

Agricultural saltland ecology: the seasonal effects of leaf litter and microsite on seedling recruitment in an alley-planted *E. sargentii* and *Atriplex* spp. system

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Introduction

This study examines whether microsites (tree/shrub) and litter-cover facilitate seedling recruitment on salt-affected agricultural land in a low rainfall Mediterranean climate. In this system, litter from *E. sargentii* tree rows is redistributed and trapped by seeding mounds of *Atriplex* spp. (saltbush) rows, with increased litter under trees and in proximal saltbush rows (Farrell 2008).

As perennial components of this system are arranged in repeating units of tree rows and mounded shrub inter-rows, naturally occurring banded semi-arid systems provide useful comparisons. Banded systems occur globally as a result of water redistribution from bare areas onto vegetated bands, trapping water and nutrient resources, enhancing colonization and forming plant mounds (El-Bana et al. 2003). Plant-trapped mounds ameliorate abiotic stress compared to surrounding bare soil, resulting in favourable microsites for seedling recruitment (El-Bana et al. 2003). Accumulated litter ameliorates environmental harshness through moderated soil water contents and temperatures. Litter also directly influences plant diversity and productivity through mechanical/chemical effects on seeds and seedlings (Facelli et al. 1999).

Perennials also directly modify seedling environments through competition and facilitation. These interactions occur simultaneously, although the relative importance varies with abiotic stress (Pugnaire and Luque 2001). In semi-arid or salt-marsh environments, positive effects of shading on increased water availability, reduced evaporation and temperature extremes outweigh negative effects of reduced light availability on growth rates (Calloway 1994). These interactions vary with species and size and generally positive interactions dominate harsh environments (Pugnaire and Luque 2001).

It is hypothesised that microsite and litter amelioration of abiotic stresses (salinity, water availability and temperature) will facilitate seedlings, resulting in increased seedling densities. Further, as annual species largely complete their life-cycles before onset of severe abiotic stress in summer, these species should be less reliant on facilitation than perennial species.

Materials and methods

The study site was located on Michael and Margaret Lloyd's 'Bundilla' property, approximately 27 km SE of Pingaring, south-eastern wheatbelt of Western Australia (S 32°55'31.3" and E 118°48'37.1"). Annual average rainfall is 333 mm per annum and is winter dominant. Annual rainfall for 2004 was 249 mm, with 196 mm falling within the growing season.

Seasonal soil sampling

Soil sampling was carried out (Jan, Apr, Jul, Nov 2004 and Jan 2005) in 4 blocks across the site. Samples were taken from paired bare (litter removed) and litter-covered areas within microsites (tree row, saltbush row 1 and saltbush mid-row). Saltbush row 1 and mid-row microsites were saltbush seeding rows (4 and 10 m) adjacent to tree rows. Saltbush row samples were taken from depressions adjacent to seeding mounds (6 - 11 cm tall) and tree row samples were taken 2 m from trunks. Samples were taken from 0 - 2 (surface, sand), 2 - 10 (sub-surface sand, A horizon) and 10 - 20 (clay subsoil, B horizon) cm for salinity (EC 1:5) and water content measurements (data from 0 - 2 cm presented). Soil temperatures were measured and logged using iButton temperature loggers (DS1921G, Dallas Semiconductor, Inc.) buried 0.5 - 1 cm in bare and littered microsites. (September 2004 - August 2005).

Seasonal seedling distributions

Seedling parameters were assessed seasonally within a 2500 m² (0.25 ha) grazing enclosure. Three permanent belt transects (14 x 1 m) perpendicular to the tree row, including tree and saltbush row 1 and mid-row microsites, were used to map seedling distributions. Litter-cover for each seedling position was also assessed (0 = bare, 1 = < 50 % litter, 2 = > 50 % litter).

Data analyses

Two-way ANOVA GenStat 7.2 (2004) tested effect of microsite and litter on seedling and soil parameters. All ANOVA statistics were done within months. Data were transformed where appropriate for univariate normality. All graphs and tables present non-transformed data.

Results and discussion

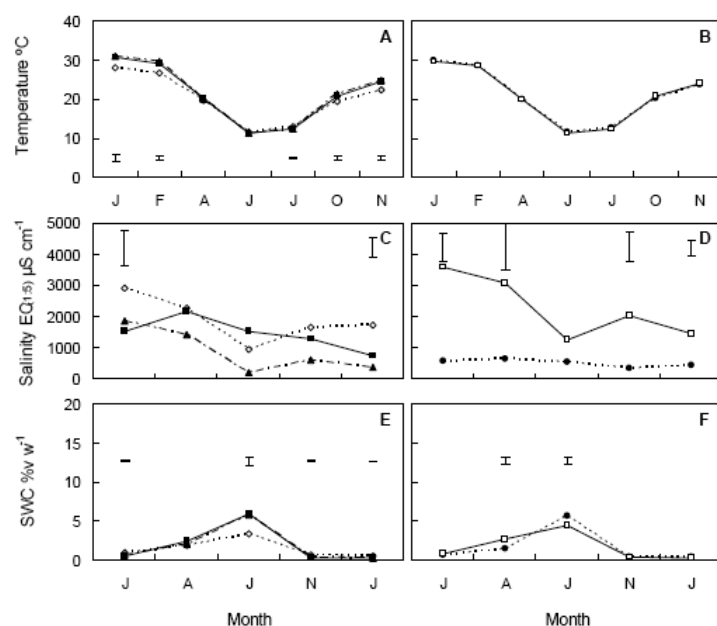


Figure 1 Effects of microsite (A, C and E) and litter-cover (B, D, F) on mean soil temperature, salinity (EC 1:5; $\mu\text{S}/\text{cm}$) and volumetric soil water content at 0-2 cm. \diamond = tree row, \blacksquare = saltbush row 1, \blacktriangle = saltbush mid-row, \bullet = litter-cover and \square = bare. Bars (LSD) denote significant differences from 2-way ANOVA within months (temperature, microsite $n = 4$, litter cover $n = 6$; salinity and water content, microsite $n = 9$, litter cover $n = 18$). Interaction P-values were not significant

Winter abiotic amelioration

As facilitation of seedling growth and survival increases with increased abiotic stress, moderate winter temperatures and increased water availability (Figure 1) should reduce the need for facilitation at this site. Winter conditions generally were not markedly different between microsites or litter levels. Soil salinities were reduced in bare and litter-covered microsites (compared with summer) as a result of late autumn and early winter rains leaching salt from the soil (Figure 1). Soil water contents (Figure 1) were also similar across microsites and may have been a result of water 'ponding' by leaf litter, which commonly occurs in semi-arid banded vegetation, increasing soil water contents. It is also likely that water contents of bare soils in winter were enhanced by reduced surface sealing and the mulching effect of annuals.

Winter seedling recruitment

Evenly distributed seedlings across all microsites in winter (Table 1), despite shading differences, supported the hypothesis of reduced facilitation/interference with reduced abiotic stress. In contrast, litter-cover resulted in increased seedling densities (Table 1), despite similar abiotic conditions (Figure 1). The influence of litter on seedling distributions varied with litter density and species longevity, with annuals predominantly in low litter and

perennials dominating dense litter-covered microsites (Table 2). This may have been due to mechanical effects of litter suppressing germination and emergence of small-seeded annuals (*M. nodiflorum*) (Foster and Gross 1997). With litter acting as a filter for seed size, this may have resulted in increased seedling densities of large-seeded perennials such as *Atriplex* spp. in dense litter-covered microsites (Table 1). Humid conditions and warmer temperatures of tree microsites in winter (Figure 1) may also result in annual establishment in dense litter, despite mechanical impairment (Facelli et al. 1999). Overall, preference of litter-covered microsites is likely due to increased trapping of redistributed seeds, as shown in a parallel study of seedbank densities at this site (Farrell 2008).

Seasonality of germination is also likely to have influenced seedling distribution. Annuals, germinating following autumn and winter rains completing their lifecycle before the onset of abiotic stress, are less likely to benefit from dense litter-cover, reflected by even distribution across microsites (Table 1). Conversely, long-lived perennial species, such as *Atriplex* spp., germinate following summer/autumn rains when temperatures are greater than 25°C. However, high salinity and temperatures interact to inhibit germination of halophytes, reducing the window for successful germination. Consequently moderate temperatures and salinities afforded by dense litter-covered microsites during warmer months (Figure 1) are likely to be more favourable for germination and establishment of *Atriplex* spp.

Table 1 Effects of microsite and litter cover on 2004 mean seedling recruitment. Tree row, Sb row 1 and Sb mid refer to tree row, saltbush row 1 and saltbush mid-row, respectively. Different letters denote significant differences within months (M) (2-way ANOVA; microsite and litter cover). Litter 0, 1 and 2 refer to bare, < 50 % cover and > 50 % cover, respectively. M *L denotes microsite x litter interaction P-value. * denotes P-value derived from square-root transformed data. All data is non-transformed. *M. nodiflorum*/m² includes dead seedling counts in Feb. *Atriplex* spp. includes *A. semibaccata*, *A. undulata* and *A. nummularia* seedlings. Total number of annual and perennial seedlings includes *M. nodiflorum* and *Atriplex* spp., respectively.

Parameter	M	Litter cover			P-value	Microsite			P-value	M*L
		0	1	2		Tree row	Sb row 1	Sb mid		
Total seedlings /m ²	Feb	1.49 a	4.74 b	5.95 b	0.005	2.52 a	3.01 a	6.65 b	0.005	0.905
	Jun	2.47 a	15.5 b	3.45 a	0.026	5.6 a	8.8 a	6.96 a	0.806	0.427
	Oct	1.7 a	4.06 b	2.21 a	0.008	2.7 ab	1.72 a	3.56 b	0.013	0.451*
<i>Atriplex</i> spp. /m ²	Feb	0 a	0.36 b	0.26 c	<0.001	0.21 a	0.18 b	0.24 a	0.001	<0.001*
	Jun	0.35 a	0.11 a	1.11 b	<0.001	0.69 a	0.73 a	0.16 a	0.064	0.008
	Oct	0 a	0.33 b	0.21 c	<0.001	0.30 a	0 b	0.24 a	<0.001	<0.001
<i>M. nodiflorum</i> /m ²	Feb	1.49 a	3.97 b	3.97 b	0.002	2.22 a	2.38 a	4.83 b	0.026	0.198
	Jun	1.86 a	12.5b	1.27 a	0.011	4.33 a	6.28 a	5.99 a	0.873	0.572
	Oct	1.3 a	2.52 b	0.8 a	0.045	2.0 a	0.72 b	1.89 a	0.023	0.365
Total annuals /m ²	Feb	1.49 a	4.21 b	5.6 b	0.015	2.22 a	5.38 a	6.33 b	0.009	0.956
	Jun	2.04 a	15.2 b	2.28 a	0.020	4.86 a	8.07 a	6.64 a	0.803	0.449
	Oct	1.61 a	3.54 a	1.94 a	0.210	2.29 a	1.73 a	3.07 a	0.494	0.862
Total perennials /m ²	Feb	0 a	0.53 b	0.35 c	<0.001	0.29 a	0.27 a	0.32 a	0.200	<0.001
	Jun	0.43 a	0.22 a	1.17 b	0.004	0.77 a	0.73 a	0.32 a	0.757	0.081
	Oct	0.09 a	0.53 b	0.27 b	<0.001	0.39 a	0 a	0.49 b	<0.001	<0.001

Spring, Summer and Autumn abiotic amelioration

Spring and summer/autumn mean temperatures varied greatly with microsite, with increased temperatures measured in both saltbush microsites (Figure 1). This indicates that shading by *E. sargentii* trees had no influence on temperatures of proximal saltbush row 1 microsites. However, proximity to the tree row resulted in differences in soil temperatures through differences in litter quantity. In warmer months increased litter in tree and saltbush row 1 microsites resulted in reduced temperature variability, ‘insulating’ the soil (data not shown). Summer soil water contents (Figure 1) were greater in bare soils irrespective of microsite, despite the fact that mulching by litter should reduce evaporation. Litter-cover reduced

salinity two to five fold (Figure 1), therefore it follows that litter reduced evaporation, thus conserving soil water.

Spring, Summer and Autumn seedling recruitment

As for winter, spring seedling densities of perennials (*Atriplex* spp.) and *M. nodiflorum* across microsites were also influenced by seed trapping. *Atriplex* spp. seedlings were preferentially distributed in saltbush microsites (Table 1), as their wind-dispersed seeds are readily trapped in nearby saltbush microsites (Farrell 2008). By contrast, water-dispersed *M. nodiflorum* seedlings were more abundant in tree and saltbush mid-row litter-covered microsites (Table 1) as a result of run-on (Farrell 2008). Following increased summer temperatures, *Atriplex* spp., total seedlings, *M. nodiflorum* and annuals were all preferentially distributed in litter-covered saltbush mid-row microsites (Table 1).

As amelioration of temperatures and soil water were greatest in the tree row (Figure 1), it is clear that facilitation was negated by increased salinities (Figure 1) and potential tree interference (competition or shade). During summer, tree microsite densities of total seedlings, *M. nodiflorum* seedlings and total annuals were reduced (Table 1). Reduced densities in tree microsites cannot be attributed to litter quantity alone, as seedling densities were highest in low and high litter levels across the site (Table 1). Despite large expanses of dense litter under trees increasing salinity (Figure 1) germination and establishment of *M. nodiflorum* should have been unaffected. Therefore the effect of litter on seedlings may be a matter of scale. Litter under saltbush shrubs was highly heterogeneous with a higher proportion of bare areas compared to tree microsites which were dominated by low and high density litter-covered areas (Farrell 2008). Saltbush row 1 also had larger areas of dense litter, therefore it is probable that litter heterogeneity in saltbush mid-rows resulted in more favourable conditions. Distribution of *Atriplex* spp. in saltbush microsites was likely due to litter density, as seedlings densities were highest in low litter and lowest under trees (Table 2).

Conclusions

Shrubs indirectly facilitated seedling recruitment through litter trapping; reducing salinity and temperatures. Trees directly inhibited recruitment through increased salinities and shade. Despite negative interactions, trees also indirectly facilitated recruitment elsewhere through litter provision. Redistribution of litter (wind/water) results in a heterogeneous litter mosaic altering abiotic conditions and creating recruitment niches suitable for a range of annual and perennial species at this saline site.

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