

Animal foraging pit soil enhances the performance of a native grass under stressful conditions

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Abstract

Background and Aims In line with the Stress Gradient Hypothesis, studies of facilitation have tended to focus on plant–plant interactions (biotic nurses), while the relative role of abiotic nurses has been little studied. We assessed the role of biotic and abiotic nurses, and their interaction, on soil enhancement and the consequential performance of a native annual grass, *Dactyloctenium radulans*.

Methods We used a growth chamber study with two levels of water application to compare the performance of *D. radulans* growing in soil from foraging pits of the Short-beaked echidna (*Tachyglossus aculeatus*;

abiotic nurse) and non-pit soil from either under tree canopies (biotic nurse) or surrounding open areas.

Results All measures of plant performance were more pronounced under the high than the low water treatment. The greatest differences between pit and surface Microsites occurred under the low water application, reinforcing our view that facilitatory effects are greater in resource-limited environments. Despite tree canopy soil having greater N, there was no significant effect on plant performance, nor any significant interaction with Microsite.

Conclusions Our study provides strong evidence that foraging pits enhance soil properties and this soil, in turn, facilitates plant growth; and supports previous work documenting the positive effect of nurse-protégé interactions under greater levels of abiotic stress.

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Dactyloctenium radulans · Facilitation · Nurse objects ·
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Abbreviations

N Nitrogen
C Carbon

Introduction

Resource dynamics, and hence ecosystem productivity, can be controlled by plants (bottom-up ecosystem control), the activity of animals (top-down ecosystem control; see Meserve et al. 2003) and by either the

biotic or abiotic components of both trophic groups (Castro et al. 2010; Eldridge and Mensinga 2007; Facelli and Brock 2000). While the relative importance of both trophic groups in regulating ecosystem processes is well known for aquatic or more mesic terrestrial systems, it remains rather illusive for semi-arid environments (Meserve et al. 2003). Studies aimed at clarifying the relative importance of top-down versus bottom-up control in ‘harsh’, resource-limited environments have focused mainly on the negative effects of biotic interactions among plants i.e. competition, or consumption by herbivores (Grime 1973; Meserve et al. 2003). Over the past two decades however, a more explicit acknowledgement has emerged of the role of positive plant-plant interactions, i.e. facilitation, in shaping plant communities, particularly in harsh environments (Callaway 2007; Flores and Jurado 2003). Current plant-plant paradigms now explicitly acknowledge the positive effects of organisms in ecosystems as well as the degree of environmental stress imposed on a system (e.g. Stress Gradient Hypothesis; Bertness and Callaway 1994). Thus recent studies of facilitation highlight the need to consider positive interactions if we are to appreciate the importance of vegetation and soil nutrient controls in shaping natural communities (Hacker and Gaines 1997; Michalet et al. 2006).

It is well established that in harsh, arid and semi-arid environments, plant establishment and productivity are co-limited by the availability of two critical resources; water and nutrients, particularly nitrogen (Sankaran et al. 2005). These resources have an uneven spatial distribution, with disproportionately large differences between resource-accumulating and resource-shedding areas (Ludwig and Tongway 1995). Animal disturbances, particularly those in arid and semi-arid environments, represent sites where limiting resources are concentrated (Whitford 2002). Small surface depressions such as foraging pits capture water, sediment, organic matter, litter and seeds (James et al. 2009), creating soils with a higher infiltration capacity, greater respiration and altered physical characteristics compared with surrounding soils (Eldridge et al. 2010; Eldridge and Mensinga 2007). Foraging pits also act as safe sites for germination by increasing seed longevity and seedling establishment (Rotundo and Aguiar 2005). All of these positive effects on soils have extended, though generally unspecified, legacy effects (*sensu* van der

Putten 2009), as microbial and chemical changes persist after the initial physical structure has been lost or infilled (van der Putten 2009). These abiotic nurses are formed by animals when they construct habitat or forage for food (Byers et al. 2006). Although the roles of biotic nurses have been studied extensively (see recent review in Callaway 2007), the positive effects of abiotic nurses such as these pits and depressions created by animals, and logs and rocks, are poorly represented in the literature (though see Castro et al. 2010; Munguia-Rosas and Sosa 2008; Peters et al. 2008).

Abiotic nurses could potentially have facilitatory effects on plants as dramatic as those reported for biotic nurses simply through their role as sinks for resources (Flores and Jurado 2003; Schlesinger et al. 2009; James et al. 2010). Further, in some situations, abiotic-nurse associations may be both more frequent and/or more important drivers of community structure and productivity than traditional biotic associations (Munguia-Rosas and Sosa 2008; Peters et al. 2008). This could happen because the effects of abiotic nurse objects are more persistent under extremely stressful or resource-limited conditions or where the vegetation community is dominated by plants with allelopathic properties. In these situations, biotic nurses such as plants might collapse (Michalet et al. 2006). Conceivably, abiotic structures might be the only ones creating favourable microhabitats, thereby expanding the range of less tolerant species, enabling them to survive in environments far beyond their physiological tolerances (Day et al. 2003). Under extreme environmental conditions therefore, abiotic nurses would be expected to play substantial roles in structuring communities and enhancing diversity, potentially overwhelming biotic nurse facilitation, which is known to wane at extremely high stress levels (Belcher et al. 1995).

In this study we assessed the relative importance and the joint soil-mediated effects of both plant-plant interactions and animal foraging pits on the growth and productivity of the annual, highly palatable *C*₄ grass *Dactyloctenium radulans* R.Br. P. Beauv (button grass), under two contrasted water scenarios in a controlled growth chamber experiment. In the context of this study we adopt the broader definition of facilitation as an interaction that directly or indirectly reduces abiotic environmental stress or increases resource availability, resulting in an increase in

productivity, survival or fitness of a photosynthesising organism (Brooker and Callaway 2009). The roles of our biotic nurses *Eucalyptus* and our phytometer *Dactyloctenium* are reasonably well known. *Dactyloctenium radulans* is widespread throughout semi-arid Australia and is grazed by both native and introduced vertebrate and invertebrate herbivores including the Greater bilby *Macrotis lagotis*, (Gibson 2001), the Australian plague locust *Chortoicetes terminifera*, (Clissold et al. 2006), a range of unspecified invertebrates, and domestic sheep and cattle. The response of *Dactyloctenium* to soil nitrogen is positive, with increased growth from high nitrogen soils. *Tachyglossus aculeatus* Shaw (Short-beaked echidna), is ubiquitous over much of continental Australia, and its foraging disturbances have been shown to have substantial effects on a wide range of soil and ecological processes such as nutrient enhancement, enhanced decomposition and moderation of temperature and water (Eldridge and Mensinga 2007) that persist long after the initial structure has been lost. The facilitatory role of our biotic nurse, *Eucalyptus* spp. on seedling establishment and growth in arid and semi-arid Australia is somewhat limited. However, a recent study has shown that a large number of perennial understorey plants in the study area are either facilitation beneficiaries (~60%) or facilitation obligates (~40%) to large eucalypt canopies (Soliveres et al. 2011). Part of this effect is thought to be due to their role in moderating environmental condition such as shade and temperature (Soliveres et al. 2011) as well as improving soil chemical properties (Jeddi et al. 2009).

We hypothesised that the accumulated soil in foraging pits would enhance the growth and survival of vascular plants indirectly *via* their positive effects on soil fertility (Eldridge and Mensinga 2007). This effect has been shown to persist for at least five years (D. Eldridge, unpubl.). We compared the relative importance of foraging pit (abiotic nurse) vs. *Eucalyptus intertexta* tree (biotic nurse) effects and the potential for a synergistic interaction between them, on soil properties and on the performance of our phytometer *Dactyloctenium*. Finally, we tested for shifts in these effects under either a low or high water regime, thereby inducing two levels of abiotic stress. Overall, we predicted a greater soil fertility and plant performance in foraging pit or tree canopy soils than those growing in surrounding surface soil; and a

synergistic effect of both nurse types or with increased water availability when acting together. By considering the role of both biotic and abiotic nurses under two different watering regimes, we aimed to increase our mechanistic understanding of the relative importance of animals and existing plants defining seedling performance in semi-arid environments.

Methods

Field site

Soils were collected from Yathong Nature Reserve in central New South Wales, Australia (32°35'S, 145°35'E). Rainfall is highly variable within and among years (BOM 2010) and averages 383 mm annually. Average maximum temperatures range from 33.1°C in January to 14.3°C in July (BOM 2010). The vegetation is predominantly open woodland dominated by western red box (*Eucalyptus intertexta*) with canopy cover ranging from 18–70% (Keith 2004). The understorey is dominated by perennial grasses, which include speargrass (*Austrostipa* spp.), wiregrass (*Aristida* spp.) and white-top grass (*Austrodanthonia caespitosa*). Annual grasses such as *Dactyloctenium radulans* appear in the warmer months, however their abundance varies on an annual basis depending upon recent climatic conditions. Above 40% of the surface is covered by biological soil crusts (Eldridge and Greene 1994). The soils at our study site, classified as red Kandosols, had loam to clay-loam surface textures to 1 m deep, overlying light-medium clay B horizons (Eldridge and Mensinga 2007).

Sampling procedure

Soil samples were collected in cylindrical steel cores 100 mm high × 70 mm diameter, driven 90 mm into moist soil. Thirty-two soil cores were randomly collected from 18-month old echidna pits (hereafter Pit), which we had been monitoring since excavation, at sites under the canopy of large *Eucalyptus intertexta* canopies (hereafter Canopy) and in the Open. With every pit sampled, a surface soil core (hereafter Surface) was also collected in a random direction, but consistent distance of 0.5 m, from the pit. Canopy soil was collected within the drip line, i.e.

about 15 m from the base of mature trees, while open soils were >20 m from any tree canopy. The soils collected from under the canopy were typically overlaid by a shallow <1 cm deep layer of leaves which was not removed during sampling.

Plant growth

Soil cores from each of the four combinations of pit and surface by canopy and open, were equally assigned randomly into two Water treatments: low water 6 ml and high water 15 ml administered daily. The determination of the two Water treatments was based on an earlier pilot trial (S. Travers, unpubl.) designed to test the response of plants across a range of moisture regimes, and were based on thresholds of the soils' active moisture range. Cores were placed in a growth chamber, which was set at 24°C diurnal temperature, 17°C night temperature and 14 hours of light, representative of average spring conditions for the field site (BOM 2010). Cores were randomly arranged into eight blocks within the growth chamber. In other words, the relative positions of each of the 64 cores taken from the field did not reflect their final position in the growth chamber. Each block contained each of the eight separate treatment combinations. In total therefore there were 64 soil cores comprising 2 Microsites (pit, surface) by 2 Cover categories (canopy, open) by 2 levels of Water applications (low, high) and 8 replicates of each combination.

Dactyloctenium radulans was chosen as the phytometer from a selection of local native grasses in a previous pilot trial based on plant response to nitrogen. The pilot trial (S. Travers, unpubl.) contained three locally native grass species whose germinants were subjected to three levels of nitrogen equivalent to 0 kg ha⁻¹, 60 kg ha⁻¹ and 120 kg ha⁻¹ (Badgery et al. 2005). *Dactyloctenium* was chosen over *Enteropogon acicularis* Lindl. Lazarides and *Chloris truncata* R.Br. as it had the greatest positive response to nitrogen in terms of relative growth. *Dactyloctenium* seeds were collected from the study area in early autumn and kept in a cool room until the following summer. Seeds were germinated in a separate tray and a single *Dactyloctenium* seedling 5–10 mm tall was transplanted into each undisturbed core. Any seedlings that died were replaced as required until day 5 of the trial. Plants were watered daily at either the high or low water regime, during

which plant height, leaf count, length of the longest leaf, stem count and flower count were recorded every 3–5 days. Any germinants sprouting from the natural seed bank were removed on emergence. After 64 days, plants were removed from the growth chamber and left to dry for two weeks. Plants were separated into leaves, roots, stems and flowers. Each component was oven-dried for 24 hours at 60°C before mass was measured. Seeds were separated from flowers and counted. The dried leaves were ground and total nitrogen and carbon determined using a high combustion LECO CNS-2000 Analyser.

Soil properties

The chemical and physical properties of the soil were also analysed. Following the same experimental design and sample size as described above, soil cores were dried in an oven at 55°C for 15 days to assess bulk density. Low oven temperatures were used so that the nitrogen content was not compromised. A 100 g sample of topsoil was ground for chemical analysis. Total nitrogen (N) and carbon (C) were determined using a high combustion LECO CNS-2000 Analyser. The active labile C fraction of the soil was measured according to the method of Weil et al. (2003). Soils were also analysed for mineralisable N according to Method 4 of Gianello and Bremner (1986). This method measures the amount of N mineralised over a 16 h anaerobic digestion at 100°C, providing an index of the potential pool of N available to plants present at the time of sampling. Although this index cannot be compared numerically with NH₄⁺ and NO₃⁻, the values are highly correlated with exhaustive aerobic soil incubation for N mineralisation (Gianello and Bremner 1986).

Statistical analyses

We derived three measures of performance of *Dactyloctenium* in relation to the various treatments; 1) total biomass, which is highly correlated with our individual measures of plant growth performance such as height and leaf length, 2) root to shoot ratio, which assesses plant response to changing levels of resources, and 3) proportional reproductive effort, measured as the ratio of the mass of reproductive structures to total biomass. Except for data on temporal changes in plant attributes (see below), soil and plant attributes (total biomass, root:

shoot ratio, proportional reproductive effort) were analysed using a balanced randomized complete block ANOVA. Data for total leaf C and N were analysed using General Linear Models as there was insufficient material available from some samples and therefore the analyses were unbalanced. Our analyses considered Block (or replicate; $n=8$) effects (random), and the main order effects of Microsite (fixed effect: pit, surface), Cover (fixed effect: canopy, open) and Water regime (fixed effect: low, high) and their two- and three-way interactions. Data were tested for homogeneity of variance using Levene's test, and diagnostic tests were run in the Minitab statistical software (Minitab, version 15.1, Minitab Inc, 2006) prior to analysis. \log_{10} transformations of leaf N % and total plant N were required to stabilize the mean–variance relationship prior to interpreting the ANOVA.

Temporal changes in plant height, number of leaves and stems, and the length of the longest leaf were examined using a linear mixed-model. Since the focus was on the time response, data for these repeated measurements were analysed using the cubic smoothing spline approach (Verbyla et al. 1999). The modelling process began by fitting a 'saturated' model that included all fixed and random terms; then in turn, each random term was dropped and the model refitted, with the subsequent change in model deviance (d) noted. The significance of the test that each variance component (a single random term) was zero was given by $0.5[\Pr(X^2 > d)]$ with $X^2 \sim \phi_1^2$ (Orchard et al. 2000). Non-significant random terms were dropped from the final model where hypothesis tests assessed the significance of fixed effects using the Wald statistic an approximate F -test. Graphs of predicted smooth response profiles were prepared for significant treatment combinations. All analyses were run using the GenStat statistical software (Payne et al. 2007) packages. Data for the number of leaves and number of stems were $\log_e(x+1)$ -transformed prior to ANOVA.

Results

Soil properties

Soil bulk density was lower in Pit than Surface soils ($F_{1, 49}=70.0$, $P<0.01$), and the effect was greatest

under the canopy (Microsite by Cover interaction: $F_{1, 49}=4.27$, $P=0.04$, Table 1). Total soil C was greater in pit soil under the canopy (3.42%) than pit soil in the open (2.26%; Microsite by Cover interaction: $F_{1, 49}=4.11$, $P=0.04$, Table 1). Overall, soils under the canopy had about 25% more labile C and 40% more total C than those in the open ($F_{1, 49}=6.6$ and 8.92 , $P<0.01$, respectively; Table 1, Online Resource 1)

The percentage of total nitrogen N in the soil followed a similar trend to total soil C (Table 1). Pit and canopy soils contained more total N than their "unengineered" analogues ($F_{1, 49}=58.5$ and 12.1 , $P<0.01$, respectively; Table 1). However, the magnitude of the difference in total N between pit and surface was greater (eight-fold) in the open than under the canopy (5.6-fold; Microsite by Cover interaction: $F_{1, 49}=4.71$, $P=0.05$; Table 1). Total soil N concentration also varied significantly in relation to watering regime, with 60% more N in the low than the high water treatment ($F_{1, 49}=7.69$, $P<0.01$; Fig. 1a) suggesting possible leaching under the high water treatment. However, there was no significant effect of the Water treatments on mineralisable available N ($P=0.51$) or on the total soil mineralisable N pools ($P=0.59$; see Online Resource 2).

Mineralisable N concentrations were greater in canopy than open soils ($F_{1, 49}=6.17$, $P=0.02$), though the denser soils in the open meant that we did not detect a significant difference in total mineralisable N pools between canopy and open sites ($P=0.75$; Online Resource 2). Concentrations and total pools of mineralisable N were greater in pit soils than surface soils ($F_{1, 49}=92.97$ and 33.22 , $P<0.01$, respectively, Table 1). Overall total N concentrations were greatest in pit soils under the canopy, suggesting a synergistic effect (Cover by Microsite interactions $F_{1, 49}=6.17$, $P=0.04$).

Plant growth: biotic and abiotic nurse effects on plant growth

Total biomass of plants growing in soils from the open or in soil from under the canopy did not differ ($P=0.25$). Pit soil produced significantly larger plants than surface soil ($F_{1, 49}=89.65$, $P<0.001$), and the high water treatment produced significantly larger plants than the low water treatment ($F_{1, 49}=48.32$, $P<0.001$, Fig. 1b). Overall the relative effect of pit soil on plant biomass was greater under the low than

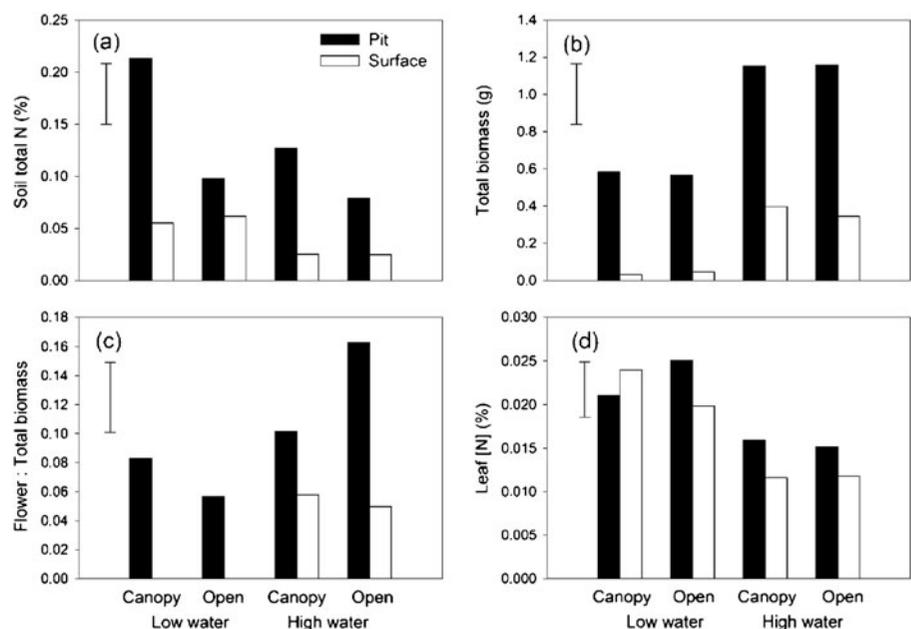
Table 1 Soil attributes. Mean soil attributes of plants in relation to Water regime low, high, Cover canopy, open and Microsite pit, surface. Within an attribute, the 5% L.S.D. for the Water by Cover by Microsite interaction is given

Water	Cover	Microsite	Bulk density (Mg m ⁻³)	Carbon		Nitrogen		
				Labile (mg kg ⁻¹)	Total (%)	Mineralisable (mg kg ⁻¹)	Mineralisable pool (mg per core)	Total (%)
High	Canopy	Pit	1.11	460.11	3.24	7.99	21.41	0.13
		Surface	1.45	320.03	1.18	4.19	14.47	0.02
	Open	Pit	1.34	388.74	2.11	6.31	22.55	0.08
		Surface	1.55	260.20	0.90	2.60	9.59	0.01
Low	Canopy	Pit	1.20	530.01	3.61	7.30	20.39	0.21
		Surface	1.51	446.71	1.13	3.07	10.96	0.04
	Open	Pit	1.37	284.63	2.41	6.96	22.63	0.10
		Surface	1.55	371.32	0.96	2.81	10.08	0.03
L.S.D. 5% value			0.13	178.81	0.93	0.06	0.73	0.02

the high water regime (Microsite by Water interaction: $F_{1, 49}=8.08$, $P=0.007$, Fig. 1b). Ultimately, pit soil under the low water treatment produced plants of greater biomass than those on surface soil under the high water treatment. Despite significant Water treatment effects on plant biomass, there were no significant effects of any factor on root to shoot ratio ($P>0.21$, Online Resource 2).

Pit soil produced plants which had a significantly greater proportional reproductive effort than surface soil plants (flower: total biomass: $F_{1, 49}=38.10$, $P<0.001$; Fig. 1c). The high water treatment also produced plants that had a greater proportional reproductive effort than their low water counterparts ($F_{1, 49}=23.49$, $P<0.001$; Fig. 1c). There were no significant effects of Cover on proportional reproductive effort ($P=0.57$).

Figure 1 Mean of **a** total plant biomass, **b** proportional reproductive effort (flower and seeds to total biomass ratio), **c** leaf nitrogen concentration, and **d** soil nitrogen concentration in relation to Microsite, Cover and Water regime. The bars indicate the 5% LSD for the Microsite by Water interaction. Overall, there are significantly greater plant biomass, proportional reproductive effort and soil N in pit soil than surface soil. There are inconsistent trends between Cover and Water treatments



Plant growth: biotic and abiotic nurse effects on plant growth rate

Averaged over time, the high water regime resulted in greater plant height and number of stems ($P < 0.01$, Online Resource 3). Significant Microsite by Time, and Water by Time interactions (Online Resource 3) indicated that pit soil and high water availability increased the rate of plant, leaf and stem growth (Fig. 2). Over time, plants growing in pit soil had more stems and longer leaves than those in surface soil (Wald statistic=43.21 and 1.07, $P < 0.01$, respectively; Fig. 2c, d), but there were no differences in total plant height (Fig. 2a & b) nor the number of leaves ($P > 0.30$, Online Resource 3). Significant Microsite by Water by Time interactions were also observed for the number of stems and longest leaf length (Online Resource 3), indicating a substantial temporal increase in the Microsite by Water interaction on the number of stems and the length of the

longest leaf (Fig. 2c, d). Increased soil nutrient concentrations under the canopy were not reflected in any observable changes in plant growth.

Plant growth: biotic and abiotic nurse effects on leaf nutrients

Although there was a significant Cover effect on leaf carbon concentration ($F_{1,49} = 5.52$, $P = 0.024$; Online Resource 2), this did not mean that soil from under tree canopies produced plants with higher carbon concentrations. Instead soil from open sites produced plants with greater leaf carbon concentration (Online Resource 1). Pit soil also produced plants containing significantly greater concentrations of carbon than surface soil ($F_{1,49} = 6.35$, $P = 0.016$).

There were no significant effects of Cover ($P = 0.92$) nor Microsite ($P = 0.20$) on leaf nitrogen concentration. There was, however, a significant Water treatment effect, with a significantly greater concentration

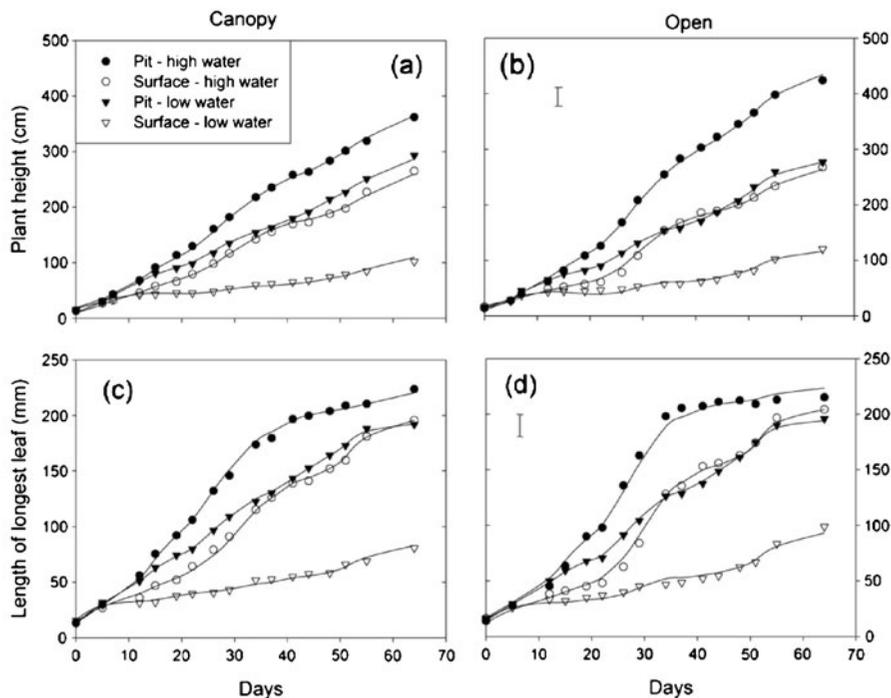


Figure 2 Plant growth rate. Changes in plant height (cm: a, b) and length of the longest leaf (mm: c, d) for plants growing in pits and surface soils under a regime of low or high water within canopy or open soils. Curves represent average values for canopy and open Microsites. The bars indicate the 5% LSD for the Microsite by Water interaction. For both longest leaf length and plant height, there were consistent trends across

Canopy and Open. Plants under the high water treatment growing in pit soil were consistently the most productive, while plants from surface soil under low water were consistently the least productive. The trajectories for high water surface soil plants and low water pit soil plant were consistently similar across both open and canopy treatments

of leaf nitrogen in plants under the low than the high water treatment ($F_{1, 49}=23.19$, $P<0.001$, Fig. 1d)

Discussion

The concept of abiotic nurse is relatively new (Munguia-Rosas and Sosa 2008), with few studies explicitly acknowledging their importance in the facilitation process (e.g. Castro et al. 2010; Parker 1989; Peters et al. 2008). Our study is unique in that we compared both an abiotic and a biotic nurse, allowing for their potential combined effects on plant growth. Our results indicated a positive effect of increasing water on plant biomass and proportional reproductive effort, and, irrespective of watering regime, a positive effect of canopy cover and pits on soil C and N. We found that soil from both the foraging pit (abiotic nurse) and canopy (biotic nurse) significantly enhanced almost every measurement of physical and chemical soil property compared with the surrounding ‘unengineered’ soil.

The defining feature of both biotic and abiotic nurses is their facilitatory effect on plant growth and/or survival through the amelioration of abiotic stresses such as unfavourable soil physical structure, temperature and solar radiation, or a combination of both (Bertness and Callaway 1994; Castro et al. 2010; Maestre et al. 2009; Peters et al. 2008). The substantial point of difference between these different nurse types is the absence of direct competition from abiotic nurses (Munguia-Rosas and Sosa 2008), though for both types to be effective, they must enhance the growth or survival of their protégé species. Both nurses ameliorated soil physical conditions by reducing bulk density and increasing organic matter and nitrogen compared with either surface soils or those from the open. Both nurses have been shown to enhance soil infiltration or water retention (Eldridge and Mensinga 2007; Raffaele and Veblen 1998), and create a more favourable rooting environment (Pugnaire et al. 2004) compared with their ‘unengineered’ analogues.

Although biotic and abiotic nurses accumulate resources through similar mechanisms (e.g. wind and water; Flores and Jurado 2003), they may differ in the efficacy of their actions. For example, decomposition of organic matter in arid environments follows different decay mechanisms depending on

whether materials are on or below the surface. Surface decomposition with biotic nurses such as shrubs and trees is generally much slower (Moorhead and Reynolds 1993) and is often dominated by photo-oxidation processes (Austin and Vivanco 2006). Abiotic nurses such as our foraging pits, however, bring organic matter into direct contact with the soil, allowing mineralised nutrients to be returned to the soil organic pool. Thus in our study, pit soils under the canopy contained the highest C and N levels, followed by open pit soils, then canopy surface soils.

A simple way of measuring the success of nurse associations is to assess the quality of protégé plants produced (Butterfield 2009). As expected, foraging pit soil resulted in greater productivity (nine-times greater biomass), and greater proportional reproductive effort and growth rate than those growing on surface soils. Plants growing in pit soil also had a greater percentage of leaf C. Indeed, the facilitatory effect of pit soil on productivity alone, under water-limited conditions, was equivalent to additional water being added to a non-pit surface. Interestingly, the growth trajectories of plants growing in pit soil on the low water treatment were the same as those growing on the surface at the higher water treatment. The addition of water may be seen as an attempt to compensate for *in situ* effects of our biotic nurse. For example, Eldridge and Mensinga (2007) found significantly greater volumetric soil moisture in pit than non-pit soil up to 6 months after rainfall. Shade from biotic nurse canopies has previously been documented to increase soil moisture by reducing temperature and evaporation (Pugnaire et al. 2004). In addition, large trees also provide hydraulic lift, increasing soil moisture from subsurface reservoirs (Caldwell and Richards 1989). Our work suggests that pits have the capacity to ameliorate the effects of water stress on plant growth, which will likely expand the realized niche for some plants during periods of low rainfall (Michalet et al. 2006), allowing them to occupy otherwise inhospitable habitat (Hastings et al. 2007).

Studies that have directly compared nurse plants and nurse objects *in situ* suggest that they may differ in the benefits they provide to the protégé (Flores and Jurado 2003; Munguia-Rosas and Sosa 2008; Parker 1989). *In situ* canopy cover may have negative effects on soil water availability, such as interception of rainfall and competition for soil moisture. However,

the benefits of shade on the protégé through reduced evaporation and increased soil moisture are also well recognised (e.g. Cody 1993). Nurse plants generally provide shade for longer than abiotic nurses, depending on the nurse plants' species and their foliage filtering effects, and, to some extent, the intensity of solar radiation (Munguia-Rosas and Sosa 2008). In contrast, nurse objects such as rocks and logs only allow for direct sun or full shade, while foraging pits themselves do not provide any shade, except perhaps during the early seedling stage (Pugnaire et al. 2004). Our high water treatment could arguably have been a substitute for the lack of shade within the growth chamber. Our set-up effectively isolated a soil effect from other *in situ* effects associated with the positive moderation of the abiotic environment, such as hydraulic lift and shade. We also essentially removed all sources of direct competition from our biotic nurse and expected positive outcomes for our protégé. Despite this, in the absence of direct competition, and with favourable water, plants were still more productive in soils that had not been engineered by the biotic nurses. In contrast to pit soil, we found no consistent effect of canopy soil on any measurement of plant performance, despite the enhanced physical and chemical status of canopy soil compared with the matrix (Facelli and Brock 2000) and thus its greater potential to ameliorate abiotic stress.

In contrast with previous studies (Soliveres et al. 2011), we did not find any facilitatory effect of canopy soils on our phytometer *D. radulans*. Two possible explanations arise that might explain these contrasting results: 1) with our experimental approach we were only able to detect the effect of soil mediated by trees. Thus the direct effects of shade, an important factor driving facilitation in water-limited environments (Callaway 1995; Maestre et al. 2003) were largely ignored. However, the most important facilitatory outcome of shade is reduced temperature stress and indirectly enhanced water availability to the protégé. The positive effects of shade were mimicked to a certain degree by our watering treatment; however we still did not find substantial effects of soil from under tree canopies under the different watering treatments assayed. 2) The most plausible explanation for the lack of a facilitory effect of canopy soils, therefore, is the allelopathic effect that Eucalypt litter is known to have on nutrient uptake and germination of some species (e.g. May and Ash 1990) The fact that higher soil N% and

mineralisable N under the canopy was not reflected in higher leaf N or reproductive effort suggests to us that our canopy soils may inhibit N uptake and usage by plants. However our pits also captured Eucalypt leaf litter, but there was no negative effects of plant growth or reproductive effort from the high N pit soils. This suggests that the allelopathic properties of Eucalypts leaf litter require time to accumulate to levels deemed inhibitive to plant growth. The contrasting results found between our work and previous studies (e.g. Soliveres et al. 2011) suggest a high species-specific response to the effects of trees with allelopathic compounds on their neighbours (Callaway 2007). As with most other grass species *D. radulans*, seemed sensitive to allelopathic compounds derived from Eucalypts (Tilman 1988). Overall, our study clearly shows that *D. radulans* grows better in soils that differ from those found beneath the canopy of Eucalypts.

Water availability could also affect the N-transfer relationship. Plants under the low water treatment generally had higher total soil N% than soil under the high water treatment (possibly due to leaching), which translated to high leaf N%. However reproductive effort was low compared to plants under the high water treatment, where soil total N and mineralisable N was low, leaf N% was low and reproductive effort was high. This may indicate that low water availability reduces reproductive effort as plant N is locked up in photosynthetic enzymes in leaves.

Our study indicates that the soil from an abiotic nurse had substantial effects on plant productivity and proportional reproductive response, unlike soil from a more nutrient-enriched biotic nurse. The greater difference between pit soil and surface soil Microsites under the moisture stressed regime supports empirical observations and theoretical predictions that small increases in resources can have much greater effects in resource-limited environments (Day et al. 2003). Although the phenomenon of abiotic nurse-associations will never truly be captured by the 'stress gradient hypothesis' literature, our pits still attain the same facilitative outcomes as traditional biotic nurses, albeit through markedly different underlying mechanisms.

Our study has broad ecosystem relevance given the extensive global distribution of soil-disturbing animals (Whitford 2002). A fuller knowledge of the direct and indirect, positive and negative effects of plants and animals is therefore requisite to our

understanding of bottom-up versus top-down controls on resource regulation in harsh environments (e.g. Eldridge et al. 2010; Riginos and Grace 2008). This will provide some clarity in the debate over the relative importance of positive and negative effects of herbivores as drivers of top-down ecosystem control, and enhance our understanding of their potential roles in restoring degraded systems (e.g. Byers et al. 2006).

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References

- Austin AT, Vivanco L (2006) Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. *Nature* 442:555–558
- Badgery WB, Kemp DR, Michalk DL, King W (2005) Competition for nitrogen between Australian native grasses and the introduced weed *Nassella trichotoma*. *Ann Bot* 96:799–809
- Belcher JW, Keddy PA, Twolanstrutt L (1995) Root and shoot competition intensity along a soil depth gradient. *J Ecol* 83:673–682
- Bertness MD, Callaway R (1994) Positive interactions in communities. *Trends Ecol Evol* 9:191–193
- BOM (2010) Bureau of Meteorology. Australian Government. <http://www.bom.gov.au/>
- Brooker RW, Callaway RM (2009) Facilitation in the conceptual melting pot. *J Ecol* 97:1117–1120
- Butterfield BJ (2009) Effects of facilitation on community stability and dynamics: synthesis and future directions. *J Ecol* 97:1192–1201
- Byers JE, Cuddington K, Jones CG, Talley TS, Hastings A, Lambrinos JG, Crooks JA, Wilson WG (2006) Using ecosystem engineers to restore ecological systems. *Trends Ecol Evol* 21:493–500
- Caldwell MM, Richards JH (1989) Hydraulic lift—water efflux from upper roots improves effectiveness of water-uptake by deep roots. *Oecologia* 79:1–5
- Callaway RM (1995) Positive interactions among plants. *Bot Rev* 61:306–349
- Callaway RM (2007) Positive Interactions and Interdependence in Plant Communities. Springer, Dordrecht
- Castro J, Allen CD, Molina-Morales M, Marañón-Jiménez S, Sánchez-Miranda Á, Zamora R (2010) Salvage logging versus the use of burnt wood as a nurse object to promote post-fire tree seedling establishment. *Restor Ecol* 19:537–544
- Clissold FJ, Sanson GD, Read J (2006) The paradoxical effects of nutrient ratios and supply rates on an outbreaking insect herbivore, the Australian plague locust. *J Anim Ecol* 75:1000–1013
- Cody ML (1993) Do Cholla cacti (*Opuntia* spp. subgenus *cylindropuntia*) use or need nurse plants in the Mojave desert? *J Arid Environ* 24:139–154
- Day RL, Laland KN, Odling-Smee J (2003) Rethinking adaptation—the niche-construction perspective. *Persp Biol Med* 46:80–95
- Eldridge DJ, Greene RSB (1994) Assessment of sediment yield by splash erosion on a semiarid soil with varying cryptogam cover. *J Arid Environ* 26:221–232
- Eldridge DJ, Mensinga A (2007) Foraging pits of the short-beaked echidna (*Tachyglossus aculeatus*) as small-scale patches in a semi-arid Australian box woodland. *Soil Biol Biochem* 39:1055–1065
- Eldridge DJ, Bowker MA, Maestre FT, Alonso P, Mau RL, Papadopoulos J, Escudero A (2010) Interactive effects of three ecosystem engineers on infiltration in a semi-arid mediterranean grassland. *Ecosystems* 13:499–510
- Facelli JM, Brock DJ (2000) Patch dynamics in arid lands: localized effects of *Acacia papyrocarpa* on soils and vegetation of open woodlands of South Australia. *Ecography* 23:479–491
- Flores J, Jurado E (2003) Are nurse-protége interactions more common among plants from arid environments? *J Veg Sci* 14:911–916
- Gianello C, Bremner JM (1986) Comparison of chemical methods of assessing potentially available organic nitrogen in soil. *Comm Soil Sci Plant Anal* 17:215–236
- Gibson LA (2001) Seasonal changes in the diet, food availability and food preference of the greater bilby (*Macrotis lagotis*) in south-western Queensland. *Wildl Res* 28:121–134
- Grime JP (1973) Competitive exclusion in herbaceous vegetation. *Nature* 242:344–347
- Hacker SD, Gaines SD (1997) Some implications of direct positive interactions for community species diversity. *Ecology* 78:1990–2003
- Hastings A, Byers JE, Crooks JA, Cuddington K, Jones CG, Lambrinos JG, Talley TS, Wilson WG (2007) Ecosystem engineering in space and time. *Ecol Lett* 10:153–164
- James AI, Eldridge DJ, Hill BM (2009) Foraging animals create fertile patches in an Australian desert shrubland. *Ecography* 32:723–732
- James AI, Eldridge DJ, Moseby KE (2010) Foraging pits, litter and plant germination in an arid shrubland. *J Arid Environ* 74:516–520
- Jeddi K, Cortina J, Chaieb M (2009) *Acacia salicina*, *Pinus halepensis* and *Eucalyptus occidentalis* improve soil surface conditions in arid southern Tunisia. *J Arid Environ* 73:1005–1013
- Keith DA (2004) Ocean shores to desert dunes : the native vegetation of New South Wales and the ACT Dept. of Environment and Conservation (NSW), Hurstville, NSW
- Ludwig JA, Tongway DJ (1995) Spatial-organization of landscapes and its function in semiarid woodlands, Australia. *Landscape Ecol* 10:51–63
- Maestre FT, Bautista S, Cortina J (2003) Positive, negative and net effects in grass-shrub interactions in Mediterranean semiarid grasslands. *Ecology* 84:3186–3197

- Maestre FT, Callaway RM, Valladares F, Lortie CJ (2009) Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *J Ecol* 97:199–205
- May FE, Ash JE (1990) An assessment of the allelopathic potential of *Eucalyptus*. *Aust J Bot* 38:245–254
- Meserve PL, Kelt DA, Milstead WB, Gutierrez JR (2003) Thirteen years of shifting top-down and bottom-up control. *Bioscience* 53:633–646
- Michalet R, Brooker RW, Cavieres LA, Kikvidze Z, Lortie CJ, Pugnaire FI, Valiente-Banuet A, Callaway RM (2006) Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecol Lett* 9:767–773
- Moorhead DL, Reynolds JF (1993) Changing carbon-chemistry of buried creosote bush litter during decomposition in the Northern Chihuahuan Desert. *Am Midl Nat* 130:83–89
- Munguia-Rosas MA, Sosa VJ (2008) Nurse plants vs. nurse objects: Effects of woody plants and rocky cavities on the recruitment of the *Pilosocereus leucocephalus* columnar cactus. *Ann Bot* 101:175–185
- Orchard BA, Cullis BR, Coombes NE, Virgona JM, Klein T (2000) Grazing management studies within the temperate pasture sustainability key program: experimental design and statistical analysis. *Aust J Exp Agric* 40:143–154
- Parker KC (1989) Nurse plant relationships of columnar cacti in Arizona. *Phys Geogr* 10:322–335
- Payne RW, Harding SA, Murray DA, Soutar DM, Baird DB, Welham SJ, Kane AF, Gilmour AR, Thompson R, Webster R, Tunnicliffe Wilson G (2007) The Guide to GenStat Release 10, Part 2: Statistics. VSN International, Hemel Hempstead
- Peters EM, Martorell C, Ezcurra E (2008) Nurse rocks are more important than nurse plants in determining the distribution and establishment of globose cacti (*Mammillaria*) in the Tehuacan Valley, Mexico. *J Arid Environ* 72:593–601
- Pugnaire FI, Armas C, Valladares F (2004) Soil as a mediator in plant-plant interactions in a semi-arid community. *J Veg Sci* 15:85–92
- Raffaele E, Veblen TT (1998) Facilitation by nurse shrubs of resprouting behavior in a post-fire shrubland in northern Patagonia, Argentina. *J Veg Sci* 9:693–698
- Riginos C, Grace JB (2008) Savanna tree density, herbivores, and the herbaceous community: bottom-up vs. top-down effects. *Ecology* 89:2228–2238
- 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
- Sankaran M, Hanan NP, Scholes RJ, Ratnam J, Augustine DJ, Cade BS, Gignoux J, Higgins SI, Le Roux X, Ludwig F, Ardo J, Banyikwa F, Bronn A, Bucini G, Caylor KK, Coughenour MB, Diouf A, Ekaya W, Feral CJ, February EC, Frost PGH, Hiernaux P, Hrabar H, Metzger KL, Prins HHT, Ringrose S, Sea W, Tews J, Worden J, Zambatis N (2005) Determinants of woody cover in African savannas. *Nature* 438:846–849
- Schlesinger WH, Belnap J, Marion G (2009) On carbon sequestration in desert ecosystems. *Glob Chang Biol* 15:1488–1490
- Soliveres S, Eldridge DJ, Maestre FT, Bowker MA, Tighe M, Escudero A (2011) Microhabitat amelioration and reduced competition among understorey plants as drivers of facilitation across environmental gradients: towards a unifying framework. *Perspec Plant Ecol Evol Syst* (in press)
- Tilman D (1988) Plant strategies and the dynamics and structure of plant communities. Princeton University Press, USA
- van der Putten WH (2009) A multitrophic perspective on functioning and evolution of facilitation in plant communities. *J Ecol* 97:1131–1138
- Verbyla AP, Cullis BR, Kenward MG, Welham SJ (1999) The analysis of designed experiments and longitudinal data by using smoothing splines. *J Royal Stat Soc Ser C Appl Stat* 48:269–300
- Weil RR, Islam KR, Stine MA, Gruver JB, Samson-Liebig SE (2003) Estimating active carbon for soil quality assessment: a simplified method for laboratory and field use. *Am J Altern Agric* 18:3–17
- Whitford WG (2002) Ecology of Desert Ecosystems. Academic Press, London