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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-occuring 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.

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 McPeek, 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-occuring 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 (Gutterman 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 shuttered 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.

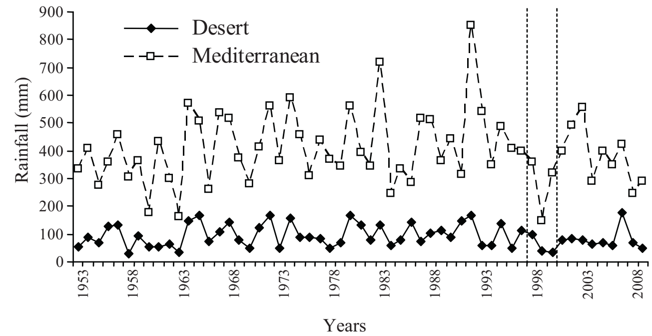

Fig. 1. Annual precipitation at the two studied locations over the last half century. Dotted lines indicate the period of demographic observations.

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.