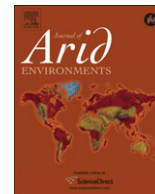




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Short communication

Foraging pits, litter and plant germination in an arid shrubland

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ABSTRACT

Many animals create soil surface depressions (pits) while foraging for subterranean resources. Foraging pits typically fill with litter, organic debris and seed, retain moisture, and become hotspots for plant germination. This study aimed to examine whether artificial foraging pits, which mimic those created by Greater bilbies (*Macrotis lagotis*) and Burrowing bettongs (*Bettongia lesueur*), develop into patches of enhanced plant germination due to accumulation of leaf litter, or whether physical characteristics of the pits such as temperature and soil moisture influence germination, irrespective of the presence of litter. Compared with the soil surface, significantly more plants germinated in artificially-created foraging pits, irrespective of whether they received added litter. Daytime temperatures were 17–31% (7–11 °C) cooler in foraging pits than on the adjacent soil surface, and pits retained significantly more moisture up to 5 days after rainfall. Our results suggest that the mesic conditions in foraging pits may be more important in promoting germination of vascular plants than the presence of litter.

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1. Introduction

Germination in the arid zone is a sporadic event that is limited by the co-occurrence of critical levels of soil moisture, temperature, nutrients and seed. Scarce resources are not distributed evenly across the landscape, rather they are concentrated into fertile patches; areas where run-on water and leaf litter accumulate (Garcia-Moya and McKell, 1970; Noy-Meir, 1973). The accumulation of leaf litter moderates soil surface temperatures and provides habitat for microbes and micro-arthropods involved in litter decomposition, resulting in higher nutrient concentrations (Eldridge and Mensinga, 2007; James and Eldridge, 2007). Fertile patches also contain greater densities of seed, and often show increased plant germination compared with the surrounding soil surface (Brooker et al., 2008).

At large spatial scales, fertile patches are formed by landscape topography and maintained by abiotic processes such as runoff and deposition. At smaller scales, however, they are primarily associated with the processes of sediment accumulation around

perennial vegetation or around the base of fallen logs, which obstruct the flow of wind and water (Tongway and Ludwig, 1994). However, soil-foraging animals also create fertile patches when they create small depressions in the soil (known as foraging pits) while foraging for epigeic invertebrates, roots, seeds and bulbs (Whitford and Kay, 1999).

Foraging pits play a pivotal role in maintaining small-scale spatial and temporal heterogeneity as they have high turnover rates and are an important source of new patch creation (Whitford, 2002). Whitford (2002) suggests that they are probably more important than shrub canopies as patch generators due to the importance of surface disturbances in seed accumulation (Reichman, 1984). Litter and seed in depressions are likely to be quickly anchored by wind-transported soil eroded from the ejecta piles created while animals dig the foraging pits. Litter in depressions is exposed to lower temperatures and reduced evaporation compared to surface litter, and the mechanism of decomposition is primarily biotic rather than by phytodegradation (Elkins and Whitford, 1982; Parker et al., 1984; Santos et al., 1981). Litter therefore decomposes faster, providing nutrients and increasing the waterholding capacity of the pit (Whitford, 2002).

The effects of litter on seed density, longevity, germination and establishment has been shown to vary across arid zone sites. In many arid areas, litter has a positive effect by providing shade and

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retaining moisture (Facelli and Pickett, 1991), while in some cases, germination is reduced when litter reduces the degree of soil-seed contact (Rotundo and Aguiar, 2005). Other studies have shown that litter has little or no effect (Eldridge and Westoby, 1991; Fowler, 1988; Hastwell and Facelli, 2000). Litter-filled pits however generally have higher germination than the surrounding soil matrix (Whitford and Kay, 1999). For example in the Great Basin Desert of western United States virtually all patches of Indian rice grass (*Oryzopsis hymenoides*) occurred when seeds were trapped with litter in rodent excavations (Longland, 1995), while in the Negev desert in Israel, the Indian crested porcupine (*Hystrix indica*) produced pits that contained greater abundance, biomass and diversity of seedlings compared to the soil matrix (Boeken et al., 1995).

The qualities that make a foraging pit a fertile microsite are likely due to the interaction between the effects of pit morphology on abiotic factors such as temperature and moisture and the ability of the pit to trap litter and seed, creating a biologically active fertile patch. The aim of this study was to examine the relationships between litter accumulation in foraging pits and resulting plant germination to determine whether foraging pits promote germination due to the fact they accumulate leaf litter, or whether there are some unique physical characteristics of foraging pits that promote germination, regardless of the presence of litter. Foraging pits were created to imitate those of two Australian soil-foraging animals, the Greater bilby (*Macrotis lagotis*) and the Burrowing bettong (*Bettongia lesueur*) and litter presence in the pits and on the surface was manipulated. Our study also aimed to determine those conditions that differ between foraging pits and the surface by comparing temperatures and soil moisture after rainfall in animal-created pits.

2. Methods

2.1. The study site

The studies reported here were conducted at Arid Recovery, an 86 km² vermin-proof fenced reserve 20 km north of Roxby Downs in arid South Australia (30°29'S, 136°53'E). Rainfall in the area is both unpredictable and highly variable, with a long-term annual average of 160 mm of rain, which fails to fall in 60% of years (Olympic Dam Operations, 1994). The landscape is characterized by west–east trending linear sand dunes, approximately 200 m wide, separated by inter-dunal swales approximately 500 m wide. Dunes have a low (<10%) clay content and are dominated by the shrubs *Acacia ligulata* and *Dodonea viscosa*, while swales have sandy clay topsoils (35–40% clay) and are characterized by low sub-shrubs *Atriplex vesicaria* and *Maireana astrotricha* from the family Chenopodiaceae. Throughout the reserve, groves of mulga (*Acacia aneura*) trees occur on sandy soils in the swales.

2.2. The litter study

In June 2006, leaves and attached twigs up to 10 cm long were collected from five live mulga trees and air-dried in the open for 2 weeks. Leaves and twigs from all trees were combined then sorted and weighed, and separated into 50 portions each of 40 g (90% litter, 10% twigs by weight). We selected 25 locations (Blocks) from a total area of about 1000 m² within a typical mulga grove. Four treatments were applied at each location; two levels of Microsite (pit, surface) each with two levels of litter cover (litter, no litter). Pits were created artificially using a pick, and were roughly circular in shape, about 15–20 cm in diameter and 8 cm deep, representing an average sized bilby-bettong foraging pit (James and Eldridge, 2007). Soil removed from the pits was deposited on the western

side of the pit in an arc halfway around the perimeter of the pit, simulating natural pits in the area. Litter was swept from the surface of all soils prior to imposition of the treatments. The prior cover of litter at all blocks was approximately 20%. We placed 40 g of mulga leaf litter in one pit and on one surface at each of the 25 locations, and covered each pit and surface with a 40 cm² piece of plastic netting with a grid size of 2 cm × 2 cm. The netting, which was secured to the ground using metal pins, prevented additional litter >2 cm in length from falling into the pits. About 100 ml of rainwater was applied to each of the four treatments to stimulate germination. In April 2007, 10 months later, we recorded the abundance and diversity of all plant seedlings emerging from pits and surfaces. During this time seedlings received 123 mm of natural rainfall, with 51% of that rain falling in January 2007. Data were $\sqrt{(x+0.1)}$ – transformed and analyzed with a factorial randomized complete block ANOVA using Minitab (2007) to test for differences in abundance and diversity of seedlings in relation to Block, Microsite, Cover and the Microsite by Cover interaction. Data were checked for normality and homogeneity of variance (Levene's test) prior to ANOVA. We used permutational multi-variate analysis of variance (PERMANOVA, Anderson et al., 2008) to examine whether plant composition varied between Microsites, Cover and their interaction.

2.3. Pit moisture and temperature studies

Soil moisture samples were taken from five paired pit and surface microsite locations at three sites 300 m apart, in two landscapes (an ecotone and adjacent swale) 1, 3 and 5 days after a rainfall event of 7.5 mm on 26th May 2006. The pits were all created by animals. Approximately 50 g samples were taken from each microsite (i.e. bottom of pit or soil surface), placed in zip-lock plastic bags and weighed. Samples were then oven-dried at 104 °C for 24 hrs and reweighed to determine gravimetric moisture content. Differences in soil moisture in relation to microsite, landscape, time and their interactions were examined using a repeated measures ANOVA with three strata; one accounting for Landscapes, a second accounting for Treatment and its interaction with Landscape, and a third accounting for changes over time and its two and three-way interactions with Landscape and Microsite. To account for possible autocorrelation between successive sampling times, the degrees of freedom for the Time, Treatment by Time and Landscape by Time interactions were adjusted using the Greenhouse-Geisser epsilon measure within the Genstat package (Payne et al., 1993). A Greenhouse-Geisser epsilon value of 0.735 indicated that there was little correlation between sampling dates. Data were checked for normality and homogeneity of variance (Levene's test) prior to ANOVA.

Soil temperatures were measured at the base of 20 pit and adjacent surfaces, in both a dune and swale at 10.30 h when the ambient temperature was 34.1 °C using a digital thermometer. The depth of each pit was also recorded. All pits were in full sun at the time of sampling and had very sparse litter cover. Differences in temperature were analyzed on log₁₀-transformed data, using a two-way ANOVA (Minitab, 2007). Simple linear regression analysis was performed to explore the relationship between pit depth and temperature in the pits.

3. Results

3.1. Germination in relation to pits and litter

Pits supported 3.5–times more seedlings (2.57 ± 0.72 ; mean \pm SEM) than an equal area of the surface (0.73 ± 0.19 ; $F_{1,42} = 8.66$, $P = 0.005$; Fig. 1a). Three plant species (*Salsola kali*, *Sida fibulifera*, *Tragus australianus*) were found only in the pits, while seven other

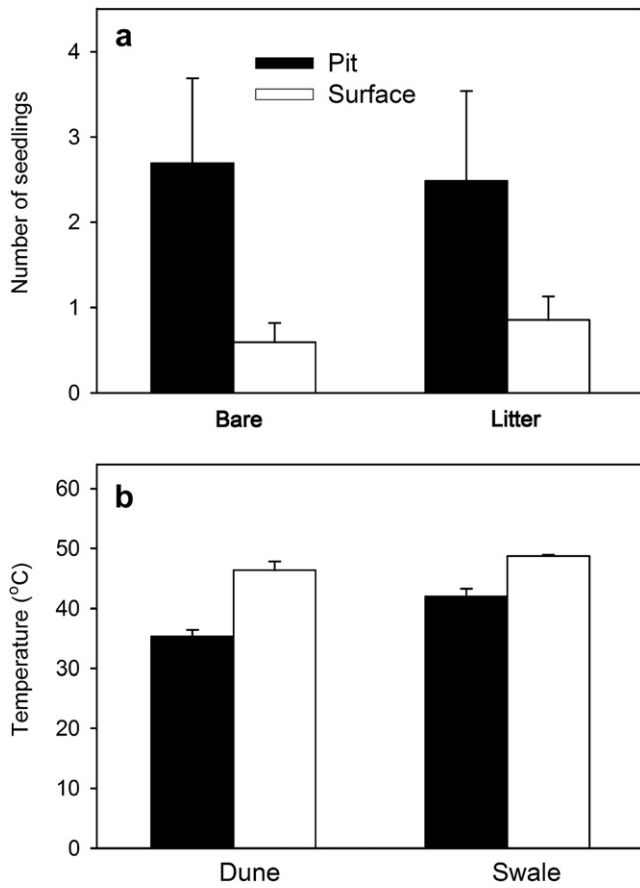


Fig. 1. Mean (\pm SEM) (a) number of seedlings recorded from bare- and litter-covered pit and surface sites and (b) average daytime temperature ($^{\circ}$ C) from pit and surface microsites in the dunes and swales.

species (*Zygophyllum* sp., *Enneapogon* sp., *Eragrostis dielsii*, *Portulaca oleracea*, *Chamaesyce drummondii*, *Aster* sp., *Tribulus terrestris*) were found in both the pits and on the surface. All species except *Tribulus terrestris* are native. Plant diversity in the pits (1.23 ± 0.28 species pit $^{-1}$) was twice that of an equivalent area of surface (0.60 ± 0.14 species pit $^{-1}$; $F_{1,42} = 6.39$, $P = 0.015$) but there was no difference in abundance ($P = 0.71$) nor diversity ($P = 0.90$) in relation to the litter treatment. The composition of plants also differed between pits and surface ($F_{1,42} = 3.42$, P (perm) = 0.014), but not between litter and litter-free surfaces (P (perm) = 0.40).

3.2. Pit moisture and temperature

Soil moisture was about seven-times greater in pits in the swales compared with the swale surfaces or pits and surfaces in the ecotones (Landscape by Treatment interaction: $F_{1,4} = 37.37$, $P = 0.004$; Fig. 2). Overall, the decline in soil moisture was greatest in the swale pits over the first three days of measurements, whereas the decline in the other treatment by landscape combinations was more gradual (Treatment \times Landscape \times Time interaction: $F_{2,16} = 11.03$, $P < 0.001$).

Pits in the dunes were on average 11 $^{\circ}$ C (31%) cooler than dune surfaces, while pits in the swales were only 7 $^{\circ}$ C (17%) cooler than the surface (Landscape \times Microsite interaction: $F_{1,27} = 5.4$, $P = 0.028$; on log $_{10}$ -transformed data; Fig. 1b). There was a significant decrease in temperature with increasing pit depth for the swales ($R^2 = 0.68$, $F_{1,8} = 17.04$, $P = 0.003$, $y = -0.84x + 47.44$) but not for the dunes ($R^2 = 0.24$, $F_{1,8} = 2.57$, $P > 0.05$).

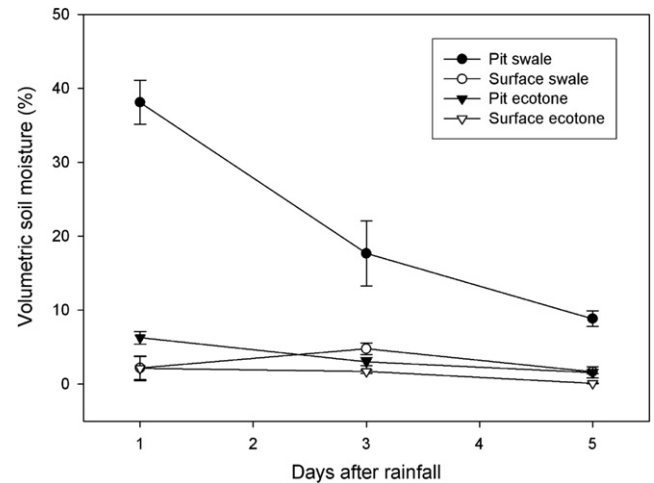


Fig. 2. Mean (\pm SEM) volumetric soil moisture (%) in the pits and on adjacent surface 1, 2 and 3 days after rainfall in the swales and ecotones.

4. Discussion

In arid and semi-arid environments, the environment surrounding a seed can have a profound influence on a seed's prospects for germination and survival. Since seedling mortality is the main filter for recruitment, the seedling stage is the most critical to plant population dynamics, and is largely governed by seed dispersal and the availability of favorable microsites (Barbera et al., 2006; Fowler, 1988). Foraging pits act as microsites of enhanced plant germination, due to number of factors that bring seeds into contact with soil moisture in a nutrient-rich patch that is more mesic than the surrounding surface (Alkon, 1999).

This study aimed to test whether foraging pits are suitable microsites for seedlings because they contain more litter, or whether there are other intrinsic qualities of the pit that promote germination. We found that the effect of pits on plant germination was unrelated to the presence of accumulating litter. We suspect that enhanced germination was primarily due to the physical environment of the pits, which is known to differ markedly from that at the surface (e.g. Eldridge and Mensinga, 2007). The effects of litter on seedlings can be physical, chemical or biological (Facelli and Pickett, 1991). In many arid areas litter has a positive effect on seed density, seed longevity and microsite quality, as it traps seeds and provides shade and wind-protection, which reduces soil temperature and retains moisture (Aguiar and Sala, 1997; Bertiller, 1992; Bertiller and Coronato, 1994; Facelli and Pickett, 1991). Litter can also have negative effects on seeds. Germination is often reduced if litter prevents seeds from coming into direct contact with the soil surface (Rotundo and Aguiar, 2005). Litter may also promote seed pathogens or release toxic substances (Facelli and Pickett, 1991; Fowler, 1988). However, Rotundo and Aguiar (2005) found that the positive effect of litter on seed density and longevity outweighed any negative effects associated with reduced soil-seed contact. Litter effects can also be indirect, for example; establishment of perennials may be facilitated by litter suppressing the emergence of herbaceous competitors (Hastwell and Facelli, 2000). The combination of positive and negative effects can also vary among different plant species and different conditions (Rotundo and Aguiar, 2005). Thus, while litter has generally been found to promote increased germination in arid areas (Evans and Young, 1970; Milton, 1995), other studies have shown little or no effect on germination (Eldridge and Westoby, 1991; Fowler, 1988; Hastwell and Facelli, 2000). Results are likely dependent on the amount of

litter present and the length of time that litter has been decomposing in the pit. In our study litter had been present in the pits for 10 months. While it was partially decomposed and buried by soil it would likely continue to break down for years, creating different conditions in the pit at different times. Gutterman et al. (1990) showed that density, biomass and seed production from pit-resident plants were greatest when the pits were about 60% full, which represented a trade-off between substantial organic matter and seed accumulation, and adequate capacity to trap and hold runoff water.

The physical shape of pits likely confers some advantages to germinating seeds by altering the abiotic environment compared with the surface, irrespective of the presence of litter. Similar to the pits of porcupines (Alkon, 1999) and echidnas (*Tachyglossus aculeatus*; Eldridge and Mensinga, 2007), pits of bilbies and bettongs were more mesic than the soil surface. Temperatures in the pits in the present study were substantially lower than those on the soil surface, similar to porcupine pits, which exhibited lower temperatures during the day but higher temperatures at night (Gutterman, 1997). Temperature is an important trigger for plant germination in many arid environments, and may also control dormancy in some desert annuals, preventing germination after rainfall if extreme temperatures are likely to reduce seedling survival (Pake and Venable, 1996).

Soil moisture was also higher in the pits up to three days after rainfall, with water initially ponding in pits. Small scale variability in water distribution plays an important role at the scale of individual seedlings (Milchunas et al., 1989), and increased germination in depressions has been attributed to altered soil moisture regimes (Harper et al., 1965). Different plant species respond differently to increased moisture in the pits. For example, the arid zone plant (*Picris cyanocarpa*) responds negatively to moisture in porcupine pits, while abundance of the Mediterranean species *Bromus rubens* was greatest in pits at the wettest sites (Shachak et al., 1991). Given the marked differences in plant responses, Shachak et al. (1991) suggest that species responses to porcupine disturbances should be viewed as a continuum along a gradient in soil moisture, with the greatest moisture associated with the pits and the lowest associated with the surface.

Although this study has demonstrated that the presence of a pit, irrespective of its litter cover, appears to be a strong determinant of plant germination, longer term studies are needed to identify those factors that are most influential in driving germination. Many studies of plant germination in arid areas have demonstrated that the optimum microsite for germination and seedling survival changes with different seedling cohorts and is rarely constant for more than a few months (Eldridge and Westoby, 1991; Fowler, 1988). Thus, different species appear in the same habitats in different months or years (Gutterman et al., 1990) dependent on many factors such as the timing or seasonality of rainfall or seed storage or maturation conditions (Gutterman et al., 1990). Finally, the capacity of the pits to support germinating plants is likely to be a function of pit age. Pits of different sizes and ages will likely vary in the amount of litter present, temperature and soil moisture status, with interactions between these factors. Important issues that require further examination are whether our observations are consistent for pits of different ages and for pits with different quantities of litter, and the extent to which our observations are consistent across different seasonal conditions.

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