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Fire frequency regulates tussock grass composition, structure and resilience in endangered temperate woodlands

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Abstract The importance of disturbance for regulating the structure and diversity of grassy ecosystems is widely recognized, but disturbance-mediated interactions between grassland composition and grassland resilience, and consequent implications for conservation management, are less well documented. We established replicated burning, mowing and (non-livestock) grazing regimes in two contrasting grassy woodland remnants in south-eastern Australia, and monitored the dynamics and resilience of the matrix-forming tussock grasses, *Poa sieberiana* (*Poa*) and *Themeda australis* (*Themeda*), over twelve years. Introduction of frequent burning to a *Poa*-dominated understorey in a rarely-burnt woodland enhanced dominance by *Themeda*, and conversely, reduced fire frequency in a frequently-burnt *Themeda* grassland substantially increased *Poa* abundance. Burning was potentially detrimental in the *Poa*-dominated woodland, but sward resilience (recovery after the 2002 burn) increased as *Themeda* increased with repeated burning. By contrast, the *Themeda* grassland was resilient to 4 and 8-yearly burning, but biennial burning led to poor resilience and high tussock mortality under drought conditions. Contrary to other mesic grasslands, cessation of burning had not caused sward collapse by 14 years post-fire despite high litter accumulation, potentially due to compensatory growth of *Poa*, lower site productivity and drought. Biennial mowing without slash removal was similar to 4-yearly burning in effects, while exclusion from kangaroo and rabbit grazing significantly increased sward biomass and contributed to increased *Poa* cover and inflorescence production. We conclude that functional complementarity associated with mixed dominants enhances resilience to variable disturbance regimes, and that below certain thresholds of abundance of each dominant, this resilience declines. Conservation management of *Themeda-Poa* ecosystems should thus aim to maintain an effective balance of these dominants.

Key words: disturbance, functional diversity, grasslands, mowing, *Themeda*, thresholds

INTRODUCTION

The importance of disturbance for regulating the diversity and structure of grassy ecosystems is recognized worldwide (McNaughton 1985; Collins & Wallace 1990; Belsky 1992; Noy-Meir 1995; Grime 2001; Lunt & Morgan 2002). At local scales, grasslands are often dominated by a few abundant, matrix-forming species, particularly graminoids (Collins & Gibson 1990), and the dynamics of these dominants can be pivotal in the response of the grassland to disturbance. In productive grasslands and grassy woodlands, reducing the biomass of the dominant matrix to maintain an open structure is often considered critical for maintaining sward health and subsidiary plant species diversity (Collins & Gibson 1990; Belsky 1992; Morgan & Lunt 1999), and lack of disturbance can lead to excessive litter accumulation and reduced plant productivity, at times resulting in ecosystem collapse and weed invasion (Knapp & Seastedt 1986; Morgan & Lunt 1999). At the other extreme, productivity can be reduced by poor resilience of dominants to the disturbance regime (Bennett *et al.* 2002). As well as directly influencing sward structure and productivity, disturbance can alter the species composition of the dominant matrix, reflecting the resilience of potential dominants to the disturbance regime. This can lead to more complex and potentially compensatory interactions between disturbance, vegetation composition, and grassland resilience (the ability of ecosystem properties to recover from disturbance), and optimizing these interactions provides an important challenge for conservation management (Collins & Gibson 1990; Belsky 1992; Menges & Hawkes 1998; Lavorel 1999).

Temperate lowland grasslands and grassy woodlands dominated by the tussock grasses *Themeda australis* (R. Br.) Stapf and/or *Poa sieberiana* Spreng. were once widespread and common in the more mesic regions of the wheat-sheep belt of south-eastern Australia (>550mm rainfall, Prober & Thiele 2005). These ecosystems have become seriously threatened through extensive clearing and agricultural development, and an understanding of

their response to disturbance is critical for guiding conservation and restoration efforts (Lunt & Morgan 2002; Prober & Thiele 2005). Since European settlement, a broad range of disturbance regimes have been introduced, the most pervasive being set-stocking with domestic livestock. The effects of set-stocking are increasingly well-documented, and provide an illustration of potential interactions among disturbance, vegetation composition and resilience that influence biodiversity management. Set-stocking modifies the dominant matrix from a mix of tall perennial tussock grasses, typically *Themeda australis* and *Poa sieberiana*, to a sward of more grazing-tolerant native perennial grass species and an increasing abundance of exotic annuals (Moore 1953; Moore 1993; Prober & Thiele 1995). These changes enhance the resilience of the grassy sward to livestock grazing, but in turn influence optimal disturbance regimes for subsequent maintenance of native plant diversity and biomass control (Kirkpatrick *et al.* 2005; Prober & Thiele 2005).

The dynamics of *Themeda-Poa* communities in relation to natural disturbance regimes are less well understood. Marsupial grazing, disturbance by fossorial mammals and fire are thought to have been the major forms of disturbance in *Themeda australis* ecosystems prior to European settlement (Lunt & Morgan 2002; Martin 2003), and as in African and American grasslands, are likely to have interacted to form a complex disturbance regime influencing patch structure and community diversity at a range of scales (Collins & Gibson 1990; Belsky 1992). Effects of fossorial mammals are unlikely to be easily elucidated, owing to the near-extinction of such species from these ecosystems (Lunt & Bennett 1999; Martin 2003). Several studies of woodland vegetation in south-eastern Australia have indicated damaging effects of preferential marsupial grazing after burning (Leigh & Holgate 1979; Meers & Adams 2003), and detrimental effects of kangaroos on establishment of *Themeda australis* and woodland trees (Allcock & Hik 2004). However the more general effects of marsupial grazing on the structure and composition of Australian grassy ecosystems remain poorly known.

Fire is a practical management tool relevant to the conservation and restoration of temperate Australian grasslands and grassy woodlands, but limited information on fire regimes is available to inform land managers (Lunt & Morgan 2002). Only two prior studies have experimentally manipulated fire frequency (Robertson 1985; Henderson 1999), and both were in degraded sites in Melbourne, Victoria. Opportunistic studies of *Themeda* grasslands on the fertile basalt plains in Victoria have indicated that frequent (1-5 year) burning is important for maintaining sward vigour and diversity (Morgan & Lunt 1999; Lunt & Morgan 2002), and other observational evidence similarly indicates the significance of fire or other disturbance for promoting *Themeda* swards in mesic climates (Moore 1953; Stuwe & Parsons 1977; Belsky 1992). However, studies in more arid areas indicate that burning can reduce productivity and seedling establishment in *Themeda* grasslands (e.g. Bennett *et al.* 2002; Snyman 2004), and hence the broader applicability of the Victorian studies is unclear. Further, these studies have focused on grasslands dominated by *Themeda*, and little attention has been given to effects of fire on other potential native dominants, particularly *Poa sieberiana*, and implications for grassland productivity and resilience.

We undertook a 12-year experimental study of *Themeda-Poa* understoreys of temperate woodlands in south-eastern Australia, to investigate the effects of autumn-winter burning and other disturbances on sward structure and species composition, and subsequent interactions with sward resilience. The study was undertaken in two contrasting remnants of temperate grassy white box (*Eucalyptus albens* Benth.) and yellow box (*Eucalyptus melliodora* A. Cunn. ex Schauer) woodland that were largely uninfluenced by post-European disturbances such as livestock grazing. We compared four burning frequencies (2 year, 4 year, 8 year and nil), and at one site monitored interactions with non-livestock (kangaroo, rabbit and hare) grazing. We also applied a biennial mowing regime as a potential alternative to burning at one site.

In this paper we report the effects of differing disturbance type and frequency on the composition, structure and resilience of the dominant grassy sward; effects on subsidiary plant species composition and diversity will be reported in a later paper. This study represents the first long-term, replicated experimental study of fire frequency in Australian temperate grassy ecosystems.

METHODS

Study sites

Experimental trials were established in October 1993 at two high quality remnants (Monteagle, 34°12' S, 148°21' E and Woodstock, 33°46' S, 148°51') of white and yellow box grassy woodland, located 70 km apart on the Central Western Slopes of New South Wales, Australia. Both four hectare remnants occur on arable mid-slopes between cropping and grazing paddocks, in undulating terrain typical of white and yellow box woodlands in the region. Subsoils at both sites are deep red clays, overlain at Monteagle by moderately-acidic fine sandy clay loams (derived from Devonian granodiorites) and at Woodstock by slightly-acidic clay loams to light clays (derived from Ordovician volcanics and limestones). Average annual rainfall is approximately 600 mm, although this is highly variable.

Both remnants are in little-used country cemeteries with a history of minimal livestock grazing and thus represent some of the least-degraded understoreys of grassy woodland in the region. The ground layer at both sites is dominated by *Themeda australis* (kangaroo grass) and *Poa sieberiana* (snow tussock), thought to be the natural dominants in this ecosystem prior to European settlement (Prober & Thiele 1995). *Themeda australis* (hereafter *Themeda*) is a warm-season C4 perennial tussock grass native to tropical and temperate Australia (commonly considered synonymous with *Themeda triandra* Forsskal from Africa and Asia),

while *Poa sieberiana* (hereafter *Poa*) is a cool-season, C3 perennial tussock grass widely distributed in mesic woodlands and forests of south-eastern Australia (Wheeler *et al.* 2002). A high diversity of native herbaceous plants occurs among the dominant grasses, with few shrubs and relatively low exotic species abundance.

While both sites represent high quality native woodland understoreys, their management regimes have differed since European settlement. Monteagle has a history of frequent burning (c. 4-8 year intervals, last burnt 1991), and is largely treeless due to historical clearing. Woodstock retains a discontinuous canopy of mature trees and prior to this experiment had not been burnt for at least 60 years.

Experimental design

Separate trials were established within a treeless area at Monteagle and a wooded area at Woodstock. Three burning frequencies (2, 4 and 8 year intervals) and an undisturbed treatment were incorporated into the experimental design at both sites (hereafter referred to as 2-, 4- or 8-year and unburnt plots). At Monteagle, biennial mowing was also included, leading to a 5 disturbance x 4 replicate trial arranged in a randomized complete block design. At Woodstock, a grazing-exclosure treatment was included in factorial combination with burning, leading to a 4 burning frequency (whole plot) x 2 fencing (sub-plot) x 4 replicate trial in a split-plot, randomized complete block design. Experimental plots were 5 x 5 m (10 x 5 m whole plots at Woodstock), separated by 5 m buffers.

Burning and mowing were conducted in late autumn to early winter, the typical season for prescribed burning in this region. Grassy swards at Monteagle generally burnt well, leaving blackened tussock bases, minimal live vegetation and sparse litter. At Woodstock, burns were more variable, but often mild due to damp eucalypt litter and sparser tussock grasses, killing

most top-growth but leaving some of the litter layer unburnt. Burns were unsuccessful at Woodstock in 2004, thus 2-year plots remained unburnt for a third year by 2005 measurements. Mowing was to 10-15 cm height without slash removal, reflecting a common technique used by land managers in the region. For practical reasons and for comparability with the 2 year burning treatment, mowing frequency was lower than generally used for amenity purposes. Exclosures consisted of 1.5m wire netting fences that excluded kangaroos, rabbits and hares, all of which were regularly seen at the site in low numbers. Although it was not possible to measure grazing pressure, an Eastern Grey Kangaroo (*Macropus giganteus* Shaw) camp was present within 50 m of the experimental site, and there was ongoing evidence of grazing, with sparse droppings, scratchings and grazed plants evident on most unfenced plots throughout the experimental period.

Monitoring

Abundance of *Themeda* and *Poa* within each plot was estimated using a point-intercept technique (modified from Everson & Clarke 1987), in October 1993 prior to any treatments and every 1-3 years during October or November until 2005. An 8 mm dowel was placed vertically at each of 50 points on a grid across each plot; the abundance ('points') for each grass species was the number of points at which one or more live leaves, stems or inflorescences intercepted the dowel. This technique provided an objective measure of abundance reflecting but not equivalent to projective cover, and is hereafter referred to as 'cover'.

Detailed measurements of the structure, density, basal area and reproductive output of the dominant grasses were made in spring to summer 2003-4, 15 to 18 months after burning or mowing treatments were applied to all but untreated plots in 2002. Comparisons among disturbed plots at this date thus represent outcomes of differing disturbance frequency and

type over the past 10 years, independent of time since disturbance. Note that the period following the 2002 burn coincided with severe drought conditions, particularly during the *Themeda* growing season from October 2002 to January 2003 when rainfall was c. 20% of average.

Understorey structure was documented using point quadrats (Kent & Coker 1992), for all plots at Monteagle and all fenced plots at Woodstock. A frame consisting of 20 vertical, 4 mm diameter pins, each 10 cm apart, was placed in the centre of each plot and the height of contact for all intercepted leaves and inflorescences (live and attached dead) of *Themeda* and *Poa* were recorded at each pin.

Basal area and tussock density were estimated for each of the dominant grasses by estimating the average diameter of each live and dead tussock within four subsamples (totaling 0.54 m²) at Monteagle and six subsamples (totaling 1.5 m²) at Woodstock. We defined a tussock as an individual separated by >3 cm from another individual of the same species.

Total biomass for each plot was estimated using a rising plate meter (Earle & McGowan 1979), with 20, 0.1 m² samples per plot. Fifteen (Monteagle) and 20 (Woodstock) 0.1 m² samples from an appropriate range of swards outside experimental plots were also measured using the rising plate meter, then harvested by removing all live and dead material to ground level. These samples were dried at 60°C for 24 hours and weighed, and simple linear regression (Monteagle $r^2=0.80$, Woodstock $r^2=0.84$, $P<0.001$) was used to convert rising plate measurements from each plot to biomass.

Densities of grass seedlings were estimated in October 2003-2005 in four, 0.25 m² subsamples per plot. Inflorescence densities were estimated by counting all inflorescences within a 5 x 1 m strip in each plot in January 2004. Ten inflorescences were randomly

selected from each plot, dried and weighed to estimate mean inflorescence dry weight. Inflorescence weight per square metre was calculated from inflorescence density x mean dry weight.

Data analysis

Data were analysed using analysis of variance in Genstat (Genstat 2003). Cover data were analysed by repeated measures analysis, which included an adjustment of the degrees of freedom in the time.treatment stratum (Greenhouse-Geissler Epsilon) to account for association of plots across time. Analysis of initial (1993) data indicated that at Woodstock, there was confounding between treatment and initial tussock cover, so we analysed changes in cover since 1993 rather than absolute values for *Themeda*, *Poa* and total grass cover. At Monteagle there were no initial biases so we used initial data as a covariate in repeated measures analyses. Where appropriate, data were transformed using logarithmic or square root transformations, and Fischer's Protected Least Significant Differences were used to compare among treatment means. General linear and polynomial regressions were also used to further explore relationships among disturbance treatments and final cover estimates.

RESULTS

Changes in tussock grass dominance due to disturbance

At Monteagle, grassy swards were initially dominated by *Themeda*, but became increasingly co-dominated by *Poa* with decreasing disturbance frequency (Figs. 1a, 2a). Repeated-measures data indicated a dramatic increase in *Poa* over time on unburnt plots, evident as early as 1996 and peaking at 400% of initial cover by 2002. This contrasts with a minimal increase in *Poa* on 2-year and mown plots, and slower increases on 4- and 8-year plots (Fig 1a). Data from 2004 for *Poa* basal area, tussock density and contacts with live and dead

leaves showed similar trends (Fig. 3a), and regression analysis indicated that burning frequency and mowing explained 80% of the variance in *Poa* cover in 2003 (Fig. 2a).

Themeda cover at Monteagle fluctuated seasonally and in relation to time since disturbance, but there was little evidence for long term trends by 2002. *Themeda* usually recovered within one to two seasons of disturbance (Fig. 1a), and recovery was faster on mown than burnt plots (e.g. 1994, 2002, 2003). In spring 2003 after a period of severe drought, live *Themeda* cover declined on unburnt plots to less than half initial levels and was significantly lower than on burnt and mown plots (Figs. 1a,2a). However, a decline on undisturbed relative to disturbed plots was not evident from abundance estimates made after the following growing season (summer 2004), and cover on unburnt plots had begun to recover by 2005.

At Woodstock, trends in sward composition were the converse of trends at Monteagle. Swards were initially dominated by *Poa*, but *Themeda* became increasingly prominent under higher burning frequencies, evident from 1999 on 2-year plots, and 2003 on 4-year plots (Fig. 1b). Regression analysis indicated that initial *Themeda* cover explained 40% of the variance in final (2005) *Themeda* cover, and addition of burning frequency to the model increased the variance explained to 84% (Fig. 2b). Data from 2004 for *Themeda* basal area, tussock density and contacts with live and dead leaves similarly indicated considerably higher *Themeda* abundance on 2-year plots, although these data could not be corrected for initial biases (Fig. 3b).

As at Monteagle, *Themeda* cover at Woodstock generally recovered rapidly after burning (within one to two seasons), whereas *Poa* took at least three seasons to return to cover levels on unburnt plots (Fig. 1b). As a consequence, *Poa* did not recover on 2-year plots over the course of the study. In 2002-3, *Poa* cover at Woodstock declined on unburnt plots compared with relatively steady cover levels from 1993-9, probably in relation to severe drought in

2002-3. Nevertheless, *Poa* cover (Figs. 1b, 2b) and basal area (Fig. 3b) on unburnt plots remained significantly higher than on burnt plots through to 2004-5.

Poa cover was significantly greater within exclosures than in grazed plots, consistent across burning treatments and throughout the experimental period (Fig. 4). No effects of fencing were detected for *Themeda* cover, or for *Themeda*, *Poa* or total tussock numbers or basal area.

Sward resilience

Measures of tussock survival and abundance in 2003-4, two seasons after all burn plots were burnt, indicated differences in sward vigour related to fire history. At Monteagle, 2-year plots recovered poorly after the 2002 burn, with notably greater mortality of *Themeda*, and significantly lower tussock cover (Fig 1a), total biomass (Table 1), and tussock basal area and productivity (live+dead contacts, Fig. 3a) than other plots. Biennially mown plots were more robust than biennially burnt plots, with post-fire measures of biomass (Table 1) and *Themeda* and *Poa* abundance (Fig. 3a) often intermediate between 2-year and 4-year plots.

In striking contrast with trends at Monteagle, sward recovery after the 2002 burn at Woodstock was fastest on the most frequently burnt plots. Tussock cover (2002, 2005 Fig. 1b), total biomass (2004, Table 1), and tussock basal area and productivity (2004, Fig. 3b) were all significantly greater on 2-year plots than on 4- and 8-year plots (but note 2004 data could not be corrected for initial biases, Fig. 3b). By 2005, tussock cover on burnt plots directly reflected burning frequency, with highest cover on 2-year plots, intermediate cover on 4-year plots and lowest cover on 8-year plots. Tussock cover on 2-year plots had surpassed cover on unburnt plots, whereas on 8-year plots it remained significantly lower than on unburnt plots (Fig. 1b). Note also that a similar effect was observed after the 1998 burn (of 2-

and 4-year plots only), with more rapid recovery on 2- than 4-year plots (Fig. 1b). Minimal tussock mortality was recorded at Woodstock.

Sward structure

Measurements of sward structure at Monteagle (Fig. 5a) indicated the build up of a dense layer (to 12 cm) of dead grass on unburnt plots. Despite this, live leaves were frequent at all heights to 33 cm, and in total were more abundant than on frequently disturbed (2-4-year) plots. Burnt plots had considerably less dead material than unburnt plots, but build-up of dead leaves was more rapid in plots that had undergone fewer burns prior to 2002. Similarly, numbers of live leaves showed an inverse relationship with fire frequency and average sward height increased from c. 15 cm on 2-year plots to c. 24 cm on 8-year plots (Fig. 5a). The structure of mown plots differed from burnt plots, with more dead leaves concentrated in the 0-3 cm layer, and live leaves most abundant at 6-18 cm.

Quantities of dead grass on unburnt plots at Woodstock were lower than at Monteagle, partly due to lower overall tussock densities (c. one-third, Fig. 3). Effects of burning were similar to Monteagle, with removal of most dead grass and concentration of live growth closer to ground level (0-9 cm) in burnt plots (Fig. 5b). However, the build-up of live and dead leaves on 2-year plots was more rapid than on 4- and 8-year plots, probably related to its higher *Themeda* component, and there was more live growth on 2-year than unburnt plots.

Total tussock densities at both sites did not vary significantly with disturbance treatment, but there was significant variation in tussock size. At Monteagle, *Themeda* and *Poa* tussocks were concentrated in the smaller size classes, with the majority of tussocks $< 5 \text{ cm}^2$ for all treatments. However, larger *Poa* tussocks developed on less frequently burnt plots, with mean *Poa* tussock size greatest on unburnt plots. Mean tussock size for *Themeda* did not differ

significantly across treatments, but the trend was towards greater tussock size on unburnt plots, and there were significantly greater numbers of large tussocks ($> 60 \text{ cm}^2$ basal area, $P = 0.009$) on unburnt than on mown, 2-year and 8-year plots.

At Woodstock, *Poa* tussocks were again concentrated in the $< 5 \text{ cm}^2$ size class, and mean tussock size was greatest on unburnt plots (Table 1). *Themeda* tussocks were often $> 5 \text{ cm}^2$, but were significantly larger on 2-year plots than on 8-year and unburnt plots.

Reproductive output

Few *Themeda* germinants appeared in 2004 and 2005 and only 2003 data are presented. At Monteagle, *Themeda* germination was greatest on 4- and 8-year plots (9-18 seedlings/m²), poor on mown and 2-year plots and absent from unburnt plots. These trends did not reflect *Themeda* inflorescence production (in the following season), which was generally superior on unburnt plots, intermediate on mown plots and inferior on burnt plots (Table 1).

Themeda germination at Woodstock reflected *Themeda* cover, with nearly 12 germinants/m² on 2-year plots, declining to 0.5/m² on unburnt plots. Similarly, there were more *Themeda* inflorescences on 2-year plots, although differences in total inflorescence weight per square metre were not quite significant (Table 1). Fencing had no significant effects on net *Themeda* reproductive output, but results did indicate a lower dry weight per *Themeda* inflorescence inside exclosures (Fig. 3).

Poa germinants at both sites were too infrequent for statistical analysis. *Poa* inflorescence production at Monteagle was poorest on 2-year and mown plots and highest on 8-year and unburnt plots, particularly due to higher numbers of inflorescences on 8-year plots, and higher dry weight per inflorescence on unburnt plots (Table 1). At Woodstock, main effects of

burning on *Poa* inflorescence production were usually not significant, but there were significant interactions with fencing that indicated poorer inflorescence production on plots burnt every 2 years (whether grazed or ungrazed), or burnt less frequently in combination with grazing (Fig. 4).

DISCUSSION

Composition of the dominant matrix

Application of different burning frequencies to experimental sites over 12 years provided strong evidence that the relative dominance of *Themeda* and *Poa* in mesic temperate grasslands and grassy woodlands of southern Australia is regulated by fire frequency. *Themeda* recovered more rapidly from burning than *Poa*, and introduction of frequent burning to the rarely-burnt woodland with high initial *Poa* (Woodstock) enhanced the abundance, tussock size, inflorescence production and germination of *Themeda*. Conversely, reduced burning frequency in the *Themeda* grassland (Monteagle) dramatically increased the abundance, tussock size and inflorescence production of *Poa*.

The importance of burning for promoting *Themeda* in south-eastern Australia has been inferred from the prominence of this species in frequently-burnt remnants (Moore 1953; Stuwe & Parsons 1977), however this study provides the first experimental demonstration of a competitive advantage of *Themeda* over other temperate Australian native perennial grasses under frequent burning. These responses to burning are additional to other factors known to influence the relative abundance of *Themeda* and *Poa*; in particular, *Themeda* is favoured in open areas, whilst *Poa* is often more abundant beneath trees (Prober *et al.* 2002).

Effects of burning on native grasses other than *Themeda* are less-well understood. Our study indicates *Poa* is less resilient to burning, but plays an increasingly important role in these

ecosystems as disturbance frequencies decrease. *Poa* is uncommon in *Themeda* grasslands of the basalt plains of Victoria, where most previous Australian *Themeda* grassland studies have been undertaken (McDougall 1989; Lunt & Morgan 1999; Morgan & Lunt 1999), perhaps explaining the lack of attention to this species in the past (Prober *et al.* 2002). Indeed it is possible that widespread frequent burning (1-5 yr) in remnants of these grasslands over long time-frames has contributed to the generally low prevalence of *Poa*.

Sward resilience

Fire frequency strongly influenced the resilience of grassy swards to burning, as evidenced by sward recovery after the 2002 fire. Effects differed between sites, with most rapid recovery on the most frequently burnt plots (2-year) at Woodstock and the least frequently burnt plots (8-year) at Monteagle. These apparently contrasting results may be attributed to differing initial tussock composition of the two sites, in turn related to long-term burning history.

At Woodstock, it is likely that greater resilience in frequently burnt swards resulted from the more rapid change from *Poa* to *Themeda* dominance. Infrequent burning, on the other hand, was potentially adverse to the grassy sward at Woodstock, with tussock cover on 8-year plots remaining significantly lower than on unburnt plots for up to four seasons after burning (Fig. 1b), probably due to poorer resilience of *Poa* and inadequate opportunity for transition to dominance by the more fire-resilient *Themeda*.

At Monteagle, the highest burning frequency (2-year) led to higher *Themeda* mortality, lower *Themeda* germination and poorer sward recovery after the 2002 burn than lower burning frequencies. While differing environmental conditions (e.g. higher fire intensity, lack of tree cover) probably contributed to differing responses between sites, it is likely that high *Themeda* cover on infrequently burnt plots at Monteagle contributed to higher resilience to

burning than at Woodstock (c. 60%, compared with c. 20% at Woodstock in 2003). Relative abundance of *Themeda* and *Poa*, and hence resilience to burning, may continue to change over time, however. It is also of interest that no other, more fire resilient tussock grasses were readily available to compensate for the decline in *Themeda* on 2-year plots.

The detrimental effects of biennial burning at Monteagle are in striking contrast with recommendations for one to five yearly burning to maintain plant diversity, grassland structure and *Themeda* productivity in other temperate Australian *Themeda* grasslands with similar annual rainfall (Morgan & Lunt 1999; Lunt & Morgan 2002), and for frequent disturbance to maintain productivity in other mesic grasslands (Knapp & Seastedt 1986, Belsky 1992). Our results showed that biennial burning can weaken *Themeda* tussocks in the central NSW region, reducing resilience of the sward to further burning and potentially leading to poorer (e.g. hotter and drier) conditions for further *Themeda* recruitment (Snyman 2004). These results are likely however, to have been exacerbated by dry conditions. In semi-arid *Themeda* grasslands in northern Australia and Africa, burning has similarly been associated with reduced grassland productivity, especially during drought (e.g. Bennett *et al.* 2002), and Hodgkinson and Muller (2005) demonstrated that drought is an important cause of mortality of other perennial tussock grasses in semi-arid eucalypt woodlands.

In further contrast to earlier studies in mesic *Themeda* grasslands (McDougall 1989; Lunt & Morgan 1999; Morgan & Lunt 1999), cessation of burning for a 14 year period did not lead to sward collapse in the grassland at Monteagle. There was an accumulation of dead material in unburnt plots and evidence for a decline in live tussock cover following the 2002-3 drought, but recovery was evident in the following seasons. We suggest three factors that may have contributed to this result:

1. The 2003 decline in the unburnt sward at Monteagle was largely due to a decline in *Themeda*. Total sward cover was buffered by the increasing dominance of *Poa* (Fig.

- 1), suggesting that changes in the relative dominance of *Themeda* and *Poa* may enhance the ability of the sward to adapt to reduced burning frequencies. This is further supported by the long-term survival of *Poa* dominated understorey in the long-unburnt woodland at Woodstock, and contrasts with basalt grasslands in Victoria where *Poa* may be too infrequent to respond rapidly to reduced fire frequency.
2. Due to lower fertility, productivity at Monteagle may be lower than in the Victorian basalt grasslands, leading to slower build-up of dead material. Total biomass in unburnt plots at Monteagle (13 years post-fire) was generally lower than, but approaching that observed in 11-year unburnt *Themeda* swards by Morgan and Lunt (1999), so the relevance of this factor remains to be tested.
3. Drought is likely to have reduced growth of perennial grasses, potentially decreasing biomass production:decomposition ratios, and limiting accumulation of undecomposed litter. In effect, drought may contribute significantly to biomass reduction, and can be viewed as another form of disturbance (Collins & Gibson 1990). Higher *Themeda* flowering on unburnt plots (cf. Morgan & Lunt 1999) may similarly have been related to recovery after drought.

Informal observations at Monteagle indicate that eventual degeneration of the grassy sward may still occur in the absence of burning or mowing, but time-frames over which this occurs are likely to be greater than 10 years.

Mowing and grazing

Mowing is often recommended as an alternative disturbance for maintaining *Themeda* grasslands, especially in urban situations (McDougall 1989; Lunt 1991; Kirkpatrick *et al.* 2005). Biennial mowing resulted in effects intermediate between 2- and 4-yearly burning, and

less *Themeda* mortality than frequent burns. With respect to sward vigour, mowing at this relatively low frequency thus provides a viable alternative to burning, particularly where more frequent biomass removal is needed for other (e.g. amenity) purposes. However, it has been proposed that mowing without slash removal leads to weed invasion and reduced diversity (Lunt 1991), and these issues require further consideration. Negative impacts of frequent mowing on *Poa* may also decrease adaptability to less frequent disturbance (see below).

Exclosure from grazing by native and feral herbivores led to less substantial effects on sward composition and structure than burning. This contrasts with African *Themeda triandra* grasslands, where Belsky (1992) found that grazing had greater impacts on species cover and diversity than fire. Further, the combination of small patch burns and grazing did not lead to severely detrimental effects, unlike observations in related vegetation (Leigh & Holgate 1979; Meers & Adams 2003). Our results presumably reflect lower grazing intensities than other studies, and the problems of preferential grazing that can be associated with patch burning (Leigh & Holgate 1979; Meers & Adams 2003) may have been ameliorated by the small size of our woodland remnant combined with higher availability of palatable pasture in neighbouring paddocks.

While they were more moderate than effects of fire, some effects of exclosure from grazing were evident. These included an increase in plant biomass by approximately one-third, and an increase in *Poa* cover. There was also an interaction between grazing and burning that indicated a decline in *Poa* reproductive output on the most disturbed plots. Inflorescence production was inhibited by all burning frequencies when subject to the additional disturbance of grazing, but in the absence of grazing *Poa* inflorescence production was resilient to 4 and 8 year burning (Fig. 4). These effects on *Poa* further confirm the vulnerability of *Poa* to disturbance in this region.

Functional diversity and resilience

The resilience of ecosystems to disturbance or other stressors is dependent on the capacity of the component species to recover from degradation, as well as compensatory mechanisms associated with diversity that enable alternative species to restore ecosystem functions (May 1973; Westman 1978; Tilman 1996; Peterson *et al.* 1998). Recovery of *Themeda-Poa* swards from burning depended on the abundance and vigour of *Themeda* tussocks, and conversely, *Poa* may have enhanced resilience of the sward to stresses related to the absence of disturbance. Taken together, these results indicate that different components of the dominant sward in temperate grassy eucalypt woodlands confer resilience in the face of different natural disturbance regimes. Functional complementarity between *Themeda* and *Poa* may thus engender resilience in a broader sense, i.e. resilience or adaptability to variable disturbance regimes (Malanson 1987), supporting the notion that species and/or functional diversity confer ecological resilience (May 1973; Tilman 1996; Peterson *et al.* 1998; Walker *et al.* 1999). Conversely, as *Themeda* declined under repeated burning at Monteagle, it appeared that sward resilience was impeded by a lack of readily available complementary species to restore grassland productivity.

Walker *et al.* (1999) argued that subsidiary species are important for restoring ecosystem functions when dominants are displaced through disturbance. In *Themeda-Poa* ecosystems, this is consistent for grazing-tolerant native grasses that become important under set stocking, as these were uncommon in pre-European mesic grassy eucalypt woodlands (Moore 1953; Moore 1993, Prober 1995). Resilience of *Themeda-Poa* ecosystems to variable fire regimes on the other hand, may be constrained by initial abundances of these species. *Poa*-dominated understoreys at Woodstock were slow to adapt to burning (as evidenced by poor recovery after the 2002 fire on infrequently burnt plots), despite an initial average *Themeda* cover of c. 20%. At Monteagle, initial *Poa* cover of c. 10% allowed an effective response to cessation of

disturbance, but this contrasts strongly with productive *Themeda* grasslands with sparse *Poa* that appear incapable of adapting to infrequent disturbance (Morgan & Lunt 1999). *Poa* germination was also very low, so it remains unclear whether *Poa* abundance at Monteagle can increase sufficiently to facilitate adaptation to a longer fire-free term. Resilience to variable fire regimes in *Themeda-Poa* ecosystems is thus likely to be greatest where both species remain in moderate abundance, and it is likely that beyond certain thresholds of *Themeda* and *Poa* abundance, variable disturbance regimes are more detrimental. Conservation management of *Themeda-Poa* ecosystems should thus aim to maintain an effective balance of these dominants.

Mixed dominance by *Themeda* and *Poa* may also influence the composition and diversity of subsidiary species in grasslands and grassy woodlands. High species or functional plant diversity can reduce invasion risk in grassy ecosystems (Tilman 1997; Hector *et al.* 2001; Kennedy *et al.* 2002), implying that ecosystems with mixed dominants may be more resistant to exotic invasion than ecosystems dominated by one species. Conversely, high ecosystem resilience imposed by complementary canopy species may constrain recruitment by native species (Levine & D'Antonio 1999; Davis *et al.* 2000). Interactions among these processes may thus have important implications for biodiversity conservation, and require further investigation.

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Table 1. Effects of disturbance on total biomass, and tussock size and reproductive output of *Themeda* and *Poa* at Monteagle (M) and Woodstock (W) in 2003-4. Different superscripts indicate significant differences at $P < 0.05$. Further details of fencing effects and burning x fencing (b x f) interactions are given in Fig. 4. Some analyses (n/a) could not be performed owing to high numbers of zeros.

	Site	2 year mow	2 year burn	4 year burn	8 year burn	unburnt	P burning	P fencing	P b x f
<i>Total biomass</i> (g/m ²)	M	240.5 ^b	172.5 ^a	281.9 ^{bc}	321.1 ^c	611.2 ^d	<0.001		
	W	-	317.6 ^a	204.0 ^b	209.8 ^b	313.5 ^a	0.031	0.002	ns
<i>Themeda</i>									
Mean tussock size (cm ²)	M	2.4	2.2	2.7	2.5	3.0	0.128		
	W	-	26.8 ^a	21.5 ^{ab}	14.2 ^b	16.7 ^b	0.032	ns	ns
Germinants/m ² (spring 2003)	M	1.2 ^a	0.7 ^a	9.5 ^b	18.5 ^b	0 ^{n/a}	<0.001		
	W	-	11.9 ^a	3.4 ^{ab}	1.6 ^b	0.5 ^b	0.049	ns	ns
Inflorescences/m ²	M	14.7 ^{ab}	9.5 ^{bc}	11.2 ^{bc}	8.1 ^c	20.4 ^a	0.009		
	W	-	2.3 ^a	0.8 ^b	1.0 ^b	1.49 ^b	0.009	ns	ns
Dry weight of 10 inflorescences (g)	M	0.75 ^a	0.99 ^{ab}	0.91 ^{ab}	0.72 ^a	1.24 ^b	0.044		
	W	-	1.46	1.05	1.43	1.69	ns	<0.001	ns
Inflorescence weight (g/m ²)	M	1.08 ^b	0.89 ^{ab}	0.92 ^{ab}	0.55 ^a	2.47 ^c	0.002		
	W	-	1.53	0.25	0.36	0.88	0.074	ns	ns
<i>Poa</i>									
Mean tussock size (cm ²)	M	3.9 ^a	1.2 ^a	3.8 ^a	4.9 ^{ab}	8.0 ^b	0.006		
	W	-	3.0 ^a	3.7 ^a	4.1 ^a	13.0 ^b	0.009	ns	ns
Germinants/m ² (spring 2003)	M	0.5	0.5	0.5	0.9	0.00	n/a		
	W	-	0.1	4.1	0.8	0.8	n/a	ns	ns
Inflorescences/m ²	M	3.4 ^a	2.6 ^a	7.9 ^a	16.7 ^b	6.0 ^a	<0.001		
	W	-	2.5	3.7	4.7	5.1	ns	<0.001	0.007
Dry weight of 10 inflorescences (g)	M	0.65 ^a	0.55 ^a	0.70 ^a	0.63 ^a	1.09 ^b	<0.001		
	W	-	1.26 ^b	0.93 ^a	1.28 ^b	1.47 ^b	0.022	ns	ns
Inflorescence weight (g/m ²)	M	0.23 ^{ab}	0.16 ^a	0.56 ^{bc}	0.99 ^c	0.66 ^c	0.004		
	W	-	0.32	0.38	0.64	0.71	ns	0.003	0.009

Figures

Fig. 1. (a) Cover (points out of 50) of the dominant grasses over 12 years at Monteagle (adjusted for 1993 cover), and (b) change in cover of the dominant grasses since 1993 at Woodstock. Significance levels (P) indicate significance of the year x burning interaction, least significant differences (lsd, 5%) apply to comparisons within years. Year of burning and mowing applications are indicated by 2 (2-year burn or mow), 4 (4-year burn) and 8 (8-year burn).

Fig. 2. Optimal regressions of *Themeda* and *Poa* cover at (a) two (Monteagle, 2003) and (b) four (Woodstock, 2005) seasons since the 2002 burn, against burning and mowing variables (No. burn= number of burns since 1993, mow= mown (1) or unmown (0)), incorporating initial abundance where significant. Note burning and mowing not combined; adjusted R² shown.

Fig. 3. Effects of burning (2, 4 and 8 year frequencies), mowing (stippled) and no disturbance (nil) on measures of *Themeda*, *Poa* and total tussock grass abundance in January 2004. Negative values (grey) indicate dead tussocks or leaves. Different letters indicate significant differences at P<0.05. For Woodstock, initial cover values are also shown to indicate initial confounding (see methods). Some analyses (n/a) could not be performed owing to high numbers of zeros.

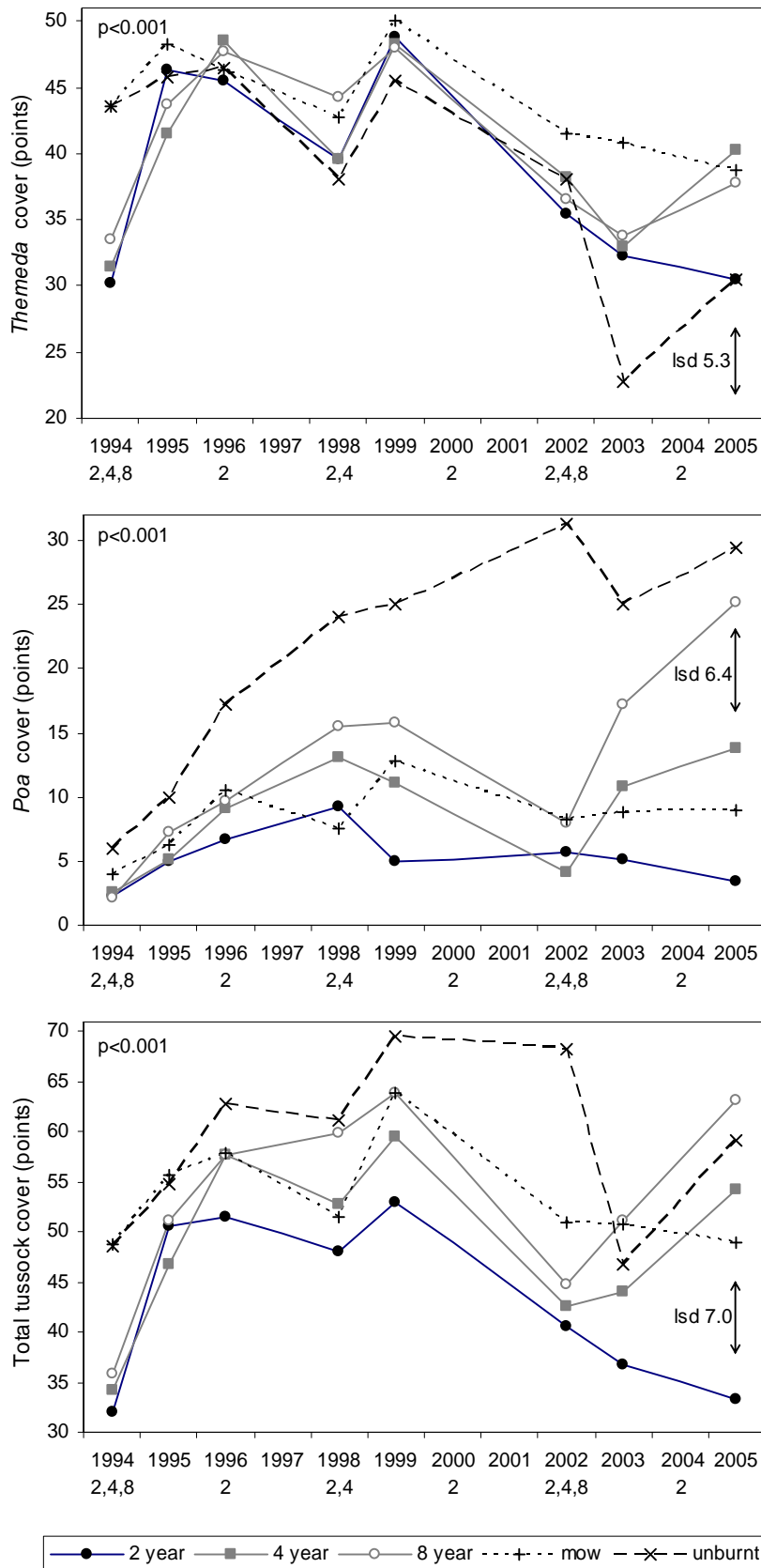
Fig. 4. Effects of grazing exclusion (fencing) on total biomass (2004), *Poa* cover (averaged across 1994-2005) and inflorescence production (2004) at Woodstock (b x f = burning x fencing interaction; only significant effects shown).

Fig. 5. Height distribution of live (positive values) and dead (negative values) leaves and inflorescences of *Themeda* and *Poa* (per 20 points, averaged over four replicates) across

different disturbance treatments at (a) Monteagle and (b) Woodstock. Note differing scales.

Figure 1.

(a)



b)

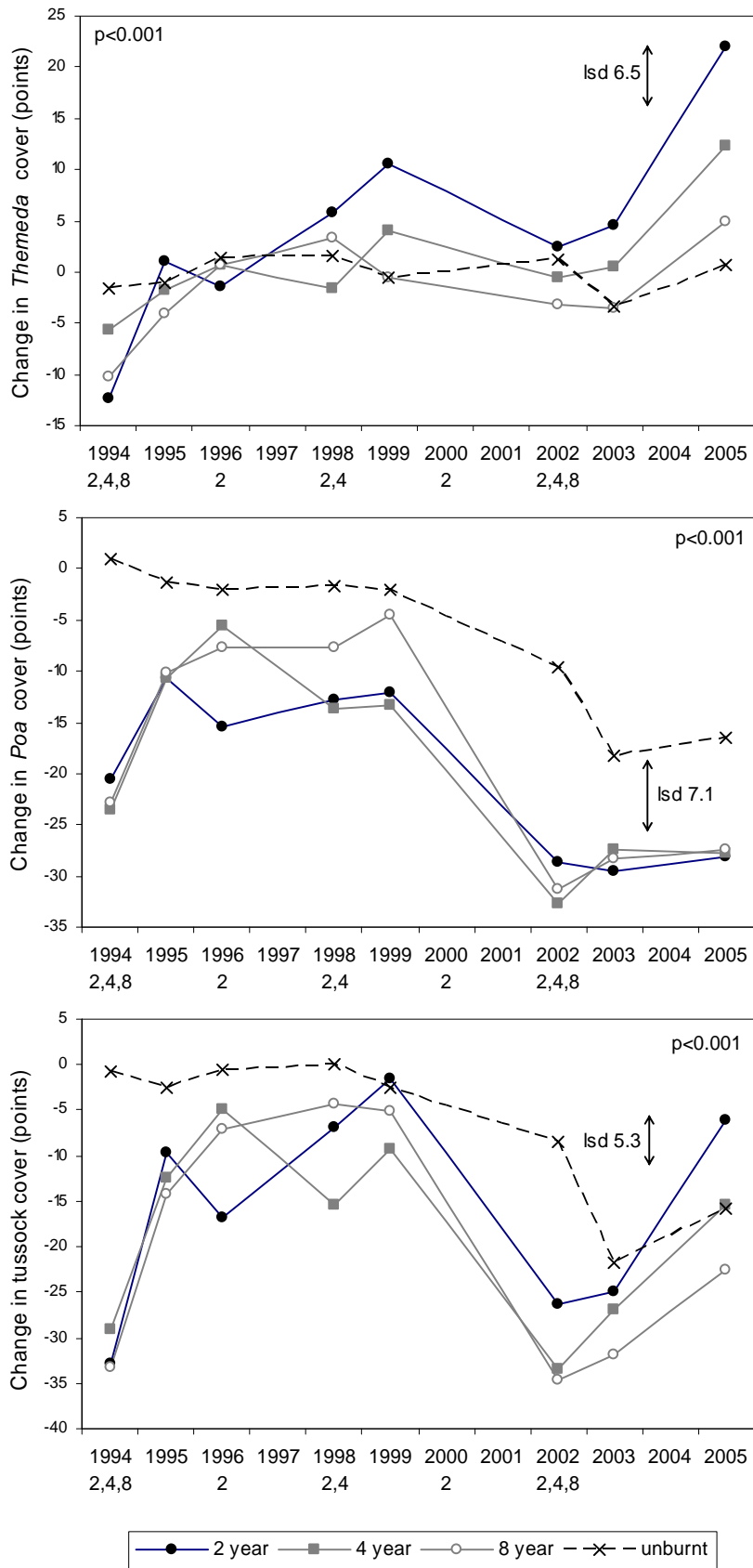
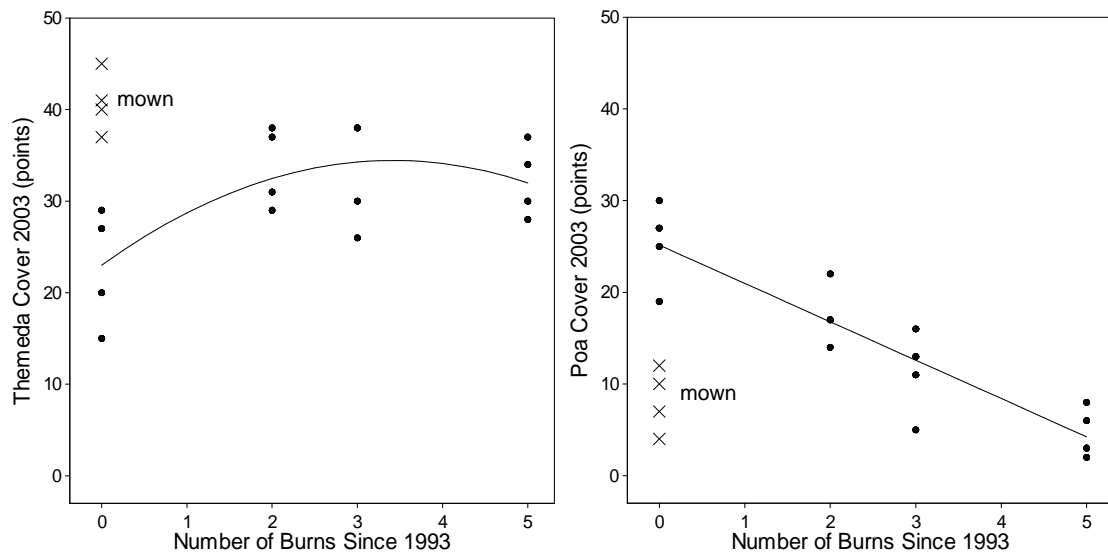


Figure 2.

(a) Monteagle

Themeda 2003 cover = $23 + 17.75 (\text{mow}) + 6.69 (\text{no. burn}) - 0.979(\text{no. burn})^2$. $R^2=55.6\%$, $n=20$, $P<0.001$

Poa 2003 cover = $25.14 - 16.89 (\text{mow}) - 4.183 (\text{no. burn})$. $R^2=79.6\%$, $n=20$, $P<0.001$



(b) Woodstock

Themeda 2005 cover = $1.83 + 0.67 (\text{Themeda 1993 cover}) + 4.838 (\text{no. burn})$. $R^2=84.0\%$, $n=32$, $P<0.001$

Poa 2005 cover = $23.53 - 2.73 (\text{no. burn})$. $R^2=29.9\%$, $n=32$, $P<0.001$

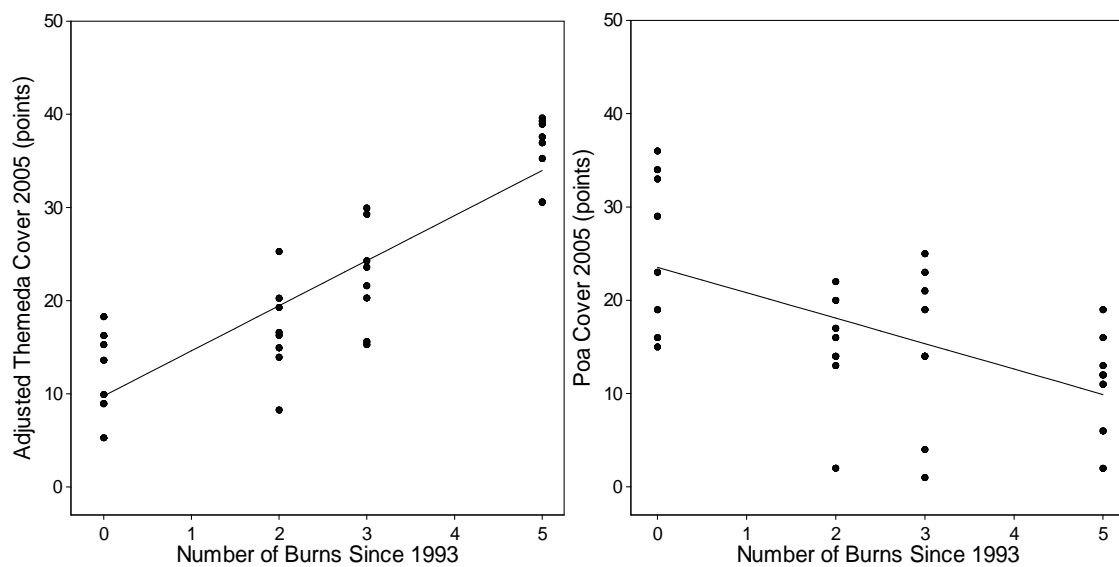
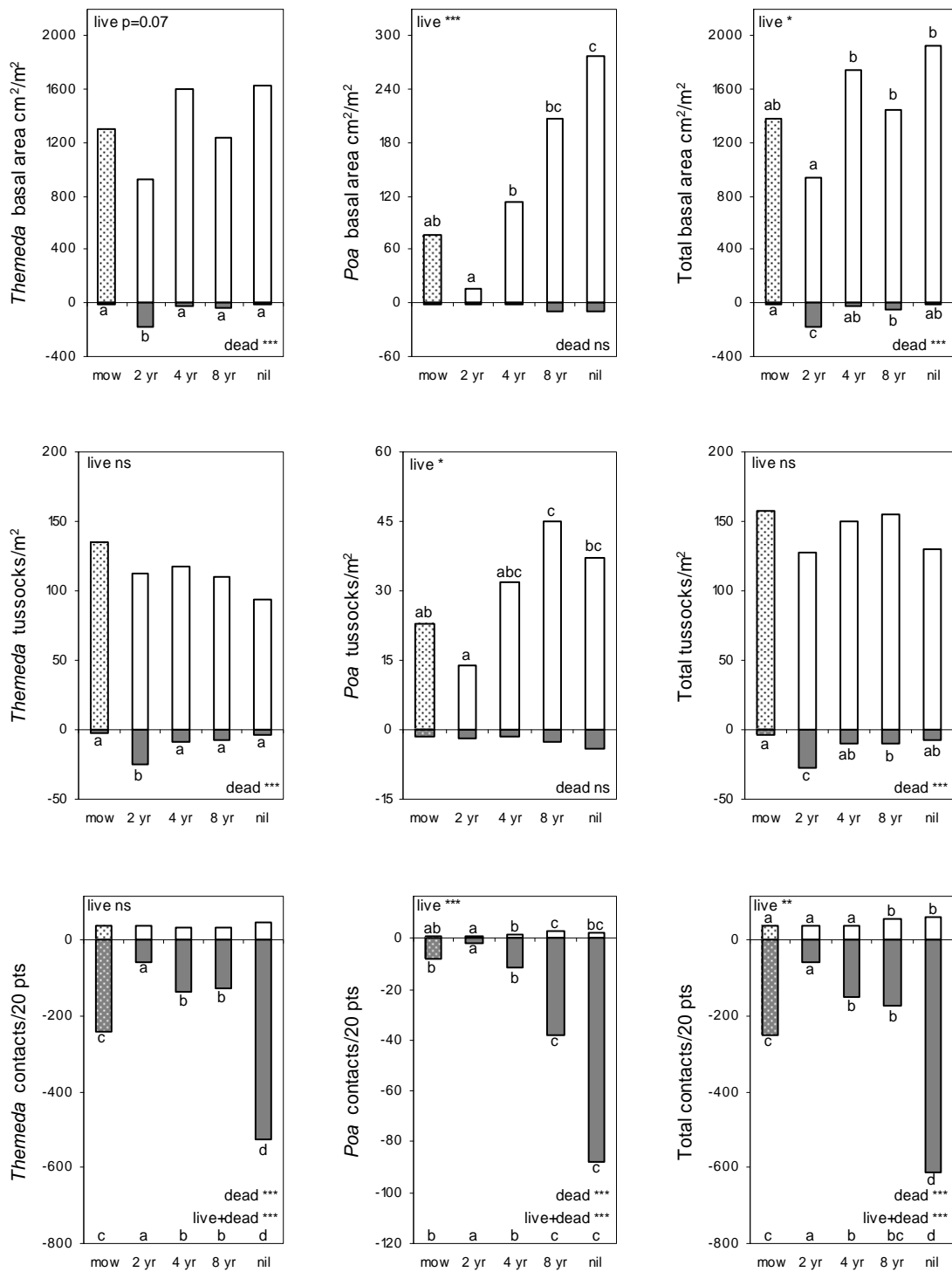


Figure 3.

(a) Monteagle



(b) Woodstock

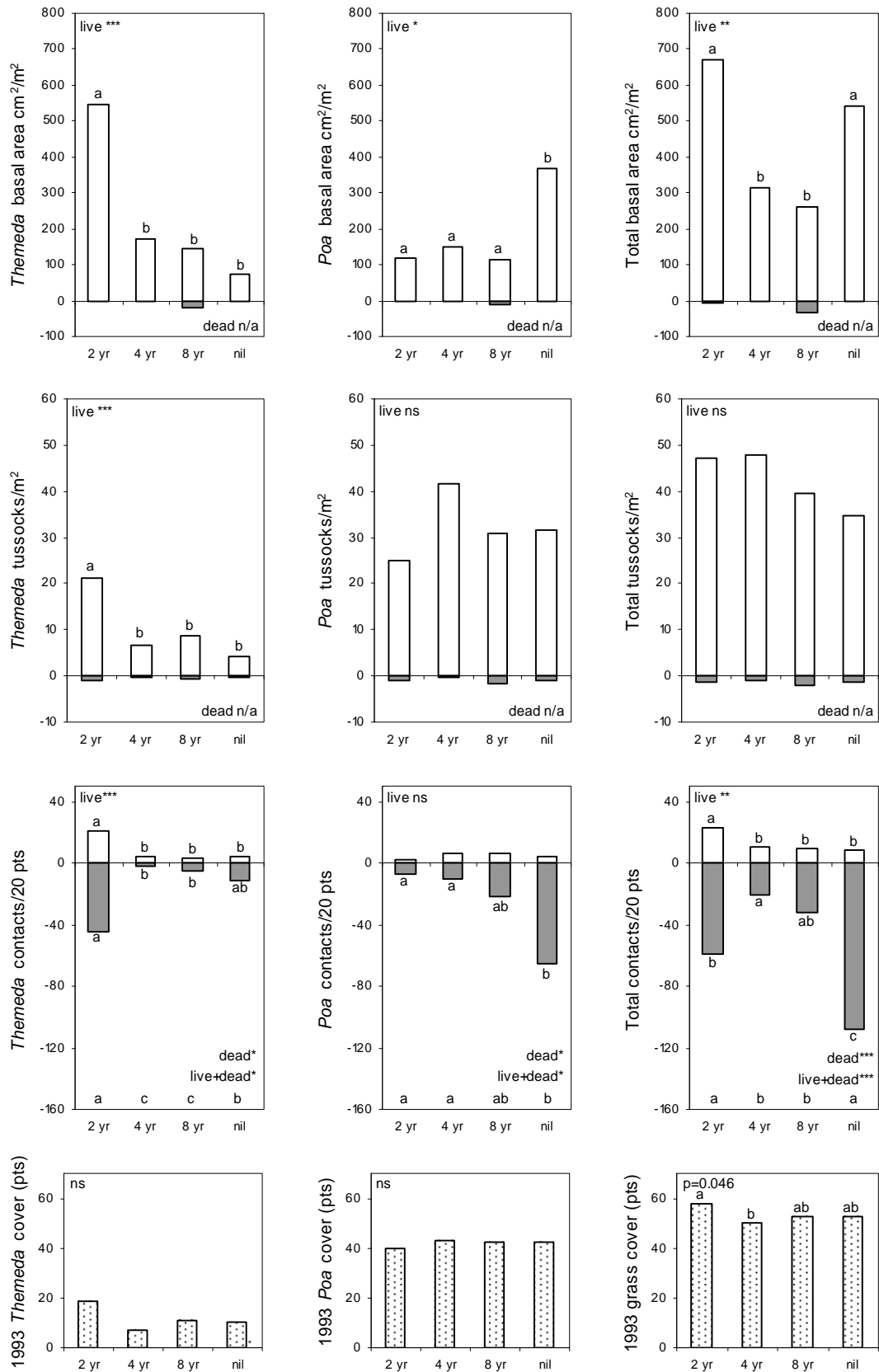


Figure 4.

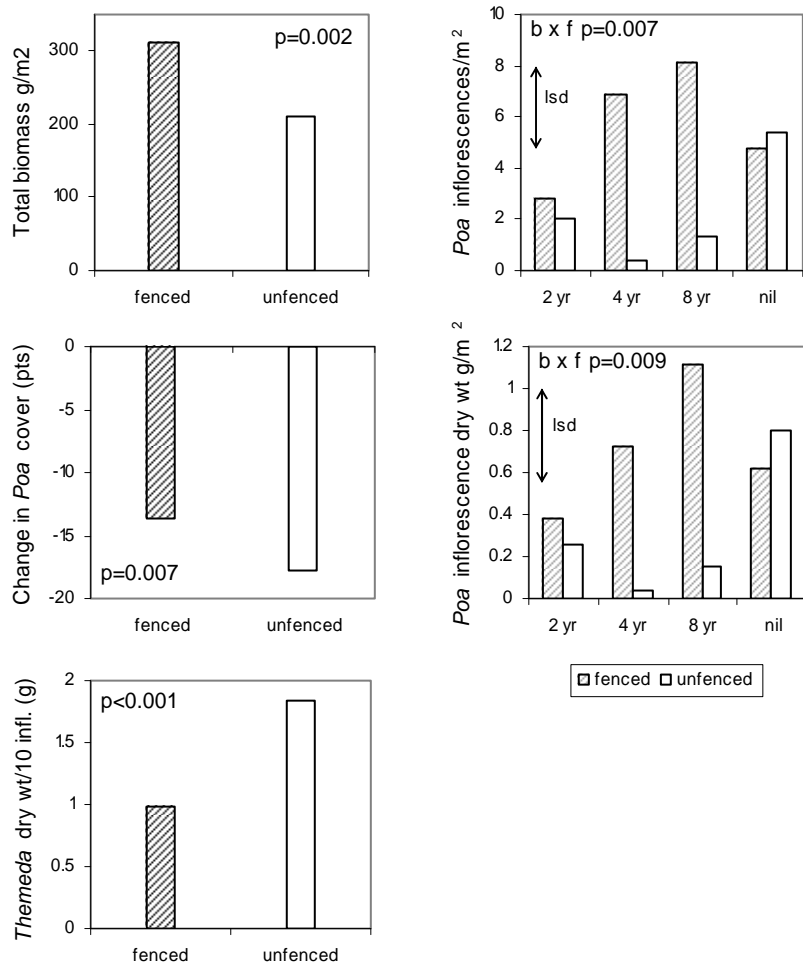


Figure 5.

