

BIDIRECTIONAL FACILITATION AND INTERFERENCE BETWEEN SHRUBS AND ANNUALS IN THE MOJAVE DESERT

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Abstract. Composition and structure of plant communities can be strongly influenced by plant interactions. Interactions among plants commonly comprise positive and negative effects operating simultaneously and bidirectionally. Thus, a thorough understanding of plant interactions requires experimental separation and quantitative assessment of the bidirectional positive and negative effects that add up to the net effects of plant interactions. Using the close spatial association of annual plants with a desert shrub (*Ambrosia dumosa*) in a sandy area of the Mojave Desert of California as a test system, we separated and quantified negative and positive effects of annuals on shrubs and of shrubs on annuals. We achieved the separation of negative and positive effects with an experimental design that included reciprocal removals of neighbors and simulations of physical effects of neighbors using artificial structures. All experimental manipulations were conducted on space originally occupied by *Ambrosia* shrubs to focus on immediate effects of neighbors on water availability rather than on long-term microenvironmental effects (e.g., nutrient accumulation). We quantified positive effects by calculating the difference between performance parameters of neighbors growing with artificial structures (thatch to mimic the physical effects of the presence of annuals and artificial canopies to mimic the physical effects of shrubs) and those of neighbors growing alone (removals). We estimated negative effects by calculating the difference between plant performance on control plots (shrubs and annuals growing together) and performances of plants growing with the artificial structures. Annuals had simultaneously strong negative and weak positive effects on shrub water status, growth, and reproductive output. Annuals also had an impact on the sex expression of shrubs by inducing shifts toward a higher male proportion in inflorescences of monoecious *Ambrosia*. In contrast, we found strong positive and weak or no negative effects of the shrubs on survival, biomass production, and seed production of the entire annual community and of selected annual species (the abundant native *Chaenactis fremontii* and the two dominant introduced annual species *Bromus madritensis* ssp. *rubens* and *Schismus barbatus*). Overall, in net effect, the interaction between shrubs and annuals can be described as facilitation or positive net effects of shrubs on annuals, and interference or negative net effects of annuals on shrubs. However, during the growing season, the ratios between positive and negative effects shifted. Annual plants benefited from the presence of shrubs to the greatest extent early in the growing season, and initial negative effects of annuals on shrubs declined as annuals senesced later in the season. Results of this study support the view that an experimental resolution of bidirectional positive and negative effects is necessary to achieve an accurate, mechanistic understanding of species interactions.

Key words: *Ambrosia dumosa*; coexistence; competition; desert; desert annuals and shrubs; facilitation; interference; Mojave Desert, California; phenology; species interaction.

INTRODUCTION

Understanding the relationships of coexisting species forms a central theme of community ecology (Watt 1947, Roughgarden and Diamond 1986). Composition and structure of a community are shaped by both abiotic factors and interactions among organisms. While the structure of plant communities can be characterized with descriptive methods, the specific types of interactions partly responsible for that structure are usually

less evident, and their resolution requires thorough, experimental analysis. Even though positive interactions between plant species have been described in the scientific literature since the turn of the century (Phillips 1909, see also Kropotkin 1902 for a general account), research in community ecology has focused primarily on negative interactions, and interference has often been considered the key factor shaping communities (Clements et al. 1929, Schoener 1983, Keddy 1989, Cornell and Lawton 1992). Only after it became evident that negative interactions alone could not account for all observed vegetation patterns (see Schoener 1982, Goldberg 1990), were positive interactions

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considered again (e.g., Hunter and Aarssen 1988, Wilson and Agnew 1992, Bertness and Callaway 1994, Bertness and Hacker 1994, Callaway 1995, Callaway and Walker 1997).

That both positive and negative effects can be important simultaneously in interactions between species has been by now demonstrated in a number of studies (e.g., Walker and Chapin 1986, Callaway et al. 1991, Aguiar et al. 1992, Bertness and Shumway 1993, Aguiar and Sala 1994), and the interaction between positive and negative effects has been discussed (Callaway 1994, Callaway and Walker 1997, Holmgren et al. 1997). However, even though it has been recognized that the overall or net effect of one species on another may be the sum of both positive and negative effects (Callaway 1995), net effects have never been experimentally dissected into their positive and negative components. Such a dissection would allow an evaluation of the degree to which positive and negative effects compensate for each other and result in variations in net effects through space and time. Net effects can result in facilitation (positive effects > negative effects) or interference (positive effects < negative effects) of one neighbor by another. Furthermore, positive and negative interactions between neighbors are very likely to be bidirectional, including positive and negative effects in both directions. This bidirectionality has seldom been assessed. Most studies have addressed only the effects of one neighbor on another. Thus, a truly mechanistic understanding of plant interactions and of the long-term changes or stability in plant associations which such interactions direct, will be possible only after the bidirectional interplay between positive and negative effects of neighboring species on each other is quantitatively assessed.

The apparent structural simplicity and stark, salient abiotic features of deserts, plus the prevalence of close, preferential associations between shrubs and herbaceous plants (often annuals) in many deserts of the world (West and Klemmedson 1978, Noy-Meir 1979) suggest that the desert shrub/annual association provides an ideal model system for a quantitative evaluation of bidirectional, positive and negative interactions among neighboring plants. Facilitative effects of shrubs on annuals have been described in the deserts of the southwestern United States (Went 1942, Muller 1953, Muller and Muller 1956, Halvorson and Patten 1975, Patten 1978, Shmida and Whittaker 1981) and the Middle East (Zohary 1973, Sarig et al. 1994, Tielbörger and Kadmon 1995, 1997). In contrast, reports on interference, such as apparent allelopathic suppression of annuals by shrubs (Friedman et al. 1977) or resource competition between herbaceous plants and shrubs, are comparatively rare for deserts (Casper 1996, Tielbörger and Kadmon 1997). Facilitation in arid areas often involves water and/or nutrient availability. Microclimates beneath shrubs are characterized by lower radiation exposures and thermal amplitudes,

and, therefore, lower evaporative demands compared to conditions in open, inter-shrub areas (e.g., Keeley and Johnson 1977, Nobel 1980, Fuentes et al. 1984, Belsky et al. 1989, Vetaas 1992). Soil surface coverage by herbaceous plants and their litter has the potential of increasing soil water content by increasing infiltration and decreasing evaporation from the soil surface (Evans et al. 1981, Knoop and Walker 1985). "Hydraulic lift" (Richards and Caldwell 1987) is a mechanism by which deep roots of woody plants can transport water to shallow soil layers, where it may be utilized by associated shallow-rooted plants (Caldwell 1990, Dawson 1993). Elevated concentrations of nutrients in the soil under woody plants as compared to that in open interstices between woody plants have been found in numerous studies of arid ecosystems (Radwanski and Wickens 1967, Garcia-Moya and McKell 1970, Bate 1981, Weltzin and Coughenour 1990). These "islands of fertility" (Garcia-Moya and McKell 1970) appear to be due to accumulation of wind-borne organic material and litter deposition (Radwanski and Wickens 1967, Bernhard-Reversat and Poupon 1980, McNaughton 1983, Caldwell and Manwaring 1994).

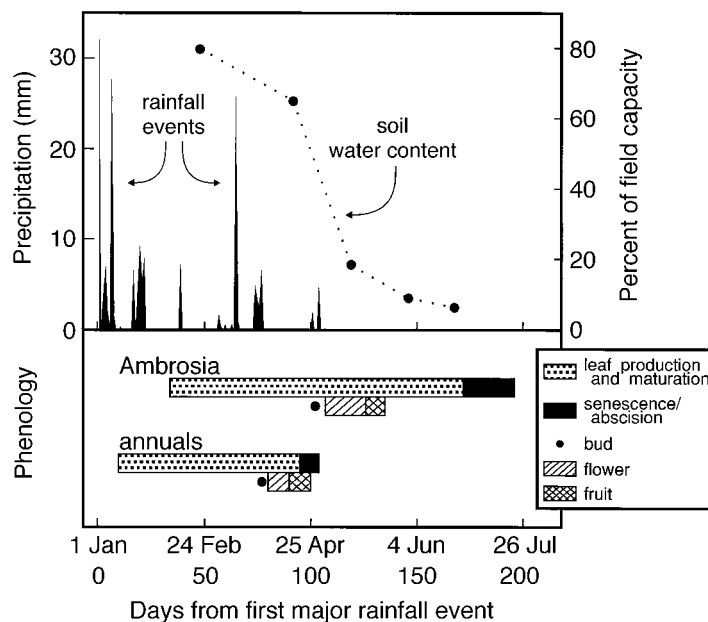
Here, we chose a floristically simple, northern Mojave Desert community in which we attempted to experimentally dissect and quantify the bidirectional, positive and negative effects involved in the interaction between a dominant shrub, *Ambrosia dumosa* (A. Gray) Payne, and the annuals commonly associated with it. We focused the study on short-term interactions through water relations rather than on long-term interactions through changes in soil nutrients. Our experimental manipulations involved plant removals and installations of artificial structures simulating specific aspects of the presence of the removed plants.

METHODS

Study site, species, and phenology

In the winter of 1994/1995 a research site was established in a sandy valley bottom in Fremont Valley in the northern Mojave Desert of California, USA (elevation 804 m, 35.4° N, 117.6° W) with the cooperation of the Bureau of Land Management (Ridgecrest Resource Area). Precipitation at the site is concentrated in winter and spring (>75% of annual total from November to April) with an annual average of 149 mm (1937–1996 Randsburg, California; 4.5 km SE from and 284 m higher than the site; National Climatic Data Center). We conducted the study during winter and spring 1994/1995, which was a relatively moist season with 250 mm of rainfall at the study site (November–April). The general vegetation in Fremont Valley is a typical Mojave Desert *Larrea–Ambrosia* scrub community (Turner 1994). At the research site, the plant community consisted of a relatively homogenous mixture of three dominant shrub species, which accounted

FIG. 1. Precipitation events, soil water content in open, inter-shrub areas (at 5–15 cm soil depth; right-hand axis), and phenology of the shrub *Ambrosia dumosa* and associated annual plants in the growth period in the winter/spring of 1994/1995.



for most of the perennial biomass: *Larrea tridentata* (DC.) Cov., nomenclature after Hickman (1993) (Zygophyllaceae; 175 individuals/ha; density data after H. J. Schenk, *unpublished data*), *Ambrosia dumosa* (A. Gray) Payne (Asteraceae; 2825 individuals/ha), and *Acamptopappus sphaerocephalus* (A. Gray) A. Gray (Asteraceae; 1425 individuals/ha). *Ambrosia* was chosen as the shrub species for detailed investigation because of its abundance at the site and its importance over most of the Mojave Desert. *Ambrosia* is a low-growing, drought-deciduous shrub; its growth commences following the onset of winter rains. It flowers in late spring when the leaves start to senesce (Turner and Randall 1987).

At the research site, winter annuals were abundant in the subcanopies of all shrub species. The annual community was dominated by the non-native grasses *Bromus madritensis* (L.) ssp. *rubens* (L.) and *Schismus barbatus* (L.) Thell., Poaceae, and an array of native forbs including *Chaenactis fremontii* A. Gray, Asteraceae. *Bromus* and *Schismus* have been naturalized in the Mojave Desert for many decades (Beatley 1966, Johnson et al. 1975). In the winters of 1994/1995 and 1995/1996 these two grass species accounted for 60 and 68%, respectively, of the density of all annual plants in the subcanopy of *Ambrosia*.

We recorded the phenological states of the annual plants and the shrub *Ambrosia* along with rainfall amounts and gravimetric measurements of soil water contents (Fig. 1). Germination of annual plants took place relatively late in our sampling season after the first substantial rainfalls on 5 January 1995. Annuals disseminated seeds and senesced >2 mo before shrubs became dormant for the dry summer season.

Experimental design

To quantitatively resolve interactions between the annuals and *Ambrosia*, we conducted a field experiment that included reciprocal removals of neighbors and replacements of neighbors by artificial structures (Fig. 2). These artificial structures were used to separate positive and negative effects of neighbors on water availability by mimicking positive effects without negative effects. Inherent in this experimental design is the assumption that positive effects on water availability are mainly due to physical properties (canopy shading of shrubs and thatch effects of annuals), and that negative effects on water availability are largely due to competitive resource uptake. The experiments were designed to elucidate the immediate facilitative effects of shrubs (shading) and of annuals (thatch effect) with the expectation that both effects increase water availability. Variations in soil properties were avoided by locating all experimental treatment sites on soil that was originally under *Ambrosia* shrubs. Long-term changes of the soil induced by shrubs or by annuals (e.g., increases in nutrient availability) were not addressed in this study.

We assessed the effects of annuals on shrubs in two treatments ($n = 20$): (1) annuals removal (S; only the shrub is present), which involved removal of annuals from around shrubs; and (2) artificial annuals ((A)S), which involved removal of annuals from around shrubs and their replacement with thatch, consisting of dry plant matter (straw) fixed in place with coarse plastic mesh. Soil water content measurements supported the prediction that this thatch would decrease evaporative losses of water from the soil (Table 1, experiment I).

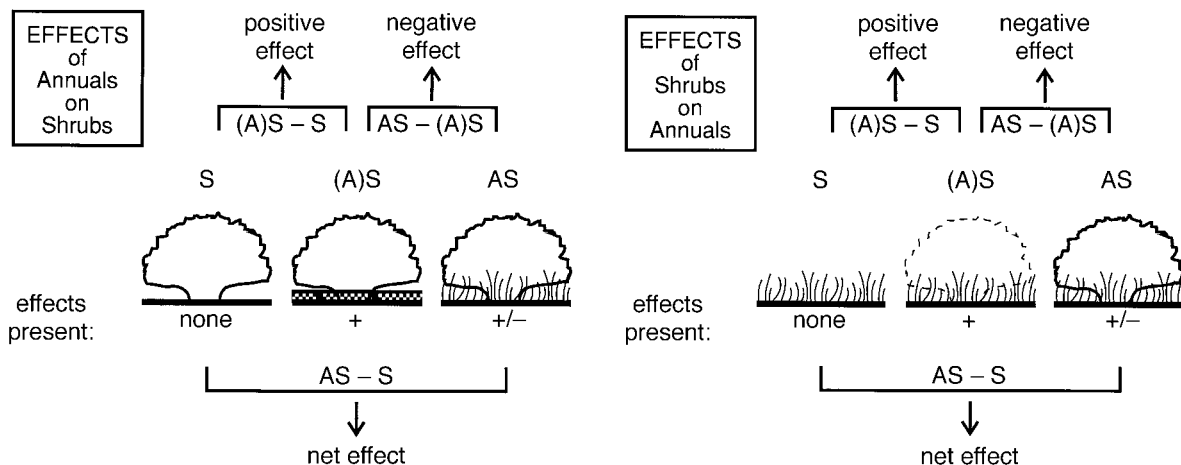


FIG. 2. Experimental design for separating and quantifying bidirectional effects (for description of treatments see *Methods*): S = annuals removal, shrub alone; (A)S = artificial annuals (thatch) and shrub; AS = control, annuals and shrub; A = shrub removal, annuals alone; A(S) = artificial shrub, annuals growing under artificial canopy. Effects presumably present in treatments are shown under the treatment depictions (+, potential positive effects; -, negative effects). The mode of calculation of positive and negative interaction effects is shown above the treatment depictions.

We also experimentally tested whether the thatch accurately simulated the physical, aboveground presence of annuals (Table 1, experiment II). In experiment II, a series of 20×20 cm plots located on former shrub sites were subjected to three different treatments: (1) all annuals removed, (2) annuals were killed with herbicides and left standing dead, and (3) annuals were removed and replaced by thatch. We irrigated all plots on 7 April with an equivalent of 25 mm precipitation and measured soil water content gravimetrically 5 d later. Soil water contents under thatch and under dead annuals were not different from each other, but both were significantly greater than in plots from which annuals had been removed (Table 1, experiment II).

The effects of shrubs on annuals were addressed with two treatments ($n = 20$): (1) shrub removal (A; only the annuals are present), in which the shrub was cut

off at ground level in the fall of 1994, and its remaining roots were killed by carefully applying triclopyr (3,5,6-trichloro-2-pyridinyloxyacetic acid ("brush-b-gon," Chevron Chemical Company, San Ramon, California) to the remaining stump; and (2) artificial shrub (A(S)), which included removal of shrubs as in 1, but the effects of a shrub canopy were simulated by attaching the canopy of a dead shrub in the same location from which the previously existing shrub was removed. This design has the benefit of more closely simulating the shading of a real three-dimensional shrub than conventional shade cloth. To ensure shading regimes comparable to live individuals, the leaf canopies of the affixed shrubs were artificially amended with additional twigs cut from living plants. Light measurements on 23 June 1995 showed no significant differences between control and artificial canopies (t test, $P = 0.314$). Concurrent feasibility studies showed that soil under these artificial canopies had water contents significantly greater than those under shrub removals (Table 1, experiment I).

Controls for both sets of experiments (shrubs on annuals and annuals on shrubs) consisted of undisturbed shrubs with naturally occurring annuals (AS). The five experimental treatments and controls were grouped together in an unreplicated randomized complete block design. These blocks ($n = 20$) were scattered randomly over a homogenous area of roughly 1 ha. Treated shrubs and controls were selected to be similar in size and overall growth condition prior to the experiment.

Assessment of plant performance

The performance measures assessed for *Ambrosia* included predawn xylem pressure potentials (PDXPP), growth, and reproductive output. We measured PDXPP

TABLE 1. Effect of artificial structures (shrub canopies and annual thatch) on soil water availability.

Experiment	Soil water content (% of field capacity)
I ($n = 10$), effect of thatch and artificial canopies (4 May 1995)	
No artificial canopy, no thatch (control)	$18.53^c \pm 3.018$
Thatch only	$26.26^b \pm 2.81$
Artificial canopy only	$32.54^a \pm 2.691$
II ($n = 5$), effect of thatch and standing dead annuals (12 April 1995)	
Open areas (control)	$43.6^b \pm 3.5$
Dead annuals	$66.4^a \pm 2.5$
Thatch	$67.3^a \pm 3.4$

Notes: Means of treatments are given with two standard errors. Different lowercase letters indicate significant differences among means of treatments (independent t test for arcsine-transformed percentages, $P < 0.05$).

TABLE 2. Multiple regression models of production and reproduction with nondestructive measurements for the shrub *Ambrosia dumosa*, the annual community as a whole, and the three annual plant species chosen for individual analysis in 1995 (P of all $r^2 < 0.001$).

Dependent variable	Independent variables and coefficients	df	r^2
<i>Ambrosia dumosa</i> , shoot elongation (cm)			
23 March	$-0.1585(\text{cover}^\dagger) + 18.56$	19	0.662
6 April	$-0.0872(\text{cover}) + 14.03$	29	0.633
14 May	$-0.0739(\text{cover}) + 15.12$	26	0.446
Biomass of annual community (mg/100 cm ²)	$66.31(\text{height}^\ddagger) + 7.75(\text{cover}[\%])$	72	0.887
<i>Bromus</i> biomass (mg/plant)	$2.32(\text{height}) + -24.07(\text{tillers}) + 10.21(\text{leaves})$	84	0.695
<i>Schismus</i> biomass (mg/plant)	$1.94(\text{height}) + 1.61(\text{tillers})$	160	0.654
<i>Chaenactis</i> biomass (mg/plant)	$-10.54(\text{height}) + 6.26(\text{leaves}) + 94.74(\text{heads})$	107	0.879
Seeds per spikelet of <i>Bromus</i> §	$1.41(\text{length})$	46	0.990
Seeds per head of <i>Chaenactis</i>	$79.79(\text{diameter}¶)$	23	0.979

† Cover is portion (%) of shrub undergoing active growth.

‡ All heights are measured in cm to the tip of uppermost leaf.

§ Spikelets of *Schismus barbatus* contained an average of 5.42 seeds.

|| Total length of spike in cm.

¶ Diameter of flowering heads in cm.

using a pressure chamber (Scholander et al. 1965) in the field at six dates throughout the growth season. For each shrub, a single twig was taken and measured immediately to avoid evaporative losses. We estimated growth of shrubs by measuring elongation of 20 twigs (per shrub) produced during the current year. These measurements were taken on three sampling dates from the middle to the end of the growth period. Preliminary measurements showed that annual shoot elongation was inversely related to the proportion of an individual shrub's canopy that underwent active growth in that year. To remove this bias and to examine only the effects of the treatments on shoot elongation, we developed linear regression models between measurements of shoot elongation and visual estimations of the portion of an entire shrub canopy undergoing active growth. For these correlations we used shrubs that were not in our experiments (Table 2). Deviations from these regressions were used to calibrate the actual effects of the treatments on shoot elongation. Reproductive outputs of *Ambrosia* were estimated by counting all male and female flower heads (inflorescences) on thirty randomly chosen spikes per shrub. In this monoecious species, heads are unisexual (staminate or pistillate) and mixed in single spikes. Individual female heads produce a single fruiting involucre (Payne 1963) containing two to four seeds (Murbeck 1943). Field and greenhouse trials showed that only one of the seeds is readily germinable (J. Schenk, *personal communication*). Therefore, the number of fruiting involucres can be used as an estimate of maximum of seed production (one flower head = one fruiting involucre = one germinable seed).

The performance measures assessed for annuals included biomass, reproduction, density, and survival. We took measurements on 10 × 20 cm, permanently marked plots placed in the northern quadrant of the subcanopy area of control and artificial shrubs. Such

plots were also located similarly at the northern side of shrub removal treatments. Aboveground biomass of the entire annual community, and of selected individual annual species, was estimated at several sampling dates throughout the growing season. For this, we determined aboveground biomass of the entire annual communities nondestructively from estimations of aerial cover and height using regressions of these quantities against dry mass of plants harvested from similar plots in adjacent areas (Table 2). Likewise for individual species, aboveground plant dry masses (for 10 plants per plot) were nondestructively estimated from regressions of height and number of leaves (and/or tillers) against plant dry mass above ground (Table 2). We estimated survival until reproduction from comparisons of initial seedling densities with final mature plant densities. We established initial densities with repeated seedling counts to account for possible separate germination events. Estimates of seed production by annuals were made at the end of the growing season with nondestructive measurements using regressions between numbers and sizes of spikes and actual seed counts (Table 2). Survival data were arcsine-transformed and all other measurements were log(+1) transformed prior to performing two-way ANOVA (treatment and block effects). We used the statistical packages SPSS/PC+ (V3.0, Norusis 1988) and SYSTAT (V5.0, Wilkinson et al. 1992) for data analysis.

Quantification of interaction effects

Positive and negative effects were calculated based on the formulas in Fig. 2. We estimated positive effects of annuals on shrubs by calculating the difference between performance parameters of shrubs (water potential, growth, fruit production) with that (artificial annuals treatment (A)S, only positive effects active) and those of shrubs growing alone (annuals removal treatment S, neither negative nor positive effect of annuals

present). Similarly, negative effects of annual plants on shrubs were estimated by calculating the difference between performance parameters of shrubs when annuals and shrubs were growing together (control AS, positive and negative effects present) and performance parameters of shrubs growing with artificial annuals (treatment (A)S, only positive effects present). Positive effects of shrubs on annuals were estimated by calculating the difference between the performance of annuals under artificial canopies (treatment A(S), only positive effects) and that of annuals growing alone (treatment A, neither negative nor positive effect of shrub present). The negative effects of shrubs on annual plants were estimated by calculating the difference between performance parameters of annuals (e.g., survival, biomass, seed production) when annuals and shrubs were growing together (control AS, positive and negative effects present) and performance parameters of annuals growing under artificial shrubs (treatment A(S), only positive effects present). To quantify the net effects of annuals on shrubs, the performance of shrubs growing alone was subtracted from the performance of shrubs when growing with annuals. The net effect of shrubs on annuals was quantified by subtracting the performance of annuals growing alone from their performance when shrubs are present.

We standardized the magnitudes of positive, negative, and net effects calculated from different performance parameters so that effects could be compared as unitless quantities readily across different performance measures and between annuals and shrubs. This standardization follows the recommendations for treatment comparison used within meta-analysis (Hedges and Olkin 1985, Gurevitch and Hedges 1993). Each effect was divided by the pooled standard deviation of the two subtracted performance parameters (Eqs. 1 and 2), and the effects were corrected for sample size bias by multiplication with the term J (Eq. 3):

$$d = \frac{\bar{X}_1 - \bar{X}_2}{s_p} J \quad (1)$$

$$s_p = \sqrt{\frac{(N_1 - 1)(s_1)^2 + (N_2 - 1)(s_2)^2}{N_1 + N_2 - 2}} \quad (2)$$

$$J = 1 - \frac{3}{4(N_1 + N_2 - 2) - 1} \quad (3)$$

where d = effect size, \bar{X} = mean of the groups (treatments) 1 or 2, s_p = pooled standard deviation of the groups 1 and 2, s = standard deviation of the groups 1 or 2, and N = total number of individuals in groups 1 or 2.

RESULTS

Effects of annuals on shrubs

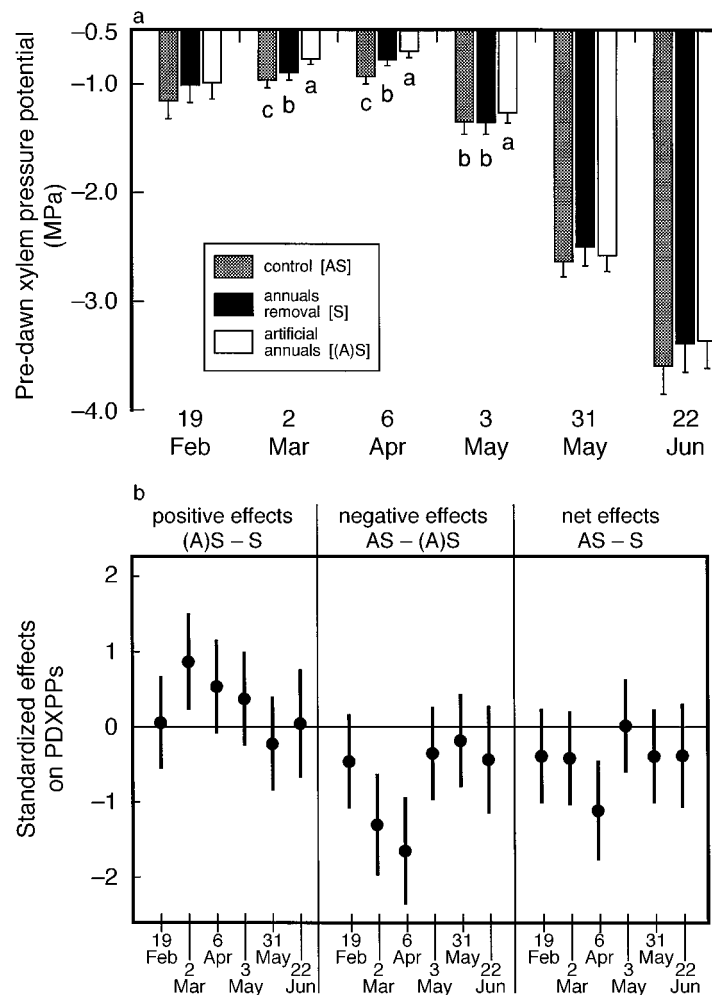
The decrease in predawn xylem pressure potentials (PDXPPs) of *Ambrosia* in all treatments from 19 February to 22 June (Fig. 3a) reflected normal, seasonal,

soil drying (Fig. 1). On 19 February we found no differences in PDXPPs between different shrub treatments. However, on the two subsequent dates, untreated control shrubs (annuals and shrubs growing together) had more negative PDXPPs than shrubs that had annual neighbors removed (shrubs alone and with artificial annuals). On all of these dates the PDXPPs of *Ambrosia* in the artificial annual (thatch) treatments were even higher than those in the annual removal treatments. Later in the season all differences vanished as soil water availability continued to decrease and annuals senesced (see Fig. 1). The magnitudes of the positive and negative effects of annuals on the PDXPPs of shrubs changed differently through the growing season (Fig. 3b). Annuals, simulated as thatch in our experiments, had significant positive effects on PDXPPs of shrubs (the confidence interval of the mean does not overlap zero) at only one sampling date (2 March), which occurred during the beginning of the growing season. In contrast, negative effects of living annuals were significant at two dates (2 March and 6 April) in the beginning of the season. Both positive and negative effects of annuals on PDXPPs of shrubs decreased in magnitude later in the season, and from 3 May on they were no longer significant. Positive and negative effects did cancel out at some of the sampling dates and annuals, therefore, significantly decreased PDXPPs of shrubs in net effect only on 6 April.

Twigs of shrubs growing without living annuals (annuals removal and artificial annuals treatments) elongated to a greater extent (by 1.4 cm and 2.7 cm more, respectively) than twigs of shrubs with living annual neighbors present (control) (Fig. 4a). Shrubs growing with artificial annuals (thatch) had the longest twig lengths on 6 April (2.0 cm more than controls and 0.9 cm more than annuals removals). The differences between treatments indicated that both positive and negative effects of annuals on shoot elongation were present (Fig. 4b). Thatch had a positive effect on shrub shoot elongation, but living annuals also had a negative effect on shrub shoot elongation. This negative effect tended to decrease as annuals senesced. The net effect of annuals on shrub shoot elongation was to depress it on all three sampling dates. This negative net effect tended to decrease toward the end of the growth season.

Shrubs growing without annual neighbors produced up to 30% more male inflorescences and up to 41% more germinable seeds (equals flower heads) than shrubs associated with living annual neighbors (Table 3). Additionally, shrubs growing with thatch produced more male inflorescences than shrubs with annual neighbors removed. Comparing the results for different treatments, annuals had significant, positive effects and negative effects on both male and female flower head production. These opposing positive and negative effects did not cancel out completely, and the net effects of annuals on shrubs were significantly negative for production of both male and female flower heads. The

FIG. 3. Effects of annuals on predawn xylem pressure potential (PDXPP) of the shrub *Ambrosia dumosa*. (a) Impacts of different treatments are shown over the growth season ($n = 20$). Different lowercase letters indicate significant differences (Tukey test after ANOVA conducted for each date separately, $P < 0.05$); error bars indicate 2 SE. (b) Standardized positive, negative, and net effects of annuals on PDXPP of the shrubs are shown over time as means with 95% confidence interval (for mode of calculation see *Methods*).



ratio of male/female flower heads on *Ambrosia* was significantly lower for shrubs growing without living annuals (Table 3), indicating that the production of female flower heads was more negatively affected by the presence of annuals than that of male flower heads.

Effects of shrubs on annuals

The number of species of annual plants germinating on plots where shrubs were removed, or where shrubs were replaced with artificial canopy structures, was not different from that of control plots, all had five to six species per plot (Table 4). Therefore, at least over the time span of the experiment, we found no significant effects of *Ambrosia* on species richness (or composition) of the annual community.

The aboveground biomass of the annual community, measured throughout the growing season was, with exception of the first date, significantly lower (29 and 36% less) in the shrub-removal treatment compared to the control and the artificial shrub treatment (Fig. 5a). In the beginning of the growing season shrubs did not have any positive effect on annual biomass, but later

positive effects of living and artificial shrubs were consistently detected (Fig. 5b). This effect tended to increase in magnitude from the first (27 January) to the third sampling date (9 March). Shrubs did not negatively affect annuals on any date. Consequently, the net effect of shrubs on annual biomass was positive at all sampling dates but the first.

As with the effects of shrubs on the whole annual community, we found significant positive effects and no significant negative effects of shrubs on the aboveground biomasses of individuals of each of the three annual species (Fig. 6). As a consequence, net effects were nearly always significantly positive. Biomasses of *Schismus* individuals were the lowest on both sampling dates in plots from which shrubs had been removed (25–34% less than in the other two treatments), and they were affected to a larger extent than biomasses of the other two species. Additionally, toward the end of their life span (23 March), *Schismus* individuals under artificial canopies increased by 8% in biomass compared to individuals growing under living shrubs. Individuals of *Bromus* in plots from which shrubs had

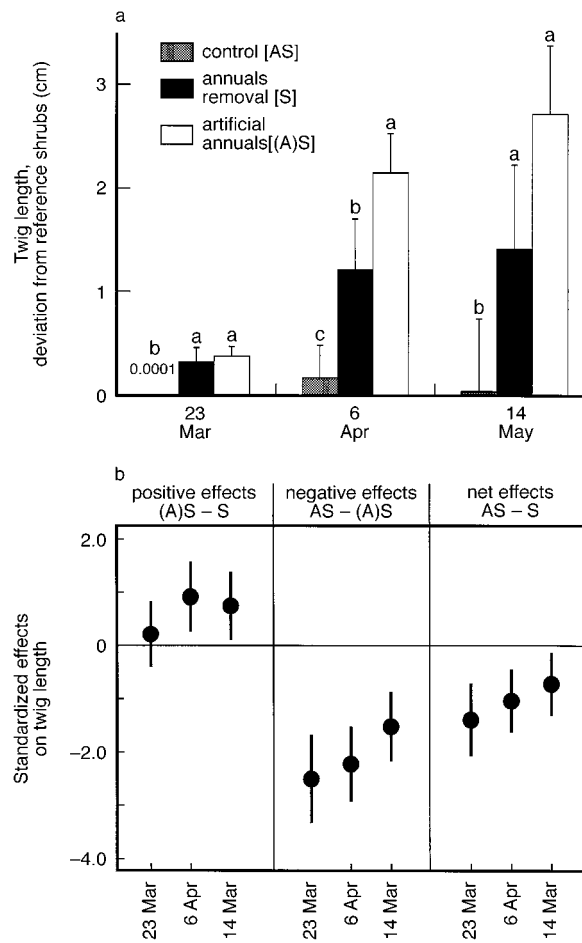


FIG. 4. Effects of annuals on twig elongation of the shrub *Ambrosia dumosa*. The twig elongation is expressed as deviation from the elongation of untreated reference shrubs (see *Methods*; $n = 20$). (a) Impacts of different treatments are shown for three dates. Different lowercase letters indicate significant differences (Tukey test after ANOVA conducted for each date separately, $P < 0.05$); error bars indicate 2 SE. (b) Standardized positive, negative, and net effects of annuals on twig elongation of the shrubs are shown over time as means with 95% confidence interval (for mode of calculation see *Methods*).

been removed were significantly smaller and had up to 13% less biomass than those in other plots at peak biomass (4 April). Individuals of *Chaenactis* in plots from which shrubs had been removed were significantly smaller (by 10%) than those in other plots well before peak biomass (February 22). Toward the end of their life span (April 20) average individual biomasses of *Chaenactis* in both the control and the shrub removal treatment were ~20% smaller than in plots that had been provided with artificial canopies (Fig. 6).

The percentage of all emergent, annual plants that survived through reproduction was significantly higher in those treatments that provided the shelter of a shrub canopy (control, 77% or artificial shrub treatment, 79%) than in the shrub removal treatment (60%, Table 4). As a result, shrub effects on annual plant survival were positive. Negative effects of the shrubs on survival of all annuals taken collectively were statistically not significant. Therefore the net effects of shrubs on all annuals were positive.

Effects of treatments on the survival of individual annual species (Table 5) were similar to the effects on all annuals collectively, except that shrubs negatively affected survival of *Schismus* and *Chaenactis*. The three annual species differed mainly in the magnitude of their responses to the treatments. Survival of *Schismus* was affected positively by shrub canopies to the largest extent, and *Chaenactis* survival was affected negatively to the largest extent. Shrubs had the weakest positive and negative effects on survival of *Bromus*.

Seed production of each of the three species was up to 81% higher in the control and the artificial shrub treatments than in the shrub removal treatments (Table 5). We found no differences between the seed production of annuals growing under artificial canopies and that of annuals under living shrub canopies. Therefore, shrubs had strong positive effects on seed production for the three annual species and only weak negative effects, which were significant only in one species (*Schismus*). Net effects of shrubs on all species were positive (facilitation).

TABLE 3. Influence of annual treatments on reproductive performance of the shrub *Ambrosia dumosa* and derived interaction effects.

Treatments and interaction effect	Performance parameter		
	Number of male flower heads per spike	Number of female flower heads per spike	Male/female ratio
Control, AS	14.17 ^c ± 0.74	13.04 ^b ± 1.11	1.17 ^a ± 0.07
Annuals removal, S	16.07 ^b ± 0.96	16.32 ^a ± 1.16	1.01 ^b ± 0.03
Artificial annuals, (A)S	18.51 ^a ± 1.58	18.45 ^a ± 1.55	1.02 ^b ± 0.05
Positive effects	0.801 ± 0.644	0.669 ± 0.638	
Negative effects	-1.320 ± 0.685	-1.721 ± 0.726	
Resulting net effects	-0.680 ± 0.638	-1.241 ± 0.676	

Notes: Means of treatment effects are given with two standard errors ($n = 20$). For each of the 20 shrubs, 30 twigs were measured, and their mean was used in the analysis. The standardized interaction effects ($n = 20$) are listed with their 95% confidence intervals. Different lowercase letters indicate significant differences among means of treatments (Tukey test after ANOVA, $P < 0.05$). Bold numbers indicate significant interaction effects (confidence intervals do not overlap zero). For abbreviations of treatments and their description see Fig. 2.

TABLE 4. Influence of shrub treatments on species richness and survival of the annual plant community and derived interaction effects.

Treatment and interaction effect	Performance parameter	
	Number of species (in seedling stage)/200 cm ²	Survival until reproduction stage (% of seedlings)
Control, AS	5.15 ^a ± 0.48	76.53 ^a ± 2.15
Shrub removal, A	5.15 ^a ± 0.66	60.10 ^b ± 3.24
Artificial shrub, A(S)	5.45 ^a ± 0.81	79.17 ^a ± 2.46
Positive effects	0.175 ± 0.619	2.850 ± 0.881
Negative effects	-0.194 ± 0.619	-0.490 ± 0.629
Resulting net effects	0.000 ± 0.619	2.569 ± 0.839

Notes: Means of treatment effects are given with two standard errors ($n = 20$), and the standardized interaction effects ($n = 20$) are listed with their 95% confidence intervals. Different lowercase letters indicate significant differences among means of treatments (Tukey test after ANOVA, $P < 0.05$). Bold numbers indicate significant interaction effects (confidence intervals do not overlap zero). For abbreviations of treatments and their description see Fig. 2.

DISCUSSION

The results of our study, using an experimental approach, show that net interactions among desert shrubs and annuals include both positive and negative effects acting simultaneously and bidirectionally. We found

within-season shifts in positive and negative effects, which caused the net effect of annuals on shrubs and that of shrubs on annuals to change through time as well.

Positive and negative effects of annuals on shrubs

The results of the experiments in which the positive effects of annuals on shrubs were mimicked by artificial thatch show that annuals have the potential to significantly improve water status (Fig. 3) and increase biomass production (Fig. 4) and reproductive output of *Ambrosia* (Table 3). However, living annuals actually caused shrub water potentials to become more negative in net effect, indicating that the negative effects of annuals on shrubs significantly exceeded the positive effects. This negative effect of annuals on shrubs could be due to resource competition (most likely for water), but other types of interference such as allelopathic interactions can not be ruled out. To our knowledge, this is the first time that annual plants have been experimentally shown to interfere with desert shrubs. Previously, neutral to positive effects of annuals on shrubs have been observed in removal experiments in the association of a Sonoran desert shrub with summer annuals (Cable 1969). Nobel (1989) found evidence for competition for water in the interaction between a perennial desert grass species and sheltered young perennial succulents. The results of the present study stand in contrast to a nonexperimental study by Pugnaire et al. (1996), who found that the presence of herbs under shrub canopies in a semiarid region was correlated with enhanced water relations of the shrubs. They did not report any negative effects in this association, and they interpreted their findings as indications of positive net effects of understory herbs on shrubs, while acknowledging that factors other than the presence of herbs could be responsible for the enhanced performance of the shrubs. Our experimental approach controlled for environmental factors and therefore allowed a clear separation between possible confounding factors such as microsite, shrub age differences, and biotic interactions. Our findings also contrast with ob-

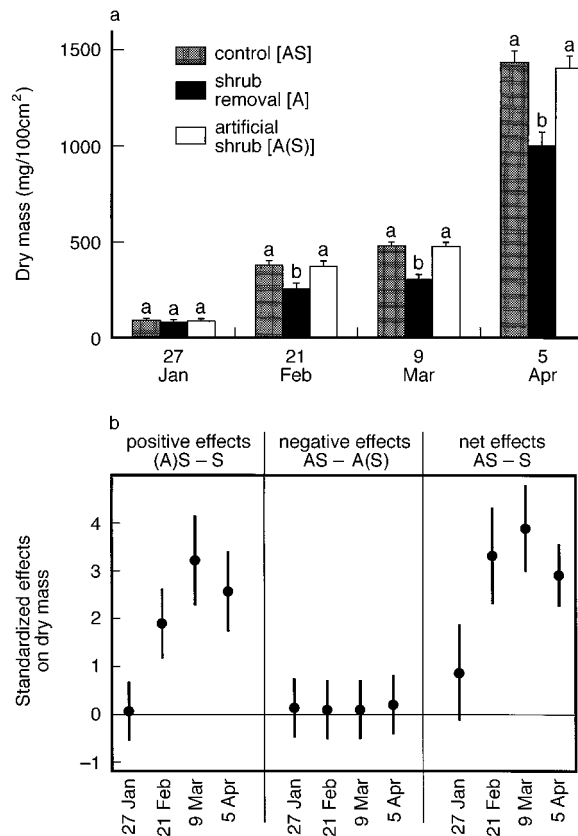


FIG. 5. Effects of shrubs on aboveground biomass of the annual community. (a) Impacts of different treatments are shown over the growth season ($n = 20$). Different lowercase letters indicate significant differences (Tukey test after ANOVA conducted for each date separately, $P < 0.05$); error bars indicate 2 SE. (b) Standardized positive, negative, and net effects of shrubs on annual biomass are shown over time as means with 95% confidence interval (for mode of calculation see *Methods*).

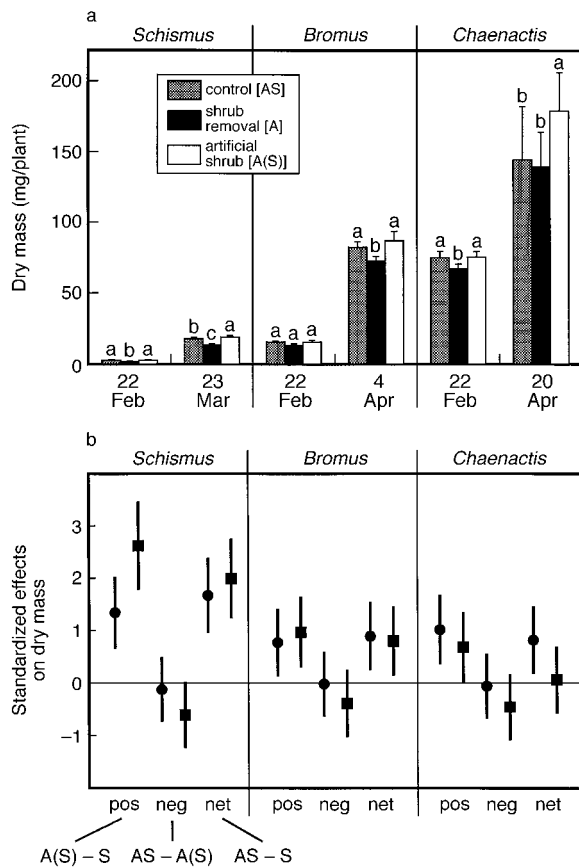


FIG. 6. Effects of shrubs on aboveground biomasses of individuals of selected annual species: *Schismus barbatus*, *Bromus madritensis* ssp. *rubens*, and *Chaenactis fremontii*. (a) Impacts of different treatments are shown for two sampling dates ($n = 20$). Different lowercase letters indicate significant differences (Tukey test after ANOVA conducted for each date separately, $P < 0.05$); error bars indicate 2 SE. (b) Standardized positive (pos), negative (neg), and net effects of shrubs on the biomass of annual individuals are shown over time as means with 95% confidence intervals (for mode of calculation see *Methods*). Different symbols indicate the mean effects at two different sampling dates: during mid-development of the plants (●) and at the peak of plant development (■).

servations made by Muller (1953), who postulated the existence of resource partitioning between roots of annuals and *Ambrosia dumosa*. Similar resource partitioning has been experimentally demonstrated for shrubs and perennial grasses in semiarid South America (Sala et al. 1989). However, our data suggest that shrubs and annuals compete for the same resources at least to some degree. This may be particularly likely when an overlap of the roots of annuals and shrubs occurs, as is probable in the case of *Ambrosia dumosa*, which has a relatively shallow rooting zone (Wallace et al. 1980).

Interference by annuals decreased the reproductive output and influenced the sex ratio of inflorescences on these monoecious shrubs. The shift toward a higher

proportion of male reproductive units in shrubs with annuals present is similar to that found previously for woody perennials undergoing water stress (Willson 1983, Waller 1988). Freeman et al. (1981) state that "costly" female reproductive success is more likely to be limited by water stress than male reproduction. This view is in agreement with findings of Dawson and Ehleringer (1993) that within a population of a streamside dioecious tree, female individuals occupied moist sites with male individuals relegated to less favorable xeric sites.

Positive and negative effects of shrubs on annuals

In general, shrubs had stronger positive effects than negative effects on annuals. Whereas species richness (or composition) of the annual community was not affected by treatments (Tables 4), increased survival (Tables 4 and 5), greater biomass production (Figs. 5 and 6), and greater seed production of annuals growing under shrub canopies (both alive and artificial, Table 5) compared to that of annuals growing without the shelter of canopies, clearly demonstrated that shrubs have positive effects on annuals. The absence of significant differences between the performance of annuals under artificial canopies and the performance under living canopies indicates that, in general, shrubs have only a small negative effect on annuals.

Our experiment controlled for potentially confounding differences in soil texture and nutrient status, since all experimental plots were located on subcanopy soil. Therefore, observed positive effects of shrubs on annuals were most likely due to the effect of shading by shrub canopies on temperature and water availability. A potentially confounding factor in our experiment was the effect of shrub removal on herbivory of annuals (e.g., Jaksic and Fuentes 1980). However, careful monitoring showed that the degree of herbivory was very low in all treatments and controls. Enhancement of water availability has been postulated in other systems involving facilitation by shrubs (Nobel 1980, Fuentes et al. 1984), and the current study provides the strongest experimental evidence to date for shrub-induced amelioration of water stress conditions and consequent enhancement of annual plant performance.

Compared to *Bromus* and *Chaenactis*, populations of *Schismus* experienced the most pronounced negative effects of shrubs and the strongest positive effects for almost all performance measures. *Schismus* was abundant under shrub canopies as well as in open intershrub areas, whereas *Bromus* and *Chaenactis* were more restricted to the more mesic shrub canopies. *Schismus* belongs to the group of generalist species, placed in between the two groups of shrub-restricted and shrub-avoiding annual species distinguished first by Went (1942) and later by Shmida and Whittaker (1981). It is not known what traits make *Schismus* more responsive than *Bromus* and *Chaenactis* to interactions with the shrub *Ambrosia*.

TABLE 5. Influence of shrub treatments on survival and seed production of three dominant annual plant species and derived interaction effects.

Treatment and interaction effect	<i>Schismus barbatus</i>	<i>Bromus madritensis</i> ssp. <i>rubens</i>	<i>Chaenactis fremontii</i>
Survival until reproductive stage (%)			
Control, AS	75.82 ^a ± 4.20	86.11 ^a ± 4.88	82.48 ^a ± 7.15
Shrub removal, A	62.43 ^b ± 3.62	72.89 ^a ± 6.989	61.99 ^b ± 11.57
Artificial shrub, A(S)	82.62 ^a ± 4.31	88.70 ^a ± 5.67	92.96 ^a ± 4.81
Positive effects	2.180 ± 0.782	1.095 ± 0.678	1.538 ± 0.723
Negative effects	− 0.687 ± 0.638	−0.215 ± 0.638	− 0.831 ± 0.704
Resulting net effects	1.467 ± 0.698	0.966 ± 0.673	0.933 ± 0.712
Seeds produced per plant			
Control, AS	66.12 ^a ± 589	50.15 ^a ± 6.27	100.68 ^a ± 18.02
Shrub removal, A	41.30 ^b ± 5.66	28.09 ^b ± 3.83	71.44 ^b ± 14.82
Artificial shrub, A(S)	74.47 ^a ± 4.97	49.17 ^a ± 8.37	111.41 ^a ± 16.02
Positive effects	2.675 ± 0.852	1.426 ± 0.712	1.163 ± 0.707
Negative effects	− 0.658 ± 0.635	−0.058 ± 0.635	−0.273 ± 0.632
Resulting net effects	1.846 ± 0.741	1.869 ± 0.762	0.775 ± 0.670

Notes: Means of treatment effects are given with two standard errors ($n = 20$). For each of the 20 plots 10 individuals were measured, and their mean was used in the analysis. Standardized interaction effects ($n = 20$) are listed with their 95% confidence intervals. Different lowercase letters indicate significant differences among means of treatments (Tukey test after ANOVA, $P < 0.05$). Bold numbers indicate significant interaction effects (confidence intervals do not overlap zero). For abbreviations of treatments and their description see Fig. 2.

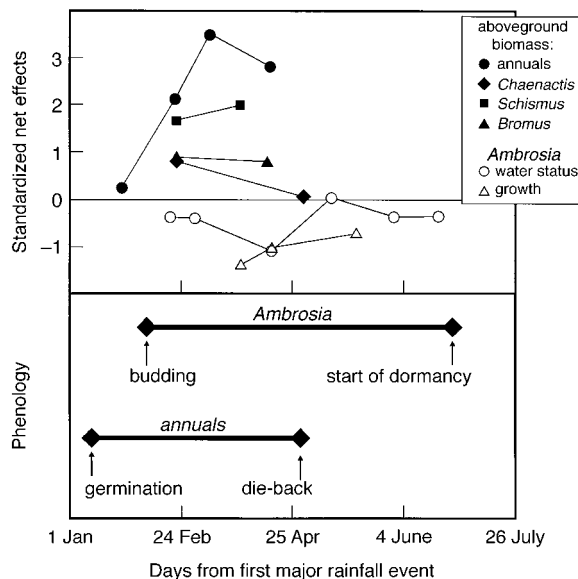


FIG. 7. Change in net effects of shrubs on annuals and of annuals on shrubs through time in relation to the phenology of shrubs and annuals. The top panel shows the means of standardized net effects through the growing season. Net effects of shrubs on annuals (filled symbols) were calculated from performance measures of annuals. These measures included biomass of the entire annual community (annuals) and the individual biomasses of the three selected plant species (*Chaenactis*, *Schismus*, and *Bromus*). Net effects of annuals on the shrub *Ambrosia dumosa* (open symbols) were based on measurements of shrub performance (water status expressed as predawn xylem pressure potential and growth expressed as shoot elongation). In the lower panel a generalized phenology diagram is given, marking the time period in which the two interacting life forms stayed active.

Seasonal shifts of positive and negative effects

Positive and negative effects of shrubs on annuals and of annuals on shrubs were not constant over the course of the experiment. During the growing season, the ratio between these effects shifted, tending to result in temporal changes in the net effects (Fig. 7). Annual plants benefited in net effect from the presence of shrubs to the largest extent in the beginning of their growing season. Annuals had their strongest negative net effects on shrubs during the first half of the growing season of the shrubs. The strong initial negative net effect of annuals on shrubs weakened later in the season, and their effect on shrub water status vanished when the annuals senesced (shown schematically in Fig. 7). However, there appeared to be a residual, negative net effect of annuals on shrub growth that extended beyond senescence of the annuals. This may be due to resource depletion by annuals earlier in the growing season, or to a carry-over effect on the shrub growth capabilities. The peak of the positive net effects of shrubs on annuals was reached during the middle of the life span of annuals. The shrubs stayed active for more than two months longer than the annuals, thereby escaping, to a degree, interference by annual plants for part of their active growth period. Similar, short-term, temporal separations between phenological stages of shrubs and annuals were described by Cable (1969) and Halvorson and Patten (1975) for the Sonoran Desert. Phenological differences between associated plants have the potential to compensate and/or avoid otherwise overwhelming negative or positive interactions. Such temporal partitioning within a single growth season ameliorate factors leading to competitive exclusion and may contribute to species coexistence just as spatial or resource partitioning is understood to promote

species diversity (May and MacArthur 1972, Whittaker 1972, Bengtsson et al. 1994).

Long-term shifts in net effects, from facilitation to interference or vice versa, have been reported previously. They are typical for the interaction of young perennials with nurse plants in arid and semiarid regions, where small plants are initially favored by sheltering host plants, but as the small plants continue to grow they eventually interfere with the former benefactor (McAuliffe 1984, 1988, Archer et al. 1988, Valiente-Banuet et al. 1991). Environmentally caused shifts in net effects also have been demonstrated over consecutive years for bunchgrass communities (Greenlee and Callaway 1996). There is a need for long-term studies (>1 yr) to determine how negative, positive, and net effects fluctuate through several seasons, and how they affect long-term changes and stability of community structure. The findings of between-year shifts in net effects (as demonstrated by Greenlee and Callaway 1996), and within-year variation in net effects for a single growth season (this study) suggest that temporal shifts in net effects make long-term studies necessary for accurate perceptions of interactions among plants in the field. Our study, which was conducted in a wetter than average year, showed that positive effects of shrubs on annuals were strong, while positive effects of annuals on shrubs were weak. Bertness and Callaway (1994) and Callaway and Walker (1997) hypothesized that the importance of positive interactions should increase with greater abiotic stress. If so, positive effects between desert shrubs and annuals would be even more pronounced in dry years. However, Casper (1996) and Tielbörger and Kadmon (1997) did not find that net facilitation of herbaceous plants by desert shrubs was necessarily stronger in drought years. Tests of these contradictory views will require long-term studies that differentiate between positive and negative effects simultaneously in addition to assessing net effects.

Balance of positive and negative effects, the net effect of interaction

Previous studies have recognized that the net effects of facilitation (Morris and Wood 1989, Chapin et al. 1994) or interference (Ellison and Houston 1958, Walker and Chapin 1986, Callaway et al. 1991, Walker and Vitousek 1991, Maron and Connors 1996) represent the sum of unequal negative and positive effects. The experimental separation of negative and positive effects in our study allowed us to quantitatively perceive that the strong negative effects of annuals on shrubs were only partly offset by the weak positive effects of annuals on shrubs that lasted only a fraction of each year, resulting in net interference of shrubs by annuals. On the other hand, the strong positive effects of shrubs on annuals were only partially offset by the weak negative effects of shrubs on annuals, resulting in net facilitation of annuals by shrubs that lasted the entire

annual life span. Thus the long-term existence of a close, spatial association of shrubs and annuals may be strongly promoted by facilitation of annuals through their entire life span and by amelioration of negative effects of annuals on shrubs by opposing positive effects and by the longevity of shrubs relative to the duration of these negative effects.

To our knowledge, an experimental approach that achieves a resolution of bidirectional positive and negative effects has not been attempted before. The attempt to do this in the present study is sound to the degree that the artificial structures employed (thatch and dead shrub canopies) mimic the positive effects of neighboring plants on each other at least with regard to soil water availability. We were able to show in a parallel field trial (Table 1, experiment II) that thatch as a mimic for the physical effects of annuals had similar effects on soil water availability as annuals had. Other than this, we have not been able to devise means to independently test the fidelity of these mimics. They probably had no negative effects on soil water status that the living plants did not also have, but it is possible that the living plants had additional positive effects that the mimics did not possess. For example, a living shrub could have increased water availability to the annuals by hydraulic lift (Richards and Caldwell 1987), a phenomenon recently confirmed to occur in *Ambrosia dumosa* (C. N. Yoder and R. S. Nowak, *personal communications*). If such additional positive effects of living shrubs were present, our estimates of rather strong positive effects of shrubs on annuals are conservative, and actual effects might be even stronger. In addition to water availability, a number of other factors may contribute important positive effects in arid environments that were beyond the scope of this study. These include nutrient availability (e.g., Garcia-Moya and McKell 1970) and the poorly understood role of mycorrhizae and microorganisms as possible mediators between annual and perennial plants (Allen and Allen 1986, Allen and Allen 1990, Sarig et al. 1994).

This study demonstrates that an observed net effect, whether it is facilitation or interference, can result from independent positive and negative effects counteracting each other. The predominance of interference over facilitation in characterizations of plant–plant interactions found in the scientific literature is not necessarily due to such a predominance in nature. It may be due to positive effects being undetected in past studies simply because they were masked by negative effects, or because the complexities of plant–plant interactions have seldom been fully anticipated in research designs.

Interactions among plants in an association will tend to drive that association to change unidirectionally to the degree that such interactions are simple, direct, and constant. But if interactions are complex amalgams of positive and negative effects that also ebb and flow independently through time, as this study demonstrates for a desert shrub–annual association, then associations

may not be driven to change directionally by apparently dominant interactions. Rather they may be caused to fluctuate about a rough mean. Consequently, the experimental separation and quantification of bidirectional positive and negative effects is necessary to gain a mechanistic understanding of plant interactions sufficient to provide assessment of the status of an association at any particular time and to allow predictions of long-term fluctuations of that association.

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ERRATA

In the article by Christopher R. Tracy (1999) entitled “Differences in body size among chuckwalla (*Sauromalus obesus*) populations,” *Ecology* **80**(1):259–271, the first line of the first full paragraph on p. 260 should read as follows: “The association between small lizards with larger fat stores in areas with **low** plant diversity vs. large lizards with lesser fat stores in areas with **higher** plant diversity might represent a trade-off in resource allocation” (corrected wording appears here in bold type).