

Aspects of litter dynamics in semi-arid environments in eastern Australia

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Aspects of litter dynamics in semi-arid environments in eastern Australia



Samantha K. Travers

A thesis in the fulfilment of the requirements for

Doctorate of Philosophy



School of Biological, Earth & Environmental Sciences

University of New South Wales

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Leaf litter is an important resource and a fundamental component of all terrestrial ecosystems. The senescence and decay of leaves, bark and other organic material provides a mechanism for carbon, nitrogen and other critical elements to be transported and incorporated into the soil. This process is particularly important in arid and semi-arid ecosystems where resources are limited and unevenly distributed spatially and temporally. There are many drivers that modulate surface litter accumulation, litter fall rates and litter decay rates. This thesis examines how these aspects of litter dynamics are moderated by abiotic (e.g. soil, landform, fire, rainfall) and biotic (e.g. vegetation communities, individual species) factors in semi-arid woodlands and shrublands in eastern Australia. Chapter 1 provides an overview of the importance of litter in semi-arid woodlands, describing previous research on leaf litter dynamics in arid and semi-arid ecosystems. Chapter 2 examines litter fall rates in response to abiotic conditions, with a focus on the fall rates of reproductive structures (seeds, flowers and fruits) from three species that differ in their life histories. Chapter 3 and 4 focus on the accumulation and spatial arrangement of surface litter. Chapter 3 describes the shift in litter bed size and composition under two Eucalypt Mallee species (*Eucalyptus socialis*, *E. dumosa*) along a 42 year chronosequence of fire histories. Chapter 4 examines properties of spatial self-organisation exhibited by litter patches, assessing litter patch cover, size and degree of spatial association between surface litter and perennial vegetation across four different landscapes. Chapters 5 and 6 focus on aspects and implications of litter decomposition in the foraging pits of mammals. Chapter 5 examines the relative importance of biotic and abiotic factors during the decomposition process of substrates in the foraging pits of short-beaked echidnas (*Tachyglossus aculeatus*), greater bilbies (*Macrotis lagotis*) and burrowing bettongs (*Bettongia lesueur*). Chapter 6 examines the conditions under which litter decomposition in echidna foraging pits facilitates seedling growth by assessing water stress and the proximity of foraging pits to large trees. Chapter 7 is a summation of the previous chapters, highlighting the implications and limitations of these novel studies, and providing direction for future work in this field.

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Preface

This dissertation consists of five chapters (Chapters 2 to 6) written as separate manuscripts that have been published, accepted, or are intended for publication in peer-reviewed journals. Each chapter is self-contained with references and appendices. Consequently, there will be some repetition among chapters.

This thesis is a compilation of my own work, with guidance from my supervisor David Eldridge. All chapters were conceptualised either by myself or jointly with David Eldridge. I wrote and illustrated the manuscripts and conducted most data analyses. Specific details for each chapter and the contribution of co-authors are detailed below.

Chapter 2: S. K. Travers and D. J. Eldridge. Chapter 2. Increased rainfall frequency triggers an increase in litter fall rates of reproductive structures in an arid eucalypt woodland. Accepted in the 'The Greening of Arid Australia' special edition of *Austral Ecology*, doi: 10.1111/aec.12055.

Study was conceptualised by Samantha Travers and David Eldridge. Data collection and laboratory analyses were undertaken by Samantha Travers. All data analyses were conducted by Samantha Travers, with the exception of the SEM, which was executed by David Eldridge. David Eldridge provided guidance on the study design and structure of the manuscript in his role as academic supervisor.

Chapter 3: S. K. Travers and D. J. Eldridge. Landscape modulators and resource accumulation in a post-fire eucalypt woodland. *Forest Ecology and Management*, 285: 11–19.

Study was conceptualised by Samantha Travers. Data collection and laboratory analyses were carried out by Samantha Travers. All data analyses were undertaken by Samantha Travers, with the exception of the SEM which was executed by David

Eldridge. David Eldridge provided guidance on the structure of the manuscript in his role as academic supervisor.

Chapter 4: S. K. Travers and D. J. Eldridge. Evidence for the spatial self–organisation of litter patches in a semi–arid woodland.

Study was conceptualised by Samantha Travers and David Eldridge. Data analyses were conducted by Samantha Travers. David Eldridge provided guidance on the study design, analyses and structure of the manuscript in his role as academic supervisor.

Chapter 5: S. K. Travers and D. J. Eldridge. Foraging pit morphology influences decomposition in a semi-arid woodland.

Study was conceptualised by Samantha Travers and David Eldridge. Data collection and laboratory analyses were carried out by Samantha Travers. Data analyses were conducted by Samantha Travers with assistance from Terry Koen and David Eldridge. David Eldridge provided guidance on the study design and structure of the manuscript in his role as academic supervisor.

Chapter 6: Samantha K. Travers, David J. Eldridge, Terry B. Koen, Santiago Soliveres. Animal foraging pit soil enhances the performance of a native grass under stressful conditions. *Plant and Soil*, 352: 341–351.

Study was conceptualised by Samantha Travers and David Eldridge. Laboratory analyses were organised by Samantha Travers. David Eldridge provided guidance on the structure of the manuscript in his role as academic supervisor. Terry Koen assisted experimental design and structure of the statistical analyses. Santiago Soliveres contributed intellectually to the development of the manuscript.

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Abstract

Leaf litter is an important resource and a fundamental component of all terrestrial ecosystems. The senescence and decay of leaves, bark and other organic material provides a mechanism for carbon, nitrogen and other critical elements to be transported and incorporated into the soil. This process is particularly important in arid and semi-arid ecosystems where resources are limited and unevenly distributed spatially and temporally. There are many drivers that modulate surface litter accumulation, litter fall rates and litter decay rates. This thesis examines how these aspects of litter dynamics are moderated by abiotic (e.g. soil, landform, fire, rainfall) and biotic (e.g. vegetation communities, individual species) factors in semi-arid woodlands and shrublands in eastern Australia. Chapter 1 provides an overview of the importance of litter in semi-arid woodlands, describing previous research on leaf litter dynamics in arid and semi-arid ecosystems. Chapter 2 examines litter fall rates in response to abiotic conditions, with a focus on the fall rates of reproductive structures (seeds, flowers and fruits) from three species that differ in their life histories. Chapter 3 and 4 focus on the accumulation and spatial arrangement of surface litter. Chapter 3 describes the shift in litter bed size and composition under two Eucalypt Mallee species (*Eucalyptus socialis*, *E. dumosa*) along a 42 year chronosequence of fire histories. Chapter 4 examines properties of spatial self-organisation exhibited by litter patches, assessing litter patch cover, size and degree of spatial association between surface litter and perennial vegetation across four different landscapes. Chapters 5 and 6 focus on aspects and implications of litter decomposition in the foraging pits of mammals. Chapter 5 examines the relative importance of biotic and abiotic factors during the decomposition process of substrates in the foraging pits of short-beaked echidnas (*Tachyglossus aculeatus*), greater bilbies (*Macrotis lagotis*) and burrowing bettongs (*Bettongia lesueur*). Chapter 6 examines the conditions under which litter decomposition in echidna foraging pits facilitates seedling growth by assessing water stress and the proximity of foraging pits to large trees. Chapter 7 is a summation of the previous chapters, highlighting the implications and limitations of these novel studies, and providing direction for future work in this field.

Table of Contents

Originality Statement	ii
Copyright Statement	iii
Authenticity Statement	iii
Preface	iv
Acknowledgements	vi
Abstract	ix
Table of Contents	x
List of Tables	xv
List of Figures	xvii
List of Appendices	xxii

Chapter 1. General introduction..... 1

1.1 An introduction to leaf litter dynamics	2
1.1.1 Broad-scale variability drives resource availability in semi-arid environments	3
1.1.2 Resource patch dynamics drive fine-scale heterogeneity	5
1.1.3 Leaf Litter as an important resource and ecological component	6
1.1.4 Alterations to leaf litter dynamics	8
1.2 Thesis objectives	9
1.3 References	11

Chapter 2. Increased rainfall frequency triggers an increase in litter fall rates of reproductive structures in an arid eucalypt woodland 19

2.1 Abstract	20
2.2 Introduction	21
2.3 Methods	25
2.3.1 Study site	25
2.3.2 Study species	25
2.3.3 Sampling Design	27
2.3.4 Annual production rates of reproductive structures	28
2.3.5 Generalised linear modelling and multi-model inference	28
2.3.6 Structural Equation Modelling	29
2.4 Results	30
2.5 Discussion	36

2.5.1 Rainfall frequency affects fall rates of reproductive structures	36
2.5.2 Fall rates of reproductive structures vary among species.....	37
2.5.3 Wind and other meteorological conditions affect the fall rate of reproductive structures.....	41
2.5.4 The importance of response diversity and episodic events	42
2.6 Acknowledgements.....	43
2.7 References	44

Chapter 3. Landscape modulators and resource accumulation in a post-fire eucalypt woodland 67

3.1 Abstract.....	68
3.2 Introduction	69
3.3 Methods.....	72
3.3.1 Field site.....	72
3.3.2 Experimental design	73
3.3.3 Measuring tree and litter bed patch layers	73
3.3.4 Statistical methods: tree and litter patch dimensions.....	74
3.3.5 Spatial and temporal development of the multi-layered patch.....	74
3.3.6 Compositional shifts in the litter patch	75
3.3.7 Tree, litter and fire as a system	75
3.4 Results.....	76
3.4.1 Spatial and temporal development of the multi-layered patch.....	76
3.4.2 Compositional shifts in the litter patch	79
3.4.3 Tree, litter and fire as a system	82
3.5 Discussion.....	83
3.5.1 Fire drives litter patch development	84
3.5.2 Litter patch development affects fuel loads and fauna.....	87
3.6 Conclusions	89
3.7 Acknowledgements.....	89
3.8 References	90

Chapter 4. Evidence for the spatial self-organisation of litter patches in a semi-arid woodland 97

4.1 Abstract.....	98
4.2 Introduction	99
4.3 Methods.....	102
4.3.1 Study site	102

4.3.2 Field measurements	103
4.3.3 Cover of perennial and litter patches.....	103
4.3.4 Size distribution of perennial and litter patches	104
4.3.5 Spatial distribution of perennial and litter patches	104
4.4 Results	107
4.4.1 Cover of perennial and litter patches.....	107
4.4.2 Size distribution of perennial and litter patches	107
4.5 Discussion	115
4.5.1 Perennial patch cover reflects litter cover	116
4.5.2 Size and frequency of litter and perennial patches differs	117
4.5.3 Litter does not accumulate in perennial patches by positive feedback mechanisms.	119
4.5.4 Perennial patch arrangement may influence the spatial variability of litter patches.	120
4.5.5 A half-century legacy effect of land clearing on litter	121
4.6 Conclusions.....	122
4.7 Acknowledgements	122
4.8 References	123

Chapter 5. Foraging pit morphology influences decomposition in a semi-arid woodland..... 137

5.1 Abstract	138
5.2 Introduction.....	139
5.3 Methods	142
5.3.1 Study site	142
5.3.2 Foraging pit morphologies	143
5.3.3 Litter substrates.....	144
5.3.4 Decomposition study.....	144
5.3.5 Relative success of fungicide and termiticide	146
5.3.6 Measures of decomposition and infiltration of soil into the litter bags	146
5.3.7 Modelling decomposition rates	147
5.4 Results	148
5.4.1 Relative success of fungicide and termiticide	148
5.4.2 Organic mass loss	151
5.4.3 Litter mass loss adjusted for rainfall	153
5.4.4 Infiltration of inorganic material into the litter bags	154
5.4.5 Modelling decomposition rates	155
5.5 Discussion	157
5.5.1 Effects of foraging pit morphology.....	158
5.5.2 The importance of substrate and soil contact	159
5.5.3 The effect of decomposer exclusion	161

5.5.4 Modelling decomposition over time	162
5.6 Conclusion.....	163
5.7 Acknowledgements.....	164
5.8 References	164

Chapter 6. Animal foraging pit soil enhances the performance of a native grass under stressful conditions..... 179

6.1 Abstract.....	180
6.1.1 Background and Aims	180
6.1.2 Methods.....	180
6.1.3 Results.....	180
6.1.4 Conclusions	180
6.2 Introduction	181
6.3 Methods.....	184
6.3.1 Field site	184
6.3.2 Sampling procedure.....	185
6.3.3 Plant growth	185
6.3.4 Soil properties.....	186
6.3.5 Statistical analyses	187
6.4 Results.....	188
6.4.1 Soil properties.....	188
6.4.2 Plant growth: Biotic and abiotic nurse effects on plant growth.....	190
6.4.3 Plant growth: Biotic and abiotic nurse effects on plant growth rate	191
6.4.4 Plant growth: Biotic and abiotic nurse effects on leaf nutrients.....	193
6.5 Discussion.....	193
6.6 Acknowledgments.....	198
6.7 References	198

Chapter 7. Thesis discussion 207

7.1 Key findings of this thesis.....	208
7.2 Temporal and spatial variability in drivers of leaf litter dynamics.....	211
7.2.1 Temporal heterogeneity	211
7.2.2 Spatial heterogeneity.....	212
7.3 Implications of this work.....	212
7.4 Hindsight and forethought: Scope for future research	214
7.4.1 General hindsight and forethought	214
7.4.2 Chapter-specific hindsight and forethought	216

7.5 Towards a holistic understanding of litter dynamics 219

7.6 References 219

List of Tables

Table 2.1. Mean (\pm SE) annual reproductive structure fall rate ($\text{g m}^{-2} \text{day}^{-1}$) and proportional mass (% fraction of the total litter fall for each year) for the three species. Significant differences among years are indicated for each species.	30
Table 2.2. The relative importance of the variables for each species for each model part. Zero-inflated models contain two parts. Part 1 explanatory variables explain the negative binomial-distributed “count” data (zeros and non-zeros), while Part 2 explanatory variables are for the additional zeros in a binomial distribution.	33
Table 2.3. Pathway coefficients for the Structural Equation Models (from Figure 2.3) for all species. Remaining path coefficients for the three models were the same.	35
Table 2.4. Total Standardized Effects for the Structural Equation Models (from Figure 2.3 and Table 2.3) for each species.	35
Table 3.1. Eigenvectors are the coefficients in the linear combinations of PCA components making up the first principal component for Patch Size score and composition score. These scores represent the weightings given to each component in the overall final summary score. The total variance explained by this first axis is also indicated.	79
Table 3.2. Path coefficients and goodness of fit tests for time since fire pathways for each component. Each row represents a model containing the response variable listed in the leftmost column. Otherwise, the model structure is identical to that in Figure 3.5, but with different path coefficients. The next five columns list the path coefficients corresponding to the direct and indirect pathways in the models. R^2 is proportion of variance explained in the response variables listed in the leftmost column. All tests reported here indicate a good fit. All models are saturated.	83
Table 4.1. Summary of SADIE and LISA indices for each patch type and each community. Peren. = perennial patch. Superscripts indicate significant differences. .	112

Table 4.2. Averaged semi-variogram parameters for litter and perennial patch data for each community. All models were spherical.	114
Table 4.3. Pearson's correlation (r) between the litter patch range (A_0) and the mean and median patch and inter-patch sizes.	115
Table 5.1. Summary of results for Olson's negative exponential model ($K \text{ days}^{-1}$) of decomposition averaged for each factor. B/ B = bilby/ bettong, Land. = landform, Treat. = chemical treatment, F + T = both fungicide and termiticide, T = termiticide, F = fungicide, C = control.	156
Table 6.1. Soil attributes. Mean soil attributes of plants in relation to Water regime low, high, Cover Canopy, Open and Microsite Pit, Surface. Within an attribute, the 5 % LSD for the Water by Cover by Microsite interaction is given.	189

List of Figures

- Figure 1.1.** Conceptual diagram of leaf litter dynamics. Black arrows indicate the links between the stages of the litter cycle, grey dotted arrows indicate the connection of each stage to chapters in this thesis. 2
- Figure 1.2.** Location of study sites in NSW, Australia. **Error! Bookmark not defined.**
- Figure 2.1.** a) meta-model and b) conceptual model of the relationships between rainfall variables, other climatic variables, soil variables and the litter fall rate of reproductive structures. Variables in the conceptual model include average rainfall event size in the past 12 months (Event size), number of rain days in the past 12 months (Rain days), cumulative daily solar radiation during each collection window (Radiation), average daily maximum wind speed (Wind speed), average daily evaporation (Evaporation) during each collection window, and categorical landscape location of dune or swale landforms (Landform). 24
- Figure 2.2.** Fall rates of reproductive structures for a) *Senna artemisioides*, b) *Acacia burkittii*, c) *Eucalyptus gracilis* for 2009, 2010 and 2011. The histogram represents cumulative rainfall for each collection window. 31
- Figure 2.3.** Structural equation model for *Eucalyptus gracilis*. Path width indicates the relative strength of the relationship, as indicated by the path coefficient. The overall model explained 23 % of the variance in the litter fall rates of reproductive structures (log₁₀ scale; d.f. = 6; Chi-square = 4.83; $P = 0.56$), as indicated by the R^2 value. The results for the two shrub species are given in Table 2.3. 34
- Figure 3.1.** Mean (\pm SE) for all tree and litter bed dimensions for both species, for sampled years since fire. The black circles represent *Eucalyptus dumosa* while the white circles represent *Eucalyptus socialis*. The y axis units are given in the subtitle for each individual graph. 77
- Figure 3.2.** Linear regression of (a) litter bed area (triangles) and litter bed mass (circles) on tree canopy area and (b) Litter bed volume on tree height (squares). Black

symbols represent *Eucalyptus dumosa* and white symbols represent *Eucalyptus socialis*. Linear regression models: Fourth-root of Litter bed area (m^2) = $0.539 \times \text{Log}_e(\text{Canopy area } (\text{m}^2) + 1) - 0.441$ ($R^2 = 0.70$; $P < 0.001$); Fourth-root of litter bed mass (kg) = $0.202 \times \text{Log}_e(\text{Canopy area } (\text{m}^2) + 1) - 0.215$ ($R^2 = 0.57$; $P < 0.001$); Fourth-root of Litter bed volume (m^3) = $0.462 \times \text{Log}_e(\text{Tree height } (\text{m}) + 1) - 0.048$ ($R^2 = 0.66$; $P < 0.001$). Long dash lines represent 95 % confidence band and dotted lines represent 95 % prediction band. 78

Figure 3.3. Mean (\pm SE) litter loads (kg m^{-2}) with increasing time since fire. Black symbols and solid line represent *Eucalyptus dumosa* and white symbols and dashed line represent *Eucalyptus socialis*. The regression for each species shows an insignificant change difference between the two species and represents a non-significant amount of variation in the data, suggesting no change in litter. Regression equations: (*E. dumosa*: $\text{kg m}^{-2} = 0.003 \times \text{Time since fire (yr)} + 1.465$, $R^2 = 0.02$, $P = 0.72$; *E. socialis*: $\text{kg m}^{-2} = 0.004 \times \text{Time since fire (yr)} + 1.405$, $R^2 = 0.02$, $P = 0.69$)..... 80

Figure 3.4. Mean (\pm SE) percent mass (\pm SE) for every burn site (years since fire) for each species' litter components: a) leaves b) bark c) stick d) seed and e) fragments. Black circles represent *Eucalyptus dumosa* and white circles represent *Eucalyptus socialis*. 81

Figure 3.5. Time since fire–litter composition model. The R^2 value above litter composition indicates that canopy size, litter bed area and time since fire account for 53 % of the variance in litter composition. Thickness of pathways is directly proportional to the strength of the path coefficients. The model is saturated, therefore the Chi-squared statistic = 0 with 0 d.f. 82

Figure 4.1. The cover of litter patches (% cover) in relation to the cover of perennial patches (% cover). A strong linear relationship exists between perennial patch cover and litter patch cover across all communities, with an increase in patch cover from plains to swale to dune communities. Regression equation: Litter cover (%) = $0.77 \times \text{Perennial patch cover } (\%) + 0.68$; $R^2 = 0.76$ 108

Figure 4.2. Average cover (%) of Litter and (combined) Perennial patches, and the contribution of each perennial patch type and litter patches in each community. Within a component, different superscripts indicate a significant difference in means at $P < 0.05$. All patches = all perennial patches combined; CWD = coarse woody debris.	109
Figure 4.3. Summed patch size distributions for a) perennial patches and b) litter patches for each community. Patch size distributions were summed across all replicates and fitted with a truncated power law, using an exponential cut off ($y = ax^b \cdot \exp^{-c \cdot x}$). Model parameters are given in Appendix 4.1.	110
Figure 4.4. Quantile–Quantile plots of litter patch size distribution (x axis, cm) compared with perennial patch size distribution (y axis, cm) for a) dune b) swale c) uncleared plain and d) cleared plain communities. The line in each plot represents $x = y$ (1:1 line).	111
Figure 4.5. The distribution of litter (L) and perennial patches (P) at a typical site for each community. The black represents the presence of a litter or perennial patch and the white indicates the bare inter–patch area.	113
Figure 5.1. The mean (\pm SE) incidence of fungal presence for each chemical treatment over the four collection intervals. The bar indicates the 5 % LSD for the Treatment by Time interaction. The incidence of fungal presence is given by the percentage of litter bags with fungi spores present for each factor. F + T = both fungicide and termiticide, T = termiticide, F = fungicide, C = control.	150
Figure 5.2. The mean (\pm SE) incidence of detritivory by non–targeted soil biota at the final (4 th) collection interval (396 days) for each chemical treatment with significant differences indicated. The incidence of detritivory is measured as the percentage of litter bags with evidence of activity (e.g. silk webbing, faeces, tunnels) from organisms other than fungi or termites for each chemical treatment. There were no observations of non–target biotic activity during collection intervals 1–3. F + T = both fungicide and termiticide, T = termiticide, F = fungicide, C = control.	150

Figure 5.3. The mean (\pm SE) % organic material remaining over time for each factor. F + T = both fungicide and termiticide, T = termiticide, F = fungicide, C = control. 152

Figure 5.4. Three-way interaction of Grass type, Landform and Treatment at collection interval 4 (396 days) for the remaining % organic material. The LSD at 5 % is given for the three-way interaction. F + T = both fungicide and termiticide, T = termiticide, F = fungicide, C = control. 153

Figure 5.5. Relationship between the inorganic content of the litter bags (g) and the mass of organic material lost per mm of rainfall (g mm^{-1}). Collection times are represented as: Time 1 = white triangles, Time 2 = black triangles, Time 3 = white squares, Time 4 = black squares. Quantile regression was performed across all collection times. The 90th (solid line: Coefficient = -0.00448 ; $t = -11.44$; $P < 0.001$), 95th (dashed line: Coefficient = -0.0047 ; $t = -9.56$; $P < 0.001$) and 99th (dotted line: Coefficient = -0.00436 ; $t = -11.44$; $P = 0.14$) quantiles regression lines are shown.... 154

Figure 5.6. Modelled half life (\pm SE) for our Landform by Treatment interaction. The time of the half life is indicated in days (y axis). F + T = both fungicide and termiticide, T = termiticide, F = fungicide, C = control. 157

Figure 6.1. Mean of (a) total plant biomass, (b) proportional reproductive effort (flower and seeds to total biomass ratio), (c) leaf nitrogen concentration, and (d) soil nitrogen concentration in relation to Microsite, Cover and Water regime. The bars indicate the 5 % LSD for the Microsite by Water by Cover interaction. Overall, there is significantly greater plant biomass, proportional reproductive effort and soil N in Pit soil than Surface soil. There are inconsistent trends between Cover and Water treatments. 191

Figure 6.2. Plant growth rate. Changes in plant height (mm: a, b) and length of the longest leaf (mm: c, d) for plants growing in Pits and Surface soils under a regime of low or high water within Canopy or Open soils. Curves represent average values for Canopy and Open Microsites. The bars indicate the 5 % LSD for the Microsite by Water interaction. For both longest leaf length and plant height, there were consistent trends across Canopy and Open. Plants under the high water treatment growing in Pit soil

were consistently the most productive, while plants from Surface soil under low water
were consistently the least productive. The trajectories for high water Surface soil
plants and low water Pit soil plant were consistently similar across both Open and
Canopy treatments.192

List of Appendices

Appendix 2.1. Details of our generalised linear modelling and multi-model inference.	51
Appendix 2.2. Summary of the final meteorological variables selected for each species. The best representative measure (Best Rep.) of each meteorological condition is given for each species, as determined by the lowest AIC of a single explanatory variable model. Variance Inflation Factors (VIF) are given for the final candidate set of explanatory variables used in the global model for each species.	54
Appendix 2.3. Table of <i>Eucalyptus gracilis</i> models ranked according to the quasi-likelihood form of Akaike's information criterion for all models with $\Delta_i \leq 2$. Zero-inflated models contain two parts, and thus require two sets of explanatory variables. The Part 1 explanatory variables explain the negative binomial-distributed "count" data (zeros and non-zeros), while Part 2 explanatory variables are for the additional zeros in a binomial distribution. QAIC, quasi-likelihood form of Akaike's information criterion; K, number of explanatory parameters in the model; d.f., model degrees of freedom; logLik, log likelihood ratio of model; $\Delta_i = \text{QAIC}_i - \text{QAIC}_{\min}$; ω_i , Akaike weight; Av3Cl, Average 3pm cloud 8ths; CuSol, cumulative solar exposure; AvMiTp Average minimum temperature; Ldfm, landform; MxWd, maximum wind speed; RnEv12, Average rainfall event size over past 12 months; RnDy12, number of rain days in the past 12 months.	55
Appendix 2.4. Table of <i>Senna artemisioides</i> models ranked according to the quasi-likelihood form of Akaike's information criterion for all models with $\Delta_i \leq 2$. Zero-inflated models contain two parts, and thus require two sets of explanatory variables. Part 1 explanatory variables explain the negative binomial-distributed "count" data (zeros and non-zeros), while Part 2 explanatory variables are for the additional zeros in a binomial distribution. QAIC, quasi-likelihood form of Akaike's information criterion; K, number of explanatory parameters in the model; d.f., model degrees of freedom; logLik, log likelihood ratio of model; $\Delta_i = \text{QAIC}_i - \text{QAIC}_{\min}$; ω_i , Akaike weight; Av9Cl, Average 9am cloud 8ths; CuSol, cumulative solar exposure; Yr, year; Ldfm, landform;	

MxWd, maximum wind speed; RnEv12, Average rainfall event size over past 12 months; RnDy8, number of rain days in the past 8 months.57

Appendix 2.5. Table of *Acacia burkittii* models ranked according to the quasi-likelihood form of Akaike’s information criterion for all models with $\Delta_i \leq 2$. Zero-inflated models contain two parts, and thus require two sets of explanatory variables. Part 1 explanatory variables explain the negative binomial-distributed “count” data (zeros and non-zeros), while Part 2 explanatory variables are for the additional zeros in a binomial distribution. QAIC, quasi-likelihood form of Akaike’s information criterion; K, number of explanatory parameters in the model; d.f., model degrees of freedom; logLik, log likelihood ratio of model; $\Delta_i = QAIC_i - QAIC_{min}$; ω_i , Akaike weight; Av9Cl, Average 9am cloud 8ths; AvMiTp, Average minimum temperature; CuSol, cumulative solar exposure; Yr, year; Ldfm, landform; MxWd, maximum wind speed; RnEv12, Average rainfall event size over past 12 months; RnDy4, number of rain days in the past 4 months.60

Appendix 2.6. Model-averaged coefficients (and standard errors) and top model coefficients for the three species. The zero-inflated models were run as two parts. Part 1 is for the negative binomial distributed “count” data and Part 2 for the binomial distributed excess zero data. The coefficients for categorical factors (i.e. Year and Landform) are relative to the missing categories (i.e. Year = 2009, and Landform = dune). Lag times for rainfall variables are indicated in months (mth). Wind speed (max) is average daily maximum wind speed; cloud cover is average daily cloud 8ths at either 9am or 3pm; solar exposure is cumulative daily solar exposure (cum.) for the given collection window; temperature is either maximum or minimum daily temperature (Temp.) averaged (avg) for each collection window.65

Appendix 4.1. Average \pm SE of truncated power law parameters ($y = ax^b \cdot \exp^{-c \cdot x}$) for patch size distribution of litter and perennial patches. Average (range) of R-squared values are given. Superscripts indicate significant differences among the communities.131

Appendix 4.2. Summary of Permutational ANOVA results for spatial indicators.

Significant results are **bolded**. For X community d.f. = 3, 32. For all other measures community d.f. = 3, 32; Patch type d.f. = 1, 32; Community × Patch = 3, 32. I_a is index of aggregation; V_i is the index of clustering into patches; V_j is the index of clustering into gaps; X is correlation coefficient of the Local Indicator of Spatial Association; A_0 is Range; C_0 is nugget; $C_0 + C$ is sill; $C / (C_0 + C)$ is spatial structure. 132

Appendix 4.3. Linear regression between perennial patch size and the averaged local indicator of spatial association index (LISA: X) for individual perennial patches. LISA values greater than zero indicate a positive association between litter and perennial patches, while values less than zero indicate a negative association between litter and the perennial patch. Coarse woody debris patches are indicated in grey triangles ($X_{CWD} = 0.06 \times \ln(\text{patch size}) + 0.44$; $P = 0.70$); Shrub patches are white squares ($X_{shrub} = 0.17 \times \ln(\text{patch size}) - 0.26$; $F_{2, 229} = 3.99$; $P = 0.70$; $R^2 = 0.01$); and trees are indicated by black circles ($X_{tree} = 0.27 \times \ln(\text{patch size}) - 0.68$; $F_{2, 229} = 15.79$; $P < 0.001$; $R^2 = 0.06$). 133

Appendix 4.4. Semi-variogram parameters for litter and perennial patch data for each replicate in each community. All models were spherical. 134

Appendix 5.1. F -ratios and P -values from the ANOVA for each collection interval (1–4) for % organic material remaining. Bl = Spatial blocking term, La = Landform (Dune, Swale), Tr = chemical treatment (F + T, F, T, C), Gr = grass type (*Austrostipa*, *Triodia*), Pi = Pit morphology (echidna, bilby/ bettong). Significant P -values are in **bold**. 173

Appendix 5.2. F -ratios and P -values from the ANOVA for each collection interval (1–4) for mass loss adjusted by rainfall (g mm^{-1}). Bl = Spatial blocking term, La = Landform (Dune, Swale), Tr = chemical treatment (F + T, F, T, C), Gr = grass type (*Austrostipa*, *Triodia*), Pi = Pit morphology (echidna, bilby/ bettong). Significant P -values are in **bold**. 174

Appendix 5.3. The mean (\pm SE) soil infiltration into the litter bags (% inorganic material) over time for each factor. F + T = both fungicide and termiticide, T = termiticide, F = fungicide, C = control. 175

Appendix 5.4. <i>F</i> -ratios and <i>P</i> -values from the ANOVA for % inorganic material. Bl = Spatial blocking term, La = Landform (Dune, Swale), Tr = chemical treatment (F + T, F, T, C), Gr = grass type (<i>Austrostipa</i> , <i>Triodia</i>), Pi = Pit morphology (echidna, bilby/ bettong). Significant <i>P</i> -values are in bold	176
Appendix 5.5. <i>F</i> -ratios and <i>P</i> -values from the ANOVA for modelled decay rates and half life of % organic material. K = Olson's negative exponential decomposition decay rate (days), Bl = Spatial blocking term, La = Landform (Dune, Swale), Tr = chemical treatment (F + T, F, T, C), Gr = grass type (<i>Austrostipa</i> , <i>Triodia</i>), Pi = Pit morphology (echidna, bilby/ bettong). Significant <i>P</i> -values are in bold	177
Appendix 6.1. Plant growth attributes. Mean of each plant growth attribute in relation to Water regime (low, high), Cover (Canopy, Open) and Microsite (Pit, Surface). The 5 % LSD values are given.	204
Appendix 6.2. Summary of the analysis of variance (ANOVA) for soil physical and chemical properties and for measurements of plant growth and leaf chemistry for Microsite, Cover, and Water treatment effects and their interactions. d.f. = 1, 49. Min. = mineralisable.	205
Appendix 6.3. Wald statistics and <i>P</i> -values for main order effects and 2- and 3-way interactions for plant height, number of leaves, no. of stems and length of the longest leaf. d.f. = 1, 56.....	206

Chapter 1. General introduction

Samantha K. Travers

1.1 An introduction to leaf litter dynamics

Deceased organic matter is one of the few features common to all ecosystems on Earth. The (re-)cycling of carbon, nitrogen and other fundamental elements is critical for sustaining life, particularly in ecosystems where these resources are limited. This thesis covers aspects of leaf litter dynamics in a resource-limited semi-arid ecosystem where leaf litter is an important and often overlooked component of ecosystem function. In the following chapters I evaluate the effects of biotic and abiotic drivers on multiple stages of the litter cycle in semi-arid woodland and shrubland communities (Figure 1.1). First however, I highlight the importance of leaf litter as a resource and an important ecological component in these systems.

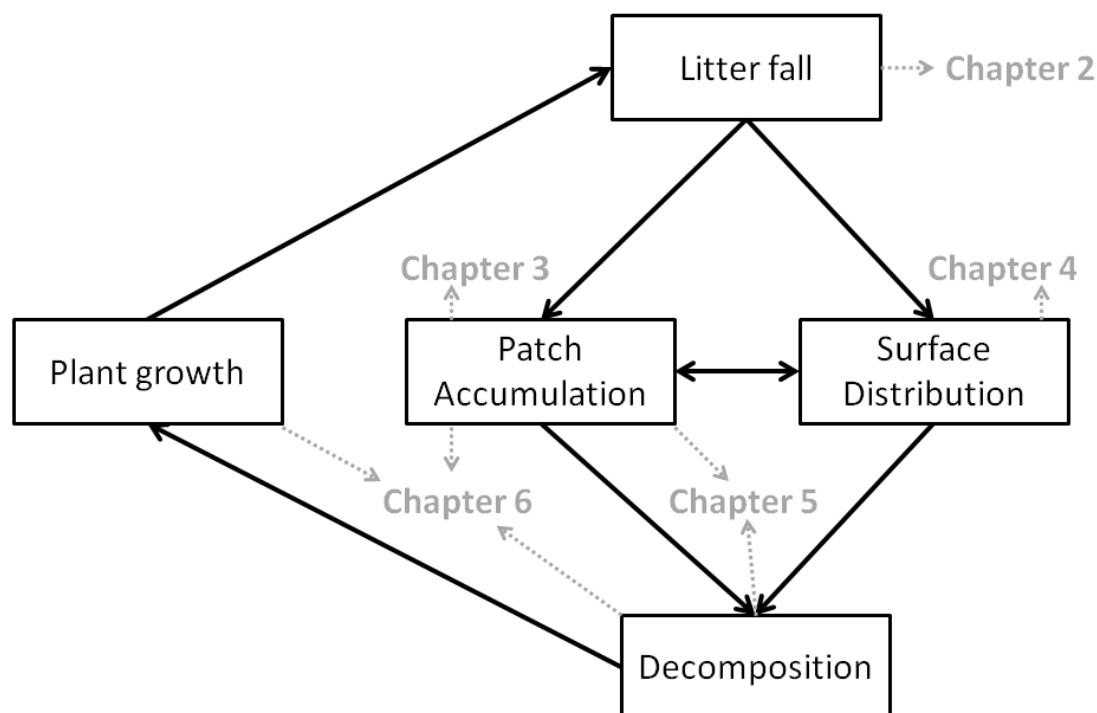


Figure 1-1. Conceptual diagram of leaf litter dynamics. Black arrows indicate the links between the stages of the litter cycle, grey dotted arrows indicate the connection of each stage to chapters in this thesis.

1.1.1 *Broad-scale variability drives resource availability in semi-arid environments*

In arid and semi-arid environments resources are often limited and are highly spatially and temporally variable (Noy Meir 1979). Although there is an abundance of sunlight, productivity in these systems is generally limited by essential resources such as water, carbon, nitrogen and phosphorus and is further inhibited by extreme temperatures, low humidity and high rates of evaporation (Noy Meir 1985; Whitford 2002). Although arid and semi-arid environments are characterised by infertile soils and variable rainfall, these features are particularly accentuated in the arid systems in Africa, South America and Australia when compared to their northern hemisphere counterparts (Morton *et al.* 2011).

Temporal variability in resource availability is largely driven by variation in rainfall (Stafford Smith and McAllister 2008). In arid and semi-arid environments the amount and frequency of rainfall can be highly variable within and among years. The variability of rainfall in Australia's systems is especially unpredictable and is unlike any other continent (Morton *et al.* 2011). In Australia, large inter-annual rainfall events are strongly tied to the patterns of air movements across the Pacific Ocean (Vines 2008). During high rainfall years the extreme increase in water availability creates an abundance of resources which flows through all trophic levels, leading to 'booms' in ecosystem productivity and populations (e.g. Kingsford *et al.* 1999). Once resources are exhausted, productivity and populations rapidly diminish. This creates inter-annual 'boom and bust' cycles of resources, ecosystem productivity and populations of all taxa (Letnic and Dickman 2006). Fire regimes are also linked to these cycles, with increases in ecosystem productivity generating large amounts of potential fuel and increasing landscape connectivity. This leads to an increase in severe fires in response to years of above average rainfall (Bradstock 2010).

1. Introduction

Spatial heterogeneity in resource limited landscapes presents itself at a range of spatial scales and is quite complex in terms of its causes and consequences (Levin 1992; Tongway and Ludwig 1996). At broad landscape scales, resource heterogeneity may occur in response to topographic features and shifts in soil texture across the landscape. Topographic features, such as dunes, create clear distinctions between areas where resources run-off and run-on (Ludwig *et al.* 1999a). In arid and semi-arid systems dominated by dune and swale landforms there is generally repeated patterns of vegetation communities across the landscape. However the dune-swale pattern may be spatially heterogeneous with mega-dunes or prolonged swales (plains) disrupting a seemingly regular pattern. These anomalies can affect the distribution of resources among landforms (Cain *et al.* 1999). Soil texture can further determine the availability of limited resources, particularly the availability of water and nitrogen amongst landforms. Fine-textured soils with high clay content generally have a greater nitrogen content than coarse-textured soils (Li *et al.* 2009). However, in low rainfall, high evaporation conditions the fine textured soils may be less conducive to retaining soil moisture than coarser-textured soils (Noy Meir 1973; Sala *et al.* 1988). There are strong links between plant life forms and their associated soil texture soils. Coarse-textured soils tend to produce taller and denser vegetation than finer textured soils (Noy Meir 1973).

Arid and semi-arid ecosystems also contain an inherently diverse range of vegetation. Typically in ecosystems where resources tend to be limited and unpredictable there tends to be a diverse range of structural and functional adaptations amongst co-existing species (Golluscio and Sala 1993; Westoby *et al.* 2002). These differences tend to relate to resource acquisition and use, allowing co-existing species to efficiently use resources in different spatial and temporal ways. Furthermore, this diversity is hypothesised to reduce inter-specific competition (Campanella and Bertiller 2008). For example, plants may respond to vertical spatial heterogeneity of resources with deep root systems which allow them greater access to more stable water supplies such as groundwater, rather than relying on surface water reserves from recent rainfall.

1.1.2 Resource patch dynamics drive fine-scale heterogeneity

At a smaller spatial scale, arid and semi-arid ecosystems concentrate limited resources into resource-rich patches, further driving the spatial and temporal heterogeneity of resources in these systems (Ludwig *et al.* 1997). A combination of both abiotic and biotic mechanisms contribute to patch formation and patch maintenance (Schlesinger and Pilmanis 1998; Ludwig *et al.* 1999b). For example, small-scale resource patches develop around perennial features in the landscape such as perennial vegetation, logs, rocks and surface depressions where wind and water resources deposit material (Ludwig and Tongway 1996). These discrete resource-rich patches are surrounded by a matrix of relatively bare resource-poor inter-patch areas (Tongway and Ludwig 1996). This configuration maximises the effective use of limited-resources such as water and nitrogen (Ludwig and Tongway 1996).

Perennial vegetation modulates resources by accumulating leaf litter and aeolian sediments and by 'mining' their surrounding matrix for water and soil nutrients. The surface litter provides shelter and foraging substrates for a range of biota, some of which are heavily dependent upon these resources (Shachak *et al.* 2008). The soil patches associated with perennial vegetation attracts soil foraging mammals, whose soil disturbing activities further contribute to the capture and augmentation of resources in these patches (Schlesinger and Pilmanis 1998; Whitford and Kay 1999).

There has been substantial work on the spatial self-organisation of perennial vegetation in arid and semi-arid systems (e.g. Klausmeier 1999; Rietkerk *et al.* 2002; Kefi *et al.* 2007; Pueyo *et al.* 2008; Kefi *et al.* 2010). Most of these studies have described the shapes of patches, and the mechanisms driving the arrangement of vegetation. While the specifics of the proposed mechanisms of spatial self-organisation differ, the general process relates to the dynamics of water, which acts as an important transport mechanism as well as a resource. The movement of water throughout arid and semi-arid landscapes has also been the focus for many studies (Evans and Ehleringer 1994; Eddy *et al.* 1999), given its importance in driving resource

1. Introduction

heterogeneity in these ecosystems. Similarly great attention has also been paid to spatial dynamics of elements such as nitrogen and phosphorus. More conspicuous resources, such as leaf litter, however, have often been overlooked in these systems.

1.1.3 Leaf Litter as an important resource and ecological component

Leaf litter is an important resource and a fundamental component of all terrestrial ecosystems. The cycling of leaf litter is crucial for the cycling of fundamental soil elements and nutrients. The senescence and decay of leaves, bark and other organic material provides a mechanism for carbon, nitrogen and other critical elements to be transported and incorporated into the soil. In arid and semi-arid ecosystems surface litter represents a major store of nutrients (Facelli and Pickett 1991; Moretto *et al.* 2001). Surface litter is also an important ecosystem component, providing shelter, foraging and breeding habitat for a range of arthropods, reptiles and birds (Kelly *et al.* 2010; Haslem *et al.* 2011). The presence of surface litter protects the top soil from wind and water impact and shearing and can also significantly alter soil moisture, light profiles and temperature regimes (Hysell and Grier 1996). This influences the density of invertebrates in mineral soil layer (Doblas-Miranda *et al.* 2007, 2009). In arid systems surface litter can also facilitate seedling germination (Facelli and Ladd 1996).

Elements of the litter cycle are inherently variable, particularly in resource-limited ecosystems with discontinuous canopy cover (Pressland 1982). In any given ecosystem, seasonal variability in the rates of leaf litter production and decomposition, along with episodic deposition and removal give rise to high temporal and spatial variability in the amount of surface litter (Hart 1995; Facelli and Carson 1991). There are clear links between the different stages of the litter cycle. For example, the amount of litter falling, the timing of litter fall, and the chemistry of falling litter control the decomposition and subsequent mineralisation of carbon, nitrogen and many other elements (Campanella and Bertiller 2008).

There is substantial variation in the amount of surface litter between vegetation communities (Hart 1995). The diversity of species and life-forms contributing to the litter pool affects all components of the litter cycle. For example, species differ markedly in their leaf litter chemistry due to differences in mechanical structures, chemical defences, methods of carbon fixation and nutrient conservation strategies (Campanella and Bertiller 2008). These plant strategies can affect the quantity, timing and rate of decay of senescent litter (Cornwell *et al.* 2008).

The surface arrangement of litter is often highly variable (Facelli and Carson 1991), particularly in arid and semi-arid systems (Eddy *et al.* 1999). Unlike mesic environments where surface litter is much more uniformly distributed, the open canopies of semi-arid systems lead to a highly spatially variable arrangement of litter (McElhinny *et al.* 2010). Perennial vegetation is understood to play an important role in determining litter composition and accumulation. Litter patches under trees and shrubs contain different litter components to those that form where perennial vegetation is absent (Martin and Major 2001).

Modelling decomposition in arid environments is complicated by the fact that the predictors of decomposition in mesic environments are not always good predictors of rates of decomposition. Decomposition is typically predicted by rainfall, temperature, the lignin and nutrient content of the decomposing substrate, and the presence of soil fauna. However, studies in arid and semi-arid ecosystems have shown that rainfall frequency (Austin *et al.* 2004), physical fragmentation (Mackay *et al.* 1994), photo degradation (Austin and Vivanco 2006), consumption by soil biota (Santos and Whitford 1981), and soil abrasion (Throop and Archer 2008) play important roles in decay in arid environments (Parton *et al.* 2007). Furthermore, the exposure of decomposing substrates also plays an important role. Buried material tends to decompose more rapidly in arid and semi-arid environments, due to a mediation of microclimatic conditions by the soil (Moorhead and Reynolds 1991; Austin *et al.* 2009).

1. Introduction

1.1.4 Alterations to leaf litter dynamics

Beyond the intrinsic spatial and temporal drivers of heterogeneity in the litter cycle there are other biotic and abiotic drivers that can further exacerbate variability in litter dynamics. Land management regimes may alter grazing and fire frequency and intensity, which directly and indirectly alters the structure and composition of vegetation communities. Such shifts are likely to affect the amount and composition of leaf litter in the system (Lindsay and Cunningham 2009).

Alterations to ecosystem processes provided by organisms may also affect leaf litter dynamics. For example, soil foraging mammals can play disproportionately large roles in the dynamics of leaf litter and nutrients in resource limited ecosystems (Jones *et al.* 1997; Eldridge 2011). Their foraging pits promote the burial of leaf litter and nitrogen-rich aeolian sediments in a depression that also captures water (Whitford and Kay 1999). The combination of soil, moisture and organic substrates provide conditions conducive for fungi and soil biota to interact and rapidly decompose organic material (Elkins and Whitford 1982; Hawkins 1996). Alterations to the populations of soil foraging animals could have substantial impacts on the mechanisms and rate of decomposition, particularly if the loss of soil foraging activities reduces the amount of litter undergoing sub-surface decomposition.

There have been many attempts to link components of the litter fall cycle within given ecosystems. Litter fall rates, forest floor mass and decomposition rates have been combined as measures of ecosystem productivity (Pressland 1982), steady state equilibrium (Turner and Lambert 2002), rates of nutrient cycling, distribution and fluxes (Burrows 1976) or various other ecosystem indices (Olson 1963). Rather than providing a comprehensive measure of litter dynamics for a specific ecosystem, this thesis focuses on the effects of various events and biotically-induced activities on aspects of litter dynamics. We know that events such as inter-decadal rainfall events, fire, shrub encroachment due to prior land clearing and shifts in soil foraging mammals are responsible for redistributing nutrients in ways that can reconfigure the landscape

(Schlesinger and Pilmanis 1998). However there have been few attempts to link these events with aspects of the litter cycle, which is a primary transport medium for the cycling of nutrients. Understanding how various parts of the litter cycle respond to such disturbances is crucial to understanding fundamental components of ecosystem function.

1.2 Thesis objectives

There are many drivers that modulate litter dynamics. The main objective of this thesis is to examine how litter dynamics (Figure 1.1) are moderated by abiotic (e.g. soil, landform, fire, rainfall) and biotic (e.g. vegetation communities, individual species) elements of semi-arid woodlands and shrublands in eastern Australia (Figure 1.2).

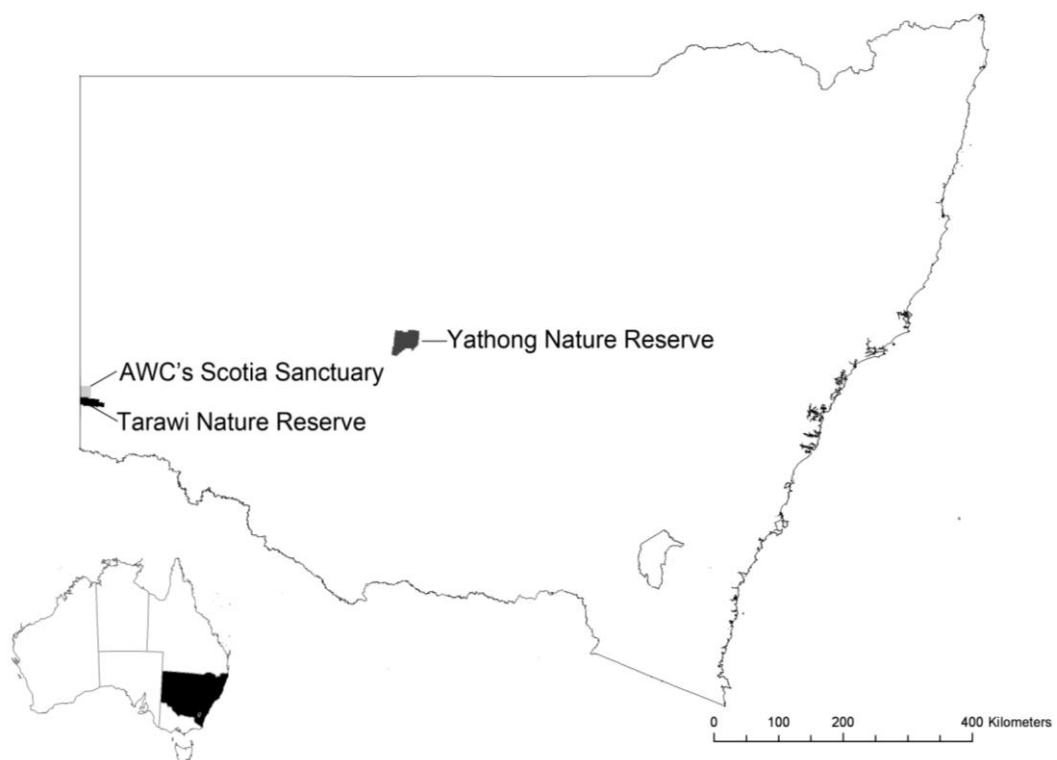


Figure 1-2. Location of study sites in NSW, Australia.

1. Introduction

Chapter 1 provides an overview of the importance of litter as a resource and ecosystem component in semi-arid woodlands, highlighting important findings from previous research on leaf litter dynamics in arid and semi-arid ecosystems.

Chapter 2 focuses on the relative importance of abiotic conditions in driving the litter fall rates of reproductive structures (seeds, flowers and fruits) from three species — two shrub species *Senna artemisioides* subsp. *filifolia* and *Acacia burkittii*, and one tree, *Eucalyptus gracilis*. This chapter monitors the response of these species to relatively fine-scale shifts in meteorological conditions (i.e. rainfall, wind speed, evaporation), to determine the relative importance of these conditions on the litter fall process. We also compared the response of these species between two different landforms to consider the effects of soil texture in moderating this process. This work has been submitted to the “Greening of Arid Australia” special edition of *Austral Ecology*.

Chapter 3 assesses the patch development of surface litter by landscape modulating mallee trees in response to fire. To measure shifts in surface litter in response to fire we compared the litter bed size and composition under two species, *Eucalyptus socialis* and *E. dumosa*, along a 42 year chronosequence of fire histories. This work has been published in *Forest Ecology and Management*.

Chapter 4 examines the evidence for the spatial self-organisation of litter patches across four different woodlands and shrublands. This chapter tests for evidence of scale-dependent feedbacks and disturbance-recovery mechanisms of self-organisation by comparing the cover, patch size and spatial arrangement of litter patches and perennial vegetation patches and assessing their spatial association with each other.

Chapter 5 compares abiotic and biotic interactions involved in the decomposition of litter in native mammal foraging pits. This chapter compares two foraging pit shapes, shallow wide pits created by short-beaked echidnas (*Tachyglossus aculeatus*) and

deeper cylindrical pits created by locally extinct greater bilbies (*Macrotis lagotis*) and burrowing bettongs (*Bettongia lesueur*). Using a litter bag study, this chapter describes how soil texture (landform), rainfall, substrate and the chemical exclusion of termites and fungi affect organic mass loss between the two foraging pit shapes.

Chapter 6 assesses how litter that decomposes under trees and in foraging pits contributes to seedling growth. This study is based on a growth chamber experiment that uses seedling growth of *Dactyloctenium radulans* (Button grass) to compare the individual and combined facilitatory “nurse” effects of short-beaked echidna (*Tachyglossus aculeatus*) foraging pits and the litter patch which accumulates under large trees. The relative effects of our treatments on plant growth are tested by inducing a water stress treatment. This work has been published in *Plant and Soil*.

Chapter 7 provides a summation of the previous chapters and highlights the implications and shortcomings of these novel studies. This chapter also provides direction for future studies in this field.

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1. Introduction

Chapter 2. Increased rainfall frequency triggers an increase in litter fall rates of reproductive structures in an arid eucalypt woodland

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Abbreviations:

AIC — Akaike's Information Criterion

GLM — Generalised Linear Models

PERMANOVA — Permutational Multivariate Analysis of Variance

QAIC — Quasi-likelihood Akaike Information Criterion

SEM — Structural Equation Model

VIF — Variance Inflation Factor



Flowers of *Acacia burkittii* (left), *Senna artemisioides* (top right) and *Eucalyptus gracilis* (bottom right)

2. Fall rates of reproductive structures

2.1 Abstract

The diversity of responses to episodic rainfall events among perennial plant species is critical for the maintenance of ecosystem functions in arid systems. We use a litter fall study to capture the responses of three species to shifts in environmental conditions. We examined the effects of landform, rainfall and other meteorological variables (temperature, evaporation, relative humidity, solar exposure, wind speed and cloud cover) on the mass of reproductive structures falling from two shrubs (*Senna artemisioides* subsp. *filifolia*, *Acacia burkittii*) and one tree (*Eucalyptus gracilis*) species in a eucalypt mallee woodland in semi-arid eastern Australia. Data were collected over three years. The first year received below-average rainfall and the following years received about twice the average annual rainfall. We assessed the relative importance of our explanatory variables, for each species separately, comparing the results using two methods: (1) multi-model inference of a zero-inflated negative binomial generalised linear model, and (2) structural equation modelling. Multi-model inference showed rainfall frequency, at species-specific lag intervals, to be of highest relative importance for all three species. Wind speed was also relatively important for all three species. Structural equation modelling supported these results, with strong, direct path coefficients for the number of days of rainfall in the past 12 months. There was, however, no strong effect of the average rainfall event size. Our analyses demonstrate the strong, direct and positive effect of rainfall, and highlight the importance of rainfall frequency rather than rainfall event size. Furthermore, we found species-specific responses to environmental variables associated with wind, solar exposure and landform, further driving the litter fall of reproductive structures in perennial plants in semi-arid environments. Understanding how different species respond to rainfall and other meteorological conditions can give us greater insights into the capacity of these systems to adapt, which will be important in a changing climate.

2.2 Introduction

The ability of ecosystems to respond to large, infrequent rainfall events and to support irruptions in populations of higher, trophic-level organisms depends on both their functional and response diversity (Ludwig and Tongway 1995; Walker *et al.* 1999; Elmqvist *et al.* 2003). The combination of functional diversity and response diversity is critical for maintaining an adaptive, functional and resilient ecosystem (Walker *et al.* 1999; Elmqvist *et al.* 2003). Functional diversity enhances the ability of an ecosystem to capture and retain critical resources (Ludwig and Tongway 1995). Response diversity (*sensu* Elmqvist *et al.* 2003) is the range of reactions to shifts in environmental conditions among species contributing to the same ecosystem function. These species-specific responses enhance the adaptive capacity of an ecosystem when more than one species contributes to the same functional role within a given ecosystem (Elmqvist *et al.* 2003). Plants exhibit species-specific responses to episodic rainfall events (Westoby 1980). While rainfall generally leads to increases in the productivity of ecosystems, response diversity enhances the way that ecosystems capture and use resources, thereby increasing ecosystem productivity.

Shifts in ecosystem productivity in response to changing meteorological conditions can be assessed by measuring litter fall rates (Pressland 1982). This method works well in deciduous-dominated ecosystems where there are clear growing seasons, but estimating ecosystem productivity is much more complex in systems dominated by evergreen, long-lived perennial plants. In these systems total litter fall is a crude measure of the overall ecosystem response, while the subtle shifts in the composition of senescing litter allows us to monitor species-specific responses. Although perennial plant species vary in how they shed their reproductive structures within years, there is strong inter-annual variability among years, driven by variation in meteorological conditions. Favourable meteorological conditions may induce mass flowering events by increasing the availability of other resources such as nitrogen (Janzen 1971; Kelly and Sork 2002; Liebhold *et al.* 2004) or soil moisture (Pressland 1982; Smaill *et al.*, 2011). Species may respond to favourable meteorological and abiotic conditions in

2. Fall rates of reproductive structures

different ways such as ‘resource matching’ (*sensu* Kelly 1994; Smaill *et al.* 2011), ‘resource switching’ (*sensu* Norton and Kelly 1988), or ‘resource accumulation’ (*sensu* Kelly and Sork 2002). Meteorological conditions may further affect the output of reproductive structures indirectly by altering pollination success. Animal pollinators are strongly aligned with the variable concentration of resources such as nectar and can vary greatly in abundance and behaviour in response to changing weather conditions (Aide 1986; Sampson *et al.* 1995; Martínez–Garza *et al.* 2011).

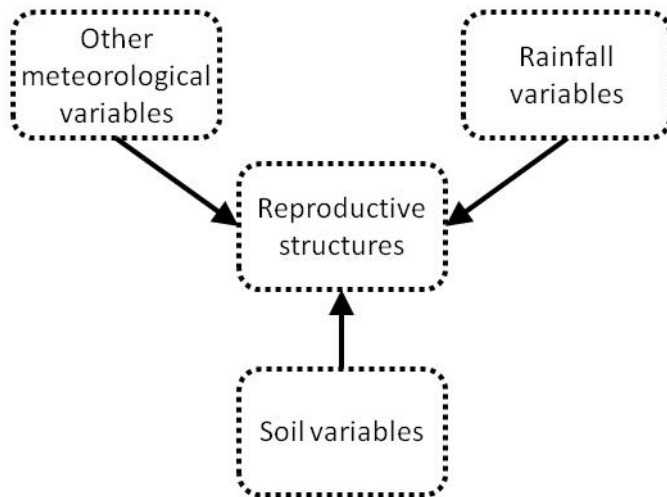
While there has been a heavy focus on the mechanisms, causes, temporal patterns and variability of reproductive structure fall rates between years (Kelly and Sork 2002), there have been few studies that have focused on smaller temporal scale patterns of reproductive structure fall rates. Furthermore, few studies have focused on the degree to which meteorological conditions contribute to intra–annual variability in reproductive structure fall rates and whether these small temporal scales capture a representative measure of response diversity among species. Australia’s arid and semi–arid ecosystems are subject to high inter– and intra–annual variability in rainfall (Morton *et al.* 2011). Between 2010 and 2011, Australia experienced an annual rainfall high, with large parts of arid and semi–arid Australia recording their largest falls for more than 30 years (BOM, 2012). This inter–decadal event created an abundance of surface water and therefore favourable growing conditions (Cookson *et al.* 2006) that are critical for driving ecosystem–wide responses in higher trophic levels (Letnic and Dickman 2006). It also provided a unique opportunity to examine the response of different species to relatively extreme episodic rainfall events and to gauge the role of abiotic conditions in driving fine–scale temporal patterns of senescence.

Here we examine the fine–scale temporal variability of reproductive structure fall rates of three perennial plant species in relation to selected abiotic conditions. We used two modelling approaches that compare the relative importance of our abiotic predictor variables on our response variable, rather than seeking to construct a single predictive model. One method, multi–model inference, uses direct effects only, while structural equation modelling calculates the relative importance of variables using a combination

of direct and indirect effects of our predictor variables on our response variable. We measured landform (as a surrogate for soil and topography), rainfall quantity and frequency, and a range of other meteorological conditions (Figure 2.1a). We measured fall rates of reproductive structures from two shrub species (*Senna artemisioides* subsp. *filifolia* (Benth.) Randall and *Acacia burkittii* F. Muell. ex Benth) and one tree (*Eucalyptus gracilis* F. Muell) species over a period of three years. Annual rainfall was below-average during the first year (2009), and well above-average during 2010 and 2011. We expected the effect of landform to vary between the dry and wet years in line with the Inverse Texture Hypothesis (Noy Meir 1973). The Inverse Texture Hypothesis predicts that under low rainfall (< 500 mm) conditions, coarse-textured sandy soils, typical of our dune landform, would likely be more productive than finer-textured soils (our swale landform), due to the hydrodynamics of evaporation. We expect this to be the case between the years of below- and above-average rainfall.

Given the important role of rainfall in driving ecosystem productivity, we expected that rainfall would be an important driver of reproductive structure fall. Due to the diversity of life histories among our species (Cunningham *et al.* 2011), we expected differential responses to rainfall to be reflected in shifts in litter fall composition. Furthermore, we expected temperature to be a relatively important indicator of reproductive structure fall as a general seasonal cue or as a specific trigger for capsules and legumes to release their seeds (Cunningham *et al.* 2011). In addition, we also considered the relative effects of meteorological conditions related to temperature and water availability by including variables such as wind speed, evaporation, solar radiation, relative humidity and cloud cover in our models. Few litter fall studies have comprehensively considered different meteorological conditions as drivers of litter fall rates. Understanding how different species respond to rainfall and other meteorological conditions gives us better insights into the ability of our ecosystem to adapt, which will be important in predicting the likely effects on plant communities of a changing climate.

(a)



(b)

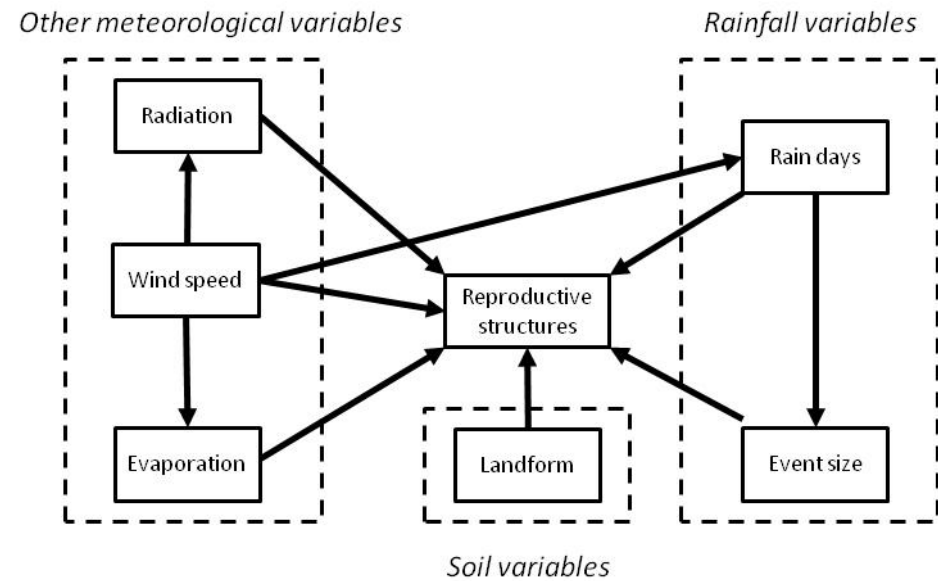


Figure 2-1. a) meta-model and b) conceptual model of the relationships between rainfall variables, other climatic variables, soil variables and the litter fall rate of reproductive structures. Variables in the conceptual model include average rainfall event size in the past 12 months (Event size), number of rain days in the past 12 months (Rain days), cumulative daily solar radiation during each collection window (Radiation), average daily maximum wind speed (Wind speed), average daily evaporation (Evaporation) during each collection window, and categorical landscape location of dune or swale landforms (Landform).

2.3 Methods

2.3.1 Study site

Our study was undertaken within Australian Wildlife Conservancy's Scotia Sanctuary in south western, New South Wales, Australia (33°43' S, 143°02' E). This area is semi-arid, receiving about 251 ± 26 mm annual rainfall based on records since 1995. Rainfall is highly spatially and temporally variable. Winters are mild, with daily mean maximum temperatures of 17 °C and daily mean minimum temperatures of 6 °C in July. Summers are hot with a January mean daily maximum temperature of 33 °C and a mean daily minimum of 19 °C (BOM 2012).

Our study was conducted in dune mallee communities; a low open woodland located on long, low (relief to 7 m) east–west trending sand dunes. Dune mallee is dominated by an overstorey of mallee trees (*Eucalyptus gracilis*, *Eucalyptus dumosa* A. Cunn. ex J. Oxley and *Eucalyptus socialis* F. Muell. ex Miq.) and an understorey of scattered perennial hummock grasses (*Triodia scariosa* N.T. Burb). Shrub cover to 2 m is sparse on the dunes, with widely–spaced individuals of predominantly *Senna artemisioides* subsp. *filifolia* and *petiolaris* Randell, and *Acacia burkittii* (Keith 2004). At our study site, the soils are a mixture of loamy calcareous earths and brownish, siliceous sands both sparsely capped with biological soil crusts. Our specific study area had not been burnt by wildfire in more than 40 years.

2.3.2 Study species

Senna artemisioides ssp. *filifolia* (Fabaceae) is a 1–3 m tall, relatively short-lived (~ 10 years) perennial shrub (Cunningham *et al.* 2011). Small yellow flowers (~ 8 mm) are produced from September to October (Cunningham 2000). The apical anther pores suggest this species is buzz pollinated (Cunningham 2000) however sexual reproduction occurs only rarely with apomictic seeds most commonly produced (Randell 1989; Holman and Playford 2000). Leguminous fruit mature in early

2. Fall rates of reproductive structures

December, with a pod size of 2–8 cm long (7–9 mm wide) containing 10–15 seeds.

Senna is a prolific seeder known to respond rapidly to rainfall and is recognised as an invasive native scrub in areas of altered grazing and fire regimes (Cunningham *et al.* 2011).

Acacia burkittii (Fabaceae) is a perennial shrub that can grow up to 4m tall and live up to 250 years (Crisp and Lange 1976). Small (8–10 mm) bright yellow flowers are produced between July and October with male and bisexual flowers produced in each head (Cunningham *et al.* 2011). *Acacia burkittii* flowers do not produce nectar, though their phyllode glands do. This attracts ants, bees, butterflies, wasps, beetles and other insects which are likely responsible for pollination. Seeds are produced in papery pods 5–12 cm long (5–7 mm wide) and are dispersed by ants and birds from the legume, which opens under hot summer temperatures (Cunningham *et al.* 2011). Population studies by Crisp and Lange (1976) suggest that reproduction by seed is continuous and neither droughts nor large rainfall events appear to have influenced regeneration at sites monitored between 1925 and 1970 at Koonamore station.

Eucalyptus gracilis (Myrtaceae) is a mallee (multi-stemmed) tree that grows approximately 8 m tall and lives for hundreds of years. Creamy white flowers are produced generally between April and October (Cunningham *et al.* 2011), however flowering events have been reported during November, February and March (Paton *et al.* 2004; Pestell and Petit 2007; Marrant *et al.* 2010). *Eucalyptus gracilis* is pollinated by a variety of birds (Paton and Ford 1977) and small mammals such as the western pygmy possum (*Cercartetus concinnus*, Marrant *et al.* 2010), and is an important resource for South Australian apiarists (Paton *et al.*, 2004). *Eucalyptus gracilis* produces fruits which are ovoid to urceolate shape; 4–7 mm long and 3–5 mm in diameter (Cunningham *et al.* 2011). Eucalypt species are generally serotinous with limited seed fall except in response to fire (Lamont *et al.* 1991).

2.3.3 Sampling Design

Litter fall was collected in standing litter traps between December 2008 and July 2011. Each litter trap consisted of a collection unit suspended in a steel frame 1 m above the ground. Collection units were UV-resistant mesh conical bags with a collection area of 0.07 m² and a mesh aperture of 2 mm². Litter traps were placed at fifteen sites within a 37 km² grazing-free enclosure. At each site, our selected species were sampled on two different landscapes, (1) a dune crest (dune) and (2) the base of the dune (swale) with a total of six litter traps per site ($n = 90$).

Traps were emptied approximately once every five weeks for 36 months (total 29 collections). Collected material was oven dried at 60 °C for 24 hrs and sorted into seven categories and weighed. Categories included *Eucalyptus* leaves, *Acacia burkittii* phyllodes, *Senna artemisioides* ssp. *filifolia* leaves, non-target species leaves, sticks and bark of all woody species, reproductive structures of all species (flowers, seeds, fruit, etc.) and 'other' (typically frass, invertebrates and faecal pellets). This study focuses on the reproductive structures only.

We converted the total capture of reproductive structures to an average fall rate (g m⁻² day⁻¹) to adjust for differences in the interval between sampling. The fall rate was multiplied by 10 000 and rounded to the nearest whole number prior to analyses, which require the response variable to be positive integers. Rainfall and other meteorological data for the 15 sites were collected on-site and supplemented with other meteorological data from nearby weather stations (BOM 2012).

Meteorological observations were used as explanatory variables, along with landform (dune, swale) and year (2009, 2010, 2011), for each collection window. Averaged, cumulative and extreme (i.e. minimum and maximum) values were calculated for the following categories of daily meteorological conditions: temperature (both minimum and maximum), evaporation, wind speed, relative humidity (at 9am and 3pm), cloud cover (at 9am and 3pm) and solar exposure. Additionally, for rainfall data, the average

2. Fall rates of reproductive structures

and cumulative rainfall, average event size and number of rain days were calculated for each collection window and for extended windows of the previous 1, 2, 3, 4, 5, 6, 8 and 12 months to account for possible lag effects.

2.3.4 Annual production rates of reproductive structures

We analysed the annual reproductive structure fall rates using a two-factor Permutational Analysis of Variance (PERMANOVA; Anderson *et al.* 2008). We compared the effects of year (fixed) and landform (fixed) on average annual litter fall rates ($\text{g m}^{-2} \text{ day}^{-1}$) for each species separately. Data for each species were transformed using a Euclidean resemblance matrix and analysed with 9999 permutations with Type III error. Analyses were performed in the +PERMANOVA package for PRIMER (Anderson *et al.* 2008).

2.3.5 Generalised linear modelling and multi-model inference

We analysed reproductive structure fall rates using separate generalised linear models (GLMs) for each of our three species. A full description of the modelling process is given in Appendix 2.1. We used a zero-inflated model with a negative binomial error structure ('pscl' package version 1.03.10 in R version 2.15.1; Zeileis *et al.* 2008; Jackman 2011; R Core Team 2012) and Akaike's Information Criterion (AIC) to select the best measurement for each meteorological condition, or the best lag interval for the rainfall measurements, as a representative explanatory variable for our final model (Anderson *et al.* 2001; Zuur 2009). To reduce collinearity, only some categories of meteorological conditions were represented in the final candidate set of explanatory variables for each species (Appendix 2.2).

To determine the relative importance of the meteorological conditions on reproductive structures for each species, we used multi-model inference (Burnham and Anderson 1998; Burnham *et al.* 2011). Due to the over-dispersed nature of our data, we calculated the Quasi-likelihood Akaike information criterion (QAIC) as an

indicator of model parsimony. Models were ranked by their QAIC criterion and we computed the differences (Δ_i) between the QAIC of the candidate models and the QAIC of the best model (lowest QAIC) (Anderson *et al.* 2001; Zuur 2009). Model averaging was conducted on models with $\Delta_i \leq 10$ as this is the model set with strongest support, however for brevity we only present $\Delta_i \leq 2$ (Appendix 2.3, 2.4 and 2.5; Burnham and Anderson 1998; Anderson *et al.* 2001).

2.3.6 Structural Equation Modelling

We used Structural Equation Modelling (SEM) to test and parameterise an *a priori* conceptual model illustrating the causal relationships among a set of environmental variables (Shipley 2000) predicted to influence the mass of reproductive structures falling from woody plants. Our SEM models are presented graphically by means of arrows (pathways) with associated standardised path coefficients that describe the precision of the relationship between two variables of interest. The path coefficient is equivalent to a regression weight or partial correlation coefficient. Path coefficients were estimated using a maximum-likelihood algorithm, and overall model fit was tested using a χ^2 goodness-of-fit test. Non-significant χ^2 values ($P > 0.05$) indicate that the predicted covariance structure from our *a priori* model does not deviate significantly from our observed covariances (Iriondo *et al.* 2003). We examined correlations among the potential predictors which we had previously identified from linear GLM models. These variables were \log_{10} transformed, where appropriate, to improve linear relationships among them. Separate models were developed for the three woody species because we expected the causal relationships among variables to be strongly species-specific. Landform (dune, swale) was converted to an ordinal variable prior to analyses. Our model posits that climatic variables (radiation, wind speed, relative humidity) and rainfall variables (event size, number of rain days) will have both direct and indirect effects on the fall rates of reproductive structures (Figure 2.1b). We compared the relative strength of these factors by considering all direct and indirect effects as a measure of their total standardized effects on the response. Modelling was performed using AMOS 20.0 software (SPSS).

2.4 Results

Total annual rainfall during the study varied markedly among years. Total annual rainfall in 2009 (195 mm) was below average, but during the following two years, almost twice the average annual rainfall for the site was received in each year, with 481 mm falling in 2010 and 455 mm falling in 2011.

Over the period of the study we recorded a general increase in the fall rate of total litter and reproductive structures; and an increase in the relative proportional mass of reproductive structures of total litter fall (Table 2.1, Figure 2.2). For all species, the fall rate of reproductive structures peaked during the 2010–2011 summer (Dec–Feb) but the specific changes varied among the three species (Figure 2.2). The average annual litter fall rate of reproductive structures for *Eucalyptus gracilis* was five–times greater in 2011 than 2009 (Year: Pseudo- $F_{2, 864} = 29.74$; $P < 0.001$; Table 2.1). For *Senna artemisioides*, the 2011 reproductive structure fall rate was 28–times greater than in 2009 (Year: Pseudo- $F_{2, 864} = 33.08$; $P < 0.001$). For *Acacia burkittii* the reproductive structure fall rate peaked in 2010, and was 70–times greater than 2009 (Year: Pseudo- $F_{2, 864} = 19.31$; $P < 0.001$; Table 2.1). Our multi–model inference also yielded similar results. For all three species, the coefficients for the years 2010 and 2011 were both

Table 2.1. Mean (\pm SE) annual reproductive structure fall rate ($\text{g m}^{-2} \text{day}^{-1}$) and proportional mass (% fraction of the total litter fall for each year) for the three species. Significant differences among years are indicated for each species.

Year	<i>Senna artemisioides</i>		<i>Acacia burkittii</i>		<i>Eucalyptus gracilis</i>	
	$\text{g m}^{-2} \text{day}^{-1}$	%	$\text{g m}^{-2} \text{day}^{-1}$	%	$\text{g m}^{-2} \text{d}^{-1}$	%
2009	$0.007 \pm 3.2\text{E}^{-3} \text{ a}$	2.7	$0.003 \pm 5.8\text{E}^{-4} \text{ a}$	1.5	$0.017 \pm 2.4\text{E}^{-3} \text{ a}$	8.5
2010	$0.196 \pm 2.7\text{E}^{-2} \text{ b}$	35.5	$0.210 \pm 4.1\text{E}^{-2} \text{ b}$	56.7	$0.023 \pm 2.9\text{E}^{-3} \text{ a}$	7.9
2011	$0.202 \pm 2.3\text{E}^{-2} \text{ b}$	26.7	$0.170 \pm 2.3\text{E}^{-2} \text{ b}$	40.3	$0.087 \pm 9.5\text{E}^{-3} \text{ b}$	13.7

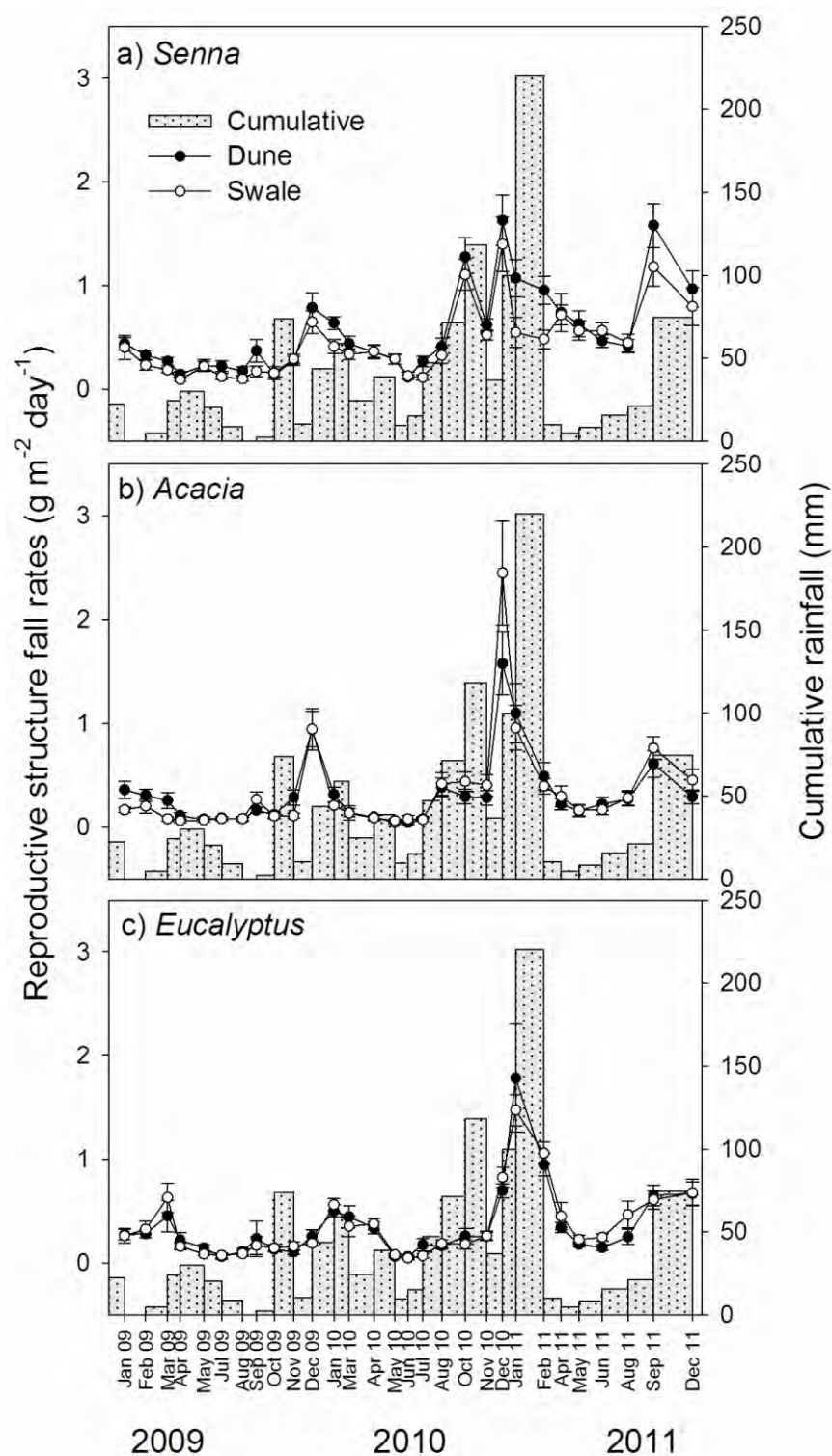


Figure 2-2. Fall rates of reproductive structures for a) *Senna artemisioides*, b) *Acacia burkittii*, c) *Eucalyptus gracilis* for 2009, 2010 and 2011. The histogram represents cumulative rainfall for each collection window.

2. Fall rates of reproductive structures

greater than 2009 (Appendix 2.6). The litter fall rate of reproductive structures was disproportionate to other components of litter fall, with the relative proportional mass of reproductive structures also increasing throughout the study (Table 2.1).

The litter fall rates of reproductive structures for the two shrub species were not significantly different between the two landforms (*Senna artemisioides*: $P = 0.35$; *Acacia burkittii*: $P = 0.051$). However there were much greater litter fall rates of *Eucalyptus gracilis* reproductive structures in the swale in 2009 and 2011, but no difference in fall rates between the two landforms in 2010 (Year by Landform interaction: Pseudo- $F_{2,864} = 9.31$; $P < 0.001$). Again this was also supported by our multi-model inference and structural equation modelling (see below). Our multi-model inference found landform to be relatively important for *Eucalyptus gracilis* (Table 2.2), with the model averaged coefficient showing eucalypts growing in swales produced more reproductive structures than those growing on dune crests (Table 2.2, Appendix 2.6).

Across all three species we found that the number of rain days was the strongest variable determining the fall rates of reproductive structures with the relative importance of rain days greater than 0.9 for one or both parts of the models (Table 2.2). However, there were differences between the species in the optimal lag interval for the number of rain days. The relative importance of the remaining variables was species-dependent. Cumulative solar exposure was the second most important variable identified by the model averaging procedure for *Senna artemisioides*, while average maximum wind speed was the second most important variables for both *Eucalyptus gracilis* and *Acacia burkittii* (Table 2.2). Details of the coefficients for the top model (QAIC_{min}) for each species are given in Appendix 2.6.

Variables	Relative Importance	
	Part 1	Part 2
<i>Senna artemisioides</i>		
Rain days 8 mth	0.47	1.00
Solar exposure (cum.)	0.87	0.49
Wind speed (max)	0.55	0.44
Rain event Size 12 mth	0.39	0.35
Year	0.57	0.17
Cloud cover (9am)	0.36	0.31
Landform	0.28	0.28
<i>Acacia burkittii</i>		
Rain days 4 mth	1.00	0.96
Wind speed (max)	0.74	0.33
Cloud cover (9am)	0.55	0.30
Rain event Size 12 mth	0.36	0.49
Maximum temp. (avg)	0.29	0.49
Year	0.35	0.29
Landform	0.27	0.35
<i>Eucalyptus gracilis</i>		
Rain days 12 mth	0.92	0.89
Landform	0.68	0.60
Wind speed (max)	0.73	0.28
Solar exposure (cum.)	0.37	0.60
Minimum temp. (avg)	0.25	0.57
Rain event Size 12 mth	0.33	0.29
Cloud cover (3pm)	0.34	0.24
Year	0.17	0.19

Table 2.2. The relative importance of the variables for each species for each model part. Zero-inflated models contain two parts. Part 1 explanatory variables explain the negative binomial–distributed “count” data (zeros and non–zeros), while Part 2 explanatory variables are for the additional zeros in a binomial distribution.

2. Fall rates of reproductive structures

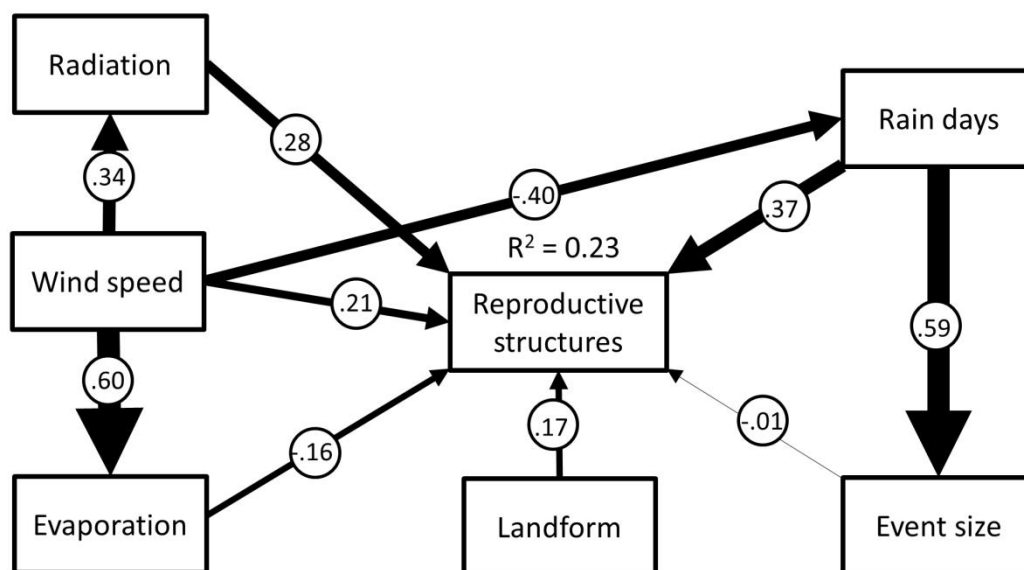


Figure 2-3. Structural equation model for *Eucalyptus gracilis*. Path width indicates the relative strength of the relationship, as indicated by the path coefficient. The overall model explained 23 % of the variance in the litter fall rates of reproductive structures (\log_{10} scale; d.f. = 6; Chi-square = 4.83; $P = 0.56$), as indicated by the R^2 value. The results for the two shrub species are given in Table 2.3.

Our structural equation models also indicated that the number of rain days had the strongest direct effect on the fall rate of reproductive structures (Figure 2.3; Table 2.3). For *Acacia burkittii*, average daily evaporation had an equally strong direct positive effect as the number of rain days (Table 2.3). The indirect effect of wind speed mediated by evaporation (indirect pathway coefficient = 0.27) was also relatively strong for *Acacia burkittii*. For *Eucalyptus gracilis* and *Senna artemisioides*, cumulative solar exposure was strongly positively related to reproductive structure fall rates, consistent with the results of our multi-model inference for *Senna artemisioides*. Landform had a strong direct effect on reproductive structure fall rates for *Eucalyptus gracilis*, but not for *Senna artemisioides* or *Acacia burkittii*, which is again consistent with our multi-model inference and annual averaged litter fall rates. The total standardized effects of our abiotic variables show that rain days in the past 12 months had the strongest total (direct and indirect) effect on the fall rate or reproductive

structures across all three species (Table 2.4). The total standardized effect was also relatively high for evaporation for *Acacia burkittii* only. Overall, our structural equation models explained 23 %, 23 % and 21 % of the variation in reproductive structure fall rates for *Eucalyptus gracilis*, *Senna artemisioides* and *Acacia burkittii*, respectively.

Table 2.3. Pathway coefficients for the Structural Equation Models (from Figure 2.3) for all species. Remaining path coefficients for the three models were the same.

Pathway	<i>Senna artemisioides</i>	<i>Acacia burkittii</i>	<i>Eucalyptus gracilis</i>
Rain days → Reproductive structures	0.34	0.46	0.37
Rain event size → Reproductive structures	0.09	0.06	−0.01
Radiation → Reproductive structures	0.17	−0.29	0.28
Wind speed → Reproductive structures	0.13	0.09	0.21
Evaporation → Reproductive structures	0.06	0.45	−0.16
Landform → Reproductive structures	−0.03	0.07	0.17
Model R²	0.23	0.21	0.23

Table 2.4. Total Standardized Effects for the Structural Equation Models (from Figure 2.3 and Table 2.3) for each species.

Predictor	<i>Senna artemisioides</i>	<i>Acacia burkittii</i>	<i>Eucalyptus gracilis</i>
Rain days	0.396	0.493	0.364
Rain event size	0.089	0.063	−0.008
Radiation	0.170	−0.287	0.279
Wind speed	0.066	0.071	0.064
Evaporation	0.061	0.455	−0.162
Landform	−0.030	0.071	0.166

2.5 Discussion

Our study showed that rainfall frequency (i.e. the number of days of rainfall) was consistently the strongest predictor of the mass of reproductive structure collected in the litter traps, despite marked differences in the response (*sensu* response diversity; Elmqvist *et al.* 2003) of our three woody plants. Although rainfall has been identified as an important driver of variation in litter fall rates (Pressland 1982), other meteorological conditions also contributed to variation in fall rates of reproductive structures among our three species. From the meteorological conditions we considered, only average maximum wind speed was an important predictor for all species. The relative importance of other rainfall measurements, meteorological conditions and landform varied substantially among our three species. Below we describe how the different species responded to altered meteorological conditions, and how this may relate to idiosyncratic responses of individuals to episodic rainfall events.

2.5.1 Rainfall frequency affects fall rates of reproductive structures

Rainfall frequency was more indicative of the response of each species than rainfall event size, or average or cumulative rainfall. An increase in rainfall frequency creates an increase in conditions that are conducive to soil biological activity, which enhances nitrogen mineralisation and therefore the availability of soil nitrogen (Walse *et al.* 1998; Paul *et al.* 2003; Sinclair 2005). However, increases in soil productivity from increased rainfall are heavily dependent upon soil texture (Noy Meir 1973). Although neither soil moisture nor soil texture were explicitly measured in our study, we did account for broad variations in soil texture and microtopography by assessing the response of our model plants across two landforms that differed markedly in soil texture and therefore, water holding capacity. We used these differences in soil texture between years of above– and below–average rainfall to measure the effects of the Inverse Texture Hypothesis (*sensu* Noy Meir 1973). Landform, however, was only significant for *Eucalyptus gracilis*, with greater litter fall rates of reproductive

structures in swale sites than dune sites during 2009 and 2011. *Acacia burkittii* followed similar trends, with swales more productive across all years, though the difference was not great enough to be significant.

The Inverse Texture Hypothesis holds that finer (more clay) soil textures such as those at our swale sites would retain more water near the surface. In contrast, rainfall on coarse-textured (more sandy) soils such as those at our dune sites, freely drains to deeper soil layers. Near-surface water retention is favourable for plant growth in wetter years, but during drier years evaporates quickly, resulting in lower ecosystem productivity compared with coarser soils (Noy Meir 1973). This trend, however, was not apparent in our data. Given the topographic location of swales, they would also have benefited from runoff from the dunes, and conceivably, their lower elevation positions would give plants a greater access to groundwater (Eberbach 2003).

2.5.2 Fall rates of reproductive structures vary among species

The fall rate of abscised reproductive structures of our three species varied both within and among years. Within a given year, the fall rates of reproductive structures followed similar seasonal patterns. The fall rates of both *Senna artemisioides* and *Acacia burkittii* consistently peaked during August–October and again in December. The earlier peaks likely correspond to flower fall, while the December peaks are likely due to fruit fall (Cunningham *et al.* 2011). The fruits of these species likely contribute to greater bulk mass than if seeds alone were released from fruits that remain on the plant. *Eucalyptus gracilis*, however, produced only a single peak in the fall rates of reproductive structures during late summer. While the timing of these peaks was consistent for each species among the three years, there were large inter-annual differences in amount of material these peaks represent.

The magnitude of response of each species differed greatly among years. *Senna artemisioides* appeared to mirror rainfall, with reproductive structure fall rates exaggerated in quantity and proportional composition during the years of above–

2. Fall rates of reproductive structures

average rainfall (2010, 2011). Given the apomictic nature of *Senna artemisioides* (i.e. asexual reproduction; Randell 1989; Holman and Playford 2000), there are likely to be relatively few constraints on the turnover rates of flowers to seeds. This supports the previous findings of research showing that *Senna artemisioides* is a prolific seeder during periods of high rainfall (Cunningham *et al.* 2011), and may suggest a strategy of ‘resource matching’ for this species (Kelly 1994; Kelly and Sork 2002). However, to confirm this, further information on vegetation growth and reproductive material produced each year would be needed. It is also important to consider that material would not necessarily fall within the year that it was produced.

There were high fall rates of reproductive structures from *Eucalyptus gracilis* during the 2010–2011 summer. However, unlike the shrubs species, there was only a small increase in the proportion of reproductive material falling between years. Previous studies show evidence of inter–annual variability in flowering for *Eucalyptus gracilis* (Paton *et al.* 2004) and other eucalypt mallees (Burrows and Burrows 1992; Paton *et al.* 2004), consistent with our data. However previous litter fall studies in mallee have found that light seed rain occurs throughout the year, rather than, as we found, a single peak (Wellington and Noble 1985). It is possible that this single peak in reproductive structures is due to physical damage from relatively large vertebrate pollinators (Burrows and Burrows, 1992) such as the western pygmy possum (Morrant *et al.* 2010). For *Eucalyptus gracilis* only, we found that peaks in reproductive structure abscission coincided with peaks in fall rates of non–plant material (i.e. scats and insects, S. Travers, unpublished data, 2012), providing strong circumstantial evidence for higher visitation rates during this period.

While many species show inter-annual variability in their reproductive output, it is likely that when the variability in fall rate of reproductive structures exceeds that of weather conditions alone, as observed in *Acacia burkittii*, other factors are likely driving the variation in fall rates (Koenig and Knops 2000; Kelly and Sork 2002). We found that the peak in reproductive structure fall rate for *Acacia burkittii* during December 2010 was much greater than that in December 2009 or 2011, despite similar

rainfall during 2010 and 2011. Although we found strong relative effects of rainfall frequency on reproductive structure fall rates, there are many possible reasons for this observed trend. For example, nitrogen reserves may have been exhausted during the 2010 production of reproductive structures; the slow growth rate of this species and year of relative fast growth (2010) may render it unable to maintain the same growth rate in the following year despite optimal rainfall; there may have been insufficient temperatures during the study window to trigger the 2012 seed fall; or there may have been sub-optimal climatic conditions during floral development, leading to a reduced output in December 2011 (Davies 1976; Smaill *et al.* 2011). While we found a strong relative importance of rainfall on the fall rate of *Acacia burkittii* reproductive structures, and the relatively largest increase between 2009 and 2010 of the three species, there may not be successful conversion from increased seeds to increased seedlings.

Previous studies have shown that the regeneration of *Acacia burkittii* does not increase after years of above-average rainfall, nor is its regeneration adversely affected by drought (Crisp and Lange 1976; Woodell 1990). The quality of seeds produced in years of high seed production may be low, leading to fewer successful germinations. Alternatively, there may be important post-seedfall ecological processes that differ in response to rainfall. For example, the elaiosome attached to *Acacia* seeds makes them particularly susceptible to removal by ants, with previous studies in mallee communities reporting high proportions of surface seed loss due to ants (65–100 % removed; Wellington and Noble 1985; Andersen 1987). While it is unclear whether this removal is predatory or facilitatory for seedling growth, the activity of ants may not differ substantially in response to rainfall, contributing to a lack of continuous, rather than pulsed, rainfall-driven regeneration of *Acacia burkittii*.

Temporal scale is important to consider when monitoring rates of change over time. Litter fall studies are commonly used as an indicator of annual ecosystem productivity (Olson 1963; Carneiro *et al.* 2009), monitoring the response of species to shifts in resource availability between years. Similarly, the production of reproductive

2. Fall rates of reproductive structures

structures is considered to be the reproductive effort of an individual when considered as a fraction of total biomass production over the scale of a growing season or year. In systems where plants are predominantly deciduous, the production and reproductive effort within a growing season has a clear cycle with calculable reproductive effort. However in systems where long-lived evergreen species dominate, such as the one we have studied, the link between vegetative production and fall rates are temporally disjunct within and between years. The whole production, growth and senescence process can be attributed to various aspects of rainfall and other meteorological conditions. For example, the production of new material may be dependent upon conditions such as temperature and nitrogen availability during resource priming in the previous year (Smaill *et al.* 2011). Determining rates of abscission however, in relation to abiotic conditions, as we have done in this study, is further complicated by the length of time at which structures remain on the plant. Some structures, such as reproductive structures may remain on the plant for much shorter time spans than other plant structures such as leaves, complicating calculations of reproductive effort or ecosystem productivity. Here we demonstrated that at small temporal scales, meteorological conditions, particularly rainfall contribute to variability in litter fall rates among species. However it is important to note that the inherent differences among species still account for much of the inter-species variation in fall rates, with our models including abiotic conditions explaining no more than 23 % of the variation in reproductive structure fall rates. The relationships with abiotic conditions will be dependent on the time scale over which fall rates were calculated. When fall rates are averaged over large time scales, such as a year, the drivers of small scale temporal variability such as daily maximum wind speed will be of less importance. However, we found that when fall rates are measured at temporal scales relevant to the effects of small-scale temporal drivers, the effects of larger temporal scales such as year become much less relevant. The exceptions to this in our data were the lag intervals in rainfall. Rainfall in the previous months was relatively more important than the measures of rainfall during litter fall collection windows. It is likely that rainfall is an indicator for the amount of reproductive material produced.

2.5.3 Wind and other meteorological conditions affect the fall rate of reproductive structures

Average maximum wind speed was a relatively important explanatory variable for all three species. This is likely due to the physical force of wind inducing litter fall in pre-abscission or abscising structures. Relatively few studies have considered the effects of wind on litter fall rates (Staelens *et al.* 2003), with most litter fall studies concentrating on the effects of rain, solar exposure and temperature. This is likely due to the larger temporal scales of these studies, with variability in maximum wind speed over a few weeks likely not significantly impacting annual fall rates.

We expected temperature to be correlated with seed fall of *Acacia burkittii* as these leguminous fruits require high temperatures to open (Cunningham *et al.* 2011). Rather, we found that average daily evaporation was more important in our models, suggesting that evaporation is a more biologically relevant indicator of seed fall than temperature. Given that high evaporation rates coincide with high temperatures, evaporation is likely more biologically relevant when evaluating heat or moisture stress induced on plants in hot, dry conditions, as moisture stress appears to be the precursor to seed fall. Temperature is also considered important for seed fall in *Eucalyptus* species *sens. lat.*, as heat induces capsule dehiscence and fall, though this is generally in response to fire (Lamont *et al.* 1991). We found average minimum temperature was moderately important in explaining the excess zero part of our model. This is due to few reproductive structures of *Eucalyptus gracilis* falling during cold months.

Solar exposure was also an important indicator of the loss of reproductive structures, for both *Senna artemisioides* and *Eucalyptus gracilis*, supporting previous studies on productivity (Cunningham 2000; Whitehead and Beadle 2004). For example, Cunningham (2000) showed that *Senna artemisioides* produced larger amounts of flowers and fruits in fragmented landscapes by using its high water use efficiency to capitalize on the enhanced light availability.

2. Fall rates of reproductive structures

Without measuring vegetative growth, it is difficult to assess how variations in fall rates between years reflect species responses to annual shifts in resources. However by understanding how abiotic conditions may contribute to variability in fine-scale fall rates of reproductive structures within a year, we may be able to interpret species responses to both inter- and intra-annual variability in abiotic conditions. This study has linked variation in litter fall rates to current weather variables that are used in climate prediction models. These meteorological conditions are also likely to change given predicted climate scenarios (i.e. shifts in rainfall frequency, greater temperature extremes, and shifts in cloud cover and atmospheric vapour; IPCC 2007). While there have been relatively few attempts to monitor biological interactions with shifts in fine-scale meteorological conditions, there have been many studies which have concluded that shifts in climate might be important for small-scale ecological processes (Morton *et al.* 2011; Wang *et al.* 2012).

2.5.4 *The importance of response diversity and episodic events*

Inter-annual variability in reproductive effort, whether due to resource matching or other reproductive response strategies, is prevalent in long-lived plants that can afford to have low reproductive output in some years (Kelly 1994). The advantage of inter-annual variability in the rate of fall of reproductive structures has been attributed to numerous factors including pollinator efficiency (Nilsson and Wastljung 1987), predator satiation (Janzen 1971), differences in seed dispersal modes and resource availability (see Herrera *et al.* 1998; Kelly and Sork 2002; Koenig and Knops 2005).

There is evidence that increased reproductive effort during years of above-average rainfall is critical for the long-term survival of many plant species. Large fall rates of reproductive structures over short time periods can lead to large pulses in the availability of nitrogen-rich substrates being incorporated into the soil and may increase the availability of seeds, and broad-scale germination and regeneration of these species. Wotton and Flannigan (1993) demonstrated that large episodic rainfall

events were important for the establishment of pearl bluebush (*Maireana sedifolia* (F.Muell.) Paul G.Wilson) as specific conditions were required for flowering, fruiting, germination and establishment.

The response of the vegetation to episodic rainfall events can vary widely among species, as we have demonstrated in this study. Soil, rainfall and other meteorological conditions (Figure 2.1) combine to trigger a diversity of responses in our plants, which in turn, likely affects ecosystem productivity and diversity. From a functional perspective, response diversity within a given functional role boosts the capacity of an ecosystem to adapt and maintain critical ecosystem functions that are necessary for the maintenance of ecosystem resilience (Elmqvist *et al.* 2003). By understanding how various components of an ecosystem respond to abiotic conditions, we gain greater insights into the adaptive capacity of an ecosystem. This knowledge helps us to better understand the likely impacts of changes in meteorological conditions as a result of a changing climate.

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2. Fall rates of reproductive structures

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2. Fall rates of reproductive structures

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2. Fall rates of reproductive structures

Zuur, A.F., Ieno, E. N., Walker, N. J., Saveliev, A. A., Smith, G. M., 2009. *Mixed Effects Models and Extensions in Ecology With R*. Springer Science and Business Media. New York.

Appendix 2.1. Details of our generalised linear modelling and multi-model inference.*Generalised linear modelling*

We analysed reproductive structure fall rates using a separate generalized linear model (GLM) for each of our three species. To account for the large number of zeros in our response variables we used a zero-inflated model with a negative binomial error structure ('zeroinfl' function in the 'pscl' package version 1.03.10 in R version 2.15.1; Zeileis *et al.* 2008; Jackman 2011; R Core Team 2012). Zero-inflated models are two-part models that simultaneously estimate the data (zeros and non-zeros) using a negative binomial distribution, as well as the additional zeros, which would not be explained by the negative binomial distribution, in a binomial error structure. The negative binomial error structure allows for greater over-dispersion in the data than the Poisson error structure (Zuur 2009). To select the appropriate error structure for each species, we ran every possible explanatory variable as a single predictor for each model part and for both model parts separately of the zero-inflated model, for each species. We first ran these models with a Poisson error structure and a 'log' link function (Zuur 2009). We then repeated this process with the negative binomial error structure with a 'log' link function. We selected the negative binomial error structure models over Poisson error structure models as the former consistently produced more normally distributed homogeneous residuals and lower Akaike's Information Criterion (AIC) values than the Poisson models, for all explanatory variables for all species (Zuur 2009). This process was also used to select the best measurement for each meteorological condition as a representative explanatory variable for our final model.

Explanatory variables were selected using the standard model selection methods (see Zuur 2009). Akaike's Information Criterion (AIC) were calculated for each single predictor model and the measure with the lowest AIC was selected to represent that meteorological condition. For rainfall data, the AIC was used to select the best rainfall lag interval for each rainfall measurement. All representative meteorological explanatory variables for each species were tested for collinearity. To avoid overfitted

2. Fall rates of reproductive structures

models, and to reduce collinearity, not all categories of meteorological conditions were represented in the final candidate set of explanatory variables for each species (Burnham and Anderson 2002). As correlation coefficients only show pairwise correlations, we used variance inflation factors (VIF) to determine which explanatory variables are collinear and should be dropped (Zuur 2009). All terms were included and dropped one by one until all remaining VIF values were less than three (Appendix 2.2).

Multi-model inference

For each species, the global model included Landform (categorised as dune or swale) and collection year (categorised as 2009, 2010, 2011) and their own candidate set of explanatory variables for meteorological conditions (Appendix 2.2). No interaction terms were considered. To determine the relative importance of the meteorological conditions on reproductive structures for each species, we used multi-model inference. Multi-model inference uses a weighted combination of results from all the models in the set, giving a better measure of precision and reducing bias in estimated parameters compared to estimates from a single “best model” approach (Burnham and Anderson 1998; Burnham *et al.* 2011). A set of alternative models was constructed for all linear combinations of all explanatory variables using MuMIn package (version 1.7.2; Barton 2012). Due to the over-dispersed nature of our data, we calculated the Quasi-likelihood Akaike information criterion (QAIC) for every model as an indicator of model parsimony. Models were ranked by their QAIC criterion and computed the differences (Δ_i) between the QAIC of the candidate models and the QAIC of the best model (lowest QAIC) as well as the Akaike weights (ω_i) (i.e. relative variance explained by each model) (see Appendix 2.3, 2.4, 2.5) (Anderson *et al.* 2001; Zuur 2009). Model averaging was conducted on models with $\Delta_i \leq 10$ to gain a more robust insight into the importance of each explanatory variable to the response variable in the final model; however for brevity we only present $\Delta_i \leq 2$ in Appendices 2.3, 2.4 and 2.5. We calculated average parameter estimates and their standard deviations estimates following Burnham and Anderson (1998). All analyses were conducted in with R (version 2.15.1; R Core Team 2012).

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Appendix 2.2. Summary of the final meteorological variables selected for each species. The best representative measure (Best Rep.) of each meteorological condition is given for each species, as determined by the lowest AIC of a single explanatory variable model. Variance Inflation Factors (VIF) are given for the final candidate set of explanatory variables used in the global model for each species.

Meteorological Conditions	<i>Eucalyptus gracilis</i>		<i>Senna artemisioides</i>		<i>Acacia burkittii</i>	
	Best rep.	VIF	Best rep.	VIF	Best rep.	VIF
Rainfall						
Average	12 month lag	–	12 month lag	–	12 month lag	–
Cumulative	12 month lag	–	12 month lag	–	12 month lag	–
Avg. event size	12 month lag	2.99	12 month lag	2.89	12 month lag	2.61
No. rain days	12 month lag	2.55	8 month lag	2.39	4 month lag	2.49
Temperature	Average min.	2.58	Average max.	–	Average max.	1.99
Wind speed	Maximum	1.85	Maximum	1.75	Maximum	1.85
Evaporation	Maximum	–	Maximum	–	Maximum	–
Relative humidity	Average 9am	–	Average 9am	–	Average 3pm	–
Cloud cover	Average 3pm	1.81	Average 9am	1.36	Average 9am	2.33
Solar Exposure	Cumulative	2.23	Cumulative	1.27	Average	–

Appendix 2.3. Table of *Eucalyptus gracilis* models ranked according to the quasi-likelihood form of Akaike's information criterion for all models with $\Delta_i \leq 2$. Zero-inflated models contain two parts, and thus require two sets of explanatory variables. The Part 1 explanatory variables explain the negative binomial-distributed "count" data (zeros and non-zeros), while Part 2 explanatory variables are for the additional zeros in a binomial distribution. QAIC, quasi-likelihood form of Akaike's information criterion; K, number of explanatory parameters in the model; d.f., model degrees of freedom; logLik, log likelihood ratio of model; $\Delta_i = \text{QAIC}_i - \text{QAIC}_{\min}$; ω_i , Akaike weight; Av3Cl, Average 3pm cloud 8ths; CuSol, cumulative solar exposure; AvMiTp Average minimum temperature; Ldfm, landform; MxWd, maximum wind speed; RnEv12, Average rainfall event size over past 12 months; RnDy12, number of rain days in the past 12 months.

Model	Part 1 Explanatory variables	Part 2 Explanatory variables	K	d.f.	logLik	QAIC	Δ_i	ω_i
Eu 1	Ldfm, MxWd, RnDy12	AvMiTp, Ldfm, RnDy12	6	9	-4382.17	873.0	0.00	0.006
Eu 2	Ldfm, MxWd, RnDy12	CuSol, Ldfm, RnDy12	6	9	-4382.86	873.2	0.13	0.005
Eu 3	Ldfm, MxWd, RnDy12	AvMiTp, RnDy12	5	8	-4395.53	873.6	0.60	0.004
Eu 4	Ldfm, MxWd, RnDy12	CuSol, RnDy12	5	8	-4396.14	873.8	0.72	0.004
Eu 5	Ldfm, MxWd, RnDy12	AvMiTp, CuSol, Ldfm, RnDy12	7	10	-4377.95	874.2	1.18	0.003
Eu 6	MxWd, RnDy12	AvMiTp, Ldfm, RnDy12	5	8	-4399.02	874.3	1.28	0.003
Eu 7	Av3Cl, Ldfm, MxWd, RnDy12	AvMiTp, Ldfm, RnDy12	7	10	-4378.99	874.4	1.38	0.003
Eu 8	CuSol, Ldfm, MxWd, RnDy12	AvMiTp, Ldfm, RnDy12	7	10	-4379.22	874.5	1.43	0.003
Eu 9	MxWd, RnDy12	CuSol, Ldfm, RnDy12	5	8	-4399.77	874.5	1.43	0.003
Eu 10	Av3Cl, Ldfm, MxWd, RnDy12	CuSol, Ldfm, RnDy12	7	10	-4379.68	874.5	1.52	0.003

Eu 11	CuSol, Ldfm, MxWd, RnDy12	CuSol, Ldfm, RnDy12	7	10	-4379.96	874.6	1.57	0.003
Eu 12	Ldfm, MxWd, RnDy12	AvMiTp, Ldfm, RnEv12, RnDy12	7	10	-4380.38	874.7	1.65	0.002
Eu 13	Ldfm, MxWd, RnDy12	CuSol, Ldfm, RnEv12, RnDy12	7	10	-4380.52	874.7	1.68	0.002
Eu 14	Ldfm, MxWd, RnEv12, RnDy12	AvMiTp, Ldfm, RnDy12	7	10	-4380.66	874.7	1.71	0.002
Eu 15	Ldfm, MxWd, RnDy12	AvMiTp, Ldfm, MxWd, RnDy12	7	10	-4381.06	874.8	1.78	0.002
Eu 16	Ldfm, MxWd, RnDy12	CuSol, Ldfm, MxWd, RnDy12	7	10	-4381.10	874.8	1.79	0.002
Eu 17	Ldfm, MxWd, RnDy12	AvMiTp, CuSol, RnDy12	6	9	-4391.46	874.8	1.81	0.002
Eu 18	Ldfm, MxWd, RnEv12, RnDy12	CuSol, Ldfm, RnDy12	7	10	-4381.36	874.9	1.84	0.002
Eu 19	MxWd, RnDy12	AvMiTp, RnDy12	4	7	-4412.90	875.0	1.98	0.002
Eu 20	Ldfm, MxWd, RnDy12	Av3Cl, AvMiTp, Ldfm, RnDy12	7	10	-4382.09	875.0	1.98	0.002
Eu 21	Av3Cl, Ldfm, MxWd, RnDy12	AvMiTp, RnDy12	6	9	-4392.38	875.0	1.99	0.002
Eu 22	AvMiTp, Ldfm, MxWd, RnDy12	AvMiTp, Ldfm, RnDy12	7	10	-4382.11	875.0	1.99	0.002

Appendix 2.4. Table of *Senna artemisioides* models ranked according to the quasi-likelihood form of Akaike's information criterion for all models with $\Delta_i \leq 2$. Zero-inflated models contain two parts, and thus require two sets of explanatory variables. Part 1 explanatory variables explain the negative binomial-distributed "count" data (zeros and non-zeros), while Part 2 explanatory variables are for the additional zeros in a binomial distribution. QAIC, quasi-likelihood form of Akaike's information criterion; K, number of explanatory parameters in the model; d.f., model degrees of freedom; logLik, log likelihood ratio of model; $\Delta_i = \text{QAIC}_i - \text{QAIC}_{\min}$; ω_i , Akaike weight; Av9Cl, Average 9am cloud 8ths; CuSol, cumulative solar exposure; Yr, year; Ldfm, landform; MxWd, maximum wind speed; RnEv12, Average rainfall event size over past 12 months; RnDy8, number of rain days in the past 8 months.

Model	Part 1 Explanatory variables	Part 2 Explanatory variable:	K	d.f.	logLik	QAIC	Δ_i	ω_i
Sen 1	CuSol, Yr, MxWd	CuSol, RnDy8	5	9	-4049.52	876.9	0.00	0.005
Sen 2	CuSol, RnDy8	CuSol, RnDy8	4	7	-4070.27	877.3	0.39	0.004
Sen 3	CuSol, MxWd, RnEv12	CuSol, RnDy8	5	8	-4062.03	877.6	0.65	0.003
Sen 4	CuSol, Yr	CuSol, RnDy8	4	8	-4062.48	877.7	0.74	0.003
Sen 5	CuSol, Yr, MxWd, RnDy8	CuSol, RnDy8	6	10	-4043.70	877.7	0.77	0.003
Sen 6	CuSol, Yr, MxWd	RnDy8	4	8	-4063.11	877.8	0.87	0.003
Sen 7	Av9Cl, CuSol, Yr	CuSol, RnDy8	5	9	-4054.16	877.9	0.98	0.003
Sen 8	CuSol, Yr, MxWd	MxWd, RnDy8	5	9	-4054.78	878.0	1.11	0.003
Sen 9	CuSol, RnDy8	RnDy8	3	6	-4083.57	878.1	1.21	0.002
Sen 10	CuSol, MxWd, RnEv12	RnDy8	4	7	-4074.16	878.1	1.21	0.002

Sen 11	CuSol, RnDy8	MxWd, RnEv12, RnDy8	5	8	-4064.95	878.2	1.26	0.002
Sen 12	Av9Cl, CuSol, Yr, MxWd	CuSol, RnDy8	6	10	-4046.50	878.3	1.36	0.002
Sen 13	CuSol, RnDy8	MxWd, RnDy8	4	7	-4074.98	878.3	1.39	0.002
Sen 14	CuSol, Yr, MxWd	MxWd, RnEv12, RnDy8	6	10	-4046.88	878.4	1.44	0.002
Sen 15	CuSol, MxWd, RnDy8	CuSol, RnDy8	5	8	-4065.79	878.4	1.44	0.002
Sen 16	CuSol, Yr, MxWd	CuSol, RnEv12, RnDy8	6	10	-4047.26	878.4	1.52	0.002
Sen 17	CuSol, Yr, MxWd, RnDy8	RnDy8	5	9	-4056.80	878.5	1.54	0.002
Sen 18	Av9Cl, CuSol, Yr, MxWd, RnDy8	CuSol, RnDy8	7	11	-4038.22	878.5	1.61	0.002
Sen 19	CuSol, MxWd, RnEv12, RnDy8	CuSol, RnDy8	6	9	-4057.16	878.5	1.62	0.002
Sen 20	CuSol, Yr, MxWd	Av9Cl, RnDy8	5	9	-4057.16	878.5	1.62	0.002
Sen 21	CuSol, Yr, MxWd	CuSol, MxWd, RnDy8	6	10	-4047.84	878.6	1.64	0.002
Sen 22	CuSol, Yr	MxWd, RnDy8	4	8	-4066.80	878.6	1.66	0.002
Sen 23	Yr, MxWd	CuSol, RnDy8	4	8	-4066.86	878.6	1.67	0.002
Sen 24	CuSol, RnDy8	CuSol, RnEv12, RnDy8	5	8	-4067.02	878.6	1.70	0.002
Sen 25	CuSol, Yr	RnDy8	3	7	-4076.54	878.6	1.72	0.002
Sen 26	CuSol, Yr, MxWd	CuSol, Ldfm, RnDy8	6	10	-4048.24	878.6	1.73	0.002
Sen 27	CuSol, MxWd, RnEv12	MxWd, RnDy8	5	8	-4067.20	878.7	1.74	0.002
Sen 28	CuSol, Ldfm, Yr, MxWd	CuSol, RnDy8	6	10	-4048.40	878.7	1.76	0.002
Sen 29	Av9Cl, CuSol, Yr	RnDy8	4	8	-4067.58	878.7	1.82	0.002
Sen 30	CuSol, Yr	MxWd, RnEv12, RnDy8	5	9	-4058.17	878.7	1.83	0.002

Appendix 2.4 Continued

Model	Part 1 Explanatory variables	Part 2 Explanatory variables	K	d.f.	logLik	QAIC	Δ_i	ω_i
Sen 31	Av9Cl, CuSol, Yr	MxWd, RnDy8	5	9	-4058.28	878.8	1.85	0.002
Sen 32	CuSol, Yr, RnEv12	CuSol, RnDy8	5	9	-4058.60	878.8	1.92	0.002
Sen 33	CuSol, Yr, MxWd, RnDy8	MxWd, RnDy8	6	10	-4049.20	878.9	1.93	0.002
Sen 34	CuSol, Yr, MxWd	Av9Cl, CuSol, RnDy8	6	10	-4049.33	878.9	1.96	0.002
Sen 35	Av9Cl, CuSol, Yr, RnDy8	CuSol, RnDy8	6	10	-4049.34	878.9	1.96	0.002
Sen 36	CuSol, RnDy8	CuSol, MxWd, RnDy8	5	8	-4068.42	878.9	2.00	0.002
Sen 37	CuSol, Yr, MxWd, RnEv12	CuSol, RnDy8	6	10	-4049.52	878.9	2.00	0.002

Appendix 2.5. Table of *Acacia burkittii* models ranked according to the quasi-likelihood form of Akaike's information criterion for all models with $\Delta_i \leq 2$. Zero-inflated models contain two parts, and thus require two sets of explanatory variables. Part 1 explanatory variables explain the negative binomial-distributed "count" data (zeros and non-zeros), while Part 2 explanatory variables are for the additional zeros in a binomial distribution. QAIC, quasi-likelihood form of Akaike's information criterion; K, number of explanatory parameters in the model; d.f., model degrees of freedom; logLik, log likelihood ratio of model; $\Delta_i = \text{QAIC}_i - \text{QAIC}_{\min}$; ω_i , Akaike weight; Av9Cl, Average 9am cloud 8ths; AvMiTp, Average minimum temperature; CuSol, cumulative solar exposure; Yr, year; Ldfm, landform; MxWd, maximum wind speed; RnEv12, Average rainfall event size over past 12 months; RnDy4, number of rain days in the past 4 months.

Model	Part 1 Explanatory variables	Part 2 Explanatory variables	K	d.f.	logLik	QAIC	Δ_i	ω_i
Ac 1	Yr, MxWd, RnDy4	AvMaTp, RnDy4	5	9	-4403.79	876.1	0.00	0.004
Ac 2	Av9Cl, MxWd, RnDy4	AvMaTp, RnEv12, RnDy4	6	9	-4404.11	876.2	0.06	0.004
Ac 3	Av9Cl, MxWd, RnDy4	RnEv12, RnDy4	5	8	-4414.55	876.2	0.09	0.004
Ac 4	Yr, MxWd, RnDy4	AvMaTp, RnEv12, RnDy4	6	10	-4393.98	876.2	0.09	0.004
Ac 5	Yr, MxWd, RnDy4	RnEv12, RnDy4	5	9	-4404.77	876.3	0.19	0.004
Ac 6	Av9Cl, MxWd, RnDy4	AvMaTp, RnDy4	5	8	-4415.06	876.3	0.19	0.004
Ac 7	Av9Cl, MxWd, RnEv12, RnDy4	RnEv12, RnDy4	6	9	-4405.08	876.4	0.25	0.003
Ac 8	MxWd, RnDy4	AvMaTp, RnEv12, RnDy4	5	8	-4415.48	876.4	0.27	0.003
Ac 9	Av9Cl, MxWd, RnEv12, RnDy4	AvMaTp, RnDy4	6	9	-4405.35	876.4	0.30	0.003
Ac 10	Av9Cl, RnDy4	AvMaTp, RnDy4	4	7	-4426.05	876.5	0.33	0.003

Appendix 2. 5. Continued									
Model	Part 1 Explanatory variables	Part 2 Explanatory variables	K	d.f.	logLik	QAIC	Δ_i	ω_i	
Ac 11	Av9Cl, RnDy4	AvMaTp, RnEv12, RnDy4	5	8	-4415.84	876.5	0.34	0.003	
Ac 12	Av9Cl, MxWd, RnEv12, RnDy4	AvMaTp, RnEv12, RnDy4	7	10	-4395.34	876.5	0.36	0.003	
Ac 13	MxWd, RnDy4	AvMaTp, RnDy4	4	7	-4426.49	876.6	0.41	0.003	
Ac 14	Av9Cl, RnDy4	RnEv12, RnDy4	4	7	-4426.72	876.6	0.46	0.003	
Ac 15	MxWd, RnDy4	RnEv12, RnDy4	4	7	-4427.15	876.7	0.54	0.003	
Ac 16	Av9Cl, MxWd, RnDy4	MxWd, RnEv12, RnDy4	6	9	-4407.49	876.9	0.72	0.003	
Ac 17	Av9Cl, Yr, MxWd, RnDy4	AvMaTp, RnDy4	6	10	-4397.72	877.0	0.82	0.003	
Ac 18	MxWd, RnEv12, RnDy4	AvMaTp, RnDy4	5	8	-4418.35	877.0	0.83	0.003	
Ac 19	Av9Cl, Yr, MxWd, RnDy4	RnEv12, RnDy4	6	10	-4397.80	877.0	0.83	0.003	
Ac 20	MxWd, RnEv12, RnDy4	AvMaTp, RnEv12, RnDy4	6	9	-4408.29	877.0	0.87	0.003	
Ac 21	Yr, MxWd, RnDy4	MxWd, RnEv12, RnDy4	6	10	-4398.09	877.0	0.89	0.003	
Ac 22	Av9Cl, Yr, MxWd, RnDy4	AvMaTp, RnEv12, RnDy4	7	11	-4387.85	877.0	0.90	0.002	
Ac 23	Av9Cl, RnDy4	MxWd, RnEv12, RnDy4	5	8	-4418.85	877.1	0.93	0.002	
Ac 24	Av9Cl, MxWd, RnEv12, RnDy4	MxWd, RnEv12, RnDy4	7	10	-4398.52	877.1	0.98	0.002	
Ac 25	MxWd, RnEv12, RnDy4	RnEv12, RnDy4	5	8	-4419.33	877.2	1.02	0.002	
Ac 26	Yr, MxWd, RnDy4	AvMaTp, Ldfm, RnDy4	6	10	-4399.14	877.2	1.10	0.002	
Ac 27	Yr, MxWd, RnDy4	AvMaTp, Ldfm, RnEv12, RnDy4	7	11	-4389.25	877.3	1.17	0.002	
Ac 28	Av9Cl, MxWd, RnDy4	AvMaTp, Ldfm, RnEv12, RnDy4	7	10	-4399.57	877.3	1.18	0.002	

Ac 29	MxWd, RnDy4	MxWd, RnEv12, RnDy4	5	8	-4420.37	877.4	1.22	0.002
Ac 30	Av9Cl, MxWd, RnDy4	Ldfm, RnEv12, RnDy4	6	9	-4410.20	877.4	1.25	0.002
Ac 31	Yr, MxWd, RnDy4	Ldfm, RnEv12, RnDy4	6	10	-4400.22	877.5	1.31	0.002
Ac 32	Av9Cl, MxWd, RnDy4	Yr, RnDy4	5	9	-4410.54	877.5	1.31	0.002
Ac 33	Av9Cl, MxWd, RnDy4	AvMaTp, Ldfm, RnDy4	6	9	-4410.57	877.5	1.32	0.002
Ac 34	Yr, MxWd, RnDy4	AvMaTp, MxWd, RnDy4	6	10	-4400.28	877.5	1.32	0.002
Ac 35	Yr, MxWd, RnDy4	Av9Cl, RnEv12, RnDy4	6	10	-4400.55	877.5	1.37	0.002
Ac 36	MxWd, RnDy4	AvMaTp, Ldfm, RnEv12, RnDy4	6	9	-4410.88	877.5	1.38	0.002
Ac 37	Av9Cl, MxWd, RnEv12, RnDy4	Ldfm, RnEv12, RnDy4	7	10	-4400.67	877.5	1.39	0.002
Ac 38	Av9Cl, MxWd, RnEv12, RnDy4	AvMaTp, Ldfm, RnDy4	7	10	-4400.80	877.6	1.42	0.002
Ac 39	Av9Cl, MxWd, RnDy4	Av9Cl, RnEv12, RnDy4	6	9	-4411.16	877.6	1.43	0.002
Ac 40	Av9Cl, RnDy4	AvMaTp, Ldfm, RnDy4	5	8	-4421.59	877.6	1.46	0.002
Ac 41	Av9Cl, MxWd, RnEv12, RnDy4	AvMaTp, Ldfm, RnEv12, RnDy4	8	11	-4390.74	877.6	1.46	0.002
Ac 42	Av9Cl, RnDy4	AvMaTp, Ldfm, RnEv12, RnDy4	6	9	-4411.31	877.6	1.46	0.002
Ac 43	Yr, MxWd, RnDy4	Yr, RnDy4	5	10	-4401.05	877.6	1.47	0.002
Ac 44	Av9Cl, MxWd, RnDy4	AvMaTp, MxWd, RnDy4	6	9	-4411.38	877.6	1.48	0.002
Ac 45	Av9Cl, MxWd, RnEv12, RnDy4	Yr, RnDy4	6	10	-4401.10	877.6	1.48	0.002
Ac 46	Av9Cl, Yr, MxWd, RnDy4	MxWd, RnEv12, RnDy4	7	11	-4390.98	877.7	1.51	0.002
Ac 47	Av9Cl, MxWd, RnEv12, RnDy4	RnDy4	5	8	-4421.88	877.7	1.52	0.002
Ac 48	Yr, MxWd, RnDy4	RnDy4	4	8	-4421.89	877.7	1.52	0.002
Ac 49	MxWd, RnDy4	AvMaTp, Ldfm, RnDy4	5	8	-4421.94	877.7	1.53	0.002

Appendix 2.5. Continued								
Model	Part 1 Explanatory variables	Part 2 Explanatory variables	K	d.f.	logLik	QAIC	Δ_i	ω_i
Ac 50	Av9Cl, MxWd, RnDy4	AvMaTp, Yr, RnDy4	6	10	-4401.65	877.7	1.58	0.002
Ac 51	Av9Cl, RnDy4	Ldfm, RnEv12, RnDy4	5	8	-4422.39	877.8	1.62	0.002
Ac 52	MxWd, RnDy4	AvMaTp, MxWd, RnDy4	5	8	-4422.43	877.8	1.62	0.002
Ac 53	MxWd, RnDy4	Av9Cl, RnEv12, RnDy4	5	8	-4422.44	877.8	1.63	0.002
Ac 54	Av9Cl, MxWd, RnEv12, RnDy4	AvMaTp, MxWd, RnDy4	7	10	-4401.97	877.8	1.65	0.002
Ac 55	Ldfm, Yr, MxWd, RnDy4	AvMaTp, RnDy4	6	10	-4401.99	877.8	1.65	0.002
Ac 56	Av9Cl, RnDy4	Yr, RnDy4	4	8	-4422.61	877.8	1.66	0.002
Ac 57	Av9Cl, MxWd, RnEv12, RnDy4	Av9Cl, RnEv12, RnDy4	7	10	-4402.04	877.8	1.66	0.002
Ac 58	Yr, MxWd, RnDy4	AvMaTp, Yr, RnDy4	6	11	-4391.79	877.8	1.67	0.002
Ac 59	MxWd, RnDy4	Ldfm, RnEv12, RnDy4	5	8	-4422.72	877.8	1.68	0.002
Ac 60	Av9Cl, RnDy4	AvMaTp, MxWd, RnDy4	5	8	-4422.94	877.9	1.72	0.002
Ac 61	Av9Cl, MxWd, RnDy4	RnDy4	4	7	-4433.24	877.9	1.73	0.002
Ac 62	Ldfm, Yr, MxWd, RnDy4	AvMaTp, RnEv12, RnDy4	7	11	-4392.17	877.9	1.74	0.002
Ac 63	Av9Cl, AvMaTp, MxWd, RnDy4	AvMaTp, RnEv12, RnDy4	7	10	-4402.56	877.9	1.76	0.002
Ac 64	MxWd, RnDy4	Yr, RnDy4	4	8	-4423.17	877.9	1.77	0.002
Ac 65	Av9Cl, AvMaTp, MxWd, RnDy4	RnEv12, RnDy4	6	9	-4412.97	877.9	1.78	0.002
Ac 66	MxWd, RnEv12, RnDy4	MxWd, RnEv12, RnDy4	6	9	-4413.04	877.9	1.80	0.002
Ac 67	Av9Cl, RnDy4	Av9Cl, RnEv12, RnDy4	5	8	-4423.38	878.0	1.81	0.002
Ac 68	MxWd, RnDy4	AvMaTp, Yr, RnDy4	5	9	-4413.10	878.0	1.81	0.002

Ac 69	Av9Cl, AvMaTp, MxWd, RnEv12, RnDy4	RnEv12, RnDy4	7	10	-4402.89	878.0	1.82	0.002
Ac 70	Yr, MxWd, RnEv12, RnDy4	AvMaTp, RnDy4	6	10	-4402.92	878.0	1.83	0.002
Ac 71	Ldfm, Yr, MxWd, RnDy4	RnEv12, RnDy4	6	10	-4402.93	878.0	1.83	0.002
Ac 72	Av9Cl, MxWd, RnDy4	Ldfm, MxWd, RnEv12, RnDy4	7	10	-4403.03	878.0	1.85	0.002
Ac 73	Av9Cl, RnDy4	AvMaTp, Yr, RnDy4	5	9	-4413.33	878.0	1.85	0.002
Ac 74	Av9Cl, MxWd, RnEv12, RnDy4	AvMaTp, Yr, RnDy4	7	11	-4392.82	878.0	1.87	0.002
Ac 75	Yr, MxWd, RnEv12, RnDy4	AvMaTp, RnEv12, RnDy4	7	11	-4393.00	878.0	1.90	0.002
Ac 76	Av9Cl, AvMaTp, MxWd, RnDy4	AvMaTp, RnDy4	6	9	-4413.68	878.1	1.92	0.001
Ac 77	Av9Cl, RnDy4	RnDy4	3	6	-4444.55	878.1	1.92	0.001
Ac 78	Av9Cl, Yr, MxWd, RnDy4	AvMaTp, Ldfm, RnDy4	7	11	-4393.12	878.1	1.93	0.001
Ac 79	Av9Cl, AvMaTp, MxWd, RnEv12, RnDy4	AvMaTp, RnDy4	7	10	-4403.42	878.1	1.93	0.001
Ac 80	MxWd, RnEv12, RnDy4	AvMaTp, Ldfm, RnDy4	6	9	-4413.74	878.1	1.93	0.001
Ac 81	AvMaTp, Yr, MxWd, RnDy4	AvMaTp, RnDy4	6	10	-4403.46	878.1	1.93	0.001
Ac 82	Av9Cl, AvMaTp, MxWd, RnEv12, RnDy4	AvMaTp, RnEv12, RnDy4	8	11	-4393.19	878.1	1.94	0.001
Ac 83	Yr, MxWd, RnDy4	Av9Cl, AvMaTp, RnDy4	6	10	-4403.51	878.1	1.95	0.001
Ac 84	Av9Cl, Yr, MxWd, RnDy4	Ldfm, RnEv12, RnDy4	7	11	-4393.33	878.1	1.97	0.001
Ac 85	MxWd, RnEv12, RnDy4	AvMaTp, Ldfm, RnEv12, RnDy4	7	10	-4403.62	878.1	1.97	0.001
Ac 86	Yr, MxWd, RnDy4	Ldfm, MxWd, RnEv12, RnDy4	7	11	-4393.44	878.1	1.99	0.001
Ac 87	Av9Cl, MxWd, RnDy4	AvMaTp, MxWd, RnEv12, RnDy4	7	10	-4403.76	878.1	1.99	0.001
Ac 88	Av9Cl, Yr, MxWd, RnDy4	AvMaTp, Ldfm, RnEv12, RnDy4	8	12	-4383.19	878.1	1.99	0.001
Ac 89	Av9Cl, MxWd, RnDy4	Yr, MxWd, RnDy4	6	10	-4403.80	878.1	2.00	0.001

Appendix 2.6. Model-averaged coefficients (and standard errors) and top model coefficients for the three species. The zero-inflated models were run as two parts. Part 1 is for the negative binomial distributed “count” data and Part 2 for the binomial distributed excess zero data. The coefficients for categorical factors (i.e. Year and Landform) are relative to the missing categories (i.e. Year = 2009, and Landform = dune). Lag times for rainfall variables are indicated in months (mth). Wind speed (max) is average daily maximum wind speed; cloud cover is average daily cloud 8ths at either 9am or 3pm; solar exposure is cumulative daily solar exposure (cum.) for the given collection window; temperature is either maximum or minimum daily temperature (Temp.) averaged (avg) for each collection window.

Variables	Model Averaged Coefficients		Top Model Coefficients	
	Part 1	Part 2	Part 1	Part 2
<i>Senna artemisioides</i>				
Intercept	-0.15 (4.68)	9.58 (2.99)	-2.58 (1.15)	7.95 (0.77)
Year (2010)	2.43 (0.64)	-0.88 (0.50)	2.78 (0.30)	–
Year (2011)	2.07 (0.89)	-2.07 (1.60E ⁺²)	2.67 (0.25)	–
Landform (swale)	-0.24 (0.17)	0.35 (0.23)	–	–
Rain event size 12mth	0.21 (0.33)	-0.25 (0.15)	–	–
Rain days 8 mth	6.33E ⁻² (2.02E ⁻²)	-0.25 (3.72E ⁻²)	–	-0.25 (2.79E ⁻²)
Wind speed (max)	0.15 (5.47E ⁻²)	-0.10 (4.37E ⁻²)	0.14 (2.66E ⁻²)	–
Cloud cover (9am)	-0.52 (0.28)	0.16 (0.44)	–	–
Solar exposure (cum.)	2.34E ⁻³ (4.24E ⁻⁴)	-1.71E ⁻³ (5.27E ⁻⁴)	1.93E ⁻³ (2.98E ⁻⁴)	-1.75E ⁻³ (3.63E ⁻⁴)

<i>Acacia burkittii</i>				
Intercept	-0.62 (3.40)	6.80 (2.80)	-3.52 (0.73)	8.78 (1.20)
Year (2010)	1.01 (0.37)	-1.27 (0.40)	1.00 (0.24)	–
Year (2011)	1.66 (0.47)	-2.10 (0.89)	1.73 (0.26)	–
Landform (swale)	0.16 (0.14)	-0.59 (0.20)	–	–
Rain event size 12 mth	0.11 (0.22)	-0.33 (0.18)	–	–
Rain days 4 mth	0.19 (2.9E ⁻²)	-0.26 (9.4E ⁻²)	0.15 (1.3E ⁻²)	-0.39 (4.5E ⁻²)
Wind speed (max)	0.12 (2.9E ⁻²)	-3.47E ⁻² (6.0E ⁻²)	0.14 (1.6E ⁻²)	–
Cloud cover (9am)	-0.64 (0.18)	0.13 (0.48)	–	–
Maximum temp. (avg)	-4.63E ⁻⁴ (3.0E ⁻²)	-0.12 (4.5E ⁻²)	–	-0.14 (2.6E ⁻²)
<i>Eucalyptus gracilis</i>				
Intercept	1.64 (2.55)	5.56 (1.58)	-0.85 (0.62)	5.50 (0.48)
Year (2010)	0.26 (0.43)	-0.37 (0.41)	–	–
Year (2011)	0.58 (0.83)	-1.57 (1.39)	–	–
Landform (swale)	0.59 (0.10)	-0.89 (0.18)	0.58 (9.7E ⁻²)	-0.88 (0.17)
Rain event size 12 mth	-0.15 (0.12)	-0.16 (0.12)	–	–
Rain days 12 mth	4.23E ⁻² (9.3E ⁻³)	-8.84E ⁻² (1.6E ⁻²)	4.12E ⁻² (3.3E ⁻³)	-9.77E ⁻² (9.1E ⁻³)
Wind speed (max)	9.64E ⁻² (1.9E ⁻²)	-4.11E ⁻² (2.5E ⁻²)	0.11 (1.28E ⁻²)	–
Cloud cover (3pm)	-0.24 (0.12)	-6.52E ⁻² (0.24)	–	–
Minimum temp. (avg)	-7.17E ⁻³ (2.3E ⁻²)	-0.13 (4.34E ⁻²)	–	-0.16 (1.9E ⁻²)
Solar exposure (cum.)	4.91E ⁻⁴ (2.5E ⁻⁴)	-2.20E ⁻³ (6.6E ⁻⁴)	–	–

Chapter 3. Landscape modulators and resource accumulation in a post–fire eucalypt woodland

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Keywords: *Eucalyptus dumosa*; *Eucalyptus socialis*; fire; leaf litter; patch; woody debris.

Abbreviations:

ANCOVA — Analysis of Covariance

N — Nitrogen

PCA — Principal Components Analysis

PERMANOVA — Permutational Multivariate Analysis of Variance

SEM — Structural Equation Model



Eucalypt mallee trees modulating resources at 8 (left), 14 (middle) and 32 (right) years since fire.

3.1 Abstract

In resource-limited environments patch development is a critical component of ecosystem function. Resource patches at both fine and broad scales are temporally dynamic, and the resources they provide change in response to broad-scale ecological disturbances such as fire. Here we consider temporal changes in perennial vegetation patches by measuring the fine-scale development of physical patch layers in response to a broad-scale abiotic process, fire. Until recently, such fundamental shifts in patch structure have, for the most part, been widely assumed and quantitatively ignored. Fundamental shifts in post-fire litter composition are important for predicting fire behaviour and may be useful in identifying the range of conditions or thresholds under which the arrangement of fuel components affects future fire behaviour. We describe the post-fire development of physical patch layers associated with two eucalypt mallee tree species (*Eucalyptus dumosa* and *Eucalyptus socialis*). We quantified tree, litter bed and canopy dimensions for sites with fire histories ranging from 4 to 42 years, focussing on the development of the sub-canopy litter bed. There were strong linear relationships between tree size and litter bed size with increasing time since last fire. After we accounted for tree and litter bed size, fire history still had a significant effect on the composition of the litter bed with sticks, seeds and fragments generally increasing and leaves generally decreasing with greater time since fire. There were no significant differences between the two tree species studied for any relationship with time since fire. Our results document the temporal, fine-scale changes in litter accumulation and composition following fire in a mallee woodland, indicating that substantial shifts in composition occur, likely affecting the flammability of the litter bed. More specifically, we have shed light on post-fire trends in litter accumulation, a fundamental component of patch development. This study provides us with a better understanding of fine-scale resource patch development, allowing us to predict shifts in resources at broader scales. By understanding how landscape modulators and their surrounding environment influence the development of patches, we are in a better position to predict how changes in these drivers are likely to affect ecosystem processes.

3.2 Introduction

Arid and semi-arid ecosystems function effectively by concentrating limited resources into discrete patches (Noy Meir 1979; Ludwig *et al.* 1997). These nutrient- and water-rich resource patches can buffer surface temperatures and provide habitat for organisms (Whitford and Kay 1999). The stark contrast in resource quality and quantity between the resource patch and the surrounding matrix can also significantly alter local species assemblages. Some resource patches are constructed by organisms that exploit, modify and concentrate resources. Examples include the resource-rich pits created by soil foraging animals (Whitford and Kay 1999) and the resource patches that form around perennial vegetation (Shachak *et al.* 2008). Widespread fine-scale patch creation and development by dominant biota, such as perennial plants, can significantly alter landscape productivity and resource diversity at broad spatial scales (Ludwig *et al.* 1997), which, in turn, affects the abundance and diversity of patch-dependent biota (Shachak *et al.* 2008). Organisms that create and maintain resource patches and are dominant at broad scales are known as landscape modulators (*sensu* Shachak *et al.* 2008).

At broad scales, landscape patchiness and associated biodiversity are also driven by abiotic processes such as fire. Such broad-scale abiotic processes have long been recognised as major drivers of biodiversity (Bradstock *et al.* 2005). Current literature, however, suggests that fine-scale resource patches created and maintained by biota may be more important for maintaining biodiversity than those created and maintained by broad-scale abiotic processes such as fire (Loreau *et al.* 2001; Shachak *et al.* 2008). Fire can modify the spatial and temporal arrangement of broad- and fine-scale patches and affect their constituent biota for many decades after the event (Russell-Smith *et al.* 2010). In highly flammable communities, a regime of regular, natural fires of varying intensity and size can structure landscapes into a mosaic of different patches, each with different stages of recovery (Gill *et al.* 2003; Bradstock *et al.* 2005). Fire is, therefore, an important modulator of resources and resource patches, and in resource-limited environments such as semi-arid woodlands, this has

3. Post–fire litter bed accumulation

dramatic effects on ecosystem structure and productivity (Noble 1989; Cohn and Bradstock 2000). At finer spatial scales, fire homogenises resource patches formed around trees, reducing resource diversity at the fine patch and inter–patch scales. However, this fine–scale loss of resource diversity is often short–lived due to the temporal dynamics of patches. Shachak *et al.* (2008) proposed that patches such as those associated with perennial vegetation are temporally dynamic and cycle through stages of resource contrast with their surrounding matrix. As patches develop, they become increasingly more complex, physically and chemically altering soil properties and providing a greater array of habitats and potential food sources for organisms across both small and large spatial scales. When patches decay through processes such as fire, resource contrast with the surrounding matrix is initially reduced, but develops again over time (Shachak *et al.* 2008).

The development of post–fire species assemblages is generally related to the extent to which patch types re-establish after fire. A range of patch types co-exist after fire, providing a multi–layered habitat for diverse groups of fauna. However, not all patch types co-exist at the same time. For example, over time a tree can create spatially complex patches, with multiple layers such as litter beds that develop rapidly on the soil surface, hollows that develop slowly in the canopy, and strips of bark on the trunk that develop at an intermediate rate. A classic example of such multi–layered resource patches occurs in Mediterranean woodlands where evergreen, sclerophyllous shrubs and trees are dominant at broad scales, creating and maintaining resource patches (Gabay *et al.* 2012). In Australia’s Mediterranean climatic zones, mallee (*Eucalyptus* spp.) is the dominant vegetation community. Mallee trees have a growth form characterised by multiple stems that develop from a lignotuber root system. They are well adapted to periodic fires, and the stems resprout in as little as two weeks after fire (Noble 1997). A range of fire histories typically occur across an entire landscape, resulting in a mosaic of multi–layered resource patches that vary in size and development. The physical elements of these multi–layered resource patches such as litter beds, canopy, trunks and arboreal bark strips also provide fuel for future fires.

Despite considerable debate on the importance of fire for mallee-dependent fauna (e.g. Driscoll and Henderson 2008), many studies have demonstrated strong relationships between the post-fire recovery of mallee communities and a range of taxa (Clarke *et al.* 2010) such as reptiles (Caughley 1985), birds (Woinarski 1999), arthropods (Noble *et al.* 1990) and mammals (Kelly *et al.* 2010). Although there has been a significant focus on post-fire shifts in plant and animal assemblages in mallee communities, there are few data, to our knowledge, on the post-fire changes to the multi-layered resource patches that typify mallee communities (but see Haslem *et al.* 2011).

Our study examines the spatial and temporal changes in multi-layered resource patches after fire in mallee communities. We investigate resources at the scale of individual trees (*sensu* Shachak *et al.* 2008) using white mallee (*Eucalyptus dumosa* A. Cunn. ex J. Oxley) and red mallee (*Eucalyptus socialis* F. Muell. ex Miq.) as models of landscape modulators. We measure the spatial shift in resource patch size in response to fire history along a continuum of fire histories across the landscape. Given the identical structure of these two species, we did not expect to record differences in relationships between patch layers. However, given that litter fall can be species-specific (Miller and Urban 1999) we compared them to test whether there was any species-dependent variation in the composition of the litter bed across the different fire histories. We expected that changes within the canopy and trunk of our mallee models would correspond with shifts in the environment of the sub-canopy patch. We quantified the dimensions of the physical patch elements, i.e. the tree and litter layer associated with our mallee trees across a range of fire histories, focussing on the spatial and compositional development of the litter patch (litter bed layer), quantifying and comparing litter bed dimensions and composition as a function of time since fire.

3.3 Methods

3.3.1 Field site

Our study was undertaken inside two large conservation areas, Tarawi Nature Reserve and Australian Wildlife Conservancy's Scotia Sanctuary in south western New South Wales, Australia (33°43' S, 143°02' E). This area is semi-arid, receiving about 280 mm annual rainfall, however there are very few years in which this amount is actually received. Rainfall is highly irregular throughout the year and spatially variable across a scale of tens of kilometres. Winters are mild, with daily mean maximum temperature of 17 °C and a daily mean minimum temperature of 6 °C in July. Summer is typically hot with a January mean daily maximum temperature of 33 °C and a mean daily minimum of 19 °C (BOM 2011).

Our study was conducted in a dune mallee community; a low open woodland located on long, low (relief to 7 m) east-west trending sand dunes. Dune mallee is generally dominated by an open overstorey of mallee (multi-stemmed) trees (*Eucalyptus gracilis* F. Muell, *Eucalyptus dumosa*, *Eucalyptus socialis*) and an understorey of scattered perennial hummock grasses (*Triodia scariosa* N. T. Burb. subsp. *scariosa*). However as mallee trees resprout from lignotuberous roots after fire, in recently burnt sections mallee appear as hummock- to shrub-sized plants for approximately ten years after fire. Individual trees grow as a cluster of stems, which may be isolated or clumped with other individuals, forming large connected litter layers. The perennial hummock grasses that dominate the inter-tree matrix are highly flammable and their role in fuel connectivity is well established (Noble 1989, 1997). Shrub cover to 2 m is sparse on the dunes, with widely-spaced individuals of predominantly *Senna artemisioides* subsp. *filifolia* (Benth.) Randall and *petiolaris* Randell, and *Acacia burkittii* F. Muell. ex Benth (Keith 2004). At our study site, the soils are mainly calcareous, brownish and siliceous sands sparsely capped with biological soil crusts.

3.3.2 Experimental design

In January 2011, we sampled nine areas with known fire histories ranging from 4 to 42 years since fire. All sampled areas were located within 20 km of each other, and were assumed to have burned under equivalent, relatively high intensity fires based on vegetation characteristics. More specifically the mallee vegetation at all sites had re-sprouted from lignotubers, rather than continuing growth from stems which existed before the fire which can happen after low intensity fires.

At each of our nine burn areas, we randomly selected 20 sites. At each site we measured two trees, one of each species (total $N = 360$). To minimize edge effects we did not sample within 30 meters of the edge of a given burn area. Sampling was limited to *Eucalyptus socialis* and *Eucalyptus dumosa*. We identified these species based on leaf and bark traits, and fruits where possible. Due to size limitations of some burn areas we could not always find an equal number of each species (i.e. 20 of each species) at each burn area. At worst a minimum of 16 individuals representative of a species were selected for sampling. However, in this case 24 individuals of the other species were sampled to maintain orthogonality at the burn area level. This restricted our use of 'species' as to a covariate, rather than a factor in our parametric analyses (see section 3.3.5 below).

3.3.3 Measuring tree and litter bed patch layers

A range of measurements were made at each tree including tree height, elliptical canopy area, and diameter of the largest stem ~ 30 cm above the ground surface, consistent with recent studies in mallee (i.e. Clarke *et al.* 2010). Litter bed size was recorded on six radial transects crossing the entire litter patch. Along these transects we measured the depth of the litter bed and the distance to the edge of the continuous litter patch in order to calculate a litter bed depth profile for each transect. Litter volume was calculated from the sum of six partial volumes derived from the integrated area under the curve of quadratic equations fitted ($R^2 > 0.99$) to each

3. Post-fire litter bed accumulation

individual length and depth transect measurements. A standardised sample of litter in a 0.2 m diameter quadrat was collected at the midpoint of the first transect at each tree. Litter was dried at 60 °C to a constant weight, sieved to remove soil and particles less than 2 mm², hand-sorted into five components (leaves; sticks; bark; seeds; fragments < 4 mm²) and weighed. Litter load (kg m⁻²) and bulk density (kg m⁻³) were calculated from this sample, in combination with the measurements taken from the *in situ* litter bed. Litter bed mass was approximated by adjusting the litter bed volume with the bulk density of litter (Bradstock and Gill 1993).

3.3.4 Statistical methods: tree and litter patch dimensions

Tree height, canopy area and the diameter of the largest stem were log_e(x + 1) transformed and litter area, mass and volume fourth-root (x^{0.25}) transformed to ensure homogeneity of residuals prior to analysis.

3.3.5 Spatial and temporal development of the multi-layered patch

Linear regressions were used to quantify all possible combinations of allometric relationships between the litter bed dimensions (litter area, litter mass, litter volume) and tree dimensions (tree height, canopy area, largest stem diameter). The best linear relationship for each litter bed dimension is reported. A Principal Components Analysis (PCA) was then used to reduce all tree and litter bed dimension data to a single unitless Patch Score for each tree. The Patch Scores were compared across treatments with a nested two-factor Analysis of Covariance (ANCOVA) where species was binary-transformed and used as the covariate. Factors included our nine levels of time since fire (burn area, fixed) and site nested within time since fire (random). The ANCOVA was run in the Minitab (2007) package.

3.3.6 *Compositional shifts in the litter patch*

To quantify litter bed properties, we calculated litter load and litter composition (i.e. the proportional mass of each individual component, leaves, sticks, bark, reproductive structures and frass). To quantify shifts in litter load with increasing time since fire, the mean for each species at each burn site was used in a linear regression.

For shifts in composition, we used a Permutational Multivariate Analysis of Variance (PERMANOVA) with Patch Score as a covariate to account for pre-existing differences in tree and litter bed size. Factors included time since fire (fixed) and species (fixed) and their two- and three-way interactions with the covariate. The analyses were performed on a Euclidean distance-based resemblance matrix of the proportional mass data of the five litter components with 9999 permutations (type III sums of squares). Except for ANCOVA (Minitab 2007), all analyses were performed in the PRIMER v6 program with the additional PERMANOVA+ statistical package (Anderson *et al.* 2008).

3.3.7 *Tree, litter and fire as a system*

We used Structural Equation Modelling (SEM) to test the relationships among time since fire, canopy area, litter bed area and litter composition. SEM accounts for the direct and indirect effects of each variable on the response variable and estimates the strength of these effects (Grace 2006). The SEM consists of a diagram of complex multivariate cause-effect relationships. An *a priori* causal framework is constructed to logically represent the expected multivariate relationships, against which field data are tested. This is done by comparing the covariance structure of the data that are implied in the *a priori* model with the covariance structure of the observed data (Grace 2006). We used a maximum likelihood based goodness-of-fit test to assess the degree of fit between observed and predicted covariance structures. Our model posits that time since fire has both a direct effect on litter bed composition but also indirect effects, which are moderated by canopy area or litter bed area. With five separate models, we

3. Post-fire litter bed accumulation

examined the direct and indirect effects on the proportional mass of leaves, sticks, bark, seeds and fragments. The proportional mass of each component was $\log_e(x + 1)$ transformed prior to analysis. Each of our models was saturated, i.e. all possible pathways between all variables were accounted for. The significance of our models could therefore not be tested, but their relative strengths are based on the amount of variance explained in our five response variables (Grace 2006). All SEM models were performed in AMOS 20.0 (SPSS Inc. 2009) software.

3.4 Results

3.4.1 Spatial and temporal development of the multi-layered patch

There was a general increase in the size of the trees and their associated litter patches for both tree species with increasing time since fire (Figure 3.1), but considerable spatial variability among trees within the same fire history. The strongest linear relationships among tree and litter bed dimensions occurred between canopy area and litter bed area ($R^2 = 0.70$, $P < 0.001$; Figure 3.2a), canopy area and litter bed mass ($R^2 = 0.57$, $P < 0.001$; Figure 3.2a), and tree height and litter bed volume ($R^2 = 0.66$, $P < 0.001$; Figure 3.2b), where each litter bed dimension increased with greater time since fire.

Our Patch Score, which integrated all canopy and litter patch dimensions and was derived from the Principal Components Analysis (Table 3.1), explained 86 % of the variation in the multi-layered patch data. We found significant shifts in the Patch Score with increasing time since fire, indicating that overall patch size is increasing ($F_{8, 171} = 107.30$, $P < 0.001$). There was also significant spatial variability in Patch Score among our sites within a fire history ($F_{171, 179} = 1.45$, $P = 0.007$). However there was no significant variation explained when the two species were considered as covariates of Patch Score ($P = 0.45$).

3. Post-fire litter bed accumulation

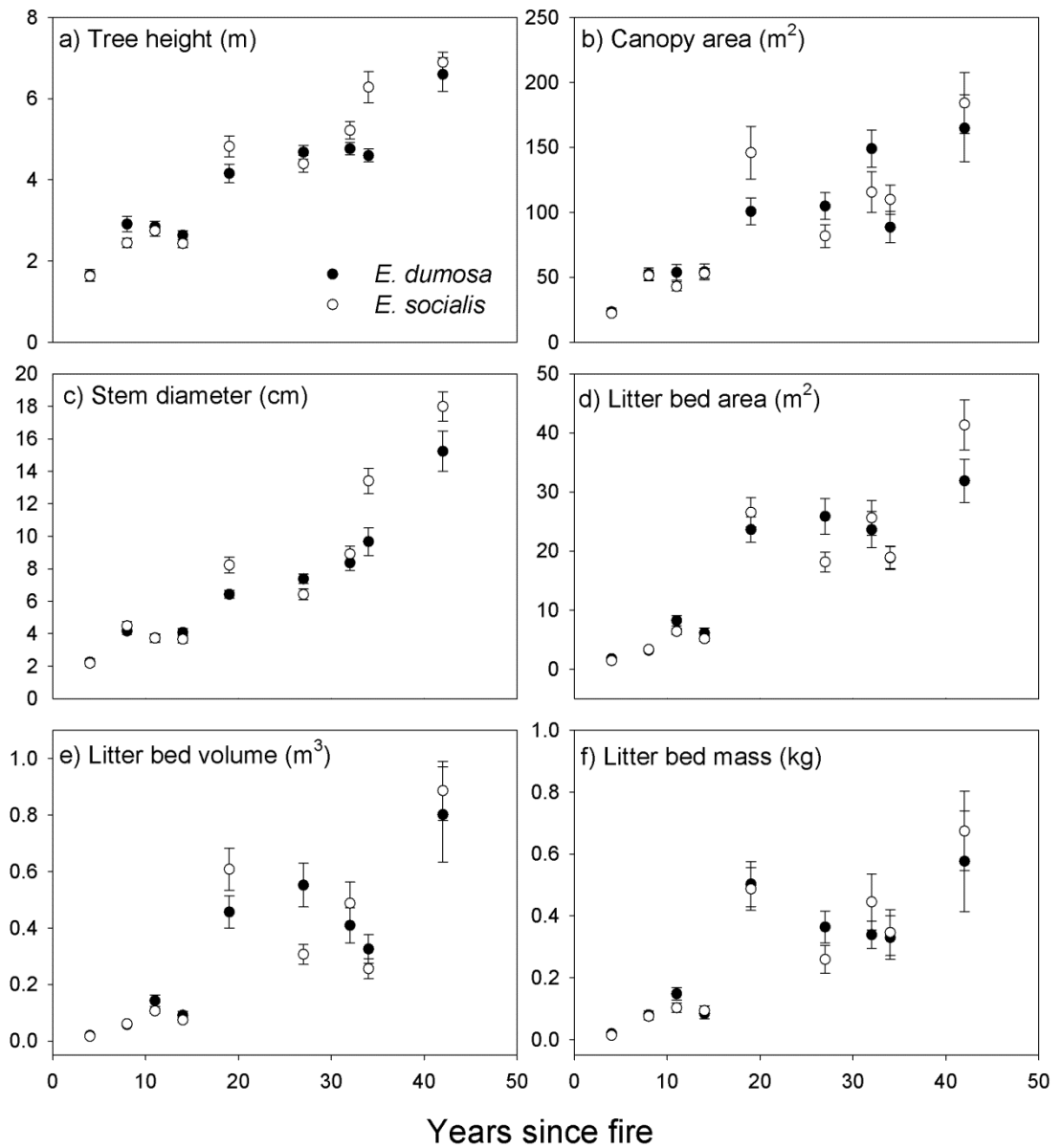


Figure 3-1. Mean (\pm SE) for all tree and litter bed dimensions for both species, for sampled years since fire. The black circles represent *Eucalyptus dumosa* while the white circles represent *Eucalyptus socialis*. The y axis units are given in the subtitle for each individual graph.

3. Post-fire litter bed accumulation

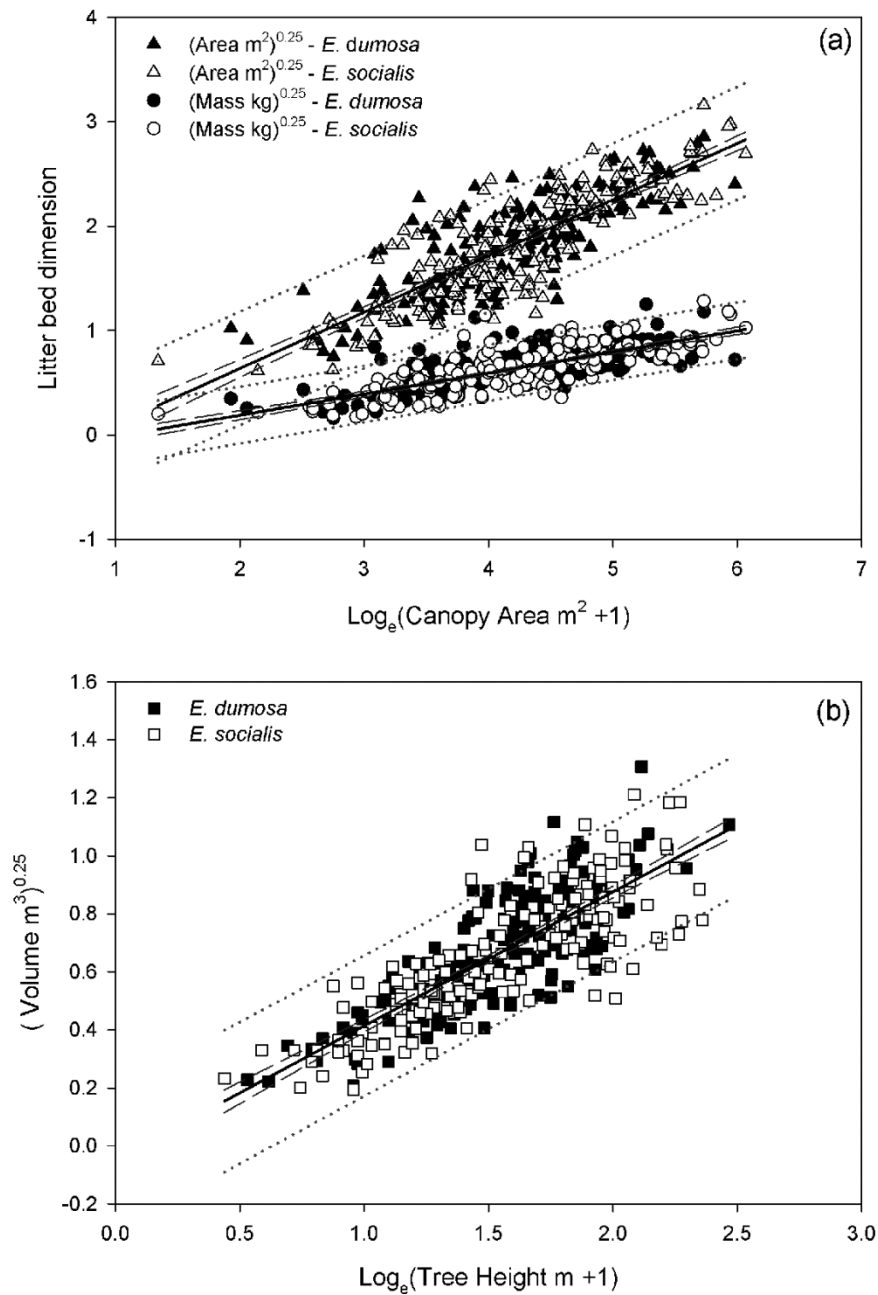


Figure 3-2. Linear regression of (a) litter bed area (triangles) and litter bed mass (circles) on tree canopy area and (b) Litter bed volume on tree height (squares). Black symbols represent *Eucalyptus dumosa* and white symbols represent *Eucalyptus socialis*. Linear regression models: Fourth-root of Litter bed area (m^2) = $0.539 \times \text{Log}_e(\text{Canopy area (m}^2) + 1) - 0.441$ ($R^2 = 0.70$; $P < 0.001$); Fourth-root of litter bed mass (kg) = $0.202 \times \text{Log}_e(\text{Canopy area (m}^2) + 1) - 0.215$ ($R^2 = 0.57$; $P < 0.001$); Fourth-root of Litter bed volume (m^3) = $0.462 \times \text{Log}_e(\text{Tree height (m)} + 1) - 0.048$ ($R^2 = 0.66$; $P < 0.001$). Long dash lines represent 95 % confidence band and dotted lines represent 95 % prediction band.

Table 3.1. Eigenvectors are the coefficients in the linear combinations of PCA components making up the first principal component for Patch Size score and composition score. These scores represent the weightings given to each component in the overall final summary score. The total variance explained by this first axis is also indicated.

Patch Size		Composition	
PCA component	Score	PCA component	Score
	Eigenvectors		Eigenvectors
$\text{Log}_e(\text{Tree Height} + 1)$	-0.310	Leaf mass %	-0.834
$\text{Log}_e(\text{Canopy Area} + 1)$	-0.673	Bark mass %	0.018
$\text{Log}_e(\text{Stem Diameter} + 1)$	-0.460	Stick mass %	0.420
$(\text{Litter Bed Area})^{0.25}$	-0.427	Seed mass %	0.040
$(\text{Litter Bed Volume})^{0.25}$	-0.177	Fragment mass %	0.356
$(\text{Litter Bed Mass})^{0.25}$	-0.158		
Total variance explained	86.0 %	Total variance explained	55.9 %

3.4.2 Compositional shifts in the litter patch

Litter load (kg m^{-2}) was highly spatially variable, did not differ between tree species, and showed no obvious trend with time since fire (Figure 3.3). Linear regression analyses did not reveal any significant variation within the data for either species (*E. dumosa* $P = 0.72$; *E. socialis*, $P = 0.69$; Figure 3.3). Despite no shifts in litter load, there were, however, significant shifts in litter composition.

Some litter bed components followed clear trends across fire histories, although there were no distinct trends between the two species. Each component shifted independently with increasing time since fire resulting in dramatic changes in overall litter bed composition. The proportion of leaves declined with increasing time since fire, with a suggestion of a plateau around 20 years since fire (Figure 3.4a). This pattern mirrored that for sticks, which gradually increased, peaking at around 30 years post-fire (Figure 3.4b). Trends for the proportion of bark were inconsistent, commencing at

3. Post-fire litter bed accumulation

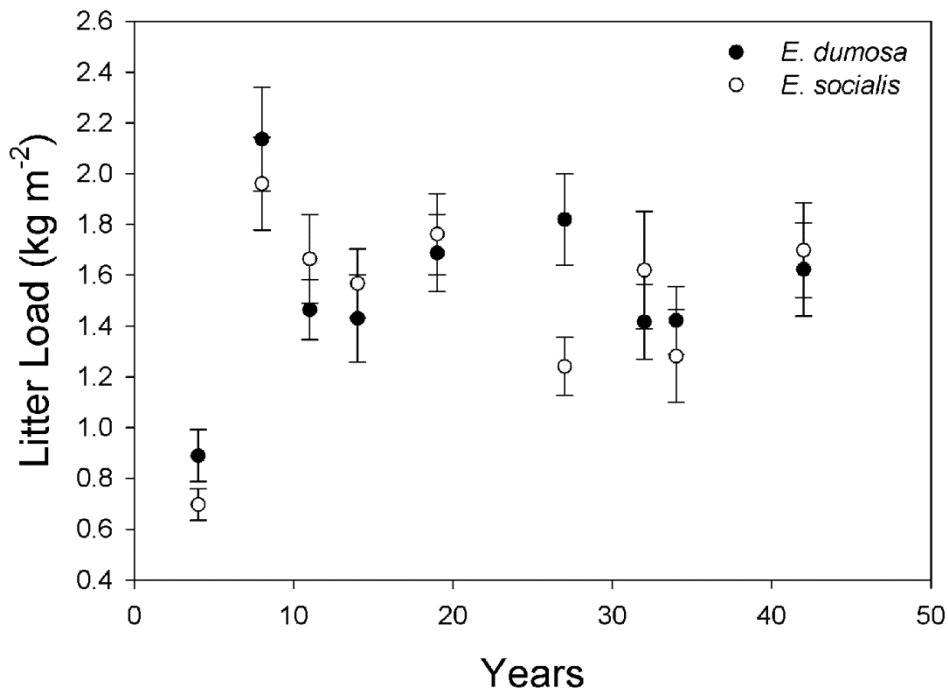


Figure 3-3. Mean (\pm SE) litter loads (kg m^{-2}) with increasing time since fire. Black symbols and solid line represent *Eucalyptus dumosa* and white symbols and dashed line represent *Eucalyptus socialis*. The regression for each species shows an insignificant change difference between the two species and represents a non-significant amount of variation in the data, suggesting no change in litter. Regression equations: (*E. dumosa*: $\text{kg m}^{-2} = 0.003 \times \text{Time since fire (yr)} + 1.465$, $R^2 = 0.02$, $P = 0.72$; *E. socialis*: $\text{kg m}^{-2} = 0.004 \times \text{Time since fire (yr)} + 1.405$, $R^2 = 0.02$, $P = 0.69$).

relatively high proportions, but showing substantial variation across the time since fire gradient (Figure 3.4c). The proportion of seeds and fragments followed a similar upward trend with increasing time since fire (Figures 4d, e).

Patch Score, our measure of patch size, explained a significant amount of variation in the PERMANOVA model of litter composition (Pseudo- $F_{1, 324} = 77.06$, $P < 0.001$). Once allowing for the effect of patch size, there was still a significant effect of time since fire on litter composition (Pseudo- $F_{8, 324} = 10.35$, $P < 0.001$), suggesting that changes in litter bed composition occur irrespective of changes in tree and litter bed size.

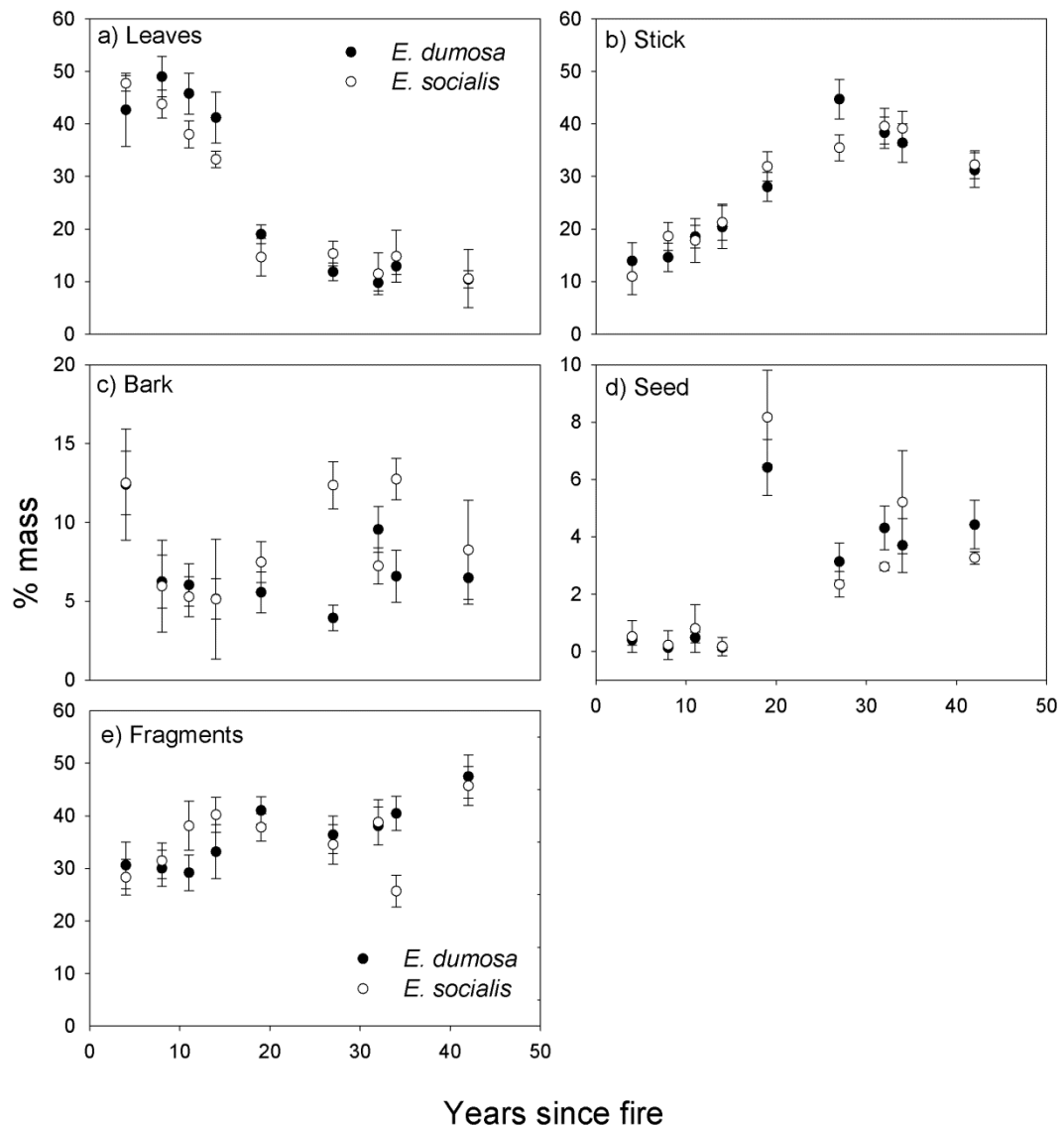


Figure 3-4. Mean (\pm SE) percent mass (\pm SE) for every burn site (years since fire) for each species' litter components: a) leaves b) bark c) stick d) seed and e) fragments. Black circles represent *Eucalyptus dumosa* and white circles represent *Eucalyptus socialis*.

However, there was no significant effect of species on litter bed composition ($P = 0.35$). Furthermore, there were significant interactions between our measure of patch size score and time since fire (Pseudo- $F_{8, 324} = 1.59$, $P = 0.025$) and between patch size score and species (Pseudo- $F_{8, 324} = 1.89$, $P = 0.004$) suggesting different rates of change in litter bed composition among burn sites and between species. Our Principal Component Analysis-derived score for litter composition (% mass) explained 55.9 % of the variation in litter composition (Table 3.1).

3. Post-fire litter bed accumulation

3.4.3 Tree, litter and fire as a system

For the leaf components of the litter bed, time since fire, canopy and litter bed area explained 55 % of the variation in the composition scores (Figure 3.5). We found that time since fire alone had the strongest, direct effect on the leaf components. Canopy area had a positive direct effect on the proportion of leaves, while litter bed area had a negative direct effect.

We identified different causal effects for each remaining component (e.g. sticks, bark etc.) separately (Table 3.2). For bark, the indirect effect of time since fire mediated by canopy area had a stronger causal effect than the direct effect of time since fire alone. Time since fire, mediated by litter bed area, was the strongest causal effect of sticks, seeds and fragments in our models.

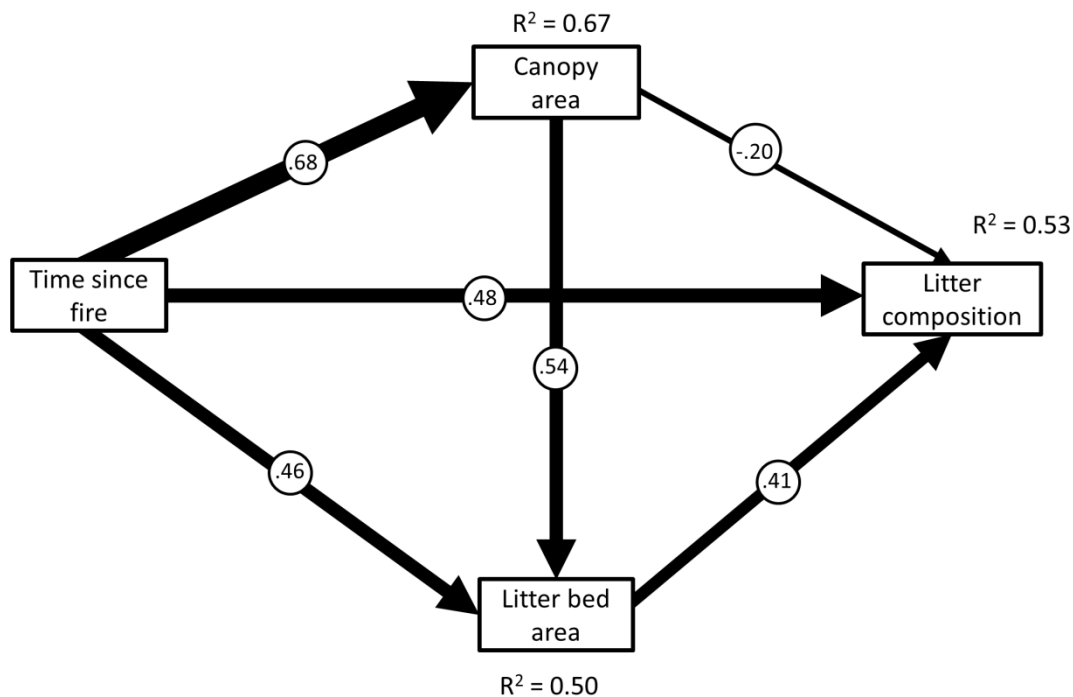


Figure 3-5. Time since fire–litter composition model. The R^2 value above litter composition indicates that canopy size, litter bed area and time since fire account for 53 % of the variance in litter composition. Thickness of pathways is directly proportional to the strength of the path coefficients. The model is saturated, therefore the Chi-squared statistic = 0 with 0 d.f.

Table 3.2. Path coefficients and goodness of fit tests for time since fire pathways for each component. Each row represents a model containing the response variable listed in the leftmost column. Otherwise, the model structure is identical to that in Figure 3.5, but with different path coefficients. The next five columns list the path coefficients corresponding to the direct and indirect pathways in the models. R^2 is proportion of variance explained in the response variables listed in the leftmost column. All tests reported here indicate a good fit. All models are saturated.

Response variable	Direct paths			Indirect paths		Model R^2
	TSF to individual component	Canopy area to component	Litter bed area to component	Time since fire via canopy area	Time since fire via litter bed area	
Leaves	0.43	0.27	-0.15	0.19	-0.07	0.55
Bark	0.03	0.06	0.06	0.04	0.03	0.11
Sticks	0.15	0.10	0.36	0.07	0.17	0.40
Seeds	0.06	0.10	0.46	0.07	0.21	0.35
Fragments	0.09	0.16	0.33	0.11	0.15	0.36

3.5 Discussion

Our study examined the post-fire development of multi-layered resource patches comprising trees, their canopies and associated litter beds in a eucalypt mallee community in eastern Australia. Using a space-for-time approach we measured the physical patch layers to monitor resource patch development by our landscape modulators. Consistent with our expectations, we found strong positive relationships between tree size and litter bed size, with patch size generally increasing with increasing time since last fire. Overall, there were no differences between the two eucalypt species, nor any trends between litter bed load (expressed as a mass per unit area) and time since fire. We did, however, find substantial shifts in litter bed composition which appeared to be driven largely by fire history.

3. Post-fire litter bed accumulation

3.5.1 Fire drives litter patch development

For many ecosystems, the processes surrounding post-fire litter dynamics, in particular, litter bed composition, are complex and poorly understood (but see Raison *et al.* 1983; Miller and Urban 2000; Haslem *et al.* 2011). We found strong relationships between fire history and the temporal development of a multi-layered resource patch system, comprising the tree stem and its canopy and litter bed. More importantly, we found significant relationships among each resource patch layer across all fire histories.

Our process model indicated that the indirect effect of fire history mediating litter bed area had a stronger effect on more litter bed components than the direct effect of fire history or the indirect effects of canopy area. This reinforces the notion that resource patch development by a landscape modulator is dependent upon its surrounding environment (Shachak *et al.* 2008). For example, recently burnt sites are characterised by greater wind speed due to surfaces lacking plant cover (Gill and Allan 2008), potentially enhancing aeolian transport of materials. We also observed smaller trees (< 2.3 m), with a higher proportion of leaves in the litter bed (~ 40 %) in recently burnt sites than sites burnt more than 20 years ago (~ 4.5 m tall, < 20 % leaves), suggesting that resource heterogeneity, in terms of litter composition, is occurring at broad scales. Resource heterogeneity is driven by processes occurring at multiple spatial scales. At a fine scale, landscape modulators drive resource patch development. Our data show that the temporal stage of litter patch development can define the quantity and composition of the litter. This patch development is intrinsically linked to broader scale processes such as fire. The mosaic of fire histories at a broader-scale leads to further resource heterogeneity. In terms of litter beds, a mosaic exists where sections of the landscape vary in terms of their litter quantity and composition.

The modelling of individual litter layer components indicated that leaves were the only resource component to have time since fire as the strongest causal factor. Three main

leaf attributes may account for the variation in litter bed leaf accumulation. Firstly, the production of leaf litter varies greatly over time, with relatively more leaves senescing in younger growth stages than in mature growth stages (Attiwill 1979). Also immediately after a fire, there appears to be a large input of leaves from stags that were not completely consumed by the fire. Secondly, the lanceolate shape of *Eucalyptus* spp. leaves allows them to be readily transported by wind. Senescing leaves may land directly in an existing litter patch or in the unvegetated interspaces where they can be subjected to redistribution processes (*sensu* Schlesinger *et al.* 1990). In the first few years after fire, mallee trees represent the only areas of resource accumulation until hummock grasses re-establish from seed (Cohn and Bradstock 2000). Thus litter beds receive proportionally less of the wind-transported leaves with increasing time since fire. Thirdly, relatively rapid decomposition rate of leaf material, compared with fine woody materials, results in a faster loss of leaves from mature litter beds, further decreasing the relative mass of leaves, and likely contributing to the relative increase of 'fragments' in the litter bed with greater time since fire.

The accumulation of more woody resource components in the litter bed is likely due to variations in litter fall rates and the build-up of recalcitrant material with inherently low levels of decomposition (Cornwell *et al.* 2008). We found that sticks, seeds and fragments increased with greater time since fire. However when modelled, these components were driven by a relatively stronger mediating effect of time since fire on litter bed area, suggesting that post-fire litter bed development plays an important role in their accumulation. Current literature predicts a greater accumulation of poorly decomposing woody components with greater time since fire (Miller and Urban 2000). Both fine and coarse woody material may take many years to decompose in semi-arid environments (Sinclair 2004), with < 25 % mass loss of buried root material after 53 months (Noble *et al.* 2009). Removal of leaf material would therefore likely lead to an increase in litter fragments, as we found in our model. Seeds were the smallest mass fraction of the litter bed, and did not appear in the litter bed until approximately 20 years after fire, when the canopy and litter bed were already well established. This is likely due to the serotinous nature of *Eucalyptus* spp. (Lamont *et al.* 1991).

3. Post–fire litter bed accumulation

Despite clear post–fire shifts in litter bed composition, we detected highly variable litter bed loads, expressed as a mass per unit area, with no trends with respect to fire history or tree size. Previous research in open woodland ecosystems indicates that litter loads under individual tree canopy crowns vary with tree size and distance from the main stem (Bradstock and Cohn 2002; McElhinny *et al.* 2010). For mallee, specifically, we found that litter load was largely independent of the diameter of the litter bed, supporting findings of Bradstock and Gill (1993). We focused on mid–bed litter loads, recording an average litter load of 1.5 kg m^{-2} across all fire histories, and within current estimates for mallee of 0.5 to 1.5 kg m^{-2} (Noble *et al.* 1984; Bradstock and Gill 1993). In general, larger trees have larger litter resource patches than smaller trees as larger litter loads reflect a greater crown volume per unit area of surface (McElhinny *et al.* 2010). This may also explain fine–scale patterns of litter arrangement, where litter depth attenuates with increasing distance from the main stem, reflecting the decrease in canopy volume with distance from the main stem (McElhinny *et al.* 2010).

Litter fall rates are generally species–specific (Miller and Urban 1999), however we found no significant difference in litter composition between our two species. It seemed possible that patch development in response to fire may differ between species, consistent with the notion of response diversity (*sensu* Elmqvist *et al.* 2003). However our two mallee species are basically structurally and functionally identical. As we found no difference between our two species, it might be possible to extrapolate these trends in litter bed composition across other mallee species that share the same structure and functional roles. This would be beneficial from a management perspective, where a one–size–fits–all approach may be taken more confidently when predicting litter composition.

3.5.2 Litter patch development affects fuel loads and fauna

Despite numerous studies on the succession of post-fire flora and fauna (Haslem *et al.* 2011; Kelly *et al.* 2011), there have been relatively few empirical insights into post-fire litter accumulation (Bradstock 2010). Litter is a crucial resource for fauna, providing habitat, foraging substrate and breeding resources (Haslem *et al.* 2011). From a functional perspective the accumulation of litter after fire is important, as fire alters landscape-level connectivity of different fuels, potentially affecting future fire regimes (Turner and Romme 1994; Miller and Urban 2000; Scarff and Westoby 2006). Changes to litter composition may shift fine-scale thresholds of fuel composition and connectivity. When optimal conditions for fine-scale connectivity occur in conjunction with optimal landscape and meteorological conditions for fuel connectivity, they could provide conditions required for the peak flammability observed in similar mallee communities (Noble 1989; Turner and Romme 1994; Bradstock *et al.* 2010).

Despite the recognition of fuel load and composition as important indicators of fire intensity, the complex composition of fuel is rarely considered in fuel load models (e.g. Scarff and Westoby 2006). This study provides new insights into the fine-scale shifts in fuel composition and complexity in response to fire history and patch size. Shifts in post-fire litter composition are important for predicting fire behaviour (Bradstock 2010) and may be useful in identifying the range of conditions or thresholds under which the arrangement of fuel components affects fire behaviour (Turner and Romme 1994). Fire return intervals of 15 to 30 years are typical of dune mallee ecosystems (Bradstock 1990; Noble and Vines 1993). In our study, we found a ~ 20 % decrease in the proportion of leaves, and ~ 20 % increase in sticks in the 15–30 years period since fire. At greater times since fire, fragments account for more than 40 % of proportional litter bed mass. Changes in composition affect litter bed flammability by altering the combustion rate, silica-free mineral content, low heat value, surface area to volume ratio, particle density, ventilation and depth of the litter bed (Bradstock and Gill 1993; van Wagendonk *et al.* 1996; Scarff and Westoby 2006), which ultimately affect the potential fire intensity. Specifically, leaves are well-ventilated and readily combustible

3. Post–fire litter bed accumulation

(Scarff and Westoby 2006). Sticks, however, require greater energy to combust, but will produce a much more intense fire, and likely structure a well–ventilated litter bed. In contrast, fragments are densely packed, and induce a low intensity, smouldering fire because of the poor ventilation (Schwilk and Caprio 2011). Therefore, shifts in composition will alter fuel properties. In light of our results, time since fire plays a significant role in determining fuel properties of the litter bed, with evidence to suggest that peaks in community flammability coincide with peaks in fuels that burn at relatively high intensities.

At any given time, the resource patches associated with our landscape modulators will be in different developmental stages across the landscape as a result of a mosaic of fire histories. The development stage of resource patches will determine fuel connectivity and thus potential flammability at a local scale (i.e. within an area of common fire history). Also, the connectivity of areas with different potential flammability (as determined by fire history) will affect fuel connectivity at a landscape scale. The connectivity and potential flammability of mosaics is critical to fire management strategies. From a biotic perspective, this mosaic is crucial for landscape–scale diversity in habitat and resources.

In mallee, particularly, the interactions among fire history and litter bed cover and composition have important outcomes for litter–dependant flora and fauna. This interaction can also affect soil stability by limiting the area colonisable by biological soil crusts (Eldridge and Bradstock 1994). The litter layer is a resource and its availability can affect the sheltering, feeding and breeding habitats of ground–foraging birds, litter dwelling reptiles, and ground dwelling mammals (Kelly *et al.* 2010; Haslem *et al.* 2011; Kelly *et al.* 2011). Litter can also directly influence the distribution and abundance of arthropods (Schlesinger *et al.* 1997). To effectively incorporate our knowledge into management plans, we need to understand the basics of these fundamental interactions. Morton *et al.* (2009) draw attention to the importance of recognising the subtle differences, such as shifts in litter composition, in these interactions between

different components of ecological communities, particularly in the face of climate change and therefore altered fire regimes.

3.6 Conclusions

The importance of episodic events, such as fire, and their effects on ecosystem structure and function, are well recognised (Stafford Smith and Morton 1990; Morton *et al.* 2009). However, there is a general lack of knowledge surrounding the processes driving the recovery of ecosystems after such episodic events. Fundamental shifts in ecosystem structure and function, such as shifts in landscape modulation and resource patch creation and development have, for the most part, been widely assumed and quantitatively ignored. Here we present a quantitative description of post-fire modulation and resource patch development in a dune mallee ecosystem. Although we focus on the physical components, there is much further scope for quantifying entire resource patch development, such as shifts in soil nutrient concentration.

Understanding the functional response of ecosystems to episodic events such as fire and the successional processes affecting flora and fauna can allow us to improve our predictions about how vegetation will likely change with projected changes in climate (Morton *et al.* 2011). Here we have demonstrated the complexities involved in post-fire litter accumulation. More specifically, we have shed light on post-fire trends in litter accumulation, a fundamental component of patch development. Patch creation and development are the basis of ecosystem function. By understanding how landscape modulators and their surrounding environment influence the development of patches, we are in a better position to predict how changes in these drivers are likely to affect ecosystem processes.

3.7 Acknowledgements

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3. Post–fire litter bed accumulation

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3. Post-fire litter bed accumulation

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Chapter 4. Evidence for the spatial self-organisation of litter patches in a semi-arid woodland

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Keywords: litter dynamics, mallee, organization, power law, shrubland.

Abbreviations:

ANOVA — Analysis of Variance

CWD — Coarse Woody Debris

LISA — Local Indicator of Spatial Association

PERMANOVA — Permutational Multivariate Analysis of Variance

Q-Q — Quantile-Quantile

SADIE — Spatial Association by Distance Indices



Litter patches in a Sand Plain Mallee Woodland

4.1 Abstract

In arid and semi-arid ecosystems, regular and irregular patterns commonly form in the arrangement of perennial vegetation. Multiple mechanisms have been proposed to explain this self-organisation phenomenon, such as scale-dependent feedbacks and disturbance recovery mechanisms. There is, however, limited empirical evidence for the spatial self-organisation of leaf litter despite its obvious presence within the self-organised vegetation patches. This study aims to measure the spatial association between litter patches and perennial vegetation patches and to identify whether surface litter is self-organised via mechanisms consistent with scale-dependent feedbacks and or disturbance-recovery mechanisms. We measured the cover, size distribution and spatial arrangement of perennial vegetation patches and surface litter patches in three semi-arid open woodland communities. The density of shrubs in one of the communities had been modified by vegetation clearance 50 years prior, providing a 'cleared' and 'uncleared' analogue of this community. Across all communities we found a high correlation in the percent cover between litter and perennial patches but a low to moderate spatial association between them. There was also a mismatch with the size of litter patches and perennial patches, with large perennial patches tending to form multiple smaller litter patches. The effects of prior vegetation clearance were still evident 50 years later, with greater perennial patch cover and greater variability in surface litter arrangement. The variability of litter patches was positively correlated with the distance between perennial patches in the undisturbed communities but strongly negatively correlated in the cleared analogue. We found no evidence to support scale dependent feedbacks occurring between litter and perennial patches with perennial patch size not affecting the strength of its association with litter. The distribution of litter patch sizes however, was consistent with a truncated power law relationship, suggesting that disturbance-recovery mechanisms may play an important role in spatial self-organisation of litter.

4.2 Introduction

Spatial self-organisation is a phenomenon evident in a broad range of ecosystems (Rohani *et al.* 1997; Peterson 2002; Rietkerk and Van de Koppel 2008). Spatial self-organisation is a process where initial disordered conditions are transformed into large-scale patterns through smaller-scale, dissipative interactions among organisms and their environment (Kessler and Werner 2003; Rietkerk and Van de Koppel 2008). Spatial organisation manifests itself as a wide range of large- and intermediate-scale, regular and irregular patterns, forming shapes such as spots, stripes, labyrinths, bands, rings and polygons (Ludwig *et al.* 1999a; Tongway *et al.* 2001; Kessler and Werner 2003). Such regular and irregular patterns have been observed in intertidal mussel beds (Guichard *et al.* 2003), fire-prone forests (Malamud *et al.* 1998), polar and high alpine stone and soil arrangement (Kessler and Werner 2003), savannah vegetation cover (Lejeune *et al.* 2002) and semi-arid vegetation cover (Rietkerk *et al.* 2002; Kefi *et al.* 2007). While regular patterns are generally easy to model, the irregular patterns are more difficult as they tend arise where abiotic features or processes, such as variation in topography or soil amplify slight small-scale variability (Klausmeier 1999). Understanding the mechanisms behind spatial self-organisation is a key component of managing self-organised systems, as the patterns are important drivers of ecological diversity, stability and resilience in these systems (D'Odorico *et al.* 2005; Pascual and Guichard 2005; Rietkerk and Van de Koppel 2008).

Spatial self-organisation has been explained by a variety of mechanisms such as oscillating consumer-prey interactions (Rohani *et al.* 1997), scale-dependent feedbacks (Rietkerk and Van de Koppel 2008) and disturbance-recovery mechanisms (Pascual and Guichard 2005). Scale-dependent feedbacks involve a feedback cycle between an organism and its environment which switches from being positive at small scales to negative at larger scales (Rietkerk and Van de Koppel 2008). Positive feedbacks may involve organisms modifying the environment to facilitate the survival of others. Negative feedbacks occur at a large scale when, for example, organisms deplete resources, resulting in competition. In the case of water availability in arid

4. Self-organisation of surface litter

systems, perennial vegetation facilitates seedlings at small spatial scales by creating conditions that enhance water availability through increased shade, reduced temperatures, reduced wind speed, and higher soil infiltration (Bertness and Callaway 1994). At larger scales, however, there is competition for the limited water resources. These scale-dependent feedbacks result in the spatial self-organisation of vegetation (Klausmeier 1999; HilleRisLambers *et al.* 2001; Rietkerk *et al.* 2004). In comparison, the disturbance-recovery mechanisms can be applied at any level of organisation, spatial or temporal, as an adaptive cycle of an ecosystem (Pascual and Guichard 2005). Disturbance-recovery mechanisms involve a large-scale disturbance prompting small-scale interactions to promote recovery. Some types of disturbance-recovery mechanisms, such as self-organised criticality (Pascual and Guichard 2005) or robust scaling (Guichard *et al.* 2003; Kefi *et al.* 2011) can result in the size-frequency of clusters produced being best described by a power law relationship, i.e., the number of patches appears as a straight line when plotted as a function of patch size on a logarithmic scale. Scale-dependent feedbacks and disturbance-recovery mechanisms have both been applied to the way in which perennial vegetation functions and self-organises in arid and semi-arid ecosystems (Rietkerk and Van de Koppel 2008; Kefi *et al.* 2011).

Shrubs, trees and perennial grasses are critically important patch types for functioning ecosystems, particularly in resource-limited arid and semi-arid environments (Schlesinger *et al.* 1990; Ludwig and Tongway 1995). Perennial vegetation is known to facilitate (Callaway 1995; Brooker and Callaway 2009), engineer (Jones *et al.* 1994; Hastings *et al.* 2007) and modulate (Shachak *et al.* 2008; Travers and Eldridge 2012) landscapes by concentrating essential resources into discrete zones in the landscape (resource-rich patches, fertile patches, resource islands). These patches retain soil, water, nutrients and leaf litter, providing essential resources for patch-dependent taxa (Shachak *et al.* 2008; Badano and Cavieres 2006) and increasing the efficiency with which resources are allocated and used (Schlesinger *et al.* 1990; Ludwig and Tongway 1995; Rietkerk *et al.* 2011). Leaf litter is a particularly important resource as it provides fuel for fire, a source of carbon, nitrogen and other trace elements, and feeding,

breeding and sheltering habitat for a variety of arthropods, reptiles, mammals and birds (Haslem *et al.* 2011). Leaf litter is often spatially associated with its source, and there is a suggestion that the properties of the litter bed are strongly linked to those of the canopy from where the material is derived (McElhinny *et al.* 2010; Travers and Eldridge 2012). While leaf litter generally accumulates around the base of perennial vegetation, there is limited empirical evidence for the spatial self-organisation of leaf litter despite its obvious presence with self-organised vegetation patches.

This study focuses on field evidence to support the notion that leaf litter self-organises in response to the arrangement of perennial patches. It aims to identify the mechanisms involved in driving the spatial self-organisation of leaf litter. Our study was conducted in a semi-arid woodland where the modulation of litter by woody plants has been shown to be a substantial biophysical process (Travers and Eldridge 2012). Our system allowed us to examine a group of woody modulators (trees and shrubs, *sensu* Shachak *et al.* 2008), whose size and spatial distribution vary among different geomorphic locations. We examined the spatial pattern of perennial patches and litter patches in a dune-swale ecosystem comprising different complements of woody modulators, ranging from a community dominated by eucalypt trees lacking a woody understorey, through to a more open community of eucalypts with isolated shrubs, to an open woodland with and without a dense shrubby understorey resulting from previous soil disturbance.

Our study was carried out in an area that (1) had not burned in over 50 years, (2) has a short history of light grazing-induced disturbance (Westbrooke 2012); and (3) is currently free from any disturbance effects created by introduced mammalian herbivores. This allowed us to examine the undisturbed process of litter patch formation and spatial organisation. We expected to find litter patterns consistent with either scale-dependent feedback mechanisms or disturbance-recovery mechanisms, or a combination of both. We hypothesised that if litter accumulates around perennial patches consistent with a positive feedback mechanism, the strength of the association between a perennial patch (modulator) and associated litter patch would

4. Self-organisation of surface litter

be dependent upon the size and spatial arrangement of perennial patches. If litter accumulates consistent with a disturbance–recovery mechanism, we should find evidence of power–laws in the size class distribution of litter patches. To test this, we measured the cover, size distribution and spatial arrangement of perennial patches and patches of surface litter, independently, to assess their degree of association and alignment.

4.3 Methods

4.3.1 Study site

Our study was undertaken within the Australian Wildlife Conservancy’s Scotia Sanctuary in south western, New South Wales, Australia (33°43’ S, 143°02’ E). This area is semi–arid, receiving about 250 mm annual rainfall. Rainfall is highly spatially and temporally variable, across a scale of tens of kilometres. Average daily winter (July) temperatures range from a minimum of 6 °C to a maximum of 17 °C while summer (January) daily temperatures range from a minimum of 19 °C to a maximum of 33 °C (BOM 2012). The soils at our site are mainly calcareous, brownish and siliceous sands. Our specific study area had not been burned by wildfire for more than 40 years.

Data were collected from four vegetation communities; three were in “natural” states and one a modified state with significantly different vegetation composition to its “natural” analogue. All four communities occur in a repeated pattern across the Scotia landscape (Westbrooke *et al.* 1998). Dune Mallee Woodland (henceforth known as dune) occurs on the sandy dune crests of long, low (relief to 7 m) east–west trending sand dunes. The overstorey vegetation is dominated by eucalypt mallee trees (*Eucalyptus gracilis*, *E. dumosa* and *E. socialis*) and the understorey by scattered perennial hummock grasses (*Triodia scariosa* N.T. Burb). Shrub cover to 2 m is sparse on the dunes (Keith 2004). Semi–arid Sand Plain woodlands (henceforth known as Uncleared plain or cleared plain; see below) occurs on soil with alkaline calcareous subsoils, supporting the growth of large (to 8 m tall) *Casuarina pauper* Auth. trees,

which are the dominant overstorey species. Other perennial species dominating this community include *Alectryon oliefolius* subsp. *canescens*, *Eremophila sturtii*, *Senna artemisioides* and *Dodonaea viscosa* subsp. *angustissima*. Some areas of this community had been cleared during the 1960s (cleared plain), with widespread removal of the large *C. pauper* trees. The remains of these trees are still visible on the surface where they form large debris piles of coarse woody debris. Sand Plain Mallee Woodland (henceforth known as swale) occurs as a transitional community between the dunes and the plains. The overstorey is dominated by Eucalypt mallee trees (*E. gracilis*, *E. dumosa*, *E. socialis*), while the understorey is dominated by the perennial shrubs *Eremophila sturtii*, *Senna artemisioides*, *Dodonaea viscosa* subsp. *angustissima* and *Acacia burkittii* (Westbrooke *et al.* 1998; Keith 2004).

4.3.2 Field measurements

Data were collected from nine replicate sites in each of the four communities (Dune, Swale, Uncleared Plain and Cleared Plain, N = 36) in January 2009. At each site we established a 50 m long by 2 cm wide transect along which we measured, using the line–intercept method, the cover of two types of patches; (1) perennial patches associated with tree and shrub canopies, and coarse woody debris (logs, stumps and sticks > 5 cm across) to the nearest 1 cm (henceforth ‘perennial patches’) and (2) surface–resident litter patches (henceforth ‘litter patches’, ≥ 2 cm across the litter patch) to the nearest 1 cm. We also recorded the type of perennial patch i.e. tree, shrub, coarse–woody debris.

4.3.3 Cover of perennial and litter patches

We used linear regression (Minitab 2010) to examine potential relationships between the cover of perennial patches and litter patches based on the percentage of the transect that they occupied. We used a one–way ANOVA to compare the percentage cover of perennial and litter patches among communities. All data, except total

4. Self-organisation of surface litter

combined perennial patches, were \log_{10} -transformed to meet the assumptions of ANOVA.

4.3.4 Size distribution of perennial and litter patches

To compare the sizes of perennial and litter patches among communities, we plotted the normalised frequency distribution of their patch sizes, after \log_{10} transformation, using bin widths of 0.1 increments (i.e. 0–0.1, 0.11–0.2 etc) (White *et al.* 2008). Truncated power laws with an exponential cut-off ($ax^b \cdot \exp^{-c \cdot x}$) (Pueyo 2011) were fitted to the size frequency distributions for each of the 36 transects. To compare potential differences in perennial patch and litter patch sizes among communities, we used a one-way Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson *et al.* 2008) on a matrix of 36 sites by the three parameters of the truncated power law equations (a, b, c). Data were analysed with 9999 unrestricted permutations of the raw data with Type III error.

Due to the large differences in the number of perennial patch sizes and the number of litter patch sizes within each community, we used two methods to compare their size distributions. Firstly, two sample Mann–Whitney U tests were used to compare the medians of patch sizes (Minitab 2010). Secondly, we used two-sample Quantile–Quantile plots which, by visual inspection, compare whether the distribution of patch sizes is equivalent i.e. whether they follow a 1:1 line. If the distribution of patches is different, the differences in variance (deviations from the 1:1 line), size (either above or below the 1:1 line) and relationship (e.g. non-linear, skewed distributions) can be determined (Thas 2010). Quantile–Quantile plots were constructed using the ‘stats’ package in R (version 15.2, R Core Team 2012).

4.3.5 Spatial distribution of perennial and litter patches

The spatial arrangement of perennial and litter patches was determined with Spatial Association by Distance Indices (SADIE, Perry 1998; Perry *et al.* 1999). SADIE is

designed to measure properties of the spatial arrangement of count, binary or continuous data that are not required to meet any particular distribution prior to analysis. This method is based on a 'distance to regularity', where a regular state is where all sampling units have the same value of the measured variable. The distance to regularity is the distance that the measured variable would need to move to achieve this arrangement. The division of each distance by the mean distance gives an index of aggregation (I_a), which indicates whether the units are clumped ($I_a > 1$), regular ($I_a < 1$) or randomly ($I_a \approx 1$) distributed. SADIE also produces an index of clustering (v), which measures the degree to which the objects under consideration cluster into patches (areas with above average values; $v_i > 1.5$) or gaps (areas with below average values; $v_j < -1.5$).

To determine the association between litter and perennial patches we used a Local Indicator of Spatial Association (LISA, Anselin 1995; Perry and Dixon 2002). This calculates the relative contribution of each sampling unit towards (χ) the overall correlation coefficient (X) between perennial plant and litter patch distributions (Perry and Dixon 2002; Maestre 2003). From the SADIE index of clustering (v_k) the local spatial association for each unit k , and the overall correlation are determined by (Winder *et al.* 2001; Perry and Dixon 2002):

$$\chi_k = n(v_{k1} - q_1)(v_{k2} - q_2) / [\sum_k (v_{k1} - q_1)^2 \sum_k (v_{k2} - q_2)^2]^{0.5}$$

$$X = (\sum_k \chi_k) / n$$

Here v_{k1} and q_1 represent the cluster indices and their mean for the litter patches while v_{k2} and q_2 represent the perennial patches. In our study, the total number of sampling units (n) was 500 with each unit representing 10 cm of summed binary data. Positive values of χ_k indicate the coincidence of patches or gaps in both data sets, while negative values indicate a misalignment, with a patch occurring in one data set and a gap in the other (Winder *et al.* 2001).

4. Self-organisation of surface litter

To test for similarities in spatial arrangement between the cover of perennial and litter patches we constructed semi-variograms for each patch type at each site. We used binary data to indicate the presence (1) or absence (0) of a patch to the nearest centimetre for each 50 m transect prior to analysis. The semi-variograms provide two measures of the spatial arrangement of the data: (1) the nugget (C_0), which represents the random variance occurring at a scale less than that used for field sampling; and (2) the range (A_0), the distance separating sampling points at which semi-variance reaches an asymptote or the maximum range of autocorrelation. The magnitude of spatial structure was obtained using the index of $C / (C_0 + C)$, where C is the difference between the nugget and the sill ($C_0 + C$). A greater proportion of the total sample is spatially structured if the index approaches 1. Our semi-variograms fitted well with spherical models, which have been proven useful in the interpretation of two-dimensional spatial data (e.g. Wang *et al.* 2007). The spherical models had high r^2 , minimal extrapolation of semi-variance at spatial scale < 5 cm, and fitted model shape (e.g. Wang *et al.* 2007). Semi-variograms were modelled with the GS⁺ software Vers. 9 (Robertson 2000).

To compare the spatial indices, we used Permutational Multivariate ANOVA (PERMANOVA). Resemblance matrices were constructed with Euclidean distances and data analysed with 9999 permutations with Type III error rates (Anderson *et al.* 2008). All spatial indices (I_a , v_i , v_j , A_0 , C_0 , $C_0 + C$, $C / (C_0 + C)$) with the exception of X , were compared in a mixed-models PERMANOVA with community and patch type as fixed factors. The first stratum considered Community, and the second stratum Patch (Perennial vs. Litter), and its interaction with community. We were most interested in the interaction, in order to determine whether the spatial indices for each patch type varied with community. The degree of association between litter and perennial patches X , in relation to the single fixed factor community was analysed with a one-way PERMANOVA (Anderson *et al.* 2008).

To determine whether the strength of the association between perennial patches and litter patches differed between perennial patch sizes and types (X_{tree} , X_{shrub} , X_{CWD}), we

plotted LISA values (X) against perennial patch size and fitted a linear regression model. Perennial patch size was $\ln(x)$ transformed prior to analysis. To further explain the spatial patterns in our data, we considered the semi-variogram range, A_0 . The A_0 is generally driven by the size of the anomalies in the landscape (Barnes 2004), such as, in our case, perennial plant patches. To determine if perennial patches are driving the scale of maximum litter variability, we used a Pearson's correlation to determine the strength of the linear relationship between litter variance (A_0) and the mean and median size of the perennial patches, and the mean and median size of the inter-patch (bare) areas.

4.4 Results

4.4.1 Cover of perennial and litter patches

The cover of litter patches increased strongly with increases in the cover of perennial patches ($F_{1,34} = 105.00$, $P < 0.001$, $R^2 = 0.76$; Figure 4.1). Perennial patch cover varied significantly among the four communities ($F_{3,32} = 3.88$, $P = 0.018$; Figure 4.2), with the greatest cover in the dunes and the least cover in the uncleared plains. Similarly the cover of litter patches was also greatest in the dunes, and lowest in the uncleared plains ($F_{3,32} = 5.64$, $P = 0.003$; Figure 4.2). The composition of perennial patches also varied significantly among communities, with the greatest tree cover in the dunes ($F_{3,32} = 13.7$, $P < 0.001$) and greatest shrub cover in the uncleared plains ($F_{3,32} = 28.7$, $P < 0.001$; Figure 4.2). The cover of coarse woody debris (CWD) did not differ significantly among communities ($P = 0.11$).

4.4.2 Size distribution of perennial and litter patches

We found no differences in the modelled distribution of perennial patch size between the communities (Figure 4.3a), with no significant differences in the three model parameters describing the shape of the truncated power law curve ($P = 0.57$; Figure 4.3a; Appendix 4.1). For litter patches, however, we detected significantly smaller

4. Self-organisation of surface litter

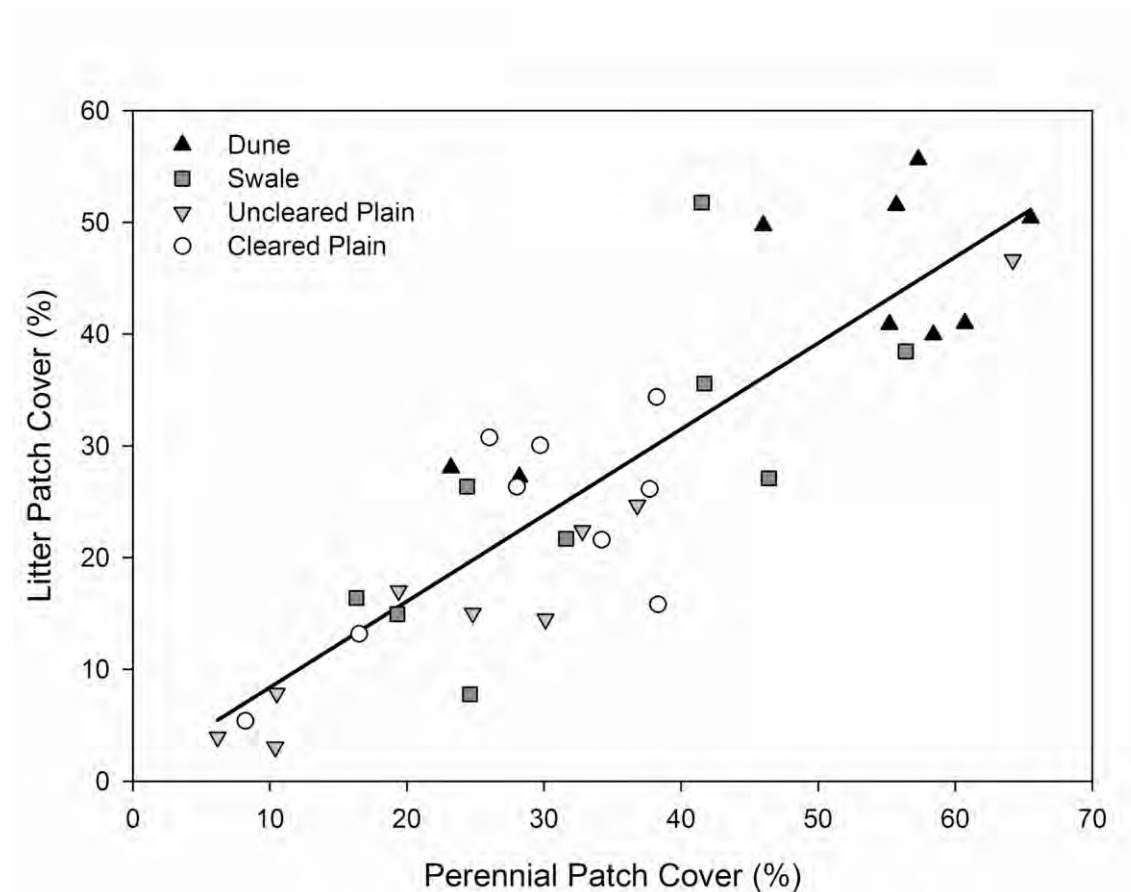


Figure 4-1. The cover of litter patches (% cover) in relation to the cover of perennial patches (% cover). A strong linear relationship exists between perennial patch cover and litter patch cover across all communities, with an increase in patch cover from plains to swale to dune communities. Regression equation: Litter cover (%) = $0.77 \times$ Perennial patch cover (%) + 0.68; $R^2 = 0.76$.

patch sizes in the uncleared plain than the other communities (*Pseudo- $F_{3, 32} = 5.27$; $P = 0.0017$*), as indicated by the earlier peak in size frequency, and a steeper decline for the uncleared plains, relative to the remaining communities (Figure 4.3b).

Within each community, however, there were significant differences in the size distribution of perennial and litter patches (Mann–Whitney $W > 63\,425$, $P < 0.001$). For perennial patches compared with litter patches, the median size of perennial patches was 53 cm larger in the cleared plain, 63 cm larger in the dunes, 72 cm larger in the uncleared plains and 90 cm larger in the swales, (position of peaks in Figure 4.3a c.f. Figure 4.3b). For all communities perennial patches were larger than litter patches,

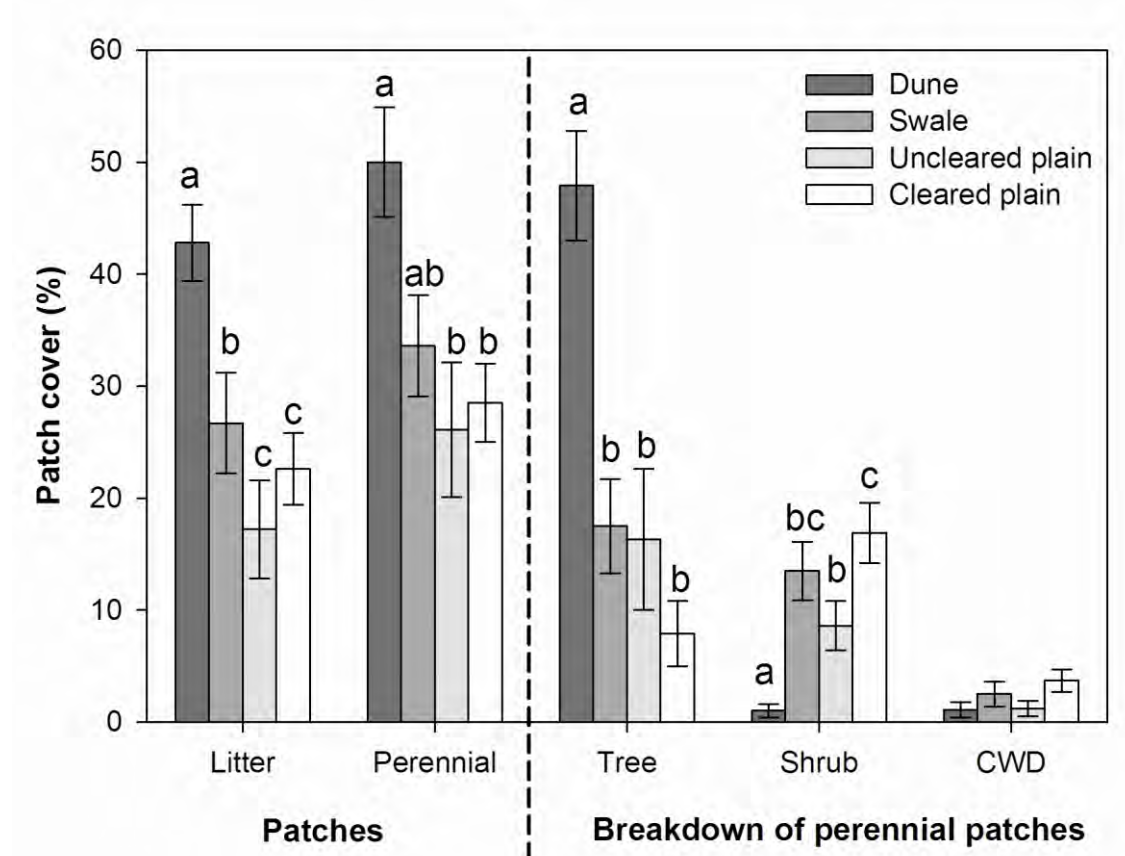


Figure 4-2. Average cover (%) of Litter and (combined) Perennial patches, and the contribution of each perennial patch type and litter patches in each community. Within a component, different superscripts indicate a significant difference in means at $P < 0.05$. All patches = all perennial patches combined; CWD = coarse woody debris.

with the plotted points on the Quantile–Quantile plots consistently falling above the 1:1 line (Figure 4.4). The fact that plotted points did not follow the 1:1 line suggests that the variance in perennial patch size exceeds that of litter patch size. The non-linear relationship between the perennial patch size and litter patch size indicates substantial differences in the mean and variance of the distributions, with the largest patch sizes not always producing the largest patches of litter.

4. Self-organisation of surface litter

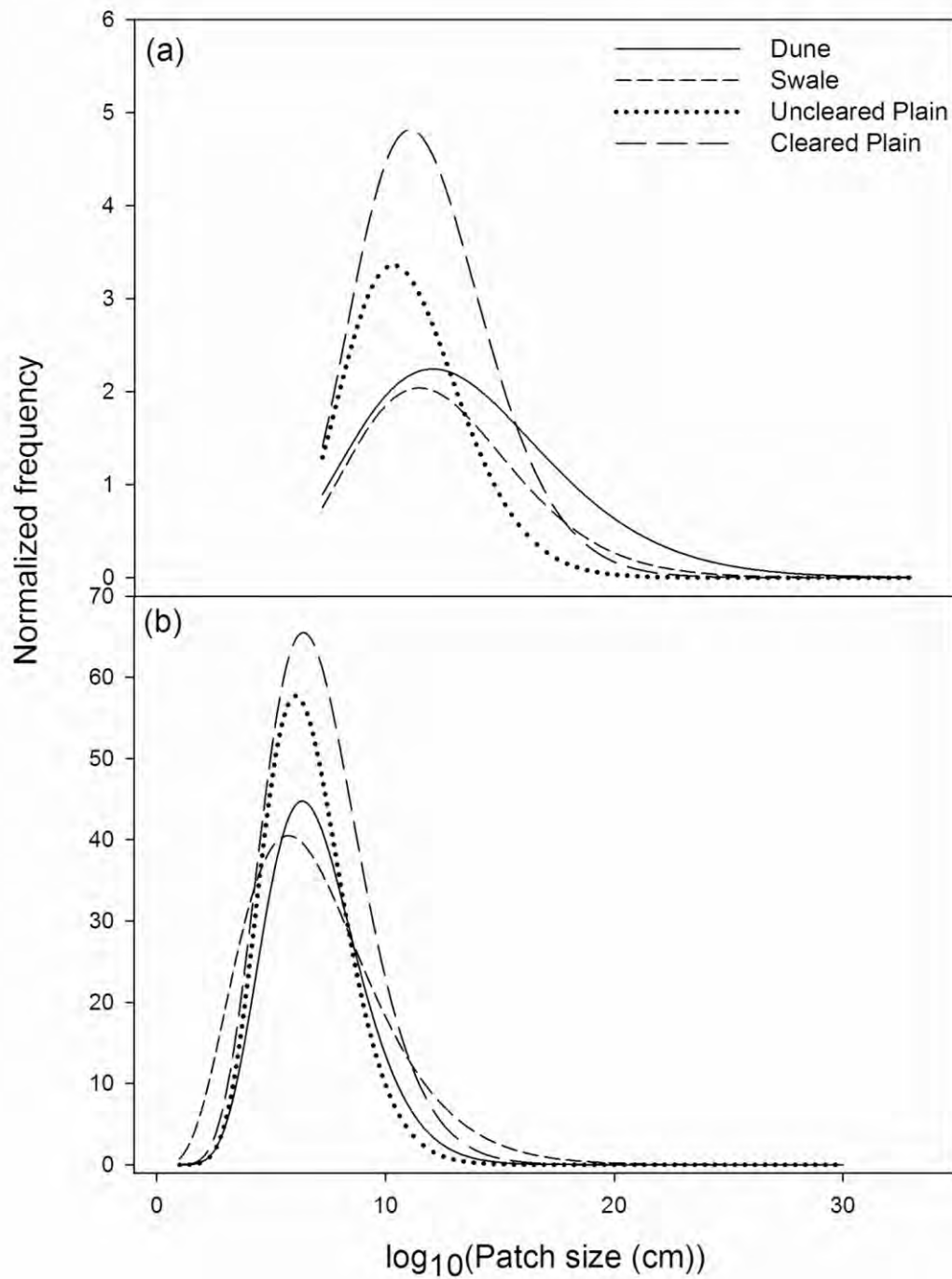


Figure 4-3. Summed patch size distributions for a) perennial patches and b) litter patches for each community. Patch size distributions were summed across all replicates and fitted with a truncated power law, using an exponential cut off ($y = ax^b \cdot \exp^{-c \cdot x}$). Model parameters are given in Appendix 4.1.

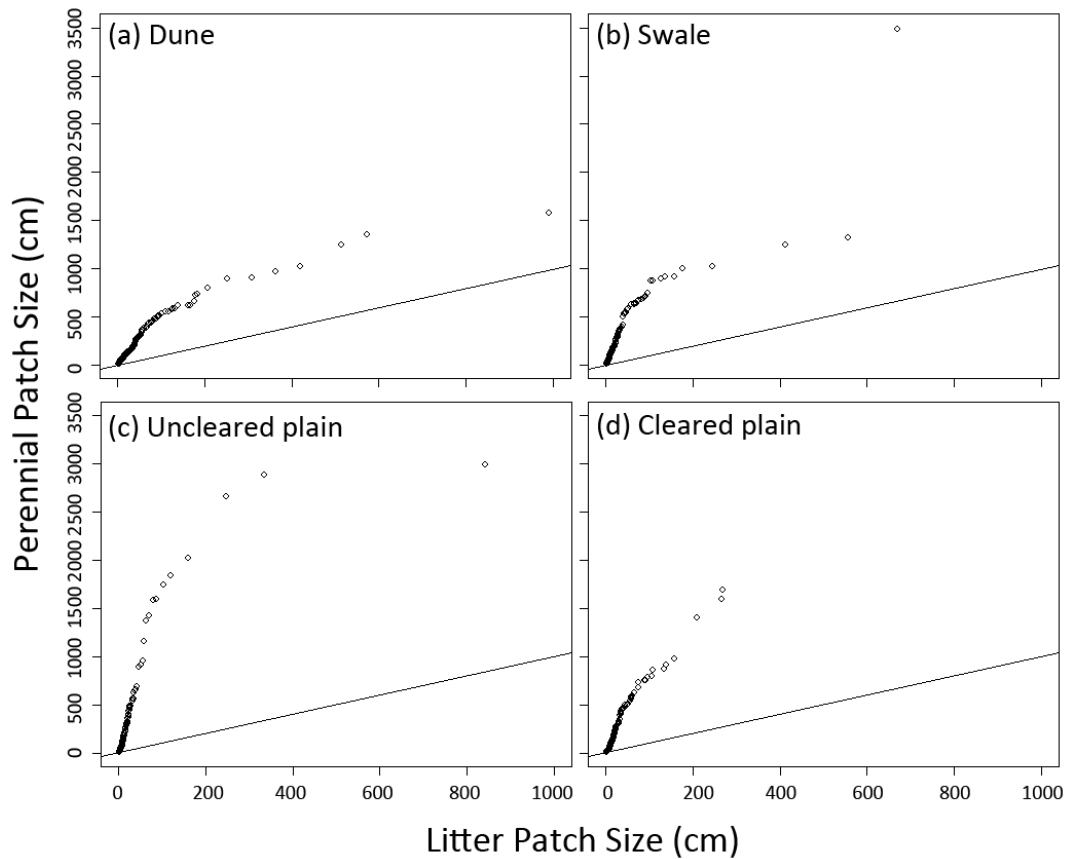


Figure 4-4. Quantile–Quantile plots of litter patch size distribution (x axis, cm) compared with perennial patch size distribution (y axis, cm) for a) dune b) swale c) uncleared plain and d) cleared plain communities. The line in each plot represents $x = y$ (1:1 line).

Spatial distribution of perennial patches and litter patches

Perennial patches and litter patches were spatially clumped ($I_a \gg 1$; Table 4.1), with clearly defined “patch” and “gap” configurations for both patch types across all communities ($v_i \gg 1.5$; $v_j \gg -1.5$; Table 4.1). The index of aggregation and degree of clustering were greatest in the swales and least in the cleared plains for both patch types, though there were only significant differences among communities in the degree of clustering into “patches” (v_i : $Pseudo-F_{3, 32} = 3.07$; $P = 0.040$; Appendix 4.2). There were no significant differences between litter and perennial patches for any of the other SADIE indices (I_a : $P = 0.26$; v_i : $P = 0.50$; v_j : $P = 0.56$; Appendix 4.2).

4. Self-organisation of surface litter

The degree of association (X) between the perennial patches and litter patches was moderate, with mostly positive correlations between the arrangement of both patch types in all communities (Figure 4.5; Table 4.1). There were no significant differences in the degree of association between perennial patches and litter among the communities ($P = 0.58$). Local association (χ_k) between perennial and litter patches ranged from -12.2 to 28.3 across all communities, with 30 % of local associations negative.

The size of perennial patches did not appear to enhance the strength of their association with litter patches. Though there were weak positive relationships ($R^2 \leq 0.06$) between perennial patch size and the strength of the local associations for perennial patch type (X_{shrub} , X_{tree} , X_{CWD} ; Appendix 4.3), this relationship was only significant for shrub and tree patches (Shrub: $X_{\text{shrub}} = 0.17 \times \ln(\text{patch size}) - 0.26$; $F_{2, 229} = 3.99$; $P = 0.70$; $R^2 = 0.01$. Tree: $X_{\text{tree}} = 0.27 \times \ln(\text{patch size}) - 0.68$; $F_{2, 229} = 15.79$; $P < 0.001$; $R^2 = 0.06$).

Table 4.1. Summary of SADIE and LISA indices for each patch type and each community. Peren. = perennial patch. Superscripts indicate significant differences.

Landform	Patch Type	Index of aggregation		Clustering into patches		Clustering into gaps		Association	
		I_a	SE	V_i	SE	V_j	SE	X	SE
Dune	Litter	6.48	1.0	6.80 ^a	1.1	-7.15	1.3	0.51	0.12
	Peren.	5.79	0.9	5.96 ^a	0.9	-6.66	1.3		
Swale	Litter	7.75	1.6	9.49 ^{ab}	2.2	-8.60	1.8	0.64	0.06
	Peren.	7.36	1.4	9.44 ^{ab}	2.3	-8.19	1.6		
Uncleared	Litter	6.49	1.1	7.17 ^a	1.1	-6.94	1.2	0.50	0.12
Plain	Peren.	6.14	1.1	6.93 ^a	1.3	-6.86	1.4		
Cleared Plain	Litter	4.58	0.8	4.74 ^b	1.0	-4.55	0.7	0.47	0.09
	Peren.	4.46	0.3	4.80 ^b	0.5	-4.61	0.4		

Most perennial patches appeared to accumulate litter (Figure 4.5), though litter patches may occur without spatial association with a perennial patch. Furthermore, larger perennial patches were sometimes associated with a number of smaller litter patches rather than a single large litter patch (Figure 4.5), providing further support for our Q–Q plot analyses. This phenomenon was particularly evident in the cleared plains (Figure 4.5).

The spatial distribution of litter and perennial patches had a high proportion of structured spatial variance in all communities (structural component: $C / (C_0 + C) > 0.6$; Nugget: $C_0 < 0.09$; Table 4.3; Appendix 4.4). However, there were no significant differences in the proportion of spatially structured variance among communities ($C / (C_0 + C)$: $P = 0.16$; C_0 : $P = 0.12$; Table 4.2; Appendix 4.2). The distance over which patch distributions were autocorrelated (Range: A_0), did not differ significantly among

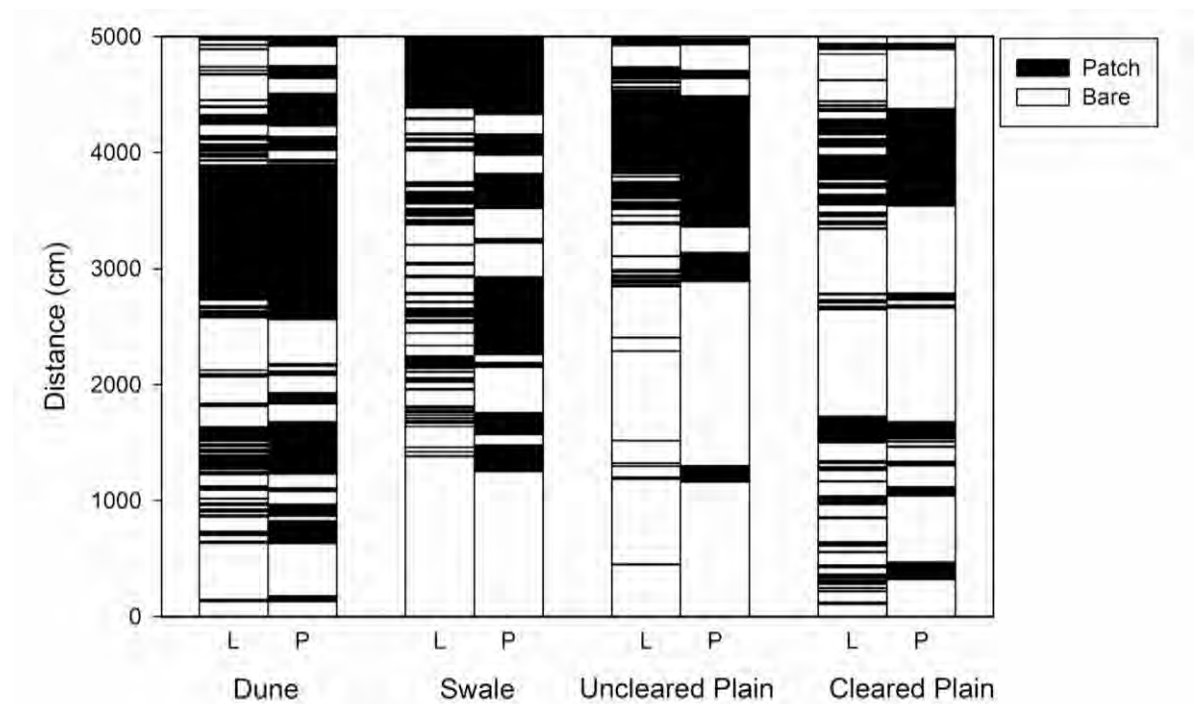


Figure 4-5. The distribution of litter (L) and perennial patches (P) at a typical site for each community. The black represents the presence of a litter or perennial patch and the white indicates the bare inter-patch area.

4. Self-organisation of surface litter

communities for either perennial or litter patches (Community: $P = 0.08$; Patch: $P = 0.09$; Table 4.2). The cleared plains, however, had the smallest range for perennial and litter patches, indicating that it had the highest spatial variability of the four communities sampled.

With the exception of the cleared plains, the average range of litter was greater than the average range of perennial patches within each community, indicating that perennial patches are more spatially variable than litter patches. The range of the semi-variogram is often correlated with the average size of physical anomalies within the landscape, however, there were relatively weak correlations between the range and the mean or median patch size for all four communities ($r < 0.65$; Table 4.3). Rather, we found relatively strong correlations between the semi-variogram range (A_0) and the size of the inter-patch areas, (i.e. the unvegetated areas between perennial patches) for both the swales and cleared plains ($r > 0.81$; Table 4.3).

Table 4.2. Averaged semi-variogram parameters for litter and perennial patch data for each community. All models were spherical.

Community	Patch type	Nugget (C_0)	Sill ($C_0 + C$)	Range (m) (A_0)	Structural Component $C/(C_0 + C)$	R^2
Dune	Litter	0.069	0.28	16.66	0.78	0.67
	Perennial	0.041	0.24	6.02	0.84	0.59
Swale	Litter	0.024	0.21	12.67	0.90	0.60
	Perennial	0.037	0.23	8.65	0.84	0.64
Uncleared Plain	Litter	0.047	0.13	11.14	0.76	0.60
	Perennial	0.017	0.18	8.61	0.91	0.68
Cleared Plain	Litter	0.010	0.16	1.60	0.95	0.39
	Perennial	0.086	0.20	3.86	0.60	0.47

Table 4.3. Pearson’s correlation (r) between the litter patch range (A_0) and the mean and median patch and inter-patch sizes.

Correlation with A_0	Dune	Swale	Uncleared Plain	Cleared Plain
Mean Patch size	0.08	0.26	0.41	−0.38
Median Patch size	0.64	−0.21	0.41	−0.42
Mean inter-patch size	0.15	0.75	0.22	−0.83
Median inter-patch size	0.10	0.81	0.37	−0.65

4.5 Discussion

Many semi-arid ecosystems show strong evidence of self-organisation developing between the arrangement of woody vegetation and their poorly vegetated interspaces (Pueyo *et al.* 2008; Kefi *et al.* 2010). The self-organisation of woody plants occurs as a consequence of these relatively large structures accumulating resources when both alive and dead (Tongway and Ludwig 1990; Eldridge and Wong 2005). Despite the generally widespread notion that litter tends to accumulate under perennial vegetation (e.g. Facelli and Pickett 1991; McElhinny *et al.* 2010), there is limited empirical evidence that self-organising mechanisms also apply to litter resources. We measured the cover, size distribution and spatial arrangement of perennial patches and patches of surface litter, separately, to test for possible evidence of the self-organisation of litter in response to perennial patch arrangement. Specifically we measured the spatial arrangement of litter; testing for evidence of litter accumulating in perennial patches in through positive feedback mechanisms; and whether litter patch size arrangement followed a truncated power law function across a range of communities. We found that the elevated environment surrounding patches of perennial vegetation were poorly associated, spatially, with patches of surface litter. However, both perennial patches and litter exhibited a strong “patch” and “gap” spatial arrangement. There was a high correlation between the percentage cover of litter and perennial patches among all communities. We found however, only weak

4. Self-organisation of surface litter

concordance between the size frequency of perennial patches and that of litter patches, with a greater number of smaller litter patches than the number and size of perennial patches. Furthermore, when we measured the spatial arrangement of patches at the smallest spatial scale (centimetres), we detected only a moderate spatial association between perennial patches and litter patches. Contrary to our expectation of the existence of positive feedback mechanisms to enhance litter accumulation, i.e. larger perennial patches to have stronger spatial associations with accumulated litter, no increasing trend was evident between perennial patch length and the strength of their association with litter. We did find, however, that litter patch size was consistent with a truncated power law relationship in all communities. This suggests that local interactions, such as disturbance–recovery mechanisms may play an important role in the spatial self–organisation of litter.

4.5.1 Perennial patch cover reflects litter cover

Numerous studies have demonstrated that perennial vegetation modifies its environment by accumulating resources at a scale consistent with, or greater than the area and time that it occupies the landscape (Badano *et al.* 2006; Wright and Jones 2006). This can affect larger–scale resource distribution (Shachak *et al.* 2008) and spatial patterns within the landscape (Ludwig *et al.* 1999a). Litter shedding by woody plants and its accumulation in the zone under the canopy is a form of allogenic engineering (*sensu* Jones *et al.* 1994). This accumulation is expected to result from small–scale (metres) positive feedback mechanisms (Levin and Segel 1985; Rietkerk and Van de Koppel 2008) or localised processes of disturbance and recovery (Pascual and Guichard 2005) whereby perennial plants create conditions favourable for the accumulation of litter (e.g. by increasing threshold velocities for the entrainment of organic matter) and facilitate further deposition of litter at the base of perennial plants (Dean *et al.* 1999; Okin *et al.* 2009). Previous studies have found strong links between canopy dimensions and associated litter bed dimensions for open woodlands (McElhinny *et al.* 2010; Travers and Eldridge 2012). We expected, therefore, that, within a given community, the density and size of perennial vegetation would

determine the total cover of perennial patches and therefore the cover of surface litter. The communities we studied varied markedly in their cover and composition of perennial vegetation. At a scale of tens of metres we found a strong positive linear relationship between the percentage cover of perennial patches and the cover of surface litter across a range of communities. Our results support previous findings that perennial patch cover is indicative of litter cover in these open woodlands and shrublands (McElhinny *et al.* 2010).

4.5.2 Size and frequency of litter and perennial patches differs

Power law size distributions or, more correctly, truncated power law size distributions (Pueyo 2011) are found in a wide range of natural and man-made systems (Kefi *et al.* 2011). There are a number of mechanisms which have been proposed to explain the presence of power laws in size classes in ecological systems (e.g. Mitzenmacher 2003; Newman 2005, Pascual *et al.* 2002). However, of these, few involve mechanisms involving local interactions, which are important for determining size distribution of patches (Kefi *et al.* 2011). Disturbance–recovery mechanisms are the likely candidate for explaining the power law relationships in patch formation, as there are a variety of time scales applicable to the disturbance and recovery processes, which we discuss below. Evidence for disturbance–recovery mechanisms contributing to the power law size distribution of patches has been found in mussel beds in intertidal mudflats (Guichard *et al.* 2003; Weerman *et al.* 2012); arid vegetation (Klausmeier 1999; Kefi *et al.* 2007); and aquatic vegetation (Schoelynck *et al.* 2012) in response to a range of abiotic disturbance processes such as wind, fire and water. We found truncated power laws described the size arrangement of both perennial and litter patches very well. Interestingly, there were no differences in perennial patch size arrangement among our selected communities, despite clear differences in perennial patch cover and composition. Assuming that disturbance recovery mechanisms are behind this patch formation pattern, this may be explained by the same disturbance and recovery processes occurring across all four communities (e.g. similar fire histories, wind exposure, solar exposure, rainfall etc.) leading to the same perennial patch size

4. Self-organisation of surface litter

arrangement. There were, however, significant differences among communities in the litter patch size arrangement. Litter patches were relatively smaller in the uncleared plain than the other communities. This may have been due to different amounts of surface litter or different leaf shapes among the vegetation communities, or different disturbance or recovery processes driving litter patch formation among the communities (Rietkerk and Van de Koppel 2008). Differences might also have been due to subtle variation in perennial patch size distribution, amplifying to significant differences in litter patch arrangement among communities (e.g. resilience mechanisms, Holling 2001; Jenerette *et al.* 2012)

Within each community we found that perennial patch sizes were generally larger and more variable than corresponding litter patch sizes. Perennial patches greater than four metres across tended to create numerous smaller litter patches, while smaller perennial patches appeared to accumulate more litter than expected, given their size, which is likely due to their spatial arrangement in relation to other patches. The dissociation between larger perennial patch size and associated litter patch size may be due to limited litter resources; ineffective harvesting of litter from bare, non-patch areas, or perhaps small-scale, abiotically-driven disturbances. For example, perennial plants in water-limited environments are effective at harvesting rainfall and channelling it to their roots. However if water ponds on the surface at the immediate base of the trunk, litter can be re-distributed away from perennial plants, creating gaps in the litter patch (Mayor *et al.* 2009; McElhinny *et al.* 2010). Small-scale disturbances less than one metres are often overlooked in larger-scale studies, however they may provide important information on how the same abiotic processes can act as disturbance or recovery processes at different scales.

Without further modelling, we cannot determine the specific disturbance-recovery mechanisms driving our observations of truncated power law size clusters of litter patches. Disturbance-recovery mechanisms encompass a range of spatial systems where the specific properties of the disturbance and recovery processes determine the conditions under which spatial distributions are expressed as power laws. The specific

properties of the processes can be important for determining properties of threshold behaviour and resilience within these ecosystems (Pascual and Guichard 2005). Pascual and Guichard (2005) describe three types of systems: 'classical phase transitions', 'self-organised criticality' and 'robust criticality'. In 'classical phase transition' systems, power laws only occur in the spatial arrangement of the system when critical points of transition are reached (i.e. when disturbance and recovery mechanisms approach a point of catastrophic change in state of the ecosystem, Pascual and Guichard 2005). In contrast, the remaining two types of systems exhibit power law distributions more readily due to local interactions (Kefi *et al.* 2011). 'Self-organised criticality' systems exhibit power laws in size clusters of recovering areas when disturbance and recovery occur at different spatial scales (Kefi *et al.* 2011). For example, fire patterns in forests have fast, wide-spread, temporally variable fire disturbance while recovery is relatively slow and constant (Grassberger 1993; Clar *et al.* 1997). 'Robust criticality' is similar to self-organised criticality however these systems lack the temporal separation between disturbance and recovery mechanisms. Instead, processes of disturbance and recovery at local scales result in distributions resembling power laws over a range of environmental conditions (Kefi *et al.* 2011). Due to the wide range of conditions under which power laws, or truncated power laws (Pueyo 2011), manifest in ecosystems, specific spatial and temporal properties of the disturbance and recovery processes need to be considered before inferences on temporal dynamics or threshold behaviours are made (Pascual and Guichard 2005). Given the broad range of conditions under which litter patches persist, it is likely that the spatial distribution of litter responds as either a self-organised or robust criticality system.

4.5.3 *Litter does not accumulate in perennial patches by positive feedback mechanisms*

Litter is often used as a surrogate for sites of enhanced nutrients or faunal habitat due to its apparent connection with perennial vegetation patches from where it is derived (Dean *et al.* 1999). However when we measured patches in fine detail, at a scale of centimetres, perennial patches and their "associated" litter patches were only weakly

4. Self-organisation of surface litter

to moderately spatially associated. Further, we found no apparent increase in the strength of their association with increasing perennial patch size. These observations do not support the hypothesis that perennial patches facilitate litter accumulation in a positive feedback mechanism at small scales, i.e. perennial patches increase litter accumulation, increased litter accumulation increases perennial patch size, increasing further litter accumulation. While we found no evidence for small-scale positive feedback mechanisms accumulating litter, water and other resources may still accumulate in this manner (Rietkerk and Van de Koppel 2008).

Scale-dependent feedback mechanisms may still play an important role in litter accumulation as only long-range negative feedbacks are required for regular pattern formation (Rietkerk and Van de Koppel 2008). While we did find litter to have a distinct clumped configuration, we did not measure processes linked to large-scale feedback mechanisms. Perennial patch size alone may not be indicative of the spatial arrangement of litter. It may be important, however, when perennial patch spatial arrangement is considered (Ludwig *et al.* 1999a; Boeken *et al.* 2004).

4.5.4 Perennial patch arrangement may influence the spatial variability of litter patches

Previous studies have found that the number and spatial arrangement of perennial patches may play important roles in accumulating resources (Tongway *et al.* 2001; Bouma *et al.* 2009). Although perennial patch size alone was not indicative of litter patch size, we did find some relationships between litter patch spatial variability and the spatial arrangement of perennial patches. Despite no significant differences in the degree of spatial variability of litter patches among our communities, we found different relationships with perennial patches. In the tree-dominated community where perennial and litter patch cover was the greatest, the variability in the litter was positively correlated with perennial patch size. In the shrub-dominated communities, however, variability in litter was correlated with the distance between perennial patches (inter-patch size). In the uncleared “natural” communities (uncleared plains

and swale), this was a positive correlation, with greater distances between shrubs resulting in larger litter patches. However in the modified community (cleared plains) the correlation was negative. The spatial arrangement of perennial patches, and the distance between them directly influences the micro-scale fetch length of wind, affecting wind speed and consequently aeolian transport capabilities (Li *et al.* 2009). Our results support previous findings that perennial patch size, spatial arrangement, and inter-patch distance may differ in their importance for resource variability among communities (Ludwig and Tongway 1995; Ludwig *et al.* 1999b).

4.5.5 A half-century legacy effect of land clearing on litter

The shift we observed in the cleared plain community is important to note as the effects of clearing appear to still be manifest more than sixty years after clearance. Clearing has resulted in a shift in the composition of perennial patches, with a significant increase in the number of perennial shrub patches. This is consistent with observations of shrub encroachment in many arid and semi-arid ecosystems globally (Eldridge *et al.* 2011). The removal of trees, which persist as decaying logs, has produced a more spatially variable landscape in terms of perennial patch and litter arrangement, than its uncleared analogue. The relationship between litter spatial viability and inter-patch distance has remained equal in magnitude but has switched to a negative correlation from the unmodified analogue with an equivalent density of shrubs (swale community). This could suggest alternative disturbance and recovery processes are occurring in the modified system.

From a management perspective, it appears that shifts in vegetation cover will affect the surface cover of litter, irrespective of whether the ecosystem has been subjected to clearing-induced vegetation change. This is particularly important for management, as perennial vegetation cover can readily be controlled by land managers. However, modifying vegetation structure and composition may have irreversible effects on relationships between litter accumulation and perennial patch size and arrangement. However, without a clear understanding of what drives the organisation of surface

4. Self-organisation of surface litter

litter, we cannot understand how processes and mechanisms might shift with vegetation modification.

4.6 Conclusions

In this study we have highlighted why the relationship between perennial patches and litter patches is more complex than has been generally reported (Shachak *et al.* 2008). While there were strong relationships between the percentage cover of perennial and litter patches, we detected only weak to moderate spatial association between them. It is likely that both litter and perennial patches are subject to self-organisation mechanisms, but the drivers of spatial arrangement are likely different. The nature of the size class distribution of litter patches suggests that disturbance-recovery mechanisms are likely occurring; though the mechanisms specific to leaf litter are different to those shaping perennial patches. We found no evidence to suggest that litter accumulates with perennial patches in a linear positive-feedback mechanism. This does not however, exclude the possibility of other properties of perennial patches inducing scale-dependent feedbacks in litter arrangement. The distance between perennial patches in shrub-dominated communities may have had strong effects on litter spatial variability. However this relationship appears to be sensitive to modification of vegetation structure and composition, such as tree clearing. Determining what drives the variability in patch spatial arrangement among communities, and between perennial patches and litter within a community is a complex task. This has important implications for the practical applications of self-organisation models to real ecosystems. Without further modelling and specific measurements of the drivers of litter arrangement it is difficult to determine what may be driving surface litter arrangement.

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Appendix 4.1. Average \pm SE of truncated power law parameters ($y = ax^b \cdot \exp^{-c \cdot x}$) for patch size distribution of litter and perennial patches. Average (range) of R-squared values are given. Superscripts indicate significant differences among the communities.

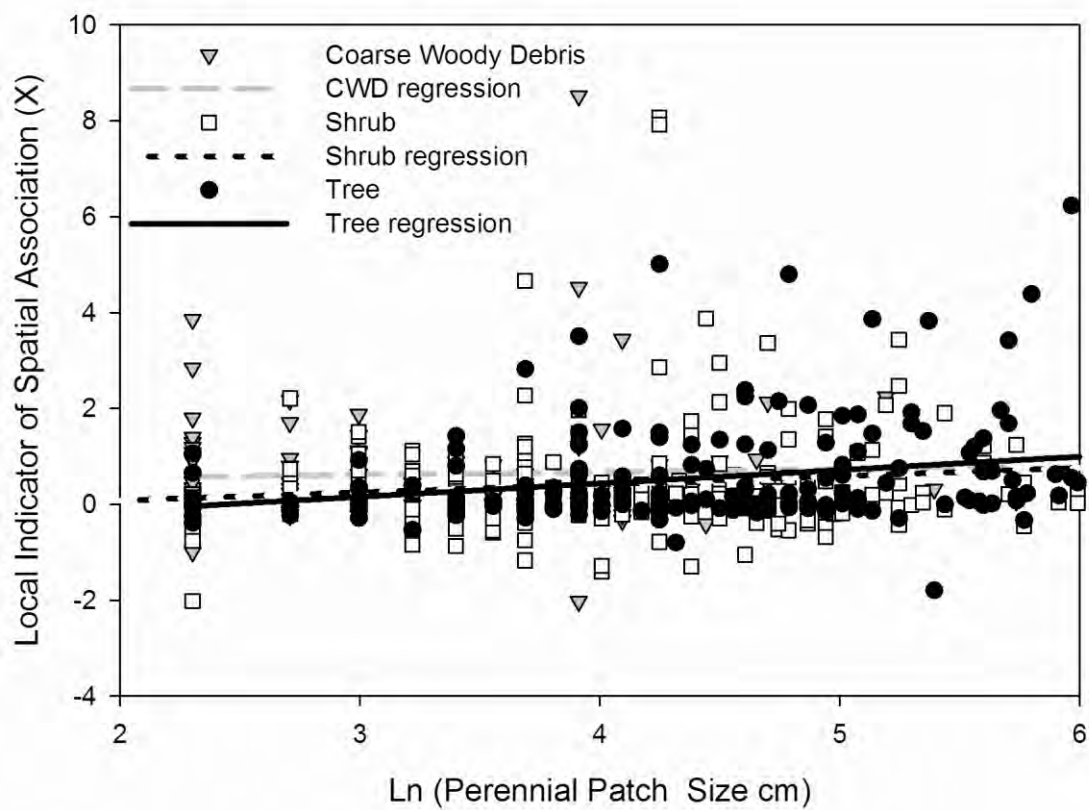
Community	a	b	c	Adj R ²
Litter				
Dune ^a	0.19 \pm 0.1	9.56 \pm 2.08	1.23 \pm 0.29	0.71 (0.31–0.87)
Swale ^a	1.47 \pm 0.8	7.26 \pm 2.01	0.92 \pm 0.22	0.67 (0.34–0.95)
Uncleared Plain ^b	0.29 \pm 0.21	62.12 \pm 23.19	9.05 \pm 3.45	0.79 (0.53–0.97)
Cleared Plain ^a	0.08 \pm 0.04	8.44 \pm 0.94	1.08 \pm 0.14	0.66 (0.44–0.80)
Perennial Patches				
Dune	3.36 \pm 3.07	53.51 \pm 27.46	5.12 \pm 2.8	0.51 (0.21–0.86)
Swale	0.21 \pm 0.21	97.04 \pm 31.54	8.08 \pm 2.65	0.67 (0.04–0.99)
Uncleared Plain	0.01 \pm 0.01	100.54 \pm 30.19	9.36 \pm 2.79	0.71 (0.22–0.99)
Cleared Plain	0.88 \pm 0.88	59.97 \pm 26.84	5.96 \pm 2.87	0.65 (0.10–0.99)

4. Self-organisation of surface litter

Appendix 4.2. Summary of Permutational ANOVA results for spatial indicators. Significant results are **bolded**. For X community d.f. = 3, 32. For all other measures community d.f. = 3, 32; Patch type d.f. = 1, 32; Community \times Patch = 3, 32. I_a is index of aggregation; V_i is the index of clustering into patches; V_j is the index of clustering into gaps; X is correlation coefficient of the Local Indicator of Spatial Association; A_0 is Range; C_0 is nugget; $C_0 + C$ is sill; $C / (C_0 + C)$ is spatial structure.

Measures	Community		Patch Type		Community \times Patch	
	Pseudo- F	P	Pseudo- F	P	Pseudo- F	P
I_a	1.86	0.152	1.32	0.261	0.41	0.750
V_i	3.07	0.040	0.47	0.500	0.14	0.937
V_j	1.04	0.389	0.34	0.561	0.13	0.939
X	0.68	0.582	–	–	–	–
A_0	2.38	0.081	3.06	0.088	0.39	0.768
C_0	2.07	0.126	0.49	0.486	0.95	0.420
$C_0 + C$	2.80	0.057	1.66	0.208	0.26	0.856
$C / (C_0 + C)$	1.84	0.160	0.168	0.681	1.49	0.239

Appendix 4.3. Linear regression between perennial patch size and the averaged local indicator of spatial association (LISA: X) for individual perennial patches. LISA values greater than zero indicate a positive association between litter and perennial patches, while values less than zero indicate a negative association between litter and the perennial patch. Coarse woody debris patches are indicated in grey triangles ($X_{\text{CWD}} = 0.06 \times \text{Ln}(\text{patch size}) + 0.44$; $P = 0.70$); Shrub patches are white squares ($X_{\text{shrub}} = 0.17 \times \text{Ln}(\text{patch size}) - 0.26$; $F_{2, 229} = 3.99$; $P = 0.70$; $R^2 = 0.01$); and trees are indicated by black circles ($X_{\text{tree}} = 0.27 \times \text{Ln}(\text{patch size}) - 0.68$; $F_{2, 229} = 15.79$; $P < 0.001$; $R^2 = 0.06$).



Appendix 4.4. Semi-variogram parameters for litter and perennial patch data for each replicate in each community. All models were spherical.

Litter Patch					Perennial Patch				
Nugget (C ₀)	Sill (C ₀ + C)	Range (cm) (A ₀)	Structural Component C/ (C ₀ + C)	R ²	Nugget (C ₀)	Sill (C ₀ + C)	Range (cm) (A ₀)	Structural Component C/ (C ₀ + C)	R ²
Dune									
0.09	0.26	965	0.65	0.69	0.01	0.24	207	0.98	0.50
0.12	0.44	4931	0.74	0.97	0.06	0.23	1065	0.73	0.56
0.01	0.24	165	0.96	0.27	0.02	0.25	385	0.94	0.34
0.13	0.3	2776	0.56	0.97	0.04	0.27	702	0.87	0.75
0.00	0.19	173	1.00	0.35	0.01	0.2	418	0.97	0.31
0.15	0.36	4311	0.58	0.98	0.08	0.28	709	0.71	0.70
0.09	0.26	1296	0.65	0.87	0.06	0.21	834	0.70	0.74
0.02	0.26	203	0.92	0.39	0.06	0.27	484	0.80	0.53
0.01	0.24	170	0.96	0.57	0.04	0.25	614	0.83	0.86
Swale									
0.01	0.25	188	0.96	0.37	0.07	0.27	998	0.73	0.55
0.00	0.18	207	1.00	0.50	0.06	0.25	542	0.76	0.59
0.01	0.17	142	0.94	0.41	0.08	0.25	759	0.68	0.69
0.00	0.12	123	0.97	0.46	0.02	0.16	188	0.91	0.47

Appendix 4.4. Continued									
Litter Patch					Perennial Patch				
Nugget (C ₀)	Sill (C ₀ + C)	Range (cm) (A ₀)	Structural Component C/ (C ₀ + C)	R ²	Nugget (C ₀)	Sill (C ₀ + C)	Range (cm) (A ₀)	Structural Component C/ (C ₀ + C)	R ²
Swale (Continued)									
0.07	0.36	4450	0.80	0.99	0.03	0.24	877	0.86	0.69
0.00	0.07	117	0.95	0.07	0.02	0.19	159	0.91	0.32
0.01	0.24	195	0.95	0.64	0.02	0.28	451	0.94	0.56
0.05	0.19	1390	0.73	0.96	0.03	0.18	864	0.82	0.93
Uncleared Plain									
0.09	0.21	1495	0.57	0.96	0.00	0.39	2374	1.00	0.99
0.08	0.2	2667	0.62	0.94	0.07	0.26	2019	0.73	0.97
0.00	0.04	140	1.00	0.27	0.00	0.05	162	1.00	0.22
0.12	0.26	775	0.55	0.85	0.03	0.24	575	0.89	0.80
0.00	0.03	111	1.00	0.08	0.02	0.1	626	0.76	0.71
0.00	0.06	148	1.00	0.20	0.00	0.08	181	1.00	0.41
0.05	0.15	3330	0.64	0.98	0.02	0.18	867	0.88	0.55

0.01	0.13	140	0.89	0.24	0.01	0.21	135	0.94	0.56
0.07	0.17	1221	0.57	0.91	0.00	0.19	806	1.00	0.94
Cleared Plain									
0.01	0.19	161	0.96	0.42	0.05	0.21	563	0.74	0.69
0.01	0.12	120	0.90	0.27	0.01	0.14	196	0.96	0.23
0.03	0.23	180	0.88	0.36	0.09	0.21	554	0.59	0.59
0.00	0.18	150	1.00	0.28	0.09	0.25	1111	0.64	0.74
0.00	0.20	189	0.99	0.45	0.01	0.21	177	0.97	0.27
0.02	0.24	216	0.90	0.52	0.02	0.25	242	0.92	0.36
0.01	0.17	159	0.94	0.54	0.02	0.23	268	0.92	0.45
0.00	0.12	142	1.00	0.31	0.01	0.24	225	0.96	0.69
0.00	0.05	122	0.94	0.35	0.00	0.07	142	0.96	0.20

Chapter 5. Foraging pit morphology influences decomposition in a semi–arid woodland

Samantha K. Travers, David J. Eldridge

Keywords: *Austrostipa scabra*; fungicide; mallee; quantile regression; termites; *Triodia scariosa*.

Abbreviations–

ANOVA — Analysis of Variance

C — Control

F — Fungicide

LSD — Least Significant Difference

PERMANOVA — Permutational Multivariate Analysis of Variance

T— Termiticide



Typical foraging pit of a greater bilby or burrowing bettong (left) and short–beaked echidna (right)

5.1 Abstract

In ecosystems around the world humans have introduced or altered fundamental ecosystem processes either directly or as a consequence of their actions. The loss of native soil foraging mammals, such as the greater bilby (*Macrotis lagotis*) and burrowing bettong (*Bettongia lesueur*), throughout vast areas of Australia has potentially altered fundamental soil processes such as decomposition. Little is known about whether surviving native soil-disturbing animals, such as the short-beaked echidna (*Tachyglossus aculeatus*), have assumed the ecosystem role of these locally-extinct native animals. We used a litter bag study to compare abiotic and biotic mechanisms of decomposition within the foraging pits of two native mammals. Specifically we compared whether decomposition rates differed between landforms, which we used as a surrogate for soil texture; grass species *Austrostipa scabra* subsp. *scabra* and *Triodia scariosa* subsp. *scariosa*, which we used as our substrates; and the effects of chemically excluding fungi and/ or termites. We found initial differences in the organic mass loss between the echidna and bilby/ bettong foraging pits, yet there was no overall effect on the decomposition rate over 396 days. There was no evidence that landform (soil texture) or chemical exclusion of termites and fungi significantly reduced our measures of decomposition, despite significant effects at 396 days. The two grass species lost significantly different amounts of organic material at each collection interval, providing the most consistent effect on decomposition over the duration of the study. Our data highlights temporal idiosynchronies in the various drivers of decomposition. Overall this study provides evidence that the foraging pits of the short-beaked echidna do not differ markedly from those of the locally extinct greater bilby and burrowing bettong in terms of their capacity to maintain rates of decomposition at an annual scale. However, foraging pit morphology does affect initial rates of decomposition.

5.2 Introduction

Humans have caused major shifts in ecosystems globally, by inducing or altering fundamental ecosystem processes (Hughes *et al.* 2003; Hooper *et al.* 2005; Halpern *et al.* 2008). Some of the relatively rapid and recent changes have occurred within Australia's arid and semi-arid environments, with substantial changes in natural fire (Bradstock 2010) and grazing regimes (Facelli and Springbett 2009; Read and Cunningham 2010), declines in soil health (Eldridge *et al.* 2011), shifts in climate (Greenville *et al.* 2012), introduction of feral carnivores (Smith and Quin 1996) and herbivores (Edwards *et al.* 2004), and widespread extinctions of small to medium sized mammals (Short and Smith 1994; Johnson 2006). Such rapid changes have culminated in widespread reductions in ecosystem function (Ludwig and Tongway 1996; Morton *et al.* 2011). While the direct impacts of these changes are readily identifiable, there are still unknown indirect effects that take many decades to emerge, largely because of the slow nature of ecological change in these systems (Stafford Smith and Morton 1990; Morton *et al.* 2011).

A relatively slow, yet fundamental process in arid and semi-arid environments is the decomposition of organic material (Moorhead and Reynolds 1991; Throop and Archer 2008; Cornwell *et al.* 2009). Although litter chemistry, rainfall and temperature are closely linked to global trends in litter decomposition (Aerts 1997; Cornwell *et al.* 2008; Brandt *et al.* 2010), decomposition rates in semi-arid and arid environments are generally faster than predicted by these abiotic factors alone. Evidence to date suggests that substrate fragmentation, comminution to coarse soil fragments, soil texture, solar exposure and nitrogen availability also play important roles (Austin and Vivanco 2006; Parton *et al.* 2007; Throop and Archer 2008). One important factor driving decomposition is burial, with buried organic material decomposing faster than litter residing on the soil surface (Moorhead and Reynolds 1991; Austin *et al.* 2009). Thus, abiotic factors that vary with soil depth are likely more important for decomposition than abiotic factors that vary only spatially at the surface (Moorhead and Reynolds 1989; Doblas-Miranda *et al.* 2009a). The burial of organic material

5. Decomposition in foraging pits

reduces photodegradation, which can have significant impacts on the mineralisation and incorporation of nitrogen and carbon into soil organic pools (Austin and Vivanco 2006; Austin *et al.* 2009). Burial also buffers extreme temperatures, prolongs exposure to moist conditions, and brings organic material into direct contact with soil-borne fungi and microarthropods. These conditions create an environment conducive to sustaining stable populations of decomposers (Elkins and Whitford 1982; Santos and Whitford 1983; Moorhead and Reynolds 1993).

Despite the importance of decomposition, relatively few recent studies have focussed on the biotic interactions driving decomposition in arid and semi-arid environments (but see Doblas-Miranda *et al.* 2009b; Farji-Brener 2010; Buitenwerf *et al.* 2011; Megias *et al.* 2011). There are suites of soil biota that interact to disperse, comminute, digest and mineralise organic material in arid systems. However, biotic activity generally tends to be inhibited by the extreme abiotic conditions in arid and semi-arid environments (Elkins and Whitford 1982; Wall and Virginia 1999). Interactions between biota however, can enhance decomposition. For example soil arthropods and some vertebrate fauna transport the immobile decomposers, such as fungi, between decomposition hotspots (Elkins and Whitford 1982; Hawkins 1996; Whitford 2002). Fungi are important decomposers (Santos and Whitford 1981; Parker *et al.* 1984; Santos *et al.* 1984) as they are capable of digesting recalcitrant materials such as cellulose, hemicellulose and lignin (Parker *et al.* 1984; Hawkins 1996; Cornwell *et al.* 2009). Their activity, however, is limited by nitrogen availability, as they tend to immobilise nitrogen during the decay process for use in their digestive enzymes (Parker *et al.* 1984; Moorhead and Reynolds 1993). Termites also have an important role in decomposition as they are responsible for both above- and below-ground decomposition (Whitford *et al.* 1982; Gutierrez and Whitford 1989). Termites are highly abundant in Australia's arid and semi-arid regions (Noble *et al.* 1989; Whitford *et al.* 1992; Noble *et al.* 2009). Australian termites are unique as they tend to be detritivores rather than herbivores, feeding upon 'fungal gardens' of senescent plant material stored in subterranean galleries (Watson *et al.* 1973; Noble *et al.* 2009).

Together, the combination of termites and fungi are presumed to be responsible for substantial amounts of decomposition in Australia's arid and semi-arid environments.

Perhaps of equal or greater importance to decomposition in these environments are the organisms that act relatively independently of seasonal environmental constraints, such as soil foraging animals (Steinberger and Whitford 1983; Whitford 2002). In resource-limited ecosystems throughout the world, soil foraging animals contribute to fundamental ecosystem processes and landscape heterogeneity by burying organic material and creating patches of fertile soil through their foraging activities (Whitford and Kay 1999; Eldridge 2011). Pits and depressions created by soil foraging animals capture and retain nitrogen- and carbon-rich sediments, water, litter, faeces and seed, bringing these essential resources together in time and space (Boeken *et al.* 1995; Eldridge 2011). Together, these resources increase microbial and arthropod activity, which leads to enhanced decomposition (Santos *et al.* 1981; Whitford 2002). By controlling the availability of resources to other organisms, foraging pits enable organisms with different resource requirements to co-exist, and can expand the distribution of patch-dependent organisms (Day *et al.* 2003; Crain and Bertness 2006).

During the past 200 years in Australia, soil disturbing animals such as the greater bilby (*Macrotis lagotis*) and burrowing bettong (*Bettongia lesueur*), have had their inhabitable range substantially reduced (Strahan 1995; Johnson 2006; Woinarski *et al.* 2011). Given their important role in small scale patch formation in semi-arid systems (Garkaklis *et al.* 2004; James *et al.* 2009), the loss of these animals is likely to have widespread effects on processes in the soil, such as decomposition. Little is known about whether surviving and analogous native soil-disturbing animals such as the short-beaked echidna (*Tachyglossus aculeatus*) have assumed the ecosystem role of these locally-extinct animals. Given that foraging pits dug by short-beaked echidnas differ in size, shape, frequency of construction and location to the foraging pits dug by greater bilbies and burrowing bettong, there may be important differences in the decomposition rate of substrates in these foraging pits

5. Decomposition in foraging pits

In this study we assess whether pit morphology affects the abiotic and biotic drivers of decomposition rates. Specifically, we compared decomposition rates in relation to foraging pit shape, landform, substrate type, and detritivore activity. We designed a litter bag study using two pit types, that vary in morphology (shape) that were either (1) shallow basin-shaped pits (echidna), or (2) deep, cylindrical-shaped pits (bilby/bettong). We expected faster decomposition within deeper pits due to the more rapid, deeper burial of litter. The effect of soil texture was assessed by comparing decomposition on a dune (sand) with an inter-dunal swale (loam). We adopted a reciprocal transplant approach using two grass substrates; a dune species (*Triodia scariosa* subsp. *scariosa* N.T. Burb.) and a swale species (*Austrostipa scabra* subsp. *scabra* (Lindl.) S. W. L. Jacobs & J. Everett) and expected greater decomposition of swale substrates in the swales and *vice versa* ('home field advantage'; *sensu* Milcu and Manning 2011). To assess detritivore effects, we used four treatments involving the use of a termiticide, fungicide, both or none, and predicted that decomposition would be greatest where neither termiticide nor fungicide were applied to the substrates.

5.3 Methods

5.3.1 Study site

This study was undertaken inside Australian Wildlife Conservancy's Scotia Sanctuary in south western New South Wales, Australia (33°43' S, 143°02' E). This area is semi-arid, receiving approximately 250–280 mm rainfall annually, based on records since 1995. However there are very few years where this amount is actually received due to the spatial and temporal variability of rainfall within and between years. Average daily temperatures range from a minimum of 6 °C to a maximum of 17 °C in winter (July), and from a minimum of 19 °C to a maximum of 33 °C in summer (January, BOM 2012). The soils at our sites are a mixture of brownish and siliceous sands and loamy calcareous earths.

Our study was conducted in two open woodland communities that occur on different landforms: (1) Dune mallee woodlands (henceforth Dune) and (2) Semi-arid Sand Plain woodlands (henceforth Swale) (Keith 2004). The Dune mallee woodland occurs on the crests of long, low (relief to 7 m) east–west trending sand dunes. The overstorey is dominated by Eucalypt mallee trees, *Eucalyptus gracilis*, *E. dumosa* and *E. socialis* with an understorey dominated by scattered perennial hummock grasses (*Triodia scariosa*) (Keith 2004). The Semi-arid Sand Plain woodlands tend to occur on soils which have calcareous subsoils. The overstorey is dominated by *Casuarina pauper* Auth. The understorey is predominantly perennial shrubs, including *Alectryon oleifolius* subsp. *canescens*, *Eremophila sturtii*, *Senna artemisioides*, *Acacia burkitti* and *Dodonaea viscosa* subsp. *angustissima*. Ground cover is predominantly *Austrostipa* spp., however ground cover is highly variable and heavily dependent on annual rainfall (Westbrooke *et al.* 1998).

5.3.2 Foraging pit morphologies

We used the foraging pits of three different soil disturbing animals, short-beaked echidnas and greater bilbies or burrowing bettongs, to compare litter decomposition rates. The structural integrity of foraging pits is highly dependent upon soil texture, with much greater pit turnover rates in highly erodible, coarse-textured soils (James *et al.* 2009; Eldridge *et al.* 2012).

Echidna foraging pits are typically elliptical shaped, ranging from 15–25 cm in diameter, 5–15 cm deep (Eldridge and Mensinga 2007) and are approximately 0.0096 m³ in volume (James and Eldridge 2007; Eldridge *et al.* 2012). These pits are typically surrounded by large clods of soil, which are ejected during pit excavation. In coarse-textured soils the ejected soil clods are relatively poorly aggregated, with their degree of aggregation increasing in finer soil textures (Eldridge and Mensinga 2007).

Bilbies and burrowing bettongs dig pits while foraging for seeds, invertebrates, bulbs and fungi. Their pits are cylindrical-shaped, approximately 15 cm wide and 10–20 cm

5. Decomposition in foraging pits

deep, on average, 0.0099 m³ in volume (James and Eldridge 2007) and are largely indistinguishable. In coarse-textured soils, bilby and bettong pits tend to be deeper (James and Eldridge 2007). The material ejected from these pits is generally piled into a neat mound at the base of the pit.

5.3.3 Litter substrates

We selected two perennial grasses, one from each landform. From the swale we selected *Austrostipa scabra* subsp. *scabra* (henceforth *Austrostipa*) and from the dune we selected *Triodia scariosa* (henceforth *Triodia*) as our litter substrates. *Austrostipa* is a C3, tufted perennial grass which grows up to 0.5 m high. It has a soft, light texture with a small surface area to weight ratio. *Austrostipa* is one of the dominant grass species in the swales, but occasionally grows on the dune crests. *Triodia*, commonly known as porcupine grass, is a C4 perennial hummock grass which grows up to 0.6 m high with flower stems up to 0.9 m high. Hummocks range from 0.6 to 1.2 m in width and may form rings up to 3 m in diameter. *Triodia* has a dense, rigid texture with a high surface area to weight ratio due to the high silica content in the leaves (Dengler *et al.* 1994; Reid and Hill 2013). *Triodia* is found almost exclusively on the crest of sandy dunes. Both grasses flower in response to rainfall.

5.3.4 Decomposition study

To provide a chemically and physically consistent substrate, living material of *Austrostipa* and *Triodia* was collected from the study site in January 2009. While living material may not be completely chemically equivalent to freshly senesced material, particularly in nitrogen content, the use of senesced material poses issues for capturing the initial stages of decomposition. Grass samples were air-dried at room temperature and stored in the dark for three months before use. Four grams (± 0.5 g) of either *Austrostipa* or *Triodia* were weighed and sealed into aluminium flyscreen bags (12.5 cm \times 12.5 cm; mesh size 2 mm). Five additional bags of each grass type and

treatment were used to calculate transport and handling loss from the experiment bags as a 'transport and handling' control. Ten additional grass samples of each species were weighed and oven-dried at 60 °C for 72 hrs to measure dry mass. All bags were soaked in tap water for 2 hrs and air dried in the dark for a week prior to treatment to remove any dust and any other surface residues which may contribute to errors in mass calculations.

Litterbags of both grass species were divided into four treatments, termiticide only (T), fungicide only (F), both termiticide and fungicide (F + T) and no treatment (control, C). Treatment solutions were mixed, with 0.05 % bifenthrin solution which is used primarily as a termiticide — but can affect bees, flies, cockroaches, mosquitoes, spiders, ants, aphids, leaf-feeding caterpillars, wasps, weevils, leaf miners and leaf hoppers. We used 0.03 % triforine solution used as a fungicide, which is commonly used to control blackspot, rust and powdery mildew. Litterbags requiring only a termiticide or fungicide treatment were soaked for 12 hrs in their respective solution. Litterbags requiring both treatments were soaked in the termiticide solution for 6 hours, air dried for a week then soaked in the fungicide solution for 6 hrs. Control litterbags were soaked for 12 hrs in water. All treated bags were air dried in a dark location for a week. Once dried, all field experiment bags and 'transport and handling' control bags were transported to the field site in plastic zip-lock bags.

At the field site, litterbags were placed in four 'blocked' sites. At each site, bags were placed in two landforms: 1) a sandy dune crest (Dune) and 2) an adjacent swale (Swale). In each landform, pairs of foraging pits were located representing one of each morphological shape (echidna and bilby/ bettong). Pairs were less than 2 m apart. Litterbags with matching grass type (*Austrostipa*, *Triodia*) and chemical treatment (F + T, F, T, C) were placed into each pair of pits and tethered into the pit with a wire peg. Each pit contained only one litter bag to avoid disturbance with litterbag removal over time. Litterbags were deployed on 16th May 2009. Paired litterbags were collected at one of four time periods, 30, 63, 130 and 396 days since placement (Total N = 512). At each collection, litterbags were collected and transported in individual paper bags.

5. Decomposition in foraging pits

Litterbags were returned to the laboratory, oven-dried at 60 °C for 72 hrs, and the soil and leaves that had accumulated on the outside of the bags were gently removed and discarded. Bags were visually inspected for the presence of fungal spores and termite damage before and after oven drying. Once dried, the entire contents of each litter bag was removed and weighed. Two subsamples (0.5–1 g) from each litter bag were ashed at 550 °C for 6hrs, cooled overnight in a dessicator and weighed to assess the mass of inorganic matter. This process removes all organic material in the subsample and allows an average calculation of the organic and inorganic content for each litter bag (Throop and Archer 2007). This process was also used on the ‘transport and handling’ controls to calculate initial organic and inorganic contents for each grass type and each chemical treatment. We used these controls to calculate the proportion of organic and inorganic content remaining for each sample (as a percentage of the initial material).

5.3.5 Relative success of fungicide and termiticide

We assessed the relative success of our fungicide and termiticide treatments with a two-way Permutational Analysis of Variance (PERMANOVA). Our factors included treatment (F, T, F + T, C) as a fixed factor and collection interval as a random factor. We used a binary presence/ absence to measure the presence of fungi, termite, and “other” soil biota activity in the litter bags. Data were transformed using a Bray Curtis resemblance matrix with a dummy variable. We ran each of the three response variables (fungi, termite, other) in a separate PERMANOVA using 9999 permutations with Type III error in the +PERMANOVA package for PRIMER (Anderson *et al.* 2008).

5.3.6 Measures of decomposition and infiltration of soil into the litter bags

We used two measures of decomposition, percent (%) of initial organic material remaining and the grams of material lost per mm of rainfall. Rainfall data were

collected at the study site and measured as the total mm rainfall over the duration of each collection interval. We used the % of organic material remaining in each litter bag to determine how many grams of organic material were lost from the initial weight of each litter bag. We divided the grams of material lost in each litter bag by the mm of rainfall to standardise for the effects of rainfall on mass loss. Soil infiltration was assessed as both a total mass and a proportion of the inorganic content of the initial material (% inorganic material).

To determine how our factors influenced our measures of decomposition and soil infiltration, we ran several split plot, five-factor, Analysis of Variance's (ANOVA). Our design compared the effects of Block (random), Landform (fixed), Grass type (fixed), Chemical treatment (fixed) and Pit shape (fixed), and their interactions. Each collection interval (Times 1–4) was analysed separately to simplify the model. Data were tested for homogeneity of variance using Levene's test prior to analysis and no transformations were required. These analyses were performed in the Minitab version 16 statistical software (Minitab Inc, 2010).

5.3.7 Modelling decomposition rates

To assess whether soil infiltration (mass of inorganic material in the litter bags) influenced the mass of substrate lost per mm of rainfall, we fitted a quantile regression to the data. Quantile regression allows for changes in central tendency between the response and predictor variables, heterogeneous variance in the relationship, and changes to the shape of the distributions of y variables across the predictor (x) variables (Cade and Noon 2003). Quantile regressions are commonly applied to ecological data to demonstrate the boundaries of limiting factors when only a subset of limiting factors are measured. In these situations there is a focus on the rates of change in quantiles near the limiting responses (Cade and Noon 2003). However a change in central tendency, variance, and shape of distributions may also occur in observational data due to model misspecification. For example, where other potentially limiting factors were not measured or not included in the model, or due to inappropriate functional forms (e.g. using a linear model instead of a non-linear

5. Decomposition in foraging pits

model). Analyses were performed in the “quantreg” package in R version 2.15.1 (Koenker 2012; R Core Team 2012).

To model the relationship between the % litter mass remaining and time (days), we fit a negative exponential decomposition model to all replicates (Olson 1963):

$$\ln (X_n / X_0) = -kt$$

where X_0 is the initial amount of material, X_n is the amount of material at time = n , and t is the measure of time in days (Olson 1963). We used linear regressions to calculate decay rates (k -values), where the coefficients of determination (R^2) express the variance explained by the model. To calculate the half-life of litter (i.e. the time required for 50 % decomposition) from our models we used Olson’s (1963) formula:

$$t_{0.5} = 0.6931 / k$$

To assess the effects of our factors on the decomposition rates and half-lives of our litter, we used the five-factor, split plot ANOVA described above. K values were multiplied by 1000 prior to analysis.

5.4 Results

5.4.1 Relative success of fungicide and termiticide

The relative success of our chemical treatments was dependent upon two factors: 1) the incidence of detritivory by our target organism and 2) the relative effectiveness of the treatment at inhibiting the target organisms. Fewer fungal spores were evident on the litter bags treated with fungicide (Pseudo- $F_{3,496} = 12.7$, $P = 0.002$; Figure 5.1). The incidence of fungal activity varied over time, with fewer litter bags showing evidence of fungal activity in the final collection (Pseudo- $F_{3,496} = 3.8$, $P = 0.009$). The reduction

in apparent shifts in fungal activity made the relative success of our fungicide vary over time (Pseudo- $F_{9,496} = 2.2$, $P = 0.020$; Figure 5.1).

The effectiveness of reducing termite activity was difficult to assess as few litter bags showed evidence of termite activity. There were no differences in the incidence of termite activity among treatments ($P = 0.06$) or collection intervals ($P = 0.51$).

However, the fungicide and termiticide were effective at reducing activity of other detritivores, such as insect larvae. The litter bags collected at the final collection interval (396 days) were the only bags where the incidence of activity by non-target detritivores was evident (collection intervals: Pseudo- $F_{3,496} = 229.3$, $P < 0.001$). From these litter bags all chemically treated litter bags reduced the incidence of breakdown by non-target organisms (chemical treatment by collection interval interaction: Pseudo- $F_{9,496} = 5.5$, $P < 0.001$; Figure 5.2).

5. Decomposition in foraging pits

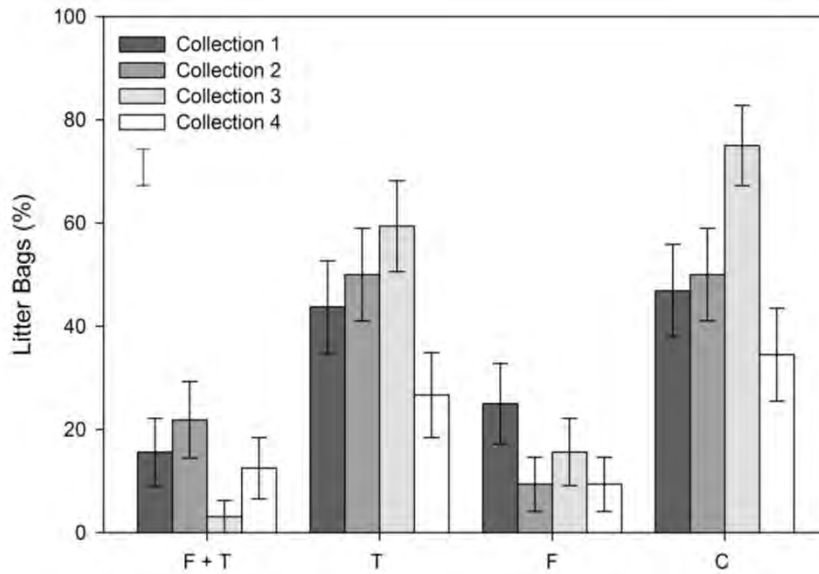


Figure 5-1. The mean (\pm SE) incidence of fungal presence for each chemical treatment over the four collection intervals. The bar indicates the 5 % LSD for the Treatment by Time interaction. The incidence of fungal presence is given by the percentage of litter bags with fungi spores present for each factor. F + T = both fungicide and termiticide, T = termiticide, F = fungicide, C = control.

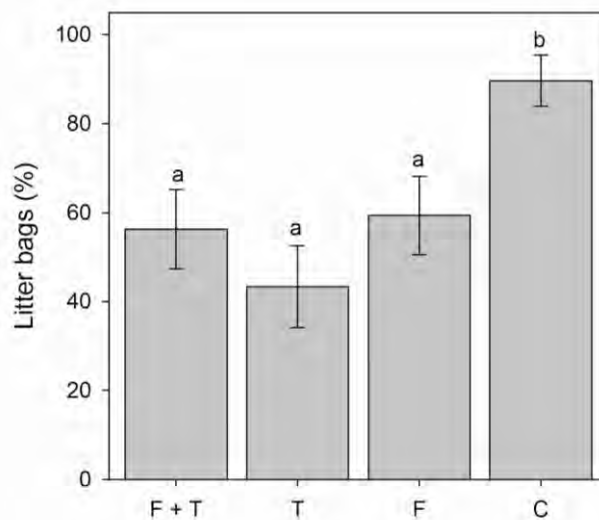


Figure 5-2. The mean (\pm SE) incidence of detritivory by non-targeted soil biota at the final (4th) collection interval (396 days) for each chemical treatment with significant differences indicated. The incidence of detritivory is measured as the percentage of litter bags with evidence of activity (e.g. silk webbing, faeces, tunnels) from organisms other than fungi or termites for each chemical treatment. There were no observations of non-target biotic activity during collection intervals 1–3. F + T = both fungicide and termiticide, T = termiticide, F = fungicide, C = control.

5.4.2 Organic mass loss

Across all collection periods, we found a significant difference in the % organic material remaining for both grass species (Time 1: $F_{1,42} = 14.2$; Time 2: $F_{1,42} = 7.71$; Time 3: $F_{1,42} = 7.59$; Time 4: $F_{1,42} = 6.77$; $P < 0.02$; Figure 5.3; Appendix 5.1). *Austrostipa* lost more organic material than *Triodia* for the first three collection intervals. However, at the final collection (396 days) *Triodia* had less % organic material remaining than *Austrostipa* (Figure 5.3). We found that the significance of our remaining factors, and their interactions, varied over time.

There were significant differences in the % organic material remaining between our two pit types initially. After 30 days there was less % organic material remaining in the bilby/ bettong pits than the echidna pits ($F_{1,48} = 9.31$; $P < 0.01$; Appendix 5.1), but after 63 days, significantly less % organic material remained in the echidna pits ($F_{1,48} = 8.28$; $P < 0.01$; Figure 5.3; Appendix 5.1). By our third and fourth collection intervals there were no differences % organic material remaining between pit types ($P > 0.3$; Appendix 5.1).

For our chemical treatments, there was no significant difference in the % organic material remaining until the fourth collection interval ($P > 0.09$ for the first three time periods). After 396 days (Time 4) a greater % organic material remained for the chemically treated (F, T, F + T) than the untreated ($F_{3,42} = 4.38$; $P = 0.011$; Appendix 5.1; Figure 5.3) litter bags.

We detected no main effect of landform on % organic material remaining, however there were significant interactions with landform (Appendix 5.1). For example, after 396 days, we detected a significant three-way interaction between landform, treatment and grass ($F_{3,42} = 3.28$; $P = 0.033$; Appendix 5.1), with the application of fungicide to *Austrostipa* significantly enhancing the % organic material lost in the swale only (Figure 5.4). This interaction demonstrated that the difference in % organic

5. Decomposition in foraging pits

material remaining between the two grass types was more pronounced in the swale, with *Triodia* generally losing a greater % organic material than *Austrostipa* (Figure 5.4).

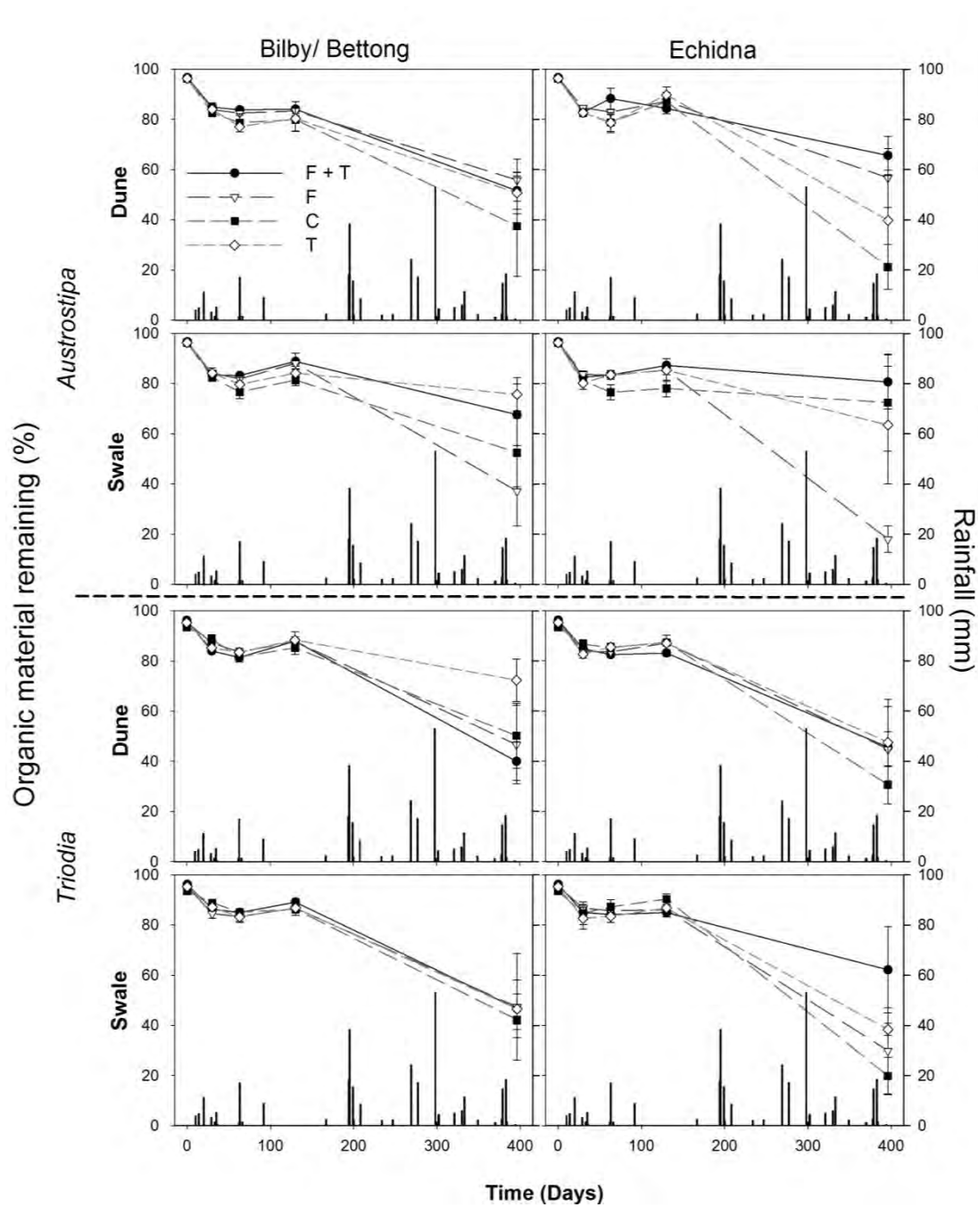


Figure 5-3. The mean (\pm SE) % organic material remaining over time for each factor, and total daily rainfall (mm) during the study period. F + T = both fungicide and termiticide, T = termiticide, F = fungicide, C = control.

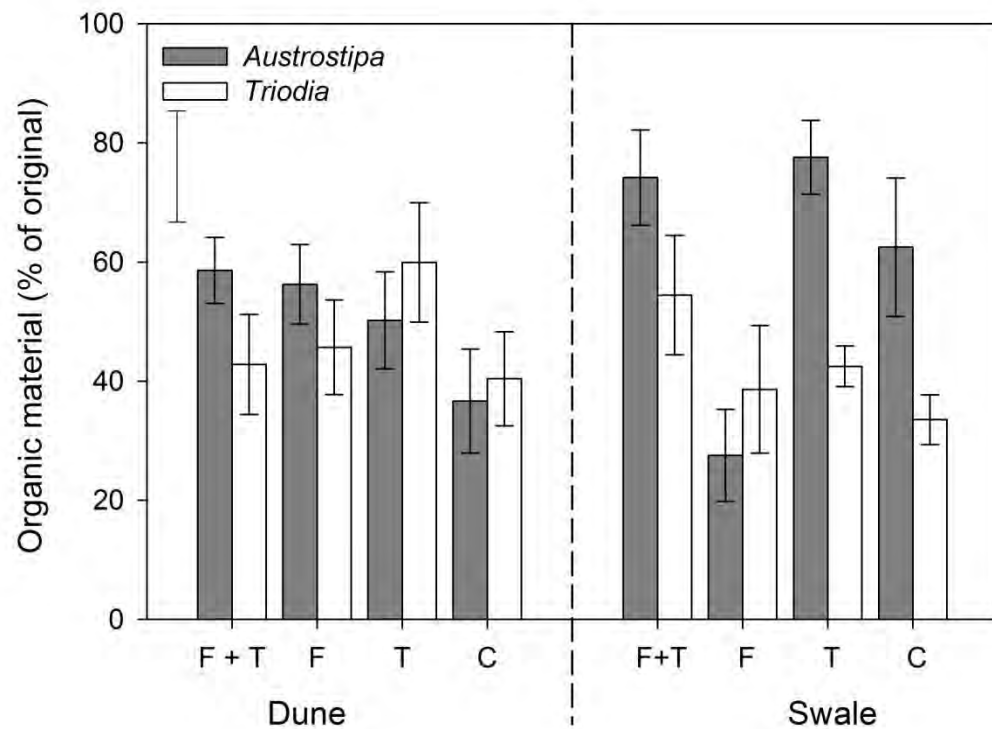


Figure 5-4. Three-way interaction of Grass type, Landform and Treatment at collection interval 4 (396 days) for the remaining % organic material. The LSD at 5 % is given for the three-way interaction. F + T = both fungicide and termiticide, T = termiticide, F = fungicide, C = control.

5.4.3 Litter mass loss adjusted for rainfall

The loss of organic material was still significantly different among our factors when we accounted for the effects of rainfall. However, the results were time-dependent.

Austrostipa lost a significantly greater mass of organic material per mm of rainfall than *Triodia* over the first three collection intervals ($F_{1,42} \geq 6.99$; $P < 0.02$; Appendix 5.2).

We recorded a greater loss of organic material per mm of rainfall in echidna than bilby/ bettong pits up to 63 days ($F_{1,48} = 5.13$; $P < 0.028$; Appendix 5.2) but any pit effect diminished after this ($P \geq 0.11$). Rainfall-adjusted mass varied significantly with treatment only after 396 days, with termiticide-treated bags (T and F + T) retaining significantly more organic material per mm of rainfall than bags subjected to fungicide only or no chemical treatment ($F_{3,42} = 3.12$; $P = 0.039$; Appendix 5.2).

5. Decomposition in foraging pits

Rainfall-adjusted mass of organic material varied inversely with the content of inorganic material (e.g. sand) in the litter bags. The results, however, are not clear cut, as the infiltration of inorganic material increases over time (Figure 5.5).

5.4.4 Infiltration of inorganic material into the litter bags

The inorganic content of our litterbags increased with time (Appendix 5.3). However the rate of increase varied among treatments with a significantly greater % inorganic

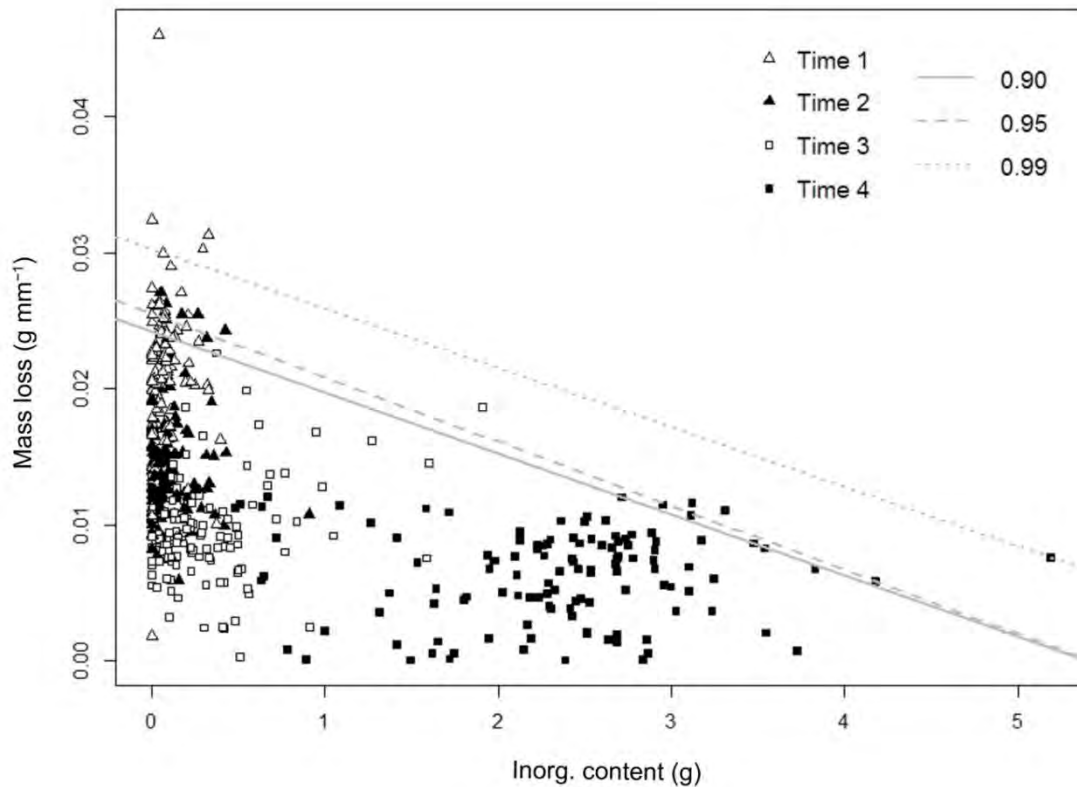


Figure 5-5. Relationship between the inorganic content of the litter bags (g) and the mass of organic material lost per mm of rainfall (g mm^{-1}). Collection times are represented as: Time 1 = white triangles, Time 2 = black triangles, Time 3 = white squares, Time 4 = black squares. Quantile regression was performed across all collection times. The 90th (solid line: Coefficient = -0.00448 ; $t = -11.44$; $P < 0.001$), 95th (dashed line: Coefficient = -0.0047 ; $t = -9.56$; $P < 0.001$) and 99th (dotted line: Coefficient = -0.00436 ; $t = -11.44$; $P = 0.14$) quantiles regression lines are shown.

material in the *Austrostipa* than the *Triodia* litter bags up until 196 days ($F_{1,42} \geq 4.7$; $P < 0.04$; Appendix 5.3, 4). Initially we also detected a greater % inorganic material in litter bags placed in the bilby/ bettong pits than echidna pits on the dunes, but not in the swales (Pit \times Landform interaction: $F_{1,48} = 4.2$; $P = 0.046$; Appendix 5.4).

The % inorganic material did not differ among chemical treatments for the first 63 days ($P > 0.39$), but at 196 days, all fungicide-treated bags (F and F + T) contained a lower % inorganic material than the other treatments ($F_{1,42} = 5.74$; $P = 0.003$; Appendix 5.4). Further, after 396 days, all termiticide-treated litter bags (T and F + T) contained greater % inorganic material than the control litter bags. Termiticide and fungicide-treated bags (F + T) contained greater % inorganic material than those treated only with fungicide ($F_{1,42} = 4.42$; $P = 0.01$; Appendix 5.4).

5.4.5 Modelling decomposition rates

The exponential decomposition models used to describe the loss of % organic material fit our empirical data well (R^2 range = 0.41–0.98; Table 5.1). The K-values from our modelled decay rates (% organic remaining day⁻¹) did not differ significantly among any of the treatments or their interactions ($P > 0.07$; Appendix 5.5).

The modelled half life of our litter did not differ significantly in relation to our chemical treatments ($P > 0.1$; Appendix 5.5) except for control litter bags in the swales, which had a greater half life than those under any other chemical or landform combinations (Treatment \times Landform interaction: $F_{3,42} = 2.88$; $P = 0.049$; Figure 5.6; Appendix 5.5).

5. Decomposition in foraging pits

Table 5.1. Summary of results for Olson's negative exponential model ($K \text{ days}^{-1}$) of decomposition averaged for each factor. B/ B = bilby/ bettong, Land. = landform, Treat. = chemical treatment, F + T = both fungicide and termiticide, T = termiticide, F = fungicide, C = control.

Land.	Pit	Treat.	<i>Austrostipa</i>			<i>Triodia</i>		
			K	SE	Adj. R^2	K	SE	Adj. R^2
Dune	B/ B	F + T	0.0018	9.6E-05	0.79 – 0.91	0.0021	1.8E-04	0.74 – 0.90
Dune	B/ B	T	0.0018	1.6E-04	0.81 – 0.98	0.0014	1.1E-04	0.81 – 0.94
Dune	B/ B	F	0.0017	1.1E-04	0.81 – 0.89	0.0019	2.0E-04	0.77 – 0.91
Dune	B/ B	C	0.0015	3.8E-04	0.78 – 0.93	0.0018	2.0E-04	0.80 – 0.95
Dune	Echidna	F + T	0.0015	1.4E-04	0.83 – 0.91	0.0020	1.7E-04	0.77 – 0.86
Dune	Echidna	T	0.0017	3.5E-04	0.41 – 0.91	0.0019	4.2E-04	0.73 – 0.85
Dune	Echidna	F	0.0016	1.7E-04	0.79 – 0.89	0.0018	1.8E-04	0.77 – 0.85
Dune	Echidna	C	0.0023	2.7E-04	0.84 – 0.89	0.0021	1.9E-04	0.73 – 0.83
Swale	B/ B	F + T	0.0020	2.8E-04	0.77 – 0.87	0.0021	1.8E-04	0.74 – 0.90
Swale	B/ B	T	0.0021	9.1E-05	0.84 – 0.94	0.0014	1.1E-04	0.81 – 0.94
Swale	B/ B	F	0.0021	3.6E-04	0.69 – 0.91	0.0019	2.0E-04	0.77 – 0.91
Swale	B/ B	C	0.0018	2.8E-04	0.61 – 0.85	0.0018	2.0E-04	0.80 – 0.95
Swale	Echidna	F + T	0.0012	1.8E-04	0.89 – 0.98	0.0017	3.2E-04	0.77 – 0.95
Swale	Echidna	T	0.0018	3.2E-04	0.70 – 0.92	0.0021	7.5E-05	0.81 – 0.92
Swale	Echidna	F	0.0022	9.1E-05	0.80 – 0.97	0.0021	1.7E-04	0.73 – 0.94
Swale	Echidna	C	0.0014	5.1E-04	0.92 – 0.97	0.0018	4.5E-04	0.65 – 0.89

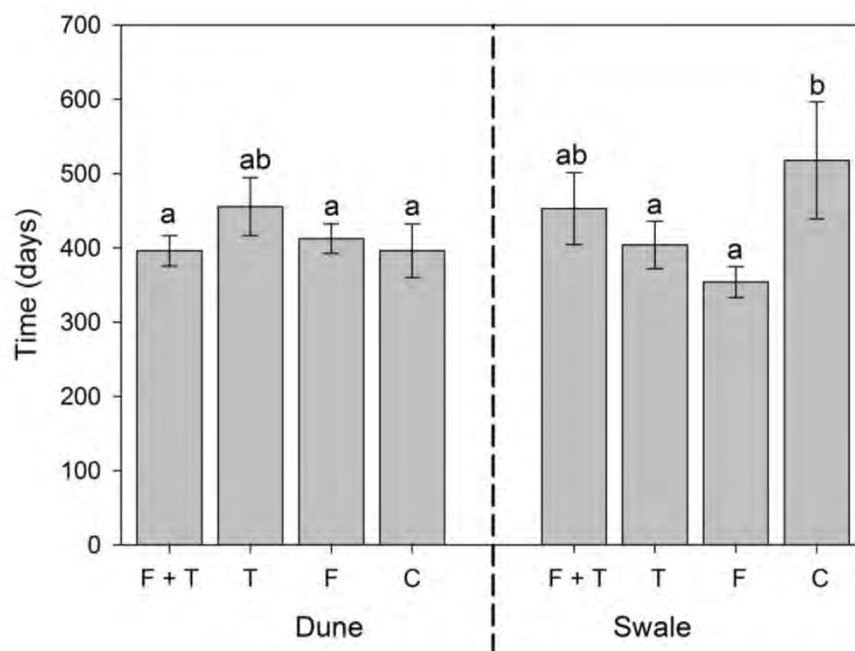


Figure 5-6. Modelled half life (\pm SE) for our Landform by Treatment interaction. The time of the half life is indicated in days (y axis). F + T = both fungicide and termiticide, T = termiticide, F = fungicide, C = control.

5.5 Discussion

This study examined whether mechanisms underlying the decomposition of leaf litter differed between the foraging pits of native soil-foraging mammals. We assessed whether pits constructed by echidnas and bilbies/ bettongs, which varied markedly in morphology, influence decomposition rates across different landforms, substrates, and decomposer communities. We detected initial differences in our measures of decomposition between echidna and bilby/ bettong pits. At the completion of the study (396 days), however, there was no overall difference in the modelled decomposition rates between the two pit types. The most consistent difference in our measures of decomposition and soil addition over the duration of the study was between our two grass species. There was no consistent evidence that landform or chemical exclusion of decomposers (i.e. termites and fungi) significantly reduces the % organic material lost, despite significant effects at the final stages of our study.

5. Decomposition in foraging pits

5.5.1 *Effects of foraging pit morphology*

The loss of soil foraging mammals from large parts of arid and semi-arid Australia could potentially alter carbon and nutrient dynamics in these systems. While arid and semi-arid Australia still supports some soil foraging animals such as goannas (Whitford 1998), echidnas (Eldridge and Mensinga 2007) and rabbits (James *et al.* 2011), their foraging pits are morphologically distinct and are constructed at different locations and frequencies to those constructed by locally extinct bilbies and bettongs (James *et al.* 2009; Eldridge *et al.* 2012). While echidnas, bilbies and bettongs all produce similar size excavations, they differ in shape and the depth to which they dig (James and Eldridge 2007).

Foraging pit morphology initially affected rates of organic mass loss, but the trends we found were contrary to our initial expectations. Our expectation of greater decomposition in bilby/ bettong pits was upheld initially. We found a greater % organic mass loss in bilby/ bettong pits after 30 days. This may have been due to a greater initial infiltration of soil into the litter bags in the bilby/ bettong pits, particularly in coarse-textured dune soils. However, when organic mass loss was adjusted for the possible effects of rainfall, the initial loss of organic material was greater in the echidna pits. The % organic mass loss was also significantly greater in the echidna foraging pits after 63 days. Our results suggest that variation between echidna and bilby/ bettong pits, in depth and shape, has a negligible effect on the long-term process of decomposition. Although the initial burial and rates of organic mass loss may vary between these two markedly different pit shapes, differences are short-lived, lasting for only a few months. This suggests that, unlike rabbits (James *et al.* 2011), the foraging pits of short-beaked echidnas have similar functional roles to the foraging pits from the locally extinct bilbies and burrowing bettongs.

5.5.2 The importance of substrate and soil contact

Foraging pits enhance decomposition by promoting the rapid burial of organic material (Whitford 2002). Rates of decay can shift with changes in abiotic conditions such as season and climate (Moorhead and Reynolds 1991; Austin *et al.* 2009). However, there is mounting evidence to suggest that the physical and chemical properties of the decomposing substrate are significant drivers of decomposition rates (Aerts 1997; Cornwell *et al.* 2008). At global scales, the decomposability of a litter is consistently correlated with the ecological strategy of individual species making up that litter, given that plant functional traits tend to overlap substantially in their leaf traits (Wright *et al.* 2004; Cornwell *et al.* 2008). We found that the two different substrates provided the most consistent effect on our measures of decomposition, with significant differences between the substrates at almost every collection. While both of these perennial grasses have a thin cylindrical structure, they do differ markedly in their leaf density due to the high silica content in *Triodia* (Dengler *et al.* 1994; Reid and Hill 2013). Such differences in density affect the surface area to weight ratio which may affect mass loss rates as equal masses, not equal volumes of each grass, were used in each litter bag. Some studies have shown that leaves with a high mass per unit area have low rates of decomposition (Wright *et al.* 2004; Cornwell *et al.* 2008).

Soil contact is reported to play a critical role in decomposition in arid and semi-arid ecosystems (Moorhead and Reynolds 1991; Throop and Archer 2007; Throop and Archer 2008). When substrates are mixed with, or buried by, soil, there is greater contact with bacteria, fungi, termites and other soil microbes and fauna which enhance decomposition rates. We found soil infiltration increased with time as did the incidence of fungi on the control and termiticide treated bags over the first 196 days. The infiltration of soil did not appear to affect subsequent infilling, however this may be an artefact of the temporal spacing of our collection intervals. Throop and Archer (2007) found that soil infiltration into litter bags was strongly correlated with the proportion of mass remaining. We found the mass loss of organic material per mm of rainfall is not well predicted by the amount of soil which infiltrates the litter bags

5. Decomposition in foraging pits

alone, as shown in Figure 5.5. This relationship shows a shift in central tendency and variance suggesting that additional response variables are required to adequately model the relationship (Cade and Noon 2003). While there are clear trends that soil infiltration into the litter bags increased over time, time masks many other underlying, unmeasured factors which may also contribute to organic material mass loss.

The positive effects of soil contact may depend upon soil texture. Soil texture has a significant effect on foraging pit longevity (Eldridge *et al.* 2012), with lower half-lives of pits formed on coarse-textured than fine-textured soils (Eldridge 2011). Our results suggest that soil texture affects the rates of substrate burial and initial decomposition. We used landform as a surrogate for soil texture, comparing decomposition rates from sandy dune crests with loamy inter-dunal swales. While we found no direct effects of our two landforms on decomposition, soil texture appeared to mediate other interactions. For example, the modelled half-life of litter was greatest for litter bags placed in the swale with no chemical treatment. This observation is consistent with predictions under the inverse texture hypothesis (*sensu* Noy Meir 1973), where coarse textured sandy soils are more productive than finer-textured soils in low rainfall (< 300–500 mm) environments due to the hydrodynamics of evaporation (Noy Meir 1973). Not all landform interactions, however, were consistent with the inverse texture hypothesis. For example, after 396 days there was a greater proportion of mass loss for the fungicide-treated *Austrostipa* litter bags in the swales than in the dunes.

We found no evidence to support a ‘home-field advantage’ (*sensu* Milcu and Manning 2011; Fraser and Hockin 2013) of decomposition for our substrates in the landforms from which they were derived. After 396 days both untreated grasses had lost equal proportions of organic material in the dunes, and *Triodia* had lost a significantly greater proportion in the swale than the locally native *Austrostipa*. This supports previous studies which have also failed to find evidence that plants encourage soil biota which decompose their litter quicker (e.g. Ayres *et al.* 2006).

5.5.3 *The effect of decomposer exclusion*

While some studies have shown that fungi and/ or termites are important decomposers in semi-arid systems (Noble *et al.* 1989; Noble *et al.* 2009), we found no strong evidence for this in our study. We expected that excluding detritivores would decrease both the proportional and rainfall-adjusted organic mass loss. However this did not occur until the final collection at 396 days. Furthermore, the chemical treatments did not clearly reveal the extent to which fungi or termites decomposed the material. While there was a significantly higher incidence of fungi on the litter bags which were not treated with fungicide (i.e. termiticide and control bags) there appeared to be temporal variation in the presence of fungi with a peak in the incidence of fungi at the second and third collection intervals (63 and 196 days). This may have been due to seasonal variation and the timing of our collection intervals, with the second and third collection intervals occurring in the warmer months. This interval of increased fungal presence may also correspond to period where the physical and chemical state of our substrate is optimal for fungi to proliferate.

The litter bags collected at the final interval were heavily consumed by non-target insect larvae, with a high concentration of faunal silk tunnels penetrating the litter bags. Given the large rainfall events which occurred during summer, between the third and final collection intervals (196 days and 396 days) it is unknown whether insect larvae usually play such a large role in decomposition or whether it was due to the abnormally wet summer. Detritivory by similar insect larvae has been recorded in decomposition studies conducted during years of above average rainfall in eucalypt-pine woodlands in the Pilliga area in north-central New South Wales (Hart 1995). It appears that the chemical treatments we applied simply reduced the incidence of decay by these insect larvae rather than excluding termites or fungi. This is an issue with using chemical treatments, as chemicals are rarely species specific and may have unknown, confounding effects on non-target biota. Their effectiveness at controlling organisms may also not be consistent over the time.

5. Decomposition in foraging pits

Chemical treatment was however, related to the infiltration of soil into the litter bags in the latter stages of our study. The fungicide-treated bags had less infiltration of soil at 196 days. Fungi are generally responsible for enzymatic-induced breakdown of organic matter (Hawkins 1996; Cornwell *et al.* 2009), and their presence is reported to increase with soil contact (Moorhead and Reynolds 1991; Throop and Archer 2008). We found that by excluding fungi we have reduced the ability of soil to adhere to the substrate. It is possible that the physical structure of fungal hyphae may be important for binding soil particles to the substrate.

In arid and semi-arid systems, soil biotic activity is concentrated in the top few centimetres of the soil, where nutrients are also concentrated (Whitford 2002; Tongway *et al.* 2003). This also coincides with the part of the soil profile that is heavily disturbed by soil foraging animals (James *et al.* 2009; Eldridge *et al.* 2012). There are conflicting views about whether soil disturbance by animals disrupts or encourages the activities of soil biota such as termites (Gibb 2012). We found little evidence, overall, of termite activity in our litter bags, which is interesting given that termites are recognised as important decomposers in these systems (Noble *et al.* 2009). At sites supporting high populations of both termites and beetles, termites tend to be far more important consumers, particularly of material with high levels of lignin (Wood and Sands 1978; Cornwell *et al.* 2009). Our results, however, indicate that insect larvae, which likely include beetles and moths, may be as equally as important for the decomposition of sub-surface material as termites, and this might be the case elsewhere in semi-arid Australia (Hart 1995).

5.5.4 Modelling decomposition over time

Decomposition is a complex process to model. The negative exponential model of decomposition (Jenny *et al.* 1949; Olson 1963) is commonly used to compare relative rates of mass loss, i.e. slow (< 0.005), medium ($0.005\text{--}0.010$) and fast ($0.010\text{--}0.015$; Petersen and Cummins 1974; Boulton and Boon 1991). Despite widespread use, this model assumes that mass loss from organic material is a constant, decreasing fraction

of the material remaining and that mass loss equates with decomposition. It also integrates the decay of a number of components that vary in their decay rates and interact synergistically and antagonistically with each other, affecting the overall substrate decay rate (Boulton and Boon 1991). While the decomposition model of Olsen (1963) was a good fit to our data, obtaining a high coefficient of determination does not mean that the model adequately describes the complexity of biological interactions operating during the decomposition process (Boulton and Boon 1991). We found no significant differences in decomposition rate among any of our factors despite observing significant differences among the factors at separate collection periods. For example, when analysed separately, we found that the effects of pit morphology were short-lived and that a switch occurred in the relative % organic mass loss of the two substrates over time.

The inconsistent temporal effects that we found amongst our factors highlight the importance of model selection and temporal scale in decomposition studies. Some studies have overcome some of these issues by using different measures of decomposition and factors such as temperature and moisture, rather than simply time (e.g. Throop and Archer 2008; Fraser and Hockin 2013). Although the most parsimonious model may have been overly simplistic or had too few data points, the time frame over which we measured may have captured a large shift in factors driving the decomposition processes. Previous work has suggested that studies of decomposition need to be conducted over standard time periods to allow for these temporal idiosynchronies (e.g. Boulton and Boon 1991).

5.6 Conclusion

This study measured abiotic and biotic mechanisms of decomposition within the foraging pits of two native mammals. We found that the effects of foraging pit morphology were relatively short-lived, and there were no differences in the overall decomposition rate between the two types of pits over the total duration of our study. Our data highlights the importance of temporal variability in driving differences in

5. Decomposition in foraging pits

decomposition, and supports the notion that the properties of the decomposing substrate are an important driver of decomposition. Overall this study provides evidence that the foraging pits of the short-beaked echidna do not differ markedly from those of the locally extinct greater bilby and burrowing bettong, in terms of their capacity to maintain decomposition. Despite this, a diverse community which contains an array of resource patch-creating species is likely more functional than one where species have been lost.

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Appendix 5.1. *F*-ratios and *P*-values from the ANOVA for each collection interval (1–4) for % organic material remaining. Bl = Spatial blocking term, La = Landform (Dune, Swale), Tr = chemical treatment (F + T, F, T, C), Gr = grass type (*Austrostipa*, *Triodia*), Pi = Pit morphology (echidna, bilby/ bettong). Significant *P*-values are in **bold**.

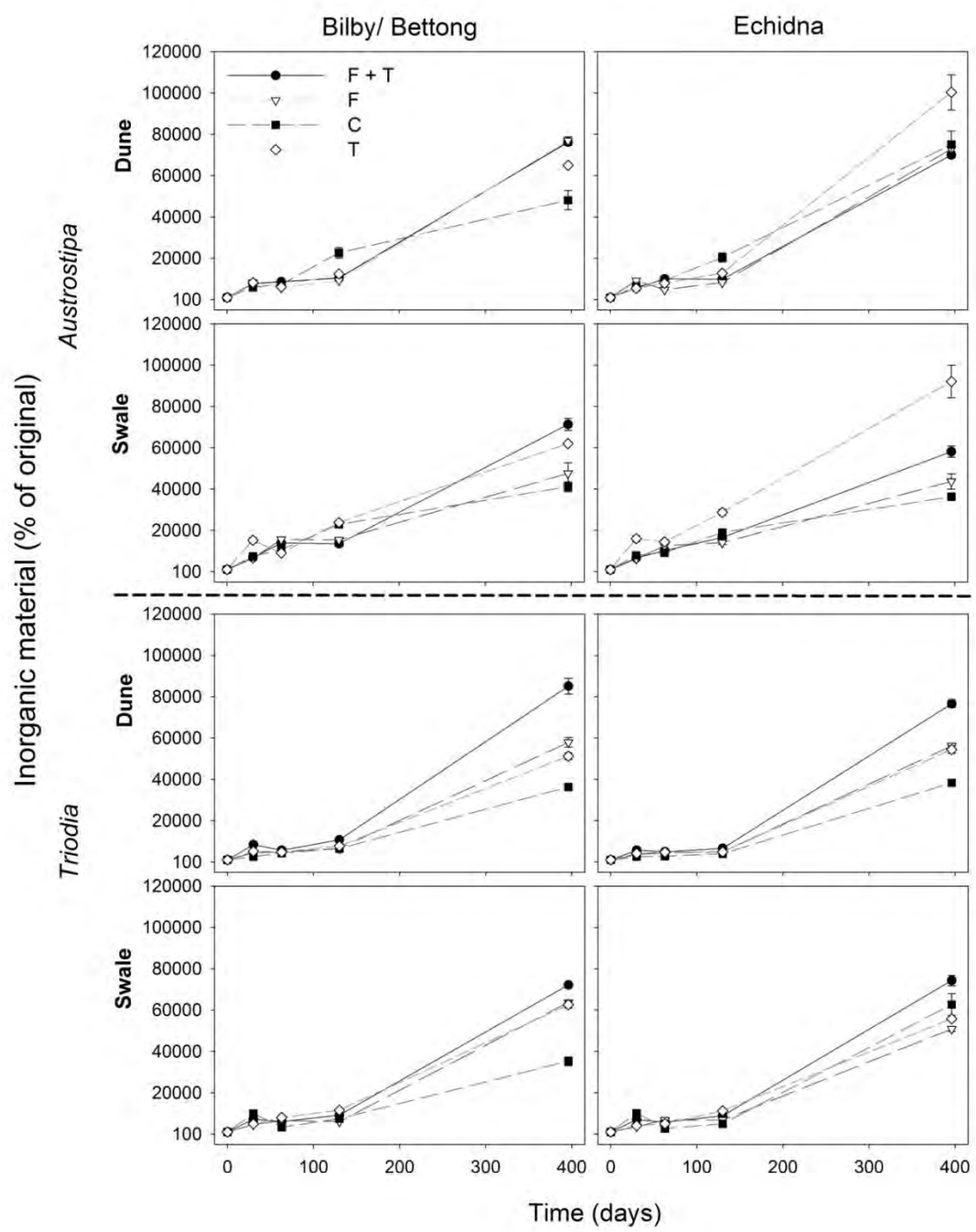
Factor	d.f.	1		2		3		4	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Bl	3	0.57	0.685	N/A	N/A	1.26	0.425	0.68	0.626
La	1	0.49	0.536	0.54	0.515	0.08	0.795	1.85	0.267
Bl × La	3	2.42	0.603	0.14	0.932	2.28	0.287	N/A	N/A
Tr	3	1.20	0.322	2.38	0.093	1.21	0.318	4.38	0.011
Gr	1	14.2	0.001	7.71	0.010	7.59	0.009	6.77	0.014
La × Tr	3	0.51	0.678	0.41	0.744	0.98	0.412	2.93	0.048
Tr × Gr	3	1.30	0.287	3.86	0.021	2.27	0.096	0.88	0.463
La × Gr	1	1.11	0.298	0.23	0.634	0.00	0.961	3.31	0.078
La × Tr × Gr	3	0.91	0.445	2.10	0.125	1.38	0.265	3.28	0.033
Pi	1	9.31	0.004	8.28	0.006	0.35	0.554	0.75	0.391
La × Pi	1	0.39	0.535	1.60	0.212	2.43	0.125	0.31	0.581
Tr × Pi	3	1.47	0.235	0.13	0.940	1.62	0.196	1.59	0.203
Gr × Pi	1	0.73	0.398	0.08	0.776	1.72	0.196	1.44	0.236
La × Tr × Pi	3	0.75	0.529	1.18	0.329	0.18	0.911	0.99	0.406
La × Gr × Pi	1	0.18	0.673	0.11	0.741	4.39	0.042	0.03	0.869
Tr × Gr × Pi	3	0.43	0.735	0.62	0.602	0.71	0.551	0.33	0.807
La × Tr × Gr × Pi	3	1.13	0.345	0.69	0.562	0.32	0.813	0.52	0.673

5. Decomposition in foraging pits

Appendix 5.2. *F*-ratios and *P*-values from the ANOVA for each collection interval (1–4) for mass loss adjusted by rainfall (g mm^{-1}). Bl = Spatial blocking term, La = Landform (Dune, Swale), Tr = chemical treatment (F + T, F, T, C), Gr = grass type (*Austrostipa*, *Triodia*), Pi = Pit morphology (echidna, bilby/ bettong). Significant *P*-values are in **bold**.

Factor	d.f.	1		2		3		4	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Bl	3	2.33	0.915	0.22	0.878	1.35	0.402	0.27	0.847
La	1	0.07	0.808	0.02	0.885	0.05	0.843	0.77	0.445
Bl × La	3	1.89	0.493	1.02	0.476	2.87	0.313	N/A	N/A
Tr	3	1.17	0.333	0.12	0.946	1.07	0.372	3.12	0.039
Gr	1	12.5	0.001	9.35	0.004	6.99	0.012	3.39	0.074
La × Tr	3	0.09	0.965	1.37	0.267	0.89	0.455	2.33	0.092
Tr × Gr	3	2.80	0.053	0.84	0.482	3.01	0.042	0.58	0.632
La × Gr	1	2.13	0.153	0.08	0.773	0.00	0.961	2.98	0.093
La × Tr × Gr	3	0.29	0.829	0.82	0.490	1.46	0.242	2.78	0.056
Pi	1	5.13	0.028	2.71	0.106	0.42	0.521	1.18	0.284
La × Pi	1	0.01	0.941	0.31	0.579	2.65	0.110	0.07	0.799
Tr × Pi	3	0.64	0.596	0.77	0.516	1.73	0.172	1.7	0.179
Gr × Pi	1	1.04	0.312	0.07	0.799	1.88	0.176	0.55	0.462
La × Tr × Pi	3	0.46	0.709	0.87	0.463	0.15	0.931	0.65	0.587
La × Gr × Pi	1	0.04	0.844	0.15	0.699	4.57	0.038	0.01	0.908
Tr × Gr × Pi	3	0.26	0.856	0.32	0.814	0.70	0.557	0.33	0.807
La × Tr × Gr × Pi	3	0.89	0.455	0.7	0.558	0.33	0.806	0.56	0.646

Appendix 5.3. The mean (\pm SE) soil infiltration into the litter bags (% inorganic material) over time for each factor. F + T = both fungicide and termiticide, T = termiticide, F = fungicide, C = control.



5. Decomposition in foraging pits

Appendix 5.4. *F*-ratios and *P*-values from the ANOVA for % inorganic material. Bl = Spatial blocking term, La = Landform (Dune, Swale), Tr = chemical treatment (F + T, F, T, C), Gr = grass type (*Austrostipa*, *Triodia*), Pi = Pit morphology (echidna, bilby/ bettong). Significant *P*-values are in **bold**.

Factor	d.f.	1		2		3		4	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Bl	3	0.99	0.504	1.95	0.407	0.41	0.831	N/A	N/A
La	1	1.55	0.302	2.84	0.191	2.79	0.194	8.85	0.059
Bl × La	3	N/A	N/A	1.40	0.322	1.33	0.398	0.38	0.826
Tr	3	0.53	0.663	1.02	0.398	4.95	0.007	4.42	0.010
Gr	1	4.70	0.037	31.9	0.000	65.2	0.000	1.38	0.249
La × Tr	3	1.45	0.244	1.64	0.199	3.14	0.040	0.31	0.816
Tr × Gr	3	1.74	0.175	0.33	0.802	5.74	0.003	1.46	0.243
La × Gr	1	0.00	0.955	4.42	0.043	3.62	0.067	3.06	0.090
La × Tr × Gr	3	1.76	0.172	0.43	0.730	0.91	0.447	0.50	0.682
Pi	1	6.96	0.011	0.73	0.398	0.57	0.455	1.09	0.301
La × Pi	1	4.20	0.046	1.94	0.170	0.63	0.431	0.22	0.643
Tr × Pi	3	2.52	0.069	1.63	0.194	0.34	0.797	2.27	0.093
Gr × Pi	1	1.07	0.305	1.65	0.204	0.44	0.510	0.79	0.379
La × Tr × Pi	3	2.28	0.091	0.59	0.623	0.21	0.887	0.07	0.976
La × Gr × Pi	1	0.26	0.614	0.94	0.338	0.02	0.884	0.89	0.349
Tr × Gr × Pi	3	0.36	0.781	4.59	0.007	0.29	0.832	1.47	0.234
La × Tr × Gr × Pi	3	1.20	0.319	3.64	0.019	0.05	0.984	1.00	0.402

Appendix 5.5. *F*-ratios and *P*-values from the ANOVA for modelled decay rates and half life of % organic material. K = Olson's negative exponential decomposition decay rate (days), BI = Spatial blocking term, La = Landform (Dune, Swale), Tr = chemical treatment (F + T, F, T, C), Gr = grass type (*Austrostipa*, *Triodia*), Pi = Pit morphology (echidna, bilby/ bettong). Significant *P*-values are in **bold**.

Factor	d.f.	Decay rate (K days ⁻¹)		Half life (days)	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
BI	3	1.81	0.477	3.33	0.604
La	1	0.59	0.499	3.03	0.180
BI × La	3	0.36	0.792	0.09	0.960
Tr	3	0.58	0.629	1.40	0.258
Gr	1	1.59	0.215	1.75	0.194
La × Tr	3	2.46	0.078	2.88	0.049
Tr × Gr	3	2.00	0.131	1.21	0.320
La × Gr	1	0.32	0.573	0.02	0.878
La × Tr × Gr	3	0.46	0.709	0.11	0.954
Pi	1	0.00	0.949	1.33	0.255
La × Pi	1	1.44	0.236	2.49	0.121
Tr × Pi	3	1.90	0.142	0.95	0.425
Gr × Pi	1	1.52	0.223	0.87	0.356
La × Tr × Pi	3	1.32	0.278	2.52	0.069
La × Gr × Pi	1	1.29	0.261	0.82	0.371
Tr × Gr × Pi	3	0.98	0.411	0.86	0.471
La × Tr × Gr × Pi	3	0.25	0.860	0.19	0.901

5. Decomposition in foraging pits

Chapter 6. Animal foraging pit soil enhances the performance of a native grass under stressful conditions

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Keywords: biotic nurse; biotic–nurse interactions; *Dactyloctenium radulans*; facilitation; nurse objects; *Tachyglossus aculeatus*.

Abbreviations:

ANOVA — Analysis of Variance

C — Carbon

LSD — Least Significant Difference

N — Nitrogen



The effects of our different treatments on plant growth. From left to right: (1) Open Pit low water, (2) Open Surface low water, (3) Canopy Pit low water, (4) Canopy Surface low water, (5) Open Pit high water, (6) Open Surface high water, (7) Canopy Pit high water, (8) Canopy Surface high water.

6. Pit soil enhances plant growth

6.1 Abstract

6.1.1 Background and Aims

In line with the Stress Gradient Hypothesis, studies of facilitation have tended to focus on plant–plant interactions (biotic nurses), while the relative role of abiotic nurses has been little studied. We assessed the role of biotic and abiotic nurses, and their interaction, on soil enhancement and the consequential performance of a native annual grass, *Dactyloctenium radulans*.

6.1.2 Methods

We used a growth chamber study with two levels of water application to compare the performance of *D. radulans* growing in soil from foraging pits of the short-beaked echidna (*Tachyglossus aculeatus*; abiotic nurse) and non-pit soil from either under tree canopies (biotic nurse) or surrounding open areas.

6.1.3 Results

All measures of plant performance were more pronounced under the high than the low water treatment. The greatest differences between pit and surface Microsites occurred under the low water application, reinforcing our view that facilitatory effects are greater in resource-limited environments. Despite tree canopy soil having greater N, there was no significant effect on plant performance, nor any significant interaction with Microsite.

6.1.4 Conclusions

Our study provides strong evidence that foraging pits enhance soil properties and this soil, in turn, facilitates plant growth; and supports previous work documenting the positive effect of nurse–protégé interactions under greater levels of abiotic stress.

6.2 Introduction

Resource dynamics, and hence ecosystem productivity, can be controlled by plants (bottom–up ecosystem control), the activity of animals (top–down ecosystem control; see Meserve *et al.* 2003) and by either the biotic or abiotic components of both trophic groups (Facelli and Brock 2000; Eldridge and Mensinga 2007; Castro *et al.* 2010). While the relative importance of both trophic groups in regulating ecosystem processes is well known for aquatic or more mesic terrestrial systems, it remains rather elusive for semi–arid environments (Meserve *et al.* 2003). Studies aimed at clarifying the relative importance of top–down versus bottom–up control in ‘harsh’, resource–limited environments have focused mainly on the negative effects of biotic interactions among plants i.e. competition, or consumption by herbivores (Grime 1973; Meserve *et al.* 2003). Over the past two decades however, a more explicit acknowledgement has emerged of the role of positive plant–plant interactions, i.e. facilitation, in shaping plant communities, particularly in harsh environments (Flores and Jurado 2003; Callaway 2007). Current plant–plant paradigms now explicitly acknowledge the positive effects of organisms in ecosystems as well as the degree of environmental stress imposed on a system (e.g. Stress Gradient Hypothesis — where a gradient of increasing physical stress leads to an increase in the incidence of positive interactions between individuals —; Bertness and Callaway 1994). Thus recent studies of facilitation highlight the need to consider positive interactions if we are to appreciate the importance of vegetation and soil nutrient controls in shaping natural communities (Hacker and Gaines 1997; Michalet *et al.* 2006).

It is well established that in harsh, arid and semi–arid environments, plant establishment and productivity are co–limited by the availability of two critical resources; water and nutrients, particularly nitrogen (Sankaran *et al.* 2005). These resources have an uneven spatial distribution, with disproportionately large differences between resource–accumulating and resource–shedding areas (Ludwig and Tongway 1995). Animal disturbances, particularly those in arid and semi–arid environments, represent sites where limiting resources are concentrated (Whitford

2002). Small surface depressions such as foraging pits capture water, sediment, organic matter, litter and seeds (James *et al.* 2009), creating soils with a higher infiltration capacity, greater respiration and altered physical characteristics compared with surrounding soils (Eldridge and Mensinga 2007; Eldridge *et al.* 2010). Foraging pits also act as safe sites for germination by increasing seed longevity and seedling establishment (Rotundo and Aguiar 2005). All of these positive effects on soils have extended, though generally unspecified, legacy effects (*sensu* van der Putten 2009), as microbial and chemical changes persist after the initial physical structure has been lost or infilled (van der Putten 2009). These abiotic nurses are formed by animals when they construct habitat or forage for food (Byers *et al.* 2006). Although the roles of biotic nurses have been studied extensively (see recent review in Callaway 2007), the positive effects of abiotic nurses such as these pits and depressions created by animals, and logs and rocks, are poorly represented in the literature (though see Munguia–Rosas and Sosa 2008; Peters *et al.* 2008; Castro *et al.* 2010).

Abiotic nurses could potentially have facilitatory effects on plants as dramatic as those reported for biotic nurses simply through their role as sinks for resources (Flores and Jurado 2003; Schlesinger *et al.* 2009; James *et al.* 2010). Further, in some situations, abiotic–nurse associations may be both more frequent and/ or more important drivers of community structure and productivity than traditional biotic associations (Munguia–Rosas and Sosa 2008; Peters *et al.* 2008). This could happen because the effects of abiotic nurse objects are more persistent under extremely stressful or resource–limited conditions or where the vegetation community is dominated by plants with allelopathic properties. In these situations, biotic nurses such as plants might collapse (Michalet *et al.* 2006). Conceivably, abiotic structures might be the only ones creating favourable microhabitats, thereby expanding the range of less tolerant species, enabling them to survive in environments far beyond their physiological tolerances (Day *et al.* 2003). Under extreme environmental conditions therefore, abiotic nurses would be expected to play substantial roles in structuring communities and enhancing diversity, potentially overwhelming biotic nurse facilitation, which is known to wane at extremely high stress levels (Belcher *et al.* 1995).

In this study we assessed the relative importance and the joint soil-mediated effects of both plant–plant interactions and animal foraging pits on the growth and productivity of the annual, highly palatable C₄ grass *Dactyloctenium radulans* R.Br. P. Beauv (button grass), under two contrasted water scenarios in a controlled growth chamber experiment. In the context of this study we adopt the broader definition of facilitation as an interaction that directly or indirectly reduces abiotic environmental stress or increases resource availability, resulting in an increase in productivity, survival or fitness of a photosynthesising organism (Brooker and Callaway 2009). The roles of our biotic nurses *Eucalyptus* and our phytometer *Dactyloctenium* are reasonably well known. *Dactyloctenium radulans* is widespread throughout semi–arid Australia and is grazed by both native and introduced vertebrate and invertebrate herbivores including the greater bilby (*Macrotis lagotis*, Gibson 2001), the Australian plague locust (*Chortoicetes terminifera*, Clissold *et al.* 2006), a range of unspecified invertebrates, and domestic sheep and cattle. The response of *Dactyloctenium* to soil nitrogen is positive, with increased growth from high nitrogen soils. *Tachyglossus aculeatus* Shaw (short–beaked echidna), is ubiquitous over much of continental Australia, and its foraging disturbances have been shown to have substantial effects on a wide range of soil and ecological processes such as nutrient enhancement, enhanced decomposition and moderation of temperature and water (Eldridge and Mensinga 2007) that persist long after the initial structure has been lost. The facilitatory role of our biotic nurse, *Eucalyptus* spp. on seedling establishment and growth in arid and semi–arid Australia is somewhat limited. However, a recent study has shown that a large number of perennial understorey plants in the study area are either facilitation beneficiaries (~ 60 %) or facilitation obligates (~ 40 %) to large eucalypt canopies (Soliveres *et al.* 2011). Part of this effect is thought to be due to their role in moderating environmental condition such as shade and temperature (Soliveres *et al.* 2011) as well as improving soil chemical properties (Jeddi *et al.* 2009).

We hypothesised that the accumulated soil in foraging pits would enhance the growth and survival of vascular plants indirectly *via* their positive effects on soil fertility

6. Pit soil enhances plant growth

(Eldridge and Mensinga 2007). This effect has been shown to persist for at least five years (D. Eldridge, unpubl.). We compared the relative importance of foraging pit (abiotic nurse) vs. *Eucalyptus intertexta* tree (biotic nurse) effects and the potential for a synergistic interaction between them, on soil properties and on the performance of our phytometer *Dactyloctenium*. Finally, we tested for shifts in these effects under either a low or high water regime, thereby inducing two levels of abiotic stress. Overall, we predicted a greater soil fertility and plant performance in foraging pit or tree canopy soils than those growing in surrounding surface soil; and a synergistic effect of both nurse types or with increased water availability when acting together. By considering the role of both biotic and abiotic nurses under two different watering regimes, we aimed to increase our mechanistic understanding of the relative importance of animals and existing plants defining seedling performance in semi-arid environments.

6.3 Methods

6.3.1 Field site

Soils were collected from Yathong Nature Reserve in central New South Wales, Australia (32°35' S, 145°35' E). Rainfall is highly variable within and among years (BOM 2010) and averages 383 mm annually. Average maximum temperatures range from in 33.1 °C in January to 14.3 °C in July (BOM 2010). The vegetation is predominantly open woodland dominated by western red box (*Eucalyptus intertexta*) with canopy cover ranging from 18–70 % (Keith 2004). The understorey is dominated by perennial grasses, which include speargrass (*Austrostipa* spp.), wiregrass (*Aristida* spp.) and white-top grass (*Austrodanthonia caespitosa*). Annual grasses such as *Dactyloctenium radulans* appear in the warmer months, however their abundance varies on an annual basis depending upon recent climatic conditions. Above 40 % of the surface is covered by biological soil crusts (Eldridge and Greene 1994). The soils at our study site, classified as red Kandosols, had loam to clay-loam surface textures to 1 m deep, overlying light-medium clay B horizons (Eldridge and Mensinga 2007).

6.3.2 Sampling procedure

Soil samples were collected in cylindrical steel cores 100 mm high × 70 mm diameter, driven 90 mm into moist soil. Thirty-two soil cores were randomly collected from 18-month old echidna pits (hereafter Pit), which we had been monitoring since excavation, at sites under the canopy of large *Eucalyptus intertexta* canopies (hereafter Canopy) and in the Open. With every pit sampled, a surface soil core (hereafter Surface) was also collected in a random direction, but consistent distance of 0.5 m, from the pit. Canopy soil was collected within the drip line, i.e. about 15 m from the base of mature trees, while Open soils were > 20 m from any tree canopy. The soils collected from under the canopy were typically overlaid by a shallow < 1 cm deep layer of leaves which was not removed during sampling.

6.3.3 Plant growth

Soil cores from each of the four combinations of Pit and Surface by Canopy and Open, were equally assigned randomly into two Water treatments: low water 6 ml and high water 15 ml administered daily. The determination of the two Water treatments was based on an earlier pilot trial (S. Travers, unpubl.) designed to test the response of plants across a range of moisture regimes, and were based on thresholds of the soils' active moisture range. Cores were placed in a growth chamber, which was set at 24 °C diurnal temperature, 17 °C night temperature and 14 hours of light, representative of average spring conditions for the field site (BOM 2010). Cores were randomly arranged into eight blocks within the growth chamber. In other words, the relative positions of each of the 64 cores taken from the field did not reflect their final position in the growth chamber. Each block contained each of the eight separate treatment combinations. In total therefore there were 64 soil cores comprising 2 × Microsites (Pit, Surface) by 2 × Cover categories (Canopy, Open) by 2 × levels of Water applications (low, high) and 8 × replicates of each combination.

6. Pit soil enhances plant growth

Dactyloctenium radulans was chosen as the phytometer from a selection of local native grasses in a previous pilot trial based on plant response to nitrogen. The pilot trial (S. Travers, unpubl.) contained three locally native grass species whose germinants were subjected to three levels of nitrogen equivalent to 0 kg ha⁻¹, 60 kg ha⁻¹ and 120 kg ha⁻¹ (Badgery *et al.* 2005). *Dactyloctenium* was chosen over *Enteropogon acicularis* Lindl. Lazarides and *Chloris truncata* R.Br. as it had the greatest positive response to nitrogen in terms of relative growth. *Dactyloctenium* seeds were collected from the study area in early autumn and kept in a cool room until the following summer. Seeds were germinated in a separate tray and a single *Dactyloctenium* seedling 5–10 mm tall was transplanted into each undisturbed core. Any seedlings that died were replaced as required until day 5 of the trial. Plants were watered daily at either the high or low water regime, during which plant height, leaf count, length of the longest leaf, stem count and flower count were recorded every 3–5 days. Any germinants sprouting from the natural seed bank were removed on emergence. After 64 days, plants were removed from the growth chamber and left to dry for two weeks. Plants were separated into leaves, roots, stems and flowers. Each component was oven-dried for 24 hours at 60 °C before mass was measured. Seeds were separated from flowers and counted. The dried leaves were ground and total nitrogen and carbon determined using a high combustion LECO CNS–2000 Analyser.

6.3.4 Soil properties

The chemical and physical properties of the soil were also analysed once plants were removed from the cores. Following the same experimental design and sample size as described above, soil cores were dried in an oven at 55 °C for 15 days to assess bulk density. Low oven temperatures were used so that the nitrogen content was not compromised. A 100 g sample of topsoil was ground for chemical analysis. Total nitrogen (N) and carbon (C) were determined using a high combustion LECO CNS–2000 Analyser. The active labile C fraction of the soil was measured according to the method of Weil *et al.* (2003). Soils were also analysed for mineralisable N according to Method 4 of Gianello and Bremner (1986). This method measures the amount of N mineralised

over a 16 hr anaerobic digestion at 100 °C, providing an index of the potential pool of N available to plants present at the time of sampling. Although this index cannot be compared numerically with NH_4^+ and NO_3^- , the values are highly correlated with exhaustive aerobic soil incubation for N mineralisation (Gianello and Bremner 1986).

6.3.5 Statistical analyses

We derived three measures of performance of *Dactyloctenium* in relation to the various treatments; 1) total biomass, which is highly correlated with our individual measures of plant growth performance such as height and leaf length, 2) root to shoot ratio, which assesses plant response to changing levels of resources, and 3) proportional reproductive effort, measured as the ratio of the mass of reproductive structures to total biomass. Except for data on temporal changes in plant attributes (see below), soil and plant attributes (total biomass, root: shoot ratio, proportional reproductive effort) were analysed using a balanced randomized complete block ANOVA. Data for total leaf C and N were analysed using General Linear Models as there was insufficient material available from some samples and therefore the analyses were unbalanced. Our analyses considered Block (or replicate; $n = 8$) effects (random), and the main order effects of Microsite (fixed effect: Pit, Surface), Cover (fixed effect: Canopy, Open) and Water regime (fixed effect: low, high) and their two- and three-way interactions. Data were tested for homogeneity of variance using Levene's test, and diagnostic tests were run in the Minitab statistical software (Minitab, version 15.1, Minitab 2007) prior to analysis. Log_{10} transformations of leaf N % and total plant N were required to stabilize the mean-variance relationship prior to interpreting the ANOVA.

Temporal changes in plant height, number of leaves and stems, and the length of the longest leaf were examined using a linear mixed-model. Since the focus was on the time response, data for these repeated measurements were analysed using the cubic smoothing spline approach (Verbyla *et al.* 1999). The modelling process began by fitting a 'saturated' model that included all fixed and random terms; then in turn, each

6. Pit soil enhances plant growth

random term was dropped and the model refitted, with the subsequent change in model deviance (d) noted. The significance of the test that each variance component (a single random term) was zero was given by $0.5[\Pr(X^2 > d)]$ with $X^2 \sim \chi_1^2$ (Orchard *et al.* 2000). Non-significant random terms were dropped from the final model where hypothesis tests assessed the significance of fixed effects using the Wald statistic an approximate F -test. Graphs of predicted smooth response profiles were prepared for significant treatment combinations. All analyses were run using the GenStat statistical software (Payne *et al.* 2007) packages. Data for the number of leaves and number of stems were $\log_e(x + 1)$ -transformed prior to ANOVA.

6.4 Results

6.4.1 Soil properties

Soil bulk density was lower in Pit than Surface soils ($F_{1,49} = 70.0$, $P < 0.01$), and the effect was greatest under the canopy (Microsite by Cover interaction: $F_{1,49} = 4.27$, $P = 0.04$, Table 6.1). Total soil C was greater in Pit soil under the Canopy (3.42 %) than Pit soil in the Open (2.26 %; Microsite by Cover interaction: $F_{1,49} = 4.11$, $P = 0.04$, Table 6.1). Overall, soils under the canopy had about 25 % more labile C and 40 % more total C than those in the Open ($F_{1,49} = 6.6$ and 8.92 , $P < 0.01$, respectively; Table 6.1, Appendix 6.1)

The percentage of total nitrogen N in the soil followed a similar trend to total soil C (Table 6.1). Pit and Canopy soils contained more total N than their “unengineered” analogues ($F_{1,49} = 58.5$ and 12.1 , $P < 0.01$, respectively; Table 6.1). However, the magnitude of the difference in total N between Pit and Surface was greater (eight-fold) in the Open than under the Canopy (5.6-fold; Microsite by Cover interaction: $F_{1,49} = 4.71$, $P = 0.05$; Table 6.1). Total soil N concentration also varied significantly in relation to watering regime, with 60 % more N in the low than the high water treatment ($F_{1,49} = 7.69$, $P < 0.01$; Figure 6.1a) suggesting possible leaching under the high water treatment. However, there was no significant effect of the Water

Table 6.1. Soil attributes. Mean soil attributes of plants in relation to Water regime low, high, Cover Canopy, Open and Microsite Pit, Surface. Within an attribute, the 5 % LSD for the Water by Cover by Microsite interaction is given.

Water	Cover	Microsite	Bulk	Carbon		Nitrogen		
			density	Labile	Total	Mineralisable	Mineralisable pool	Total
			(mg m ⁻³)	(mg kg ⁻¹)	(%)	(mg kg ⁻¹)	(mg per core)	(%)
High	Canopy	Pit	1.11	460.11	3.24	7.99	21.41	0.13
		Surface	1.45	320.03	1.18	4.19	14.47	0.02
	Open	Pit	1.34	388.74	2.11	6.31	22.55	0.08
		Surface	1.55	260.20	0.90	2.60	9.59	0.01
Low	Canopy	Pit	1.20	530.01	3.61	7.30	20.39	0.21
		Surface	1.51	446.71	1.13	3.07	10.96	0.04
	Open	Pit	1.37	284.63	2.41	6.96	22.63	0.10
		Surface	1.55	371.32	0.96	2.81	10.08	0.03
LSD 5 % value			0.13	178.81	0.93	0.06	0.73	0.02

6. Pit soil enhances plant growth

treatments on mineralisable available N ($P = 0.51$) or on the total soil mineralisable N pools ($P = 0.59$; see Appendix 6.2).

Mineralisable N concentrations were greater in Canopy than Open soils ($F_{1,49} = 6.17$, $P = 0.02$), though the denser soils in the Open meant that we did not detect a significant difference in total mineralisable N pools between Canopy and Open sites ($P = 0.75$; Appendix 6.2). Concentrations and total pools of mineralisable N were greater in Pit soils than Surface soils ($F_{1,49} = 92.97$ and 33.22 , $P < 0.01$, respectively, Table 6.1).

Overall total N concentrations were greatest in Pit soils under the Canopy, suggesting a synergistic effect (Cover by Microsite interactions $F_{1,49} = 6.17$, $P = 0.04$).

6.4.2 Plant growth: Biotic and abiotic nurse effects on plant growth

Total biomass of plants growing in soils from the Open or in soil from under the Canopy did not differ ($P = 0.25$). Pit soil produced significantly larger plants than Surface soil ($F_{1,49} = 89.65$, $P < 0.001$), and the high water treatment produced significantly larger plants than the low water treatment ($F_{1,49} = 48.32$, $P < 0.001$, Figure 6.1b). Overall the relative effect of Pit soil on plant biomass was greater under the low than the high water regime (Microsite by Water interaction: $F_{1,49} = 8.08$, $P = 0.007$, Figure 6.1b). Ultimately, Pit soil under the low water treatment produced plants of greater biomass than those on Surface soil under the high water treatment. Despite significant Water treatment effects on plant biomass, there were no significant effects of any factor on root to shoot ratio ($P > 0.21$, Appendix 6.2).

Pit soil produced plants which had a significantly greater proportional reproductive effort than Surface soil plants (flower: total biomass: $F_{1,49} = 38.10$, $P < 0.001$; Figure 6.1c). The high water treatment also produced plants that had a greater proportional reproductive effort than their low water counterparts ($F_{1,49} = 23.49$, $P < 0.001$; Figure 6.1c). There were no significant effects of Cover on proportional reproductive effort ($P = 0.57$).

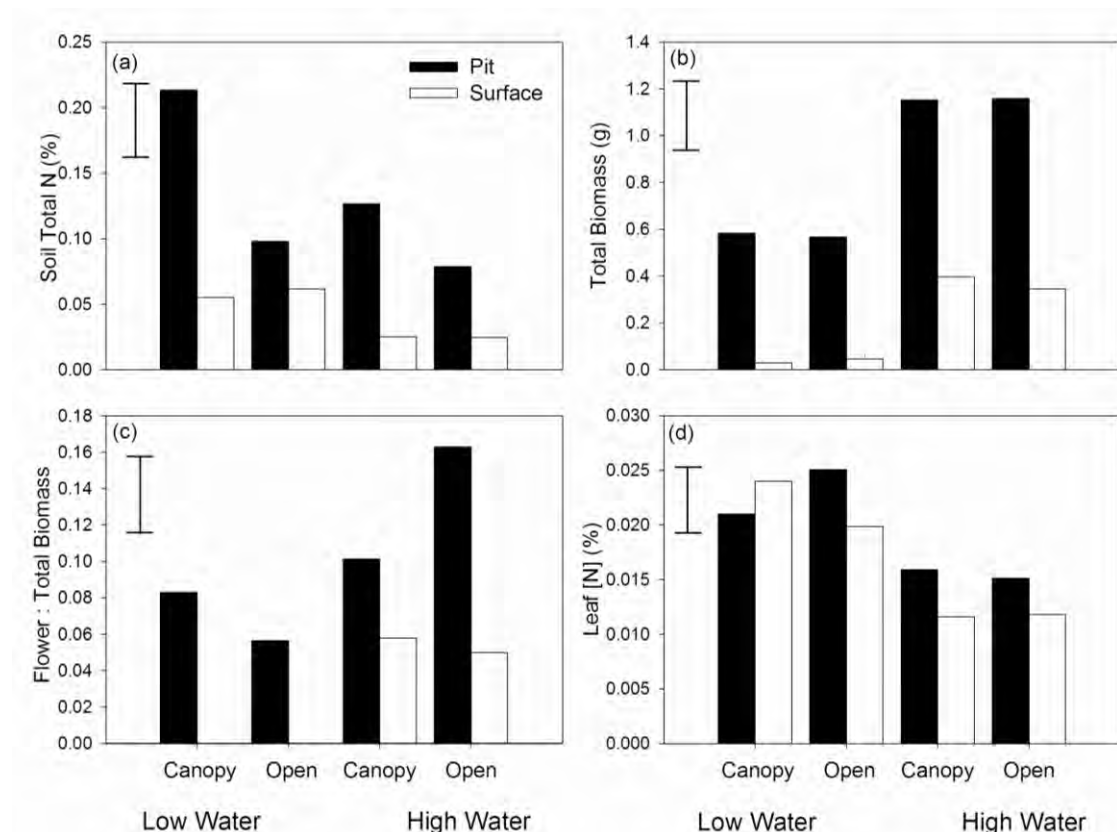


Figure 6-1. Mean of (a) total plant biomass, (b) proportional reproductive effort (flower and seeds to total biomass ratio), (c) leaf nitrogen concentration, and (d) soil nitrogen concentration in relation to Microsite, Cover and Water regime. The bars indicate the 5 % LSD for the Microsite by Water by Cover interaction. Overall, there is significantly greater plant biomass, proportional reproductive effort and soil N in Pit soil than Surface soil. There are inconsistent trends between Cover and Water treatments.

6.4.3 Plant growth: Biotic and abiotic nurse effects on plant growth rate

Averaged over time, the high water regime resulted in greater plant height and number of stems ($P < 0.01$, Appendix 6.3). Significant Microsite by Time, and Water by Time interactions (Appendix 6.3) indicated that Pit soil and high water availability increased the rate of plant, leaf and stem growth (Figure 6.2). Over time, plants growing in Pit soil had more stems and longer leaves than those in Surface soil (Wald statistic = 43.21 and 1.07, $P < 0.01$, respectively; Figure 6.2c, d), but there were no

6. Pit soil enhances plant growth

differences in total plant height (Figure 6.2a, b) nor the number of leaves ($P > 0.30$, Appendix 6.3). Significant Microsite by Water by Time interactions were also observed for the number of stems and longest leaf length (Appendix 6.3), indicating a substantial temporal increase in the Microsite by Water interaction on the number of stems and the length of the longest leaf (Figure 6.2c, d). Increased soil nutrient concentrations under the canopy were not reflected in any observable changes in plant growth.

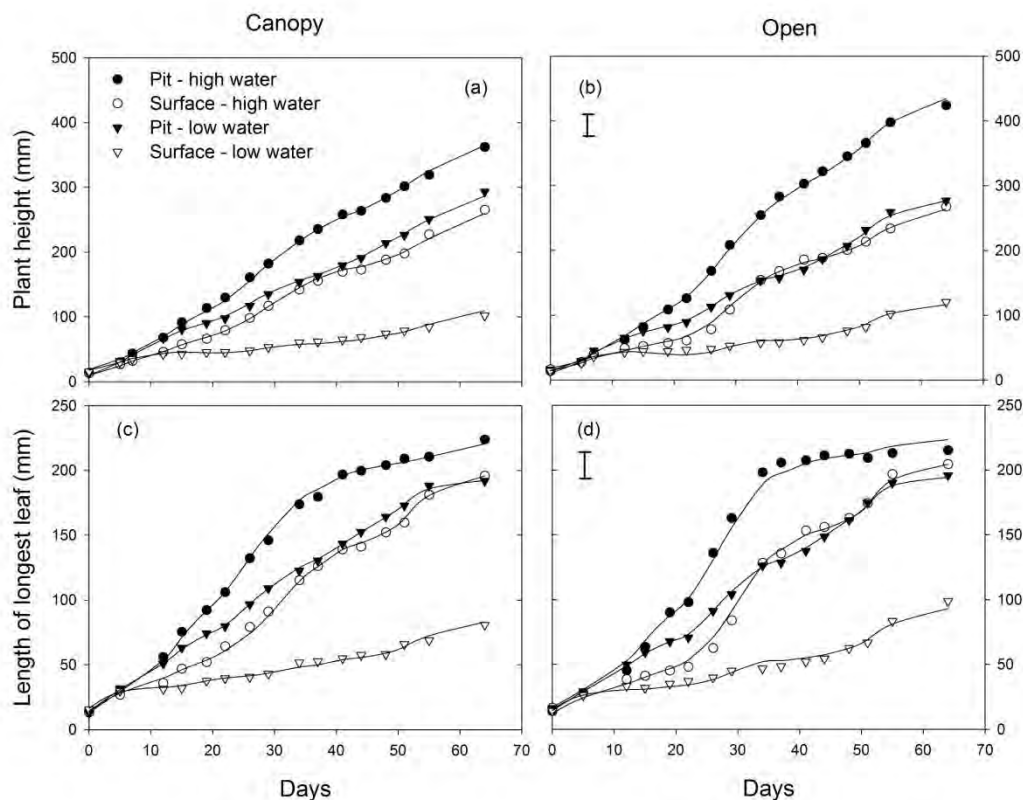


Figure 6-2. Plant growth rate. Changes in plant height (mm: a, b) and length of the longest leaf (mm: c, d) for plants growing in Pits and Surface soils under a regime of low or high water within Canopy or Open soils. Curves represent average values for Canopy and Open Microsites. The bars indicate the 5 % LSD for the Microsite by Water interaction. For both longest leaf length and plant height, there were consistent trends across Canopy and Open. Plants under the high water treatment growing in Pit soil were consistently the most productive, while plants from Surface soil under low water were consistently the least productive. The trajectories for high water Surface soil plants and low water Pit soil plant were consistently similar across both Open and Canopy treatments.

6.4.4 Plant growth: Biotic and abiotic nurse effects on leaf nutrients

Although there was a significant Cover effect on leaf carbon concentration ($F_{1,49} = 5.52$, $P = 0.024$; Appendix 6.2), this did not mean that soil from under tree canopies produced plants with higher carbon concentrations. Instead, soil from Open sites produced plants with greater leaf carbon concentration (Appendix 6.1). Pit soil also produced plants containing significantly greater concentrations of carbon than Surface soil ($F_{1,49} = 6.35$, $P = 0.016$).

There were no significant effects of Cover ($P = 0.92$) nor Microsite ($P = 0.20$) on leaf nitrogen concentration. There was, however, a significant Water treatment effect, with a significantly greater concentration of leaf nitrogen in plants under the low than the high water treatment ($F_{1,49} = 23.19$, $P < 0.001$, Figure 6.1d).

6.5 Discussion

The concept of abiotic nurses is relatively new (Munguia–Rosas and Sosa 2008), with few studies explicitly acknowledging their importance in the facilitation process (e.g. Parker 1989; Peters *et al.* 2008; Castro *et al.* 2010). Our study is unique in that we compared both an abiotic and a biotic nurse, allowing for their potential combined effects on plant growth. Our results indicated a positive effect of increasing water on plant biomass and proportional reproductive effort, and, irrespective of watering regime, a positive effect of canopy cover and pits on soil C and N. We found that soil from both the foraging pit (abiotic nurse) and canopy (biotic nurse) significantly enhanced almost every measurement of physical and chemical soil property compared with the surrounding ‘unengineered’ soil.

The defining feature of both biotic and abiotic nurses is their facilitatory effect on plant growth and/ or survival through the amelioration of abiotic stresses such as unfavourable soil physical structure, temperature and solar radiation, or a combination

6. Pit soil enhances plant growth

of both (Bertness and Callaway 1994; Peters *et al.* 2008; Maestre *et al.* 2009; Castro *et al.* 2010). The substantial point of difference between these different nurse types is the absence of direct competition from abiotic nurses (Munguia–Rosas and Sosa 2008), though for both types to be effective, they must enhance the growth or survival of their protégé species. Both nurses ameliorated soil physical conditions by reducing bulk density and increasing organic matter and nitrogen compared with either Surface soils or those from the open. Both nurses have been shown to enhance soil infiltration or water retention (Raffaele and Veblen 1998; Eldridge and Mensinga 2007), and create a more favourable rooting environment (Pugnaire *et al.* 2004) compared with their ‘unengineered’ analogues.

Although biotic and abiotic nurses accumulate resources through similar mechanisms (e.g. wind and water; Flores and Jurado 2003), they may differ in the efficacy of their actions. For example, decomposition of organic matter in arid environments follows different decay mechanisms depending on whether materials are on or below the surface. Surface decomposition with biotic nurses such as shrubs and trees is generally much slower (Moorhead and Reynolds 1993) and is often dominated by photo–oxidation processes (Austin and Vivanco 2006). Abiotic nurses such as our foraging pits, however, bring organic matter into direct contact with the soil, allowing mineralised nutrients to be returned to the soil organic pool. Thus in our study, Pit soils under the Canopy contained the highest C and N levels, followed by Open Pit soils, then Canopy Surface soils.

A simple way of measuring the success of nurse associations is to assess the quality of protégé plants produced (Butterfield 2009). As expected, foraging pit soil resulted in greater productivity (nine–times greater biomass), and greater proportional reproductive effort and growth rate than those growing on surface soils. Plants growing in Pit soil also had a greater percentage of leaf C. Indeed, the facilitatory effect of Pit soil on productivity alone, under water–limited conditions, was equivalent to additional water being added to a non–pit Surface. Interestingly, the growth trajectories of plants growing in Pit soil on the low water treatment were the same as

those growing on the Surface at the higher water treatment. The addition of water may be seen as an attempt to compensate for *in situ* effects of our biotic nurse. For example, Eldridge and Mensinga (2007) found significantly greater volumetric soil moisture in pit than non-pit soil up to 6 months after rainfall. Shade from biotic nurse canopies has previously been documented to increase soil moisture by reducing temperature and evaporation (Pugnaire *et al.* 2004). In addition, large trees also provide hydraulic lift, increasing soil moisture from sub-surface reservoirs (Caldwell and Richards 1989). Our work suggests that pits have the capacity to ameliorate the effects of water stress on plant growth, which will likely expand the realized niche for some plants during periods of low rainfall (Michalet *et al.* 2006), allowing them to occupy otherwise inhospitable habitat (Hastings *et al.* 2007).

Studies that have directly compared nurse plants and nurse objects *in situ* suggest that they may differ in the benefits they provide to the protégé (Parker 1989; Flores and Jurado 2003; Munguia-Rosas and Sosa 2008). *In situ* canopy cover may have negative effects on soil water availability, such as interception of rainfall and competition for soil moisture. However, the benefits of shade on the protégé through reduced evaporation and increased soil moisture are also well recognised (e.g. Cody 1993). Nurse plants generally provide shade for longer than abiotic nurses, depending on the nurse plants' species and their foliage filtering effects, and, to some extent, the intensity of solar radiation (Munguia-Rosas and Sosa 2008). In contrast, nurse objects such as rocks and logs only allow for direct sun or full shade, while foraging pits themselves do not provide any shade, except perhaps during the early seedling stage (Pugnaire *et al.* 2004). Our high water treatment could arguably have been a substitute for the lack of shade within the growth chamber. Our set-up effectively isolated a soil effect from other *in situ* effects associated with the positive moderation of the abiotic environment, such as hydraulic lift and shade. We also essentially removed all sources of direct competition from our biotic nurse and expected positive outcomes for our protégé. Despite this, in the absence of direct competition, and with favourable water, plants were still more productive in soils that had not been engineered by the biotic nurses. In contrast to Pit soil, we found no consistent effect of Canopy soil on any

6. Pit soil enhances plant growth

measurement of plant performance, despite the enhanced physical and chemical status of canopy soil compared with the matrix (Facelli and Brock 2000) and thus its greater potential to ameliorate abiotic stress.

In contrast with previous studies (Soliveres *et al.* 2011), we did not find any facilitatory effect of canopy soils on our phytometer *D. radulans*. Two possible explanations arise that might explain these contrasting results: 1) with our experimental approach we were only able to detect the effect of soil mediation by trees. Thus the direct effects of shade, an important factor driving facilitation in water-limited environments (Callaway 1995; Maestre *et al.* 2003) were largely ignored. However, the most important facilitatory outcome of shade is reduced temperature stress and indirectly enhanced water availability to the protégé. The positive effects of shade were mimicked to a certain degree by our watering treatment; however we still did not find substantial effects of soil from under tree canopies under the different watering treatments assayed. 2) The most plausible explanation for the lack of a facilitatory effect of canopy soils, therefore, is the allelopathic effect that Eucalypt litter is known to have on nutrient uptake and germination of some species (e.g. May and Ash 1990). The fact that higher soil N % and mineralisable N under the canopy was not reflected in higher leaf N or reproductive effort suggests to us that our canopy soils may inhibit N uptake and usage by plants. However our pits also captured Eucalypt leaf litter, but there were no negative effects on plant growth or reproductive effort from the high N Pit soils. This suggests that the allelopathic properties of Eucalypts leaf litter require time to accumulative to levels deemed inhibitive to plant growth. The contrasting results found between our work and previous studies (e.g. Soliveres *et al.* 2011) suggest a high species-specific response to the effects of trees with allelopathic compounds on their neighbours (Callaway 2007). As with most other grass species *D. radulans*, seemed sensitive to allelopathic compounds derived from Eucalypts (Tilman 1988). Overall, our study clearly shows that *D. radulans* grows better in soils that differ from those found beneath the canopy of Eucalypts.

Water availability could also affect the N–transfer relationship. Plants under the low water treatment generally had higher total soil N % than soil under the high water treatment (possibly due to leaching), which translated to high leaf N %. However reproductive effort was low compared to plants under the high water treatment, where soil total N and mineralisable N was low, leaf N % was low and reproductive effort was high. This may indicate that low water availability reduces reproductive effort as plant N is locked up in photosynthetic enzymes in leaves.

Our study indicates that the soil from an abiotic nurse had substantial effects on plant productivity and proportional reproductive response, unlike soil from a more nutrient–enriched biotic nurse. The greater difference between Pit soil and Surface soil Microsites under the moisture stressed regime supports empirical observations and theoretical predictions that small increases in resources can have much greater effects in resource–limited environments (Day *et al.* 2003). Although the phenomenon of abiotic nurse–associations will never truly be captured by the ‘stress gradient hypothesis’ literature, our pits still attain the same facilitative outcomes as traditional biotic nurses, albeit through markedly different underlying mechanisms.

Our study has broad ecosystem relevance given the extensive global distribution of soil–disturbing animals (Whitford 2002). A fuller knowledge of the direct and indirect, positive and negative effects of plants and animals is therefore requisite to our understanding of bottom–up versus top–down controls on resource regulation in harsh environments (e.g. Riginos and Grace 2008; Eldridge *et al.* 2010). This will provide some clarity in the debate over the relative importance of positive and negative effects of herbivores as drivers of top–down ecosystem control, and enhance our understanding of their potential roles in restoring degraded systems (e.g. Byers *et al.* 2006).

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Appendix 6.1. Plant growth attributes. Mean of each plant growth attribute in relation to Water regime (low, high), Cover (Canopy, Open) and Microsite (Pit, Surface). The 5 % LSD values are given.

Water	Cover	Microsite	Biomass (g)						Root: Shoot	Flower: Total biomass	No. Of Flowers	No. of Seeds	Leaf Carbon		Leaf Nitrogen	
			Leaf	Stem	Flowers + Seeds	Total above ground	Roots	Total					Leaf C (g)	Leaf C (%)	Leaf N (g)	Leaf N (%)
High	Canopy	Pit	0.549	0.456	0.148	1.152	0.112	1.264	0.088	0.101	4.875	161.13	0.225	40.65	0.007	1.231
		Surface	0.211	0.148	0.037	0.396	0.042	0.438	0.077	0.058	1.875	30.88	0.084	40.08	0.002	1.065
	Open	Pit	0.683	0.633	0.265	1.581	0.172	1.753	0.102	0.163	7.375	316.63	0.284	41.60	0.011	1.193
		Surface	0.196	0.128	0.022	0.345	0.070	0.414	0.212	0.050	1.375	4.13	0.079	40.28	0.002	1.074
Low	Canopy	Pit	0.309	0.211	0.063	0.583	0.063	0.646	0.092	0.083	2.250	72.13	0.127	40.74	0.006	1.433
		Surface	0.022	0.008	0.000	0.031	0.002	0.033	0.254	0.000	0.000	0.00	0.007	39.75	0.000	1.541
	Open	Pit	0.317	0.205	0.043	0.566	0.099	0.665	0.201	0.056	1.375	32.13	0.130	40.93	0.008	1.576
		Surface	0.034	0.012	0.000	0.046	0.010	0.055	1.746	0.000	0.000	0.00	0.011	41.00	0.001	1.412
LSD 5 % value			0.141	0.138	0.069	0.325	0.067	0.372	1.444	0.048	2.121	98.00	0.059	0.96	0.002	0.229

Appendix 6.2. Summary of the analysis of variance (ANOVA) for soil physical and chemical properties and for measurements of plant growth and leaf chemistry for Microsite, Cover, and Water treatment effects and their interactions. d.f. = 1, 49. Min. = mineralisable.

Component	Microsite		Cover		Water		Microsite × Water		Microsite × Cover		Water × Cover		Microsite × Cover × Water	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Bulk density (mg m ⁻³)	70.0	<0.01	18.0	<0.01	1.7	0.19	0.2	0.69	4.3	0.04	1.0	0.33	0.0	0.99
Labile C (mg kg ⁻¹)	2.3	0.14	6.6	0.01	1.3	0.25	2.4	0.13	1.1	0.31	1.2	0.37	0.8	0.37
Total C (%)	59.9	<0.01	8.9	0.01	0.5	0.47	0.5	0.49	4.1	0.04	0.0	0.98	0.0	0.85
Min. N (mg kg ⁻¹)	93.0	<0.01	6.2	0.02	0.4	0.51	0.5	0.49	0.7	0.41	2.8	0.10	0.3	0.57
Total N (%)	55.8	<0.01	12.1	<0.01	7.7	0.01	0.7	0.40	4.7	0.04	0.7	0.40	2.3	0.14
Min. N (mg per core)	33.2	<0.01	0.1	0.75	0.3	0.59	0.1	0.78	1.6	0.22	0.5	0.49	0.2	0.69
Total biomass (g)	89.7	<0.01	1.3	0.25	48.3	<0.01	8.1	0.01	1.9	0.18	1.4	0.25	2.5	0.12
Root: shoot	1.6	0.22	1.5	0.23	1.6	0.21	1.3	0.26	1.1	0.30	1.0	0.32	0.8	0.38
Flower : total biomass	38.1	<0.01	0.3	0.57	23.5	<0.01	0.1	0.72	0.8	0.37	2.8	0.10	4.0	0.05
Leaf [N] (%)	1.7	0.20	0.0	0.92	23.2	<0.01	0.6	0.46	1.0	0.32	0.0	0.94	1.5	0.23
Leaf [C] (%)	6.4	0.02	5.5	0.02	0.0	0.87	0.1	0.39	0.1	0.78	0.1	0.80	2.7	0.11

Appendix 6.3. Wald statistics and *P*-values for main order effects and 2- and 3-way interactions for plant height, number of leaves, no. of stems and length of the longest leaf. d.f. = 1, 56.

Attribute	Plant height		No. of leaves		No. of stems		Length longest leaf	
	Wald statistic	<i>P</i> -value	Wald statistic	<i>P</i> -value	Wald statistic	<i>P</i> -value	Wald statistic	<i>P</i> -value
Cover	2.39	0.13	0.09	0.77	0.83	0.37	0.09	0.47
Microsite	0.73	0.40	1.07	0.31	43.21	<0.01	1.07	<0.01
Water	10.83	<0.01	1.32	0.26	26.89	<0.01	1.32	0.51
Cover.Microsite	0.38	0.54	0.99	0.32	0.38	0.54	0.99	0.77
Cover.Water	0.83	0.37	0.00	0.95	0.46	0.50	0.00	0.93
Microsite.Water	1.16	0.29	3.53	0.07	0.03	0.87	3.53	0.08
Cover.Microsite.Water	0.79	0.38	0.57	0.45	0.44	0.51	0.57	0.84
Time	659.60	<0.01	1493.20	<0.01	421.80	<0.01	1493.21	<0.01
Time.Cover	2.31	0.13	3.14	0.08	6.71	0.01	3.14	0.37
Time.Microsite	74.62	<0.01	100.96	<0.01	54.69	<0.01	100.96	<0.01
Time.Water	68.91	<0.01	50.48	<0.01	12.90	<0.01	50.48	<0.01
Time.Cover.Microsite	0.67	0.42	0.17	0.68	0.03	0.87	0.17	0.71
Time.Cover.Water	1.70	0.20	0.32	0.58	0.01	0.92	0.32	0.78
Time.Microsite.Water	0.87	0.35	2.77	0.10	5.12	0.03	2.77	<0.01
Time.Cover.Microsite.Water	1.51	0.22	0.19	0.66	0.06	0.81	0.19	0.98

Chapter 7. Thesis discussion

Samantha K. Travers

The objective of this thesis is to examine how litter dynamics are moderated by abiotic and biotic features in semi arid woodlands and shrublands. Specifically, I investigated how multiple stages of leaf litter dynamics were affected by drivers such as rainfall, fire, vegetation community, landform type and plant species in these communities. The implications of biotically-induced ecosystem changes to leaf litter dynamics (e.g. vegetation clearance, changes in soil foraging mammal communities) are highlighted in some chapters. In general, a recurring theme in this thesis is the marked effects of rainfall and landform type across multiple stages of the leaf litter cycle. Similarly, intrinsic differences among plant species, and therefore plant communities, are strong drivers of the leaf litter dynamics. This research has advanced our understanding of leaf litter as an important component of semi-arid environments that contributes to maintaining a function and dynamic ecosystem.

7.1 Key findings of this thesis

Chapter 2 provides a detailed description of reproductive structure fall rates of three woody plant species in response to abiotic conditions in a mallee woodland. For our three species, abiotic conditions explained about 23 % of the variation in the mass of reproductive structures falling over a three year period. Of the meteorological conditions we used as predictors, rainfall frequency was the strongest predictor for all species, followed by maximum wind speed. The importance of other environmental variables such as solar exposure and evaporation differed among our species. Greater amounts of reproductive material fell from *Eucalyptus gracilis* in the swale landforms, which was likely due to the effects of soil texture and topography.

In Chapter 3 we report on the post-fire modulation of litter patches under mallee eucalypt trees that we measured using a space-for-time approach. The structure of mallee trees appears to regulate litter accumulation as there were few differences between the two eucalypt species. We found clear trends between tree size and litter bed size. Both trees and litter beds increased in size with increasing time since last fire, and there were few differences in these trends between species. The composition of

the litter bed also appears to be largely driven by fire history, with substantial shifts in the proportion of leaves, bark and seeds over time. Despite shifts in litter bed depth and composition, the mass of litter per unit area did not appear to vary with time since fire. An important implication of this work is that peak flammability in this system, which occurs about 15–30 years after fire, coincides with a peak components of the litter bed which are highly flammable and burn at high intensities. This is an important issue that needs to be considered when devising management strategies for the control of fire in mallee landscapes.

In Chapter 4 we provide evidence for the spatial self-organisation of surface litter. We found a high correlation between perennial patch cover and litter cover, but only a moderate spatial association between them. Also, there was weak concordance between the size frequency of perennial patches and litter patches, with a greater number of smaller litter patches compared to perennial patches. The variability in the spatial arrangement of litter patches was positively correlated with perennial patch size in the mallee community. However in the shrublands, the variability in litter arrangement was correlated with the distance between perennial patches (inter-patch size), and the sign of this relationship appeared to depend on the history of clearing. We found no evidence that litter accumulates under perennial patches in a positive feedback mechanism, i.e. a correlation between increasing perennial patches size and an increase in the strength of its association with litter. However, the size distribution of the patches suggests that disturbance-recovery mechanisms may play an important role in spatial self-organisation of litter, with the size distributions of litter patches well described by truncated power laws.

In Chapter 5 and 6 we focus on the role of native mammal foraging pits and their effects on decomposition and plant growth. In Chapter 5 we used a litter bag study to measure biotic and abiotic drivers of decomposition in foraging pits created by mammals. Our results suggest that the foraging pits of short-beaked echidnas (*Tachyglossus aculeatus*) provide an environment that results in similar rates of decomposition as the pits of locally-extinct native mammals such as the greater bilby

(*Macrotis lagotis*) and the burrowing bettong (*Bettongia lesueur*), with substrates decomposing *via* the same mechanisms. Foraging pit morphology did however, affect initial organic mass loss, with a greater mass loss in the bilby or bettong foraging pits after 30 days, but greater organic mass loss in the echidna pits after 60 days. From the biotic and abiotic drivers we measured in this study, the most consistent differences in decomposition rates were between the two plant species we used as substrates (i.e. *Austrostipa scabra* subsp. *scabra* and *Triodia scariosa* subsp. *scariosa*). The different landforms, used as a surrogate for soil texture, and the exclusion of fungi and/ or termites, did not affect overall decomposition rates, although they did influence organic mass loss in the later stages of our study (at 196 and 396 days). Overall, we found that the foraging pits of short-beaked echidnas contributed to leaf litter decomposition in ways that are functionally analogous to the locally-extinct burrowing bettongs and greater bilbies. This suggests that extant populations of echidnas, which are widely distributed over continental Australia, may be performing the same role as bilbies and bettongs, though the extent of this functional role is unknown.

In Chapter 6 we report on a growth chamber experiment which compares the combined facilitatory “nurse” effects of echidna foraging pits and trees on seedling growth and production. We found that the soil that develops under the litter layer beneath tree canopies and in foraging pits contains favourable physical and chemical properties that facilitate seedling growth. However, the soil that forms within foraging pits under the canopy contains more soil carbon and nitrogen than the non-pit soils under the canopy, which demonstrates that foraging pits further concentrate carbon and nitrogen. We also found strong evidence that foraging pits have the capacity to ameliorate the effects of water stress on plant growth. The growth trajectories for plants growing in pit soil under low water conditions were the same as those growing in non-pit soil under high water conditions. This indicates that pits and pit soils may provide refugia for plants during dry times, enabling them to persist in otherwise inhospitable habitats (Hastings *et al.* 2007).

7.2 Temporal and spatial variability in drivers of leaf litter dynamics

A quintessential characteristic of arid and semi-arid ecosystems is their temporal and spatial variability in resources. Throughout this thesis I have shown that leaf litter is a highly dynamic resource and ecological component across a variety of spatial and temporal scales. The temporal and spatial variability in the extent and composition of litter production, and the rate of decomposition is driven by processes and events that are also highly variable in both time and space.

7.2.1 Temporal heterogeneity

At large temporal scales, inter-decadal and inter-annual variability in rainfall and fire regimes drive the amount and composition of litter, which accumulates as surface litter (Pook *et al.* 1997). Coupled with the relatively slow nature of surface decay rates in these systems (Moorhead and Reynolds 1991; Cornwell *et al.* 2008), large rainfall events or fires, and their interaction, are likely to affect surface litter and associated resources for years or decades after such events. It is highly likely that similar shifts occur in leaf litter in other communities, particularly in those communities where production is driven by large temporal variability in rainfall and fire regimes (Sinclair 2005; D'Odorico *et al.* 2007).

At finer temporal scales, it is also apparent that drivers of litter dynamics vary from month to month and season to season. The fall rates of reproductive structures and the decomposition rates of substrates in animal foraging pits were driven by fine-scale temporal shifts in biotic and or abiotic conditions. While some of these fine scale temporal processes are tied to the availability of resources at larger spatial and temporal scales (e.g. litter fall rates increase due to prolonged above average rainfall), the fine scale drivers (e.g. wind speed) may further exacerbate temporal patterns or the rates of processes (Scheffer *et al.* 2001). Furthermore, fine scale temporal variability may not cause substantial changes in processes when viewed at larger temporal scales, as I found in my study of decomposition rates (Chapter 5). However,

7. Discussion

the specific timing of fine scale temporal drivers may be critically important for other processes, such as mast seeding events (Kelly and Sork 2002).

7.2.2 Spatial heterogeneity

Throughout this thesis I address spatial variability in drivers of litter dynamics at multiple spatial scales. At fine spatial scales, litter patch development is driven by the growth of individual plants, fire history and the structure, size and density of vegetation (Chapters 3 and 4). The fine scale spatial arrangement of litter patches, and the specific ways in which litter accumulates (i.e. under vegetation, in a surface depression, etc.) can have important implications for the rate at which litter decomposes (Throop and Archer 2008). Furthermore, the specific arrangement of litter patches can have important implications for plant growth resulting from such litter patches, as I indicate in Chapter 6.

At broader spatial scales, we can see that processes that are temporally variable can interact and induce broad-scale spatial variability in litter and many other resources. This is evident in the spectrum of fire histories across the landscape, which is described in Chapter 3. The mosaic of fire histories across the mallee landscape contributes to the diversity of litter loads and litter composition. We also found evidence that different vegetation communities, which occur in a repeatable pattern across the landscape, affect litter dynamics at smaller spatial scale e.g. surface litter distribution (Chapter 4). The dune and swale landforms further contribute to variability in litter dynamics with the differences between the two landforms mediating some litter fall rates and decomposition rates (Chapters 2 and 5, respectively).

7.3 Implications of this work

The extreme variability in amount, composition and rate of litter production and its decomposition has important implications for ecosystem function, particularly as litter is used as a resource by many species (Haslem *et al.* 2011) and contributes to soil

carbon and nitrogen pools (Throop and Archer 2008). The spatial diversity in the availability of leaf litter has direct effects on the spatial distribution of litter-dependent fauna. Many arthropods are exclusively limited to, or are heavily dependent upon, the presence of surface litter (Uetz 1979; Kwok 2012). Many reptiles, such as Boulenger's skink (*Morethia boulengeri*) and bird species, such as the mallee fowl (*Leiopoa ocellata*), are also dependent upon litter for habitat foraging and nesting in the mallee (Benshemesh 1989; Haslem *et al.* 2011). There is also evidence that seedling growth is facilitated by the presence of surface litter (Facelli and Pickett 1991). By understanding how surface litter and associated resources shift in space and time, we gain much greater insight into litter dynamics, and how alterations to ecosystems may affect the distribution and abundance of litter and litter-dependent species.

The variation in the leaf litter dynamics between individual plant species is important for ecosystem resilience. This thesis highlights the ways in which individual plant species differ markedly in rates of litter production, litter patch formation and decomposition. We did find, however, that similarly structured species (i.e. two eucalypt mallee species in Chapter 3, *Eucalyptus socialis*, *E. dumosa*) may have similar responses to the some drivers such as fire (Clarke *et al.* 2010). In general, the diversity of species responses, or response diversity (*sensu* Elmqvist *et al.* 2003), is important for building ecosystem resilience. Ecosystems become more resilient when two or more species that respond differently to the same conditions also have similar functional roles (Elmqvist *et al.* 2003; Folke *et al.* 2004). A diversity of responses enhances the capacity of ecosystems to adapt to shifts in biotic and abiotic conditions. By understanding the many ways in which species respond to the same conditions, we gain a greater understanding of the resilience of ecosystems to future changes. By assessing the nature of changes in different systems that have been altered, we gain greater insights into the severity or long term implications of changes such as vegetation clearance, shifts in soil foraging mammal communities or climate change.

There are two clear land management implications arising from the work reported in this thesis. Firstly, when monitoring fuel loads in mallee, land managers can capitalise on “one size fits all” allometric relationships across a broad range of eucalypt mallee species (see Bradstock and Gill 1993; Noble 1997; Clarke *et al.* 2010). Additionally, it is clear from my work that litter cover is correlated vegetation (see Chapter 4). Thus land managers can estimate surface fuel from perennial vegetation cover. The relationships presented in this thesis can be used to estimate standing fuel loads in dune mallee communities using simple field-based approaches such as measuring tree height. The results however could be strengthened by undertaking further replication to verify associated errors, as we discuss below. Secondly, for management regimes that are aimed at restoring ecosystem functions, we found the foraging pits of short-beaked echidnas contribute to decomposition processes in a similar functional role as the pits created by the locally extinct greater bilbies and burrowing bettongs. This process of patch formation is particularly important in resource-limited environments where the restoration of ecosystem function is promoted by reinstating patches in the landscape (Whitford 2002; James *et al.* 2009)

7.4 Hindsight and forethought: Scope for future research

7.4.1 General hindsight and forethought

Aspects of litter dynamics have been used in many terrestrial ecosystems around the world, for many different purposes. Future research in this field may benefit from recent technologies for data collection and analyses. For example *in situ data* loggers (e.g. ibuttons Hubbart *et al.* 2005) are becoming readily available and more affordable and may assist with monitoring abiotic conditions during litter fall or decomposition studies such as those described in Chapter 2 and Chapter 5. This may be particularly important in arid and semi-arid environments where there is high spatial variability in abiotic conditions such as wind-speed and rainfall among sample sites. Similarly high resolution “gigapixel” photo point photography may be useful for monitoring real-time or hourly responses of litter dynamics, such as surface litter distribution during

high wind or rainfall events (Brown 2012). Data analyses which require large numbers of iterations or permutations (e.g. PERMANOVA, Multi-model inference), such as those used in Chapter 2, 3, 4 and 5, are still relatively computer intensive. Such analyses will benefit from recent developments and future improvements in computing power to maximise the number of unique permutations or iterations against which inferences are made.

As is the case with many studies, in many disciplines, repetition in both space and time is the key to unmasking the universality of observed patterns and processes. However, pseudoreplication is a common issue that hinders the generalisation of observed trends. For example, in Chapter 2 we recorded litter fall rates during a very unique rainfall event when average annual rainfall was nearly double the recorded average rainfall. While this provides a unique opportunity to observe the magnitude at which species respond to these events, this study is arguably temporally pseudoreplicated. The same high rainfall conditions were also prevalent in Chapter 5. We attempted to account for the effects of high annual rainfall in Chapter 5 by measuring decomposition as percentage organic mass loss and grams lost per mm of rainfall. As large rainfall events are unlikely to occur at equivalent magnitudes again in the next few decades, it is difficult to replicate these studies and yield similar results.

Spatial pseudoreplication, however, is relatively easier to address. We used spatial blocking factors to account for spatial heterogeneity (Chapters 2, 4, 5 and 6), although broad-scale replication would be ideal. In contrast there is limited scope for expanding the decomposition study reported in Chapter 5 as there are only a few locations at which greater bilbies and/ or burrowing bettongs are found, either captive or in wild populations. Nevertheless, the study does provide an insightful case study for the environment in which it was conducted. The study area reported in Chapter 3 provided a unique challenge in terms of spatial heterogeneity as each fire only burnt one patch of land, which was generally spatially isolated from other burn areas. While similar aged burns are available to measure within the region (see Clarke *et al.* 2010), it was beyond the scope of our study to expand the study over such a large region.

7.4.2 Chapter-specific hindsight and forethought

In Chapter 2 we present a unique insight into the role of weather in driving variation in litter fall. While these links were limited by the coarse scale at which some of the weather variables were measured, there is scope for similar studies, with more accurate, *in situ* observations, as I mentioned above (See section 7.4.1.). Given that the same types of weather observations are scaled up for large scale climate predictions, it seems that using the same measures would be a logical way to scale down weather observations to match ecological responses at the landscape level. A similar issue was posed by Morton *et al.* (2009). These authors also identified a need to find non-linear responses between climate and substrate or biotic interactions to improve our understanding of ecosystem function and the distribution of species (Morton *et al.* 2009). Additionally, there is further scope to address nutrient limitations that likely contributed to the fall rates of reproductive structures. Given that arid and semi-arid systems are both water- and nutrient-limited, and that rainfall can affect nutrient availability at daily and sub-daily scales (Wang *et al.* 2009), it is likely that some of the variance which was not explained by our models can be attributed to nutrient dynamics. Accounting for nutrient dynamics in future litter fall studies may enhance our understanding of the mechanisms behind plant responses to meteorological conditions, particularly where plant responses are measured at fine temporal scales. From the links we found in Chapter 2, breaking down time scales in which we view processes, to time scales finer than has been set by preceding studies is critical to furthering our knowledge on these processes. It allows one to see the nature of responses before we can understand the causes of non-linear responses. This applies not just to litterfall studies, but to any process that exhibits temporal variation. Understandably however, smaller time scales are not always practical in terms of logistics in data collection.

Monitoring fuel loads is important for land managers, particularly in fire-prone landscapes and in the face of shifts in changing climate and consequent shifts in fire

regimes. Chapter 3 provides clear links between fire history, tree size and fuel composition. While these specific relationships have limited use in vegetation beyond mallee communities, there is scope for research on shifts in litter composition in other fire-prone landscapes, both as long-term monitoring and as snapshot ‘space-for-time’ studies. There needs to be future consideration of shifts in litter bed composition between the inner and outer areas of the litter bed, which affects the flammability of the litter bed (Bradstock and Gill 1993). This shift in composition may also differ with fire history and could contribute to the way in which biota interact with litter resources in the years following a fire. Despite the recognition of fuel load and composition as important indicators of fire intensity, the complex composition of fuel is rarely considered in fuel load models (e.g. Scarff and Westoby 2006, but see Bradstock and Gill 1993), and this could be a fruitful area of further research. Monitoring shifts in the composition and chemistry of litter beds may also shed light on the modification of soil structure and nutrients by fire (Morton *et al.* 2011).

While it is somewhat obvious that shifts in vegetation density from clearing or woody encroachment would affect litter dynamics, it was interesting to discover that differences are still manifest 60 years later in ways that we did not expect (Chapter 4). There remains scope for further study to assess what drives variability in the spatial arrangement of litter and its relationship with perennial patch size or cover. Comparing the effects of structure or life form (i.e. shrub, tree) or perennial patch cover (i.e. 30 % cover vs. 50 % cover) may provide a foundation for such research. Our study was also limited by the use of a linear transect rather than a 2-dimensional plot to measure patch distribution. It would be of further interest to assess the variability in spatial heterogeneity between a transect approach and one that is plot-based. Admittedly, though, the fine scale resolution (cm) which we report on in Chapter 4 and which would be necessary to measure spatial association accurately, may prove to be a tedious task in a representative area of vegetation, such as 20 × 20 m or 50 × 50 m size quadrats.

As mentioned earlier, the unusual rainfall events during the decomposition study (reported in Chapter 5) may substantially alter decomposition processes that prevail in drier years. However, the unique circumstances under which this study was conducted have provided some novel insights into possible decomposition processes. In particular, the litter bags which were exposed during the warm summer period with above average rainfall succumbed to relatively heavy detritivory by insect larvae. While this has been observed at least once before in semi-arid Australia (Hart 1995), it is reported that termites are the predominate decomposers in some semi-arid environments (Noble *et al.* 2009). However, the question remains, how important are termites as decomposers in arid Australia (Morton *et al.* 2011)? It appears as though insect larvae, such as those of beetles and moths, may play a significant role in decomposition under some conditions, however further work is required to address this research question. In light of our current study, i.e. the role of foraging pit morphology on decomposition, arguably there is a need to compare the role of these native species to introduced species such as the European rabbit (*Oryctolagus cuniculus*), to measure their comparative role in foraging pit construction and associated decomposition. Progress on this specific question is already underway (Travers and Eldridge, unpublished data).

As with many laboratory-based studies, there is limited scope for 'real world' applications without further *in situ* assessments. In Chapter 6 we present a growth-chamber based study showing clearly that the soil developing within echidna foraging pits has physical and chemical properties that substantially enhance plant growth and development. This study would benefit from a complimentary field-based experiment which gives realistic effects of temperature, shade and other features which affect water dynamics. Also, further studies on seedling germination and a greater range of plant types (e.g. C3, C4; annual, perennial; grass, shrub, tree; etc.) would assist in giving a greater understanding of this process.

7.5 Towards a holistic understanding of litter dynamics

Despite the conspicuous presence of leaf litter in all terrestrial communities, it is often an overlooked and understudied component of these ecosystems. Here we have provided a unique insight into the spatial and temporal variability in the abiotic and biotic drivers that influence aspects of leaf litter dynamics. Such drivers often interact, creating complex patterns in litter fall, surface distribution, patch formation and decomposition. While it is difficult to accurately describe all factors that contribute to the cycling of leaf litter, there needs to be greater acknowledgment of the drivers of litter dynamics at multiple spatial and temporal scales.

Leaf litter is a valuable and critical resource and ecological component in many terrestrial ecosystems. Although it provides habitat for a vast range of species, relatively few studies have examined how specific shifts in litter and associated resources affect the biota and their communities and functions. This is particularly important where threatened, vulnerable and endangered species are dependent on the presence of leaf litter. Beyond habitat, leaf litter also provides a source of fuel, and is functionally important for nutrient cycling and transport. While specific rates of processes may be unique to individual plant species, this diversity contributes to the overall functional diversity of any given ecosystem, which is important for maintaining ecosystem resilience. By understanding how different drivers operate and alter leaf litter processes under different conditions, we gain greater insights into the functional role of litter, its importance as a resource, and its complex dynamics as a fuel in these resource-limited ecosystems.

7.6 References

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7. Discussion

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