

Coexistence of shrubs and grass in a semi-arid landscape: a case study of mulga (*Acacia aneura*, Mimosaceae) shrublands embedded in fire-prone spinifex (*Triodia pungens*, Poaceae) hummock grasslands

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Abstract. The persistence of relatively fire-sensitive mulga (*Acacia aneura* F. Muell. ex Benth., Mimosaceae) shrublands within a landscape matrix of highly flammable spinifex (*Triodia* spp. R.Br., Poaceae) hummock grassland is a central question in the ecology of semiarid Australia. It is also a special case of questions about the coexistence of grasses and woody plants that have general application in semiarid rangelands and tropical savannas. With the use of field surveys and a 24-year fire history, we examined their coexistence on a sandplain in the Tanami Desert, Northern Territory, Australia. Mulga and spinifex each formed discrete monodominant stands with generally abrupt boundaries that did not correspond to obvious edaphic or topographic discontinuities. Spinifex hummock grasslands burnt almost three times as often as mulga shrublands and tended to occur on lighter soils with less biological crusting and more physical soil crusting. A combination of fire and soil variables described the environmental partitioning better than did either alone. Biological crusting increased with time since fire in both vegetation types. The demographic structure of mulga stands reflected their fire history, the more frequently burnt stands comprising almost entirely small plants. One fifth of mulga plants <0.5 m tall were resprouts. Our data provide support for the hypothesis that abrupt boundaries between mulga shrublands and spinifex hummock grasslands can be generated across diffuse environmental gradients by fire–soil–vegetation feedback loops. The oft-severe demographic impact of fire on mulga that is burnt raises questions about the appropriateness of frequent intense fires in this landscape.

Introduction

Fire is a major force restraining the distribution of woody plants and promoting pyrophilic grasslands globally (Bond *et al.* 2005). Notwithstanding, shrubs and trees persist in many fire-prone grassland regions either as discrete islands within a fire-prone matrix (e.g. Bowman 2000; Heisler *et al.* 2004; Hennenberg *et al.* 2006; Coblenz and Keating 2008) or as scattered individuals among grasses, as in the tropical savannas (Mistry 2000). The mechanisms and dynamics of the coexistence of woody plants and grasses are thus of considerable ecological interest (House *et al.* 2003; Sankaran *et al.* 2004). Much attention has been paid to the phenomenon of shrub invasion of grasslands following reduction in the frequency and/or intensity of fire (e.g. Brown and Carter 1998; Roques *et al.* 2001; Briggs *et al.* 2005), a situation that may arise from fire management and/or reduction in grassy fuel loads with intensification of pastoral activities (e.g. Brown and Sieg 1999; Roques *et al.* 2001). Somewhat less attention has been paid to the converse, in which elevated fire frequencies and/or intensities may promote the spread of grassland at the expense of woody vegetation.

Spinifex hummock grasslands occupy 18% of the Australian continent, and mulga shrublands and woodlands a similar proportion, both occurring mainly in arid and semiarid regions

(DEH 2007). The two vegetation types frequently abut, with Griffin and Hodgkinson (1986) suggesting that the boundary between them is the longest ecotone in Australia. Although the boundaries are often abrupt, they frequently correspond with no more than subtle differences in soils (van Etten 1988; Bowman *et al.* 1995, 2007; Nano and Clarke 2008). Whereas spinifex is pyrophilic and pyrogenic (Suijendorp 1981; Allan and Southgate 2002), mulga is somewhat fire-sensitive (Hodgkinson and Griffin 1982; Griffin *et al.* 1983; Hodgkinson 2002; Williams 2002; Wright and Clarke 2007), prompting invocation of fire as a key player in generating and/or maintaining the ecotone (Bowman *et al.* 1995; Nano and Clarke 2008). Nevertheless, even correlative evidence for this proposition is scant (Bowman *et al.* 2008) and it remains unclear how abrupt boundaries could be maintained by fire and whether they are robust to changes in fire regime (however, see below). Thus, the interaction between spinifex and mulga is a key dynamic in the ecology of the Australian continent that continues to raise intriguing questions about the forces that shape it.

Most spinifex species have limited palatability to stock and are thus not particularly vulnerable to overgrazing. Being hummock-forming, they accumulate fuel loads over several to

many years (Griffin *et al.* 1990; Russell-Smith *et al.* 1998; Allan and Southgate 2002). Concern has been expressed that, with the collapse of traditional Aboriginal fire regimes, more frequent and intense fires supported by a combination of spinifex and interstitial annuals that are episodically abundant may adversely affect mulga communities and their associated fauna (Kimber 1983; Griffin and Hodgkinson 1986; Start 1986; Latz 1991, 1995; Allan and Southgate 2002; Smyth and James 2004). The collapse of traditional Aboriginal fire regimes is thought to be associated with major changes to a range of vegetation types in Australia (Ellis 1985; Bowman and Panton 1993; Harrington and Sanderson 1994; Latz 1995; Hodgkinson 2002; Russell-Smith *et al.* 2004), variously triggered by the exclusion of fire or increases in its frequency and/or intensity in the absence of Aboriginal management.

Bowman *et al.* (1995) found that mulga–spinifex boundaries on conglomerate hills in central Australia are essentially stable. At a scale of several thousands of years, the boundaries on a sandplain site have also been essentially stable (Bowman *et al.* 2007). However, at a decadal scale at the same site, there has been considerable lability in the area of mulga, with changes all occurring within 50 m of boundaries with spinifex hummock grasslands (Bowman *et al.* 2008). Correlative evidence suggests that these changes are related to the occurrence of fire (Bowman *et al.* 2008).

In the present study, we examine the floristic, structural and gross soil patterns, and a 24-year fire history, of sandplain vegetation – patches of mulga shrubland embedded in a matrix of spinifex hummock grassland – on the southern fringe of the Tanami Desert in the Northern Territory of Australia. Our study area is the same as that of Bowman *et al.* (2007, 2008) and our study extends previous work to floristic, edaphic and

demographic considerations. We consider the following three specific questions: (1) do the vegetation boundaries correspond to edaphic and/or floristic disjunctions; (2) how do fire frequencies vary with vegetation type; and (3) what impact has fire had on the structure of mulga stands? Our more general aims are to explore how mulga patches have been able to persist in a fire-prone spinifex matrix, and to consider whether prevailing fire regimes are a threat to their persistence.

Materials and methods

Study area and key species

The 512-km² study area is in the northern, mostly ungrazed portion of Mt Denison Station (22°07'50"S, 132°04'54"E), a pastoral property on the southern edge of the Tanami Desert, Northern Territory, Australia (Fig. 1; see Bowman *et al.* 2008 for more detail). Red sands and earths predominate, with alluvial deposits along adjacent floodplains, the underlying geology being Redhackle Granite with subordinate Lander rock formation (sandstone and siltstone) (N. Donnellan, pers. comm.). The mean annual rainfall is 363 mm, with 73% falling in the summer months November–March, although monthly and annual totals are extremely variable. Average monthly maximum temperatures at Yuendumu, 45 km north-east of the study area, range from 40°C in summer to 26°C in winter, whereas average minimum temperatures range from 21°C in summer to 5°C in winter (Bureau of Meteorology 2005).

Spinifex hummock grasslands dominate the flat landscape. Approximately 70 patches of mulga shrubland, ranging in area from 0.002 km² to 25 km², are scattered widely throughout the matrix of spinifex hummock grassland (Bowman *et al.* 2008). The spinifex species is the stoloniferous form of



Fig. 1. Location within Australia of Mt Denison Station, on which the study was conducted. State and territory borders are shown.

Triodia pungens R.Br., a long-lived, hummock-forming, highly flammable and spiny grass whose foliage in the mature state is largely inedible for mammalian herbivores. In the study area it resprouts freely from rootstocks when burnt, although this is not so throughout its range (Rice and Westoby 1999). Mulga (*A. aneura* var. *tenuis*) is a tall shrub or small tree and is often multi-stemmed. Variety *tenuis* displays a strong tendency to form monodominant stands on a range of soils, and especially on red earths, and is widespread in arid and semiarid Australia (Hodgkinson 2002).

Field survey

Plots were placed in a wide range of fire ages (see below) for each of the three vegetation types, except that sites burnt in the previous 12 months were avoided. The vegetation types were mulga shrubland ($n=42$ plots), spinifex hummock grassland ($n=39$ plots) and mixed ($n=24$ plots) (total $n=105$). Mulga shrubland was defined as being dominated by *A. aneura*, with <1% cover of *T. pungens*, and spinifex hummock grassland as being dominated by *T. pungens*, with <1% cover of *A. aneura*. Mixed plots had greater than, and mostly much greater than 1% cover of both *A. aneura* and *T. pungens*.

Plots were 80 × 20 m, a plot size and shape found by S. J. van Leeuwen (unpubl. data, cited in van Leeuwen *et al.*, 1995) to be optimal to sample 95% of the perennial flora in a Western Australian mulga woodland. In each plot, we recorded the cover of each long-lived perennial species (trees, shrubs or hummock grass) in modified Braun–Blanquet classes (1 = <1%, 2 = 1–5%, 3 = 6–10%, 4 = 11–25%, 5 = 26–50%, 6 = 51–75% and 7 = 76–100%). Forbs and other grasses were not recorded because their cover responds rapidly to rain and fire. The number of live *A. aneura* were recorded in height classes (<0.5, 0.5–1, 1–3, 3–5 and >5 m). Live *A. aneura* <0.5 m tall were classified as resprouts or seedlings, depending on the proximity (direct contact = resprout) to a burnt, dead stem. A sample of ~10 were excavated and confirmed as resprouts.

The unvegetated ground in each plot was described at 100 points placed at 1-m intervals along a transect across the plot. Each point was scored as one of sand, gravel, physical soil crust or biological crust rated against standard photographs (Nicholas 2007). The texture of the soil was determined by the squeeze test described by Handreck and Black (1999) and graded as sandy, loamy sand, clayey sand, sandy loam, fine sandy loam or sandy clay loam. Two 7.5-cm soil cores of standard volume (117.1 cm³) were collected from each plot for later analysis.

Soil analysis

Soil samples were dried overnight in an oven at 100°C. The mass of each sample was measured with an electronic balance to the nearest milligram and converted to bulk density (mass volume⁻¹) by using the standard volume. The pH of each sample was determined with a pHep3 pH meter (Hanna Instruments Pty Ltd, Melbourne, Australia) to one decimal place.

Fire-scar analysis

In this landscape, fire scars on LANDSAT images remain visually detectable by colour differences for several years. Examination of a sequence of images for the period 1980–2004 was used to

identify 14 images that displayed evidence of fires during the previous 2 months. Plot locations were projected onto these images with the GIS computer program ArcView 9.0 (Environmental Systems Research Institute Inc., Redlands, CA, US). The number of fires and intervals between them were summarised for each plot.

Data analysis

We used the Bray–Curtis distance measure and multidimensional scaling (NMS) ordination (PC-Ord; MJM Software Design 2006) of plant cover-class data (modified Braun–Blanquet scores) to identify floristic patterns in the vegetation in one to six dimensions. A maximum of 400 iterations were allowed to generate minimum-stress solutions. The optimal dimensionality was identified by comparing the ordination stress of real and randomised data for each dimension, the aim being to minimise both the stress and the number of dimensions.

Multinomial generalised linear modelling with a logit link function was used to relate the three vegetation types to environmental variables. Environmental variables (all continuous) examined were cover of gravel and physical soil crust, texture, bulk density, pH of the soil and the number of fires during the 24-year period. The six texture classes were treated as a continuous variable based on their particle size and ranging from sandy to sandy clay loam.

We used a linear model to explore predictors of the percentage cover of biological crusting (arcsin square-root transformed). Response variables were time since last fire (a continuous variable) and vegetation type (a categorical variable). These analyses were modelled with the generalised linear model module in Statistica7 (StatSoft Inc. 2006). The strength of support for all possible subsets of explanatory variables was evaluated with the Akaike Information Criterion (AIC_C) and the percentage of deviance explained (Burnham and Anderson 2002).

The structure and skewness (Krebs 1989) of *A. aneura* stands in mixed and mulga plots was summarised graphically with the use of the five recorded height classes. In this context, skewness is a measure of relative dominance of small or large plants, with positive values indicating dominance by the former and negative values dominance by the latter. A two-factor ANOVA with interaction was used to examine the relationship between skewness and the number of fires (in Classes 0, 1 and 2+) and vegetation type (mulga shrubland, mixed).

Results

The mulga–spinifex mosaic

For the most part, the occurrence of *A. aneura* and *T. pungens* was discrete and they were separated by abrupt boundaries (Fig. 2). It was estimated from air photographs and ground surveys that less than 1% of the landscape comprised codominant mixtures of the two species.

Fifty-three long-lived perennials were recorded, with a mean of 11.1 species per plot (range 4–22). Thirty-six species (68%) occurred in both mulga shrubland and spinifex hummock grassland, and no species was unique to mixed vegetation. Species that occurred in more than 50% of plots within either mulga shrubland or spinifex hummock grassland were also

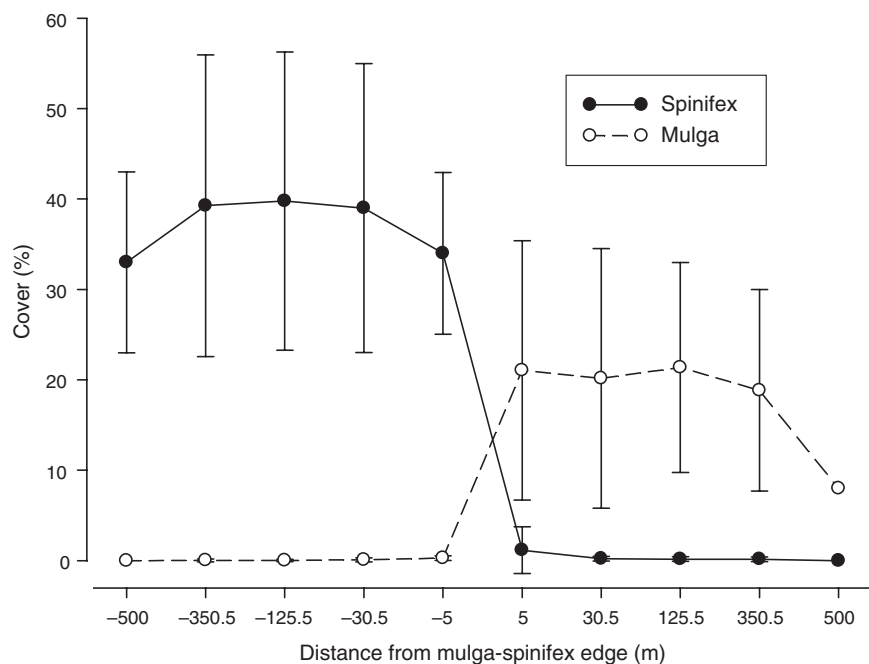


Fig. 2. Cover of mulga (*Acacia aneura*) and spinifex (*Triodia pungens*) across sharp boundaries. Values are means \pm s.d. in 81 plots, divided into classes on the basis of distance from the boundary (class midpoint distances shown). Samples sizes for classes, from left to right, are 4, 12, 13, 5, 5, 9, 15, 11, 6, 1. Plots in mixed stands, which comprised less than 1% of the landscape, are not included.

recorded in at least three plots (7%) of the alternative vegetation type. No species other than *A. aneura* and *T. pungens* had a median cover greater than 5% in any vegetation type.

Floristic ordination of plots demonstrated a clear graded sequence from spinifex hummock grassland through mixed vegetation to mulga shrubland (Fig. 3a). However, when *A. aneura* and *T. pungens* were excluded this sequence largely disappeared (Fig. 3b), although spinifex plots are mostly aggregated into the top right section of the graph and the distinction among *a priori* groups remained highly significant (MRPP $t = -22.7$, $P < 0.001$).

In all, 14 of the 97 fires detected in the study area during the 24-year study period burnt plots. Summer fires were more extensive, two such fires burning 56 and 31% of plots, respectively. Spinifex hummock grassland plots were burnt a mean of 2.8 times, almost three times as frequently as mulga shrubland plots, with mixed plots having an intermediate frequency (Fig. 4). Burnt stumps and charcoal were found in all mulga shrubland and mixed plots, and only in a few spinifex plots, even though 33% of mulga shrubland plots and 21% of mixed plots were not burnt during the study period. All spinifex plots were burnt during the study period. Minimum inter-fire intervals of less than or equal to 5 years were recorded for 64% of spinifex hummock grassland plots, 8% of mixed plots and 5% of mulga shrubland plots, and minimum intervals of 15 years in 72, 21 and 7% of plots, respectively. Notwithstanding, 38 spinifex plots (97%) experienced an inter-fire interval of greater than 10 years (mulga 100%; mixed 96%) and 28 spinifex plots (72%) experienced an inter-fire interval of greater than 15 years (mulga 95%; mixed 83%). (Note that the plots represent the range of fire ages and are thus not a random sample.)

A combination of fire and soil variables better described the environmental partitioning of mulga shrubland, mixed vegetation and spinifex hummock grassland vegetation types than did either alone (Table 1). The most well supported model, which accounted for 51% of the deviance, included soil texture, the number of fires and percentage physical soil crusting. Spinifex hummock grassland occurred on sandier soils with greater physical soil crusting and more frequent fires, and mulga shrubland at sites with loamier soils and the lowest fire frequency (Fig. 4). There was no support for an effect of bulk density, and pH explained only an additional 0.9% of the deviance. There was a considerable environmental overlap among vegetation types, least so for soil texture.

The cover of biological crusting varied among vegetation types and with time since the last fire (Table 2, 45% of deviance explained), being lower in spinifex hummock grassland, and in recently burnt plots in all vegetation types (Fig. 5).

Mulga structure

Mulga shrublands with numerous young *A. aneura* (<1 m) mostly had few or no mulga plants greater than 1 m tall (Fig. 6). The converse was also true. Skewness was related to the number of fires (2-factor ANOVA: fire – $F_{2,60} = 5.76$, $P = 0.005$), whereas it was not significantly related to the vegetation type (mulga or mixed) or to the interaction between the number of fires and vegetation type ($P > 0.50$ for both). Mulga shrublands dominated by younger *A. aneura* showed a strong tendency to have been more frequently burnt (Fig. 7).

Of 1673 *A. aneura* plants that were <0.5 m tall, 79.2% were seedlings and 20.8% were resprouts.

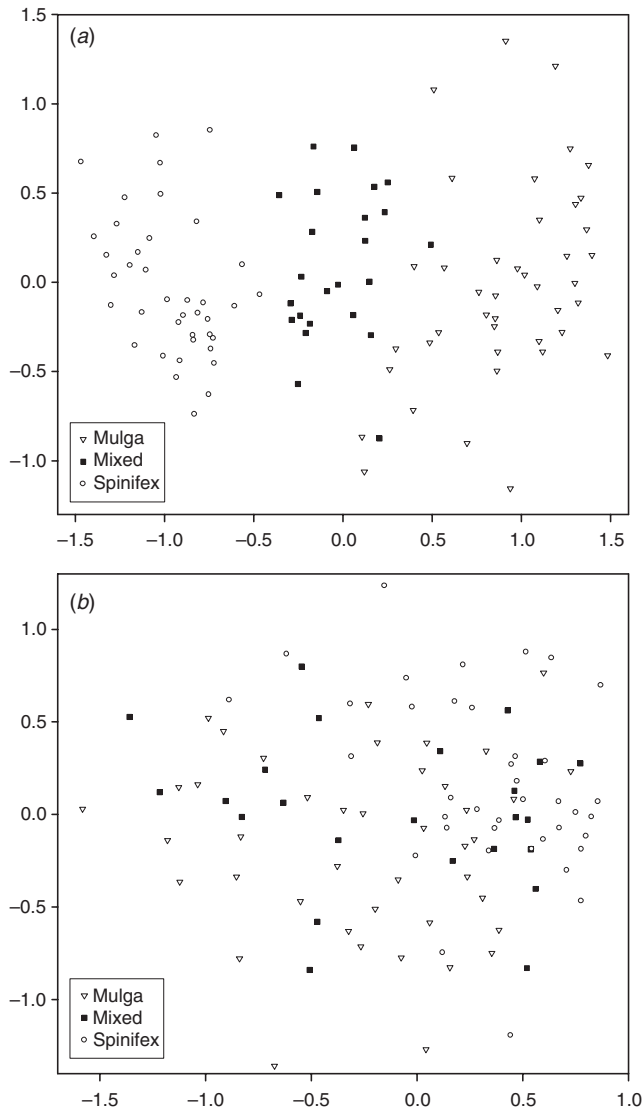


Fig. 3. Ordinations of 105 plots on a mulga–spinifex sand plain, based on cover-class scores of long-lived perennials: (a) a two-dimensional ordination with all except rare species included (final stress = 17.9); (b) the first two dimensions of a three-dimensional ordination with *Acacia aneura* and *Triodia pungens* excluded (final stress = 18.2).

Discussion

The vegetation matrix and its environmental correlates

The mulga–spinifex mosaic of Mt Denison Station is a particular case, in a semiarid landscape, of a general phytogeographical ‘problem’ of forest islands embedded in fire-prone matrices in the absence of sharp environmental discontinuities (e.g. Bowman et al. 1990; Hennenberg et al. 2006). The Mt Denison sandplain was overwhelmingly characterised by discrete, monodominant stands of just two species, the shrub *A. aneura* and hummock grass *T. pungens*, with generally abrupt boundaries between shrubland and hummock grassland. No other woody or long-lived perennial plant species was strongly associated with this dichotomy. Nano and Clarke (2008) noted that community-level floristic discontinuities occurred at some but not all

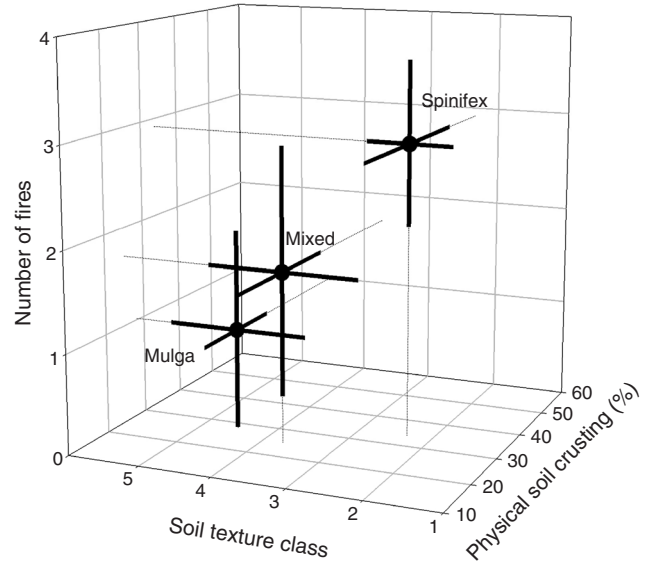


Fig. 4. Mean and standard deviation of variables identified (Table 1) as best describing the environmental partitioning of mulga shrubland, mixed vegetation and spinifex hummock grassland. Texture classes are on a particle-size gradient from 1 = sandy to 6 = sandy clay loam (see Materials and methods).

Table 1. Multinomial linear models identifying support for variables that describe the environmental partitioning of mulga shrubland, mixed vegetation and spinifex hummock grassland in the Mt Denison study area

The predictor variables are ordered for their importance in the model. *K* = the number of parameters in the model; ΔAIC_C = the difference in AIC_C scores between the specified model and the most well supported model; %DE = the percentage of deviance explained. Of all possible subsets, we have presented the three most well supported models (1–3), the two most well supported models containing soil variables alone (4, 5) and the number of fires alone (6)

Model	<i>K</i>	ΔAIC_C	%DE
1. Texture, no. of fires, %physical soil crusting	8	0	51.1
2. Texture, no. of fires, %physical soil crusting, pH	10	2.80	52.0
3. Texture, no. of fires, %physical soil crusting, %gravel	10	2.95	52.0
4. Texture, %physical soil crusting	6	10.71	44.3
5. Texture, %physical soil crusting, %gravel	8	14.35	44.7
6. No. of fires	4	52.27	23.8

Table 2. Linear models identifying the level of support for variables that describe the occurrence of biological crusting in the Mt Denison study area

The explanatory variables are ordered for their importance in the model

Model	<i>K</i>	ΔAIC_C	%DE
Time since last fire, vegetation type	4	0	45.2
Time since last fire	2	3.82	36.1
Vegetation type	3	11.52	31.8

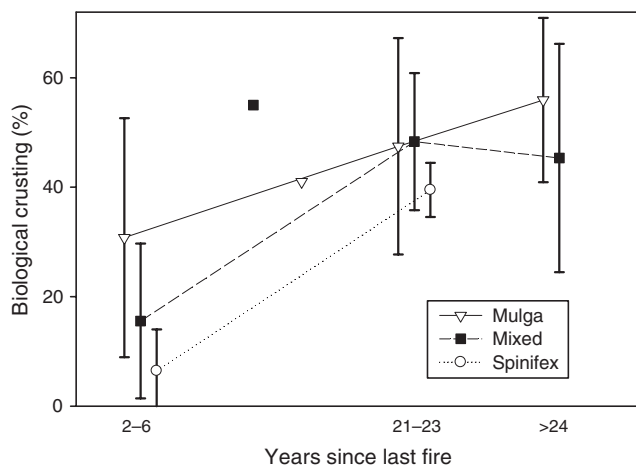


Fig. 5. Mean and standard deviation of variables identified (Table 2) as best describing the occurrence of biological crusting on Mt Denison station. For graphic purposes, the number of years since last fire has been aggregated into three classes, with two outliers also shown.

mulga–spinifex boundaries and that, whereas these floristic discontinuities were associated with distinct edaphic changes, boundaries that lacked associated community-level floristic discontinuities were associated with diffuse environmental gradients. Our results are consistent with this in that although mulga shrublands characteristically occurred on heavier-textured soils with more surface biological crusting and less physical soil crusting than for spinifex hummock grasslands, there was an extensive overlap between vegetation types in these characters. Neither pH nor bulk soil density contributed usefully to the discrimination between vegetation types. At this site, Bowman *et al.* (2007) found that mulga grew on soils that were more clay-rich and had higher levels of nitrogen, phosphorous and potassium than those of the hummock grasslands; however, the differences were not great and were gradational rather than abrupt at the vegetation boundary. Although further analysis of soils would doubtless add detail to the picture, our data and that of Bowman *et al.* (2007) are, we believe, sufficient to conclude that it is unlikely that *A. aneura* and *T. pungens* differ in their fundamental niche sufficiently to generate the sharp boundaries evident at the present site.

The occurrence of mixed vegetation provides further evidence that the fundamental niches of *A. aneura* and *T. pungens* overlap. Mixed vegetation occurred at sites that were, on average, intermediate between mulga and spinifex plots with regard to soil texture, physical and biological soil crusting, and fire frequency. There is no direct evidence about the origins of mixed vegetation. That it occupies only a small portion of the landscape reflects, we believe, the high level of antagonism between the two species, and we postulate that mixed vegetation represents an unstable transitional state whose subsequent trajectory will depend on chance fire events.

Both biological and physical soil crusts are a feature of many semiarid regions. Biological crusts fix nitrogen, improve moisture penetration, reduce erosion and enhance the germination and survival of seedlings (Eldridge and Greene 1994; Evans and Johansen 1999; Belnap *et al.* 2001). In contrast, physical soil

crusting decreases moisture penetration and increases erodibility (Rostagno *et al.* 1999; Ribolzi *et al.* 2006), and may arise in direct consequence of fire or other disturbance or as a result of the exposure to wind that follows a disturbance-induced reduction in vegetation cover. Our finding that the cover of biological crusts was greater in areas that have not been burnt for >20 years is consistent with the generality that cryptogams are fire-sensitive (Eldridge and Greene 1994; Evans and Johansen 1999). Whereas some biological crusts recover within several years of a fire (Johansen *et al.* 1993), our data infer recovery over longer periods, as noted by Eldridge and Bradstock (1994) in mallee also on red-earth soils. Although biological crusts favour the growth of mulga shrublands (Tongway and Ludwig 1990; Dunkerley 2002), it is noteworthy that we found considerable biological crusting in the few areas of spinifex hummock grassland that had not been burnt for >20 years, a state that may predispose them to colonisation by *A. aneura*. Markedly lower levels of biological crusting in recently burnt spinifex grasslands compared with recently burnt mulga shrubland (Fig. 5) may reflect a history of multiple fires in the former rather than a recent fire *per se*. This and the strong association of physical soil crusting with spinifex hummock grasslands may represent a process of soil degradation by fire and wind erosion (Warcup 1983; Fayos 1997; Ravi *et al.* 2006) that parallels changes from shrubland to grassland induced by grazing (Mills and Fey 2004).

The interaction between fire and biological crusting, along with our finding that a combination of fire frequency and physical soil crusting explained the occurrence of the vegetation types better than did either alone provides support for, and some additional dimensions to the suggestion (e.g. Bowman *et al.* 2008; Nano and Clarke 2008) that soil–fire–vegetation feedback loops play a key role in converting gentle edaphic gradients into sharp environmental boundaries in the mulga–spinifex system. The capacity of *A. aneura* to fix nitrogen and improve soil moisture retention through root nodulation (Winkworth 1973; Tongway and Ludwig 1990; Dunkerley 2002) is another dimension to these loops, as also is the pyrogenic nature of spinifex hummock grasslands and somewhat fire-retardant nature of mulga shrublands, along with possible shading effects of *A. aneura* on *T. pungens* and other possible competitive interactions (van Etten 1988; Nano 2005).

Consequences of fire for mulga

The strong tendency observed in the present study for mulga shrublands to be dominated by one or two similar height classes, with great variation in the dominant height class among plots, suggests marked temporal instability in mulga stand structures (cf. Rubin *et al.* 2006). We have shown that the demographic structure of mulga shrublands is related to fire history. A direct causal link, in which mature plants are killed by fire whereas germination is stimulated by it, is strongly inferred from the abundance of seedling and/or resprout *A. aneura*, and the scarcity of larger *A. aneura*, in plots burnt more than once in the previous 24 years. Conversely, plots that were not burnt in the study period were dominated by larger shrubs. In parallel, Bowman *et al.* (1990) reported that

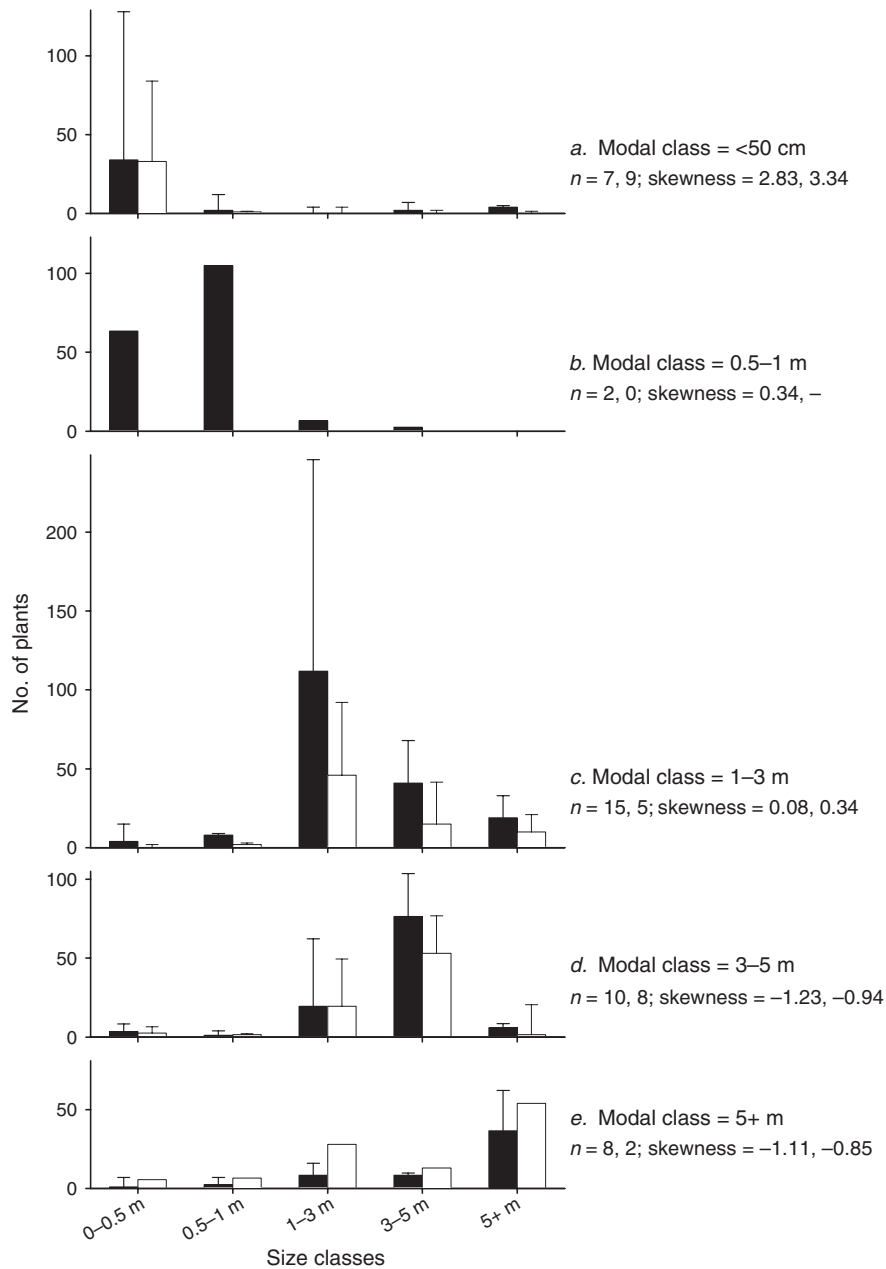


Fig. 6. Height profiles (medians and 75th percentiles) of live *Acacia aneura* in mulga shrubland (black) and mixed vegetation (white) in plots grouped by their modal height class. Positive skewness represents numerical dominance by smaller plants and negative skewness dominance by larger plants.

A. auriculiformis in forest islands suffered substantial mortality in the event of fire, and that seedlings were more prevalent in burnt than unburnt islands. Although *A. aneura* is frequently, although not invariably, killed by fire (Hodgkinson and Griffin 1982), we found numerous basal resprouts, demonstrating a regenerative capacity also reported by Wright and Clarke (2007), which may be a feature of var. *tenuis*. Thus, fire and even a sequence of fires need not cause local extirpation of *A. aneura*. However, the record of air photography for the site (Bowman *et al.* 2008) shows that local extirpations of – and

colonisation by – *A. aneura* have occurred and are concentrated along the fringes of mulga shrublands which are, by definition, exposed to spinifex-fuelled fires. Combining the results of that study and the present one, the reasonable conclusion is that demographic shifts compounded by multiple fires can exhaust the regenerative capacity of mulga shrublands, creating a fire-trap for seedlings and a demographic bottleneck *sensu* Trollope (1984) and Higgins *et al.* (2000), and also that *A. aneura* is actively colonising spinifex hummock grasslands that remain long unburnt.

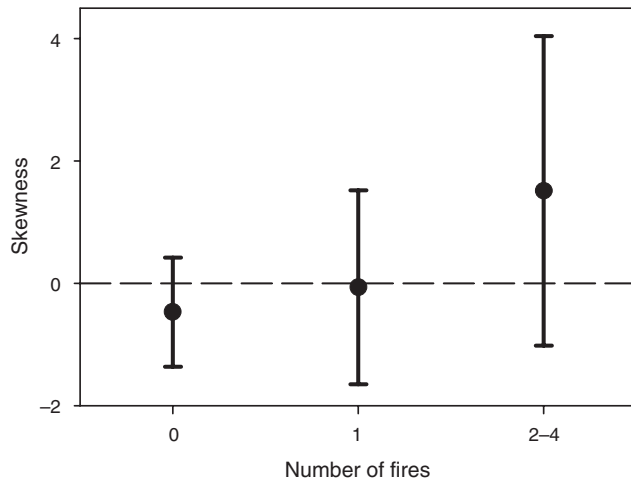


Fig. 7. Mean and standard deviation of the skewness of *Acacia aneura* height classes in mulga shrubland and mixed vegetation with different fire histories. Positive skewness represents numerical dominance by smaller plants and negative skewness dominance by larger plants.

The fire-free interval required by seedlings and resprouts of *A. aneura* var. *tenuis* to flower and produce seed is not well documented, although D. Albrecht and P. Latz (pers. comm., 2007) have suggested that it ranges from 5 to 15 years, depending on rainfall. Most spinifex hummock grassland plots experienced both a fire return time of <5 years and one >15 years during the 24-year study period, whereas return times for shrubland plots were mostly >15 years, even though all displayed evidence of fire. Thus, fire return times are within the frame that could trigger dynamic responses, particularly in the form of invasion and attrition of *A. aneura* seedlings within spinifex hummock grassland. The intensity and perhaps also the timing of fire are likely also to be relevant.

Mulga–spinifex boundaries at this site are more dynamic than at some other sites (cf. Bowman *et al.* 1995; Nano 2005), which most likely reflects high fire frequencies combined with the absence of topographic fire protection and the subtle and diffuse nature of edaphic gradients. The trend over the two decades to 2002 has been one of slight increase in the area of mulga shrubland, following three decades of decline (Bowman *et al.* 2008). Thus, the demographic impact of fire strongly inferred from the present study does not indicate an imminent collapse of the mulga–shrubland system. However, it does suggest a mechanism for the attrition of mulga along boundaries and the elimination of small patches demonstrated by Bowman *et al.* (2008), providing support for the suggestion that high fire frequencies maintained over long time periods will adversely affect the mulga ecosystem.

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