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## COMPETITION IN TWO SPECIES OF DESERT ANNUALS ALONG A TOPOGRAPHIC GRADIENT<sup>1</sup>

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**Abstract.** Details on the nature of density-dependent processes in desert annuals and their interaction with density-independent factors are critical to an understanding of adaptation to variable environments and the role of environmental variation in the maintenance of species coexistence. In this study we examined intra- and interspecific competitive interactions along a topographic gradient for two co-occurring species of desert winter annuals, *Plantago patagonica* and *Pectocarya recurvata*. This investigation was carried out in a creosote flat in the Sonoran Desert during 1987–1988, a growing season with high plant densities and low rainfall. Three stations were established along the topographic gradient: one in the sandy rivulets of a tertiary wash or arroyo, one in the sandy clay soil at the base of a small hill, and the third on the southeast side of the gently sloping (9°) hill. The wash habitat had the greatest moisture availability (soil water potential) shortly after rainfall. Yet it dried out quickly, presumably due to greater evaporation and percolation, leaving the base of the hill with the greater average moisture availability. The slope had the lowest moisture availability. Competition experiments were set up at each station using a neighborhood design with varying density in either mono- or mixed cultures. Target plants were scored for survival, fecundity, and size. *Plantago* and *Pectocarya* were found to have equivalent competitive effects in all three habitats using either species as a target: the species identity of neighbors had no measurable effects so that competition coefficients appear to be equal. However, density-response curves had different slopes in the different habitats along the gradient: both species had flat density-response curves on the slope, while *Plantago* had its steepest curve in the wash and *Pectocarya* had its steepest curve at the base of the hill. While density-dependent processes were important determinants of success for these desert annuals in this low-rainfall year, the strength of the density response varied spatially. We argue that the habitat–density interactions that differ among species may promote their coexistence.

**Key words:** coexistence; density dependence; desert annuals; fecundity; interspecific competition; intraspecific competition; neighborhood interactions; *Pectocarya recurvata*; *Plantago patagonica*; spatial variation; survival.

### INTRODUCTION

Annuals constitute a major proportion of the plant diversity of deserts. Because of the clear role of environmental variability in arid habitats, the population dynamics of desert annuals have been frequently studied in terms of density-independent abiotic factors such as precipitation and temperature (Went 1949, Tevis 1958, Shreve and Wiggins 1964, Beatley 1967, Gutierrez and Whitford 1987). However, desert plants are also affected by biotic interactions. Seeds of desert annuals, along with those of co-occurring perennials, are known to support large populations of granivorous ants and rodents (e.g., Brown et al. 1979). Manipulative

studies in natural populations have also demonstrated the existence of competition among desert annuals (Klikoff 1966, Inouye et al. 1980, Kadmon and Shmida 1990a, b; see Fowler [1986] for a review). We still do not know much about the frequency of occurrence, intensity, and spatial patterns of density-dependent processes in desert annuals nor how such processes interact with density-independent factors. Such details are critical to an understanding of adaptation to variable environments (Venable 1989, Venable and Brown 1993) and an understanding of the role of environmental variation in the maintenance of species coexistence (Shmida and Ellner 1985, Chesson and Huntly 1989).

In this paper we ask under what conditions competition is an important determinant of survival and reproductive success in two species of desert annual populations. The objectives are (1) to document competitive interactions in natural populations of two winter annual species; (2) to report spatial variation in density effects along a topographic gradient; (3) to de-

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termine whether spatial variation along a topographic gradient affects the intensity of competition differently for the two species; (4) to assess the relative strengths of intra- and interspecific competition in a particular habitat; and (5) to consider the implications of these results for the population dynamics and coexistence of these species.

Topographic gradients can create substantial spatial variation in the productivity of desert annuals. Position along a water runoff gradient can substantially influence soil water availability (Evenari et al. 1982), which in turn can directly determine plant reproductive success. For example, seed production of *Stipa capensis*, an annual plant of the Judean Desert in Israel, was found to be lowest on a dry slope, moderate in shallow water-catching depressions, and highest in a wadi (wash) (Kadmon and Shmida 1990a, b). An observational study by Loria and Noy-Meir (1979–1980) also showed greater survival and reproductive success of old world desert annuals in wetter runoff-receiving sites in a relatively dry year.

In mesic communities, variation in the productivity of different habitats can influence the intensity of competition among plants for resources. Competitive interactions are generally expected to be most intense in more productive habitats where density or biomass is greatest (Grime 1977, Goldberg 1982, Wilson and Keddy 1986, Campbell and Grime 1992). Goldberg (1990) has argued that this is because the greatest magnitude of resource depletion, i.e., the greatest "effect" on resources, occurs where plants are large and closely spaced. Intense competition in productive habitats where nutrients and light are limiting is well documented (e.g., Mahmoud and Grime 1976, Keddy 1981, Reader and Best 1989, Reader 1990, Morris and Myerscough 1991), and several studies have demonstrated an increase in the intensity of competition along a gradient of increasing moisture availability (e.g., Del Moral 1983, Gurevitch 1986, Kadmon and Shmida 1990a, b).

However, reports of intense competition in unproductive environments (Tilman 1989; see Fowler [1986] for review of competition in arid and semi-arid environments) or no consistent relationship with abiotic stress (Welden et al. 1988) have also been documented. Intense competition in less productive habitats may occur as a result of greater resource limitation (Tilman 1982, 1988), while the absence of any relationship between competition and productivity gradients may be a consequence of variation in the importance of competition relative to other density-dependent and density-independent processes in the environment (Welden and Slauson 1986).

Previous studies of competition among desert annuals have used quadrat methods to demonstrate reduced survival or fecundity at higher densities (e.g., Klikoff 1966, Inouye et al. 1980). We used a neighborhood approach, which allowed us to assess com-

petition at the finer scale at which plants actually interact. Thus we analyzed the responses of individual target plants to conditions within local competitive neighborhoods, defined as the area around a target plant circumscribing all other plants with which it competes (Pacala and Silander 1985). We systematically varied both the density and frequency of neighbor species in order to separate intra- from interspecific competitive effects (cf. Firbank and Watkinson 1985, Law and Watkinson 1987, Connolly 1988).

## METHODS

### *Study site and species*

This study was conducted during the winter and spring season of 1987–1988 at the northwest base of Tumamoc Hill at the Desert Laboratory of the University of Arizona in Tucson, Arizona. The topography is characterized by rolling hills and small meandering washes. Study plots were located in open sites (between shrubs) at three stations along a topographic gradient: (1) the southeast side of a gently sloping (9°) hill, (2) the base of the hill (4–6°), and (3) an adjacent wash consisting of a series of shallow (<0.5 m deep) and narrow (2–3 m wide) dry drainage channels.

Rainfall at Tumamoc Hill averages  $\approx 250$  mm/yr. Almost half of this precipitation falls during the summer months, and the rest is unevenly distributed between October and April. Winter annuals typically germinate between October and January. Plants set seed and die in March or April, before the hottest and driest months of the year, May and June. Precipitation and temperature data from October 1987 through May 1988 were recorded daily at the Desert Laboratory (Fig. 1). This was a relatively dry year with little germination-inducing precipitation prior to December 1987 and not much rain during the first 3 mo of 1988, the critical growing season. There was, however, high germination during the relatively wet December resulting in high plant densities.

The soil on the slope is composed of basaltic andesite (Phillips 1976) with a coarse sandy-loam texture (67% sand, 20% silt, 13% clay) and with fragments of basaltic rocks embedded in the surface. The surrounding lower areas have recently derived alluvial soil, including sandy-clay soil at the base of the hill (54% sand, 22% silt, 24% clay) and loamy-sand soil in the wash (79% sand, 10% silt, 10% clay). The slope was rockier (50% gravel) than the base of the hill (20% gravel) or the wash (25% gravel).

The perennial vegetation is dominated by *Larrea tridentata* (creosote bush) and *Ambrosia deltoidea* (bursage), with *L. tridentata* predominant at the base of the hill and wash, and *A. deltoidea* more common on the slope. *Opuntia fulgida*, *O. phaeacantha*, and *Carnegiea gigantea* (saguaro) are scattered throughout the area. Among the winter annuals, *Plantago patagonica* and *P. insularis* are generally common at the study site

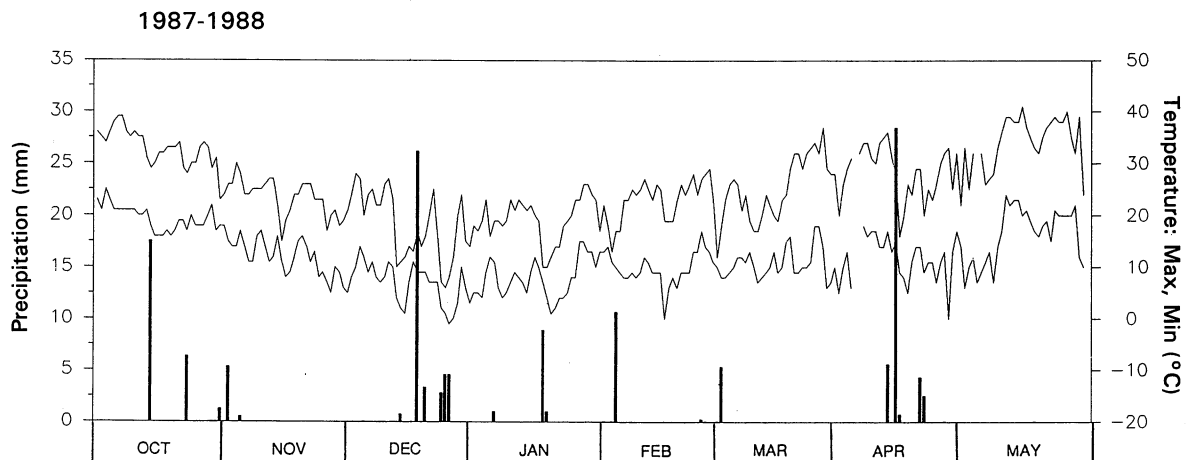


FIG. 1. Daily precipitation (vertical bars) and maximum and minimum temperatures (solid lines) at Tumamoc Hill (Arizona, USA) from October 1987 through May 1988.

every season while some species, such as *Pectocarya recurvata* and the grass *Schismus barbatus*, have population sizes that fluctuate greatly from year to year (D. L. Venable and A. Caprio, unpublished data).

This study focused on the two most abundant winter annual species of the 1987–1988 season, *Plantago patagonica* Jacq. (Plantaginaceae) and *Pectocarya recurvata* Johnston (Boraginaceae). *Plantago patagonica* forms rosettes whereas *Pectocarya recurvata* tends to be erect and branched from the base. At the peak of their vegetative growth in 1988, plants of both species were quite small at the study site, reaching only 1–2 cm in height. During this year the two species occurred in near monoculture or mixed stands with each other.

#### Analysis of soil water potential

Soil samples from the wash, base of the hill, and slope were collected at depths of 3 and 8 cm on two occasions: during a cool, wet day on 6 January 1990 (15 mm of rain fell on 3 January) and during a warm day on 6 April 1990 (12°/29°C min/max temperature) about a week after two rainfall events (12 and 6 mm on 29 and 31 March 1990). Four samples for each treatment combination were collected on each date. The soil samples were collected in tightly covered cans, and the percentage of water content was determined gravimetrically. Additional samples were analyzed for percentage of water content at  $-0.33$ ,  $-0.1$ ,  $-0.3$ , and  $-1.5$  MPa by the Soil, Water, and Plant Analysis Laboratory at the University of Arizona. The results of this second analysis were used with the data from the first analysis to calculate the mean soil water potential for each combination of habitat, depth, and day.

#### Design of the competition experiments

To choose the appropriate neighborhood radius for the plants at this desert site during the 1987–1988 season, data from an experiment on *Plantago* performed

in the wash habitat the previous year were used (M. Pantastico-Caldas and D. L. Venable, unpublished manuscript). Following the procedure suggested by Silander and Pacala (1985), plant performance (mean number of seeds produced by reproductive plants) was regressed against the number of neighbors in neighborhoods of different radii at the end of the growing season. The radius that minimized the residual sum of squares,  $1 - R^2$ , was considered to be the appropriate neighborhood size (sensu Silander and Pacala 1985). A neighborhood radius of 4 cm was chosen because it was the smallest neighborhood radius that provided a relatively low residual sum of squares. Below 4 cm the  $1 - R^2$  values were considerably higher, while values between the 4 and 8 cm radii varied only slightly (M. Pantastico-Caldas and D. L. Venable, unpublished manuscript). The use of the same neighborhood size for *Pectocarya* seemed reasonable because it has an above- and belowground plant size similar to *Plantago*.

There was little germination of *Plantago* or *Pectocarya* in October and November of 1987 and most seedlings germinated in late December. The experiments were set up during the 2nd wk of January 1988 when most plants were at the early seedling stage (1–2 wk old; plants that had emerged prior to December had mostly died and were not included in these experiments). Mortality from the time of emergence in late December to the time the experiments were set up in January was negligible because of cool moist weather.

Randomly chosen neighborhoods (target plants and their neighbors within a 4-cm radius; an area of 0.50 dm<sup>2</sup>) in high-density stands of *Plantago* and *Pectocarya* at the three sites were marked with color-coded toothpicks and nails. These dense stands appeared to be fairly homogeneous, resource-rich patches in the areas between shrubs within each habitat type. Thinning treatments were randomly assigned to manipulate both

the density and species of neighbors, and plants other than *Plantago* and *Pectocarya* were removed from the neighborhoods. Uprooting the seedlings did not significantly disturb the soil because the seedlings had not yet become completely established and were only rooted by short primary roots. These two species represented  $\approx 70\%$  of the total density of annuals at the study site that year (D. L. Venable and A. Caprio, unpublished data).

Two sets of neighborhoods were produced, one with *Plantago* and the other with *Pectocarya* as the target plant. In each habitat the neighborhoods were thinned to three density levels: 1, 4, and 24 plants/neighborhood (including the target), with two frequencies for densities  $> 1$  plant/neighborhood: monoculture (1 : 0) and mixed stand of even proportions of *Plantago* and *Pectocarya* (1 : 1). Note that these frequencies were based on species identities of all plants within the circular area with a radius of 4 cm (Table 1). We examined the effects of neighbor density and frequency more intensively at one site (the base of the hill) by adding an additional density: 8 plants/neighborhood, and two additional frequencies: neighborhoods with predominantly conspecific target and neighbor species (3 : 1) and neighborhoods with predominantly heterospecific target and neighbor species (1 : 3). Our design frequencies included the target plant so that frequencies of neighbors alone actually varied slightly with density (Table 1). Eight replicates were used for each treatment combination. Altogether, 104 neighborhoods were established at the base of the hill for each species acting as target and 40 neighborhoods each for the wash and slope habitats, for a total of 184 neighborhoods per species for the whole experiment.

This design reduces most of the statistical difficulties associated with neighborhood designs. These include lack of independence (each plant was utilized only once as a neighbor or target) and confounding of density with spatially varying microhabitat variables (density manipulations were randomly assigned).

The locations of the target plants and their neighbors were recorded by placing a mapping table over the neighborhoods and marking plant positions on acetate sheets. The same acetate sheets were used through the entire season, and the mapping table was placed in a standard position next to permanent toothpicks and nails in order to assure reliable identification of plants.

Survival to reproduction was scored as "1" if an individual target plant produced at least one seed and "0" if not. Fecundity of surviving targets was measured by counting the seeds on each plant. Two measurements of size were obtained for each surviving target: height and number of leaves for *Plantago* and height and number of basal shoots for *Pectocarya*. We used survival and reproduction as the primary determinant of plant success and the size measurements as further description of morphological changes during growth. Height was measured as the length of the longest leaf

TABLE 1. Experimental design of the competition experiments.

Habitat	Species frequency*	Neighborhood density (plants/0.5 dm <sup>2</sup> )			
		1	4	8	24
		Neighbor identity†			
Slope	Monoculture 1:0	...	3:0	...	23:0
	Mixed stand 1:1	...	1:2	...	11:12
Base	Monoculture 1:0	...	3:0	7:0	23:0
	Mixed stand 3:1	...	2:1	5:2	17:6
	1:1	...	1:2	3:4	11:12
	1:3	...	0:3	1:6	5:18
Wash	Monoculture 1:0	...	3:0	...	23:0
	Mixed stand 1:1	...	1:2	...	11:12

\* Relative proportions of the two species within the neighborhoods, including the target plants.

† Ratio of number of neighbors conspecific with the target plant to number of neighbors heterospecific to the target plant.

for *Plantago* and the length of the tallest basal shoot for *Pectocarya*. Fecundity and height were measured at the last census (19–23 March). The number of leaves or basal shoots was counted during the peak of vegetative growth (28 February–1 March), and the mortality of the target plants was also monitored at both censuses.

Variables for different groupings of target plants were  $l$ , the probability of surviving from emergence to reproduction (calculated as the proportion of emerged seedlings that were able to successfully reproduce);  $b$ , the expected fecundity of reproductive plants (calculated as the mean number of seeds produced by reproductive plants);  $l_b$ , the expected fecundity of emerged seedlings (calculated as the mean number of seeds produced by emerged seedlings); and the means of the various measures of plant size.

#### Analyses of the competition experiments

In order to have balanced design matrices, the results were analyzed in three ways: (1) a two-way factorial with three levels of neighborhood density (1, 4, and 24 plants/neighborhood), three habitats (wash, base of the hill, and slope), and eight replicates per treatment combination, for a total of 72 target plants per species; (2) a three-way factorial with two levels of neighborhood density (4 and 24 plants/neighborhood), three habitats (wash, base of the hill, and slope), two frequencies (1 : 0, 1 : 1), and eight replicates per treatment combination, for a total of 96 target plants per species; and (3) a two-way factorial design for targets at the base of the hill with three levels of neighborhood density (4, 8, and 24 plants/neighborhood), four frequencies (1 : 0, 3 : 1, 1 : 1, and 1 : 3), and eight replicates per treatment combination, for a total of 96 targets per species.

The three analyses were performed separately for *Plantago* and *Pectocarya*. Fecundity and size measurements of the target plants were analyzed with

TABLE 2. Soil water potential (MPa) at 3 and 8 cm depth in the wash (W), base of the hill (B), and on the slope (S) on a "wet day" (6 January 1990, 3 d after 15 mm of precipitation on 3 January) and a "dry day" (6 April, 1 wk after 18 mm of rain).

Soil depth (cm)	Wet day			Dry day		
	W	B	S	W	B	S
3	-.076	<-1.5	<-1.5	<-1.5	<-1.5	<-1.5
8	-.025	-.046	<-1.5	<-1.5	-.64	<-1.5

ANOVA (SAS Institute 1988: GLM Procedure, factorial model). The variables  $b_r$ ,  $l_r b_r$ , height, and number of leaves or basal shoots were log-transformed to homogenize variances. The Student–Newman–Keuls (SNK) test was used to compare the means when main effects were significant.

Survival to reproduction was analyzed with a maximum-likelihood logit model (SAS Institute 1988: CATMOD Procedure, Linear Categorical Models). These models are preferred over least squares regression and ANOVA because they take into account the underlying binomial nature of the probability of surviving to a particular time or state. They properly weight

variances according to sample sizes and proximity of the survival probabilities to 0 or 1 and they also have the desirable property that predicted survival probabilities are bounded by 0 and 1. In our model the independent variables were categorical, as in an ANOVA, while the dependent variable was the logit (or log-odds) of  $l_r$ , i.e.,  $\ln(l_r/(1 - l_r))$ . For these analyses,  $\chi^2$  rather than  $F$  statistics are used to test the significances since model parameters are estimated using maximum likelihood rather than least squares. To compare treatment means for significant main effects having more than two levels, a randomly chosen pair of levels was analyzed. If the difference was significant, one of the levels was compared with the level that was left out initially. If the initial difference was not significant, the two levels were lumped and compared with the third level.

## RESULTS

### Soil water potential

On 6 January (3 d after rain) the wash habitat had high soil water potential at both 3 cm and 8 cm depth (Table 2). The base of the hill had a similar high soil water potential at 8 cm though there was little moisture at 3 cm depth. On the drier day, 6 April (1 wk after rain), the wash had dried out and the base of the hill had the highest soil water potential. The slope of the hill had the lowest water potential at all depths and dates.

The lower water availability in the wash several days after rainfall is likely to be the result of high percolation and evaporation rates. The wash receives the most runoff during the rain but its sandy soil is less effective in retaining moisture than the sandy clay at the base of the hill.

### Competition experiments

In the monoculture analysis, density explained 15% of the variation in the expected (i.e., mean) fecundity of emerged seedlings ( $l_r b_r$ ), of *Plantago* ( $P < .01$ ) and 22% for *Pectocarya* ( $P < .001$ ), with  $l_r b_r$  being generally lower at higher densities (Figs. 2 and 3;  $F$  values in Table 3A). Habitat effects were not significant for either species, but habitat  $\times$  density interactions explained an additional 13% in  $l_r b_r$  for *Plantago* and 11% for *Pectocarya* ( $P < .05$  for both species). This interaction resulted principally from the contrasting behavior in different habitats of the isolated plants when compared

TABLE 3. (A)  $F$  values (and  $\chi^2$  values for  $l_r$ ) and significance levels for the two-way ANOVA of monocultures of *Plantago patagonica* and *Pectocarya recurvata* and (B)  $F$  values and significance levels of  $l_r b_r$  for the one-way ANOVA of monocultures of *Plantago patagonica* and *Pectocarya recurvata* within each habitat,  $df = 2, 63$ .

Species	Variables*	Error df	Source of variation		
			Density (df = 2)	Habitat (df = 2)	Density $\times$ Habitat (df = 4)
<i>Plantago</i>	$l_r$	...	4.56 <sup>NS</sup>	6.50 <sup>†</sup>	6.07 <sup>NS</sup>
	$b_r$	46	9.94 <sup>§</sup>	0.03 <sup>NS</sup>	1.20 <sup>NS</sup>
	$l_r b_r$	63	7.08 <sup>‡</sup>	2.24 <sup>NS</sup>	2.91 <sup>†</sup>
	Leaves	61	9.12 <sup>§</sup>	0.42 <sup>NS</sup>	0.82 <sup>NS</sup>
	Height	58	2.44 <sup>NS</sup>	0.67 <sup>NS</sup>	0.67 <sup>NS</sup>
<i>Pectocarya</i>	$l_r$	...	0.32 <sup>NS</sup>	2.83 <sup>NS</sup>	4.47 <sup>NS</sup>
	$b_r$	54	7.89 <sup>§</sup>	0.02 <sup>NS</sup>	1.73 <sup>NS</sup>
	$l_r b_r$	63	10.49 <sup>§</sup>	0.71 <sup>NS</sup>	2.59 <sup>†</sup>
	Shoots	61	5.96 <sup>‡</sup>	2.67 <sup>NS</sup>	1.56 <sup>NS</sup>
	Height	55	1.91 <sup>NS</sup>	8.48 <sup>§</sup>	0.45 <sup>NS</sup>

Species	Habitat	Source of variation
		Density
<i>Plantago</i>	Slope	0.10 <sup>NS</sup>
	Base	1.78 <sup>NS</sup>
	Wash	11.03 <sup>§</sup>
<i>Pectocarya</i>	Slope	0.63 <sup>NS</sup>
	Base	12.00 <sup>§</sup>
	Wash	3.05 <sup>NS</sup>

\*  $l_r$  = the probability of surviving from emergence to reproduction;  $b_r$  = the expected fecundity of reproductive plants;  $l_r b_r$  = the expected fecundity of emerged seedlings.

† = .05  $\geq P > .01$ ; ‡ = .01  $\geq P > .001$ ; § = .001  $\geq P > .0001$ ; <sup>NS</sup> =  $P > .05$ .

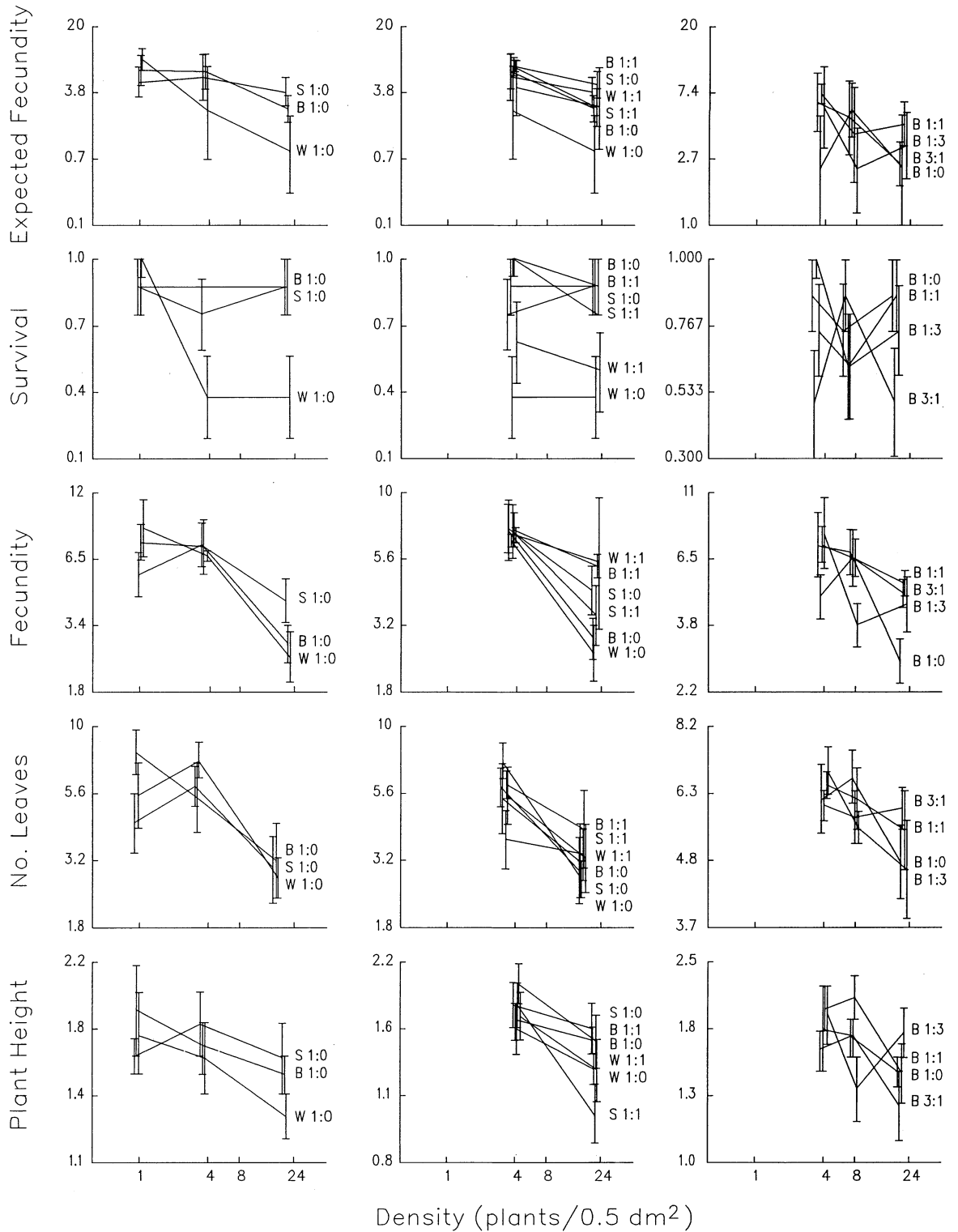


FIG. 2. Performance of *Plantago patagonica* as a function of habitat, density, and species frequency. Rows are the expected fecundity of emerging seedlings,  $l_b$ ; survival to reproduction,  $l_r$ ; fecundity of reproductive plants,  $b_r$ ; number of leaves per plant; and height. The columns correspond to the analysis of habitat and density in monocultures (left), habitat, density, and species frequency (center), and more levels of density and frequency at the base of the hill (right). Data are means, and vertical bars represent  $\pm 1$  SE. S = slope, B = base of hill, W = wash. Species frequencies are given as ratios of the numbers of plants of the target species (here, *P. patagonica*) to the numbers of plants of the neighbor species, within a circle of 4-cm radius.

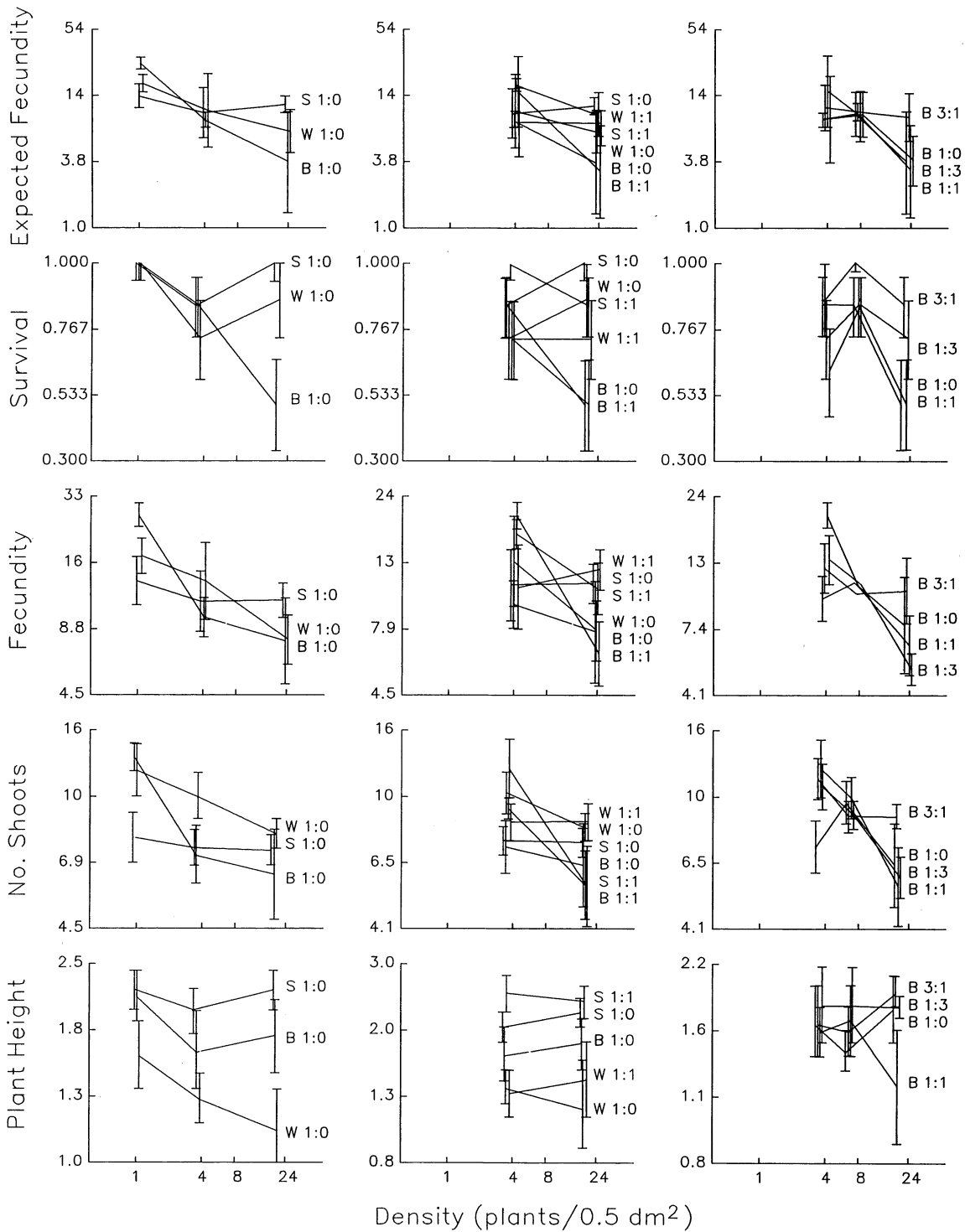


FIG. 3. Performance of *Pectocarya recurvata* as a function of habitat, density, and species frequency. Data presentation as in Fig. 2.

to plants with neighbors (when the data were reanalyzed without the isolated plants, the density  $\times$  habitat interaction was not significant,  $P < .20$  for both species).

Given the significant habitat  $\times$  density interactions, it is informative to repartition the sum of squares to look at the effects of density within each habitat. When this was done, we found that the habitat  $\times$  density



interactions were due to strong density effects at the base of the hill and wash but virtually no density effect on the slope (Figs. 2 and 3;  $F$  values in Table 3B). In the wash, isolated *Plantago* targets (2 plants/dm<sup>2</sup>) had much higher  $l, b_r$  than the target plants with neighbors (8 and 48 plants/dm<sup>2</sup>;  $P < .001$  for density effects in the wash habitat;  $P < .05$ , SNK for comparison of means). At the base of the hill, a similar but less pronounced trend of density-dependent reduction in  $l, b_r$  of *Plantago* was not statistically significant ( $P < .19$ , density effects at the base of the hill). In contrast,  $l, b_r$  of *Pectocarya* was most affected by competition at the base of the hill ( $P < .001$ ). There, increasing the neighborhood density from 1 to 4 plants/neighborhood and from 4 to 24 plants/neighborhood significantly reduced  $l, b_r$  of *Pectocarya* ( $P < .05$ , SNK for comparison of means). In the wash the density-dependent reduction in  $l, b_r$  of *Pectocarya* was smaller in magnitude and only marginally significant ( $P < .07$ ). On the slope the density curves are essentially flat for both species.

For *Plantago* the effects of competition were also manifested in a reduction of the expected fecundity of reproductive plants ( $b_r$ ) and a reduced number of leaves (Fig. 2;  $F$  values in Table 3A). Density explained 28% of the variation in  $b_r$  ( $P < .001$ ) and 22% of the variation in the number of leaves ( $P < .001$ ). The effects of density on survival to reproduction ( $l_r$ ) and plant height were not statistically significant. There were significant habitat effects on  $l_r$  due to low values in the wash ( $P < .05$ ). The pattern was that these plants mostly survived until the last census but died without producing any seeds (note that  $l_r$  was calculated as survival to reproduction). While the habitat  $\times$  density interaction for  $l_r$ ,  $b_r$ , number of leaves, and height were not significant, the same trends that were seen for  $l, b_r$  were apparent for these variables: the size and fecundity of *Plantago* appeared to be least affected by density on the slope and most affected in the wash, and  $l_r$  was only low for target plants with neighbors in the wash (Fig. 2).

For *Pectocarya*, competitive effects were manifested in reduced  $b_r$  and number of basal shoots (Fig. 3;  $F$  values in Table 3A). Density explained 21% of the variation in  $b_r$  ( $P < .001$ ) and 14% of the variation in the number of basal shoots ( $P < .01$ ). Isolated plants had higher  $b_r$  and number of basal shoots than plants in low- and high-density neighborhoods ( $P < .05$ ). While  $b_r$  did not vary with habitat, there was a tendency for the two measures of plant size to be affected in opposite ways by habitat. Plants were significantly taller ( $P < .001$ ) but had fewer basal shoots ( $P < .08$ ) on the slope. These opposing trends in the effects of habitat on plant height and number of basal shoots apparently canceled one another, resulting in the absence of a habitat effect on  $b_r$ . As was found for *Plantago*, no significant interactions were apparent for  $l_r$ ,  $b_r$ , or plant size despite a clear tendency for greater density effects at the base of

the hill than in the wash, and in the wash than on the slope (Fig. 3).

The main contribution of the three-way analysis of habitat, density, and frequency was to show that the frequency of neighbor species (monoculture vs. 1 : 1 mixture) had no measurable effect on any of the plant performance variables (Figs. 2 and 3;  $F$  values in Table 4A). Neither species frequency nor its interactions with other factors were significant for any performance variable for either species. The habitat and density effects in this analysis were basically the same as those found in the monoculture analysis presented above, except that the important comparisons with isolated plants were not made.

The more detailed two-way analysis of density and frequency at the base of the hill further confirmed that the species identity of neighbors (monocultures and two-species mixtures with 3 : 1, 1 : 1 and 1 : 3) had no significant effect on the performance of either species (Figs. 2 and 3;  $F$  values in Table 4B). This analysis also showed that increasing the density from 4 to 8 plants/neighborhood (8 to 16 plants/dm<sup>2</sup>) at the base of the hill did not result in any significant decrease in size, survival, or reproductive success of plants of either species (Figs. 2 and 3;  $P < .05$ , SNK for comparison of means).

## DISCUSSION

### *Competition in a high-density low-rainfall year*

In 1987, 43 mm of rain fell between 14 and 28 December, resulting in the emergence of seedlings at the second highest densities for the 9 yr on record (1982–1983 to 1990–1991; D. L. Venable and A. Caprio, unpublished data). The mean of the natural background density for combined populations of *Plantago* and *Pectocarya* at the study site in 1987–1988 was  $\approx 25$  seedlings/dm<sup>2</sup> or  $\approx 11$  neighbors/neighborhood as compared to  $\approx 6$  seedlings/dm<sup>2</sup> or 2 neighbors/neighborhood in the previous year (Table 5).

Following this wet December, only 27 mm of precipitation fell during the period of rapid vegetative growth and reproduction from January through March of 1988 (Fig. 1). The plants encountered successive droughts of at least 3-wk duration including one beginning in early March which lasted  $> 1$  mo. This last big drought was particularly critical, occurring just prior to reproduction when the plants should have been at the peak of vegetative growth. Survival and reproductive success were low compared to the previous year on plots located on the same topographic gradient (Table 5).

Thus our data show that in a high-density, low-rainfall year both *Plantago patagonica* and *Pectocarya recurvata* experienced competitive conditions in two of the three habitats investigated. Such density-dependent inhibition in a year when rainfall was infrequent and low has been previously reported for another desert

TABLE 4. *F* values (and  $\chi^2$  values for  $l_r$ ) and significance levels for (A) the three-way ANOVA of *Plantago patagonica* and *Pectocarya recurvata* and (B) two-way ANOVA of *Plantago patagonica* and *Pectocarya recurvata* at the base of the hill.

		Source of variation							
Species	Variables*	Error df	Density (df = 1)	Habitat (df = 2)	Frequency (df = 1)	Density × Habitat (df = 2)	Density × Frequency (df = 1)	Habitat × Frequency (df = 2)	Density × Habitat × Frequency (df = 2)
<i>Plantago</i>	$l_r$	...	1.14 <sup>NS</sup>	15.20§	1.79 <sup>NS</sup>	...	2.08 <sup>NS</sup>	0.07 <sup>NS</sup>	...
	$b_r$	59	18.69§	0.05 <sup>NS</sup>	1.62 <sup>NS</sup>	0.01 <sup>NS</sup>	1.71 <sup>NS</sup>	1.37 <sup>NS</sup>	1.06 <sup>NS</sup>
	$l_r b_r$	84	7.88‡	8.93§	3.07 <sup>NS</sup>	0.23 <sup>NS</sup>	0.53 <sup>NS</sup>	0.51 <sup>NS</sup>	0.78 <sup>NS</sup>
	Leaves	82	15.26§	0.47 <sup>NS</sup>	0.01 <sup>NS</sup>	0.62 <sup>NS</sup>	2.04 <sup>NS</sup>	0.62 <sup>NS</sup>	0.19 <sup>NS</sup>
	Height	79	14.82§	1.15 <sup>NS</sup>	0.13 <sup>NS</sup>	0.34 <sup>NS</sup>	2.96 <sup>NS</sup>	2.19 <sup>NS</sup>	0.48 <sup>NS</sup>
<i>Pectocarya</i>	$l_r$	...	0.31 <sup>NS</sup>	5.64 <sup>NS</sup>	0.12 <sup>NS</sup>	...	0.26 <sup>NS</sup>	0.06 <sup>NS</sup>	...
	$b_r$	64	6.85†	0.83 <sup>NS</sup>	2.03 <sup>NS</sup>	1.04 <sup>NS</sup>	0.60 <sup>NS</sup>	0.07 <sup>NS</sup>	2.74 <sup>NS</sup>
	$l_r b_r$	84	4.15†	4.67†	0.11 <sup>NS</sup>	2.39 <sup>NS</sup>	0.71 <sup>NS</sup>	0.08 <sup>NS</sup>	0.70 <sup>NS</sup>
	Shoots	79	7.85‡	1.44 <sup>NS</sup>	0.09 <sup>NS</sup>	0.92 <sup>NS</sup>	2.37 <sup>NS</sup>	0.70 <sup>NS</sup>	1.92 <sup>NS</sup>
	Height	67	0.02 <sup>NS</sup>	15.12§	0.01 <sup>NS</sup>	0.10 <sup>NS</sup>	0.31 <sup>NS</sup>	1.35 <sup>NS</sup>	0.80 <sup>NS</sup>

		Source of variation			
Species	Variables	Error df	Density (df = 2)	Frequency (df = 3)	Density × Frequency (df = 6)
<i>Plantago</i>	$l_r$	...	0.35 <sup>NS</sup>	3.87 <sup>NS</sup>	...
	$b_r$	60	4.70†	0.57 <sup>NS</sup>	1.87 <sup>NS</sup>
	$l_r b_r$	84	1.51 <sup>NS</sup>	1.46 <sup>NS</sup>	1.77 <sup>NS</sup>
	Leaves	80	3.20†	0.19 <sup>NS</sup>	0.78 <sup>NS</sup>
	Height	77	3.57†	1.06 <sup>NS</sup>	1.51 <sup>NS</sup>
<i>Pectocarya</i>	$l_r$	...	5.52 <sup>NS</sup>	3.41 <sup>NS</sup>	...
	$b_r$	63	7.15‡	0.54 <sup>NS</sup>	1.44 <sup>NS</sup>
	$l_r b_r$	84	5.50‡	1.24 <sup>NS</sup>	0.58 <sup>NS</sup>
	Shoots	78	7.92§	1.05 <sup>NS</sup>	1.38 <sup>NS</sup>
	Height	66	0.06 <sup>NS</sup>	0.75 <sup>NS</sup>	0.58 <sup>NS</sup>

\* For explanation of species variables, see Table 3.

† = .05 ≥ *P* > .01; ‡ = .01 ≥ *P* > .001; § = .001 ≥ *P* > .0001; <sup>NS</sup> = *P* > .05.

winter annual in Arizona, *Plantago insularis* (21 mm between 22 January and 27 May; Klikoff 1966). In Israel, Kadmon and Shmida (1990a) also found intense competition in another desert annual *Stipa capensis* when natural rainfall during the year was relatively low (60 mm for the 1985–1986 season). It would, therefore, seem that it is not unusual for competitive inhibition of desert annuals to occur under conditions that are unfavorable for the growth of large, fecund plants.

#### Differential competitive response along the gradient

The salient pattern in our results was that competition tended to be weak at the slope and more intense

at the two habitats below it. For each of the two species, the performance curves crossed at low densities.

We evaluated two aspects of spatial environmental variation along the topographic gradient: soil texture and soil water potential. The loamy-sand soil in the wash received pulses of abundant soil moisture associated with rainfall, while the sandy-clay soil at the base of the hill retained moisture longer. The slope had lower moisture availability than the other two habitats.

In order to survive in sandy soils, seedlings must be able to quickly utilize moisture from the rapidly drying soil surface. Without neighbors a plant has a high probability of reaching deeper moist soil layers before the

TABLE 5.  $l_r$ ,  $b_r$ ,  $l_r b_r$ , and seedling density in unmanipulated plots of the two species investigated for 2 yr in the open habitats (from D. L. Venable and A. Caprio, unpublished data). For explanation of species variables, see Table 3.

Year	<i>Plantago patagonica</i>			<i>Pectocarya recurvata</i>		
	$l_r$	$b_r$	$l_r b_r$	$l_r$	$b_r$	$l_r b_r$
1986–1987	0.80	17.9	14.3	0.79	49.0	38.5
Density (seedlings/dm <sup>2</sup> )		4.8			1.7	
1987–1988	0.30	3.6	1.1	0.32	8.4	2.7
Density (seedlings/dm <sup>2</sup> )		11.6			13.1	

soil surface dries, increasing the likelihood of successful reproduction. High density in a habitat where abundant moisture occurs in pulses may result in numerous small plants that survive until late in the season without reproducing. This scenario could account for the intense competitive inhibition in *Plantago* in the wash. *Pectocarya* was also marginally affected by competition in the wash but experienced the most pronounced density effects at the base of the hill.

The reasons for these apparent species-specific plastic responses to habitat and density differences are not yet apparent. The species differences are, however, not surprising if they are mediated by a difference in the mechanism of tolerance to competition (i.e., a differential "response" to competition; Goldberg and Fleetwood 1987, Goldberg 1990). Competitive traits associated with high tolerance of low resource levels, such as increased resource uptake, decreased resource loss, increased efficiency of conversion of resource to growth, or storage during periods of temporary resource abundance, are determined by physiological mechanisms that may be species-specific (Goldberg 1990). Explorations of the physiological responses of these plants to habitat and density would be necessary to sort out the exact mechanisms involved.

A factor that may have contributed to the weak density effects on the slope is rockiness, both above- and belowground. The rocks may have significantly partitioned the resource pool, thus isolating the portion available to each plant. This might have reduced the ability of high-density neighbors to inhibit one another. This idea of lateral constraint was consistent with the observation that *Pectocarya* tended to be taller but less branched on the slope.

Our results showed that the increasing intensity of competition from the slope downwards was not simply the result of overall higher moisture availability at the base and wash. In this scenario, intense competition at the base of the hill or wash would be due to greater plant growth in response to greater soil moisture potential. The absence of competition on the slope would result from minimal interaction among small plants with extremely small competitive neighborhoods. This scenario explained Kadmon and Shmida's (1990b) results for *Stipa capensis* where the range of densities along the topographic gradient was more than three orders of magnitude. In contrast, we controlled for density when comparing intensity of competition along this particular topographic gradient, and we found that on the slope plants were similar in size to those below but with higher  $l, b$ , at high density levels. Thus, the slope appeared to be more favorable than the other two habitats when density was high, despite having the lowest average soil moisture potential. One possible reason for this pattern was that average soil moisture potential may not have been an appropriate measure of moisture availability at the slope. The presence of rocks may not only have partitioned the resource pool

but may have also created small pockets of moist soil underneath them that plants were able to utilize during long periods of drought.

The results we present demonstrate the need to pay attention to subtle aspects of spatial heterogeneity and temporal variability (e.g., effects of pulses of resource availability during the growing season) in order to more fully understand the role of competition in the dynamics of natural populations.

#### *Equivalent competitive effects*

Our species frequencies are based on the densities of neighbors plus the target, thus the frequency of neighbors varies slightly with density in our design. Also we did not include 100% heterospecific neighbors as a treatment. However, we find it compelling that there was no significant effect of species frequency or any interaction with species frequency for either species across all habitats and densities for any of our five performance variables (Tables 2 and 3, Figs. 2 and 3). Even at the base of the hill where a greater range of neighbor species frequencies was investigated, the performances of *Plantago* and *Pectocarya* were not affected by neighbor species frequency. Thus it would seem that the two species are equivalent in their competitive effects on target plants.

Since individuals of the two species had roughly the same size and growth form, this result was consistent with Goldberg and Werner's (1983) prediction that species of similar growth forms may exhibit a large degree of equivalence of competitive effects. They argued that plant size, more than the identity of species, is likely to influence competitive abilities that act via effects on resource uptake, i.e., larger plants, regardless of species, can generally take up more resources than smaller plants (Goldberg and Fleetwood 1987, Goldberg 1990). Competitive equivalence was also found for *Plantago patagonica* and *Schismus barbatus* in 1986–1987 (M. Pantastico-Caldas and D. L. Venable, unpublished manuscript).

#### *Implications for population dynamics and coexistence*

This study suggested that in a high plant density but low rainfall year, competition may play a significant role in the population dynamics of *Plantago* and *Pectocarya* in two of three habitats in the open sites of our study area in Arizona. The survival and reproductive success of the two species were reduced considerably by the presence of neighbors (of either species) in the two habitats below the slope. In this year type, subpopulations on the slope may contribute more to the seed bank than those from the other two habitats. In wetter years, however, pulses of abundant moisture in the wash and base of the hill may allow greater reproductive success among populations below the slope.

The differences in the responses of *Plantago* and *Pectocarya* to competition in the three habitats also

suggest the possibility of density- and habitat-dependent competitive superiority. During years of high density and low rainfall, *Plantago* will tend to be more susceptible to competitive inhibition in the wash whereas *Pectocarya* will be more suppressed at the base of the hill. On years when seedling densities are low, however, such differences may not occur. Thus, in each habitat, competitive superiority may shift from one species to the other, depending upon density. If density varies from year to year (perhaps due to variation in the previous year's seed production, germination conditions, or predation intensity), such shifts in competitive superiority should promote coexistence by delaying, or even totally preventing, competitive exclusion (Chesson and Huntly 1989).

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