

An experimental test for effects of the maternal environment on delayed germination

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Summary

1. Recent models on bet-hedging germination in annual plants assume a negative relationship between the proportion of offspring that germinate and the quality of the maternal environment. An increase in the proportion of seeds remaining dormant in the next year, when produced in seasons with high reproduction may result from selection that avoids overcrowding in the following year.

2. We present the first empirical test of this prediction by utilizing a field experiment in Israel which manipulated the entire maternal environment. We subjected semi-arid and Mediterranean annual plant communities to different rainfall treatments: control, reduced and increased rainfall. We then related maternal environment quality to offspring germination fractions for three focal species in two consecutive seasons.

3. There was a negative relationship between the quality of the maternal environment and offspring germination fraction in four out of twelve cases. The negative relationship was stronger for the least competitive species and in the environment with high competition intensity, supporting the role of competition for the observed pattern.

4. Our results suggest that competition with all neighbours is more likely to explain the pattern than sib competition.

5. *Synthesis.* Our findings provide the first experimental evidence of a highly reliable cue (productivity of maternal environment) that allows for plants to respond to their future biotic environment. There is an urgent need for testing predictions of theoretical models in natural populations and for incorporating the role of density dependence in studies of bet-hedging germination.

Key-words: adaptive strategy, annual plants, bet hedging, *Biscutella didyma*, *Bromus fasciculatus*, competition, field rainfall manipulations, *Hymenocarpus circinnatus*, predictive germination, seed dormancy

Introduction

Seed dormancy in annual plants inhabiting unpredictable environments allows avoidance of temporally unfavourable conditions. By spreading germination over several seasons, extinction risk is reduced and, on average, plants may exploit more favourable conditions. Numerous studies have modelled optimal germination fractions of annual plants. Most of these were based on the pioneering model of Cohen (1966), which assumes that germination probabilities of all seeds in the seed bank are equal, constant across seasons, and proportional to the probability of experiencing a favourable season. Later studies have extended this model and relaxed two of the most restrictive assumptions. First, germination rates were allowed to vary according to environmental cues indicative of the favourability of the next season (so-called ‘predictive germina-

tion’ *sensu* Cohen 1967; Venable & Lawlor 1980; Ellner 1985a). Secondly, Cohen’s density-independent case was expanded to a situation, where sibling competition reduces individual seed yield (Westoby 1981; Bulmer 1984; Ellner 1985a,b; Léon 1985; Ellner 1986, 1987; Nilsson *et al.* 1994; Kobayashi & Yamamura 2000). While the number of models on bet-hedging germination of annuals is extremely large, empirical evidence from natural populations testing their predictions has lagged far behind (Philippi 1993a,b; Pake & Venable 1996; Clauss & Venable 2000; Venable 2007).

A common assumption of these models is a homogeneous seed bank, i.e. at a given time all seeds in the soil share the same germination probability. However, empirical studies have shown that this assumption is unrealistic because germination fractions may vary with respect to the rainfall history that the seeds have experienced, and with the size and fecundity of the mother plant (Zammit & Zedler 1990; Philippi 1993b; Tielbörger & Valleriani 2005). Nevertheless, several decades

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passed since Cohen's pioneering model before it was shown theoretically that heterogeneous seed banks could be selected for (Tuljapurkar & Istock 1993; Tielbörger & Valleriani 2005; Valleriani & Tielbörger 2006). Such a pattern may emerge, when predictive germination is coupled with density-dependent seed yield. In this case, seeds produced in favourable (high yield) seasons should have lower proportional germination than seeds produced in unfavourable (low yield) seasons. This can be explained as follows: if dormancy is higher after favourable seasons, the offspring may reduce negative effects of crowding in the following year (Tielbörger & Valleriani 2005; Valleriani & Tielbörger 2006).

In this context, one must properly distinguish between two aspects of 'crowding' that can have different evolutionary consequences. Most previous models have focused on crowding among sibs of the same parent, where higher dormancy increased the fitness of the individual mother plant by reducing the negative effects of sibling competition (e.g. Bulmer 1984; Ellner 1986). A conceptual derivative of these models (the so-called sib-competition hypothesis), which assumes a heterogeneous seed bank, has been tested empirically. The prediction of this hypothesis, which has received some empirical support in the field (Zammit & Zedler 1990; weak support by Hyatt & Evans 1998) and in greenhouse studies (Philippi 1993b), is that seeds of mother plants with many seeds exhibit higher dormancy than seeds from small seed families.

Another aspect of crowding includes competition among all plants (intraspecific and interspecific) in a community. Because plants use essentially the same resources and because most neighbours are non-sibs and interspecific neighbours rather than sibs alone, overall community (diffuse) competition should be much more important than sib competition. Also, the negative consequence of this type of crowding is effective not only at an individual level. It also reduces average individual fitness in a population and therefore also reduces population growth rate. Mechanisms to avoid general competition thus serve not only to increase individual fitness but also to enhance the long-term persistence of a species. A recent model therefore proposed that higher dormancy in seed families that were generated in favourable years resulted from competition among all seedlings, irrespective of their sibship (Tielbörger & Valleriani 2005). The prediction of this model is a negative relationship between the quality of the maternal environment and the average offspring germination fraction.

One challenge of studying predictive germination (*sensu* Cohen 1967) empirically is to find a reliable cue of year quality that can be detected by the seed prior to germination. Previous studies have focused on abiotic cues such as the first rainfall of a season. Usually there was no positive correlation between the first major rain event of a season that triggers germination and the total rainfall of a season (but see Pake & Venable 1996). The intriguing consequence of the germination models that incorporate general competition is that community performance in the previous year can be a better indicator of the current-year quality, at least in terms of the biotic environment into which the seed will germinate (Tielbörger & Valleriani 2005). The precise cue from community performance that gives

rise to a change in germination rate could be related to many different aspects of quality in the maternal environment, both biotic (e.g. competition) or abiotic (e.g. water, nutrient fluxes) (Platenkamp & Shaw 1993). Testing models of predictive germination with general density dependence rather than with sib-competition alone poses a conceptual and methodological challenge. Although theory provides a very clear prediction, large-scale manipulations under field conditions are needed to mimic all possible cues for maternal environmental quality. This is because, unlike models of sib competition, the cue for competitive conditions in the following year cannot be related to the size and fecundity of the mother plant which may vary with local conditions. Instead, the size and fecundity of all plants in the maternal environment are indicative of the potential number of neighbours in the following year. Indeed, earlier studies show that a reliable cue for a productive year may be closely related to neighbour density or productivity in the previous year (Platenkamp & Shaw 1993; Crone 1997). This is also supported by the idea that if maternal and offspring environments are similar, maternal environment effects are adaptive (see review by Galloway 2005).

Because potential cues for environmental quality are difficult to separate experimentally, one should ideally manipulate the entire plant community in the field. Here, we were able to utilize a field experiment in two different climatic regions, where annual rainfall has been manipulated to test whether (prospective) general competition is important in determining offspring germination. It is important to demonstrate the existence of such a relationship, because this may indicate a simple but effective mechanism by which seeds can partly 'predict' the future quality of their environment despite its apparently unpredictable character.

In this study, we present the first experimental test for such a mechanism. To test for the generality of maternal environment effects on germination, we performed the experiments under conditions that differed in the importance of competition for plant performance. Namely, we selected two sites that differ markedly in climate and competition intensity and importance and three coexisting species that differ in their competitive response. We predicted that: (i) offspring germination fraction is negatively correlated with maternal environmental quality. As we assume that competition is the ultimate reason for the existence of such maternal environment effects, we further hypothesized that (ii) the negative relationship would be more pronounced in sites with high competition intensity and for less competitive species.

Materials and methods

FIELD RAINFALL MANIPULATIONS

The study was conducted at two sites in a transition zone between arid and mesic climatic regions in Israel. In the following, we refer to the sites as 'semi-arid' (300 mm mean annual rainfall, Israeli Meteorological Service) and 'Mediterranean' (540 mm mean annual rainfall), respectively. The semi-arid site is located 20 km north of Beer Sheva in the northern Negev desert, and the Mediterranean site is

15 km southwest of Jerusalem. Both sites are situated on south-facing slopes and have the same calcareous bedrock. The vegetation at both sites is open shrubland dominated by *Sarcopoterium spinosum* and by *Thymelaea hirsuta* and *Calicotome villosa* in the semi-arid and the Mediterranean sites, respectively (species names after Feinbrun-Dothan & Danin 1991). At the semi-arid site, annuals may reach 15% cover and often grow under the canopy of shrubs. At the Mediterranean site, annuals attain up to 60% cover in the open patches between shrubs (Holzapfel *et al.* 2006). The sites were suited to test our two hypotheses because competition differs considerably, with neutral or positive interactions at the semi-arid site and predominantly competitive interactions at the Mediterranean site (Holzapfel *et al.* 2006; Schiffers & Tielbörger 2006).

Rainfall at both sites was manipulated during two consecutive growing seasons (*c.* November–April), 2002–03 and 2003–04. Naturally occurring rainfall was reduced in dry plots by manually closing roofs of standard PVC rainout shelters constructed 1 m above-ground surface during targeted rain showers. Following the same rainfall events, the wet plots were irrigated by drizzle sprinklers installed at 50 cm above the ground. Plots with unmanipulated rainfall are referred to as ‘control’ plots. There were five randomly located plots of 10 × 25 m for each of the three rainfall treatments (dry, control, wet) at each site. Manipulations continued until rainfall was reduced or increased by 30% of the long-term average annual rainfall at the sites. Rainfall was not manipulated during seed set and dispersal.

The rainfall manipulations were effective in both years. In the first season (2002–03), total rainfall exceeded the long-term average at both sites by 144% at the semi-arid site and 156% at the Mediterranean site. The rainfall manipulations changed total rainfall amounts to 83% and 113% of the current rainfall at the semi-arid site, and to 74% and 119% at the Mediterranean site, respectively (Fig. 1). The following season (2003–04) was drier with 89% of the long-term average at the semi-arid site and 81% at the Mediterranean site. In this season, the rainfall manipulations reduced and increased the current rainfall

amounts to 58% and 134% at the semi-arid, and 68% and 141% at the Mediterranean site, respectively (Fig. 1).

It is important to note that rainfall varies unpredictably both within years, because the large rain systems do not reach the study area at the beginning of the rainy seasons (Aviad, Kutiel & Lavee 2004, 2009), and rainfall also varies unpredictably between years (Zhang *et al.* 2005). Thus, neither the rainfall in the previous year nor the first rainfall that triggers germination in a year is a good predictor of the quality of the coming growing season. Therefore, there should be strong selection pressure on the traits that give rise to a ‘prediction’ in the quality of the environment into which a seed germinates, fulfilling a requirement of our hypothesis. For illustrating the inherent unpredictability of rainfall at our field sites, we used data on plant emergence, survival and growth in permanent quadrats, and *in situ* rainfall measurements over 6 years (2001/02–2007/08, no measurements in 2004/05). The plant data provided: (i) average biomass per unit area as a proxy for year quality, and (ii) an estimate for the amount of rainfall that triggered the major germination event. Correlating the amount of effective rainfall with average biomass per unit area yielded non-significant results for both sites (semi-arid: $r = 0.21$, Mediterranean: $r = 0.46$).

STUDY SPECIES

We studied three native winter annuals with a wide distribution across Israel (Feinbrun-Dothan & Danin 1991), high abundance at both study sites, and differences in seed dormancy strategy. *Bromus fasciculatus* (L.) is a grass with low dormancy. *Biscutella didyma* (L.) is a crucifer with intermediate seed dormancy. *Hymenocarpus circinnatus* (L.) Savi is a legume with pods containing two seeds with high dormancy. The species also differ in competitive response ability and are thus likely to differ in their response to maternal environmental quality (hypothesis 2). *Hymenocarpus circinnatus* is the strongest competitor and *B. didyma* and *B. fasciculatus* are weak competitors (Schiffers & Tielbörger 2006; C. Ariza & K. Tielbörger, unpubl. data).

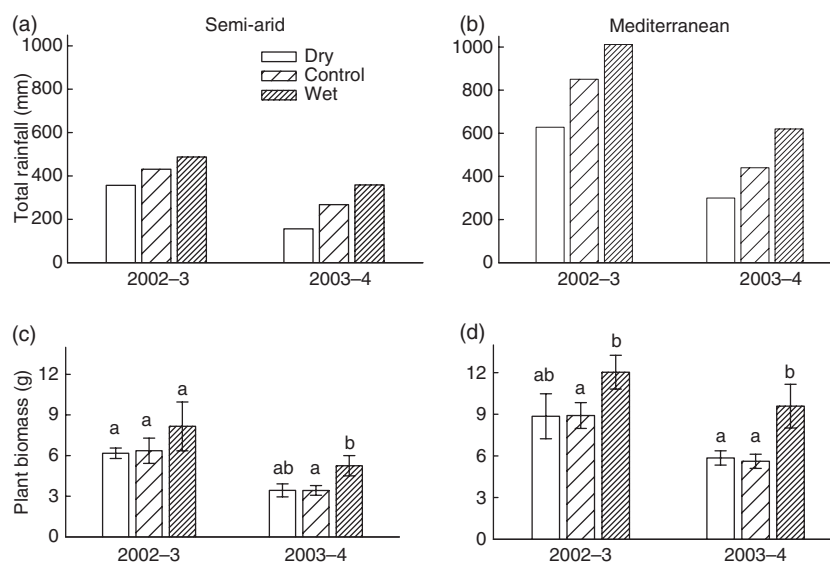


Fig. 1. Total rainfall (a), (b) and mean (\pm SE) community biomass of plants per 20 × 20 cm (c), (d) established under different maternal environments (dry, control and wet) in 2002–03 (‘first generation’) and 2003–04 (‘second generation’). Biomass values with similar letters do not differ from each other (one-tailed *t*-tests corrected for false discovery rate).

ESTIMATING ENVIRONMENTAL QUALITY

Community biomass was used as the main predictor of the environmental quality experienced by the mother plant and of the potential density of competitors in the following season. This proxy is best suited for testing our main hypothesis because it indicates the productivity of the environment, and because it is likely to correlate with seed production per unit area. For example, we have found a positive correlation between above-ground biomass and fecundity for *c.* 50 species in the study sites (W. Siewert & K. Tielbörger, unpubl. data). It should be noted that we did not use total annual rainfall as an indicator of maternal environment quality, because the favourability of a season is also determined by the within-year distribution of rain and not only by its total. This was also supported by correlation analyses for long-term data for our stations (correlations between rainfall and biomass: Mediterranean: $r = 0.83$, $P < 0.05$; semi-arid: $r = 0.62$, NS). Figure 1 confirms this assumption in that the treatments did affect biomass, but higher total rain was not consistently correlated with biomass. Specifically, the irrigation markedly increased biomass, but the dry treatment had no effect.

Community biomass data were obtained from a parallel study, where above-ground biomass was harvested annually at peak season from five randomly located 20×20 cm quadrats per plot (a total of 25 per treatment and site, J. Kigel & I. Konsens, unpubl. data). Biomass was harvested each year and in each maternal environment.

DIAPORE COLLECTION AND STORAGE

Diaspore collection and handling followed a protocol from previous studies (Petrú *et al.* 2006; Petru & Tielbörger 2008), based on the need of desert annual seeds to experience high temperatures to break summer dormancy (e.g. Boeken *et al.* 2004). We collected ripe diaspores from the treatments in both seasons, at the time of seed set and dispersal (April–May). Seeds were collected over 4–5 different days during the fruiting period by carefully scanning the entire area within a treatment for ripe seeds and collecting no more than three seeds per plant to minimize the impact on the sites. Diaspores from the first season are referred to as ‘first seed generation’. In the second season, plants were collected at a distance of at least 2 m from the plot’s edge (mean dispersal distances of most annual species are in the range of a few centimetres, Siewert 2008), to ensure that collections included only diaspores of plants established from seeds produced within the treatment plots. Therefore, this ‘second seed generation’ experienced two consecutive seasons of rainfall treatments. For naturally breaking summer dormancy, we stored the diaspores collected in each season in their original sites over the summer in bags made of organza (permeable transparent synthetic fabric), attached to the ground surface. Each season in September, we collected the bags from the field, transferred them to a laboratory for seed counting into equal portions and immediately sowed them into an environmentally controlled germination experiment.

SEED VIABILITY TESTING

Seeds that are stored in the field over summer for dormancy breaking may lose their viability. Also, seeds produced under different conditions could differ in their viability, which would affect germination fractions. For example, seeds produced under wet conditions may be more prone to fungal attack and thus be less viable. Seeds produced in bad conditions could also be less viable because of lack of resources. We examined the viability of five times 20 seeds per species, site and treatment, by germinating them under laboratory conditions

(23 °C) for 10 days and subsequently poking ungerminated seeds to examine whether the embryos were fleshy and viable (see Pake & Venable 1996). The three species had high viability in both sites and seasons with no significant variation among the maternal environments (*B. didyma* 81–91%, *B. fasciculatus* 62–96%, *H. circinnatus* 90–100%).

CONTROLLED GERMINATION TRIALS

To avoid confounding with numerous factors that control germination in the field (e.g. soil type, neighbour conditions, on-site rainfall; see Petru & Tielbörger 2008), we carried out germination trials in a growth chamber (further ‘Phytotron’) at the Hebrew University in Rehovot, Israel, in mid-November each season, for each species separately. We added 20 *B. didyma* seeds, 40 and 30 *B. fasciculatus* (in the first and second season, respectively) or 40 *H. circinnatus* seeds (20 fruits; each enclosing 2 seeds) to pots measuring 12 cm in diameter and 12 cm in depth, filled with vermiculite and soaked with tap water with no added nutrients. To prevent desiccation, we covered the seeds with a 1-cm layer of well-moistened vermiculite. We exposed the seeds to a temperature range of 16 °C day/10 °C night and watered them excessively twice a day. In each season, the experimental design (2 sites \times 3 species \times 3 maternal environments) had 20 replicates, resulting in a total of 360 pots. The first seedlings emerged 1 week after initiation of the experiment. Subsequently, we counted seedlings every other day and removed them from the pots. The experiment was completed in 4 weeks, when no additional seedlings emerged. Results from parallel experiments (Eberhart 2006) and viability tests indicated that most seeds (90–100%) that did not germinate in the first season were dormant and not dead.

DATA ANALYSES

To directly test for the predicted site \times treatment and species \times treatment interactions on germination (hypothesis 2), we performed ANOVAS. In these tests, the proportion of offspring seeds germinating per sample was evaluated for the rainfall treatments, species and sites in a full factorial design (2 sites \times 3 species \times 3 rainfall treatments). We tested effects of the rainfall treatments on the second seed generation in separate ANOVAS, because the second season was not a true replication of the first season’s experiment. Namely, seeds produced in the first season experienced one season of rainfall manipulation, while seeds produced in the second season came from plants whose mothers had already experienced a manipulated season. The ANOVA model for germination was the same for both generations. Germination data from both seasons did not require transformation. Tukey’s multiple range *post hoc* tests ($P < 0.05$) evaluated pairwise differences between rainfall treatments within species and sites.

While the ANOVAS tested for the statistical interactions, we also predicted a specific negative effect of maternal environmental quality on offspring germination. Average biomass of annuals indicates maternal environmental quality and potential neighbour density in the next year. We then tested for the predicted negative relationship between average biomass per treatment and average offspring germination fraction (hypothesis 1), using linear regressions. The hypothesized statistical interactions were then obtained from the above ANOVAS. We corrected for false discovery rate with the procedure of Benjamini & Hochberg (1995), which has recently been advocated for ecological studies (Verhoeven, Simonsen & McIntyre 2005).

Results

ANALYSES OF VARIANCE AND MULTIPLE TESTS

Germination in the first season differed significantly between sites (Table 1) with higher average germination for seeds from the Mediterranean site (Fig. 2b). Differences among rainfall treatments were significant for the Mediterranean site and non-significant for the semi-arid site (significant interaction site \times rainfall treatment, Table 1; Fig. 2). For two species (*B. didyma*, *B. fasciculatus*) from the Mediterranean site, germination fractions were significantly greater for the dry

treatment than for the control, and germination for controls was greater than for the wet treatment, while germination of *H. circinnatus* did not differ between treatments (Fig. 2a,b; Table 1: significant two-way and three-way interactions between site, species and rainfall treatment). Average germination in the second season was higher for seeds from the semi-arid site (Fig. 2c). The site and species effects as well as all interactions were significant (Table 1), indicating species-specific and site-specific responses to the rainfall treatments. Namely, seeds of *B. didyma* from the wet treatment had lower germination (Fig. 2d) than those from the two drier treatments for the Mediterranean site, while germination of *B. fasciculatus* and *H. circinnatus* differed significantly between stations and treatments but did not show any consistent pattern across sites and treatments (Fig. 2c,d).

Table 1. Results of ANOVAS for proportional offspring germination (G) for 2 years, two sites (semi-arid and Mediterranean), three species (*Biscutella didyma*, *Bromus fasciculatus* and *Hymenocarpus circinnatus*) and three rainfall treatments (dry, control and wet)

	d.f.	G 2003–04		G 2004–05	
		F	P	F	P
Site	1	21.22	< 0.001	104.75	< 0.001
Species	2	1158.89	< 0.001	27.33	< 0.001
Rainfall treatment	2	36.81	< 0.001	2.46	0.087
Site \times species	2	54.95	< 0.001	70.79	< 0.001
Site \times rainfall treatment	2	22.48	< 0.001	13.63	< 0.001
Species \times rainfall treatment	4	20.19	< 0.001	9.00	< 0.001
Site \times species \times rainfall treatment	2	16.71	< 0.001	18.79	< 0.001

REGRESSION ANALYSES

The regression analyses using biomass as predictor for offspring germination confirmed the findings of the ANOVAS. Eight regressions showed a negative slope but this was significant only in four cases. Namely, biomass in the Mediterranean site was negatively correlated with germination fractions of *B. didyma* in both years, for *B. fasciculatus* in the first year, and for *H. circinnatus* in the second year (Table 2). There was no significant negative correlation for any species in the semi-arid site. A (significant) positive slope between biomass and germination was detected in two cases (*H. circinnatus* Mediterranean first generation, *B. fasciculatus* Mediterranean second generation).

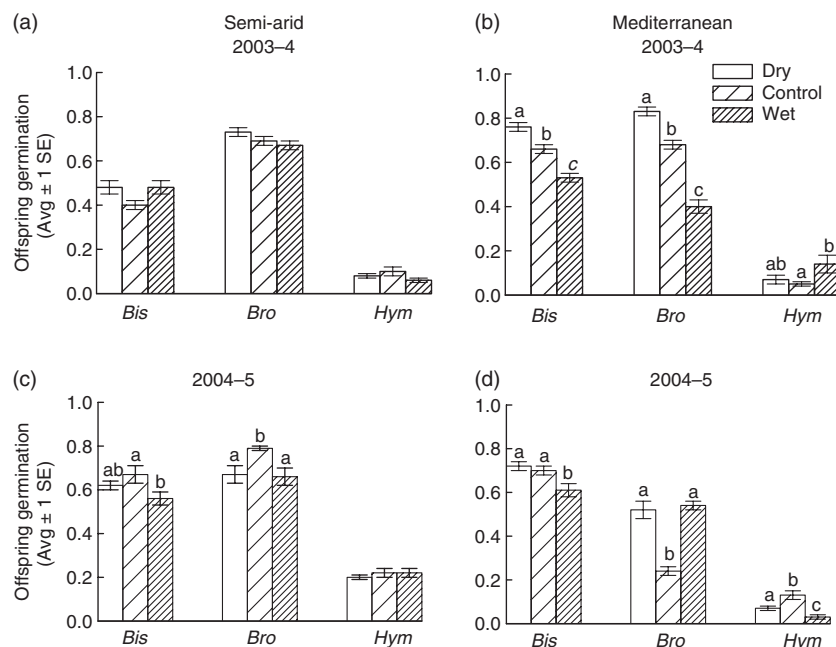


Fig. 2. Mean proportional germination of seeds collected in 2002–03 (a, b) and 2003–04 (c, d) from different maternal environments (dry, control and wet) at a semi-arid (a, c) and Mediterranean (b, d) site. Seeds were germinated under controlled conditions in the following season. Different letters above error bars indicate significant pairwise differences between maternal environments within species and site (Tukey's multiple range tests, $P < 0.05$). *Biscutella didyma* (= Bis), *Bromus fasciculatus* (= Bro) and *Hymenocarpus circinnatus* (= Hym).

Table 2. Results of regression analyses (r^2) testing in two sites, 2 years and for three species *Biscutella didyma*, *Bromus fasciculatus* and *Hymenocarpus circinnatus*, for a negative relationship between average biomass per unit area and offspring germination fraction (G)

	G		
	<i>B. didyma</i>	<i>B. fasciculatus</i>	<i>H. circinnatus</i>
Biomass 2002–03 semi-arid	0.21	0.05	0.32
Biomass 2002–03 Mediterranean	0.38*	0.68*	0.10*
Biomass 2003–04 semi-arid	0.08	0.05	0.01
Biomass 2003–04 Mediterranean	0.17*	0.21*	0.36*

Asterisks indicate significant results ($P < 0.05$) after correction for false discovery rate. Bold values indicate negative slopes consistent with the predicted relationship.

Discussion

Our findings suggest that seed dormancy in annual plants inhabiting unpredictably varying habitats may be affected by the quality of the maternal environment. However, this predicted negative correlation between maternal environmental quality and offspring germination was not consistent among species and environments. In the following, we discuss first the supporting evidence for our main prediction and then suggest explanations for the cases that did not confirm our first hypothesis.

In line with our initial hypotheses, the negative correlation between maternal environment quality and offspring germination was only observed in environments with high competition intensity (e.g. Schiffrers & Tielbörger 2006) and was stronger for competitively inferior species. *Biscutella didyma* from the Mediterranean site exhibited a consistently negative relationship between rainfall in the season of seed set and offspring germination, and the two other species showed this pattern in one of the years. This is the first empirical evidence for such effects from field-manipulated populations of plants. Therefore, our results represent a first experimental support for the theoretically predicted pattern of environmental maternal effects on germination (Tielbörger & Valleriani 2005). Based on this model, we suggest that the pattern observed here is adaptive, and that it is the result of selective constraints induced by generalized competition after favourable seasons. This simple mechanism allows seeds to respond to their future competitive environment long before germination. Our findings thus corroborate models about predictive germination (Cohen 1967; Venable & Lawlor 1980; Ellner 1985a), which indicate that fitness is maximized when the germination fraction is correlated with an environmental cue that reliably indicates the favourability of the next season. The few attempts to demonstrate such a mechanism in nature have encountered the difficulty of relating an abiotic cue (e.g. first rainfall of a season) to the

quality of the coming year (but see Pake & Venable 1996). Because this correlation does not exist in many environments, including ours, the alternative cue we suggest here could be very important. Unlike the first rainfall of the season, the maternal environment is a highly reliable signal for environmental conditions (here: neighbour densities) in the following season. This indicates that diffuse competition may be a strong selective force for determining predictive germination.

Besides the supporting evidence, there were several deviations from the predicted optimal behaviour. We suggest that these may be explained by the fact that negative density dependence (diffuse competition) is the ultimate reason for the evolution of a negative relationship between maternal environmental quality and offspring germination fraction (Tielbörger & Valleriani 2005). Such effects should be more detectable in more productive environments and environments where competition intensity is high. Our study supports this suggestion by finding the effects of maternal environment only at the Mediterranean site. Recent investigations at our study sites showed that indeed, competition between plants at the Mediterranean site is always intense, while facilitation dominates in dry seasons at the semi-arid site and balances negative interactions in wet years (Holzapfel *et al.* 2006; Schiffrers & Tielbörger 2006). The lack of evidence in the semi-arid environment also indicates that the pattern we detected is unlikely to result from non-adaptive effects (e.g. differences in nutrient content of seeds from different treatments) on seed germination.

Another interesting deviation from our prediction is that *H. circinnatus* and *B. fasciculatus* did not exhibit a consistent response to the rainfall treatments. Similar to the differences between sites, such species-specific patterns could also be partly explained by the role of competition. Seeds of *H. circinnatus* are among the largest within our plant communities, and previous experiments have indicated that this species is a superior competitor (Schiffrers & Tielbörger 2006; C. Ariza & K. Tielbörger, unpubl. data). Therefore, competition is a less important selective force for this species and maternal environment effects should be less likely to occur. Another, more speculative, explanation for the lack of consistent evidence in *B. fasciculatus* and *H. circinnatus* may be related to the general germination strategy exhibited by legumes and grasses. In our system, legumes have a thick seed coat and very high dormancy, while grasses usually have consistently low dormancy, i.e. high germination (Kigel & Galili 1995; Petru & Tielbörger 2008). This may make germination fractions relatively invariable and result in rather small responses of germination to external cues. Overall, the species-specific patterns we detected indicate that the mechanism for predictive germination we propose here may not be important on a community level. Therefore, multi-species studies should be performed to test models of optimal germination (e.g. Venable 2007).

It should be emphasized that unlike previous empirical and theoretical studies, we were searching for effects of the maternal environment at the population level. These effects are the result of generalized or diffuse competition as opposed to the so-called sib-competition hypothesis. The sib-competition

hypothesis predicts that seeds of large families are selected to have lower germination rates due to the detrimental effects of sibling competition on parental fitness (Westoby 1981; Ellner 1986; Nilsson *et al.* 1994; Kobayashi & Yamamura 2000). The test of this hypothesis involves collecting sibling seeds from mother plants of different fecundity within a population and season and measuring their germination fractions (Zammit & Zedler 1990; Hyatt & Evans 1998). The authors of these and a similar study (Philippi 1993b) suggested that information about the quality of the maternal season may be transferred to the offspring via maternal effects (Roach & Wulff 1987). An indication of the occurrence of such individual maternal effects could be a negative correlation between maternal seed production and offspring germination. Although our design did not aim at testing the sib-competition hypothesis, we also looked at average fecundity per study species as a predictor of offspring germination. Compared to measures of general competition such as rainfall or productivity, maternal fecundity was a relatively poor predictor of offspring germination, with only one significant negative correlation (see Appendix S1 in Supporting Information). This observation also finds support in a parallel study that has directly tested, and failed to support, the sib-competition hypothesis for our three focal species (Eberhart 2006). We therefore suggest that individual maternal effects are unlikely to determine the pattern detected here. Yet, studies are needed that are explicitly designed to differentiate between our new hypothesis and the sib-competition hypothesis.

A recent study showed that the phytochrome system may be involved in germination responses to seasonal cues, including maternal effects on germination (Donohue *et al.* 2007). Thus, an alternative way of 'detecting' the favourability of a season independent of individual maternal performance may be via high densities of plants around the mother (Platenkamp & Shaw 1993; Crone 1997) utilizing different red : far red ratios. Indeed, we found negative relationships between site productivity in the year of seed production and offspring germination. Productivity should correlate with abundance of neighbours, and this may be an even better cue for predicting overcrowding than maternal fecundity because it is not affected by chance effects on the individual mother plant. Also, such a mechanism would allow prediction of the potential intensity of generalized competition (as modelled by Tielbörger & Valleriani 2005), independent of the density of siblings. Clearly, the mechanisms behind the patterns observed here merit more attention in physiological studies on seed dormancy.

In summary, our findings suggest that there may be a simple but effective mechanism allowing seeds to 'predict' their future success by utilizing information about the environment of their mother. However, the relative importance of this mechanism probably depends on whether or not competition is a strong selective force and whether or not there is strong selection on seed dormancy. Because our study is the first of its kind, we call for further experiments testing the generality of the theoretically predicted behaviour and the species- and site-specific patterns observed here.

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References

- Aviad, Y., Kutiel, H. & Lavee, H. (2004) Analysis of beginning, end, and length of the rainy season along a Mediterranean–arid climate transect for geomorphic purposes. *Journal of Arid Environments*, **59**, 189–204.
- Aviad, Y., Kutiel, H. & Lavee, H. (2009) Variation of Dry Days Since Last Rain (DDSLR) as a measure of dryness along a Mediterranean – Arid transect. *Journal of Arid Environments*, **73**, 658–665.
- Benjamini, Y. & Hochberg, Y. (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society B*, **57**, 289–300.
- Boeken, B., Ariza, C., Gutterman, Y. & Zaady, E. (2004) Environmental factors affecting dispersal, germination and distribution of *Stipa capensis* in the Negev Desert, Israel. *Ecological Research*, **19**, 533–540.
- Bulmer, M.G. (1984) Delayed germination of seeds: Cohen's model revisited. *Theoretical Population Biology*, **26**, 367–377.
- Clauss, M.J. & Venable, D.L. (2000) Seed germination in desert annuals: an empirical test of adaptive bet hedging. *American Naturalist*, **155**, 168–186.
- Cohen, D. (1966) Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology*, **12**, 119–129.
- Cohen, D. (1967) Optimizing reproduction in a randomly varying environment when a correlation may exist between the conditions at the time a choice has to be made and the subsequent outcome. *Journal of Theoretical Biology*, **16**, 1–14.
- Crone, E.E. (1997) Parental environment effects and cyclical dynamics in plant populations. *American Naturalist*, **150**, 708–729.
- Donohue, K., Heschel, M.S., Chiang, G.C.K., Butler, C.M. & Barua, D. (2007) Phytochrome mediates germination responses to multiple cues. *Plant, Cell and Environment*, **30**, 202–212.
- Eberhart, A. (2006) Do siblings avoid each other? An empirical test of the sibling competition hypothesis along a steep climatic gradient. Diploma Thesis, University of Tübingen, Tübingen, Germany.
- Ellner, S. (1985a) ESS germination strategies in randomly varying environments. I. Logistic type models. *Theoretical Population Biology*, **28**, 50–79.
- Ellner, S. (1985b) ESS germination strategies in randomly varying environments. II. Reciprocal yield-law models. *Theoretical Population Biology*, **28**, 80–115.
- Ellner, S. (1986) Germination dimorphisms and parent-offspring conflict in seed germination. *Theoretical Population Biology*, **123**, 173–185.
- Ellner, S. (1987) Competition and dormancy: a reanalysis and review. *American Naturalist*, **130**, 798–803.
- Feinbrun-Dothan, N. & Danin, A. (1991) *Analytical Flora of Eretz-Israel*. Cana Publishing House Ltd., Jerusalem.
- Galloway, L.F. (2005) Maternal effects provide phenotypic adaptation to local environmental conditions. *New Phytologist*, **166**, 93–100.
- Holzapfel, C., Tielbörger, K., Parag, H.A., Kigel, J. & Sternberg, M. (2006) Annual plant–shrub interactions along an aridity gradient. *Basic and Applied Ecology*, **7**, 268–279.
- Hyatt, L.A. & Evans, A.S. (1998) Is decreased germination fraction associated with risk of sibling competition? *Oikos*, **83**, 29–35.
- Kigel, J. & Galili, G. (1995) *Seed Development and Germination*. Dekker, New York.
- Kobayashi, Y. & Yamamura, N. (2000) Evolution of seed dormancy due to sib competition: effect of dispersal and inbreeding. *Journal of Theoretical Biology*, **202**, 11–24.
- Léon, J.A. (1985) Germination strategies. *Evolution. Essays in Honour of John Maynard Smith* (eds P.J. Greenwood, P.H. Harvey & M. Slatkin), pp. 129–143. Cambridge University Press, London.
- Nilsson, P., Fagerström, T., Tuomi, J. & Åström, M. (1994) Does seed dormancy benefit the mother plant by reducing sib competition? *Evolutionary Ecology*, **8**, 422–430.
- Pake, C.E. & Venable, D.L. (1996) Seed banks in desert annuals: implications for persistence and coexistence in variable environments. *Ecology*, **77**, 1427–1435.

- Petrů, M. & Tielbörger, K. (2008) Germination behaviour of annual plants under changing climatic conditions: separating local and regional environmental effects. *Oecologia*, **155**, 717–728.
- Petrů, M., Tielbörger, K., Belkin, R., Sternberg, M. & Jeltsch, F. (2006) Life history variation in an annual plant under two opposing environmental constraints along an aridity gradient. *Ecography*, **29**, 1–9.
- Philippi, T. (1993a) Bet-hedging germination of desert annuals: beyond the first year. *American Naturalist*, **142**, 474–487.
- Philippi, T. (1993b) Bet-hedging germination of desert annuals: variation among populations and maternal effects in *Lepidium lasiocarpum*. *American Naturalist*, **142**, 488–505.
- Platenkamp, G.A.J. & Shaw, R.G. (1993) Environmental and genetic maternal effects on seed characters in *Nemophila menziesii*. *Evolution*, **47**, 540–555.
- Roach, D.A. & Wulff, R.D. (1987) Maternal effects in plants. *Annual Review of Ecology and Systematics*, **18**, 209–235.
- Schiffers, K. & Tielbörger, K. (2006) Ontogenetic shifts in interactions among annual plants. *Journal of Ecology*, **94**, 336–341.
- Siewert, W. (2008) The dispersal dormancy trade-off in annual plants: putting model predictions to the test. Diploma Thesis, University of Tübingen, Tübingen, Germany.
- Tielbörger, K. & Valleriani, A. (2005) Can seeds predict their future? Germination strategies of density-regulated desert annuals. *Oikos*, **111**, 235–244.
- Tuljapurkar, S. & Istock, C. (1993) Environmental uncertainty and variable diapause. *Theoretical Population Biology*, **43**, 251–280.
- Valleriani, A. & Tielbörger, K. (2006) Effect of age on germination of dormant seeds. *Theoretical Population Biology*, **70**, 1–9.
- Venable, D.L. (2007) Bet-hedging in a guild of desert annuals. *Ecology*, **88**, 1086–1090.
- Venable, D.L. & Lawlor, L. (1980) Delayed germination and dispersal in desert annuals: escape in space and time. *Oecologia*, **46**, 272–282.
- Verhoeven, K.J.F., Simonsen, K.L. & McIntyre, L.M. (2005) Implementing false discovery rate control: increasing your power. *Oikos*, **108**, 643–647.
- Westoby, M. (1981) How diversified seed germination behaviour is selected. *American Naturalist*, **118**, 882–885.
- Zammit, C. & Zedler, P.H. (1990) Seed yield, seed size, and germination behaviour in the annual *Popogyne abramsii*. *Oecologia*, **84**, 24–28.
- Zhang, X., Aguilar, E., Sensoy, S., Melkonyan, H., Tagiyeva, U., Ahmed, N. *et al.* (2005) Trends in Middle East climate extreme indices from 1950 to 2003. *Journal of Geophysical Research*, **110**, D22104.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Evaluation of possible effects of maternal fecundity on offspring germination.

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