

Minerva Access is the Institutional Repository of The University of Melbourne

Author/s:

Farrell, C;Hobbs, RJ;Colmer, TD

Title:

Microsite and litter cover effects on seed banks vary with seed size and dispersal mechanisms: Implications for revegetation of degraded saline land

Date:

2012-07-01

Citation:

Farrell, C., Hobbs, R. J. & Colmer, T. D. (2012). Microsite and litter cover effects on seed banks vary with seed size and dispersal mechanisms: Implications for revegetation of degraded saline land. *Plant Ecology*, 213 (7), pp.1145-1155. <https://doi.org/10.1007/s11258-012-0072-y>.

Persistent Link:

<https://hdl.handle.net/11343/282903>

Microsite and litter cover effects on seed banks vary with seed size and dispersal mechanisms: implications for revegetation of degraded saline land

Claire Farrell ^{ab*}, Richard J Hobbs ^a, Timothy D Colmer ^a

^a School of Plant Biology (MO84), Faculty of Natural and Agricultural Sciences, The University of Western Australia, 35 Stirling Highway, Crawley, Western Australia 6009, Australia

^b Present address: Melbourne School of Land and Environment, The University of Melbourne, 500 Yarra Boulevard, Richmond, Victoria 3121, Australia

* Corresponding author. Phone +61 03 9250 6849. Fax +61 03 9250 6885. Email address: c.farrell@unimelb.edu.au

Proofs should be sent to Claire Farrell, Melbourne School of Land and Environment, The University of Melbourne, Richmond, Victoria 3121, Australia

Word count: 5999

Abstract

Seed movements and fates are important for restoration as these determine spatial patterns of recruitment and ultimately shape plant communities. This paper examines litter cover and microsite effects on seed availability at a saline site revegetated with *Eucalyptus sargentii* tree rows interplanted with 5 – 6 rows of saltbush (*Atriplex* spp.). As litter accumulation decreases with increasing distance from tree rows, soil seed banks were compared between paired bare and litter covered zones within three microsites; tree row, saltbush row closest to tree row and saltbush mid-row (middle row of saltbush between tree rows). Germinable seed banks of the four most abundant species with contrasting seed-sizes and dispersal mechanisms were assessed to test the hypotheses that: (i) microsites with litter cover contain higher seed densities than bare areas, but that (ii) microsite and litter effects will vary depending on seed size and dispersal mechanisms. Overall, litter cover increased seed densities, however litter effects varied with seed size, with no effect on small-seeded species and litter increasing densities of large-seeded species. Seed bank composition also differed between tree and shrub microsites due to differences in seed morphology and dispersal mechanisms. Water-dispersed species were unaffected by microsite but densities of wind-dispersed species, including *Atriplex* spp., were higher in saltbush microsites. Densities of wind-dispersed species also differed between the two saltbush microsites despite similar litter cover. Future plantings should consider row spacing and orientation, as well as the dimensions of seeding mounds and associated neighboring depressions, to maximize litter and seed trapping by microsites.

Keywords: Recruitment; banded vegetation; salinity; and leaf litter

Introduction

Human induced salinity affects many areas of the world, including America, Asia and Australia (Ghassemi et al. 1995) and has been attributed to land use practices such as clearing native vegetation and overgrazing (Hoy et al. 1994). ‘Dryland’ salinity results from rising water tables and re-vegetation of salt-affected areas is seen as a means of amelioration, ideally reflecting pre-cleared vegetation structure, function and complexity (Hobbs and Cramer 2003). In many regions, such as Western Australia, large scale restoration of agricultural land is required to address the problems associated with salinity (Standish et al. 2007) . However, long term vegetation dynamics in these restored areas is yet unknown and success of revegetation will be dependent on recruitment to maintain water table drawdown. As seed dispersal determines spatial patterns of recruitment and ultimately shape plant communities (Caballero et al. 2008), effective restoration requires knowledge of seed movements and fates (Chambers 2000).

Seed dispersal is affected by numerous biotic and abiotic factors (Chambers and MacMahon 1994). The present study is predominantly interested in factors which affect horizontal and vertical redistribution of seeds (phase II dispersal) following primary dispersal as vegetation patterning and seed fates are closely linked to Phase II dispersal (Chambers and MacMahon 1994). Phase II dispersal is affected by abiotic and biotic factors such as soil texture, seed size and morphology and plant life-cycle (Chambers and MacMahon 1994). Seed size is a critical

determinant of vertical redistribution, with small seeds becoming more readily integrated into soil profiles than larger seeds, although this varies with soil particle size (Chambers et al. 1991). Seed morphology and dispersal appendages also affect redistribution. Large seeds with awns such as grasses, or wing-like morphologies e.g. *Atriplex* spp., are readily horizontally redistributed by wind due to large exposed surface areas, consequently microtopography and litter are important for seed retention (Chambers et al. 1991; Rotundo and Aguiar 2005; Chambers 2000).

Vegetation and microtopographical variations (microsite) and litter effects on seed bank dynamics have been widely studied in semi-arid systems (Rotundo and Aguiar 2005; Boeken and Orenstein 2001; Aguiar and Sala 1997). For example, Reichman (1984) found that seed densities in the Sonoran desert were higher in depressions and under shrub canopies than in open areas between shrubs. In semi-arid banded vegetation, wind-blown or runoff transported sediment is trapped by shrubs, forming mounds, which enhances trapping of litter and propagules, supporting colonization by successive shrubs and understorey species (Dunkerley and Brown 1999). Vegetation patches act as both seed sources and seed sinks by trapping seeds from adjacent bare areas (Caballero et al. 2008). Shrubs and other vegetation trap seeds by modifying small scale wind patterns, creating eddies and turbulence which slow prevailing winds and cause release of entrained seeds (Reichman 1984). Wind velocities in interspaces can be up to four times those under shrubs and seed entrapment in sparse or low vegetation occurs predominantly under canopies (Van Oudtshoorn and Van Rooyen 1999). Horizontal seed

redistribution is also affected by preferential flow of runoff onto vegetated bands which is likely to increase recruitment in these areas (Aguiar and Sala 1999), overcoming limitations of short-distance dispersal mechanisms present in many annual and semi-arid species (Mott 1973).

Litter also reduces runoff and litter addition onto bare crusted soils has been shown to increase seed densities in semi-arid ecosystems (Boeken and Orenstein 2001). Conversely, litter can reduce seed densities through increased predation by birds and ants (Guttermann et al. 1990). Inconsistent effects of litter on seed densities reported in the literature may be due to differences in seed size and shape (Rotundo and Aguiar 2005).

We evaluated the importance of microsite and litter cover on seed trapping and retention in a revegetated saline agricultural grazing system alley-planted with tree (*Eucalyptus sargentii* Maiden) rows inter-planted with 5 – 6 saltbush (*Atriplex* spp.) rows. Although artificially constructed, the composition of this mixed planting is analogous to natural systems in low rainfall woodlands of Western Australia where eucalypts such as *E. salmonophloia* F.Muell (salmon gum) (Yates et al. 2000) and *E. kondininensis* Maiden & Blakely (Kondinin blackbutt) (pers. obs.) form natural associations with understorey saltbush species. Not all of the saltbush species at this site are indigenous, however, the altered chemical and physical conditions of saline land often requires the introduction of salinity tolerant non-local species (Standish et al. 2008). In this mixed-planting, litter from tree rows is horizontally redistributed and trapped by vegetation and microtopographical depressions formed by planting mounds, creating a mosaic of

bare and litter covered areas across the site. As previous research at this site has shown that litter accumulation decreases with increased distance from the tree row (Farrell et al. 2011), soil seed bank will be compared between paired bare- and litter covered zones within each of three microsites; tree row, saltbush row 1 (row closest to the tree row) and saltbush mid-row (middle row of saltbush between tree rows). Evaluation of soil seed banks in this study will determine the importance of spatial heterogeneity of microsites and litter cover for recruitment patterns.

Germinable seed banks of the four most abundant species with contrasting seed sizes and dispersal mechanisms were assessed to test the hypotheses that: (i) microsites with litter cover will contain higher seed densities than bare-covered areas, due to increased seed trapping and retention, through protection from seed removal processes such as wind, runoff and predation but that (ii) the effects of litter and microsites will vary depending on seed size and dispersal mechanisms; with increased densities of larger seeds in litter than in bare microsites and increased quantities of *Atriplex* spp. in saltbush microsites, compared with more distant tree microsites. Seed densities are also expected to vary between the three microsites due to decreasing litter quantity with increased distance from the tree row (Farrell et al. 2011).

Although the effects of microsite on seed density are widely known, little information exists on how different microsites influence seedling density and composition (Caballero et al. 2008). This study will enable the comparison between tree and shrub microsites, also with comparison between shrub microsites with different litter quantities. Further, the effects of litter on seed

bank composition and densities are usually compared between bare-open microsites and litter covered tree/shrub microsites. This study offers the unique opportunity to compare bare and litter covered areas within the same microsite. Knowledge of how seed bank densities relate to microsite and litter spatial heterogeneity has important implications for restoration practices (Maestre et al. 2003).

Materials and methods

Study site and species

The study site was located at Michael and Margaret Lloyd's Bundilla property, approximately 27 km SE of Pingaring in the south-eastern wheatbelt of Western Australia, Australia (S 32°55'31.3" and E 118°48'37.1"). The climate is a Mediterranean-type with hot, dry summers and wet winters. Mean annual rainfall is 333 mm and is winter dominant, with 70 % falling during the growing season (autumn, winter and spring). Annual rainfall for 2004 was 249 mm, with 196 mm falling within the growing season. 2003 annual rainfall was 362 mm with 229 mm during the growing season. Daily mean soil temperatures (1 cm below soil surface) ranges between 11.3 °C (winter) and 31.3 °C (summer), with litter reducing extremes (Farrell et al. 2011). The topography is flat (< 1% slope) and the soils are shallow (A horizon < 20 cm) yellow duplex soils (solonetzic) of sand over clay. Soil salinity (EC_{1:5}) of the top 10 cm ranges from 0.21 to 3.59 dS m⁻¹, with litter cover reducing salinity 2 to 5 times in warmer months (Farrell et al. 2011). Prior to clearing for cropping the original vegetation consisted of multi-stemmed

eucalypt species (mallee) including *E. salubris* F.Muell and *E. salmonophloia* (salmon gum) communities (Beard 1968) and remnants exist in surrounding paddocks.

The site was re-vegetated with *E. sargentii* tree seedlings in 1989 with the aim to reduce rising water tables for continued inter-row cropping. *E. sargentii* is a salt-tolerant, locally endemic eucalypt species which naturally occurs around salt-lake margins (Brooker and Kleinig 2001). Cropping was discontinued in 1996 following un-seasonal heavy summer rains, and inter-rows were mounded and seeded with saltbush. The site is now utilized as productive grazing land in summer and autumn (10-15 dry sheep equivalents (DSE) for 6-8 weeks duration) (M. Lloyd, pers. com.) but was not grazed during this study. Vegetation at the 60 ha site is arranged with rows of *Eucalyptus sargentii* trees spaced 10 - 15 m apart (approximately 10 m spacing within rows) and mounded (6 - 11 cm high) inter-rows of *Atriplex* spp. (saltbush) shrubs. Saltbush rows are spaced 1.5 m apart (2 m spacing within rows) and include *A. nummularia* Lindl., *A. undulata* (Moq.) De Dietr. and *A. semibaccata* R.Br. Rows were orientated north-south in the area sampled. Understorey species were predominantly agricultural weeds, including *Mesembryanthemum nodiflorum* L. and *Rumex bucephalorus* L., or pasture species such as *Lolium rigidum* Gaud..

Litter from *E. sargentii* tree rows is horizontally redistributed and trapped by microtopographical depressions in front of saltbush seeding mounds, with most litter under trees and in proximal saltbush rows (Farrell 2007). Litter distribution also varies within microsites, with bare and litter

covered areas. Across the site as a whole, litter cover accounts for 85% of the area within all microsites, with litter in tree rows accounting for 62% of the total area (Farrell 2007). Bare and litter covered areas were compared within three microsites in the present study: ‘tree row’, ‘saltbush row 1’ and ‘saltbush mid-row’. Tree row microsites included the area around each tree. Saltbush row 1 was the row of saltbush shrubs closest to the eastern tree row ((approximately 4 m from tree row). Saltbush mid-row was the third saltbush row east of the tree row (approximately 10 m from tree row). Tree row microsites account for 69% of the total trapping area across the site and saltbush row 1 and saltbush mid-row microsites account for 12 and 20% , respectively (Farrell 2007).

Spatial variation in soil seed bank

Soil seed bank sampling occurred in April 2004 (late autumn), prior to break of season rainfall and germination events. Seed bank sampling methodology was informed by previous seed bank collections from the site which determined species composition, number of samples and seasonal variability. The regular planting structure of the site and homogenous soils meant that sampling blocks were representative of site conditions. Four blocks spaced at least 100 m apart were randomly sampled to obtain four replicates (one from each block) from each of three microsites: tree row, first row saltbush and mid-row saltbush. These two saltbush microsites were sampled to determine the effects of different litter densities (increased litter closest to tree rows) within the same vegetation type. We sampled from specific microsites due to the regular planting structure of the site. In each microsite, samples were taken from bare and litter covered soil

surfaces (samples < 1 m apart). Bare areas were areas with no litter or sparse litter cover (less than 1 %). Tree row samples were taken 2 m from tree trunks, approximately at canopy edge, on eastern side of rows closest to saltbush rows. Saltbush row samples were taken from trapping zones (depressions formed by seeding mounds which collect litter, predominantly leaves with some other debris) located on western sides of north-south orientated seeding mounds. Samples were taken from 25 x 25 cm quadrats to a depth of 2 cm. This depth was considered appropriate as soils are heavily crusted and integration of seed into the profile was therefore low, also germination of native species was unlikely below this depth (Tacey and Glossop 1980). Samples within large areas of litter, for example under tree canopies, always included the exposed edge. Litter and the top 2 cm of soil were collected from the sampled area and bagged together in clear plastic bags and stored under black plastic for less than one week in shaded, dry conditions.

Germinable seed bank assessment and litter quantity

Soil seed bank samples were sieved (0.8 cm² mesh) to remove litter and homogenize samples. Litter was oven-dried at 70°C for one week before being weighed to determine quantity. Soil samples were spread evenly (2 cm depth) in seedling trays (27.5 x 33 cm) over 2 cm of moist medium-grade vermiculite and a paper towel lining. The entire sample was used because previous experiments (unpublished) using a thin layer, 0.5 cm, experienced surface crusting and frequently dried out due to water repellency. Trays were randomized on benches within a glasshouse. Samples were watered regularly to maintain germination conditions. Emergents were counted and discarded every two weeks. Unidentified individuals were planted in pots

containing potting mix and grown until identification could be made. Assessment of germinable seed bank abundance and composition occurred from 23 April to 30 September 2004, until no more seedlings appeared. As the soil seed bank of our study site was composed mainly of pasture and weed species which germinate following autumn rains this method of seed bank evaluation is suitable when studying the spatial segregation of species (López-Pintor et al. 2003).

Data analyses

Germinable seed densities (number of emergents) and litter quantity were calculated on a per m² basis. Seed densities were analyzed using 2-way ANOVA with litter cover (2 levels) and microsite (3 levels) as fixed factors. 2-way ANOVA was appropriate as levels of litter cover were sampled in each microsite and were spatially independent of each other. Significant differences were determined by Tukey's post hoc test ($P < 0.05$). Data were square-root transformed where necessary to ensure univariate normality. All data presented in figures are non-transformed data. Univariate data analyses used GenStat 7.2 (2004). Permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001) was used to examine differences in seed bank species composition between litter cover, microsites and their interaction. Canonical Analysis of Principle coordinates (CAP) (Anderson and Robinson 2003) was then used to determine which species were responsible for differences in species composition between microsites with and without litter cover.

Results

Litter cover, total number of germinants and species

A total of 3841 seedlings germinated from the soil seed bank samples collected in this study. The number of seedlings per sample ranged from 0 to 938 (mean 160). 15 species were found and the number of species in each sample ranged from 0 to 9 (mean 4.0), with significantly more species found in saltbush mid-row microsites (mean = 6.9 species) compared to the other microsites (saltbush row 1 = 2.9 species and tree row = 2.4 species) ($P < 0.001$; $n = 4$). There was no significant effect of litter cover on species number. All species were annual except for *Atriplex* spp. (*A. semibaccata*, *A. nummularia* and *A. undulata*).

Litter cover (quantity of litter removed from seed bank samples) was significantly higher in litter covered microsites than bare microsites and there was an interaction between litter cover and microsite ($P = 0.048$). Bare microsites, as defined in the methods, were areas with no appreciable litter cover ($< 1\%$) and litter quantities from these microsites were minimal and were not different from each other (tree row 45.9 g m^{-2} ; saltbush row 1 = 48.9 g m^{-2} ; saltbush mid-row = 17.2 g m^{-2}). In litter-covered microsites, litter quantities were highest in tree microsites (2940 g m^{-2}) and litter quantities were not significantly different in the two saltbush microsites (saltbush row 1 = 1898 g m^{-2} ; saltbush mid-row = 1660 g m^{-2}).

Effect of litter cover on seed densities

Densities of germinable seeds were greater in litter covered microsites for six of the nine species present (Table 1). Total germinable seed bank density was significantly greater in litter covered

microsites ($P = 0.01$). Of the most abundant species present in the seed bank, only *R. bucephalophorus* and *M. nodiflorum* were not significantly different in bare and littered microsites. Seed densities of non-abundant species (*Hypochaeris radicata* L., *Eragrostis dielsii* Pilg. and *Plantago coronopus* L.) were not affected by the lack of litter.

Insert Table 1.

Effect of litter cover and microsite on seed bank composition and seed densities

Seed bank composition differed across microsites and litter cover with a significant microsite and litter cover interaction (P (perm) = 0.004). Seed bank composition in saltbush mid-row microsites with- and without- litter cover were significantly different to the other microsites with- and without- litter cover (P (perm) = 0.001; CAP). These differences were attributed to increased seed densities of *Lolium rigidum*, *Spergularia diandra* and *Vulpia* spp. in saltbush mid-row microsites.

Insert Figure1

The effect of litter cover on average total germinable seed density varied with microsite, with no significant differences for tree row and saltbush row 1 microsites (Fig. 1). Litter resulted in increased germinable seed densities compared to bare areas in saltbush mid-row microsites ($P = 0.01$) and there was an interaction between saltbush mid-row and litter ($P = 0.024$). Overall

saltbush mid-row microsites had significantly greater germinable seed densities than saltbush row 1 or tree microsites ($P = 0.001$).

Insert Figure 2.

Effects of litter cover and microsite on germinable seed density of the most abundant three species present in the seed bank and of the target perennial shrubs, *Atriplex* spp., are shown in Figure 2. Of the four species, seed densities of *M. nodiflorum* did not vary with microsite or litter cover ($P = 0.29$ and 0.27 respectively). Seed densities of *Atriplex* spp. were significantly larger in saltbush mid-row microsites ($P = 0.01$) and there was a significant interaction with litter cover ($P = 0.027$). *Lolium rigidum* showed a similar pattern of seed density distribution to *Atriplex* spp. with the greatest number of seeds in litter covered saltbush mid-row microsites, litter cover, microsite and litter x microsite were all highly significant ($P < 0.001$). Seed densities of *R. bucephalophorus* were significantly larger in saltbush mid-row microsites ($P = 0.015$) but litter cover was not significant ($P = 0.244$).

Effect of litter and microsite on wind- and water-dispersed seeds

Seed densities of wind- and water-dispersed seeds were not statistically different between litter and bare surfaces (wind-dispersed seeds $P = 0.89$ and water-dispersed seeds $P = 0.62$) (Fig. 3). Microsite differences influenced the densities of wind- and water-dispersed seeds, with more

water-dispersed seeds in tree and saltbush row 1 microsites ($P = 0.02$) and more wind-dispersed seeds in saltbush mid-row microsites ($P = 0.01$).

Insert Figures 3 and 4.

Discussion

This study evaluated the importance of microsite and litter cover on seed bank densities on revegetated agricultural saline land. Overall seed densities were greater in litter covered microsites when compared with bare soil in the same microsites, supporting the hypothesis that litter increases seed densities due to increased seed trapping and retention. However, when species were considered individually, litter had differential effects on seed densities. This was likely due to species differences in dispersal mode, seed shape and size, as seed redistributions are affected by seed sizes relative to soil particle size (Chambers et al. 1991) and seed appendages for burial and retention (Chambers 2000).

Seed size was important for determining seed densities of the four most abundant species, with larger-seeded *Atriplex* spp. and *L. rigidum* having higher seed densities in litter covered microsites than bare sites. Conversely, densities of small-seeded *R. bucephalophorus* and *M. nodiflorum* were un-affected by litter cover. These results are consistent with Boeken and Shackak (1994) and Chambers (2000) who found that small seeds were less dependent on seed

traps such as litter and microtopographical depressions than larger seeds due to reduced surface areas limiting redistribution but promoting soil retention.

Dispersal mechanisms also influenced seed densities in litter covered microsites. Within wind-dispersed species (*Atriplex* spp., *L. rigidum* and *R. bucephalophorus*) differences in seed size and seed morphology, aiding wind-dispersal and preventing redistribution via phase II dispersal in runoff, probably account for differences in litter effects on seed densities. Litter was more important for seed retention of larger seeded *Atriplex* spp. and *L. rigidum*. *Atriplex* spp. seeds are enclosed within bracteoles that provide a flattened, wing-like structure for dispersal, and these remain until abraded following desiccation (Beadle 1952). The dart-like seeds of *L. rigidum*, a grass, require wind or animal disturbance to be released and dispersal is limited around parent plants (Blanco-Moreno et al. 2004). However, litter had no effect on seed densities of *R. bucephalophorus*, the smallest of the wind-dispersed seeds (1 mm diameter) (Hanf 1983), which may have been due to hook-like appendages and small seed size (Hussey et al. 1997) preventing redistribution.

Litter also had no effect on densities of water-dispersed *M. nodiflorum* seeds, again likely due to dispersal mechanisms and proximity to parent plants (Van Oudtshoorn and Van Rooyen 1999). Although *M. nodiflorum* is small seeded like *R. bucephalophorus*, it lacks burial or retention appendages, and instead has a mucilaginous coating and becomes glued onto soil crusts during rain dispersal (Guterman 1994). This prevents redistribution by runoff (García-Fayos et al.

2010) and litter can impede seed adherence (Chambers 2000). Seeds of *M. nodiflorum* are released from the parent plant over a greater period of time (Guterman 1994), reducing the importance of litter protection from seed predation (Kemp 1989). Litter cover is also less important for seed retention as seeds often become trapped by dead remains of parent plants (Guterman 1981).

Seed bank species composition, seed densities and number of species varied greatly between microsites, regardless of litter cover. This was to be expected as patch attributes strongly influence seed banks in vegetation where structure and composition varies (Caballero et al. 2008). The number of species and densities were greatest in shrub microsites furthest from tree rows, regardless of litter cover, which did not differ between the two saltbush microsites. Shrub microsites furthest from tree rows were also different in terms of species composition, attributable to annual grasses. Previous research at the site found that these microsites were the most favourable for seedling recruitment, with greater seedling densities, due to amelioration of soil salinity and temperature (Farrell et al. 2011). Therefore, it follows that seed densities would be higher in these microsites where previous individuals had successfully completed their life-cycles and deposited seeds, further enhancing seed bank patchiness (Kemp 1989).

The effect of tree and shrub microsites on seed distributions also differed amongst species. Microsite had no effect on *M. nodiflorum* distribution, which again is probably explained by poor dispersal and proximity to parent plants (Van Oudtshoorn and Van Rooyen 1999). In contrast,

microsite influenced seed densities of the other abundant species, with highest seed densities in saltbush mid-row microsites and equally low densities in other microsites. For wind-dispersed *L. rigidum* and *Atriplex* spp. there was an interaction between litter cover and microsite, with highest seed densities in saltbush mid-row microsites with litter cover. Increased seed densities of *Atriplex* spp. in saltbush microsites supported the hypothesis of increased *Atriplex* spp. seed distribution within saltbush microsites due to seed production and trapping (Aguilar and Sala 1999). Increased seed trapping and retention in saltbush microsites were likely due to shrub morphology effects on small scale wind patterns, causing seed release and preventing re-distribution (Reichman 1984). Facelli and Temby (2002) also found increased seed densities under *Atriplex* spp. shrubs when compared with surrounding open-bare areas.

Differences in tree versus saltbush row microsites may be due microtopography. Tree row microsites were relatively flat, whereas saltbush row microsites were 0.5 to 2 cm deeper than surrounding flat areas. This may also account for differences in distribution of wind- and water-dispersed seeds between tree and shrub microsites, as wind-dispersed seeds are dominant in depressions (Boeken and Shachak 1998) and densities declines as depressions are filled by sediment and debris (Guterman et al. 1990).

Microtopographic features have been used as a means of promoting diversity in restoration activities through increased habitat heterogeneity and resource capture (Biederman and Whisenant 2011). In degraded semi-arid landscapes, artificial depressions and mounds have

promoted seed trapping and germination. Depressions increased vegetation cover in the Negev desert (Boeken and Shachak 1994) and led to autogenic restoration in semi-arid rangelands (Whisenant et al. 1995). While mounds stimulated plant colonization through improved water harvesting in arid north-western Australia (Kok et al. 1986). The mounds at the present site were established to reduce waterlogging and increase salt leaching from the root-zone, but have a long-term benefit to plant recruitment as well.

Seed bank dynamics vary seasonally with rainfall extremes and production ‘pulses’ (Marone et al. 2000; Mott 1973), consequently this study does not reflect temporal variation in seed bank. Seed bank compositions can also vary markedly between years, however, as sampling occurred following an above average rainfall year these results may provide upper thresholds of soil germinable seed banks. Further, as samples were taken from traps under trees and shrubs, seed bank densities might not show high variation through time, as found by Reichman (1984). Caballero *et al.* (2005) found seed bank composition remained seasonally constant and microsites were more important for determining composition. Low species diversity in seed bank observed in our study is also reflective of site history as non-native annual grasses dominate seed banks in agricultural landscapes, even after 45 years of abandonment (Standish et al. 2007). However, increased annual species abundance relative to perennials has also been observed in natural chenopod shrublands (Meissner and Facelli 1999). Periodic grazing during autumn and summer in previous years may have reduced seed availability (Hunt 2001). Absence of *E. sargentii* from the soil seed bank despite seed availability (pers. obs.), is most likely due to

large aerial seed bank, high predation and low seed viability, common in mallee and other low rainfall eucalypts (Wellington and Noble 1985; Yates et al. 1995).

Although the present study was restricted to one site due to novel revegetation structure and arrangement, this study enabled a mechanistic understanding of how litter cover and microsites interact to influence seed bank composition and densities in a degraded saline agricultural system. Other studies assessing microsite and litter effects on seed bank dynamics have compared seed densities between litter covered shrub microsites and bare open areas (Facelli and Temby 2002; Reichman 1984). However, the present study was unique in that it compared bare and litter covered areas within the same microsite.

Conclusions

Recruitment dynamics and effects of microsite and litter cover have important consequences for restoration of degraded landscapes. Site preparation including creation of depressions and mounds resulted in favourable microsites for litter accumulation and seed trapping, and thus for recruitment. Microsite and litter effects on individual species seed densities differed according to seed size and dispersal mechanisms. Modification of mounds and depressions to increase litter and seed trapping may result in increased understorey biodiversity and recruitment.

Consideration of species dispersal mechanisms may also enhance revegetation success, for example selecting water-dispersed species for revegetation of flat, scalded and waterlogged

valley floors. Future plantings should also consider row spacing and orientation to maximize litter and seed trapping.

Acknowledgements

The authors would like to thank Chris Szota and Aleida Williams for invaluable assistance in the field. Thanks also to Michael and Margaret Lloyd for allowing us to work on their property. This research was funded through a PhD scholarship from The University of Western Australia and the Co-operative Research Centre (CRC) for Plant-based Management of Dryland Salinity.

Literature cited

- Aguiar MR, Sala OE (1997) Seed distribution constrains the dynamics of the Patagonian steppe. *Ecology* 78:93-100
- Aguiar MR, Sala OE (1999) Patch structure, dynamics and implications for the functioning of arid ecosystems. *Tree* 14:273-277
- Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecol* 26:32-46
- Anderson MJ, Robinson J (2003) Generalised discriminant analysis based on distances. *Australia and New Zealand Journal of Statistics* 45:301-318
- Beadle NCW (1952) Studies in halophytes. 1. The germination and establishment of the seed and establishment of the seedlings of five species of *Atriplex* in Australia. *Ecology* 33:49-62
- Beard JS (1968) Vegetation survey of Western Australia. Vegmap publications, Sydney
- Biederman L, Whisenant S (2011) Using Mounds to Create Microtopography Alters Plant Community Development Early in Restoration. *Restor Ecol* 19:53-61
- Blanco-Moreno JM, Chamorro L, Masalles RM, Recasens J, Sans FX (2004) Spatial distribution of *Lolium rigidum* seedlings following seed dispersal by combine harvesters. *Weed Research* 44:375-387
- Boeken B, Orenstein D (2001) The Effect of Plant Litter on Ecosystem Properties in a Mediterranean Semi-Arid Shrubland. *J Veg Sci* 12 (6):825-832

- 424 Boeken B, Shachak M (1994) Desert plant communities in human-made patches: Implications
425 for management. *Ecol Appl* 4 (4):702-716
- 426 Boeken B, Shachak M (1998) Colonization by annual plants of an experimentally altered desert
427 landscape: source—sink relationships. *J Ecol* 86 (5):804-814
- 428 Brooker I, Kleinig D (2001) Field guide to Eucalypts, vol 2. Bloomings books, Melbourne
- 429 Caballero I, Olano J, Escudero A, Loidi J (2008) Seed bank spatial structure in semi-arid
430 environments: beyond the patch-bare area dichotomy. *Plant Ecol* 195 (2):215-223
- 431 Caballero I, Olano J, Luzuriaga A, Escudero A (2005) Spatial coherence between seasonal seed
432 banks in a semi-arid gypsum community: density changes but structure does not. *Seed*
433 *Sci Res* 15 (02):153-160
- 434 Chambers JC (2000) Seed movements and seedling fates in disturbed sagebrush steppe
435 ecosystems: Implications for restoration. *Ecol Appl* 10:1400-1413
- 436 Chambers JC, MacMahon JA (1994) A day in the life of a seed: Movements and fates of seeds
437 and their implications for natural and managed systems. *Ann Rev Ecol Syst* 25:263-292
- 438 Chambers JC, MacMahon JA, Haefner JH (1991) Seed entrapment in alpine ecosystems: Effects
439 of soil particle size and diaspore morphology. *Ecology* 72:1668-1677
- 440 Dunkerley DL, Brown KJ (1999) Banded vegetation near Broken Hill, Australia: significance of
441 surface roughness and soil physical properties. *CATENA* 37:75-88
- 442 Facelli JM, Temby AM (2002) Multiple effects of shrubs on annual plant communities in arid
443 lands of South Australia. *Austral Ecol* 27 (4):422-432
- 444 Farrell C (2007) Leaf-litter and microsite on seedling recruitment in an alley-planted *E. sargentii*
445 and *Atriplex* spp. saline agricultural system. PhD Thesis, The University of Western
446 Australia, Perth.
- 447 Farrell C, Szota C, Hobbs RJ, Colmer TD (2011) Microsite and litter cover effects on soil
448 conditions and seedling recruitment in a saline agricultural system. *Plant Soil* 348:397-
449 409
- 450 García-Fayos P, Bochet E, Cerdà A (2010) Seed removal susceptibility through soil erosion
451 shapes vegetation composition *Plant Soil* 334:289-297
- 452 Genstat (2004) Genstat Version 7.2 Lawes Agricultural Trust, Rothamsted Experimental
453 Research Station, Harpenden, Hertfordshire, UK.,
- 454 Ghassemi F, Jakeman AJ, Hix HA (1995) Salinisation of land and water resources; human
455 causes, extent, management and case studies. University of NSW Press, Sydney
- 456 Gutterman Y (1981) Annual rhythm and position effect in the germinability of
457 *Mesembryanthemum nodiflorum*. *Isr J Bot* 29:93-97
- 458 Gutterman Y (1994) Long-term seed position influences on seed germinability of the desert
459 annual *Mesembryanthemum nodiflorum* L. *Isr J Plant Sci* 42:197-205
- 460 Gutterman Y, Golan T, Garsani M (1990) Porcupine diggings as a unique ecological system in a
461 desert environment. *Oecologia* 85:122-127
- 462 Hanf M (1983) The arable weeds of Europe with their seedlings and seeds. BASF, Ludwigshafen
- 463 Hobbs RJ, Cramer VA (2003) Natural ecosystems: Pattern and process in relation to local and
464 landscape diversity in southwestern Australian woodlands. *Plant Soil* 257:371-378

- Hoy NT, Gale MJ, Walsh KB (1994) Revegetation of a scalded saline discharge zone in Central Queensland. 1. Selection of tree species and evaluation of an establishment technique. *Aust J Exp Agric* 34:765-776
- Hunt LP (2001) Low seed availability may limit recruitment in grazed *Atriplex vesicaria* and contribute to its local extinction. *Plant Ecol* 157:53-67
- Hussey BMJ, Keighery GJ, Cousens RD, Dodd J, Lloyd SG (1997) Western weeds: A guide to the weeds of Western Australia. The Plant Protection Society of Western Australia (Inc.), Perth
- Kemp P (1989) Seed banks and vegetation processes in deserts. In: Leck MA, Parker VT, Simpson RL (eds) *Ecology of soil seed banks*. New York: Academic Press, pp 257-281
- Kok B, George PR, Stretch J (1986) Saltland revegetation with salt-tolerant shrubs. *Reclam Reveg Res* 5:501-507
- López-Pintor A, Espigares T, Rey Benayas J (2003) Spatial segregation of plant species caused by *Retama sphaerocarpa* influence in a Mediterranean pasture: a perspective from the soil seed bank. *Plant Ecol* 167 (1):107-116
- Maestre F, Cortina J, Bautista S, Bellot J, Vallejo R (2003) Small-scale environmental heterogeneity and spatiotemporal dynamics of seedling establishment in a semiarid degraded ecosystem. *Ecosystems* 6 (7):630-643
- Marone L, Horno ME, Gonzalez dSR (2000) Post-dispersal fate of seeds in the Monte desert of Argentina: Patterns of germination in successive wet and dry years. *J Ecol* 88 (6):940-949
- Meissner RA, Facelli JM (1999) Effects of sheep exclusion on the soil seed bank and annual vegetation in chenopod shrublands of South Australia. *J Arid Environ* 42 (2):117-128
- Mott JJ (1973) Temporal and spatial distribution of an annual flora in an arid region of Western Australia. *Trop Grassl* 7:89-97
- Reichman OJ (1984) Spatial and temporal variation of seed distributions in Sonoran Desert soils. *J Biogeogr* 11:1-11
- Rotundo JL, Aguiar MR (2005) Litter effects on plant regeneration in arid lands: a complex balance between seed retention, seed longevity and soil-seed contact. *J Ecol* 93:829-838
- Standish R, Cramer V, Wild S, Hobbs R (2007) Seed dispersal and recruitment limitation are barriers to native recolonization of old fields in western Australia. *J Appl Ecol* 44 (2):435-445
- Standish R, Cramer V, Yates C (2008) A revised state-and-transition model for the restoration of woodlands in Western Australia. *New Models for Ecosystem Dynamics and Restoration*
- Tacey WH, Glossop BL (1980) Assessment of topsoil handling techniques for rehabilitation of sites mined for bauxite within the jarrah forest of Western Australia. *Journal of applied ecology* 17:195-201
- Van Oudtshoorn K, Van Rooyen M (1999) *Dispersal biology of desert plants*. Springer Verlag, Wellington
- AB, Noble IR (1985) Seed Dynamics and Factors Limiting Recruitment of the Mallee *Eucalyptus Incrassata* in Semi-Arid Southeastern Australia. *J Ecol* 73:657-666
- Whisenant SG, Thurow TL, Maranz SJ (1995) Initiating autogenic restoration on shallow semiarid sites. *Restor Ecol* 3 (1):61-67

- 506 Yates CJ, Hobbs RJ, Atkins L (2000) Establishment of perennial shrub and tree species in
507 degraded *Eucalyptus salmonophloia* (Salmon gum) remnant woodlands: Effects of
508 restoration treatments. Restor Ecol 8:135-143
- 509 Yates CJ, Taplin R, Hobbs RJ, Bell RW (1995) Factors limiting the recruitment of *Eucalyptus*
510 *salmonophloia* in remnant woodlands .2. Post-dispersal seed predation and soil seed
511 reserves. Aust J Bot 43:145-155
512
513

Table 1 Effect of litter cover on mean number of seed bank emergents (seedlings m⁻² in late autumn). All microsites (tree row, saltbush row 1 and saltbush mid-row) pooled for comparisons of litter covered and bare samples. Group abbreviations; A = annual, P = perennial; H = herb, G = grass, S = shrub; E = exotic, N = native. *Trifolium* spp. included *T. tomentosum* and *T. glomeratum*. *Vulpia* spp. included *V. bromoides* and *V. myuros*. *Atriplex* spp. included *A. semibaccata*, *A. nummularia* and *A. undulata*. One-way ANOVA was performed on square root transformed data, original means and SE are shown. (* P≤0.05, ** P≤ 0.01 and *** P≤ 0.001; n.s. = not significant; n = 12)

Species	Group	Number of emergents m ⁻²		P-value
		Litter	Bare	
Wind dispersed				
<i>Rumex bucephalophorus</i> L.	AHE	312 (±140)	659 (±332)	0.244 n.s.
<i>Lolium rigidum</i> L.	AGE	1137 (±493)	250 (±143)	<0.001***
<i>Spergularia diandra</i> (Guss.) Heldr.	AHE	239 (±107)	27 (±19)	0.002**
<i>Trifolium</i> spp.	AHE	24 (±19)	5.3 (±5.3)	0.013*
<i>Vulpia</i> spp.	AGE	53 (±26)	4.4 (±4.4)	0.014**
<i>Atriplex</i> spp.	PSN/E	32 (±13)	2.7 (±1.8)	0.001***
<i>Hypochaeris radicata</i> L.	PHE	4.0 (±2.9)	0	0.113 n.s.
<i>Eragrostis dielsii</i> Pilg.	PGN	0	4.0 (±4.0)	0.333 n.s.
Water dispersed				
<i>Mesembryanthemum nodiflorum</i> L.	AHE	489 (±141)	336 (±129)	0.441 n.s.
<i>Cotula australis</i> (Sieber ex Spreng.)Hook F.	AHE	34 (±26)	1.5 (±1.5)	0.011*
<i>Plantago coronopus</i> L.	PHE	0	1.3 (±1.3)	0.333 n.s.

Figure captions

Fig. 1 Canonical Analysis of Principle coordinates (CAP) (Anderson and Robinson 2003) showing differences in species composition between microsites with and without litter cover (Bray-Curtis dissimilarities, $n = 4$, data square root transformed). Open and closed symbols represent litter and bare, respectively. Triangles = tree row microsites; diamonds = saltbush row 1 microsites (approximately 4 m from the tree row); and squares = saltbush mid-row microsites (approximately 10 m from the tree row) - 'mid' refers to the middle row of saltbush between rows of trees. Seed bank composition in saltbush mid-row microsites with- and without- litter cover were significantly different to the other microsites with- and without- litter cover (P (perm) = 0.001; CAP).

Fig. 2 Average number of total seed bank emergents per m^2 (in a glasshouse test) in soil from bare and litter covered microsites (average quantity of litter from littered microsites was 2165 g dry weight per m^2) (means $\pm$ SE, $n = 4$). Open and closed bars represent litter and bare, respectively. Saltbush row 1 microsites (approximately 4 m from the tree row); saltbush mid-row microsites (approximately 10 m from the tree row) - 'mid' refers to the middle row of saltbush between rows of trees. Two-way ANOVA showed significant differences ($P \leq 0.05$). Different letters denote significant differences between litter cover and microsite.

Fig. 3 Average number of total seed bank emergents per m^2 (in a glasshouse test) of four species (A *Atriplex* spp., B *Mesembryanthemum nodiflorum*, C *Lolium rigidum* and D *Rumex bucephalophorus*) in bare and litter covered microsites (mean $\pm$ SE, $n = 4$). Open and closed

bars indicate litter and bare, respectively. Saltbush row 1 microsites (approximately 4 m from the tree row); saltbush mid-row microsites (approximately 10 m from the tree row) - 'mid' refers to the middle row of saltbush between rows of trees. Different letters denote significant differences (two-way ANOVA, $P \leq 0.05$) between litter cover and bare areas across microsites, for each species. Note different scales in the four parts of the figure.

Fig. 4 Variation in the percentage of wind- and water-dispersed seeds (seed bank emergents in a glasshouse test) in bare and litter covered microsites (mean $\pm$ SE, $n = 4$). Open and closed portions of bars indicate wind- and water-dispersed seeds, respectively. Sb1, saltbush row 1 microsites (approximately 4 m from the tree row); Sb mid, saltbush mid-row microsites (approximately 10 m from the tree row) - 'mid' refers to the middle row of saltbush between rows of trees. There were no significant differences between litter covered and bare microsites. Saltbush mid-row was significantly different to tree row and saltbush row 1 microsites for wind-dispersed seeds (ANOVA, $P = 0.01$) and from the tree row for water-dispersed seeds (ANOVA, $P = 0.02$).

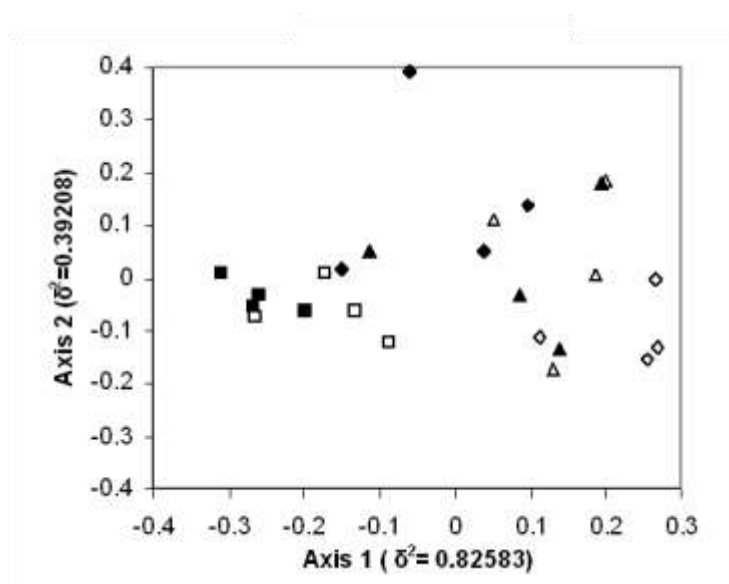
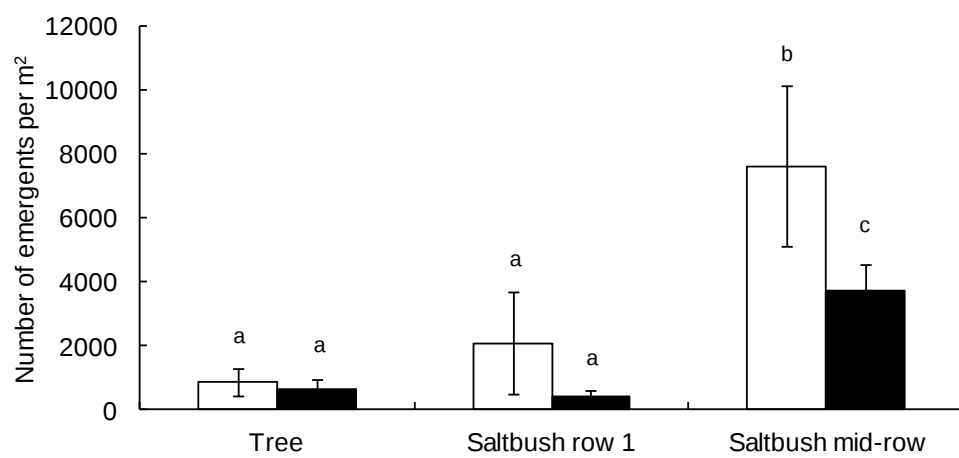
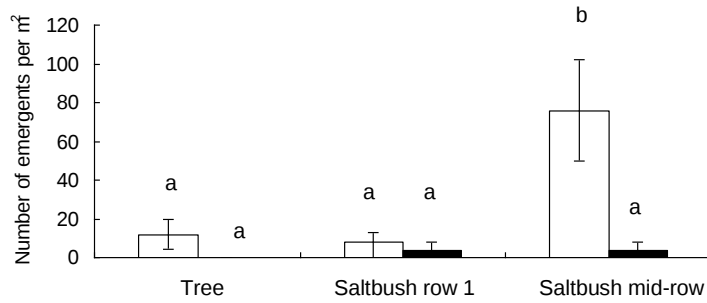


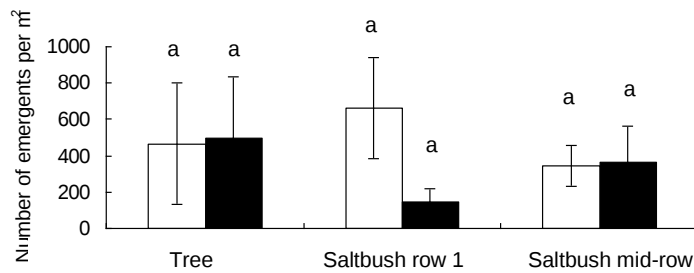
Fig.1

**Fig.2**

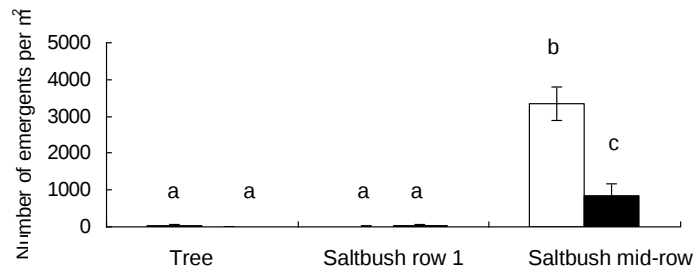
A *Atriplex* spp.



B *Mesembryanthemum nodiflorum*



C *Lolium rigidum*



D *Rumex bucephalophorus*

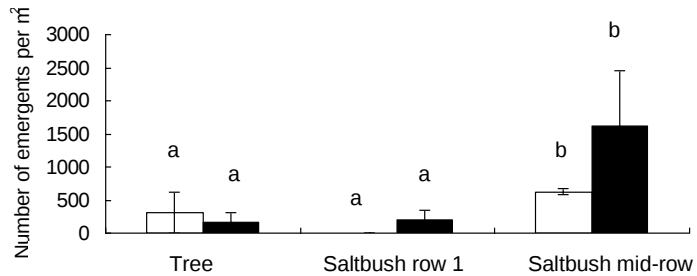
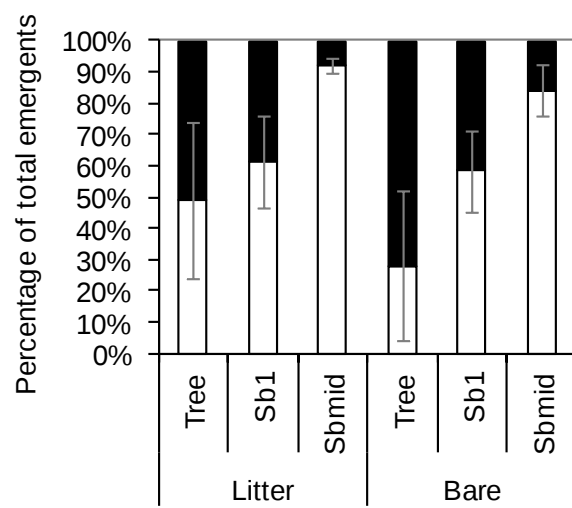


Fig.3

**Fig.4**