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How do fire regimes affect ecosystem structure, function and diversity in grasslands and grassy woodlands of southern Australia?

Ian D Lunt, Suzanne M Prober and John W Morgan

Introduction

Grasslands and grassy woodlands are widespread across southern Australia, occurring in the transitional zone between forests in higher rainfall areas and the shrublands and hummock grasslands of the drier interior. The conservation status of grassy ecosystems in southern Australia varies from relictual fragments in intensively-used agricultural regions to well-conserved, intact ecosystems in the Australian alps. In this chapter, we briefly describe the distribution of grasslands and grassy woodlands in southern Australia, and then review three major ways in which fire regimes can affect the distribution, structure, dynamics and composition of these ecosystems. We ask three questions that have received considerable attention globally – to what extents do fire regimes in grassy ecosystems in southern Australia influence: (1) boundaries between treeless grasslands and timbered woodlands; (2) the cover or abundance of woody plants within grassy woodlands; and (3) the productivity, structure, function and diversity of ground vegetation in grasslands and grassy woodlands?

Ecosystem descriptions

This chapter covers native grasslands and grassy woodlands in southern Australia. Arid, subtropical and tropical ecosystems, and grassy woodlands dominated by genera other than *Eucalyptus* are excluded. We use the collective term ‘grassy ecosystems’ to refer to both grasslands and grassy woodlands. Southern grassy ecosystems extend in a broad arc from southern Queensland, through New South Wales and Victoria, to eastern South Australia. They also occur in Tasmania and south-western Australia (Yates and Hobbs 1997; DEWR 2007). Structurally, they range from low open woodland with less than 10% foliage projective cover in drier zones to tall woodland with up to 30% projective foliage cover in high rainfall regions (Yates and Hobbs 1997). In this review, we divide southern grassy ecosystems into three broad climatic categories: semi-arid, mesic and alpine/sub-alpine. Semi-arid grassy ecosystems occur in dry regions with around 200–400 mm mean annual rainfall, in all mainland states. Mesic grassy ecosystems occur in regions with 400–1000 mm mean annual rainfall, excluding sub-alpine and alpine areas. Mesic ecosystems range from the boundary of the semi-arid zone to tablelands and coastal regions in south-east Australia, and occur in all southern states. Mesic ecosystems are often referred to as ‘temperate’, but we avoid this term due to its variable usage. Sub-alpine and alpine ecosystems occur at high elevation (>915 m in Tasmania and >1370 m on mainland Australia: Williams and Costin 1994), and receive regular snow fall.

Two distinct understorey types occur in grassy woodlands: shrubby and grassy. Shrub understoreys predominate in semi-arid woodlands and on more skeletal soils in mesic regions (Yates and Hobbs 1997), and are not the focus of this chapter. Grassy understoreys support a ground-layer of annual and perennial grasses and forbs, with only scattered shrubs, and may also be called forb-rich woodlands if forbs are more prominent than grasses. They are common on relatively fertile soils, especially in mesic regions (Yates and Hobbs 1997). Sub-alpine woodlands support both grassy and shrubby understoreys depending on site factors and disturbance history (Williams and Costin 1994). Mesic grasslands generally occur on heavy soils in valley bottoms and plains (Kirkpatrick *et al.* 1995; Lunt and Morgan

2002; Keith 2004). These are most prominent in south-eastern Australia, although limited areas of mesic grasslands probably once occurred in south-western Australia (O'Connor 2001). At higher elevations, alpine grasslands occur above the tree-line and sub-alpine grasslands occur in frost hollows below the tree-line (Williams and Costin 1994). Small mesic grasslands also occur within eucalypt forest and rainforest mosaics in high rainfall (700–1800 mm) areas in eastern Australia (Ellis 1985; Fensham and Fairfax 1996; Stubbs 2001); these are referred to as 'grassy balds' in this review, following Fensham and Fairfax (1996).

Grasslands generally have a similar plant composition to the understorey in nearby woodlands. The perennial native grasses, *Themeda australis* (syn. *T. triandra*) and *Poa* species dominate understoreys in mesic, sub-alpine and alpine zones. Other native grasses – particularly *Austrodanthonia*, *Austrostipa* and *Enteropogon* species – are often dominant in semi-arid regions and in many mesic ecosystems, including those with less than 550 mm mean annual rainfall, poor soils, and following heavy grazing by livestock. Other distinctive grassy ecosystems occur in areas with heavy cracking-clay soils and summer-dominant rainfall, such as the Darling Downs of southern Queensland (Groves and Williams 1981; Keith 2004). Perennial forbs are abundant in grassy ecosystems in mesic and alpine regions, whereas native annuals and shrubs become more abundant in semi-arid regions.

Of all of Australia's major vegetation types, mesic grassy ecosystems have undergone the greatest decline since European settlement (DEWR 2007). Grassy ecosystems in agricultural regions have been fragmented and degraded by widespread clearing, cultivation, fertilisation and livestock grazing. Most remnants are weed-invaded and managed for purposes other than biodiversity conservation (Yates and Hobbs 1997). By contrast, grassy ecosystems remain more intact, and more native species persist, in regions with less extensive cropping and pasture improvement (McIvor and McIntyre 2002), especially in alpine areas. In sub-alpine and alpine regions, grassy ecosystems were historically grazed by livestock in summer until grazing controls were introduced over the last 50 years (Williams and Costin 1994). Most subalpine and alpine regions are no longer grazed by domestic stock.

Fire and grassland–woodland boundaries

Frequent burning maintains boundaries between treeless grasslands and wooded ecosystems in many regions around the globe (Backéus 1992; Bond 2008). However, the relative influence of top-down processes, such as fire, and bottom-up (resource-constrained) processes, such as soil water availability, on grassland boundaries has been debated for many decades (e.g. Sauer 1950; Bond 2008). In southern Australia, tree–grassland boundaries in lowland, montane and alpine areas may each be regulated by differing combinations of top-down and bottom-up processes.

Mesic grassy ecosystems

Mesic grassy ecosystems have been extensively cleared for agriculture, but pre-European boundaries between grasslands and woodlands are clearly shown on historical survey plans. Many early maps show sharp boundaries that accord closely with soil and topographic patterns (e.g. Fensham and Fairfax 1997; Lunt 1997). Mesic grasslands predominantly occurred on heavy clay soils, and many were subject to seasonal waterlogging and inundation (Beadle 1981; Kirkpatrick *et al.* 1995; Keith 2004). Morcom and Westbrooke (1998), for example, noted that treeless grasslands and timbered woodlands in the Wimmera in western Victoria occupied subtly distinct micro-topographic positions, with grasslands on low-lying clay soils and woodlands on slightly elevated areas that were inundated less frequently. Heavy, waterlogged and/or cracking clay soils constrain establishment of tree seedlings, particularly when combined with low–moderate rainfall (350–700 mm generally), summer droughts, low winter temperatures and, in some regions, frequent frosts. Consequently, bottom-up, soil and topographic processes are widely seen as the principal regulators of boundaries between mesic grasslands and woodlands at the time of European settlement, rather than fire or other top-down processes (Beadle 1981; Kirkpatrick *et al.* 1995; Keith 2004). By contrast, since European settlement, a wide variety of disturbances (i.e. top-down processes) have enabled grasslands to expand at the expense of woodlands, including clearing, cropping and heavy grazing.

Alpine and sub-alpine areas

In contrast to lowland grasslands, temperature controls boundaries of sub-alpine and alpine grasslands. Alpine grasslands occur above the climatic limit for tree growth. Globally tree-lines occur where the mean temperature in the growing season is 5.5–7.5°C (Körner and Paulsen 2004). In Australia, most tree-lines are between 1700 and 1950 m elevation (Moore and Williams 1976). Subalpine grasslands occur below the climatic limit for tree growth (mostly 1200–1650 m above sea level), where nocturnal cold air drainage creates intense frosts that kill tree seedlings (Moore and Williams 1976). Alpine tree-lines are extremely stable over century time periods, and they do not appear to move after individual fires (Green 2009; Rumpff 2009), except where heavy grazing after fire kills regenerating seedlings (Wimbush and Forrester 1988). Again, bottom-up processes appear to control this major ecosystem boundary.

Although alpine tree-lines appear to be controlled by climatic constraints, fires may affect boundaries between alpine shrublands and grasslands (McDougall 2003). Figure 12.1a provides a conceptual model summarising hypothesised dynamics between alpine grasslands and shrublands, based on published literature. Shrub-grass dynamics are cyclic, with grasses replacing shrubs over time in the absence of major disturbance. Disturbances that create bare ground, including fire, trigger the cycle of shrub regeneration, followed by establishment of grasses beneath senescing shrubs (Williams and Ashton 1988; McDougall 2003). As shrubs become more dominant, they can promote larger fires because shrubs are more flammable than alpine grasses (Williams *et al.* 2006). Future studies assessing the effects of recent wildfires will greatly increase our understanding of fire dynamics in alpine shrublands and grasslands.

Montane grassy balds

Fire may also contribute to the maintenance of grassy balds in high rainfall (700–1800 mm), montane areas in eastern Australia (Ellis 1985; Fensham and Fairfax 1996; Stubbs 2001). These small grassland patches occur within mosaics of eucalypt forests and rainforests. It has been speculated that these grassland patches are ‘Pleistocene relicts’ that have been progressively invaded by forests over the past 10 000 years, except where frequent burning by Aborigines has prevented tree encroachment (Webb 1964; Fensham and Fairfax 1996). Alternatively, grassland patches may have been created more recently, by forest disturbances (e.g. fire, wind or frost) followed by repeated Aboriginal burning that prevented tree encroachment (Ellis 1985; Stubbs 2001; Fensham and Fairfax 1996; Fairfax *et al.* 2009). Notably, grassy balds are largely restricted to mountain regions supporting fire-sensitive rainforests, and are absent from many other forest areas. This suggests that balds may represent a transitional state derived from fire-sensitive rainforests rather than from eucalypt forests (Ellis 1985).

In contrast to other continents, we conclude that the distribution of extensive grasslands in southern Australia at the time of European settlement was primarily controlled by bottom-up, resource constraints, rather than fire (a top-down disturbance). Fire has been a conspicuous component of Australian ecosystems for at least 15 million years (Kershaw *et al.* 2002) and, during this period, the genus *Eucalyptus* has evolved a formidable array of characteristics that enable populations to dominate under a wide range of fire regimes (Gill 1997). Adaptations include a long (>200 year) lifespan, thick fire-resistant bark, epicormic buds, fire-resistant seed capsules and a basal lignotuber (Gill 1997; Burrows 2002). Consequently, tree-less grasslands appear to be largely restricted to environments that exceed the physiological tolerance of eucalypts. The most notable constraints are: (1) a combination of climate-edaphic and competitive interactions on heavy clay soils on lowland plains; and (2) low temperatures in alpine areas.

Fire regimes and woodland structure

Globally, rainfall and temperature are the principal determinants of maximum potential primary productivity in woodlands and forests (Sankaran *et al.* 2005). However, frequent fires and other disturbances can reduce woody plant cover and biomass below their climatic potential (Bond and

Keeley 2005; Sankaran *et al.* 2005). Consequently, many areas of the globe support vegetation that is more open than would be expected climatically (Bond and Keeley 2005).

Much of the evidence for fire-induced constraints on the cover of woody plants has come from evidence of encroachment by woody plants following reductions in fire frequency. Woody plant encroachment has been widespread across the globe over the past 100–200 years (Scholes and Archer 1997; Asner *et al.* 2004). The most commonly cited mechanism involves a reduction in fire intensity, frequency and size, which is caused by heavy grazing of grass fuels, usually by livestock. Lower fire occurrence, in turn, increases the establishment and longevity of woody plants, particularly of species unpalatable to livestock (Noble 1997; Scholes and Archer 1997; Asner *et al.* 2004). A number of positive feedback loops reinforce this process, including: (1) competitive suppression of grasses by woody plants, which further reduces fuel loads and fuel connectivity, and (2) increased seed production by larger populations of woody plants, which further promotes encroachment. Depending on the strength of positive feedback loops, alternative stable states may develop (e.g. dense shrubland cf. open grassy woodland), which cannot easily be reversed within management timeframes (Suding *et al.* 2004).

Did pre-European fire regimes deplete woody plants below climatically and edaphically determined maxima in southern Australian woodlands? Unfortunately, this question is difficult to answer because there is little quantitative information on pre-European vegetation patterns (i.e. basal area and cover of woody plants) or pre-European disturbance regimes in grassy ecosystems. This uncertainty has promoted many popular debates about how woodland stand structures have changed since European settlement. In the following section, we describe observed changes in woody plant abundances in semi-arid and mesic woodlands, and how fire regimes may have contributed to these changes.

Semi-arid woodlands

Woodland stand structures in semi-arid woodlands at the time of European settlement are poorly described. In some semi-arid regions, such as the Great Western Woodlands of Western Australia, woodland understoreys appear to be naturally shrub-dominated (Hobbs 2002). In others, archival records document widespread recruitment by woody plants since European settlement, including *Acacia*, *Callitris*, *Dodonaea*, *Eremophila* and *Senna* species (Noble 1997). This has been particularly prominent on the Cobar-Byrock Pediplain of western New South Wales (Noble 1997). This process is widely interpreted by the global model of semi-arid encroachment by woody plants (Figure 12.1b). Thus, heavy grazing by livestock depleted the grass cover, which reduced competition against shrub seedlings and prevented landscape fires, leading to widespread, pulsed recruitment of woody plants (Hodgkinson and Harrington 1985; Noble 1997). Additionally, trees were ringbarked across large areas in the late 1800s and early 1900s, further reducing competition against encroaching shrub species (Noble 1997).

Events surrounding periods of high rainfall appear critical in regulating this dynamic. Shrub recruitment is restricted to periods of high rainfall because seedlings require high levels of soil moisture in summer. Harrington (1991) estimated that there were only six opportunities for mass seedling recruitment during the previous century. On the other hand, high rainfall also promotes vigorous growth of grasses, which provides contiguous fuel for landscape fires. Large fires can only occur after wet years, when grass biomass is high (Hodgkinson and Harrington 1985). Consequently, potential control of shrubs using fire is restricted to intermittent ‘big grass’ years. However, dense shrubs can inhibit fire propagation (Harrington 1979) by restricting grass growth (Walker *et al.* 1972), although the magnitude of this effect is poorly quantified. Reduced flammability of dense shrub stands thus allows the development of ‘alternate stable states’, whereby positive feedback loops prevent encroached stands from returning to open, grass-dominated conditions (Suding *et al.* 2004).

We note that shrub encroachment associated with fire suppression in semi-arid woodlands appears counter to that in alpine grasslands, where encroachment may be driven by increasing fire (Figure

12.1). This could be due to differing flammability of shrubs and grasses in the two ecosystems and differing spatial arrangements of fuels. In semi-arid woodlands, dense stands of shrubs, such as *Callitris*, *Dodonaea* and *Eremophila* species, are less flammable than grass swards (Harrington 1979; Cohn *et al.* 2011), so shrub encroachment reduces fire intensity and spread. By contrast, in the alps, shrub cover may be continuous and shrubs are more flammable than the grass swards, so encroaching shrubs increase potential fire frequency and spread (Williams *et al.* 2006). As well, the consequences of fire on shrub establishment may differ. Increasing bare ground after fire in alpine areas will promote shrubs, whereas in semi-arid woodlands, shrub establishment is limited to periods of high rainfall.

Mesic woodlands

A number of studies have documented the establishment of dense stands of trees and shrubs in recent decades in mesic woodlands (reviewed in Lunt *et al.* 2010). These examples of woody plant encroachment are thought to be caused by different processes than occur in rangeland areas. In mesic woodlands, dense recruitment of woody plants has often followed reductions in European disturbances, especially livestock grazing, as illustrated by the following scenario. Mesic eucalypt woodlands are assumed to have had a relatively open canopy and grassy understorey before European settlement. Most fragmented remnants have rarely been burnt since European settlement, owing to habitat fragmentation, fire suppression and heavy grazing by livestock (Lunt and Bennett 2000; Parsons and Gosper 2011). In contrast to semi-arid woodlands, heavy (often continual) livestock grazing in mesic woodlands prevented, rather than promoted, recruitment of woody species (Fischer *et al.* 2009). Dense recruitment of woody plants has often occurred where livestock (and other human disturbances) have been removed from mesic woodlands, and fires have remained infrequent. For example, Franco and Morgan (2007) reported that the understorey shrub *Acacia paradoxa* increased from 8% to 42% cover between 1972 and 2002 in a mesic woodland in southern Victoria, following the removal of livestock grazing and regular soil disturbance. This process is more akin to successional models in the 'land abandonment' or 'old-field' literature (Cramer and Hobbs 2007) than to the semi-arid model of woody plant encroachment (Figure 12.1b).

Unfortunately, few studies have compared stand basal area between pre-settlement and current time periods in mesic woodlands. Without this information, we cannot make inferences about the degree to which fire regimes (or other processes) constrained tree stocking levels in pre-settlement woodlands below climatic and edaphic limits. Comparisons of tree density between current and pre-settlement periods are not particularly informative, because a dense stand of small trees may thin slowly to form an open stand dominated by fewer, large trees, as may have existed at the time of European settlement. Lunt *et al.* (2006) compared basal area between pre- and post-settlement periods in *Eucalyptus*–*Callitris* woodlands at the overlap zone between semi-arid and mesic woodlands in central New South Wales. Stand basal area increased by 46% over the period, from 10.7 to 15.6 m² ha⁻¹. Some of this increase may be due to an under-estimation of original tree densities (due to decomposition of stumps). However, the results suggest that there has been a substantial increase in basal area following *Callitris* establishment, consistent with the semi-arid encroachment model. Unfortunately, no comparable studies have been conducted in mesic woodlands that receive higher rainfall.

A notable feature of the woody plant literature from mesic woodlands is the lack of studies that have experimentally manipulated fire regimes. Indeed we are aware of only two studies that used 'natural experiments' (and none that used planned experiments) to compare woody plant densities across areas with different fire histories (Kirkpatrick 2004; Watson *et al.* 2009). Watson *et al.* (2009) found that the native shrub *Bursaria spinosa* was more abundant in rarely burnt woodlands than in woodlands that had been burnt every 10 years or more frequently. Additionally, little information is available on the successional dynamics of many woody plants, which hinders predictions of long-term dynamics in encroaching mesic woodlands.

To summarise, there is good evidence that historical changes to fire regimes, in combination with intensive grazing, caused substantial changes to the stand structure of many semi-arid woodlands. These structural changes and driving mechanisms are consistent with the global literature on woody

plant encroachment in semi-arid areas (Figure 12.1b). By contrast, there is little compelling evidence that historical changes to fire regimes caused substantial changes to the structure of most mesic woodlands, perhaps because other concurrent disturbances, such as heavy grazing by livestock, also affected stand dynamics. In the absence of robust, natural or planned experiments, the impacts of current fire regimes on woody cover in mesic woodlands remain highly speculative.

Fire effects on grassy ground vegetation

In this section, we focus on the herbaceous vegetation, dominated by grasses and forbs, that occurs in grasslands and in the understorey of grassy woodlands. In highly productive sites, grasses can produce abundant plant material that, when dry, provides a readily combustible fuel. Consequently, rates of grass production strongly influence potential fire regimes. In addition to fuelling fires, accumulated plant material (live and dead) regulates many ecosystem functions, including nutrient cycling, population dynamics, plant diversity and animal habitat (Knapp and Seastedt 1986). Consequently, fire regimes can indirectly influence the function, structure and composition of grassy ecosystems by altering herbaceous biomass (Figure 12.2a; Knapp and Seastedt 1986).

Rates of biomass accumulation are dictated by the rates of primary production and decomposition, both of which are regulated by climate and, at smaller scales, by soil fertility (Lauenroth and Sala 1992; Aerts 1997). As a result, productivity gradients controlled by climatic and edaphic factors regulate: (1) potential fire regimes (by controlling fuel levels); (2) the degree to which fire is important for maintaining plant diversity and ecosystem function; and (3) the resilience of grassy ecosystems to fire (by influencing recovery rates and functional composition). This interplay between productivity, accumulated biomass and fire means that variations in fire regimes may have more substantial impacts in high-productivity grasslands than in low-productivity grasslands. In high-productivity grasslands, different fire regimes can lead to large variations in biomass and ecosystem processes. By contrast, in low-productivity grasslands, biomass accumulates more slowly and has less impact on ground flora. Additionally, the slow rate of biomass accumulation in low-productivity grasslands reduces fire frequency and intensity, so variations in fire regimes may have less impact than in high-productivity grasslands. By contrast, slow recovery rates may reduce the resilience of low-productivity grasslands to frequent fires or other disturbances.

In the following section we ask how fire regimes affect the structure, function and diversity of the herbaceous understorey in southern grassy ecosystems. We compare the responses of ecosystems of low and high productivity, and summarise our conclusions in Figure 12.2. We restrict this review to lowland ecosystems, given the paucity of fire research in alpine grasslands in Australia.

Rates of biomass accumulation

Surprisingly few studies have compared rates of productivity or biomass accumulation across natural grassy ecosystems in southern Australia. An exception is Schultz *et al.* (2011), who compared long-term biomass accumulation in undisturbed (ungrazed and unburnt) grassy ecosystems across Victoria. Biomass varied more than 30-fold among sites: from 28 g m⁻² to 944 g m⁻². It accumulated fastest on fertile soils in high rainfall areas, and was lower than otherwise expected beneath trees. Dead grass litter accumulates rapidly in mesic *Themeda* grasslands (Morgan and Lunt 1999; Prober *et al.* 2007), but does not accumulate over long periods in drier grasslands; instead, it appears to decay (or blow away) relatively quickly. For example, Conway (2000) found that litter cover declined from over 50% to less than 10% in a single year during drought in northern Victoria. Despite lower soil moisture, decomposition can be rapid in semi-arid grasslands owing to abiotic processes and photochemical degradation by UV light (Vanderbilt *et al.* 2008).

Fires, biomass and ecosystem functioning

As elsewhere across the globe, accumulated vegetation greatly affects ecosystem processes in grassy ecosystems of high productivity in southern Australia. Rates of soil biological activity, decomposition

and soil turnover by invertebrates are faster in dense, undisturbed *Themeda* swards than in frequently burnt swards, possibly because of greater soil moisture beneath the former (Prober *et al.* 2008; O'Bryan *et al.* 2009). Consequently, soils beneath closed swards may be less compacted and have faster infiltration rates than those beneath open swards (Prober *et al.* 2008). On the other hand, closed swards reduce the amount of sunlight that reaches the soil surface, reducing soil temperatures (Lunt 1995). Rates of seed germination, seedling establishment, emergence from subterranean organs, plant growth, flowering and seed production by many species can also be lower in closed swards (reviewed in Lunt and Morgan 2002). Accumulated litter also affects growth of dominant grasses. In highly productive, undisturbed grasslands, *Themeda* swards can suffer widespread senescence (with up to 75% mortality of tussocks) as live tissues are 'smothered out' by dense litter (Morgan and Lunt 1999).

Although fire regulates biomass, biomass is also likely to regulate fire frequency and intensity in intact (i.e. non-fragmented) grassy ecosystems (Figure 12.2). Compared with other ecosystems, fire intensities in remnant *Themeda* grasslands are usually low (99–1147 kW m⁻¹) owing to benign weather conditions at the time of prescribed burning (Morgan 1999). By contrast, fire intensities in northern Australia savannas can reach 18 000 kW m⁻¹ (Williams *et al.* 1998). Surface soils reach high temperatures for short periods during fires (350–525°C for <5 minutes), but deeper soils are minimally affected (<10°C increase at 10 cm depth: Morgan 1999; Bennett *et al.* 2002). Consequently, fires may kill surface tissues, shallow buds and seeds, but not deeper roots or rootstocks.

The effects of fires on soil chemical properties are poorly documented in southern grassy ecosystems, but appear to be minor. Experimental fires in a mesic *Themeda* grassland marginally increased levels of soil ammonium, nitrate and available phosphorus at 1–2 years after burning, but repeated low-intensity fires had no impacts on total nitrogen or carbon after 12 years (Prober *et al.* 2008). Even at the opposite extreme of the productivity gradient (in a semi-arid, sub-tropical *Themeda* grassland), single fires had negligible effects on soil chemical properties immediately after burning, including total nitrogen and phosphorus (Bennett *et al.* 2002). On the other hand, high frequency fires (every 1–2 years) can expose bare soils to the elements, which promotes soil crusting and compaction, and reduces water infiltration, soil biological activity and consequent grassland productivity (Prober *et al.* 2008). These changes are driven by insulation *between* fires, rather than fire *per se*, and are likely to result from any disturbances that create open bare soils (e.g. heavy grazing).

Fire effects on microphytic crusts, which can reduce soil erosion, vary across the productivity gradient. In a semi-arid woodland, fire greatly reduced cryptogam cover (predominantly lichens), which took 4 years to return to pre-fire levels (Greene *et al.* 1990). By contrast, cryptogams in mesic grasslands recover rapidly after fires, and cover may rapidly exceed levels in undisturbed areas due to reduced competition from dominant grasses (Ferguson *et al.* 2009; O'Bryan *et al.* 2009). Thus, Morgan (2006) reported that bryophytes attained over 80% cover 3 months after burning, and Ferguson *et al.* (2009) found that bryophyte cover 3 months after a low-intensity fire was twice that in unburnt plots. Thus, frequent fires appear to have little impact on soils and long-term productivity in mesic grassy ecosystems, except under the highest frequencies (1–2 years) where – in some areas at least – soil productivity declines owing to prolonged soil exposure to sunlight and rainfall (Prober *et al.* 2008).

Functional composition of herbaceous species

Fire regimes may also alter ecosystem functioning by influencing the abundance of species with different functional traits (e.g. C4 versus C3 grasses, annuals versus perennials). In mesic ecosystems co-dominated by C4 *Themeda* and C3 *Poa* species, dominance ratios are strongly dependent on fire frequency, with the C4 *Themeda* increasing under more frequent fires and C3 *Poa* increasing in the absence of fire. These, in turn, influence resilience to repeated fire, with lower resilience in *Poa*-dominated ecosystems (Prober *et al.* 2007). The impacts of these shifts on other ecosystem functions, such as biomass accumulation and subsidiary plant diversity, require further investigation.

Fire can also promote exotic C3 annuals. In intact *Themeda* grasslands, exotic annuals are generally sparse owing to low levels of phosphorus and available nitrogen (Morgan 1998; Prober *et al.* 2002). Fires may temporarily promote exotic annuals, but do not promote a large increase in their biomass because exotics remain constrained by low nutrient levels (Prober *et al.* 2008). In degraded ecosystems, where exotic annuals are more persistent, fire can be used to manipulate weed seed banks and establishment conditions, to favour re-establishment of native grasses. In particular, burning in spring, before exotics set seed, can reduce the abundance of exotic annual grasses in subsequent years by destroying seeds held in the plant canopy (Prober *et al.* 2004). Interestingly, Henderson (1999) found that annual burning in autumn also reduced the cover of exotic annuals, compared with triennial autumn burning. The mechanism by which this reduction occurred is unknown. Fire-induced reductions in exotic annuals are usually temporary unless perennial species achieve dominance.

Diversity of herbaceous species

Fires and other disturbances are expected to have contrasting impacts on plant diversity at opposite ends of the productivity gradient (Huston 1979, 2004). In highly productive environments, large dominant species (usually grasses) can monopolise resources and competitively exclude smaller species. Disturbances can promote plant density and diversity by constraining potentially dominant species, unless disturbances occur too frequently for species to withstand. The intermediate disturbance hypothesis predicts that species density will be low at extremely high and low disturbance intensities or frequencies, and high at 'intermediate' levels (Grime 1973). By contrast, competitive exclusion is less critical in low-productivity systems, because low resource levels restrict the growth of all species, including potential dominants. Huston (1979, 2004) predicted that 'mortality-causing disturbances' would promote diversity in high-productivity systems by preventing competitive exclusion by dominant species, but would reduce diversity in low-productivity systems by increasing the mortality of slow-growing species. This prediction has been supported by experiments and meta-analyses of data from marine, freshwater, and terrestrial ecosystems (Hillebrand *et al.* 2007).

Data are inadequate to test these predictions in grassy ecosystems in southern Australia, but inferences can be made from a number of observational studies and experiments. It has long been recognised that frequent fires can maintain native plant diversity in mesic *Themeda* grasslands by reducing shoot competition (Stuwe and Parsons 1977; Lunt and Morgan 2002). In a 3-year experiment in a mesic grassy woodland, Robertson (1985) found that small-scale richness of plant species increased with increasing fire frequency, and did not decline under the highest fire frequency possible (annual burning). Instead, annual burning consistently maintained lower biomass and slightly higher species richness than biennial burning or unburnt controls. Morgan (1999) concluded that burning was unlikely to lead to a decline in species richness or density in *Themeda* grasslands that were burnt annually because most perennials avoided summer fires by being dormant at the time of burning; thus, annual fires do not necessarily constitute a 'mortality-causing disturbance' *sensu* Huston (1979, 2004). Similarly, O'Bryan *et al.* (2009) found that burning every 2 years led to an increase in cryptogam diversity compared with lower fire frequencies.

Unpublished data from a recent 11-year fire experiment, however, suggests that fire impacts on diversity may vary according to longer term fire history and/or functional composition of the dominant grasses. In a *Themeda*-dominated site that was historically burnt every 4–8 years, fire exclusion for 12 years led to a decline in native species richness and forb abundance. By contrast, in a nearby *Poa*-dominated site that had remained unburnt for over 60 years, native forb abundance remained high when unburnt, but declined when burnt every 2 years (Prober and Thiele *pers. comm.*).

From this, we conclude that fire regimes maintain or increase plant diversity in highly productive *Themeda* grasslands, even under very frequent burning (every 1–2 years). Although some fire-sensitive species may have been eliminated long ago, repeat surveys of sites that were frequently burnt during the 20th century show that extinction rates have been greatest where fire frequencies have declined in recent decades (Williams *et al.* 2006).

Unfortunately, little information is available from low-productivity grasslands dominated by species other than *Themeda* and *Poa*. In a 3-year study, Foreman (1996) compared the effects of a single fire (in year 1) against annual burning (in years 1–3) on the richness of native and exotic species in low-productivity *Austrodanthonia* grasslands. Both fire regimes reduced richness of exotic (but not native) species compared with undisturbed controls, but there was no significant difference between the two burning treatments. Thus, consistent with theory, burning did not promote plant richness in this low-productivity grassland, presumably because fires did not greatly alter the cover of dominant grasses (*Austrodanthonia* spp.), which had relatively low biomass before burning. Potential adverse effects of frequent burning on low-productivity grasslands are poorly documented, but frequent fires may lead to a decline in resource levels due to slow rates of post-fire recovery (Greene *et al.* 1990; Prober *et al.* 2008).

To summarise, Australian grasslands appear to operate like grasslands elsewhere in the world. Productivity is controlled by climate and soil fertility. Fires predominantly affect grassland functioning by consuming biomass, and thereby altering the availability of resources and competitive interactions (Figure 12.2). Although data are meagre (especially for low-productivity grasslands), grassland fires appear to have little direct impact on soil chemistry, and physical changes to soils induced by different fire regimes seem to be largely mediated by insolation between fires. In highly productive grasslands, plant abundances can decline in the absence of fire (or other disturbances); declines in plant diversity are widely assumed, but are poorly documented. In contrast to expectations under the intermediate disturbance hypothesis, plant diversity does not appear to always decline under very high fire frequencies, perhaps because fire-induced mortality is low. In less-productive environments, the resilience of grasslands to fire and the effects of fire on diversity are poorly understood.

Fire and climate change

Climate change is likely to affect all aspects of grassy ecosystems in southern Australia, both directly and indirectly via a multitude of interacting and cascading ecosystem processes (Dunlop and Brown 2008; Williams *et al.* 2009). Climate change will alter fire regimes, which will cause vegetation changes, which, in turn, will lead to further changes in fire regimes. Although considerable uncertainty surrounds future climate predictions – especially rainfall – higher temperatures, lower mean annual rainfall and changing rainfall seasonality are expected (CSIRO 2007; IPCC 2007). Climate change is likely to increase the frequency of severe fire weather in many regions (Lucas *et al.* 2007), but will also influence the distribution of fuels through its influence on vegetation structure and productivity. The net result is difficult to predict. Where rates of biomass production decline, fire intensity (and perhaps frequency) may decline, despite more frequent, severe weather events (Bradstock 2010). However, in agricultural and urban regions, where fires are rare and rapidly suppressed, changes in fire weather and fuel loads may not affect ultimate fire regimes.

Grassland–woodland boundaries

Because most grassland–woodland boundaries appear to be controlled by climatic and edaphic factors, climate change is likely to affect grassland–woodland boundaries directly. Increasing temperatures may promote expansion of trees into alpine grasslands and sub-alpine ‘frost hollow’ grasslands (e.g. Wearne and Morgan 2001), and reduced waterlogging might enable trees to establish in some lowland grasslands. Likely fire-mediated changes are more difficult to predict. Hotter, drier conditions could promote more frequent alpine fires, enabling shrublands to expand into alpine grasslands (Williams *et al.* 2006). As well, fire may hasten expansion of grasslands into woodland areas if soil moisture deficits are sufficient to cause extensive tree dieback, especially in semi-arid woodlands (Fensham *et al.* 2009). However, in fragmented grasslands in lowland areas and grassy balds in high-rainfall areas, where fire regimes are actively controlled by people, woodland–grassland boundaries may not be greatly affected by climate-driven changes to fire regimes.

Woodland structure

Climate change will affect woodland structure in complex ways. A number of processes are expected to promote shrubs. Rising CO₂ may directly favour C3 woody species above herbaceous species (Bond and Midgley 2000; Hovenden and Williams 2010). This, in turn, will affect fire regimes, depending on the relative flammability of dominant shrubs and grasses, potentially promoting shrubs in alpine and semi-arid ecosystems via the various pathways shown in Figure 12.1. In montane and sub-alpine woodlands, higher temperatures may enable more frequent fires by reducing fuel moisture content (Bradstock 2010), further promoting shrub invasion into alpine grasslands (McDougall 2003).

On the other hand, some processes could limit CO₂-induced shrub encroachment. In drier regions, establishment and growth of woody species may be hindered by the severity of hot, dry conditions (Vesk and Dorrough 2006; Fensham *et al.* 2009). Further, in regions with a Mediterranean climate, some climate scenarios suggest an increase in summer rainfall, despite an overall decline in rainfall (CSIRO 2007). This could promote intermittent growth of warm-season grasses, leading to a build-up of ground fuels, which may lead to an increase in fire frequency. This scenario is considered a serious threat to the shrubby Great Western Woodlands in semi-arid Western Australia, where many overstorey trees are fire-sensitive.

Grassy ground vegetation

Climate change is also likely to affect the balance between productivity, disturbance and diversity in grasslands and woodland understoreys. Drier conditions are likely to slow the rate of biomass accumulation, which may lead to a lower propensity for fire, less need for fire to maintain the diversity of ground plants, and perhaps a lower resilience to repeated fires. Increasing concurrence of fire and moisture stress may also lead to more frequent failure of seedling recruitment of forbs and grasses, and increased plant mortality (Prober *et al.* 2007; Hovenden *et al.* 2008).

In contrast to changes in lowland ecosystems, higher temperatures in alpine areas may lengthen the growing period and promote increased grass dominance and productivity in the absence of fire, especially in habitats with relatively short growing seasons such as snow-patch herblands (Edmonds *et al.* 2006). This could lead to a decline in plant diversity at patch and landscape scales (i.e. a decline in alpha and beta diversity).

Conclusion

In this chapter, we have highlighted the role of fire in regulating grassland–woodland boundaries, woodland structure, and grassland function and diversity in southern Australia. From the limited data available, Australian grassy ecosystems generally operate like grassy ecosystems elsewhere in the world. Apparent exceptions include the relatively small influence of fire on grassland–woodland boundaries, and the potential for plant diversity to be maintained under very high fire frequencies in highly productive grasslands. However, our confidence in these conclusions is tempered by the paucity of experimental studies in many grassy ecosystems in southern Australia, especially studies stratified across climate-regulated productivity gradients. Such studies would also provide a far stronger basis from which to predict impacts of climate change on southern grassy ecosystems. This need is especially critical in fragmented grassy ecosystems that are currently subjected to numerous ecosystem stresses.

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Figure 12.1. Conceptual models contrasting hypothesised (a) alpine and (b) semi-arid shrub-grass dynamics, as influenced by fire regimes, climate and major disturbances. Central components shared by both systems are shown in black. **Alpine dynamics:** (a) increased [CO₂] promotes growth of C3 shrubs; (b) flammable shrubs promote fires, which (c) create gaps that promote shrub establishment; (d) heavy grazing reduces grass cover, which (e) creates gaps that promote shrub establishment; (f) grasses re-establish beneath shrubs over the long-term; (g) low rainfall (during drought) and (h) higher temperatures (global warming) reduce fuel moisture levels, which (i) promotes fire intensity and spread. **Semi-arid dynamics:** (a) irregular high rainfall promotes grass growth; (b) dense grass restricts woody plant recruitment, but (c) promotes fire spread; (d) fire kills seedlings and mature plants of some woody species; (e) irregular high rainfall promotes woody plant establishment, which, in the absence of fire, (f) promotes cover of woody plants; (g) increased [CO₂] may also promote growth of C3 woody plants; (h) dense woody plants and (i) heavy grazing restrict grass biomass; which (c) reduces fire frequency and spread; (j) fire suppression and/or landscape fragmentation further restrict fire spread.

Figure 12.2. Conceptual models hypothesising interactions between resources, fires and grassland structure, function and diversity in: (a) mesic and (b) semi-arid grassy ecosystems. Arrow widths indicate process strength. Large arrows (at bottom) highlight contrasting process directions in the two systems. Major processes in **mesic systems:** (a) Climatic-edaphic resources regulate productivity and decomposition, which control biomass accumulation, which, in turn (b) controls fires that (c) reduce biomass levels; (d) accumulated biomass strongly regulates available resource levels, which (e) control plant composition and diversity. **Semi-arid systems:** (a) Climatic-edaphic resources, especially intermittently high summer rainfall, regulate biomass accumulation, which (b) controls fire regimes. In contrast to mesic systems, (c) dense biomass accumulation is more limited by low productivity than by fire frequency, and (d) accumulated biomass may maintain resource levels by reducing soil insolation and enhancing infiltration; potentially reducing resource losses through erosion; that is, the reverse of process (a).