



Annual plant–shrub interactions along an aridity gradient

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Received 2 February 2005; accepted 19 August 2005

KEYWORDS

Annuals;
Shrubs;
Desert;
Mediterranean;
Facilitation;
Competition;
Environmental
gradient;
Climatic gradient;
Life stage;
Rainfall

Summary

Annual plants in semi-arid and arid areas are often closely associated with shrubs. The degree of association largely depends on the balance of negative and positive effects between these contrasting plant life-forms, ranging from interference to facilitation. Since positive interactions are predicted to become less important with increasing rainfall, the interaction balance is expected to shift along aridity gradients. However, this prediction has not been tested on a community level and for different life-history stages across large geographical gradients. Here, we show such changes for annual plant populations and communities in four contrasting sites along a steep climatic gradient, ranging from the arid desert to mesic Mediterranean regions in Israel. Above-ground productivity, richness, seedling density, and seed bank density of the annual plant community, as well as fecundity of annual plant populations, were generally higher under shrubs than in areas between shrubs at the arid end of the gradient, but significantly lower at the humid end. Net effects of shrubs on annuals expressed as relative interaction intensity indicated a steady and consistent shift from net positive or neutral effects in the desert to net negative effects in the mesic part of the gradient. These findings emphasize the usefulness of studies along large-scale gradients encompassing a wide range of environmental conditions for understanding community level interactions among coexisting species. © 2005 Gesellschaft für Ökologie. Published by Elsevier GmbH. All rights reserved.

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Zusammenfassung

Annuelle Pflanzen in semiariden und ariden Gebieten sind häufig eng mit Sträuchern assoziiert. Das Ausmaß dieser Assoziation hängt in hohem Maße von der Balance zwischen negativen und positiven Interaktionen ab. Da die Bedeutung von positiven Interaktionen im allgemeinen mit steigendem Niederschlag abnimmt, sollte sich die Balance zwischen den beiden Interaktionstypen entlang von Ariditätsgradienten verschieben. Diese Vorhersage ist jedoch nicht auf einer Gemeinschaftsebene, für verschiedene Lebensstadien und für ausgedehnte geographische Gradienten getestet worden. Hier zeigen wir solche Veränderungen für Pflanzenpopulationen und -gemeinschaften in vier sehr stark unterschiedlichen Untersuchungsgebieten entlang eines steilen Klimagradients in Israel. Oberirdische Produktivität, Artenreichtum, Keimlingsdichte, Dichte in der Samenbank, sowie Fekundität von annuellen Populationen waren generell höher unter Sträuchern als zwischen Sträuchern am ariden Ende des Gradienten, jedoch signifikant niedriger unter feucht-mediterranen Bedingungen. Nettoeffekte der Sträucher auf Annuelle, basierend auf allen gemessenen Parametern, deuteten auf eine stetige und konsistente Verschiebung von insgesamt positiven oder neutralen Effekten in der Wüste zu insgesamt negativen Effekten in den humiden Bereichen des Gradienten hin. Diese Ergebnisse zeigen deutlich die Nützlichkeit von Untersuchungen entlang von großskaligen Gradienten mit sehr verschiedenen Umweltbedingungen für ein Verständnis der Interaktionen zwischen koexistierenden Arten.

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Introduction

Interactions among species are among the most important determinants of structure and dynamics of ecological communities. Therefore, the interplay of positive and negative interactions has become one of the major emerging themes in community ecology (Bruno, Stachowicz, & Bertness, 2003). It has been predicted that positive interactions (facilitation) among plants are stronger in stressful sites, while negative interactions (interference) predominate in less stressful environments (Bertness & Callaway, 1994; Callaway & Walker, 1997). Many empirical studies have attempted to test this prediction along resource gradients in various regions of the world (e.g., Bertness & Hacker, 1994; Callaway, 1998; Callaway, DeLucia, Moore, Nowak, & Schlesinger, 1996; Callaway et al., 2002; Pugnaire & Luque, 2001; Walker & Chapin III, 1986). These studies emphasize the need for investigations over a wide range of environmental conditions to advance our understanding of the processes involved in the interactions among coexisting species. Unfortunately, the majority of previous studies have either used very short-scale gradients with limited species turnover (e.g., Donovan & Richards, 2000; Maestre & Cortina, 2004a; Schenk, Holzapfel, Hamilton, & Mahall, 2003) or they have investigated two extremes instead of real gradients (e.g., Kadmon, 1997; Pugnaire & Luque, 2001; Tielbörger &

Kadmon, 2000a). The problem with the latter approach is that conclusions about shifts in interaction strength are unjustified, since the progression of interaction type between the extremes may take any possible shape. This highlights that gradients encompassing a wide range of conditions and communities, e.g., geographical gradients, may add important insights to the more commonly investigated small-scale gradients.

Though there has been relatively little debate about the increasing importance of facilitative interactions with increasing stress (but see Maestre & Cortina, 2004a, b; Pennings, Selig, Houser, & Bertness, 2003), the pattern and strength of competition along resource gradients are still heavily debated and empirical results are inconclusive. Studies across geographical resource gradients that follow the approaches used in macroecological research (Blackburn, 2004; Storch & Gaston, 2004) can address this controversy. Namely, when the geographical gradient is large, both environmental conditions and plant communities change, and differences in the crucial processes that drive community assembly can be detected. Relatively few studies have addressed variation in plant interactions along climatic gradients spanning over large geographical ranges (Bertness & Ewanchuk, 2002; Pennings et al., 2003; Tewksbury & Lloyd, 2001) and none of those involved complete community shifts along those gradients, such as shifts in species richness or

community structure. Such studies should also involve widely differing communities, with a comparatively large set of species.

Here, we utilize a unique environmental gradient with high species turnover in order to unravel the nature of the changes in species interactions along spatial gradients in limiting resources. More specifically, we analyzed the variation in the shrub–annual plant association along a steep climatic gradient in Israel, ranging from the desert to the mesic Mediterranean, in which water is the main limiting factor (Aronson & Shmida, 1992). We tested for the theoretically predicted shift from net positive to net negative effects with increasing rainfall (i.e., decreasing drought stress) (Bertness & Callaway, 1994; Brooker & Callaghan, 1998). Also, since the life-history stage at which the interactions are studied is of crucial importance for the detected outcome (Callaway & Walker, 1997; Goldberg, Rajaniemi, Gurevitch, & Stewart-Oaten, 1999), we focused on various demographic parameters of the annual plant populations and communities.

Methods

The climatic gradient

Field studies were carried out in four experimental sites along a climatic gradient in Israel running from North to South (length: 245 km). Environmental conditions at these sites represent mesic Mediterranean, “typical” Mediterranean, semi-arid, and arid conditions. All sites share the same calcareous bedrock and are positioned on south-facing slopes. The basic climate is Mediterranean with rainy winters (October–April) and prolonged rainless summers. The growing season of plants commences soon after the first rains, between October–December each year. The arid site is situated in the Negev Desert near Sde Boqer (N 30°52′ E 34°46′) at 470 m a.s.l., on desert Lithosol (soil nomenclature: Dan, Yaalon, Koyumdijsky, & Raz, 1976). Average annual rainfall is 90 mm with >30% inter-annual variation and 19.1 °C mean annual temperature. The open vegetation of the site is dominated by small shrubs such as *Zygophyllum dumosum* Boiss. *Artemisia sieberi* Besser and *Hammada scoparia* (Pomel) Iljin (nomenclature: Feinbrun-Dothan & Danin, 1991) and sparsely growing desert annuals and geophytes. The semi-arid site is located near Lahav (N 31°23′ E 34°54′) between the southern Judean Mountains and the Northern Negev, at 590 m a.s.l., on Light

Brown Rendzina. Average annual rainfall is 300 mm with 25% inter-annual variation, and mean annual temperature of 18.4 °C. The vegetation is dominated by dwarf-shrubs of *Sarcopoterium spinosum* (L.) Spach and *Coridothymus capitatus* (L.) Reichenb. fil. associated with herbaceous (chiefly annual) plants. The Mediterranean site is located 18 km south-west of Jerusalem, near Matta (N 31°42′ E 35°3′) at 620 m a.s.l., on Terra Rossa. The climate is characterized by 537 mm average annual rainfall with 22% inter-annual variation and 17 °C mean annual temperature. The vegetation is dominated by *Sarcopoterium spinosum* and large numbers of herbaceous (mostly annual) plant species. The mesic Mediterranean site is near Ein Ya’aqov (N 33°0′ E 35°14′) in the northern Galilee mountains at an elevation of 500 m a.s.l., on montmorillonitic Terra Rossa, with 780 mm mean annual rainfall, <20% inter-annual variation, and with 18.1 °C mean annual temperature. The vegetation varies from closed oak maquis (*Quercus calliprinos* Webb) to more open garrigue dominated by several shrub species (e.g., *Sarcopoterium spinosum*, *Cistus* ssp., *Calicotome villosa* (Poiret) Link). Herbaceous vegetation, mainly composed of annuals, coexists with shrubs. The plant communities in the four sites differ strongly in their species composition. Species turnover is approximately 80% from the arid to the semi-arid site (including the dominant shrub species), 70% to the Mediterranean and about 40% to the mesic Mediterranean (unpubl. data).

The research was carried out during the winter 2001/2002, that ranked as a slightly above average rainfall year. The arid site received 111% of the long-term average rainfall, the semi-arid site 113%, the Mediterranean site 134%, and the mesic Mediterranean site 112%. Parallel investigations indicated that soil water content, the most important factor for plants with respect to water availability, was positively correlated with actual and long-term average rainfall (Pariante et al., unpubl. data).

Sampling

In each of the four sites, we investigated the annual community under the canopy of the dominant shrub species (understory) and in open areas between them. In the three moister sites, the semi-globular dwarf-shrub species *Sarcopoterium spinosum* (Rosaceae), was selected while *Artemisia sieberi* (Asteraceae), was chosen in the most arid site, where *S. spinosum* is not present. We have

chosen *A. sieberi* because of its high abundance at the arid site and its overall resemblance to *S. spinosum* in canopy structure. Five blocks of approx. 10 m × 20 m in size were marked at a distance of 50–80 m from each other across the southern slope at each site, and five mature shrubs were selected randomly within each block. Permanent quadrats (20 cm × 20 cm) were established under the eastern side of the selected shrubs, with the center of the quadrat placed approximately at the canopy edge. A corresponding quadrat was placed in the open area next to each selected shrub. In each site, 5 blocks with 5 quadrat pairs were monitored.

Annual plant performance

Above-ground biomass of the herbaceous community beneath the shrubs and between shrubs was evaluated non-destructively from aerial cover and plant height once at peak vegetation development, using regressions of these quantities against dry mass of plants harvested from similar plots in adjacent areas (Table 1). Non-destructive measures were used since the plots were intended for long-

term monitoring which does not allow selective removal. Due to different phenology among the sites, sampling dates were for the arid site March 17, the semi-arid site March 26, the Mediterranean site March 13, and the mesic Mediterranean site May 1.

Per-quadrat density and species richness (number of species per quadrat) of seedlings were determined with repeated counts, taking into account separate germination events. Our measure of species richness underestimated actual richness, since seedlings could not always be separated to the species level and some recorded taxa may contain several species. However, since we assessed richness at early life stages of all plant species, we obtained the maximal potential species number. Data on density and species richness of adult plants were collected too. They are not presented since observed trends were qualitatively similar to those found for seedling density.

For fecundity measurements, 3–5 dominant annual plant species were chosen in each site: *Stipa capensis* Thunb. (Poaceae), *Schismus arabicus* Nees (Poaceae), and *Astragalus tribuloides* Delile (Fabaceae) in the arid site; *Crithopsis delileana* (Schultes et Schultes fil.) Roshev. (Poaceae), *Carrichtera annua* (L.) DC. (Brassicaceae) and

Table 1. Allometric linear regression models of biomass production by herbaceous (mostly annual) vegetation and seed production by dominant annuals based on non-destructive measurements ($p < 0.001$ in all cases)

Dependent variable	Intercept	Independent variables and slopes	df	r^2
Biomass of herbaceous vegetation^a				
Arid site	0.0038	Cover (%) × 0.015 (height not significant)	35	0.724
Semi-arid site	5.75	Cover (%) × 1.72 + height ^b × 3.86	59	0.437
Mediterranean site	2.85	Cover (%) × 1.68 + height × 6.47	144	0.491
Mesic Mediterranean site	19.94	Cover (%) × 2.45 (height not significant)	66	0.580
Seeds per individual				
<i>Stipa capensis</i>	147.01	Length of panicle ^c × 15.6 × panicles	23	0.795
<i>Crithopsis delileana</i>	−2.71	Length of spike × 0.227 × spikes	40	0.850
<i>Filago contracta</i>	−15.3	Width of capitula × 5.68 × capitulae	24	0.897
<i>Plantago afra</i>	−3.85	Length of capitula × 1.58 × capitulae ^d	24	0.615
<i>Bromus fasciculatus</i>	−99.7	Length of panicle × 2.42 × panicles	37	0.827
<i>Brachypodium distachyon</i>	−3.01	Length of spike × 0.392 × spikes	32	0.755
<i>Plantago cretica</i>	1.33	Diameter of capitula × 0.651 × capitulae ^d	36	0.945
<i>Hedypnois rhagadioloides</i>	−6.3	Number of outer florets × 2.93 × capitulae	28	0.801

^amg per 200 cm².

^bAverage height in cm.

^cAll length or diameters in mm.

^dEach floret contains 2 seeds (values multiplied by 2).

Filago contracta (Boiss.) Chrtek et Holoub (Asteraceae) in the semi-arid site; *Bromus fasciculatus* C. Presl (Poaceae), *Plantago afra* L. (Plantaginaceae), *Valantia hispida* L. (Rubiaceae), *Galium judaicum* Boiss. (Rubiaceae) and *Crepis sancta* (L.) Bornm. (Asteraceae) in the Mediterranean site; *Brachypodium distachyon* (L.) Beauvois (Poaceae), *Plantago cretica* L. (Plantaginaceae), *Hedypnois cretica* (L.) Dum.-Courset (Asteraceae), and *Picris galilaea* (Boiss.) Eig (Asteraceae) in the mesic Mediterranean site. Where possible, seeds were counted directly on reproductive plants. In some species, seed production had to be estimated using allometric relationships between seed number and non-destructive measures of fecundity (Table 1). In each quadrat, 10–15 individuals were measured and the average was used in further analyses.

To estimate the size of the germinable seed bank in the soil we collected paired soil samples (5 cm × 5 cm, 5 cm depth) in the shrub understory and between shrubs at the end of the summer drought and before the fall rains (September 2001). Soil samples included seeds on the surface and litter. Ten such pairs were taken in each of the five blocks in all sites. These samples were spread on a gauze sheet in plastic containers (12 cm × 14 cm, 6.5 cm deep) with drainage holes, on top of a 3 cm vermiculite layer, and were irrigated during the winter in a nethouse in the Botanical Gardens at Tel Aviv University. Emerging seedlings were identified, counted and continuously removed until no further emergence was observed (mid-March).

Data analysis

For statistical analyses, we calculated per-block means of all dependent variables and used the averages as observations. Such pooling was done since sampling of some dependent variables (e.g., fecundity) resulted in a slightly unbalanced design, error distributions were not homogeneous for all variables, and loss of power due to the averaging turned out to be negligible. After averaging, designs were balanced, variances were homogeneous, and data was normally distributed for all dependent variables. Therefore, similar analyses could be used for all dependent variables, facilitating interpretation and comparison of results. Due to pooling, habitat types were not independent. Therefore, separate repeated-measures ANOVAs were employed for each dependent variable, with habitat (shrub vs. open space) as within-subject factor, site as between-subject factor and between-block variation as error term. The depen-

dent variables in the models were the per-block means of seedling density, richness, above-ground biomass, fecundity, and size of germinable seed bank. Significant site × habitat interactions were interpreted as support for our hypothesis of predictable shifts in net interactions along the aridity gradient. In addition to the ANOVAs, we conducted post hoc pairwise *t*-tests for each site separately, to evaluate differences between habitats. In these tests, we did not correct for multiple comparisons, since our main goal was to search for general trends in the direction and strength of interactions along the gradient, rather than looking for specific differences between habitat types.

To test the net effects of shrubs on annual plants, performance of the annuals was compared between different neighbor conditions by using the Relative Interaction Intensity (RII) index: $RII = (P_{+N} - P_{-N}) / (P_{-N} + P_{+N})$; where *P* is a measure of performance of annuals in the presence (+N) and absence (−N) of shrubs. This index has been recently shown to be superior to the commonly used RNE (Armas, Ordiales, & Pugnaire, 2004). RII was calculated for each block separately. We tested our prediction of increasingly negative RII with increasing rainfall using linear regression models with RII as dependent variable and the average rainfall at each site as independent variable. We additionally performed one way ANOVAs with site as independent variable (*df* = 4) and RII as dependent variable. RII was $\log(x + 1)$ transformed for the biomass data in order to improve homogeneity of variances. Post hoc tests (Duncan tests) were done to evaluate differences between the RII among sites.

In order to address the problem of confounding effects of shrub species and site, we performed additional analyses for the three wetter sites only, which shared *Sarcopoterium spinosum* as the common shrub species, and we obtained qualitatively similar results compared to the analysis involving all four sites and thus two different shrub species. Therefore, in order to highlight the generality of our findings, we present the results from the analyses with the complete data set.

Results

Above-ground biomass

Annual plant biomass production in open areas increased with rainfall along the gradient, with a marked difference between the desert and the three wetter sites (Fig. 1A). Large increases were

found in the understory from the arid site to the semi-arid site, whereas understory productivity decreased strongly towards the Mediterranean and the mesic Mediterranean. There were no

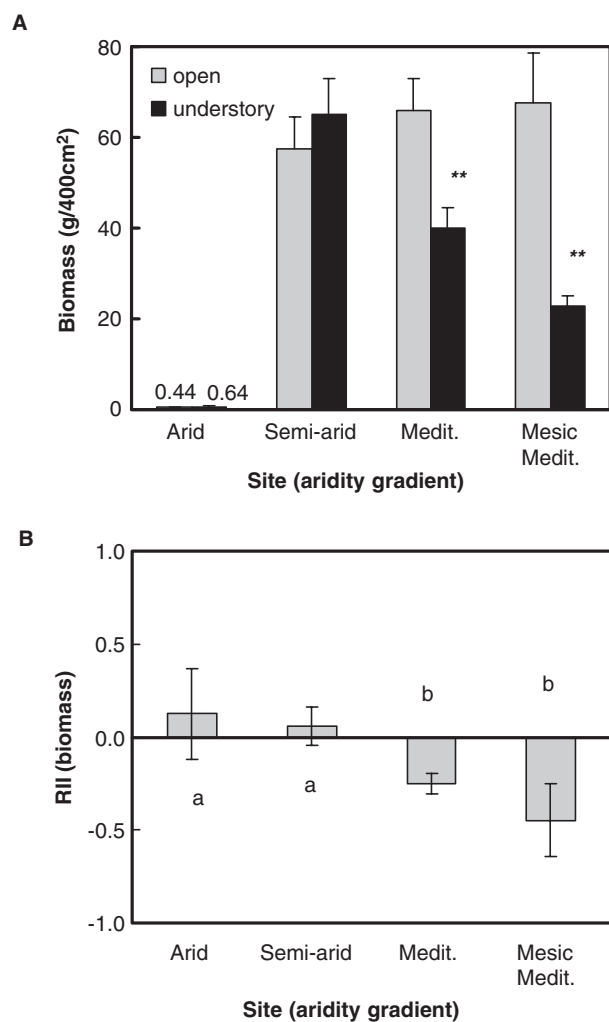


Figure 1. Above-ground biomass of herbaceous plants in areas between (open) and under shrubs (understory) along the aridity gradient. (A) Biomass (means \pm SE). Asterisks indicate significant differences between habitat types at a given site (pairwise *t*-tests, $**p < 0.01$). (B) Net effect of shrubs on herbaceous biomass expressed as mean Relative Interaction Intensity (RII) of the five blocks (\pm 95% confidence interval). Means with shared letters do not differ from each other (Duncan tests, $p > 0.05$).

significant differences between biomass in understory and open areas in the arid and semi-arid site, but understory biomass was significantly lower in the Mediterranean (61% of open) and the mesic Mediterranean (34%). These site-habitat interactions were highly significant (Table 2). Differences in RII were marginally significant in oneway-ANOVA ($F = 3.1$, $p = 0.058$), but pairwise differences were significant between the two arid and the two humid sites (Fig. 1B).

The net effect of shrubs on productivity of annual communities ranged from neutral (nominal positive) net effect to increasingly negative effects with increasing average rainfall amount. This trend was highly significant in the regression analyses (Table 3).

Seedling density

Seedling density of the annual plant communities both in open areas and in the understory increased greatly from the arid to the semi-arid site and decreased towards the Mediterranean sites, however more markedly in the shrub understory (Fig. 2A). With the exception of the arid site, where density was 3.6 times higher under shrubs than between shrubs, densities in the understory were consistently lower at the other sites. The reduction in seedling density under shrubs became stronger with increasing rainfall (semi-arid: 67% of open, Mediterranean: 63%, mesic Mediterranean: 34%), but these habitat \times site interactions were not significant (Table 2). RII differed markedly between sites ($F = 10.96$; $p < 0.001$) and there was a highly significant trend of decreasing RII values with increasing rainfall (Fig. 2B, Table 3).

Species richness

The number of species/taxa in open areas between shrubs increased from the arid to the Mediterranean site, followed by a decrease in the mesic Mediterranean site (Fig. 3B). The pattern under shrubs was similar but with no difference in richness between the two central sites. Compared to the understory, richness tended to be lower in

Table 2. Results (*F*-values) of repeated-measures ANOVA for testing the effect of habitat (open vs. under shrubs, within-subject factor) and site (between-subject factor) on mean above-ground biomass, seedling density, species richness and seed bank density ($*p < 0.05$; $**p < 0.01$; $***p < 0.001$)

Source of variation (df)	Biomass	Density	Richness	Seed bank
Site (3)	24.94 ^{***}	5.19 [*]	22.75 ^{***}	11.12 ^{***}
Habitat (1)	24.01 ^{***}	8.37 [*]	1.96	11.87 ^{**}
Site \times habitat (3)	13.99 ^{***}	1.25	6.15 ^{**}	8.57 ^{**}

Table 3. Results of linear regression with Relative Interaction Intensity (RII) of above-ground biomass, seedling density, species richness, seed bank density, and fecundity, respectively, as dependent variable and average rainfall at each site as independent variable (** $p < 0.01$; *** $p < 0.001$)

RII for:	r^2	F	Slope
Biomass	0.30	9.02**	-0.58
Density	0.54	23.70***	-0.75
Richness	0.61	31.21***	-0.80
Seed bank	0.50	19.90***	-0.73
Fecundity	0.59	92.20***	-0.77

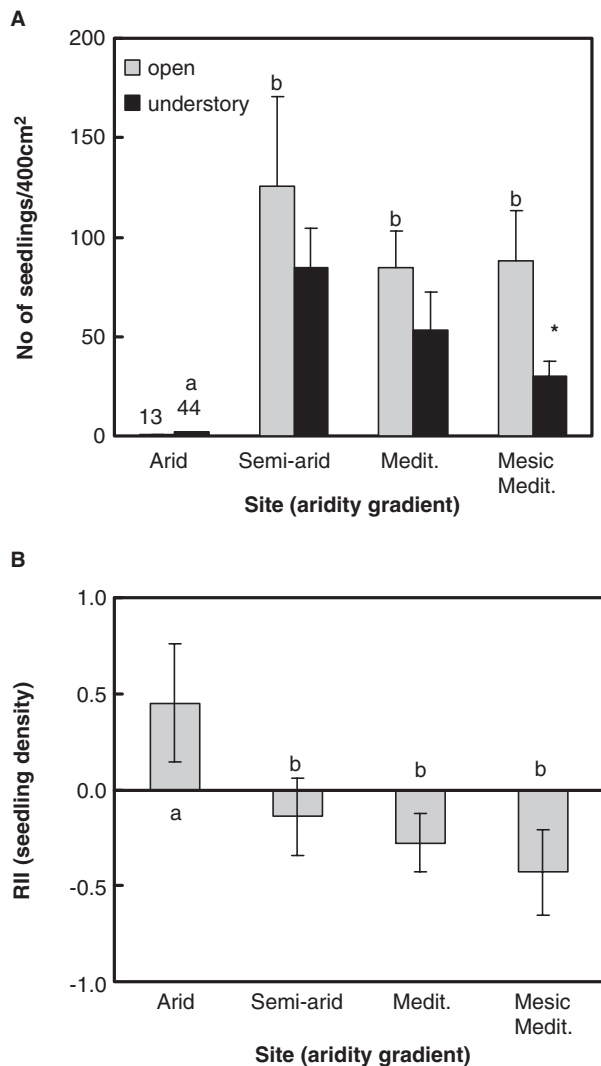


Figure 2. Seedling density in areas between (open) and under shrubs (understory) along the aridity gradient. (A) Density (means + SE). Asterisks indicate significant differences between habitat types at a given site (pairwise t -tests, * $p < 0.05$). (B) Net effect of shrubs on seedling density expressed as mean Relative Interaction Intensity (RII) of the five blocks ($\pm 95\%$ confidence interval). Means with shared letters do not differ from each other (Duncan tests, $p > 0.05$).

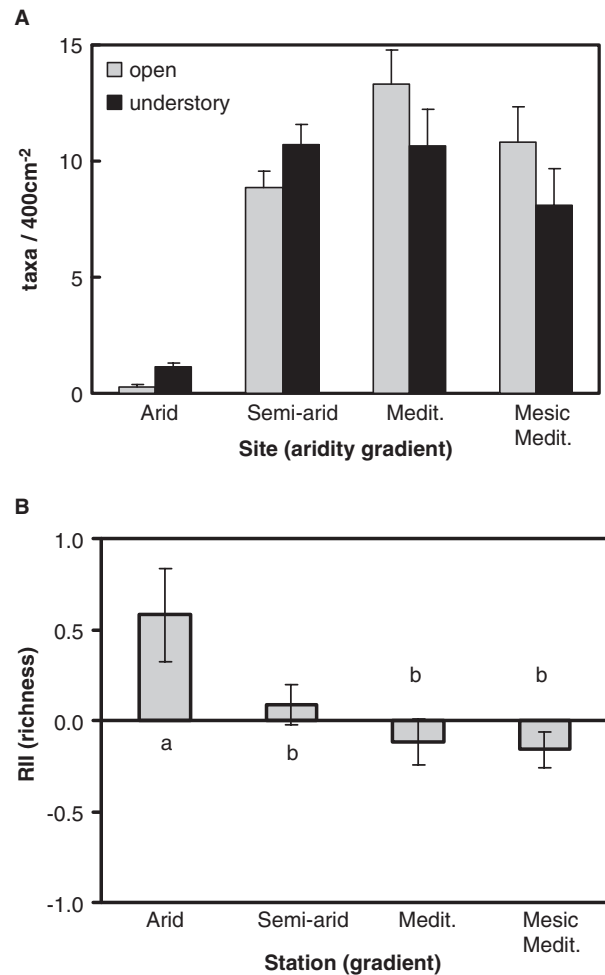


Figure 3. Richness in areas between (open) and under shrubs (understory) along the aridity gradient. (A) Taxa richness (means + SE). Asterisks indicate significant differences between habitat types at a given site (pairwise t -tests, * $p < 0.05$). (B) Net effect of shrubs on richness expressed as mean Relative Interaction Intensity (RII) of the five blocks ($\pm 95\%$ confidence interval). Means with shared letters do not differ from each other (Duncan tests, $p > 0.05$).

open areas in the two drier sites (25% and 83% of shrubs, respectively) and higher in the two moister sites (understory richness: 80% and 75% of open, respectively). This site \times habitat interaction was significant (Table 2) and mirrored the shift of the RII along the gradient (Fig. 3B, Table 3). There was a clear trend of decreasing RII on richness from positive to negative effects with increasing rainfall ($F = 17.48$, $p < 0.001$; Table 3).

Seed bank

The amount of seeds in soil and litter that were readily germinable increased from the arid site to

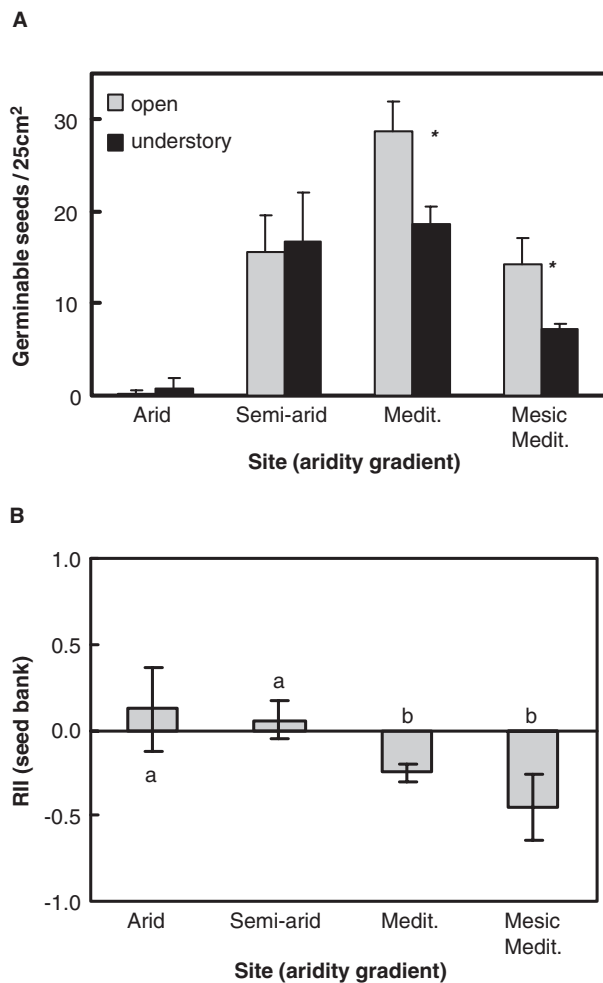


Figure 4. Size of germinable seed bank in areas between (open) and under shrubs (understory) along the aridity gradient. (A) Density (means + SE). Asterisks indicate significant differences between habitat types at a given site (pairwise *t*-tests, $*p < 0.05$). (B) Net effect of shrubs on seed bank density expressed as mean Relative Interaction Intensity (RII) of the five blocks ($\pm 95\%$ confidence interval). Means with shared letters do not differ from each other (Duncan tests, $p > 0.05$).

the Mediterranean site and decreased again in the mesic Mediterranean site (Fig. 4A). The peak at the Mediterranean site was much more pronounced in the open than under shrubs. Understory samples had similar amounts of germinable seeds as open areas in the arid and semi-arid site, but significantly lower amounts in the Mediterranean (65%) and the mesic Mediterranean (50%), resulting in a significant habitat \times site interaction in the ANOVA (Table 2). RII differed largely between sites ($F = 8.80$; $p = 0.001$), indicating that the net effect of shrubs on seed densities in the soil and litter changed from positive effects in the arid site to increasingly negative effects in the moist part of the gradient (Fig. 4B, Table 3).

Fecundity

All three desert annual species showed higher seed production under shrubs than in the open, but differences were not statistically significant (Fig. 5A, Table 4). The pooled RII differed significantly between sites (Fig. 5b, $F = 53.06$, $p < 0.001$). In the three moister sites, plants produced either similar numbers or less seeds in the understory compared to plants growing between shrubs (Fig. 5A, Table 4). These differences tended to increase with increasing rainfall, resulting in a significant, overall trend of increasingly negative RII with increasing rainfall (Fig. 5B, Table 3).

Discussion

Altogether, our findings provide clear evidence that shrubs tended to have positive or neutral net effects (i.e., positive RII) on associated annuals in arid environments and strong negative net effects in mesic environments. This is mostly in line with the predicted shift from positive to negative net interactions with decreasing environmental stress (Bertness & Callaway, 1994; Brooker & Callaghan, 1998). Similar patterns along geographical gradients have been shown before (Callaway & Pugnaire, 1999). However, the strength of our approach lies in the fact that in contrast to most previous studies, we assessed the net effect of shrubs on annuals for a wide range of community and population performance parameters. It has been previously shown that different life history stage parameters as for instance growth and fecundity can differ strongly in their dependency on environmental conditions (Goldberg, Turkington, Olsvig-Whittaker, & Dyer, 2001; Hastwell & Facelli, 2003). In contrast, all our parameters showed a fairly similar dependency on the gradient. We therefore suggest that the observed interaction shift may be characteristic for the coexistence of annual plants with shrubs along aridity gradients in general.

Productivity of the herbaceous community in the open spaces between shrubs increased steadily with rainfall. In contrast, seedling density and seedling species richness showed a unimodal pattern, with a peak in density at the semi-arid site and a marked peak in richness at the Mediterranean site. Such hump-shaped curves appear to be typical of diversity-productivity relationships and have been demonstrated for many ecosystems (Rosenzweig & Abramsky, 1993; Tilman, 1982) among which are similar aridity gradients in Israel (Aronson & Shmida, 1992;

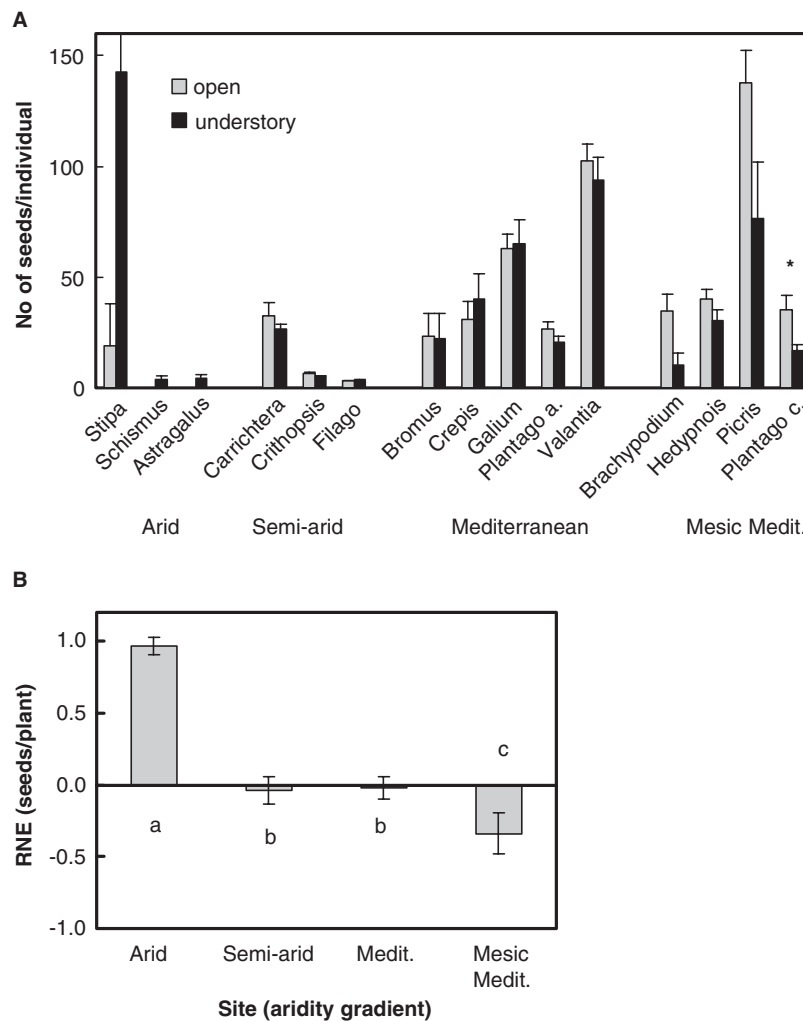


Figure 5. Seed production in areas between (open) and under shrubs (understory) along the aridity gradient. (A) Seeds per plant (means + SE) of dominant annual species. Asterisks indicate significant differences between habitat types at a given site (pairwise t -tests, $*p < 0.05$). Note that the large error bar of *Stipa* (understory, SE = 99) had to be truncated for scaling purposes. (B) Net effect of shrubs on seed production expressed as mean Relative Interaction Intensity (RII) of the five blocks (\pm 95% confidence interval); species are lumped. Means with shared letters do not differ from each other (Duncan tests, $p > 0.05$).

Table 4. Results (F -values) of repeated-measures ANOVAs for mean fecundity with habitat (shrubs vs. open) as within-subject factor and species as between-subject factor ($**p < 0.01$; $***p < 0.001$)

Source of variation (df)	Arid	Semi-arid	Mediterranean	Mesic Mediterranean
Species (2–4)	2.57	143.6 ^{***}	16.19 ^{***}	40.63 ^{***}
Habitat (1)	1.81	0.67	0.49	8.94 ^{**}
Species \times habitat (2–4)	2.11	0.48	0.86	8.57 ^{**}

Holzapfel, Schmidt, & Shmida, 1992; Osem, Per-evolotsky, & Kigel, 2002). Richness and densities of seedlings in the understory also followed a unimodal pattern in relation to the aridity gradient, but for richness the peak was shifted towards the drier

sites. More remarkably, in contrast to the open areas, productivity showed a unimodal pattern similar to richness and density, with a peak at the semi-arid site. Such a relationship between richness and productivity has not been predicted by

previous models. This observation is striking since the annual communities in the open areas, i.e., in immediate vicinity of the understory, show a different relationship between productivity and richness. These are strong indications for shrubs altering the relationship of plant performances with overall productivity along resource gradients. These results emphasize the importance of including species interactions when studying community processes, such as diversity–productivity relationships, in general (Bruno et al., 2003).

The mechanisms underlying the shift from facilitation or neutral interactions to interference cannot be addressed with a purely observational study. A more mechanistic understanding needs to experimentally separate positive and negative effects (Holzapfel & Mahall, 1999). However, since water is the main limiting factor for plant growth in the studied system, we suggest that the facilitative net interactions at the arid end of the gradient are the result of positive effects of shrubs like amelioration of drought stress by canopy shade (see summary in Callaway & Pugnaire, 1999; Maestre, Bautista, & Cortina, 2003) or improved soil structure and infiltration patterns under shrubs (Pariante, 2002). Though previous studies have indicated that desert shrubs may intercept rainfall (Sala, Golluscio, Lauenroth, & Soriano, 1989; Tielbörger & Kadmon, 2000b; Tromble, 1988), parallel studies have indicated that water content is higher under shrubs than in the open at the arid end (Pariante et al., unpubl. results). Such patterns have been demonstrated for a range of arid environments (e.g., Holzapfel & Mahall, 1999; Pugnaire, Haase, & Puigdefábregas, 1996). In contrast, competition for light, nutrients, and water are most likely a main cause for net negative effects of shrubs on understory plants in the less arid part of the gradient (Specht, Grundy, & Specht, 1990). These negative factors are commonly implicated as the chief negative agents in plant interactions at the rich end of resource gradients (e.g., Holmgren, Scheffer, & Huston, 1997). Research in close vicinity to our mesic Mediterranean site indicated that nutrients, namely phosphorus, are indeed limiting factors in the interaction between shrubs and herbaceous vegetation (Henkin, Noy-Meir, Kafkafi, Gutman, & Seligman, 1996). Interestingly, it has been found for a semi-arid environment that below-ground competition intensity between the shrub *Retama sphaerocarpa* and its understory plants was more intense in arid than in humid sites (Pugnaire & Luque, 2001). Based on our data, we cannot exclude any of the two possible patterns of negative interactions along stress gradients, as

they are disputed in the “Grime–Tilman debate” (Grime, 1973; Thompson & Grime, 1988; Tilman, 1987). However, increasing importance of facilitative interactions with aridity alone may explain the observed shift from negative net interaction to positive net interactions, regardless of whether competitive effects stay constant or decrease with stress.

We were not able to study a single shrub species along the aridity gradient. Thus, differences in shrub–annual interactions between the arid vs. the three moister sites may be attributed also to species-specific effects of different shrubs. Nevertheless, even when we compared the response to *Sarcopoterium* alone at the three moister sites, a clear reduction of negative effects on performance of annuals was observed with increasing aridity. On the other hand, the scope of our research was to assess the robustness of the Bertness–Callaway model for a whole range of different communities. Specific and ecotypic differences among the studied organisms, such as differential response to competition (Petrů et al., unpubl. results) are a necessary part of such an approach. In fact, our observation of consistent shifts in interaction strength across a wide range of parameters, species and environmental conditions highlights the robustness and validity of our findings.

In conclusion, our findings based on large-scale spatial variation in resource availability across a climatic gradient, provide support for the theoretical predictions of Bertness and Callaway (1994) and Brooker and Callaghan (1998), i.e., shifts from positive to negative interactions with decreasing stress. Yet, temporal variation in the environment may not lead to the theoretically predicted pattern in species interactions, particularly in years with high drought stress (Casper, 1996; Tielbörger & Kadmon, 2000b). This highlights the need for long-term studies encompassing a wide range of environmental conditions and communities, in order to separate between the effects of spatial and temporal variation in resource availability on positive vs. negative plant interactions along environmental gradients.

Acknowledgments

Eyal Sachs, Martina Petrů, Katja Schiffers, Muriel Shamla, Ralfi Bali, Azaria Lupo, and Tal Israel made our challenging work easier, thank you all! We are grateful to two anonymous, thorough reviewers. This study is part of the GLOWA Jordan River project funded by the German Federal Ministry of

Education and Research (BMBF) in collaboration with the Israeli Ministry of Science and Technology (MOST).

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