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Competition intensity as a function of resource availability in a semiarid ecosystem

Abstract Two field experiments were conducted using three dominant perennial species of the Chihuahuan Desert: *Hilaria mutica* (a tussock grass), *Larrea tridentata* (a microphyllous shrub) and *Opuntia rastrera* (a flat-stemmed succulent cactus). Two hypotheses concerning competition in arid plant communities were tested. (1) Marked resource partitioning with no interspecific competition could be expected since the three species belong to different life-forms, and that plant growth in deserts is basically limited by harsh environmental conditions. (2) Alternatively, resource scarcity (particularly water) will result in strong plant competition. In a 1-year removal experiment, water status and plant growth of the three species were monitored in twelve 10 m × 10 m plots randomized in three blocks and assigned to the following treatments: (a) removal of all species, except *H. mutica*; (b) removal of all species, except *L. tridentata*; (c) removal of all species, except *O. rastrera*, and (d) control without any manipulation. In a watering experiment, under two neighbourhood conditions (growing isolated or in associations of plants of the three species in plots of 20 m^2), the water status of the three species and the growth of *H. mutica* and *L. tridentata* were studied for 32 days after an irrigation equivalent to 30 mm of rain, similar to a strong storm event at the site. In the removal experiment, where plants were free to capture water, no evidence of competition was observed. However, during the watering experiment, in which water was forced into the soil, competitive effects were observed. Associated individuals of *L. tridentata* had lower xylem water potentials and osmotic potentials (OPs) and produced shorter twigs and less leaves and nodes. Although less pronounced, neighbours also had a negative effect on the OP in *O. rastrera*. According to these results, the intensity of the interspecific competition for water seems to depend on the level of resource availability in the soil. Thus, the validity of the two hypotheses tested in this study also depends on the level of resources. Competition could be absent or very low in years of low precipitation, as in the year of this study (173 mm against a 25-year average of 264 mm). However, when soil water availability is high, e.g. following heavy rain, the negative interactions between species could be more intense.

Key words Plant competition · Chihuahuan Desert ecology · *Hilaria mutica* · *Larrea tridentata* · *Opuntia rastrera*

Introduction

Water availability is a critical factor for the establishment and growth of desert plants (Noy-Meir 1973), which have therefore developed a wide array of physiological, morphological and life history adaptations to maximize survivorship during dry periods (Ehleringer 1985; Nobel 1988).

Although water scarcity in arid lands suggests that plants should compete (sensu Tilman 1988) for moisture in the soil, there are contradictory views among authors regarding the importance of competition. Some authors have denied the existence of plant competition in arid lands (Shreve 1951; Went 1955). Connel (1975) considers that, either due to harsh physical conditions of the environment or to heavy predation during juvenile stages, many species seldom attain densities high enough to provoke competition. Cody (1986) argues that differences in plant life-forms allow interspecific segregation, and hence species coexistence, due to differences in the way that light, water and nutrients are captured. Kemp (1983) found groups of plants of different life-forms and photosynthetic pathways whose different phenological

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behaviours allowed them to grow in different seasons of the year. The model ruderal-competitor-stress tolerator of Grime (1979) suggests that competition is of very low importance in environments under a high degree of stress, a high rate of disturbance and low levels of resources and that, contrariwise, the intensity of competition must increase as the productivity of the community increases. Most of the evidence of competition in arid-land plants comes from observational studies on the spatial pattern of plant distribution (Fowler 1986 and references therein), but several studies have experimentally assessed the effects of competition in arid-land plants, involving grasses and forbs (Friedman and Orshan 1974; Robberecht et al. 1983; Nobel and Franco 1986; Olson and Richards 1989), shrubs (Friedman 1971; Fonteyn and Mahall 1981; Ehleringer 1984; Manning and Barbour 1988), and a combination of shrubs and grasses (Cable 1969; Sala et al. 1989), while there is only one study of a succulent species (Burger and Louda 1995). All the evidence supports the hypothesis that competition is a relatively frequent plant-plant interaction in arid and semiarid plant communities (Fowler 1986). However, as water availability fluctuates temporally and spatially in these ecosystems, it can be postulated that the intensity of competition likewise fluctuates (Weins 1977; Chesson 1986; Grant 1986; Schmitt and Holbrook 1986).

In this paper, the competition between individuals of three species, of different life-forms, was assessed in two field experiments in the Chihuahuan Desert, Mexico. Water status within the plants, growth, and flower or fruit production of *Hilaria mutica* Buckl. (Benth.), *Larrea tridentata* (DC.) Cov. and *Opuntia rastrera* Weber were measured after removal of all non-conspecific neighbours and in control plants growing without removal treatments. Additionally, in a watering experiment, the effect of neighbours on the water status of plants of the three species, and on the growth of *H. mutica* and *L. tridentata*, was studied after a single watering equivalent to a strong rain event, when the plants were growing in two neighbouring conditions: in isolation or in associations of individuals of the three species.

Two mutually exclusive hypotheses concerning competition in arid zones were tested (Shreve 1951; Went 1955; Noy-Meir 1973; Grime 1979; Fonteyn and Mahall 1981; Robberecht et al. 1983; Ehleringer 1984; Cody 1986; Sala et al. 1989). (1) Marked resource partitioning with no competition between species could be expected since the three species belong to different life-forms, and that growth in these plants is basically limited by harsh environmental conditions. (2) Alternatively, resource scarcity (particularly water) will result in strong plant competition.

Materials and methods

Field work was done at Mapimí Biosphere Reserve (Chihuahuan Desert, Mexico, 26°N 103°W, 1100 m altitude, 264 mm of annual rainfall concentrated in summer, mean temperature 20.8°C). The species studied were *L. tridentata* (a perennial microphyllous shrub), *O. rastrera* (a succulent cactus with flat-stemmed cladodes) and *H. mutica* (a perennial tussock-grass). The study site was dominated by *L. tridentata* and *O. rastrera* and was located in a bajada (slope 2% to 6%) with Haplic Yermosol soils (FAO/UNESCO 1976).

Removal experiment

All removal treatments were made on 16 May 1989 and the measurement of the response variables (water status and production of vegetative and reproductive structures) began in October 1989, after the rainy season was over, and finished in April 1990, just before the onset of the rainy season. Total rainfall during that period was 173 mm. The mean minimum temperature in January was 2.6°C and mean maximum temperature in June was 36.8°C.

The experiment was conducted in a 9-year exclosure for large herbivores, and during the experiment small mammals were also excluded. The 80 m × 37 m enclosure was divided in three rectangular blocks perpendicular to the slope. Four 10 m × 10 m plots were randomized in each block and assigned to the following treatments: (a) removal of all species, except *H. mutica*; (b) removal of all species, except *L. tridentata*; (c) removal of all species, except *O. rastrera*, and (d) control without any manipulation.

Aerial biomass was removed by manually clipping and any subsequent regrowth was eliminated. In all cases, the clipped biomass remained in situ to mitigate the microclimatic changes that can be expected around removed plants. Adult individuals of similar size were selected within each species for the measurement of response variables.

After the application of the removal treatment, the mean plant cover (in all cases $n = 3$) was 15.95 (SE = 4.71), 12.43 (SE = 1.36) and 2.66 m^2 (SE = 0.04) when all aerial biomass was eliminated except for *O. rastrera*, *L. tridentata* or *H. mutica*, respectively. The plots with only *O. rastrera* had 65.0 (SE = 17.35) plants on average, with only *L. tridentata*, 5.3 (SE = 0.88) and with only *H. mutica*, 25.7 (SE = 3.33). In the control plots, the mean plant density was 51.3 (SE = 10.87), 4.0 (SE = 0.58), 12.6 (SE = 2.19) and 8.9 plants (SE = 1.38) for *O. rastrera*, *L. tridentata*, *H. mutica*, and other species, respectively. In the same order, the mean plant cover was 12.99 (SE = 2.66), 15.98 (SE = 3.08), 2.55 (SE = 0.34), and 4.12 m^2 (SE = 0.56).

Response variables

Predawn xylem water potentials (XWPs) of *H. mutica* and *L. tridentata* were measured with a pressure chamber with a 0–7 MPA gauge (PMS Instruments, Corvallis, Ore.; Turner 1981), using two culms (shoots) of two tussocks of *H. mutica* and two twigs of two plants of *L. tridentata* per plot. Osmotic potential (OP) of sap extract from *O. rastrera* was measured using a dew-point microvoltmeter connected to a C-52 sample chamber (Wescor, Logan, Utah; Turner 1981; Koide et al. 1989). As *O. rastrera* is a CAM species, the plant tissue was obtained between 0900 and 0930 hours, when nocturnal gas exchange was over and stomata were closed. The sample was obtained with aluminium sample cores 0.5 cm in diameter from two terminal cladodes facing E-W of two plants per plot.

The number of culms and inflorescences produced during the experiment were counted in five tussocks of *H. mutica* per plot. Ten twigs of three *L. tridentata* plants were randomly selected and tagged in each plot. The growth in length and the number of leaves, nodes and new shoots produced by the terminal bud of each twig were determined on October 15, November 11 and January 23. The fruits produced by the terminal bud were counted. The survivorship of terminal cladodes, the number and area of the new cladodes and the number of flowers produced per individual were measured in ten plants of *O. rastrera* per plot.

Watering experiment

Watering was done in circular plots of 20 m^2 delimited with metallic sheets 60 cm in height and buried 30 cm in the soil. This plot size was sufficient to water a surface larger than the area of influence of the root system of all three species, which were 13.91 m^2 for *L. tridentata*, 6.61 m^2 for *O. rastrera* and 0.51 m^2 for *H. mutica* (Briones et al. 1996). This experiment was done in March–April 1990. During these months, mean minimum and maximum temperature were 12.6°C and 30.4°C and rain only fell once during that time (5 mm, 5 days after watering).

Twelve plots were used, three had individuals of all three species (associated plants) and the remaining nine plots (isolated plants) had, in the centre, only one individual of *L. tridentata* (three plots), only one individual of *O. rastrera* (three plots) and up to three tussocks of *H. mutica* (three plots). The number of species in the plots of associated plants varied between four and five. The mean density of individuals was 23.3 per 20 m^2 and the mean plant cover was 6.27 m^2 for the same area. One plant of each shrub species and three plants of the grass species were randomly selected inside each associated plot to monitor response variables.

Mean cover of isolated individuals were 3.68 m^2 (SE = 0.591, $n = 3$), 0.26 m^2 (SE = 0.019, $n = 3$) and 0.16 m^2 (SE = 0.019, $n = 9$) for *L. tridentata*, *O. rastrera* and *H. mutica*, respectively. In the same order, the cover of the measured plants in the plots with associated individuals were 2.85 m^2 (SE = 1.727, $n = 3$), 0.33 m^2 (SE = 0.044, $n = 3$) and 0.19 m^2 (SE = 0.033, $n = 6$).

The plots were flooded with the water volume required to simulate 30 mm of rainfall on the evening of 23 March 1990. Plant water potentials and growth, and soil water potential (SWP) of each plot were measured from the 2nd to the 32nd day after watering. After that period, water potentials were near their prewatering values and, consequently, too low to be accurately measured.

To assess the effect of watering on each species, three nearby unwatered and isolated individuals of each species were randomly selected for plant and soil water potential measurements at the beginning and at the end of the experiment. The dimensions of these unwatered individuals were similar to those of the watered plants.

Response variables

XWP and OP were measured as in the removal experiment. Additionally, the predawn OP of sap extracts from *L. tridentata* and *H. mutica* leaves (two samples per plant) was determined.

SWP at three depths (0–0.10 m, 0.10–0.20 m and 0.20–0.30 m) was measured with the psychrometric technique employed for OP determinations using soil samples collected with an auger bucket 7 cm in diameter. In extremely dry samples, when the psychrometer failed to condense water within the sample chambers, an arbitrary value of −10.1 MPa was assigned to that sample.

Length growth and the number of leaves, nodes, flowers and shoots produced by the terminal bud of ten randomly selected twigs in each *L. tridentata* plant were determined 32 days after the watering. All biomass produced was collected and oven dried at 80°C until it reached constant weight.

Five culms of two plants per plot were used for analysing *H. mutica* growth. The culms, which originated after irrigation, were in the periphery of the tussocks. Shoot length (from the base of the culm up to the top of the last fully expanded leaf), number of leaves and their phenology were registered at 6, 9, 16, 21 and 32 days after watering. At the end of the experiment, all shoots were collected and oven dried at 80°C until of constant weight.

Statistical analyses

Removal experiment

Variations in XWP and OP were analysed using repeated-measures analysis of variance (ANOVAR) because successive measurements were made on the same plants. To avoid pseudoreplication, the mean of the plant water potentials in each plot were used (i.e. $n = 3$). The analyses were performed using blocks and removal treatments (control vs removal plots) as between-subject effects, and time, time × removal and time × block as within-subject effects. The analyses were done using the BMDP statistical package (Dixon et al. 1988). The same model was used for the log of twig lengths and the square root of the number of nodes and shoots produced by plot of *L. tridentata*. These data transformations were necessary to normalize the distribution of the variables.

The square root of the number of culms of *H. mutica*, number of cladodes of *O. rastrera* and number of the reproductive structures produced by plot of each species were analysed by ANOVA using removal treatments and block effects as explanatory variables. The same model was used for the cladode area of *O. rastrera*. Differences in survivorship of *O. rastrera* cladodes between removal treatments, categories (live, dead, semidead) and time were assessed through analysis of the standardized residuals of the contingency table where all those factors were crossed (Everitt 1977), using the GLIM statistical package (Aitkin et al. 1989; Crawley 1993).

Watering experiment

Variations in XWP and OP of *H. mutica* and *L. tridentata* and OP of *O. rastrera* were analysed by ANOVAR using the neighbourhood condition (associated or isolated plants) as between-subjects effect, and time and time × neighbourhood condition as within-subjects effect. To avoid pseudoreplication, the mean plant water potential per plot was used (i.e. $n = 3$). Despite the absence of normality, SWP variability was assessed through an ANOVAR using the neighbourhood condition as between-subjects effect, and time, depth and all interactions as within-subjects effect.

Shoot length, square root of the number of leaves and arcsine of the proportions of green leaf blades per plant of *H. mutica* were analysed with ANOVAR models as used for plant water potentials. The effects of the neighbourhood condition on the aerial biomass of *H. mutica* and length and biomass of twigs, square root of the number of leaves, nodes, shoots and flowers per plant of *L. tridentata* were analyzed with a one-way ANOVA.

Results

Removal experiment

XWP differed between dates ($P < 0.05$, Fig. 1) but the removal treatment had no significant effect on the water potential of the three species. Variables measuring vegetative growth and reproductive effort (number of culms and inflorescences in *H. mutica*, elongation of twigs, number of leaves, nodes, new shoots and fruits in *L. tridentata*, and the survivorship of cladodes, and number and area of new cladodes and flowers in *O. rastrera*) did not differ between removal treatments. Except for *L. tridentata* XWP, differences in the response variables were small as well as non-significant. This suggests that the non-significance in the results does not arise from an experimental error inflated by uncontrolled sources of variation inherent to removal experiments (Aarsen and Epp 1990), such as plant density among others.

Watering experiment

All species showed a clear response to watering. Isolated plants of *L. tridentata* had significantly higher
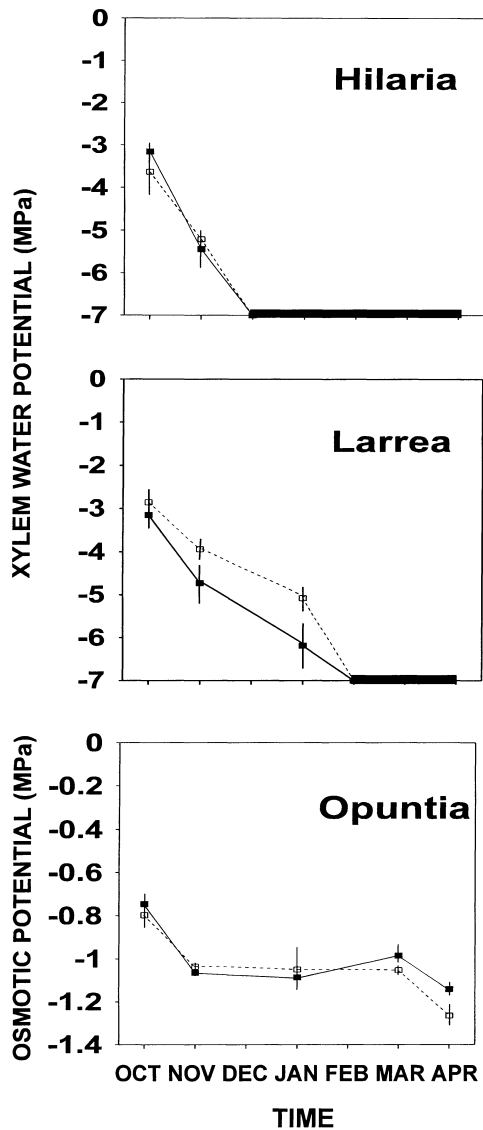
Fig. 1 Time course of predawn xylem water potential (XWP) of *Hilaria mutica* and *Larrea tridentata*, and osmotic potential (OP) of *Opuntia rastrera* in a Chihuahuan Desert scrub. Mean ± 1 SE for three plots, where all other species were removed (*filled squares*), on 16 May 1989 and for three plots without any manipulation (*open squares*). The value for each plot was obtained by averaging four measurements (two measurements of two plants). The plant water potential of the three species was registered five times from October to April (i.e. just when the 1989 rainy season was over and before the start of the next one). The *solid bar* running along the horizontal axis indicate the period when XWP was below −7 MPa

Fig. 2 Time course of predawn XWP of isolated (+) and associated (×) plants of *H. mutica* and *L. tridentata* growing in a Chihuahuan Desert scrub. Plants received an experimental irrigation equivalent to 30 mm of rain on day zero (23 March 1990). Each point represents the mean ± 1 SE for three plants (two measurements per plant). Three non-watered and isolated plants of each species were also sampled but XWP was always below the minimum range of measurements (−7 MPa)

XWP than the associated ones, whereas XWP of *H. mutica* plants did not differ between treatments (Fig. 2). OP was also higher in isolated than in associated plants of *L. tridentata* and nearly so in *O. rastrera* plants ($P = 0.056$), whereas the OP of *H. mutica* plants did not differ between treatments (Fig. 3). The XWP of non-irrigated plants of *L. tridentata* and *H. mutica* was always outside the range of the pressure chamber (−7 MPa), and it was impossible to obtain expressed
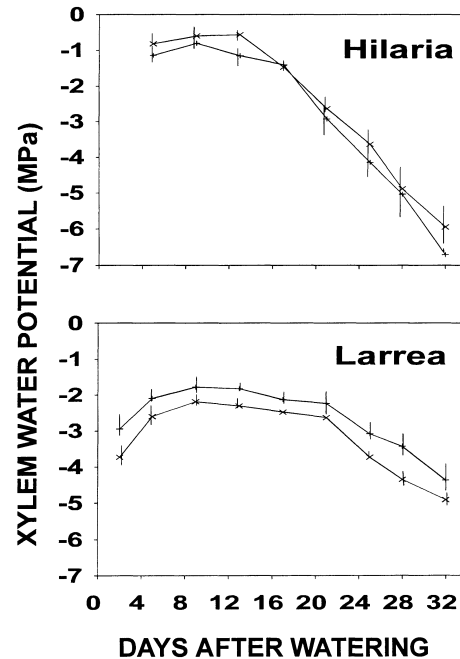
sap to measure OP in these plants. As expected, the OP of *O. rastrera* was higher in irrigated than in non-irrigated plants (Fig. 3).

SWP differed between depths ($P < 0.00001$, Fig. 4) but did not differ between neighbourhood conditions ($P > 0.2$) according to the exploratory ANOVAR. SWP averaged over all plots and dates was −6.31 MPa in the 0–0.10 m layer, −4.88 MPa in the 0.10–0.20 m layer and −6.99 MPa in the 0.20–0.30 m layer. SWP of the surface soil layer (0–0.10 m) was very high immediately after irrigation and then decreased sharply, whereas between 0.10 and 0.20 m it increased steadily during the first 10 days and then remained stable until day 20, when it began to drop. Variation in the SWP in the 0.20–0.30 m layer had the same pattern but values were lower than at 0.10–0.20 m (Fig. 4). Water percolated up to 0.20–0.30 m in the plots.

Twig length growth, and numbers of nodes and leaves produced were significantly higher in isolated than in associated plants of *L. tridentata* (Table 1). In the same way, the biomass and the number of shoots and flowers produced were higher in isolated than in associated plants of *L. tridentata*, but these differences were non-significant. Variables measuring vegetative growth (shoot length and biomass, number of leaves and their phenology) of *H. mutica* did not differ between neighbourhood conditions ($P > 0.05$).
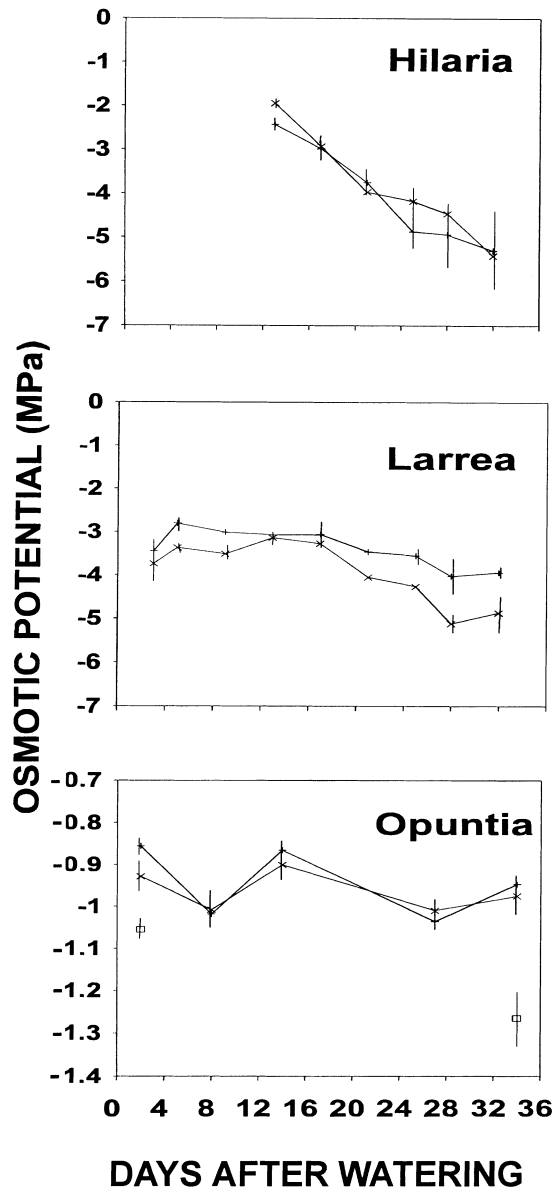
Fig. 3 Time course of OP of isolated (+) and associated (×) plants of *H. mutica*, *L. tridentata* and *O. rastrera* growing in a Chihuahuan Desert scrub. Plants received an experimental irrigation equivalent to 30 mm of rain on day zero (23 March 1990). Each point represents the mean ± 1 SE for three plants (two measurements per plant). Three non-watered and isolated plants of each species were also sampled at the beginning and at the end of the experiment but only *O. rastrera* OP (*open squares*) could be measured, as it was impossible to obtain expressed sap to measure OP in non-watered *H. mutica* and *L. tridentata*

Fig. 4 Time course of soil water potential (SWP) between 0–0.10 m (*filled squares*), 0.10–0.20 m (*open squares*) and 0.20–0.30 m (*crosses*) depth during a 32-day period after an experimental irrigation equivalent to 30 mm of rain. Each point represents the mean ± 1 SE for 12 watered plots of a Chihuahuan Desert scrub. Three plots had individuals of three species (associated plants) and nine plots (isolated plants) had only one individual of *L. tridentata* (three plots), of *O. rastrera* (three plots), and up to three tussocks of *H. mutica* (three plots). Data were pooled after ANOVAR showed no difference between treatments ($P > 0.05$). The *solid bar* running along the horizontal axis indicates the period when SWP was below −10.1 MPa

Discussion

Removal experiment

Neighbour removal experiments have been the most successful approach to study competition in plant communities. Often, the species remaining after the removal showed a positive response in density and survival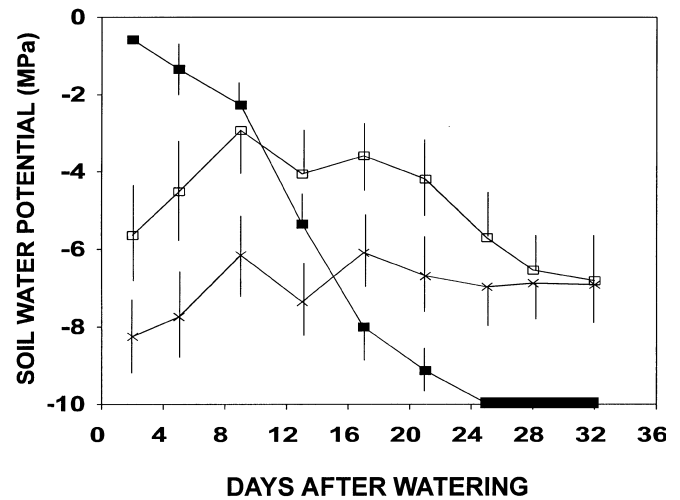 or in growth and water status (Fonteyn and Mahall 1981; Fowler 1986; Aarsen and Epp 1990). However, evidence of plant competition was not found in the present removal experiment, since plant elimination did not have effects on the remaining individuals.

In agreement with the results reported in this paper, some experiments in arid lands and elsewhere have revealed no effect at all after neighbour removal (Fowler 1986; Aarsen and Epp 1990). Sala et al. (1989) found no effects in the XWP and primary production of the grass *Poa ligularis* after the removal of the shrub *Mulinum spinosum* in the Patagonian steppe. In another experiment involving two shrubs of an arid Californian ecosystem, Manning and Barbour (1988) found that the XWP of *Crysothamnus teretifolius* did not change after the removal of *Haploppapus cooperi*.

Niche differentiation (e.g. different rooting depths) between species has been suggested as a general explanation for the absence of effects in the plants remaining after neighbour removal (Cody 1986; Fowler 1986). Different morphological and physiological adaptations to water stress have also been invoked as mechanisms of coexistence between species (Kemp 1983; Ehleringer 1985; Nobel 1988). Indeed, the three species studied here show different adaptations to drought. *L. tridentata* is a microphyllous perennial shrub capable of maintaining the activity of photosynthetic tissues and plant growth when severely water stressed (Odening et al. 1974; Meinzer et al. 1986). In addition, leaf movements in this species are interpreted as a mechanism to reduce or avoid water losses through evapotranspiration (Ezcurra et al. 1992). Being a succulent with CAM metabolism,

Table 1 Growth of isolated and associated plants of *Larrea tridentata* 32 days after experimental watering equivalent to 30 mm of rain in a Chihuahuan Desert scrub. The mean and 1 SE (in parentheses) of twig length (cm), dry mass (g), and square root of number of shoots, nodes, leaves and flowers on twigs produced by a randomly selected terminal bud in each of three plants per neighbourhood condition are shown (* $P < 0.05$)

Treatments	Length of twigs	Dry mass	Number of shoots	Number of nodes	Number of leaves	Number of flowers
Isolated	0.97* (0.121)	0.023 (0.0058)	0.23 (0.047)	0.47* (0.031)	0.79* (0.037)	0.46 (0.077)
Associated	0.42 (0.097)	0.013 (0.0159)	0.12 (0.024)	0.36 (0.008)	0.64 (0.020)	0.37 (0.048)

O. rastrera can store water and maintain high water potentials during dry periods, avoiding water loss through high cuticular and stomatic resistances (Nobel 1988). *H. mutica* is a tussock-grass with moderately thick scaly rhizomes. It develops green leaves during the hot and rainy summers and rolls up its leaf blades during dry periods. However, the evidence for interspecific competition found through size-distance analyses (Briones et al. 1996) does not support the hypothesis that niche differentiation is sufficiently important for the species studied in this work to avoid competition. The failure to detect evidence for competition following the removals could be due to very low levels of resources (soil water) during the experiment (see below).

Watering experiment

Differences in response variables (water status and growth in *L. tridentata*, and OP in *O. rastrera*) found between isolated and associated plants can be explained by competition for soil water, and other soil resources (e.g. N) that can be limiting when water is added to the system (Sharifi et al. 1988) and then can magnify the effect of irrigation (Fowler 1986). Each plant can extract water and soil resources up to a maximum depth determined by root extension and root resistance to water flow (Sala et al. 1981; Fitter and Hay 1987; Rundel and Nobel 1991). *H. mutica* and *L. tridentata* have roots through the entire profile (0–0.75 m) in the study site, but *H. mutica* has 70% of its roots between 0.05 and 0.30 m, and *L. tridentata* has 71% of its roots between 0.10 and 0.30 m. *O. rastrera* has no roots below 0.30 m and 87% of the roots are between the surface and 0.15 m depth (Briones et al. 1996).

The level of water resources provided by irrigation triggered flowering in both associated and isolated plants of *L. tridentata* compared to non-irrigated plants. Furthermore, the level of resources also determined competitive effects. Partial overlap of vertical root distribution makes *L. tridentata* a potential competitor of *H. mutica* all along the soil profile, and of *O. rastrera* in the first centimetres. Its unique ability to tap water from extremely dry soils (Odening et al. 1974) probably renders *L. tridentata* an efficient competitor under low water supply. But this is not necessarily true under high water supply, where a low root density may result in reduced water uptake compared to coexisting species with higher root densities. The root density of *L. tridentata* is 2.8 and 1.4 times lower than those of *H. mutica* and *O. rastrera*, respectively, within the layers where root profiles overlap (Briones et al. 1996). In the case of *O. rastrera*, it is even possible that water uptake had increased immediately after irrigation due to a fast and efficient root response to irrigation, as recorded in other desert succulents (Rundel and Nobel 1991; Dougherty et al. 1996).

Potential water competition by *O. rastrera* is not only spatially limited to the first centimetres of the soil profile but it is also temporally limited. In fact, *O. rastrera* may have competed for water with its neighbours only during the first days after irrigation due to the high water potential maintained inside its tissues. The OP was −1.2 MPa at the end of the dry season and −0.9 MPa 2 days after irrigation (Figs. 1, 3). Nobel (1988) reports that after a 4-month dry season, water uptake by desert succulents was only possible when the SWP was higher than −1.0 MPa.

Temporal fluctuations in competition intensity

The results suggest that the intensity of interspecific competition can vary according to the fluctuations of resource availability. Consequently, the validity of the two hypotheses tested in this work depends on the level of the resources. In the removal experiment, no evidence of competition was observed when plants were free to capture rain water in a relatively dry year (173 mm of total rainfall against a 25-year average of 264 mm). However, competitive effects were detected during the watering experiment, in which water was forced into the soil.

Some authors have mentioned that temporal and spatial fluctuation in resource availability (principally water) can modify competitive interactions in desert ecosystems. (Weins 1977, 1986; Fonteyn and Mahall 1981; Fowler 1986; Grant 1986; Chesson 1986; Schmitt and Holbrook 1986; Aguiar et al. 1992). In the Negev Desert, Friedman and Orshan (1974) found that fruit production of two *Medicago laciniata* varieties increased after neighbour removal only if they were irrigated. In the Sonoran Desert, Klikoff (1966) found that the survival rate of the annual *Plantago insularis* was density dependent (i.e. survival was higher in the sites with lower

initial density) only when the sites were moderately irrigated. Similarly, in the Mohave Desert, a strong increment in soil water availability due to 60 mm of rain triggered reciprocal competitive interactions between *L. tridentata* and *Ambrosia dumosa* as revealed by a decrease in the XWP of both shrubs (Fonteyn and Mahall 1981). In contrast, Burger and Louda (1995) found that the removal of the surrounding grassland vegetation increased the number and size of new cladodes of *O. fragilis* in two successive wet summers, but supplemental water had no significant effect on *O. fragilis* growth. In this case, the authors concluded that competition for a non-water resource, such as light, was the mechanism implied in the interaction.

The results of the watering experiment sustain the premise that water is a limiting resource and that species compete for it. However, fluctuations in competition intensity due to varying resource levels (as revealed comparing the results of the watering experiment with those of the removal experiment) and the possible concurrence of positive interactions (Silvertown and Wilson 1994) preclude long-term predictions of the interaction effect. Related studies made with the same three species in the same plant community using size-distance relationships (Briones et al. 1996) showed that intraspecific competition has occurred between plants of *H. mutica*, *L. tridentata* and *O. rastrera*, as well as between the interspecific pairs *H. mutica–O. rastrera* and *L. tridentata–O. rastrera*. This indicates that competition has been operating in the community for some time, influencing the spatial pattern of individuals. That period could be as long as the age of the oldest plants living in the site (Welden et al. 1988). There are no data on the age of the plants in the study site, but it must be mentioned that age estimations of *L. tridentata* in the Sonoran Desert suggest that it is one of the longest-lived plants of desert ecosystems (Vasek 1980).

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