POSITIVE, NEGATIVE, AND NET EFFECTS IN GRASS–SHRUB INTERACTIONS IN MEDITERRANEAN SEMIARID GRASSLANDS

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Abstract. Current theoretical models and field evidence suggest that facilitation and interference act simultaneously in the field, but there is little information on their joint dynamics under varying abiotic conditions. We evaluated spatial and temporal variations in the positive, negative, and net effects of the tussock grass *Stipa tenacissima* on the shrub *Pistacia lentiscus* in Mediterranean semiarid grasslands. We performed a field experiment in which positive (microclimatic amelioration and water inputs from runoff) and negative (belowground competition) effects were experimentally manipulated under contrasting levels of stress. The environment provided by *S. tenacissima* (tussock treatment) improved the survival and physiological status of planted *P. lentiscus* seedlings. The elimination of shade and competition from *S. tenacissima* significantly decreased and increased, respectively, seedling performance as compared to the tussock treatment. We found evidence that microclimatic amelioration is the main positive factor involved in the interaction under study, and that it can balance the negative effects of belowground competition. The latter was also important, especially after major rainfall events. In contrast with previous studies, both the water inputs from runoff and the soil chemical fertility were found to have a relatively weak effect in the interaction under study. The net effect of *S. tenacissima* on *P. lentiscus* was always facilitative, but the magnitude of this effect increased with the harshness of the environmental conditions in both space and time. Despite this, the mechanisms underlying plant–plant interaction responded unequally to small-scale environmental variation. Our results agree with models suggesting that the magnitude of facilitation may increase under stressful conditions, and provide evidence of the dynamic nature of positive and negative interactions in the field.

Key words: competition; facilitation; Mediterranean grassland; Pistacia lentiscus; plant species interactions; positive and negative effects; semiarid grassland; Stipa tenacissima.

INTRODUCTION

Positive interactions between plant species have been acknowledged since the early days of ecology (Went 1942, Muller 1953). Nevertheless, for many decades, negative interactions have been considered the major force driving interspecific interactions in plant communities (Keddy 1989), and most research on this topic has focussed on the identification and quantification of interference (Gurevitch et al. 1992, Goldberg and Novoplansky 1997). In the last years, there has been an increasing interest in facilitation, and its importance for plant community dynamics is now widely recognized (Bertness and Hacker 1994, Callaway 1995). A large set of field studies supports the idea that both processes act simultaneously, and that the net interaction between two plant species results from unequal negative and positive effects (e.g., Callaway et al. 1991, Bertness and Shumway 1993, Aguiar and Sala

1994). Nevertheless, much remains unknown about the balance between positive and negative interactions, the way they are related to species traits and environmental conditions, and their spatial and temporal variation in the field (Callaway et al. 2002). It has been suggested that interference is more important in wet and cold years, and that facilitation dominates in hot and dry years (Greenle and Callaway 1996). However, the opposite pattern has also been reported (Tielbörger and Kadmon 2000). Temporal changes from facilitation to interference have also been associated with changes in the life cycle or in the ecophysiology of the species involved, even within the same year (Pugnaire et al. 1996, Barnes and Archer 1999, Holzapfel and Mahall 1999). On a spatial scale, several studies support the hypothesis that facilitation increases in importance along a gradient of abiotic stress (Greenle and Callaway 1996, Pugnaire and Luque 2001). Thus, a comprehensive assessment of plant interactions in the field must incorporate both the temporal and spatial variability in the abiotic conditions.

Facilitative interactions have been described mainly for harsh conditions, such as those occurring in semi-arid environments (Callaway 1995). The mechanisms

of facilitation in these areas are diverse, and include improved soil fertility (Moro et al. 1997), microclimatic amelioration (Franco and Nobel 1989), and increased water availability (Raffaele and Veblen 1998) under the canopy of the facilitator species. These mechanisms often act together, but empirical knowledge on their relative importance under field conditions is scarce (Callaway 1995). In semiarid environments, competition for water is more important than competition for light or nutrients (Casper and Jackson 1997), but there are still experimental gaps about how resource dynamics affects negative interactions in these areas (Goldberg and Novoplansky 1997).

To our knowledge, very few studies have performed manipulative field experiments to dissect the net effects of a given plant-plant interaction into their underlying positive and negative effects (Holzapfel and Mahall 1999). None of these studies has used this kind of approach to jointly evaluate the spatial and temporal variation in these effects, and the mechanisms underlying them, under varying abiotic conditions in the field. We aimed to do this for the effects of the perennial tussock grass *Stipa tenacissima* L. on the native late-successional shrub *Pistacia lentiscus* L. in semiarid Mediterranean grasslands. Recent studies show that *S. tenacissima* facilitates the establishment of shrubs in semiarid areas (Maestre et al. 2001, 2002*a*), but the relative importance of the mechanisms underlying this interaction is unknown. Facilitation of woody by herbaceous species has rarely been reported (De Stevens 1991, Gill and Marks 1991, Berkowitz et al. 1995), and the described interaction between *S. tenacissima* and shrubs provides the first evidence for net facilitation of shrub seedlings by perennial grasses in semiarid ecosystems. In these areas, numerous studies have reported facilitation of grasses by shrubs, or of shrub and tree seedlings by adults, either conspecific or not (e.g., Franco and Nobel 1989, Pugnaire et al. 1996, Moro et al. 1997).

We hypothesize that changes in abiotic conditions modify the positive, negative, and net effects according to the predictions of Bertness and Callaway (1994), i.e., the importance of positive vs. negative effects increases as the abiotic stress increases. The objectives of this study were to (1) assess the relative importance of the positive and negative effects of *S. tenacissima* on *P. lentiscus*, (2) elucidate the mechanisms underlying them, and (3) evaluate their dynamics, and that of the net effect, under contrasting stress conditions. To achieve these objectives, we manipulated the positive (microclimatic amelioration and water inputs from runoff) and negative (belowground competition) effects involved in the interaction under study on two sites differing in their degree of abiotic stress. We also performed a growth chamber experiment to test the effect of soil fertility on this interaction.

METHODS

Study area

Field experiments were conducted at two sites (Aguas and Ballestera) located in southeastern Spain (Aguas, 38°31′ N, 0°21′ W, 460 m above sea level, 12° slope, 160° aspect; Ballestera, 38°28′ N, 0°22′ W, 140 m above sea level, 21° slope, 170° aspect). Their climate is semiarid, with a mean annual precipitation below 390 mm and an intense summer drought. Soils are loamy to silty loam, Lithic Calciorthid, derived from marls and limestone. Vegetation is dominated by *S. tenacissima*, but sparse perennial grasses, such as *Brachypodium retusum* (Pers.) P. Beauv., and shrubs, such as *Globularia alypum* L. and *Rhamnus lycioides* L., can also be found. Although both sites share the same soil type, vegetation, and aspect, and they are only 10 km apart, they show important differences in rainfall amounts. Short-term (1999–2001) on-site recordings showed that the annual rainfall at Ballestera was 36% lower than at Aguas (153 vs. 239 mm mean rainfall). Long-term (1960–1990) recordings at the nearest weather stations (38°35′ N, 0°18′ W, 429 m above sea level, and 38°24′ N, 0°26′ W, 40 m above sea level for Aguas and Ballestera, respectively) followed the same trend, with Ballestera showing a 43% lower annual rainfall than Aguas (220 mm vs. 388 mm mean rainfall). Thus, we assume the presence of higher abiotic stress in Ballestera than in Aguas.

Experimental design and measurements

Field experiment.—We selected two main treatments for this experiment: ''tussock'' and ''open.'' The tussock treatment was located upslope and adjacent to isolated *S. tenacissima* tussocks; the open treatment was located in the intertussock areas devoid of vascular vegetation (see Maestre et al. 2001 for details). In addition, we added three manipulative treatments: (1) removal of belowground competition from *S. tenacissima*, (2) removal of shade from the canopy of *S. tenacissima*, and (3) preventing water inputs due to runoff from arriving at *S. tenacissima* tussocks, respectively. Hereafter, they are referred to as ''herbicide,'' ''no-shade,'' and ''no-runoff'' treatments, respectively. In the herbicide treatment, we killed *S. tenacissima* tussocks by applying herbicide (glyphosate 36% [weight:volume], [Insecticidas Mafa, Nules, Spain]), avoiding any damage to the surrounding vegetation. After herbicide application, we did not remove dead plants. In the no-shade treatment, we bent *S. tenacissima* canopies with the help of metallic cables fixed to the ground. After bending, measures of photosynthetically active radiation (PAR) showed no differences with those recorded for the open treatment (see *Results*). In the no-runoff treatment, we inserted a 20 cm high, 120 cm long, metallic sheet in the ground at a depth of 6 cm. It formed a

120° angle to divert runoff, and was placed 25 cm upslope of the edge of *S. tenacissima*.

Before planting, we randomly selected 25 planting points per treatment and site. The application of herbicide and the bending of *S. tenacissima* tussocks were performed two weeks before planting, and the installation of metallic sheets took place immediately after planting. Nine-month-old seedlings of local provenance were planted in manually dug planting holes (25 × 25 × 25 cm) in late winter (22–23 January 2001). The seedlings were purchased from a commercial nursery located 60 km from the study sites (Viveros Todolí, Palmera, Spain). To ensure successful establishment, each seedling was irrigated with 2 L of water at planting. Due to the extremely low rainfall registered during the first months of the experiment, we performed additional irrigations with the same amount of water on 12 April and 15 July 2001.

We used survival and chlorophyll fluorescence to evaluate seedling response to the experimental treatments. Survival was recorded at 2–4 wk intervals between January and September 2001, and monthly between December 2001 and May 2002. We performed chlorophyll fluorescence measurements in Aguas on five dates between April and September 2001 (11 April, 31 May, 11 July, 21 August, and 8 September). We used a portable, pulse-modulated fluorometer (PAM-2000, Walz, Effeltrich, Germany), equipped with a leaf clip holder (2030-B, Walz) and sensors for incident photosynthetically active radiation (PAR). Predawn and midday measurements of maximal (F_m) and minimal (F_0) fluorescence were used to calculate the maximum efficiency of the photosynthetic energy conversion of PSII ($F_v/F_m = [F_m - F_0]/F_m$), where F_v is the variable fluorescence. Predawn measurements were performed before sunrise; midday measurements were performed between 1230 and 1400 hours (local time, Greenwich Mean Time + 2 h), after a 30-min dark adaptation. Six individuals per treatment and sampling date were randomly selected for the physiological measurements.

We measured soil moisture and PAR for all treatments by using time-domain reflectometry (TDR, Topp and Davis 1985) and the fluorometer described above, respectively. During the planting process in Aguas, we vertically installed TDR probes of 20 cm in length in 12 randomly selected planting holes per treatment. We used a Tektronix 1502C metallic TDR cable tester (Tektronix, Beaverton, Oregon, USA) for measurements, and a site-specific calibration factor for the soils of the study area. Measurements were performed at 1–6 wk intervals between January 2001 and May 2002, and provide an integration of volumetric soil moisture content at 0 to 20 cm depth. We measured PAR between 1100 and 1230 hours (local time, Greenwich Mean Time + 2 h) during the ecophysiological surveys.

Growth chamber experiment.—For this experiment, soils from 12 randomly selected tussock and open treatments were collected at both field sites during January 2002. The soil was taken to the laboratory, sieved through an 8-mm mesh, and dried at 60°C to constant mass. Forty-eight 150-cm³ pots were filled with field soil following a fully randomized factorial design, with 12 replicates per combination of treatment and site. A 1-wk-old *P. lentiscus* seedling previously germinated from seed was added to each pot. Seeds of local provenance—originating 60 km from the study sites—were collected by the local Forest Services in 1998. Seedlings were subsequently grown for 65 d in a growth chamber (model MLR-350, Sanyo Electric, Tokyo, Japan), which was maintained at day : night air temperatures of 26:20°C, PAR of 300:0 μmol·m⁻²·s⁻¹ and photoperiod of 14 h. All pots were irrigated with 50 mL of deionized water twice a week during the experiment, and they were randomly rotated twice a month. At the end of the experiment, we measured basal diameter, stem height, and number of leaves of all seedlings; after that the seedlings were harvested and divided into roots, stems, and leaves. The harvested material was dried at 65°C to constant mass. Soils from tussock and open treatments are very similar in physiochemical properties (Maestre et al. 2001). However, we performed a control assessment of the soil organic matter (SOM) content in the soils used in this experiment by means of the loss-on-ignition method (soils were heated in a furnace at 550°C for 2 h). These estimations may be biased by the high carbonate content of the soils (59–85%, Maestre et al. 2001), but as the carbonate content was homogeneous within each site, we considered loss-on-ignition values to be acceptable for comparison purposes.

Quantification of positive, negative, and net effects in the field

We assume that the net effect of *S. tenacissima* on *P. lentiscus* results from the sum of unequal negative and positive effects. The negative effects in this interaction are likely to be driven by resource competition—probably for water—between both species. Preliminary measurements showed that roots of *S. tenacissima* colonized the planting holes in the tussock treatment six months after planting (data not shown). Since water limits physiological activity in *S. tenacissima* (Haase et al. 1999) and *P. lentiscus* (Flexas et al. 2001), we expected competition for this resource under the conditions of the present study and predicted an increase in its magnitude as the soil moisture decreased during summer. We identified soil conditions (fertility, surface properties, and physical characteristics), microclimatic amelioration, and water inputs from runoff as the main positive factors. In the field, we manipulated three main factors involved in the interaction under study: belowground competition (negative), microclimatic amelioration (positive), and water inputs from runoff (positive). This approximation, which necessarily oversimplifies reality, does

not explicitly take into account the differences in soil chemical and physical properties between treatments. However, their role can be inferred from the comparative analysis of the factors studied, and from the growth chamber experiment.

We quantified positive, negative, and net effects in the field between March and October 2001, when most seedling mortality took place. To assess the net effect of *S. tenacissima* on *P. lentiscus*, we compared seedling performance in the tussock and open treatments. Negative effects of competition by *S. tenacissima*, positive effects of microclimatic amelioration, and positive effects of runoff water were obtained for a given variable as the difference in seedling performance between tussock and herbicide, tussock and no-shade, and tussock and no-runoff treatments, respectively. For survival data, the effects were quantified by calculating the relative differences in survival between pairs of treatments. For predawn F_v/F_m measurements, effects were calculated by using "Hedges' *d* index" as described in Gurevitch and Hedges (2001).

Statistical analyses

We evaluated the positive, negative, and net effects of *S. tenacissima* on soil moisture by using "Hedges' *d* index." Chlorophyll fluorescence and PAR data were analyzed by two-way (treatment and sampling date) ANOVA, with treatment as a fixed factor and sampling date as a random factor. Seedling survival was analyzed by calculating Kaplan-Meier estimates of survival curves followed by a log-rank test to evaluate differences between treatments. Data from the growth chamber experiment were analyzed separately for each site by one-way ANOVA. In all cases, the Student-Newman-Keuls (SNK) test was used to evaluate differences between treatments when appropriate. Prior to ANOVA, data were checked for normality and homogeneity of variances, and were log-transformed when necessary to correct for deviations from these assumptions. All statistical analyses were performed with the use of the SPSS 9.0 package (SPSS, Chicago, Illinois, USA).

RESULTS

Field experiment

Rainfall during the first 15 mo after planting was 280 mm and 192 mm at Aguas and Ballestera, respectively (Fig. 1). Differences between sites gradually increased throughout the spring and summer of 2001—by the end of summer, Ballestera had received 40% less rainfall than Aguas—and decreased thereafter. The net effect of *S. tenacissima* on soil moisture was positive and significant during most of the study period (tussock–open graph in Fig. 2); it was especially evident after the main rainfall events, and became less important as soil moisture decreased (Ap-
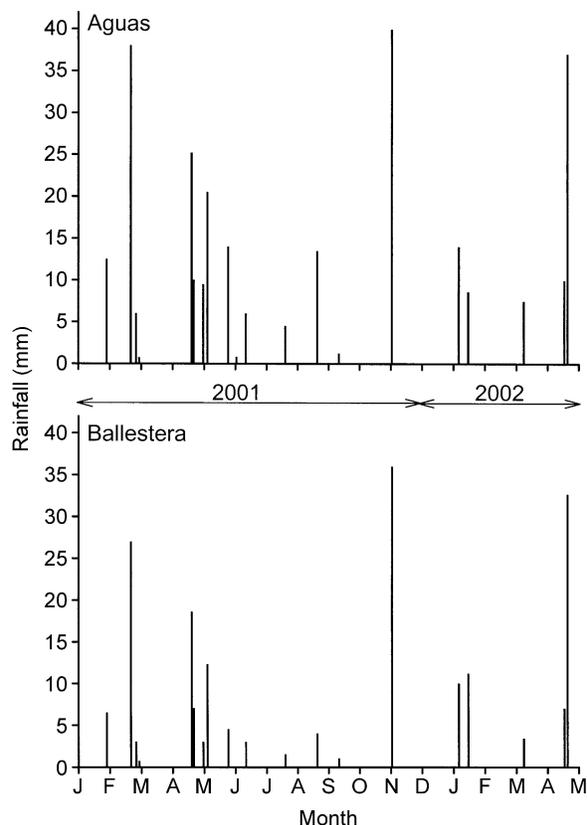

FIG. 1. On-site recordings of rainfall at the study sites throughout the study period.

pendix A). The effect of competition on soil moisture was negative and significant during most of the period (tussock–herbicide graph in Fig. 2). Microclimatic amelioration had a positive and significant effect on soil moisture during spring and early summer (tussock–no-shade graph in Fig. 2). On the other hand, the effect of water inputs from runoff was negligible; it was significant only after the main rainfall event that took place during the spring (no-runoff–tussock graph in Fig. 2).

By the end of the experiment, the survival rate of *P. lentiscus* ranged between 0% and 36% in Ballestera and 32% and 96% in Aguas, and was 28–60% lower for a given treatment in the former (Fig. 3). Seedlings planted in the herbicide treatment showed significantly higher survival rates than those planted in the other treatments. Survival rates were similar for the tussock and no-runoff treatments, but significantly lower for the no-shade treatment as compared to both of them. No differences in the dynamics of survival between the tussock and open treatments were found, but they were marginally significant in Aguas ($P = 0.078$). Incoming PAR was highly decreased by *S. tenacissima* tussocks (Fig. 4). At predawn, seedlings planted in the herbicide treatment
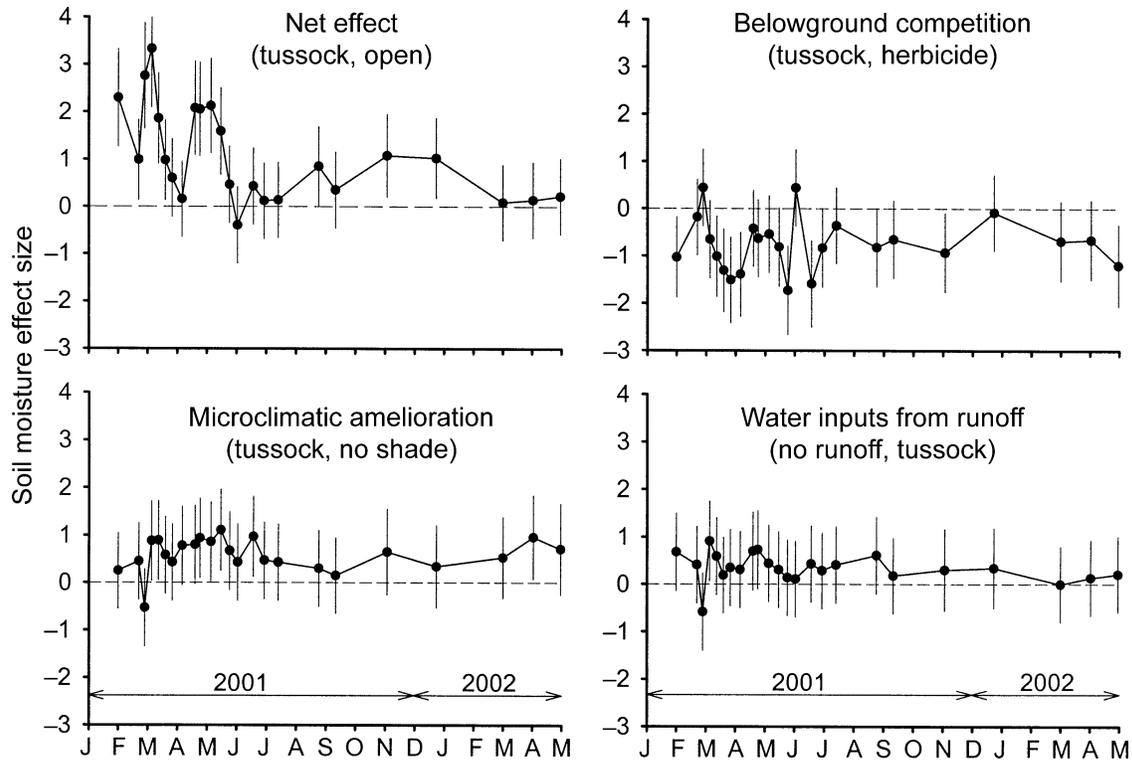
FIG. 2. Dynamics of the positive, negative, and net effects of *Stipa tenacissima* on soil moisture at Aguas. Data represent mean effect size (Hedges' *d* index) ± 95% confidence intervals. To calculate each effect we used data from the treatments shown in parentheses.

had higher F_v/F_m than those planted in the other treatments (Fig. 4). This variable was also higher in the tussock and no-runoff treatments than in the no-shade and open treatments. Similar patterns were found at midday, but values of F_v/F_m values were substantially lower, especially in unshaded treatments (Fig. 4). Additional data on seedling performance can be found in Appendix B.

Growth chamber experiment

Pistacia lentiscus stem height was higher when seedlings were grown with tussock soils from Aguas (Table 1). Other morphometric variables showed a similar trend, but the differences between treatments were not statistically significant. In Ballestera, where no differences in seedling performance were found, soil organic matter (SOM) did not show significant differences between treatments (5.70 ± 0.21% in tussock treatment vs. 5.66 ± 0.35% in open treatment [mean ± 1 SE, n = 12]; one-way ANOVA, $F = 0.01$, df = 1, 22, $P =$ 0.926). In Aguas, the differences between treatments in SOM were marginally significant (5.17 ± 0.34% in tussock treatment vs. 4.39 ± 0.24% in open treatment [mean ± 1 SE, n = 12]; one-way ANOVA, $F = 3.48$, df = 1, 22, $P = 0.076$).

Dynamics of positive, negative, and net effects

The net effect of *S. tenacissima* on *P. lentiscus* survival was facilitative at both sites throughout the study period (Fig. 5). It increased at both sites during the summer, but was always higher in Ballestera than in Aguas; differences between sites in the size of this effect increased concomitantly with the differences in rainfall between them. The dynamics of the positive and negative effects of *S. tenacissima* on *P. lentiscus* survival were similar at both sites, but their size was generally higher in Ballestera than in Aguas (Fig. 6). The size of the negative effects mediated by competition and of the positive effects mediated by microclimatic amelioration and water inputs from runoff increased during the course of the summer. Within the latter, the size of the effect of microclimatic amelioration was higher than that of water inputs from runoff. Results obtained with predawn F_v/F_m measurements followed a similar trend (Fig. 7). The net effect of *S. tenacissima* on *P. lentiscus* F_v/F_m was positive and significant in spring and late summer. The size of the negative effects mediated by competition increased during the summer, and was significant by the end of the study period. The size of the positive effect mediated by microclimatic amelioration was significant in early spring and late summer. The effect of water
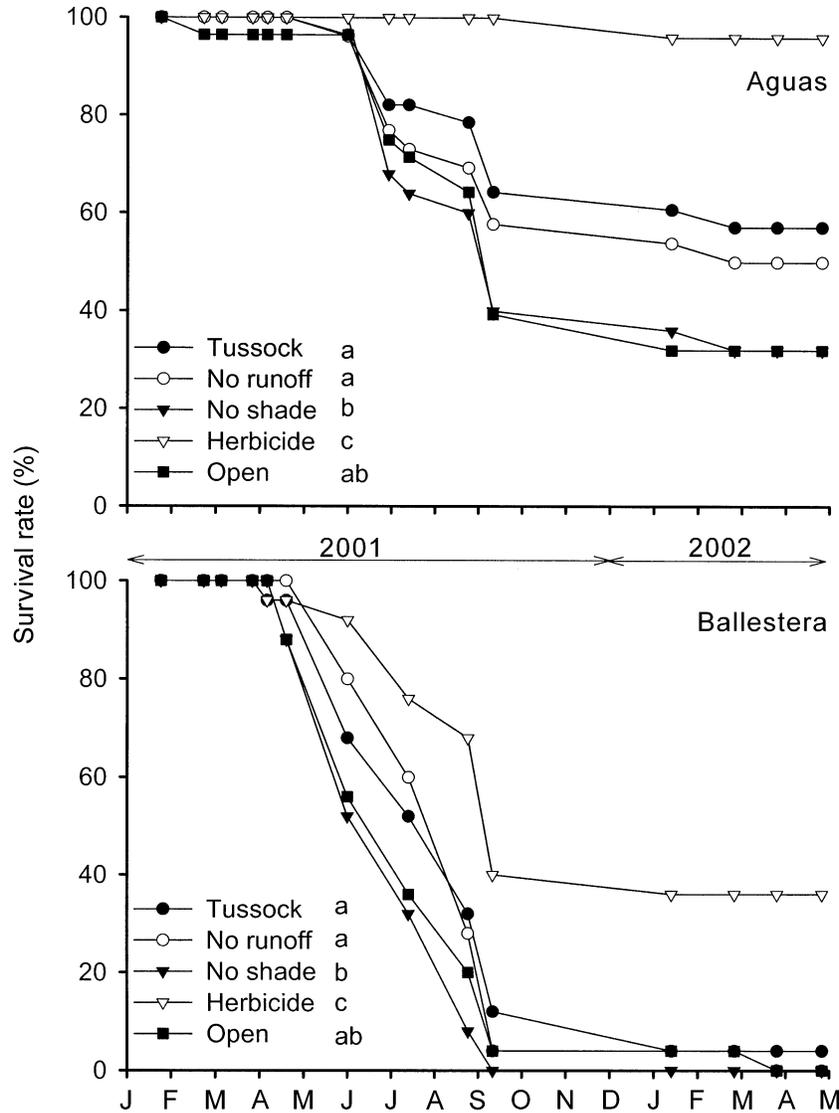
FIG. 3. Survival of *Pistacia lentiscus* seedlings planted under different treatments. The number of seedlings planted for each combination of treatment and site was 25. Planting was on 22–23 January 2001. Shared letters after the key to symbols indicate no significant differences between treatments (log-rank test, $P > 0.05$).

inputs coming from runoff was not significant for any sampling date.

DISCUSSION

Soil moisture dynamics

We found a positive and significant effect of *S. tenacissima* on soil moisture during most of the study period. Interestingly, the size of this effect was often larger than that derived from the sum of the negative and positive effects evaluated. This suggests that other factors not fully incorporated in our experimental design, such as soil physical properties and water inputs from sources like dew, may influence soil moisture

dynamics in these *S. tenacissima* steppes. But it is also likely that the various factors affecting soil moisture interact with each other in a nonadditive way. Our results suggest that water uptake by *S. tenacissima* is high enough to affect soil moisture content, especially after the main spring rainfall events. The size of the effects of microclimatic amelioration and competition on soil moisture were similar throughout the study period, providing evidence that shading by *S. tenacissima* canopy may balance the negative effect promoted by its own water uptake. These results suggest that microclimatic amelioration plays a major role in the maintenance of soil moisture underneath
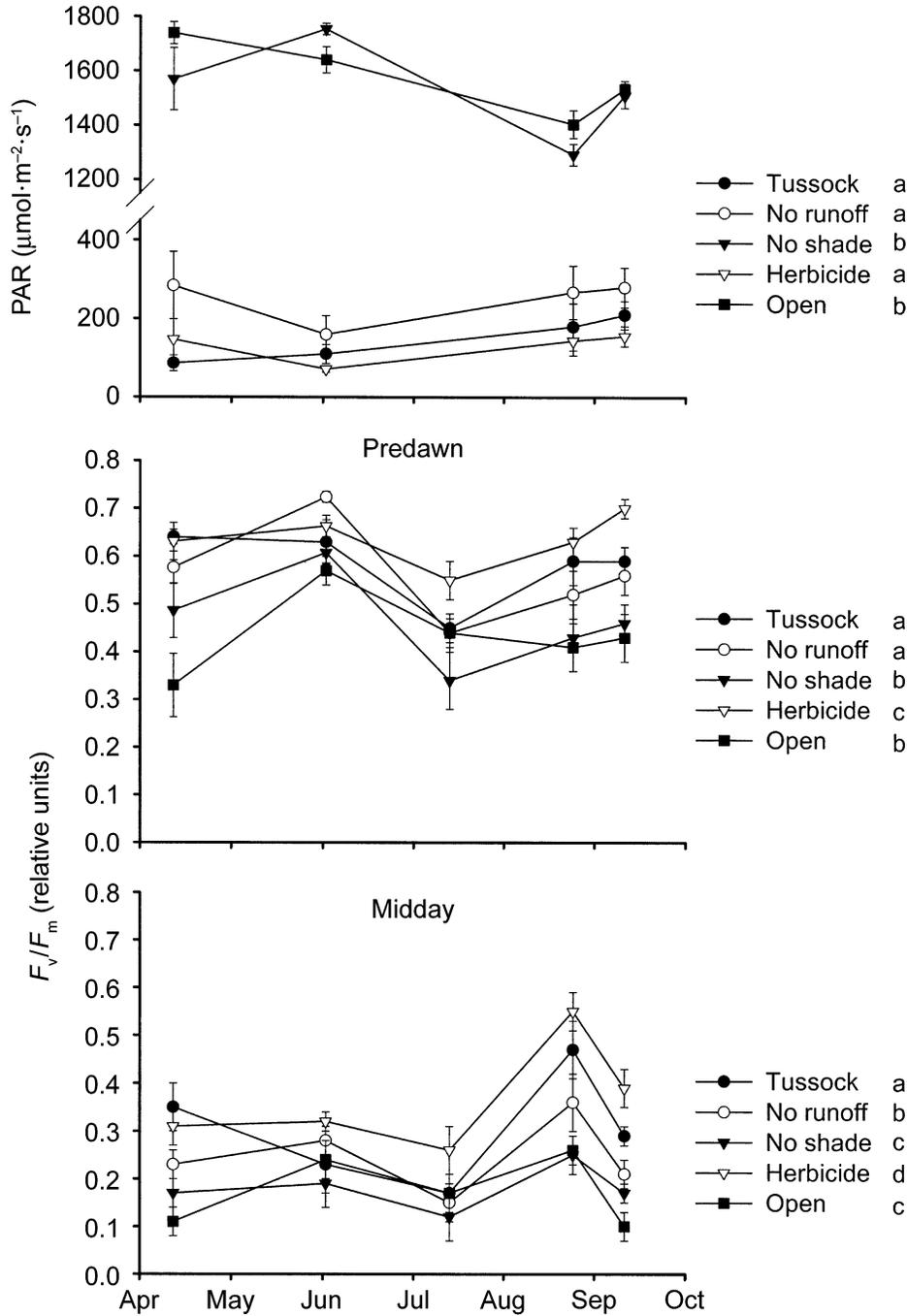
FIG. 4. Dynamics of photosynthetically active radiation (PAR), and of maximum efficiency of PSII (F_v/F_m) of *Pistacia lentiscus* seedlings, under different treatments at Aguas. Data represent means $\pm$ 1 SE ($n = 6$). Shared letters after the key to symbols indicate no significant differences between treatments (SNK test, $P > 0.05$).

the canopy of *S. tenacissima*, and support previous studies that emphasize its importance for retaining soil moisture in semiarid areas (Breshears et al. 1998). The negligible effects of runoff diversion on soil moisture dynamics under the canopy of *S. tenacissima* were unexpected, and contrast with previous work

performed in Almería (Spain) showing lower soil moisture content in tussock treatments when runoff water was diverted (Puigdefábregas and Sánchez 1996). This discrepancy could be associated to differences in soil depth, since the study in Almería focussed on changes in the 0–5-cm layer whereas in our

TABLE 1. Characteristics of *Pistacia lentiscus* seedlings harvested at the end of the growth chamber experiment, and results of one-way ANOVA tests to evaluate the effect of microsite on seedling growth.

a) Seedling characteristics

Variable	Aguas		Ballestera	
	Tussock	Open	Tussock	Open
Basal diameter (mm)	0.96 ± 0.06	0.86 ± 0.04	1.02 ± 0.05	0.89 ± 0.06
Height (cm)	4.55 ± 0.25	3.83 ± 0.21	4.52 ± 0.31	3.99 ± 0.26
Number of leaves	11.92 ± 0.54	11.48 ± 0.75	12.67 ± 0.70	12.08 ± 1.03
Foliar biomass (g)	8.42 ± 1.26	6.04 ± 0.43	8.94 ± 1.02	6.68 ± 0.99
Stem biomass (g)	1.38 ± 0.25	1.01 ± 0.10	1.72 ± 0.27	1.27 ± 0.22
Root biomass (g)	4.66 ± 0.77	4.15 ± 0.79	4.78 ± 0.70	4.51 ± 0.98
R:S	0.50 ± 0.08	0.61 ± 0.13	0.46 ± 0.05	0.55 ± 0.06

b) ANOVA results

Variable	Aguas			Ballestera		
	F	df	P	F	df	P
Basal diameter	1.69	1, 22	0.207	2.49	1, 22	0.129
Height	4.94	1, 22	**0.037**	1.70	1, 22	0.206
Number of leaves	0.29	1, 22	0.596	0.22	1, 22	0.645
Foliar biomass	3.16	1, 22	0.089	2.51	1, 22	0.128
Stem biomass	1.89	1, 22	0.283	1.64	1, 22	0.214
Root biomass	0.21	1, 22	0.655	0.05	1, 22	0.821
R:S	0.55	1, 22	0.468	1.272	1, 22	0.272

Notes: For seedling characteristics, data are means ± 1 SE ($n = 12$). R:S = root-to-shoot ratio (belowground/aboveground biomass). Significant effects ($P < 0.05$) are in bold.

study we measured soil moisture content down to a depth of 20 cm. But it may also reflect differences in the relative importance of the factors regulating soil moisture dynamics.

Mechanisms of facilitation of Pistacia lentiscus by Stipa tenacissima

Stipa tenacissima was able to facilitate *P. lentiscus* under the conditions of our study. These results agree with previous observations (Maestre et al. 2001, 2002*a*), providing further evidence that the facilitative effect of *S. tenacissima* is consistent. The positive but weak effect of soil fertility on *P. lentiscus* growth agrees with a previous work on the same experimental sites, which reported only marginal differences in soil chemical properties between treatments (Maestre et al.

2001) and with the SOM values measured in this work. However, this effect contrasts with other studies performed in semiarid areas, which identify soil fertility as one of the main mechanisms driving facilitation (Moro et al. 1997, Walker et al. 2001). It is interesting to note that the positive effect of soil fertility was observed only for soils from Aguas and that the experiment was performed in a controlled environment, which permitted an optimal seedling development. We speculate that, under field conditions, soil chemical fertility will play a minor role as compared to other environmental modifications promoted by *S. tenacissima*. However, as we did not manipulate fertility in the field, we were not able to quantify its relative importance against the remaining factors involved in the interaction under study. From the comparison of the factors

FIG. 5. Dynamics of the net effect of *Stipa tenacissima* on *Pistacia lentiscus* survival (solid lines), and cumulative differences in rainfall between Aguas and Ballestera (bars). This effect is estimated as $(S_T - S_O)/S_O$, where S_T and S_O are the survival rates for the tussock and open treatments, respectively. Note that the values of the net effect are not presented as cumulative.
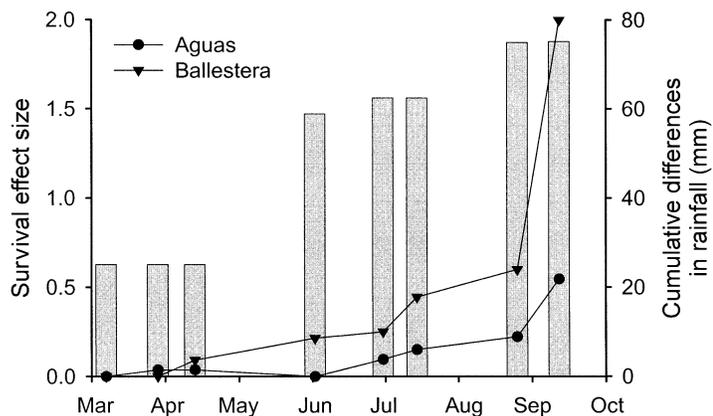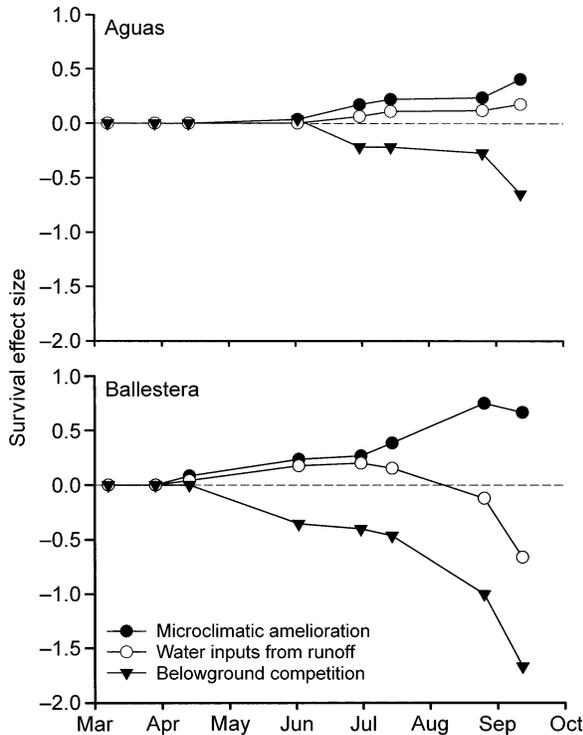
FIG. 6. Dynamics of the positive and negative effects of *Stipa tenacissima* on *Pistacia lentiscus* survival. The effects of microclimatic amelioration, water inputs from runoff, and belowground competition are estimated as $(S_{NS} - S_T)/S_T$, $(S_{NR} - S_T)/S_T$, and $(S_H - S_T)/S_T$, respectively, where S_T, S_{NS}, S_{NR}, and S_H are the survival rates for the tussock, no-shade, no-runoff, and herbicide treatments, respectively. To help with interpretation of the results, the sign of the effects of microclimatic amelioration and belowground competition has been changed. Note that the values of the positive and negative effects are not presented as cumulative.

manipulated in our field study, and with the data obtained in previous studies (Maestre et al. 2001, 2002*b*), we suggest that differences in physical properties between tussock and open treatments are more relevant than differences in soil chemical fertility for the interaction under study. Further manipulative experiments are needed to test this assumption.

Our results regarding the role of microclimatic amelioration agree with studies stressing its importance as a mechanism of facilitation in arid and semiarid environments (Nobel 1984, Franco and Nobel 1989, Fulbright et al. 1995). Our findings also suggest that water inputs from runoff are not an important factor in the facilitation of *P. lentiscus* by *S. tenacissima*. This contrasts with current knowledge, which highlights the importance of this water source in the maintenance of two-phase semiarid vegetation (Aguiar and Sala 1999, Valentin et al. 1999). Nevertheless, to date few experiments have manipulated runoff fluxes to elucidate their role on plant performance. Puigdefábregas and Sánchez (1996) showed that diverting the runoff significantly

reduced *S. tenacissima* growth. In contrast, Seghieri and Galle (1999) did not find a significant effect of this water source on the phenological and physiological activity of the shrub *Combretum micranthum* in a "tiger bush" ecosystem. The latter authors argued that high infiltration rates in vegetated patches could be enough to maintain shrub water status. Furthermore, the differences in infiltration rates between bare ground and vegetated patches have been identified as a key factor for explaining the maintenance and dynamics of semiarid vegetation (Hillerislambers et al. 2001). In *S. tenacissima* steppes, the infiltration rates are substantially higher underneath the tussocks than in open areas (Maestre et al. 2002*b*). Thus, the changes in microclimate and infiltration rates associated with *S. tenacissima* may be more important than runoff water for maintaining the physiological activity of planted seedlings.

We found strong belowground competition between *S. tenacissima* and *P. lentiscus*. The competition between shrubs and grasses in water-limiting ecosystems has been thoroughly described in the ecological literature (Bush and Van Auken 1989, Aguiar and Sala 1994). It can be especially important during the seedling stage of shrubs, when their rooting area is shared with that of herbaceous species (Montaña et al. 1995). We provide evidence that the mechanisms underlying the positive effects were able to offset the belowground competition, and that microclimatic amelioration was the main positive effect involved in the facilitation of *P. lentiscus* by *S. tenacissima*. But it is interesting to note that by the end of summer the effect of competition on survival was higher than the sum of the positive effects analyzed. As discussed above, this suggests that other factors that were not considered in the field experiment, such as differences in soil physical fertility and mycorrhizae (Azcón-Aguilar et al. 2003), may be playing a role in the interaction under study, or that a synergistic interaction between the positive factors involved in this interaction is taking place.

Dynamics of the positive, negative, and net effects

Understanding the links between abiotic conditions and species interactions is crucial for increasing our understanding of plant community dynamics, for accurately predicting the impacts of global climatic change on natural ecosystems, and for improving ecosystem management activities (Berkowitz et al. 1995, Bertness and Ewanchuk 2002). We did not find a tradeoff between facilitation and interference, but the magnitude of the positive, negative, and net effects showed strong differences coupled with small-scale changes in abiotic conditions as predicted by Bertness and Callaway (1994). We have used a manipulative experimental approach to evaluate for the first time the joint dynamics of facilitation and interference over time in habitats varying in apparent abiotic stress. Although in our case the net effect was always facilitative, the re-
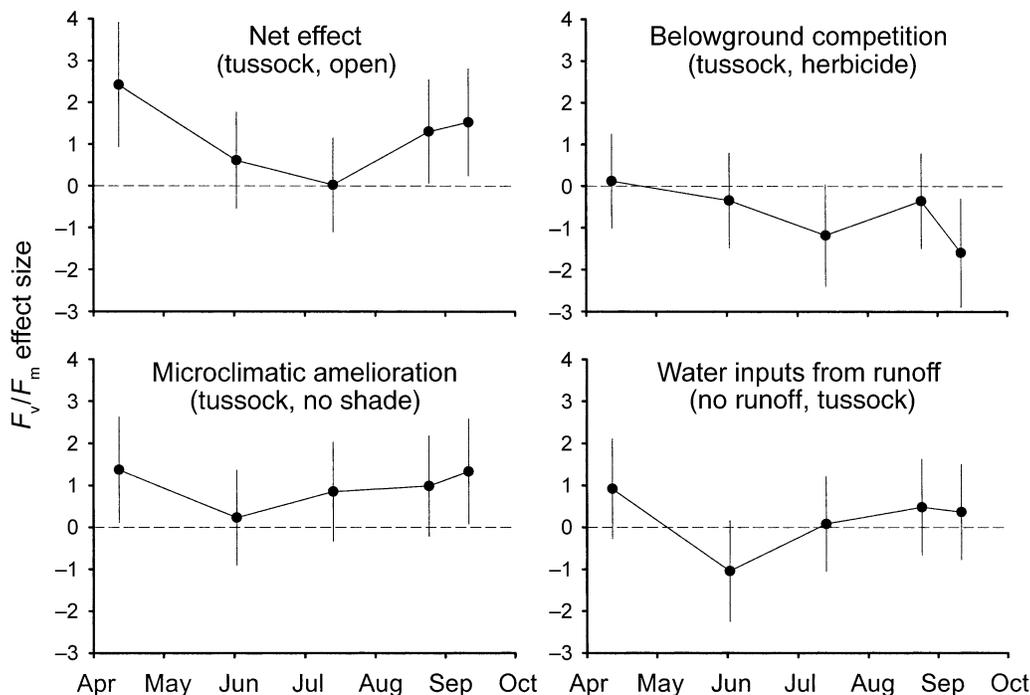
FIG. 7. Dynamics of the positive, negative, and net effects of *Stipa tenacissima* on *Pistacia lentiscus* predawn maximum efficiency of PSII (F_v/F_m) at Aguas. Data represent mean effect size (Hedges' *d* index) $\pm$ 95% confidence intervals. To calculate each effect we used data from the treatments shown in parentheses.

sults indicate that the mechanisms underlying plant–plant interaction may respond unequally to small-scale environmental variation, with the balance between their effects leading either to facilitation or to interference. The use of single-year observations did not allow us to evaluate how interannual variations in climatic conditions might change the dynamics of positive and negative effects in the interaction under study. However, we evaluated a crucial period for seedling establishment in Mediterranean ecosystems (Rey and Alcántara 2000), and the net effect observed was consistent with previous studies performed under lower rainfall conditions (Maestre et al. 2001, 2002*a*).

Stipa tenacissima is now occupying areas formerly dominated by shrublands and open woodlands (Le Houérou 2001). If, as suggested by recent studies (De Luis 2000), the amount of rainfall in the study area is decreasing as a consequence of climatic change, the positive effect of *S. tenacissima* on shrub seedlings is likely to increase in the future. This would promote the recolonization of *S. tenacissima* grasslands by late-successional shrubs; however, it is unknown whether this positive effect could offset current limitations to this process, such as lack of seed sources and high seedling mortality during summer drought. Brown et al. (1997) report a threefold increase in the density of woody shrubs in a Chihuahuan arid grassland during the last 30 yr in response to climatic change. We speculate that such scenarios are unlikely to occur in *S. tenacissima* grasslands, at least at that temporal scale. However,

elucidation of the long-term consequences of changes in the size of *S. tenacissima* effects on shrubs in response to climatic change merits further study.

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APPENDIX A

A figure showing the dynamics of soil moisture for different treatments throughout the study period is available in ESA's Electronic Data Archive: *Ecological Archives* E084-086-A1.

APPENDIX B

A figure showing predawn water potential of *Pistacia lentiscus* seedlings measured in Aguas on 16 June 2001 is available in ESA's Electronic Data Archive: *Ecological Archives* E084-086-A2.