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Seed Germination in Desert Annuals: An Empirical Test of Adaptive Bet Hedging

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abstract: Temporal variability in survivorship and reproduction is predicted to affect the evolution of life-history characters. Desert annual plants experience temporal variation in reproductive success that is largely caused by precipitation variability. We studied several populations of the desert annual *Plantago insularis* along a precipitation gradient. Whereas models of bet hedging in unpredictable environments generally predict one optimal germination fraction for a population, empirical studies have shown that environmental conditions during germination can cause a range of germination fractions to be expressed. In a 4-yr field study, we found that populations in historically more xeric environments had lower mean germination fractions, as is predicted by bet-hedging models. However, populations exhibited significant variation in germination among years. Two experimental studies measuring germination under several environment conditions were conducted to elucidate the source of this in situ variation. Germination fractions exhibited phenotypic plasticity in response to water availability and date within the season. Populations differed in their norms of reaction such that seeds from more xeric populations germinated under less restrictive conditions. A pattern of delayed germination consistent with among-year bet-hedging predictions arose in the field through the interaction of seed germinability and the distribution of environmental conditions during germination.

Keywords: desert annual plant, bet hedging, phenotypic plasticity, seed germination, variable environments, life history.

Temporal variability in survivorship and reproduction has important consequences for life-history evolution and population dynamics (Cohen 1966; Levins 1968; Gillespie 1981; Stearns 1992; Rhodes et al. 1996). When temporal variability is large, such that in some years most individuals in a particular developmental stage die, selection will favor life-history strategies that reduce variance in fitness (Cohen 1966; Tuljapukar 1990). Annual plants in highly variable environments such as deserts are particularly vulnerable to mortality during the vegetative phase (Beatley 1974; Venable and Pake 1999). Delay in germination of some seeds is predicted to reduce temporal variance in individual fitness in desert annuals. When seeds of a genotype germinate over a number of years, the probability that all seedlings will die before reproducing is lowered. Delayed germination is a bet-hedging strategy if it reduces temporal variance in reproductive success for a genotype and also reduces arithmetic mean fitness. Bet hedging is adaptive if it increases geometric mean fitness (Seger and Brockmann 1987). Delayed seed germination as an adaptive bet-hedging strategy has been the subject of a large number of theoretical models (Cohen 1966, 1967; MacArthur 1972; Venable and Lawlor 1980; Bulmer 1984; Cohen and Levin 1985; Ellner 1985, 1986, 1987; Leon 1985; Brown and Venable 1986; Klinkhamer et al. 1987; Venable and Brown 1988; Venable 1989) and a much smaller number of rigorous empirical tests (Philippi 1993*b*; Pake and Venable 1996; Venable and Pake 1999).

Conditions under which fitness (*W*) is maximized by bet hedging via delayed seed germination in unpredictably variable environments can be found from the following fitness equation:

$$\overline{W} = [s(1 - G) + YG]^{P_g} \times [s(1 - G)]^{P_b}, \tag{1}$$

where *s* is the survival rate to the following year of nongerminated seeds, *G* is the fraction of seeds germinating, P_g and P_b are the probabilities of good and bad years, *Y* is the average seed yield per germinated seed (reproductive success) in good years, and reproductive success is assumed to be 0 in bad years (Cohen 1966). When *Y* is large, the germination fraction that maximizes fitness is approximately equal to the probability a year will be good for the survivorship and reproduction of germinated seedlings, P_g. Thus, populations that differ in probability of a

good year will differ in optimal germination fraction (G^*).

Empirical tests of adaptive variation in germination fractions generally use seeds collected from maternal plants in natural populations that differ in climate. Because direct estimates of the probability of a good year for multiple populations are rare, climatic differences are assumed to reflect variation in P_g and thus selection on germination. For example, precipitation and temperature have been used to characterize the frequency of good and poor year types in multiple populations of a desert annual (Philippi 1993*b*). Seed germination fractions are then determined in the greenhouse or growth chamber (e.g., Jain 1982; Philippi 1993*b*). Such studies record germination fractions in benign environments that are conducive to germination of nondormant seeds, and under these conditions, populations have been shown to differ significantly, yet without a consistent relationship to the climatic gradient under investigation (Jain 1982; Hacker 1984; Gutterman and Edine 1988; Philippi 1993*b*; Kigel 1995). Several empirical studies have focused on additive genetic variation, dominance and epistatic effects, as well as maternal effects to explain such population differences (Schmitt et al. 1992; Philippi 1993*b*; Platenkamp and Shaw 1993; Wulff et al. 1994; Wulff 1995).

Less emphasis has been placed on the role of environmental conditions during germination for observed differences among populations. Environmental factors such as water, temperature, and photoperiod have been found to affect germination responses in almost all species investigated (Gutterman 1993; Baskin and Baskin 1998). Furthermore, the phenotypic response to these factors can differ among species, populations, and genotypes (Schmitt et al. 1992; Beckstead et al. 1996; Baskin and Baskin 1998). Therefore, germination fractions in the field may differ among years and populations and from those observed in controlled conditions, simply as a result of variation in environmental conditions during germination. Such phenotypic variability could cause actual germination fractions to deviate in a nonadaptive manner from any optimum predicted by bet-hedging models. Alternatively, if conditions during germination are predictive of future survival and reproduction, then phenotypic plasticity in germination is expected to evolve and to give rise to predictive germination (Cohen 1967). Understanding variation in germination fractions along environmental gradients requires consideration of systematic differences among populations, both in environmental conditions during the germination season and in the probability of a good year determined by the postgermination environment. Neither the among-year distribution of environmental conditions during the germination season nor the effect of environmental conditions on germination has been considered in previous empirical studies of bet hedging.

We conducted a multiyear study of germination in several populations of the desert winter annual *Plantago insularis*. The goal was to estimate optimal germination fractions for populations of this species and to determine whether the observed variation supported microevolutionary predictions for temporally varying environments. Populations were chosen along a precipitation gradient. Optimal germination fractions for each population were estimated from the proportion of good years in the historical precipitation record. Germination fractions were then measured in three environmental settings. In situ seed germination in four populations of *P. insularis* was observed in 4 yr, including one El Niño season. In a common garden experiment with five populations, we tested the effects of water quantity and date within the season on germination fractions. Finally, we assessed differentiation across the geographic range of the species by sampling the soil seed bank from 12 populations in southwestern Arizona and southern California and measuring germination fractions in a growth chamber.

Species, Populations, and Precipitation

Plantago insularis Eastw. [incl. var. *fastigiata* (E. Morris) Jepson] (section *Leucopsyllium*, Plantaginaceae) (desert Indian wheat) is a scapose winter annual endemic to the Sonoran and Mohave Deserts of the southwestern United States and northwestern Mexico. The species occurs on low-elevation desert bajadas and flood plains (0–1,000 m) in association with other annuals, such as *Amsinckia intermedia*, *Chorizanthe rigida*, *Erodium texanum*, *Lepidium lasiocarpum*, *Pectocarya recurvata*, and *Schismus barbatus*, as well as perennial vegetation dominated by *Ambrosia dumosa*, *Atriplex canescens*, *Carnegiea gigantea*, *Larrea tridentata*, and *Opuntia* spp. *Plantago insularis* is one of the most abundant winter annual species and is a preferred native forage species of desert herbivores (Reichman 1975; Krausman et al. 1989; Seegmiller et al. 1990). Seeds of Sonoran and Mohave Desert winter annuals germinate between September and March in response to cool temperatures and rainfall events >15–25 mm (Juhren et al. 1956; Tevis 1958*a*, 1958*b*; Beatley 1974). When germination is followed by rain in the subsequent several months, high plant survivorship and reproduction result in positive population growth rates (Beatley 1974; Loria and Noy-Meir 1979/1980; Venable and Pake 1999). Plants set seed and senesce before onset of the arid foresummer. A persistent soil seed bank is formed when seeds remain ungerminated in the soil after the end of the germination season (Pake and Venable 1996).

The 12 study populations of *P. insularis* are located in

Table 1: Winter precipitation (mm between September and March) at 12 locations in southern Arizona and California

Location	Abbreviation	Latitude and longitude	n	Mean[a]	Variance	CV	$P_{g\|r}$ [b]	G_r^{*} [c]
Florence, Ariz.	FL	111°20′W, 33°08′N	58	171[A]	5,296	43	.78	.78
Organ Pipe Cactus National Monument, Ariz.	OP	112°46′W, 32°05′N	46	142[B]	5,197	51	.63	.63
Gila Bend, Ariz.	GB	112°48′W, 32°36′N	100	99[C]	3,052	56	.56	.56
Barstow, Calif.	BA	116°59′W, 34°52′N	38	81[CD]	1,843	53	.48	.47
Needles, Calif.	NE	114°45′W, 34°55′N	91	80[CD]	2,495	62	.42	.41
Blythe, Calif.	BL	114°45′W, 33°40′N	76	71[C]	1,962	63	.21	.20
Wellton, Ariz.	WE	114°10′W, 32°40′N	47	70[C]	2,424	70	.26	.25
Sentinel, Ariz.[d]	SE	113°15′W, 32°57′N	23	69[C]	2,315	70	.11	.10
Indio, Calif.	IN	116°05′W, 33°45′N	89	69[C]	2,458	72	.23	.22
Eagle Mountain, Calif.	EM	115°05′W, 33°50′N	56	63[C]	2,072	73	.25	.24
Yuma, Ariz.	YU	114°32′W, 32°24′N	120	59[C]	1,617	69	.14	.13
Brawley, Calif.	BR	115°26′W, 32°58′N	80	53[C]	1,530	73	.18	.17

Note: Mean, variance, coefficient of variation (CV), probability of a good year ($P_{g\|r}$), and optimal germination fraction (G_r^{*}) were calculated for a sample of n winters with complete precipitation records. Locations are listed in order of decreasing mean winter precipitation.

[a] Means with different letters are significantly different ($P < .05$) in Student-Newman-Keuls a posteriori multiple comparison; $F = 30.0$, df = 11, 812, $P < .001$.

[b] Proportion of good years given germination rain calculated with 17/24/30 threshold (see "Estimation of Optimal Germination Fractions").

[c] Optimal germination fractions calculated from equation (2), with $P_{g\|r}$ estimated from 17/24/30; $s = 1.0$, $Y_g = 100$, $Y_p = 0$.

[d] Long-term data from Dateland, Ariz.

the Arizona Upland and Lower Colorado Valley subdivisions of the Sonoran Desert and in the Mohave Desert. Each population is within 20 km of a weather station for which climatic data are available from the National Oceanic and Atmospheric Administration (NOAA). The historical precipitation record depicts significant differences among the 12 locations (table 1). Mean winter rainfall (September–March) ranged from a low of 53 mm (Brawley, Calif.) to 171 mm at the most mesic site (Florence, Ariz.; table 1). Populations with lower mean winter precipitation had higher coefficients of variation (table 1). The slope of the linear regression of log standard deviation and log mean winter precipitation ($b = 0.552$) was significantly <1 ($F = 67.91$, df = 1, 10, $P < .001$), indicating that more xeric populations had proportionately greater standard deviations. Although all populations are found in dry desert environments, we refer to populations as relatively more mesic and more xeric throughout this article.

El Niño–Southern Oscillations (ENSO), during which southwestern North America receives more than average winter precipitation (Ropelewski and Halpert 1986), affect the study populations differently. We identified ENSO years from sea-surface temperatures (Japan Meteorological Agency) and calculated total winter precipitation in all ENSO and non-ENSO years from 1949 to 1990 for each population. ENSO years had higher mean winter precipitation than non-ENSO years for all 12 populations ($P < .05$ for nine of 12 populations). A linear regression of log-transformed population mean precipitation in ENSO years versus in non-ENSO years estimated a slope of 0.73. This

value was significantly <1 ($F = 6.87$, df = 1, 10, $P = .026$), indicating that more xeric populations received proportionately more precipitation during ENSO years. ENSO also affected the timing of precipitation during the winter. In non-ENSO years, the month during which the most rain fell was December or January in 11 of 12 populations. In contrast, significantly fewer populations (three of 12) had maximal rainfall in December or January in ENSO years ($\chi^2 = 8.4$, df = 1, $P < .005$). During ENSO years, most populations had maximal rainfall in either October or March, when average day length was longer and temperatures were higher (Sellers and Hill 1974). Florence and Organ Pipe, the two most mesic populations, had maximal rain in December in ENSO as well as non-ENSO years.

Estimation of Optimal Germination Fractions

The model of Cohen (1966) in equation (1) calculates the optimal constant germination fraction assuming that seeds can germinate in every year. However, real desert annuals are faced with years in which there is inadequate rain for germination. Because it is meaningless to ask what fraction of seeds should germinate in these dry years, we modified the Cohen (1966) model to include a third year type: years with inadequate rain for germination. With this modification the model becomes

$$\overline{W} = [s(1 - G_r) + YG_r]^{P_r \times P_{g\|r}} \times [s(1 - G_r)]^{P_r \times P_{b\|r}} \times s^{P_n}, \quad (2)$$

where G_r is the germination fraction in years with adequate

rain for germination and where the germination fraction is constrained to equal 0 in years with inadequate germination rain. The probability of a year without germination rain is P_n, and P_r is the probability of a year with adequate rain for germination. The probability of a good year for survival and reproduction, given that there was adequate rain for germination, is $P_{g|r}$, and $P_{b|r}$ is the probability of a bad year for survival and reproduction, given that there was adequate rain for germination. The optimal germination fraction for this model is given by

$$G_r^* = \frac{P_{g|r}Y - s}{Y - s}, \qquad (3)$$

which approximately equals $P_{g|r}$ when Y is large.

Thus, G_r^* should be approximately equal to the proportion of good years among years with enough rain for germination. This result is similar to that of Cohen (1967), except that not germinating with inadequate germination rain is a constraint rather than an optimal strategy in response to a cue predicting a poor year. The amount of germination rain may still act as a cue predicting higher survival and reproduction in subsequent months (Cohen 1967).

We used estimates of precipitation requirements for germination, growth, and reproduction, together with historical precipitation records for each of the 12 populations, to predict probabilities of good years and optimal germination fractions, as follows. For each weather station and in each winter season with a complete record, we assessed whether any 1 mo between September and March had greater than the 17 mm rainfall that we considered necessary for germination. Years meeting this criterion were designated as having adequate rain for germination. Then, for each month with >17-mm rain, we determined whether the following 2 mo had greater than the 24 mm or 30 mm, respectively, that are required for growing to reproductive maturity. The season was designated as good if at least one sequence of months fulfilled the above criteria. By this definition, a good year reflects both the amount and timing of germination and growth rains within a season. The probability of a good winter season given adequate rain for germination ($P_{g|r}$) was estimated as the proportion of years with germination rains that were good (referred to as 17/24/30). We then calculated $P_{g|r}$ with two more permissive sets of threshold values (17/20/20 and 5/20/20).

The proportion of good years given germination rain (17/24/30) varied widely, from 0.11 at Sentinel to 0.78 at Florence (table 1). Although the proportion of good years was affected by the threshold values used, the rank orders, and therefore the positions of the populations along the precipitation gradient, were highly correlated for alter-
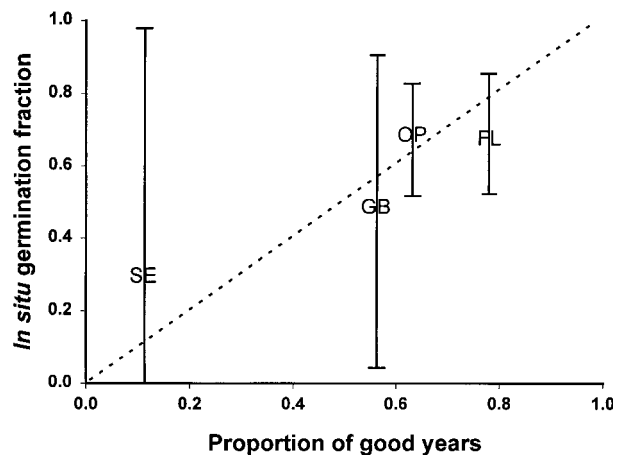

Figure 1: In situ germination fractions in four populations of *Plantago insularis*. Two-letter population abbreviations are positioned at population means: *SE* = Sentinel, *GB* = Gila Bend, *OP* = Organ Pipe, *FL* = Florence. Bars represent the range of germination fractions observed in 4 yr. Populations are placed along the abscissa according to their proportions of good years ($P_{g|r}$) calculated by using the 17/24/30 threshold. The dotted line indicates optimal germination fractions predicted for different values of the $P_{g|r}$.

native calculations ($r_s > 0.75$, $P < .005$). The three measures of proportion of good years (17/24/30, 17/20/20, and 5/20/20) were also positively correlated with the mean winter precipitation ($r_s > 0.88$, $P < .001$) and negatively correlated with the coefficient of variation ($r_s < -0.59$, $P < .04$).

We then estimated the optimal germination fraction for each population by maximizing W in equation (2) with respect to G_r. Optimal germination fractions (G_r^*) were <1 at all populations (table 1). When $P_{g|r}$ was calculated with the 17/24/30 threshold, $s = 1$ and $Y = 100$, G_r^* was approximately equal to $P_{g|r}$ (table 1). Increasing Y from five to 500 caused G_r^* to approach $P_{g|r}$ from below. When seed survival was increased from 0.1 to 1, G_r^* decreased slightly from $P_{g|r}$, as seen in table 1 for the more xeric populations. Deviations in G_r^* as a result of varying s, Y, and the threshold criteria were small relative to among-population variation in G_r^*. Populations of *Plantago insularis* were predicted to differ systematically in G_r^*; populations that are more xeric should experience selection for lower germination fractions in any single year (table 1).

Though the model discussed previously assumes density-independent population dynamics, a similar selective gradient was predicted assuming density dependence. In a density-dependent model of the evolution of seed germination, Ellner (1985) incorporates differences in variance of reproductive success under high and low density. The subset of assumptions in Ellner's model most ap-

Table 2: Seedling density (L), seed density after germination (D), and germination fraction ($G = L/[D + L]$) in four populations of *Plantago insularis* in 4 yr

Population	Seedlings/m²[a]	Seeds/m²[b]	Germination fraction	Total winter precipitation (mm)
1994–1995:				
Sentinel	1,052[B]	4,787[A]	.18	82.8
Gila Bend	291[C]	36[B]	.89	127.0
Organ Pipe	519[C]	453[B]	.53	243.8
Florence	2,163[A]	417[B]	.84	220.0
1995–1996:				
Sentinel	13[C]	3,656[A]	.003	2.5
Gila Bend	2,254[A]	1,178[B]	.66	49.0
Organ Pipe	1,495[B]	997[B]	.60	91.4
Florence	2,313[A]	1,994[B]	.54	84.3
1996–1997:[c]				
Sentinel	0[A]	1,037[A]	.00	9.6
Gila Bend	24[A]	358[B]	.06	59.2
Organ Pipe	97[A]	26[C]	.79	57.9
Florence	91[A]	40[C]	.69	67.5
1997–1998:				
Sentinel	486[A]	13[B]	.97	167.6
Gila Bend	128[B]	298[A]	.30	136.6
Organ Pipe	57[B]	13[B]	.81	245.4
Florence	90[B]	52[B]	.63	295.2

Note: Total winter precipitation (September to March) was measured at nearby National Oceanic and Atmospheric Administration weather stations.

[a] Population: $F = 57.3$, df $= 3, 544$, $P < .0001$; year: $F = 56.6$, df $= 3, 544$, $P < .0001$; population $*$ year: $F = 28.1$, df $= 9, 544$, $P < .0001$. Letters indicate significant differences among populations in Student-Newman-Keuls a posteriori multiple comparison for each year separately.

[b] Population: $F = 14.3$, df $= 3, 424$, $P < .0001$; year: $F = 11.7$, df $= 3, 424$, $P < .0001$; population $*$ year: $F = 5.7$, df $= 9, 424$, $P < .0001$. Letters indicate significant differences among populations in Student-Newman-Keuls a posteriori multiple comparison for each year separately.

[c] For 1996–1997 only, D was estimated as the mean pregermination densities in the common garden experiment minus mean seedling density in the field for each population. ANOVA was conducted on pregermination seed densities in replicate trays.

plicable to this desert annual system are intermediate levels of seed survivorship, variance in total reproductive yield that is large, and the possibility of years with zero reproductive yield (Clauss 1999). Simulations with these conditions for the 12 populations showed that the density-dependent model predicts optimal germination fractions that are <1 and that are qualitatively similar (although somewhat lower) to the predictions from the density-independent model (M. Clauss and D. Venable, unpublished data).

Characterizing temporal variability in reproductive success by using historical precipitation records provides long-term information not generally available from demographic studies. For *P. insularis*, we can confirm the existence of large temporal variability from field obser-

vations of per capita survival and reproduction (Y) in four populations (Clauss 1999). Geometric mean growth rates of hypothetical genotypes ranging from $G_r = 0$ to $G_r = 1$ were calculated for each population from equation (2), allowing each year to be a separate year type occurring with equal probability. Using estimates of Y from field observations in 4 yr and assuming 100% seed survival in the soil, we found that hypothetical germination fractions of 0.5, 0.8, and 0.6 maximized growth rates for three populations. Only at the most mesic population, Florence, did a hypothetical genotype with no delayed germination ($G_r^* = 1$) have greatest fitness in this 4-yr period. Florence also had the greatest G_r^* as calculated from the historic precipitation data (table 1). Thus, direct measures of temporal variability in reproductive success in *P. insularis* con-
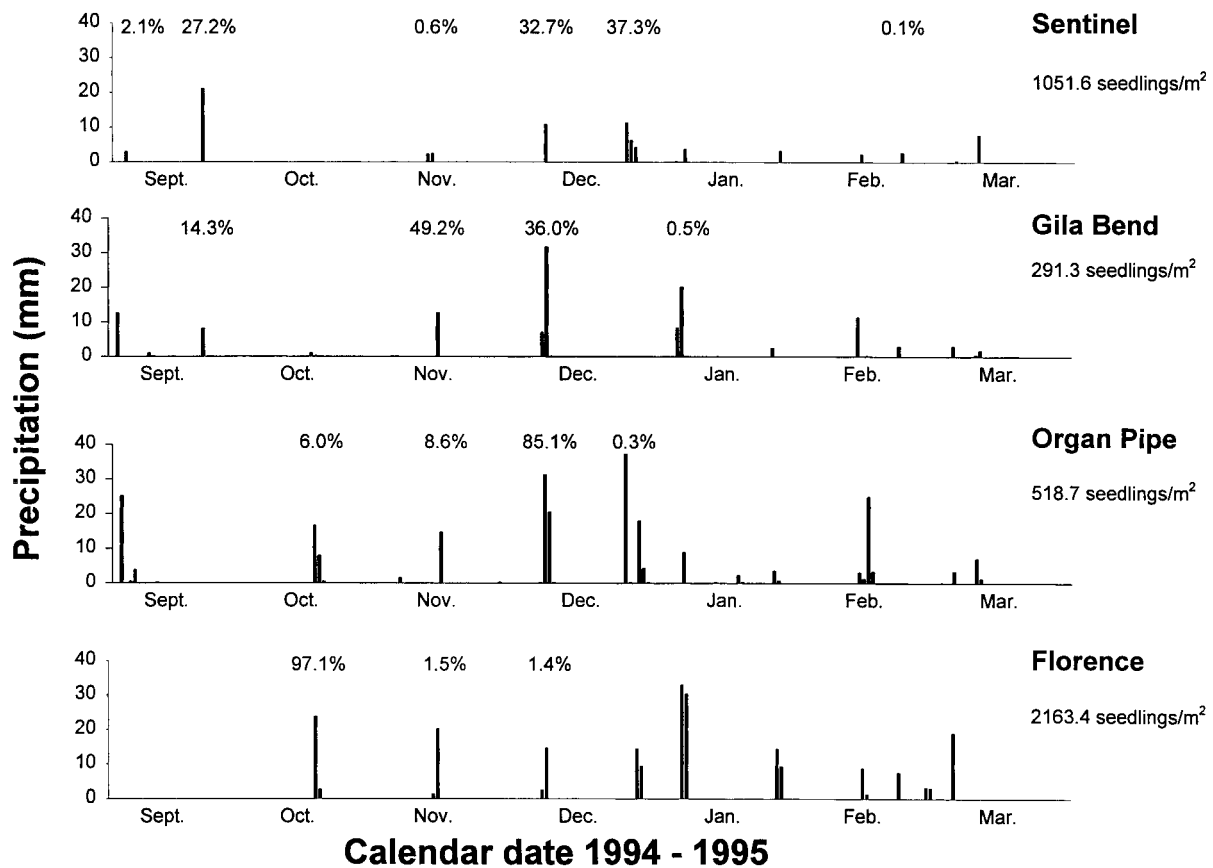
Figure 2: Daily precipitation amount (*mm*) and timing of germination for *Plantago insularis* at four populations in southern Arizona in the winter of 1994–1995. The size of the germination cohort measured as the percentage of total seedling density is indicated above the rainfall event that resulted in germination. Total density of seedlings is given under each population name.

firm the prediction for three of four populations that bet hedging via delayed seed germination should be an adaptive strategy.

Measurement of Germination Fractions

Study 1: In Situ Germination at Four Populations

Methods. Germination under natural conditions was studied in four populations of *Plantago insularis* in southern Arizona between September 1994 and March 1998. Populations at Florence, Organ Pipe, Gila Bend, and Sentinel were chosen because they span a wide range in proportion of good years (table 1). At each population, five sites were deployed at 1-km intervals, each containing eight quadrats, for a total of 40 permanent quadrats. The eight quadrats per site were positioned by using stratified random sampling within a 25 × 20-m area divided into 5 × 5-m grid squares. Within-grid squares, quadrats were located ran-

domly with the provision that the minimum distance between two quadrats was 2 m and that each quadrat be located >1 m from the edge of any shrub. Quadrat sizes were allowed to vary between 0.0225 and 0.25 m² to maintain adequate sample sizes in the face of fluctuating seedling density. Over 15,000 individuals of *P. insularis* germinating within quadrats were mapped on acetate sheets by using a clear plexiglas table during 10, eight, nine, and 13 censuses in 1994–1995, 1995–1996, 1996–1997, and 1997–1998, respectively. By surveying the populations after all rainfall events between September and March, we determined the timing and amount of precipitation that resulted in seedling emergence. Germination did not occur outside this 7-mo period. Seedlings emerge within 12 d of a rainfall event (M. J. Clauss, personal observation), and all newly germinated seedlings recorded during a census constitute a germination cohort.

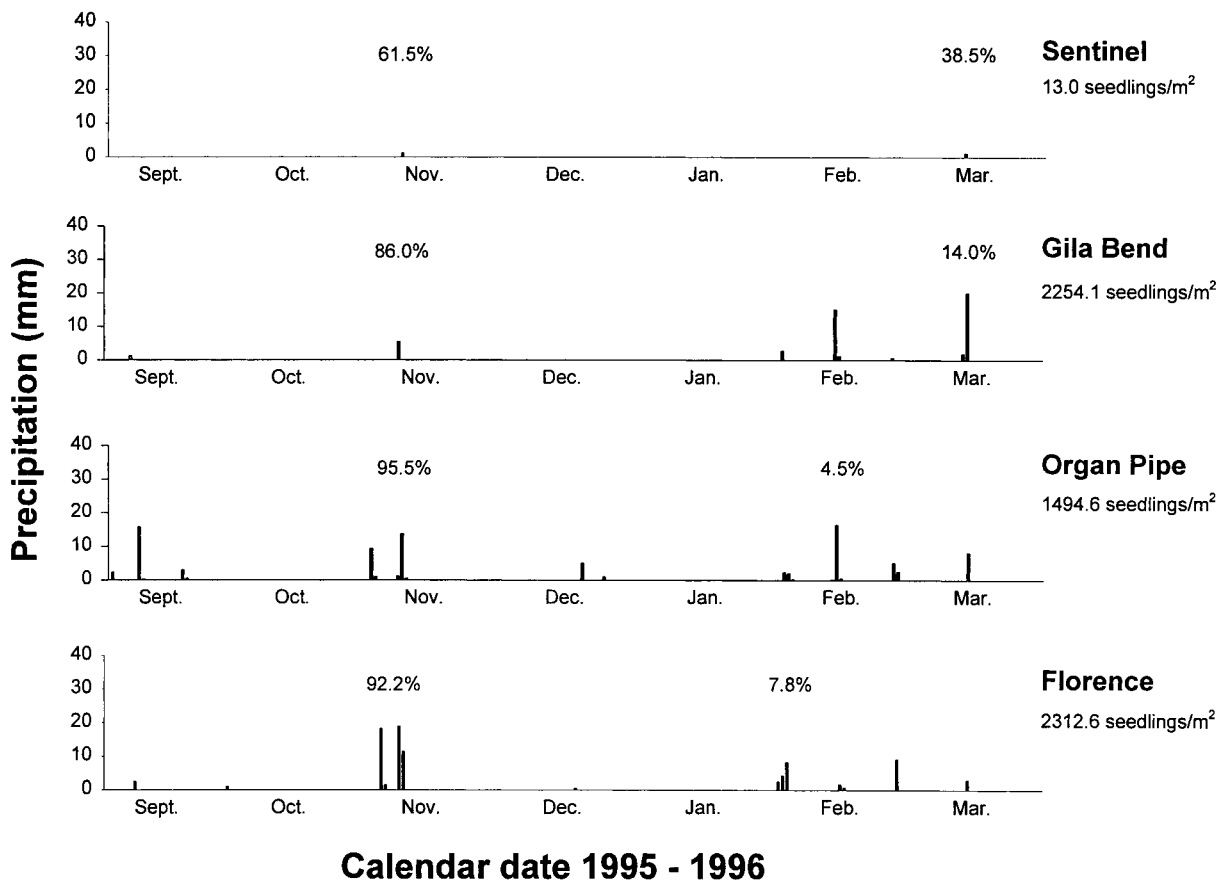We estimated in situ germination fractions (*G*) for each

Figure 3: Daily precipitation amount (*mm*) and timing of germination for *Plantago insularis* at four populations in southern Arizona in the winter of 1995–1996. The size of the germination cohort measured as the percentage of total seedling density is indicated above the rainfall event that resulted in germination. Total density of seedlings is given under each population name.

population in each season. Germination fractions were calculated from the density per square meter of seedlings (*L*; from the germination monitoring described previously), and the density per square meter of viable seeds in the soil seed bank after germination (*D*), determined as follows. In 3 of 4 yr, we estimated the seed bank by sampling $22.06\text{-cm}^2 \times 2\text{-cm-deep}$ soil cores in early March, after the last germination cohort and before the dispersal of new seeds. Shallow soil cores provide an appropriate estimate of the seed bank because most (>89%) viable seeds lie within the top 2 cm of the soil surface in desert sites (Reichman 1984; Pake and Venable 1996). In March 1995, one core was collected adjacent to each of five randomly chosen permanent plots at each of the five sites per population (for a total of 25 samples per population). In March 1996, one core was taken adjacent to six plots at each of the five sites (30 samples per population). In March 1998, one soil core was collected adjacent

to each of seven permanent plots at each of five sites (35 samples per population). For these 3 yr, the sum of the average density of viable nongerminated seeds and the average seedling density for that season equals the density of seeds in the soil before germination (*L* + *D*), assuming no seed mortality during the germination period. For 1996–1997, seed density before germination was estimated from 16 $480\text{-cm}^2 \times 2\text{-cm-deep}$ soil samples taken from each population in November 1996 for the common garden experiment (see study 2, "Methods"). In all years, the soil from each sample was sieved, all *P. insularis* seeds were removed, and viable seeds were counted. All seeds were cut or poked through the seed coat to determine viability. Seeds with fleshy endosperm were regarded as viable. We found this technique for testing seed viability superior to using tetrazolium chloride because some deeply dormant viable seeds show minimal staining with tetrazolium and because embryos and endosperm in the field usually un-
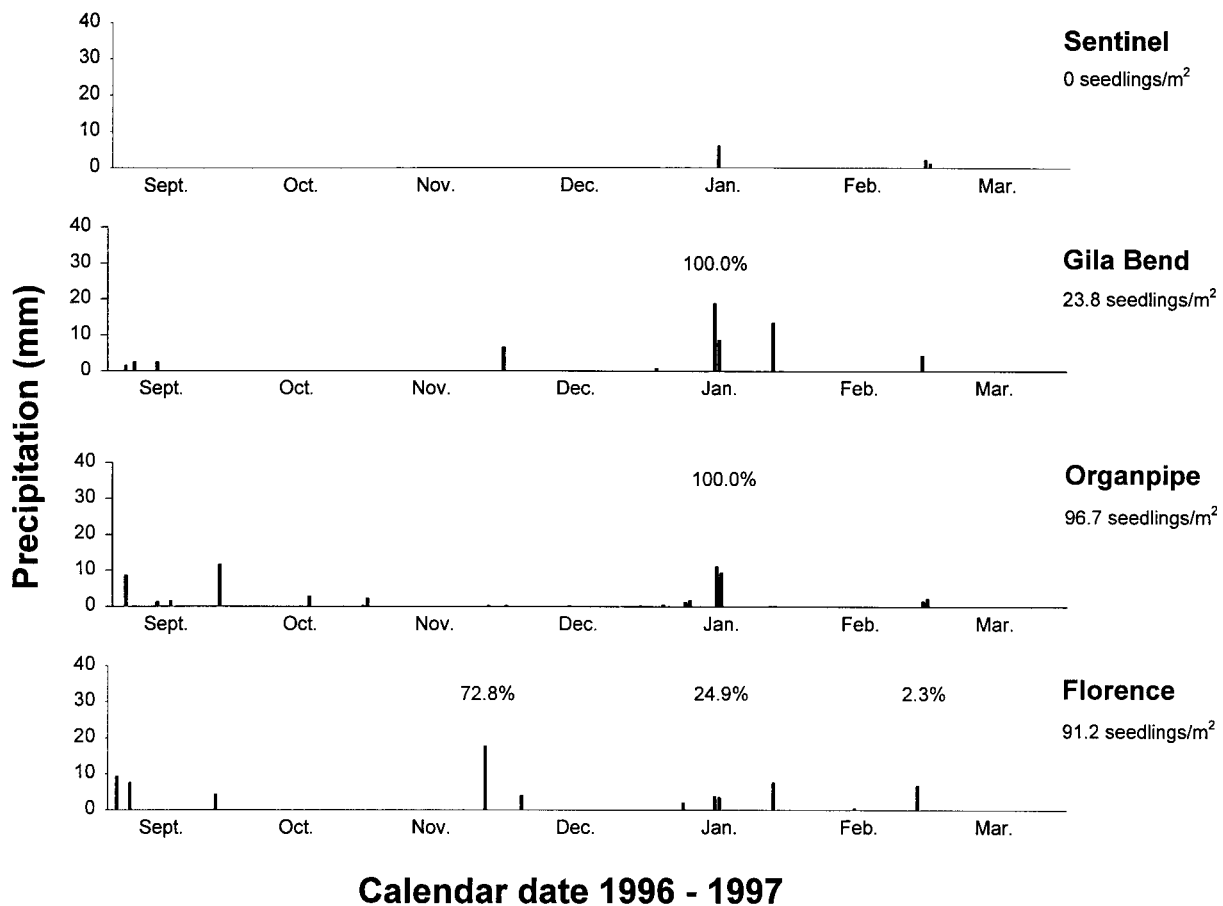
Figure 4: Daily precipitation amount (*mm*) and timing of germination for *Plantago insularis* at four populations in southern Arizona in the winter of 1996–1997. The size of the germination cohort measured as the percentage of total seedling density is indicated above the rainfall event that resulted in germination. Total density of seedlings is given under each population name.

dergo easily recognizable changes upon death (e.g., desiccation, decay). In each year and population, the germination fraction was calculated by dividing the seedling density in the field by the seed density before germination ($G = L/[D + L]$).

Results. Average in situ germination fractions were lower in populations with a lower proportion of good years (fig. 1; Pearson's $r = 0.935$, $P = .065$). Germination fractions differed greatly among populations and among years because both seed (D) and seedling densities (L) varied significantly (table 2). The two populations in more xeric environments, Sentinel (SE) and Gila Bend (GB), had greater ranges of germination fractions among years than the populations in more mesic environments (fig. 1). Whereas all populations had high G (>0.80) in at least one season, SE and GB had both the highest (0.97 and 0.89,

respectively) and the lowest (<0.07) germination fractions. The lowest germination fractions for the more mesic populations were 0.53 and 0.54 for Organ Pipe (OP) and Florence (FL), respectively.

These germination fractions represent the accumulation of multiple germination cohorts emerging over the 7-mo winter period in response to discrete rainfall events (figs. 2–5). Winter storm systems are regional in the Sonoran Desert, and most populations experienced most rainfall events (figs. 2–5). However, the historically more xeric populations generally received less rainfall per event and, as a result, less total winter rainfall than the more mesic populations (table 2). If we assume similar positive reaction norms for seed germination in response to water availability at all populations, we would expect fewer germination cohorts at more xeric sites. However, in most years, germination occurred as often, or more often, at SE
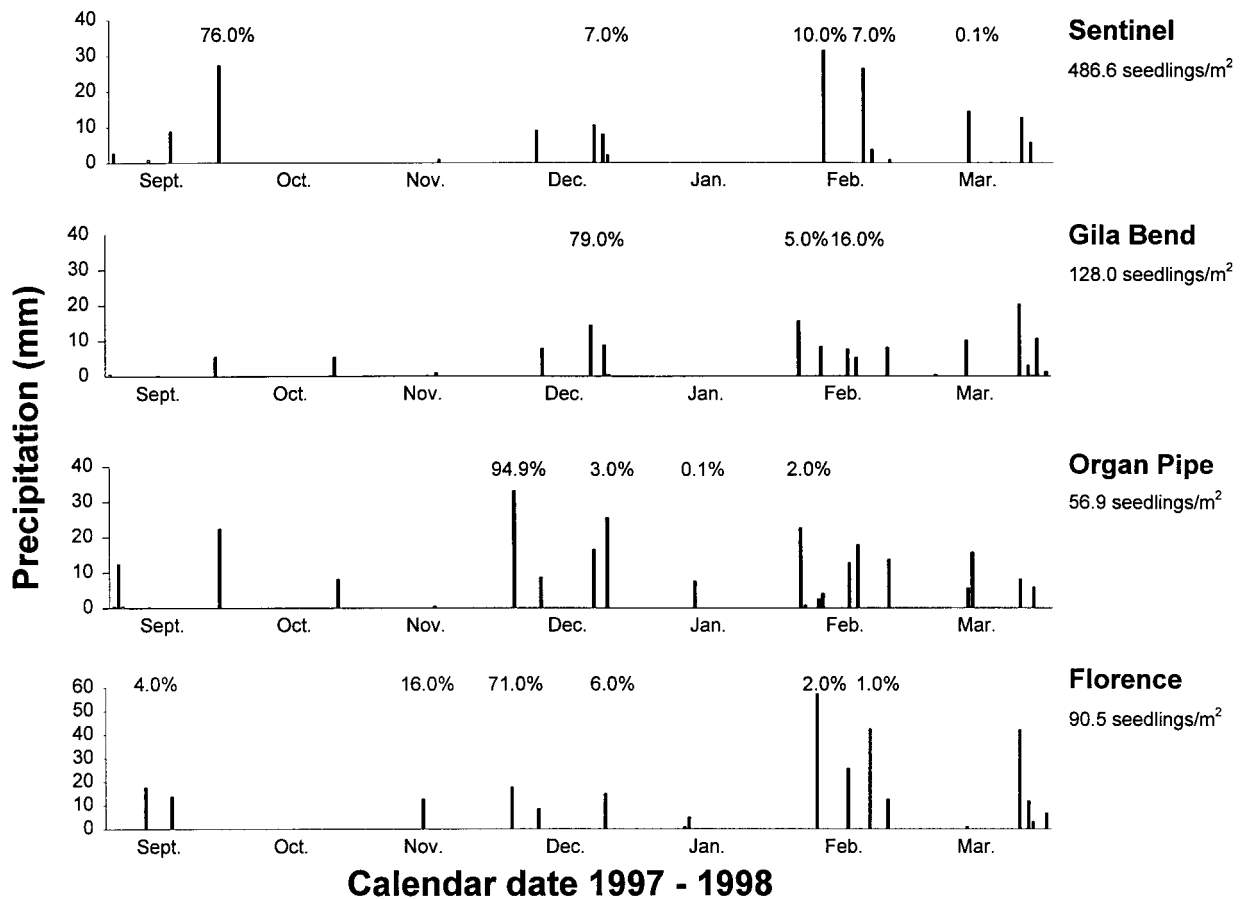
Figure 5: Daily precipitation amount (*mm*) and timing of germination for *Plantago insularis* at four populations in southern Arizona in the El Niño–Southern Oscillation winter of 1997–1998. The size of the germination cohort measured as the percentage of total seedling density is indicated above the rainfall event that resulted in germination. Total density of seedlings is given under each population name.

and GB in comparison to OP and FL (table 3). The unexpectedly high number of germination cohorts at more xeric populations occurred because seeds responded to small rainfall events at SE and GB (table 3). At SE, seeds germinated in response to rainfall events that registered as little as 1.3 mm at the nearby weather station. Furthermore, even with less total winter precipitation, germination at SE occurred over the widest range of dates, spanning 5–6 mo in 3 of 4 yr. Seeds at SE germinated in September in both of the years that had September precipitation (figs. 2, 5). Even though OP and FL received >17 mm precipitation in September during 4 and 3 yr, respectively, FL had only one small germination cohort this early in the season (figs. 2, 5). Similarly, both SE and GB had March germination cohorts in at least 1 yr, whereas seeds never germinated in March at the more mesic OP and FL populations, even when there was substantial rainfall (figs. 2–5). Thus, shorter germination seasons at more

mesic populations were the result of neither a lack of rainfall nor a lack of seeds in the soil seed bank (table 2).

Study 2: Common Garden Germination Trials with Five Populations

Methods. To compare germination responses for seeds originating from historically mesic and xeric environments under similar conditions, we conducted an outdoor common garden experiment in Tucson, Arizona. Seeds from the soil seed banks of the four populations in study 1 plus those from Yuma, Arizona, were tested for germination in four trials during the 1996–1997 winter. Soil samples were collected from each population in November 1996 before any in situ germination. We allowed seeds to experience ripening, oversummering, and early fall conditions in situ because environmental conditions during this time can have significant effects on germination responses of desert

Table 3: Mean and minimum precipitation (mm) that resulted in germination cohorts at four populations of *Plantago insularis* in 4 yr and in all years combined

Population	1994–1995			1995–1996			1996–1997			1997–1998			All years		
	n	Mean	Min.	*n*	Mean	Min.	*n*	Mean	Min.	*n*	Mean	Min.	*n*	Mean	Min.
Sentinel	6	10.8	3.0	2	1.3	1.3	0	…	…	5	25.0	14.5	13	12.4	6.3
Gila Bend	4	22.2	8.1	2	13.8	5.6	1	24.4	24.4	3	17.4	12.9	10	18.9	12.7
Organ Pipe	4	37.8	14.7	2	21.3	17.3	1	20.4	20.4	4	35.5	7.6	11	28.7	15.0
Florence	3	21.8	17.2	2	32.8	15.2	3	10.7	6.8	6	53.1	12.7	14	29.6	13.0

Note: Precipitation falling within 48 h was summed and recorded as one event; *n* = the number of germination cohorts. There was no germination at Sentinel in 1996–1997. Because rainfall is from nearby weather stations, the minimum precipitation resulting in germination is approximate.

winter annuals, including *P. insularis* (S. Adondakis, unpublished data). In each population, 16 soil samples 480 cm² × 2 cm in depth were taken in a stratified random manner (one random sample in each 10-m block along four 40-m transects). Transects were separated by 1 km. At Florence, Organ Pipe, Gila Bend, and Sentinel, the transects were within 50 m of the permanent quadrats at sites 1–4 described in study 1. The 16 samples from each population containing seeds and soil were combined, well mixed, and divided into four equal parts. The soil was stored outside of the University of Arizona greenhouses and was protected by a roof from rain. For each germination trial in December 1996 and in January, February, and March 1997 (table 4), one-fourth of the soil from each population was used as a seed source. A 500-cm³ sample of the soil seed bank was placed on 7,500 cm³ of commercial topsoil in each of 50 26 × 53 × 6-cm trays. The sample constituted a layer ∼4 mm deep in each tray. Five populations and two watering treatments were arranged in a randomized complete block design with five blocks and no replication within blocks. The trays in the high-watering (HW) treatment received 100 mL in both morning and evening daily for 30 d. Trays in the low-watering (LW) treatment received 100 mL daily, only in the morning. Five additional trays with only topsoil were used as controls for seed contamination and received the HW treatment. The amount of water in the HW treatment was chosen to simulate high soil humidity after large winter rains. This treatment kept the soil surface damp at all times in the December trial. Soil surfaces underwent daily periods of drying in LW trays during the December trial and in both treatments for all subsequent germination trials. Germination trays were protected from natural rains with clear plastic sheets that were removed immediately after rainfall. All trays were covered with 40% shade cloth to reduce evaporation.

Newly germinated seedlings were individually marked with colored toothpicks and counted every 5 d. Trials lasted 30 d, by the end of which no new seedlings had emerged for 5 d. Seedling survivorship was recorded at the end of the 30-d trial. All soil from each tray was then sieved, and all remaining seeds of *P. insularis* were removed, tested for viability, and counted. The number of viable seeds remaining in the soil (D) and the number of germinating seedlings (L) in each tray were used to calculate the germination fraction, $G = L/(D + L)$, assuming no seed mortality in the soil. The total number of all seeds and seedlings in the experiment was converted to density per square meter based on the area of the original soil samples and provided an estimate of the in situ seed bank before germination in the fall of 1996. All *P. insularis* seeds and seedlings originated from the field collected seed banks because no individuals were found in the control trays. Germination fractions were analyzed with a generalized linear model assuming a binomial response variable and using a logit link function (PROC GENMOD, SAS Institute 1989), and adjusting χ^2 to account for overdispersion (Crawley 1993). Germination fraction means and SEs given in the tables and figures were back transformed after calculation on logit-transformed data ($\log [\{a + 0.5\}/\{b + 0.5\}]$, where a is the number of germinated seeds and b is the number of nongerminated seeds; Sokal and Rohlf 1995).

Results. Mean germination fractions differed significantly among populations in the common garden experiment (YU = 0.44, SE = 0.27, FL = 0.26, GB = 0.19, OP = 0.17; table 5, population). These population differences are interpreted further in this article in the context of the significant two-way interactions, with emphasis on the differences among populations in response to watering treatment and trial date.

Germination fractions for all populations declined when water was limiting (HW = 0.38, LW = 0.16; table 5, water), though the phenotypic response to water availability varied among populations (fig. 6; table 5, water ∗ population interaction). In the HW treatment, YU and SE, the two most xeric populations with the lowest proportion of good years, had higher germination fractions than more mesic populations (fig. 6). Decreasing water availability by half

Table 4: Environmental conditions during four germination trials in a common garden experiment conducted in Tucson, Arizona, December 1996–April 1997

	December	January	February	March
Dates	12/12/96–1/10/97	1/15/97–02/13/97	02/21/97–03/22/97	03/25/97–04/23/97
Average temperature (°C)	10.9	12.4	16.0	18.3
Maximum temperature (°C)	25.0	25.0	33.3	32.8
Minimum temperature (°C)	−3.3	−3.3	0	4.4
Total precipitation (mm)[a]	18	2	16	13
Average day length	10 h, 5 min	10 h, 37 min	11 h, 37 min	12 h, 42 min

[a] Germination trays were covered during rainfall but seeds were exposed to changes in relative humidity and air temperature.

caused the largest decline in *G* for these two xeric populations, and as a result, there was no systematic variation in germination response along the selective gradient in the LW treatment (fig. 6).

Trials conducted later in the winter season had lower average germination fractions (December = 0.45, January = 0.19, February = 0.25, March = 0.16; table 5, trial). Aside from the low *G* in January (table 6), average differences among trials coincided with seasonal changes in the environment (table 4). However, populations differed significantly in their response to germination trials (fig. 7; table 5, population ∗ trial interaction). Whereas there was a decline in *G* in later trials for the more mesic populations (FL, OP, GB), *G* values were high throughout the season for SE and even tended to increase in March for YU (fig. 7). Thus, lower average *G* values for the more mesic populations were primarily because of declining germination in January, February, and March trials (fig. 7). This pattern is consistent with our in situ observations that seeds in SE germinated more with late (and early) rains than did seeds in more mesic populations (figs. 2, 3, 5).

The two-way interaction between water and trial was also significant (table 5). Whereas germination declined monotonically with trial date in the HW treatment, a seasonal decline in *G* was interrupted in the LW treatment by unexpectedly low germination in January (table 6). During the January trial, there was less natural rainfall (table 4), and therefore seeds experienced fewer days with cloud cover and increased relative humidity.

Population, watering, and trial date treatments had strong effects on the survivorship of seedlings. In December, all germinated seedlings survived to day 30 of the trial (fig. 8). Seedlings receiving the HW treatment had higher survivorship than individuals in LW trays in January. In February and March, no seedlings survived to day 30, with the exception of the YU high-water treatment, in which survival to day 30 was 0.89 and 0.49, respectively (fig. 8).

Study 3: Growth Chamber Germination Trials with 12 Populations

Methods. We tested for population differentiation at the regional level by collecting soil seed banks from populations throughout the geographic range of *P. insularis* and determining seed germination fractions in two growth chamber trials. In October 1995, before any in situ germination, we collected six soil cores in a stratified random fashion along a 60-m transect (one sample from each 10-m block) from each of 12 populations in southern Arizona and California (table 1). At Florence, Organ Pipe, Gila Bend, and Sentinel, the transect began within 50 m of the permanent quadrats at site 1 described in study 1. Each core sampled an area of 98.2 cm² × 2 cm in depth. All *P. insularis* seeds were removed from the sample and rinsed with a 2% solution of bleach to reduce superficial fungal and bacterial contaminants. For each trial, 10 seeds per sample were weighed and placed on 0.4 cm³ of water-saturated silica sand (P. W. Gillibrand Filter Sand 20) in a 15-mm-deep petri dish with a 90-mm diameter. The 72

Table 5: Generalized linear model analyzing germination fraction (number of germinated seeds/total number of seeds) for *Plantago insularis* in a common garden experiment

Source	df	*F*[a]	*P*
Population	4	51.8	<.0001
Water	1	47.3	<.0001
Trial	3	48.1	<.0001
Water ∗ population	4	13.5	<.0001
Population ∗ trial	12	45.9	<.0001
Water ∗ trial	3	14.7	<.0001

Note: Block effect and three-way interaction term were not significant and were removed from the model.

[a] To correct for overdispersion in the data, χ^2 was divided by Pearson's χ^2/df (3.18); *F*-test denominator, df = 170.
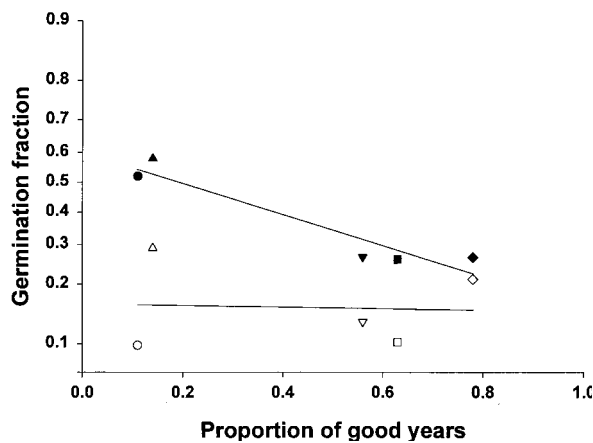
Figure 6: Mean seed germination fractions on a logit scale for five populations of *Plantago insularis* in a common garden experiment with two watering treatments. Populations are placed along the abscissa according to their proportions of good years calculated by using the 17/24/30 threshold. Filled symbols denote high water and open symbols denote low water. *Triangle*, Yuma; *circle*, Sentinel; *inverted triangle*, Gila Bend; *square*, Organ Pipe; *diamond*, Florence.

dishes were placed into a growth chamber, and positions were rerandomized daily. Growth chamber environmental conditions were set to average temperatures and photoperiod across the environmental gradient and were adjusted as the season progressed. The first trial was conducted from October to December 1995. The growth chamber was set to 26°/10°C day and night temperatures with 11 h 30 min of daylight in October. In November, the conditions were adjusted to 23°/7°C with 10 h 15 min of daylight and in December to 18°/3°C with 10 h of daylight. Water was supplemented as required to maintain saturation of the sand. Germination was scored daily until there was no germination for five consecutive days. Seeds not used in the first germination trial were stored outside the University of Arizona greenhouses in Tucson, Arizona, where they experienced natural fluctuations in light, temperature, and humidity but were protected from direct precipitation. A second, midseason trial was conducted from January through March 1996 with the growth chamber set to 18°/3°C with 10 h of daylight in January, 23°/7°C and 10 h 30 min of daylight in February, and 26°/10°C with 11 h 45 min of daylight in March. Population differences in germination fraction were analyzed with a generalized linear model assuming a binomial response variable and using a logit link function (PROC GENMOD, SAS Institute 1989) and adjusting χ^2 to account for overdispersion (Crawley 1993). Variation in seed mass among populations was compared using ANOVA.

We analyzed the relationships between germination fraction and three measures of the proportion of good years, as well as the mean winter precipitation and the coefficient of variation of winter precipitation for the 12 populations. The proportions of good years were estimated as detailed in "Estimation of Optimal Germination Fractions." We tested for linear trends among populations in *G* by using linear contrasts within the generalized linear models described. The linear contrasts were constructed by weighting the populations by their position along the selective gradient. Separate analyses were conducted for each of the five measures of the gradient. The same five linear contrasts were conducted for variation in seed mass among populations.

Results. Germination fractions differed significantly among populations and among trial dates (table 7, main effects). On average, *G* values were higher in January than in October (fig. 9); however, populations differed significantly in their response to trial date (table 7, population * trial).

A significant proportion of the variation among populations in germination fraction was explained by the position of populations along the selective gradient in four of five linear contrasts (table 7, linear contrasts). Populations with low proportions of good years expressed the highest germination fractions (fig. 9). The relationship between germination fraction and the selective gradient was significantly negative when the gradient was measured, first, by the probability of a good year ($P_{g|r}$) by using the 17/24/30 threshold (table 7, linear contrasts); second, by two sets of more permissive threshold values for evaluating $P_{g|r}$ (table 7, 17/20/20 and 5/20/20); or, third, by the mean precipitation (table 7). The germination fraction did not vary significantly with the coefficient of variation of precipitation (table 7). Thus, there was no evidence of the predicted positive relationship between germination fractions and the selective environment from which populations originated.

Seed mass varied significantly among populations but not among trial dates (population: $F = 28.8$, df = 11, 127, $P < .001$; trial: $F = 1.25$, df = 1, 127, $P = .266$; interaction term was not significant and was removed from the model). Linear contrasts testing for differentiation of seed mass along the selective gradient indicated a positive relationship (fig. 10) that was significant in four of five comparisons (results not shown).

Discussion

Seeds of *Plantago insularis* exhibited delayed germination under all conditions; germination fractions of viable seeds were always <1. Delayed germination functions as a bet-hedging mechanism in *P. insularis* because it reduces both the arithmetic mean and variance in population growth (i.e., fitness) across years, relative to a strategy in which

all seeds germinate every year (Clauss 1999). Is this bet hedging adaptive? Delayed germination was predicted to be adaptive in all populations of *P. insularis* (table 1). By using the historical precipitation record to estimate the probability of a good year given germination rain, we found a bet-hedging model predicts lower optimal germination fractions for populations in more xeric environments. Furthermore, significant differences among individual maternal plants in the germination fractions of their offspring suggest the potential for evolutionary response to this selective gradient (Clauss 1996).

In the field, mean germination fractions were lower for populations with lower proportions of good years (fig. 1). This is the first study to measure in situ germination fractions for more than one population in multiple years. Fluctuations in germination fractions among years exhibited two unexpected elements. First, the more xeric populations, Sentinel and Gila Bend, exhibited the greatest range in *G* among years, including very high germination fractions. Second, Sentinel, which received the least rainfall throughout the study, had the widest range of germination dates in 3 of the 4 yr. In the following two sections, we address these field observations in the context of results from the germination experiments.

Among-Year Variation in Germination Fractions

Populations differed in their phenotypic response to environmental conditions during germination. The highest in situ germination fractions were recorded at Gila Bend and Sentinel in the wet 1994–1995 and 1997–1998 years, respectively, even though the more mesic populations received more precipitation (table 2). Caution must be exercised when interpreting field germination fractions in
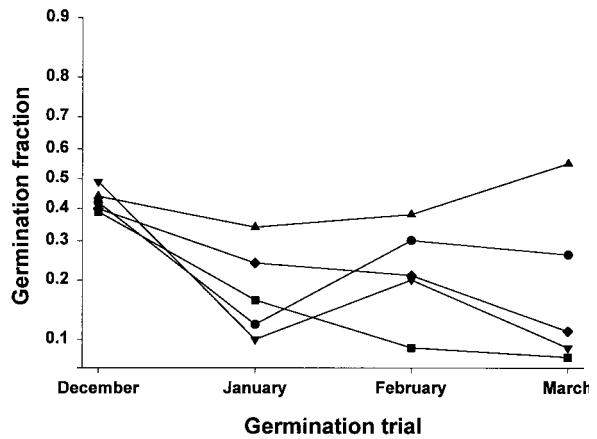

Figure 7: Mean seed germination fractions on a logit scale for five populations of *Plantago insularis* in a common garden experiment during four germination trials. *Triangle*, Yuma; *circle*, Sentinel; *inverted triangle*, Gila Bend; *square*, Organ Pipe; *diamond*, Florence.

only 4 yr. Yet, when seeds were supplied with ample water in common garden and growth chamber experiments, germination fractions were again as high or higher for xeric, in comparison to mesic, populations of *P. insularis* (figs. 6, 9; tables 6, 7). These high germination fractions expressed by seeds from more xeric populations were opposite from the G_r^* predicted by the bet-hedging model for unpredictably variable environments (table 1). Higher optimal germination fractions would be predicted for xeric populations if germination occurred in response to a cue predictive of high future reproductive success (Cohen 1967). Precipitation during the germination season could be such a cue, yet low-optimal germination fractions were predicted for xeric populations, even though our method

Table 6: Germination fractions for populations of *Plantago insularis* in each trial date and water treatment combination of a common garden experiment

Trial and water	Yuma		Sentinel		Gila Bend		Organ Pipe		Florence	
	Mean	SE bounds	Mean	SE bounds	Mean	SE bounds	Mean	SE bounds	Mean	SE bounds
December:										
High	.487	.429–.546	.658	.596–.714	.603	.539–.663	.614	.355–.822	.431	.299–.574
Low	.410	.322–.503	.269	.180–.382	.392	.335–.452	.220	.120–.368	.446	.362–.534
January:										
High	.696	.672–.720	.496	.445–.547	.179	.105–.289	.280	.211–.362	.330	.269–.380
Low	.115	.070–.181	.021	.009–.047	.056	.033–.093	.102	.075–.137	.184	.110–.290
February:										
High	.626	.518–.723	.546	.507–.584	.275	.232–.323	.163	.105–.245	.356	.226–.510
Low	.345	.295–.400	.148	.096–.222	.163	.107–.241	.058	.050–.067	.228	.160–.315
March:										
High	.772	.720–.816	.539	.423–.650	.132	.089–.192	.102	.078–.134	.124	.097–.157
Low	.501	.410–.592	.093	.051–.163	.058	.043–.078	.093	.076–.113	.148	.112–.193

Note: Means and standard errors (SE) were calculated on logit-transformed data and then back transformed.
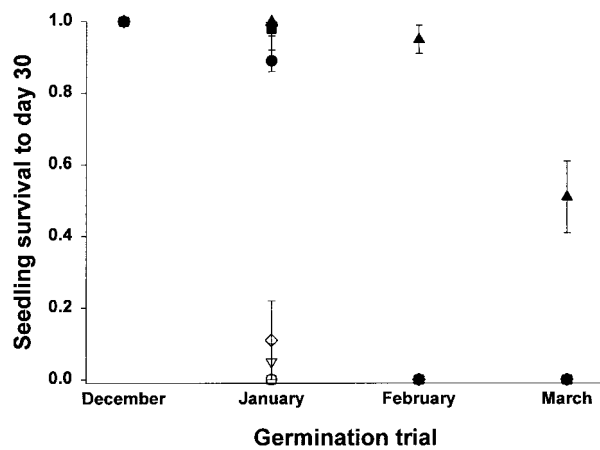
Figure 8: Proportion of seedlings surviving 30 d in each of four germination trials for five populations of *Plantago insularis* in a common garden experiment with two watering treatments. Means and standard errors of proportions were calculated for arcsine-transformed data and then back transformed. Filled symbols denote high water and open symbols denote low water. *Triangle*, Yuma; *circle*, Sentinel; *inverted triangle*, Gila Bend; *square*, Organ Pipe; *diamond*, Florence.

of identifying good years would have resulted in increased $P_{g|r}$ had there been a positive correlation between germination and growth rains. Thus, there is no hint in the precipitation data that early germination rain is more predictive of later growth rain in the more xeric environments. Greater predictability in xeric populations would have to be caused by differences in the response of germinated seedlings to the environment itself. This possibility is discussed in the section on interactions among traits.

Within-Season Variation in Germination Fractions

A second unexpected aspect of in situ seed germination for *P. insularis* was the large range of germination dates within the season for the most xeric population. Although Sentinel received much less winter precipitation than the more mesic populations, seeds germinated in response to multiple rainfall events spanning from September to March in both wet years (table 3; figs. 2, 5). Seeds in more mesic populations generally did not germinate early and late in the season even when there was ample rainfall (figs. 2–5). In a 15-yr study of an even more mesic desert annual community near Tucson, Arizona, germination dates for *P. insularis* have consistently been after October 1 and before the end of February (Venable and Pake 1999). A similar distinction between mesic and xeric populations was seen in the common garden experiment, where more mesic populations experienced a sharp decline in *G* later in spring and the more xeric populations did not (table

5; fig. 7). Variation among populations in their response to increasing temperatures and longer days (table 4) may have caused these differences in germination season (Gutterman 1993; Baskin and Baskin 1998).

Increased germination early and late in the season in the more xeric populations may be favored by the seasonal distribution of precipitation during El Niño–Southern Oscillations (ENSO; see "Species, Populations, and Precipitation"). ENSO seasons are disproportionally wet in xeric environments and are likely to contribute disproportionately to population growth because the amount of seasonal precipitation is positively correlated with survival and reproduction in annual plants (Beatley 1974; Loria and Noy-Meir 1979/1980; Templeton and Levin 1979; Brown and Venable 1986; Clauss 1999; Venable and Pake 1999). In more xeric populations, the additional rain in ENSO seasons falls early and late in the season, at a time when there is little rain in non-ENSO years. Thus, given that germination has a genetic basis in this species, genotypes with the ability to germinate early or late in the season will increase in frequency during ENSO years and have a disproportionate impact on evolutionary change.

One consequence of less restrictive germination requirements in more xeric environments is that populations will have an increased number of potential ger-

Table 7: Analysis of germination fractions at two trial dates for 12 populations of *Plantago insularis* and linear contrasts testing whether among-population variation was significantly explained by the location of the populations along the precipitation gradient

	df	F[a]	P
Effects:			
Population	11	83.5	<.0001
Trial	1	56.7	<.0001
Population ∗ trial	11	72.9	<.0001
Linear contrasts:			
17/24/30	1	6.2	<.05
17/20/20	1	12.6	<.002
5/20/20	1	10.5	<.005
Mean precipitation	1	24.4	<.001
CV	1	1.2	<.50

  Note: For main effects and interactions, a generalized linear model was used assuming a binomial response variable and applying a logit link function. For linear contrasts, the gradient was measured by three sets of threshold criteria for the proportion of good years given germination rain (see "Estimation of Optimal Germination Fractions"). The gradient was also described by the mean winter precipitation and the coefficient of variation (CV) of winter precipitation.

  [a] To correct for overdispersion in the data, χ^2 was divided by Pearson's χ^2/df (1.58); F-test denominator df = 120.
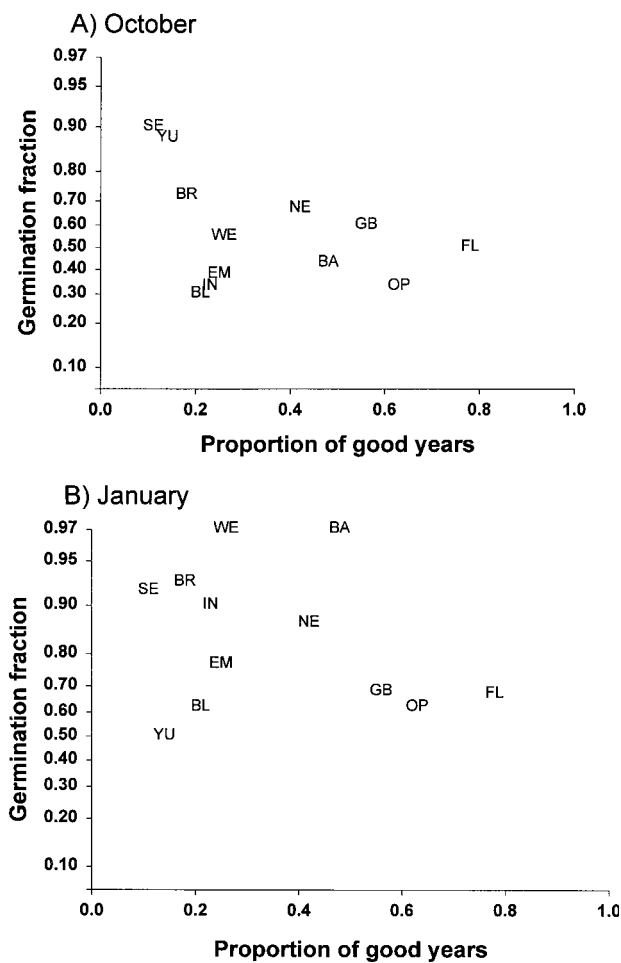
A) October

B) January

partly substitutable (King and Roughgarden 1982; Ritland 1983; Venable and Brown 1988; Evans and Cabin 1995). High seedling survival in hot and dry conditions, as seen for Yuma in March (fig. 8), may increase the probability of survival to reproduction for germinated seedlings, thereby reducing variance in reproductive success among years. Phenologic observations at the four field populations of *P. insularis* over four seasons indicate that plants at more xeric locations can have a younger age at maturity, set seeds earlier in the season, and can set seed with the moisture provided by one germination rainfall event (M. J. Clauss, unpublished data). These postgermination traits may increase the probability that $Y > 1$, even in years only receiving germination rains, thereby reducing the unpredictable temporal variance in reproductive success. This variance reduction via postgermination traits may allow selection for the high germination fractions observed in more xeric populations. Although data of in situ germination fractions for other desert annuals are not widely available (but see Venable and Pake 1999), there are multiple reports of unusually high population densities in years with high seasonal rainfall (Beatley 1974; Gutterman 1993; Polis et al. 1997), suggesting that the results reported here may represent a common pattern in extremely xeric environments. High temporal variance in survival and reproduction can also select for increased seed size or seed dispersal into dissimilar patches (Venable and Brown 1988). In *P. insularis*, seed mass varied significantly among the 12 populations, but more xeric populations had lower, not greater, seed mass (fig. 10). Neither seed morphology related to dispersal nor habitat patchiness varied syste-
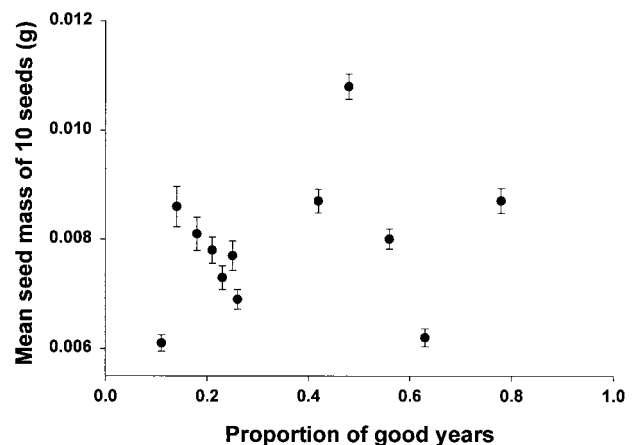
Figure 9: Seed germination fractions on a logit scale for 12 populations of *Plantago insularis* in two growth-chamber trials at ambient conditions in (*A*) October and (*B*) January, plotted against proportions of good years calculated by using the 17/24/30 threshold. The slope of the relationship between *G* and proportion of good years did not differ significantly among trials ($F = 0.025$, df = 1, 140, $P < .5$). Population abbreviations as in table 1.

mination opportunities within a year. As opposed to spreading the risk among years, differences in success of early-, middle-, and late-germinating offspring may provide a hedge against reproductive failure (Leon 1985; Venable 1989). Germination responses in *P. insularis* suggest that species under strong selection for variance reduction may have the ability to combine within-year and among-year strategies for bet hedging.

Interactions among Traits

The variance-reducing properties of germination, postgermination, and other seed traits can interact and are

Figure 10: Mean mass and standard error of 12 groups of 10 seeds from 12 populations of *Plantago insularis* plotted against proportions of good years calculated by using the 17/24/30 threshold. Linear contrast: $F = 18.78$, df = 1, 116, $P < .001$.

matically across the precipitation gradient (M. J. Clauss, personal observation).

Germination Fractions across Environments: Previous Empirical Evidence

In the past 20 yr, a number of empirical studies have compared germination responses among populations differing in historical precipitation regimes. Generally, seeds are collected from maternal plants in a number of wet and dry populations, and germination is monitored under common conditions resembling a good year for germination in the field (providing a measure of first-year germination; Philippi 1993*a*). The results of these studies have not provided consistent support for bet-hedging predictions. In a study of seven grassland annuals, Jain (1982) observed higher seed dormancy (lower G) in the laboratory for populations with higher probabilities of precipitation. Comparing 12 populations of *Digitaria milanjiana* from a combination of wet and dry African tropical and equatorial habitats, Hacker (1984) found that, after one generation in a common garden, populations from habitats with higher rainfall had higher average growth chamber germination fractions than populations from drier habitats. However, there was a great deal of variation in G among equatorial and tropical habitats of similar rainfall, as well as among seeds harvested in different seasons. By using a similar experimental design, Hacker and Ratcliff (1989) showed that equatorial populations of *Cenchrus ciliaris* experiencing high rainfall also had higher G. In contrast, in tropical habitats, it was populations of *C. ciliaris* with intermediate rainfall that had maximal G. Gutterman and Ednine (1988) found that, for two species of *Helianthemum*, populations from drier and hotter locations had higher G. Seeds originating from a xeric population of *Anthoxanthum odoratum* had higher G in a growth chamber than seeds from a mesic population after a reciprocal transplant experiment (Platenkamp 1991). In the most exhaustive comparison to date, Philippi (1993*b*) showed a significant positive correlation between G in a growth chamber and rainfall among 11 populations of *Lepidium lasiocarpum* in the southwestern United States. However, on the basis of further experiments with this species, Philippi (1993*b*) concluded that this correlation was most likely driven by variation in maternal plant size among populations in the years of seed production. Kigel (1995) observed the opposite pattern with drier populations of *Stipa capensis* in Israel exhibiting higher G in a growth chamber than those from wetter habitats. In a comparison among populations from wet, dry, and intermediate habitats for 29 Mediterranean leguminous species, Ehrman and Cocks (1996) found significantly more hard seededness (lower G) at drier sites for only five species.

The remaining 24 species exhibited no ecotypic differentiation among sites that differ up to 88% in seasonal precipitation. The results of our study suggest that it is difficult to draw conclusions concerning evolution in response to variable environments from such data, as a key factor is the interaction between germinability and the distribution of the climatic conditions encountered in the field during germination.

Conclusions

This investigation of bet hedging in *Plantago insularis* differs from previous studies because we measured germination fractions in several populations over multiple years in the field and under experimental conditions. Variability in reproductive success among years inferred from the historical precipitation record predicts delayed seed germination as a form of adaptive bet hedging for all populations. A complex picture arose from the empirical data for germination fractions in this winter annual plant. Mean in situ germination fractions increased with increasing proportion of good years. In contrast, germination fractions in common environment experiments were constant or decreased with increasing proportion of good years. Germination fractions exhibited phenotypic plasticity in response to water availability and date within the season. Thus, if the mean in situ germination fractions reflect adaptations to variable environments, *P. insularis* did not attain this strategy through constant optimal germination fractions, as a simple interpretation of bet-hedging models would suggest (i.e., Sentinel seeds should have lower G than Florence seeds under any conditions tested). Rather, the mean response was attained through an interaction between the distribution of germination environments and phenotypic plasticity in germination. Populations in mesic environments generally received more rainfall, had intermediate seed germination fractions, and had a narrow germination season. Populations in more xeric environments received less rainfall, had high seed germination fractions when water was available, and had a longer germination season. The phenotypic variability in germination fraction among years may reflect constraint or adaptation. Physiological limitations to adjusting germination responses to water availability and season may prevent germination fractions from attaining a bet-hedging optimum in every year. Adaptive plasticity in germination is predicted when a cue during germination is correlated to future reproductive success. Although there was no evidence of such a correlation in the historical precipitation record, the field data suggest that postgermination traits in the most xeric population may have evolved to

increase the predictability of reproductive success for germinated individuals.

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