

Secondary seed dispersal of *Erodiophyllum elderi*, a patchily distributed short-lived perennial in the arid lands of Australia

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Abstract We investigated secondary dispersal of propagules of *Erodiophyllum elderi* (Asteraceae), a short-lived perennial plant growing in small patches in the arid lands of southern Australia. In spite of its importance for population dynamics, secondary dispersal is a little understood process. We monitored the dispersal of 2280 large woody capitula (seed heads) released in six *E. elderi* patches for 9 months. Colour-coded seed heads were located at night using UV light and their distance and direction from the release point were measured. Over the 9-month period, more seed heads moved, and those that did, moved further in areas with high herbivore activity. Overall dispersal distance across the ground was limited to less than 30 m. Dispersal patterns were related to the topographical slope at the release site: seed heads moved further, and more dispersed on steeper slopes unless the steep slopes had sandy soil in which case seed heads were buried, caught or there was reduced sheet water flow limiting their dispersal potential. After several months, seed head dispersal virtually ceased as seed heads became stuck in the debris and soil after heavy rains or further dispersal became unlikely when seed heads reached locally low-lying areas. Secondary dispersal patterns suggest two distinctly different influences associated with the presence of herbivores: the direct movement of seed heads by trampling from sheep (an introduced herbivore) and the indirect effect of a reduced standing biomass from grazing. Reduced vegetation cover allows seed head redistribution via sheet water flow during large rainfall events.

Key words: above-ground seed bank, *Erodiophyllum elderi*, patchy distribution, secondary dispersal, xeric vegetation.

INTRODUCTION

Arid land regions are notoriously patchy in terms of the quality of sites suitable for seed germination, the subsequent survival of seedlings and the resources available for plant growth. Factors promoting spatial heterogeneity of the distribution of arid land plants include the patchy nature of resource accumulation (e.g. water and nutrients, Noy-Meir 1973; Friedman & Stein 1980; Tongway & Ludwig 1994), the preferential survival of plants in particular areas (Osborn *et al.* 1932; Schupp 1995; Schupp & Fuentes 1995) and the directed dispersal of seeds to areas with favourable conditions

(Howe & Smallwood 1982). Because of the heterogeneity that exists within arid lands, dispersal is a critical component of a plant's life cycle in determining the fate and success of a seed. Seeds that disperse to areas unsuitable for germination constitute a net loss from the seed bank. Conversely, seeds that disperse to areas favourable for germination and establishment (Chambers & MacMahon 1994), are more likely to contribute to the persistence of the species in the community (Howe & Miriti 2004).

The seed dispersal process occurs in two or more phases. The first of these, primary dispersal, typically involves the movement of propagules from the parent plant to the ground at various distances depending on seed characteristics and dispersal vectors. The next phase, secondary dispersal, involves movement once propagules have reached the ground and often involves different dispersal agents and can involve the vertical movement of seeds in the soil profile. Both phases can offer benefits to plants (Vander Wall & Longland

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Accepted for publication October 2009.

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2004). Dispersal is notoriously difficult to study because seeds and seed propagules (i.e. dispersal units containing seed/s) are often small and almost impossible to relocate and there are typically large losses from the seed bank (Winn 1989). Consequently, most experiments have focused on the initial movement from the parent plant to the ground (Chambers & MacMahon 1994), which is often limited in distance and duration (e.g. Stamp & Lucas 1990). In a review on dispersal, Chambers and MacMahon (1994) concluded that we know very little about a single day in the life of a seed, let alone over a longer timescale. Little has changed since their review. In particular, secondary seed dispersal remains one of the most important yet least studied aspects of plant population ecology (e.g. see Cain *et al.* 2000; Howe & Miriti 2004).

A great diversity of dispersal methods exist for seeds of arid land species. The frequency and distance of seed dispersal is influenced by morphological characteristics including seed or propagule size, shape and the presence of plumes, wings or thorns (Guterman 1994). Of the 229 central Australian plant species examined by Jurado *et al.* (1991), 40% of the diaspores were unassisted, 38% were wind-dispersed and 22% were animal-dispersed. Ellner and Schmid (1981) found that an even greater proportion of the desert plants in Israel lack dispersal-promoting structures and yet other species have morphological characteristics that inhibit dispersal. Such morphological characteristics are proposed to be a mechanism that reduces the chance of seeds encountering unsuitable habitat (Ellner & Schmid 1981; Venable *et al.* 2008). However, the lack of dispersal-promoting characteristics does not preclude biotic or abiotic dispersal, particularly for secondary and subsequent phases of dispersal, and the interaction between seeds and their environment can profoundly influence their dispersal ability. For example, steep terrain can result in the downhill movement of seeds (e.g. Venable *et al.* 2008), wind contributes to their horizontal surface movement, and sufficient precipitation results in overland flows that can transport seeds (e.g. Friedman & Stein 1980; Chambers & MacMahon 1994; Vander wall *et al.* 2005). Biotic factors include seed dispersal aided by animals (e.g. Tester *et al.* 1987) and the presence of plant litter that can trap seeds and limit their dispersal (e.g. Watkinson 1978; Venable *et al.* 2008).

The often reported disruption of ecosystem structure and function from the introduction of large vertebrates or plants species (Peters *et al.* 2006) may, in part, be due to changes in dispersal processes. For example, the introduction of sheep into the Australian arid lands has had a profound and often negative influence on the vegetation (e.g. Jessup 1948; Hall *et al.* 1964; Lange 1985; Williams 1985; Whelan 1989; Morton 1990; Friedel *et al.* 1993; McIntyre & Lavorel

1994; Landsberg *et al.* 1997). Dramatic and widespread changes in the soil structure, productivity and species composition of these areas have occurred, particularly in the years immediately following the introduction of sheep when stocking rates were high (Morton 1990). The potential effects of such changes on the fate and dispersal of seeds is recognized but remains largely unknown (Tremont 1994). It is unclear exactly how introduced herbivores might affect seed dispersal processes or whether their influence is on long-distance dispersal, short-distance dispersal or both. Clearly, changes in dispersal processes are likely to have important consequences for species distributions, their population dynamics and potentially their persistence. To understand what the consequences are however, we need to improve our understanding of the patterns of, and processes influencing, secondary dispersal of seeds in arid lands.

Therefore, our objectives were to examine the potential for secondary dispersal of the propagules (referred to as seed heads henceforth) of the arid land short-lived perennial composite *Erodiohyllum elderi* (F. Muell.) as well as to determine the potential interactive effects of grazing, topography, rainfall and soil characteristics on these dispersal processes. Specifically, we asked: (i) Does dispersal concentrate seed heads into the naturally occurring patches? (ii) How are dispersal patterns influenced by the topographical slope of these patches? (iii) How does seed head dispersal depend on the timing and amount of rainfall? and (iv) How are seed head dispersal patterns affected by the activity of vertebrates, in particular by large introduced herbivores (sheep) compared with their native counterparts (kangaroos)?

METHODS

The focal species for this research, *E. elderi* (Koonamore Daisy) is a short-lived perennial found in semi-arid and arid areas of southern Australia. It grows in distinct 'patches' consisting of up to several thousand plants spread over an area of several hundred square metres. These patches mostly coincide with low-lying areas across the landscape. The flowers develop into hard woody capitula, roughly cylindrical, 20 mm diameter and 20 mm high and weighing up to 2.5 g (Emmerson, unpubl. data, 1995). Each capitulum holds up to 120 seeds forming an above-ground seed bank from which seeds are released over a period of up to two decades as a response to sufficient rainfall and seed head decay. Seed head decay takes many years and would certainly not occur over the time frame over which dispersal was recorded here. The primary phase of *E. elderi* dispersal is limited because the intact seed heads mostly drop to the ground below the parent

plant. As with many other species from xeric environments, *E. elderi* seed heads lack obvious structures to promote dispersal.

Site description

The study was conducted at Koonamore Station (32°07'S, 139°22'E), located in the mid-east of South Australia. Koonamore Station receives an average annual rainfall of 215 mm, and although there are more rain days per month during winter, individual rainfall events are typically larger during summer. The daily maximum temperature in summer (December–February) averages 32°C, while in the winter (June–August) it averages 15°C. The study site is characterized by a gentle undulating topography with clay pans bordered by small sandy dunes. The vegetation is a chenopod shrubland dominated by *Atriplex vesicaria* (bladder saltbush), *Maireana sedifolia* (pearl bluebush), and *M. pyramidata* (black bluebush) and scattered trees mainly *Acacia aneura* (mulga) and *Myoporum platycarpum* (false sandalwood). Annual plant species are often prominent in the low-lying areas after rains promote germination and plant growth (Osborn *et al.* 1932; Carrodus *et al.* 1965). *Erodiophyllum elderi* is one of the larger herbaceous plants growing in the flats and low-lying areas.

In addition to topographical variation creating a series of low-lying areas suitable for short-lived species, variation in the intensity of sheep grazing also creates variable conditions for the species inhabiting the area. Approximately 390 ha of Koonamore Station were fenced to exclude sheep in 1925 (Osborn *et al.* 1935), hereafter referred to as the Reserve. A rabbit eradication programme was started in the 1970s in this reserved area and there is currently little evidence of rabbit activity in the Reserve.

Seed head dispersal

Seed head dispersal was monitored by painting seed heads and relocating them either during the day or at night time with a UV lamp. Prior to the establishment of this experiment we conducted a separate experiment comparing painted seed heads with seed heads marked with incised crosses. These tiny superficial crosses in no way damaged the seed head structure and allowed us to check for their presence without making the seed heads obvious or attractive to animals. Painted and incised seed heads were placed in small 'corrals' made with sticks and small branches. The results indicated that over 4 months, painted seed heads were no more or less likely to be removed by

animals than unpainted seed heads. Thus, we are confident that painting did not unduly affect seed head dispersal.

Seed head dispersal patterns were monitored in six *E. elderi* patches located within 15 km of each other. These patches ranged from 50 m across to over 500 m across. Two patches were inside the Reserve where kangaroos are the main herbivores (R1 and R2) and the other four patches were outside the Reserve and subject to sheep grazing in addition to the presence of kangaroos. Here we designate inside Reserve patches with an 'R' and outside Reserve patches with an 'O'. Of the outside Reserve patches, two (O1 and O2) were closer to water points and therefore expected to experience a higher sheep grazing pressure and more moving sheep per unit area (Lange 1985) and the other two were away from watering points (O3 and O4). None of the patches had rabbit warrens present. While sheep are reported to browse *E. elderi* foliage when other forage is scarce it is certainly not a large component of their diet (Cunningham *et al.* 1992). There is no evidence that kangaroos graze the foliage. Emus are a less common vertebrate in the area inside and outside the Reserve.

A focal point near the centre of each patch was marked and six transects spaced 60 m apart were established continuing radially outward from this central location. Transects continued until they were 15 m beyond the edge of the patch or reached 100 m and remained within the patch; points along the transect were deemed to be in the patch if there was an *E. elderi* plant or large seed head concentration within 3 m either side of each transect. At the midway point along each transect, at the edge of the patch and the end of the transect as well as at the central location post, 20 painted seed heads were deployed within a 0.2 × 0.2 m area (referred to as a release site). Release sites were permanently marked with small poles to allow their precise relocation. The 20 seed heads deployed in each release site were painted the same fluorescent colour combination, requiring 19 different colour combinations for the 19 release sites in each patch to identify their original position. Each patch had 19 separately identifiable release sites.

The change in elevation was measured at 5 m intervals along each of these transects as well as at each release site and 5 m either side of each release site to determine a unique slope for each release site that we refer to as the topographical slope. The gently undulating nature of the area meant that the topography within a patch changed by just over 2 m along transects of length 150 m. Hence, the dimensionless topographical slopes recorded here were typically less than 0.03 and had a maximal value of 0.08.

Seed head dispersal was measured by locating the painted seed heads at night with a portable UV lamp. A painted rock was placed by the seed head to allow its

relocation the following morning, when the direction and net distance moved for each seed head in relation to their corresponding release site was measured. The number of seed heads remaining in each release site was also noted. Seed heads were released on 19 October 1994 and dispersal measured on 17 December 1994, 4 February 1995, 5 March 1995, 9 June 1995 and 17 July 1995 (2, 4, 5, 8 and 9 months, respectively, after deployment). Frequently measuring seed head dispersal enhanced our ability to relocate a maximum number of seed heads.

Photographs were taken from permanent photo-points located in each patch to determine changes in standing biomass (including living vegetation and dead vegetation) between dispersal measurement occasions as well as allowing a comparison of standing biomass between the patches. Photos were ranked according to the standing biomass from one to six (lowest to highest) at each of the dispersal measurement occasions with the method used by Noble and Crisp (1979/80). Standing biomass was interpreted as an indication of the amount of material that could hinder dispersal by snagging seed heads. Differences in standing biomass were due to different initial conditions, the differential growth of plants when rainfall produced favourable conditions and the disintegration of the herbaceous vegetation afterwards.

In addition to the position of the patches in relation to inside or outside the Reserve and the relative ranking of the standing biomass, we also quantified herbivore activity by counting the amount of egesta (dung or droppings) present. Droppings were counted in each of 15 1-m² plots in each patch at the end of the dispersal experiment noting the herbivore responsible and were used to calculate a mean value per patch. Because dung does not persist for more than a year in the field but does persist for a period of months (Emmerson, unpubl. data, 1995), this value represents the cumulative herbivore activity in each patch over the course of the experiment. Very few kangaroo droppings were found and all of them were in patches inside the Reserve. There were no sheep droppings present inside the Reserve. Total rainfall between dispersal measurement occasions was recorded in rainfall gauges placed in each patch.

DATA ANALYSIS

Data were analysed with a two-step process, the first of these was to consider the proportion of the seed heads that moved from each release site, and the second was to consider the distance that seed heads moved conditional on them moving. This approach is common for zero-inflated data (Martin *et al.* 2005). To account for spatial dependence of seed heads released in the same release site (in the case of the distance seed heads

moved) or from release sites along the same transect, data were analysed with mixed-effects models including release site and transect as random components. The mixed-effects models were fitted in R v.2.3.1 (R Development Core Team 2006) using the *lmer* function in the *lme4* library (Pinheiro & Bates 2000; Bates & Sarkar 2006) that produces sensible restricted likelihood estimates from unbalanced data, which is of benefit in this case. Variance components were estimated with restricted maximum likelihood when comparing models with different random-effects components and maximum likelihood to compare models with similar random-effects components but different fixed-effects structures (Crawley 2002). A binomial error structure was used to analyse the proportion of seed heads moved, which is preferential to either transforming proportional data or analysing raw proportions (Crawley 2002).

Generalized linear mixed-effects models included all patches simultaneously at both the initial and final measurement occasions. Because of the association between egesta counts, the ranking of standing biomass and the identity of the major herbivores as determined by whether the patch was inside or outside the Reserve, only one of these was included in the statistical analyses; we used egesta counts because they were quantitative compared with the more subjective rankings of the photos or the reduced information offered by position in relation to the Reserve only. Full statistical models included topographical slope at each release site and egesta counts as explanatory variables as well as the interaction term between the two. Random-effect terms included transect (each of six directions) and, in the case of distance moved, release site within transect (referred to as 1- or 2- level random-effects components).

To determine the most suitable random-components structure, the full model including all random- and fixed-effects terms was compared with simpler models by systematically removing each random-effect term and choosing the model with the smallest Akaike's information criterion (AIC). In this case the AIC indicates the best model by providing a measure of fit penalized by the number of parameters estimated (Akaike 1974). Once the important random effects, if any, had been identified, deletion tests for the fixed effects were performed using this model as the starting point. Systematic deletion of each of the fixed-effects terms starting with the interaction term was examined for their impact on model deviance. The significance of each term after removal was determined by using the change in deviance compared against the χ^2 distribution until a final model was established.

To determine whether seed heads moved predominantly towards or away from each patch, the direction of seed head movement was examined. This was only

possible for release sites at the edge or outside the patch because the direction of either towards or away from the patch was ambiguous for release sites located within the patch. For each patch at each time, Wilcoxon rank sum tests were used to determine whether the median distance moved when considering away movement as positive and towards movement as negative, were significantly different to zero. If the median distance moved was greater than zero then movement is predominantly away from the patch while the converse is true for a median distance less than zero. While seed heads moving from the same release site may exhibit spatial dependence, this analysis reflects the direction that seed heads typically move even for seed heads aggregated over a small scale, which is typical in the field.

Only one patch (O1) was closely bounded by small sand dunes and we recorded whether the release sites in that patch had sandy or clay soil. This allowed us to compare the effect of soil type and topographical slope on dispersal patterns as well as including an interaction term in the statistical models. Once more, seed head dispersal was examined in terms of individual movement for each seed head and the proportion of seed heads moving per release site. In both cases, we took account of potential spatial dependence by using a mixed-effects model with an appropriate random-effects structure. As with the previous analyses, this began with an assessment of the relevant random effects in statistical models; random components included transect, and in the case of distance moved, release site within transect (referred to as 1- and 2-level random-effects components). Deletion tests were assessed using a χ^2 -test until a minimal model with appropriate random and fixed effects was determined. Data from the sandy soil release sites in this patch were excluded from the across patch analyses described above.

Statistical analyses are presented for data collected 2 months (17 December 1994) and 9 months after deployment (17 July 1995). Statistical analyses were conducted with the statistical package R v. 2.3.1 (R Development Core Team 2006), except for the Wilcoxon rank sum tests that were conducted with GraphPad PRISM.

RESULTS

Ninety-nine per cent of seed heads were recovered after 2 months and 95% 9 months after the seed heads were released. Most of the seed heads that were not recovered were released in sandy areas in and around patch O1. These areas were subsequently raked and most seed heads were recovered by this process; the results from the buried seed heads were excluded from analyses.

Seed head dispersal distances varied among patches at all measurement times (Figs 1,2). After the first 2 months very little dispersal had occurred in three of the six *E. elderi* patches; two of which were inside the Reserve (R1 and R2). There was an additional pulse of dispersal in the outside Reserve patches, particularly patch O1, between 2 and 4 months corresponding to the occurrence of two large rainfall events (12 and 29 mm) (Figs 1b,3a). Subsequent dispersal between 4 and 9 months was limited (Figs 1c,d,2) despite several rainfall events greater than 20 mm (Fig. 3a). At this stage, many seed heads had become physically trapped by vegetation and other debris on the ground and, along with the seeds from other species, were caught in slight depressions or were stuck in the soil as a consequence of water pooling after a large rainfall. Despite the limited dispersal during the latter part of the experiment, some seed heads continued to move, particularly in patch O3, which by this stage, had very little standing biomass remaining. After 2 months, maximum dispersal distances were 10.75 m outside the Reserve and 0.35 m inside, while the maximum dispersal at the completion of the experiment (9 months after seed head release) was 27.50 m outside the Reserve and 1.09 m inside.

There was a great deal of variation in both the proportion of seed heads moving and the distances moved by seed heads. This was across all sources of variation, including, in the case of distance moved, seed head movement for seed heads within a given release site (models including 2-level random effects had minimal AIC values; Table 1). In some cases, all seed heads from a release site moved and moved similar distances in the same direction, while few seed heads moved from other release sites and did so in a scattered manner in terms of the direction and distance moved (Fig. 4). These were considered to be the result of two distinctly different dispersal processes, the first being movement through sheet water flow carrying seed heads following a large rainfall event (Fig. 4a,b), and the second being the scattering of seed heads due to sheep moving through the area, inadvertently kicking them along the way (Fig. 4c,d). However, both water and sheep trampling are likely to simultaneously influence seed head dispersal patterns outside the Reserve and we cannot exclude the possibility of a contribution to the dispersal patterns observed here from other potential vectors, such as wind blow. What was obvious is that the movement of seed heads through sheet water flow often resulted in seed heads gathering in areas with other drift material including the seeds from other species, small twigs and other pieces of vegetation and animal dung. Such movement occurred in a typically downhill direction from the release site.

When the dispersal experiment was established, the two outside Reserve patches considered to have highest levels of herbivore activity based on their

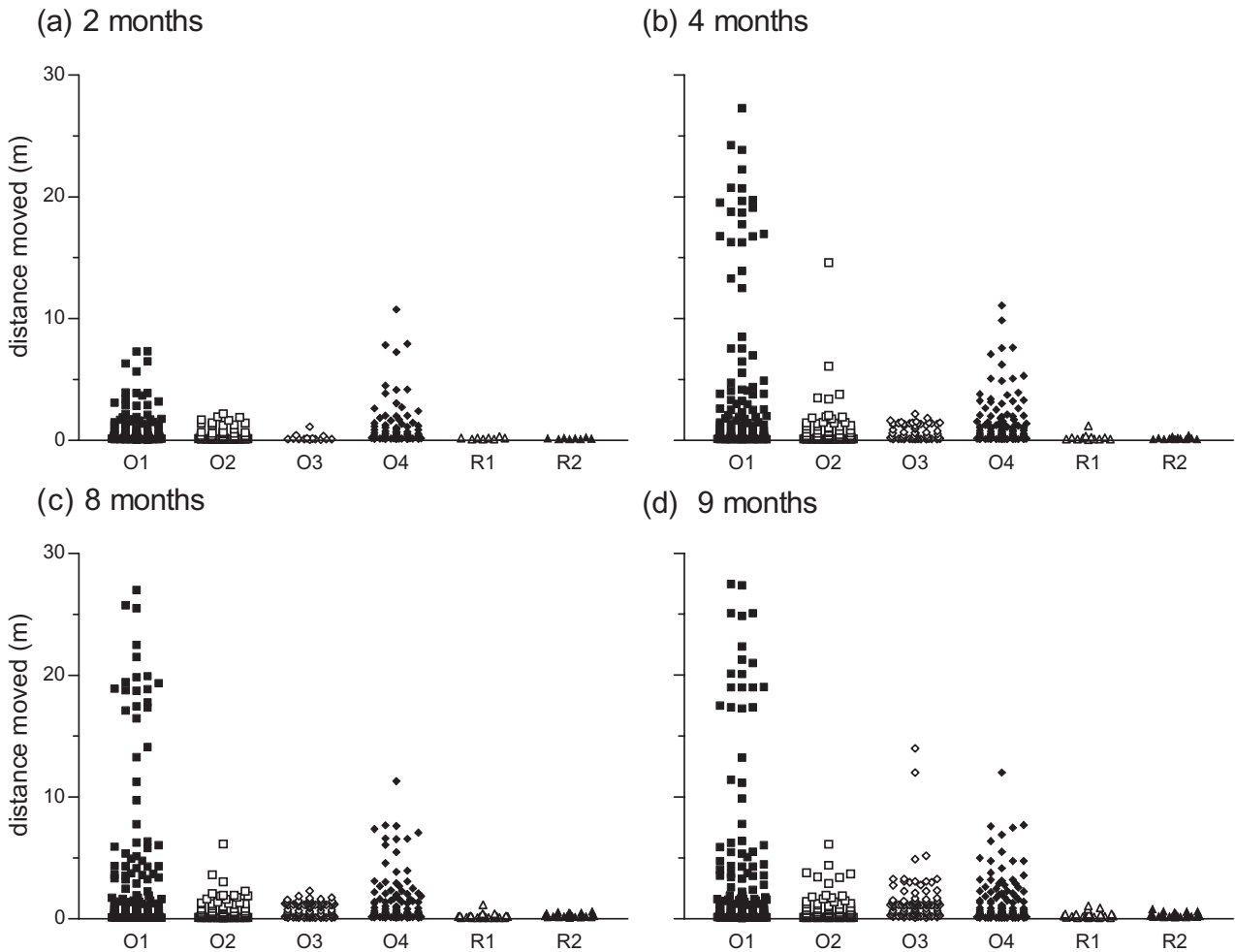


Fig. 1. Individual seed head movement throughout the course of the dispersal experiment in different *Erodiohyllum elderi* patches either inside (R) or outside (O) a vegetation reserve. Seed head dispersal measured 2, 4, 8 and 9 months after deployment (a–d). The horizontal spread of the points is for visual purposes and is not statistically or biologically important. Statistical analyses take into account issues relating to spatial dependence of dispersal recorded for seed heads released from the same release site.

proximity to water, also had the smallest amount of standing biomass present (O2 and O1, two furthest right closed triangles; Fig. 3b). Furthermore, these two sites also had the highest egesta counts at the end of the experiment, which confirmed the idea that they had the highest levels of herbivore activity. In contrast, both patches inside the Reserve (R1 and R2; open triangles) had high levels of standing biomass and the lowest egesta counts, while the two patches considered to have lowest sheep activity (O3 and O4, two furthest left closed triangles) had higher ranks of standing biomass and lower egesta counts compared with O1 and O2.

The rankings of standing biomass remained the same for the first 4 months after which there was less standing biomass in the patches inside the Reserve than in the two patches with low herbivore activity outside the Reserve. This was primarily because the

standing biomass that consisted mainly of dead *E. elderi* plants in the outside Reserve location was large and slightly woody and, once dead, remained as part of the standing biomass. In contrast, the vegetation inside the Reserve was comprised of grasses as well as *E. elderi* plants, and the rapid disintegration of the grasses upon their death left little standing biomass. The relative amount of standing biomass in each patch based on photographic comparisons at the beginning of the experiment was strongly and negatively correlated with mean egesta counts (Spearman rank correlation: $r = -0.89$, $P = 0.033$). In patches with higher abundance of dung there was less standing biomass.

Rainfall was consistent in each of the six *E. elderi* patches examined in this study (Fig. 3a); there was never more than 10 mm difference between patches between any two consecutive readings, and the overall pattern was highly synchronous. Over the duration of

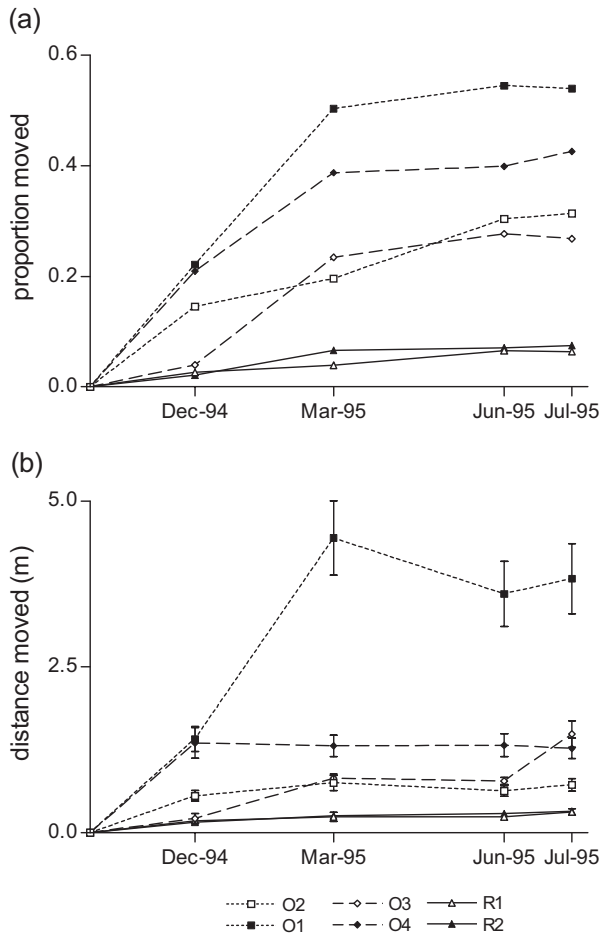


Fig. 2. Dispersal over a period of 9 months for seed heads released in each of six patches: (a) proportion of seed heads moving per patch and (b) mean distance moved for moving seed heads (\pm SEM). Statistical analyses take into account spatial dependence of seed head movement from the same release site.

the experiment, there were several rainfall events over 20 mm. The first of these occurred between the 2- and 4-month period when there was a simultaneous substantial movement of seed heads in one of the outside Reserve patches (O1: Fig. 1a,b).

Seed heads moved further both towards and away from the patches in patches outside the Reserve compared with seed head movement inside Reserve patches. The initial maximum distance that any seed head moved away from a patch was 10.75 m outside the Reserve compared with 0.22 m inside. Likewise, after 2 months the maximum distance that any seed head moved towards a patch was 4.5 m outside the Reserve and 0.15 m inside. After 9 months the maximal seed head dispersal distance away from the patch was 14 m outside the Reserve compared with 1.09 m inside the Reserve. Maximum dispersal distances towards the patch were 12 m outside the

Reserve and 0.41 m inside the Reserve. Seed heads moving away from patches were often scattered rather than moving as a group from a particular release site. Seed heads from patch O3 moved predominantly towards the patch for the 4 and 8 month dispersal measurements (Wilcoxon rank sum test: $W = -439$, $P = 0.01$, $n = 54$ and $W = -527$, $P = 0.01$, $n = 49$ for 4 and 8 months, respectively), while in patch O4, seed heads moved predominantly away from the patch for the final measurement (Wilcoxon rank sum test: $W = 1412$, $P = 0.006$, $n = 97$).

The topographical slope at the release site did not significantly affect the proportion of seed heads moving after 2 months but influenced both the proportion moved and the distance moved at the final measurement; seed heads moved further when the slope at the release sites was steeper at high egesta count sites (Fig. 5a,d, Tables 1,2). Within the various patches, the regression slope of this relationship differed (O3: 111.9, O4: 5.0, O2: 28.3, O1: 433.5 (clay) and 2.88 (sand); Fig. 6 for results from patch O1) and the slopes were not significantly different from zero for the inside Reserve patches. There was a strong overall influence on both the proportion of seed heads moving and the distance they moved depending on the activity of large herbivores as indicated by egesta counts but which also relates to the amount of standing biomass present and whether the patch was inside or outside the Reserve (Fig. 5b,c, Tables 1,2). After 2 and 9 months, the proportion of seed heads moving was greater where egesta counts were higher. After 9 months seed heads also moved further where egesta counts were higher but this was not apparent after 2 months (Fig. 5, Table 1).

Figure 5c and f show model predictions over the range of egesta counts and topographical slopes recorded in the study for each of the minimal models for proportion moving and distance moved, respectively, based on 9 months of dispersal. The proportion of seed heads moving from each release site is predicted to decrease as a function of topographical slope but increase as a function of egesta counts (Fig. 5c). In some ways this reduced dispersal potential at the larger slopes is unexpected and may be due to some of the steeper slopes having sandy soil instead of clay soil (discussed below). The distance that seed heads are expected to disperse is less than 2 m for sites inside the Reserve (egesta counts less than 10 m^{-2}) irrespective of topographical slope, whereas at higher egesta counts there is a clear expectation that seed heads will disperse further on steeper topographical slopes (Fig. 5f).

The effect of soil type on seed head dispersal

In patch O1, seed heads were more likely to move from clay release sites rather than sandy soil release sites

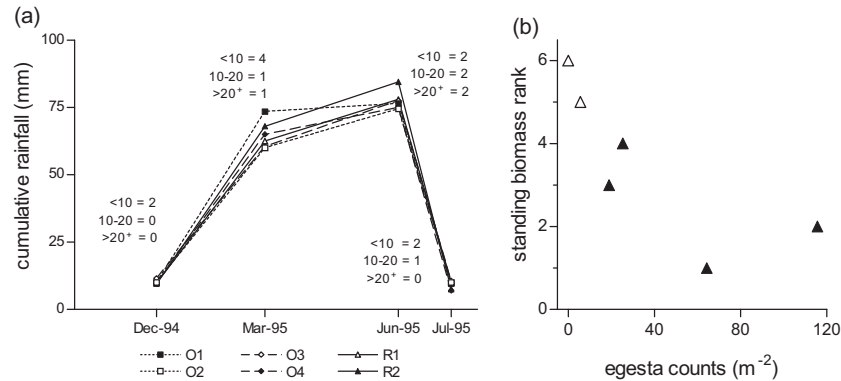


Fig. 3. (a) Cumulative rainfall between consecutive seed head dispersal readings for each *Erodiophyllum elderi* patch; the number of rainfall events between consecutive readings of <10, 10–20 and >20 mm indicated at each time, and (b) the rank of standing biomass in each patch plotted against egesta counts. Solid triangles represent outside vegetation reserve patches and open triangles represent inside vegetation reserve patches. A rank of 1 indicates the patch with the lowest standing biomass present through to 6 for the highest standing biomass.

Table 1. Deletion test results for models of the distance moved by seed heads after 2 and 9 months

	Initial (2 months)	Final (9 months)
2-level LME	AIC = 835	AIC = 2566
1-level LME	AIC = 839	AIC = 2657
LM (no random effects)	AIC = 875	AIC = 2704
Variable		
Interaction term	$\Delta\text{Dev} = -0.85, P = 0.771$	$\Delta\text{Dev} = -8.73, P = 0.003$
Egesta counts	$\Delta\text{Dev} = -2.61, P = 0.106$	Not tested
Topographical slope	$\Delta\text{Dev} = -0.62, P = 0.431$	Not tested

Initial model includes no terms and final model includes interaction term and both main effects. Inclusion of random effects examined in LME model by comparing AIC values. Model with smallest AIC used in deletion tests to examine fixed effects (in bold). Change in deviance on removal of a given explanatory variable is tested against the χ^2 distribution: each explanatory variable is associated with 1 d.f. AIC, Akaike's information criterion; Dev, deviance; LM, linear model; LME, linear model effects.

2 months after deployment, while 9 months after deployment this pattern was not apparent and the proportion of seed heads moving was only influenced by the topographical slope of the release site (Table 3 and Fig. 6a). For a given topographical slope, seed heads were more likely to move further if released on clay soils compared with sandy soil release sites (Fig. 6b) as indicated by the significant interaction term (Table 3) between topographical slope and soil type and the magnitude of the slopes of the relationship in the following equations (final: distance = $433.5 \times \text{topographical slope} + 1.45$ (clay), distance = $2.88 \times \text{topographical slope} + 0.65$ (sand)). This result persisted throughout the duration of the experiment.

DISCUSSION

This study has clearly shown that secondary dispersal of propagules of *E. elderi*, an arid land species with no obvious dispersal-promoting characteristics, is influenced by a range of abiotic and biotic factors. The

genuine difficulty in measuring dispersal, especially secondary dispersal, has resulted in conclusions about dispersal potential being based on morphological characters of the seeds (e.g. Ellner & Shmida 1981; Jurado *et al.* 1991). In particular, for the seeds of arid land species, this has resulted in many seeds being categorized as 'unassisted' with a consequent expectation of limited seed dispersal (Wilson 1993). While such a conclusion is generally appropriate for the primary dispersal phase, our results show that such seeds may have complex secondary dispersal processes involving vectors and factors that are not obvious based on seed morphological characteristics alone.

In this particular instance, dispersal was mainly restricted to the redistribution of *E. elderi* propagules within a patch with maximum dispersal distances of around 30 m over a 9-month period. While this is far greater than the seed dispersal of three Sonoran Desert winter annuals (Venable *et al.* 2008), it is far less than the 100 m distance considered as long-distance dispersal in Cain *et al.* (2000). Dispersal was greatly limited inside a reserved area from which sheep had

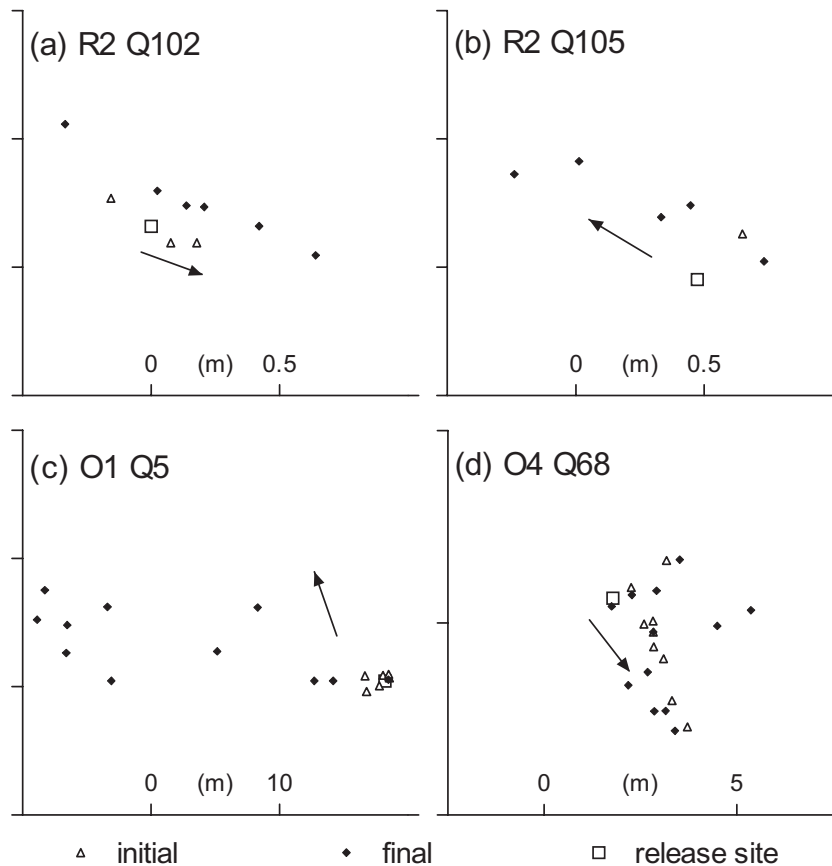


Fig. 4. Seed head movement for four example release sites, two were in patches inside the vegetation reserve and two were outside the vegetation reserve. Included on each map is release site, initial movement after 2 months and final movement after 9 months. Arrow indicates the direction of downhill slope. Note that each release site has its own scale.

been excluded since 1925 (see Osborn *et al.* 1935 for details) where maximum distances were recorded to be just over a metre. Consequently, this study provides clear evidence that the introduction of sheep into the Australian arid landscape is likely to have had a profound influence on the fate and dispersal of seeds for this and other species.

We attribute the strong influence of the presence and activity of the main herbivores on *E. elderi* seed head movement to their direct interactions with seed heads and indirectly through their influence on the abiotic and biotic environment. We have tried here to distinguish between the effects of the amount of standing biomass, the intensity of herbivore activity as well as the effect of the identity of the main herbivores. In reality, however, these three aspects are confounded. For example, the standing biomass depends on the current grazing pressure (Tongway & Ludwig 1994), the condition of the soil environment from past herbivore activity (Stafford-Smith & Pickup 1990), the quality of the seed bank, as well as plant survival and growth (Friedel *et al.* 1990; Ludwig *et al.* 1994). Consequently, in heavily grazed patches, vegetation and

dead material are unlikely to build up to the same extent as in lightly grazed areas and this will have consequences for seed dispersal patterns. In this particular instance, neither kangaroos nor sheep were likely to browse *E. elderi* foliage (Cunningham *et al.* 1992), instead preferring other species. Hence, the observed effects are mediated by the impacts of introduced sheep on the abiotic environment and on the biotic environment via their effects on other plant species growing in the low-lying herbaceous communities. Additionally, the amount of standing biomass is critically dependent on rainfall in the preceding months or years (Morton 1990).

The potential for greater dispersal in areas with reduced standing biomass is partly because woody litter and small branches trap windblown and water-washed material (Friedel *et al.* 1990; Ludwig *et al.* 1994) but also because of differences in water flow across the landscape. For example, water was channelled intensely in areas with reduced standing biomass compared with its movement through less disturbed sites (Ludwig *et al.* 1994). We could see clearly in the field, particularly after deluges of rain in

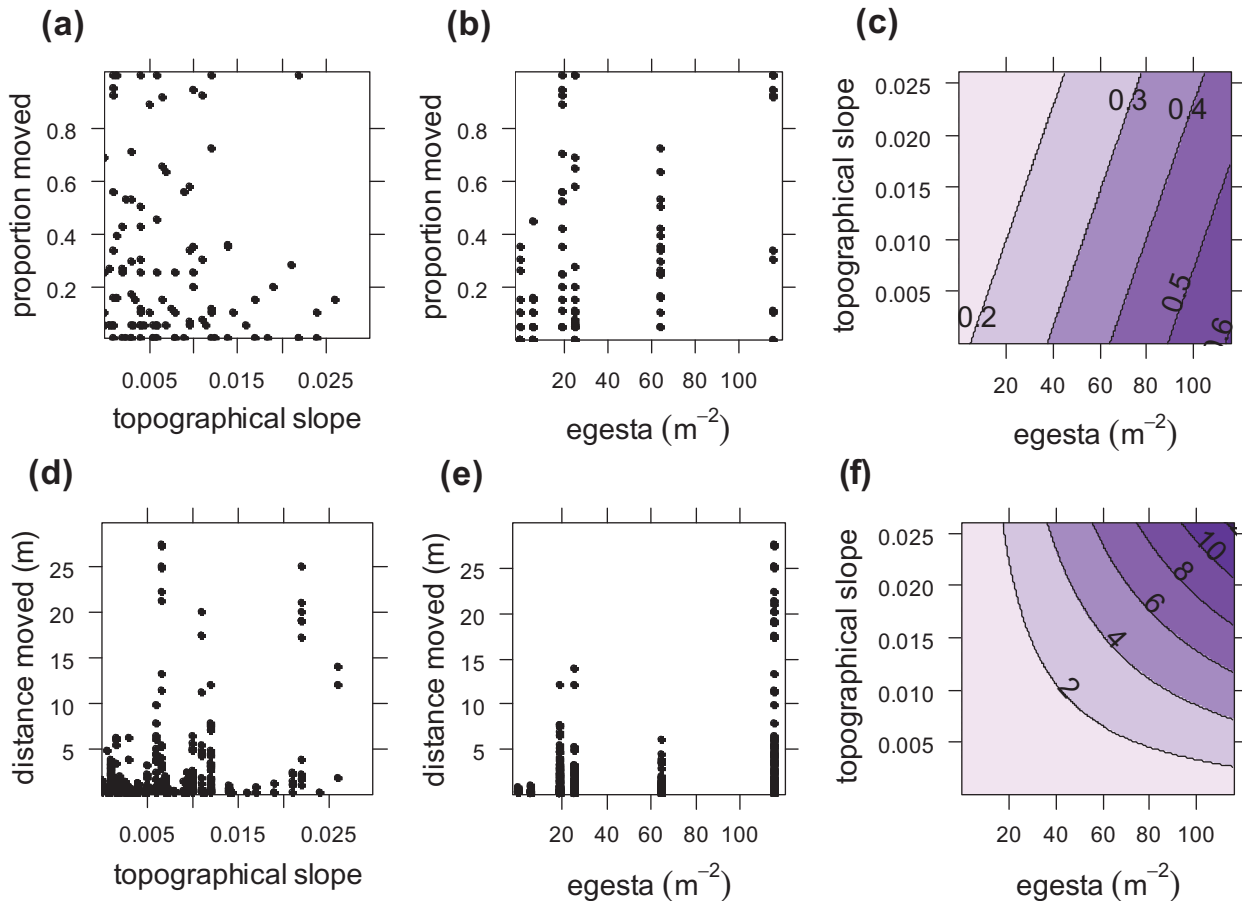


Fig. 5. Proportion of seed heads moved from each release site after 9 months as a function of (a) topographical slope, (b) egesta density, (c) generalized linear model prediction of the proportion of seed heads moved based on the minimal model. The distance that seed heads moved in relation to (d) topographical slope at each release site, (e) egesta counts and (f) model prediction of the distance moved based on fixed effects coefficients from minimal mixed-effects model. Linear mixed-effects model included random effects terms to take into account spatial dependence of seed head movement for seed heads from the same release site.

Table 2. Deletion test results for models of the proportion of seed heads that moved from each release site after 2 and 9 months

	Initial (2 months)	Final (9 months)
1-level GLMM	AIC = 8169	AIC = 14484
GLM (no random effects)	AIC = 721	AIC = 1044
Variable		
Interaction term	$\Delta\text{Dev} = -0.99, P = 0.321$	$\Delta\text{Dev} = -3.49, P = 0.062$
Egesta counts	$\Delta\text{Dev} = -96.32, P < 0.001$	$\Delta\text{Dev} = -130.95, P < 0.001$
Topographical slope	$\Delta\text{Dev} = -0.27, P = 0.61$	$\Delta\text{Dev} = -7.67, P = 0.005$

Initial model includes egesta counts and final model includes egesta counts and topographical slope. Inclusion of random effects in GLMM examined by comparing AIC values. Model with smallest AIC used in deletion tests to examine fixed effects (in bold). Change in deviance from the minimal AIC model on removal of a given explanatory variable is tested against the χ^2 distribution: each explanatory variable is associated with 1 d.f. AIC, Akaike's information criterion; Dev, deviance; GLM, generalized linear model; GLMM, generalized linear mixed-effects model.

sites with limited standing biomass, areas where seed heads, seeds from other species and water-washed material such as twigs and dung had accumulated. Such water-washed material is noted in other studies

as well (Ludwig & Tongway 1995; Vittoz & Engler 2007; Venable *et al.* 2008). Our results are consistent with an indirect effect of herbivores on seed head dispersal patterns through their impact on water flow

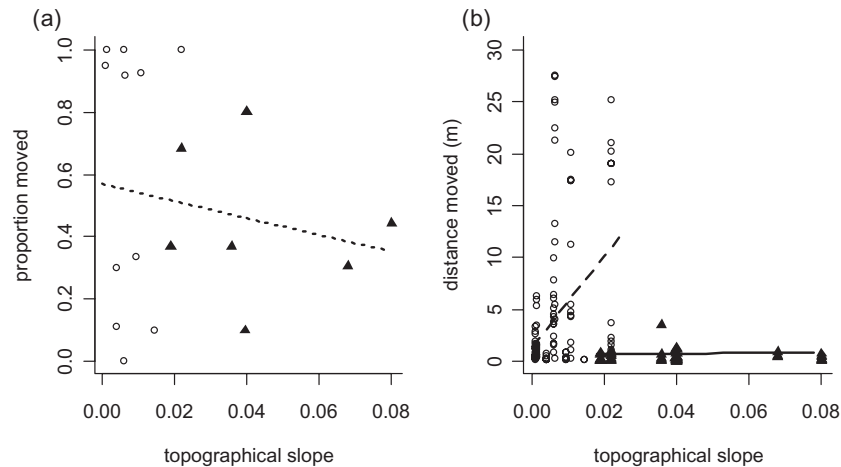


Fig. 6. Effect of soil type and topographical gradient on (a) proportion of *Erodiohyllum elderi* seed heads moved from each release site and (b) the distance moved by seed heads after 9 months of dispersal. Solid triangles represent sandy soil release sites and open circles represent clay soil. Dotted line indicates predicted proportion of seed heads moved for combined soil type from generalized linear model. Predicted dispersal distance for seed heads on clay soil (dashed line) and sandy soil (solid line) as a function of topographical slope using coefficients of fixed effects terms from linear mixed-effects model.

Table 3. Modelling results for the proportion and distance moved by seed heads in relation to release site soil type and topographical slope

Model	Initial (2 months)	Final (9 months)
(a) Proportion moved: 1-level GLMM	AIC = 2891	AIC = 3338
GLM (no random effects)	AIC = 190	AIC = 237
Variable: interaction term	$\Delta\text{Dev} = -3.91, P = 0.04$	$\Delta\text{Dev} = -0.08, P = 0.78$
Soil type	Not tested	$\Delta\text{Dev} = -0.23, P = 0.64$
Topographical slope	Not tested	$\Delta\text{Dev} = -4.41, P = 0.04$
(b) Distance moved: 2-level LME	AIC = 271	AIC = 941
1-level LME	AIC = 269	AIC = 955
LM (no random effects)	AIC = 325	AIC = 1005
Variable: interaction term	$\Delta\text{Dev} = -9.92, P = 0.002$	$\Delta\text{Dev} = -15.71, P < 0.001$
Soil type	Not tested	Not tested
Topographical slope	Not tested	Not tested

Initial models include interaction terms and final model includes topographical slope for proportion moved and the interaction term for the distance moved. Inclusion of random effects determined by finding minimal AIC values (in bold). Change in deviance from the minimal AIC model on removal of a given explanatory variable is tested against the χ^2 distribution: each explanatory variable is associated with 1 d.f. Main effects terms not tested when interaction term required in model. AIC, Akaike's information criterion; Dev, deviance; GLM, generalized linear model; GLMM, generalized linear mixed-effects model; LM, linear model; LME, linear mixed effects model.

across the soil surface via the reduction in standing biomass and changes in soil stability. In areas where sheep activity is high for example, the run-off for a given rainfall is higher where vegetation cover is reduced and infiltration is reduced because of increased soil erodibility (Stafford-Smith & Pickup 1990). Hence it is not surprising that seed head dispersal is reduced and less likely inside the vegetation reserve where there are no sheep.

Water flow, which seemingly moves seed heads downhill, can be a major dispersal agent for arid land seeds (Friedman & Stein 1980; Gutterman 1994; Gutterman & Ginott 1994; Vittoz & Engler 2007) as

reflected in our results by the increased dispersal observed after heavy rainfall as well as the impact of the topographical slope on seed head dispersal. The consequences of downhill, rainfall-driven dispersal is that seeds are likely to disperse to areas with relatively high water availability, such as local depressions or creek beds (Friedman & Stein 1980; Vittoz & Engler 2007). While such movement can be beneficial for subsequent seed germination and seedling establishment by moving seeds to where water and nutrients are also likely to accumulate, seed aggregation may increase the potential for intraspecific competition because of the large density of seeds that can

germinate (Inouye 1980; Schupp 1995; Schupp & Fuentes 1995). We speculate that the consequence of water flow-driven dispersal for *E. elderi* propagules is that it allows a packet of seeds to disperse through space, potentially avoiding the pitfalls of competition with maternal plants, which could occur if primary dispersal was the only dispersal method. Such downhill movement would be to a desirable location for subsequent germination and growth and, once there, the maternal tissue of the seed head ensures that competition with siblings will be reduced as not all seeds are released simultaneously. However, this does not exclude the possibility of intraspecific competition with seeds from other seed heads.

After several months, many seed heads became lodged in depressions or caught in seed traps, such as vegetation or debris on the ground. It may be possible that open bracts effectively hold seed heads to the ground to a limited extent, unless there is sufficient sheet water flow to move them. Similarly, dispersal for other arid land seeds and seed capsules depends on the quantity of rainfall (Venable *et al.* 2008). For example, the true rose of Jericho (*Antastica hierochuntia*) seeds are anchored to the ground immediately after they are dislodged from the maternal plant (Friedman & Stein 1980) and only during sufficiently large rainfall events are carried downstream. Reduced *E. elderi* seed head dispersal was recorded in the small sand dunes that often border patches, which we attribute to their burial in the sand and the lack of water flowing across sandy areas because it soaks rapidly into the sand. While we did not explicitly examine the process here, the burial of seed heads and hence the movement of seeds in the soil profile, may influence subsequent seed germination. Despite the lack of dispersal-promoting characters, we observed isolated or small numbers of seed heads in areas between Koonamore Daisy patches, even uphill on the small dunes between patches and hence longer-distance uphill dispersal is obviously possible. While this study has focussed on several vectors for dispersal it does not exclude the possibility that other vectors, such as wind, also disperse *E. elderi* seed heads. This would be particularly apparent in areas with little or no standing biomass that would allow stronger wind effects on the soil surface.

An unexpected outcome of this experiment was the pattern of seed head dispersal that was consistent with trampling by large vertebrates, principally sheep, resulting in seed heads being scattered around a release site and movement against the topographical slope. Despite this, there does not appear to be any specific adaptation for animal-aided dispersal. Scattered seed heads were mainly apparent in the presence of sheep and we believe it unlikely that there are adaptations for native animals to disperse *E. elderi* seed heads. Furthermore, the lack of *E. elderi* seedling

emergence from dung collected from within *E. elderi* patches suggests that ingestion of seeds or seed heads does not contribute to dispersal (Emmerson, unpubl. data, 1995).

Dispersal patterns of *E. elderi* seed heads were highly variable between patches and within patches, even between seed heads released in the same 0.2×0.2 m release site. We did not record enough detail about microfeatures of the release sites, such as the presence of small ephemeral herbs, twigs or branches or whether there was a smaller scale topographical variation within the release site to determine if these things were responsible. In some cases, it is possible that sheep intersected only part of the release site knocking only some of the seed heads away but this can only explain some of the variability that we observed. Furthermore, seed head dispersal from neighbouring release sites varied dramatically, particularly in patches outside the vegetation reserve. Hence dispersal can potentially be influenced by small and unobvious aspects of the seeds location and this requires further investigation to improve our understanding of what drives dispersal for this and other xeric species.

The short-distance dispersal reported here for *E. elderi* seed heads is likely to be typical of other xeric species (e.g. Venable *et al.* 2008), particularly those that release seed from their fruits over a period of time. In the absence of introduced herbivores, such dispersal patterns are likely to maintain a patchy distribution for *E. elderi*, whereas in areas with high sheep activity, the dispersal patterns reported here have the potential to reduce patchiness by redistributing seed heads uphill against the topographical slope at least temporarily. A reduction in patchiness has been reported in other Australian arid ecosystems as a result of the effect that grazers have on soil stability, and the consequence that has on water run-off and hence resource redistribution available for subsequent plant establishment or growth (Morton 1990; Stafford-Smith & Pickup 1990; Ludwig *et al.* 1994; Ludwig & Tongway 1995) and, for these systems, the reduction in patchiness has a negative outcome. A change in seed dispersal potential in these ecosystems combined with changes in resource distribution may magnify the impacts from the introduction of sheep.

ACKNOWLEDGEMENTS

Our heartfelt thanks to those who searched for seed heads during the night and woke the following morning to measure their movement, in particular Jemery Day, David Ladd and David Bigham. Corinna Lange spent many artistic hours in the field setting up this experiment. Natalie Kelly provided valuable statistical advice. LE was supported by a Faculty of Science Scholarship from the University of Adelaide

and a Collaborative Research Scholarship from RSBS at the Australian National University. Lachlan McLachlan kindly provided access to Koonamore Station throughout this research. Russ Sinclair enthusiastically allowed access to the TGBO Reserve records and the use of Bindy-i Research Centre.

The anonymous reviewers provided valuable comments.

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