a particular fire frequency (van Wilgen *et al.* 1994). Others also advocate burning the landscape in a mosaic pattern, reflecting the natural variation in fire season, intensity, frequency and extent of fire (Specht 1981a; Avis 1993; van Wilgen *et al.* 1994).

Central to many fire management plans is the desire to maintain or even enhance species diversity. This then poses an interesting problem for management, regarding the spatial and temporal scale at which species extinctions are allowable (Bradstock *et al.* 1995). Bradstock (1995) suggest that a conservative approach would be to avoid even small-scale extinctions. However, this is likely to be unworkable, owing to differing species densities and the natural variability in factors such as fire intensity (Hobbs & Atkins 1988), which may adversely affect populations at a very small scale. Instead, a more sensible aim may be to avoid extinction within a broader landscape or area (Bradstock *et al.* 1995). This issue has been clearly illustrated in this study, where total species richness was found to decline with time since fire at smaller scales but not at the scale of the entire site, implying that local extinctions were scale-dependent. Therefore, park managers must define the spatial scale(s) at which they wish to manage rare or threatened species and the heathland as a whole. Otherwise, there is no benchmark from which to manage the heathland.

There are a few minor threats to the continued persistence of species occurring in the heath, including infection of the soil with *Phytophthora cinnamomi*^m (Kennedy & Weste 1986), inappropriate fire control measures (Caling & Adams 1999) and weed invasion (Cheal 1996). However, the greatest danger is the potentially negative effect on biodiversity of particular fire regimes, whether naturally-occurring, or implemented by park management (Gill 1999). Ideally, all information concerning the 'vital attributes' (Noble & Slatyer 1980) of each species would be available, rendering the determination of optimal fire frequencies a relatively simple process. However, there is a large gap in the data, particularly relating to seed longevity in the soil. Therefore, any estimate of

desirable fire frequencies would be purely speculative and fall somewhere within the existing estimates previously mentioned for heaths in south-east Australia.

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APPENDIX 1: Estimating time since fire

INTRODUCTION

Many methods have been used to determine fire history, or the time since the last fire at a given site. These methods include the use of fire history maps (Ough & Ross 1992; Wright *et al.* 1994), detailed fire history records (Cary & Morrison 1995; Fox *et al.* 1996), satellite imagery, aerial photographs (Keith 1995; Bradstock *et al.* 1997), historical records (Bowman 1998) and local knowledge of residents and park rangers (Ough & Ross 1992; Bennett 1994). Often, detailed and accurate records or maps are unavailable, and historical sources of information are lacking, in which case, tree rings (Banks 1988; Jarman *et al.* 1988), dendrochronology (Burrows *et al.* 1995), *anthorrhoea* banding patterns (Lamont *et al.* 1999; Ward *et al.* 2001) and charcoal data from cores (Gell *et al.* 1993) are often used to determine site fire history. However, these methods can be time consuming and some may be destructive to the environment. Individually, these methods may yield valuable information but records are often incomplete and/or inaccurate, therefore, the use of multiple methods may give more accurate results.

In addition to the methods listed above, a number of studies have used a simple technique whereby growth nodes are counted in Proteaceous species, particularly of the genus *Banksia*, to determine individual plant age (Cowling & Lamont 1985; Lamont 1985; Cowling *et al.* 1987; Witkowski *et al.* 1991; Witkowski *et al.* 1992), and/or site age (time since fire) (Specht *et al.* 1958; Bond 1980; Brown & Podger 1982; Bond *et al.* 1984; Hoffman *et al.* 1987; Jarman *et al.* 1988; Marsden-Smedley *et al.* 1999).

This method has been employed because some *Banksia* species produce a distinctive annual branching pattern, with small, circular swellings formed at the junction (node) of each annual growth increment (refer to Lamont 1985). These swellings, or nodes, can be counted on seedlings or sprouts from the outermost branch to the base of the trunk, to give an estimate of above-ground plant age. As most species (including *Banksia*) in the fire-prone environments of Australia regenerate prolifically in the first year or two following fire (Specht *et al.* 1958; Cowling *et al.* 1987; Wark *et al.* 1987; Gill 1993), the estimate of plant age derived from the *Banksia* node count method should theoretically

correspond with site age (time since last fire). *Banksia marginata* is one such species that occurs commonly from sea level to sub-alpine areas in south-east Australia (Holliday & Watton 1990). This species is very variable, growing as a shrub, or a tree up to 10 m, and regenerating from seed, or by resprouting after fire (George 1987). It leaves recognisable node scars after each growing season, which are thought to be one per year, usually between November and March (Specht *et al.* 1958; Specht *et al.* 1981). In some circumstances, it can be relatively long-lived, living up to 150 years (J. Marsden-Smedley pers. comm.), and therefore, it can potentially be used to determine the time since last fire, even at sites unburnt for long periods.

Although a number of studies have used the *Banksia* node count method to estimate site age (e.g. Specht *et al.* 1958; Brown & Podger 1982; Jarman *et al.* 1988; Marsden-Smedley *et al.* 1999), there appear to be no published data regarding the reliability of this method. This study aims to determine the accuracy of the *Banksia* node count method by using the method to date sites of known time since fire. After verifying the validity of the method, time since fire for study sites of previously unknown age were estimated using *Banksia* node counts and other complementary methods, namely aerial photographs and newspaper records.

METHODS

Banksia marginata nodes were counted on shrub-form individuals at nine 4 ha sites of different time since fire, in April 2001 (March 1999 for GP-23). To ascertain the accuracy of the *Banksia* dating method, node counts were made at five sites burnt between 1980 and 1997 and cross-checked with the actual site age known from Department of Natural Resources and Environment (DNRE) fire-history records and mapping. In addition, four sites last burnt before the commencement of DNRE fire-history mapping in 1981 were sampled to estimate time since fire at these sites.

At each of the nine sites, nodes were counted on 50-61 haphazardly located *B. marginata* individuals, although only 14 individuals were assessed at GP-23. Plants that were obviously young root suckers at older sites were not assessed. To gain a more accurate estimate of above-ground plant age, a figure of one was added to the node count of each individual (Marsden-Smedley *et al.* 1999), as this gives the actual number of growth increments (internodes), which corresponds with plant age; rather than the number of junctions (or nodes) between growth increments.

In addition to the *Banksia* dating method, aerial photographs of the study area were examined as far back as 1970, to determine whether any evidence of fire was present. Although photographs were taken in 1970, 1976-1979, 1984, 1986 and 1991, the entire study area was not covered in each of these years, meaning that records were incomplete. Newspaper records from 1964-1971 were also checked for the *Gippsland Times*, a newspaper based in Sale, which is the nearest major town to the study area. No fires were reported within the study area for this period. Newspaper records from 1972-1980 were unable to be checked. Finally, growth rings on a sample of *B. marginata* and *Leptospermum myrsinoides* individuals were counted in an attempt to further cross-check the *Banksia* node count method (Brown & Podger 1982; Marsden-Smedley *et al.* 1999). However, rings were found to be difficult to distinguish and determine to the same level of accuracy as the node count method, therefore, they were not used in determining site age.

Data analysis

Banksia marginata displays a distinctive pulse of regeneration following fire. However, some individuals regenerate from root suckers in the inter-fire period, while others may

escape above-ground death by fire if fires are patchy. Owing to the episodic nature of the regeneration event following fire, the modal internode count (Marsden-Smedley *et al.* 1999) was used to estimate the time since fire at each site. Modal counts were used instead of means (e.g. Witkowski *et al.* 1992), because mean values are potentially influenced by individuals that either escaped fire, or have regenerated in the inter-fire period, and may therefore give spurious site age estimates. Pearson correlation was used to examine the relationship between known time since fire and mode of the internode count, for the five sites of known time since fire. The critical level for hypothesis testing was $\alpha = 0.05$. Data were square-root transformed to improve homogeneity of variances.

RESULTS

Modal *B. marginata* internode counts for the five youngest sites (Figure 1) were found to be significantly correlated with known time since fire ($R = 0.98$, $p = 0.005$). At four out of the five sites, the *Banksia* node count method is accurate to within a year either side of the modal count for a range of ages, from 4-21 years post-fire (Table 1). However, T4-14 was anomalous in that the modal count was three years less than the actual age at the date of sampling (Table 1). Given the very similar number of individuals from 12-15 years (Figure 1), the 'true' mode may be anywhere within this range. Assuming that the significant relationship between modal internode counts and site age continues as plants grow older, GP-23 is estimated to be 22 years old; T4-25, 27 years old; SS-26, 24 years old; and, T2-27, 28 years old at the date of *Banksia* sampling (Figure 1, Table 2).

Some of the four oldest sites lack a distinctive modal peak, compared with sites such as BS-1.5 and SS-16, which indicate a significant post-fire regeneration event (Figure 1). Therefore, a potential age range has been included for the modal counts of GP-23, T4-25, SS-26 and T2-27 (Table 2), based on the frequency histograms in Figure 1. Using this method, GP-23 appears to be 22 years old, with an age range of 21-26 years, T4-25 appears to be 27 years old, with an age range of 25-30 years, T2-27 appears to be 28 years old, with an age range of 22-29 years, while SS-26 appears to be 24 years old, with an age range of 23-36 years (Figure 1).

When aerial photographs are considered in conjunction with internode counts, estimates of site age are further clarified. Aerial photographs indicated that T4-25, T2-27 and SS-26 had not been burnt by March-April 1976. As there was no evidence of fire scarring at these sites, the most recent fire is assumed to have occurred at least two years prior to aerial photographs being taken, indicating that these sites were last burnt in 1974, or earlier (checks on three independent fires indicated that fire scars remain recognisable on aerial photographs for at least 2-3 years). This finding increased the age estimate for SS-26 and narrowed the potential age range (error) for all three sites (Table 2). Because internode counts were made up to two years following vegetation sampling, the final determination of site age was changed accordingly, indicating that T4-25 was 25 (25-28) years old at the time of vegetation sampling, SS-26, 26 (26-35) years old, and T2-27, 27 (26-28) years old (Table 2). In contrast to the previous three sites, a fire scar was

evident at GP-23, which suggests it was probably burnt sometime within the two years prior to 1976. This indicated that site age for GP-23 at the time of vegetation sampling was 23 (23-26) years (Table 2).

DISCUSSION

The mode of the *Banksia* node count method proved to be accurate to within one year either side of the actual site age, for four of the five sites up to 21 years old. The only exception to this was T4-14, however, this was probably an artefact of the low intensity, and therefore patchy nature of the most recent fire at the site (B. Houghton pers. comm.), resulting in two broad age classes (Figure 1). Although there was some variability in the accuracy of the *Banksia* node count method, overall, it corresponded closely with the actual site age determined from DNRE fire history mapping. Therefore, there is a strong basis for using the *Banksia* node count method to determine site age for patches that pre-date the commencement of fire history mapping in 1981.

As site age increased, it became increasingly difficult to identify distinct phases of episodic recruitment following fire (Figure 1). Although GP-23, T4-25, SS-26 and T2-27 have distinct modal internode counts, there are other peaks in the frequency histograms that complicate interpretation of the data. For instance, SS-26 possessed a peak at 36 years of age, only one count below the modal peak at 24 years. This suggests the possibility of two fires within the past 36 years, with the fire 24 years ago quite patchy, owing to 46% of the sampled individuals being older than 24 years (Figure 1). Conversely, there may have been only one fire, 36 years ago, with continuous regeneration of *Banksia marginata* occurring in the interim. However, newspaper reports suggest an absence of fire within the study area from 1964-1971, implying that no sites were aged between 30 and 37 years at the time of *Banksia* sampling.

Despite the reported success of the *Banksia* node count method, there are factors influencing its accuracy. As *B. marginata* grows older, nodes often become indistinct toward the base of the plant, particularly prior to branching of the main trunk (Lamont 1985). This makes assessment of nodes on the lower trunk increasingly difficult. Another potential error arises if more than one growth spurt occurs in a single year. Specht (1958) indicated that *B. marginata* only actively grew above certain temperatures that were only met during the summer months, however, in particularly long summers, secondary growth spurts may occur.

Previous studies that have used the *Banksia* node count method to estimate site age have employed a small number of samples. For example, Marsden-Smedley (1999)

recommended a minimum of six individuals be sampled per site, Jarman (1988) used only one or two individuals, while Specht (1958) and Brown (1982) do not state the number of samples used in determining site age. In environments where fire has been patchy (resulting in multiple age classes) and *B. marginata* is suckering in the inter-fire period (e.g. this present study), a much larger sample size is required to accurately estimate time since fire. This study suggests that 50 samples are generally sufficient to confidently estimate site age.

In addition to sample number, the method by which site age is actually determined is not always given in some studies, i.e. is the mean, median or mode of all node counts used? Owing to this lack of information, it is therefore difficult to ascertain the reliability of site age estimates for some studies.

This study provides empirical evidence regarding the accuracy and validity of the *Banksia* node count method. The method is not intended to give a definitive site age, but rather, an informed estimate based on rigorous sampling and use of complementary techniques. Fifty samples per site were generally appropriate, however, for sites older than 21 years, sample size may need to be greater, owing to the potentially greater error in counting internodes, variability in stand age caused by fire patchiness and regeneration by root suckering in the inter-fire period.

Table 1. Site age estimates based on the modal age class derived from the *Banksia marginata* node count method, for sites of known age

Site	<i>n</i>	Site age (DNRE fire history mapping)	Modal internode count	Difference between mode and age at date of <i>Banksia</i> sampling
BS-1.5	50	4	4	0
TT-9	56	11	12	+1
T4-14	55	16	13	-3
SS-16	52	18	17	-1
UT-19	51	21	21	0

Table 2. Site age estimates for sites pre-dating DNRE fire history mapping. Age estimates are based on aerial photographs and the modal age class derived from the *Banksia marginata* node count method.

Site	<i>n</i>	Mode (potential age range) -- see Figure 1	Previous fire (according to aerial photographs)	Adjusted site age estimate based on aerial photographs	Adjusted site age estimate (± 2)	Difference between vegetation and <i>Banksia</i> sampling date (yrs)	Final estimate of site age at date of vegetation sampling
GP-23	14	22 (23-26)	< April 1976	23 (23-26)	23 (23-26)	0	23 (23-26)
T4-25	61	27 (25-30)	< March 1976	27 (25-30)	27 (27-30)	2	25 (25-28)
SS-26	50	24 (23-36)	< April 1976	25 (25-36)	27 (27-36)	1	26 (26-35)
T2-27	54	28 (22-29)	< March 1976	28 (25-29)	28 (27-29)	1	27 (26-28)

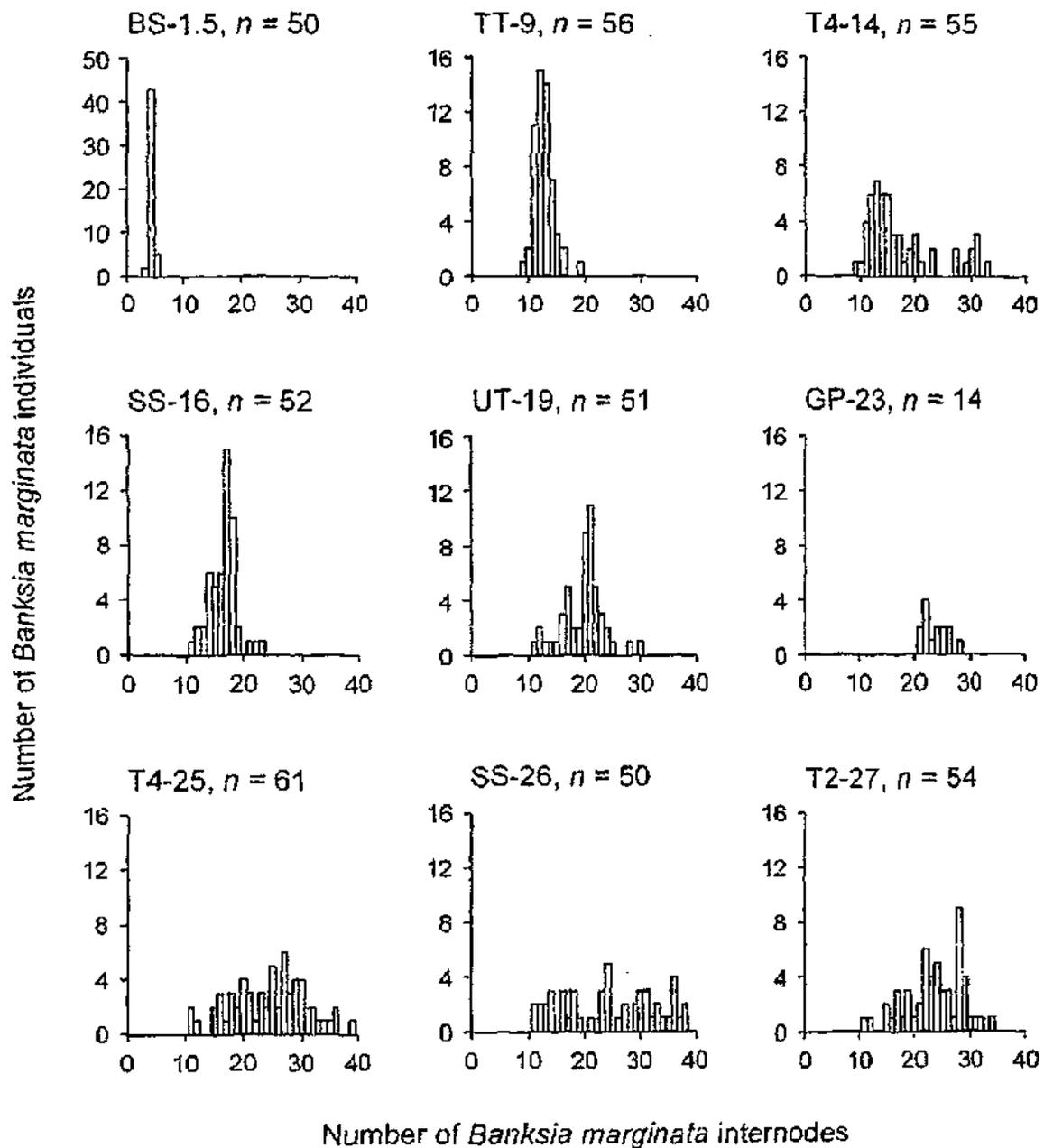


Figure A1. *Banksia marginata* internode counts for sites sampled in April 2001 (March 2001 for GP-23).

APPENDIX 2: Plant species list (inclusive of all scales sampled)

* non-native species

Ferns

DENNSTAEDTIACEAE

Pteridium esculentum

Monocotyledons

CYPERACEAE

Caustis pentandra

Isolepis marginata

Lepidosperma concavum

Schoenus imberbis

LILIACEAE

Caesia parviflora

Laxmannia orientalis

Thelionema sp.

ORCHIDACEAE

Caladenia alata

Caladenia carnea var. *carnea*

Caladenia sp.

Caleana major

Calochilus robertsonii

Calochilus sp.

Genoplesium sp. aff. *rufum*

Glossodia major

Pterostylis parviflora

Pterostylis sp.

Pyrorchis nigricans

POACEAE

* *Aira caryophyllea*

Anisopogon avenaceus

Austrodanthonia geniculata

Poaceae sp. 1

Poaceae sp. 2

Poa sieberiana var. *sieberiana*

* *Vulpia bromoides*

RESTIONACEAE

Hypolaena fastigiata

XANTHORRHOEACEAE

Lomandra filiformis ssp. *filiformis*

Lomandra glauca

Lomandra longifolia

Xanthorrhoea australis

Xanthorrhoea minor ssp. *lutea*

Dicotyledons

AIZOACEAE

Carpobrotus rossii

APIACEAE

Platysace ericoides

Xanthosia pilosa

ASTERACEAE

* *Conyza* sp.

Euchiton sphaericus

* *Hypochoeris radicata*

CAMPANULACEAE

Wahlenbergia gracilentia

CASUARINACEAE

Allocasuarina littoralis

Allocasuarina misera

Allocasuarina paludosa

Allocasuarina paradoxa

Allocasuarina sp.

CRASSULACEAE

Crassula sieberiana

DILLENIACEAE

Hibbertia acicularis

Hibbertia fasciculata var. *prostrata*

Hibbertia riparia

Hibbertia virgata

DROSERACEAE

Drosera peltata

EPACRIDACEAE

Astroloma pinifolium

Brachyloma daphnoides

Epacris impressa

Leucopogon ericoides

Leucopogon virgatus var. *virgatus*

Monotoca scoparia

EUPHORBIACEAE

- Amperea xiphoclada* var. *xiphoclada*
Ricinocarpus pinifolius

FABACEAE

- Aotus ericoides*
Bossiaea cinerea
Bossiaea heterophylla
Bossiaea obcordata
Dillwynia glaberrima
Dillwynia sericea
Gompholobium huegelii

GOODENIACEAE

- Dampiera stricta*

HALORAGACEAE

- Gonocarpus tetragynus*

T.AURACEAE

- Cassytha glabella*
Cassytha melantha
Cassytha pubescens

LORANTHACEAE

- Amyema pendula* ssp. *pendula*

MIMOSACEAE

- Acacia longifolia* var. *longifolia*
Acacia oxycedrus
Acacia suaveolens

MYRTACEAE

- Baeckea ramosissima* ssp. *prostrata*
Calytrix tetragona
Eucalyptus aff. *willisii* (Gippsland Lakes)
Eucalyptus viminalis ssp. *pryoriana*
Eucalyptus viminalis ssp. *pryoriana* X *Eucalyptus cephalocarpa*
Leptospermum continentale
Leptospermum myrsinoides
Thryptomene micrantha

PITTOSPORACEAE

- Rhytidosporum procumbens*

POLYGALACEAE

- Comesperma calymega*

PROTEACEAE

- Banksia marginata*
- Banksia serrata*
- Grevillea chrysophaea*
- Persoonia juniperina*

RUTACEAE

- Boronia anemonifolia* ssp. *anemonifolia*
- Correa reflexa* var. *speciosa*
- Zieria veronicea*

STYLIDIACEAE

- Stylidium* sp. 2

THYMELAEACEAE

- Pimelea linifolia* ssp. *linifolia*

TREMADRACEAE

- Tetratheca pilosa* ssp. *latifolia*