

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

SAMANTHA K. TRAVERS* AND DAVID J. ELDRIDGE

Evolution and Ecology Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia (Email: s.travers@unsw.edu.au)

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* ssp. *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 generalized 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.

Key words: *Acacia burkittii*, *Eucalyptus gracilis*, ecosystem function, mallee, mass flowering, multi-model inference, response diversity, *Senna artemisioides*.

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 & 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 & 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.

*Corresponding author.

Accepted for publication April 2013.

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 & 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 different ways such as ‘resource matching’ (*sensu* Kelly 1994; Smaill *et al.* 2011), ‘resource switching’ (*sensu* Norton & Kelly 1988), or ‘resource accumulation’ (*sensu* Kelly & 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; Martinez-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 & 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 & 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 (SEM) 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 (Fig. 1a). We measured fall rates of reproductive structures from two shrub species (*Senna artemisioides* ssp. *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

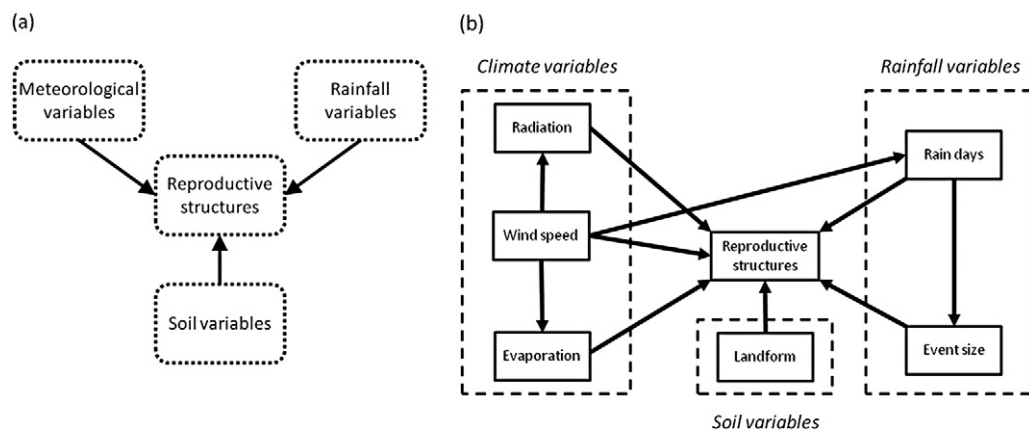


Fig. 1. (a) Metamodel and (b) conceptual model of the relationships among rainfall variables, other climatic variables, soil variables and the litter fall rate of reproductive structures. Variables in the conceptual model include average rainfall event size in the past 12 months (Event size), number 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).

(< 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.

METHODS

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 (*E. 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 *S. artemisioides* ssp. *filifolia* and *petiolaris* Randell, and *A. burkittii* (Keith 2004). At our study site, the soils are mainly calcareous, brownish and siliceous sands. Our specific study area had not been burnt by wildfire in more than 40 years.

Study species

Senna artemisioides ssp. *filifolia* (Fabaceae) is a 1–3 m tall, relatively short-lived (approx. 10 years) perennial shrub (Cunningham *et al.* 2011). Small yellow flowers (approx. 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 & Playford 2000). Leguminous fruit mature in early 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 recognized 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 4 m tall and live up to 250 years (Crisp & 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 that 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 & Petit 2007; Marrant *et al.* 2010). *Eucalyptus gracilis* is pollinated by a variety of birds (Paton & 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 that 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).

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 h and sorted into seven categories and weighed. Categories included *Eucalyptus* leaves, *A. burkittii* phylloides, *S. 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 ($\text{g m}^{-2} \text{day}^{-1}$) 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 9.00 hours and 15.00 hours), cloud cover (at 9.00 hours and 15.00 hours) and solar exposure. Additionally, for rainfall data, the average and cumulative rainfalls, 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.

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).

Generalized linear modelling and multi-model inference

We analysed reproductive structure fall rates using separate generalized linear models (GLMs) for each of our three species. A full description of the modelling process is given in Appendix S1. 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 *et al.* 2009). To reduce collinearity, only some categories of meteorological conditions were represented in the final candidate set of explanatory variables for each species (Appendix S2).

To determine the relative importance of the meteorological conditions on reproductive structures for each species, we used multi-model inference (Burnham & 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 *et al.* 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 $\Delta_i \leq 2$ (Appendixes S3, S4 and S5; Burnham & Anderson 1998; Anderson *et al.* 2001).

Structural equation modelling

We used SEM to test and parameterize 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 standardized 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 a nominal 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 (Fig. 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).

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

Table 1. Mean 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

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

Significant differences (a, b) among years are indicated for each species.

structures; and an increase in the relative proportional mass of reproductive structures of total litter fall (Table 1, Fig. 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 (Fig. 2). The average annual litter fall rate of reproductive structures for *E. gracilis* was five-times greater in 2011 than 2009 (Year: Pseudo- $F_{2, 864} = 29.74$; $P < 0.001$; Table 1). For *S. 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 *A. 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 1). Our multi-model inference also yielded similar results. For all three species, the coefficients for the years 2010 and 2011 were both greater than 2009 (Appendix S6). 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 1).

The litter fall rates of reproductive structures for the two shrub species were not significantly different between the two landforms (*S. artemisioides*: $P = 0.35$; *A. burkittii*: $P = 0.051$). However there were much greater litter rates of *E. gracilis* reproductive structures in the swale in 2009 and 2010, 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 SEM (see below). Our multi-model inference found landform to be relatively important for *E. gracilis* (Table 2), with the model averaged coefficient showing eucalypts growing in swales produced more reproductive structures than those growing on dune crests (Table 2, Appendix S6).

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). 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-

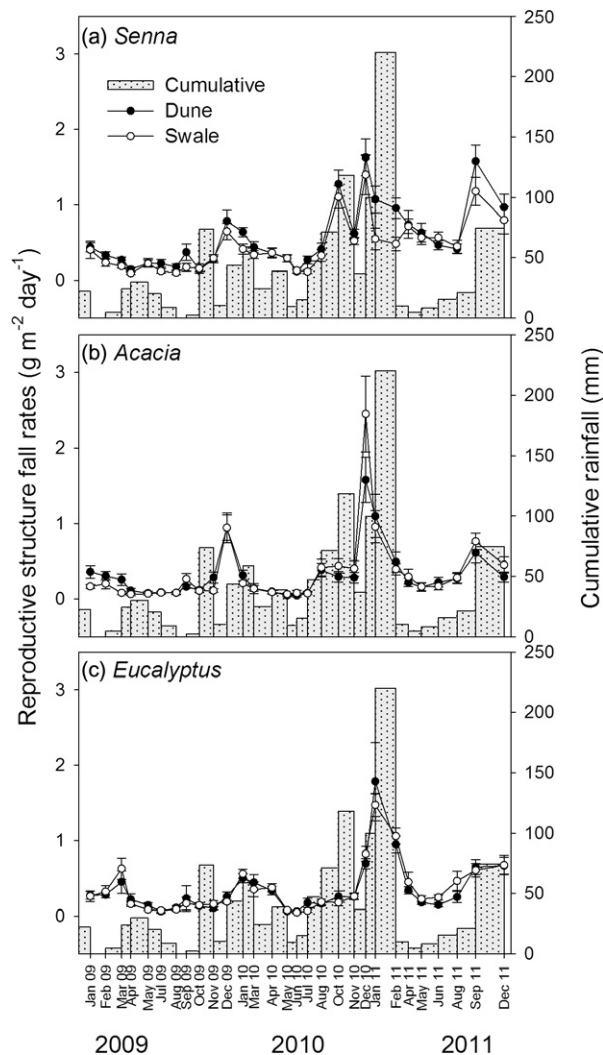


Fig. 2. Fall rates of reproductive structures for (a) *Senna artemisioides*, (b) *Acacia burkittii*, (c) *Eucalyptus gracilis* for 2009, 2010 and 2011. The histogram represents cumulative rainfall for each collection window.

dependent. Cumulative solar exposure was the second most important variable identified by the model averaging procedure for *S. artemisioides*, while average maximum wind speed was the second most important variables for both *E. gracilis* and *A. burkittii* (Table 2).

Table 2. The relative importance of the variables for each species for each model part

Variables	Relative importance	
	Part 1	Part 2
<i>Senna artemisioides</i>		
Rain days 8 months	0.47	1.00
Solar exposure (cumulative)	0.87	0.49
Wind speed (max)	0.55	0.44
Rain event Size 12 months	0.39	0.35
Year	0.57	0.17
Cloud cover (9.00 hours)	0.36	0.31
Landform	0.28	0.28
<i>Acacia burkittii</i>		
Rain days 4 months	1.00	0.96
Wind speed (max)	0.74	0.33
Cloud cover (9.00 hours)	0.55	0.30
Rain event Size 12 months	0.36	0.49
Maximum temperature (average)	0.29	0.49
Year	0.35	0.29
Landform	0.27	0.35
<i>Eucalyptus gracilis</i>		
Rain days 12 months	0.92	0.89
Landform	0.68	0.60
Wind speed (max)	0.73	0.28
Solar exposure (cumulative)	0.37	0.60
Minimum temperature (average)	0.25	0.57
Rain event Size 12 months	0.33	0.29
Cloud cover (15.00 hours)	0.34	0.24
Year	0.17	0.19

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.

Details of the coefficients for the top model (QAIC_{min}) for each species are given in Appendix S6.

Our structural equation models also indicated that the number of rain days had the strongest direct effect on the fall rate of reproductive structures (Fig. 3; Table 3). For *A. burkittii*, average daily evaporation had an equally strong direct positive effect as the number of rain days (Table 3). The indirect effect of wind speed mediated by evaporation (indirect pathway coefficient = 0.27) was also relatively strong for *A. burkittii*. For *E. gracilis* and *S. artemisioides*, cumulative solar exposure was strongly positively related to reproductive structure fall rates, consistent with the results of our multi-model inference for *S. artemisioides*. Landform had a strong direct effect on reproductive structure fall rates for *E. gracilis*, but not for *S. artemisioides* or *A. 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 4). The total standardized

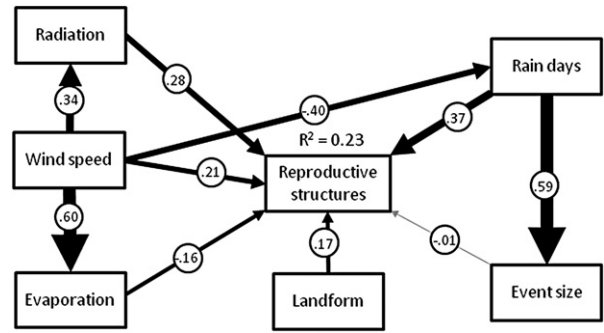


Fig. 3. Structural equation model for *Eucalyptus gracilis*. Path width indicates the relative strength of the relationship, as indicated by the path coefficient. The overall model explained 23% of the variance in the litter fall rates of reproductive structures (log₁₀ scale; d.f. = 6; $\chi^2 = 4.83$; $P = 0.56$), as indicated by the R² value. The results for the two shrub species are given in Table 3.

Table 3. Pathway coefficients for the structural equation models (from Fig. 3) for all species

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 R ²	0.23	0.21	0.23

Remaining path coefficients for the three models were the same.

Table 4. Total standardized effects for the structural equation models (from Fig. 3 and Table 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

effect was also relatively high for evaporation for *A. burkittii* only. Overall, our structural equation models explained 23%, 23% and 21% of the variation in reproductive structure fall rates for *E. gracilis*, *S. artemisioides* and *A. burkittii*, respectively.

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.

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 mineralization 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 *E. 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).

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 *S. artemisioides* and *A. 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 structure 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-average rainfall (2010, 2011). Given the apomictic nature of *S. artemisioides* (i.e. asexual reproduction; Randell 1989; Holman & 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 *S. 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 & 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 *E. 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 *E. gracilis* (Paton *et al.* 2004) and other eucalypt mallees (Burrows & 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 & Noble 1985). It is possible that this single peak in reproductive structures is due to physical damage from relatively large vertebrate pollinators (Burrows & Burrows 1992) such as the western pygmy possum (Morrant *et al.* 2010). For *E. 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, unpubl. data, 2012), providing strong circumstantial evidence for higher visitation rates during this period.

When the variability in fall rate of reproductive structures exceeds that of weather conditions alone, as observed in *A. burkittii*, other factors are likely driving the variation in fall rates (Koenig & Knops 2000; Kelly & Sork 2002). We found that the peak in reproductive structure fall rate for *A. 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; 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 *A. 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 *A. burkittii* does not increase after years of above-average rainfall, nor is its regeneration adversely affected by drought (Crisp & 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 & 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 *A. 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 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 life span of structures. Some structures, such as reproductive structures may have much shorter life 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 a surrogate for the amount of reproductive material produced.

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 *A. 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 more a biologically relevant indicator of seed fall than temperature. Given that high evaporation rates coincide with high temperatures, evaporation is likely more biologically relevant to evaluating heat or moisture stress induced on plants in hot, dry conditions. 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 that average minimum temperature was moderately important in explaining the excess zero part of our model. This is due to few reproductive structures of *E. gracilis* falling during cold months.

Solar exposure was also an important indicator of the loss of reproductive structures, for both *S. artemisioides* and *E. gracilis*, supporting previous studies on productivity (Cunningham 2000; Whitehead & Beadle 2004). For example, Cunningham (2000) showed that *S. 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.

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 predic-

tion 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 that have concluded that shifts in climate might be important for small-scale ecological processes (Morton *et al.* 2011; Wang *et al.* 2012).

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 & Wastljung 1987), predator satiation (Janzen 1971), differences in seed dispersal modes and resource availability (see Herrera *et al.* 1998; Kelly & Sork 2002; Koenig & 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 (Fig. 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.

ACKNOWLEDGEMENTS

We thank Terry Koen for his advice on experimental design and Aaron Greenville for guidance with Generalized Linear Modelling. We are grateful for the substantial financial, field and logistical support provided by the Australian Wildlife Conservancy, with special thanks to Jennifer Cathcart, Felicity L'Hotellier, Joanne Stephens, Matt Hayward, Tony Cathcart and Joe Stephens for their continued support and assistance. We thank James Val, Alan Kwok, Alex James, Erin Rogers and many other volunteers for their assistance with field work; and Gabriella Radnan, Alan Kwok, Marta Ruiz-Colmenero, Jasmine Robinson and Aaron Lee for their assistance with separating litter samples. We also thank Alan Kwok and Matt Hayward for their comments on the manuscript.

REFERENCES

- Aide T. M. (1986) The influence of wind and animal pollination on variation in outcrossing rates. *Evolution* **40**, 434–5.
- Andersen A. N. (1987) Effects of seed predation by ants on seedling densities at a woodland site in SE Australia. *Oikos* **48**, 171–4.
- Anderson D. R., Link W. A., Johnson D. H. & Burnham K. P. (2001) Suggestions for presenting the results of data analyses. *J. Wildl. Manage.* **65**, 373–8.
- Anderson M. J., Gorley R. N. & Clarke K. R. (2008) *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods*. PRIMER-E, Plymouth.
- BOM (2012) Bureau of Meteorology. Australian Government. [Cited 3 May 2012.] Available from URL: <http://www.bom.gov.au/>.
- Burnham K. P. & Anderson D. R. (1998) *Model Selection and Inference: A Practical Information-Theoretic Approach*. Springer, New York.
- Burnham K. P., Anderson D. R. & Huyvaert K. P. (2011) AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behav. Ecol. Sociobiol.* **65**, 23–35.
- Burrows D. M. & Burrows W. H. (1992) Seed production and litter fall in some eucalypt communities in central Queensland. *Aust. J. Bot.* **40**, 389–403.
- Carneiro M., Serrao V., Fabiao A., Madeira M., Balsemao I. & Hilario L. (2009) Does harvest residue management influence biomass and nutrient accumulation in understory vegetation of *Eucalyptus globulus* Labill. plantations in a Mediterranean environment? *For. Ecol. Manage.* **257**, 527–35.
- Cookson W. R., Muller C., O'Brien P. A., Murphy D. V. & Grierson P. F. (2006) Nitrogen dynamics in an Australian semiarid grassland soil. *Ecology* **87**, 2047–57.
- Crisp M. D. & Lange R. T. (1976) Age structure, distribution and survival under grazing of arid-zone shrub *Acacia-burkittii*. *Oikos* **27**, 86–92.
- Cunningham G. M., Mulham W. E., Milthorpe P. L. & Leigh J. H. (2011) *Plants of Western New South Wales*. CSIRO Publishing, Melbourne.
- Cunningham S. A. (2000) Effects of habitat fragmentation on the reproductive ecology of four plant species in mallee woodland. *Conserv. Biol.* **14**, 758–68.
- Davies S. J. J. F. (1976) Studies of flowering season and fruit production of some arid zone shrubs and trees in Western Australia. *J. Ecol.* **64**, 665–87.
- Eberbach P. L. (2003) The eco-hydrology of partly cleared, native ecosystems in southern Australia: a review. *Plant Soil* **257**, 357–69.
- Elmqvist T., Folke C., Nystrom M. *et al.* (2003) Response diversity, ecosystem change, and resilience. *Front. Ecol. Environ.* **1**, 488–94.
- Herrera C. M., Jordano P., Guitián J. & Traveset A. (1998) Annual variability in seed production by woody plants and the masting concept: reassessment of principles and relationship to pollination and seed dispersal. *Am. Nat.* **152**, 576–94.
- Holman J. E. & Playford J. (2000) Molecular and morphological variation in the *Senna artemisioides* complex. *Aust. J. Bot.* **48**, 569–79.
- IPCC (2007) *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds S. Solomon, D. Qin, M. Manning *et al.*). Cambridge University Press, Cambridge.
- Iriondo J. M., Albert M. J. & Escudero A. (2003) Structural equation modelling: an alternative for assessing causal relationships in threatened plant populations. *Biol. Conserv.* **113**, 367–77.
- Jackman S. (2011) *Pscl: Classes and Methods for R Developed in the Political Science Computational Laboratory*, Stanford University. Stanford University, Stanford.
- Janzen D. H. (1971) Seed predation by animals. *Annu. Rev. Ecol. Syst.* **2**, 465–92.
- Keith D. A. (2004) *Ocean Shores to Desert Dunes: The Native Vegetation of New South Wales and the ACT*. Department of Environment and Conservation (NSW), Hurstville.
- Kelly D. (1994) The evolutionary ecology of mast seeding. *Trends Ecol. Evol.* **9**, 465–70.
- Kelly D. & Sork V. L. (2002) Mast seeding in perennial plants: why, how, where? *Annu. Rev. Ecol. Syst.* **33**, 427–47.
- Koenig W. D. & Knops J. M. H. (2000) Patterns of annual seed production by northern hemisphere trees: a global perspective. *Am. Nat.* **155**, 59–69.
- Koenig W. D. & Knops J. M. H. (2005) The mystery of masting in trees. *Am. Sci.* **93**, 340–7.
- Lamont B. B., Lemaitre D. C., Cowling R. M. & Enright N. J. (1991) Canopy seed storage in woody plants. *Bot. Rev.* **57**, 277–317.
- Letnic M. & Dickman C. R. (2006) Boom means bust: interactions between the El Niño/Southern Oscillation (ENSO), rainfall and the processes threatening mammal species in arid Australia. *Biodivers. Conserv.* **15**, 3847–80.
- Liebhold A., Sork V., Peltonen M. *et al.* (2004) Within-population spatial synchrony in mast seeding of North American oaks. *Oikos* **104**, 156–64.
- Ludwig J. A. & Tongway D. J. (1995) Spatial-organization of landscapes and its function in semiarid woodlands, Australia. *Landscape Ecol.* **10**, 51–63.
- Martínez-Garza C., Osorio-Beristain M., Valenzuela-Galván D. & Nicolás-Medina A. (2011) Intra and inter-annual variation in seed rain in a secondary dry tropical forest excluded from chronic disturbance. *For. Ecol. Manage.* **262**, 2207–18.

- Morrant D. S., Petit S. & Schumann R. (2010) Floral nectar sugar composition and flowering phenology of the food plants used by the western pygmy possum, *Cercartetus concinnus*, at Innes National Park, South Australia. *Ecol. Res.* **25**, 579–89.
- Morton S. R., Stafford Smith D. M., Dickman C. R. *et al.* (2011) A fresh framework for the ecology of arid Australia. *J. Arid Environ.* **75**, 313–29.
- Nilsson S. G. & Wastjung U. (1987) Seed predation and cross-pollination in mast-seeding beech (*Fagus sylvatica*) patches. *Ecology* **68**, 260–5.
- Norton D. A. & Kelly D. (1988) Mast seeding over 33 years by *Dacrydium cupressinum* Lamb. (rimu) (Podocarpaceae) in New Zealand: the importance of economies of scale. *Funct. Ecol.* **2**, 399–408.
- Noy Meir I. (1973) Desert ecosystems: environment and producers. *Annu. Rev. Ecol. Syst.* **4**, 25–51.
- Olson J. S. (1963) Energy-storage and balance of producers and decomposers in ecological-systems. *Ecology* **44**, 322–31.
- Paton D. C., Crossfield E. L., Hurrell B. & Rogers D. J. (2004) *Floral Resources Used by the South Australian Apiary Industry* (ed. Rural Industries Research and Development Corporation). Australian Government, Canberra.
- Paton D. C. & Ford H. A. (1977) Pollination by birds of native plants in South Australia. *Emu* **77**, 73–85.
- Paul K. I., Polglase P. J., O'Connell A. M., Carlyle J. C., Smethurst P. J. & Khanna P. K. (2003) Defining the relation between soil water content and net nitrogen mineralization. *Eur. J. Soil Sci.* **54**, 39–47.
- Pestell A. J. L. & Petit S. (2007) Diet of the western pygmy possum, *Cercartetus concinnus* gould (Marsupialia: Burramyidae), at Innes National Park, South Australia, and evaluation of diet sampling methods. *Aust. J. Zool.* **55**, 275–84.
- Pressland A. J. (1982) Litter production and decomposition from an overstorey of *Eucalyptus* spp. on two catchments in the New England region of New South Wales. *Aust. J. Ecol.* **7**, 171–80.
- R Core Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Randell B. R. (1989) Revision of the Cassiinae in Australia. 2. *Senna miller* sect. *Psilorhagma* (J. Vogel) Irwin & Barneby. *J. Adelaide Bot. Garden* **12**, 165–272.
- Sampson J. F., Hopper S. D. & James S. H. (1995) The mating system and genetic diversity of the Australian arid zone mallee, *Eucalyptus rameliana*. *Aust. J. Bot.* **43**, 461–74.
- Shipley B. (2000) *Cause and Correlation in Biology: A User's Guide to Path Analysis, Structural Equations and Causal Inference*. Cambridge University Press, Cambridge.
- Sinclair R. (2005) Long-term changes in vegetation, gradual and episodic, on the TGB Osborn Vegetation Reserve, Koonamore, South Australia (1926–2002). *Aust. J. Bot.* **53**, 283–96.
- Smaill S. J., Clinton P. W., Allen R. B. & Davis M. R. (2011) Climate cues and resources interact to determine seed production by a masting species. *J. Ecol.* **99**, 870–7.
- Staelens J., Nachtergale L., Luyssaert S. & Lust N. (2003) A model of wind-influenced leaf litterfall in a mixed hardwood forest. *Can. J. For. Res.* **33**, 201–9.
- Walker B., Kinzig A. & Langridge J. (1999) Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems* **2**, 95–113.
- Walse C., Berg B. & Sverdrup H. (1998) Review and synthesis of experimental data on organic matter decomposition with respect to the effect of temperature, moisture, and acidity. *Environ. Rev.* **6**, 25–40.
- Wang L., D'Odorico P., Evans J. P. *et al.* (2012) Dryland ecohydrology and climate change: critical issues and technical advances. *Hydrol. Earth Syst. Sci.* **16**, 2585–603.
- Wellington A. B. & Noble I. R. (1985) Seed dynamics and factors limiting recruitment of the mallee *Eucalyptus-incrassata* in semi-arid, southeastern Australia. *J. Ecol.* **73**, 657–66.
- Westoby M. (1980) Elements of a theory of vegetation dynamics in arid rangelands. *Israel J. Bot.* **28**, 169–94.
- Whitehead D. & Beadle C. L. (2004) Physiological regulation of productivity and water use in *Eucalyptus*: a review. *For. Ecol. Manage.* **193**, 113–40.
- Woodell S. R. J. (1990) Regeneration in the shrub *Acacia-burkittii* from ex benth in the arid zone of South-Australia. *Biol. Conserv.* **51**, 39–48.
- Wotton B. M. & Flannigan M. D. (1993) Length of the fire season in a changing climate. *For. Chron.* **69**, 187–92.
- Zeileis A., Kleiber C. & Jackman S. (2008) Regression Models for Count Data in R. *J. Stat. Softw.* **27**, 1–25.
- 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 & Business Media, New York.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Details of generalized linear modelling and multi-model inference.

Appendix S2. The final meteorological variables selected for each species.

Appendix S3. *Eucalyptus gracilis* models ranked according to the quasi-likelihood form of Akaike's information criterion.

Appendix S4. *Senna artemisioides* models ranked according to the quasi-likelihood form of Akaike's information criterion.

Appendix S5. *Acacia burkittii* models ranked according to the quasi-likelihood form of Akaike's information criterion.

Appendix S6. Model-averaged coefficients and top model coefficients for the three species.