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Competition between three Chihuahuan desert species: evidence from plant size-distance relations and root distribution

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Abstract. Using size-distance data we tested the intensity and importance of competition between *Hilaria mutica* (a tussock grass), *Larrea tridentata* (a microphyllous shrub) and *Opuntia rastrera* (a succulent) in the Chihuahuan desert. We also compared the vertical and horizontal distribution of roots to assess the potential degree of overlap in the use of soil resources. The relationships between sizes and distances of nearest-neighbour plants suggested that intraspecific competition is generally more important than interspecific competition. However, evidence of stronger inter than intraspecific competition was found in some cases. Species combinations showing significant interspecific competition involved always *Opuntia*, whereas *Larrea* and *Hilaria* did not influence each other. The analysis of the symmetry of competition showed that *Opuntia* was adversely affected by the presence of *Hilaria* or *Larrea*.

Although differences were found in the distribution of roots, the results of the size-distance study support the idea that, (particularly) *Opuntia*, below-ground niche differentiation is not sufficiently important to totally avoid the negative effects of plant competition.

Keywords: *Hilaria mutica*; *Larrea tridentata*; *Opuntia rastrera*; Plant interaction; Root system; Spatial pattern.

Introduction

Since water is the most important limiting factor for plant growth in arid ecosystems (e.g. Ehleringer 1985; Nobel 1988) it has been suggested that desert plants must compete for it (e.g. Fowler 1986). There is experimental evidence that desert plants compete for water (Fonteyn & Mahall 1981; Robberecht et al. 1983; Ehleringer 1984) but this does not exclude the possibility of competition for other resources (West & Skujins 1978; Fisher et al. 1988). The great diversity of life forms found in deserts has been interpreted as the result of niche differentiation in order to reduce competition among species (Shreve 1951; Cody 1986).

The effects of competition in plant communities can be inferred from the study of the relationship between distance and size of neighbouring plants (Pielou 1962, 1983; Fowler 1986; Welden et al. 1988; Keddy 1989;

Campbell et al. 1991; Wilson 1991). The hypothesis is that competition between neighbours results in density-dependent growth and mortality; consequently, closely spaced plants will be small and have low survivorship (Pielou 1962; Fowler 1986). This implies three hypotheses: (1) resources (with a spatially uniform distribution) limit plant growth, (2) resource capture is proportional to plant size and (3) resources not used by a plant may be used by neighbours (Caldwell 1990).

A positive correlation between the sum of neighbour plant sizes and the distances separating them can be interpreted as the result of competition, and the lack of such a correlation as the result of the absence of competition (Pielou 1962; Yeaton & Cody 1976; Yeaton et al. 1977; Gulmon et al. 1979; Fuentes & Gutierrez 1981; Welden et al. 1988; Wilson 1991).

In addition, it has been pointed out by Welden & Slauson (1986), two different aspects of competition should be distinguished: intensity and importance. Competition intensity is the absolute severity of physiological strain induced upon competing plants, and importance of competition is the relative degree to which competition determines the physiological status or fitness of individuals. The importance of competition is necessarily relative to the importance of other factors (such as abiotic stress) influencing plant performance. If regression analysis is used to measure the relationships between size of, and distance between, neighbour plants, the importance of competition is indicated by the coefficient of determination; the slope provides information on the intensity of competition (Welden & Slauson 1986; Welden et al. 1988).

The differentiation of root systems has been advocated as a mechanism that reduces competition and facilitates species coexistence (Cable 1969; Parrish & Bazzaz 1976; Berendse 1981; Davis & Mooney 1985; Manning & Barbour 1988; Caldwell 1990; Rundel & Nobel 1991), particularly in deserts (Cody 1986). Moreover, below-ground niche differentiation might be more important for plant coexistence than above-ground niche differentiation (Fitter 1987). Hence, the analysis of root systems, by allowing the assessment of the degree of

underground resource partitioning, might be used to explain the spatial distribution of plants (Cody 1986; Manning & Barbour 1988).

In this paper the above-ground spatial size-distance patterns and the root systems of species representing three perennial life forms from the Chihuahuan desert were studied in order to test for evidence of competition, both intra and interspecific, to determine whether the importance or intensity of competition varied among species combinations, and to determine if the root systems differentially explore the soil.

Methods

Study area and species

The study area is located in the Mapimí Biosphere Reserve, Chihuahuan desert (26° N, 103° W, at an altitude of 1100 m a.s.l.). Rainfall is concentrated in summer (72 % of the annual average of 264 mm falls between June and September). The mean annual temperature is 20.8 °C. Vegetation corresponds to the 'xerophytic scrub' described by Rzedowski (1978) and to Brown's (1982) 'Chihuahuan desert scrub'. A general description of the vegetation can be found in Montaña (1990).

The species studied represent three typical life forms of the Chihuahuan desert. *Larrea tridentata* is a perennial microphyllous shrub common in the hot deserts of southwestern USA and Mexico; *Opuntia rastrera* is a succulent with flat-stemmed cladodes which appears in dense associations in the southern Chihuahuan desert, and *Hilaria mutica* is a perennial tussock-grass common in playas and bajadas of the Chihuahuan desert.

The study site, dominated by *L. tridentata* and *O. rastrera*, was located in a 2 % to 6 % sloping bajada, i.e. a weakly sloping plain connecting footslopes with floodplains. Soils were of the Yermosol Haplic type (Anon. 1976) developed on colluvial deposits with elements of medium to small size overlying on calcareous claystone at 0.80 m to 1.2 m depth. Soils are characterized by a clay-loam horizon between zero to 0.25 m and a clay horizon below (Delhoume 1988). The study was conducted in a 1600-m^2 (80 m × 20 m) plot where *O. rastrera*, *L. tridentata* and *H. mutica* contributed 41 %, 40 % and 5 % respectively of a total cover of 33 m^2/100 m^2, and 63 %, 7 % and 14 % respectively of a total density of 87.2 plants/100 m^2.

Importance and intensity of competition

Field measurements. All plants of the three species in the 1600-m^2 plot were labelled and each was taken as a focal plant. Species identity, sizes and distance between each focal plant and its first nearest neighbour were recorded for each pair of plants so defined. When two plants were each other's nearest neighbour the same set of readings was used twice. When the nearest neighbour of a focal plant was outside the limits of the plot, its size and the distance between them were recorded and included in the analysis. The number of pairs *Larrea-Larrea* found inside the 1600-m^2 plot was 22, the number of *Larrea-Hilaria* pairs was 19. In order to have a minimum number of 50 pairs of each combination of species, additional pairs of *Larrea-Larrea* and *Larrea-Hilaria* were randomly chosen in a contiguous plot of 5760 m^2. Sizes were estimated as plant cover. *Larrea* and *Hilaria* cover was calculated as the area of a circle by averaging two canopy diameters at right angles. In the case of *Opuntia* a regression between number of cladodes (NC) and cover (CO) was established using 163 randomly chosen plants:

$$CO \text{ (in cm}^2\text{)} = 672.8 + 99.3 * NC \qquad (1)$$

This relation, which is significant ($r^2 = 0.81$, $P < 0.01$) was used to calculate the cover of individuals by counting the number of cladodes. Distances were measured to the center of the plants due to the absence of a single shoot in the species. Special precautions were taken to define if each clump of shoots belonged to one or more individuals (Ebert & McMaster 1981) and, in cases of doubt, the first 10 cm of roots below the crown were exposed by carefully digging into the soil.

Regressions between size and distance. All data were sorted into pairs of intraspecific and interspecific species combinations: *Larrea-Larrea*, *Hilaria-Hilaria*, *Opuntia-Opuntia*; *Hilaria-Larrea*, *Hilaria-Opuntia*, *Larrea-Opuntia*. This means that each nearest-neighbour pair was identified as belonging to only one of these categories. The sizes of both plants in each pair were added upp, and the regression of these sum of neighbour plant-sizes on the distances separating them were calculated for every intra and interspecific species combination, after appropriate transformation and standardization of variables (see below). The regression model is:

$$S_c = a + bD + e \qquad (2)$$

where S_c = is the sum of the cover values for the focal plant and its nearest neighbour, and D, the independent variable, is the distance separating them.

Positive correlations (r) in a size-distance relationship indicate the existence of competition among plants (Pielou 1962; Yeaton & Cody 1976; Yeaton et al. 1977; Gulmon et al. 1979; Fuentes & Gutierrez 1981; Welden & Slauson 1986; Welden et al. 1988; Wilson 1991). The determination coefficient of the regression (r^2) meas-

ures the importance of competition because it indicates how much of the variation of S_c is explained by D relative to other (unknown) variables influencing plant size. The slope of the relationship measures the intensity of competition as far as it describes the rate at which the sum of neighbour sizes varies with distance (Welden & Slauson 1986; Welden et al. 1988; Wilson 1991).

If competition is affecting plant growth, a steeper slope in the regression S_c on D indicates that the competition is less intense than in cases where shallower slopes are found. In order words, for the same change in distance the change in combined size will decrease as competition intensity increases. Thus, intensity of competition increases with decreasing steepness of the slope (Welden & Slauson 1986; Welden et al. 1988; Wilson 1991). To test if the intensity of competition is symmetric within each interspecific combination, two separate regressions (one for each species of the pair) between plant size and distance were performed (after transformation and standardization of both variables, see below). The regression model is:

$$C_i = a_i + b_i * D + e_i; \ (i = 1, 2) \tag{3}$$

where C_i is plant size and the subindexes 1 and 2 represent the focal plant and the nearest neighbour, respectively. If the two regression slopes are different from zero, significant differences between the slopes will indicate asymmetry in the competition intensity experienced by both species. If one slope is different from zero but the other is not, asymmetry can be inferred because the size of one species varies with distance, whereas the other does not. Obviously, if the two regression slopes are not different from zero, asymmetry cannot be inferred.

Although the importance and intensity of competition in a population of plants may be different for different individuals (i.e. the effects of the competition could be very important or intense for some plants and barely important or intense for others), the coefficient of determination and the slope of a size-distance regression detect the average effect of competition experienced by all measured plants (Welden & Slauson 1986). However, we should not hope that the importance and intensity of the competition in a population are necessarily correlated (Welden & Slauson 1986; Welden et al. 1988; Wilson 1991). For example, if the fitness of the plants is essentially affected only by competition this interaction may have a low or high intensity but is very important or, if the fitness is determined by other factors (e.g. abiotic stress, disturbance, herbivory, parasitism) then the competition could be of low or high intensity but is unimportant (Welden & Slauson 1986).

As there is no statistical test to compare coefficients of determination (Sokal & Rohlf 1981), differences between coefficients of correlation (r) were taken as differences of the importance of competition (Welden et al. 1988; Wilson 1991). The r-values were transformed to z-values (Fisher values), and Tukey-type multiple comparisons tests were used to compare significant r-values after a χ^2 test showed that the hypothesis of non-differences among them could be rejected. Tukey-Kramer multiple comparisons tests were used to make comparisons between slopes that were significantly different from zero, after rejecting the hypothesis of non-differences between them by an F-test (Zar 1974).

Transformation and standardization of variables. The normality of both variables, sum of sizes and distance, was obtained through a $\log_{10}$ transformation after an analysis of residuals and a search of the best fit of the regression models. This was achieved by the use of the Box-Cox method (Sokal & Rohlf 1981) included in the GLIM statistical package (Generalized Linear Iterative Modeling; Crawley 1993). Plant density and size affect the slope of the relationship between sum of sizes and distances. Standardization will remove these influences and allow true comparisons of competion intensity between species combinations (Wilson 1991). As ANOVAs showed that both variables ($\log_{10}$ sum of sizes and $\log_{10}$ distance) varied between species combinations (see Table 1), they were standardized by dividing each value by the average calculated within each species combination (Wilson 1991). Thus, each standardized variable had a mean of 1.

Root distribution

Vertical distribution was measured in three isolated adult individuals of each species using the profile wall method (Böhm 1979). The profile was cut smoothly at 15 cm from the center of the plant in *Larrea* and *Opuntia* and from the periphery of the tussock in *Hilaria*. The number of roots intersecting a grid of 5 cm × 5 cm was recorded. The measured profile was 75 cm deep and 75 cm wide in *Hilaria* and 210 cm wide in the other species. Some roots < 1 mm in diameter may have been lost; this is of minor importance since sampling occurred at the end of the dry season (April) when the number of very fine roots is at its lowest. Mean cover was 0.13 m² (S.D. = 0.04) for *Hilaria*, 1.88 m² (S.D. = 0.66) for *Larrea* and 0.28 m² (S.D. = 0.001) for *Opuntia*.

The horizontal distribution of roots was mapped in a second set of three isolated adult plants of each species with the aid of a grid after a careful hand-excavation of the full root system up to a maximum depth of 28 cm for *Larrea*, 16 cm for *Opuntia* and 19 cm for *Hilaria*. Maximum depth of each species was reached when soil compactness and root resistance to mechanical damage

Table 1. Mean $\log_{10} S_c$ (sum of plant cover) and $\log_{10} D$ (nearest neighbour distance) values between plants of *Hilaria mutica*, *Larrea tridentata* and *Opuntia rastrera* in six combinations in the Chihuahuan desert. Different letters in the same column indicate significant differences between means (Tukey-test, $P < 0.01$). ** indicate $P < 0.01$ for ANOVA F-values.

Species combination	No. of neighbour pairs	Log$_{10}$ S_c (cm^2)	Log$_{10}$ D (cm)
Hilaria-Hilaria	61	3.0685306 a	1.4785547 a
Larrea-Larrea	50	4.4801190 d	2.0017291 d
Opuntia-Opuntia	578	3.4057335 b	1.6560965 b
Hilaria-Larrea	50	4.8274110 e	1.7037261 bc
Hilaria-Opuntia	101	3.5602055 c	1.5530832 a
Larrea-Opuntia	53	4.3330635 d	1.8412421 cd
$F(5,887)$		390.180 **	32.591 **

resulted in the impossibility of exposing roots without damage. The study of the vertical distribution of root systems showed that the proportion of roots below those depths were around 10% in *Opuntia*, 20% in *Larrea* and 50% in *Hilaria*. Influence area was calculated as the area of a circle with a radius defined by the mean of the longest lateral roots: i.e. longer than 1 m in *Larrea* and *Opuntia*, and longer than 0.30 m in *Hilaria*. Influence volume was calculated as the volume of a cylinder having a base equal to the influence area and a height equal to the maximum root depth. The total length of roots per unit of soil volume (a measure of how densely roots explore the soil) was also calculated. Mean plant cover of the randomly selected individuals were:

Hilaria   0.19 m^2 (S.D. = 0.04)
Larrea   3.15 m^2 (S.D. = 0.74)
Opuntia   0.25 m^2 (S.D. = 0.0007).

Results

Regressions between size and distance

All species combinations except *Hilaria-Larrea* showed a significant positive correlation in the relationships between the standardized $\log_{10}$ sum of sizes and standardized $\log_{10}$ distance (Fig. 1). The variation in size accounted for by distance was higher in intraspecific than in interspecific combinations (Fig. 2), i.e. coefficients of determination in the *Hilaria-Hilaria*, *Larrea-Larrea* and *Opuntia-Opuntia* pairs were greater than in their interspecific combinations, although there were no significant differences at $P = 0.05$ (as indicated by a Tukey multiple-comparison test of the r^2 values, Fig. 2).

The rate at which the sum of neighbour sizes changes with distance did vary among species combinations (Fig. 2). For some species, regression slopes were sig-

nificantly steeper in intraspecific than in interspecific combinations. The slope of the size-distance regression was steeper between individuals of *Opuntia* than between plants of the couple *Opuntia-Larrea*. In the same way, the slope between individuals of *Hilaria* was steeper than between pairs of *Hilaria-Opuntia*.

When the effect of distance between neighbours over the plant size of each species was analyzed (i.e. when the symmetry of the size-distance relationship was investigated) within each interspecific combination, only the size of *Opuntia* increased significantly with distance (Table 2). The sizes of *Hilaria* and *Larrea* were not affected by the distance in any case.

Root distribution

The vertical distribution of the root system differed between species as shown by a significant interaction between species and depth (Fig. 3, F-test, $P < 0.0001$). The highest proportion of roots was found near the soil surface (0-0.30 m). *Hilaria* and *Larrea* had roots through the entire profile (0-0.75 m), but *Hilaria* had 70% of its roots interceptions between 0.05 and 0.03 m and *Larrea* had 71% of its roots between 0.10 m and 0.30 m. *Opuntia* did not have roots below 0.30 m and 87% of the roots were between the surface and 0.15 m depth.

Species also differed in the horizontal distribution of their root systems. Influence area, influence volume and length of roots per unit volume were different (F-test, $P < 0.05$, Table 3).

Discussion

Importance and intensity of competition

The relationships between sizes and distances of nearest-neighbour plants suggest that individual plant growth and spatial distribution of plants have been influenced by competitive interactions, except for the *Hilaria-Larrea* combination.

Table 2. Slopes of the regressions between plant size and distance to the nearest neighbour. Results for each species of three interspecific combinations are shown. Significance for departures from zero slopes are: ** $P < 0.01$, NS = $P > 0.05$.

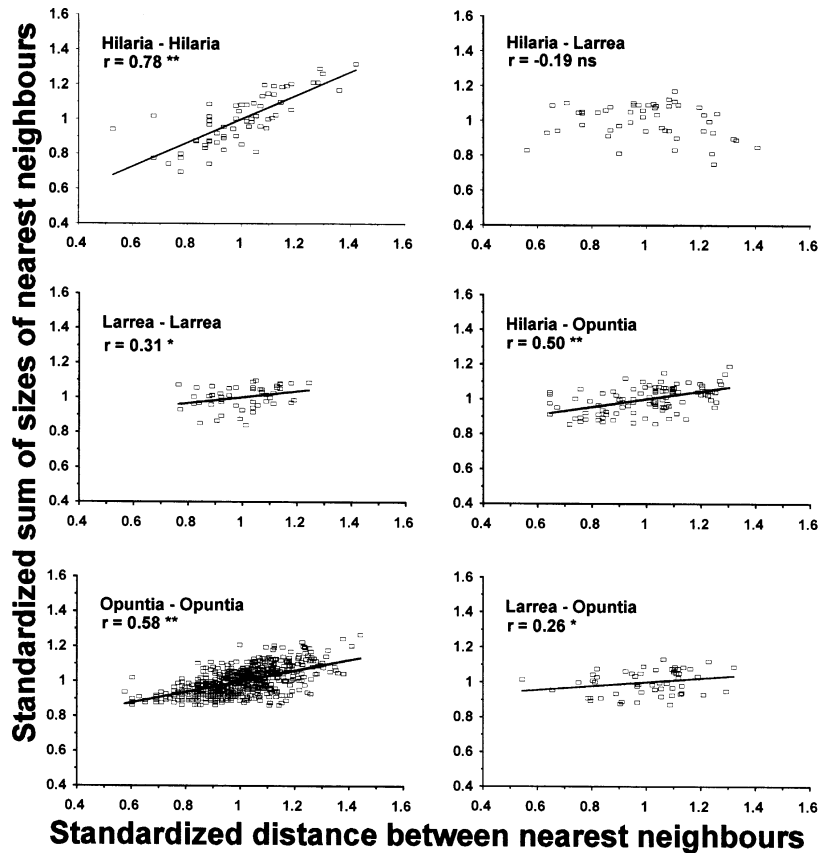| Species combination	Species in focus	n	Slope
Hilaria-Larrea	*Hilaria*	50	− 0.0595 NS
	Larrea	50	− 0.0945 NS
Hilaria-Opuntia	*Hilaria*	101	0.3015 NS
	Opuntia	101	0.2055 **
Larrea-Opuntia	*Larrea*	53	0.1041 NS
	Opuntia	53	0.1717 **

Fig. 1. Relationship between standardized $\log_{10}$ sum of cover of nearest neighbour plants and standardized $\log_{10}$ distance between plants for six species combinations: *Hilaria-Hilaria* (*n* = 61), *Larrea-Larrea* (*n* = 50), *Opuntia-Opuntia* n = 578), *Hilaria-Larrea* (*n* = 50), *Hilaria-Opuntia* (*n* = 101) and *Larrea-Opuntia* (*n* = 53). Coefficients of correlation (*r*) and regression lines are shown. Significance levels for *r* are: * = *P* < 0.05, ** = *P* < 0.01, NS = *P* > 0.05).

Several community processes could have produced these results. An original spatial clumping arising from vegetative reproduction and a subsequent self-thinning with partial competitive exclusion of other life forms could have produced the observed pattern of plant sizes and distances (Pielou 1961, 1962; Phillips & MacMahon 1981). *H. mutica* is a perennial grass forming dense tussocks of shoots emerging from rhizomes with very short internodes. *O. rastrera* is a cactus producing semi-prostrate rows of cladodes that can develop roots and constitute new individuals when severed from the mother plant. *L. tridentata* has been reported as having vegetative and sexual reproduction in other regions (Phillips & MacMahon 1981) however, at the study site it seems to reproduce mainly by seeds. Experimental and observational evidence that *L. tridentata* competes with other species have been reported by other authors (e.g. Yeaton et al. 1977; Fonteyn & Mahall 1981; Fowler 1986). Nobel (1981, 1983) and Nobel & Franco (1986) also found experimental and observational evidence of intraspecific competition in *H. rigida*, a species similar to *H. mutica*.

If competition was of paramount importance, the determination coefficient for the relationship between sizes and distances of nearest-neighbour plants would equal one. The variation found in r^2 values (0.07 - 0.61) between our species combinations indicate that other factors besides competition could be regulating interac-
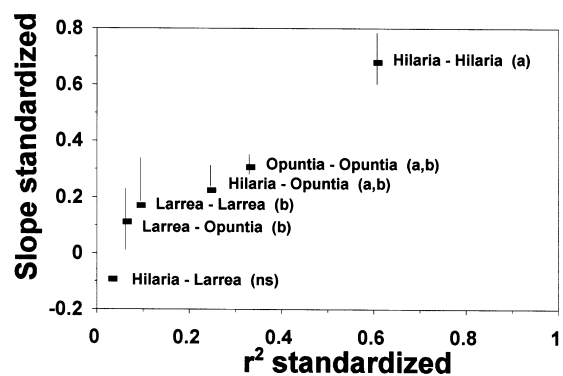

Fig. 2. Relationship between the slopes of sum of nearest neighbour size-distance regressions and the coefficient of determination r^2 of the same regressions for six species combinations in the Chihuahuan desert. Sum of size and distance were $\log_{10}$ transformed and standardized by their means. 95 % confidence intervals for slopes are shown. Different letters indicate significant differences among the coefficients of correlation corresponding to each r^2. NS = not significantly different from zero (*P* < 0.05).
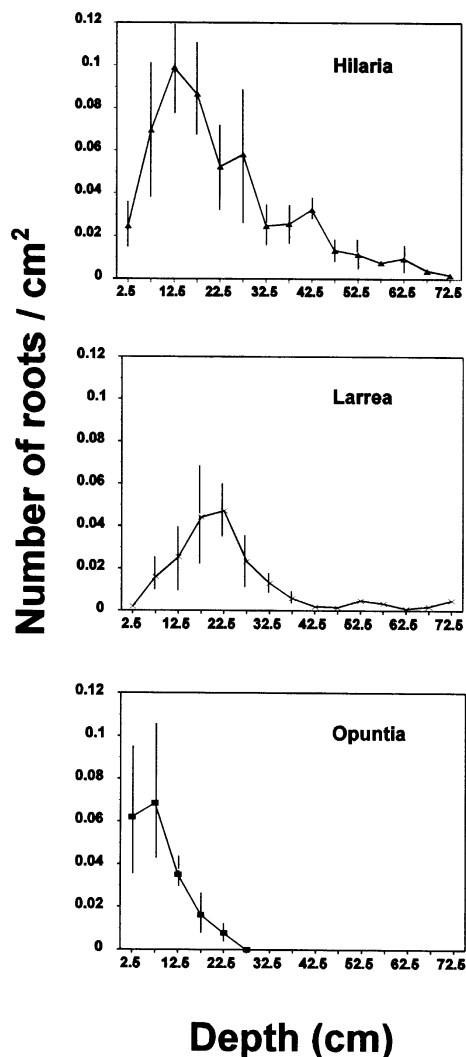
Fig. 3. Vertical distribution of roots of *Larrea tridentata, Hilaria mutica* and *Opuntia rastrera*. Mean number of roots (± 1 S.E., *n* = 3) intercepted at different depths along vertical profiles ranging from the surface up to 0.75 m are shown.

tions. Indeed, the size-distance patterns found in this study can be partially explained by adaptations to use unevenly distributed soil water, which is common in

deserts due to differences in microtopography or soil texture (Pielou 1961; Schulter 1984). Short seed-dispersal distances (Pielou 1962; Manning & Barbour 1988), allelopathy, pathogen dispersal pattern, or disturbances could also be used to explain spatial patterns of plant distribution (Welden et al. 1988).

The importance of competition varied between species combinations as indicated by a χ^2-test for overall comparison between r^2 values. Multiple comparison of determination coefficients suggests that intraspecific competition has been more important than interspecific competition, i.e. the determination coefficient in each intraspecific combination was always higher than in the two corresponding interspecific combinations (although these specific comparisons were non-significant). In some species combinations, regression slopes indicate that the intensity of competition was stronger in inter than in intraspecific pairs. Competition between individuals of *Opuntia* was significantly less intense than between individuals of the *Opuntia-Larrea* pair. Similarly, competition between *Opuntia-Hilaria* pairs was significantly more intense than between *Hilaria* individuals.

The study of the symmetry of competition intensity within interspecific pairs showed that *Opuntia* is severely affected by other species. The hypothesis of no competition could not be rejected in either of the two interspecific combinations where *Opuntia* was involved, and in both cases *Opuntia* was suffering the effects of competition, i.e. its size varied with distance whereas the size of the other species did not. The study of symmetry also showed that neither of the species of the combination *Larrea-Hilaria* registered any negative effect as may have been expected from the fact that the hypothesis of no competition could not be rejected.

Other studies in desert environments also suggest that intraspecific could be more important that interspecific competition. Yeaton & Cody (1976) used correlation coefficients between distances and sizes of neighbour plants to measure intra and interspecific competition between two *Opuntia* species and *Yucca* in the Mojave desert. They report higher *r*-values for intra

Table 3. Horizontal distribution of roots of *Hilaria mutica*, *Larrea tridentata* and *Opuntia rastrera* growing in a Chihuahuan desert scrub. Values represent means for three plants of each species. ANOVA *F*-values are shown in the last row (* = $P < 0.05$, NS = $P >$ 0.05). Different letters in the same column indicate significant differences (Tukey-test, $P < 0.05$). Average length was calculated for the longest roots, i.e. longer than 1 m in *Larrea* and *Opuntia*, and longer than 0.30 m in *Hilaria*.

Species	Plant cover (m²)	Max. depth (m)	Mean length (m)	Total length (Tl, m)	Influence area (m²)	Influence volume (Iv, m³)	Tl/Iv ratio (m/m³)
Hilaria	0.19	0.19	0.39 a	14.31 a	0.51 a	0.09 a	152.4 a
Larrea	3.29	0.28	2.10 b	33.42 a	13.91 b	3.94 b	10.11 b
Opuntia	0.25	0.16	1.42 b	24.80 a	6.61 ab	1.16 ab	26.08 b
F(2,6)			14.1 *	4.4 ns	6.6 *	8.2 *	92.1 *

than for interspecific combinations. Yeaton et al. (1977) investigated competition between five species including *Larrea tridentata* and found that all five intraspecific correlations were positive and significant, against only four out of nine interspecific correlations.

Studies in *L. tridentata* suggest that the relative importance of competition between conspecifics of this species would vary in the North American deserts. In the Sonoran and Chihuahuan deserts the relationships among sum of sizes and distance between nearest neighbours indicate that the importance of competition within *L. tridentata* is low: $r^2 = 0.11$ in the Sonoran desert (Yeaton et al. 1977), and $r^2 = 0.15$ (our data). However, in the Mojave desert the importance of intraspecific competition in *L. tridentata* is relatively high with $r^2 = 0.48$ (Fonteyn & Mahall 1981). In the same study, a removal experiment showed that competition between *L. tridentata* and *Ambrosia dumosa* was more intense than competition within species. Our results shows the same tendency of higher importance but lower intensity in intra than in interspecific *Larrea* combinations.

On the other hand, the importance of intraspecific competition in *Hilaria* could be high, as indicated by the r^2 values for *H. mutica* in our Chihuahuan desert study site ($r^2 = 0.61$) and for *H. rigida* in the Sonoran desert ($r^2 = 0.78$; Nobel 1981). However, the intensity of competition could be low in both sites. In our study the *Hilaria-Hilaria* regression showed the steepest slope: 0.681. Nobel (1981) reported a slope of 1.216 for the *H. rigida* intraspecific combination after regression of unstandardized $\log_{10}$ size versus unstandardized $\log_{10}$ distance data. If unstandardized $\log_{10}$-$\log_{10}$ data was used in our study, a very similar size-distance slope of 1.413 was found for the *H. mutica* intraspecific combination. Experimental removal studies have also demonstrated the presence of intraspecific competition in *Hilaria rigida* growing in the Sonoran desert (Nobel 1983; Nobel & Franco 1986).

Root systems

Essentially similar root systems to those found at our site have been reported for *Hilaria* and *Opuntia* species in other places. A deep fibrous root system not extending laterally, has been observed in *H. mutica* growing in swales of the northern Chihuahuan desert (Ludwig 1975). The shallow root system of *O. rastrera* is similar to those of other cacti (Ludwig 1975; Rundel & Nobel 1991).

Although differences were found in the distribution of root systems of isolated plants, the degree of possible vertical overlap of roots coupled with soil texture characteristics indicate that they are potential competitors for soil resources. The fact that all three species have a high proportion of shallow roots suggests that soil water competition can exist if most of the annual precipitation falls as small rains and is stored only in the shallow soil horizons. In the study site, small rains (less than 5 mm) accounted for 59 % of the number of rains and 17 % of the total rainfall in a 28-yr period; also - the heavy soil textures found below 30 cm do not allow easy, deep percolation of soil water.

In summary, our results support the hypothesis that competition is an important force in structuring a desert plant community. Importance and intensity of competition differed between life forms, which supports the idea that, in particular for *Opuntia*, below-ground niche differentiation is not sufficiently important to avoid plant competition for soil resources. *Opuntia* is always adversely affected when competing whether with the grass or with the shrub, whereas the shrub and the grass are not mutually affected.

References

Anon. 1976. *Soils Map of the World, 1/5 000 000 (Vol. 1).* Legende FAO/ UNESCO, Paris.

Barbour, M.G., Cunningham, G., Oechel, W.C. & Bamberg, S.A. 1977. Growth and development, form and function. In: Marby, T.J., Hunziker, J.H. & DiFeo, D.R. (eds.) *Creosote Bush. Biology and Chemistry of Larrea in the New World Deserts*, pp. 48-91. Dowden, Hutchinson & Ross, Stroudsburg, PA.

Berendse, F. 1981. Competition between plan populations with different rooting depths II. Plot experiments. *Oecologia* (*Berl.*) 48: 334-341.

Böhm, W. 1979. *Methods of studying root systems.* Springer-Verlag, Berlin.

Brown, D.E. 1982. Biotic communities of the American Southwest United States and Mexico. Chihuahuan Desert Scrub. *Desert Plants* 4: 169-179.

Cable, D.R. 1969. Competition in the semidesert grass-shrub type as influenced by root systems, growth habitats, and soil moisture extraction. *Ecology* 50: 27-38.

Caldwell, M.M. 1990. Competition between root systems in natural communities. In: Gregory, P.J., Lake, J.V. & Rose, D.A. (eds.) *Root development and function*, pp. 167-185. Cambridge University Press, Cambridge.

Campbell, B.D., Grime, J.P., Mackey, J.M.L. & Jalili, A. 1991. The quest for a mechanistic understanding of resource competition in plant communities: the role of experiments. *Funct. Ecol.* 5: 241-253.

Cody, M.L. 1986. Structural niches in plant communities. In:

Diamond, J. & Case, T.J. (eds.) *Community ecology*, pp. 381-405. Harper & Row, New York, NY.

Crawley, M.J. 1993. *GLIM for ecologists.* Blackwell, Oxford.

Davis, S.D. & Mooney, H.A. 1985. Comparative water relations of adjacent California shrub and grassland communities. *Oecologia* (*Berl.*) 66: 522-529.

Delhoume, J.P. 1988. Distribution spatiale des sols le long d'une toposéquence représentative. In: Montaña, C. (ed.) *Estudio integrado de los recursos vegetación, suelo y agua en la Reserva de la Biosfera de Mapimí*, pp. 135-165. Instituto de Ecología, México.

Ebert, T.A. & McMaster, G.S. 1981. Regular pattern of desert shrubs: A sampling artefact? *J. Ecol.* 69: 559-564.

Ehleringer, J.R. 1984. Intraspecific competitive effects on water relations, growth and reproduction in *Encelia farinosa. Oecologia* (*Berl.*) 63: 153-158.

Ehleringer, J.R. 1985. Annual and perennials of warm deserts. In: Chabot, B.F. & Mooney, H.A. (eds.) *Physiological ecology of North American plant communities*, pp. 162-180. Chapman & Hall, New York, NY.

Fisher, F.M., Zack, J.C., Cunningham, G.L. & Whitford, W.G. 1988. Water and nitrogen effect on growth and allocation patterns of creosote bush in the northern Chihuahuan Desert. *J. Range Manage.* 41: 387-391.

Fitter, A.H. 1987. Spatial and temporal separation of activity in plant communities: prerequisite or consequence of co-existence? In: Gee, J.H.R. & Giller, P.S. (eds.) *Organization of communities. Past and present*, pp. 119-139. Blackwell, Oxford.

Fonteyn, P.J. & Mahall, B.E. 1981. An experimental analysis of structure in a desert plant community. *J. Ecol.* 69: 883-896.

Fowler, N. 1986. The role of competition in plant communities in arid and semiarid regions. *Annu. Rev. Ecol. Syst.* 17: 89-110.

Fuentes, E.R. & Gutierrez, J.R. 1981. Intra- and interspecific competition between matorral shrubs. *Oecol. Plant.* 16: 283-289.

Gulmon, S.L., Rundel, P.W., Ehleringer, J.R. & Mooney, H.A. 1979. Spatial relationships and competition in a Chilean desert cactus. *Oecologia* (*Berl.*) 44: 40-43.

Keddy, P.A. 1989. *Competition. Population and Community Biology Series.* Chapman & Hall, London.

Ludwig, J.A. 1975. Distributional adaptations of root systems in desert environments. In: Marshall, J.K. (ed.) *The belowground ecosystem: A synthesis of plant-associated process*, pp. 85-91. Range Sci. Dept., Colorado State Univ., Fort Collins, CO.

Manning, S.J. & Barbour, M.G. 1988. Root system, spatial patterns, and competition for soil moisture between two desert subshrubs. *Am. J. Bot.* 75: 885-893.

Montaña, C. 1990. A floristic-structural gradient related to land forms in the southern Chihuahuan Desert. *J. Veg. Sci.* 1: 669-674.

Nobel, P.S. 1981. Spacing and transpiration of various sized clumps of a desert grass, *Hilaria rigida. J. Ecol.* 69: 735-742.

Nobel, P.S. 1983. Experimental removal of intraspecific competitors - effects on water relations and productivity of a desert bunchgrass, *Hilaria rigida. Oecologia* (*Berl.*) 60: 21-24.

Nobel, P.S. 1988. *Environmental biology of agaves and cacti.* Cambridge University Press, Cambridge.

Nobel, P.S. & Franco, A.C. 1986. Annual root growth and intraspecific competition for a desert bunchgrass. *J. Ecol.* 74: 1119-1126.

Parrish, J.A.D. & Bazzaz, F.A. 1976. Underground niche separation in successional plants. *Ecology* 57: 1281-1288.

Phillips, D.L. & MacMahon, J.A. 1981. Competition and spacing patterns of desert shrubs. *J. Ecol.* 69: 97-115.

Pielou, E.C. 1961. Segregation and symmetry in two-species populations as studied by nearest-neighbour relationships. *J. Ecol.* 49: 255-269.

Pielou, E.C. 1962. The use of plant-to-neighbour distances for the detection of competition. *J. Ecol.* 50: 357-367

Pielou, E.C. 1983. *Population and community ecology. Principles and methods.* Gordon & Breach Sci. Publ., New York, NY.

Robberecht, R., Mahall, B.E. & Nobel, P.S. 1983. Experimental removal of intraspecific competitors - effects on water relations and productivity of a desert bunchgrass, *Hilaria rigida. Oecologia* (*Berl.*) 60: 21-24.

Rundel, P.W. & Nobel, P.S. 1991. Structure and function in desert root systems. In: Atkinson, D. (ed.) *Plant root growth. An ecological perspective*, pp. 349-378. Blackwell Sci. Publ., Oxford.

Rzedowski, J. 1978. *Vegetación de México.* Limusa, México.

Schulter, D. 1984. A variance test for detecting species associations, with some example applications. *Ecology* 65: 998-1005.

Shreve, F. 1951. Vegetation of the Sonoran Desert. *Carnegie Inst. Washington Publ.* 591: 1-192.

Sokal, R.R. & Rohlf, F.J. 1981. *Biometry. The principles and practice of statistics in biological search. 2th ed.* W.H. Freeman, San Francisco, CA.

Welden, C.W. & Slauson, W.L. 1986. The intensity of competition versus its importance: an overlooked distinction and some implications. *Quart. Rev. Biol.* 61: 23-44.

Welden, C.W., Slauson, W.L. & Ward, R.T. 1988. Competition and abiotic stress among trees and shrubs in northwest Colorado. *Ecology* 69: 1566-1577.

West, N.E. & Skujins, J. 1978. *Nitrogen in desert ecosystems.* US/IBP Synthesis Series 9, Dowden, Hutchinson & Ross, Stroudsburg, PA.

Wilson, S.D. 1991. Variation in competition in eucalypt forests: the importance of standardization in pattern analysis. *J. Veg. Sci.* 2: 577-586.

Yeaton, R.I. & Cody, M.L. 1976. Competition and spacing and plant communities: The northern Mohave desert. *J. Ecol.* 64: 689-696.

Yeaton, R.I., Travis, J. & Gillinsky, E. 1977. Competition and spacing in plant communities: The Arizona upland association. *J. Ecol.* 65: 587-595.

Zar, J.H. 1974. *Biostatistical Analysis. 2th ed.* Prentice Hall, Inc. Englewood Cliffs, NJ.