Flammable Australia
The Fire Regimes and Biodiversity of a Continent

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Fig. 8.2. Species-rich, annually burnt, *Themeda triandra*-dominated grassland in western Victoria. Note the abundance of bare ground and low levels of grass biomass.

Fig. 8.3. A dense, closed sward of *Themeda triandra* in an undisturbed, species-poor grassland in the Australian Capital Territory. Compare grass biomass levels and the amount of bare ground against the frequently burnt remnant in Fig. 8.2.
The role of fire regimes in temperate lowland grasslands of southeastern Australia

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Abstract
The role of fire regimes in temperate lowland grasslands in Australia is discussed. Over 99% of native grasslands in most regions have been destroyed or highly modified for agriculture. Fire is excluded from most agricultural operations and is regularly used in only a small proportion of grassland remnants. Most of the grassland fire literature focuses on frequently burnt grasslands dominated by *Themeda triandra* in western Victoria, and little information is available on grasslands dominated by other species. *Themeda* grasslands tolerate frequent burning, and many remnants with a diverse flora are burnt at 1-3-year intervals. The fire ecology of *Themeda* grasslands is discussed in detail, and a conceptual model is developed which highlights the importance of disturbances such as fire for preventing competitive exclusion by the dominant grasses. Relatively little fire research has been conducted in Australian temperate grasslands compared to sclerophyllous ecosystems. Issues requiring further research include: experimental studies of ecosystem responses to particular fire regimes; identifying processes that promote seedling recruitment; and the effects of different fire regimes on grassland fauna and soil nutrient fluxes.

Introduction
Before European colonisation, natural and Aboriginal-lit fires may have played a pivotal role in controlling the ecological structure and functioning of the grassy plains of southeastern Australia. The importance of fire regimes in the original landscape will probably never be known, however, since the natural grasslands were rapidly and completely transformed to agricultural crops and pastures after settlement. Nowadays, biomass on the plains is controlled by introduced stock and mechanical harvesters, not by flames. Frequent burning of native grasslands is increasingly becoming an anachronistic oddity, confined to small, isolated sites on roadsides and rail easements where fragments of the original vegetation have been protected from landscape disturbance regimes such as those due to cropping and grazing. Many of these small fragments are critically important for the conservation of Australia’s temperate grassland estate (Stuwe 1986; McDougall and Kirkpatrick 1994).

In this chapter, we review the effects of fire regimes on temperate, lowland (non-alpine) grassland communities in southeastern Australia. Whilst we focus on natural, treeless grasslands, we also include relevant information from secondary grasslands derived from other ecosystems such as grassy woodlands and shrublands. Our focus is on native vegetation, and grasslands composed predominantly of exotic species are excluded.

Compared to fire-prone ecosystems such as heathlands and wet sclerophyll forests, very little research has been undertaken on fire effects in temperate Australian grasslands. Since virtually all published information is on flora rather than fauna, and most published studies are from grasslands dominated by *Themeda triandra* (kangaroo grass), especially on the western basalt plains of Victoria, botanical studies from this ecosystem inevitably dominate this review.

Ecosystem distribution
Prior to European colonisation, natural grasslands occupied large areas of southeastern Australia,
most notably on the basalt plains of western Victoria, in south-central South Australia (SA), and in the Riverina region of northern Victoria. The Riverina region of south-central New South Wales (NSW) is generally considered to have been originally dominated by woodlands of *Acacia pendula* and *Atriplex nummularia*, with both species being rapidly eliminated by heavy stock grazing to form extensive secondary grasslands (Moore 1953; Leigh and Noble 1972). However, little accurate information is available on original vegetation structure in the region, and it has been argued that at least some areas in NSW may always have been treeless grasslands (McDougall and Kirkpatrick 1994). Smaller areas of grassland occurred in the Wimmera and Gippsland in Victoria, on the NSW Southern Tablelands and Tasmanian Midlands (Fig. 8.1).

These grassland regions share a suite of similar climatic and geomorphological features including: relatively low rainfall (usually 400–600 mm mean annual rainfall, grading into drier, semi-arid ecosystems in the NSW Riverina and in South Australia); flat to gently undulating topography; and heavily textured, poorly drained soils of relatively high fertility. The combination of fertile soils on gentle slopes permitted widespread agricultural development after European colonisation, causing a dramatic decline in the extent and integrity of natural grasslands. Today, lowland temperate grasslands in all regions are threatened ecosystems. Most remnants are small, isolated, and managed for purposes other than biodiversity conservation (McDougall and Kirkpatrick 1994).

**Plant composition**

Natural temperate grasslands are typically dominated by perennial tussock grasses with inter-tussock forbs, smaller grasses and sedges (see Fig. 8.2, colour plate). Dominant grass genera include *Themeda*, *Austrodanthonia* (formerly *Danthonia*), *Austrostipa* (formerly *Stipa*) and *Poa*. *Themeda triandra* or *Poa* species dominate remnants in areas of relatively high rainfall (e.g. southern Victoria, NSW Southern Tablelands and the Tasmanian Midlands), whereas *Austrodanthonia* and *Austrostipa* species co-dominate the Riverine plains and south-central SA (with *Lomandra* species). *Austrodanthonia* and *Austrostipa* species are also widespread in higher-rainfall regions in dry, stony sites and where stock grazing has depleted the original dominant *Themeda triandra* (C. W. E. Moore 1953; R. M. Moore 1962; Willis 1964; Sharp 1995). Tussock grasses often contribute most of the above-ground (and presumably below-ground) biomass in undisturbed *Themeda* and *Poa*-dominated communities (see Fig. 8.3, colour plate; McDougall 1989; Morgan and Lunt 1999). By contrast, biomass is usually considerably lower in *Austrodanthonia* and *Austrostipa* grasslands (Williams 1970; Williams and Roe 1975).

In all but the driest regions (i.e. NSW Riverina and south-central SA), most native species are herbaceous perennials (Costin 1954; Willis 1964; Benson 1994; McDougall and Kirkpatrick 1994; Tremont and McIntyre 1994). By contrast, native annuals (many shared by semi-arid ecosystems further inland) are abundant in south-central South Australia (Davies 1997) and the Riverina (Foreman 1996; Benson et al. 1997). In all regions, most perennial species are hemicryptophytes or geophytes which possess regenerative buds at or below the soil surface (McIntyre et al. 1995; Morgan 1998a). Indeed, almost 90% of species in frequently burnt *Themeda* grasslands in southern Victoria belong to one of these two life-form groups (Morgan 1999). In contrast to the predominance of perennial species in the native flora, many exotic species are annuals (therophytes). Exotic annual grasses and forbs are now abundant in most grassland remnants in all regions (McDougall and Kirkpatrick 1994).

**Grassland fire regimes**

Grassland burning regimes can conveniently be divided into three broad phases: (1) pre-European fire regimes; (2) traditional European regimes (late 1800s–1970s); and (3) recent burning practices (post-1980), which include the use of fire for conservation management.

**Pre-European fire regimes**

The nature of pre-European burning regimes in grasslands remains largely unknown. It is widely
assumed that grasslands were often burnt by fires ignited by Aborigines and lightning, but little information exists to support this belief, apart from many brief historical references which mention widespread burning by Aborigines.

Considerable debate has taken place in other continents over whether grassland areas were 'natural' vegetation formations or artefacts of the burning practices of indigenous peoples (e.g. Sauer 1950; Stewart 1956; Vogl 1974; Axelrod 1985). Several recent regional historical studies from southeastern Australia have demonstrated high fidelities between
regional grassland and woodland boundaries and soil distributions (e.g. Fensham 1989; Foreman 1996; Fensham and Fairfax 1997; Lunt 1997a; Morcom and Westbrooke 1998). Consequently, it seems most likely that absence of trees was controlled by a combination of soil and regional climatic features, with pre-European fire regimes playing a minor role in controlling tree regeneration. Over short time periods, competition between tree seedlings and established grass tussocks may also prevent tree recruitment in productive grasslands (Fensham and Kirkpatrick 1992), but it is difficult to envisage this mechanism operating over millennia.

A number of recent invasions by native trees and shrubs into small grasslands on hillside 'balds' and coastal headlands have been attributed to fire exclusion since European settlement (e.g. Howitt 1890; Fensham and Fairfax 1996; Costello 1998). Similar processes have occurred in a variety of woodland ecosystems (e.g. Withers and Ashton 1977; Allen 1998; Lunt 1998). Thus, it is possible that frequent burning before European colonisation may have maintained small, treeless areas in mountainous and coastal regions and in some woodlands, but there is no evidence of large-scale tree or shrub invasion across extensive grassland ecosystems.

Traditional European fire regimes

Despite the paucity of information on pre-European burning regimes, it is widely assumed that the dominant landscape disturbance agent in grasslands has changed from burning under low grazing pressures before European colonisation, to grazing with little burning since (Groves and Williams 1981; Mack 1989). All temperate grassland regions in southeastern Australia are now utilised for stock grazing and other agricultural pursuits, including irrigation and cropping. In most temperate grassland regions, few grazing enterprises involve regular burning.

At local scales, however, many small sites in some regions have been burnt frequently for over a century as a means of fire protection for rural communities. Annual and biennial summer burning have traditionally been conducted by local fire brigades for fire control along roadsides in western Victoria, at least since the 1940s (Morgan 1998a, b). Increasingly, however, these practices are being phased out and burning is being replaced by ploughed firebreaks and herbicides. Similarly, state railway authorities traditionally burnt rail-line easements (often annually in late spring) since the creation of rail-lines in the 19th century. Annual burning was a vital means of fire control in an era when steam trains often started fires from sparks in smoke. Ongoing rail closures (which have continued throughout the 20th century) have contributed to the demise of rail-line burning.

Small rail reserves and some road easements are amongst the few places in most grassland regions where frequent burning has continued in the absence of stock grazing. Many of these sites now contain some of the highest quality grassland remnants, in terms of biodiversity conservation, in southeastern Australia, and they contain many endangered plant species (Scarlett and Parsons 1993; McDougall and Kirkpatrick 1994). Indeed, Scarlett (1994) has described the frequently burnt rail reserve remnants of western Victoria as the 'working model' of the original grassland vegetation.

Recent fire regimes

Since the early 1980s, increasing attention has been given to the use of fire as a management tool to maintain plant diversity in remnant Themeda triandra grasslands, especially in southern Victoria. Nowadays, two types of grassland are regularly burnt: (1) small, narrow rail and road easements, which historically have been burnt by railway staff or local fire brigades for fire control purposes; and (2) previously grazed (and rarely burnt) paddocks which are now being burnt to maintain grassland diversity by state conservation agencies. The different management authorities tend to use different fire regimes. Roadside remnants are often burnt early in summer (late December and January) after curing of the grasses, whilst conservation reserves are usually burnt in early autumn (late March and April) after the end of the fire control season. Burning regimes in conservation reserves have tended to be erratic, and conservation agencies have
given a far lower commitment to implementing planned regimes than have rural fire brigades or railway agencies (Lunt and Morgan 1999a). Fragmentation of natural grasslands into small, isolated remnants has had inevitable consequences for grassland fire regimes. Contemporary fires in natural grasslands are small, tightly controlled, and usually intentionally lit. Landscape-scale wildfires very rarely occur.

Fire behaviour

Grassland management fires usually only burn small areas and are ignited when weather conditions are calm. Consequently, the rate of forward spread is slow and fire intensity is usually low. Recorded fire intensities from *Themeda triandra* grasslands range from 100 to 1200 kW m$^{-1}$ (Groves 1974; Morgan 1999). By contrast, intensities up to 18000 kW m$^{-1}$ have been recorded from savanna fires in the Northern Territory (Williams et al. 1998).

Morgan (1999) described the characteristics of a number of management burns in *Themeda* grasslands in western Victoria. Fire intensity was found to be positively correlated with the rate of forward spread, but was not significantly correlated with fuel load, which indicates the importance of weather conditions in controlling fire behaviour. Maximum fire temperatures at ground level were highly variable, and ranged from 98 °C to 522 °C at the base of *Themeda* tussocks (Morgan 1999). Maximum temperatures were as high in annually burnt sites as in sites burnt 4 and 7 years previously (mirroring the similar fire intensities between sites), but temperatures were more variable and the duration of soil surface heating was much shorter at annually burnt sites. Temperatures at the soil surface exceeded 100 °C for less than 1 min in an annually burnt grassland, compared to 2–3 min in sites burnt less frequently (Fig. 8.4). All grassland fires were rapid events, and ambient soil temperatures returned within 5 min of the passage of the firefront (Morgan 1999). Fires had little effect on soil temperatures at 10 mm depth (Morgan 1999).
presumably because the fire front passed quickly (Groves 1974) and because temperature changes at depth are determined by surface fuel consumption (Bradstock and Auld 1995). Substantial and prolonged soil heating is more likely to occur in the months after a fire due to solar radiation absorption by the bare earth (Lunt 1995; Auld and Bradstock 1996; Morgan 1999).

Responses to single fires

Grassland structure

In grasslands dominated by large, long-lived, perennial tussock grasses such as Themeda triandra and Poa species, the biomass of the dominant grasses is at least one to two orders of magnitude greater than that of most inter-tussock species. As biomass accumulates after burning (or the absence of other disturbance regimes), the dominant grasses often contribute over 90% of community biomass (McDougall 1989; Tremont 1994).

The rate of biomass accumulation after burning is extremely variable in Themeda triandra grasslands in southeastern Australia (Fig. 8.5). Biomass levels generally increase up to about 10 years, but accumulation rates in the first 2–5 years vary both between sites (according to site productivity) and within sites, according to seasonal moisture availability (Fig. 8.5). Biomass levels recorded 1 year after burning range from 0.9 to 4.0 t ha$^{-1}$, and after 2 years from 1.0 to 4.8 t ha$^{-1}$ (Groves 1965; Lunt 1995; Morgan and Lunt 1999). A maximum level of 11.6 t ha$^{-1}$ (mostly Themeda) was recorded from areas of the Laverton North Grassland Reserve (in western Melbourne) which were unburnt and ungrazed for 9–10 years (McDougall 1989).

Groves (1974) recorded a declining rate of biomass production from Themeda triandra as time progressed after burning, with rapid growth in the first 2 years, and considerably slower growth from 2 to 5 years. It was suggested that after 5 years, a steady state might be achieved with new growth being balanced by death and decomposition of old tissue (Groves 1974). More recent results, however, have questioned the stability of long-undisturbed Themeda stands. McDougall (1989) documented substantial differences in Themeda biomass and tussock densities between areas burnt 2 and 9 years previously. Tussock density in the long-unburnt area was only 25% of that in the recently burnt area, and most unburnt tussocks were poorly rooted, had a
small basal area and were easily killed by trampling. McDougall (1989) predicted that long-unburnt Themeda tussocks would die, and that most litter would decompose after tussocks senesced.

This prognosis was confirmed by a recent chronosequence study which found that Themeda populations declined in the absence of burning or grazing. Morgan and Lunt (1999) compared Themeda biomass, cover, tiller and tussock densities between areas unburnt for varying periods, and documented a decline in tussock and tiller densities from 6 years after burning. By 11 years after fire, few live tillers or tussocks remained in the sward, and dead grass formed a thick layer of thatch over the soil surface. Almost 75% of Themeda tussocks died in this period. The cause of Themeda death was assumed to be self-shading by accumulated litter. Thus, instead of a steady state of balanced biomass production and litter decomposition, undisturbed Themeda swards may accumulate large quantities of litter which smother and kill tussocks long before substantial decomposition occurs. Thus, productive grasslands dominated by dense Themeda swards may not be sustainable over long periods of time unless accumulated grass litter is periodically removed by burning, grazing, slashing or some other mechanism. Before European colonisation, patches of senescent grassland presumably existed across the landscape, to be subsequently recolonised by propagules from nearby areas. Nowadays, the small size of most remnants makes such losses unsustainable, and areas of dead grass are quickly occupied by exotic species, against which a healthy Themeda sward provides considerable defence (Lunt and Morgan 1999b). In contrast to Themeda triandra, Poa species appear to be able to maintain their dominance without disturbance by burning or other forms of biomass removal. However, little is known of the fire ecology of these grasslands.

Few fire studies have been conducted in grasslands dominated by Austrodenanthia and Austrostipa species (Foreman 1996). Austrodenanthia and many Austrostipa species typically have less biomass and shorter life spans than Themeda triandra or Poa species (Williams 1970; Williams and Roe 1975). Consequently, litter accumulation and competitive exclusion occur much more slowly (if at all) in these low productivity grasslands, and biomass removal (by fire, grazing or other means) is not necessarily required in order to maintain plant diversity (Williams 1969). Williams (1969) recorded little accumulation of biomass after 16 years of grazing and burning where exclusion in an Austrodenanthia grassland at Deniliquin (although changes in plant composition did occur during this period).

Botanical composition

Accumulating grass biomass leads to changes in the resources available to inter-tussock species. Closed grass swards control access to space, nutrients, water and light, creating adverse conditions for many associated species and consequent species poverty (Grubb 1977; Grime 1979). A strong, negative correlation exists between biomass levels in Themeda grasslands and the amount of photosynthetically active radiation which is transmitted through the grass canopy, with less than 10% of incident sunlight reaching the ground level beneath grasslands of 4 t ha⁻¹ biomass (Fig. 8.6); this amount of biomass is commonly attained within 2–4 years of burning (Fig. 8.5). Dense grass litter presumably also influences soil moisture and nutrient levels, although little information is available from Australia (but see Wijesuriya and Hocking 1999). Grass biomass also affects fauna habitat structure (e.g. Baker-Gabb 1993; Osborne et al. 1995), including herbivore abundances. In a seed burial experiment, Watson (1995) found substantial seed predation (assumed to be by rodents and invertebrates) beneath a dense grass cover, but little seed predation in burnt, open areas. Similar results have been obtained outside Australia (e.g. Reader 1992).

Little information is available on the shade tolerance of most inter-tussock forbs, but indirect evidence suggests that ramets and genets of many species are intolerant of prolonged deep canopy shading (Stuwe and Parsons 1977; Scarlett and Parsons 1990; Morgan 1997a). For example, Scarlett and Parsons (1990) documented numerous declines of the endangered daisy Rutilosis leptorrhynchos, as a result of grass competition in the absence of frequent burning. Subsequent experimental studies
have shown that the species requires open conditions to recruit, grow and flower (Morgan 1995, 1997a). It would appear that high species richness can only be maintained at the small scale where grassland canopies are naturally sparse or frequently destroyed.

Effects of fires on demographic processes

Fires can affect plant populations at all stages of the plant life cycle. Consequently, an understanding of plant demographic processes and population biology is required to predict the impacts of different fire regimes in grasslands. In this section, we summarise some distinctive features of the grassland flora of southeastern Australia and describe the implications of these characteristics for fire management.

Recent studies have documented short-term fire effects in temperate grasslands (e.g. McDougall 1989; Lunt 1990a, 1994; Morgan 1996; Briggs and Muller 1997; Gilfedder and Kirkpatrick 1998a, b; Lunt and Morgan 1999c). Common outcomes from these studies include: a short-term decline in the biomass and cover of the dominant grasses (and all other species) as a result of burning (all studies); a short-term increase in the abundance of opportunistic post-fire colonisers, most of which are annual exotic species which recruit from a large soil seed bank (Lunt 1990a, b; Briggs and Muller 1997; Gilfedder and Kirkpatrick 1998a); vigorous resprouting by all perennial species, with no obligate seed regenerators except annuals (Lunt 1990a; Morgan 1996); little or no post-fire seedling recruitment by many perennials (Lunt 1990a; Morgan 1998b); enhanced vigour and flower production of many perennial herbs in the spring after burning (Lunt 1994; Morgan 1996; Gilfedder and Kirkpatrick 1998b); and little change in plant composition after burning (Lunt 1990a; Morgan 1996, 1999; Briggs and Muller 1997). These trends are discussed in more detail below.

Seasonal phenology

Most grassland species exhibit strong seasonal growth patterns. In southern Victoria, above-ground vegetative growth commences from dormant buds in late autumn or winter after drought-breaking rains, then continues rapidly through spring when flowering is most pronounced, before seed is shed in December or January (Groves 1965; Morgan 1999). The above-ground parts of most plant species
(including therophytes, geophytes and hemicryptophytes) then die back to dormant buds (or seeds for therophytes) to avoid the summer drought period (Morgan 1999). *Themeda triandra*, and other summer growing C4 grasses, are an obvious exception to this general pattern. *Themeda* commences rapid growth in late spring (October) before flowering and shedding seed in midsummer (January–February). It can remain green through most of summer, responding quickly to summer rainfall, before autumn frosts and low temperatures reduce growth rates in winter (Groves 1974; McDougall 1989).

Such strong growth rhythms presumably have great implications for burning in different fire seasons. Fires in summer and early autumn (before the autumn rainfall break) occur at a time when most grassland species are dormant (Morgan 1999). Hence, few plants are directly exposed to fire and, because grassland fires barely raise soil temperatures, dormant buds in the soil are unlikely to be affected by burning. Carbohydrate levels are often at a maximum in root storage organs at the time of summer burning. Presumably, since little labile carbohydrate is lost from plants in fire events, respouting can be maximised in the post-fire conditions where light and (potentially) water availability are high. Of those species exposed to fire, many have their regenerative buds tightly held in tussock bases (e.g. *Themeda triandra*) and thus, buds are effectively insulated from direct fire damage. Buried seeds are unaffected by the passage of fire (Morgan 1999), presumably because soil heating is minimal during grassland fires. However, most seeds on the soil surface are incinerated (Morgan 1999).

**Vegetative resprouters**

Virtually all perennial grassland plants resprout after burning (Lunt 1990a; Morgan 1996, 1999), and 64% of perennial species in annually burnt grasslands in western Victoria were classed as obligate resprouters by Morgan (1999). A further 28% of species were classed as 'autoregenerating long-lived sprouters' (sensu Bell et al. 1984), i.e. species with good success at vegetative respouting after fire coupled with limited successful seedling germination. The respouting of native grassland plants in the absence of substantial seedling regeneration is similar to the obligate vegetative sprouting syndrome described by Bell et al. (1984) for sandplain species in Western Australia.

Obligate seed regenerators (non-resprouting species which rely on seedling recruitment for postfire regeneration) are very sensitive to frequent burning, as repeated fires may kill regenerating plants before they reach reproductive maturity (Gill 1981; Keith 1996). No perennial plants in temperate grasslands are known to possess this strategy, although it is possible that any species which did may have been eliminated by frequent burning in the past. The ability to resprout after burning, grazing or summer moisture stress appears to be shared by virtually all perennial grassland species in southeastern Australia.

**Flower promotion**

Many herbaceous species flower prolifically in the spring after burning, provided that adequate soil moisture is available (Lunt 1994; Morgan 1996). Flower abundance then declines in successive years as shoot competition from the dominant grasses increases. Exceptions to this generalisation include *Themeda triandra*, for which flowering was reduced by 70% after a late-summer fire (McDougall 1989), and the orchids *Diuris punctata* and *D. fragrantissima*, which appear to flower most prolifically in the second spring after autumn fires (Cropper 1993; Lunt 1994). For most perennial grassland species, the secondary juvenile period (i.e. the time required for resprouting plants to flower and set seed after burning: Johnson et al. 1994) would appear to be very short (i.e. <12 months) with most species capable of flowering in the first spring after an autumn fire (Lunt 1990a, 1994; Morgan 1996, 1999).

How fire promotes flowering remains poorly understood. Changes in daily temperature fluctuations, increased light penetration and soil temperatures, changes in physical and chemical characteristics of the soil, reduced competition, increased water availability, leaf removal and the production of ethylene have all been postulated as being important in other ecosystems (Hulbert 1988; Bond and van Wilgen 1996), and may also play a role.
in Australian temperate grasslands. For many grassland species, post-fire pulse flowering does not appear to be restricted to the period immediately after burning (e.g. 12 months), but appears to continue for as long as grass biomass levels remain low. This suggests that competition for light is a driving force influencing flower production in herbaceous species.

**Soil seed banks**

A conspicuous feature of the grassland flora of southeastern Australia is that many species shed readily germinable seed (Willis and Groves 1991; Lunt 1995; Morgan 1998d) and form small, transient soil seed banks (Gilfedder and Kirkpatrick 1993; Morgan 1995, 1996c; Lunt 1996, 1997d). For example, a seed burial study on the endangered daisy Rulidosis leproborhynchoidea found that all viable seeds germinated promptly in response to the autumn rainfall 'break' and no seeds survived in the soil for more than 16 weeks after burial (Morgan 1995).

In general, it would appear that only small-seeded, perennial forb species, such as Hypericum gramineum, Juncus and Wahlenbergia species form large, persistent soil seed banks (Lunt 1990b, 1997d; Willis et al. 1997; Morgan 1998c), as has been found in many soil seed bank studies in other ecosystems (Leck et al. 1989; Thompson et al. 1993). By contrast, annual species (most of which are exotic) typically form large soil seed banks and can account for more than 80% of seeds present in grassland seed banks (Lunt 1990b, 1997d; Gilfedder and Kirkpatrick 1993; Morgan 1998c). The absence of a soil seed bank means that the persistence of many species relies upon the maintenance of a resprouting 'bud and tuber bank' in the existing plant population. If existing plants die, then future recruitment cannot occur. This problem is accentuated in fragmented remnants as the chance of new propagules disseminating into isolated remnants is very low.

**Seedling recruitment**

Perhaps as a consequence of small soil seed banks, single grassland fires do not promote mass seed germination of most perennial species (Lunt 1990a; Pyrke 1993; Foreman 1996; Morgan 1997b, 1999), in contrast to their effects on seedling recruitment in many heathland and forest communities (Wark et al. 1987). Seedling recruitment appears to occur infrequently for many native perennial species (Pyrke 1993; Morgan 1998d, 1999). In a 4-year study, Morgan (1997b) found seedling recruitment of native species to be rare in high quality, species-rich Themeda grasslands in western Victoria, even though over 70% of perennial native species were ultimately dependent on seedlings for regeneration. Given the widespread distribution of grassland species (McIntyre et al. 1993), a similar scenario may exist in other grassland regions of southeastern Australia. The 'storage effect' recruitment model proposed by Warner and Chesson (1985) appears to be relevant to productive Themeda grasslands. Under this model, infrequent but successful recruitment events are 'stored' into the adult population, allowing persistence during periods of extended, low-level recruitment.

The absence of a persistent soil seed bank for many species has significant implications for potential post-fire recruitment. If few seeds are produced in the year immediately before a fire, little seedling recruitment is possible in the year after burning. Since flower and seed production are strongly inhibited by a dense, closed grass layer, little seedling recruitment may be expected when a long-undisturbed, dense grass canopy is finally burnt. Instead, pulse flowering in the spring after burning may enhance opportunities for seedling recruitment in the second autumn–winter after burning (Lunt 1994). Thus, rather than directly triggering seedling recruitment, grassland fires may facilitate deferred post-fire recruitment, by providing open conditions for successful seed production in the following spring–summer, thereby permitting seedling recruitment in following years. Whilst this model would seem a logical consequence of transient soil seed banks, few empirical data are yet available, and further recruitment studies are needed.

Seedling survival is tightly coupled to light availability at ground level. In the absence of gaps in the canopy that allow high light levels to penetrate to
the ground, seedling survival is negligible for many species (Morgan 1997a, b). Indeed, for some native species, gaps greater than 30 cm diameter are necessary to promote seedling survival (Morgan 1997a). Since grass biomass rapidly accumulates and gaps quickly disappear in productive grasslands (Figs 8.5, 8.6), only short periods (of 1–2 years) after burning may be suitable for abundant seed production and successful recruitment. Thus, fire may provide brief “windows of opportunity” during which plants can successfully set seed and regenerate whilst grass biomass is low.

Fire regimes and fauna

The effects of grassland fire regimes on fauna have been poorly studied. Only one quantitative experimental study is available (Greenslade 1997), and most published information is based on casual observations of short-term responses of endangered reptiles and invertebrates to single fires. Despite this limited information base, frequent burning is widely perceived as having negative impacts on many fauna; particularly small species that are relatively immobile.

A number of reports on threatened grassland lizards, including the striped legless lizard (Delma impar) and grassland earless dragon (Tympanocryptis lineata pinguecula) suggest that light grazing might be a more suitable management regime than frequent burning (Webster et al. 1992; Robertson and Cooper 1997; Robertson 1999).

Coulson (1990) recorded mortality of the threatened striped legless lizard (Delma impar) during a grassland fire, and suggested that predation was likely to increase as a result of the post-fire reduction in vegetation cover. Subsequent management recommendations for grasslands containing D. impar suggest that burning be conducted in late summer or autumn, when the dry clay soils are extensively cracked, to enable lizards to avoid incineration by hiding in deep cracks (Webster et al. 1992; Craigie 1995). Robertson and Cooper (1997) reported deaths of the endangered grassland earless dragon (Tympanocryptis lineata pinguecula) due to incineration, although some individuals were able to escape by retreating to burrows and perhaps remaining in them for long periods. Appropriate fire regimes have yet to be determined for this species.

The endangered golden sun-moth (Synemon plana) is most abundant in the Australian Capital Territory (ACT) in native grasslands that are grazed or mown rather than burnt. Frequent burning is considered likely to be detrimental to the species (ACT Government 1998). Sun-moth larvae feed on plant roots, especially Austrodanthonia species, and it has been suggested that root reserves would be reduced after burning as plants vigorously resprout, thereby reducing the food supply to larvae (ACT Government 1998). However, no information is available on postfire changes in root reserves, and it is questionable whether root reserves are substantially reduced by fires.

In contrast to the above species, which usually occur in large, unburnt paddocks rather than small, frequently burnt grassland remnants, the endangered morabine grasshopper (Keyarca scurr) occurs in rail-line remnants in the ACT and NSW Southern Tablelands. These sites were historically burnt every 1–3 years. Little is known about the effects of fire on the species, but it is thought that burning in autumn (when eggs are hatching) or in spring (when adults are active) might present a hazard to these slow-moving flightless grasshoppers. On the other hand, post-fire reduction in grass competition is likely to aid the survival of food plants (Rowell and Crawford 1995).

Greenslade (1997) studied the responses of grassland invertebrates for 16 months after an autumn fire in an experimental small-plot study. She found that fire caused a short-term reduction in invertebrate richness and abundances compared to unburnt plots, but that these differences had disappeared after 16 months. The species composition of Collembotha differed between burnt and unburnt plots at 16 months, which was considered to be due to differences in postfire vegetation structure.

The challenge for managers of small grassland remnants that contain a diverse flora and endangered fauna is to maintain an open vegetation structure to maintain plant diversity whilst maintaining viable fauna populations. Where fire is used, far
more information is required to balance short-term fire effects (e.g. immediate mortality and restricted foraging and/or elevated predation risk after burning), and the longer-term impacts on fauna populations. Short-term losses may only be sustainable if fauna benefit from post-fire conditions in the medium term, or can immigrate from nearby sites. However, the highly fragmented nature of grassland remnants strongly minimises opportunities for dispersal. Many grasslands containing threatened fauna may be easier to manage using intermittent, light grazing rather than frequent burning. Clearly, far more work is required to identify the responses of grassland fauna to long-term fire regimes.

Responses to fire regimes

Grassland plant species demonstrate considerable resilience to single fires. However, observations on the short-term impacts of single fires provide little insight into the effects of consecutive fires. As in other ecosystems, attributes of fire regimes including fire intensity, seasonality and frequency of occurrence are all likely to have significant effects on grassland composition and functioning. However, little is known about many of these factors.

The effects of grassland fire regimes have been investigated in two ways: (1) by regional comparisons of sites that have experienced different burning regimes for many decades (e.g. Stuwe and Parsons 1977; Lunt 1997b; c; Morgan 1998c) and (2) a small number of experimental studies (e.g. Robertson 1985; Foreman 1996; Henderson 1999).

Effects of historical fire regimes

In an early study, Stuwe and Parsons (1977) compared the plant composition of remnant Themeda triandra grasslands with different management histories in western Victoria. Remnants on rail easements which were ungrazed and frequently burnt (every 1–3 years in summer) were found to be significantly richer in native species than remnants in unburnt, lightly grazed paddocks or those on unburnt and ungrazed road reserves (these sites were probably grazed in the past). Inter-tussock forbs such as Chrysocephalum apiculatum, Leptorhynchos squa-
matus and Plantago gaudichaudii were best represented in frequently burnt sites, and no native species were favoured by fire exclusion. These differences were interpreted as responses to grazing and burning history, mediated through competition from the dominant grass, Themeda triandra (Stuwe and Parsons 1977). This study laid a firm foundation for the ongoing emphasis on frequent burning as a management tool in Victorian grasslands.

In a similar regional study, Lunt (1997b) compared the composition of frequently burnt, ungrazed, secondary grasslands in eastern Victoria (most of which were on rail easements), against unburnt and intermittently grazed, grassy forest and woodland remnants in the region. All remnants were assumed to be derived from the same grassy woodland ecosystem originally. Frequently burnt rail remnants possessed a different suite of plants to unburnt woodland remnants, and these differences reflected different management regimes rather than underlying soil features. Tall forbs were abundant in frequently burnt sites and relatively rare in grazed sites, whereas short species were abundant in intermittently grazed woodlands and rare in frequently burnt sites. Lunt (1997c) hypothesised that tall species were depleted in woodland sites by past stock grazing and that short species were depleted in frequently burnt sites as a result of competition from the dominant perennial grass, Themeda triandra, which dominated the burnt remnants. The second hypothesis is intriguing since it suggests that the depletion of many forbs in frequently burnt sites was a result of strong inter-specific competition between fire events rather than being a direct negative impact of frequent burning per se. If correct, this finding again suggests that the effects of grassland burning regimes are mediated through their effects on the dominant species. Burning regimes which promote dense swards of a competitively superior dominant (such as Themeda triandra) might be expected to deplete small species which are readily out-competed beneath a closed grass sward.

Are species-rich rail-line grasslands diverse because they have been frequently burnt, or because they have rarely been grazed? Unfortunately, the
effects of historical patterns of grazing and fire management are not easily separated in regional studies such as Stuwe and Parsons (1977) or Lunt (1997b). However, many of the species reported from frequently burnt grazing refugia by Stuwe and Parsons (1977) and McDougall and Kirkpatrick (1994) are also abundant in rarely burnt grazing refugia, such as travelling stock reserves and cemeteries, in *Eucalyptus albida* grassy woodlands in central NSW (Prober and Thiele 1995). This suggests that fire is not critically important to the perpetuation of these species.

Regional studies of fire history have provided invaluable information on the long-term effects of particular fire regimes (especially frequency and seasonality) on plant composition. In southern Victoria, many annually burnt grasslands are among the richest and most important remnants for plant conservation (Scarlett et al. 1992; McDougall and Kirkpatrick 1994). *Ipso facio,* such regimes are unlikely to be deleterious to species which are abundant in these sites. Surprisingly, relatively few grassland species appear to have been grossly depleted or eliminated by burning at such high frequencies. A notable exception may be members of the Fabaceae, including *Glycine, Psoralea, Desmodium, Swainsona* and *Lotus* species. Scarlett and Parsons (1982) suggested that these taxa were underrepresented on frequently burnt (1–3 years) rail and road remnants, and speculated that annual burning in late spring and early summer may have resulted in their demise.

Based on the 'intermediate disturbance hypothesis' (Grime 1979), one might theoretically expect diminished species diversity in sites subjected to extremely high fire frequencies (e.g. annual burning). In practice this does not seem to occur. Many annually burnt sites are very species-rich and very important for grassland conservation (McDougall and Kirkpatrick 1994). This unexpected response might reflect the fact that annual summer fires may not act as a 'disturbance' for many species — if disturbance is interpreted as 'partial or total destruction of the plant biomass' (Grime 1979, p. 7) — since at the time of summer burning, most plants are reduced to dormant rootstocks at or below ground level, and thereby escape destruction by fire.

Only one study is available which compares the effects of frequent burning against the long-term exclusion of fire and other disturbances (e.g. grazing): an unreplicated comparison of a long-unburnt area and an adjacent, frequently burnt area of productive *Themeda* grassland in western Melbourne (Lunt and Morgan 1999c). The long-unburnt area remained unburnt for 17 years from 1978 until 1995, whilst the frequently burnt zone was burnt six times, at 2–5 year intervals, during this period. In 1997 the rarely burnt zone was dominated by exotic species (49% exotic cover cf. 40% native cover), whereas the frequently burnt zone was dominated by native species (72% cover) with just 7% exotic cover. The most dramatic differences in species abundances between the two zones were for the exotic daisy *Hypochaeris radicata* which attained 33% mean cover in the rarely burnt zone compared to just 1% in the frequently burnt zone, and *Themeda triandra* which attained 22% in the rarely burnt zone compared to 63% in the frequently burnt zone. The density of live *Themeda* tussocks in the rarely burnt area was only 30% of that in the frequently burnt zone (Lunt and Morgan 1999c). Thus, the long-term absence of burning appears to have killed many *Themeda* tussocks (as has been recorded elsewhere; Morgan and Lunt 1999) and promoted many perennial, exotic weeds.

Experimental fire studies

Apart from those studies which have described the outcomes of historical burning practices, most fire studies from temperate Australian grasslands have described short-term responses after single fire events. Few experimental manipulations of different fire regimes have been undertaken (Robertson 1985; Foreman 1996; Henderson 1999). Foreman (1996) conducted a replicated, small-plot experiment over 3 years to investigate the effects of burning, grazing and cultivation on a species-rich *Austrodanthonia* grassland in northern Victoria. Data were analysed by univariate statistics to describe changes in cover and density of functional plant groups (including annuals, perennials, forbs, grasses, exotics, natives). Burning reduced the cover
of all functional groups compared to the control treatment, including annual and perennial native and exotic species. The notable exception was an increase in abundance of the exotic geophyte, Romulea minutiflora. For annual species, in particular, the changes induced by burning were of lesser magnitude than those caused by climatic variations during the experiment (i.e. drought). It should be noted that these results are not necessarily transferable to larger paddock scales, since all above-ground vegetation was consumed with an oxygen/acetylene torch and much of the vegetation would not have carried a fire normally.

Despite considerable conjecture, little is known of the effects of burning in different seasons. In the conservation management literature, spring burning has often been suggested as a possible mechanism to deplete annual exotic species in invaded grasslands by reducing their flowering and seed set (e.g. Stuwe 1986; McDougall 1989). Over several years, repeated spring burning may exhaust seed supplies and deplete these species from the community. By contrast, autumn fire regimes may help to promote exotic annual grasses by providing competition-free sites for establishment. Few data are available to support these hypotheses.

In an early study, Robertson (1985) documented the short-term effects (over 3 years) of annual and biennial burning in a long-grazed and rather species-poor Eucalyptus camaldulensis–E. melliodora open woodland with Themeda triandra-dominated understorey west of Melbourne. Annual burning consistently maintained lower biomass and slightly greater richness of herbaceous species than biennial burning or unburnt controls. By 2 years after burning, biennially burnt plots were similar in structure and floristics to unburnt areas. However, few significant differences were observed between spring and autumn burning, which had similar effects.

An ongoing experimental study near Melbourne may address a number of important questions about the effects of frequency and seasonality of burning on species composition, structure and nutrient cycling in productive, species-poor Themeda grasslands (Henderson 1999; Wijesuriya and Hocking 1999). A preliminary report by Henderson (1999) demonstrated substantial differences in the post-fire weed flora according to fire frequency, with annual autumn burning leading to a marked reduction in the abundance of the large-seeded, exotic annual grass Briza maxima, compared to triennial autumn burning. Furthermore, the total cover of exotic annual species was markedly lower in annual burnt plots than under triennial burning or annual or triennial slashing (Henderson 1999). Further long-term experimental studies are obviously required to identify the effects of different fire regimes.

Synthesis

From the above review, it is clear that further research is needed to broaden our understanding of most aspects of fire ecology in remnant native grasslands. Some of the many topics which deserve attention include: experimental studies of ecosystem responses to particular fire regimes (especially to compare the effects of different fire frequencies and seasons); seedling recruitment (when does it occur, under what conditions, how does fire affect it, how often is it necessary?); and the effects of different fire regimes on grassland fauna and soil nutrient fluxes.

Despite our limited understanding of grassland ecology and fire effects, we have attempted to develop a simple conceptual model of how productive Themeda grasslands might respond to different fire regimes, based on the studies reviewed above. Insufficient information is available to generalise to other grassland ecosystems. Our model Themeda grassland possesses the following characteristics.

It is dominated by a vigorous perennial grass which rapidly outcompetes associated species through biomass accumulation. The many, smaller, inter-tussock species are primarily herbaceous perennials, which suffer minimal mortality of genets and ramets due to burning, and possess small, transient soil seed banks. Seedling recruitment is not directly promoted by fire, but instead is relatively rare and may require a combination of open gap conditions and uncommon climatic events. Most
plants die back to buds or tubers at or below ground level over summer. Climatic conditions permitting, plants flower and set seed abundantly when biomass levels are low. Most plants flower abundantly in the first spring after burning (climate permitting), and plant vigour and reproductive output decline as biomass levels accumulate. Ultimately, many plants die beneath a dense grass sward, and in the absence of a persistent soil seed bank, complete mortality of mature plants is irreversible, especially in small isolated remnants.

We do not wish to imply that all grassland species possess all of these characteristics (some certainly do not). However, apart from speculation about the conditions that might promote rare recruitment events, this character suite does appear to be shared by many grassland species in temperate Australia. It should also be noted that these characteristics are not necessarily shared by all grassy ecosystems, especially grassy woodlands and secondary grasslands with abundant shrubs. Frequent burning may deplete or eliminate woody species in these ecosystems.

What role might fire play in such a system? The major ecological force driving the model system is inter-specific competition, or more specifically, resource acquisition through biomass accumulation by the dominant grasses. Any activities which constrain the dominant grasses will facilitate coexistence of other subordinate species. This is Grime’s (1979) archetypical ‘competitive environment’. The primary role of burning would appear to be to reduce biomass accumulation and shoot competition from the dominant grasses. Fire is not critical to this process, since biomass can be removed or altered in structure in a number of ways, including burning, grazing and slashing. In relatively unproductive environments, accumulation rates may be so slow that no biomass reduction is necessary to maintain species richness and ecological processes. Furthermore, in this model ecosystem there appear to be few critical ecological processes that only fire can fulfil. Thus, burning may be more exchangeable as a management tool in grasslands than in other ecosystems such as heathlands or wet sclerophyll forests where critical ecosystem processes (such as fire-stimulated seed germination) can only be practically accomplished by using fire.

In the model system, the processes which take place between fire events (which are driven by grass dominance) are likely to have more impact on ecosystem structure and composition than the fire events themselves or their immediate after-effects. Fire frequency, and in particular, the variable ‘timesince-fire’, is likely to exert the most profound influence on grassland composition and structure (rather than other attributes of the fire regime, such as fire season or intensity), simply because fire frequency exerts the greatest influence on accumulated biomass and structural dominance. As time extends after fire and biomass levels accumulate, the potential reproductive output and survival of inter-tussock species declines. The longer the interval between fires, the lower the potential for future re-establishment and recruitment.

It is clear that far more ecological research is required to enable burning regimes to be confidently tailored to individual grassland remnants. In the meantime, however, many productive grassland remnants need to be continually burnt to prevent further declines in plant diversity. We hope that the insights provided here may help to stimulate more applied research to be undertaken and to avert diversity losses until future results become available.

References


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