Seed Banks in Desert Annuals: Implications for Persistence and Coexistence in Variable Environments

Catherine E. Pake; D. Lawrence Venable

Ecology, Vol. 77, No. 5. (Jul., 1996), pp. 1427-1435.

Ecology, 77(5), 1996, pp. 1427–1435

SEED BANKS IN DESERT ANNUALS: IMPLICATIONS FOR PERSISTENCE AND COEXISTENCE IN VARIABLE ENVIRONMENTS[1]

Catherine E. Pake and D. Lawrence Venable
Department of Ecology and Evolutionary Biology,
University of Arizona, Tucson, Arizona 85721 USA

Abstract. It is widely believed that desert annual plants maintain between-year seed banks, yet few field studies actually have measured the proportion of the viable seed bank that remains dormant through a season. Dormancy and germination fractions were quantified for a guild of winter annuals on a creosote flat in the Sonoran Desert for three years. Predictions from two types of theoretical models applicable to temporally variable environments were examined: (1) the evolution of life history traits promoting persistence in the face of temporal variation and (2) the role of temporal variation in mediating species coexistence. The density of ungerminated seeds was estimated by collecting soil samples after germination, but prior to new seed set. Seedlings were followed in nearby plots to estimate the density of germinated seedlings and their reproductive success. Long-term data collected from permanent plots over a 10-yr period were used to calculate temporal variation in reproductive success for each species. Species with higher temporal variation in reproductive success had lower germination fractions and smaller seeds, consistent with the theory that seed dormancy and large seed size are partially substitutable bet-hedging strategies. The data also suggested that this system possesses traits that are necessary for temporal variation to promote coexistence. First, between-year seed banks, necessary to buffer populations in unfavorable years, were documented for 17 species. Second, there was a strong tendency for year-to-year variation in germination fractions to vary among species. Finally, plants germinated more in years of higher reproductive success. We discuss how a correlation between germination and reproductive success enhances the role of temporal variance in success hierarchies in promoting species coexistence.

Key words: desert annual plants; dormancy; field experiment; life history traits; predictive germination; reproductive success; seed banks; Sonoran Desert; spatial variation; species coexistence; temporal variation.

INTRODUCTION

It is widely assumed that desert annual plants have seed banks. However, close inspection of the literature (e.g., Nelson and Chew 1977, Freas and Kemp 1983, Reichman 1984, Price and Reichman 1987) shows that little work has been done that actually quantifies the proportion of viable seeds that remain dormant in the soil after a germination event (but see Venable 1989). Long-lived seeds and species-specific germination requirements have been hypothesized to explain observed fluctuations in population density among species (Went 1949, Juhren et al. 1956, Tevis 1958, Shreve and Wiggins 1964). Yet, early workers typically observed only the number of seedlings emerging, without quantifying the seed bank.

Recently, a few desert annual species have been studied in well-controlled tests in growth chambers (Freas and Kemp 1983, Baskin et al. 1993, Philippi 1993*a*, *b*). These laboratory studies have generally shown that a fraction of viable seeds remains dormant, even under ideal germination conditions. Here we document natural germination fractions (the proportion of viable seeds that germinate in a given year's germination season) for a guild of Sonoran Desert winter annuals under spatially and temporally varying field conditions.

We use these results to test predictions from two types of theoretical models applicable to temporally variable environments: (1) the evolution of life history traits that promote persistence in the face of temporal uncertainty, and (2) the role of temporal variation in mediating species coexistence. Deserts tend to be highly variable through time; indeed, the coefficient of variation in potential evapotranspiration among years is greater in hot deserts than in any other biome (Frank and Inouye 1994). Such environmental fluctuations can produce a large variance in reproductive success among years (Venable et al. 1993, Pake and Venable 1995, Venable and Pake, *in press*).

A temporally variable environment may favor life history traits that reduce fitness variance, even if they result in some reduction of expected or mean fitness (Venable and Lawlor 1980, Philippi and Seger 1989). For annual plants, fractional germination (i.e., between-year seed banks) provides a variance-reducing mechanism. Delayed germination of a fraction of a

---

[1] Manuscript received 10 July 1995; accepted 28 August 1995; final version received 6 October 1995.

plant's progeny buffers it from the consequences of near or complete reproductive failure in unfavorable years. It also reduces variance by lowering success in favorable years, when greater fitness would have resulted from germination. Thus, all else being equal, populations that experience more temporal variation are predicted to have lower germination fractions and a higher fraction of their seeds in between-year seed banks than populations that experience less temporal variation.

Seed size is likely to be another variance-reducing trait that may modify the strength of selection for delayed germination in desert annuals. Large seeds may buffer seedlings from some of the negative effects of dry years by promoting faster root development and earlier access to deep water reserves (Baker 1972). Yet, for the same reproductive allocation, a large-seeded plant will produce fewer seeds than a small-seeded plant under favorable conditions. Thus, both large seeds and between-year dormancy should lower temporal variation in fitness in places where rainfall is highly variable. Since the variance-reducing effects of large seed size and dormancy are partly substitutable, having one of these traits should reduce selection for the other (Venable and Brown 1988). Thus, all else being equal, populations with larger seeds should experience less temporal variation in reproductive success and, therefore, have higher germination fractions, than populations with smaller seeds.

Annual plants not only persist in the variable environment of the desert, they also coexist with a diverse array of other annual plant species. Annuals comprise ≈50% of the species in a number of regional floras of the Sonoran Desert (Venable et al. 1993, Venable and Pake, *in press*). Because of this diversity in an environment with high temporal variability, desert annuals have frequently been cited as an example of a biological system in which temporal variation may be promoting coexistence (Shmida and Ellner 1984, Warner and Chesson 1985, Ellner 1987, Chesson and Huntly 1988, 1989, Chesson 1994).

Model systems in which temporal variation in environmental conditions promotes coexistence have three elements: (1) species with a long-lived, resistant life history phase that buffers populations from unfavorable conditions, (2) species-specific responses to temporal variation, so that species are not completely correlated in which years are the most favorable for population growth, and (3) when a species is abundant, it tends to both experience and exert strong competitive effects in its favorable years (Chesson and Huntly 1988, 1989, Chesson 1994). When all three of these elements are present, each species tends to increase from low density, and coexistence is favored.

All of these characteristics are found in annual plant systems if species maintain between-year seed banks and have species-specific germination responses to the environment (Chesson and Huntly 1988, 1989, Chesson 1994). In addition, if germination fractions are higher in years of greater reproductive success ("predictive germination," cf. Venable and Lawlor 1980), then the ability of variable germination fractions to promote coexistence is enhanced (Venable et al. 1993, Pake and Venable 1995).

In this study we ask: Do species with higher temporal variation in reproductive success have lower germination fractions? and Do larger seeded species have lower variation in reproductive success and higher germination fractions than smaller seeded species?

With respect to coexistence mediated by temporal variance, we ask: Is the production of a between-year seed bank common in this guild of plants? Do germination responses in different years vary in a species-specific way? Is there a positive correlation between germination fraction and reproductive success (i.e., predictive germination)? Do germination differences between shrub-covered and open microhabitats vary in a species-specific fashion, suggesting a possible role for habitat partitioning in mediating coexistence?

METHODS

Study system

This study took place from 1989–1990 to 1991–1992 at the University of Arizona's Desert Laboratory on the northwest side of Tumamoc Hill, just west of Tucson, Arizona. Rainfall data collected by the Desert Laboratory were used to characterize study years. On average, 25.0 cm of precipitation falls annually near Tucson, with over half falling during the summer months of July, August, and September. Most of the remaining rain falls between October and April, the growing season for winter annuals.

The site (725 m elevation) is a gently sloped creosote flat dominated by *Larrea divaricata* (creosote bush), which has 50% cover. More than 30 species of winter annuals have been documented on permanent plots followed by D. L. Venable since 1982–1983 at the site. Winter annuals at the site typically germinate with the onset of autumn (October to December) rains, and grow and reproduce until March or April. Species may have different tolerances for water stress at different phases of plant development, and there are differences among years in the amounts and timing of rainfall (Fig. 1). A more detailed description of the site, rainfall, and species can be found in Pake and Venable (1995).

Field methods

Estimating germination fractions.—Germination fraction was defined as the proportion of viable seeds that germinated in a given year (cf. Cohen 1966, Venable and Lawlor 1980). In order to estimate germination fractions, the density of seedlings was determined in sample quadrats, and the density of viable seeds remaining after the germination season was calculated from soil cores. Germination fraction for each species

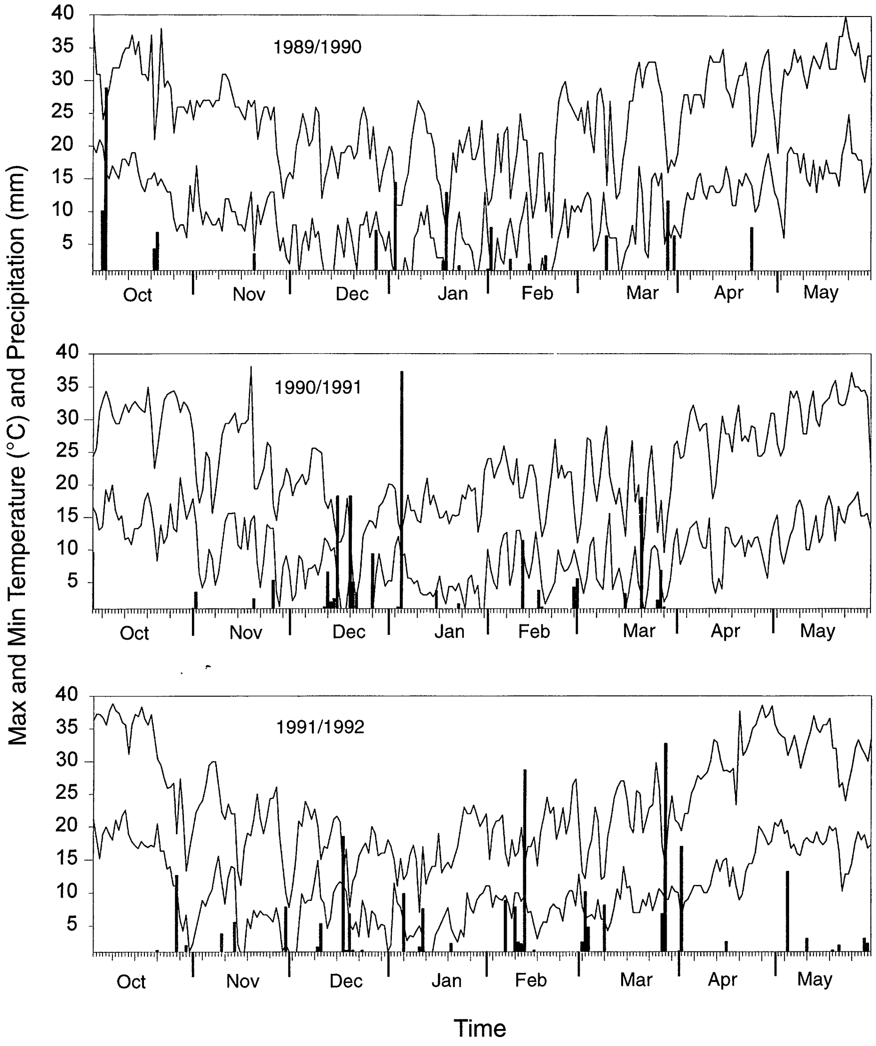

FIG. 1. Daily precipitation (vertical bars) and maximum and minimum temperatures at the Desert Laboratory at Tumamoc Hill (Tucson, Arizona) from October through May of 1989/1990, 1990/1991, and 1991/1992.

was then computed as: (seedlings/m^2)/[(seeds + seedlings)/m^2].

To estimate the density of viable seeds after the germination season, soil cores (5.4 cm diameter × 2.5 cm deep) were collected in late February to early March in each of three years along a 180-m transect, using a stratified random sampling technique (cf. Benoit et al. 1989). Because aggregated or rare species should be estimated with a sample size >100 individuals (Goyeau and Fablet 1982), 180 soil samples were taken each year. Half of samples were obtained from under creosote shrubs, and half from open sites. Cores were obtained after the germination season, but prior to seed set. Thus viable seeds found in these samples had forgone germination during at least one and possibly more seasons. Pilot studies indicated that viable seeds rarely occurred below 2.5 cm in the study area. Immediately after collection, samples were placed in paper bags and oven dried for 24–48 h at 40°C, to inhibit rot or germination.

Seeds and organic material were separated from soil particles using a repetitive frothing, flotation, and filtering technique. Prior testing showed that this technique retrieved >95% of seeds from soil samples to which a known number of seeds of three species (*Plantago patagonica, Pectocarya recurvata, Schismus barbatus*) had been added (C. Pake, *personal observation*). Individual soil samples were mixed with tap water and stirred vigorously (frothing). The suspension containing floating organic matter and small soil particles was immediately decanted through an organza-cloth filter placed in a Büchner funnel attached to suction. The filter had previously been shown to capture the smallest seeds of interest (*Evax multicaulis,* 0.025 mg). This process was repeated about six times for each soil sample, at which time the decanted liquid was virtually

TABLE 1. Characteristics of 16 desert species with between-year seed banks. All data are for three years except temporal variation in reproductive success, which is for a 10-yr period. ''undef'' refers to undefined germination fractions; ''…'' signifies data not available.

			Seed densities (no./m^2)					
	Seed mass (mg)		1989/1990		1990/1991		1991/1992	
Species	Mean	SE	Mean	95% CI	Mean	95% CI	Mean	95% CI
Bowlesia incana	0.91	0.085	178	97.5–271	115	51.2–190	724	424–1049
Cryptantha pterocarya	0.30	0.031	2.44	0–7.33	2.44	0–7.33	0	0–0
Daucus pusillus	1.07	0.079	9.75	2.44–19.5	2.44	0–7.33	21.9	4.87–48.7
Draba cuneifolia	0.06	0.0045	0	0–0	2.44	0–7.33	0	0–0
Eucrypta micrantha	0.04	0.0044	0	0–0	2.44	0–7.33	31.7	7.31–65.8
Evax multicaulis	0.025	0.002	65.8	34.1–102	124	75.5–179	41.4	19.5–65.8
Lappula redowski	1.73	0.317	9.75	0–21.9	0	0–0	0	0–0
Monoptilon belliodes	0.30	0.0098	9.75	0–21.9	0	0–0	0	0–0
Pectocarya heterocarpa	0.38	0.0496	0	0–0	0	0–0	2.44	0–7.33
Pectocarya recurvata	0.95	0.0307	7.31	0–17.1	0	0–0	0	0–0
Plantago insularis	0.95	0.0525	2.44	0–7.33	0	0–0	0	0–0
Plantago patagonica	0.88	0.044	7.31	0–17.1	4.87	0–12.2	2.44	0–7.33
Schismus barbatus	0.08	0.0055	97.5	58.5–150	283	156–470	1430	286–3610
Stylocline micropoides	0.13	0.0066	4.87	0–13.4	2.44	0–7.33	2.44	0–7.33
Sysimbrium irio	…		0	0–0	0	0–0	2.44	0–7.33
Vulpia octoflora	0.38	0.0087	2.44	0–7.33	0	0–0	0	0–0

* The proportion of viable seeds that germinate in a given year's germination season.

† SD of log per-capita reproductive success (log average seed set of germinated seeds) over 10 yr.

clear. The organza filter and debris were then placed in a labelled petri dish and oven dried again, as above.

In order to separate seeds from the organic debris, the dried, filtered portions were sieved into three fractions using a 1-mm and 500-μm mesh USA Standard Testing sieve (sieve numbers 18 and 35). Seeds were separated from each fraction using a dissecting microscope and were identified by comparison with voucher seeds. All seeds were cut or poked through the seed coat to determine viability. Seeds with juicy, oily, or fleshy embryos were regarded as viable. This technique was deemed superior to tetrazolium chloride testing for viability because of the difficulty in manipulating the smallest seeds, because some deeply dormant viable seeds show only minimal staining with tetrazolium, and because embryos and endosperm in the field usually undergo easily recognizable changes upon death (desiccation, decay).

To estimate the density of seedlings, 42 to 48 quadrats (0.05 m^2 under shrubs, 0.10 m^2 in the open) were censused each year along a 180-m transect parallel to the seed bank transect. The first year, 15 shrub and 27 open quadrats were followed. The next two years, 24 were censused in each microhabitat. The seedling transect was offset 5 m from the seed-bank transect to prevent trampling of quadrats during the intensive soil sampling. There were no obvious habitat differences between the parallel transects. Plots were initially censused 3–5 wk after the main germination flush and again at the end of the season in order to characterize the density, survivorship, and reproduction of each species. Using a Plexiglas mapping table, acetate sheets, and colored markers, each seedling was mapped with exact location and species identity. Reproductive success was computed as the average seed set per seedling in each year (proportion surviving times mean fecundity of survivors, i.e., per-capita reproductive success).

Temporal variation.—We used a long-term data set (Venable et al. 1993) to measure the level of temporal variation experienced by plants of each species. For 10 yr (1982/1983–1991/1992) winter annuals had been censused along a third, 250-m transect (near the 180-m transect described for plant censuses above). This transect had 15 permanent plots in the open microhabitat (0.05 m^2 each until 1989/1990, then increased to 0.10 m^2 each). These plots were regularly censused after fall germination-inducing rainfall events and thereafter approximately monthly for emergence, survival, and reproduction. This sampling scheme gave sample sizes of hundreds of individuals for most species in most years. Temporal variation in reproductive success was calculated as the standard deviation in the log of the average seed set of germinated seeds (per-capita reproductive success) for each species over 10 years. For a log-transformed variable, the standard deviation is a scale-invariant measure of variability and more resistant to outliers than the coefficient of variation.

Seed size.—In order to measure mean seed mass (hereafter seed size), seeds were collected from naturally occurring specimens at Tumamoc Hill. They were weighed with a Sauter AR 1014 balance, in lots of 25–100 seeds from pooled collections from several individuals. More seeds per lot were used for species with lower seed mass.

Statistics

Data were analyzed using the GLM procedure in SAS, version 6.04 (SAS Institute 1989) for analyses of variance.

TABLE 1. Continued.

Seedling densities (no./m²)						Germination fraction*			Reproductive success			
1989/1990		1990/1991		1991/1992								
Mean	95% CI	Mean	95% CI	Mean	95% CI	1989/ 1990	1990/ 1991	1991/ 1992	1989/ 1990	1990/ 1991	1991/ 1992	Temp var†
43.3	16.3–78.0	43.2	17.2–73.4	30.2	12.3–50.0	0.05	0.36	0.02	0.401	8.37	35.7	···
0	0–0	1.49	0–3.83	8.54	2.29–16.5	0	0.79	1.0	···	550	210	···
2.30	0.242–5.11	5.96	1.28–12.3	2.29	0.625–4.48	0.67	0.90	0.12	13.5	20.4	25.8	0.465
0.667	0–2.00	4.89	0.213–12.9	5.63	1.46–10.8	1.0	0.90	1.0	···	7.00	15.5	···
0	0–0	12.7	2.55–26.8	19.8	4.58–38.3	undef	0.90	0.81	···	4.10	6.94	···
0.161	0–0.484	9.36	3.83–16.0	10.8	5.73–17.3	0.002	0.07	0.21	0	185	85.7	0.807
0	0–0	0.213	0–0.638	0.833	0–2.08	0	1.0	1.0	···	232	22.0	···
0.161	0–0.484	1.70	0–4.47	0	0–0	0.01	1.0	0	0	25.0	···	0.466
0	0–0	4.26	1.28–8.09	11.9	6.25–18.3	undef	1.0	0.93	···	160	92.6	···
2.97	0.161–6.18	0.213	0–0.638	1.88	0.417–3.33	0.31	1.0	1.0	3.34	0	94.7	0.521
0.807	0.161–1.77	3.62	0.851–7.23	1.04	0–2.71	0.50	1.0	1.0	0.801	6.01	29.0	0.544
3.82	0–10.5	3.62	0.851–7.45	48.8	12.8–97.1	0.31	0.41	0.87	1.80	89.5	29.3	0.515
13.5	6.60–21.5	21.5	11.3–33.2	243	137–379	0.14	0.06	0.20	86.5	474	798	0.713
0	0–0	0	0–0	3.13	1.25–5.42	0	0	0.81	···	···	412	0.560
0	0–0	0	0–0	4.79	0–13.5	undef	undef	0.33	···	···	···	···
7.98	1.33–15.8	2.98	0–8.09	5.63	2.50–10.4	0.93	1.0	1.0	6.01	8.68	212	0.584

Mean seed and seedling densities are reported. Seeds and seedlings tended to be clustered such that most species had many soil samples with no seeds, leading to data that are skewed and kurtotic. Therefore, we bootstrapped the data to obtain confidence intervals in our estimate of the mean.

The mean seed and seedling densities for each species were used to calculate germination fractions, which were arcsine transformed for analyses. Per-capita reproductive success and seed mass data were log transformed. In each case, these transformations normalized error structures and controlled heteroscedasticity.

Type IV sums of squares were used when data were unbalanced (Shaw and Mitchell-Olds 1993). Nonunique sums of squares (designated by * in ANOVA tables) can result from unbalanced data. However, reported results are based on unique sums of squares in most cases. When differences were significant, we used Tukey's "honestly significant difference test," which holds the experimentwise error rate at a specified level, even when data sets contain unequal cell sizes (SAS Institute 1989).

Many interactions in models were not significant; when F values for interactions were close to or less than 1, we performed the analysis again without the interaction (as per Steel and Torrie 1980:446). This usually resulted in greater power with which to test other hypotheses and estimate parameters.

Two subsets of species were used. Analyses regarding the evolution of life history traits used species that were common on the permanent plots over a 10-yr period, for which we could compute temporal variation in reproductive success. For questions related to coexistence, all species present in at least two years of the 3-yr seed-retrieval portion of the study were included.

RESULTS

Natural conditions.—The three study years differed in both the total amount of seasonal rainfall and the timing of rainfall within seasons (Fig. 1). The rainfall events that caused most germination occurred in 4–5 October 1989, 12–16 December 1990, and 18–21 December 1991. Years became successively wetter from 1989/1990 to 1991/1992, both in rainfall measured over the entire growing season (October to April: 144.0, 190.0, and 231.4 mm, respectively), as well as in late-season rainfall (January to March: 75.2, 102.6, and 141.2 mm, respectively), when pre-reproductive plants frequently experience a drought. Due to drier and hotter conditions the first year, reproduction was completed by mid-March in 1990, as compared to mid-April in 1991 and 1992.

The study years followed the late 1980s' drought and were characterized by low population densities of all species, and low seed-bank densities (Venable et al. 1993, Venable and Pake, *in press*). While our seed bank and plant censuses were quite extensive, low seed and seedling densities resulted in variable germination fractions, with an increased probability of stochastic ones and zeros (due to no seeds or no seedlings, respectively).

Species composition of the seed bank.—The presence of a between-year seed bank was confirmed for 16 species along the transect over three years (Table 1). In addition, both seedlings and dormant seeds were found for a seventeenth species (*Eriastrum diffusum*) not included in Table 1. It was omitted because we did not estimate the density of the many viable dormant seeds

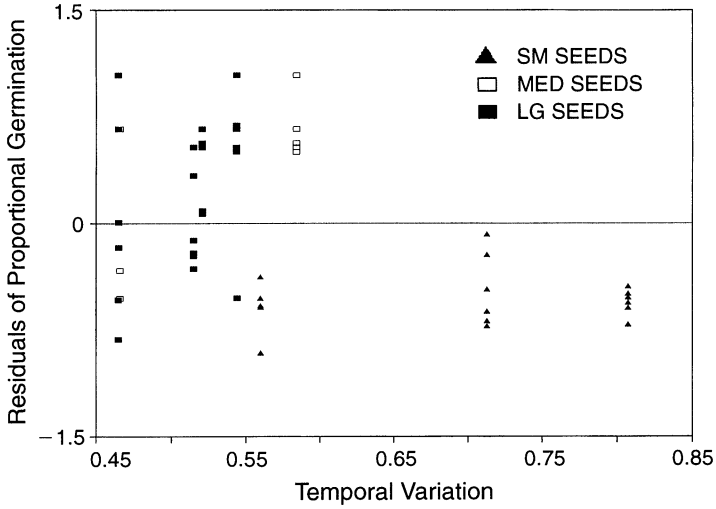

FIG. 2. Lower germination fraction for species with higher temporal variation (in mean per capita reproductive success) is illustrated here in a plot of the residuals of proportional germination (after year differences were removed) against the temporal variation experienced by each species in a 10-yr period. Germination fraction was determined as the proportion of viable seeds that germinated in a given year's germination season. Symbols illustrate the correlation between seed size and factors plotted on the axes: Smaller seeded species tended to have higher germination fractions and to fall at the higher end of temporal variation. (See Table 1 for seed mass and temporal variation by species.)

that are borne on persistent standing dead plants from previous years.

Other species (*Bromus rubens, Chaenactis brevicornu, C. stevioides, Erodium cicutarium, E. texanum, Eriogonum* spp., *Eriophyllum lanosum, Lesquerella gordonii, Lepidium lasiocarpum, Lotus* spp., *Phacelia crenulata*) occurred as seedlings in some years (5 species in 1989/1990, 9 in 1990/1991, and 10 in 1991/1992), but no dormant seeds were found. With the exception of *Bromus rubens,* this group of species had lower seedling densities than species for which dormant seeds were found ($P < 0.05$ based on nonparametric confidence limits; Snedecor and Cochran 1976). It is likely that some of these rarer plants have seed banks at densities that were too low for our sampling scheme to detect.

Life history patterns in a temporally variable environment.—Nine of the species found to have between-year seed banks occurred regularly in our long-term (1982/1983–1991/1992) data set from the permanent plots. An examination of the relationships between germination fraction, seed size, and temporal variation in per-capita reproductive success showed the patterns predicted.

Seed size was negatively correlated with temporal variation in per-capita reproductive success, as is expected if seed size tends to buffer plants from environmental variation (Spearman $r_S = -0.7448$, $P = 0.0213$; data in Table 1). Germination fraction varied among years, with year accounting for 13.05% of the total variation. The residual variation in germination fraction was significantly related to both temporal variation in reproductive success and seed size. The strong correlation between these two factors precluded our confidently inferring an independent relationship between each of these factors and germination fraction (i.e., various collinearity indices were high, cf. Mitchell-Olds and Shaw 1987). Thus, we analyzed these relationships separately. Germination fractions were lower for species with greater temporal variation in per-capita reproductive success ($F_{1,44} = 10.06$, $P = 0.0028$; Fig. 2), as is predicted by models of bet-hedging in variable environments. And, germination fractions were higher for species with larger seeds, as would be expected if seed size and delayed germination are partially substitutable buffering traits ($F_{1,44} = 20.20$, $P = 0.0001$; Fig. 2). The relationship between germination and each of these factors did not vary among years of the study.

Coexistence in a variable environment.—We have ≥2 yr of data on the germination and reproductive success of 15 species (all species in Table 1 except *Sysimbrium*), enabling us to test whether germination fraction varied with year or habitat. The variation in germination response among years differed among species (Table 2; germination response of each species each year is given in Table 1), a trait that promotes coexistence in models of annual plants in a temporally variable environment. Averaged across species and years, germination fraction was higher in the open habitat (69.8%) than under shrubs (51.6%). (Arcsine square-root transformed means with 1 SE were 0.9887 [0.0611] and 0.8017 [0.0611], respectively.) However, the difference between habitats did not vary signifi-

TABLE 2. Analysis of variance for effect of species, habitat, and year on germination fraction (proportion of seeds germinated) for 15 species that produced seed banks (data in Table 1).

Source	df	SS	MS	*F*	*P*
Species	14	12.62*	0.901	6.63	0.0001
Habitat	1	0.5503	0.550	4.05	0.0533
Year	2	3.217*	1.61	11.83	0.0002
Species × Year	25	6.369	0.255	1.87	0.0507
Error	30	4.080	0.1360		

* These sums of squares are not unique due to an unbalanced statistical design.

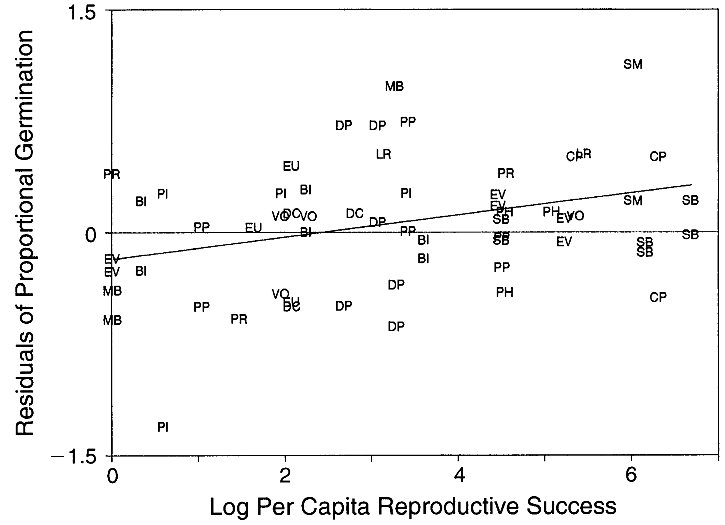

FIG. 3. The positive relationship between germination fraction and reproductive success of the current year. Points plotted along the ordinate are residuals after the effects of species differences were removed. ([Residuals to proportional germination] = 0.0714 [Per capita reproductive success] − 0.175.)

cantly among species (species × habitat interaction: $F_{13,15} = 1.05$), or year (habitat × year interaction: $F_{2,15} = 0.82$), and these terms were not included in the final model.

Relationship between germination and reproductive success.—For 15 species for which we have ≥2 yr of germination data, germination fraction was higher in years of greater reproductive success ($F_{1,51} = 5.27$; $P = 0.0258$; Fig. 3). Species differences ($F_{14,51} = 5.36$; $P = 0.0001$) accounted for 57.1% of the variation in germination fraction and reproductive success accounted for 4.01%. The interaction between species and reproductive success was nonsignificant ($F_{13,38} = 0.91$).

DISCUSSION

This study quantifies germination fractions for 16 Sonoran desert annual species under natural field conditions. These data are subsequently used to address questions posed by theories of life history evolution and coexistence in variable environments.

Life history evolution.—Larger seeded species in our study were found to have lower variance in reproductive success. This lower variance was also correlated with a smaller fraction of seeds entering a between-year seed bank. This is the first time that field data on long-term fitness variance and on germination fractions have been combined to demonstrate these patterns. These patterns support the idea that risk can be lowered either by having a large seed size, and thereby a lower variance in reproductive success of germinating seeds, or by having a large seed bank and thereby buffering against high variance in the per-capita reproductive success of germinating seeds. In our system, these alternative strategies for dealing with risk resulted in a negative correlation between seed size and dormancy, consistent with the prediction that possession of one risk-reducing trait lowers selective pressure favoring the other risk-reducing trait (Venable and Brown 1988, Venable 1989). Rees (1993) also found a trade-off between dormancy and seed size in a comparative survey of British plants.

There is some support in the literature for related ideas involving seed traits in variable environments. A trade-off between seed dormancy and seed spatial dispersal has been suggested within several seed-heteromorphic species (Venable and Lawlor 1980) and among species of British plants (Rees 1993). In growth chamber experiments, Phillipi (1993*a*) found that germination fractions in populations of a Chihuahuan Desert annual, *Lepidium lasiocarpum,* decreased along a gradient of declining rainfall. This is consistent with the prediction that annual plants with a seed bank should have higher germination fractions where the quality of good years is higher (Cohen 1966).

While our study shows patterns suggested by life history theories in variable environments, the theories are phrased in "all-else-being-equal" terms, usually thought to predict evolutionary tendencies within a species or group of related species. That these patterns should be seen across distantly related species in the same habitat suggests that there may be some strong constraints on the possible combinations of traits for these similar-sized plants growing in this common environment. Our results do not address the historical mechanism that gave rise to the pattern. Two possible mechanisms are that (1) only species with appropriate life history combinations have been able to persist and coexist in this environment, and (2) selection operated on these species (or their ancestors) in this environment, or in other similar ones, to produce species with appropriate life history combinations.

Coexistence.—Our data suggest that this system may have the characteristics required by the models of Chesson and colleagues (Chesson and Huntly 1988, 1989, Chesson 1993) for temporal variation to promote coexistence. First, many species produce a between-year seed bank. Second, the germination responses to temporal variation are species specific.

A system with the above characteristics meets the invasibility criterion for species coexistence, i.e., that the mean log growth rate of each species is positive at low density (Chesson and Ellner 1989, Chesson 1994). This occurs because in years favorable to germination an abundant species tends to experience competition, in part from high densities of conspecific seedlings. Competition in otherwise favorable years tends to prevent high population growth rates (cf. Pantastico-Caldas and Venable 1993, and Pake and Venable 1995, for studies of competition with this system). A species whose population has crashed to a low density, however, may occasionally experience a favorable year in the absence of competition (because germination responses are not completely correlated among species). This enables a low-density species to occasionally attain really high population growth rates. Therefore, as long as a between-year seed bank is present to buffer decline in unfavorable years, a low-density species tends to reinvade the system.

Our data do not suggest a role for germination in habitat partitioning. Germination responses to habitat variation (shrub-covered vs. open microhabitats) were not statistically different among species. Rather, germination for all species in all years tended to be higher in the open than under shrubs. A similar result has been found in the Mojave Desert: experimentally sown seeds of many winter-annual species had higher germination in the open than under *Larrea* shrubs (Samson 1986).

Predictive germination?—The data presented here show higher germination fractions in years that were favorable for reproductive success. The mechanism giving rise to this pattern could be as simple as having the germination fraction sensitive to temperature and water conditions that are favorable for early growth and establishment. If early growth and establishment are important components of fitness variation among years, then germination fraction would automatically be correlated with reproductive success. Alternatively, greater germination in favorable years is the adaptive pattern expected from models of predictive germination when appropriate cues are available (Cohen 1967, Venable and Lawlor 1980). At our field site, rainfall in December (frequently an important month for germination) is correlated with rainfall in February (an important month for plant growth, though it is often subject to drought: $r = 0.19$, $P = 0.04$, $N = 115$ yr, University of Arizona meteorological data). Thus, December rainfall might be an appropriate germination cue to predict reproductive success.

A positive correlation between germination fraction and germination success has been found elsewhere. Rice (1985) showed that two annual *Erodium* species exposed to spatial variation in a California grassland cue on temperature fluctuations, which indicate whether a microsite is covered or open. Germination fractions are higher in open microsites, where there tends to be higher reproductive success. It has also been shown, using four years of the long-term data set referred to here, that when there is more than one definable cohort within a season, the cohort with the higher germination tends to be the one with the higher fitness (Venable 1989). Thus, within years, the timing of germination is variable and within-year germination timing is positively correlated with fitness opportunities.

Demonstration that this pattern has evolved to increase fitness would require rigorous proof of adaptation using experimental or comparative methods beyond the scope of this study. We can only say that the pattern observed here is consistent with the hypothesis of adaptive predictive germination, and note that many other aspects of germination biology (e.g., cyclical annual dormancy, overwintering requirements, etc.) associate the germination of plants with conditions favorable for growth and reproduction (Fenner 1985).

Implications of predictive germination for coexistence.—Predictive germination has been largely ignored in published coexistence models, despite Cohen (1967) and Venable and Lawlor (1980). Yet, Venable et al. (1993) report that in computer simulations a positive correlation between germination fraction and reproductive success, like that found in this study, enhances the coexistence-promoting properties of variable and species-specific germination fractions. Therefore, regardless of the mechanisms giving rise to it, the pattern of higher germination in favorable years has important implications for species coexistence based on temporal variance.

While we found greater germination in years of higher per-capita reproductive success, and species-specific germination responses to temporal variation, these patterns are based on only three years of data on germination fractions. Although these are labor-intensive data to collect, it is desirable to obtain a larger sample of years to confirm these suggestive, statistically significant trends.

The results of this study suggest that this system has many of the population dynamic elements necessary for species coexistence based on temporal variance. Other mechanisms of species coexistence, such as types of spatial variation not investigated here, and species-specific interactions with higher trophic levels, are likely to play roles in this system as well. Yet given the plethora of coexistence mechanisms, it is important to document, with careful field investigations, the population-dynamic elements required for one likely mechanism. Such work is needed to complement recent theoretical developments in the area of coexistence.

ACKNOWLEDGMENTS

Thanks to R. Robichaux, P. Chesson, J. Bronstein, and M. Clauss for valuable comments on the manuscript. We would also like to thank A. Caprio, K. Rylander, M. Fishbein, a team of undergraduates, and the USGS at Tumamoc Hill for their support in the field, in the lab, and during discussions. This work was partially funded by an American Association of University Women fellowship and research grants from Sigma Xi and the University of Arizona to C. E. Pake and NSF BSR 91107324, National Geographic Society Grant 3924–88, and a DOD Legacy Grant to D. L. Venable.

LITERATURE CITED

Baker, H. G. 1972. Seed mass in relation to environmental conditions in California. Ecology **53**:997–1010.

Baskin, C. C., P. L. Chesson, and J. M. Baskin. 1993. Annual seed dormancy cycles in two desert winter annuals. Journal of Ecology **81**:551–556.

Benoit, D. L., N. C. Kenkel, and P. B. Cavers. 1989. Factors influencing the precision of soil seed-bank estimates. Canadian Journal of Botany **67**:2833–2839.

Brown, J. S., and D. L. Venable. 1986. Evolutionary ecology of seed-bank annuals in temporally varying environments. American Naturalist **127**:31–47.

Chesson, P. L. 1994. Multispecies competition in variable environments. Theoretical Population Biology **45**:227–276.

Chesson, P. L., and S. P. Ellner. 1989. Invasibility and stochastic boundedness in two-dimensional competition models. Journal of Mathematical Biology **27**:117–138.

Chesson P. L., and N. Huntly. 1988. Community consequence 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.

Cohen, D. 1966. Optimizing reproduction in a randomly varying environment. Journal of Theoretical Biology **12**: 119–129.

———. 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.

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.

Fenner, M. 1985. Seed ecology. Chapman and Hall, New York, New York, USA.

Frank, D., and R. S. Inouye. 1994. Temporal variation in climate of terrestrial ecosystems: patterns and ecological implications. Journal of Biogeography **21**:401–411.

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.

Goyeau, H., and G. Fablet. 1982. Etude du stock de semences de mauvaises herbes dans le sol: le probléme de l'échantillonnage. Agronomie (Paris) **2**:545–552.

Juhren, M., F. W. Went, 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.

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.

Mitchell-Olds, T., and R. G. Shaw. 1987. Regression analysis of natural selection: statistical inference and biological interpretation. Evolution **41**:1149–1161.

Nelson, J. F., and R. M. Chew. 1977. Factors affecting seed reserves in the soil of a Mojave Desert ecosystem, Rock Valley, Nye County, Nevada. American Midland Naturalist **97**:300–320.

Numerical Algorithms Group. 1987. The generalized linear interactive modelling system, release 3.77. Second edition. Royal Statistical Society, Oxford, UK.

Pake, C. E., and D. L. Venable. 1995. Is coexistence in Sonoran Desert annual plants mediated by temporal variation in reproductive success? Ecology **76**:246–261.

Pantastico-Caldas, M., and D. L. Venable. 1993. Competition of two species of desert annuals along a topographic gradient. Ecology **74**:2192–2203.

Philippi, T. 1993*a*. Bet-hedging germination of desert annuals: beyond the first year. American Naturalist 142(3): 474–487.

———. 1993*b*. Bet-hedging germination of desert annuals: variation among populations and maternal effects. American Naturalist **142**:488–507.

Philippi, T., and J. Seger. 1989. Hedging one's evolutionary bets, revisited. Trends in Ecology and Evolution **4**:41–44.

Price, M. V., and O. J. Reichman. 1987. Spatial and temporal heterogeneity in Sonoran Desert soil seed pools, and implications for heteromyid rodent foraging. Ecology **68**: 1797–1811.

Rees, M. 1993. Tradeoffs among dispersal strategies in British plants. Nature **366**:150–152.

Reichman, O. J. 1984. Spatial and temporal variation in seed distributions in desert soils. Journal of Biogeography **11**: 1–11.

Rice, K. J. 1985. Responses of *Erodium* to varying microsites: the role of germination cuing. Ecology **66**:1651–1657.

SAS Institute. 1989. SAS/STAT user's guide, version 6, fourth edition, volume 2. SAS Institute, Cary, North Carolina, USA.

Samson, D. A. 1986. Community ecology of Mojave Desert winter annuals. Dissertation. University of Utah, Salt Lake City, Utah, USA.

Shaw, R. G., and T. Mitchell-Olds. 1993. Anova for unbalanced data: an overview. Ecology **74**:1638–1645.

Shmida, A., and S. Ellner. 1984. Coexistence of plant species with similar niches. Vegetatio **58**:29–55.

Shreve, F., and I. L. Wiggins. 1964. Vegetation of the Sonoran Desert. Stanford University Press, Stanford, California, USA.

Snedecor, G. W., and W. G. Cochran. 1976. Statistical methods. Iowa University Press, Ames, Iowa, USA.

Steel, R. G. D., and J. H. Torrie. 1980. Principles and procedures of statistics: a biometrical approach. McGraw-Hill, New York, New York, USA.

Tevis, L. Jr. 1958. Germination and growth of ephemerals induced by sprinkling a sandy desert. Ecology **39**:681–688.

Venable, D. L. 1989. Modelling the evolutionary ecology of seed banks. Pages 67–90 *in* M. A. Leck, V. T. Parker, R. L. Simpson, editors. Ecology of soil seed banks. Academic Press, New York, New York, USA.

Venable, D. L., and J. S. Brown. 1988. The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. American Naturalist **131**:360–384.

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., and C. E. Pake. *In press*. The population ecology of Sonoran Desert annual plants. *In* R. Robichaux, editor. Ecology and conservation of the Sonoran Desert flora: a tribute to the Desert Laboratory. University of Arizona Press, Tucson, Arizona, USA.

Venable, D. L., C. E. Pake, and A. Caprio. 1993. Diversity and coexistence of Sonoran Desert winter annuals. Plant Species Biology **8**:207–216.

Warner, R. R., and P. L. Chesson. 1985. Coexistence mediated by recruitment fluctuations. American Naturalist **125**:769–787.

Went, F. W. 1949. Ecology of desert plants. II. The effect of rain and temperature on germination and growth. Ecology **30**:1–13.