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IS COEXISTENCE OF SONORAN DESERT ANNUALS MEDIATED BY TEMPORAL VARIABILITY IN REPRODUCTIVE SUCCESS?¹

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Abstract. Models of annual plants with a persistent seed bank have shown that temporal variation can promote coexistence if the reproductive success of species is favored in different environments determined by temporally variable conditions. This study investigates whether this mechanism may explain the coexistence of three Sonoran Desert species (*Pectocarya recurvata*, *Plantago patagonica*, *Schismus barbatus*). In a 2-yr experiment, factors that vary across years (water and seedling density) were manipulated. In addition, the dominant spatial feature, presence or absence of *Larrea* cover, was also included as a factor. Our aim was to document fitness hierarchies in different types of years. Seedlings were mapped monthly for survival and reproductive success. To compare species, we used 10 yr of data to calculate the average value that seeds of different species have for population growth. Shifts in fitness hierarchies were found for two species pairs (*Pectocarya*–*Schismus* and *Pectocarya*–*Plantago*), depending on density and either the year or the water level. Surprisingly, all species had higher survival at higher densities in one or another treatment. Habitats were not important to the fitness hierarchies; all species had higher mean survival and fitness in the open than under shrubs.

Key words: annual plants; coexistence; competition; fecundity; *Larrea divaricata*; *Pectocarya recurvata*; *Plantago patagonica*; relative fitness; *Schismus barbatus*; Sonoran Desert; spatial variation; survival; temporal variation.

INTRODUCTION

Understanding the mechanisms allowing plant species to coexist has challenged ecologists. We often find coexisting plant species that do not appear to partition any of the fundamental axes of environmental heterogeneity, such as resources, habitats, pH, temperature, relationships with predators, or response to disturbance (Silvertown and Law 1987). For example, at our study site in the Tucson Mountains, over 30 species of winter annual plants commonly co-occur where little habitat diversity exists (a creosote flat dominated by the shrub *Larrea divaricata*).

New insights into mechanisms of coexistence have been gained from models that incorporate temporal variation in the form of variation between years (as opposed to variation within a year; Chesson and Warner 1981, Ellner 1984, Shmida and Ellner 1984, Chesson 1986, Chesson and Huntly 1988). These models support the suggestions of earlier empirical work (Grubb 1977, Hutchinson 1958, 1959, 1961) that species could co-occur in the same habitat by partitioning the environment through time. These models require that species are favored in different years, have overlapping generations with one life history stage relatively invulnerable to bad years (e.g., long-lived adults or seeds), and are severely limited by competition when they are abundant in favorable years (Chesson and

Huntly 1989). In studies incorporating spatiotemporal variability, when temporal fluctuations are out of phase from patch to patch so that competitive rankings vary depending on both the patch and the year, dispersal can promote coexistence (Shmida and Ellner 1984, Chesson 1985, Comins and Noble 1985). A temporally variable environment provides windows of opportunity. If species possess different types of adaptations they may be able to take advantage of different types of opportunities.

The present study measures relative fitness to determine whether species in the same guild are favored in different years, and discusses the implications these empirical findings have for species coexistence. The guild of the Sonoran Desert winter annuals is an ideal system for investigating coexistence mediated by temporal variation in environmental conditions. First, as a consequence of high temporal variability in rainfall and temperatures, potential evapotranspiration is far more variable in hot deserts than in any other biome (D. Frank and R. S. Inouye, *in press*). Second, the biotic environment experienced by an annual plant in our system is extremely variable: seedling densities vary by nearly two orders of magnitude (Fig. 1). Third, this system is species rich and $\approx 50\%$ of plant species are annuals (Venable et al. 1993). Finally, some desert annual seeds are long lived (Freas and Kemp 1983, Kemp 1989; C. E. Pake and D. L. Venable, *unpublished manuscript*), providing a relatively invulnerable life history stage resistant to drought and competition that protects species against extinction in unfavorable years.

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A 2-yr experiment was conducted in which two factors (water and seedling density) that vary between years were manipulated, allowing us to follow aspects of both natural and simulated temporal variation. The dominant spatial feature was also incorporated: microhabitats arranged in a mosaic of shrub-covered areas and open areas between shrubs.

METHODS

Study site and species

Our study site is a gently sloping alluvial plain (725 m elevation) at the University of Arizona's Desert Laboratory near Tucson. It is dominated by *Larrea divaricata* (creosote bush; 48% cover), but includes other perennials such as *Ambrosia deltoidea*, *Acacia constricta*, *Opuntia phaeacantha*, *Krameria grayii*, and *Opuntia leptocaulis*. The area has not been grazed by livestock since 1907 (Bowers 1989, Burgess et al. 1991).

Tucson's average annual precipitation is ≈ 25 cm, and typically half falls in the summer months of July, August, and September. The remainder is spread unevenly over the rest of the year, mostly from October to April (Fig. 2).

The study species (*Pectocarya recurvata* Johnst. (Boraginaceae), *Plantago patagonica* Jacq. (Plantaginaceae), and *Schismus barbatus* (L.) Thell.; Gramineae) were three of the four most abundant species in the three seasons preceding the study and showed no obvious spatial habitat segregation. Over the last 10 yr, reproductive success among these species displayed a range of temporal variability (SD in log-realized fecundity among years for *Pectocarya* = 1.20, for *Plantago* = 1.34, and for *Schismus* = 1.71) uncorrelated

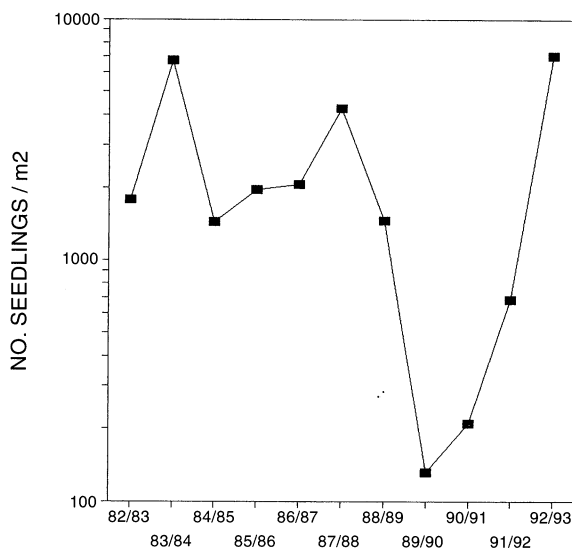


FIG. 1. Total seedling densities for all species at the University of Arizona Desert Laboratory study site near Tucson, 1982/1983–1992/1993.

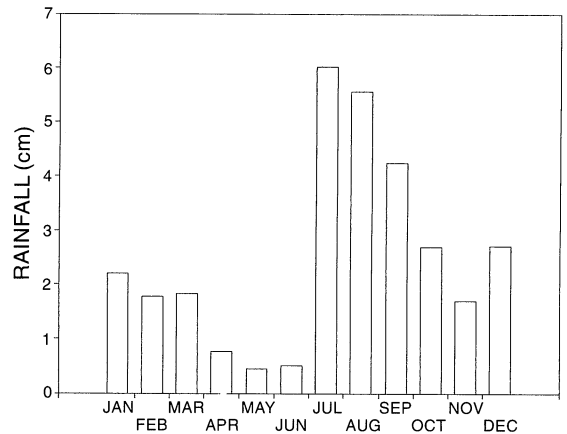


FIG. 2. Within-year distribution of monthly rainfall (National Weather Service 30-yr averages) for Tucson, Arizona.

among species (Venable et al. 1993). Both *Pectocarya* and *Plantago* are large-seeded (0.95 mg), native annuals. *Schismus*, in contrast, is a small-seeded (0.08 mg), naturalized exotic, originally from arid regions of the Near East. *Schismus* was apparently introduced to the Desert Laboratory grounds 50–76 yr ago (Burgess et al. 1991).

Winter annuals germinate as early as October, but more frequently in November or December. In both years of the present study (Fig. 3), the rainfall event that caused mass germination occurred in mid-December (12–16 December 1990 and 18–21 December 1991) with the first emergence occurring 5–6 d later (17 December 1990 and 23 December 1991), and continuing for another 7–10 d. The earliest flowering appeared mid-February in both years, the first set seeds in March. In these 2 yr, reproduction was not complete until early to mid-April. *Pectocarya* and *Plantago* had a narrower window for reproduction than *Schismus*, which in general was among the first (with *Pectocarya*) and the last (with *Plantago*) to flower, set seed, and die.

Environmental data

Pairs of calibrated maximum-minimum thermometers were placed in shrub and open microhabitats. Rain gauges were placed in the open on the experimental site (three in 1990/1991, two in 1991/1992). Gypsum blocks, calibrated to the soil type (shrub or open) in which they would be placed, were installed at 5 cm depth in the borders of 30 plots prior to germination in the 1st yr. In the 2nd yr, additional blocks were installed on five plots. Thermometers, rain gauges, and gypsum blocks were read at roughly weekly intervals.

Three soil samples each, from the shrub and open microhabitats, were analyzed for composition (sand, silt, clay, gravel) at the University of Arizona Soil, Water, and Plant Analysis Laboratory.

Experimental conditions

During 2 yr, we examined the effects of annual plant density, water addition/removal, and shrub vs. open microhabitats on the reproductive success of three annual species. In the fall of the 1st yr, 60 plots (30 × 40 cm) were located either directly under the canopy on the north side of *Larrea* shrubs (at least 1.5 m tall) or in the open spaces between shrubs (at least 0.5 m out from the edge of a shrub canopy). Contiguous groups of six shrubs and six open plots were chosen subjectively to represent homogeneous experimental blocks.

Experimental combined densities of all three study species were set at 200 plants/m² ("low"), 1000 plants/m² ("medium"), or 4000–8000 plants/m² ("high"), to cover the naturally occurring range of densities at our site (Fig. 1). Previously collected litter that contained seeds of all annual species was used to seed plots in November of each field season. After thoroughly mixing the litter and estimating the number of germinable seeds from germination trials in growth chambers, some of it was autoclaved to kill all seeds; 900 mL of litter with viable seeds were broadcast on high density plots. Lower density plots also received 900 mL in the following ratios of viable/autoclaved litter, respectively: 170/730 for medium density and 115/785 for low density.

Although the use of litter of the appropriate dilution roughly controlled densities, plots required thinning after germination to achieve exact experimental densities. Because the majority (≈80%) of the seedlings were *Pectocarya*, individuals of this species were preferentially removed during thinning to preserve the largest possible sample size for *Plantago* and *Schismus*. In addition, individuals were chosen so that, as nearly as possible, a plot had the same density in all four quarters. The relatively uncommon individuals of nonstudy species were also removed. Since seedlings were small (<1 cm), gently uprooting them with forceps enabled removal while causing minimal soil disturbance.

Previous studies at this site have shown competitive effects due to the densities of the study species, but have found no effect due to their relative proportions (M. C. Pantastico-Caldas and D. L. Venable 1993, *unpublished manuscript*). Thus, in the present study we manipulated the total density of these species but made no attempt to control their relative proportions (which, in any case, did not vary substantially).

The wet treatment was allowed access to natural rainfall, and during dry spells (when rainfall events were >5–10 d apart) plots were hand-watered every 1–3 d

by applying 600 mL to each plot (1200 cm²) using a broad, multiply perforated spout that applied a gentle stream. Watering was done at dusk or, alternatively, shade cloth (80%) was applied for 12–24 h to mimic the effect of overcast skies.

The dry treatment received natural rainfall through January in both years. However, since both winters were exceptionally wet, several late-season rainfall events were excluded with the use of temporary rain shields.

Herbivore control.—Three experimental and three natural (nonexperimental) plots were reviewed daily to determine whether herbivores might be attracted to our artificially high densities in these low density years. After observing more invertebrate damage (usually tiny bites on cotyledons) on experimental than natural plots, experimental plots were sprayed once with Sevin (a general insecticide of 3–4 d persistence) to control invertebrates (31 December 1990 and 7 January 1992). Following this intervention, invertebrate herbivore activity did not appear to be higher than the background activity on natural density plots. In addition, small chickenwire cages (60 × 60 cm in area, 25 cm tall) were placed over plots on 7–8 January 1991 and on 18 November 1991 to minimize small mammal access to the experiment.

Data collection.—Seedlings were initially mapped on acetate sheets on 8–18 January 1991 and 7–8 January 1992 (when they were 2–3 wk old) using a Plexiglas mapping table. The mapped area was 20 × 25 cm, which excluded borders of plots. A midseason census was taken on 14–26 February 1991 and 7–11 February 1992. Because flowering phenology was variable across space (the driest plots in general being the first to flower and set seed), the final census was spread over an interval: 30 March–10 April 1991 and 1–17 April 1992.

Relative performance estimated by using seed values

As a measure of fitness, we used lb_s , the mean seed set of a germinated seed. This was calculated as (total seeds produced)/(number of seedlings), on a per species per plot basis. l_r represents the proportion of germinated seeds that survived to reproduce, and b_r represents the average number of seeds produced by reproductive adults.

One of our goals was to compare reproductive success across species. However, because of differences in seed size and other seed traits, the probabilities of survival to reproduction for seeds of different species

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FIG. 3. Two winter growing seasons, 1990/1991 and 1991/1992. (A) Comparison of temperatures between habitats (■ = shrub-max, X = shrub-min; □ = open-max, X = open-min), (B) natural rainfall, (C) the wet, and (D) the dry treatments. Arrows represent the midpoint emergence (G), the initiation of separate water treatments (W), the beginning of flowering (F) and of seed set (S), and the point at which all plants have died (D).

TABLE 1. The average value that seeds of three species have for population growth (reproductive adults/seed), bootstrapped confidence intervals, and relative seed values obtained from 10 yr (1982/1983–1991/1992) of data on permanent plots at the study site. Inverse seed values estimate how many seeds, on average, are required by each species to produce a reproductive adult (seeds/reproductive adult).

	<i>Plantago</i>	<i>Pectocarya</i>	<i>Schismus</i>
Seed value (90% CI)	0.087 (0.0543–0.118)	0.0573 (0.0425–0.103)	0.0164 (0.00960–0.0216)
Relative seed value	1.00	0.710	0.203
Inverse seed value	12.4	17.5	60.9

are not the same. Thus, equal levels of seed set do not imply equal numbers of offspring. To correct for this, we used long-term demographic data (collected 1982/1983–1991/1992, from permanent plots along a 200-m transect parallel to the present experiment; D. L. Venable and A. Caprio, *unpublished data*) to quantify the average value that seeds of different species have for population growth. We estimated “seed value,” the average probability that a set seed will become a reproductive adult, or inversely, the number of seeds required on average to make a reproductive adult, as:

$$\frac{\text{number of reproductive adults produced over 10 yr}}{\text{number of seeds produced over 10 yr}}$$

Bootstrapped variances of seed values were also calculated to see how sensitive seed values were to the components making up the ten-year data set.

The calculated seed values (0.0807 adults/seed for *Plantago*, 0.0573 adults/seed for *Pectocarya*, and 0.0164 adults/seed for *Schismus*; Table 1) were “relativized” by arbitrarily setting the highest value (*Plantago*) to 1 (1.00, 0.710, and 0.203, respectively). Seed set, b_r , was multiplied by this relative seed value to compute relative b_r . Similarly, relative l_b , equals l_r times relative b_r . Thus, these demographic parameters have been scaled to take into account species differences in the average value seeds have for population growth. Accordingly, if relative b_r or relative l_b of one species is higher than that of another, it can be considered to be outperforming the other species under a specific set of conditions.

Statistics

Data were analyzed using the GLM procedure in SAS version 6.04 (SAS 1989). Survival data were arcsine transformed to meet assumptions of normality. Relative l_b , and relative b_r were log transformed, which also normalized the error structure.

To compare relative fitnesses between species within a treatment combination, we performed a global analysis using a repeated-measures design. To understand how the responses of each species contributed to significant differences between species, we analyzed the data for each species separately. The latter analyses determined whether an individual species had a significant response to year, water, density, or habitat.

The separate species analyses used a split-split plot

design. Split-plot designs have more than one size of experimental unit (the larger units containing several of the smaller units), and as a consequence have different error terms for factors assigned to different-sized units. Shrub vs. open habitat treatments were the largest experimental units, to which Error A (calculated as Habitat \times Block) applied. Because the same plots were used each year, these experimental units were subdivided by Year (Error B; Year \times Block within Habitat). The plots themselves, to which Density and Water were completely randomized, were sub-sub-divisions. The residual error applied to this level of analysis.

Repeated-measures designs differ from split-plot designs in that the levels of one or more factors cannot be randomly assigned. Because of this the corresponding error terms may have a covariance matrix that does not conform to the assumptions of split-plot analyses. Specifically, the split-plot model requires that pairs of observations on the same unit be equally correlated (Milliken and Johnson 1984, Littell et al. 1991). However, when there are only two levels of a nonrandomized factor (e.g., Habitat, Year), there is only one pair of observations on a unit, the question regarding correlation structure between pairs of observations is irrelevant, and the split-plot analysis is appropriate. Thus, while neither habitat nor year could be randomly assigned to plots, because they each have only two levels, the split-plot analysis can be used.

In the global analysis comparing species, each of our plots was essentially split again, because measurements were made for each of the three species on a plot. Since Species was not truly randomized within plots and because there were three levels of Species, we performed a repeated-measures analysis, testing the hypothesis that pairs of observations on the same unit were equally correlated. When these criteria were not met, we followed Huyhn and Feldt's (1976) Box correction, which decreases the degrees of freedom associated with the F test to adjust for correlations.

A significant Species \times Factor interaction means that species responded differently to a factor. When such interactions were significant, we compared the performance of species in each treatment combination using Fisher's protected least significant difference (Milliken and Johnson 1984, Day and Quinn 1989).

“Pairwise deletion,” a method that tends to produce the least bias in reliability, was used to estimate missing

data (Milliken and Johnson 1984; P. B. Jones, *personal communication*). Estimated data replaced missing data in the fitness analysis on five plots for *Plantago* and on seven plots for *Schismus*.

Robustness of hierarchies.—If one species had a significantly higher relative l, b , than another species in a particular treatment combination, we inferred that a fitness hierarchy existed under those conditions and that one species increased relative to the other. Since this conclusion is based on an estimate of seed value, we tested the robustness of competitive hierarchies by performing additional analyses (eight in all) using all combinations of upper and lower confidence limits of seed values (Table 1). For each hierarchy supported using our estimate of seed value, we report the number of additional analyses that also supported it at $P < 0.05$. A value of 8 means that no matter which seed values in the confidence interval were used, that competitive hierarchy was significant.

These considerations are important for evaluating significant differences between species, because the relative fitness of the species shifts with seed value. However, since seed value is a constant by which l, b , is multiplied, the significance of interactions in the repeated-measures analyses is not affected, nor is the significance of factors in the separate analyses of species.

RESULTS

Environmental data

The thermal environment in the open was more extreme than that under shrubs (Fig. 3A): maximum temperatures were higher ($P < 0.0001$) and minimum temperatures were lower ($P < 0.0001$; Wilcoxon signed-rank test). The means for percent silt and clay were higher under shrubs, whereas percent sand and gravel were higher in the open (Table 2).

Precipitation was 17.15 cm in the 1990/1991 growing season and 19.05 cm in 1991/1992 (Fig. 3B), whereas the average rainfall for this period (December through April) in Tucson is only 9.3 cm (Fig. 2). These two wet seasons differed in rainfall distribution. In 1990/1991 most precipitation occurred early (65% in the months of December and January), whereas in 1991/1992 it was more evenly distributed (30% in December and January). In both seasons, the ground remained saturated through late January. The last rains in January of both years (16–23 January 1991 and 20–21 January 1992) were followed by a period of drought and rising temperatures, which lasted 20 d in 1991 and 17 d in 1992.

Gypsum block readings before water treatments were implemented reveal how density and habitat affect water availability during the midseason drought. Five to six days after the last rainfall in January, medium density plots were less likely to be stressed (< -1.5 mPa) than other plots (low and high density combined; $\chi^2 =$

TABLE 2. Composition of soil samples taken from the shrub ($n = 3$) and the open ($n = 3$) habitats.

Habitat		Soil			Gravel (%)
		% sand	% silt	% clay	
Shrub	Mean	68.2	21.3	10.4	22.2
	SD	4.78	4.63	0.122	9.30
Open	Mean	77.9	12.6	9.43	29.0
	SD	7.05	5.37	1.68	3.93

10.19, $P < 0.005$; Fig. 4A, B). Habitats were not significantly different.

Experimental conditions

Manipulated densities did not differ substantially in the two growing seasons. In 1990/1991 and 1991/1992, respectively, the log densities per square metre (SD) for low density treatments were 2.14 (0.0886) and 2.09 (0.0500), for medium density were 2.99 (0.0514) and 2.98 (0.140), and for high density were 3.94 (0.169) and 3.59 (0.221).

Rainfall in wet treatments was augmented to 232% (1990/1991) and 273% (1991/1992) of average winter precipitation (Fig. 3C). The latter represents the extreme of wet years naturally encountered in this system. Dry treatments received 135 and 105% of average rainfall, respectively (Fig. 3D). During the 2nd yr the wet treatment received both more late season rainfall and more late season water augmentation. Similarly, the dry treatment in 1991/1992 received a higher proportion of its rainfall after 1 February than did the dry treatment in 1990/1991.

Relative performance of species

Differences in relative fitness.—Species responded differently to density depending upon the year ($P = 0.0097$, Table 3; Fig. 5F). *Pectocarya* had a peaked density response, obtaining its highest fitness at medium density in both years. In contrast, *Plantago*'s mean response to density in both years was relatively flat. Finally, *Schismus* had a peaked density response in 1990/1991, similar to that of *Pectocarya*, but a V-shaped response in 1991/1992, with a fitness at medium density lower than either low or high density.

As a consequence of these different species responses, the repeated-measures analysis revealed fitness hierarchies in all density \times year treatment combinations, except for 1990/1991 high density (Table 4A). We found shifts in fitness hierarchies for two species pairs: whether *Pectocarya* outperformed *Schismus*, or vice versa, and whether *Pectocarya* outperformed *Plantago*, or vice versa, depended on both the density and the year. In contrast, *Schismus* outperformed *Plantago* in some density \times year combinations, but this hierarchy did not shift to favor *Plantago* in other density \times year combinations.

Species also had different fitness responses to density

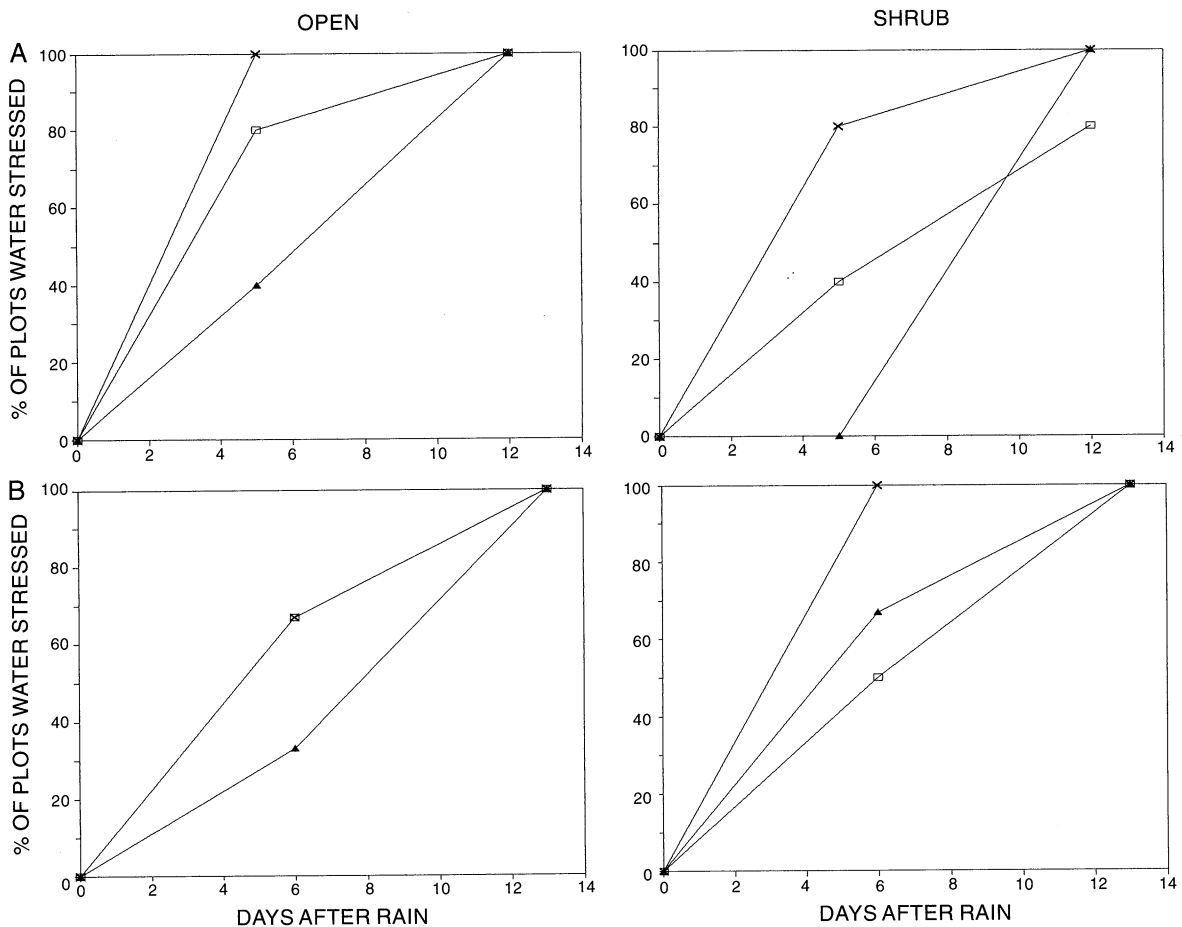


FIG. 4. Proportion of plots water stressed ($\psi < -1.5$ mPa) during a midseason drought and prior to the application of water treatments. (A) 1990/1991, $n = 5$ for each habitat-density combination; (B) 1991/1992, $n = 6$ for each, except for high density shrub where $n = 5$. \square = low density, \blacktriangle = medium density, \times = high density.

depending on water levels ($P = 0.0676$, Table 3; Fig. 5E). *Pectocarya* demonstrated the same peaked density response discussed above with a positive response to water (Fig. 5D), regardless of the density. The fitness of *Plantago*, on the other hand, did not have a similar response to water at all densities ($P = 0.0662$, Fig. 5E). Under dry conditions, it had significantly higher fitness at low than at medium density, but there were no significant differences between densities under wet conditions. The response of *Schismus* to water, like that of *Pectocarya*, was positive (Fig. 5D), and did not appear to vary much with density.

Differences in how species responded to density and water resulted in shifts in hierarchies for the same species pairs mentioned above: *Pectocarya*–*Schismus* and *Pectocarya*–*Plantago* (Table 4B). For the third species pair hierarchies did not shift: *Schismus* outperformed *Plantago* in some density \times water combinations.

Similar relative fitnesses across space.—Although our findings suggest that shrub/open habitats are important, there was no significant difference in how habitats affected species (all interactions including a species \times habitat term were not significant; Table 3). The

main effect of habitat was significant for *Plantago* ($P = 0.0294$), and all species had higher mean fitness in the open than under shrubs (Fig. 5A).

Similarly, block effects were important to each species individually ($P = 0.0181$ for *Pectocarya*, 0.0435 for *Plantago*, and 0.0215 for *Schismus*). However, in the global analysis we detected no differences in how blocks affected species (Table 3).

Differences in survival to reproduction.—As in the fitness analysis, survival varied with density in ways that depended on water levels ($P < 0.0059$), and years ($P < 0.0422$, Table 5; Fig. 6E, F). Between *Pectocarya* and *Schismus*, medium density often favored *Pectocarya* and high density often favored *Schismus*, but at low density the outcome varied each year. Between *Pectocarya* and *Plantago*, *Pectocarya* had the advantage in many density \times year and density \times water combinations, but *Plantago* had a marginal advantage in low density, dry years.

These data show that in one treatment combination or another, each species had an unexpected tendency for increasing survival with increasing density (Fig. 6C, E, F).

TABLE 3. Repeated-measures analysis comparing relative fitness (ln relative l_b) across three species (*Pectocarya*, *Plantago*, and *Schismus*). Underlined sources of variation are significant at $P < 0.10$.

Source of variation	df	MS	F	H-F* Pr > F
Species × Habitat	2	2.9888	1.06	>0.30
Error A	8	2.8112
Species × Year	2	35.7938	9.17	<u>0.0022</u>
Species × Year × Habitat	2	2.5507	0.65	<u>>0.50</u>
Error B	16	3.9045
Species	2	15.8205	9.65	<u>0.0001</u>
Species × Block	8	0.7260	0.44	<u>>0.50</u>
Species × Density	4	8.1828	4.99	<u>0.0001</u>
Species × Water	2	2.0199	1.23	<u>>0.20</u>
Species × Density × Water	4	3.6623	2.23	<u>0.0676</u>
Species × Density × Year	4	5.6688	3.46	<u>0.0097</u>
Species × Year × Water	2	0.2899	0.18	<u>>0.50</u>
Species × Habitat × Density	4	0.7444	0.45	>0.50
Species × Habitat × Water	2	3.5763	2.18	>0.10
Species × Habitat × Density × Water	4	1.1747	0.72	>0.50
Species × Year × Habitat × Density	4	0.4110	0.25	>0.50
Species × Year × Habitat × Water	2	0.2942	0.18	>0.50
Species × Year × Density × Water	4	2.4897	1.52	>0.20
Species × Year × Habitat × Density × Water	4	2.4866	1.52	>0.20
Error (residual)	160	1.6359		

* Huyhn and Feldt's (1976) Box correction.

Similar survival across space.—For all three species, survival to reproduction was higher in the open than under shrubs ($P < 0.05$ for *Pectocarya* and *Plantago*; $P < 0.06$ for *Schismus*, Fig. 6A) and the block effect was significant ($P = 0.0031$ for *Pectocarya*, 0.0141 for *Plantago*, and 0.0047 for *Schismus*). However, neither type of spatial heterogeneity contributed to significant differences in survival between species (Table 5).

Relative fecundity.—Due to low survivorship, many plots do not provide us with an estimate of reproduction (b_t). From 120 plots, potentially yielding 120 data points, no plants survived to reproduce on 27, 59, and 47 plots, respectively, for *Pectocarya*, *Plantago*, and *Schismus*. A repeated-measures analysis of variance automatically discards all data from a plot on which an estimate for one species is missing, which would leave only 44 plots for the global analysis. Estimating missing data for so many data points is risky and the P levels of the unbalanced analyses must be interpreted with extreme caution. We have chosen, therefore, to report means from the separate species analyses to illustrate how fecundity patterns (Fig. 7) interacted with survival patterns (Fig. 6) to produce fitness patterns (Fig. 5).

The fecundity means for *Plantago* and *Schismus* were higher in the open than under the shrub (Fig. 7A). *Pectocarya* had higher mean fecundity in 1990/1991 than 1991/1992, but *Schismus* and *Plantago* had higher mean fecundity in 1991/1992 than in 1990/1991 (Fig. 7B).

The patterns associated with density (Fig. 7C, E) and water (Fig. 7D, E) are consistent with resource competition. However, there was no advantage of low den-

sity relative to medium density in 1991/1992 for *Pectocarya* and *Plantago* (Fig. 7F).

DISCUSSION

This paper demonstrates that, for three species (*Pectocarya recurvata*, *Plantago patagonica*, *Schismus barbatus*), seed production of a germinated individual is affected by environmental conditions that vary between years: total seedling density, water levels, and the year of the experiment. In some species-year combinations and in some species-water combinations, density affects survival positively (Fig. 6E, F) and fecundity negatively (Fig. 7E, F). This results in fitness responses to density that are variable depending upon species, year, and water (Fig. 5E, F). Favorable conditions for one species are often not favorable conditions for another (Tables 3 and 5). Because we have computed relative fitness in population growth terms, we have strong evidence that these differences between species create fitness hierarchies with shifting dominance through time for two species pairs: *Pectocarya*–*Schismus* and *Pectocarya*–*Plantago* (Tables 4 and 6).

Meaning of shifts in fitness hierarchies through time

Models in which a temporally variable environment affects reproduction, and species coexistence, have been discussed in terms of annual plants with persistent seed banks (Ellner 1984, 1987, Shmida and Ellner 1984, Chesson and Huntly 1989, Chesson, *in press*). These models take the form:

$$X_{(t+1)} = X_{(t)}\{(1 - G)S + G[Y/(1 + C)]\}, \quad (1)$$

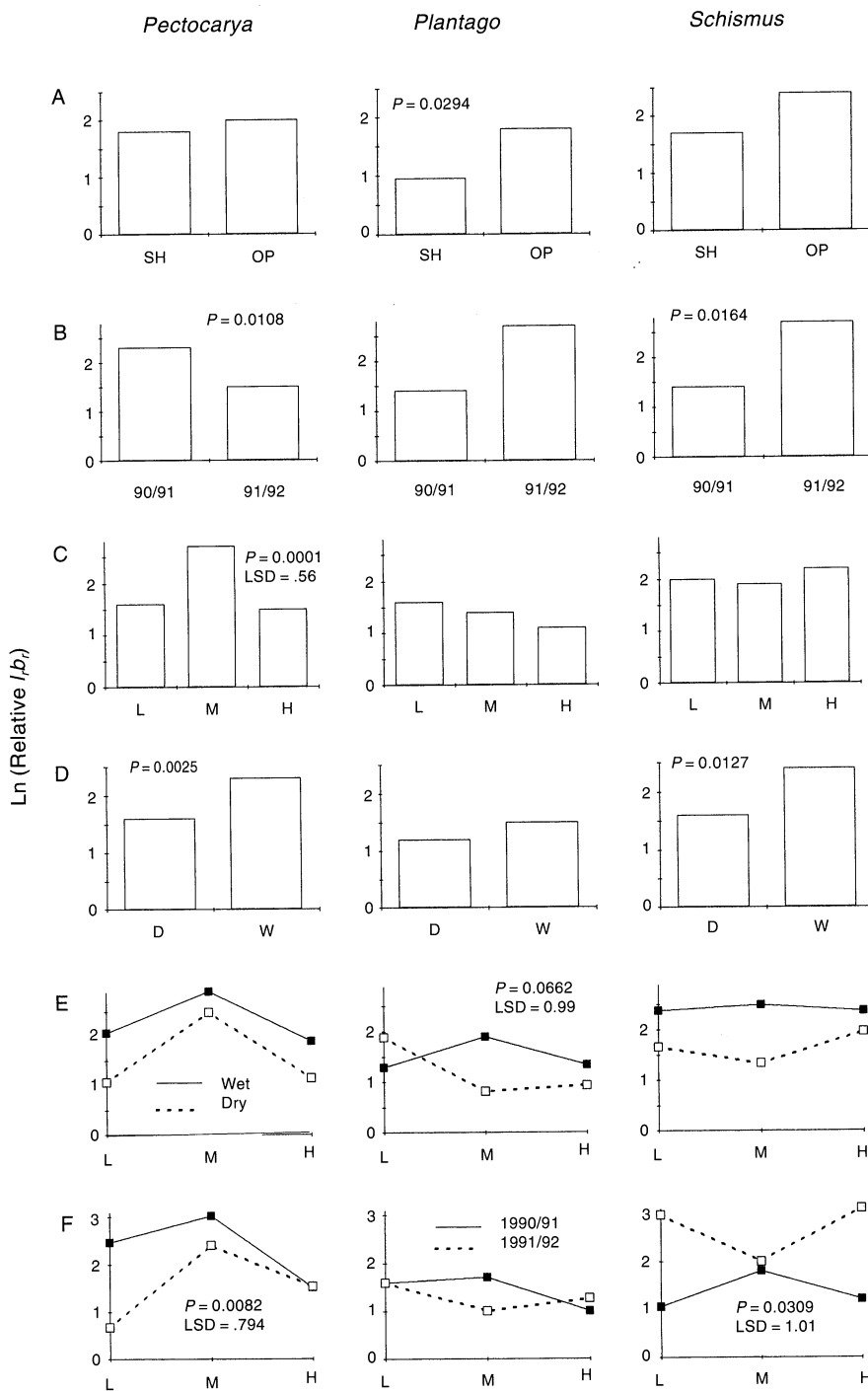


FIG. 5. Mean relative fitness (\ln Relative $l.b.$) by factors (rows) and species (columns). Rows: (A) Habitat. (SH = shrub, OP = open.) (B) Year. (C) Density. (L = low, M = medium, H = high.) (D) Water. (D = dry, W = wet.) (E) Density \times Water. (F) Density \times Year. See Table 3 for P levels from global analysis comparing species. LSD for comparing species within the same treatment combination in (E) and (F) = 0.794; resulting fitness hierarchies in Table 4. (P levels and LSD's inside each graph are from the separate species' analyses of variance. They are given if $P < 0.10$.)

where X is a vector of species densities (of seeds just prior to germination), G is germination fraction, S is survival of dormant seeds, Y is seed yield of a germinated individual in the absence of competition,

and C represents competition. In a two-species system with equivalent competitors (e.g., Pantastico-Caldas and Venable 1993), C may be represented as:

TABLE 4. Fitness hierarchies supported by the repeated-measures analysis (Table 3), followed by robustness indices (in parentheses) from additional analyses using cr 's for seed values (Table 1). An index of 8 means all additional analyses support the hierarchy. $R = Pectocarya$, $P = Plantago$, $S = Schismus$.

A) Species × Density × Year			
Year	Density		
	Low	Medium	High
1990/1991	$R > S$ (8) $R > P$ (6)	$R > S$ (6) $R > P$ (7)	...
1991/1992	$S > R$ (8) $S > P$ (7) $P > R$ (6)	$R > P$ (7) $S > P$ (5) ...	$S > P$ (8) $S > R$ (7) ...

B) Species × Density × Water			
Water	Density		
	Low	Medium	High
Dry	$P > R$ (4) ...	$R > P$ (8) $R > S$ (7)	$S > P$ (5) $S > R$ (2)
Wet	$R > P$ (5) $S > P$ (5)	$R > P$ (6) ...	$S > P$ (2) ...

$$C = G_1X_{1(t)} + G_2X_{2(t)}, \quad (2)$$

describing a negative hyperbolic relationship between seed yield and density. Certain model parameters (e.g., G_i and Y_i) may be varied with environmental conditions in year t .

In a temporally variable environment, since an equilibrium is not reached, assessing the possibility of coexistence requires that we assess whether species tend to increase when rare, rather than determine abundances at an equilibrium point. A standard invasibility

analysis involves determining if an invading species can increase in the presence of a resident species. A species will have a tendency to invade if its long-term average log growth rate ($E[\ln X_{t+1}/X_t]$) when at low density is positive (Chesson 1988, 1989).

Published theoretical works modelling annual plants report coexistence mediated by temporal variation in the germination parameter, not in seed set (Ellner 1984, Shmida and Ellner 1984, Chesson and Huntly 1988, 1989). Since this study provides empirical support for species-specific temporal variation in Y (the maximum seed production per individual), we used exploratory simulations to investigate when the invasibility criterion is met, given variation in Y and/or G , and two species with high seed survivorship (e.g., $S = 0.90$) and with identical probability distributions for environmentally dependent parameters.

Temporal variation in Y_t with <100% correlation between species, and invariant low G (e.g., 0.10) did not permit coexistence, although species tended to coexist for a long time (e.g., 5000 yr). Therefore, temporal variation in Y may slow the random walk to extinction, which would allow other coexistence promoting factors not captured in Eq. 1 to operate (e.g., spatial heterogeneity; Tilman 1982, Shmida and Ellner 1984). In contrast, when germination fraction, G_t , was temporally variable and Y was constant, the invasibility criterion was satisfied. When both G_t and Y_t varied independently, we found no suggestion that temporal variation in reproductive success enhanced the coexistence-promoting potential of variation in germination fraction alone. These results are in accordance with the work cited above.

TABLE 5. Repeated-measures analysis comparing the survival of three species (*Pectocarya*, *Plantago*, and *Schismus*). Underlined sources of variation are significant at $P < 0.10$.

Source	df	MS	F	H-F* Pr > F
Species × Habitat	2	0.2006	1.58	>0.20
Error A	8	0.1272
Species × Year	2	0.4748	2.76	<u>0.0932</u>
Species × Year × Habitat	2	0.0526	0.31	>0.50
Error B	16	0.1719
Species	2	0.7329	6.78	<u>0.0015</u>
Species × Block	8	0.0221	0.20	>0.50
Species × Density	4	0.3767	3.49	<u>0.0093</u>
Species × Water	2	0.0015	0.01	>0.50
Species × Density × Water	4	0.4069	3.77	<u>0.0059</u>
Species × Density × Year	4	0.2741	2.54	<u>0.0422</u>
Species × Year × Water	2	0.0034	0.03	>0.50
Species × Habitat × Density	4	0.0235	0.22	>0.50
Species × Habitat × Water	2	0.2426	2.24	>0.10
Species × Habitat × Density × Water	4	0.1564	1.45	>0.20
Species × Year × Habitat × Density	4	0.0116	0.11	>0.50
Species × Year × Habitat × Water	2	0.0805	0.74	>0.40
Species × Year × Density × Water	4	0.0895	0.83	>0.50
Species × Year × Habitat × Density × Water	4	0.1891	1.75	>0.10
Error (residual)	160	0.1081		

* Huyhn and Feldt's (1976) Box correction.

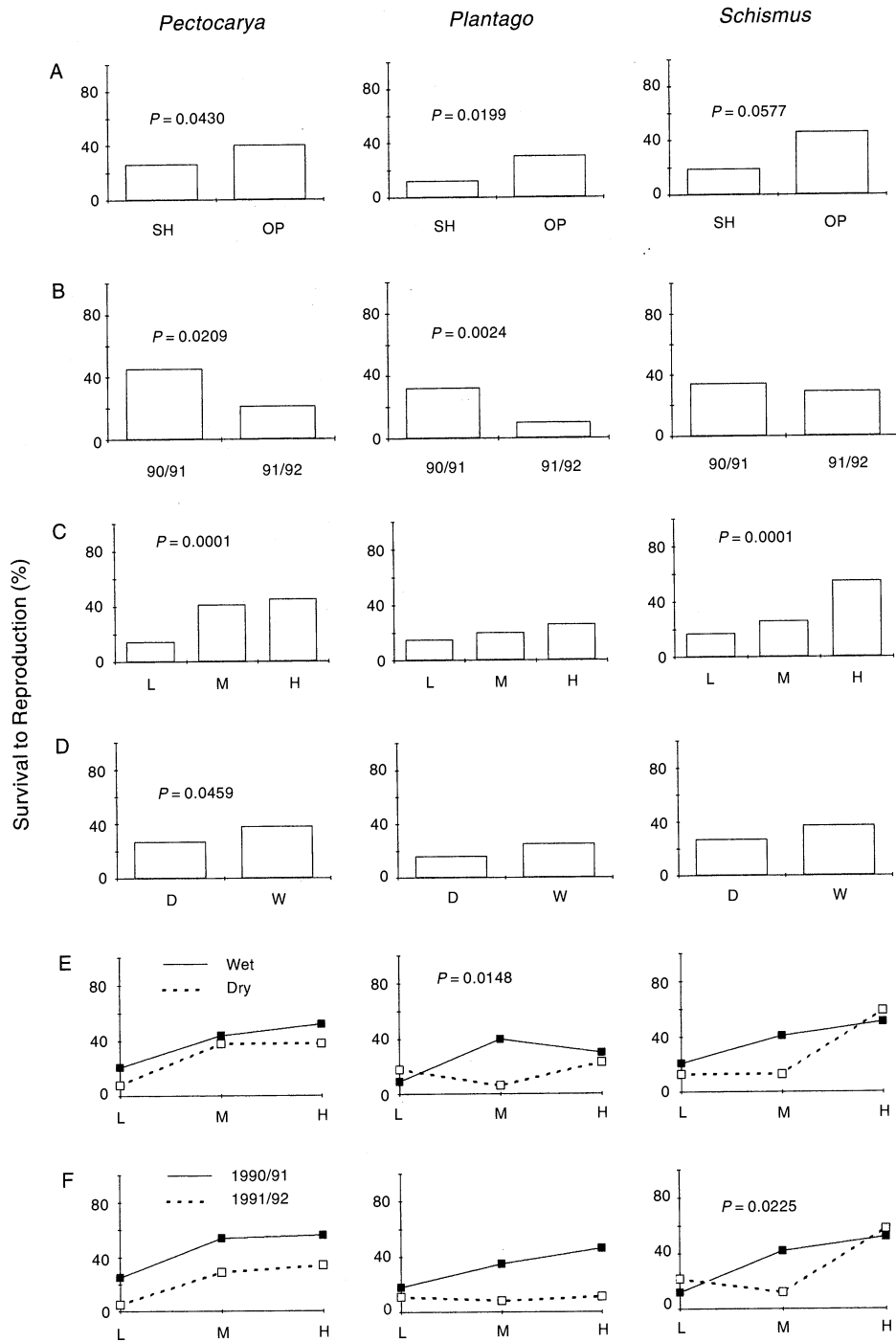


FIG. 6. Mean survival to reproduction (l_r , percent) by factors (rows) and species (columns). Rows: (A) Habitat. (SH = shrub, OP = open.) (B) Year. (C) Density. (L = low, M = medium, H = high.) (D) Water. (D = dry, W = wet.) (E) Density × Water. (F) Density × Year. Means are back transformed from angular transformation. See Table 5 for P levels from global analysis comparing species. Untransformed LSD for comparing species within the same treatment combination in (E) and (F) = 0.204; resulting survival hierarchies in Table 6. (P levels inside each graph, given if $P < 0.10$, are from separate species' analysis of variance; untransformed LSD's in (C) for *Pectocarya* = 0.148 and for *Schismus* = 0.182; in (E) for *Plantago* = 0.281; in (F) for *Schismus* = 0.257.)

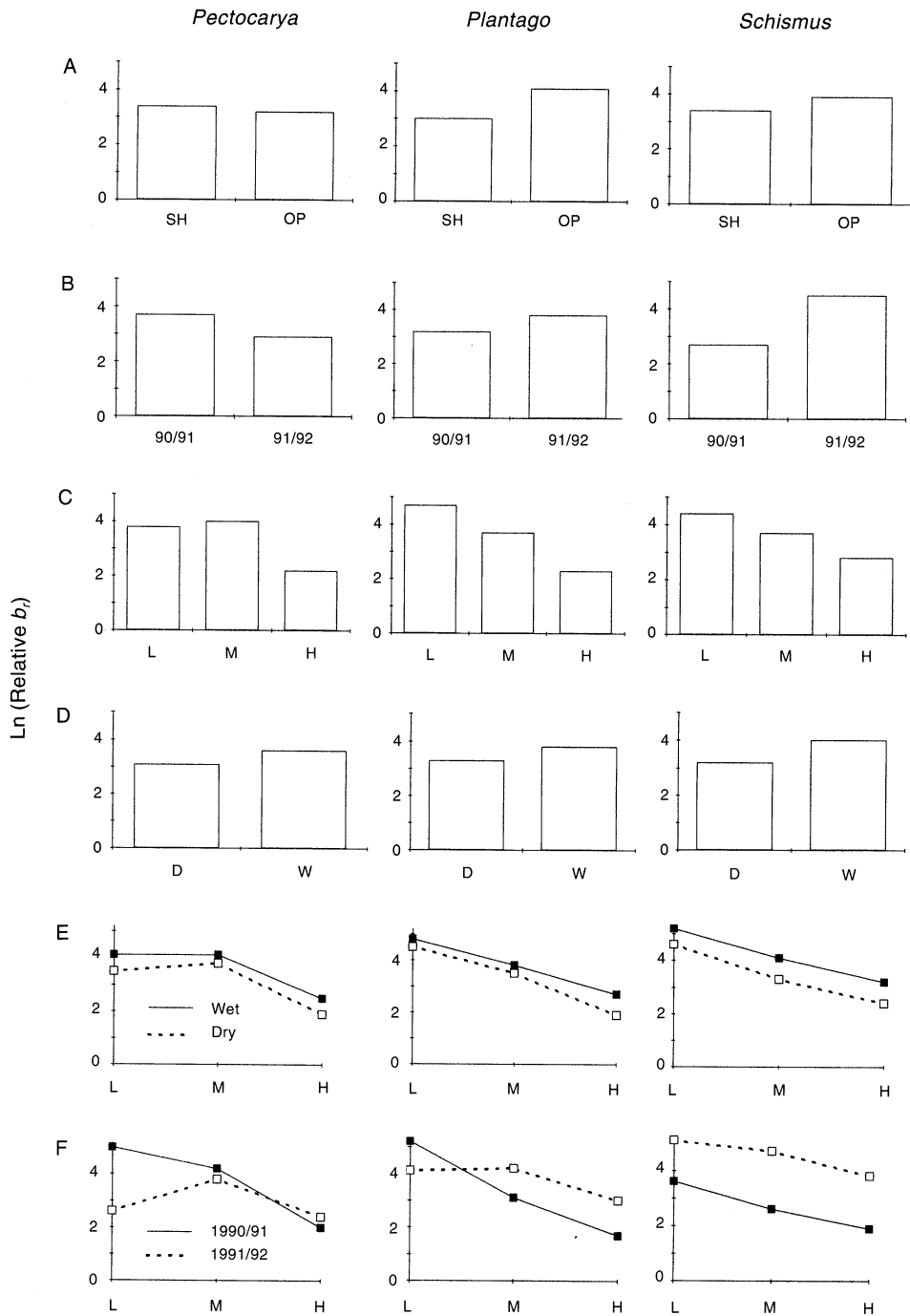


FIG. 7. Mean fecundity of surviving adults (\ln Relative b_i) by factors (rows) and species (columns). Rows: (A) Habitat. (SH = shrub, OP = open.) (B) Year. (C) Density. (L = low, M = medium, H = high.) (D) Water. (D = dry, W = wet.) (E) Density \times Water. (F) Density \times Year.

Next we looked at the effects of predictive germination (Cohen 1967, Venable and Lawlor 1980), i.e., when variation in germination is positively correlated with variation in reproductive success. Given this situation, variation in Y , augmented the tendency for variation in G , alone to promote coexistence (i.e., the long-term average log population growth of a species at low

density was higher). If the environmental conditions that cause germination either enhance the probability of survival or are correlated with other environmental conditions later in the year that enhance fitness, the existence of a positive association between germination fraction and reproductive success is plausible (Venable 1989, Venable et al. 1993).

TABLE 6. Survival hierarchies supported by the repeated-measures analysis (Table 5). $P < 0.05$, unless "+," which designates $P < 0.10$. $R = Pectocarya$, $P = Plantago$, $S = Schismus$.

A) Species \times Density \times Year			
Water	Density		
	Low	Medium	High
1990/1991	$R > S (+)$	$R > P (+)$...
1991/1992	$S > R$	$R > P$	$S > R$
	...	$R > S$	$S > P$
	$R > P$

B) Species \times Density \times Water			
Water	Density		
	Low	Medium	High
Dry	$P > R (+)$	$R > P$	$S > P$
	...	$R > S$	$S > R$
Wet	$S > P$
	$R > P$

To understand these findings, consider the biology built into the model with variable germination fractions but no predictive germination. In particular years, an abundant species germinates a high fraction of seeds, resulting in high seedling densities. Thus in years in which it emerges, the population growth of an abundant species is limited by competition (positive covariance between environment and competition; sensu Chesson and Huntly 1988, 1989). However, such a positive covariance does not occur for a rare species, since years favorable for germination are not 100% correlated among species (i.e., a year in which a low density species emerges could occasionally be a low density year). Overlapping generations in the form of a persistent seed bank prevent species from ever having really low growth rates because seeds are resistant to the effects of competition and drought.

In the model with predictive germination, germination is linked to opportunities for high growth rates, which should tend to bolster the growth rate of a species at low density. On the other hand, a species at high density is still limited by the covariance between environmental and competitive factors mentioned above, preventing a common species from ever attaining really high growth rates.

Thus, simulations suggest that temporal variation in germination fractions is essential for temporal-variability-mediated coexistence. Furthermore, assessing the importance of field-demonstrated variation in reproductive success to coexistence requires considering the possibility of a positive correlation between germination fractions and reproductive success.

A related study of 15 species at this site suggests that seed bank dynamics in this system satisfy both of these conditions (C. E. Pake and D. L. Venable, unpublished manuscript). Germination fractions were determined by estimating the densities of emergent seedlings and of postgermination dormant seeds in the soil

in each of three successive field seasons. Species-specific variation in germination fractions was found, including variable germination fractions between years for *Pectocarya* (0.31, 1.0, 1.0), *Plantago* (0.31, 0.41, 0.87), and *Schismus* (0.14, 0.06, 0.20), and germination was significantly higher in years of higher reproductive success (ANCOVA: species, $F_{7,34} = 6.22$, $P = 0.0001$; reproductive success, $F_{1,34} = 5.93$; $P = 0.0203$).

While this study shows that temporal variation in the desert is potentially important to coexistence for two species pairs (*Pectocarya-Schismus* and *Pectocarya-Plantago*), the fitness hierarchies of which change with temporally variable conditions, we do not necessarily claim it is important for all species within the guild. More empirical data on seed survivorships, fluctuations in germination fractions, and the frequency of year types, will strengthen our ability to assess the impact of environmental variability on coexistence in this system. Other mechanisms such as spatial heterogeneity (Tilman 1982), higher trophic levels (Pacala and Crawley 1992), and slow exclusion of competitive equivalents (Hubbell and Foster 1986) may be important contributors to coexistence for some species, and potentially act in concert with temporal variation (Venable et al. 1993).

Other dynamics of a system with temporal variation in Y could also provide positive covariance of environment and competition for an abundant species, and thus favor coexistence, for example, if the years that favor reproductive success also favor greater competitive effect via plant size or vigor (Chesson and Huntly 1988). However, we expect this mechanism to be of lesser importance than seed bank dynamics in this system, because of the finding of equivalent competitive effects of species (Pantastico-Caldas and Venable 1993).

Data demonstrating that temporal variability, albeit on a different scale, is important to species coexistence is not new. For example, in the Sonoran Desert where annual rainfall is bimodal, guilds of winter annuals and summer annuals germinate in entirely separate seasons (Went 1949, Juhren et al. 1956). Differences in the within-season timing of flowering, and other aspects of phenological spread (Grubb 1977), represent another important way in which species divide up their temporal environment. We know of no other field study, however, which uses relative fitness measures to demonstrate the potential importance of between-year, rather than within-year, variation in environmental conditions.

Fitness hierarchies do not shift across space

In this experiment all species had significantly higher survival in the open than under shrubs. Furthermore, in the fitness analyses, when habitat effects were significant, fitness was higher in the open. Since shrub/open habitats did not contribute to fitness hierarchies,

we have no evidence that habitat partitioning is contributing to species coexistence in a classical sense. As with habitats, block effects were important for each species individually, but did not contribute to fitness hierarchies. Of course, it is possible that our inability to detect species responding differently to spatial variation is because we only measured some aspects of temporal variation, and that other patterns occur in other years.

Spatial variation that does not result in habitat partitioning may, nevertheless, be important to coexistence in a temporally variable environment if it subdivides populations into groups affected differently by competition and temporal variation (Chesson 1990). Whether some places are less sensitive to yearly environmental variation than elsewhere and also less sensitive to competition remains to be explored.

Finding habitat effects for single species, or that the effect of habitat varies with density, is common in the desert annual literature investigating slope/wash spatial heterogeneity (Kadmon and Shmida 1990a, b, Kadmon 1993, M. C. Pantastico-Caldas and D. L. Venable, *unpublished manuscript*). In addition, several studies have suggested that Sonoran and Mojave desert annuals have a positive association with shrubs relative to the open (Went 1942, Muller 1953, Muller and Muller 1956, Halvorson and Patten 1975). Clearly our data do not support the latter hypothesis, but these earlier studies were of different species or determined productivity without respect to species identities.

Density effects and competition

In addition to temporal variation in environmentally dependent parameters (G_i and Y_i), Eq. 1 assumes that population growth is determined by competitive interactions. Our data are not always consistent with the latter assumption. For *Pectocarya* in 1991/1992, low density was significantly less favorable to fitness than medium density, and for *Schismus* in 1991/1992, medium density was significantly less favorable than high density (Fig. 5F). Whether the system can tolerate the occurrence of these unusual density responses and maintain coexistence depends on the relative frequency of such year types as well as the details of seed bank dynamics. Otherwise, significant differences in single-species analyses show the reductions in fitness between lower and higher densities captured in Eq. 2: *Plantago* in dry conditions between low and medium density, *Schismus* in 1991/1992 between low and medium density, and *Pectocarya* in both years between medium and high density (Fig. 5E, F).

We do not directly measure competition in this study. Although the fitness data reveal one species increasing relative to another, this does not necessarily mean that it does so at the expense of the other species. Nonetheless, in all studies of desert annuals, including ours, there is evidence of a negative association between density and fecundity (Fig. 7C; Inouye et al. 1980,

Kadmon and Shmida 1990a, b, M. C. Pantastico-Caldas and D. L. Venable 1993, *unpublished manuscript*). At the least, this is consistent with the idea that resource competition in the reproductive phase of plant development commonly occurs at higher densities.

With respect to survival, previous workers have found two response patterns to density: (1) no effect (Klikoff 1966, Inouye et al. 1980, Kadmon and Shmida 1990a, M. C. Pantastico-Caldas and D. L. Venable 1993, *unpublished manuscript*) and (2) a negative effect (Klikoff 1966; M. C. Pantastico-Caldas and D. L. Venable, *unpublished manuscript*). We have found a third pattern: all species, in one or another treatment combination, experienced a significant positive effect of density on survival (Fig. 6C, E, F). In aggregate, these data suggest that survival response to density varies among years. Sometimes interactions during establishment are unimportant, sometimes they may be competitive, other times they may be facilitative.

Calculation of relative fitness

Our calculation of relative fitness relies on a 10-yr data set used to estimate seed value, the species-specific probability that a set seed will become a reproductive adult. A persistent seed bank in a temporally variable environment complicates our ability to make this estimate because time lags exist between seed production and establishment of adults and because deposits into the seed bank vary substantially between years. For example, seed production per square metre for the study species varied by 2–2.5 orders of magnitude between 1982/1983 and 1991/1992 (D. L. Venable and A. Caprio, *unpublished data*). In addition, seed value itself is probably a temporally variable attribute.

We argue that our estimates of seed value should accurately represent the mean value if, on average, the number of seeds entering the seed bank over this 10-yr period roughly equals the number coming out (via death or germination), and acknowledge that data over an even longer time period would be better. Furthermore, both random and biological variation is taken into account by performing additional analyses using the extremes of seed value confidence intervals. This generates a robustness index by which to gauge faith in a result. If attention is restricted to fitness hierarchies with a robustness index of 8 (i.e., supported at $P < 0.05$ no matter which seed values within the 90% CI are used), we have evidence that a temporally variable environment causes shifts in hierarchies for one species pair, *Schismus*–*Pectocarya*, for which the discussion on the meaning of shifts in hierarchies still holds.

Factors contributing to shifts in hierarchies

It is possible that herbivory differences and rainfall distribution differences between years contributed to shifts in fitness hierarchies. For example, in Table 4A, *Pectocarya* had an advantage over *Schismus* in 1990/

1991 at some densities, but *Schismus* had the advantage in 1991/1992 at some densities. For *Pectocarya* the 2nd yr was a year of both lower survival (Fig. 6B) and higher midseason herbivory (average percent of plants chewed by herbivores at midseason per plot), which increased from 2 to 13%. *Schismus*, on the other hand, had low herbivory rates (<1%) each year and similar survival both years (Fig. 6B). In addition, it had a higher seed set in the 2nd yr (Fig. 7B, F), when both the wet and the dry treatments received a higher percentage of late season rainfall/water. *Schismus*' broader window for reproduction was pronounced the 2nd yr, when it continued to produce new seed later than the other two species (C. E. Pake, *personal observation*).

The hierarchies in Tables 4 and 6 also show that *Pectocarya* is favored at medium density while *Schismus* is favored at high density. Interestingly, the onset of drought conditions, as detected by gypsum blocks placed at 5 cm depth, is slower at medium density than at other densities (low and high combined; Fig. 4). Potential physiological or anatomical species differences responsible for shifts in hierarchies with density could involve differences in rooting morphology (C. E. Pake, *personal observation*).

CONCLUSION

For a Sonoran Desert annual, years are characterized by large variation in seedling density (simulated in our experiment by manipulating densities), in rainfall amounts (simulated by wet and dry treatments), and by other factors (obtained in our experiment by following two different years), for example herbivory and rainfall distribution. Among three seed bank annuals, reproductive success varies with temporally variable conditions in ways that create shifts in fitness hierarchies for two species pairs. The demonstrated shifts are important to temporal-variance-mediated coexistence if these species also have temporally variable germination fractions, uncorrelated between species, but with a positive correlation between germination fractions and reproductive success. A related 3-yr study has found evidence for between-year seed banks with these characteristics in this guild (C. E. Pake and D. L. Venable, *unpublished manuscript*). Spatial heterogeneity created by a shrub/open habitat mosaic was not an important axis by which these three species partitioned their environment.

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LITERATURE CITED

- Bowers, J. E. 1989. A debt to the future: scientific achievements of Desert Laboratory, Tumamoc Hill, Tucson, Arizona. *Desert Plants* **10**:9-47.
- Burgess, T. L., J. E. Bowers, and R. M. Turner. 1991. Exotic plants at the Desert Laboratory, Tucson, Arizona. *Madroño* **38**:96-114.
- Chesson, P. L. 1985. Coexistence of competitors in spatially and temporally varying environments: a look at the combined effects of different sorts of variability. *Theoretical Population Biology* **28**:263-287.
- . 1986. Environmental variation and the coexistence of species. Pages 240-256 in J. Diamond and T. J. Case, editors. *Community ecology*. Harper & Row, New York, New York, USA.
- . 1988. Interactions between environment and competition: how fluctuations mediate coexistence and competitive exclusion. *Lecture Notes in Biomathematics* **77**: 51-71.
- . 1989. A general model of the role of environmental variability in communities of competing species. *Lectures on Mathematics in the Life Sciences* **20**:97-123.
- . 1990. Geometry, heterogeneity, and competition in variable environments. *Philosophical Transactions of the Royal Society of London B* **330**:165-173.
- . *In press*. Multispecies competition in variable environments. *Theoretical Population Biology*.
- Chesson, P. L., and N. Huntly. 1988. Community consequences of life-history traits in a variable environment. *Annales Zoologici Fennici* **25**:5-16.
- Chesson, P. L., and N. Huntly. 1989. Short-term instabilities and long-term community dynamics. *Trends in Ecology and Evolution* **4**:293-298.
- Chesson, P. L., and R. R. Warner. 1981. Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist* **117**:923-943.
- Cohen, D. 1967. Optimizing reproduction in a randomly varying environment when a correlation may exist between the conditions at the time a choice has to be made and the subsequent outcome. *Journal of Theoretical Biology* **16**:1-14.
- Comins, H. N., and I. R. Noble. 1985. Dispersal, variability, and transient niches: species coexistence in a uniformly variable environment. *American Naturalist* **126**:706-723.
- Day, R. W., and G. P. Quinn. 1989. Comparisons of treatments after analysis of variance in ecology. *Ecological Monographs* **59**:433-463.
- Ellner, S. 1984. Asymptotic behavior of some stochastic difference equation population models. *Journal of Mathematical Biology* **19**:169-200.
- . 1987. Alternate plant life history strategies and coexistence in randomly varying environments. *Vegetatio* **69**: 199-208.
- Frank, D. A., and R. S. Inouye. *In press*. Temporal variation in climate of terrestrial ecosystems: patterns and ecological implications. *Journal of Biogeography*.
- Freas, K. E., and P. R. Kemp. 1983. Some relationships between environmental reliability and seed dormancy in desert annual plants. *Journal of Ecology* **71**:211-217.
- Grubb, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews* **52**:107-145.
- Halvorson, W. L., and D. T. Patten. 1975. Productivity and flowering in winter ephemerals in relation to Sonoran Desert shrubs. *American Midland Naturalist* **93**:311-319.
- Hubbell, S. P., and R. B. Foster. 1986. Biology, chance, and history and the structure of tropical rain forest tree communities. Pages 314-329 in J. Diamond and T. J. Case, editors. *Community ecology*. Harper & Row, New York, New York, USA.

- Hutchinson, G. E. 1958. Concluding remarks. Cold Spring Harbor Symposium. Quantitative Biology **22**:415-427.
- . 1959. Homage to Santa Rosalia or Why are there so many kinds of animals? *American Naturalist* **43**:145-159.
- . 1961. The paradox of the plankton. *American Naturalist* **95**:137-145.
- Huyhn, H., and L. S. Feldt. 1976. Estimation of the Box correction for degrees of freedom from sample data in the randomized block and split plot designs. *Journal of Educational Statistics* **1**:69-82.
- Inouye, R. S., G. S. Byers, and J. H. Brown. 1980. Effect of predation and competition on survivorship, fecundity, and community structure of desert annuals. *Ecology* **61**:1344-1351.
- Juhren, M., F. W. Went, and E. Phillips. 1956. Ecology of desert plants. IV. Combined field and laboratory work on germination of desert annuals at Joshua Tree National Monument, California. *Ecology* **37**:318-330.
- Kadmon, R. 1993. Population-dynamic consequences of habitat heterogeneity: an experimental study. *Ecology* **74**:816-825.
- Kadmon, R., and A. Shmida. 1990a. Competition in a variable environment: an experimental study in a desert annual population. *Israel Journal of Botany* **39**:403-412.
- Kadmon, R., and A. Shmida. 1990b. Patterns and causes of spatial variation in the reproductive success of a desert annual. *Oecologia* **83**:139-144.
- Kemp, P. R. 1989. Seed banks and vegetation processes in deserts. Pages 257-282 in M. A. Leck, V. T. Parker, and R. L. Simpson, editors. *Ecology of soil seed banks*. Academic Press, New York, New York, USA.
- Klikoff, L. G. 1966. Competitive response to moisture stress of a winter annual of the Sonoran Desert. *American Midland Naturalist* **75**:383-391.
- Littell, R. C., R. J. Freund, and P. C. Spector. 1991. SAS system for linear models. Third edition. SAS Institute, Cary, North Carolina, USA.
- Milliken, G. A., and D. E. Johnson. 1984. Analysis of messy data. Volume 1. Designed experiments. Van Nostrand Reinhold, New York, New York, USA.
- Muller, C. H. 1953. The association of desert annuals with shrubs. *American Journal of Botany* **40**:53-60.
- Muller, W. H., and C. H. Muller. 1956. Association patterns involving desert plants that contain toxic products. *American Journal of Botany* **43**:354-361.
- Pacala, S. W., and M. J. Crawley. 1992. Herbivores and plant diversity. *American Naturalist* **140**:243-260.
- Pantastico-Caldas, M. C., and D. L. Venable. 1993. Competition in two species of desert annuals: neighborhood analysis along a topographic gradient. *Ecology* **74**:2192-2203.
- SAS. 1989. SAS/STAT user's guide. Version 6. Fourth edition. Volume 2. SAS Institute, Cary, North Carolina, USA.
- Shmida, A., and S. Ellner. 1984. Coexistence of plant species with similar niches. *Vegetatio* **58**:29-55.
- Silvertown, J., and R. Law. 1987. Do plants need niches? Some recent advances in plant community ecology. *Trends in Ecology and Evolution* **2**:24-25.
- Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.
- Venable, D. L. 1989. Modelling the evolutionary ecology of seed banks. Pages 67-90 in M. A. Leck, V. T. Parker, and R. L. Simpson, editors. *Ecology of soil seed banks*. Academic Press, New York, New York, USA.
- Venable, D. L., and L. Lawlor. 1980. Delayed germination and dispersal in desert annuals: escape in space and time. *Oecologia* **46**:272-282.
- Venable, D. L., C. E. Pake, and A. Caprio. 1993. Diversity and coexistence of Sonoran Desert winter annuals. *Plant Species Biology* **8**:207-216.
- Went, F. W. 1942. The dependence of certain annual plants on shrubs in Southern California Deserts. *Bulletin of the Torrey Botanical Club* **69**:100-114.
- . 1949. Ecology of desert plants. II. The effect of rain and temperature on germination and growth. *Ecology* **30**:1-13.