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Research article

Demographic consequences of delayed germination in two annual grasses from two locations of contrasting aridity

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ABSTRACT

Delayed seed germination is considered to be a bet-hedging strategy, but experimental evidence of its adaptive role as an inherited trait is still lacking. In each of two co-occurring annual grass species, populations of Mediterranean and desert origin were studied during three consecutive years for population demography and seed germination in the reciprocally introduced experimental soil seed banks. The two environments strikingly differed in productivity (annual rainfall) and predictability (variation in amount and timing of annual rainfall). The two species exhibited highly similar pattern of seed size and dormancy across the two environments. In both species, a higher proportion of dormant seeds was observed at the desert location and for the seeds of desert origin, consistent with bet-hedging buffering against unpredictability of rainfall and high probability of drought in this environment. In addition, in both species seed mass was significantly less in plants of desert origin than in plants of Mediterranean origin. The two environments differed in demographic consequences of temporal variation in precipitation. In the Mediterranean population, even in the year of least precipitation, adults grew to maturity and seeds were produced. These seeds served to maintain population size. In contrast, in the desert population, in the year of least rainfall no seedlings survived to maturity and the soil seed bank was the only source of population persistence. Altogether, the results concur with predicted by adaptive bet hedging importance of delayed germination under marginal precipitation.

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Introduction

Delayed seed germination can be an adaptive bet-hedging strategy (Slatkin, 1974; Seger and Brockmann, 1987) if it increases the geometric mean fitness by sacrificing arithmetic mean fitness, i.e. when it reduces temporal variance in individuals' reproductive success. While delayed seed germination as an adaptive bet-hedging strategy is well studied theoretically (Cohen, 1966, 1967; Ellner, 1985; Brown and Venable, 1986; Klinkhamer et al., 1987; Venable and Brown, 1988; Sasaki and Ellner, 1995; Mathias and Kisdi, 2002; Valleriani, 2005), empirical tests are still scarce (Philippi, 1993; Pake and Venable, 1996; Venable and Pake, 1999; Clauss and Venable, 2000; Evans et al., 2007; Venable, 2007; Simons, 2009). Recognition of the adaptive role of fractional germination is technically challenging because it can be estimated only over a long-term scale and requires demonstration of (i) its direct relationship with environmental fluctuations and (ii) fitness advantage as compared with non-fractional germination (reviewed in Childs et al., 2010; Simons, 2011). One approach to provide evidence that

fractional germination is a bet hedging adaptation is to correlate variation among populations in degree of dormancy with variation in the magnitude of a surrogate for risk associated with emergence in those environments (e.g. low annual precipitation) (Philippi, 1993; Clauss and Venable, 2000). However, in studies using this approach a direct link between environmental unpredictability and fitness consequences of seed dormancy is only surmised. A better approach is one that infers long-term population consequences of delayed germination using demographic observations, parameterized population models and stochastic simulations (Kalisz and McPeck, 1993; Clauss, 1999; Evans et al., 2007). A drawback of this approach is that it is based on data gathered within a very limited time period (usually several years) and may miss the rare extreme climate fluctuations. More direct evidence was recently provided by Venable (2007) performing across species correlation between mean germination fraction and variation in per capita reproductive success based on long-term demographic data. In the study of Venable (2007), a relationship between germination strategies and population demography was analyzed via interspecific comparison at the same desert location. In this study, I investigated seed germination in relation to population demography of only two co-occurring species, but at two locations, one of which was and the second was not expected to select for delayed germination. The

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pattern of germination was tested using reciprocal introduction of seeds and with maternal effects removed prior to experiment. The latter was necessary for disentangling genetic and environmental components of environmentally-dependent seed germination, viz. role of seed origin vs. conditions experienced by a germinating/dormant seed.

In Israel the north-south aridity gradient creates steep climatic and ecological clines over relatively short distances (Bitan and Rubin, 1991; Aronson et al., 1992; Kadmon and Danin, 1997). Water is the main limiting and fluctuating resource in this area, and creates an increasingly severe productivity-predictability gradient from mesic Mediterranean to xeric desert (Aronson et al., 1992). In this study, I conducted demographic observations and reciprocally introduced experimental soil seed banks to compare population demography and pattern of germination over three years in two annual grasses, *Avena sterilis* and *Hordeum spontaneum*. Two populations of each, one representing the desert and the other the Mediterranean environment, were compared. Here, I asked (i) whether germination fractions of seeds of desert vs. Mediterranean origin and at the desert vs. Mediterranean site in the two species will correspond to what is theoretically predicted by the bet-hedging theory; and (ii) whether inter-population differences in a pattern of seed germination will have different consequences for population demography. I predicted that (i) germination fractions will be lower in the desert than in the Mediterranean environment; (ii) plants of desert origin possess traits consistent with bet-hedging such as higher seed dormancy and longer persistence in the soil; (iii) delayed germination will have a positive effect on population demography at the desert location; and (iv) the observed patterns will coincide in the two species.

Materials and methods

Study species

Hordeum spontaneum Koch (wild barley) and *Avena sterilis* L. (wild oat) are winter annual grasses that have wide and largely overlapping distributions. Both species are abundant in open vegetation formations of the Mediterranean climatic zone and penetrate into favorable desert habitats (wadi beds and loessy depressions) (Zohary, 1983). Seeds are produced in spring (April–May) and are innately dormant at dispersal requiring high temperature after ripening. A specific amount of rainfall as a single rainy event (>10 mm) is needed to trigger germination in fall (Guterman and Gozlan, 1998). Seedlings emerge in November–December, grow and mature throughout winter – early spring and senesce before summer. Seeds that do not germinate in the autumn following dispersal either die or enter the soil seed bank where they can remain dormant for several years (Volis et al., 2004; Volis, 2009). In these species, dispersal units are spikelets with a short dispersal distance from the mother plant (95% of shattered spikelets fall within 1.0 and 1.5 m, *H. spontaneum* and *A. sterilis*, respectively) (Volis, unpublished data).

Choice of populations

One research site was established in each of the Mediterranean and desert climatic zones in Israel. The Mediterranean populations (M) are in Beit Guvrin National Park located in the Shefela Hills (elevation 300 m, average annual precipitation 400 mm). The area is a semi-steppe batha on rendzina soil with mosaic of shrub–semi-shrub cover (*Sarcopoterium spinosum*, *Calicotome villosa*, *Cistus salvifolius*) and dense stands of *H. spontaneum* and *A. sterilis* among other grasses.

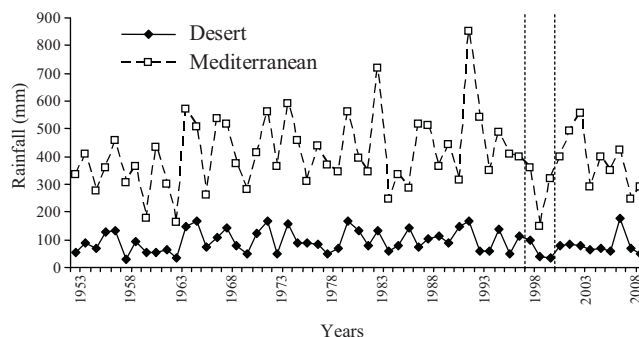


Fig. 1. Annual precipitation at the two studied locations over the last half century. Dotted lines indicate the period of demographic observations.

The desert populations (D) are in a wadi in the Negev Desert (elevation 400 m, average annual precipitation 90 mm) within a fenced experimental area of the Mitrani Department for Desert Ecology, Ben-Gurion University. There is sparse desert vegetation on loess soil (dominated by shrubs and semi-shrubs including *Retama raetam*, *Thymelea hirsuta*, *Zygophyllum dumosum*, *Hammada scoparia*) with patchily distributed *H. spontaneum* and *A. sterilis* within the wadi.

The D site was found to be less predictable in annual rainfall amount than the M site (CV in annual rainfall over 60 years is 0.43 and 0.32 in D and M site, respectively) (Israeli Meteorological Service) (Fig. 1).

Experimental design

Seed introduction experiment

In 1997, spikelets of *A. sterilis* and *H. spontaneum* were collected from randomly selected adult plants at least 2 m apart in proximity to the plots under observation. From these accessions, fifteen (*A. sterilis*) and ten (*H. spontaneum*) spikelets (one spikelet per accession) from each population were planted in the following season in a greenhouse at the Bergman Campus, Ben Gurion University in Beer Sheva (mean annual precipitation 202 mm) to obtain F1 seeds with maternal effects removed. Equal numbers of F1 seeds per parent comprised a bulk population seed sample. In fall 1998, randomly chosen seed sample spikelets from each of the two F1 populations were reciprocally buried at each transplant site. The number of spikelets buried at each site was 220 (*A. sterilis*) and 424 (*H. spontaneum*). Unequal species sample size was a result of different seed availability. A spikelet was placed in a separated cell 1.5 cm × 1.5 cm of a plastic tray filled with sieved soil (to remove the local seeds) of the transplant environment, placed flush with the ground level and covered with fine metal net to prevent seed predation by ants, rodents and birds. Two months after the first effective rains (>10 mm of rainfall) the trays were removed, brought to the laboratory and spikelets classified as germinated (with the radicle protruded) or non-germinated. The non-germinated spikelets were returned and buried again at the respective transplant sites immediately after examination and the procedure was repeated in 1999/2000; this was repeated again in 2000/2001. In *A. sterilis*, a spikelet contains more than one seed. A spikelet was considered germinated if a radical protruded from at least one of its seeds. No seed survived in the experimental soil seed bank after three years, i.e. all the seeds that did not germinate either rotted or disappeared.

Population demographic survey

Plant individuals of each species were counted at seedling and adult stage, and seed production quantified in each permanently marked 1 m² plot (30 and 50 plots at the M and D site, respectively). Emerging seedlings were censused every two weeks and marked by colored toothpicks during the first two months after germination. At maturation and prior to seed dispersal, all adult plants were counted and 12 randomly-chosen plants per plot were scored for number of panicles/spikes and number of spikelets per panicle/spike. As monitored plots remained intact throughout the study, the number of seeds per plot was estimated from the number of mature adults multiplied by the average yield per adult. Fecundity per adult was calculated for each plot.

Measuring seed weight

An experimental plot of about 100 m² was established within 500 m from each of the M and D sites. The plots were cleared of vegetation. To minimize the effects of maternal and paternal environmental variation, (i) seeds were collected in a single year (1996); (ii) ten randomly-selected field-collected seeds were germinated and grown under greenhouse conditions in a fully randomized design; (iii) the two-week old self-progeny of ten mother plants composed the seedling pools that were transplanted in each environment within two weeks after the first rain of more than 10 mm (effective rain). A randomized block design was established with each block containing plants from the two populations arranged as a lattice pattern, with 10 cm spacing. At seed maturity, 100–200 spikelets were collected from each population/block and average spikelet weight per population/block was estimated.

Data analysis

Significance of differences in seed germination between planting sites and seeds of different origin was determined by χ^2 tests with Yates correction for continuity. Mann–Whitney *U* test was used for comparison of demographic parameters between the two sites. The effects of seed origin and planting site on spikelet weight were analyzed by 2-way ANOVA.

Results

Seed introduction experiment

In both species, spikelet viability was found not to exceed 3 years and in both, the effect of introduction site and the effect of seed origin on spikelet germination were important (Fig. 2).

The spikelet germination differed between the introduction sites in the three consecutive years after introduction (oat, $\chi^2_1 = 158.0$, 14.6 and 15.9, $p < 0.001$; barley, $\chi^2_1 = 227.0$, 60.7 and 12.6, $p < 0.001$).

In oat, in the first year, lower percentage of spikelets germinated was observed at the D site (47.0 and 38.4%, D and M, respectively) as compared with the M site (81.0 and 92.0%, D and M, respectively). Spikelets of D and M origin did not differ in percent germination at the desert site ($\chi^2_1 = 2.3$, $p > 0.05$), but germination of D spikelets was lower than germination of M spikelets at the M site ($\chi^2_1 = 9.7$, $p < 0.01$). In the second year, proportion of germinated spikelets that were dormant in a previous year was higher at the D site (18.3 and 8.5%, D and M, respectively) as compared with the M site (6.6 and 3.0%, D and M, respectively). The D spikelets had significantly higher germination proportion at the D site ($\chi^2_1 = 7.7$, $p < 0.01$) but not at M site ($\chi^2_1 = 2.2$, $p > 0.05$). In the third year, germination was

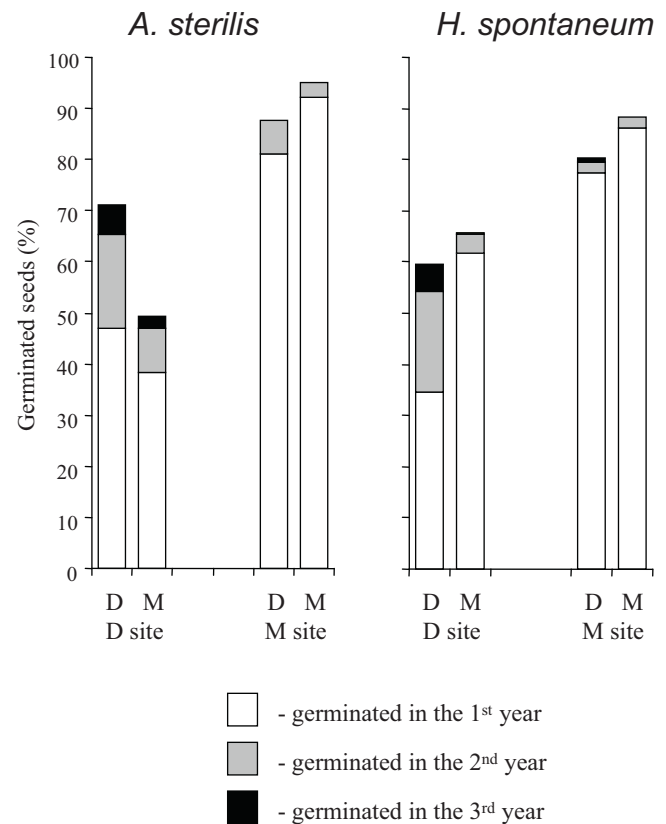


Fig. 2. Germination fractions over three years in *A. sterilis* and *H. spontaneum* experimental soil seed banks. Two bars at each introduction site denote seeds of desert (D) and Mediterranean origin (M).

higher at the D site (5.9 and 2.4%, D and M, respectively) than at the M site (0%), but the difference between D and M spikelets was not significant ($\chi^2_1 = 1.8$, $p > 0.05$).

Similarly, in barley, percentage of spikelets that germinated in the first year was lower at the D site (34.6 and 61.6%, D and M, respectively) than at the M site (77.4 and 86.3%, D and M, respectively). Germination of D spikelets was lower than germination of M spikelets at both sites ($\chi^2_1 = 57.7$ and 17.3, $p < 0.001$). In the second year, germination fraction was higher at the D site (19.7 and 3.7%, D and M, respectively) than at the M site (2.0 and 2.1%, D and M, respectively), and D spikelets had higher germination proportion than M spikelets at the D site ($\chi^2_1 = 47.1$, $p < 0.01$). Analogous results were observed in the third year (5.2 and 0.3% at the D site, and 1.0 and 0% at the M site, D and M, respectively), with higher germination of D than M spikelets at the D site ($\chi^2_1 = 16.0$, $p < 0.05$) but not at the M site ($\chi^2_1 = 2.4$, $p > 0.05$).

Demographic observations

In oat, probability of survival from seed to seedling stage in both 1997/98 and 1998/99 was significantly higher at the M site than at the D site (Mann–Whitney *U* test, $U = 82.0$ and 33.0, $p < 0.001$) (Table 1). However, the opposite was true for the probability of survival from seedling to adult (years 1997/98 and 1998/99, Mann–Whitney *U* test, $U = 368.5$ and 30.0, $p < 0.05$ and < 0.001 , respectively). There was no difference in adult fecundity between the two populations in the same year of observations (year 1997, Mann–Whitney *U* test, $U = 449$, $p > 0.05$).

In barley, probability of survival from seed to seedling stage in both 1997/98 and 1998/99 (Table 1) was significantly higher at

Table 1
Demographic parameters for two populations, Mediterranean (M) and Desert (D), in years 1997–2000. Means over plots (above) are presented with 95% confidence intervals (in parentheses).

Demographic parameters	M site		D site	
	1997/98	1998/99	1997/98	1999/2000
<i>A. sterilis</i>				
Survival from seed to seedling	0.456 (0.361–0.550)	–	0.145 (0.091–0.198)	–
Survival from seedling to adult	0.726 (0.645–0.807)	–	0.839 (0.775–0.904)	0
Fecundity	10.5 (8.8–12.3)	–	8.6 (7.4–10.5)	0
<i>H. spontaneum</i>				
Survival from seed to seedling	0.210 (0.151–0.285)	0.281 (0.215–0.344)	0.051 (0.034–0.072)	–
Survival from seedling to adult	0.557 (0.477–0.630)	0.687 (0.630–0.741)	0.717 (0.623–0.800)	0
Fecundity	22.5 (15.1–23.0)	10.5 (9.0–12.1)	35.8 (30.1–43.0)	0

–: not estimated.

Table 2

Two-way ANOVA of effects of seed origin and site of planting (both are fixed) on weight of spikelets of *A. sterilis* and *H. spontaneum*.

Source of variation	<i>A. sterilis</i>		<i>H. spontaneum</i>	
	df	F	df	F
Site	1	0.1 ns	1	0.3 ns
Origin	1	65.5***	1	175.6***
Site × Origin	1	0.5 ns	1	0.1 ns
Error	24		28	

the M site than at the D site (Mann–Whitney *U* test, χ^2 approximation = 25.5 and 47.1, both $p < 0.001$). However, the opposite was true for the probability of survival from seedling to adult (years 1997/98 and 1998/99, Mann–Whitney *U* test, χ^2 approximation = 7.4 and 14.8, $p < 0.01$ and < 0.001 , respectively) and for adult fecundity (years 1997/98 and 1998/99, Mann–Whitney *U* test, χ^2 approximation = 9.6 and 42.6, $p < 0.01$ and < 0.001 , respectively).

In both species, no plant reached maturity and produced seeds in year 1999/2000 at the D site.

Seed weight

Weight of spikelets (=dispersal units) of M and D origin grown reciprocally at both locations was significantly different in both species (Table 2). Spikelets of M origin were heavier than spikelets of D origin (58.4 ± 1.1 vs. 36.7 ± 0.9 mg and 66.0 ± 1.3 vs. 50.9 ± 1.3 mg, barley and oat, respectively). The difference in weight was independent of place of planting/growth (Table 2).

Discussion

It has been predicted that heritable differences in seed size and dormancy are expected to evolve in environments that differ in temporal climatic heterogeneity, i.e. in temporal predictability of environment (Cohen, 1966; Brown and Venable, 1986; Klinkhamer et al., 1987; Venable and Brown, 1988). Specifically, the fraction of propagules emerging is predicted to increase with the probability of years of reproductive success (Cohen, 1966), and optimal seed size to depend on biotic interactions such as intensity of competition and predation, and on other seed traits, such as dormancy (Venable and Brown, 1988; Geritz, 1998; Geritz et al., 1999).

In my study, I observed a remarkable similarity between the two annual plant species in persistence of seeds in the soil seed bank, patterns of seed germination in the desert vs. Mediterranean location, and weight of seeds of desert vs. Mediterranean origin.

For analysis of the soil seed bank, I used reciprocal introduction of seeds. Reciprocal introduction can effectively detect local adaptation as a significant genotype × environment interaction with an advantage of a genotype in its own environment (Kittelson and Maron, 2001; Volis et al., 2002; Etterson, 2004). For traits in which the relationship with fitness is not obvious, such as dormancy and persistence in the soil seed bank, reciprocal introduction can provide an important insight on the trait expression in non-native vs. native environments.

An important and novel aspect of this study was a fact that in the first year after introduction, seeds of both species experienced at the desert site relatively rare event of precipitation not sufficient for germinated seeds to develop into reproducing adults.

There were a higher proportion of dormant seeds and more sequential germination in the second and third years at the desert as compared with the Mediterranean location in the seed introduction experiment. This pattern agrees with bet-hedge buffering against unpredictability of rainfall and the higher probability of a year in which seed production fails in the desert environment.

Similarly, seeds originating in the less predictable desert environment had more sequential germination over time, i.e. higher proportion of seeds being in the soil for one and more years, in native desert compared with the Mediterranean environment.

Germination fraction does not appear to be fixed for seeds of any origin, but is a very plastic trait highly dependent on amount and timing of precipitation. On the other hand, if precipitation is far from optimal, proportion of seeds that survive in the soil seed bank and germinate in the second or third year is always higher for plants of desert origin. This means that increased persistence in soil seed bank and fractional germination are selected for in the less predictable environment and are inherited traits.

A clear genetically determined difference in size was detected between seeds of desert and Mediterranean origin. Seeds of desert origin were consistently smaller than seeds of Mediterranean origin. Seed size is positively related with seedling growth and establishment (Turnbull et al., 1999; Leishman et al., 2000; Seiwa et al., 2002; Rodriguez-Girones et al., 2003) and therefore with seedling success in competitive environments (Eriksson, 1999; Jakobsson and Eriksson, 2000; Leishman, 2001; Dalling and Hubbell, 2002; Turnbull et al., 2004; Moles and Leishman, 2008). On the other hand, large seed size may trade-off with lower persistence in the seed bank due to predation and with reduced dispersal distance (Price and Joyner, 1997; Reader, 1993; Thompson et al., 1993; Moegenburg, 1996; Gomez, 2004). Moreover, Gomez (2004) experimentally demonstrated that the optimal seed size can be a cumulative function of contrasting selective pressures involving several fitness components. In his experiment, the size of acorns of *Quercus ilex* was directly related to seedling establishment, but also was directly related to probability of seedling loss through increased predation of larger than of smaller seeds.

In my reciprocal seed transplant study, biotic interactions were excluded. This is a weakness of the experimental design and prevented assessment of the potential importance of seed predation in the environment studied. However, I observed much stronger seed predation by foraging ants, rodents and birds in the desert than in the Mediterranean environment (Volis, personal observations) due to the overall low productivity of the desert environment. Thus predation intensity may be a selective force contributing to the differences in size between the seeds of desert and Mediterranean origin.

Seed lifetime in the soil in both studied species did not exceed 3 years, which corresponded to a short-term persistent seed bank (seeds surviving 1–4 years) in classification of Thompson et al. (1997). Seed longevity of annuals is often low (Rice, 1989; Kemp, 1989; Milberg, 1995; Thompson et al., 1997) and absence of a long-term persistent seed bank in the two studied species is not surprising. However, this study demonstrated that in occasional extremely dry years when amount or timing of rainfall is insufficient for plants to mature or even for seeds to germinate, a short-term seed bank becomes the only means ensuring population persistence. Occasional occurrence of years when successful germination is followed by complete reproductive failure is a distinct feature of desert environments (Tevis, 1958; Beatley, 1967; Inouye, 1991; Venable and Pake, 1999). The results show a clear difference in demographic consequences of temporal variation in precipitation in desert vs. Mediterranean environment. In the Mediterranean population, even in the most unfavorable years, adults are present and seeds are produced. Consequently, these seeds serve to restore initial population size. In contrast, in the desert population, in years of insufficient rainfall a situation of no adults surviving to seed production is possible (as happened in season 1998–99 and in the past, see Fig. 1). Under these circumstances the only source of population recovery is the soil seed bank.

A general rule in the studied species appears to be an increasing role of germination-regulating mechanisms that reduce temporal variation in population growth rate from the more predictable Mediterranean towards less predictable desert environments.

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