

DORMANCY AND GERMINATION IN A GUILD OF SONORAN DESERT ANNUALS

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Abstract. To investigate bet hedging and species coexistence in a guild of Sonoran Desert winter annuals, we subjected seeds of eight species to factorial combinations of summer treatments (varying temperature and precipitation), germination conditions (representative of early, middle, and late germination season temperatures and day lengths), and experiment trial dates (spanning the germination season). In keeping with bet hedging theory, we found that many viable seeds would not germinate in response to any combination of treatments (germination usually <50%). In keeping with the storage effect model, we found that these coexisting species differed in their germination response to our experimental manipulations and also differed in how the experimental variables interact. Field germination data from a long-term project on population and community dynamics of this guild show that germination fractions are similar between field and growth chamber and that species that tend to germinate under early season conditions in the growth chamber also tend to do so under unmanipulated field conditions. Some species are nondormant during the summer and only acquire dormancy at the onset of the autumn germination season, while others appear to have either innate or conditional dormancy until the onset of the germination season.

Key words: *bet hedging; conditional dormancy; desert annual; early germination; secondary dormancy; seed heteromorphism; species coexistence.*

INTRODUCTION

For desert annual plants, seed germination is risky because, in the absence of a perennating vegetative structure, seeds are the only link from one year to the next and the precipitation required for germination can be different from that required for survival of the seedling (Went 1949). Deserts receive rainfall in amounts that vary substantially among years in both amount and timing. As a result, successful germination is sometimes followed by complete reproductive failure (Tevis 1958*a, b*, Beatley 1967, Burk 1982, Venable and Pake 1999). Many plant species have mechanisms that allow their seeds to remain dormant until conditions favorable for germination and survival occur. Some species also have mechanisms that insure that the seeds produced by a single individual germinate at more than one time, often over a period of years. The latter phenomenon is often understood in terms of adaptive bet hedging in the face of unpredictable environmental variation (Cohen 1966, Venable and Lawlor 1980, Venable 1985, Philippi and Seger 1989).

Long-lived seeds that spread germination over time are also thought to contribute to temporal variance-mediated species coexistence, since they may allow species to partition the environment in time (Chesson and Huntly 1989, Pake and Venable 1996). In order for

temporal variance-mediated species coexistence to occur via seed dormancy, the proportion of seeds germinating must vary among years. Also, species must respond differently to the conditions encountered in different years, so that germination responses are not completely correlated among species (Ellner 1987, Chesson and Huntly 1988, Chesson 1994). There are many ways this germination decoupling could occur.

The summer conditions that desert winter annual seeds experience before the winter germination season can affect seed dormancy (Baskin and Baskin 1976, 1979). If species respond differently to these conditions, variation in summer weather patterns may be an important contributor to species-specific responses. The temperatures and day lengths at the time of germination rains vary among years and can also affect the germination of desert annuals in different ways. For example, some species readily germinate in the early fall while others preferentially germinate in late winter (Venable 1989). However, it cannot be readily determined from field data if it is the temperature/day length combination that affects germination or if it is the result of some correlate of the actual passage of time. If the answer differs for different desert annual species, this provides a further mechanism for differential germination in different years. To distinguish these possibilities, we must determine if, given the appropriate temperature and day length, seeds will germinate differently at different times during the germination season.

In this study, we explored the germination responses of a guild of Sonoran Desert annuals to document the

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PLATE 1. Seeds of species used in this study. Row 1 (left to right): *Plantago patagonica* (Plantaginaceae), *Pectocarya recurvata* (Boraginaceae), *Eriastrum diffusum* (Polemoniaceae). Row 2: *Schismus barbatus* (Poaceae), *Evax multicaulis*, *Stylocline micropoides* (Asteraceae). Row 3: *Pectocarya heterocarpa* long seeds, *Pectocarya heterocarpa* winged seeds (Boraginaceae), and *Eriophyllum lanosum* (Asteraceae). Photo credit: G. Barron-Gafford.



extent to which they remain dormant even when given favorable conditions and to uncover differences in germination response among species that could contribute to differential germination among years under variable natural conditions. We explored the growth chamber germination responses of eight species by exposing them to factorial combinations of summer treatments (varying temperature and precipitation), germination conditions (representative of early, middle, and late germination season temperatures and day lengths), and actual trial dates (spanning the germination season). We predict fractional germination, with many viable seeds not germinating in response to any combination of treatments. We also predict divergent germination responses of the species and the species by conditions interactions that are required in versions of the storage effect model in which coexistence is driven by seed dynamics (Chesson 1994). Our results also permit us to determine the relative roles of primary and secondary dormancy vs. lack of suitable environmental conditions for nongermination of these species. This guild of plants has been monitored for 20 years to document population and community dynamics (Venable et al. 1993, Venable and Pake 1999) and has been studied from the standpoint of competitive dynamics and their variation in space and time (Pantastico-Caldas and Venable 1993, Pake and Venable 1995, 1996), life history evolution (Clauss and Venable 2000), and seed bank age structure (Moriuchi et al. 2000). Thus, these results are relevant in a broader context and we can compare some of our laboratory germination results with actual long-term patterns of germination in the field.

METHODS

Study site and species

Seeds were collected from the Desert Laboratory at Tumamoc Hill, Tucson, Arizona, USA (32°13' N,

111°01' W) from an alluvial plain dominated by *Larrea divaricata* (creosote bush). The site receives ~300 mm of annual precipitation on average, about half of which falls during the summer monsoons (July–September), with the rest occurring sporadically through the remainder of the year (Bowers and Turner 1985). We studied eight common winter annual species found in this area (see Plate 1): *Eriophyllum lanosum*, *Evax multicaulis*, *Stylocline micropoides* (Asteraceae); *Pectocarya heterocarpa*, *Pectocarya recurvata* (Boraginaceae); *Plantago patagonica* (Plantaginaceae); *Eriastrum diffusum* (Polemoniaceae); and *Schismus barbatus* (Poaceae). *Pectocarya heterocarpa* produces two types of aerial seeds (nutlets) as well as basal seeds at ground level. We refer to the two aerial seed types as “winged seeds” (nutlets with a margin covered with barbed, membranaceous wings) and “long seeds” (long, narrow nutlets with no wings). Here, we report results for only the two aerial seed types because of difficulties encountered in obtaining and separating sufficient basal seeds.

Summer treatment

We collected seeds at maturity from ~50–100 plants of each of the eight study species in the spring of 1993 and placed them in 15 fine-mesh polyorganza bags per species. Each bag contained ~2000 seeds of a single species. Five bags of seeds for each species were subjected to one of three summer treatments.

For the “dry/cool” summer treatment, the bags were unwatered and placed flat on a greenhouse table. Seeds in the dry/cool treatment experienced natural day lengths and greenhouse temperatures that did not exceed 38°C. For the “dry/hot” summer treatment, the mesh bags of seeds were placed on the ground under a transparent plastic tent at the field site where they had been collected. The tent was held ~0.5 m above

the ground by a PVC pipe frame, allowing air passage over the bags, while shielding the seeds from most of the summer rains. Summer ambient air temperature at the site regularly exceeded 40°C (on 15, 9, 4, and 0 days respectively in June, July, August, and September 1993) and soil temperatures regularly exceeded 65°C. Mean ambient daily maximum and minimum air temperatures at the site were 38.4/20.7, 38.0/23.7, 35.7/22.6, and 34.8/19.9°C for the months of June through September 1993.

For the “wet/hot” summer treatment, the mesh bags were placed on the ground at the field site and exposed to natural rainfall, which totaled 117 mm (weather data collected by staff at the Desert Laboratory). Both sets of field-placed seeds were protected from rodent and bird predation by a 1/4-inch (0.64 cm) mesh hardware cloth cage staked to the ground over the seed bags, but not touching them.

The summer treatments began in early June 1993 and ended one week before the germination trials for each of the first two trials and on 10 October 1993 for the remaining three trials. Seeds removed from the summer treatments on 10 October 1993 were kept in “October conditions” (see *Methods: Germination experiment*) in a growth chamber during the month of October. Conditions were changed each month thereafter to simulate the corresponding temperature and day length in the field until seeds were germinated.

Germination experiment

Groups of 100 seeds of each species and each summer treatment were placed on moist #20 silica sand in covered petri dishes. We ran five 14-d germination trials. The germination trials began on the following dates: 16 August 1993, 21 September 1993, 27 October 1993, 4 December 1993, 23 February 1994, hereafter referred to as the August, September, October, December, and February trials. During each germination trial, we exposed six replicate petri dishes containing seeds of each species and summer treatment to three different germination conditions in growth chambers. The germination conditions simulated averaged temperature and day-length field conditions for October (29°C day, 14°C night, 11.5 hr of daylight, hereafter referred to as OCT conditions), November (22°C day, 7°C night, 10.5 hr of daylight, hereafter referred to as NOV conditions) and December (18°C day, 3°C night, 10.25 hr of daylight, hereafter referred to as DEC conditions). After 14 d, we scored germination in each petri dish based on radicle emergence. We chose 14 d because it is unlikely that these seeds often receive favorable moist germination conditions in the field for periods in excess of 14 d, due to generally superficial seed banks and rapid drying of desert soils following infrequent precipitation (Venable and Pake 1999).

After the germination trials were complete, we tested all of the ungerminated seeds (typically 50–90 per dish) from four to eight haphazardly chosen petri dishes per

species to determine seed viability. To distinguish non-germinated seeds from dead seeds we followed the method of Pake and Venable (1996) and poked or cut through the seed coat with a dissecting needle. Seeds with juicy, oily, or fleshy embryos were counted as viable. Previous studies have shown this to be a reliable measure of viability for these species, superior to tetrazolium chloride or germination assays (Pake and Venable 1996). We calculated seed viability for each species as the sum of the number of germinated seeds and the number of viable seeds remaining after the experiment, divided by the total number of seeds. Viability was >94% for all species except *E. lanosum* for which it was 79%.

Statistical methods

Data were analyzed using a generalized linear model with a logit link function, initially assuming a binomial distribution of germination fractions. Thus, the models were analyses of variance that correspond to logistic regression. Because seeds were grouped into petri dishes, individual seeds may not be independent data points and the variance may be larger than the theoretical binomial variance for the model. To account for this overdispersion, we followed the standard procedure of dividing our test χ^2 's by the Pearson χ^2/df (Aitkin et al. 1989, Crawley 1993). This scale parameter, which has a theoretical value of 1 under strict binomial variance, was typically in the range of 1.5–2.5. Because this procedure results in dividing one χ^2 random variable by another, we tested significance with *F* tests. For model simplification, we began with all main effects and interactions. We progressively removed non-significant interactions (from higher order to lower order) until achieving a model with at least some significant effects at each remaining hierarchical level. We did not remove any main effect that was involved in a significant interaction effect, or any interaction effect that was involved in a significant higher order interaction effect. The four-way ANOVAs for all species together (Table 1) and for the seed types of *Pectocarya heterocarpa* (Appendix A: Table A2) did not converge and thus were analyzed with least-squares ANOVA on arcsine-square-root transformed petri dish means.

Comparison to field germination

Mean growth chamber germination was calculated for a subset of experimental conditions which we deemed realistic conditions likely to be encountered in the field. We did not consider the August or September trial dates to be realistic because we have never observed August germination in 19 years of observation of these species at our field site, and have observed only negligible germination in September. We further assumed that October conditions could only occur in October, that November conditions could occur in October or December and that December conditions could occur in December or February. We excluded the green-

TABLE 1. Results of the least-squares ANOVA on arcsine square-root transformed germination (%) for all species combined.

| Factor | Portion explained (%) | df | F |
|--|-----------------------|------|--------|
| Species | 49.5 | 8 | 1649.1 |
| Germination conditions | 5.0 | 2 | 671.1 |
| Trial date | 0.7 | 4 | 46.8 |
| Summer treatment | 1.5 | 2 | 201.4 |
| Species × germination conditions | 8.2 | 16 | 136.9 |
| Species × trial date | 4.1 | 32 | 33.8 |
| Species × summer | 6.4 | 16 | 107.0 |
| Germination conditions × trial date | 0.8 | 8 | 26.9 |
| Germination conditions × summer | 0.0 | 4 | 5.4 |
| Trial date × summer | 0.3 | 8 | 12.3 |
| Species × germination conditions × trial date | 3.8 | 64 | 15.8 |
| Species × germination conditions × summer | 1.5 | 32 | 12.4 |
| Species × trial date × summer | 4.2 | 61 | 18.3 |
| Germination conditions × trial date × summer | 0.03 | 16 | 5.7 |
| Species × germination conditions × trial date × summer | 2.0 | 116 | 4.7 |
| Error | 7.3 | 1937 | |

Notes: Portion explained is the percentage of the total variation (sum of squares) explained by each effect. $P < 0.0005$ for all effects.

house-stored seeds (dry/cool) for this calculation of germination in realistic conditions.

We also calculated an index of early-season germination from the laboratory results. We first determined the mean germination in each of October, November, and December conditions using only the treatments representing realistic conditions as defined in the last paragraph. An index of early germination in the lab was created by assigning October germination conditions a value of 1, November a value of 0.5, and December a value of 0. A weighted average of these values was then calculated using the mean percentage germination under each month's conditions as the weight. This index of early germination goes from a value of 0, signifying laboratory germination only under December conditions, to 1, signifying germination only under October conditions (equal germination under the three sets of conditions would give an index of 0.5).

Actual field-germination fractions are available for seven years for five of our species (Pake and Venable 1996, Venable and Pake 1999). Permanent plots have been monitored to determine the density of seeds germinating following rains. Viable seed-bank densities were assessed at the end of the germination season by sifting soil cores and removing and counting viable seeds (see Pake and Venable [1996] or Venable and Pake [1999] for methodology). Germination fraction for each year was calculated from these densities of germinated and viable ungerminated seeds. Of seven years for which germination fraction data are available, three years had low germination due to low rainfall during the germination season. We averaged the germination fractions for the remaining four years with moderate to high germination season rains and compared these means to our growth chamber germination fractions. The growth chamber germination trials were

conducted under moist conditions which mimic years with germination season rain (seeds don't germinate in the field or growth chamber without water). Thus the meaningful comparison is with field germination in years with germination season rain.

In a year when there are multiple germination cohorts in the field, we can also determine the propensity of each species to germinate early in the season. In years with only two germination cohorts, we calculated early germination as the percentage of all germinating seedlings that germinated in the first cohort. When there were three or more cohorts, the division between early and late was chosen so as to equalize them as much as possible. For example, if there were three cohorts representing 1, 5, and 94% of germinating seeds, the first two would be combined into "early germination." Then the fraction of the total germination for each species that occurred in the first two cohorts would be calculated (see Venable [1989] for methodology). While this may seem somewhat arbitrary, it works well for interspecific comparisons as long as the cohorts are used consistently for all species in any given year. We have germination data appropriate for this analysis for 19 yr, 15 of which have data for multiple cohorts. The percentage of early germination was averaged for each species over these 15 yr to compare to the growth chamber results. In both of the field vs. growth chamber comparisons, we are comparing growth chamber germination of a single year's seed production (genotypes and environment) to field data averaged over many years of seed production and genotypes.

RESULTS

To see if and how species differ in their germination responses, we analyzed the effect of species, trial date, germination conditions, and summer conditions on ger-

TABLE 2. Germination (averaged over all experimental conditions, and over those likely to be encountered in the field), and combinations of conditions giving maximum germination.

| Species | Germination (%)† | | Combination for maximum germination (trial date, germination conditions, summer treatment)‡ | |
|---|------------------|----------------------|---|------------------------|
| | All conditions | Realistic conditions | Experimental conditions | Realistic conditions§ |
| <i>Eriastrum diffusum</i> | 1.36 (0–8.83) | 2.25 (0–8.83) | February, DEC, dry/hot | |
| <i>Eriophyllum lanosum</i> | 1.58 (0–9.33) | 2.02 (0.03– | August, DEC, dry/hot | February, DEC, dry/hot |
| <i>Evax multicaulis</i> | 15.18 (0.06– | 3.83) | | |
| | 48.6) | 24.41 (2.0–48.6) | December, NOV, dry/hot | |
| <i>Pectocarya heterocarpa</i> (winged seeds) | 6.76 (0–40.2) | 8.36 (0.1–35.5) | October, NOV, dry/cool | December, NOV, dry/hot |
| <i>Pectocarya heterocarpa</i> (long seeds) | 1.45 (0–13.5) | 1.63 (0–5.0) | December, NOV, dry/cool | October, NOV, wet/hot |
| <i>Pectocarya recurvata</i> | 0.33 (0–2.33) | 0.40 (0–1.0) | October, NOV, dry/cool | October, NOV, dry/hot |
| <i>Plantago patagonica</i> | 41.7 (0–87.5) | 64.20 (11.1– | December, DEC, dry/hot | |
| | | 87.5) | | |
| <i>Schismus barbatus</i> | 17.37 (0–56.5) | 16.3 (0.4–29.8) | August, OCT, dry/hot | October, NOV, dry/hot |
| <i>Stylocline micropoides</i> | 12.45 (0.2–38.5) | 12.43 (3.3–19.5) | August, DEC, dry/hot | December, NOV, dry/hot |

Notes: See Methods: Comparison to field germination for definition of conditions likely to be encountered in the field.

† Values given are means and, in parentheses, ranges of treatment means.

‡ Experimental germination conditions: OCT, 29°C day, 14°C night, 11.5 hr daylight; NOV, 22°C day, 7°C night, 10.5 hr daylight; DEC, 18°C day, 3°C night, 10.25 hr daylight.

§ The combination giving maximum germination for realistic conditions is only listed if the combination of conditions for maximum germination in experimental conditions are not likely to be encountered in the field.

mination and found that all main effects and interactions were significant (Table 1). Species had the strongest main effect on germination of the four variables tested, highlighting the large among-species differences in mean germination percentage (see Table 1, “percentage of variation explained” column). Several species had quite low overall germination, including *Eriastrum diffusum*, *Eriophyllum lanosum*, *Pectocarya recurvata*, and the long seeds of *Pectocarya heterocarpa* (Table 2). Others, such as *Evax multicaulis*, *Schismus barbatus*, *Stylocline micropoides*, *Plantago patagonica*, and the winged seeds of *P. heterocarpa* had at least moderate germination under some conditions. Also, two-, three-, and four-way interactions involving species explained a greater percentage of variance than interactions not involving species (totaling 30% of total variance, Table 1). This suggests that species are not only different in their mean germination, but also in how they respond to the experimental variables and in how the experimental variables interact.

After species, germination conditions had the second strongest main effect on germination followed by summer conditions and finally trial date (Table 1). Likewise, in the two-way interactions with species, germination conditions explained the most variation, followed by summer and finally trial date. Thus, among experimental manipulations, day length and temperature had the strongest impact on germination. However, species differed as to which conditions provoked higher germination. *Eriophyllum lanosum* had its highest germination in December conditions (Fig. B2 in Appendix B), while both seed types of *Pectocarya heterocarpa* had highest germination in November conditions (Figs. B7 and B8 in Appendix B). *Eriastrum diffusum*, *Evax multicaulis*, *Plantago patagonica*, and *Stylocline mi-*

cropoides had higher germination in both November and December conditions (Figs. B1, B3, B4, and B6 in Appendix B), while *Schismus barbatus* germinated more in October and November conditions (Fig. B5 in Appendix B).

Following germination conditions, summer treatments had the second strongest main effects and interactions in determining germination. *Eriastrum diffusum*, *Eriophyllum lanosum*, *Evax multicaulis*, *Plantago patagonica*, *Schismus barbatus*, and sometimes *Stylocline micropoides* had higher germination following the dry/hot summer treatment. Both seed types of *Pectocarya heterocarpa* and sometimes *Stylocline micropoides* had their highest germination following dry/cool summer treatment. While hot/wet treatment was never the summer treatment to elicit the highest germination, it did not always result in the lowest germination and was a close second for *Eriastrum diffusum*, *Pectocarya recurvata*, and *Plantago patagonica* (Appendix B).

Response to actual germination trial date was even more variable. *Eriastrum diffusum* generally germinated more at later trial dates (Fig. B1 in Appendix B). *Eriophyllum lanosum* had highest germination either early or late, but not at intermediate trial dates (Fig. B2 in Appendix B). *Plantago patagonica* and *Pectocarya heterocarpa* (Figs. B3, B7, and B8 in Appendix B) had highest germination at the intermediate dates, while *Evax multicaulis* had its highest germination on intermediate or late dates (Fig. B6 in Appendix B). *Schismus barbatus* germination at different trial dates was variable depending on the combination of other experimental conditions and *Stylocline micropoides* was variable but with a tendency towards higher germination at early or intermediate trial dates.

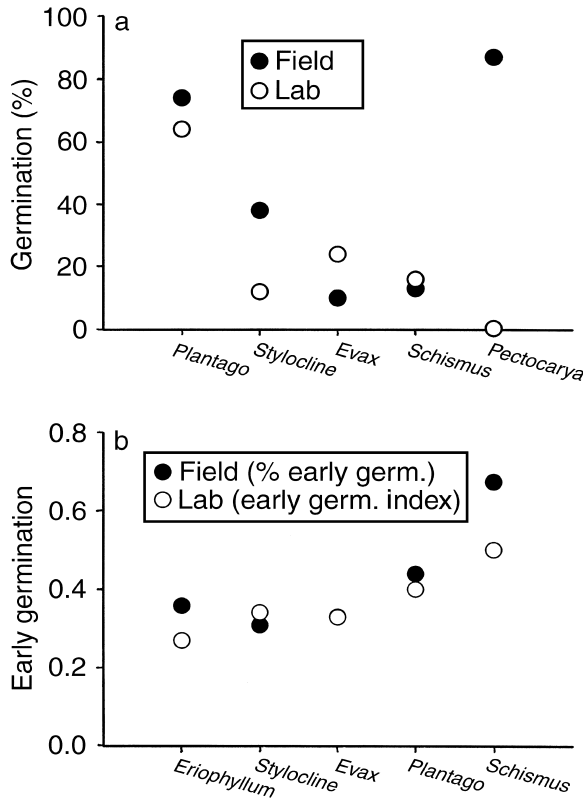


FIG. 1. Germination in the field vs. growth chamber for five species (full names in Table 2). (a) Mean germination in natural field sites (mean over four years with moderate to high rains during the germination season) compared to mean germination in the lab under realistic field conditions. (b) Early germination in the field (see *Methods: Comparison to field germination* for definition) plotted against an index of early germination in the lab under realistic conditions (see *Methods: Comparison to field germination* for calculation).

Two- and even three-way interactions among the treatments were common. Thus, these species in a guild of winter annuals differ in complex ways in their germination response to germination conditions, summer conditions, and trial date. Further insight as to the nature of these differences is revealed in separate analyses of each species (Appendix A).

Four of the five species for which we also have field germination data had mean laboratory germination (using the subset of realistic conditions) that was similar to field germination fractions averaged over years that had precipitation during the germination season (the relevant comparison, see *Methods*). *Plantago patagonica* had high germination fractions in both field and lab, while *Schismus barbatus* and *Evax multicaulis* had fairly low germination in both settings (Fig. 1a). *Stylocline micropoides* had somewhat higher germination in the field than lab. *Pectocarya recurvata*, which had virtually no germination in our lab experiments, had high germination fractions in years with germination rains (Fig. 1a). The similarity of field and lab germination

fractions for the same species is significantly greater than would be expected from the differences in germination fraction among species when the *Pectocarya* comparison is removed, but not when it is included (intraclass correlation, $r = 0.87$, $P = 0.013$ without *Pectocarya* vs. $r = 0.19$, $P = 0.34$ with *Pectocarya*).

The index of early germination in the lab (calculated using only the realistic subset of lab conditions) corresponds quite well with the percent early germination averaged over 15 yr in the field (Fig. 1b, $r = 0.83$, $P < 0.05$). *Schismus barbatus* and *Plantago patagonica* tend to germinate early, while *Eriophyllum lanosum*, *Stylocline micropoides*, and *Evax multicaulis* tended to germinate later in the field and under realistic later season conditions in the lab.

DISCUSSION

A heterogeneous set of germination responses to summer treatment, trial date, and germination conditions exists in this guild of Sonoran Desert winter annuals. Interactions abound, with no two species responding in the same way to our experimental treatments. This suggests a complex array of contingent germination strategies.

Delayed germination

We have subjected desert annual seeds to sets of summer conditions, germination trial dates, temperatures, and day lengths, most of which are representative of what they would encounter in the field (see *Methods: Comparison to field germination*). Yet, large numbers of viable seeds remained dormant under all conditions explored (usually $>50\%$, sometimes $>90\%$). It has often been suggested that desert annuals have persistent seed banks (Went 1949, Juhren et al. 1956, Tevis 1958a, Shreve and Wiggins 1964, Freas and Kemp 1983, Baskin et al. 1993, Philippi 1993a, b, Pake and Venable 1996). Low germination fractions are predicted from the theory of bet hedging due to the high variability and unpredictability of rainfall in deserts and the lack of other persistence mechanisms in annual plants (Cohen 1966, Venable and Lawlor 1980, Philippi and Seger 1989).

Four of the five species for which we have good field data on germination fractions show a good correspondence to laboratory germination fractions (Fig. 1a). Thus low germination following favorable precipitation is representative of what actually occurs in the field site from which seeds were collected and cannot be attributed to not providing the conditions that normally trigger germination. This sort of comparison of natural field germination to growth chamber results is critical to interpreting the relevance of laboratory germination results, but data to make such comparisons are not often available. Our growth chamber results for *Pectocarya* were not representative of this species' germination in the field. We have no clear explanation for

this discrepancy, but note that *P. recurvata* population dynamics over the last 18 yr correlate poorly to those of other species in the guild (Venable et al. 1993, Venable and Pake 1999). This is presumably due to idiosyncratic germination requirements.

Early vs. late germination

Our laboratory results suggest that some species, like as *Schismus barbatus*, tend to germinate more under early season conditions than others, such as *Eriophyllum lanosum*. Such tendencies reflected germination propensities in the field for the five species for which good field data are available (Fig. 1b). This correspondence once again confirms the relevance of the laboratory germination experiments to understanding germination in natural conditions in the field. It also suggests that the tendency to germinate early vs. late in the field is at least partly due to the temperature and day length conditions experienced at the time of precipitation. The tendency to germinate early should be important in determining both competitive success and mortality risk (Baskin and Baskin 1972, Venable et al. 1995, Abbott et al. 1998, Gonzalez-Astorga and Nunez-Farfan 2000). At our field site, early germination of plants in this guild has been found often to result in greater mortality due to warm early-season conditions in years with little follow-up precipitation, or in greater size, due to the extra growth opportunity in wet years (Venable 1989).

Differences in germination requirements and species coexistence

Chesson has derived general conditions under which temporal environmental variation contributes to species coexistence (Chesson 1994, 2000). Applying the general theory to a model of persistent-seed-bank-producing annuals, he has shown that species coexistence and thus diversity should be promoted if each species' germination fraction varies among years and if the germination fractions are less than perfectly correlated among species (Chesson and Huntly 1988, 1989). This can be loosely interpreted in terms of providing the species with at least partially different temporal windows combined with the buffering effects of delayed germination. The species of coexisting winter annuals we have studied differed in their germination response to our experimental manipulations and differed in how the experimental variables interact. Given the general correspondence between field and lab data, such idiosyncratic responses suggest that under one particular set of conditions in the field, a certain species may produce relatively more seedlings, yet given a different set of field conditions, another species may produce more seedlings. Not only do species differ as to which conditions at the time of rainfall result in highest germination, but the optimal conditions often varied depending on the time of year that trials occurred and on the environmental conditions experienced the previous

summer. Thus, there would be chains of circumstances involving these variables leading to different patterns of germination across species and altered aboveground community composition in different years. Investigations of the comparative germination of coexisting species such as this one, performed with a view towards disclosing differences that could contribute to coexistence, are valuable, but rarely performed (Philippi 1993a, Pierce and Moll 1994, Kotorova and Leps 1999, McIvor and Howden 2000).

Quiescence vs. primary and secondary dormancy

Germination of winter annuals does not occur under natural conditions during the summer at our field site despite the occurrence of approximately half of the mean annual precipitation during the summer. It is possible that seeds are produced in a dormant state in the spring and require some period of time to pass, perhaps at high temperatures, before losing dormancy (Baskin and Baskin 1986, Standifer and Willson 1988). An alternative is that seeds may not be dormant at the time of production or that they lose dormancy subsequent to production and only acquire or reacquire it at the time they risk ecologically inappropriate germination in the early autumn (Harper 1957). Another possibility is that seeds are not dormant, but merely quiescent, awaiting specific environmental conditions that are only available in the appropriate germination season (Harper 1957). To distinguish among these alternative possibilities, we have subjected seeds to conditions mimicking natural conditions that occur at different times in the germination season at various actual times bracketing the natural germination season.

Germination in all species varies when seeds are subjected to the same conditions at different times, indicating the importance of dormancy and the passage of time for germination. However, the experimental conditions of temperature and day length also affected germination of all species, indicating the accumulation of quiescent, nondormant seeds awaiting appropriate germination conditions. Germination of both seed types of *Pectocarya heterocarpa* tends to be restricted to the appropriate calendar date, though it is strongly affected by germination conditions as well (Figs. B7 and B8 in Appendix B). *Stylocline micropoides* provides a clear case of secondary dormancy acquired just prior to the autumn germination season. Seeds readily germinate in August given November or December germination season conditions. However, by September, seeds are dormant and do not germinate again under favorable conditions until at least October (Fig. B4d-h in Appendix B). This August window of low dormancy clearly does not affect the species in nature since it will never experience November or December conditions in August. Similarly, but only following dry/hot summer conditions, *Eriophyllum lanosum* had its highest germination in August, acquiring greater dormancy by September. Also, *Evax multicaulis* readily germinated

in August given November or December conditions, but only after wet/hot conditions *Plantago patagonica* appears to have conditional dormancy sensu Baskin and Baskin (1998). It has high germination during all trials given November or December conditions but only gradually acquires the ability to germinate under October conditions (Fig. B3g–i in Appendix B).

The complexity of these germination responses suggests that the divisions between quiescent and dormant, primary and secondary, and conditional vs. innate are simplistic for most of these species. The answers are contingent and several possibilities usually exist for a species. If such patterns are found for other plants as well, it may suggest that these simple categories underrepresent the complexity of germination biology.

This investigation has shed light on the germination biology of a guild of desert annuals. A considerable fraction of seeds do not germinate under favorable conditions either in the field or under controlled growth chamber conditions. Such seed behavior is consistent with predictions of bet hedging for desert annuals. Also, a seed-bank annual version of the storage effect model requires for coexistence that species have independently variable germination fractions (i.e., have species by condition interactions for germination percentage). By focusing on this dynamic we have shown that such interactions exist in the growth-chamber responses of eight common members of a guild of desert annuals. More specifically, we were able to show that oversummering conditions, calendar date of germination, temperature, and day length play a part in these differential responses. Furthermore, the growth-chamber germination results seem to reflect to a reasonable degree what actually happens in the field. Postgermination dynamics reported elsewhere (Pantastico-Caldas and Venable 1993, Pake and Venable 1995, 1996) will be important in determining the actual competitive outcomes. However, the species by conditions interactions for germination promote coexistence, and hence are worthy of isolation and investigation. Many of the details that determine the germination biology of plants are important in determining population and community dynamics. Thus, focused studies like the one here, conducted in the larger framework of long-term field studies, can yield a deeper understanding of plant population and community dynamics (Rees et al. 2001).

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LITERATURE CITED

- Abbott, R. J., F. C. Bretagnolle, and C. Thebaud. 1998. Evolution of a polymorphism for outcrossing rate in *Senecio vulgaris*: influence of germination behavior. *Evolution* **52**:1593–1601.

- Aitkin, M., D. Anderson, B. Francis, and J. Hinde. 1989. Statistical modelling in GLIM. Oxford University Press, Oxford, UK.
- Baskin, C. C., and J. M. Baskin. 1998. Seeds: ecology, biogeography, and evolution of dormancy and germination. Academic Press, San Diego, California, USA.
- Baskin, C. C., P. L. Chesson, and J. M. Baskin. 1993. Annual seed dormancy cycles in 2 desert winter annuals. *Journal of Ecology* **81**:551–556.
- Baskin, J. M., and C. C. Baskin. 1972. Influence of germination date on survival and seed production in a natural population of *Leavenworthia stylosa*. *American Midland Naturalist* **88**:318.
- Baskin, J. M., and C. C. Baskin. 1976. High-temperature requirement for after-ripening in seeds of winter annuals. *New Phytologist* **77**:619–624.
- Baskin, J. M., and C. C. Baskin. 1979. Effect of relative humidity on after-ripening and viability in seeds of the winter annual *Draba verna*. *Botanical Gazette* **140**:284–187.
- Baskin, J. M., and C. C. Baskin. 1986. Temperature requirements for after-ripening in seeds of nine winter annuals. *Weed Science* **33**:375–380.
- Beatley, J. C. 1967. Survival of winter annuals in northern Mojave Desert. *Ecology* **48**:745–750.
- Bowers, J. E., and R. M. Turner. 1985. A revised vascular flora of Tumamoc Hill, Tucson, Arizona. *Madrono* **32**:225–252.
- Burk, J. H. 1982. Phenology, germination, and survival of desert ephemerals in Deep Canyon, Riverside County, California. *Madrono* **29**:154–163.
- Chesson, P. 1994. Multispecies competition in variable environments. *Theoretical Population Biology* **45**:227–276.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* **31**:343–366.
- 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., and N. Huntly. 1989. Short-term instabilities and long-term community dynamics. *Trends in Ecology and Evolution* **4**:293–298.
- Clauss, M. J., and D. L. Venable. 2000. Seed germination in desert annuals: an empirical test of adaptive bet hedging. *American Naturalist* **155**:168–186.
- Cohen, D. 1966. Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology* **12**:119–129.
- Crawley, M. J. 1993. GLIM for ecologists. Blackwell Scientific, Oxford, UK.
- Ellner, S. 1987. Alternate plant life history strategies and coexistence in randomly varying environments. *Vegetatio* **69**:199–208.
- 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.
- Gonzalez-Astorga, J., and J. Nunez-Farfan. 2000. Variable demography in relation to germination time in the annual plant *Tagetes micrantha* Cav. (Asteraceae). *Plant Ecology* **151**:253–259.
- Harper, J. L. 1957. The ecological significance of dormancy and its importance in weed control. *Proceedings of the International Congress for Crop Protection* **4**:415–420.
- 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. *Ecology* **37**:318–330.

- Kotorova, I., and J. Leps. 1999. Comparative ecology of seedling recruitment in an oligotrophic wet meadow. *Journal of Vegetation Science* **10**:175–186.
- McIvor, J. G., and S. M. Howden. 2000. Dormancy and germination characteristics of herbaceous species in the seasonally dry tropics of northern Australia. *Austral Ecology* **25**:213–222.
- Moriuchi, K. S., D. L. Venable, C. E. Pake, and T. Lange. 2000. Direct measurement of the seed bank age structure of a Sonoran Desert annual plant. *Ecology* **81**:1133–1138.
- Pake, C. E., and D. L. Venable. 1995. Is coexistence of Sonoran Desert annuals mediated by temporal variability in reproductive success? *Ecology* **76**:246–261.
- Pake, C. E., and D. L. Venable. 1996. Seed banks in desert annuals: implications for persistence and coexistence in variable environments. *Ecology* **77**:1427–1435.
- Pantastico-Caldas, M., and D. L. Venable. 1993. Competition in two species of desert annuals along a topographic gradient. *Ecology* **74**:2192–2203.
- Philippi, T. 1993a. Bet-hedging germination of desert annuals—beyond the 1st year. *American Naturalist* **142**:474–487.
- Philippi, T. 1993b. Bet-hedging germination of desert annuals—variation among populations and maternal effects in *Lepidium lasiocarpum*. *American Naturalist* **142**:488–507.
- Philippi, T., and J. Seger. 1989. Hedging ones evolutionary bets, revisited. *Trends in Ecology and Evolution* **4**:41–44.
- Pierce, S. M., and E. J. Moll. 1994. Germination ecology of 6 shrubs in fire-prone Cape Fynbos. *Vegetatio* **110**:25–41.
- Rees, M., R. Condit, M. Crawley, S. Pacala, and D. Tilman. 2001. Long-term studies of vegetation dynamics. *Science* **293**:650–655.
- Shreve, F., and I. L. Wiggins. 1964. *Vegetation of the Sonoran Desert*. Stanford University Press, Stanford, California, USA.
- Standifer, L. C., and P. W. Willson. 1988. A high temperature requirement for after ripening of imbibed seeds of *Poa annua* seeds. *Weed Research* **28**:365–371.
- Tevis, L. 1958a. Germination and growth of ephemerals induced by sprinkling a sandy desert. *Ecology* **39**:681–688.
- Tevis, L. 1958b. A population of desert ephemerals germinated by less than one inch of rain. *Ecology* **39**:688–695.
- Venable, D. L. 1985. The evolutionary ecology of seed heteromorphism. *American Naturalist* **126**:577–595.
- Venable, D. L. 1989. Modeling the evolutionary ecology of seed banks. Pages 67–87 in M. A. Leck, V. T. Parker, and R. L. Simpson, editors. *The ecology of soil seed banks*. Academic Press, San Diego, California, USA.
- Venable, D. L., E. Dyreson, and E. Morales. 1995. Population-dynamic consequences and evolution of seed traits of *Heterosperma pinnatum* (Asteraceae). *American Journal of Botany* **82**:410–420.
- 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. 1999. Population ecology of Sonoran Desert annual plants. Pages 115–142 in R. H. Robichaux, editor. *The ecology of Sonoran Desert plants and plant communities*. University of Arizona Press, Tucson, Arizona, USA.
- Venable, D. L., C. E. Pake, and A. C. Caprio. 1993. Diversity and coexistence of Sonoran Desert winter annuals. *Plant Species Biology* **8**:207–216.
- Went, F. W. 1949. Ecology of desert plants. II. The effect of rain and temperature on germination and growth. *Ecology* **30**:1–13.

APPENDIX A

Tables of separate generalized linear models (GLIM) analyses for each species and for seed types of *Pectocarya heterocarpa* are available in ESA's Electronic Data Archive: *Ecological Archives* E085-076-A1.

APPENDIX B

Figures of growth chamber germination percentages for each species collapsed over nonsignificant interactions are available in ESA's Electronic Data Archive: *Ecological Archives* E085-076-A2.