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Indirect effects in a desert plant community: is competition among annuals more intense under shrub canopies?

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Abstract

An unresolved discussion in contemporary ecology deals with the relative importance of competition along environmental gradients. In deserts, local-scale differences in environmental productivity may be caused by the presence of shrubs, which represent a favorable habitat for annual populations within a nutrient-poor matrix. In this study, we attempted to test the hypothesis that facilitation of desert annuals by shrubs increase the intensity of competition among the annual plants. Such negative indirect effects have so far been ignored in studies about plant-plant interactions. We tested our hypothesis by measuring seedling survival and fecundity of four abundant annual plant species with and without neighbors in open areas and under shrub canopies in a sandy desert area. Our findings did not indicate indirect negative effects of shrubs on their understory annuals. Sensitivity to the presence of neighbors varied between species and surprisingly, the species with the smallest seeds was the only one which was not negatively affected by the presence of neighbors. In contrast to our hypothesis, there was no difference between the habitat types shrubs and openings in absolute and relative competition intensity. Our overall results suggest that negative indirect effects of shrubs are unimportant in determining demographic response of understory annual plants.

Introduction

Interactions between organisms have been recognized as a major factor in structuring natural communities. However, for unproductive environments, the importance of interactions as determinants for the long-term persistence of populations has previously been questioned (Grime 1973; Huston 1979). The above authors have argued, that competition intensity among plants is much higher in productive than in unproductive environments, because neighbor biomass is larger and interactions more frequent. However, this view has been challenged by Newman (1973) and Tilman (1982, 1988), who have argued that competition intensity is equally high along productivity gradients. These authors hypothesized that in unproductive habitats interactions among plants are mainly below-ground,

while in productive environments above ground competition (e.g., for light) dominates.

The available empirical results for competitive interactions along environmental gradients are conflicting and either of the theories has found support. It has been observed that the outcome of experiments may largely depend on the life history stage of the target plant (Goldberg et al. 1999). For example, small seedlings may be much more sensitive to the presence of neighbors than adult plants (Callaway & Walker 1997; Goldberg et al. 1999; Nash-Suding & Goldberg 1999; Foster 1999). These studies have highlighted the importance of studying responses of target plants to competition at different life history stages.

As an alternative solution for the conflicting empirical results, it has been suggested that the outcome of the experiments depends on whether *absolute* or

relative competition intensity (i.e., the net reduction in plant performance due to competition *vs.* the net reduction standardized by plant performance in the absence of competition) were measured (Grace 1993, 1995). Previous studies have indicated, that absolute competition intensity is much more sensitive to gradients in the productivity and disturbance regime of the environment (Campbell & Grime 1992; Grace 1993; Turkington et al. 1993; Kadmon 1995). Therefore, Grace (1993) has pointed to the importance of measuring both absolute and relative competition intensity in studies of competition among plants along productivity gradients.

Based on the arguments of Grime (1973) and Huston (1979), it has been assumed that in desert environments, competition plays a minor role for the performance of plants. However, results of a recent study have indicated that the likelihood of detecting a positive relationship between competitive magnitude and productivity is particularly large in unproductive habitats (Foster 1999). Arid and semi-arid ecosystems frequently exhibit a two-phase mosaic structure with patches of high and low plant cover (Aguiar & Sala 1999; Klausmeier 1999). This suggests, that the relative importance of competition may vary among such patches of different productivity (Kadmon 1995). In particular, local-scale differences in habitat productivity are often caused by the presence of perennial shrubs. It has been shown that desert shrubs serve as 'islands of fertility' with nutrient contents and water availability being much higher under the canopies of desert shrubs than in the open areas between them (Garcia-Moya & McKell 1970; Garner & Steinberger 1989; Nobel, 1989; Rostagno et al. 1991; Gutiérrez et al. 1993; Pugnaire et al. 1996; Schlesinger et al. 1996; Aguiar & Sala 1999). Therefore, density and productivity of desert annuals growing beneath the canopy of shrubs are often much higher than for conspecific plants growing in the open areas between shrubs (e.g., Went 1942; Halvorson & Patten 1975; Nelson & Chew 1977; Shmida & Whittaker 1981; Tielbörger & Kadmon 1995). One may expect that facilitation by shrubs may lead to an increasing intensity of competition among the facilitated plants. For example, Aguiar & Sala (1994) have investigated recruitment patterns of perennial grasses in a Patagonian steppe and found a shift from positive to negative effects on recruitment as densities of tussock grasses around shrubs increased. However, in spite of the large number of studies conducted to investigate direct shrub effects on desert annuals, indirect effects via density-dependent mechanisms have not been explicitly addressed before.

It has been previously suggested that seed size and competitive ability are inversely related to each other (Winn 1985; Rees 1995). Yet, empirical evidence for the existence of such a trade-off is still very limited. In this study, we wanted to test the prediction that small-seeded species suffer more from crowding effects in the productive understory than species with relatively large seeds.

Our study was conducted in a sandy desert area in the northwestern Negev desert. Densities of annual plants in this area are usually much higher under shrub canopies than in the open spaces in between shrubs (Tielbörger & Kadmon 1995, 1997). Furthermore, a recent study has indicated that differences in sand stability modify or even reverse competition intensity among annual plants in the area (Kadmon 1997). In that study it could be shown that competition among annuals was intense in stable habitats, while annuals had no effects on their neighbors in areas of high sand mobility. Shrubs are very effective in stabilizing mobile sand (Danin 1996), and it may be expected that competition intensity among understory plants will differ greatly between mobile open areas and relatively stable areas under shrub canopies. By measuring the demographic responses of annual plants to the presence of neighbors under perennial shrubs and between shrubs we attempted to investigate, whether differences in habitat productivity and surface mobility affect the intensity of competition among the annuals in a predictable manner.

In particular, we hypothesized that (1) the intensity of competition among annual plants is much higher under shrubs than between shrubs, (2) absolute competition intensity is more sensitive to differences in habitat conditions than relative competition intensity, and (3) small-seeded species are competitively inferior to large-seeded ones.

Methods

The study site

The study was conducted between March 1996 and May 1997 at the Nizzana research site in the northwestern Negev desert of Israel. The area is located about 60 km southwest of Beer 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 trending from west to east. The upper parts of the dunes are still mobile, while the lower parts and the interdune areas are partly stabilized by a microbiotic soil surface crust and a relatively dense vegetation cover (Tielbörger 1997a).

The rainy season and, accordingly, the growing season of annual plants, extends from October to May. Mean annual rainfall is 90 mm (Berkowicz et al. 1995). However, amount and distribution of yearly rainfall is highly variable. Rainfall during the study period was slightly below the long-term average and measured 80 mm.

The study was conducted in a habitat of semi-stable sand along a lower dune slope. Total cover of perennial plants in this type of habitat is 30% and the dominant perennial species are *Moltkiopsis ciliata* (Forss.) I. M. Johnst. (Boraginaceae), *Heliotropium digynum* C. Chr. (Boraginaceae) and *Stipagrostis scoparia* (Trin. & Rupr.) De Winter (Poaceae). For annual species, the environment can be divided into two distinct habitats types (Tielbörger 1997a): phytogenic hillocks formed under the canopy of perennial plants and open areas between shrubs with mobile sand covering a thin biological surface crust. Density and seed production of annual plant species are usually much higher under the canopy of perennial plants than in the open areas between them (Tielbörger & Kadmon 1995; Tielbörger 1997a). Previous studies have indicated that a major process in determining the patchy distribution of annual plants in the study site is seed trapping by shrubs and other rough elements (Prasse & Bornkamm 2000).

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 were chosen because they are among the most abundant species in the study area, they occur in both types of habitats and they differ markedly in seed size. The dwarf plant *Ifloga spicata* has the lightest seeds of all species in the study site (0.006 g), which are approximately three times lighter than the seeds of the small-seeded *Senecio glaucus* (0.018 g) . *Rumex pictus* has relatively heavy seeds (0.084 g), and *Erodium laciniatum* exhibits the largest and heaviest seeds of the studied species (0.130 g). *Ifloga spicata* is the only species which, on the average, is more abundant and reproductive in the open areas between shrubs (Tielbörger 1997b). If seed size is indicative of competitive ability,

this distribution pattern may reflect the fact that *Ifloga* suffers from competition under the densely populated shrubs.

Seedling densities

In summer 1996, four blocks (replicates) of 50 m × 50 m were marked in the study area. The area of each plot was subdivided 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, 16 randomly chosen quadrats of 25 cm × 25 cm were set up in each of the habitat types of each block. Seedlings of all annual species emerging in these quadrats were counted throughout the season. Based on these counts, we determined per-block means of density of emerging plants and of reproductive plants for each focal species in each habitat type.

Seedling survival

Seedling survival of plants growing under natural conditions was estimated for each species, habitat and block separately by dividing average densities of reproductive plants by densities of emerging plants. Survival of seedlings without neighbors was measured using neighbor removal experiments. In January 1997, short after the first major germination event, eight seedlings of each of the four species were randomly selected and marked in each block and habitat type (a total of 32 individuals per species and habitat). All neighboring seedlings were removed several times throughout the growing season, within a radius of 30 cm around each individual target plant. Preliminary observations had indicated that such a radius is sufficient to exclude above- and below-ground interactions among annual plants. The plants were monitored regularly throughout the growing season in order to determine seedling survival, i.e., the percentage of emerging seedlings surviving to seed production.

Seed production per reproductive plant

In order to determine seed production of plants under natural conditions, 32 plants (eight per block) of each of the four focal species were collected randomly in each habitat type during the time of seed set, and the number of seeds produced was counted. Seed production of the experimentally isolated plants was counted as well. However, in order to obtain similar sample

sizes for each of the four species and for control and isolated plants, a second plant was marked close to the target plant and neighbors were removed around that second plant, too. This second target plant served for seed production measurements in case the other plant died before producing seeds. Except for one case (*Ifloga spicata*, shrubs: $n = 23$), sample size was similar for all combinations of species and habitat type and varied between 30 and 32 individuals.

Reproductive success

Reproductive success (i.e., seed production per emerging plant) of individuals growing under natural densities was estimated for each block separately by multiplying the average seed production per reproductive plant by the fraction of emerging plants surviving to seed production. Reproductive success of isolated plant was measured directly by counting the number of seeds produced per target plant. Plants which died before seed set were assumed to have zero seed production.

Statistical analyses

The dependent variables for all statistical analyses were the per-block means of the measured parameters and variables ($n = 4$). This averaging procedure resulted in a paired design for both the effects of the two habitats (shrubs and open areas) and the two treatments (removal and control) in all subsequent analyses.

Between-habitat differences in natural densities of emerging plants (shrubs *vs.* open areas) were tested for each of the four focal species separately and for all emerging annual plant species by using paired *t*-tests.

Differences in competition intensity in the two habitat types were investigated using different ANOVA models. In a first set of analyses we constructed repeated measures ANOVAs (ANOVAR) with per block mean of the seed production per reproductive plant as dependent variable, treatment (control *vs.* neighbor removal) and habitat type (shrubs *vs.* openings) as within-subject factors, species as between-subject factor and among-block variation as error term. Similar models were constructed with mean seedling survival and reproductive success (i.e., seed production per emerging plant) as dependent variables. We interpreted a statistically significant treatment × habitat interaction as evidence for habitat-specific differences in competition intensity. Similarly, a significant species × treatment interaction term was interpreted

as a species-specific response to the neighbor removal. In addition, we performed paired *t*-tests, in order to compare demographic response with and without neighbors for each species in each habitat type separately. For each species, significance levels in the *t*-tests were adjusted for bias introduced by multiple comparisons using the Bonferroni-correction. Density and seed production data were $\log(x + 1)$-transformed in order to meet the assumptions of ANOVAR.

In a second set of analyses, we tested more directly whether competition intensity is larger under shrub canopies than in the open areas. Analyses were performed both for relative (RCI) as well as absolute competition intensity (ACI). For each species, habitat type and block we estimated ACI as the difference between isolated plant performance and control plant performance. RCI was estimated by dividing ACI by the isolated plant performance. We constructed ANOVAR models with per block mean of competition intensity (i.e., ACI and RCI, for each measure of plant performance) as dependent variable ($n = 4$), habitat type as within-subject factor, species as between-subject factor and among-block variation as error term. In these models, a significant effect of habitat type was interpreted as evidence for differences in competition intensity between shrubs and open areas. In order to test whether competition intensity was larger under shrub canopies than in the openings, we compared species-specific competition intensities between shrubs and open areas using paired *t*-tests.

Results

Seedling densities

Mean overall densities of annual plants were significantly (paired *t*-test, $p < 0.001$) higher under shrubs than in open areas between shrubs (shrubs: 84.7±8.9 plants/625 cm^2; openings: 19.1±3.2 plants/625 cm^2). All four focal species were considerably more abundant under the canopy of shrubs (Figure 1). However, between-habitat differences in densities were only significant in the case of *Senecio glaucus* and *Rumex pictus*.

Seedling survival

Except for *Ifloga spicata*, seedling survival tended to be higher for experimentally isolated plants than for plants growing under natural neighbor conditions (Figure 2). However, only in the case of *Rumex pictus*

Table 1. Results of repeated-measures ANOVAs with habitat (shrubs *vs.* openings) and treatment (control *vs.* isolated plants) as within-subject effects, annual plant species as between-subject effect, and number of seeds produced per reproductive plant, seedling mortality, and number of seeds produced per emerging plant as dependent variables.

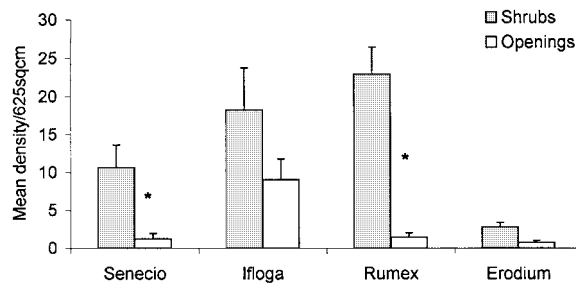| Source of variation (df)	Dependent variable		
	Seeds per reproductive plant	Seedling survival	Seeds per emerging plant
Habitat (1)	8.01*	10.132**	0.51
Treatment (1)	2.77	17.06***	11.75**
Species (3)	5.14*	21.77***	1.42
Habitat × Treatment (1)	1.26	1.25	1.90
Habitat × Species (3)	11.30***	6.05**	11.92***
Treatment × Species (3)	6.88**	1.82	8.05**
Habitat × Treatment × Species (3)	3.04	0.53	1.23
Error (12)			

$^*p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

Figure 1. Mean (± SE) densities of four dominant annual plant species for the two habitat types shrubs and open areas in the Nizzana sand field. Asterisks indicate significant differences in densities between the two habitat types (paired *t*-tests, $p < 0.05$).

(shrubs) differences between treatments were statistically significant ($p < 0.05$, paired *t*-tests). The results of the repeated-measures ANOVA did not indicate species-specific responses to the neighbor removal treatment (Table 1). A significant habitat × species interaction term indicated that there was a species-specific effect of the habitat type on seedling survival. Figure 2 shows, that for one species (*Ifloga spicata*) seedling survival was higher in the open areas, while there were no between-habitat differences in survival rates for the other three species. Seedling survival differed between species, habitats and treatments, but there was no significant interaction between habitat type and treatment (Table 1). Similarly, there was no significant effect of habitat type on relative (Table 2) and absolute competition intensity (Table 3).
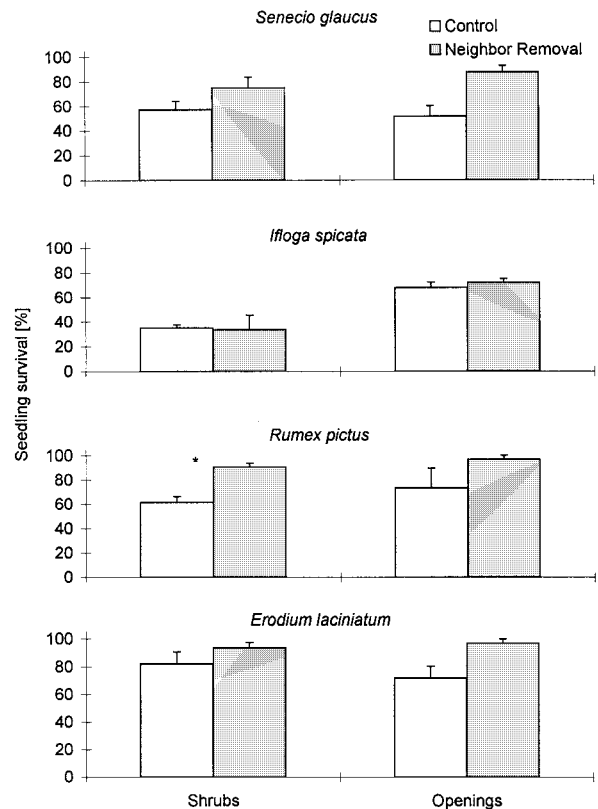

Figure 2. Mean (± SE) seedling survival for four annual plant species, two habitat types (shrubs *vs.* openings), and two treatments (control plants *vs.* experimentally isolated plants) in the Nizzana sand field. For a given species, asterisks indicate significant differences between isolated and control plants (paired *t*-tests, $p < 0.05$).

Table 2. Results of repeated-measures ANOVAs with habitat (shrubs *vs.* openings) as within-subject effect, annual plant species as between-subject effect and relative competition intensity (RCI, measured for number of seeds produced per reproductive plant, seedling mortality, and number of seeds produced per emerging plant) as dependent variable.

Source of variation (df)	Dependent variable		
	RCI for seeds per reproductive plant	RCI for seedling survival	RCI for seeds per emerging plant
Habitat (1)	0.69	0.02	0.40
Species (3)	4.74*	0.52	3.22
Habitat × Species (3)	0.84	1.51	0.05
Error (12)			

* $p < 0.05$.

Table 3. Results of repeated-measures ANOVAs with habitat (shrubs *vs.* openings) as within-subject effect, annual plant species as between-subject effect and absolute competition intensity (ACI, measured for number of seeds produced per reproductive plant, seedling mortality, and number of seeds produced per emerging plant) as dependent variable.

Source of variation (df)	Dependent variable		
	ACI for seeds per reproductive plant	ACI for seedling survival	ACI for seeds per emerging plant
Habitat (1)	0.40	1.25	0.03
Species (3)	4.29*	1.82	7.05**
Habitat × Species (3)	2.38	0.53	1.04
Eror (12)			

* $p < 0.05$; ** $p < 0.01$.

Seed production per reproductive plant

There was no consistent pattern of the effect of neighbor removal on seed production per surviving plant for the four annual species. Individuals of *Senecio glaucus* tended to produce more seeds without neighbors in both habitat types, but this effect was not significant in paired *t*-tests (Figure 3). In the case of *Ifloga spicata*, there was no effect (openings) or a significantly negative effect (shrubs) of the experimental isolation on seed production. Isolated individuals of *Rumex pictus* produced more seeds than conspecific plants growing with neighbors in the open habitat, while no such effect was observed for plants growing under shrubs. Finally, *Erodium laciniatum* did not show any significant response to the experimental isolation (Figure 3). The above described species-specific responses to the removal of neighbors was also indicated in a significant species × treatment interaction in the repeated-measures ANOVA (Table 1). There were differences between habitats in seed production of *Erodium laciniatum* and *Senecio glaucus* but not for the other species (Figure 3). This finding is reflected in the significant habitat × species interaction term of the statistical analysis (Table 1). The further results of the ANOVAs did not indicate any habitat-specific effect of the removal of neighbors: there was no significant effect of the habitat × treatment interaction on seed production, and no effect of habitat type on relative and absolute competition intensity (Tables 2 & 3).

Reproductive success

Reproductive success of isolated individuals of *Senecio glaucus* and *Rumex pictus* was higher than of plants growing under natural neighbor conditions (Figure 4). However, differences between treatments were not statistically significant for *Senecio glaucus* growing in the openings ($p > 0.05$, paired *t*-test). There was no statistically significant effect of the neighbor removal on reproductive success of *Ifloga spicata* and *Erodium laciniatum*. Similar to seed production per reproductive plant, the results of the ANOVA indicated a significant interaction between the effect of species and treatment (Table 1). The results of the various ANOVA models did not indicate,
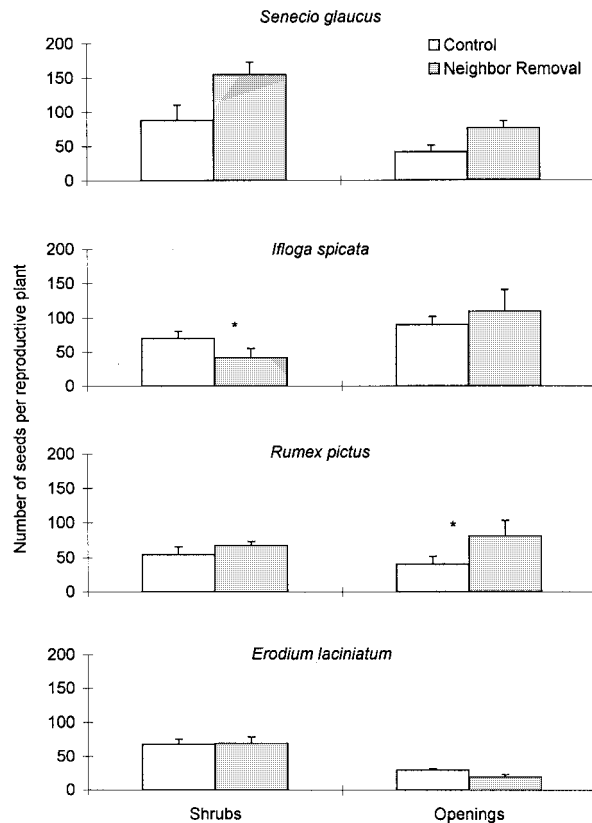
Figure 3. Mean (± SE) seed production per reproductive plant for four annual plant species, two habitat types (shrubs *vs.* openings), and two treatments (control plants *vs.* experimentally isolated plants) in the Nizzana sand field. For a given species, asterisks indicate significant differences between isolated and control plants (paired *t*-tests, $p < 0.05$).

Figure 4. Mean (± SE) seed production per emerging plant for four annual plant species, two habitat types (shrubs *vs.* openings), and two treatments (control plants *vs.* experimentally isolated plants) in the Nizzana sand field. For a given species, asterisks indicate significant differences between isolated and control plants (paired *t*-tests, $p < 0.05$).

that competition intensity was higher in either of the habitat types: There was no significant effect of the habitat × treatment interactions on reproductive success (Table 1), and no significant effect of habitat on relative and absolute competition intensity (Tables 2 and 3).

Discussion

Competition intensity and habitat productivity

Our overall results do not support the hypothesis that competition intensity is higher under shrubs than in the open areas. We could show that competition was either intense in both habitat types or did not affect annual plant performance at all. For all four annual species, absolute and relative competition intensity were similar for the two habitat types, no matter whether
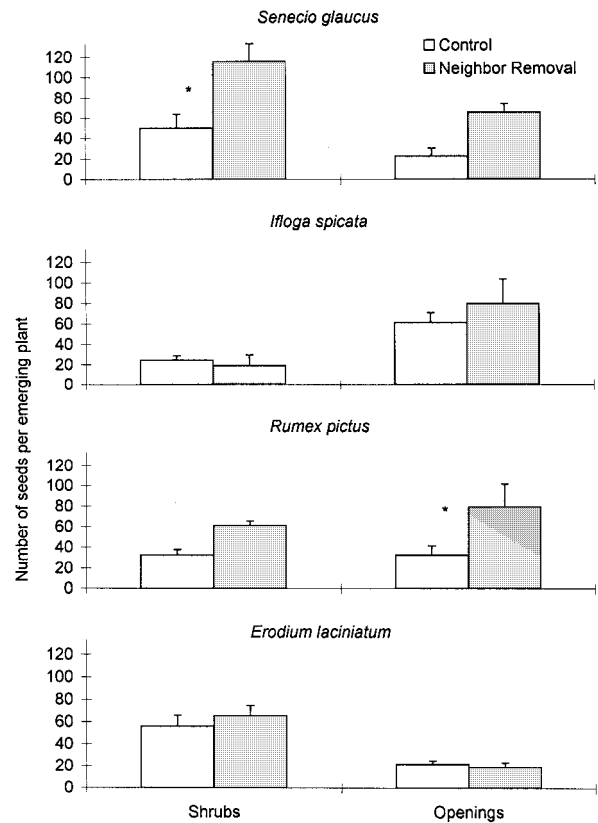
seedling survival, seed production, or the combined response (seed production per emerging plant) was considered. However, there were few cases in which either of the three demographic parameters was more sensitive to neighbor removal in one habitat type than in the other. For example, consistent with our hypothesis, survival of isolated seedlings of *Rumex pictus* and seed production per isolated emerging individual of *Senecio glaucus* were significantly higher than that of control plants under shrubs, while these differences were not statistically significant in the open areas. However, in contrast to our hypothesis, we found a larger positive response to neighbor removal in the open habitat for seed production per reproductive plant in the case of *Rumex pictus* and *Ifloga spicata*.

Previous studies indicated, that in the study area density and productivity of annuals is usually much higher under shrubs than in open areas (Tielbörger

& Kadmon 1995, 1997), and that competition intensity between annuals is higher in areas of lower sand mobility (Kadmon 1997). Furthermore, it has been hypothesized that in unproductive habitats, competition intensity is much lower than in habitats with high productivity and large amounts of standing crop (Grime 1973; Huston 1979). In the present study, overall plant densities and densities of the four target species were much larger under shrubs than in open areas between shrubs. We therefore assumed, that in the unproductive and unstable open areas competition should play a minor role for the success of the studied annual populations, while under shrubs competition should be intense. Our finding of equal competition intensities in the two habitat types contradicts this assumption and support the hypothesis of equal competition intensity along environmental gradients (Newman 1973; Tilman 1982, 1988).

Interestingly, our results are similar for the different life history stages at which the response of the target plants were observed. It has been suggested that small seedlings are more sensitive to abiotic stress and therefore profit from the presence of neighbors while negative neighbor effects predominate at later stages (Foster 1999). From our results, there is no evidence that seedling survival was less affected by neighbor competition than seed production. We detected a positive response to neighbor removal for both seedling survival and seed production per reproductive plant for species (*Rumex pictus*) and negative effects (suggesting facilitation by neighbors) on seed production of another species (*Ifloga spicata*). Therefore, our results do not support previous suggestions that the sensitivity to neighbors varies in a simple and consistent manner between different life history stages (Callaway & Walker 1997; Foster 1999; Goldberg et al. 1999).

Relative and absolute competition intensity

In a recent study, Nash Suding and Goldberg (1999) have concluded that '. . . after decades of experimental and conceptual work the debate concerning how competitive intensity varies with productivity remains unresolved'. Various attempts have been made in order to explain the conflicting results of empirical studies. For example, it has been suggested that the outcome of the experiments depends on the life history stage of the target plant (Callaway & Walker 1997; Goldberg et al. 1999), on the incorporation of plant litter effects (Nash Suding & Goldberg 1999), and on whether gradients are studied in productive or unproductive en-

vironments (Foster 1999). Another explanation was formulated by Grace (1993) who hypothesized that, consistent with Grimes ideas, absolute competition intensity increases with increasing productivity, while relative competition intensity is unaffected by the productivity of the environment. This hypothesis has been supported by several studies which indicated that ACI is much more sensitive to differences in habitat productivity and disturbance regime than RCI (Campbell & Grime 1992; Grace 1993; Turkington et al. 1993; Kadmon 1995). In a later paper, Grace (1995) has argued that only by using the standardized form of competition intensity (RCI), one can distinguish between plant responses to environmental gradients and their responses to each other. In this study, we attempted to test whether the two habitat types shrubs and open areas differ in absolute competition intensity, while relative competition intensity is similar in the two habitat types. We tested this prediction for four dominant annual species and for two different life history stages. There was not a single case in which competition intensity differed between the open areas and the areas between shrubs, and this finding did not depend on whether relative or absolute competition intensity was measured. Therefore, our results do not support the hypothesis of Grace (1993) that relative competition intensity varies along productivity gradients in a manner consistent with the ideas of Grime (1973) and Huston (1979).

Sensitivity to competition and seed size

Although our results do not indicate habitat-specific differences in competition intensity, we could show that competition was important in determining the demography of the studied annual populations. However, the four studied species differed considerably in their sensitivity to neighbor competition. Two species, *Senecio glaucus* and *Rumex pictus*, showed large differences in reproductive success of experimentally isolated plants and plants growing under natural densities, while for the other two species no such effect was detected. Therefore, our results indicate that competition may play a major role in structuring the studied annual plant community.

It has previously been suggested, that species-specific differences in competitive ability are correlated with differences in seed size (Winn 1985; Rees 1995). However, in our study there was no evidence for the fact that small-seeded species were competitively inferior to large seeded ones. Additional re-

gression analyses indicated, that average seed weight accounted for very little (between 1.4% and 19.2%, $p > 0.1$ in all cases) of the variation in RCI and ACI. Interestingly, the only species which did not show any positive, but rather a negative response to the removal of neighbors (*Ifloga spicata*), has the smallest seeds of the overall annual community of the studied system. In a long-term study in the Nizzana dunes, this dwarf annual was the only species which, on the average, was more successful in the open areas (Tielbörger 1997b). Therefore, Tielbörger & Kadmon (1995) hypothesized that reproduction of *Ifloga spicata* is limited by the highly competitive environment under shrub canopies. Our results contradict this hypothesis and indicate, that competition among annuals can not explain the fact, that the tiny composite is more successful in the open areas between shrubs.

Limitations of the study and long-term implications

For an interpretation of our results, one has to take into account that our study was conducted over a single growing season. Desert ecosystems are inherently variable and environmental conditions, particularly annual rainfall, may considerably differ between years. Consequently, annual plant densities and, accordingly, competitive regime vary between years, too. Results from three long-term studies (Tielbörger 1997; Tielbörger & Kadmon 1997, 2000) which were conducted in the same experimental system allow to evaluate, how 'representative' the conditions in the year of study were. However, these studies were only observational, and only the manipulation of neighbor conditions in the two habitat types shrubs and open areas during several growing seasons may unequivocally reveal, whether our results reflect the conditions of more than a single year. Tielbörger & Kadmon (2000) measured densities and reproductive success of the focal four annual species in several consecutive years which differed considerably in the amount of annual rainfall (between 38 mm and 178 mm). Two major findings of that study are important for interpreting the results of our present study:

First, Tielbörger & Kadmon (2000) found that in each year, reproductive success was higher in the habitat type which exhibited higher annual plant densities. This indicates that, in contrast to our main hypothesis, reproductive success was not a direct negative function of habitat productivity. The results of our present study are consistent with these findings in that they do not support the idea of higher competition intensity

beneath shrubs. We therefore suggest that although we have conducted our study over a single growing season, our findings may be representative for years with much higher or lower rainfall.

Secondly, between-habitat differences in densities and reproductive success were found to be extremely variable (Tielbörger & Kadmon 1995, 2000). When water was abundant, densities and seed production were much larger under shrubs than in open areas, while an opposite pattern was detected in drought years. A closer look at the results of Tielörger & Kadmon (1997) reveals that there was no year in which the ratio of densities under shrubs and densities in open areas was larger than in the studied season (4.6). For example, densities in the wettest year ever measured at the study site (178 mm) were 1.9 times higher under shrubs and 8.5 times higher in open areas during the driest year ever detected (38 mm). This indicates that competition intensity beneath shrubs is probably never larger than in open areas, even in years with different rainfall conditions.

On a long term, it appears unlikely that patchiness in habitat conditions considerably affects the nature of interactions between annual plants in the studied system. Direct effects of shrubs on annual plant performance like those found by Tielörger & Kadmon (2000) are probably much more important than indirect effects operating through annual plant densities. Therefore, in order to understand the long-term dynamics of the studied system, it is crucial to learn about these direct effects, rather than about the nature of interactions among the annual plants themselves.

Indirect negative interactions

The results of our study may add an interesting aspect to the topic of indirect interactions. Recently, Callaway & Walker (1997) have pointed to the importance of studying indirect interactions among plants. Indirect effects occur, if certain species modify the strength of the type of interactions between other species (Connell 1990). For example, it has been found that competitively superior species (Miller 1994) or parasitic species (Penning & Callaway 1996) may indirectly facilitate other species by directly suppressing competitively inferior species or certain host plants. While there is a relatively large number of studies reporting such 'indirect facilitation', virtually no study was designed to explicitly test for indirect negative effects in plant communities (but see Aguiar & Sala 1994). In this study we tested the hypothesis

that shrubs may impose indirect negative effects on fitness components of annuals plants, by increasing density and standing crop (and, therefore, competition intensity) below shrub canopies. Our results were consistent with previous studies in that total densities and productivity of annual plants were higher under shrubs than in the open areas. However, in contrast to our expectations, these differences were not associated with a consistent reduction in the demographic success of individual plants below shrubs canopies. Thus, our findings indicate, that facilitation of annuals by desert shrubs did not impose indirect negative effects on the understory plants by increasing inter- or intraspecific competition. Much further work is required to evaluate the role of indirect negative interactions in other plant communities.

Acknowledgements

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