

TEMPORAL ENVIRONMENTAL VARIATION TIPS THE BALANCE BETWEEN FACILITATION AND INTERFERENCE IN DESERT PLANTS

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Abstract. Recently, numerous studies have pointed to the importance of positive interactions in natural communities. There is now a broad consensus that the balance between negative and positive interactions should shift along environmental gradients, with competition prevailing under environmentally benign conditions and positive interactions dominating under harsh conditions. A commonly cited example of the importance of facilitation in harsh environments is the preference of desert annual plants for the areas under the canopy of shrubs. The recognition of apparently positive effects of desert shrubs on annuals, however, has been mostly based on density measurements, while fitness parameters of the understory plants have been ignored. Also, the temporal consistency of such effects has not been previously tested. Based on conceptual ideas about the balance between interference and facilitation, we predicted that positive effects of the shrubs on the understory should dominate in dry years, while in favorable years, negative effects would be stronger. We tested our hypothesis by measuring the direction and magnitude of the shrub effect on demographic responses of four desert annual plant species during four consecutive seasons of differing rainfall. The results contradicted our initial hypothesis. Depending on the species, the effect of the shrubs shifted from either negative to neutral or from neutral to positive with increasing annual rainfall. However, this trend was stronger for the effect of shrubs on plant reproductive success than on their densities. Our data highlight the importance of measuring fitness parameters in studies of plant–plant interactions. We suggest that the negative effects of shrubs on plant fitness were due to rainfall interception, while positive effects were related to increased nutrient availability beneath shrubs. However, the mechanisms by which the shrubs and annuals interact can only be resolved using an experimental approach. Our results contradict previous hypotheses about the relative importance of positive and negative interactions along environmental gradients. A simple conceptual model summarizing the proposed role of rainfall in determining the direction of shrub effects on their understory annuals is presented.

Key words: annual plants; desert plant community; environmental gradient; facilitation; interference; plant–plant interactions; rainfall; shrubs; temporal variation.

INTRODUCTION

Interactions between organisms are often an important force in structuring natural communities. Although the main focus of contemporary ecological research has been on negative interactions, the role of facilitation in community ecology has recently gained a great deal of attention (e.g., Bertness and Shumway 1993, Bertness and Callaway 1994, Bertness and Yeh 1994, Callaway 1995, Bertness and Leonard 1997, Callaway 1997, Callaway and Walker 1997, Hacker and Gaines 1997). These studies have pointed to the fact that positive and negative interactions act simultaneously in determining the structure of communities. It has further been hypothesized that the balance between these two types of interactions depends on the harshness of the physical environment (Bertness and Callaway 1994, Bertness and Hacker 1994, Bertness and Leonard 1997, Callaway and Walker 1997, Brooker and Callaghan

1998). The importance of facilitation should increase with increasing abiotic stress, while negative interactions should prevail under benign conditions (Bertness and Callaway 1994, Callaway and Walker 1997, Holmgren et al. 1997, Brooker and Callaghan 1998). Empirical evidence for this hypothesis stems from a variety of studies investigating interactions between organisms along spatial gradients in the physical environment (e.g., Walker and Chapin 1987, Bertness and Shumway 1993, Bertness and Hacker 1994, Bertness and Yeh 1994, Greenlee and Callaway 1996, Bertness and Leonard 1997).

Natural environments are not only variable in space, but also in time. If the importance of facilitation increases with increasing abiotic stress, one would predict that temporal fluctuations in the environment would also modify the balance between positive and negative interactions in a predictable manner (Bertness and Callaway 1994, Callaway and Walker 1997, Brooker and Callaghan 1998). Unfortunately, due to the lack of long-term field studies, empirical evidence for tem-

poral shifts in the balance between facilitation and interference in ecological communities is extremely limited (but see Casper 1996, Greenlee and Callaway 1996). In this study, we tested the hypothesis that temporal fluctuations in the environment modify the balance between positive and negative interactions in a manner consistent with the prediction of Bertness and Callaway (1994).

We focused on one of the most commonly cited examples of the importance of positive interactions in plant communities, the so-called "nurse plant syndrome" (e.g., Niering et al. 1963, Turner et al. 1966, Franco and Nobel 1989). This notion describes the phenomenon that plant seedlings tend to establish under the shelter of adults of other species. Most evidence for nurse plant effects comes from arid ecosystems. A variety of studies indicate that the density and productivity of desert plants growing beneath the canopy of shrubs are greater than for conspecifics growing in the open areas between shrubs (e.g., Went 1942, Halvorson and Patten 1975, Nelson and Chew 1977, Shmida and Whittaker 1981, Tielbörger and Kadmon 1995). Shrubs may facilitate the development of understory vegetation by ameliorating a variety of physical conditions beneath their canopies. For example, overstory plants may shade the substrate and reduce evaporation loss (Keeley and Johnson 1977, Nobel 1980, Franco and Nobel 1989, Valiente-Banuet and Ezcurra 1991), or supply higher levels of nutrients than the surrounding open areas (Garcia-Moya and McKell 1970, Ros-tagno et al. 1991, Gutiérrez et al. 1993, Pugnaire et al. 1996).

In a recent study, Hacker and Gaines (1997) have defined positive interactions as "nontrophic interactions that increase the average individual fitness of at least one species. . . ." Although most ecologists would agree with this view, fitness components like mortality or seed production have rarely been examined in studies of positive interactions in ecological systems. Similarly, in the specific case of nurse plant effects in deserts, most previous studies have focused on density measurements of understory plants (e.g., Went 1942, Halvorson and Patten 1975, Shmida and Whittaker 1981, Nelson and Chew 1997) and very few studies have measured components that contribute to individual fitness (but see Tielbörger and Kadmon 1995, Casper 1996, Holzapfel and Mahall 1999). In this study, we investigated the impact of desert shrubs on the demography of understory annual species by measuring both density and reproductive success. By measuring the responses of the annuals to the presence of shrubs during four consecutive growing seasons, we attempted to investigate how differences in annual rainfall affect the direction (i.e., positive, negative, or neutral) and the magnitude of the shrub effects. Based on the theoretical concepts discussed above, we predicted that relatively dry years would result in facilitation of annuals by shrubs, while relatively favorable years would

result in negative effects of shrubs on the annual understory.

METHODS

The study site

Our study was conducted from September 1993 to April 1997 at the Nizzana research site in the northwestern Negev desert of Israel. This area is located ~60 km southwest of Ber-Sheva at the Egyptian-Israeli border, and represents the eastern continuation of the northern Sinai continental sand fields. The topography is characterized by parallel longitudinal sand dunes running from west to east.

The rainy season and, accordingly, the growing season of annual plants, extends from October through May. Mean annual rainfall is 100 mm (Berkowicz et al. 1995). However, as is typical for desert regions, the amount and distribution of yearly rainfall are highly variable. For example, in the last five years total annual rainfall in the Nizzana area ranged from 38 to 167 mm (Arid Ecosystems Research Center, Climate Data Base, Hebrew University of Jerusalem, Israel, *unpublished data*).

The study was done in a semistable sand habitat along a lower dune slope. Total cover of perennial plants in this type of habitat is ~30% and the dominant perennial species are *Molteniopsis ciliata* (Forss.) I. M. Johnst. (Boraginaceae), *Heliotropium digynum* C. Chr. (Boraginaceae), and *Stipagrostis scoparia* (Trin. & Rupr.) De Winter (Poaceae) (Tielbörger 1997b). For annual species, this habitat can be divided into two distinct subhabitats: (1) phytogenic hillocks formed under the canopy of perennial plants, and (2) open areas with mobile sand covering a thin biological surface crust. Results from previous studies (Tielbörger and Kadmon 1995, Tielbörger 1997a) have indicated that the density and biomass of most annual plant species are much higher under the canopy of perennial plants than in the open areas between them. For the present study, four annual species were selected: *Senecio glaucus* L. (Asteraceae), *Ifloga spicata* (Forss.) Sch. Bip. (Asteraceae), *Rumex pictus* Forss. (Polygonaceae), and *Erodium laciniatum* (Cav.) Willd. (Geraniaceae). These species are among the most abundant species in the study area and they occur in both types of habitats.

Sampling design

In the first summer of the study (1993), four permanent blocks (replicates) of ~50 m × 50 m were marked in the study area. Each block was divided into two types of habitat: shrubs and openings. The shrub habitat was defined as the zone beneath the canopies of perennial plants, and the remaining area was defined as openings. Before any germination occurred in 1993, 16 randomly chosen quadrats of 25 × 25 cm were set up in each of the habitat types of each block. Seedlings of the four focal annual species emerging in these quad-

rats were counted throughout the following four seasons. Preliminary experiments indicated that counting small seedlings among dense branches of shrubs was very difficult and might have introduced bias to density estimates. We therefore corrected our density measurements using data from destructive counts in adjacent areas (for a detailed description of this procedure see Tielbörger and Kadmon 1995, Tielbörger 1997b). Counts were made several times after the first rainfall of each season, depending on amount and within-season distribution of rainfall events. More counts were made in the first and last season, when very early and very late rains resulted in germination of two separate cohorts. Based on the counts, we determined mean density of emerging plants (at the beginning of the season) and mean density of reproductive plants (at the end of the season) for each focal species in each block.

Measurements of reproductive success

To estimate reproductive success, individuals of each of the four focal species were collected randomly during the time of seed set, and the number of seeds produced per plant was determined. In the first, second, and fourth year of study, 100 individuals (25 per block) were collected for each species in each habitat type. Due to low densities and high mortality in the third season (1995–1996), no individuals could be collected for *Senecio glaucus* and *Rumex pictus*. For *Ifloga spicata*, 48 individuals (12 per block) were collected in the open areas and for *Erodium laciniatum*, 100 plants (25 per block) were collected in the openings and 52 plants (13 per block) in the shrub habitat. Reproductive success was defined as mean seed production per germinating plant. It was estimated for each block by multiplying the mean seed production per reproductive plant by the fraction of emerging plants surviving to seed production.

Statistical analysis

The hypothesis that the effect of shrubs on annual plant performance varied from one year to another was tested using analyses of variance. The dependent variables in the analyses were the per-block means of densities and reproductive success, respectively ($n = 4$). Reproductive success had to be calculated on a per-block basis, because mortality estimates were obtained using the per-block estimates of densities. Means were calculated for the density of each block, because the data based on per quadrat measurements contained many zero values and did not fulfill the assumptions of ANOVA. We are aware that the low number of replicates may have introduced Type I error into our analyses (i.e., deciding that the main effects are not significant when in fact they are). However, results from additional analyses, based on quadrats ($n = 64$) in the case of densities, and on individuals ($n = 100$, except for the drought year) in the case of seed production,

were similar to those obtained from our more conservative approach.

For each species, repeated-measure ANOVA models were constructed with per-block means of density and reproductive success as separate dependent variables, habitat type and year as a within-subject factors, and among-block variation as error term ($n = 4$). Based on our hypothesis, we expected to find a statistically significant interaction between the effect of year and habitat type on mean density and reproductive success. The above approach was based on the assumptions that the block effect did not interact with those of habitat type and year. To test this assumption, we constructed mixed-model ANOVAs with year as the within-subject factor, habitat type as the fixed effect, block as the random effect, and within-block variation (variation among quadrats, $n = 64$, in the case of the density data and among individuals, $n = 100$, in the case of the seed production data) as error term. The results obtained from these tests were consistent with our assumption and revealed no interaction between block and year or habitat type.

To evaluate whether and how the direction and magnitude of the shrub effect on the understory annuals changes with increasing annual rainfall, we defined the shrub effect on the annual populations as “positive” when densities and/or reproductive success were higher under shrubs than in open areas, and as “negative” when demographic rates were lower under shrubs than in open areas. The magnitude and direction (i.e., positive, negative, or neutral) of the effect of shrubs on density of a particular species j in a particular year t was estimated as:

$$E_{D,j,t} = [D_{j,t(\text{shrub})} - D_{j,t(\text{open})}] / D_{j,t(\text{open})}$$

where $D_{j,t(\text{shrub})}$ is the mean density of species j in year t in quadrats located under shrubs, and $D_{j,t(\text{open})}$ represents the mean density of that species in the same year in quadrats located in open areas. $E_{D,j,t}$ then represents the relative increase in density of a particular species under shrubs as compared to its density in open areas in a particular year. Similarly, the relative effect of shrubs on reproductive output of the annual plants ($E_{R,j,t}$) was estimated as

$$E_{R,j,t} = (R_{j,t(\text{shrub})} - R_{j,t(\text{open})}) / R_{j,t(\text{open})}$$

Positive values of $E_{D,j,t}$ and $E_{R,j,t}$ indicate that densities and per capita reproductive success, respectively, were higher under shrubs than in open areas, while negative values indicate negative effects of shrubs on annual plant demographic responses.

In order to test whether differences in mean density and mean reproductive success between habitat types were statistically significant, we performed paired t tests for each year and species separately. To minimize bias introduced by multiple comparisons, significance levels were adjusted using the Bonferroni correction for a particular species. All data were $\log(x + 1)$ trans-

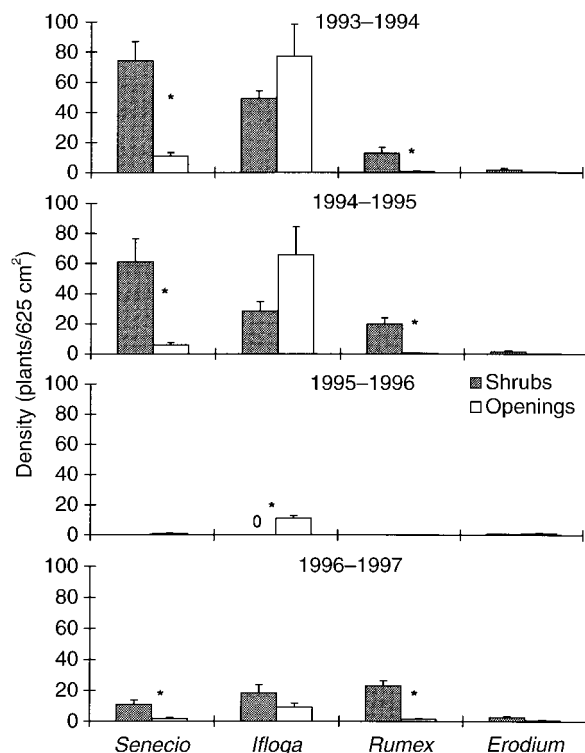


FIG. 1. Mean (± 1 SE) densities of emerging plants in the four seasons. Asterisks indicate significant differences between shrubs and openings for a given species in a given season ($P < 0.05$, paired t tests, significance levels were corrected for multiple comparisons using the Bonferroni correction). Zeros indicate zero values.

formed prior to analysis to improve the linearity of the models (Sokal and Rohlf 1995).

RESULTS

Rainfall and timing of seedling emergence

Absolute amount as well as the distribution of rainfall events differed considerably between the 4 yr of the study. Accordingly, timing and magnitude of seedling emergence varied among the 4 yr. Total precipitation was 50 mm in the 1993–1994 season, 167 mm in the 1994–1995 season, 38 mm in the 1995–1996 season, and 74 mm in the 1996–1997 season (Arid Ecosystems Research Center, Climate Data Base). The range of rainfall conditions included both the wettest (1994–1995) and the driest (1995–1996) season re-

corded since the establishment of the Nizzana research site in 1989.

In 1993–1994, one minor rainfall event (3 mm) at the end of November caused the first germination in the open habitat, but all the emerging seedlings died before the first major rainstorm (20 mm in mid-December). Following this rainstorm, which resulted in one major germination event in both subhabitats, only rain events of low intensity were measured, and the substrate dried out very quickly. Resultant seedling mortality was very high in this year.

The 1994–1995 season's precipitation was extraordinarily high and consisted of four large rainstorms the first of which (54 mm at the beginning of November) exceeded the previous year's total. This storm caused a single, major germination event in both open areas and under shrubs. Following the first rain, there were several smaller rainstorms. This indicated that water was not limiting throughout the sensitive seedling stage. The majority of emerging annual plants survived to seed production, and the high and evenly distributed rainfall resulted in an extension of the growing season through mid-summer 1995.

In the 1995–1996 season, one late, small rainstorm caused little germination, mainly in the open habitat. The only major rainstorm of that season occurred in late March, after nearly all these annual plants had died. This late-season rain did not cause any further germination.

Similar to the first season, a small rainfall in November 1996 resulted in the germination of a few plants, but all seedlings died before the first major rainstorm. This rain, which was followed by one distinct germination event, occurred very late in the season (mid-January 1997) and was followed by several smaller storms. Due to this late rain, the growing season was very short.

Seedling densities

None of the four annual species that we studied responded in a consistent manner to the presence of shrubs during the course of study (Fig. 1). As was expected, the habitat \times year interaction was statistically significant in all cases (Table 1). The values of E_D were lowest during the driest season and, with the exception of *Ifloga spicata*, highest during the wettest season (Fig. 2). With increasing annual rainfall, between-habitat differences in densities of the four spe-

TABLE 1. Summary of results of repeated-measures ANOVAs (F values) designed to test the within-subject effects of year and habitat type (shrubs vs. openings) on mean densities per block ($n = 4$) of the four focal annual plant species.

Source of variation (df)	<i>Senecio</i>	<i>Ifloga</i>	<i>Rumex</i>	<i>Erodium</i>
Year (3, 9)	88.34***	156.59***	51.22***	2.28
Habitat (1, 3)	105.86**	7.63	204.96***	4.72
Year \times Habitat (3, 9)	37.84***	30.04***	95.82***	10.03**

** $P < 0.01$, *** $P < 0.001$.

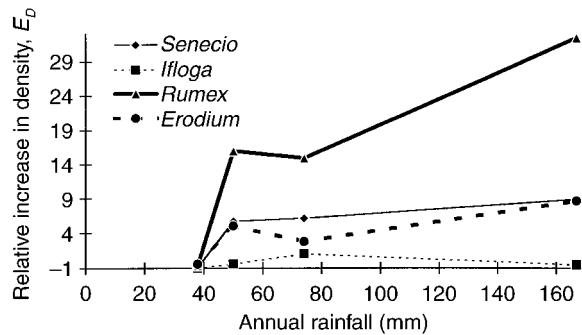


FIG. 2. Relative increase in density (E_D) of annual plants under shrubs compared to the open areas under different regimes of annual rainfall.

cies changed, either from significantly higher densities in the openings towards no between-habitat differences (*Ifloga spicata*), or from no difference, towards higher densities under shrubs (*Senecio glaucus*, *Rumex pictus*, *Erodium laciniatum*) (Fig. 1). Thus, in contrast to our expectations, there was a general trend of increasing, rather than decreasing, positive shrub effects on annual plant densities with increasing rainfall. However, this trend was not consistent for three out of the four annual species studied. For two species (*Rumex pictus* and *Erodium laciniatum*), values of E_D were not higher in the intermediate year (1996–1997) than in the driest first year, and one species, *Ifloga spicata*, had higher values of E_D in the intermediate year than in the wettest season (Fig. 2). The data furthermore indicate that differences between years in annual plant densities were larger in the shrub habitat than in open areas (Fig. 1).

Reproductive success

Like their effect on densities, shrubs did not have a consistent effect on reproductive success during the course of study (Fig. 3). Two species (*Senecio glaucus* and *Rumex pictus*) failed to reproduce during the driest season (1995–1996), and, due to division by zero, the calculation of E_R was not possible. However, within the range of existing values, E_R of all four species increased monotonically with increasing annual rainfall, and changed from negative values in drier years to positive values in wetter years (Fig. 4). The statistical results indicated that the effect of shrubs on seed production changed either from neutral (i.e., statistically not significant) to significantly positive or from significantly negative to neutral, when annual rainfall increased (Fig. 3). With the exception of *Erodium laciniatum* ($P > 0.05$), the habitat \times year interaction was highly significant for all species, confirming that the effect of shrubs on reproductive success was year dependent (Table 2). As with the density responses, between-year differences in reproductive success were larger for the shrub habitat than for the openings (Fig. 3).

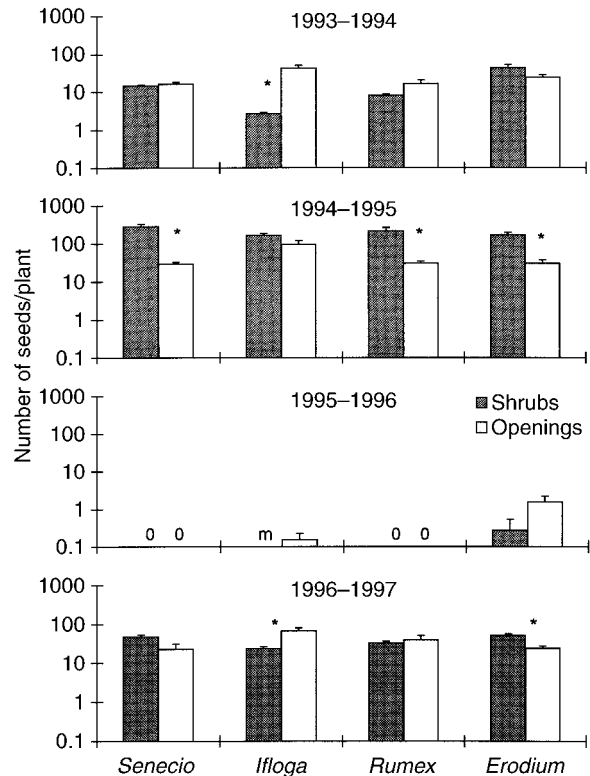


FIG. 3. Mean (± 1 SE) reproductive success in the four seasons. Asterisks indicate significant differences between shrubs and openings for a given species in a given season ($P < 0.05$, paired t tests, significance level corrected for multiple comparisons with the Bonferroni correction). Note that the scale is log₁₀. Zeros indicate zero values, m indicates missing values.

DISCUSSION

Our results indicate that the effect of desert shrubs on their understory annuals may vary considerably from one year to another. The observed range of demographic responses of individual species to the presence of shrubs, and the finding that such demographic responses may be inverse in different years, point to the importance of long-term studies to understanding

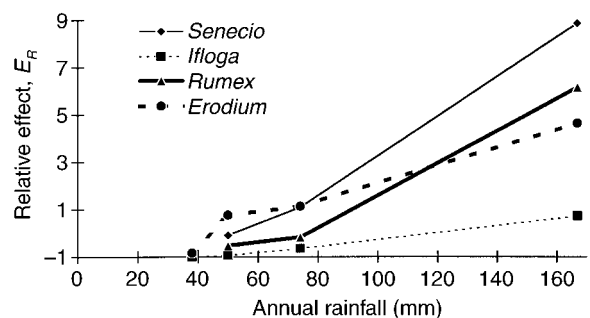


FIG. 4. Relative increase in reproductive success (E_R) of annual plants under shrubs as compared to the open areas under different regimes of annual rainfall.

TABLE 2. Summary of results of repeated-measures ANOVAs (F values) constructed to test the within-subject effects of year and habitat type (shrubs vs. openings) on mean reproductive success per block ($n = 4$) of the four focal annual plant species.

Source of variation (df)	<i>Senecio</i>	<i>Ifloga</i>	<i>Rumex</i>	<i>Erodium</i>
Year (3, 9)	153.71***	405.67***	206.56***	107.34**
Habitat (1, 3)	426.56***	131.65***	8.11	1099.19*
Year \times Habitat (3, 9)	20.36***	44.70***	13.49***	7.75

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

species interactions in desert plant communities. Unfortunately, most previous studies on the effect of shrubs on desert annuals were based on a single year of observation (e.g., Went 1942, Halvorson and Patten 1975, Shmida and Whittaker 1981, Tielbörger and Kadmon 1995, Pugnaire et al. 1996, but see Tielbörger and Kadmon 1997). Our results indicate that the interpretation of patterns observed in such short-term studies may be unreliable.

Furthermore, previous studies have suggested that the relative contribution of facilitation and interference is altered by environmental variation in a predictable manner. When environmental conditions become more severe, a shift towards stronger positive effects is predicted (Bertness and Callaway 1994, Callaway and Walker 1997, Holmgren et al. 1997, Brooker and Callaghan 1998). We therefore hypothesized that shrubs would facilitate annual species during drought years, while in relatively benign years, negative effects would prevail. Our results contradict this hypothesis and indicate that the net effect of positive and negative interactions was shifted towards positive, rather than negative effects, when environmental conditions (i.e., water availability) were more favorable.

The mechanisms by which shrubs and annuals interact are numerous, and can only be untangled using manipulation of environmental severity. For example, Callaway et al. (1991) and Holzapfel and Mahall (1999) were able to identify and separate positive and negative effects of overstory plants on their understory by using both measurements of abiotic variables and experimental manipulations. Also, without manipulations of canopy cover (e.g., Callaway 1994), one can not resolve whether shrubs and annuals really interact, or whether the observed relationships are the result of the reaction to a third factor which affects both shrubs and annuals. However, regarding the history of the study site, we believe that the patchiness in habitat conditions for the annual plants is mainly due to the presence of shrubs. The sand dunes had been nearly bare of vegetation and composed of completely open and mobile sand until 1982, because of heavy grazing by Bedouin herds (Tsoar and Møller 1986). In 1982 the area was protected from grazing, and since then, a recovery of higher vegetation and a microbiotic surface crust has taken place on the dunes. It appears unlikely that there was any patchiness in habitat conditions in the open

and mobile sand, which results in the distribution of shrubs as it is observed today.

Although our findings are based on demographic measurements along a natural environmental gradient rather than on experiments, the observed patterns of demographic response do allow us to suggest possible mechanisms for the interaction between shrubs and annuals in the studied system. Our finding that the relative effect of the shrubs on emergence and reproductive success of annual plants changes from negative to positive with increasing rainfall suggests that shrubs had an overall negative effect on water availability. This effect was particularly pronounced during the extreme drought of 1995–1996, in which emergence and reproduction under shrubs were zero or nearly zero for three of the species studied. Field observations indicated that amount and intensity of rainfall were not sufficient to wet the soil beneath the perennial plants during that season. This suggests that interception of rainfall by shrub canopies was important in limiting emergence and reproduction of understory plants during the drought year. While several previous studies have highlighted the importance of rainfall interception by the canopy of desert shrubs (Pressland 1976, Tromble 1988, Martinez-Meza and Whitford 1996), our study is the first to show that such an effect may have demographic consequences for understory plants.

Implicit in all previous studies about the importance of facilitation under harsh conditions, is the assumption that environmental harshness is ameliorated by the facilitator species. For example, Holmgren et al. (1997) have used the concept of nurse plants to illustrate how positive and negative effects of trees and shrubs on the understory shift along rainfall gradients. Based on some previous studies, they suggested that shrubs have a positive effect on water availability beneath their canopy. Consequently, they predicted that facilitation would be particularly important under conditions of high water stress. Yet, as explained above, shrubs probably had negative effects on water availability by intercepting rainfall (Pressland 1976, Tromble 1988, Martinez-Meza and Whitford 1996). Consequently, the harshness of the conditions (in terms of water availability) was intensified rather than ameliorated by the presence of shrubs. This may explain why the effect of shrubs on the understory annuals was positive only when water was abundant.

In the wettest year of study, reproductive success of all annual species was higher under perennial plants than in the openings. Although we did not measure nutrient contents in the soil, our results may be attributed to higher nutrient availability beneath shrub canopies (García-Moya and McKell 1970, Charley and West 1975, Franco and Nobel 1989, Rostagno et al. 1991, Gutiérrez et al. 1993, Sarig et al. 1994, Pugnaire et al. 1996, Moro et al. 1997). The open sands are extremely poor in nutrients (Pfisterer et al. 1996), and shrubs may represent "fertile islands" (García-Moya and McKell 1970, Garner and Steinberger 1989, Schlesinger et al. 1996) within an otherwise nutrient-poor matrix. As nutrients can be expected to track water supply, such a positive effect of shrubs is more likely to occur under wet conditions, when water is not limiting.

The trend towards stronger positive effects of shrubs with increasing precipitation was less pronounced in the case of the density data. This can be explained by the fact that individual reproduction depends directly on the amount of rainfall, whereas densities are a function of available seed supply and germination rates. Therefore, density may be much more affected by previous years' precipitation than by the rainfall in the current year. While germination rates should be directly and positively correlated with current annual rainfall, seed densities depend on fecundity during previous years (Kadmon 1993). In addition, Tielbörger (1997b) has found that not only seed production, but also the fraction of germinating seeds, may be a function of previous years' precipitation. Also, several studies focusing on desert shrublands have indicated that seeds are more likely to be trapped under shrub canopies than in the openings (Nelson and Chew 1977, Reichman 1984, Price and Reichman 1987, Mull and MacMahon 1996). This may lead to high seed densities under shrub canopies, which may explain why densities of emerging plants were higher beneath shrubs in most years of our study. Only one species (*Ifloga spicata*) tended to be more abundant in the open areas. Seed trapping by shrubs is less important for that species, because approximately 30% of the seeds of *Ifloga* are not immediately dispersed, but stay on the mother plant for ~1 yr (K. Tielbörger, unpublished data). These seeds then germinate directly on the dead mother plant in the following growing season.

Even though reproduction rather than densities should be directly affected by the actual rainfall conditions, reproductive success may also be a function of previous years' demographic rates. If high precipitation during previous years resulted in high seed production, this may affect reproductive success in the following years when survival and seed production are density-dependent (Kadmon 1995). For example, high seed densities may result in a highly competitive environment for the emerging seedlings. If competition affects either seedling mortality or seed production, or both,

reproductive success will also decrease. Due to higher seed densities under shrubs, such a carryover effect on reproductive success from previous years may be higher under shrub canopies. Competitive interactions among annuals may be even more important than interactions between the shrubs and the annuals, which would result in a misinterpretation of the shrub effects on their understory. However, in neighbor-removal experiments, only two of the four species (*Senecio glaucus*, *Rumex pictus*) exhibited density-dependent reproductive success, and competition intensity was similar in both habitats (Tielbörger and Kadmon, *in press*).

Previous attempts to investigate positive effects in plant communities have rarely examined fitness parameters of the interacting species, and most evidence for facilitation in desert plant communities is based on observed density responses rather than on measurements of demographic parameters (e.g., Went 1942, Halvorson and Patten 1975, Shmida and Whittaker 1981, Sarig et al. 1994, Pugnaire et al. 1996, though see Casper 1996). However, in our opinion, fitness parameters should be the key measure for evaluating facilitative effects of one plant on another (see also Hacker and Gaines 1997). Pure spatial associations between shrubs and annuals do not necessarily indicate that shrubs facilitate the understory annual populations. Our finding that nurse plants may have differential effects on density and reproductive success highlight the importance of measuring fitness responses in future studies on positive and negative interactions in plant communities.

Most evidence for the increasing importance of facilitation with increasing abiotic stress comes from studies that have investigated plant responses to spatial environmental gradients. It has been assumed that the above model should also apply for temporal variations in the favorability of the environment (Bertness and Callaway 1994, Callaway and Walker 1997, Holmgren et al. 1997). Unfortunately, the degree to which the relative contribution of positive and negative interactions may be altered by temporal environmental variation has hardly been studied in the field (but see Greenlee and Callaway 1996, Casper 1996). While Greenlee and Callaway (1996) reported negative effects of bunchgrasses on a rare *Lesquerella* species in a wet year and facilitation during a relatively dry year, Casper (1996) has found that drought did not intensify either positive or negative interactions between Chihuahuan desert shrubs and the herbaceous perennial *Cryptantha flava*. Our results are consistent with the latter finding that positive interactions were not more important in years of higher abiotic stress. Yet, much more empirical evidence is needed in order to understand how the nature of plant-plant interactions changes along temporal environmental gradients.

A simple conceptual model can summarize our interpretation of the role of rainfall in altering positive and negative effects of desert shrubs on their under-

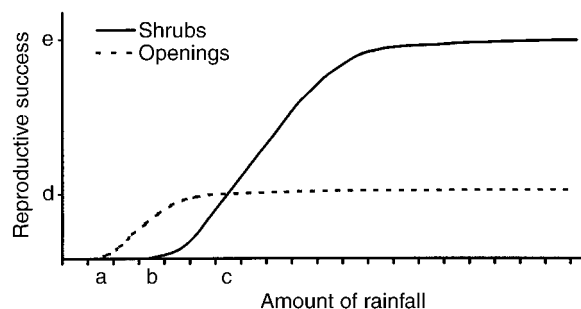


FIG. 5. Conceptual model depicting the qualitative relationships between the amount of rainfall and the reproductive success of annual plants under shrub canopies and in open areas. The model predicts negative effects of shrubs on plant reproductive success in relatively dry years (rainfall < c) but positive effects for relatively wet years (rainfall > c). Point a = threshold value of rainfall that allows reproduction in the open habitat; point b = threshold value of rainfall that allows reproduction in the shrub habitat (higher than point a due to rainfall interception by shrub canopies); point c = critical rainfall threshold above which positive effects of shrubs on plant reproductive success predominate over negative effects; below point c water is the main limiting resource under shrubs, while above c, nutrients are limiting in the open areas; point d = reproductive success in the open habitat when water is not limiting; point e = reproductive success under shrubs when water is not limiting (higher than d due to increased nutrient regeneration).

story annual populations (Fig. 5). A certain threshold of precipitation is required for successful reproduction of annual plants in the open areas (a). This threshold is higher beneath shrubs (b), due to rainfall interception by the shrub canopies. Above this threshold (b), reproductive success is positively correlated with the amount of rainfall, until a certain level of precipitation is reached, above which no further gain in reproduction is obtained and water is not limiting. The maximum reproductive success of plants inhabiting the open areas (d) is lower than that of conspecifics growing beneath shrubs (e), due to nutrient limitation in the open areas. This simple model is consistent with our empirical results, although threshold values and relative differences in reproduction between habitat types may vary in a species-specific manner. The model is also consistent with our observation that the range of demographic responses to rainfall fluctuations was larger under shrubs than in open areas. Under conditions of very low rainfall, water is more limiting under shrub canopies than in open areas, while under conditions of high water supply, reproductive success can reach much higher values under shrubs, due to higher nutrient contents. It should be noted that the validation of this model requires experimental manipulation of environmental severity (both in water and in nutrients) to elucidate the proposed mechanism of interaction among shrubs and annual plants.

While the above assumption of positive effects of desert shrubs on nutrient availability is widely supported by many previous studies (Garcia-Moya and

McKell 1970, Charley and West 1975, Franco and Nobel 1989, Rostagno et al. 1991, Gutiérrez et al. 1993, Sarig et al. 1994, Pugnaire et al. 1996, Moro et al. 1997), the effect of shrubs on water availability is less clear. Most studies of nurse plant effects in desert ecosystems have stressed the importance of positive effects of shrubs on water availability by reducing evaporative loss (Nobel 1980, Franco and Nobel 1989, Valiente-Banuet and Ezcurra 1991) or by hydraulic lift (Caldwell et al. 1998). In contrast, our results indicate that at least during very dry years, interception of rainfall by the canopy may lead to negative effects of shrubs on their understory plants. This difference may be caused by the fact that our study occurred during drier conditions than did most previous studies, in which only positive effects were documented. For example, in the only study which has tested the effect of an exceptionally dry year on the interactions between desert shrubs and understory plants (Casper 1996), rainfall in the "drought" year (105 mm) was still higher than in three of the four seasons in our study. Thus, our study is the first to be done under a range of rainfall conditions, including the level below which desert annuals were unable to germinate and reproduce. Our overall results highlight the importance of detailed long-term demographic research in order to understand how temporal environmental variation may alter the general nature of interactions among species.

ACKNOWLEDGMENTS

We would like to thank C. Holzapfel, R. Brooker, and an anonymous reviewer, for their valuable comments on an earlier version of this manuscript. R. Prasse, A. Höhn, and A. Stratmann provided help in the field. The extraordinary support of I. and H. Künne is gratefully acknowledged. The research was funded by the MINERVA foundation, the Lady Davis Fellowship Trust, the Israel Academy of Sciences and Humanities, and the German Ministry for Education and Research (BMBF). Fieldwork was done at the Nizzana research site of the Arid Ecosystems Research Center of the Hebrew University of Jerusalem and the MINERVA Foundation.

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