Chapter 7

Importance of suppression- and tolerance-based competition for seedling establishment success

Summary

1 Correlative analysis shows that species' patterning in mountain range mosaics may in part reflect the combined influence of suppression- and tolerance-based inter-specific competition.

2 Mosaic species do not exhibit a high level of regeneration niche partitioning at emergence and early survival, meaning that their within- and between-habitat distributions may result from the influence of competition with neighbouring seedlings during recruitment.

3 A multi-factor experiment was designed to tests for main and interactive effects of inter-specific competition among seedlings from different habitats (allopatric interaction), shading and edaphic variability.

4 The results provided qualified evidence for niche contraction at establishment through the interaction of edaphic and biotic effects. Specifically, when spinifex (*T. brizoides*) is grown in mulga soil it survives better with full light than with shading. Thus, in areas favouring the maximum development of a *A. aneura* canopy, hummock grass establishment is constrained by its inability to tolerate limited light conditions. Post-disturbance recruitment of mulga species in high pH spinifex soils is in turn constrained by the combined influences of edaphic effects and suppression-based competition from establishing spinifex species.

5 Within-habitat coexistence in mulga relates to the ability to recruit in mature habitat and thereby resist competitive suppression when resource levels are low. In spinifex however, coexistence is largely dependent on an ability to resist suppression by virtue of 'fugitive' traits at the establishment life phase.

6 Overall, this study highlights the importance of examining competitive interactions across the range of environmental conditions, life-history stages

and disturbance histories for understanding patterning in mulga-spinifex mosaics.

7.1 Introduction

It was demonstrated in Chapter 2 of this thesis that in the mountain range setting, minimal between-habitat floristic overlap coincides with the occurrence of widely varying environmental attributes across boundaries, while greater compositional commonality occurs when gradients are relatively weak. The results showed further that *Triodia brizoides* is likely to be less restricted by fundamental-niche constraints than is the mulga dominant, *A. aneura*, given the latter's overall reduced frequency and complete absence from certain spinifex habitats characterised by extreme edaphic characteristics (e.g. high pH and strongly-carbonated soils). In terms of the more diffuse edaphic boundaries, evidence suggested that the between-habitat distribution of these species likely relates to the combined influence of negative grass-shrub interactions and fire recurrence. Here too, it was suggested that as the shrubland dominant, *Acacia aneura* may have an intrinsic role in the maintenance of mosaic stability, primarily through positive and negative biotic effects. These ideas are in keeping with the predictions of Model III (refer Chapter 1), that competitive interactions mediate shrub-grass boundary positioning in these mosaics. While this work was successful in establishing correlative relationship, like the preceding study of central Australian range mosaics (see Bowman *et al.* 1994), it did little to disentangle cause from effect in relation to the mechanisms for species' sorting within- and between-habitat boundaries.

Subsequent experimentation examined the role of biotic interactions in mulga-spinifex mosaics by directly testing the predictions of Model III as they relate to the recruitment life phase. The model has two essential requirements for its operation. First, it is necessary to show that in the absence of disturbance, spinifex is excluded from established *A. aneura* habitat due to the superior competitive abilities of the latter; and second, that disturbance alters competitive relations such that spinifex invasion into previously unoccupied mulga habitat will be newly facilitated. These requirements are reflective of a more general debate in the ecological literature (e.g. see Cahill 2002; Goldberg & Landa 1991; MacDougall & Turkington 2004) regarding the importance of suppression ability as it relates to competitive *effect*, relative to the ability to tolerate low resource levels i.e. competitive *response*. Theory predicts that suppression- and tolerance-based competition relates to a trade-off between 1) the ability to rapidly acquire resources and dominate early successional stages by virtue of growth-rate related physical size differences (as *per* Grime's 1979 C-strategy); and 2) the ability to recruit within resource-poor mature habitats (Grime's S-strategy). This means that suppression specialists will be favoured by frequent disturbance, while tolerance specialists will dominate habitats characterised by minimal disturbance.

Evidence presented in the preceding chapter was in keeping with the above ideas in that it showed that the growth and survival of *A. aneura* seedlings were suppressed by adult *Triodia*. The Gulliver effect model (Bond & van Wilgen 1996) was used to contextualise the results within the broader debate (see especially Bond *et al.* 2005, Bond & Keeley 2005) concerning mechanisms for global-scale shrub-grass coexistence. Specifically, it was argued that in areas within the edaphic range of *A. aneura*, spinifex grassland is dependent on a fire-mediated shift in shrub-grass competitive abilities for its maintenance. This depiction was based on the untested assumption that in the post-disturbance environment, suppression-based competition by faster growing *Triodia* seedlings represents the underlying mechanism for *A. aneura* displacement. It is, however, well-recognised that seedling and adult traits do not necessarily covary (Grime 1979; Shipley *et al.* 1989), meaning that while it is clear that *A. aneura* recruitment is suppressed by adult *Triodia*, it still needs to be demonstrated that *Triodia* seedlings possess similar suppressive traits. The work presented in Chapter 5 indicated that mosaic species are unlikely to partition resources during regeneration, given they showed little variation in response to the habitat variables tested. This means that their within- and between-habitat temporal and spatial distributions may in part reflect the influence of negative interactions with neighbouring seedlings during recruitment.

One other outstanding issue relates to the exclusion of spinifex from mature mulga as *per* the other requirement of the model. Earlier, van Etten (1987) demonstrated that *Triodia pungens* is disadvantaged by shading, suggesting that the abundance of this species in mature mulga habitat – that is otherwise within its edaphic range – is kept in check by its inability to tolerate reduced light levels. This might likewise serve as an explanation for the absence or very low abundance of *Triodia brizoides* from the thick-canopied mulga patches at Tylers Pass where between-habitat edaphic gradients are relatively minor. Experimentation is required however, before these ideas can be directly applied to this situation.

This chapter examines the importance of suppression- and tolerance-based competition as underlying mechanisms for coexistence regulation in mulga-spinifex mosaics. Specifically, it seeks to determine the extent to which 1) establishing spinifex can suppress mulga seedlings in the post-disturbance environment, 2) spinifex establishment in mature mulga is constrained by its intolerance of reduced light levels; and 3) suppression- and tolerance-based competitive relationships remain stable with changing environmental condition. The questions addressed are:

1. To what extent do main and interactive effects of shading, soil type and seedling interactions mediate establishment and early survival success?
2. Do species' responses vary across habitat boundaries, and are differences sufficient to explain current mosaic patterns?

7.2 Methods

7.2.1 EXPERIMENTAL DESIGN

The experiment was arranged in two patches, separated by a distance of 10 m, in a single nursery bay at the Alice Springs Desert Park (Fig. 7.1). A replicated split-plot design was used to test the effects of soil type, shade, and seedling neighbour effects (allopatric/sympatric interaction) on seedling survival and growth. The soil treatment had two levels consisting of mulga soil and spinifex soil. The experiment comprised forty eight 25 cm diameter pots in total – 24 filled with 'non-spinifex' mulga soil and 24 with high pH and strongly-carbonated (i.e. group 5 'white') *Triodia brizoides* soil – both taken from the Hugh River region of the Brewer Conglomerate (refer Chapter 2). The 24 mulga soil pots and the 24 spinifex soil pots were then divided between the two patches such that each patch comprised 12 mulga pots and 12 spinifex pots. The shade treatment comprised two levels: canopy and no canopy, each of which were replicated across the two patches. The canopies were constructed from a piece of green nylon 70% Weathashade^{TM} shadecloth, suspended from above-ground metal posts. Canopies extended well beyond the edges of planted pots to minimise direct sunlight exposure. Finally, a seedling neighbour treatment was imposed. This had two levels: allopatric association and sympatric association.

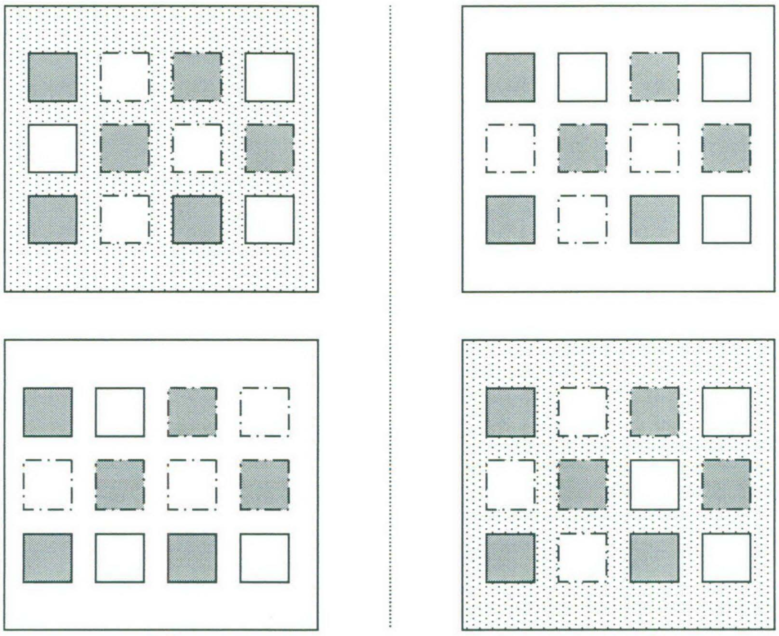

Fig. 7.1 Stylised representation of the design of the experiment testing for the effects of allopatric seedling interaction, shading and soil type. Background fill indicates shading; fine dotted line denotes spatial replication of treatments (patch 1 and 2).
(▨) mulga soil; (☐) spinifex soil; (-·) allopatric association; (—) sympatric association;

The allopatric level was created by including a mix of species (three from each habitat) in the same pot, while the sympatric level involved only species from mulga or species from spinifex habitat. Table 7.1 lists the species used in the experiment. For the majority of species, seedlings were started from seed in potting mix then transplanted to the experimental pots. An inability to germinate sufficient quantities of two of the species: *Triodia brizoides* and *Eremophila latrobei*, meant that they instead had to be propagated from cuttings. This meant that the results could be related to seedling behaviour only in relation to the size of these individuals relative to adult plants. All pots were planted with 24 individuals. For the allopatric level of the neighbour treatment, three species from each habitat were each represented by four individuals such that there were 12 mulga habitat individuals and 12 spinifex habitat individuals.

For the sympatric level, three species from either habitat were each represented by eight seedlings such that there were 24 seedlings of mulga species in one half of the sympatric pots, and 24 of spinifex species in the other half. Seedlings were planted in mid February 2000. Planting consisted of making a small depression in the soil and inserting one seedling at a time. Pots were supplied with equal amounts of water via an automated sprinkler system. Any dead individuals were replaced during a two-week initial phase. The experiment commenced at the start of March 2000. Survival counts and non-destructive repeated height measurements were taken on three and two occasions respectively throughout experimentation. The experiment was officially terminated at the end of May 2000 after three months.

Table 7.1 Attributes of species used in the experiment testing for effects of allopatric seedling interaction, shading and soil type on seedling establishment success. Mulga species are in bold.
V = variable vegetative response to fire; K = killed by fire; R = resprouts after fire.

Species & Alice Springs Desert Park voucher codes.	**Family**	**Growth-form**	**Fire Response**
***Acacia aneura* ASDP973500**	Mimosaceae	Long-lived perennial shrub	K
Acacia bivenosa 96RBB193	Mimosaceae	Short-lived perennial shrub	V (R>K)
Corymbia eremaea subsp. *oligophylla*	Myrtaceae	Long-lived perennial tree	R
***Digitaria brownii* 96A90816**	Poaceae	Short-lived perennial tussock grass	?K
Triodia brizoides	Poaceae	Long-lived perennial hummock grass	V(K>R)
Eremophila latrobei* subsp. *glabra	Myoporaceae	Long-lived perennial shrub	V (?K >R)

7.2.2 ANALYSIS

The influence of individual treatments and their interactive effects on survival and growth were analysed separately for each species using four-factor ANOVA. Soil, shade and seedling neighbour association were treated as fixed factors, whereas the two replicate patches were a nested factor. Significance for all statistical tests was determined at $P < 0.05$. Where patch effects were not evident ($P > 0.05$), results were pooled and the data reanalysed using three-factor ANOVA. Plant status (living or dead) was adjusted to the proportion of seedlings planted (eight or four, depending on the mix treatment). An angular transformation was then applied (arcsine square root) to the data to meet the assumptions of the analysis (to increase homogeneity of variance and normality). Height data were ln (x) transformed. Homogeneity of variance was checked by visually examining plots of residuals versus predicted values (see Quinn & Keough 2001).

7.3 Results

7.3.1 MAIN TREATMENT EFFECTS

Soil

None of the study species was influenced by the main effects of soil type in terms of their survival (Appendices 7.1-7.3, Fig. 7.2). Most of the species did, however, exhibit a trend towards better own soil survival by the end of the experiment. The only exception was *Triodia brizoides*, with this species surviving equally well in the two soil types. One species, *Acacia aneura*, had enhanced growth in its own soil compared with in the spinifex soil at month one ($P < 0.01$). Main soil affects were otherwise unapparent for the remaining species (Appendices 7.4-7.5, Fig. 7.3).

Shading

Main shade effects were also of minor consequence for survival (Appendices 7.1-7.3, Fig. 7.2). Only *E. latrobei* subsp. *glabra* was significantly affected, showing reduced survival at month two with shade. All species, except for the two dominants *A. aneura* and *T. brizoides*, tended towards better survival without shade, while these latter two showed no particular trend either way. Importantly though, *A. aneura*, at one point (month one) showed enhanced growth with shading ($P < 0.01$). None of the other species was influenced by main shade effects in terms of their growth (Appendices 7.4-7.5, Fig. 7.3).

Species association

Survival in the mulga grass *D. brownii* was influenced by main species association effects at months two and three, at which points it had better survival in the allopatric compared with the sympatric mix. This same pattern was apparent for *Corymbia eremaea* subsp. *oligophylla* at months two and three. Only one species, *E. latrobei* subsp. *glabra*, exhibited a trend towards better survival in the sympatric mix (Appendices 7.1-7.3, Fig. 7.2). Growth in this same species was influenced by the species' association treatment, being enhanced in the sympatric mix at months one and three ($P < 0.0001$). The mulga dominant *Acacia aneura* likewise showed enhanced growth at month one in the sympatric mix ($P < 0.01$) (Appendices 7.4-7.5, Fig. 7.3).

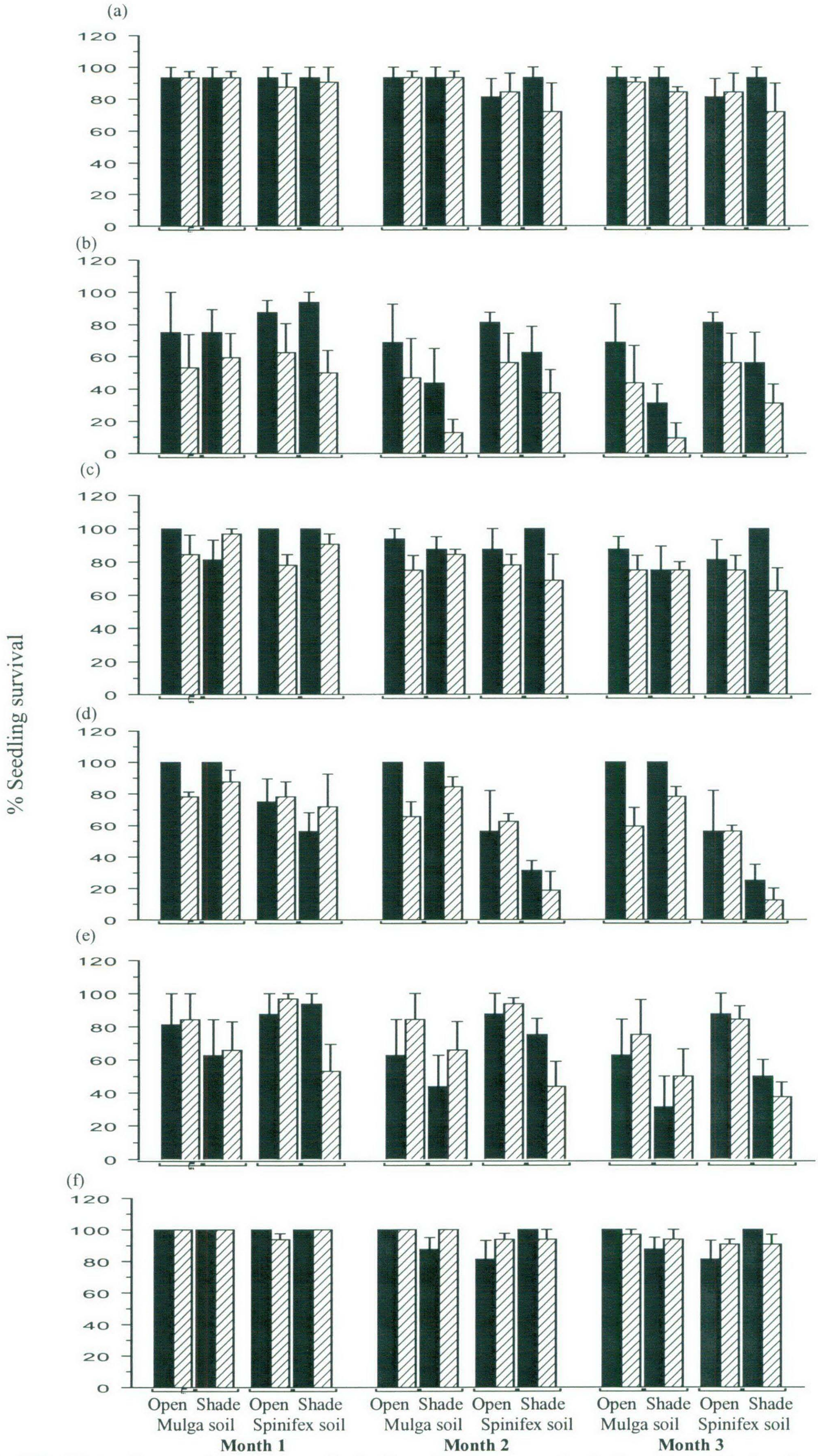

Fig. 7.2 Plots of mean (±SE) % survival of seedlings at months 1, 2 and 3. (a) ***Acacia aneura***; (b) *Acacia bivenosa*; (c) *Corymbia eremaea* subsp. *oligophylla*; (d) ***Digitaria brownii***; (e) ***Eremophila latrobei* subsp. *latrobei***; (f) *Triodia brizoides*. (■) allopatric mix; (▨) Sympatric mix. Mulga species are in bold.

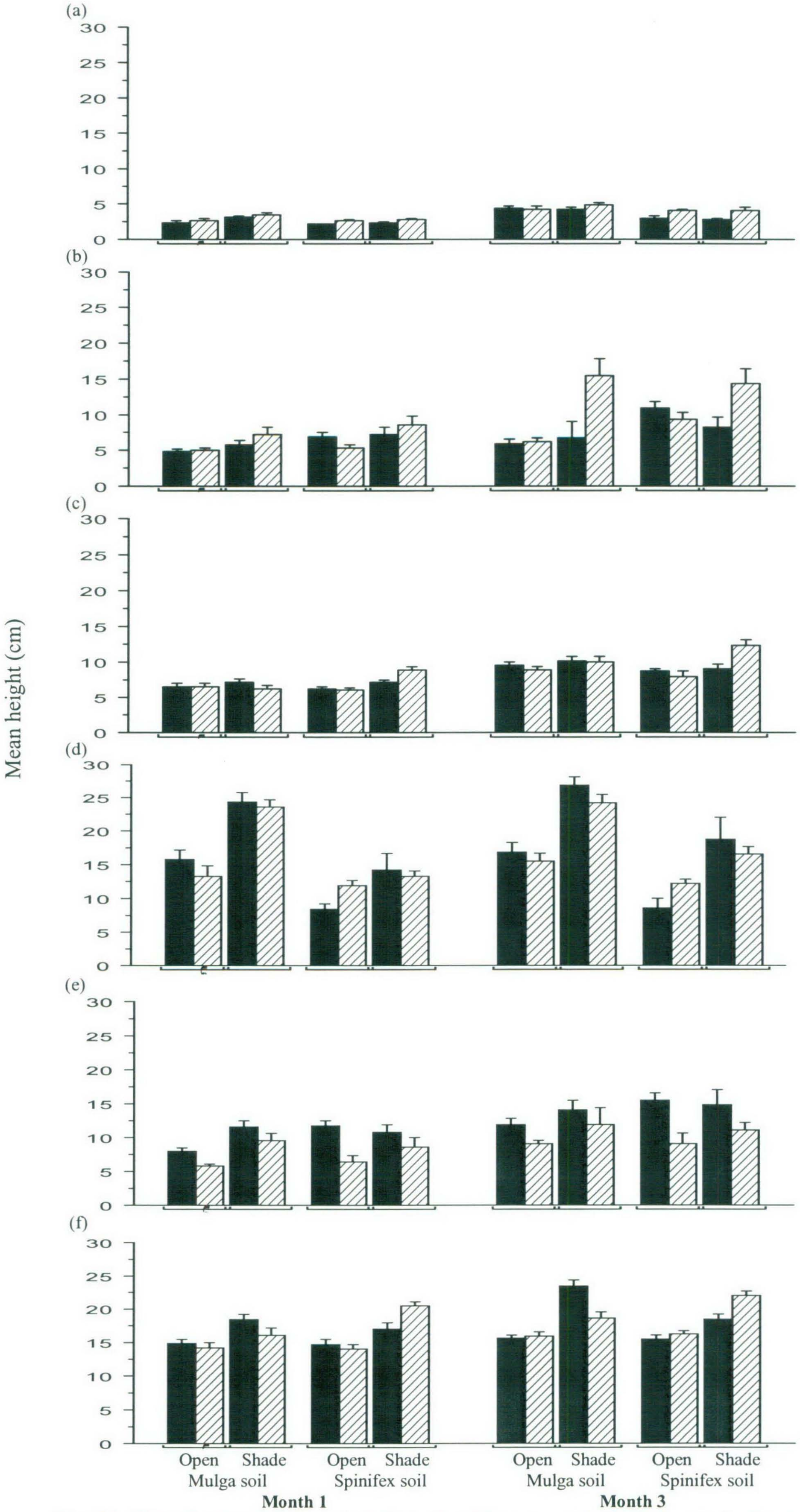

Fig. 7.3 Plots of mean (±SE) growth (height) of seedlings at months 1 and 3. (a) ***Acacia aneura***; (b) *Acacia bivenosa*; (c) *Corymbia eremaea* subsp. *oligophylla*; (d) ***Digitaria brownii***; (e) ***Eremophila latrobei* subsp. *latrobei***; (f) *Triodia brizoides*. (■) allopatric mix; (▨) Sympatric mix. Mulga species are in bold

7.3.2 TREATMENT INTERACTIONS

Treatment interactions dominated the survival results in this experiment. At month one, *D. brownii* showed better survival in mulga soil in the allopatric mix, and at the same time showed better survival in spinifex soil in the sympatric mix. At months two and three, this same species showed better survival in mulga soil under shade, and better survival in the spinifex soil in the open. The spinifex dominant *T. brizoides* showed the opposite response, i.e. better survival in the open in mulga soil, and better survival in the shade in its own soil. One species, *Corymbia eremaea* subsp. *oligophylla* had better survival without shade in the allopatric mix, and equal survival with shade and in the open in the sympatric mix (Appendices 7.1-7.3, Fig. 7.2).

At month three, *Acacia aneura* showed enhanced growth in the sympatric mix when grown in spinifex soil yet was uninfluenced by species' association in its own mulga soil ($P < 0.05$). *Digitaria brownii* exhibited the exact same response at month one ($P < 0.05$). Also at month one, two species, *Digitaria brownii* and *E. latrobei* subsp. *glabra* showed enhanced growth under the shade in their own mulga soil, but were otherwise uninfluenced by shade in the spinifex soil ($P < 0.0001$). Growth to month one in the spinifex tree *C. eremaea* subsp. *oligophylla* mirrored that of these last two species, in that it was enhanced in the shade in its native spinifex soil ($P < 0.01$). *Triodia brizoides* growth was influenced by a three-way interaction at months one and three (soil x shade x species mix) that did not provide any insight into species' patterning (Appendices 7.4-7.5, Fig. 7.3).

7.3.3 PATCH EFFECTS

Patch effects influenced the survival of two species: the first, *A. bivenosa*, at each monitoring point, and the second, *E. latrobei* subsp. *glabra*, at months one and two (Appendices 7.1-7.3). Growth in three of the species was influenced by patch effects: *Acacia bivenosa* at months one and three; *Digitaria brownii* at month three, and *Corymbia eremaea* subsp. *eremaea* at month three (Appendices 7.4-7.5).

7.4 Discussion

7.4.1 WHAT FACTORS DRIVE ESTABLISHMENT AND SURVIVAL IN MULGA-SPINIFEX MOSAICS?

Main effects of physiological constraint and biotic interactions

The results of this study add strength to the main argument presented in the previous chapter that, in isolation, physiological constraint and biotic interactions are of relatively minor consequence for seedling establishment success in mulga-spinifex mosaics. Noteworthy exceptions include the temporary positive influence of 1) the sympatric mix on growth in *Acacia aneura* (month one) and in *Eremophila latrobei* subsp. *glabra* (at months one and three); and of 2) the allopatric mix on survival in the spinifex tree *C. eremaea* subsp. *oligophylla* (at months two and three). These results confirm the importance of suppression-based competition by establishing *Triodia* plants in the determination of recruitment success in both spinifex and mulga species.

Also noteworthy was the positive effect of shading on early growth (to month one) in the mulga dominant *A. aneura*. Throughout this thesis, facilitation of seedling emergence and early survival by established *A. aneura* shrubs has been a recurrent theme, with these additional results strengthening the case for the importance of this process for regeneration in mulga habitat. The result also adds weight to the earlier depiction of *A. aneura* as a stress-tolerator (*sensu* Grime 1979) at the seedling stage, given its ability to recruit in limited light conditions. The otherwise minimal independent influence of the artificial shading treatment is again consistent with existing theory that predicts that root- compared with shoot-competition is of greatest consequence in arid habitats (Rajaniemi *et al.* 2003).

Finally, some evidence was provided for the role of edaphic constraint, primarily with regard to its influence on early growth patterns in *A. aneura*. The otherwise near absence of main soil effects is possibly reflective of the primary role of soil/water relations compared with soil nutrient gradients for seedling establishment in these arid mosaics. In this experiment, unlike in the previous one (refer Chapter 6), water and its influence on soil penetrability was never a limiting factor given that irrigation took place throughout. This meant that potential soil texture effects were, in this case, never realised. The influence of the substantial between-habitat differences in soil texture, as demonstrated by the results of Chapter 2, therefore still requires consideration.

The remaining main treatment effects offered no further insight into variable establishment success given they were suggestive of 1) enhanced survival in the mulga shrub *E. latrobei* subsp. *glabra* with increased light (i.e. conditions more characteristic of spinifex habitat), and enhanced survival in *D. brownii* in sympatric association. Again though, patch effects had consistent effects on growth and survival throughout experimentation, serving as further evidence for the high level of spatial- and temporal-heterogeneity in arid environments (see Peek & Forseth 2003).

Interactive effects of physiological constraint and biotic interactions

The results of this experiment demonstrate that the interactive effects of physiological constraint and biotic interactions are highly influential in the determination of seedling establishment success in mulga-spinifex mosaics. Specifically, it was shown that edaphic conditions affect plant growth and survival by modifying the outcome of seedling-seedling and seedling-adult interactions. Two major findings emerged from this study. First, it was shown that for certain species – namely the mulga diagnostics *A. aneura* (at month three) and *D. brownii* (at month one) – growth and survival in spinifex soil is enhanced when they are grown in sympatric- compared with allopatric-association. This means that in certain spinifex habitats, negative allopatric interactions and edaphic constraint combine to reduce the chances of successful establishment of mulga species. The result further suggests that the ability of establishing spinifex to suppress mulga seedlings is largely dependent on environmental context.

The second major finding in terms of the treatment interactions is that mulga and spinifex species potentially respond differently to shading when grown in mulga soil. Most noteworthy was the variable survival results of the mulga tussock grass *D. brownii* and the spinifex dominant *T. brizoides*, with the former exhibiting heightened survival under shaded conditions in mulga soil, and the latter with full light in mulga soil. It is possible that this result is reflective of the variable influence of established *A. aneura* shrubs on these two divergent diagnostic grasses. Specifically, it is apparent that while survival in *D. brownii* is possibly facilitated by the combined effects of shading and own soil type, that in the hummock grass is comparatively reduced in areas where *A. aneura* develops a dense canopy. It is likely therefore, that while in the post-disturbance environment, establishing *Triodia* has a strong competitive effect on neighbouring mulga seedlings, its negative influence is reduced in mature mulga because it is less able to tolerate the comparatively low resource (i.e. light) levels there. This means that in mulga habitat, the suppression ability of *Triodia* is only short-term. This same constraint is not in operation in mature spinifex habitat, given that most of the characteristic shrubs exhibit more of a fugitive strategy (*sensu* Grime 1979), and thereby do not form persistent, dense canopies. Van Etten (1987) provided a similar explanation for the comparatively low abundance of *Triodia pungens* in mulga habitat, based on the results he obtained from shading experiments. The combined influence of own soil type and shading was additionally apparent for growth in the mulga shrub *E. latrobei* subsp. *glabra*, potentially explaining the result showing that while this species is sometimes present in spinifex habitat, it most often has its greatest abundance in mature mulga (refer Chapter 2).

7.4.2 HOW IS COEXISTENCE MAINTAINED IN MULGA-SPINIFEX MOSAICS?

Between-habitat partitioning

It was suggested in the previous chapter that, in emphasising edaphic variation, the chief value of Bowman *et al.*'s first model lies in its ability to partially explain boundary formation and maintenance rather than to account for coexistence breakdown. The results of this study indicate that this also applies in the case of mountain range mulga-spinifex mosaics. Specifically, the results demonstrate that this particular example of spinifex soil – characterised by extremely high pH, high carbonate concentration, and low clay content – likely represents what Myster (2001) refers to as a 'gradient edge' for *A. aneura*, given that this species exhibited comparatively reduced early growth (to month one) in that situation. It is likely therefore, that between-habitat coexistence in these range mosaics is at least partly due to the influence of fundamental niche constraints on *A. aneura*. It is also possible that the independent influences of positive shade effects and negative allopatric seedling interactions would further act to strengthen between-habitat patterning during the early establishment phase. And at later stages, the establishment of this species outside of its normal range is evidently constrained by the interaction of edaphic and biotic factors (i.e. the negative influence of allopatric association on *A. aneura* in spinifex soil).

For other species, between-habitat partitioning is apparently foremost related to the influence of edaphic variability on the outcome of biotic interactions. Specifically, it is suggested that own-habitat establishment in the mulga species *D. brownii* and *E. latrobei* subsp. *glabra* is facilitated by a combination of soil and shade effects. Additionally, the inhibitory effects of the joint influence of soil type and allopatric seedling interactions would possibly act to constrain *D. brownii* establishment in spinifex habitat. For *Triodia brizoides*, evidence suggests that mulga soil and shading combine to reduce establishment success in this species in mature mulga. This serves as a potential explanation for the low abundance of *Triodia brizoides* in the thick stands of regenerating mulga at Tylers Pass (see Chapter 2). The results do not however, provide insight into the processes restricting the remaining two species to spinifex habitat, given that one (*A. bivenosa*) was influenced foremost by patch effects, while the other failed to respond to the habitat-related factors trialled in this experiment. Further work, perhaps focussing more on the influence of soil-water relations, is therefore necessary for the resolution of this matter.

Within-habitat coexistence

The results of this study provide further support for the idea that processes mediating within-habitat coexistence in mulga and spinifex are not equivalent. Specifically, the survival data for the spinifex tree *C. eremaea* subsp. *oligophylla* alludes to the importance of temporal fluctuations in the abundance of *Triodia* for establishment success in spinifex. This is because it was demonstrated that early survival in this species is enhanced with reduced *Triodia* abundance (as simulated by the allopatric mix) and increased light, both of which characterise early post-disturbance conditions in spinifex habitat. It is likely therefore, that coexistence in this habitat is at least partially facilitated by disturbance-mediated competitive release, combined with the fugitive strategy of establishing co-occurring seedlings that are able to escape competition by restricting recruitment to the post-disturbance environment. By contrast, the results were not indicative of a requirement for adult removal for within-habitat coexistence in mulga, and in fact alluded to the importance of the provision of shade for establishment success in this habitat.

7.4.3 CONCLUSION

This study highlights the importance of examining competitive interactions across the range of environmental conditions, life-history stages and disturbance histories for understanding patterning in mulga-spinifex mosaics. Specifically, it was shown that while interactions with establishing spinifex initially suppress *A. aneura* seedling growth in mulga soil, the ultimate outcome of this interaction is contingent on the timing of future disturbance events. If fire recurrence happens prior to *A. aneura* reaching maturity and forming a light-restricting canopy, then the chances of long-term mulga persistence will be reduced. If, on the other hand, the site experiences a long fire-return interval by virtue of patchy fire behaviour, then the suppressive effect of spinifex will diminish with time due to its inability to tolerate the debilitating interactive effects of mulga soil and shade. In habitats that are tending more towards a gradient edge for mulga species, their exclusion will instead result from the independent influence of fundamental niche constraint at early establishment, and the combined debilitating effects of edaphic and biotic interactions at later development stages. Within-habitat coexistence in mulga relates to the ability to recruit in mature habitat and thereby resist competitive suppression when resource levels are low, while that in spinifex is largely dependent on an ability to resist suppression by virtue of 'fugitive' traits at the establishment life phase.

Chapter 8

General discussion and presentation of a new model for mulga-spinifex mosaic coexistence

8.1 Introduction

The primary goal of this thesis was the identification of processes mediating within- and between-habitat coexistence in central Australian mulga-spinifex mosaics. As a rationale for the study, it was argued that in order to gauge the likelihood of mosaic coexistence breakdown, it is first necessary to gain a detailed understanding of the nature of habitat boundaries and of the factors currently contributing to their maintenance. The study used community coexistence theory as a framework for identifying 'assembly processes' (*sensu* Weiher & Keddy 1999) and for determining how they relate to the predictions of existing models for mosaic breakdown. It was characterised by a series of manipulative experiments designed to identify the critical constraints on the transference from early life stages through to adulthood within and between habitat boundaries.

Throughout this thesis, much consideration has been given to the relative merits of three divergent models for mosaic regulation. As explained, two of the models may be classed as 'non interactive' theory (*sensu* Bond & van Wilgen 1996), given their shared emphasis on the interplay of species' tolerances/requirements and on the local environment for the regulation of community dynamics. The first of these (**fire-mediated shift in site quality**) accounts for the localised extinction of *A. aneura* through the fire-induced erosion of mulga soil. In this way it suggests that current boundaries are the result of patchy resource distribution, as *per* the 'source/sink' model for mulga grove-intergrove patterning (Tongway *et al.* 2001). Model II (**fire-mediated extinction**) aligns closely with the predictions of the 'vital attributes approach' (Noble & Slatyer 1980) and the global model for grass-shrub patterning (Bond *et al.* 2005; Bond & Keeley 2005). It depicts the fire-driven localised extinction of *A. aneura* via the successive removal of fire-sensitive adults and slow-growing seedlings, and through subsequent seed bank exhaustion. In this way it suggests that current shrub-grass alterations are the result of patchy fire behaviour. The third model (**fire-mediated shift in competitive abilities)** instead falls into the 'interactive' theoretical framework given its emphasis on biotic

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Appendices

Appendix 2.1 Results of SIMPER analysis of within- and between-group similarity fro the broad- and fine-scale clusters defined by the PATN analysis of mountain range mosaic habitats.

Within-group similarity of broad-scale clusters:

i. Group A *Triodia brizoides* hummock grassland: This cluster consisted of 31 samples distributed across all four sites. It had the lowest within-group average similarity (27.83) of the three groups, indicating a comparative lack of among-sample cohesion. Two highly typical spinifex species (*sensu* Bowman *et al.* 1994) – *Triodia brizoides* and *Acacia bivenosa* – contributed approximately half (55.02%) of within-group similarity, and a further 24 species contributed over 90% (refer Table 2.2). Overall, the group had a relatively high proportion (42%) of typical spinifex species as well as a moderate proportion (19%) of typical mulga species. Though listed among the highest-order contributors, the mulga dominant, *Acacia aneura*, contributed least to within-group similarity, indicating that it occurred in low abundance or was entirely absent from samples where *Triodia brizoides* constituted the structural dominant. The 26 diagnostic species (as per the SIMPER analysis) were distributed among seven growth-form groups, with perennial shrubs having the greatest representation (ten species), followed by perennial half-shrubs (five species). The remaining groups – short-lived half-shrubs, perennial tussock grasses, trees, hummock grasses and short lived forbs – were comparatively poorly represented.

ii. Group B *Acacia aneura* shrubland: This cluster consisted of 34 samples distributed across all four sites. It had intermediate within-group average similarity (36.06) indicating a moderate degree of among-sample cohesion. Five species – *Acacia aneura*, *Sida filiformis*, *Cheilanthes lasiophylla*, *Triodia brizoides*, and *Eremophila latrobei* var. *latrobei* – contributed approximately half (50.96%) of the within-group similarity and a further 19 contributed over 90% (refer Table 2.2). Overall, the group had the highest proportion of typical mulga species (37%) and the lowest proportion of typical spinifex species (8%). Diagnostic species were distributed among eight growth-form groups, with perennial shrubs again having the greatest representation (nine species). Two groups – perennial half-shrubs and perennial tussock grasses – had intermediate representation (four species each), while the remaining groups (hummock grasses, perennial forbs, short-lived tussock grasses, ferns and short-lived half-shrubs) were each represented by one species only. While present in some Group B quadrats, the other hummock-grass, *Triodia longiceps*, made negligible contribution to the within-group similarity of this group.

iii. Group C (= Subgroup 9) *Triodia longiceps* hummock grassland (Figs 2.6 & 2.7): Samples in this cluster had a restricted distribution, being confined to north-facing slopes of one of the four sample areas – Brewer Conglomerate East (Hugh River). A section of the Bitter Springs Limestone formation occurred directly to the north of this habitat. This cluster had the highest within-group average similarity (43.77), indicating a comparatively high level of cohesion among the eight constituent mature and burnt samples. The structural dominant, *Triodia longiceps*, contributed more than half (58.76) of the within-group similarity while a further seven contributed over 90% (refer Table 2.2).

Overall, the group had a relatively high proportion of typical spinifex species (33%) and a low proportion of typical mulga species (7%). *Acacia aneura* was not included among the highest order contributors, indicating minimal co-occurrence of this species and *Triodia longiceps*. The eight diagnostic species were distributed among five growth-form groups, with perennial shrubs having the greatest representation (four species), and the remaining groups – perennial half-shrubs, hummock-grasses, mallee-shrubs, and perennial forbs – each being represented by one species only.

Between-group dissimilarity of broad-scale clusters

Groups A & C: *Triodia brizoides* and *Triodia longiceps* clusters were characterised by a very high average dissimilarity (88.64), indicating minimal floristic overlap. Seventeen species contributed approximately half (51.19%) of the between-group dissimilarity. Of these, only one species – the perennial shrub *Senna glutinosa* subsp. *glutinosa* – was twice more abundant in Group C than in Group A. Species unique to C were also relatively few and included: the hummock-grass *Triodia longiceps*, the mallee shrub *Eucalyptus eucentrica*, the tree species *Grevillea striata*, and the short-lived forb *Streptoglossa odora*. Only one species, the perennial shrub *Senna artemisioides* nothosubsp. *artemisioides*, was twice more abundant in Group A than in Group C. By contrast, as many as 33 species, representing nine growth-form groups, were unique to Group A. Most of these were perennial shrubs and half-shrubs (nine and five species each). Two other groups – perennial tussock grasses and short-lived forbs – were also well represented (four species each). Also notable was the restriction of the hummock grass *Triodia brizoides*; five species of *Acacia* (*A. melleodora*, *A. murrayana*, *A. spondylophylla*, *A. tetragonophylla* and *A. validinervia*); as well as two diagnostic mulga species (*Sarcostemma viminale* subsp. *australe* and *Eremophila latrobei* var. *latrobei*) to this cluster.

Groups A & B: *Triodia brizoides* and mulga clusters were characterised by comparatively low average dissimilarity (82.66). Twenty-five species contributed approximately half (50.52%) of the between-group dissimilarity. Of these, 14 (all diagnostic of B) were twice more abundant in Group B than in Group A. Included were: the mulga shrubs *A. aneura*, *Eremophila latrobei* subsp. *latrobei*, *E. latrobei* subsp. *glabra* and *E. freelingii*; various perennial tussock grasses (e.g. *Digitaria brownii*, *Paspalidium constrictum*, and *Tripogon loliiformis*), the ferns *Cheilanthes lasiophylla* and *C. sieberi* subsp. *sieberi*; and the chenopod half-shrubs *Enchylaena tomentosa* and *Maireana villosa*. Perennial tussock grasses (e.g. *Enteropogon acicularis*, *Neurachne tenuifolia*, *Neurachne munroi* and *Thyridolepis mitchelliana*) dominated the group of seven unique B-group species. Three Group A diagnostic species – *Triodia brizoides*, *Acacia bivenosa*, and *Scaevola spinescens* – were twice more abundant in Group A, and as many as 15 species, representing eight growth-form groups, were unique to A. Notable examples were various members of the families Myrtaceae (e.g. *Corymbia eremaea* subsp. *oligophylla* and *Eucalyptus intertexta*) and Malvaceae (e.g. *Hibiscus solanifolius* and *Gossypium sturtianum*).

Groups B & C: mulga and *Triodia longiceps* clusters were characterised by the highest average dissimilarity (89.23). Seventeen species contributed approximately half (51.13%) of the dissimilarity. Of these, three – *Triodia longiceps*, *Acacia bivenosa* and *Senna glutinosa* subsp. *glutinosa* – were twice more abundant in Group C than in Group B. Similarly few species were unique to Group C: the mallee shrub *Eucalyptus eucentrica*, the tussock grass *Paraneurachne muelleri*, and the small Proteaceous tree *Hakea suberea*. Five diagnostic mulga species were twice more abundant in B than in C. Included were: the shrubs *Acacia aneura*, *Eremophila freelingii*, and *Enchylaena tomentosa*; the fern *Cheilanthes lasiophylla*, and the tussock grass *Tripogon loliiformis*. As many as 25 species, spanning ten growth-form groups, occurred in B but not in C. Included were: two mesophyll shrubs *Canthium lineare* and *C. latifolium*; the shade-tolerant succulents *Sedopsis filsonii* and *Grahamia australiana*; the mulga fern *Cheilanthes sieberi* subsp. *sieberi*; and the semi-woody mulga climber *Sarcostemma viminale* subsp. *australe*. The group of unique B species was also comparatively rich in tussock grasses, while at the same time, including the hummock grass *Triodia brizoides*.

Within-group similarity of Group A subgroups

i. Subgroup 1 (Fig. 2.8) comprised eight samples, all of which were confined to Site 3 (Finke Gorge) and were dominated by mature stands of *Triodia brizoides*. Within-group average similarity was predictably high (57.21) indicating a high degree of among-sample cohesion. Four fire tolerant (*sensu* Latz 1995) species – *Triodia brizoides*, *Scaevola spinescens*, *Sida filiformis*, and *Acacia bivenosa* – contributed approximately half (52.76%) of the within-group similarity and a further 9 contributed 90% (refer Table 2.2). Overall, the subgroup has a relatively high (33%) proportion of typical spinifex species (*sensu* Bowman *et al.*) and a low proportion (13%) of typical mulga species. The 13 diagnostic species were distributed among six predominantly long-lived growth-form groups, with perennial shrubs and half-shrubs having the greatest representation (6 and 3 species respectively). The remaining growth-form classes – short-lived half-shrubs, hummock grasses, perennial tussock grasses, and perennial forbs – were each represented by one species only. The majority of woody diagnostics were all capable of some degree of resprouting and/or were tolerant of repeated firing by virtue of rapid life-cycle development.

ii. Subgroup 2 (Fig. 2.9) comprised eight samples, characterised primarily by mature stands of *Triodia brizoides* from two sites: 2 (Tylers Pass), where it occurred only on red-soils with sandstone and quartzite surface clasts; and 4 (Iwupataka). Also included was one sample of sparsely regenerating mulga with a dense *Triodia brizoides* understorey (sample 26). Within-group average similarity was comparatively low (36.61) possibly reflecting regional and geological differences. Only one species, the structural dominant *Triodia brizoides*, contributed half (52.5%) of the within-group similarity while a further ten contributed over 90% (refer Table 2.2). A large proportion of these were shrubs capable of withstanding repeated firing (e.g. *A. bivenosa*, *A. validinervia*, *Senna artemisioides* nothosubsp. *artemisioides*, and *A. melleodora*). This subgroup had a high proportion of typical spinifex species (25%) and a low proportion of typical mulga species (7%). While the fire-sensitive mulga dominant *Acacia aneura* was listed as diagnostic for this subgroup, its contribution was comparatively minimal.

iii. Subgroup 3 (Fig. 2.10) comprised three samples, all of which were confined to Site 3 (Finke Gorge) and were dominated by immature stands of *Triodia brizoides*. Within-group average similarity was high (63.14) indicating a high degree of cohesion. Five fire-encouraged species – *Acacia spondylophylla*, *Phyllanthus lacunellus*, *Acacia bivenosa*, *Triodia brizoides*, and *Indigofera* A86365

MacDonnell Ranges – contributed approximately half (50.72%) of the within-group similarity, and a further ten contributed 90% (refer Table 2.2). Typical spinifex species were moderately well represented (17%) while typical mulga species were few (7%). The fifteen diagnostic species were distributed across six growth-form classes, with perennial shrubs and half-shrubs having the greatest representation (five species each), followed by short-lived half-shrubs (two species). The remaining classes – hummock grasses, perennial tussock grasses, and perennial forbs – all had one species each. The majority of remaining diagnostics were classed as either fire-encouraged/tolerant (e.g. *Goodenia triodiophila*, *Abutilon leucopetalum*, *Petalostylis cassioides*, *Hibiscus solanifolius*, *Evolvulus alsinoides* var. *villosicalyx*, and *Senna artemisioides* nothosubsp. *artemisioides*).

iv. Subgroup 4 (Fig. 2.11) comprised four samples spread across Sites 1 (Hugh River) and 2 (Tylers Pass), all of which were dominated by immature stands of *Triodia brizoides*. Like those of 2, Subgroup 4 samples were confined to red-soil areas. Within-group average similarity was comparatively low (36.91), indicating a lack of cohesion and possibly reflecting regional (east-west differences). Four species – *Triodia brizoides*, *Panicum effusum*, *Paraneurachne muelleri*, and *Hibiscus sturtii* var. *grandiflorus* – contributed approximately half (53.64%) of the within-group similarity and a further 11 contributed over 90% (refer Table 2.2). This subgroup included a large proportion of typical spinifex species (42%) and a small proportion (6%) of typical mulga species. Again perennial shrubs dominated the assemblage (six species), followed by perennial half-shrubs and perennial tussock grasses (three species each). The remaining growth-form groups – short-lived half-shrubs, perennial hummock grasses, and short-lived forbs – were each represented by one species only. All of the diagnostic species (both woody and herbaceous) for this subgroup were either fire-encouraged or fire-tolerant, and most of the woody species possessed at least some degree of resprouting ability (e.g. *Acacia murrayana* and *A. validinervia*).

v. Subgroup 5 (Figs 2.12 & 2.13) comprised eight samples spread across Sites 1 (Hugh River) and 2 (Tylers Pass) and dominated by mature and immature stands of *Triodia brizoides*. All five samples were confined to 'white-soil' areas that were characterised by a wide range of surface rock types including granite, schist, gneiss, sandstone, limestone and quartz. Within-group average similarity was comparatively low (36.11), indicating a lack of cohesion and probably reflecting regional (east-west) and fire-age differences among constituent samples. Three fire-encouraged herbaceous species – *Triodia brizoides*, *Solanum ellipticum*, and *Trichodesma zeylanicum* – contributed approximately half (50.61%) of the within-group similarity and a further 13 (again including *Acacia bivenosa*) contributed 90% (refer Table 2.2). One quarter (25%) of typical spinifex species was included in this subgroup, while typical mulga species were poorly represented (6%). The 16 diagnostic species were distributed across eight growth-form groups, with short-lived forbs and perennial shrubs having the greatest representation (five and four species each). All remaining groups – trees, perennial half-shrubs, short-lived tussock grasses, hummock grasses, perennial forbs and climbers – had only minimal representation. All woody and semi-woody diagnostic species were fire-tolerant/fire-encouraged, and the majority possessed at least some resprouting ability.

Within-group similarity of Group B subgroups (all confined to red-soil areas)

i. Subgroup 6 (Figs 2.14 & 2.15) comprised 13 samples spread across two sites: 1 (Hugh River) and 3 (Finke Gorge) and was characterised primarily by mature stands of *Acacia aneura* with a *Triodia brizoides* hummock grass understorey. Also included were two samples of thick regenerating mulga with a dense understorey of *Triodia brizoides*, from north-facing slopes of site 1. Within-group average similarity was relatively high (47.67) considering the geological differences and the geographic separation of included samples. Seven species – *Triodia brizoides*, *Acacia aneura*, *Sida filiformis*, *Eremophila latrobei* var. *latrobei*, *Acacia kempeana*, *Cheilanthes lasiophylla*, and *Sarcostemma viminale* subsp. *australe* – contributed approximately half (54.61%) of the within-group similarity and a further 16 contributed over 90% (refer Table 2.2). Despite constituting a structural (shrub-grass) mix, there was a disproportionate number of typical mulga species (30%) compared with typical spinifex species (17%). The 23 diagnostic species were distributed across eight growth-form groups, with perennial shrubs and half-shrubs having the greatest representation (nine and four species each). All remaining groups – short-lived perennial half-shrubs, perennial tussock grasses, hummock grasses, short-lived tussock grasses, ferns and climbers – had only minimal representation. Unlike those of the preceding subgroups, Subgroup 6 woody and semi-woody diagnostics were largely obligate seeders (e.g. *Sida filiformis*, *Indigofera* A86365 MacDonnell Ranges, *Acacia aneura*, and *Enchylaena tomentosa*) or facultative resprouters (e.g. *Acacia kempeana*, *Eremophila freelingii*, and *Eremophila latrobei* var. *latrobei*). Samples of mature mulga from the Hugh River section were highly localised, occurring in one small area (near Point Howard), which unlike other sampled parts of the Brewer Conglomerate, was protected from fires advancing from the north by a parallel-running high quartzite range. Samples from study site 3 were largely confined to the plateau rim of the Finke Gorge range system – an area least likely to be affected by lightning strikes compared with the adjacent steep, high slopes (Figs 2.16 & 2.17).

ii. Subgroup 7 (Figs 2.18 & 2.19) comprised 14 samples spread across three sites: 1 (Hugh River), 2 (Tylers Pass), and 4 (Iwupataka). Included in this subgroup were stands of both mature and regenerating mulga. Spinifex (*T. brizoides* and *T. longiceps*) was either absent or occurs as only a very minor component of the ground stratum. Within-group average similarity was low (38.48), likely reflecting the high degree of geographic separation, the differing geological settings, and possibly different fire-ages. Four species – *Acacia aneura*, *Cheilanthes lasiophylla*, *Digitaria brownii* and *Sida filiformis* – contributed approximately half (51.59%) of the within-group similarity and a further 15 contributed over 90% (refer Table 2.2). Slightly more than one-quarter (28%) of typical mulga species was included in the group of diagnostics as was only 8% of typical spinifex species. The 19 diagnostic species were distributed across seven growth-form groups, with perennial shrubs having the greatest representation (seven species). Perennial half-shrubs and perennial tussock grasses were also well represented (four and three species respectively), while the remaining classes – short-lived tussock grasses, hummock grasses, short-lived forbs, and ferns – had low richness (one or two species). Woody and semi-woody species were either obligate seeders or facultative resprouters and only two (*Sida filiformis* and *Evolvulus alsinoides* var. *villosicalyx*) were fire-encouraged.

iii. Subgroup 8 (Figs 2.20 & 2.21) comprised seven samples that occurred in two sites: 1 (Hugh River) and 2 (Tylers Pass). Included in this subgroup were stands of both mature and regenerating mulga. Spinifex (*T. brizoides*) was present in all samples, though its abundance was variable, ranging from one to ten (mean of five). Within-cluster average similarity was relatively high (47.24), despite the geographic separation of the samples. Five species – *Acacia aneura*, *Thyridolepis mitchelliana*, *Paspalidium constrictum*, *Sida filiformis*, *Eremophila latrobei* var. *glabra*, *Triodia brizoides* – contributed approximately half (52.63%) of the within-group similarity and a further ten contributed 90% (refer Table 2.2). A moderate proportion (19%) of typical mulga species was included, as was one typical spinifex species (*Triodia brizoides*). Perennial shrubs were best represented (5 species), followed by tussock grasses and perennial half-shrubs (three species each). The remaining growth-form groups – short-lived half-shrubs, perennial forbs and ferns – were poorly represented. As with the previous two subgroups (6 and 7), the woody diagnostics (8 species) were predominantly seeders or facultative resprouters. The mature stands of mulga (four samples) had extremely dense canopies and occurred only as very small isolated patches. Each patch was confined to areas with a southern landform aspect, and was characterised by a canopy of somewhat spindly individuals, all of which appeared to be part of the same cohort. *Triodia brizoides* had a maximum abundance of three in these samples. The frequency of *Acacia aneura* in the remaining samples (all regenerating after fire) was more variable (ranging from four to eight) compared to the mature stands, while *Triodia brizoides* had a consistently high frequency (range 7 to 10).

Between-group dissimilarity of fine-scale clusters

Dissimilarity analysis was carried out only for spatially contiguous subgroups:

Subgroups 1 & 3: Finke Gorge mature and immature spinifex clusters (Fig. 2.22) were characterised by a comparatively low level of dissimilarity (71.64) – illustrating the overarching influence of geological/regional affects compared with fire history. Twelve species contributed approximately half (50.41%) of between-group dissimilarity. Of these, four species – *Phyllanthus lacunellus*, *Stenopetalum decipiens*, *Indigofera* A86365 MacDonnell Ranges, and *Acacia bivenosa* (all fire encouraged) – were twice more abundant in 3 than in 1. Nine species were unique to Subgroup 3, many of which again were fire encouraged (e.g. *Acacia spondylophylla*, *Petalostylis cassioides*, *Hibiscus solanifolius*, *Goodenia triodiophila*, and *Xerochrysum bracteatum*). Only two species – *Sida filiformis* and *Scaevola spinescens* – were twice more abundant in 1 than in 3. Seven species were unique to 1, most of which were actually diagnostic of mulga (B) habitat (e.g. *Acacia kempeana*, *Sarcostemma viminale* subsp. *australe*, *Eremophila latrobei* var. *latrobei*, *Enchylaena tomentosa*, and *Rhagodia eremaea*) and none of which were fire encouraged.

Subgroups 2 & 4: Brewer Conglomerate red-soil mature and immature spinifex clusters (Fig. 2.23) were characterised by only a moderate level of dissimilarity (78.36), again implying that fire effects were of limited impact compared with other habitat factors. Nineteen species contributed approximately half (51.24%) of between-group dissimilarity. Of these, seven (mostly fire-encouraged perennial tussock grasses and some half-shrubs) were twice more abundant in 4 than in 2:

Heliotropium tenuifolium, *Panicum effusum*, *Paraneurachne muelleri*, *Themeda triandra*, *Evolvulus alsinoides* var. *villosicalyx*, *Hibiscus sturtii* var. *grandiflorus*, and *Ptilotus schwartzii*. A large number of short-lived species were unique to 4, many of which were fire-encouraged (e.g. *Goodenia ramelii*, *Pterocaulon sphacelatum*, *Trichodesma zeylanicum*, *Phyllanthus lacunellus*, and *Streptoglossa decurrens*). Also unique to 4 were various fire-tolerant/encouraged perennial shrubs: *Eucalyptus trivalvis*, *Acacia coriacea*, *Acacia murrayana*, *Gossypium australe*, *Gossypium sturtianum*, *Hibiscus solanifolius*, *Melhania oblongifolia*, and *Senna glutinosa* subsp. *pruinosa*. No species had twice its abundance in 2 than in 4. Eight species were unique to 2 – *Cheilanthes lasiophylla*, *Eriachne mucronata*, *Eucalyptus intertexta*, *Chrysocephalum semicalvum*, *Cheilanthes sieberi* subsp. *pseudovellea*, *Hakea suberea*, *Canthium lineare*, and *Santalum lanceolatum* – none of which were fire encouraged.

Subgroups 1 & 6: Finke Gorge mature spinifex and the mixed mulga-spinifex samples of Subgroup 6 (Figs 2.24 & 2.25) were characterised by the lowest level of dissimilarity (64.09), indicating a high degree of floristic overlap. Seventeen species contributed approximately half (51.2%) of between-group dissimilarity. Of these, four – *Acacia aneura*, *Sarcostemma viminale* subsp. *australe*, *Eremophila latrobei* var. *latrobei*, and *Enneapogon polyphyllus* (all Group B diagnostics) – were twice more abundant in 6 than in 1. As many as 16 species were unique to Subgroup 6. Included awere five species of tussock grass, two ferns, the shade-tolerant succulent *Sedopsis filsonii*, as well as the highly diagnostic mulga species *Spartothamnella teucriiflora*. Only three species – *Scaevola spinescens*, *Senna glutinosa* subsp. *glutinosa* and *Acacia bivenosa* – were twice more abundant in 1 than in 6, and only one – the fire encouraged tussock grass *Paraneurachne muelleri* – was unique to 1.

Subgroups 2 & 6: Brewer Conglomerate mature red-soil spinifex and the mixed mulga-spinifex samples of Subgroup 6 were characterised by a low to moderate level of dissimilarity (76.28), indicating a relatively high degree of floristic overlap. Twenty species contributed approximately half (51.18%) of between-group dissimilarity. Of these, 11 (all Group B diagnostics) were twice more abundant in 6 than in 2: *Cheilanthes sieberi* subsp. *sieberi*, *Eremophila latrobei* var. *latrobei*, *Abutilon fraseri*, *Paspalidium constrictum*, *Digitaria brownii*, *Enchylaena tomentosa*, *Sida filiformis*, *Acacia aneura*, *Acacia kempeana*, *Eremophila freelingii*, *Eremophila latrobei* var. *latrobei*, and *Solanum quadriloculatum*. Seventeen species were unique to 6, many of which were tussock grasses (e.g. *Aristida contorta*, *Eragrostis laniflora*, *Neurachne tenuifolia*, and *Paspalidium clementii*) or were shrub species intolerant of repeated firing (e.g. *Sarcostemma viminale* subsp. *australe*, *Rhagodia eremaea*, *Maireana georgei*, *Maireana campanulata*). Also included was the shade-tolerant succulent *Sedopsis filsonii*. Only one species, the perennial grass *Eriachne mucronata*, was twice more abundant in 2 than in 6. Woody species unique to 2 were resprouters or facultative resprouters (e.g. *Eucalyptus gamophylla*, *Acacia validinervia*, *Eucalyptus intertexta*, *Acacia melleodora*, and *Hakea suberea*).

Subgroups 2 & 8: Brewer Conglomerate mature red-soil spinifex and Tylers pass dense mulga clusters (Figs 2.26 & 2.27) were characterised by a moderate to high level of dissimilarity (77.84), indicating limited floristic overlap. Thirteen species contributed approximately half (51.08%) of between-group dissimilarity. Of these, only one, *Triodia brizoides*, was twice more abundant in Subgroup 2 than in 8. Species unique to 2 were the resprouter and facultative resprouter shrubs: *Acacia bivenosa*, *Senna glutinosa* subsp. *glutinosa*, *Hakea suberea*; and *Eucalyptus gamophylla* and *Eucalyptus intertexta*, as well as the fire-encouraged grass *Paraneurachne muelleri*. Seven species were twice more abundant in 8 than in 2, with the majority of these being highly diagnostic of Group B mulga (e.g. *Sida filiformis*, *Acacia aneura*, *Canthium lineare*, *Eremophila latrobei* var. *latrobei* and *Paspalidium constrictum*). Also included was the shade tolerant succulent *Grahamia australiana*. Eight species were unique to 8, only one of which (*Solanum ellipticum*) was fire-encouraged. Included were the obligate-seeder and facultative resprouter shrubs: *Acacia macdonnelliensis*, *Rhagodia eremaea*, and *Eremophila latrobei* var. *glabra*, as well as the shade tolerant succulent *Sedopsis filsonii* and the tussock grass species *Aristida obscura* and *Thyridolepis mitchelliana*.

Subgroups 9 (= C) & 7: Brewer Conglomerate *Triodia longiceps* and spinifex-free mulga clusters (Fig. 2.28 & 2.29) were characterised by a very high level of dissimilarity (89.34), indicating minimal floristic overlap. Fourteen species contributed approximately half (51.66%) of between-group dissimilarity. Of these, only three – *Acacia bivenosa*, *Triodia longiceps* and *Senna glutinosa* subsp. *glutinosa* (all highly diagnostic of Subgroup 9) – were twice more abundant in 9 than in 7. Species unique to Subgroup 9 (*Eucalyptus eucentrica*, *Paraneurachne muelleri*, *Phyllanthus lacunellus* and *Hakea suberea*) were either fire encouraged or fire tolerant. Species twice more abundant in 7 than in 9 (*Cheilanthes lasiophylla*, *Tripogon loliiformis*, *Eremophila freelingii*, and *Acacia aneura*) were all highly diagnostic of mulga (Group B). As many as 18 species were unique to 7. Included were obligate seeder or facultative resprouter shrubs (e.g. *Acacia tetragonophylla*, *Eremophila latrobei* var. *glabra*, *Eremophila latrobei* var. *latrobei*, *Harnieria kempeana* subsp. *kempeana*, and *Spartothamnella teucriiflora*), the shade-tolerant species *Cheilanthes sieberi* subsp. *sieberi* and *Grahamia australiana*, as well as various tussock grasses (e.g. *Digitaria brownii*, *Neurachne tenuifolia*, and *Thyridolepis mitchelliana*).

Subgroups 2 & 5: Brewer Conglomerate mature red-soil, and mixed-aged white-soil spinifex clusters (Fig. 2.30) were characterised by a moderate to high level of dissimilarity (78.94), indicating little floristic overlap and implicating the role of substrate differences and perhaps fire in subgroup composition patterns. Nineteen species contributed approximately half (51.57%) of between-group dissimilarity. Of these, only one, *Sida filiformis*, was twice more abundant in Subgroup 2 than in 5. Nineteen species were unique to Subgroup 2, five of which were actually diagnostic of mulga (Group B): *Acacia aneura*; *Eremophila latrobei* var. *latrobei*; *Canthium lineare*; *Cheilanthes sieberi* subsp. *sieberi* and *Cheilanthes lasiophylla*. The remaining were mostly perennial shrubs (e.g. *Eucalyptus intertexta*, *Acacia melleodora*, *Eucalyptus gamophylla*, *Carissa lanceolata*, *Santalum lanceolatum*, *Ozothamnus kempei*). Two species were twice more abundant in 5 than in 2: the short-lived forb *Heliotropium tenuifolium*, and the Myrtaceous tree *Corymbia eremaea* subsp. *oligophylla*. As many as twenty-eight species were unique to 5, including a large number of forbs (e.g. *Chenopodium desertorum*, *Euphorbia centralis*, *Solanum ellipticum*, and *Nicotiana simulans*) as well as fire-encouraged shrubs (e.g. *Acacia murrayana*, *Gossypium sturtianum* and *Haloragis uncatipila*). Also included were certain species characteristic of high pH substrates throughout other areas of central Australia (e.g. *Vittadinia eremaea*, *Zygophyllum tesquorum*, *Anemocarpa saxatilis*, and *Sida* A90679 Limestone).

Subgroups 5 & 9: Brewer Conglomerate white-soil *Triodia brizoides* and *Triodia longiceps* clusters (Fig. 2.31) were characterised by an extremely high level of dissimilarity (94.50), indicating minimal floristic commonality. Fifteen species contributed approximately half (51.75%) of between-group dissimilarity. Of these, only two – *Senna glutinosa* subsp. *glutinosa* and *Sida filiformis* – were twice more abundant in 9 than in 5. Included in the group of species unique to 9 were two species highly diagnostic of Subgroup 9 – *Triodia longiceps* and *Eucalyptus eucentrica*. Similarly few species (*Ptilotus clementii* and *Trichodesma zeylanicum*) were twice more abundant in 5 than in 9. This contrasted with the high number (24) of species unique to Subgroup 5. This group was as rich in perennial shrubs (e.g. *Acacia murrayana*, *Acacia validinervia*, *Gossypium sturtianum*, *Melhania oblongifolia*, *Senna artemisioides* nothosubsp. *sturtii*, and *Senna artemisioides* subsp. *oligophylla*) as it was in short-lived forbs (e.g. *Heliotropium tenuifolium*, *Nicotiana simulans*, *Salsola kali*, *Swainsona phacoides*, and *Zygophyllum tesquorum*). Also noteworthy was the inclusion of three species characteristic of high pH soils: *Vittadinia eremaea*, *Sida* A90679 Limestone, and *Anemocarpa saxatilis*.

Appendix 2.2 F-values from the one-factor ANOVA of growthform- and total species-richness across the fine- and broad-scale PATN clusters.

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; Ns = Not significant.

Source of variation	d.f	Climbers	Ferns	Perennial Forbs	Short-lived Forbs	Hummock Grasses	Perennial Tussock Grasses	Short-lived Tussock Grasses	Perennial Half-Shrubs	Short-lived Half-shrubs	Mallees	Shrubs	Trees	All Species
Broad group	2	3.739*	48.806***	3.375*	1.555 NS	3.4*	19.511***	5.96**	6.156**	1.093 NS	8.103**	7.445**	3.796*	12.923***
Residual	70													
Fine group	8	2.15*	32.491***	3.972**	6.651***	3.862***	7.449***	4.142***	4.476***	4.808***	4.518***	5.096***	4.667***	6.36***
Residual	64													

Appendix 2.3 F-values from the one-factor ANOVA of fire-response group richness across the fine- and broad-scale PATN clusters.

* = $P < 0.05$; ** = P < 0.01; *** = P < 0.001; Ns = Not significant.

Source of variation	d.f.	Obligate Seeders	Facultative resprouters	Resprouters
Broad group	2	7.983***	3.823*	5.725**
Residual	70			
Finer group	8	7.797***	3.025**	10.814***
Residual	64			

Appendix 2.4 F-values from the one-factor ANOVA of *Acacia aneura* size-class frequency across the fine- and broad-scale PATN clusters.

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; Ns = Not significant.

Source of variation	d.f	<0.5m	0.5-2m	2-6m (mature)	2-6m (senescent)	Fire stag <2m	Fire stag 2-6m
Broad group	2	18.063***	21.594***	37.625***	2.367 NS	1.761 NS	49.199***
Residual	70						
Fine group	8	5.526***	5.596***	8.938***	1.150 NS	0.893 NS	13.266***
Residual	64						

Appendix 2.5 F-values from the one-factor ANOVA of edaphic variability across the fine- and broad-scale PATN clusters.

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; Ns = Not significant.

	d.f	Landscape aspect	Aspect value	CaCO3 Depth	CaCO3 Surface	% Litter	pH depth	pH surface	Soil depth	Texture depth	Texture surface	% Boulders	% Stones	% Gravel	Slope
Broad group	2	2.002 NS	0.833 NS	4.536*	5.55**	6.001**	26.809***	16.141***	4.793*	10.719***	4.375*	1.288 NS	1.810 NS	0.700 NS	5.759**
Residual	70														
Fine group	8	1.925 NS	1.117 NS	12.318***	64.141***	3.672**	18.463***	13.864***	3.20**	7.833***	1.573 NS	1.936 NS	1.312 NS	1.050 NS	3.597**
Residual	64														

Appendix 2.6 F-values from the two factor ANOVA of growthform group- and total species-richness across the *a priori* treatments habitat and fire age.
* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; Ns = Not significant.

Source of variation	d.f	Climbers	Ferns	Perennial Forbs	Short-lived Forbs	Hummock Grasses	Perennial Tussock Grasses	Short-lived Tussock Grasses	Perennial Half-Shrubs	Short-lived Half-shrubs
H (habitat)	1	1.926 NS	81.987***	0.554 NS	0.587 NS	6.265*	22.802***	5.347*	0.625 NS	0.157 NS
A (fire age)	1	11.128 NS	11.48**	0.826 NS	8.782 NS	0.789 NS	0.264 NS	0.627 NS	3.098 NS	1.002 NS
HxA	1	4.888 NS	0.764 NS	6.64*	4.897 NS	0.319 NS	1.005 NS	04.524*	4.144*	3.381 NS
Residual	69									

Appendix 2.6 Cont.

Source of variation	d.f	Mallees	Shrubs	Trees	All Species
H (habitat)	1	5.234*	5.67*	5.28*	5.30*
A (fire age)	1	1.223 NS	1.392 NS	0.217 NS	3.718 NS
HxA	1	0.221 NS	0.39 NS	0.944 NS	6.149*
Residual	69				

Appendix 2.7. F-values from the two factor ANOVA of fire-response group richness across the *a priori* treatments habitat and fire age.
* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; Ns = Not significant.

Source of variation	d.f.	Obligate Seeders	Facultative resprouters	Resprouters
H (habitat)	1	11.009**	0.663 NS	2.415 NS
A (fire age)	1	0.475 NS	0.957 NS	4.593*
HxA	1	0.201 NS	0.139 NS	0.981 NS
Residual	69			

Appendix 2.8 F-values from the two factor ANOVA of *Acacia aneura* life-stage class frequency across the *a priori* treatments habitat and fire age.
* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; Ns = Not significant.

Source of variation	d.f.	<0.5m	0.5-2m	2-6m (mature)	2-6m (senescent)	Fire stag <2m	Fire stag 2-6m
H (habitat)	1	31.406***	64.071***	51.10***	1.938 NS	0.151 NS	108.793***
A (fire age)	1	1.019 NS	1.996 NS	11.278**	1.938 NS	4.667*	11.866**
HxA	1	0.342 NS	7.112**	11.278**	1.938 NS	0.151 NS	1.551 NS
Residual	69						

Appendix 3.1 Results of SIMPER analysis of within- and between-group similarity fro the broad- and fine-scale clusters defined by the PATN analysis of dunefield mosaic habitats.

Within-group similarity of broad-scale clusters:

i. Group A 'non-spinifex' mulga shrubland: This cluster consisted of four samples distributed across two sites (Owen Springs and Orange Ck). It had intermediate within-group average similarity (50.74), indicating a moderate level of among-sample cohesion. Six species – *Aristida contorta*, *Acacia aneura*, *Enneapogon avenaceus*, *Sclerolaena convexula*, *Enneapogon polyphyllus*, *Rutidosis helichrysoides* – contributed approximately half (51.91 %) of within-group similarity, and a further 16 species contributed over 90 % (refer Table 3.2). Neither *Triodia* species contributed to within-group similarity.

ii. Group B mixture of spinifex (*Triodia basedowii*) and mixed mulga-spinifex (*Triodia basedowii*) sites. This cluster consisted of 16 samples distributed across three sites (Owen Springs, Orange Ck and Yulara lease). It had the lowest within-group average similarity (32.86), indicating relatively poor among-sample cohesion, and likely reflecting the geographic separation of the samples. Two species – *Triodia basedowii* and *Aristida holathera* var. *holathera* – contributed approximately half (53.66 %) of within-group similarity, and a further 18 contributed over 90 % (refer Table 3.2). Though listed among the highest-order contributors, the mulga dominant, *Acacia aneura*, actually contributed little to within-group similarity, indicating that it most often occurred in low abundance or was entirely absent from samples where *Triodia basedowii* dominated.

iii. Group C spinifex (*Triodia pungens*) and mulga with spinifex (*Triodia pungens*) present in the understorey. This cluster consisted of eight samples from one site only (Uluru National Park). It had the highest within-group average similarity (53.16), indicating a high level of among-sample cohesion, and likely reflecting the geographic closeness of the samples. Four species – *Monachather paradoxus*, *Calandrinia reticulata*, *Leucochrysum stipitatum* and *Goodenia occidentalis* – contributed approximately half (50.13 %) of within-group similarity, and a further nine contributed over 90 % (refer Table 3.2). The mulga dominant, *Acacia aneura*, and the spinifex dominant, *Triodia pungens*, were also listed among the highest order contributors.

Between-group dissimilarity of broad-scale clusters

Groups A & B: The non-spinifex mulga and mixed mulga-spinifex (*Triodia basedowii*) clusters were characterised by moderate average dissimilarity (86.12). Twenty species contributed approximately half (51.19 %) of the between-group dissimilarity. Of these, four were twice more abundant in Group B than in Group A – *Eragrostis laniflora*, *Aristida holathera* var. *holathera*, *Sida platycalyx* and *Triodia basedowii*. As many as 22 species were unique to B. Included were the grasses, *Eriachne aristidea*, *Monachather paradoxus*, *Paraneurachne muelleri*, *Yakirra australiensis*; various succulents, *Calandrinia reticulata* and *Calandrinia balonensis*; forbs species, *Chrysocephalum apiculatum*, *Lepidium phlebopetalum*, *Muelleranthus stipularis*, *Fimbristylis dichotoma;* half-shrubs, *Sclerolaena johnsonii*, *Solanum centrale*, *Lechenaultia divaricata*, *Scaevola parvifolia*, *Euphorbia tannensis* subsp. *eremophila*; and the shrubs, *Dicrastylis gilesii*, *Senna pleurocarpa*, *Rulingia loxophylla*, *Acacia* *melleodora*, *Eucalyptus gamophylla*, *Grevillea juncifolia* and *Aluta maisonneuvei*. Ten species were twice more abundant in A than in B. These were mainly grasses – *Enneapogon polyphyllus*, *Cenchrus ciliaris*, *Aristida contorta*, *Triraphis mollis*, *Digitaria brownii* and *Enneapogon avenaceus*, but also the mulga dominant *Acacia aneura*, and the forbs and half shrubs *Rutidosis helichrysoides*, *Abutilon otocarpum* and *Sclerolaena convexula*. Species unique to A were either grasses, e.g. *Dichanthium sericeum* subsp. *sericeum*, *Eragrostis barrelieri* and *Digitaria coenicola*; forbs, *Tribulus eichlerianus s. lat.*, *Polycarpaea arida*, *Boerhavia schomburgkiana*, *Alternanthera angustifolia*, *Wahlenbergia queenslandica*, *Rhodanthe charsleyae*, *Calotis latiuscula*, *Minuria leptophylla*; or half-shrubs such as *Sclerolaena costata*, *Maireana scleroptera*, *Swainsona flavicarinata*, *Sida fibulifera*, *Malvastrum americanum* and *Swainsona phacoides*.

Within-group similarity of Group B subgroups

i. Subgroup 2 comprised six samples from Sites 1 (Owen Springs) & 2 (Orange Creek), all of which were dominated by mature stands of *Triodia basedowii*. Within-group average similarity was comparatively low (47.61) indicating a low degree of among-sample cohesion. Three grasses – *Triodia basedowii*, *Aristida holathera* var. *holathera* and *Eragrostis laniflora* – contributed approximately half (54.59 %) of the within-group similarity and a further ten contributed 90 % (refer Table 3.2). Included were various forbs and subshrubs – *Sida platycalyx*, *Lechenaultia divaricata*, *Solanum centrale*, *Ptilotus polystachyus*, *Sclerolaena johnsonii* and *Euphorbia drummondii s. lat.* – the grasses *Eriachne aristidea* and *Enneapogon polyphyllus*, as well as the fire tolerant shrubs *Acacia murrayana* and *Acacia melleodora*.

ii. Subgroup 3 comprised four samples from Site 2 (Orange Creek), all of which were characterised by mixed stands of *Triodia basedowii* and *Acacia aneura*. Two of the samples supported regenerating mulga, and two supported mature mulga. Within-group average similarity was comparatively low (51.18), indicating a low degree of among-sample cohesion. The two structural dominants, *Acacia aneura* and *Triodia basedowii*, were foremost among the contributors of with-group similarity. Other major contributors were: *Aristida holathera* var. *holathera*, *Leucochrysum stipitatum*, *Lepidium phlebopetalum* and *Sclerolaena johnsonii*. Grasses, e.g. *Enneapogon polyphyllus*, *Monachather paradoxus*, *Eragrostis laniflora*, *Eriachne aristidea*, *Paspalidium reflexum* and *Tripogon loliiformis*; and forbs and half shrubs including *Sida platycalyx*, *Euphorbia tannensis* subsp. *eremophila*, *Muelleranthus stipularis*, *Solanum quadriloculatum*, *Euphorbia drummondii s. lat.*, *Sclerolaena convexula* and *Abutilon otocarpum* dominated the group of remaining species contributing 90 % of the within-group similarity. Also included were the chenopod shrubs *Rhagodia eremaea* and *Enchylaena tomentosa*, and the succulents *Calandrinia reticulata* and *Calandrinia balonensis*.

iii. Subgroup 4 comprised three samples from Site 4 (Yulara lease), all of which were characterised by immature stands of *Triodia basedowii*. Within-group average similarity was exceptionally high (70.01) indicating a high level of among-sample cohesion. Three species: *Triodia basedowii*, *Senna pleurocarpa* and *Aristida holathera* var. *holathera* contributed approximately half (50.87 %) of the within-group similarity and a further five contributed 90 % (refer Table 3.2). These were the grasses

Eragrostis laniflora, *Aristida contorta* and *Paraneurachne muelleri* and the woody species *Rulingia loxophylla* and *Dicrastylis gilesii.*

iv. Subgroup 5 comprised three samples from Site 4 (Yulara lease), all of which were characterised by mature stands of *Triodia basedowii.* Within-group average similarity was comparatively low (44.85) indicating a low degree of among-sample cohesion. One species *Triodia basedowii* contributed all 90% of the within-group similarity. This indicated that species richness was very low, and that most of the constituent species did not occur in more than one sample.

v. Subgroup 6 comprised four samples from Site 3 (Uluru National Park). The majority of samples were characterised by mature stands of mulga with a low coverage of *Triodia pungens* in the understorey. The remaining sample was dominated by regenerating mulga with a slightly higher abundance of *Triodia pungens* compared with the mature mulga samples. Within-group average similarity was moderately high (59.83) indicating an intermediate level of among-sample cohesion. Four species: *Calandrinia reticulata*, *Monachather paradoxus*, *Acacia aneura* and *Stenopetalum anfractum* contributed approximately half (50.87 %) of the within-group similarity and a further nine contributed 90 % (refer Table 3.2). These were predominantly grasses – *Thyridolepis multiculmis*, *Eragrostis laniflora*, *Triodia pungens*, *Aristida holathera* var. *holathera* and *Digitaria brownii*, but also forbs – *Leucochrysum stipitatum*, *Goodenia occidentalis* and *Waitzia acuminata*, and the chenopod shrub *Maireana villosa*.

vi. Subgroup 7 comprised four samples from Site 3 (Uluru National Park). The majority of samples were characterised by mature stands of *Triodia pungens*, though one also had regenerating mulga with a *Triodia pungens* understorey. Within-group average similarity was relatively high (69.43) indicating an intermediate level of among-sample cohesion. Five species – *Leucochrysum stipitatum*, *Triodia pungens*, *Eragrostis laniflora*, *Goodenia occidentalis* and *Aristida holathera* var. *holathera* – contributed approximately half (53.29 %) of the within-group similarity, and a further six contributed 90 % (refer Table 3.2). These included the grasses *Amphipogon caricinus* and *Monachather paradoxus*; the forbs *Velleia glabrata*, *Calandrinia reticulata* and *Brunonia australis*; as well as the dune specialist *Acacia ammobia*.

Between-group dissimilarity of fine-scale clusters

Dissimilarity analysis was carried out only for spatially contiguous subgroups, as summarised below:

Subgroups 6 & 7: Uluru mulga and spinifex clusters were characterised by the lowest level of dissimilarity (55.44) – illustrating the overarching influence of regional effects compared with other factors. Ten species contributed approximately half (52.35) of the between-group dissimilarity. Of these, seven species – the grasses *Triodia pungens*, *Eragrostis laniflora*, *Aristida holathera* var. *holathera* and *Amphipogon caricinus* – and the forb *Velleia glabrata*, were twice more abundant in Subgroup 7 than in 6. Four species occurred in 7 but not in 6. These were the shrubs *Aluta maisonneuvei*, *Acacia ammobia* and *Grevillea juncifolia*, and the half-shrub *Scaevola parvifolia*. Only one species, the structural dominant, *Acacia aneura* was twice more abundant in 6 than in 7, while three, *Aristida contorta*, *Thyridolepis multiculmis* and *Stenopetalum anfractum* were unique to 6.

Subgroups 4 & 5: Yulara immature and mature *Triodia basedowii* subgroups were characterised by a high level of dissimilarity (70.28), illustrating the strong influence of fire on species composition in hummock grasslands. Five species contributed approximately half (56.15) of the between-group dissimilarity. Of these, two grasses, *Aristida holathera* var. *holathera* and *Aristida contorta* were twice more abundant in 4 than in 5. Eight species – *Goodenia gibbosa*; *Scaevola parvifolia*, *Yakirra australiensis*, *Paraneurachne muelleri*, *Eragrostis laniflora*, *Rulingia loxophylla*, *Senna pleurocarpa* and *Corchorus sidoides* occurred in 4 but not in 5. No species was twice more abundant in 5 than in 4, and only two were unique to 5: *Eucalyptus gamophylla* and *Acacia ligulata*.

Subgroups 3 & 2: Spinifex (*Triodia basedowii*) and mixed mulga-spinifex (*Triodia basedowii*) subgroups were characterised by a moderate level of dissimilarity (66.54). Eighteen species contributed approximately half (50.03) of the between-group dissimilarity. Of these, seven – *Calandrinia reticulata*, *Monachather paradoxus*, *Muelleranthus stipularis*, *Leucochrysum stipitatum*, *Sclerolaena convexula*, *Solanum quadriloculatum* and *Acacia aneura* – were twice more abundant in Subgroup 3 than in 2. Sixteen species were unique to 3. These were: the forbs *Lepidium phlebopetalum* and *Rhodanthe floribunda*; the grasses *Tripogon loliiformis*, *Paspalidium reflexum*, *Aristida contorta* and *Digitaria brownii*; the chenopod shrubs *Rhagodia eremaea* and *Maireana villosa*; the mallee shrub *Eucalyptus gamophylla*; the shrubs *Eremophila latrobei*, *Eremophila longifolia*, *Acacia aneura* and *Acacia kempeana*; and the half-shrubs *Evolvulus alsinoides* var. *villosicalyx* and *Solanum chenopodinum*. Three species – *Eriachne aristidea*, *Solanum centrale* and *Lechenaultia divaricata* – were twice more abundant in 2 than in 3, while only four – *Scaevola parvifolia*, *Yakirra australiensis*, *Sida ammophila* and the introduced grass *Cenchrus ciliaris* – were unique to 2.

Subgroups 1 & 2: non-spinifex mulga and *Triodia basedowii* grassland subgroups were characterised by a very high level of dissimilarity (88.04) in spite of their immediate proximity to each other. Eighteen species contributed approximately half (50.78) of the between-group similarity. Of these, five – *Eragrostis laniflora*, *Aristida holathera* var. *holathera*, *Sida platycalyx*, *Ptilotus polystachyus* and *Triodia basedowii* – were twice more abundant in 2 than in 1. As many as 17 species were unique to 2. Most of these were forbs: *Trachymene glaucifolia*, *Calandrinia reticulata*, *Fimbristylis dichotoma*, *Calandrinia balonensis*, *Xerochrysum bracteatum*, *Chrysocephalum apiculatum;* or grasses e.g. *Yakirra australiensis*, *Aristida inaequiglumis*, *Monachather paradoxus* and *Eriachne aristidea*. The remaining species were fire-tolerant shrubs: *Grevillea juncifolia*, *Dodonaea viscosa* subsp. *angustissima* and *Acacia melleodora*; and half-shrubs, e.g. *Scaevola parvifolia*, *Lechenaultia divaricata*, *Sclerolaena johnsonii* and *Solanum centrale*. Four species were twice more abundant in 1 than in 2 – *Abutilon otocarpum*, *Sclerolaena convexula*, *Rutidosis helichrysoides* and *Acacia aneura*. A total of 28 species was unique to 1. This group was dominated by forbs – *Tribulus eichlerianus s. lat.*, *Rhodanthe floribunda*, *Polycarpaea arida*, *Portulaca oleracea*, *Boerhavia schomburgkiana*, *Alternanthera angustifolia*, *Wahlenbergia queenslandica*, *Indigofera linnaei*, *Calotis latiuscula*, *Minuria leptophylla*, *Rhodanthe charsleyae* and *Boerhavia repleta*. Also well represented were tussock grasses*:* *Panicum decompositum s. lat.*, *Eragrostis barrelieri*, *Tripogon loliiformis*, *Digitaria brownii*, *Enneapogon avenaceus*, *Aristida contorta*, *Panicum effusum* and *Digitaria coenicola;* and half shrubs e.g. *Abutilon fraseri*, *Sida fibulifera*, *Malvastrum americanum*, *Maireana* *scleroptera*, *Swainsona flavicarinata*, *Swainsona phacoides*, *Evolvulus alsinoides* var. *villosicalyx* and *Sclerolaena costata*.

Subgroups 1 & 3: non-spinifex mulga and mulga-*Triodia basedowii* mix subgroups were characterised by a high level of dissimilarity (72.49) in spite of their immediate proximity to each other. Twenty three species contributed approximately half (50.83) of the between-group similarity. Of these four – *Leucochrysum stipitatum*; *Aristida holathera* var. *holathera*; *Sida platycalyx* and *Triodia basedowii* – were twice more abundant in 3 than in 1. Twenty species were unique to 3. Of these, most were forbs: *Lepidium phlebopetalum*; *Calandrinia reticulata*; *Muelleranthus stipularis*; *Calandrinia balonensis*; *Chrysocephalum apiculatum*; *Fimbristylis dichotoma*; *Goodenia gibbosa* and *Goodenia glabra*. Also well represented were grasses: *Monachather paradoxus*, *Paspalidium reflexum*, *Eriachne aristidea*, *Eriachne helmsii*; and subshrubs e.g. *Sclerolaena johnsonii*; *Euphorbia tannensis* subsp. *eremophila* and *Solanum centrale*. Less well represented were: mallee shrubs (1 species, *Eucalyptus gamophylla*); shrubs (3 species, *Maireana villosa Senna pleurocarpa* and *Eremophila latrobei*); and trees (1 species, *Acacia estrophiolata*). Seven species were twice more abundant in 1 than in 3: the forb *Rutidosis helichrysoides*; grasses *Triraphis mollis*, *Digitaria brownii*, *Aristida contorta* and *Enneapogon avenaceus*; and subshrubs *Abutilon otocarpum* and *Sclerolaena convexula*. A total of 18 species was unique to Subgroup 1. The majority of these were herbs: *Tribulus eichlerianus s. lat.*, *Boerhavia schomburgkiana*, *Alternanthera angustifolia*, *Wahlenbergia queenslandica*, *Calotis latiuscula*, *Minuria leptophylla*, and *Rhodanthe charsleyae*; or half-shrubs: *Malvastrum americanum*, *Pterocaulon sphacelatum*, *Maireana scleroptera*, *Swainsona flavicarinata*, *Sida fibulifera*, *Swainsona phacoides*, *Sclerolaena costata*. Also included were the grasses: *Panicum effusum*, *Eragrostis barrelieri*, *Cenchrus ciliaris*; and *Digitaria coenicola*.

Appendix 4.1 Analysis of variance for the effects of heat (80°C/5 minutes), smoke and light (Exp. I) for germination in a selection of mulga-spinifex mosaic species after two weeks of incubation. Mulga species in bold. Significance ($P < 0.05$) in bold.

Source of variation	d.f.	***Acacia aneura*** **NRB 266**		*Acacia melleodora* 96RBB137		***Acacia kempeana*** **97 A93493**		***Senna artemesioides* subsp. *artemesioides*** **97-A94257**		*Acacia murrayana*		*Senna pleurocarpa* 96-RBB217		*Eucalyptus gamophylla* 96RBB180		***Enchylaena tomentosa*** **96A91830**	
		F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Heat (H)	1	0.091	0.7659	48.577	**< 0.0001**	0.092	0.7641	3.391	0.078	4.499	**0.0444**	0.65	0.428	0.133	0.7181	0.025	0.8765
Smoke (S)	1	0.605	0.4443	0.166	0.6875	1.678	0.2076	0.897	0.3530	1.045E-4	0.9919	0.086	0.7723	2.011	0.169	1.228	0.2787
Light (L)	1	1.035	0.3192	0.054	0.8190	1.805	0.1916	0.077	0.7841	0.156	0.6965	0.036	0.8504	0.900	0.3522	0.181	0.674
H x S	1	0.153	0.6994	0.013	0.9095	0.374	0.5466	1.070E-4	0.9918	0.339	0.5661	0.504	0.4844	0.549	0.4657	0.235	0.6321
H x L	1	0.451	0.5084	0.855	0.3642	1.069	0.3115	0.574	0.4559	0.112	0.7405	0.453	0.5075	0.165	0.6885	0.047	0.8307
S x L	1	1.120	0.3005	0.511	0.4816	1.945	0.1760	1.296	0.2662	2.478	0.1286	0.005	0.9432	0.163	0.6898	0.281	0.6007
H x S x L	1	0.405	0.5304	3.679	0.0671	0.318	0.5783	0.033	0.858	2.451	0.1305	0.218	0.6445	0.922	0.3466	0.705	0.4094
Cabinet	1	0.06	>0.05	3.69	> 0.05	4.975	**< 0.05**	1.92	> 0.05	4.63	**< 0.05**	4.129	> 0.05	1.21	> 0.05	6.413	**< 0.05**
Residual	24																

Appendix 4.2 Analysis of variance for the effects of heat (80°C/5 minutes), smoke and light (Exp. I) for germination in a selection of mulga-spinifex mosaic species after four weeks of incubation. Mulga species in bold. Significance ($P < 0.05$) in bold.

Source of variation	d.f.	***Acacia aneura*** **NRB 266**		*Acacia melleodora* 96RBB137		***Acacia kempeana*** **97 A93493**		***Senna artemesioides* subsp. *artemesioides*** **97-A94257**		*Acacia murrayana*		*Senna pleurocarpa* 96-RBB217		*Eucalyptus gamophylla* 96RBB180		***Enchylaena tomentosa*** **96A91830**	
		F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Heat (H)	1	1.082	0.3072	45.534	**< 0.0001**	1.671E-5	0.9968	3.849	0.0598	2.197	0.1494	0.841	0.367	0.036	0.8501	0.194	0.6627
Smoke (S)	1	3.984	0.0558	4.068	0.0534	0.111	0.741	0.781	0.3844	2.175	0.1515	0.175	0.6789	0.680	0.4166	0.194	0.6627
H x S	1	0.488	0.4906	1.061	0.3118	0.5	0.4854	0.009	0.9262	1.740	0.1978	0.085	0.7727	0.207	0.6528	2.02	0.1663
Cabinet	1	0.016	>0.05	0.73	> 0.05	0.22	>0.05	2.25	> 0.05	0.43	> 0.05	0.474	> 0.05	0.0595	> 0.05	0.01	> 0.05
Residual	24																

Appendix 4.3 Pearson product moment correlations (r^2) for seed size and germinability in Experiment I.

r^2	*P*
.216831	.244903

Appendix 4.4 Pearson product moment correlations (r^2) for seed size and germination rate in Experiment I.

r^2	*P*
.193454	.275498

Appendix 4.5. Analysis of variance for the effects of heat temperatures 120°C, 80°C and 0°C (10 minutes) (Exp. II) for germination in a selection of mulga-spinifex mosaic species after two weeks of incubation. Mulga species in bold. Significance ($P < 0.05$) in bold.

		Acacia aneura **NRB 266**		*Acacia melleodora* 96RBB132		***Acacia kempeana*** **97 A93493**		***Senna artemesioides* subsp. *artemesioides*** **97-A94257**		*Acacia murrayana*		*Senna pleurocarpa* 96-RBB217		*Eucalyptus gamophylla* 96RBB180		***Enchylaena tomentosa*** **96A91830**	
Source of variation	d.f.	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Heat (H)	1	2.459	0.1406	7.435	**0.0124**	2.989	0.1011	9.585	**0.0059**	0.699	0.5222	14.568	**0.0015**	0.341	7.197	28.536	**0.0001**
Cabinet	1	5.99	> 0.05	0.025	> 0.05	0.966	> 0.05	1.67	> 0.05	2.03	> 0.05	0.575	> 0.05	0.1	> 0.05	0.41	> 0.05
Residual	1																

Appendix 4.5 Cont.

		Acacia aneura ASDP973500		*Acacia bivenosa* 96RBB193		*Corymbia eremaea* subsp. *oligophylla*		*Digitaria brownii*		*Triodia longiceps*		*Eucalyptus eucentrica* 96RBB90	
Source of variation	d.f.	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Heat (H)	1	1.733	0.2309	7.457	**0.0123**	1.398	0.259	3.756	0.0652	40.544	**< 0.0001**	3.49	0.0755
Cabinet	1	4.44	> 0.05	0.692	> 0.05	0.47	> 0.05	3.11	> 0.05	0.18	> 0.05	1.9	> 0.05
Residual	1												

Appendix 4.6 Pearson product moment correlations (r^2) for seed size and germinability in Experiment II.

r^2	*P*
.216495	.175383

Appendix 4.6 Pearson product moment correlations (r^2) for seed size and germination rate in Experiment II.

r^2	*P*
.202513	.191893

Appendix 5.1 Pearson product moment correlations (r^2) for seed size and emergence success and speed and Spearman Rank correlations (R) for growth form and emergence success and speed.

	Emergence Success				Emergence Speed			
Experiment	Seed size		Growth form			Seed size	Growth form	
	r^2	*P*	R	*P*	r^2	*P*	R	*P*
I	0.068	0.673	-0.447214	0.450185	0.0025	0.9371	-0.802955	0.101838
III	0.013	0.787	0.603703	0.113016	0.3241	0.141	.381881	0.350541
V	0.039	0.707	0.333947	0.517700	0.234	0.331	.212512	0.686031

Appendix 5.2 Pearson product moment correlations (r^2) for seed size and survival and Spearman Rank correlations (R) for growth form and survival.

	Survival Week 2				Survival Month 2				Survival Month 6			
	Seed size		Growth form		Seed size		Growth form		Seed size		Growth form	
Experiment	r^2	*P*	R	*P*	r^2	P	R	*P*	r^2	*P*	R	*P*
I	0.477	0.309	-.3162	.68377								
III	0.451	0.098	.66815	.10089								
V	0 117	0.507	.75897	.08014	0.709	**0.036**	-0.6375	0.1733	0.670	**0.046**	-0.5161	0.2946

Appendix 5.3 Analysis of variance for the effects of habitat, predator exclusion and litter on emergence success in Experiment I. n.e. is no emergence. Mulga species in bold. $P < 0.05$ (in bold).

Source of variation	d.f.	***Acacia aneura***		*Acacia melleodora*		*Acacia murrayana*		***Enchylaena tomentosa***		*Eucalyptus gamophylla*	
		F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Habitat (H)	1	10.507	**0.002**	38.026	**<.0001**	n.e.	n.e	13.114	**0.0006**	11.401	**0.0014**
Predator exclusion (P)	2	5.961	**0.0046**	6.274	**0.0035**	n.e.	n.e	4.981	**0.0103**	2.074	0.1356
Litter cover (L)	2	5.545	**0.0065**	5.942	**0.0047**	n.e.	n.e	2.029	0.1413	2.211	0.1194
H x P	2	1.618	0.2077	2.024	0.142	n.e.	n.e	0.671	0.5154	2.074	0.1356
H x L	2	1.902	0.1592	3.521	**0.0365**	n.e.	n.e	0.768	0.4689	2.211	0.1194
P x L	4	1.55	0.2009	0.465	0.7607	n.e.	n.e	3.184	**0.0202**	1.227	0.3104
H x P x L	4	1.323	0.2732	1.144	0.3457	n.e.	n.e	3.038	**0.0248**	1.227	0.3104
Residual	54										
Patch	1	0.261	>0.05	6.192	**<0.05**			0.004	>0.05	3.16	>0.05

Appendix 5.4 Analysis of variance for the effects of habitat, predator exclusion and litter on emergence success in Experiment III. n.e. is no emergence. Mulga species in bold. $P < 0.05$ (in bold).

Source of variation	d.f.	***Acacia aneura***		*Acacia melleodora*		*Acacia murrayana*		***Enchylaena tomentosa***		*Eucalyptus gamophylla*		***Digitaria brownii***		*Senna pleurocarpa*		***Senna artemesioides* subsp. *filifolia***	
		F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Habitat (H)	1	75.355	**<.0001**	61.17	**<.0001**	16.866	**0.0001**	n.e.	n.e	41.629	**<.0001**	24.391	**<.0001**	76.22	**<.0001**	30.168	**<.0001**
Predator exclusion (P)	2	1.229	0.3005	9.378	**0.0003**	2.468	0.0942	n.e.	n.e	0.332	0.7192	0.603	0.5509	1.823	0.1714	4.212	**0.02**
Litter cover (L)	2	0.7	0.5009	0.964	0.3879	2.434	0.0973	n.e.	n.e	2.238	0.1165	2.011	0.1438	2.724	0.0746	2.784	0.0707
H x P	2	5.353	**0.0076**	3.445	**0.0391**	1.217	0.3040	n.e.	n.e	0.563	0.5728	0.603	0.5509	0.426	0.6555	4.212	**0.02**
H x L	2	0.201	0.8184	1.664	0.1989	1.918	0.1568	n.e.	n.e	1.195	0.3106	2.011	0.1438	0.406	0.6683	2.784	0.0707
P x L	4	0.431	0.7856	1.784	0.1454	0.436	0.7822	n.e.	n.e	0.98	0.4262	0.555	0.6964	1.76	0.1504	2.188	0.0825
H x P x L	4	1.417	0.2409	0.79	0.5369	0.338	0.8515	n.e.	n.e	1.142	0.3469	0.555	0.6964	0.318	0.8647	2.188	0.0825
Residual	54																
Patch	1	0.743	>0.05	6.051	**<0.05**	6.55	**<0.05**			0.062	>0.05	0.002	>0.05	1.436	>0.05	0.0044	>0.05

Appendix 5.5 Analysis of variance for the effects of habitat and soil on emergence success in Experiment V. Mulga species in bold. $P < 0.05$ (in bold).

		Acacia aneura		*Acacia melleodora*		*Acacia murrayana*		***Enchylaena tomentosa***		*Triodia basedowii*		***Digitaria brownii***	
Source of variation	d.f.	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Habitat (H)	1	0.095	0.7616	0.399	0.5347	11.901	**0.0025**	0.731	0.4026	0.91	0.3515	0.293	0.5943
Soil (S)	1	3.271	0.0856	5.483	**0.0297**	3.18	0.0897	9.487	**0.0059**	1.292	0.2691	1.728	0.2035
H x S	1	0.009	0.9238	0.433	0.5178	0.095	0.7607	1.039	0.3203	0.541	0.4704	0.092	0.7649
Residual	20												
Patch	1	2.629	>0.05	0.523	>0.05	0.315	>0.05	2.0075	>0.05	2.191	>0.05	0.043	>0.05

Appendix 5.6 Analysis of variance for the effects of habitat and soil on emergence success in Experiment VI. n.e. = no emergence. Mulga species in bold. $P < 0.05$ (in bold).

		Acacia aneura		*Acacia melleodora*		*Acacia murrayana*		***Enchylaena tomentosa***		*Triodia basedowii*		***Digitaria brownii***	
Source of variation	d.f.	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Habitat (H)	1	8.511	**0.0085**	28.754	**<0.0001**	5.813	**0.0256**	n.e	n.e	1.701	0.2070	0.955	0.3402
Soil (S)	1	0.007	0.935	11.078	**0.0034**	2.167	0.1566	n.e	n.e	1.084	0.3102	0.559	0.4633
H x S	1	0.006	0.9369	0.821	0.3757	0.68	0.4192	n.e	n.e	0.017	0.8968	13.805	**0.0014**
Residual	20												
Patch	1	0.633	>0.05	0.659	>0.05	0.6803	>0.05			1.084	>0.05	0.057	>0.05

Appendix 5.7 Analysis of variance for the effects of habitat on survival to 2 weeks in Experiment I. (a) ***Acacia aneura***; (b) *Acacia melleodora*; (c) ***Enchylaena tomentosa***. $P < 0.05$ (in bold).

(a)

Source of variation	d.f.	F	*P*
Habitat (H)	1	5.566	**0.0334**
Residual	14		
Patch	1	1.436	>0.05

(b)

Source of variation	d.f.	F	*P*
Habitat (H)	1	11.971	**0.0014**
Residual	37		
Patch	1	0.119	>0.05

(c)

Source of variation	d.f.	F	*P*
Habitat (H)	1	4.368	**0.0462**
Residual	27		
Patch	1	0.305	>0.05

Appendix 5.8 Analysis of variance for the effects of habitat on survival to 2 weeks in Experiment III. (a) ***Acacia aneura***; (b) *Acacia melleodora*; (c) *Acacia murrayana*; (d) *Eucalyptus gamophylla*; (e) *Senna pleurocarpa*. $P < 0.05$ (in bold).

(a)

Source of variation	d.f.	F	*P*
Habitat (H)	1	4.291	**0.0443**
Residual	43		
Patch	1	4.404	**<0.05**

(b)

Source of variation	d.f.	F	*P*
Habitat (H)	1	9.614	**0.0032**
Residual	50		
Patch	1	7.69	**<0.05**

(c)

Source of variation	d.f.	F	*P*
Habitat (H)	1	1.357	0.2585
Residual	19		
Patch	1	Too few cells	Too few cells

(d)

Source of variation	d.f.	F	*P*
Habitat (H)	1	12.594	**0.0019**
Residual	21		
Patch	1	Too few cells	Too few cells

(e)

Source of variation	d.f.	F	*P*
Habitat (H)	1	2.162	0.1497
Residual	38		
Patch	1	1.817	>0.05

Appendix 5.9 Analysis of variance for the effects of habitat and soil on survival to 2 weeks in Experiment V. (a) ***Acacia aneura***; (b)*Acacia melleodora*; (c) *Acacia murrayana*; (d) ***Enchylaena tomentosa***; (e) *Triodia basedowii*; (f) ***Digitaria brownii***. $P < 0.05$ (in bold).

(a)

Source of variation	d.f.	F	*P*
H (habitat)	1	2.302	0.1449
S (soil)	1	0.594	0.4498
H x S	1	0.117	0.7364
Residual	20		
Patch	1	5.651	**<0.05**

(b)

Source of variation	d.f.	F	*P*
H (habitat)	1	0.224	0.6409
S (soil)	1	2.393	0.1376
H x S	1	0.403	0.533
Residual	20		
Patch	1	0.234	>0.05

(c)

Source of variation	d.f.	F	*P*
H (habitat)	1	2.292	0.154
S (soil)	1	9.63	**0.0084**
H x S	1	4.724	**0.0488**
Residual	13		
Patch		Too few cells	Too few cells

Appendix 5.9 Cont.

(d)

Source of variation	d.f.	F	*P*
H (habitat)	1	2.572	0.1272
S (soil)	1	2.456	0.1355
H x S	1	0.440	0.5161
Residual	17		
Patch		0.685	>0.05

(e)

Source of variation	d.f.	F	*P*
H (habitat)	1	0.008	0.9292
S (soil)	1	0.867	0.379
H x S	1	0.012	0.9171
Residual	8		
Patch	1	Too few cells	Too few cells

(f)

Source of variation	d.f.	F	*P*
H (habitat)	1	0.243	0.6277
S (soil)	1	1.187	0.2897
H x S	1	0.027	0.8707
Residual	19		
Patch	1	0.726	>0.05

Appendix 5.10 Analysis of variance for the effects of habitat and soil on survival to 2 months in Experiment V. (a) ***Acacia aneura***; (b) *Acacia melleodora*; (c) *Acacia murrayana*; (d) ***Enchylaena tomentosa***; (e) *Triodia basedowii*; (f) ***Digitaria brownii***. $P < 0.05$ (in bold).

(a)

Source of variation	d.f.	F	*P*
H (habitat)	1	2.695	0.1163
S (soil)	1	0.708	0.4100
H x S	1	0.550	0.4671
Residual	20		
Patch	1	6.15	**<0.05**

(b)

Source of variation	d.f.	F	*P*
H (habitat)	1	102.128	**<0.0001**
S (soil)	1	3.216	0.0881
H x S	1	0.311	0.5831
Residual	20		
Patch	1	0.381	>0.05

(c)

Source of variation	d.f.	F	*P*
H (habitat)	1	-1.454E16	Too few cells
S (soil)	1	-1.454E16	Too few cells
H x S	1	-1.454E16	Too few cells
Residual	13		
Patch		Too few cells	Too few cells

Appendix 5.10 Cont.

(d)

Source of variation	d.f.	F	*P*
H (habitat)	1	3.647	0.0732
S (soil)	1	1.044	0.3213
H x S	1	1.029	0.3245
Residual	17		
Patch	1	5.49	**<0.05**

(e)

Source of variation	d.f.	F	*P*
H (habitat)	1	0.281	0.6104
S (soil)	1	0.391	0.5490
H x S	1	0.118	0.7396
Residual	8		
Patch	1	Too few cells	Too few cells

(f)

Source of variation	d.f.	F	*P*
H (habitat)	1	0.714	0.4086
S (soil)	1	0.903	0.3539
H x S	1	0.009	0.9247
Residual	19		
Patch	1	1.118	>0.05

Appendix 5.11 Analysis of variance for the effects of habitat and soil on survival to 6 months in Experiment V. (a) ***Acacia aneura***; (b) *Acacia melleodora*; (c) *Acacia murrayana*; (d) ***Enchylaena tomentosa***; (e) *Triodia basedowii*; (f) ***Digitaria brownii***. $P < 0.05$ (in bold).

(a)

Source of variation	d.f.	F	*P*
H (habitat)	1	2.568	0.1247
S (soil)	1	0.092	0.7650
H x S	1	1.61	0.2191
Residual	20		
Patch	1	6.810	**<0.05**

(b)

Source of variation	d.f.	F	*P*
H (habitat)	1	260.827	**<.0001**
S (soil)	1	5.249	**0.033**
H x S	1	5.249	**0.033**
Residual	20		
Patch	1	2.418	>0.05

(c)

Source of variation	d.f.	F	*P*
H (habitat)	1	6.529	**0.024**
S (soil)	1	6.529	**0.024**
H x S	1	6.529	**0.024**
Residual	13		
Patch	1	Too few cells	Too few cells

Appendix 5.11 Cont.

(d)

Source of variation	d.f.	F	*P*
H (habitat)	1	3.103	0.0961
S (soil)	1	3.190E-5	0.9956
H x S	1	1.065	0.3166
Residual	17		
Patch	1	0.637	>0.05

(e)

Source of variation	d.f.	F	*P*
H (habitat)	1	0.414	0.5378
S (soil)	1	0.684	0.4322
H x S	1	0.676	0.4348
Residual	8		
Patch	1	Too few cells	Too few cells

(f)

Source of variation	d.f.	F	*P*
H (habitat)	1	0.575	0.4578
S (soil)	1	0.152	0.7013
H x S	1	0.001	0.9762
Residual	19		
Patch	1	1.118	>0.05

Appendix 5.12 Analysis of variance for the effects of habitat and soil on survival to 2 weeks in Experiment VI. (a) ***Acacia aneura***; (b) *Acacia melleodora*; (c) *Acacia murrayana*; (d) *Triodia basedowii*; (f) ***Digitaria brownii***. $P < 0.05$ (in bold).

(a)

Source of variation	d.f.	F	*P*
H (habitat)	1	0.251	0.6245
S (soil)	1	0.686	0.4213
H x S	1	1.45	0.2484
Residual	14		
Patch	1	3.568	>0.05

(b)

Source of variation	d.f.	F	*P*
Habitat (H)	1	0.009	0.9252
Residual	17		
Patch	1	0.04	>0.05

(c)

Source of variation	d.f.	F	*P*
Habitat (H)	1	-9.896E15	Too few cells
Residual	4		
Patch	1		

(d)

Source of variation	d.f.	F	*P*
Habitat (H)	1	0.476	0.5059
Residual	10		
Patch	1	0.828	>0.05

(e)

Source of variation	d.f.	F	*P*
H (habitat)	1	0.211	0.652
S (soil)	1	4.756	**0.0435**
H x S	1	0.006	0.94
Residual	17		
Patch	1	0.983	>0.05

Appendix 5.13 Analysis of variance for the effects of habitat and soil on survival to 2 months in Experiment VI. (a) ***Acacia aneura***; (b) *Acacia melleodora*; (c) *Acacia murrayana*; (d) *Triodia basedowii*; (f) ***Digitaria brownii***. $P < 0.05$ (in bold).

(a)

Source of variation	d.f.	F	*P*
Habitat (H)	1	3.370	0.0877
Soil (S)	1	0.219	0.6465
H x S	1	1.572	0.2304
Residual	14		
Patch	1	0.4497	>0.05

(b)

Source of variation	d.f.	F	*P*
Habitat (H)	1	0.033	0.8574
Residual	17		
Patch	1	0.04	>0.05

(c)

Source of variation	d.f.	F	*P*
Habitat (H)	1	0.833	0.413
Residual	4		
Patch	1	Too few cells	Too few cells

(d)

Source of variation	d.f.	F	*P*
Habitat (H)	1	0.267	0.6328
Residual	4		
Patch	1	Too few cells	Too few cells

(e)

Source of variation	d.f.	F	*P*
H (habitat)	1	0.284	0.6010
S (soil)	1	0.800	0.3837
H x S	1	0.017	0.8976
Residual	17		
Patch	1	0.043	>0.05

Appendix 5.14 Analysis of variance for the effects of habitat, predator exclusion and litter on emergence success in Experiment II. n.e. = no emergence. Mulga species in bold. $P < 0.05$ (in bold).

Source of variation	d.f.	***Acacia aneura***		*Acacia bivenosa*		*Senna glutinosa* subsp. *glutinosa*		***Senna artemesioides* subsp. *artemesioides***		***Enchylaena tomentosa***		*Eucalyptus eucentrica*	
		F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Habitat (H)	1	n.e.	n.e	n.e.	n.e	0.734	0.3953	3.857	0.0547	2.948	0.0917	1	0.3218
Predator exclusion (P)	2	n.e.	n.e	n.e.	n.e	0.703	0.4994	3.857	**0.0272**	0.89	0.4166	1	0.3746
Litter cover(L)	2	n.e.	n.e	n.e.	n.e	2.195	0.1212	1.286	0.2848	4.039	**0.0232**	1	0.3746
H x P	2	n.e.	n.e	n.e.	n.e	1.294	0.2824	3.857	**0.0272**	0.809	0.4507	1	0.3746
H x L	2	n.e.	n.e	n.e.	n.e	0.386	0.6817	1.286	0.2848	2.5	0.0915	1	0.3746
P x L	4	n.e.	n.e	n.e.	n.e	0.684	0.6063	1.286	0.2871	1.092	0.3697	1	0.4157
H x P x L	4	n.e.	n.e	n.e.	n.e	0.337	0.8521	1.286	0.2871	0.874	0.4858	1	0.4157
Residual	54												
Patch	1					1.064	>0.05	0.429	>0.05	0.054	>0.05	1	>0.05

Appendix 5.15 Analysis of variance for the effects of habitat, predator exclusion and litter on emergence success in Experiment IV. n.e. = no emergence. Mulga species in bold. $P < 0.05$ (in bold).

Source of variation	d.f.	***Acacia aneura***		*Acacia bivenosa*		*Senna glutinosa* subsp. *glutinosa*		***Acacia kempeana***		***Enchylaena tomentosa***		*Eucalyptus eucentrica*		***Digitaria brownii***		*Triodia longiceps*	
		F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Habitat (H)	1	5.368	**0.0243**	1.588	0.213	6.165	**0.0162**	0.857	0.3587	3.888	0.0538	n.e.	n.e	48.297	**<.0001**	n.e.	n.e
Predator exclusion (P)	2	4.731	**0.0128**	1.235	0.2988	0.991	0.378	1.929	0.1552	8.232	**0.0008**	n.e.	n.e	10.757	**0.0001**	n.e.	n.e
Litter cover (L)	2	2.774	0.0713	3.353	**0.0424**	5.1	**0.0094**	2.571	0.0858	0.222	0.8014	n.e.	n.e	2.956	0.0605	n.e.	n.e
H x P	2	1.619	0.2077	3.706	**0.031**	2.887	0.0644	5.357	**0.0075**	2.057	0.1378	n.e.	n.e	4.346	**0.0178**	n.e.	n.e
H x L	2	1.975	0.1486	0.529	0.592	1.124	0.3325	0.857	0.4301	0.06	0.9416	n.e.	n.e	8.498	**0.0006**	n.e.	n.e
P x L	4	2.657	**0.0426**	0.706	0.5914	1.169	0.3348	0.643	0.6343	0.18	0.948	n.e.	n.e	0.607	0.6594	n.e.	n.e
H x P x L	4	4.449	**0.0035**	1.059	0.3859	1.11	0.3613	1.5	0.2152	0.426	0.7892	n.e.	n.e	2.221	0.0788	n.e.	n.e
Residual	54																
Patch	1	0.437	>0.05	0.176	>0.05	2.631	>0.05	0	>0.05	0.466	>0.05			1.072	>0.05		

Appendix 5.16 Analysis of variance for the effects of habitat on emergence success in Experiment VII. Mulga species in bold. $P < 0.05$ (in bold).

		Acacia aneura		*Acacia bivenosa*		*Gossypium sturtii*		***Enchylaena tomentosa***		*Corymbia eremaea* subsp. *oligohphylla*		***Digitaria brownii***	
Source of variation	d.f.	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Habitat (H)	1	1.781	0.2033	0.235	0.6351	1.472	0.2452	n.e.	n.e	0.003	0.9579	2.437	0.1408
Residual	14												
Patch	1	0.329	>0.05	0.350	>0.05	0.481	>0.05			0.043	>0.05	1.541	>0.05

Appendix 5.17 Analysis of variance for the effects of habitat on ***Enchylaena tomentosa*** survival at week 2 in Experiment II. $P < 0.05$ (in bold).

Source of variation	d.f.	F	*P*
H (habitat)	1	0.603	0.4469
Residual	19		
Patch	1	0.375	>0.05

Appendix 5.18 Analysis of variance for the effects of habitat on survival at week 2 in Experiment IV. (a) ***Acacia aneura***; (b) *Senna glutinosa* subsp. *glutinosa*. $P < 0.05$ (in bold).

(a)

Source of variation	d.f.	F	*P*
H (habitat)	1	0.143	0.7210
Residual	5		
Patch	1	Too few cells	Too few cells

(b)

Source of variation	d.f.	F	*P*
H (habitat)	1	0.256	0.6145
Residual	64		
Patch	1	0.378	>0.05

Appendix 5.19 Analysis of variance for the effects of habitat and predator exclusion on seed removal at day 8 in Experiment I. Mulga species in bold. $P < 0.05$ (in bold).

		Acacia aneura		*Acacia murrayana*		*Acacia melleodora*		***Enchylaena tomentosa***		*Eucalyptus gamophylla*	
Source of variation	d.f.	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Habitat (H)	1	0.350	0.5688	0.065	0.8043	0.221	0.6491	1.800	0.2126	0.008	0.9329
Predator exclusion (P)	2	0.983	0.411	0.490	0.628	1.088	0.3773	1.642	0.2467	3.396	0.0797
H x P	2	0.252	0.7829	0.526	0.6079	0.737	0.5054	1.642	0.2467	0.832	0.4659
Residual	9										

Appendix 5.20 Analysis of variance for the effects of habitat and predator exclusion on seed removal at day 8 in Experiment II. Mulga species in bold. $P < 0.05$ (in bold).

		Acacia aneura		*Acacia bivenosa*		***Senna artemesioides* subsp. *artemesioides***		*Senna glutinosa* subsp. *glutinosa*		*Eucalyptus eucentrica*		***Enchylaena tomentosa***	
Source of variation	d.f.	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Habitat (H)	1	0.04	0.8458	1.304	0.2830	1.668	0.2287	0.019	0.8947	0.093	0.7676	0.939	0.3579
Predator exclusion (P)	2	0.542	0.5992	6.148	0.0207	0.354	0.7115	0.605	0.5669	1.263	0.3286	2.571	0.1309
H x P	2	0.374	0.6984	1.119	0.3682	1.523	0.2692	0.097	0.9083	0.069	0.9339	0.374	0.6980
Residual	9												

Appendix 5.21 Pearson product moment correlations (r^2) for seed size and removal and Spearman Rank correlations (R) for seed coat features and removal in ant removal experiments.

Experiment	Seed size		Seed coat features	
	r^2	*P*	R	*P*
I	0.62	0.114	0.00	1.000000
II	0.39	0.25	0.447214	0.450185

Appendix 6.1 Analysis of variance for the effects of habitat, adult neighbour and soil on percent species survival after 1 month in Exp. I. Mulga species in bold.

		Acacia aneura		*Acacia melleodora*		*Acacia murrayana*		***Digitaria brownii***		***Enchylaena tomentosa***		*Triodia basedowii*		
Source of variation	d.f.	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	d.f.	F	*P*
H (habitat)	1	1.579	0.2138	1.997	0.1627	1.2	0.2777	3.333	0.0729	2.222	0.1413	1	2.709	0.1171
N (adult neighbour)	2	0.175	0.8395	1.498	0.2318	0.133	0.8754	0.933	0.3989	2.222	0.1172	2	0.287	0.7539
S (soil)	1	4.386	**0.0405**	4.529	**0.0374**	0.133	0.7163	0.133	0.7163	2.222	0.1413			
H x N	2	1.579	0.2146	0.5	0.6093	2.8	0.0688	0.933	0.3989	2.222	0.1172	2	0.892	0.427
H x S	1	1.579	0.2138	1.997	0.1627	3.333	0.0729	0.133	0.7163	2.222	0.1413			
N x S	2	0.175	0.8395	1.498	0.2318	1.733	0.1854	0.933	0.3989	2.222	0.1172			
H x N x S	2	1.579	0.2146	0.5	0.6093	0.133	0.8754	0.933	0.3989	2.222	0.1172			
R (residua)l	60													
P (patch)	1	0.175	$P > 0.05$	4.53	$\mathbf{P < 0.05}$	0.133	$P > 0.05$	1.2	$P > 0.05$	2.222	$P > 0.05$	18	3.553	$P > 0.05$

Appendix 6.2 Analysis of variance for the effects of habitat, adult neighbour and soil on percent species survival after 2 months in Exp. I. Mulga species in bold.

		Acacia aneura		*Acacia melleodora*		*Acacia murrayana*		***Digitaria brownii***		***Enchylaena tomentosa***	
Source of variation	d.f.	F	*P*	F	P	F	*P*	F	*P*	F	*P*
H (habitat)	1	1.576	0.2142	1.704	0.1967	5.532	**0.022**	12.733	**0.0007**	2.861	0.0959
N (adult neighbour)	2	3.613	**0.033**	7.226	**0.0015**	6.361	**0.0031**	2.941	0.0605	2.609	0.0819
S (soil)	1	2.021	0.1604	6.822	**0.0114**	2.64	0.1094	2.103	0.1522	1.105	0.2974
H x N	2	2.308	0.1083	3.866	**0.0263**	1.282	0.285	4.13	**0.0209**	4.79	**0.0117**
H x S	1	0.705	0.4044	0.015	0.9033	0.019	0.8918	3.919	0.0523	4.85E-05	0.9945
N x S	2	0.184	0.8321	3.663	**0.0316**	2.888	0.0635	2.313	0.1077	0.158	0.8543
H x N x S	2	1.42	0.2496	0.297	0.7445	0.005	0.995	2.246	0.1146	0.071	0.9317
R (residua)l	60										
P (patch)	1	1.96	$P > 0.05$	2.79	$P > 0.05$	4.706	$\mathbf{P < 0.05}$	0.153	$P > 0.05$	0.24	$P > 0.05$

Appendix 6.3 Analysis of variance for the effects of habitat, adult neighbour and soil on percent species survival after 6 months in Exp. I. Mulga species in bold.

		Acacia aneura		*Acacia melleodora*		*Acacia murrayana*		***Digitaria brownii***		***Enchylaena tomentosa***	
Source of variation	d.f.	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
H (habitat)	1	1.307	0.2575	21.873	**<.0001**	43.67	**<.0001**	18.06	**<.0001**	25.283	**<.0001**
N (adult neighbour)	2	5.643	**0.0057**	9.596	**0.0002**	9.818	**0.0002**	0.518	0.5983	0.916	0.4055
S (soil)	1	0.969	0.329	0.936	0.3371	0.562	0.4566	0.849	0.3604	0.436	0.5117
H x N	2	6.459	**0.0029**	3.209	**0.0474**	3.415	**0.0394**	1.037	0.3607	4.905	**0.0106**
H x S	1	0.831	0.3655	0.006	0.9369	1.33	0.2535	3.075	0.0846	0.002	0.9641
N x S	2	0.086	0.9181	0.311	0.7337	0.245	0.7832	2.15	0.1254	0.166	0.8478
H x N x S	2	0.233	0.7928	0.341	0.7125	0.115	0.8916	2.323	0.1067	1.365	0.2632
R (residua)l	60										
P (patch)	1	3.162	$P > 0.05$	0.937	$P > 0.05$	0.55	$P > 0.05$	0.275	$P > 0.05$	0.54	$P > 0.05$

Appendix 6.4 Analysis of variance for the effects of habitat, adult neighbour and soil on percent species survival after 12 months in Exp. I. Mulga species in bold.

		Acacia aneura		*Acacia melleodora*		*Acacia murrayana*		***Digitaria brownii***		***Enchylaena tomentosa***	
Source of variation	d.f.	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
H (habitat)	1	0.84	0.363	42.155	**<.0001**	151.229	**<.0001**	6.694	**0.0121**	36.794	**<.0001**
N (adult neighbour)	2	7.208	**0.0016**	13.181	**<.0001**	12.151	**<.0001**	1.092	0.342	2.243	0.1149
S (soil)	1	0.125	0.7252	0.259	0.6127	0.909	0.3443	1.447	0.2337	0.309	0.5804
H x N	2	4.689	**0.0128**	5.655	**0.0056**	12.151	**<.0001**	0.625	0.539	6.69	**0.0024**
H x S	1	2.988	0.089	0.786	0.379	0.909	0.3443	1.872	0.1764	0.787	0.3786
N x S	2	0.116	0.8902	0.017	0.9827	0.09	0.9145	1.092	0.342	0.523	0.5956
H x N x S	2	0.017	0.9833	0.307	0.7367	0.09	0.9145	1.092	0.342	2.433	0.0964
R (residua)l	60										
P (patch)	1	3.49	$P > 0.05$	0.002	$P > 0.05$	11.27	$\mathbf{P < 0.05}$	0.1197	$P > 0.05$	0.099	$P > 0.05$

Appendix 6.5 Analysis of variance for the effects of habitat, adult neighbour and soil on percent species survival after 24 months in Exp. I. Mulga species in bold.

		Acacia aneura		*Acacia melleodora*		*Acacia murrayana*		***Digitaria brownii***	
Source of variation	d.f.	F	*P*	F	*P*	F	*P*	F	*P*
H (habitat)	1	2.934	0.0916	31.902	**<.0001**	15.38	**0.0002**	3.661	0.0602
N (adult neighbour)	1	3.641	0.0609	24.944	**<.0001**	2.005	0.1435	16.878	**0.0001**
S (soil)	1	0.06	0.8074	0.254	0.6159	0.018	0.8942	0.899	0.3465
H x N	1	21.466	**<.0001**	24.944	**<.0001**	2.005	0.1435	2.278	0.1362
H x S	1	2.156	0.1469	0.254	0.6159	0.018	0.8942	1.261	0.2656
N x S	1	0.078	0.7804	1.341	0.2512	0.469	0.6279	0.296	0.5881
H x N x S	1	0.042	0.8392	1.341	0.2512	0.469	0.6279	0.517	0.4748
R (residua)l	60								
P (patch)	1	3.22	*P* > 0.05	3.566	*P* > 0.05	1.17	*P* > 0.05	1.533	*P* > 0.05

Appendix 6.6 Analysis of variance for the effects of habitat, adult neighbour and soil on species height after 1 month in Exp. I. Mulga species in bold.

		Acacia aneura		*Acacia melleodora*		*Acacia murrayana*		***Digitaria brownii***		***Enchylaena tomentosa***	
Source of variation	d.f.	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
H (habitat)	1	3.415	0.0655	38.326	**< 0.0001**	87.437	**< 0.0001**	0.73	0.3935	84.160	**< 0.0001**
N (adult neighbour)	2	1.528	0.2184	0.081	0.9226	0.477	0.6212	0.907	0.4046	7.963	**0.0004**
S (soil)	1	2.123	0.1464	9.173	**0.0026**	6.223	**0.0131**	4.637	**0.032**	0.981	0.3227
H x N	2	4.015	**0.0189**	5.455	**0.0047**	5.507	**0.0044**	7.121	**0.0009**	1.873	0.1553
H x S	1	0.194	0.6595	1.644	0.2007	0.18	0.6719	1.381	0.2408	4.654	**0.0317**
N x S	2	1.002	0.3682	6.782	**0.0013**	1.078	0.3414	0.635	0.5305	4.556	**0.0111**
H x N x S	2	0.583	0.559	6.26	**0.0021**	6.148	**0.0024**	1.267	0.2829	0.556	0.5739
R (residua)l	>120										
P (patch)	1	0.056	*P* > 0.05	1.507	*P* > 0.05	2.5	*P* > 0.05	14.57	***P* < 0.05**	22.89	***P* < 0.05**

Appendix 6.7 Analysis of variance for the effects of habitat, adult neighbour and soil on species height after 6 months in Exp. I. Mulga species in bold.

		Acacia aneura		*Acacia melleodora*		***Digitaria brownii***		***Enchylaena tomentosa***	
Source of variation	d.f.	F	*P*	F	*P*	F	*P*	F	*P*
H (habitat)	1	0.387	0.5346	6.709	**0.0107**	79.277	**<0.0001**	15.802	**<0.0001**
N (adult neighbour)	2	10.667	**<0.0001**	9.535	**0.0001**	9.56	**<0.0001**	6.959	**0.0012**
S (soil)	1	1.926	0.1667	4.078	0.455	5.027	**0.0256**	4.325	**0.0386**
H x N	2	0.066	0.9362	0.073	0.9295	6.988	**0.0011**	3.735	**0.0253**
H x S	1	2.766	0.0978	0.189	0.6646	0.068	0.7947	3.012	0.084
N x S	2	0.174	0.08404	**0.01**	0.9901	1.197	0.3033	0.54	0.5833
H x N x S	2	0.34	0.7124	0.993	0.3731	1.687	0.1868	3.735	**0.0253**
R (residual	>120								
P (patch)	1					2.195	$P > 0.05$	26.84	$\boldsymbol{P < 0.05}$

Appendix 6.8 Analysis of variance for the effects of habitat, adult neighbour and soil on species leaf number after 1 month in Exp. I. Mulga species in bold.

		Acacia aneura		*Acacia melleodora*		*Acacia murrayana*	
Source of variation	d.f.	F	*P*	F	*P*	F	*P*
H (habitat)	1	8.328	0.0041	30.635	**< 0.0001**	61.135	**< 0.0001**
N (adult neighbour)	2	0.216	0.8056	1.066	0.3456	7.112	**0.0009**
S (soil)	1	2.512	0.1139	12.019	**0.0006**	0.997	0.3188
H x N	2	2.614	0.0747	0.38	0.6841	5.554	**0.0042**
H x S	1	0.527	0.4685	0.685	0.4085	0.345	0.5571
N x S	2	2.701	0.0686	0.81	0.4456	1.128	0.3248
H x N x S	2	0.137	0.8718	0.431	0.6503	9.572	**< 0.0001**
Residual	342						
P (patch)	1	3.72	$P > 0.05$	7.8	$\boldsymbol{P < 0.05}$	Too many missing cells	

Appendix 6.9 Analysis of variance for the effects of habitat, adult neighbour and soil on species leaf number after 6 months in Exp. I. Mulga species in bold.

		Acacia aneura		*Acacia melleodora*	
Source of variation	d.f.	F	*P*	F	*P*
H (habitat)	1	1.631	0.203	10.784	**0.0013**
N (adult neighbour)	2	3.902	**0.0217**	10.192	**< 0.0001**
S (soil)	1	0.06	0.8067	4.971	**0.0275**
H x N	2	0.913	0.4028	0.173	0.8414
H x S	1	1.939	0.1653	0.220	0.6399
N x S	2	2.038	0.1329	0.729	0.4841
H x N x S	2	1.036	0.3567	0.467	0.6282
R (residual)	342				
P (patch)		Too many missing cells		Too many missing cells	

Appendix 6.10 Analysis of variance for the effects of habitat on percent survival in *Triodia basedowii* after 1 and 8months in Exp. II.

		Survival to 1 month		Survival to 8 months	
Source of variation	d.f.	F	*P*	F	*P*
H (habitat)	1	3.734	0.1015	40.630	**0.0007**
R (residual)	6				
P (patch)	1	3.733	>0.05	2.533	>0.05

Appendix 7.1 Analysis of variance for the effects of soil type, shade and species' association on survival at month one. Mulga species are in bold.

		Acacia anuera		*Acacia bivenosa*		*Corymbia eremaea* subsp. *oligophylla*		***Digitaria brownii***		***Eremophila latrobei* subsp. *glabra***		*Triodia brizoides*	
	d.f.	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Soil (S)	1	0.024	0.8783	0.222	0.6421	4.300E-4	0.9836	8.697	**0.007**	0.864	0.3618	3	0.0961
Shade (SH)	1	0.057	0.8131	1.786E-4	0.9894	0.148	0.7038	0.028	0.8687	3.852	0.0614	3	0.0961
Species' mix (M)	1	0.465	0.5020	5.193	**0.0319**	5.361	**0.0295**	1.535	0.2274	0.238	0.6298	3	0.0961
S x SH	1	0.057	0.8131	0.043	0.8367	1.430	0.2434	1.430	0.2434	0.083	0.7752	3	0.0961
S x M	1	0.024	0.8783	0.489	0.4912	4.028	0.0561	4.949	**0.0358**	0.864	0.3618	3	0.0961
SH x M	1	0.057	0.8131	0.142	0.7098	5.82	**0.0238**	1.835	0.1882	0.864	0.3618	3	0.0961
S x SH x M	1	0.057	0.8131	0.358	0.5553	0.692	0.4137	0.106	0.7474	1.340	0.2585	3	0.0961
Residual	24												
Patch	1	0.21	> 0.05	7.7	**< 0.05**	0.03	> 0.05	0.08	> 0.05	5.15	**< 0.05**	0	> 0.05

Appendix 7.2 Analysis of variance for the effects of soil type, shade and species' association on survival at month two. Mulga species are in bold.

		Acacia anuera		*Acacia bivenosa*		*Corymbia eremaea* subsp. *oligophylla*		***Digitaria brownii***		***Eremophila latrobei* subsp. *glabra***		*Triodia brizoides*	
	d.f.	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Soil (S)	1	1.408	0.2471	1.602	0.2178	0.08	0.7797	29.27	**< 0.0001**	0.802	0.3795	1.59	0.2195
Shade (SH)	1	0.015	0.9037	3.011	0.0955	0.109	0.7437	1.856	0.1858	7.38	**0.012**	0.149	0.7034
Species' mix (M)	1	0.589	0.4503	3.494	0.0739	12.366	**0.0018**	6.812	**0.0154**	0.241	0.6283	0.861	0.3627
S x SH	1	0.015	0.9037	0.224	0.6406	0.215	0.6474	6.227	**0.0199**	0.121	0.7307	4.564	**0.043**
S x M	1	0.113	0.7394	0.042	0.8398	0.582	0.4531	2.237	0.1478	2.933	0.0997	0.678	0.4185
SH x M	1	0.529	0.4739	0.102	0.7516	3.176E-4	0.9859	3.585E-4	0.9850	0.295	0.5919	0.003	0.9587
S x SH x M	1	0.529	0.4739	0.014	0.9063	1.637	0.213	1.242	0.2762	0.613	0.4414	3.252	0.0839
Residual	24												
Patch	1	0.09	> 0.05	8.20	**< 0.05**	0.46	> 0.05	1.86	> 0.05	3.41	> 0.05	0.43	> 0.05

Appendix 7.3. Analysis of variance for the effects of soil type, shade and species' association on survival at month three. Mulga species are in bold.

		Acacia anuera		*Acacia bivenosa*		*Corymbia eremaea* subsp. *oligophylla*		***Digitaria brownii***		***Eremophila latrobei* subsp. *glabra***		*Triodia brizoides*	
	d.f.	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Soil (S)	1	0.278	0.603	2.675	0.115	0.353	0.5582	30.689	**< 0.0001**	0.919	0.3474	1.008	0.3253
Shade (SH)	1	0.027	0.8697	5.826	**0.0238**	3.031E-4	0.9863	3.069	0.0926	12.930	**0.0015**	0.05	0.8255
Species' mix (M)	1	2.202	0.1508	3.597	0.07	8.428	**0.0078**	9.032	**0.0061**	0.089	0.7674	0.138	0.7136
S x SH	1	0.174	0.6801	0.472	0.4987	0.516	0.4794	6.99	**0.0142**	0.089	0.7674	4.111	0.0538
S x M	1	0.121	0.7312	0.014	0.9071	1.095	0.3057	3.589	0.0703	1.536	0.2272	0.376	0.5453
SH x M	1	1.082	0.3085	0.019	0.8919	0.935	0.3433	0.031	0.8622	0.13	0.7218	0.028	0.8681
S x SH x M	1	0.209	0.6516	0.005	0.9434	2.49	0.1277	0.513	0.4806	0.089	0.7674	2.215	0.1497
Residual	24												
Patch	1	0.17	> 0.05	5.61	**< 0.05**	0.004	> 0.05	3.24	> 0.05	5.72	**< 0.05**	1.55	> 0.05

Appendix 7.4 Analysis of variance for the effects of soil type, shade and species' association on growth at month one. (a) ***Acacia anuera***, (b) *Acacia bivenosa*, (c) *Corymbia eremaea* subsp. *oligophylla*, (d) ***Digitaria brownii***, (e) ***Eremophila latrobei* subsp. *glabra***, (f) *Triodia brizoides*.

(a)

	d.f.	F	*P*
Soil (S)	1	7.364	**0.0073**
Shade (SH)	1	7.945	**0.0054**
Species' mix (M)	1	7.934	**0.0054**
S x SH	1	2.362	0.1262
S x M	1	1.891	0.1709
SH x M	1	0.008	0.9291
S x SH x M	1	0.044	0.8344
Residual	169		
Patch	1	0.89	> 0.05

(b)

	d.f.	F	*P*
Soil (S)	1	6.926	**0.0103**
Shade (SH)	1	7.062	**0.0096**
Species' mix (M)	1	11.487	**0.0011**
S x SH	1	3.692	0.0585
S x M	1	1.544	0.2179
SH x M	1	14.441	**0.0003**
S x SH x M	1	0.026	0.8722
Residual	75		
Patch	1	12.3	> 0.05

(c)

	d.f.	F	*P*
Soil (S)	1	2.686	0.1031
Shade (SH)	1	7.126	**0.0084**
Species' mix (M)	1	0.239	0.6256
S x SH	1	7.325	**0.0075**
S x M	1	2.805	0.0958
SH x M	1	0.222	0.6383
S x SH x M	1	2.811	0.0955
Residual	166		
Patch	1	0.53	> 0.05

(d)

	d.f.	F	*P*
Soil (S)	1	47.6292	**< 0.0001**
Shade (SH)	1	39.491	**< 0.0001**
Species' mix (M)	1	0.135	0.7141
S x SH	1	4.69	**0.032**
S x M	1	5.476	**0.0206**
SH x M	1	0.102	0.7501
S x SH x M	1	3.528	0.0623
Residual	146		
Patch	1	1.24	> 0.05

(e)

	d.f.	F	*P*
Soil (S)	1	0.293	0.5891
Shade (SH)	1	11.495	**0.0009**
Species' mix (M)	1	27.025	**< 0.0001**
S x SH	1	6.424	**0.0124**
S x M	1	2.855	0.0933
SH x M	1	2.783	0.0975
S x SH x M	1	0.484	0.4876
Residual	139		
Patch	1	1.11	> 0.05

(f)

	d.f.	F	*P*
Soil (S)	1	1.096	0.2965
Shade (SH)	1	30.444	**< 0.0001**
Species' mix (M)	1	5.613E-5	0.994
S x SH	1	1.585	0.2097
S x M	1	6.666	**0.0106**
SH x M	1	0.654	0.4199
S x SH x M	1	4.959	**0.0272**
Residual	182		
Patch	1	2.13	> 0.05

Appendix 7.5 Analysis of variance for the effects of soil type, shade and species' association on growth at month three. (a) ***Acacia anuera,*** (b) *Acacia bivenosa*, (c) *Corymbia eremaea* subsp. *oligophylla*, (d) ***Digitaria brownii***, (e) ***Eremophila latrobei*** **subsp.** ***glabra***, (f) *Triodia brizoides.*

(a)

	d.f.	F	*P*
Soil (S)	1	15.007	**0.0002**
Shade (SH)	1	0.019	0.8893
Species' mix (M)	1	10.214	**0.0017**
S x SH	1	0.904	0.3432
S x M	1	5.93	**0.0169**
SH x M	1	1.086	0.2989
S x SH x M	1	0.493	0.4834
Residual	116		
Patch	1	0.53	> 0.05

(b)

	d.f.	F	*P*
Soil (S)	1	5.562	**0.02**
Shade (SH)	1	5.189	0.246
Species' mix (M)	1	0.384	0.5364
S x SH	1	0.001	0.9706
S x M	1	0.516	0.4742
SH x M	1	1.794	0.183
S x SH x M	1	0.683	0.4101
Residual	75		
Patch	1	Missing cells	Missing cells

(c)

	d.f.	F	*P*
Soil (S)	1	0.324	0.5701
Shade (SH)	1	10.001	**0.0019**
Species' mix (M)	1	0.697	0.4052
S x SH	1	2.966	0.0873
S x M	1	1.785	0.1838
SH x M	1	6.464	**0.0121**
S x SH x M	1	3.310	0.0710
Residual	139		
Patch	1	5.01	**< 0.05**

(d)

	d.f.	F	*P*
Soil (S)	1	38.956	**< 0.0001**
Shade (SH)	1	60.973	**< 0.0001**
Species' mix (M)	1	0.122	0.7271
S x SH	1	0.309	**0.5794**
S x M	1	3.832	**0.0528**
SH x M	1	3.171	0.0778
S x SH x M	1	2.579	0.1112
Residual	109		
Patch	1	6.34	**< 0.05**

(e)

	d.f.	F	*P*
Soil (S)	1	0.177	0.6749
Shade (SH)	1	2.789	0.0978
Species' mix (M)	1	12.72	**0.0005**
S x SH	1	0.328	0.5681
S x M	1	1.693	0.1960
SH x M	1	1.713	0.1934
S x SH x M	1	0.999	0.3199
Residual	139		
Patch	1	0.108	> 0.05

(f)

	d.f.	F	*P*
Soil (S)	1	0.173	0.6779
Shade (SH)	1	68.744	**< 0.0001**
Species' mix (M)	1	0.281	0.5966
S x SH	1	0.255	0.6143
S x M	1	13.377	**0.0003**
SH x M	1	1.029	0.3119
S x SH x M	1	8.101	**0.005**
Residual	174		
Patch	1	0.002	> 0.05

interactions for species patterning. It predicts that spinifex gains a competitive advantage in the context of frequent disturbance. In portraying this relationship, spinifex grassland may be described as fire-*dependent* (*sensu* Bond *et al.* 2005), given that it is excluded from otherwise suitable habitat by the presence of *A. aneura*. The model in turn highlights the broader issue of the maintenance of diversity within habitats, given its predictions for the exclusion of inferior competitors in the context of limiting resources. Though divergent in their detail, the three models may each be viewed as examples of 'niche opportunity' theory (Shea & Chesson 2002), given their shared emphasis on 1) altered site condition through exogenous disturbance, and 2) the facilitation of spinifex invasion into previously unoccupied areas once altered site conditions exceed stress thresholds for *A. aneura* population persistence.

This final chapter draws together the various findings of this investigation of mulga-spinifex boundaries and relates them to the expectations of each of the above three models. A new multi-causal coexistence model is then presented that draws on the various relevant aspects of each of the existing models as well as on community theory more generally. The chapter concludes with the recommendation that future research and management should concentrate more on the maintenance of mulga quality rather than focussing solely on the issue of fire-driven boundary shifts.

8.2 Relevance of existing models for between-habitat coexistence breakdown

This following section examines how the data presented in this thesis relate to the predictions of each of the existing three models for mosaic breakdown. The purpose of this is twofold. First, it allows consideration of the relevance of each model to current shrub-grass patterning, and second, it is designed to inform debate as to the likelihood of, and mechanisms for, coexistence breakdown in the context of novel and potentially catastrophic disturbance.

8.2.1 MODEL I: FIRE-MEDIATED REDUCTION IN MULGA SITE QUALITY

Model I requires that 1) current edaphic patterning is of primacy in the distribution of species across habitat boundaries, and 2) post-fire edaphic changes would prevent mulga re-establishment.

Do current boundaries reflect the influence of edaphic constraint?

The results of Chapters 2 and 3 demonstrated that minimal between-habitat floristic overlap most often coincides with the occurrence of distinct edaphic shifts, while greater compositional commonality usually occurs when gradients are more diffuse. Regarding the former situation, it was proposed that between-habitat segregation can be most readily explained by invoking the notion of non-overlapping fundamental niche space in the context of a spatially variable environment. In the case of the latter, edaphic constraint was viewed as being of reduced consequence for species' patterning.

Experimentation focused on boundaries characterised by marked floristic and edaphic discontinuity. The examination of dormancy and germination responses in mosaic species (Chapter 4) provided some indirect evidence for the role of edaphic control of early recruitment success for between-habitat species' sorting. Specifically, it was shown that rapid germination speed is closely associated with sandy *Triodia basedowii* habitat membership, and slow speeds with water-limiting, heavy clay *T. longiceps* habitat. It was recognised however, that further work was required to more fully understand mosaic species' patterning given the sequential and multiphase nature of the recruitment process in plant populations.

The results of Chapter 5 provided little support for the role of edaphic constraint at early life stages for mosaic structuring. Rather, they showed that most species respond in a similar way across habitat boundaries, and that among-species differences in emergence and early survival are not closely matched to habitat membership. This decoupling of seedling and adult distributions indicated that later-acting factors must operate to produce observed within- and between-habitat vegetation patterns.

A study of constraints on seedling establishment in dunefield mosaics (Chapter 6) demonstrated that the edaphic model provides only partial explanation for between-habitat segregation in that setting. Specifically, it was shown that while the expansion of *T. basedowii* and associated dune shrubs into mulga habitat is negated at the seedling establishment stage due to restrictions on root penetration, mulga species are in no way limited by edaphic conditions in neighbouring sandy spinifex habitat.

The examination of seedling survival and growth in simulated mountain range mosaic conditions (Chapter 7) further highlighted the inadequacies of the edaphic model as an independent explanation for mosaic regulation. Here, it was shown that in isolation, edaphic constraint has little influence on between-habitat species patterning in that setting. This related to the data showing that *T. brizoides* can survive and grow equally well in its own and in neighbouring mulga soil throughout the establishment phase. And while there was some suggestion that the particular example of spinifex soil used in the experiment represents what could be interpreted as a 'gradient edge' (*sensu* Myster 2001) for *A. aneura*, the negative independent influence of that substrate was shown to be only temporary.

Would boundaries shift as a result of a disturbance-mediated reduction in edaphic heterogeneity?

The results of this study can offer little support for the role of post-fire edaphic alteration in the repositioning of mulga-spinifex boundaries. In fact, data from Chapters 2 and 3 indicate that the fire-driven erosion of mulga soil would not facilitate the novel incursion of spinifex species through a process of habitat homogenisation. This is because textural variability (and on ranges, chemical differences) across mulga-spinifex boundaries increases with soil depth, meaning that the removal of mulga surface soil would result in a greater edaphic differential than that present prior to the onset of site degradation. It was further demonstrated that mulga habitats should not be considered more prone to post-fire erosion compared with spinifex. In the range setting, mulga occurs on intermediate slopes and has higher boulder coverage compared with spinifex habitats, while dunefield mulga is characterised by hard-setting soils with binding properties that would aid stabilisation. Furthermore, it was shown that mulga habitats in both settings retain fire-killed standing stags, and have an equal complement of short-lived species (especially grasses) whose rapid post-fire establishment would further aid soil stability in the immediate post-fire environment. Clearly then, other possible post-fire changes must be considered in relation to the process of mulga contraction.

Further work showed that the related view (see Latz in prep.) – that boundary shifts would result from wind-blown sand movement from burnt dune slopes to mulga swales – is likewise of little relevance in these mosaics. Specifically, the results of Chapter 6 demonstrated that unless sand deposition in the swale is well in excess of 1 m (i.e. the depth tested in this study) – which, as outlined in Buckley (1979), is highly unlikely under present climatic conditions – the successful expansion of dune species onto hard-setting swale soils is improbable due to physiological limitations during establishment. And given that mulga species can currently emerge (Chapter 5) and establish (Chapter 6) in spinifex habitats, it follows that a fire-induced shift in site quality, producing edaphic conditions more similar to spinifex habitat, would not newly act to preclude their own-habitat post-fire recruitment.

8.2.2 MODEL II: FIRE-MEDIATED EXTINCTION OF MULGA

The relevance of Model II to mulga-spinifex mosaics is contingent on the extent to which 1) current boundaries reflect differing degrees of fire frequency, and 2) increased firing results in a contraction of mulga habitat due to the inability of its constituent species to tolerate fire recurrence.

Do current boundaries reflect a successional gradient from infrequently burnt shrubland to frequently burnt grassland?

The work presented in this thesis is largely supportive of Bowman *et al.*'s own suggestion that, contrary to the predictions of theory, mulga and spinifex habitats rarely form part of a classic-style fire-successional gradient from infrequently burnt shrubland to frequently-burnt grassland. The results of visual comparisons of past and present boundaries using 1950, 1987 and 1997 aerial photography (Chapter 2), confirmed Bowman *et al.*'s original supposition that shrub-grass boundaries are, in this region at least, mostly highly stable. This was supported by the analysis of the between-habitat distribution of *Acacia aneura* life-stage classes that demonstrated a far greater association of all classes with mulga than with spinifex habitat (also Chapter 2). The result was interpreted as being inconsistent with the type of patterning that would result from a recently-initiated landscape-scale shift from shrub to grass dominance in response to increased firing. On-ground inspection revealed further, that in the majority of cases where fire incursion had taken place, stand replacement was occurring at pre-existing mulga edges. Overall, the results served to demonstrate that due to the comparatively low flammability of mulga, current firing mostly acts to reinforce, rather than dismantle existing shrub-grass boundaries.

Importantly however, this present study differs from that of Bowman *et al.* in being able to present some data that is more consistent with the predictions of the fire succession model, albeit on a very fine- and spatially-restricted scale. This relates to mulga-spinifex boundaries on Tylers Pass red-soil areas. As reported, habitats there range from non-spinifex dense-canopied mulga through to mixed stands with varying abundances of regenerating mulga and mature spinifex, and finally, to mature spinifex that has minimal floristic commonality with 'intact' mulga. Given that patterning in that area was not significantly correlated with the edaphic variables tested, it was proposed that the floristic and structural gradient relates most to varying degrees of fire recurrence.

Would increased firing cause the contraction of mulga?

The relevance of Model II to mulga-spinifex mosaics is contingent not only on regime change, but also on the extent to which the constituent habitats meet the essential criteria for its operation in terms of their inherent attributes. The results of floristic sampling and experimentation allowed for detailed consideration of one of the fundamental requirements of the model: that mulga is intolerant of repeated firing. Evidence for the first indicator of fire intolerance – the death of adult *A. aneura* plants – was obtained from the survey data of Chapter 2. This related to the regular occurrence of fire-killed adult stags and the lack of live adults in regenerating mulga stands. These results demonstrated the importance of regeneration from seed compared with vegetative resprouting in *A. aneura* as a response to disturbance. Additional data presented in Chapters 2 and 3 served as evidence for the negative influence of fire-recency in other components of mulga flora. Specifically, it was shown that certain characteristic mulga groups (e.g. perennial forbs, perennial half-shrubs, ferns and climbers) would be disadvantaged by short fire-return intervals, given that they are better represented (in terms of species' richness) in mature than in regenerating mulga. Together, these data were interpreted as being indicative of the deleterious effects of a short fire-return interval on mulga compositional- and structural-integrity.

While not being directly examined in this study, the influence of fire-frequency was also given consideration, particularly in relation to the second indicator of fire intolerance: slow seedling growth-rate. It was shown, for example, that while *A. aneura* can in certain cases emerge (Chapter 5), and establish beyond the juvenile stage in spinifex habitat where it does not currently form a canopy (Chapter 2, 3 and 6), it will rarely have the opportunity to establish a seed bank there due to the increased risk of juvenile fire death. This relates principally to the idea that in fire-prone systems, minor differences in growth rate can have major consequences for coexistence (Bond & van Wilgen 1996). This issue likewise applies to the various other slow-growing mosaic obligate seeders and passive fire tolerators that are similarly confined to, or have greater abundance in, mulga habitat due to the combined influence of their fire-response traits and their inherently slow rate of development.

Importantly though, the results of Chapter 4 indicated that *A. aneura* may not meet the criterion of fire intolerance with regard to all of its life stages. Specifically, it was shown that germination in this species is likely to be regulated by the combined influence of a range of factors, including soil-moisture content, temporal variables such as disturbance frequency and/or after-ripening, as well as seasonal influences and heating duration. It is likely, therefore, that a requirement for the combined occurrence of any of these factors would serve to limit the frequency and the size of germination events. A propensity for fractional seed bank release would in turn mean that the chance of propagule depletion, and hence localised extinction of this species, might in fact be relatively low. By invoking this notion of fractional seed bank release in *A. aneura*, some account can be made of its minimal contraction over the last half century (see above discussion), and of the regular occurrence of stand-replacement at burnt mulga habitat edges, in spite of evidence for repeated fire exposure.

8.2.3 MODEL III: FIRE-MEDIATED SHIFT IN COMPETITIVE ABILITIES

In order for Model III to be used as an explanation for mosaic patterning, it must first be demonstrated that 1) spinifex is currently excluded from mulga by negative interactions with mature *A. aneura*, and 2) spinifex in turn suppresses the establishment of mulga seedlings.

Is spinifex excluded from mulga habitat through competitive effects?

The results of this thesis provide some support for the role of competition in the determination of species' limits in these mosaics. It was suggested in Chapters 2 and 3 for example, that the absence (or otherwise very low abundance) of various spinifex *Acacia* species (e.g. *A. bivenosa*, *A. murrayana* and *A. melleodora*) from mulga habitat might result from the process of resource pre-emption by *A. aneura*. It was further reasoned that this same process may also account for the segregation of numerous other congeneric species pairs across mulga-spinifex boundaries. This work also documented the between-habitat segregation of growth-form groups with divergent leaf and shoot properties. Prominent examples include the unequal distribution of perennial tussock- and hummock-grasses, and the virtual exclusion of myrtaceous trees and mallee shrubs from mulga habitat. This pattern aligns with the current emphasis in the literature on shifts in plant functional trait combinations along habitat gradients for coexistence maintenance (Fonseca *et al.* 2000). And finally, the floristic data presented in Chapter 2 provided some suggestion that in the absence of edaphic control, the abundance of *Triodia brizoides* in mulga might relate to canopy density. This is consistent with van Etten's (1987) report of the negative influence of shade on *Triodia pungens*.

The results of Chapters 6 were unsupportive of the idea that resource pre-emption by *A. aneura* is important in the prevention of dune shrub establishment in mulga swales, given the demonstrated overarching influence of edaphic constraint there. Those of Chapter 7 differed in providing qualified support for the role of niche contraction for species' patterning in mountain range mosaics. Specifically, they showed that when *T. brizoides* is grown in non-spinifex mulga soil it survives better with full light than with shading. On the strength of this, it was argued that in certain areas where edaphic conditions favour the development of a light-inhibiting mulga canopy (e.g. south-facing slopes, low pH and clay-rich soils), hummock grass dominance is dependent on the fire-induced removal of established *A. aneura* shrubs, due to its intolerance of the combined effects of edaphic constraint and reduced light levels.

Would a fire-mediated alteration of competitive outcomes induce coexistence breakdown?

The application of the fire-dependency model additionally requires demonstration of the negative influence of *Triodia* on *A. aneura* seedling survival and growth. Interactions between *A. aneura* and two species of *Triodia* were examined in this thesis. The results of Chapter 6 clearly highlighted the negative influence of established *T. basedowii* on *A. aneura* (and associated mulga species) seedling growth and survival. Specifically, when seedlings from mulga habitat were transplanted into spinifex habitat, they became established when adult spinifex neighbours were removed, but were suppressed when neighbours were present. The results of Chapter 7 showed that *A. aneura* is, at least during the early establishment phase, negatively influenced by interactions with establishing *T. brizoides* and associated spinifex seedlings. Evidence indicates therefore, that Model III provides a sound theoretical framework for coexistence breakdown, given the demonstrated inherent slow growth rate of *A. aneura* seedlings (Chapter 6), the negative impact of spinifex on *A. aneura* growth and survival (Chapters 6 and 7), and the sensitivity of juvenile and adult *A. aneura* plants to fire (Chapters 2, 3 and 6). However, given the apparent stability of mulga-spinifex boundaries, there is currently little scope for its application to mosaic regulation.

8.3 Multi-causal model for within- and between-habitat coexistence in mulga-spinifex mosaics

While providing some insight into the various constraints on life-cycle development in mosaic species, none of the three models examined so far can, in isolation, adequately account for coexistence maintenance or breakdown. This result mirrors current claims in the wider ecological literature for the importance of multi-causal explanation for community assembly (Rees *et al.* 2001; Shea & Chesson 2002; Whitford 2002; Schenk *et al.* 2003). In recognition of the complexity of mosaic patterning throughout the central Australian landscape, a multi-causal model will now be presented that seeks to account for the segregation of species between mulga and spinifex habitats, and the coexistence of species within them.

The processes in the model start at the recruitment life stage in the post-fire environment. Established *Triodia* and *A. aneura* adults have been removed by the passage of fire. Seed removal-rates prior to disturbance were equivalent in each habitat, meaning that asymmetric dispersal and predation is unlikely to have influenced the distribution of propagules. Germination in spinifex species is highly cued to fire, resulting in a large proportion of the seed bank being expended in a single fire event. *Acacia aneura* seed banks instead undergo fractional release, meaning that a greater proportion remains dormant after the single fire event.

Fire does not result in edaphic changes that preclude the re-establishment of mulga species and at the same time newly facilitate the encroachment of spinifex species in mulga habitat. Instead, safe sites for emergence and early survival are mediated by water availability, which affects all species equally within- and between-habitat boundaries. This means that all mosaic species have equal opportunity to emerge in their own and in neighbouring habitat, independent of the level of between-habitat edaphic variability. Recruitment is largely confined to major rainfall events in both habitat types.

8.3.1 BETWEEN-HABITAT COEXISTENCE

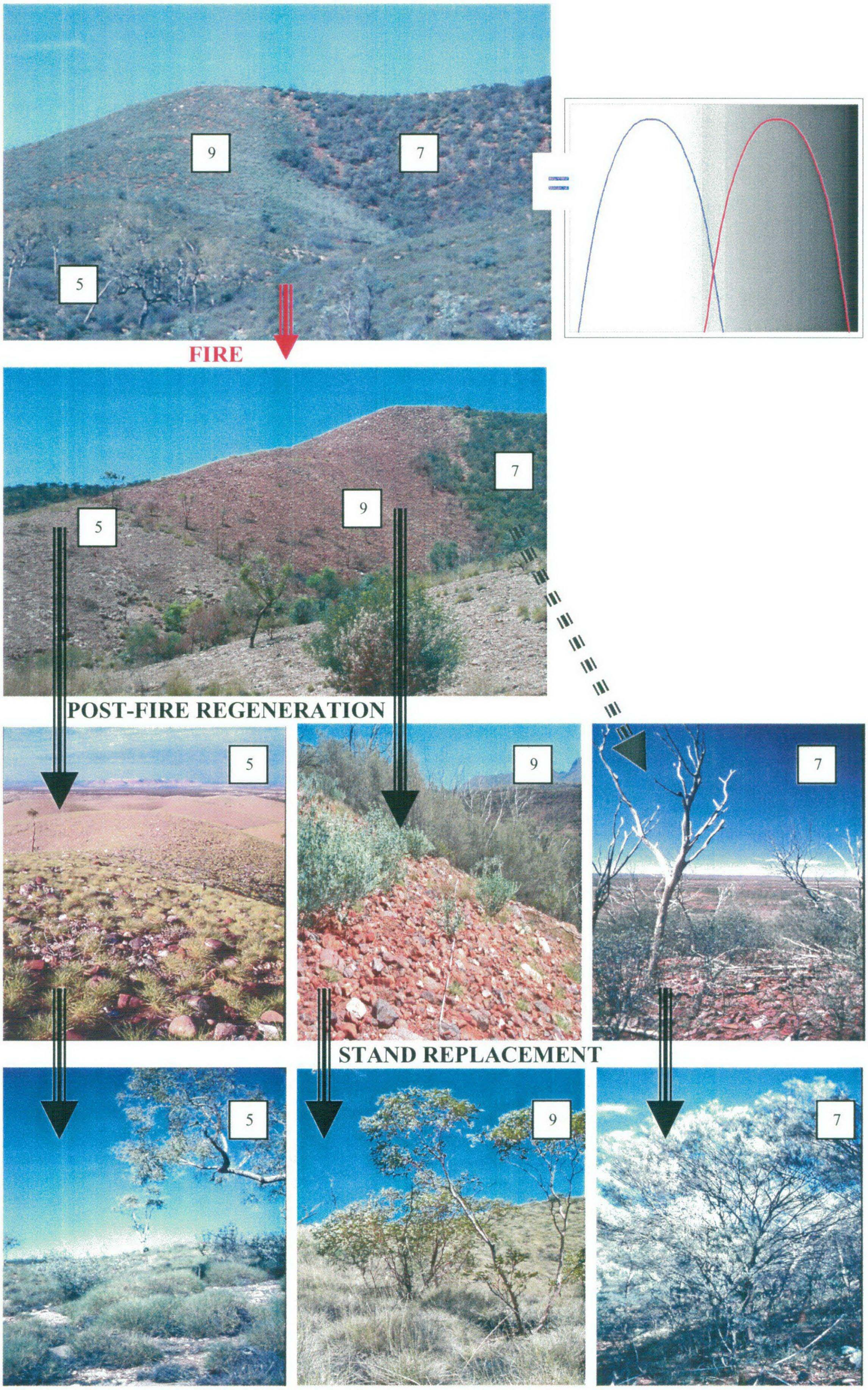
Species' sorting in these mosaics takes place through the combined effects of fundamental- and realised-niche constraints on establishment and maturation. The importance of various processes, including their main and interactive effects, varies considerably both spatially and temporally throughout mosaic landscapes. This means that processes that are important for species' segregation in some situations are largely irrelevant in others. Moreover, even in terms of the immediate mulga-spinifex boundary, the processes operating to prevent shrubland expansion are rarely equivalent to those maintaining grassland extent. And the evidence of certain situations shows that processes may affect only a portion of a habitat's flora such that some species are excluded from neighbouring habitat and others are not. Certain generalisations are, however, possible. These are outlined in the following.

Type I: Strongly contrasting between-habitat edaphic gradients

a) Fire-independent segregation. The presence of strongly contrasting edaphic conditions across habitat boundaries precludes seedling establishment in neighbouring habitat, giving rise to minimal between-habitat floristic overlap (Fig. 8.1). This means that floristic patterns result from the combined effects of non-overlapping niche-space and habitat heterogeneity. This model accounts for the between-habitat patterning of non-spinifex mulga (Subgroup 7) and *Triodia longiceps* (Subgroup 9) and 'white soil' *Triodia brizoides* (Subgroup 5) on the Brewer Conglomerate mountain range system (refer Chapter 2 herein). It has further application to the covariance of shrub-grass alterations and distinct geological/soil-parent material shifts on central Australian mountain ranges more generally. On a landscape scale however, the two-way edaphic control of shrubland/grassland extent is comparatively rare and is possibly confined to the Pertnjara land system (*sensu* Perry *et al.* 1962).

Firing is of little consequence in the exclusion of mulga (including *A. aneura* and associated diagnostics) from those spinifex habitats that are characterised by extremely high pH and strongly carbonated soils. Instead, establishment of mulga species is impeded by edaphic constraint and/or the debilitating cumulative effects of 'gradient edge' and allopatric seedling interaction. In these situations, grassland

Fig. 8.1 Boundary type I a) Fire-independent segregation due to strongly contrasting between-habitat edaphic gradients. The presence of strongly-contrasting edaphic conditions across habitat boundaries precludes seedling establishment in neighbouring habitat, giving rise to minimal between-habitat floristic overlap. This means that floristic patterns result from the combined effects of non-overlapping niche-space and habitat heterogeneity. Here, mulga (blue) and spinifex (red) occupy different fundamental niches (background shading) and have minimal floristic overlap.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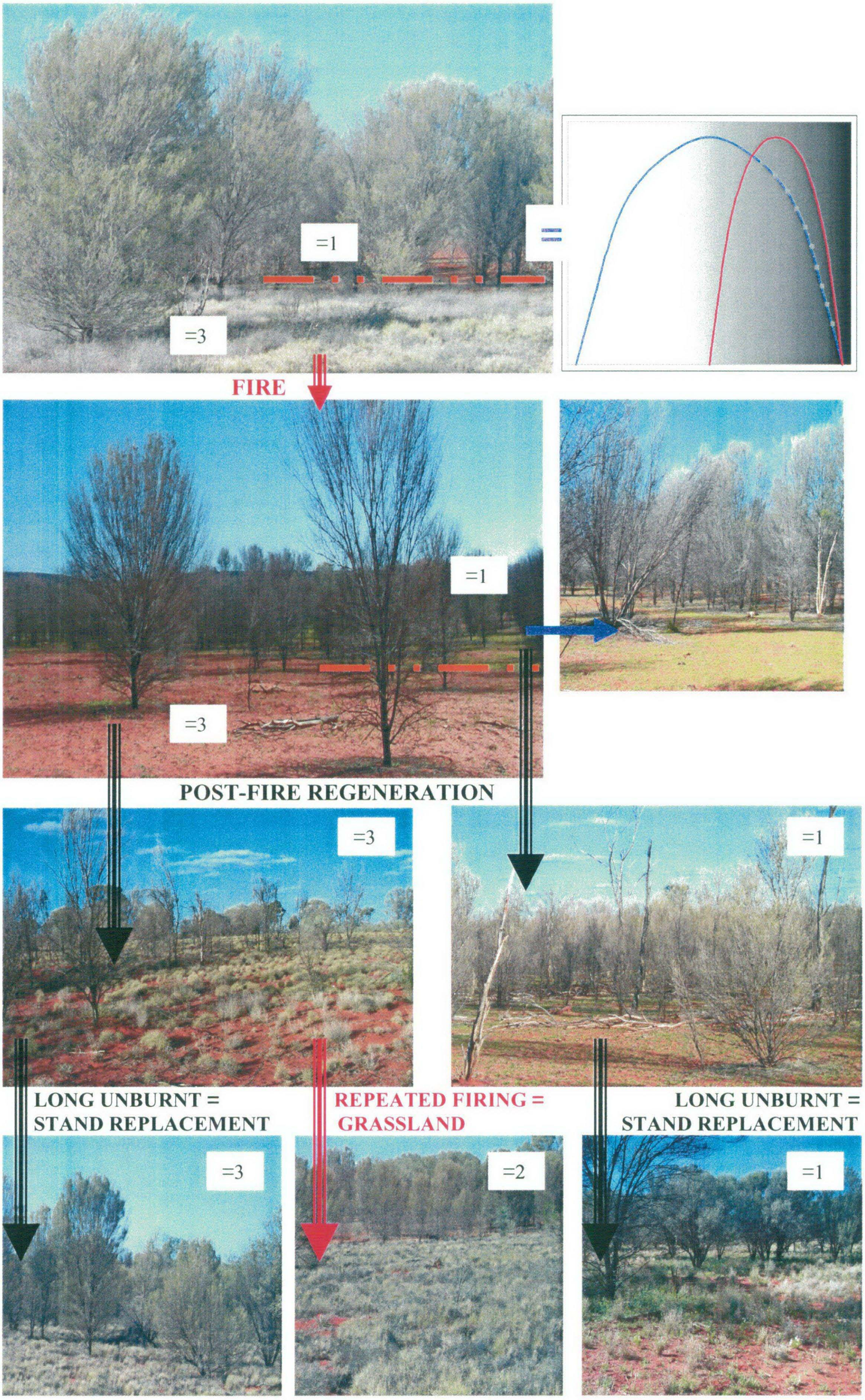
persistence is not dependent on repeated firing. Mulga habitats likewise represent an edaphic gradient edge for spinifex establishment, meaning that spinifex (including *Triodia* and associated species) is excluded from mulga simply due to its inability to tolerate the extremely acidic (pH 5-4) clay-rich soils there. This means that while these spinifex species can emerge in mulga habitat, they will not survive and grow to maturity there. Other potential influences such as fire and biotic interactions are therefore irrelevant in preventing spinifex expansion. In these situations, non-spinfex mulga habitat persists because of its reduced flammability, and because its fractional seed bank release ensures that stand replacement occurs even in the unlikely event of a short fire-return interval. Repeated firing, while likely resulting in the degradation of mulga quality (i.e. reduced functional group richness and the creation of thick, even-aged stands), will not initiate a conversion to spinifex.

b) Partially fire-dependent segregation. Minimal between-habitat floristic overlap can be only partially explained by the presence of strongly contrasting between-habitat edaphic conditions. In these circumstances, shrub-grass alterations result from the influences of physiological and demographic constraints combined with suppression-based competitive effects (Fig. 8.2). This model applies to shrub-grass alterations on central Australian dunefields that correlate with marked shifts in soil texture and penetrability. Here, as in the above situation, mulga habitat represents an edaphic gradient edge for spinifex species, meaning that while they can emerge there, they will not survive and grow to maturity due to their inability to tolerate water-limiting and hard setting soils. In this way, the realised- and fundamental-niches of spinifex species are equivalent. Here again, mulga stand-replacement takes place after a fire event and firing remains relatively infrequent due to the low flammability of this habitat.

Unlike in the previously described model however, neighbouring grassland persistence is instead mediated by the combined influence of species' fire-response traits, suppression-based competition and fire frequency. Here, the establishment of inherently slow-growing and fire-intolerant mulga species (i.e. 'the Gullivers' *sensu* Bond & van Wilgen 1996) is suppressed by the presence of faster growing and fire-tolerant *Triodia*. This alteration of competitive abilities, combined with the higher flammability of *Triodia*, ensures that shrub dominance is kept in check in the absence of edaphic control, and that grassland structure is maintained. In this situation,

Fig. 8.2 Boundary type I b) Partially fire-dependent segregation. Minimal between-habitat floristic overlap can be only partially explained by the presence of strongly contrasting between-habitat edaphic conditions. In these circumstances, shrub-grass alterations result from the influences of physiological and demographic constraints combined with suppression-based competitive effects. Mulga stand-replacement takes place after a fire event and firing remains relatively infrequent due to the low flammability of this habitat. Neighbouring grassland persistence is mediated by the combined influence of species' fire-response traits, suppression-based competition and fire frequency. Here, the fundamental niche of mulga (blue) is contracted (hashed blue) by the combined influence of competitive and fire effects. Spinifex (red) has reduced fundamental niche space independent of biotic factors compared with that of mulga.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REPEATED FIRING =
GRASSLAND
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STAND REPLACEMENT
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hummock grasslands may be described as a fire-*dependent* habitat (*sensu* Bond *et al.* 2005). Repeated firing will result in the exclusion of mulga species from this habitat. By contrast, a mixed shrub-grass formation will characterise long-unburnt areas. In this situation, the competitive displacement of *Triodia* by *A. aneura* shrubs does not take place in the absence of fire because competitive and demographic constraints on *A. aneura* combine to prevent the establishment of a dense light-inhibiting canopy.

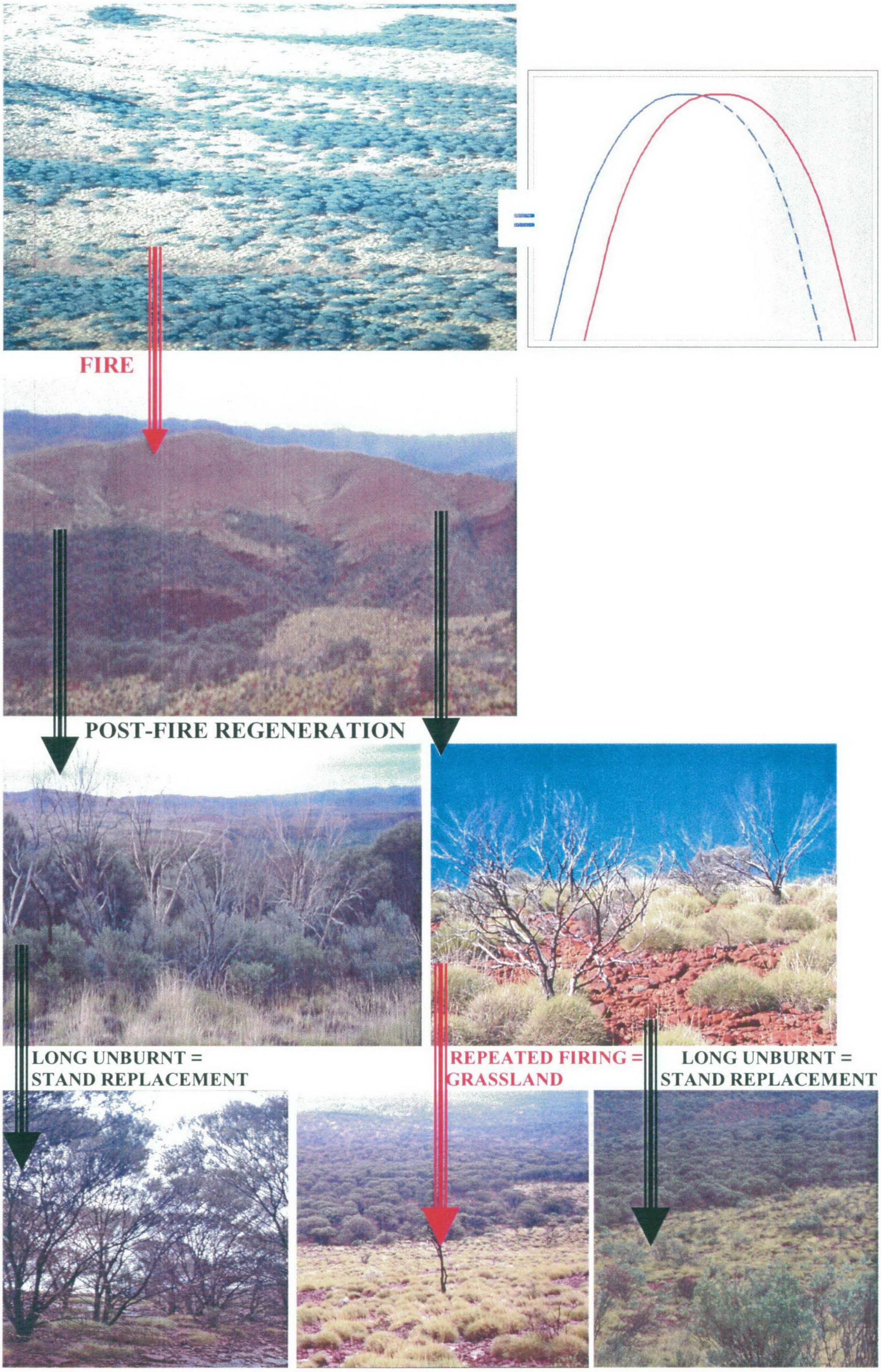
This model can be applied to several central Australian landsystems (e.g. Tietkins, Alinga, Lindavale, Karee, Bushy park, Leahy, Ewaninga and Adnera *sensu* Perry *et al.* 1962) that are characterised by sandy plains & low dunefields in which mulga occupies large areas of red clayey sands & red earth soils and spinifex and mulga-spinifex mixes occur on red sands. Spatially, it is of second-most importance for between-habitat boundary patterning throughout the central Australian landscape.

Type 2: Weakly-contrasting edaphic gradients

a) Fire-dependent segregation. Mulga-spinifex boundaries are 'artificial' (*sensu* van Etten 1997) in that while they are visible at the landscape level, they do not reflect an abrupt change in overall species composition and edaphic condition (Fig. 8.3). Here, the circumscription of individual habitats is largely dependent on the abundance of *Acacia aneura* itself, given that *Triodia* does not always vary greatly and that there is relatively high floristic commonality overall. It follows that boundary positioning largely reflects the extent to which habitat conditions facilitate the development of an *A. aneura* shrub canopy. Here, a boundary shift in the direction of mulga could easily occur in the context of high fire frequency, given that *A. aneura* is among those species least capable of withstanding repeated firing. In this situation, the loss of *Acacia aneura* represents the critical step in the conversion of shrubland to hummock grassland. In this model, as in the last, the 'Gulliver effect' operates to maintain grassland structure. These predictions align directly with the expectations of the global model for fire-mediated coexistence of grass-shrub alterations (see Bond *et al.* 2005).

This depiction of fire-mediated control, accounts for the rarity of mulga-spinifex mixes in the context of a frequently-fired landscape. It thereby raises the possibility that in the absence of fire, mixed mulga-spinifex communities could potentially dominate the landscape, while their segregation through physiological

Fig. 8.3 Boundary type II a) Fire-dependent segregation across weakly-contrasting edaphic gradients. Mulga-spinifex boundaries are 'artificial' in that while they are visible at the landscape level, they do not reflect an abrupt change in overall species composition and edaphic condition. A boundary shift in the direction of mulga could easily occur in the context of high fire frequency, given that *A. aneura* is among those species least capable of withstanding repeated firing. In this situation, the loss of *Acacia aneura* represents the critical step in the conversion of shrubland to hummock grassland. Lower slope areas are less prone to fire incursion allowing for the development of a mulga canopy. Spinifex (red) and mulga can co-occur in fire shadow areas. Here, the fundamental niche of mulga (blue) is contracted (hashed blue) by the combined influence of competitive and fire effects. Spinifex (red) and mulga can co-occur in fire shadow areas.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LONG UNBURNT =
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control at niche thresholds would be comparatively rare. In this way, the model could account for patterning on mountain ranges and dunefields throughout a vast area of the central Australian landscape. Examples of landsystems where it likely applies are: Simpson; Singleton; Angas; Aileron; Harts; Sonder; Gillen, and Middleton *sensu* Perry *et al.* 1962). This depiction is directly at odds with the commonly-held view of mulga contraction through spinifex invasion, which as Bowman *et al.* (1994) predict, first requires the fire-induced removal of *A. aneura* once edaphic, demographic and/or competitive thresholds are exceeded.

b) Partially fire-dependent segregation. Segregation occurs through the combined effects of edaphic constraint, tolerance-based competition and differences in habitat flammability (Fig. 8.4). This applies to the extremely dense mulga patches at Tylers Pass that have maintained their extent over recent times in spite of their increased vulnerability due to edge effects. In these sites, the soil type represents a niche optimum for *A. aneura* (as evinced by the exceptionally thick canopy development), yet is tending more towards a gradient-edge for *T. brizoides*. It is here that the otherwise minimal influence of edaphic constraint is magnified by this species' intolerance of low light levels, resulting in its reduced establishment success. The fire-induced removal of the dense mulga canopy would result in the temporary creation of new niche opportunities for *T. brizoides*. Ultimately though, the re-establishment of a light-inhibiting mulga canopy again serves to limit the abundance of *Triodia* in this habitat and lessen the risk of repeated firing. It is likely that these processes operate on a very limited scale throughout central Australia.

8.4.2 WITHIN-HABITAT COEXISTENCE

Fire-dependent coexistence: Species' richness decreases with time-since-fire in spinifex habitat. The establishment of weak competitors in frequently-disturbed spinifex is facilitated by a trade-off in competitive ability and rate of growth. Fast-germinating and rapidly-growing species mature and set seed well prior to becoming suppressed by slow-to-establish, but competitively superior *Triodia*. This means that while competition from *Triodia* is intense in later post-fire stages, it does not result in the exclusion of these 'fugitive' species (*sensu* Grime 1979) due to the latter's ability to rapidly establish persistent seed banks that are cued to post-disturbance conditions. Storage-effects, as they relate to dormant seed banks and vegetative buds, further

Fig. 8.4 Boundary type II b) Partially fire-dependent segregation. Segregation occurs through the combined effects of edaphic constraint, tolerance-based competition and differences in habitat flammability. This applies to the extremely dense mulga patches at Tylers Pass that have maintained their extent over recent times in spite of their increased vulnerability due to edge effects. In these sites, the soil type represents a niche optimum for *A. aneura* (as evinced by the exceptionally thick canopy development), yet is tending more towards a gradient edge for *T. brizoides*. It is here that the otherwise minimal influence of edaphic constraint is magnified by this species' intolerance of low light levels, resulting in its reduced establishment success. In this case, mulga (blue) and spinifex (red) occupy different realised niches and have minimal floristic overlap due to suppression- and tolerance-based competitive effects in the context of a frequently-fired landscape.


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STAND REPLACEMENT
LONG UNBURNT =
STAND REPLACEMENT
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2

reduce the risk of localised extinction through reproductive failure in unfavourable times.

Fire-independent coexistence: Contrasting with spinifex habitat, species richness increases with time-since-fire in mulga. With maturity, *A. aneura* shrubs facilitate the establishment of associated shade-tolerant mulga species through 'island effects' (increased shading, litter, moisture and possibly nutrients) and the provision of perch sites for seed-dispersing birds. Regeneration in *A. aneura* is continuous because soil processes (heating-cooling cycles and scarification) result in the staggered release of variable-aged seeds from the seed bank. Asymmetric competition and apparent competition do not result in reduced *A. aneura* seedling establishment success near established adults. Rather, positive adult-seedling interactions – as they relate to reduced heat and moisture stress under *A. aneura* canopies – result in enhanced seedling growth and survival during establishment. This means that while disturbance-mediated adult removal is a requirement for regeneration in spinifex habitat, it may in fact have negative consequences for mulga persistence. This relates to the idea of proportionately greater seedling losses in mulga habitat where adults have been removed by firing as compared with in mature stands. There are intrinsic opportunities for the circumvention of possible negative parent-offspring interactions at later stages of development via gap creation through the sporadic death of adults, even in the absence of fire disturbance. Thus, *A. aneura* population persistence is (at least to some degree) facilitated by a positive-feedback (*sensu* Tongway & Ludwig 1989, 1990, 1994) that equates with Rietkerk *et al.*'s (2002) concept of 'spatial self-organisation'.

Physiological control is of greater relevance for shrub diversity in mulga than is interspecific competition. Specifically, mulga habitats characterised by coarser-textured soils will support a greater range of congeneric shrubs and trees (e.g. *Acacia kempeana*; *A. estrophiolata*; *A. minyura*; *A. paraneura*; and *A. ayersiana*) than will finer-textured and hard-setting soils of which only *A. aneura* is tolerant. Competitive displacement is avoided through a high level of niche differentiation – as evinced by the greater functional diversity in mulga *cf* in spinifex; through tolerance-based competition; and through chance establishment success in the context of within-habitat environmental patchiness. Persistence throughout unfavourable drought periods is possible due to temporal storage effects as expressed by stress tolerance in established plants and to the establishment of persistent seed banks.

8.4 Conclusion

The results presented in this thesis demonstrate that patterning in mulga-spinifex mosaics results from a number of disparate processes, and quite often, their interactive effects. They show, moreover, that different processes assume varying levels of importance for coexistence depending on site conditions, plant attributes and life-history stages. Demonstration of these issues was made possible through an experimental approach to the identification of the mechanisms for species' sorting, which ultimately aided the distinction between cause and correlation. The work is of value not just in terms of its contribution to our understanding of pattern and process, but also in relation to its ramifications for conservation management. Specifically, it shows that while *A. aneura* is more resistant to fire-mediated contraction than current predictions allow, the quality and integrity (as measured by functional group diversity and uneven-aged population structure) of mulga habitat can be undermined by too-frequent firing. Importantly, this depiction of habitat degradation and possible conversion to 'less desirable alternate stable states' (see Westoby *et al.* 1989) does not depend on the novel invasion of spinifex.

Concern for mulga degradation extends well beyond central Australian mulga-spinifex mosaics. Identified common threats throughout mulga lands include excessive levels of firing, grazing and firewood extraction (Tongway & Ludwig 1997; Berg & Dunkerley 2004). Long-standing mulga researchers Tongway and Ludwig (1997) propose that these processes combine to undermine the efficacy of the 'positive feedback system' on which mulga relies for its persistence. Elsewhere, the related concept of 'negative feedbacks' (see Scheffer *et al.* 2001) has been used as a theoretical framework for understanding the global process of desertification in poorly-managed arid grass-shrub mosaics (see Whitford 2002). With this in mind, it is suggested that future detailed consideration of feedbacks (both positive and negative), particularly with regard to thresholds for seedling emergence, establishment and growth, might add considerably to our understanding of assembly and 'disassembly' (*sensu* Worm & Duffy 2003) in mulga-spinifex mosaics.