

Diversity and Coexistence of Sonoran Desert Winter Annuals

D. LAWRENCE VENABLE¹⁾, CATHERINE E. PAKE¹⁾ and ANTHONY C. CAPRIO²⁾

¹⁾ Department of Ecology and Evolutionary Biology, University of Arizona, Tucson 85721, U.S.A.

²⁾ Laboratory of Tree-Ring Research, University of Arizona, Tucson 85721, U.S.A.

Abstract Annual plants make up ca. 50% of local floras in the Sonoran Desert. As with most plant communities, there is no shortage of potential coexistence generating mechanisms, and several mechanisms are likely contributors to coexistence at different spatial scales in the Sonoran Desert, e.g. spatial heterogeneity and the behaviors of predators and grazers. We explore one mechanism of likely importance for desert annuals: temporal environmental variation. It is widely recognized that coexistence is promoted by temporal variation if species such as desert annuals have “temporal niches” in the sense that each has years in which it out-performs the others. It is usually suggested that some resistant life-history stage, such as a seed bank, is also necessary to buffer each species from the negative population dynamic impact of unfavorable years. Using ten years of demographic data, we document the large year-to-year variation in population dynamics of desert annuals and show that ten species respond differently to temporal variation. Competition experiments document reversals in competitive superiority. Also, all species have a between-year seed bank, such that only a proportion of the seed bank germinates in any given year. Thus this system meets our intuitive requirements for variance-based coexistence. Dynamic models of this system demonstrate that subtle aspects of the species biology determine whether coexistence criteria are actually met. Specifically, variable germination fractions are required and coexistence is most readily favored with “predictive” germination. Germination fractions in this system do vary among years in a species specific fashion. Also, for the three years of available data, germination was predictive, in that each species had greater germination fractions in year of greater demographic success. Thus all of the population dynamic elements necessary for temporal variance mediated coexistence seem to be present in this system.

Key words: coexistence, desert annuals, population dynamics, seed bank, temporal variance.

In this paper we will briefly introduce the patterns of diversity in Sonoran Desert annuals and then discuss mechanisms of their coexistence. While a variety of mechanisms are likely to be involved in species coexistence, we will focus most of our attention on the role of temporal heterogeneity in promoting coexistence of an assemblage of Sonoran Desert winter annuals growing near Tucson, Arizona.

Species Diversity of Sonoran Desert Annuals

The Sonoran Desert comprises a large fraction of the states of Sonora, Baja California Norte and Baja California Sur in Mexico and parts of Arizona and southern California in the United States (Shreve and Wiggins, 1964). There is a variety of habitat types for annual plants in the Sonoran Desert including volcanic fields, cinder cones and mountains, granitic mountain ranges,

giant sand dunes, and desert flats. We have tabulated the occurrence of annual plants across several local floras in Arizona and Sonora as well as by these broad habitat categories in northwestern Sonora (Tables 1 and 2). Roughly 50% of the species in these local floras consist of desert annuals and 60–80% of these are winter annuals with the rest being summer or non-seasonal annuals (Table 1). The Tucson Mountains on the eastern edge of the Sonoran Desert had the highest proportion of summer annuals corresponding to its highest proportion of summer rains. The very dry northwestern Sonoran flora where rainfall is very unpredictable had the highest proportion of non-seasonal annuals (Table 1). Across broad habitat categories, in the desert areas of Northwestern Sonora, coastal and wetland habitats had the lowest proportion of annual plants (24% and 39% respectively; Table 2). Volcanic fields and mountains and granitic mountains had an intermediate proportion of annuals (44–48%) with the driest, westernmost granitic range (Sierra del Rosario) having a still higher proportion of annuals (55%). Desert flats throughout the region have a fairly high proportion of annuals (57%) while the low precipitation, 4,400 km², giant dune fields of the Gran Desierto has the lowest species richness and the highest proportion of annuals

Table 1. Occurrence of annual plants in several Sonoran Desert floras along a precipitation gradient.

	Northwest Sonora ¹	Eastern Imperial County ²	White Tank Mtns ³	South Mtns ⁴	Tucson Mtns ⁵
Area (ha)	1,500,000	205,000	11,560	4,800	40,000
Elevation (m) (range)	0–1290 (1290)	30–664 (634)	416–1246 (828)	366–820 (454)	649–1429 (780)
Annual Rainfall (mm) ⁶	58.5	85.0	196.1	182.0	299.0
(Dec-Feb)	(51%)	(37%)	(33%)	(33%)	(22%)
(Jun-Aug)	(15%)	(24%)	(30%)	(30%)	(47%)
Number of species	560	322	332	274	587
% Annuals (of flora)	48%	48%	48%	54%	45%
% Winter annuals (of annuals)	63%	66%	77%	79%	62%
% Summer annuals	22%	22%	21%	19%	33%
% non-seasonal annuals	15%	12%	2%	2%	5%

¹ Felger 1992; ² McLaughlin, et al 1987; ³ Keil 1973; ⁴ Daniel and Butterwick 1992; ⁵ Rondeau 1991; ⁶ Rainfall is from nearby weather stations, as reported in Turner and Brown (1982).

(62%; Table 2).

The prominence of annuals in the Sonoran desert is no doubt due to the relatively low plant cover in deserts and the resulting permanently-open sites available for their establishment. Also, since annuals can complete their vegetative life cycle in much less than a year, annuals can exist in the desert without all the morphological and physiological adaptations necessary to survive the hottest driest times of year. Yet why the high diversity of species?

Coexistence Generating Mechanisms for Desert Annuals

There is no scarcity of coexistence mechanisms to choose from (Tilman and Pacala, in press), and in fact the great variety of potential contributing factors makes it difficult to unambiguously assign causality. In what follows we will briefly review some potentially important mechanisms for this system. Then, rather than extensively documenting all possible mechanisms, we will explore one potentially important one in some theoretical and empirical depth.

Table 2. Proportion of Northwest Sonoran flora comprised of annual plants by habitat¹.

Habitat	Area (km ²)	Total # species	# Summer annuals	# Winter annuals	# Nonseasonal annuals	Elevation (m)	% Annuals
Sonoyta region	1,500	314	44 (14.0%)	112 (35.7%)	23 (7.3%)	325–590	57.0%
Pinacate volcanic field, lower elevations	2,000	309	22 (7.1%)	99 (32.0%)	21 (6.8%)	200–650	46.0%
Upper elevation of Sierra Pinacate	100	165	6 (3.6%)	64 (38.8%)	9 (5.5%)	650–1290	47.9%
Granitic ranges	800	173	10 (5.8%)	54 (31.2%)	13 (7.5%)	200–900	44.5%
Sierra del Rosario	78	111	6 (5.4%)	38 (34.2%)	17 (15.3%)	100–710	55.0%
Dunes	4,400	85	8 (9.4%)	37 (43.5%)	8 (9.4%)	0–250	62.4%
Desert flats	5,900	271	40 (14.8%)	85 (31.4%)	28 (10.3%)	100–350	56.5%
Coastal habitats	75	29	0 (0%)	3 (10.3%)	4 (13.8%)	0–50	24.1%
Wetland habitats	150	76	11 (14.5%)	11 (14.5%)	8 (10.5%)	0–50	39.1%

¹ Felger 1992.

Spatial heterogeneity, the subject of classical plant ecology (Tilman, 1982), is an important contributor to desert annual species diversity at a variety of scales. There are differences in annual plant species composition among the broad habitat types mentioned above as well as along a variety of resource and environmental gradients including slope, aspect, soil type and texture and gradients of moisture and nutrient availabilities. On a local scale, the habitat heterogeneity provided by the shrub-open habitat mosaic can contribute to species diversity (Shmida and Whittaker, 1981; Sampson, 1986).

The competition-colonization dynamics that have been studied extensively in forests (Pickett and White, 1985) and grasslands (Platt and Weis, 1977) are likely to be relatively minor contributors to the coexistence of desert annuals. The regime of local disturbances followed by more or less predictable successional sequences are absent, though a related phenomenon of facilitation-colonization has been suggested for desert perennials (McAuliff, 1988).

Higher trophic levels in the form of species-specific behaviors of grazers and seed predators (Pacala and Crawley, 1992) are likely to be important contributors to species coexistence in desert annuals, though at present little good quantitative data are available. Neighborhood effects such as those resulting from intraspecific clumping (Silander and Pacala, 1990) may have some impact on transient dynamics of desert annual communities, but are not expected to play a major role in the long-term coexistence of species. Likewise, the slow exclusion of competitively identical species (Hubbell and Foster, 1986) may impact transient dynamics, but life cycles are likely to be too fast for this to have important long-term effects. Also, as will be shown below, species do not behave as competitive equals.

From the early works of ecologists such as Hutchinson (1961) and plant ecologists such as Grubb (1977) we have become aware that temporal environmental variation may promote species coexistence of organisms with different "temporal niches". More recently the importance of resistant life-history stages, such as perennating organs or seed banks, for temporal variance-mediated species coexistence has been recognized (e.g. Chesson and Huntley, 1988). Temporal heterogeneity is a factor likely to be of considerable importance in promoting coexistence in desert annuals since deserts are the biome with the greatest coefficient of variation among years in rainfall (Frank and Inouye, in press) and desert annual populations are known to fluctuate widely across years. In the remainder of this paper we will explore the population-dynamic elements underlying temporal variation as a coexistence-promoting mechanism for a guild of desert winter annuals.

Here we document the large year-to-year variation in the population dynamics of Sonoran desert winter an-

nuals and show that species respond differently to temporal variation. We also document the production of a between-year seed bank. We then explore a model of coexistence of seed-bank annuals in a temporally-varying environment which incorporates elements of the biology of this assemblage of desert winter annuals. The model suggests that some population-dynamic subtleties in addition to temporal niches and resistant life-history stages are required to generate coexistence in this system. We then document these aspects for our assemblage of annuals and evaluate the likely role of temporal-variance-mediated coexistence.

Temporal Variance and Species-Specific Responses

The data we present has been collected from an undisturbed creosote bush flat at the University of Arizona Desert Laboratory dominated by *Larrea divericata* and *Ambrosia deltoidea* that has been protected from livestock grazing for the last 90 years. Permanent quadrats were established at this site in the fall of 1982 and have been monitored every year since to measure demographic parameters of emerging winter annual seedlings. In each year we documented the density of plants emerging, survival to adulthood and average fecundity of adults by mapping individual plants beginning with each germination-inducing autumn rainfall. The species under consideration are *Plantago patagonica* and *Plantago insularis* (Plantaginaceae), *Shismus barbatus* (Poaceae) introduced from the arid Middle East, *Erodium texanum* (native) and *Erodium cicutarium* (introduced from the Mediterranean; both Geraniaceae), *Evax multicaulis*, *Stylocline micropoides*, *Monoptilon bellioides*, *Eriophyllum lanosum* (Asteraceae), and *Pectocarya recurvata* (Boraginaceae).

The total number of seedlings of all species emerging (m^{-2}) has varied by two orders of magnitude over the ten years investigated (Fig. 1). The winter droughts of 1987/88–1989/90 resulted in a winter annual population crash in 1989/90 from which populations had not fully recovered by 1991/92.

While the late 1980's population crash affected all species, annual plants tended to be individualistic in their patterns of population growth in other years. For example, while *Pectocarya recurvata* generally increased from 1982 until 1987/88, *Evax multicaulis* decreased and *Eriophyllum lanosum* remained fairly constant (Fig. 2). This individualistic responses to environmental variation can also be seen by plotting species abundance curves for emerging seedlings for different years, using the species abundance rankings from the first year, 1982/83 (Fig. 3). As the species respond differently, the initial abundance hierarchy breaks down, so that by 1988/89 the rankings are quite different.

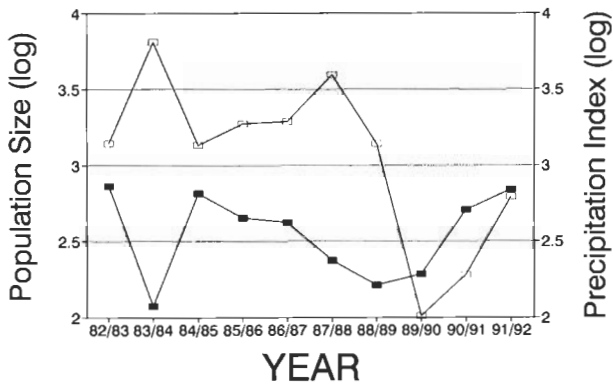


Fig. 1. Total population size (number of seedlings m^{-2} ; open squares) of all species on permanent plots tends to increase in response to the previous year's winter precipitation (indexed as total November through February precipitation in mm; filled squares).

The shifts in population sizes are driven in part by shifts in the reproductive success or realized fecundity (the probability of survival from germination to maturity times the mean fecundity of survivors) of plants in different years. There tends to be an increase in the number of seedlings emerging the year following a high per capita realized fecundity and a decline following low realized fecundity (Fig. 4). This pattern is strongly influenced by the pattern of rainfall and temperatures experienced from the time of emergence to seed set (Fig. 5). Yet the response of realized fecundity to environmental conditions in different years can be quite individualistic to the point that different species may have their best and worst performances in different

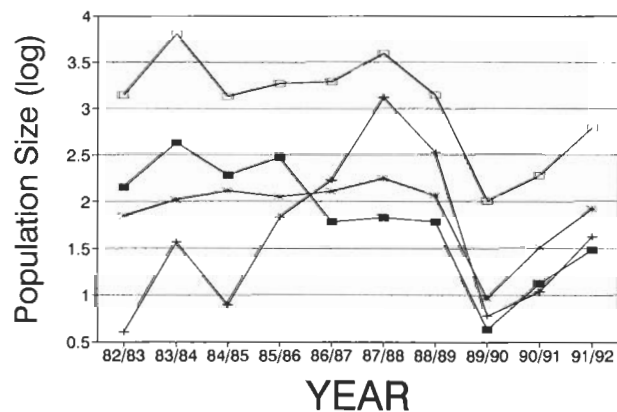


Fig. 2. Population size (number of seedlings m^{-2}) of *Pectocarya recurvata* (pluses) increased, *Evax multicaulis* (filled squares) declined, and *Eriophyllum lanosum* (asterisks) remained constant through the early 1980's, though all crashed at the end of the decade. The total population size of all species is given at the top (open squares).

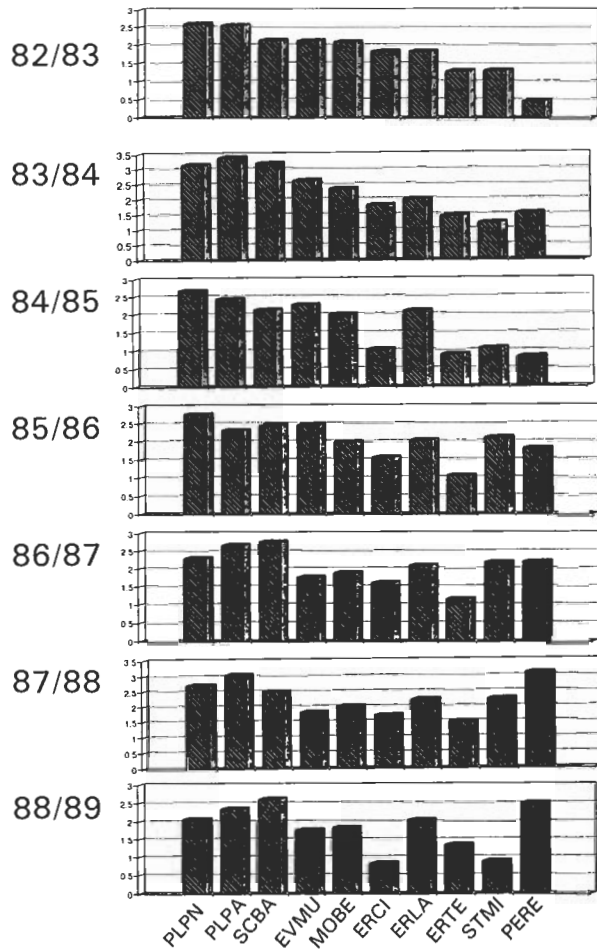


Fig. 3. The changes in relative abundance of ten species of winter annuals through time as seen from species abundance histograms for emerging seedlings. The species are ordered by their abundance rankings in the first year, 1982/83 and labelled by the first two letters of their generic and species names (see text for full names).

years (Fig. 6). Some insight into this tendency for individualistic response can be obtained by looking at the correlations among species as to how different years rank with regard to the magnitude of realized fecundity (Table 3). While some species have fairly high rank correlations with one another, many others clearly do not.

It is also possible for two species to rank years similarly with regard to realized fecundity, and yet have very different magnitudes of response. For example, one species might have high variance among years while another has a low variance. Thus while species may rank years in the same order, their relative reproductive successes may actually reverse over time. This seems to be an important phenomenon in our assemblage of annuals and an organizing life-history trait is seed size. Large-seeded plants are expected to buffer population

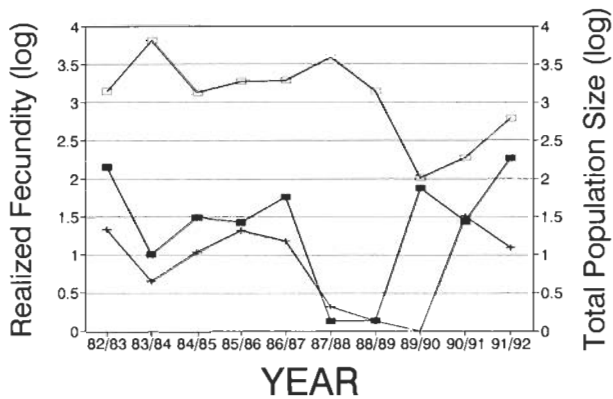


Fig. 4. Total population size (open squares) tends to rise or fall the year after changes in realized fecundity of the species in the assemblage. Realized fecundity (survival from seedling to adult times mean adult fecundity) is shown for two prominent species, *Schismus barbatus* (filled squares), and *Plantago patagonica* (pluses).

dynamics because the greater parental nutrient supply should help seedlings establish under harsh or unfavorable conditions. Yet since each seed is expensive to produce, fewer (compared to small-seeded species) are made in favorable conditions when seed size may be less important (Baker, 1972; Venable and Brown, 1988). In our assemblage, larger-seeded species have experienced less variation among years in realized fecundity than small-seeded species (Fig. 7). Thus some of the species with high rank correlations in Table 3, such as *Shismus*, *Eriophyllum* and *Plantago insularis* have different seed sizes and different year-to-year variation in demographic success (Fig. 7). For example, *Shismus* and *Plantago insularis* have a high rank correlation, but *Shismus* is a small-seeded, high-variance spe-

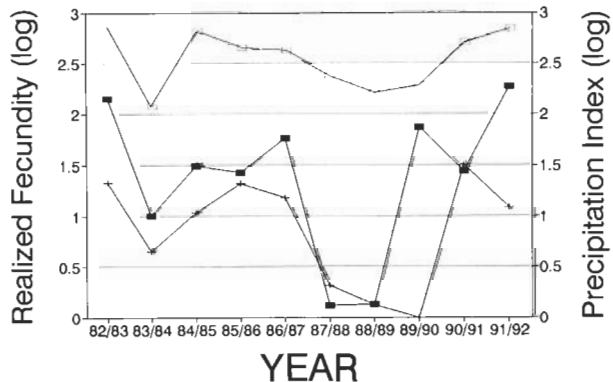


Fig. 5. Realized fecundity for two prominent species, *Schismus barbatus* (filled squares), and *Plantago patagonica* (pluses) tends to rise and fall with winter precipitation (indexed here as total precipitation from November through February; open squares).

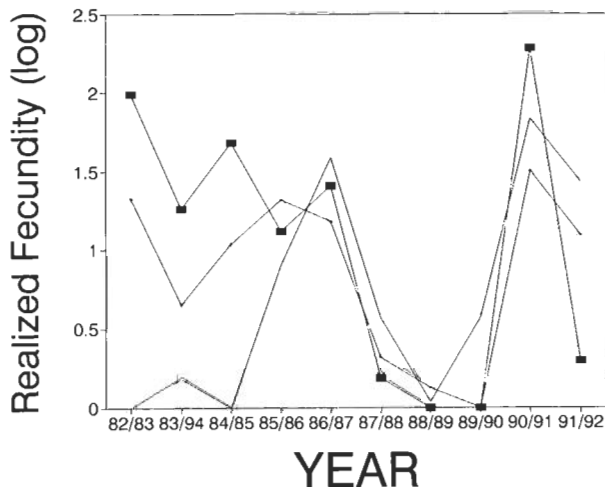


Fig. 6. Realized fecundity of three species (*Evax multicaulis*, filled squares; *Pectocarya recurvata*, open squares; and *Plantago patagonica*, asterisks) on permanent plots show individualistic responses to temporal variation.

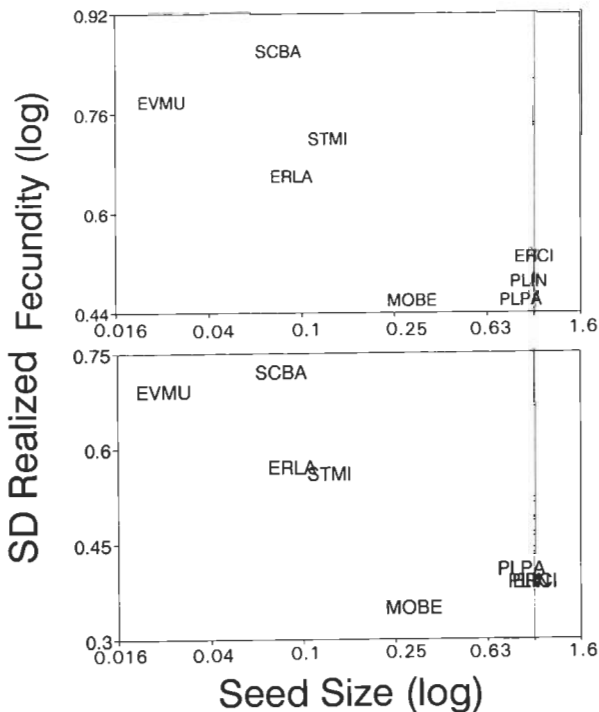
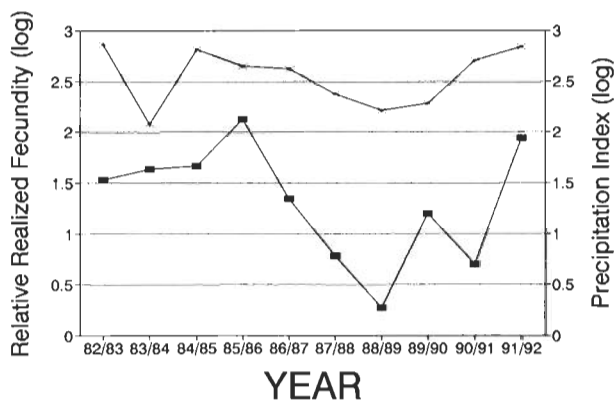


Fig. 7. Standard deviation of the logarithm of realized fecundity plotted against the logarithm of seed mass (mg) for early emerging cohorts (October–November; top graph) and late emerging cohorts (December–January; bottom graph). Standard deviations of logarithms are already corrected for differences in means (since they are based on proportional deviations from means).

Table 3. Spearman rank correlation of realized fecundity among species over ten years (1982/93 through 1991/92).

PERE	-0.45									
ERCI	0.26	0.36								
EVMU	0.53	0.09	0.35							
PLPA	0.40	0.37	0.38	0.84*						
ERLA	-0.08	0.43	0.41	0.45	0.58					
ERTE	-0.02	0.18	0.32	0.42	0.37	0.84*				
MOBE	-0.34	0.41	0.48	0.09	-0.01	0.66*	0.67*			
SCBA	0.10	0.06	0.44	0.26	0.32	0.83*	0.79*	0.67*		
PLIN	-0.08	0.30	0.70*	0.49	0.48	0.82*	0.70*	0.67*	0.73*	
	STMI	PERE	ERCI	EVMU	PLPA	ERLA	ERTE	MOBE	SCBA	PLIN

*, $P < 0.05$.**Fig. 8.** Relative realized fecundity of *Schismus barbatus* and *Plantago insularis* (filled squares) calculated as $\log(\text{realized fecundity of SCBA}/\text{realized fecundity of PLIN})$ tends to fluctuate with winter precipitation (indexed by total precipitation from November through February; asterisks).

cies while *Plantago insularis* is a large-seeded, low-variance species. Their realized fecundities shift back and forth depending on year favorability, with *Schismus* tending to do better relative to *Plantago* in favorable wet years and *Plantago* tending to do better in dry years (Fig. 8).

In addition to this long-term observational data, we also have experimental data documenting the species-specific responses to temporal variation in a natural population. For two years we systematically varied density (by manipulating the seed bank density and thinning) and water availability (by supplementing and sheltering from water) and monitored realized fecundity of three common species. There were a number of significant shifts in competitive superiority. For example, in 1991 at low density, *Pectocarya* out-performed both *Schismus* and *Plantago patagonica*, yet in 1992 at low density, *Plantago* and *Schismus* out-performed *Pectocarya* (Table 4). *Plantago* out-performed *Pectocarya* under low density dry conditions, but both *Pectocarya*

Table 4. Statistically significant differences in competitive performance in two years, three densities and two levels of water availability (reported differences were significant at $P < 0.05$ using a LSD in association with a Repeated-Measures ANOVA)¹.

	Low density		Medium density		High density	
1991	PERE	> SCBA	PERE	> SCBA		
	PERE	> PLPA	PERE	> PLPA		
1992	SCBA	> PERE	PERE	> PLPA	SCBA	> PLPA
	SCBA	> PLPA			SCBA	> PERE
	PLPA	> PERE				
DRY	PLPA	> PERE	PERE	> PLPA	SCBA	> PLPA
			PERE	> SCBA	SCBA	> PERE
WET	PERE	> PLPA	PERE	> PLPA	SCBA	> PLPA
	SCBA	> PLPA				

¹ Adapted from Pake 1993.

This model is generally similar in structure to ones used by Watkinson (1980), Pacala and Silander (1985), and Chesson and Huntley (1989) to model annual plants.

We used an invasibility criterion to judge coexistence (following Chesson and Ellner, 1989). The invasibility criterion is met when the long-term-average log growth rate, evaluated at low population size, is positive for each species, i.e. each species tends to increase when rare and thus to remain in the system (Fig. 9).

Simulations using this model indicate that, while seed banks tend to delay competitive exclusion under a wide variety of conditions, seed banks and temporal niches *per se* are not enough to generate invasibility. Rather, additional subtleties of the population dynamics are required. For example, adding variable germination fractions, not completely correlated among species, will generate invasibility. However, in this latter scenario, the magnitude of variation in realized fecundity and its correlation among species (our temporal niches) tend to have little or counterintuitive effects on coexistence. Invasibility is even more favored with predictive germination, where predictive germination is defined as variable germination with greater fractions in years of higher realized fecundity. In this scenario coexistence is strongly favored and variation in realized fecundity augments the tendency of species to increase when rare, as does differential response to environmental variation (temporal niches).

Other subtleties of the dynamics could favor invasibility as well. For example, if each species had size-specific competitive effects, such that each exerted a weaker competitive effect on itself and other species in years of low realized fecundity, the invasibility criterion would be met. However, our experimental finding of equivalent competitive effects of species despite variation in realized fecundity does not support the idea that this last mechanism operates in our system (Pantastico-Caldas and Venable, 1993).

The intuition behind these theoretical results can be grasped in the following explanation of invasibility. When a species is abundant it will always experience competition in favorable years, just due to its own abundance. Thus abundant species never achieve very high population growth rates. However, when rare, a species may occasionally experience favorable conditions in the absence of competition and have high growth rates. When rare, a species will not generate much competitive effect. Thus, if common species do not emerge or otherwise do not exert much competitive effect, a rare species may have a good year in the absence of competition. The seed bank buffers a rare species from ever having a really bad year, and this, combined with the occasional high growth rates, may result in a positive average low-density growth rate. If this scenario holds for all species, each will be able to recover from low density and they will coexist. The variable germination fraction is critical to the ability of a rare species to

have a good year in the absence of competition, since the latter only happens when rare species germinate but common species do not. With predictive germination, a rare species that germinates in the absence of competition is even more likely to have a good year, since germination is correlated with year favorability. This explanation is, of course, a simple qualitative caricature of the quantitative forces generating invasibility in the model.

Variation in Germination Fractions

Our modelling exercise suggests that to truly understand temporal-variance-based coexistence in our system, we need to know more about germination in the field in different years. For the three years of data mentioned above (Table 5) we find significant differences among years in the germination fraction and a significant interaction between species and year, indicating species-specific variation in germination fraction (Pake, 1993). Thus the basic germination requirement for variance-mediated coexistence is met. Furthermore, germination fractions are significantly higher in years of higher realized fecundity (ANOVA: Species $F_{7,34}=6.22$, $P<0.0001$; Realized Fecundity $F_{1,34}=5.93$, $P<0.02$). This result suggests predictive germination, though it is based on just three years of data. While a longer data base is needed to unequivocally show predictive germination, collecting such data will be a slow and labor-intensive endeavor. Nonetheless, our results are suggestive of the kind of germination behavior that most strongly favors species coexistence, and that makes coexistence sensitive to the kinds of temporal niche variation documented in this paper.

Predictive dormancy is not unexpected in this system since several different factors could give rise to it. First, adaptive considerations suggest that predictive germination should evolve when appropriate genetic variation exists and germination cues are available which correlate with conditions yielding success (Cohen, 1967; Venable and Lawlor, 1980). Secondly, there are several ways predictive germination could occur coincidentally, without any adaptive evolution. The germination fraction of many desert annuals varies with rainfall and temperature. These same environmental cues may also determine important components of fitness, such as seedling establishment or growth rate (i.e. the same kinds of rainfall and temperature regimes that result in high germination may result in high establishment and early growth). Alternatively, the weather conditions favoring germination may be different from but correlated with those that favor high reproduction. At our study site weather data over the last 115 years indicate a significant correlation between December rainfall (a good correlate of germination fraction) and

February rainfall (a good predictor of realized fecundity; $P < 0.04$).

Conclusions

- 1) Populations of desert winter annuals experience much year to year variation in resource availability resulting in large population fluctuations.
- 2) Species respond differently to temporal environmental variation. In some cases species differ as to which years yield higher realized fecundity, while in other cases species differ in the variance of realized fecundity due to factors such as seed size.
- 3) Desert annuals produce between-year seed banks which can buffer population decline in unfavorable years.
- 4) While temporal-variance-based coexistence might be expected due to the kinds of temporal niche differences shown here and the buffering effects of delayed germination, a model of variance-based coexistence indicates that additional subtle population dynamic elements are required.
- 5) Variable germination fractions, not completely correlated among species, will generate invasibility. When variable germination fractions are correlated with realized fecundity, the invasibility criterion is quite easily met and the species-specific reproductive responses documented for our system favor coexistence as well.
- 6) In our system, germination fractions vary across years in a species specific fashion. For the three years for which we have good field data, germination fraction is also significantly correlated with realized fecundity.
- 7) All of the elements required for variance-based species coexistence appear to be present, indicating that this is likely to be an important mechanism favoring coexistence of desert annuals.

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