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Desert shrubs have negative or neutral effects on annuals at two levels of water availability in arid lands of South Australia

James T. Weedon*† and José M. Facelli

School of Earth and Environmental Sciences, University of Adelaide, Adelaide, SA, 5005, Australia

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Abstract

1. Perennial plants have been shown to facilitate understorey annual plant species in arid lands through the modification of spatial patterns of resources and conditions. This effect can result from a balance between simultaneously positive and negative interactions, both direct and indirect. This balance may shift with temporal variability in water availability.

2. We conducted a field experiment in a chenopod shrubland in South Australia to separate the effects of shade, below-ground competition, and soil modification by shrubs on the performance of annual plants, and to determine if the strength and direction of the interaction shifted with changes in water availability.

3. Annual plant diversity and seedling density was highest in plots established in open sites away from the dominant shrubs (*Maireana sedifolia*). Experimental removal of *M. sedifolia* increased seedling density compared to plots under undisturbed shrubs and plots where the removed shrub was replaced with artificial shade. Shading of open plots also reduced seedling density. Annual plant biomass was highest in areas where shrubs had been removed and was reduced by artificial shading. Biomass was higher in open plots than under intact shrubs. Experimental water addition did not alter plant density, but increased biomass across all treatments, particularly in artificially shaded bush plots.

4. *Synthesis.* Our results show that the overall effect of shrubs on the annual plant community in the system is negative under the range of water availabilities experienced during the experiment. This negative net-effect results from a combination of simultaneous facilitation via soil modification, and above- and below-ground competition. Assessment in different systems of different combinations of mechanisms that have simultaneously positive and negative effects will allow us to refine hypotheses seeking to explain the relative importance of facilitation across spatial and temporal gradients.

Key-words: *Carrichtera annua*, chenopod shrublands, facilitation, fertility islands, *Maireana sedifolia*, *Tetragonia tetragonioides*

Introduction

The overall effect of one plant on another results from the balance between simultaneous positive and negative interactions, which can vary with life stage, abiotic conditions and resource availabilities (Callaway 1997; Holzapfel & Mahall 1999; Tielbörger & Kadmon 2000b; Pugnaire & Luque 2001). It has been suggested that facilitation is an especially important process structuring plant communities in systems such as arid lands, salt marshes and alpine vegetation, where some extreme abiotic stress limits community productivity (Bertness & Callaway 1994; Callaway & Walker 1997; Brooker & Callaghan 1998). Conversely, under more benign conditions plants are expected to grow large enough to compete for resources, making negative interactions more important in structuring communities. The evidence supporting this ‘stress gradient’ hypothesis has been recently debated (Maestre *et al.* 2005, 2006; Lortie & Callaway 2006; Brooker *et al.* 2008).

Arid lands are amongst the most studied type of ecosystem in relation to plant facilitation (Flores & Jurado 2003). Low nutrient availability, harsh conditions and, in particular, low water availability are considered the predominant abiotic forces structuring plant communities in these systems

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*Correspondence author. E-mail: jtweedon@gmail.com

†Present address: Institute of Ecological Science, Vrije Universiteit, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands

(Noy-Meir 1973) and any mitigation of these stresses should increase plant performance. The presence of long lived plants concentrates limiting nutrients, and reduces soil and air temperatures, and therefore evapotranspiration (Breshears *et al.* 1998). This creates patches of high productivity in a matrix of low productivity, sparsely vegetated space (Aguiar & Sala 1999). In spite of the relatively large number of studies there is still uncertainty about whether the intensity of facilitation increases with the stressfulness of the system (Bertness & Callaway 1994; see Callaway 2007 for a recent synthesis of the discussion). While some results do support this view (Pugnaire & Luque 2001; Maestre *et al.* 2003; Gomez-Aparicio *et al.* 2004; Callaway 2007), some others do not (Tielbörger & Kadmon 2000b; Maestre & Cortina 2004). To refine predictions of the existing models it is necessary to increase our mechanistic understanding of facilitative processes (Callaway 2007; Brooker *et al.* 2008). Relatively few studies (e.g. Holzapfel & Mahall 1999; Maestre *et al.* 2003) have tried to separate the effects of shade, which acts mainly by decreasing water stress, from soil effects, which may enhance the mineral nutrition of the plants and increase water availability through increased water retention (Facelli & Brock 2000). Because stress can be induced by deficiencies of different resources, or extreme conditions, and different species respond differentially to the various environmental factors, teasing apart these changes is of paramount importance for understanding plant interactions (Michalet 2007).

The open woodlands with chenopod understorey of the arid zone of South Australia exhibit a clear pattern of patchiness associated with the presence of perennial plants (Facelli & Brock 2000; Facelli & Temby 2002). The dominant overstorey tree, *Acacia papyrocarpa*, changes microclimate, soil properties and nutrient availability under its canopy and supports an assemblage of shrubs and annual plants distinct from that in inter-canopy spaces (Facelli & Brock 2000). At a smaller scale, chenopod shrubs favour annual plants through changes in the soil, but hinder them through shading or root competition (Facelli & Temby 2002). This is in contrast with the findings in other ecosystems (e.g. Tielbörger & Kadmon 2000b).

This study aims to separate the effects of shrubs on annual plants that are the result of soil modification, shading and belowground interactions. In addition, we included two levels of water availability to investigate the consistency of interactions with variation in water availability, the main source of inter-annual variation in the system. We predict that while soil changes favour annual plants, root competition should reduce their performance. Shading should have a negative effect under high water availabilities, but a positive one when water is limiting. Unlike previous studies (e.g. Tielbörger & Kadmon 1997), we directly manipulated water availability, rather than relying on natural variation. Our design is therefore one of the few to directly control and separate the interactive effects of shade, heterogeneity in soil properties and availability of a limiting resource. We thus provide important data on the complex interaction of simultaneous mechanisms leading to net-effects of shrubs on annuals in arid-land plant communities.

Materials and methods

The study was conducted at Middleback Field Research Centre, located 18 km west of Whyalla, South Australia (32°57′ S, 137°24′ E). The climate is arid with an average annual rainfall of 218 mm (1925–2001), although there is often considerable variation between years. Rainfall is distributed fairly evenly throughout the year, but winter rains are more regular and predictable, and fall in many small to medium size rainfall events. Temperatures range from the mean daily maximum of 28.9 °C in January to a mean daily minimum of 7.3 °C in July. Soils are red-brown calcareous earths with clay-loam texture and low fertility (Jessup & Wright 1971).

The vegetation in the area is characterised by a sparse *Acacia papyrocarpa* (Western Myall) dominated overstorey with an understorey of perennial chenopod shrubs (Specht 1972), predominantly *Maireana sedifolia*, *M. pyramidata*, and *Atriplex vesicaria*. A diverse herbaceous community is present, primarily represented by winter annuals, with *Carrichtera annua*, *Tetragonia tetragonioides*, *Danthonia caespitosa*, *Erodium cygnorum*, *Medicago minima* and *Crassula colorata* amongst the most abundant.

We set-up the experiment in a grazing exclosure established in 1972. The exclosure prevents grazing by rabbits and sheep but allows access to kangaroos. On 20–22 April 2004, autumn in the southern hemisphere, we established 80 plots, 1 m × 1 m each. Forty-eight *Maireana sedifolia* individuals of similar size and at least 3 m away from another shrub were selected, and grouped into eight groups of six shrubs each, based on spatial proximity. This allowed us to spatially stratify the assignment of microsite treatments to control for any possible underlying large scale heterogeneity in soil properties and seed-bank composition. Four additional plots per group were established in open sites between the shrubs (defined as areas at least 2 m from the nearest shrub). Within each group plots were randomly assigned to a combination of two treatments. The microenvironment treatment (henceforth, Microsite) had five levels: Bush, Bush Removed, Bush Removed + Shade, Open and Open + Shade. Across these treatments we applied a watering treatment with two levels: additional watering or control (henceforth this factor is referred to as Water).

There were thus eight replicates of each of the 10 treatment combinations. In shrub plots, 'Bush' plots were left undisturbed, 'Bush Removed' plots had all aboveground shrub biomass removed by sawing the shrubs at the base with care taken to avoid soil disturbance, 'Bush Removed + Shade' plots had the shrub removed and were covered by a shade tent constructed from 80% shade cloth (1000 mm × 1000 mm × 200 mm), attached to stakes and fixed approximately 50 cm above the soil surface. This grade of shade cloth has been used in previous studies of facilitation in arid lands (Lenz 1999) and provides a reasonable simulation of the light environment under chenopod shrub canopies without interfering with rainfall. Measurements of photosynthetically active radiation (PAR) incident at ground level on north and south sides of intact shrubs versus shade treated plots showed no differences on the south side of plots and significant differences on the north sides (see Fig. S1 in Supporting Information). The north sides of shaded plots received less radiation (equivalent to roughly 25% of ambient PAR) than the north sides of plots under intact shrubs, a fact to be borne in mind when interpreting the results. In plots without shrubs, 'Open' plots were left undisturbed, while 'Open + Shade' plots were shaded with shade tents identical to those used for plots with shrubs.

Watered plots were watered monthly from May to August (mid autumn to early spring) with the exception of July when there was heavy rainfall during the site visit. The amount of water added was calculated to augment the natural rainfall of each month to a level equivalent to the corresponding monthly rain for the 25% wettest years on record (Middleback records 1925–2000). The resulting water amounts added were: 16 mm at the end of May, 12 mm at the end of June, and 10 mm at the end of August. Water was added with watering cans at a gradual rate to minimize losses by run-off.

We counted the annual plants in each plot every month following initial emergence until the final harvest in September (early spring in the southern hemisphere). We used four fixed 25 cm × 25 cm quadrats positioned at each corner of the plot, leaving 10 cm on the outside as a buffer, to sub-sample each plot and allow the detection of within-plot patterns of distribution and abundance. Quadrats were identified by their position in the plot (north-east, north-west, south-east and south-west). In September we harvested all above-ground biomass of annual plants and sorted it by species. This harvest time coincided with the beginning of flowering for most individuals when biomass reaches its maximum (J.M. Facelli, unpublished data). In this sampling, we included a fifth quadrat at the centre of each plot. The cross sections of any shrub stumps occurring in central quadrats were measured to allow standardisation of data on a ground area basis for further analyses. All plant material was dried for 48 h at 70 °C and weighed.

Repeated measures MANOVA was applied to the pooled census data from each plot, with Microsite and Water treatment as crossed factors, and census date as the repeated measures factor. Individual species and total density were analysed in separate models. Within-group analyses were performed using Pillai trace test statistic, as it is more robust to violations of the assumptions of parametric MANOVA (Scheiner 1993).

Data from the destructive census in September were analysed separately using a partly nested ANOVA model (equation 11.6 in Quinn & Keough 2002). The model had two between plot factors (Microsite and Watering) and one within-plot factor (quadrat position). This model design uses the mean squares of plot ($n = 8$ per Microsite × Watering combination) nested within Microsite × Watering as the F-ratio denominator for between-plot terms, and the interaction of plot and quadrat as the denominator for generating F-ratios for within-plot terms. We fitted this model to density, biomass, and biomass per capita data for each species, and for total biomass and density, as well as species number per quadrat (our measure of diversity). Although the spatially stratified experimental design gives the opportunity to test for the effects of spatial groups, this would lead to a saturated model, so the eight different groups are treated as random replicates. Only *Carrichtera annua*, *Tetragonia tetragonioides*, *Erodium cygnorum* and grasses were present in more than 20% of quadrats, and therefore could be used for a meaningful analysis. All other species (none of which was present in more than 8% of quadrats) were pooled into an 'Other' category except for *Crassula colorata*, the tiny size and cryptic habit of which did not allow satisfactory census and was thus excluded from the analyses, with the exception of species richness.

Given the right-skewed distribution of all response variables we used a nonparametric, permutation approach to estimate significance levels. Following Anderson & ter Braak (2003), we generated 1000 bootstrap datasets for each model term by permuting raw observations within the levels of terms of same or lower order (e.g. to test significance of Microsite, the Microsite labels for each plot were randomly exchanged within each level of Watering). The ANOVA model was fitted to each permuted dataset to generate distributions of F-ratios, to which the F-ratios from the original dataset could be compared. Permutation tests were conducted with scripts written in R (R Development Core Team 2006). All statements of difference between treatment levels below are supported by nonparametric *post hoc* tests *t*-tests in PERMANOVA (Anderson 2001; McCardle & Anderson 2001) with significance levels corrected to maintain a family-wide Type I error-rate of $P < 0.05$.

Results

Total rainfall from 1 April until the harvest was 90.1 mm (see Fig. S2), quite close to the historical mean rainfall of 92 mm for the corresponding period. Water treatment plots received the equivalent of an extra 38 mm of rainfall. Annual plant emergence was first noted on 29 June, after a large rainfall event in the second week of June.

TEMPORAL TRENDS

The repeated-measures MANOVA model for density was significant for all species combined, *Carrichtera*, and *Tetragonia* ($P < 0.01$ for Time factor in each model, see Table S1) but not for grasses, *Erodium* and Others. Whenever the Time factor was significant there was a significant Time × Microsite interaction ($P < 0.01$) indicating different timings of emergence and/or mortality in different microenvironments. Total and *Carrichtera* density declined between July and August in the Bush Removed and Open treatments, and this decline was recovered by September (see Fig. S3). The other treatments maintained constant densities with the exception of *Tetragonia*, which declined in all treatments with a steeper decline in Bush Removed treatments.

FINAL HARVEST

There was a highly significant effect of Microsite on species number ($P < 0.01$, see Table S2 for full statistical results) because all open control plots had more species present per quadrat than bush control plots (Fig. 1d).

Microsite had a significant effect on plant density for all species combined, and for *Carrichtera*, *Tetragonia* and grasses ($P < 0.005$, Table S3) in the between-plot analysis. There was no effect of watering treatment alone on plant density for any species. Open and Bush Removed plots had the highest total density, followed by Open + Shade plots. Bush and Bush Removed + Shade plots had the lowest total plant density (Fig 1a). The patterns for *Carrichtera* density were identical, although there were no significant differences between Open + Shade and Bush plots in this case (Fig. 1b). *Tetragonia* densities were higher in Bush Removed plots than in Bush and Open Shade plots (Fig. 1c). The within plot analysis indicated a significant effect of quadrat position on total, *Carrichtera* and *Tetragonia* density ($P < 0.001$). The effect of quadrat significantly interacted with Microsite for total and *Carrichtera* density ($P < 0.001$). There was no significant effect of quadrat on Total or *Carrichtera* density for Open and Open + Shade plots but in all Bush plots (regardless of additional treatment) there was a strong general trend of the two southern quadrats having higher densities than the central and northern quadrats (Figs S4 and S5).

There was a highly significant effect of Microsite and Water on total and *Carrichtera* biomass, and of Microsite on

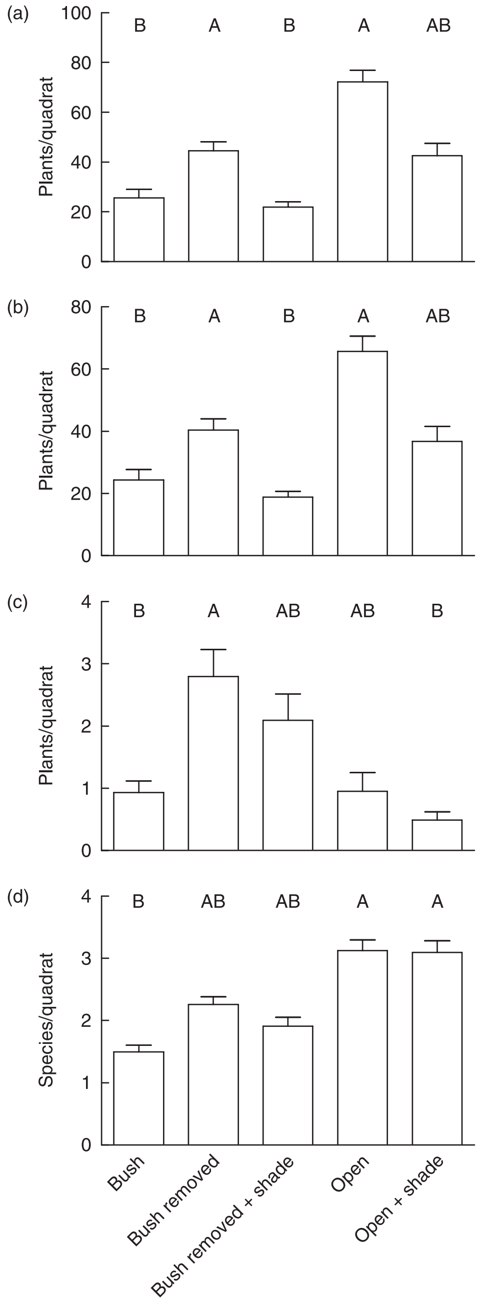

Fig. 1. Mean (± SE) plant density per 25 cm × 25 cm quadrat for (a) all species combined, (b) *Carrichtera annua* and (c) *Tetragonia tetragonioides*; and plant diversity per quadrat (d). Watered and non-watered plots are combined. Different letters indicate significant difference between treatments (Bonferroni-corrected permutation T-tests, $P < 0.05$, $n = 16$).

Tetragonia biomass across plots ($P < 0.001$, Table S4). Moreover the there was a significant Microsite × Water interaction for total biomass ($P < 0.05$). Total biomass was lower in Bush plots than in Bush Removed, Bush Removed + Shade and Open plots under watered conditions, and lower than Bush Removed plots only under ambient water levels (Fig. 2a). Identical patterns were evident in the *Carrichtera* biomass data (Fig. 2b). *Tetragonia* biomass was higher in Bush Removed plots than in Bush and Open + shade plots for both watering treatments (Fig. 2c). Biomass was consistently higher in watered plots for total, *Carrichtera* and *Tetragonia* (Fig. 2).

Quadrat position within plots showed a significant interaction with microsite ($P < 0.001$). The source of this effect was a trend for biomass to be higher in the central quadrat than in the two northern quadrats in the Bush Removed + Shade microsites, and for biomass in south-western quadrats to have more biomass than central quadrats in Bush plots. Other microsite treatments displayed no significant within plot pattern (Figs S6 and S7).

Microsite and watering treatment had significant effects on per capita biomass for Total, *Carrichtera*, and *Tetragonia* ($P < 0.01$, Table S5). Microsite and watering significantly interacted for total and *Carrichtera* per capita biomass ($P < 0.05$). Individuals of *Carrichtera* and all species combined were larger in Bush Removed and Bush Removed + Shade plots, an effect enhanced in the latter treatment by watering (Fig. S8). *Tetragonia* individuals were larger in Bush Removed plots compared with Open Control plots (Fig. S8). In all cases, watering increased per-capita biomass (Fig. S8).

Within plots per-capita biomass for all species combined and *Carrichtera* species in the central quadrat of Bush Removed and Bush Removed + Shade was significantly higher than in both southern quadrats (Figs S9 and S10). The three other microsite treatments showed no significant effect of quadrat position on per-capita biomass.

Discussion

Our results show that *Maireana sedifolia* exerts simultaneous positive and negative effects on annual plants, and that their combined outcome on diversity, growth and density is negative or null, independently of water availability within the range studied. The presence of a shrub reduced emergence of annuals under their canopy, most likely by shading, and supported a lower diversity of annual species than inter-shrub open spaces. These shrubs also reduced annual plant growth by shading and below-ground competition. Simultaneously, some aspect of the presence of the shrub, probably localised soil enrichment, has a positive effect on growth of nearby annual plants but this positive effect is only apparent when the shrub canopy is removed.

Experimental watering had no effect on annual plant density and a modestly positive effect on growth for all microsites (which was particularly pronounced in bush removed + shade plots), indicating that while the annual plants were not subject to strong stress, water was limiting. In general, emergence of annuals was reduced by shading, either by shrub canopies or artificial shade structures. Changes to soil temperature and moisture through shading have the potential to alter the fraction of seeds germinating from the seed bank. The seeds of many desert annual species have a period of dormancy controlled by a range of abiotic cues (Baskin *et al.* 1993). Previous work has shown that temperature and water availability interact to produce the germination response of several annual plants in the system (Facelli *et al.* 2005), including the dominant, *Carrichtera annua* (Facelli & Chesson 2008) and it

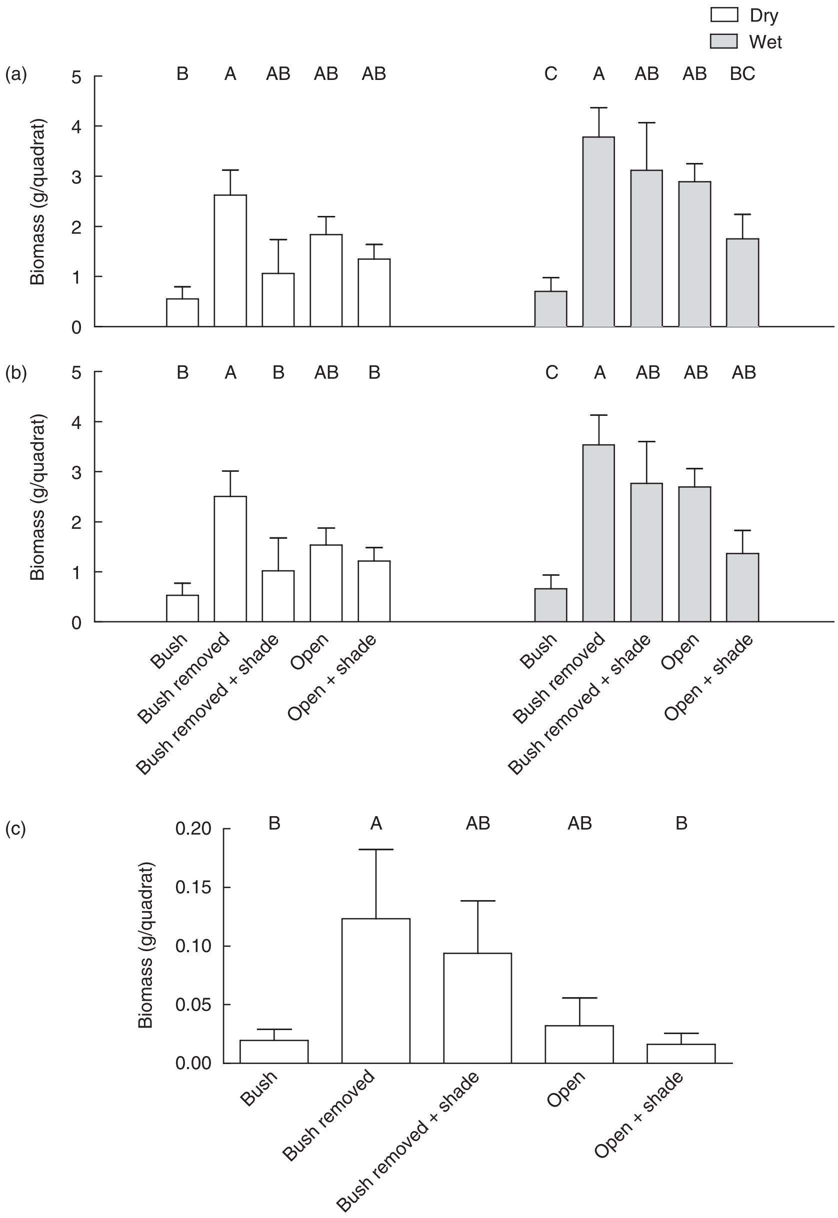

Fig. 2. Mean (± SE) above ground biomass (g) per 25 cm × 25 cm quadrat for (a) all species combined, (b) *Carrichtera annua* and (c) *Tetragonia tetragonioides*. Different letters indicate significant difference between treatments within each level of watering treatment when applicable (Bonferroni-corrected permutation T-tests, $P < 0.05$, $n = 8$).

is probable that the effect of shading on these two factors produced the differential emergence response seen in the current study.

Reduction of mortality is one of the mechanisms through which shrubs might facilitate herbaceous plants (Callaway 1995). The temporal patterns in densities we documented suggest negligible mortality for all species except for *Tetragonia*. Even the lower plant densities in August are likely to reflect counting inaccuracies caused by high densities of larger plants – this is supported by the apparent increase in density between August and the destructive count in September, a period in which clearly there was no emergence. Other studies with desert annuals have found mortality rates of up to 80% (Lortie & Turkington 2002; Tielbörger & Kadmon 2000a). Our plants were harvested towards the end of the growing season before seed set and post-reproductive mass mortality (typically in October), so it is possible that we missed differential effects of treatments on late-season survivorship. On the other hand, many plants had begun flowering, and pilot studies have shown a good correlation between September biomass and reproductive output, and low late-season pre-reproductive mortality in general (J.M. Facelli, unpublished data).

Tetragonia showed a pattern of density-distribution different from *Carrichtera*. It had higher densities at shrub sites than in open spaces, which concurs with the spatial distribution documented for the seedbank of this species in a previous study (Facelli & Temby 2002). The removal of the shrub canopy, however, increased the emergence of *Tetragonia* in a similar manner to other species. This suggests that the mechanisms leading to preferential accumulation of seeds of *Tetragonia* under shrubs occur at a different stage in the plant's life cycle (Callaway & Walker 1997) or under different conditions.

The results for the total biomass of annuals suggest interactive effects between shading, below-ground competition between shrubs and annuals, and positive effects through soil modification by the shrubs. Total biomass was reduced by shading in both open and shrub microsites, but the lower biomass of annual plants under intact shrubs than in shrub sites with artificial shade suggests that belowground competition is important in the system. This concurs with other studies that have found negative effects of shrubs on understorey plants (Swank & Oechel 1991; Forseth *et al.* 2001; Facelli & Temby 2002; Berlow *et al.* 2003). We also found evidence for light limitation of understorey plants, as reported by Forseth *et al.* (2001) in another arid system. Given that water is traditionally considered the overwhelming limiting resource in arid systems (Noy-Meir 1973), the finding that light limitation can be more important under certain circumstances suggests a need for a modification of models of arid land vegetation dynamics.

The higher biomass of annual plants in shrub removed treatments than in open sites suggests that there is some positive effect of the shrub microsite on annual plant growth. A likely mechanism is nutrient enrichment of soil under the shrub canopy, a common phenomenon in arid ecosystems (Vetaas 1992; Facelli & Brock 2000; Titus *et al.* 2002). An artificial pulse of nutrients caused by the decay of belowground biomass of the removed shrub is unlikely due to the slow nutrient flux rates in arid systems relative to the length of the study, although a transitory release of nutrients via decay of fine roots cannot be ruled out.

There is evidence for density dependent limitation of growth in plots where annuals reached high density. At the plot level per capita biomass was highest in treatments where the absolute densities were relatively lower (i.e. in the two 'Bush removed' microsite treatments vs. Open treatments). This trend is repeated within plots, individual plants tended to be bigger in parts of the plot where annual densities were lower. This pattern suggests the possibility that facilitation between guilds (i.e. positive effects of shrubs on annual plant density) may lead to increased competitive effects within the beneficiary guild, an idea tested but not supported by Tielbörger & Kadmon (2000a). Such a situation may lead to promotion of competitive dominants at the expense of diversity.

Within-plot analyses indicate a north-south pattern of plant densities in shrub sites with higher plant densities on the southern sides (shadier in the southern hemisphere) than in the northern sides of shrub plots, seemingly contradicting the negative effect of shade on emergence found in the whole plot analysis. Comparable patterns have been observed in a similar system in the Mojave Desert (Schenk & Mahall 2002). Accumulation in mounds under shrubs can be asymmetric, and transport processes such as wind and water movement may preferentially deposit seeds on the southern sides of these mounds (Reichman 1984; Oesterheld & Oyarzabal 2004). This interpretation is consistent with the prevalence of southerly winds during the seed dispersal period.

The net result of negative effects of shrubs on annuals we documented contradicts positive and neutral effects reported by other studies in arid lands (Went 1942; Muller 1953; Gutierrez *et al.* 1993; Tielbörger & Kadmon 1997; Holzapfel & Mahall 1999; Lenz & Facelli 2003). Several possible explanations may account for this. Positive effects may have been absent due to the potential species-specificity of facilitation (Callaway 1998). Given the overwhelming numerical dominance of a single annual species (*C. annua*) at our site, potentially positive effects of shrubs on other species may have been obscured in the analysis. In addition, our study was conducted in a grazing exclosure, precluding the possibility of facilitation via protection from sheep grazing, which may be critical in grazed areas at the study site (Meissner & Facelli 1999; Facelli & Temby 2002) and has been hypothesized as an important process in more productive systems (Bertness & Callaway 1994). Native mammal grazers and insect herbivores had access to the study site but we observed no evidence of significant defoliation of the annual plants.

While positive interactions are often considered to be pervasive in arid environments, we failed to find evidence for them in our system. In fact, shrubs exerted negative effects on *Carrichtera*, and null effects on *Tetragonia.* This may be a consequence of the life history of desert winter annuals, a guild that may be considered drought avoiders, rather than drought tolerant, having evolved complex adaptations to prevent their seed from germinating when conditions are, or are likely to turn, unfavourable (Baskin *et al.* 1993; Clauss & Venable 2000; Facelli *et al.* 2005; Callaway 2007). This suggests a need to define stress in terms of the physiological tolerances of the organism, rather than an *a priori* expectation (e.g. deserts are dry and sunny, therefore water stress must drive system dynamics). We have demonstrated that although water was limiting to annual plant growth, interactions between annuals and shrubs were mediated predominantly by soil nutrients and light. We offer the obvious caveat that, as our control and watering treatments represented an average and a wet year respectively, it is possible that under even drier conditions the balance of interaction mechanisms could shift to a net positive one.

Our results underline the importance of considering multiple mechanisms when characterizing shrub-understorey interactions. By separating different mechanisms of plant-plant interaction to an extent that is rare in experiments addressing facilitation in arid systems (but see Holzapfel & Mahall 1999; Maestre *et al.* 2003), we demonstrated that shrub – understorey interactions can be mediated via more than one constraining resource or condition with the result depending on the balance between them, and that different life stages (e.g. germination and growth) can be affected by different mechanisms. Attempts to refine our models of plant interactions across spatial and temporal gradients should therefore explicitly consider multiple interaction mechanisms, which may be specific to certain species, or even to different life stages within the same species.

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References

Aguiar, M.R. & Sala, O.E. (1999) Patch structure, dynamics and implications for the functioning of arid ecosystems. *Trends in Ecology & Evolution*, **14**, 273–277.

Anderson, M.J. (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, **26**, 32–46.

Anderson, M.J. & ter Braak, C.J.F. (2003) Permutation tests for multi-factorial analysis of variance. *Journal of Statistical Computation and Simulation*, **73**, 85–113.

Baskin, C.C., Chesson, P. & Baskin, J.M. (1993) Annual seed dormancy cycles in two desert winter annuals. *Journal of Ecology*, **81**, 551–556.

Berlow, E.L., D'Antonio, C.M. & Swartz, H. (2003) Response of herbs to shrub removal across natural and experimental variation in soil moisture. *Ecological Applications*, **13**, 1375–1387.

Bertness, M.D. & Callaway, R.M. (1994) Positive interactions in communities. *Trends in Ecology & Evolution*, **9**, 191–193.

Breshears, D.D., Nyhan, J.W., Heil, C.E. & Wilcox, B.P. (1998) Effects of woody plants on microclimate in a semiarid woodland: soil temperature and evaporation in canopy and intercanopy patches. *International Journal of Plant Sciences*, **159**, 1010–1017.

Brooker, R.W. & Callaghan, T.V. (1998) The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. *Oikos*, **81**, 196–207.

Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.J., Cavieres, L.A., Kunstler, G. *et al.* (2008) Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology*, **96**, 18–34.

Callaway, R.M. (1995) Positive interactions among plants. *Botanical Review*, **61**, 306–349.

Callaway, R.M. (1997) Positive interactions in plant communities and the individualistic-continuum concept. *Oecologia*, **112**, 143–149.

Callaway, R.M. (1998) Are positive interactions species-specific? *Oikos*, **82**, 202–206.

Callaway, R.M. (2007) *Positive Interactions and Interdependence in Plant Communities*. Springer, Dordrecht.

Callaway, R.M. & Walker, L.R. (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology*, **78**, 1958–1965.

Clauss, M.J. & Venable, D.L. (2000) Seed germination in desert annuals: an empirical test of adaptive bet hedging. *American Naturalist*, **155**, 168–186.

Facelli, J.M. & Brock, D.J. (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.

Facelli, J.M. & Chesson, P. (2008) Cyclic dormancy, temperature & water availability control germination of *Carrichtera annua*. *Austral Ecology*, **33**, 324–328.

Facelli, J.M. & Temby, A.M. (2002) Multiple effects of shrubs on annual plant communities in arid lands of South Australia. *Austral Ecology*, **27**, 422–432.

Facelli, J.M., Chesson, P. & Barnes, N. (2005) Differences in seed biology of annual plants in a variable environment: a key ingredient of the storage effect. *Ecology*, **86**, 2998–3006.

Flores, J. & Jurado, E. (2003) Are nurse-protege interactions more common among plants from arid environments? *Journal of Vegetation Science*, **14**, 911–916.

Forseth, I.N., Wait, D.A. & Casper, B.B. (2001) Shading by shrubs in a desert system reduces the physiological and demographic performance of an associated herbaceous perennial. *Journal of Ecology*, **89**, 670–680.

Gomez-Aparicio, L., Zamora, R., Gomez, J.M., Hodar, J.A., Castro, J. & Baraza, E. (2004) Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. *Ecological Applications*, **14**, 1128–1138.

Gutierrez, J.R., Meserve, P.L., Contreras, L.C., Vasquez, H. & Jaksic, F.M. (1993) Spatial-distribution of soil nutrients and ephemeral plants underneath and outside the canopy of *Porlieria chilensis* shrubs (Zygophyllaceae) in arid coastal Chile. *Oecologia*, **95**, 347–352.

Holzapfel, C. & Mahall, B.E. (1999) Bidirectional facilitation and interference between shrubs and annuals in the Mojave Desert. *Ecology*, **80**, 1747–1761.

Jessup, R.W. & Wright, M.J. (1971) Cenozoic sediments, soils and climates at Whyalla, South Australia. *Geoderma*, **6**, 275–308.

Lenz, T.I. (1999) *The role of facilitation in the spread of* Orbea variegata *(Asclepiadaceae) at Whyalla, South Australia*. B.Sc. (Honours) Thesis, University of Adelaide, Adelaide.

Lenz, T.I. & Facelli, J.M. (2003) Shade facilitates an invasive stem succulent in a chenopod shrubland in South Australia. *Austral Ecology*, **28**, 480–490.

Lortie, C.J. & Callaway, R.M. (2006) Re-analysis of meta-analysis: support for the stress-gradient hypothesis. *Journal of Ecology*, **94**, 7–16.

Lortie, C.J. & Turkington, R. (2002) The effect of initial seed density on the structure of a desert annual plant community. *Journal of Ecology*, **90**, 435–445.

Maestre, F.T. & Cortina, J. (2004) Do positive interactions increase with abiotic stress? A test from a semi-arid steppe. *Proceedings of the Royal Society of London B (Supplement)*, **271**, S331–S333.

Maestre, F.T., Bautista, S. & Cortina, J. (2003) Positive, negative, and net effects in grass-shrub interactions in Mediterranean semiarid grasslands. *Ecology*, **84**, 3186–3197.

Maestre, F.T., Valladares, F. & Reynolds, J.F. (2005) Is the change of plant-plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. *Journal of Ecology*, **93**, 748–757.

Maestre, F.T., Valladares, F. & Reynolds, J.F. (2006) The stress-gradient hypothesis does not fit all relationships between plant-plant interactions and abiotic stress: further insights from arid environments. *Journal of Ecology*, **94**, 17–22.

McCardle, B.H. & Anderson, M.J. (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology*, **82**, 290–297.

Meissner, R.A. & Facelli, J.M. (1999) Effects of sheep exclusion on the soil seed bank and annual vegetation in chenopod shrublands of South Australia. *Journal of Arid Environments*, **42**, 117–128.

Michalet, R. (2007) Highlighting the multiple drivers of change in interactions along stress gradients. *New Phytologist*, **173**, 3–6.

Muller, C.H. (1953) The association of desert annuals with shrubs. *American Journal of Botany*, **40**, 53–60.

Noy-Meir, I. (1973) Desert ecosystems: environment and producers. *Annual Review of Ecology & Systematics*, **4**, 25–51.

Oesterheld, M. & Oyarzabal, M. (2004) Grass-to-grass protection from grazing in a semi-arid steppe. Facilitation, competition, and mass effect. *Oikos*, **107**, 576–582.

Pugnaire, F.I. & Luque, M.T. (2001) Changes in plant interactions along a gradient of environmental stress. *Oikos*, **93**, 42–49.

Quinn, G.P. & Keough, M.J. (2002) *Experimental Design and Data Analysis for Biologists* Cambridge University Press, Cambridge.

R Development Core Team (2006) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Reichman, O.J. (1984) Spatial and temporal variation of seed distributions in sonoran desert soils. *Journal of Biogeography*, **11**, 1–11.

Scheiner, S.M. (1993). MANOVA: multiple response variables and multispecies interactions. *Design and Analysis of Ecological Experiments* (eds S.M. Scheiner & J. Gurevitch), pp. 94–112.Chapman & Hall, New York.

Schenk, H.J. & Mahall, B.E. (2002) Positive and negative plant interactions contribute to a north-south-patterned association between two desert shrub species. *Oecologia*, **132**, 402–410.

Specht, R.L. (1972) *The Vegetation of South Australia*, 2nd edn. Government Printer, Adelaide.

Swank, S.E. & Oechel, W.C. (1991) Interactions among the effects of herbivory, competition, and resource limitation on chaparral herbs. *Ecology*, **72**, 104–115.

Tielbörger, K. & Kadmon, R. (1997) Relationships between shrubs and annual communities in a sandy desert ecosystem: a three-year study. *Plant Ecology*, **130**, 191–201.

Tielbörger, K. & Kadmon, R. (2000a) Indirect effects in a desert plant community: is competition among annuals more intense under shrub canopies? *Plant Ecology*, **150**, 53–63.

Tielbörger, K. & Kadmon, R. (2000b) Temporal environmental variation tips the balance between facilitation and interference in desert plants. *Ecology*, **81**, 1544–1553.

Titus, J.H., Nowak, R.S. & Smith, S.D. (2002) Soil resource heterogeneity in the Mojave Desert. *Journal of Arid Environments*, **52**, 269–292.

Vetaas, O.R. (1992) Micro-site effects of trees and shrubs in dry savannas. *Journal of Vegetation Science*, **3**, 337–344.

Went, F.W. (1942) The dependence of certain annual plants on shrubs in southern California deserts. *Bulletin of the Torrey Botanical Club*, **69**, 100–114.

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Supporting Information

Additional Supporting Information may be found in the online vesion of this article:

Fig. S1. Comparison of photosynthetically active radiation at ground level in open, shrub and artificially shaded plots.

Fig. S2. Rainfall at field site during field experiment.

Fig. S3. Time series of plant density by microsite for Total, *Carrichtera annua* and *Tetragonia tetragonioides.*

Fig. S4. Total plant density by quadrat position.

Fig. S5. *Carrichtera annua* density by quadrat position.

Fig. S6. Total plant biomass by quadrat position.

Fig. S7. *Carrichtera annua* biomass by quadrat position.

Fig. S8. Per-capita biomass by microsite (and watering) for Total, *Carrichtera annua*, Other species and *Tetragonia tetragonioides.*

Fig. S9. Total per-capita biomass by quadrat position.

Fig. S10. *Carrichtera annua* per-capita biomass by quadrat position.

Fig. S11. Grass density in watered and unwatered plots by microsite.

Table S1. Statistical tables for repeated measures MANOVA for plant density data

Table S2. Statistical tables for permutation-based ANOVA for species number

Table S3. Statistical tables for permutation-based ANOVA for final density data

Table S4. Statistical tables for permutation-based ANOVA for final biomass data

Table S5. Statistical tables for permutation-based ANOVA for final per-capita biomass data