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Seed mass and dormancy of annual plant populations and communities decreases with aridity and rainfall predictability

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Abstract

Several theoretical and empirical studies have examined the influence of environmental conditions on seed traits and germination strategies of annual species. A positive relationship between seed mass and dormancy has been described for annuals occupying climatically unpredictable ecosystems. Larger-seeded species tend to have higher seedling survival rates, while dormancy allows a bet-hedging strategy in unpredictable environments. Until now, these ideas have been addressed primarily for only one or a few focal species, without considering differences among populations and communities. The novelty of the present study lies in the population and community-level approach, where a comprehensive seed trait database including 158 annual species occurring along a gradient of rainfall variability and aridity in Israel was used to ask the following question: Does average seed mass and dormancy of annual populations and communities decrease with increasing aridity and rainfall unpredictability?

Soil seed bank samples were collected at the end of the summer drought, before the onset of the rains, from four plant communities. Germination was tested under irrigated conditions during three consecutive germination seasons to determine the overall seed germinability in each soil sample. Seed mass was obtained from newly produced seeds collected at the study sites in late spring. The community level results showed that, in contrast to common theoretical knowledge, seed mass and dormancy of the dominant annual species decreased with increasing aridity and rainfall variability. Accordingly, a negative correlation was found between seed mass and seed germination fractions. The present study demonstrates that an analysis of seed traits along climatic gradients is significantly improved by approaches that target both population and community levels simultaneously. A critical evaluation sheds new light upon the selective pressures that act on seed ecology of annuals along a climatic gradient and facilitates formulation of more mechanistic hypotheses about factors governing critical seed traits.

Zusammenfassung

Theoretische und empirische Studien haben sich mit dem Einfluss von Umweltbedingungen auf die Eigenschaften von Pflanzensamen und auf Keimungsstrategien annueller Arten befasst. In stochastischen Ökosystemen ist eine positive Korrelation zwischen Samenmasse und Dormanz für annuelle Pflanzen als typisch beschrieben worden. Arten mit grösseren Samen neigen dazu höhere Keimlingsüberlebensraten zu haben, während erhöhte Dormanz als Absicherungsstrategie gegen unvorhersehbare Umweltbedingungen gedeutet wurde. Bis jetzt sind diese Aussagen lediglich für einzelne oder wenige Arten untersucht worden und Ansätze, die Unterschiede zwischen Populationen und Pflanzengemeinschaften berücksichtigen, fehlen weitaus.

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Die Neuheit der gegenwärtigen Untersuchung beruht auf der Fragestellung auf Populations- und Gemeinschaftsniveau. Eine umfassende Datenbank, welche die Sameneigenschaften von 158 Arten entlang eines Trockenheitsgradienten in Israel umfasst, wurde verwendet, um die folgende Frage zu untersuchen: Wie verhält sich die durchschnittliche Samenmasse und Dormanz in Bezug zu zunehmender Aridität und Niederschlagsvorhersehbarkeit?

In vier Pflanzengemeinschaften entlang des Gradienten wurden Samenbankproben am Ende der Sommertrockenheitsperiode vor den ersten Regenfällen genommen. Die Bodenproben wurden während drei aufeinanderfolgenden Wachstumsperioden bewässert, um Keimungsprozente aller Arten zu bestimmen. Samenfrischgewicht wurde anhand von in den Untersuchungsgebieten gesammelter Samen bestimmt.

Samenmasse und Dormanz nahmen auf Gemeinschaftsniveau mit zunehmender Aridität und Niederschlagsvorhersehbarkeit ab; ein Ergebnis, welches im Kontrast zu bestehender Theorie steht. Eine negative Korrelation zwischen Samenmasse und der prozentualen Keimungsrate wurde darüberhinaus gefunden. Die vorliegende Untersuchung demonstriert, dass eine umfassende Analyse von Sameneigenschaften entlang eines klimatischen Gradienten sowohl auf Populations–als auch auf Gemeinschaftsniveau unternommen werden sollte. Eine kritische Bewertung des Selektionsdruckes auf die Samenökologie aktueller Arten ist notwendig, um mechanistische Hypothesen bezüglich der Charaktereigenschaften von Pflanzensamen aufstellen zu können.

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Keywords: Desert; Germination strategies; Mediterranean; Plant community; Seed bank; Seed size

Introduction

Soil seed banks play an important role in annual plant populations by buffering populations against temporal variation (Clauss & Venable 2000) and by avoiding the demographic effects of reproductive failure (Evans & Cabin 1995). Such seed banks contain dormant seeds that did not germinate even when placed under conditions that are generally suitable for germination (Philippi 1993).

Deserts and Mediterranean-type ecosystems are good examples of ecosystems where soil seed banks play an important role in preserving plant populations and communities. This is especially true for annuals, as their seeds are the only structure linking one year to the next (Pake & Venable 1996; Adondakis & Venable 2004). Delayed germination (a bet-hedging strategy) is, in theory, one of the most efficient adaptations for annuals inhabiting arid environments, which are typically characterized by highly variable and unpredictable climatic conditions (Philippi 1993). This adaptation buffers against reproductive failure by spreading seed germination over several years, reducing the variance in fitness across years, at the cost of reducing the (arithmetic) average fitness within each year (Philippi & Seger 1989; Philippi 1993). In more mesic and climatically predictable Mediterranean-type ecosystems, the formation of soil seed banks is also regarded as an adaptive response to disturbance and grazing (Holzapfel, Schmidt, & Shmida 1993; Sternberg, Gutman, Perevolotsky, & Kigel 2003; Osem, Perevolotsky, & Kigel 2006) and/or competition (Aikio, Ranta, Kaitala, & Lundberg 2002; Volis, Mendlinger, & Ward 2002).

Seed mass, which links plant regeneration, vegetative growth, and survival, is another key functional trait for coping with environmental stress. Larger-seeded species tend to have higher seedling survival rates (e.g. Westoby, Falster, Moles, Vesk, & Wright 2002) especially under dry conditions (e.g. Baker 1972) and are thus more common in such

environments (Wright & Westoby 1999). Seedlings produced by larger seeds may be more capable of resisting environmental hazards due to larger reserves that can be exploited as a mechanism of drought resistance (Leishman & Westoby 1994).

Environmental gradients provide a useful framework for evaluating the relative importance of differential selective forces on adaptive traits (here: seed mass and dormancy) that maximize fitness among different species (Endler 1986). In the present study we used an aridity gradient as a framework for investigating the effects of climatic differences on adaptive variation in seed life traits in four annual plant communities. We focused on annual species as they encompass more than 80% of the species present in the soil seed banks at the study sites. The gradient ranges from arid desert to a mesic Mediterranean ecosystem and varies both in rainfall quantity and predictability. At the arid end of the precipitation gradient, rainfall events are highly unpredictable between years, while at the mesic end of the gradient climatic conditions are more favorable.

Previous studies have examined the influence of environmental conditions such as climatic variability and water availability on seed dormancy and seed size in annual plant species (Philippi 1993; Clauss & Venable 2000; Adondakis & Venable 2004). However, most studies have focused on only one or few focal species, without scaling up to the higher community level. We believe that scaling up from species and population level is needed in order to advance in understanding of, and ability to, predict community assembly (McGill, Enquist, Weiher, & Westoby 2006). By assembling a comprehensive database of seed life traits of the complete annual plant community, the present study combined novel population and community-level approaches. According to ecological theory, populations of annual species from climatically unpredictable arid and semiarid ecosystems should exhibit (1) lower germination rates (or a higher proportion

Table 1. Physical and biotic characteristics of the study sites along the aridity gradient. Temperature refers to annual means (mean minimum, mean and mean maximum). Rainfall coefficient of variance (CV-%) are obtained from long-term (31 years) rainfall data (Israel Meteorological Service).

| Ecosystem type | Rainfall (mm and CV) | Temperature (°C) Min. – mean – max. | Elevation (a.s.l) | Soil type |
|--------------------------------------|----------------------|--|-------------------|------------------------------|
| Arid (N30°52' E34°46') | 90 – 51 | 13.6 – 19.1 – 26.1 | 470 m | Desert Lithosol |
| Semiarid (N31°23' E34°54') | 300 – 37 | 13.2 – 18.4 – 24.8 | 590 m | Light Brown Rendzina |
| Mediterranean (N31°42' E35°3') | 540 – 30 | 12.8 – 17.7 – 23.6 | 620 m | Terra Rossa |
| Mesic Mediterranean (N33°0' E35°14') | 780 – 22 | 13.5 – 18.1 – 23.4 | 500 m | Montmorillonitic Terra Rossa |

of dormant seeds) as a bet-hedging strategy and (2) produce larger seeds than species that inhabit more predictable mesic ecosystems. We assume that higher seed mass would lead to seedlings better fitted to resist environmental risks due to larger reserves. A larger seed mass may be beneficial for rapid seedling root growth in nutrient poor environments where soil moisture is low or act as a buffer against poor environmental conditions (Leishman & Westoby 1994). In general, large seed masses should be beneficial in situations where resources are limited or are used up rapidly (Eriksson, Friis, & Lofgren 2000). Here an aridity gradient was used to study the suitability of these theoretical ideas by analyzing the relationships between climatic predictability and adaptive variations in seed life traits (here: seed mass and dormancy) of 158 annual plant species.

Materials and methods

Study sites

Soil seed banks from four field sites along a North-South aridity gradient in Israel were studied (length: 245 km, for full description see Holzapfel, Tielbörger, Parag, Kigel, & Sternberg 2006). Environmental conditions at these sites represent mesic Mediterranean, Mediterranean, semiarid, and arid conditions (Table 1). At the mesic Mediterranean site vegetation formation was characterized by a closed oak maquis (*Quercus calliprinos*) and open garrigue formations dominated by shrubs (e.g. *Calicotome villosa*, *Sarcopoterium spinosum*, *Cistus* spp.) and associated herbaceous plants. The Mediterranean site was a dwarf-shrubland dominated by *S. spinosum* and a high diversity of herbaceous (mostly annual) plant species. The semiarid site was characterized by an opened dwarf-shrubland of *S. spinosum* and *Coridothymus capitatus* associated with herbaceous (chiefly annual) plant species. The arid site was represented by an opened vegetation formation dominated by small shrubs and semi-shrubs such as *Zygophyllum dumosum*, *Artemisia sieberi* and *Hammada scoparia* and sparsely growing desert annuals, geophytes and hemicryptophytes. All sites share the same calcareous bedrock and are positioned on south-facing slopes. The typical climate is Mediterranean with rainy winters (October to April) and prolonged dry hot summers.

Germination of annuals and re-growth of most perennials occurs in October to November, soon after the first major rainfall events (~10–20 mm). The length of the typical rainy season increases from the desert (December to March) to the Mediterranean (October to May). Vegetation is dominated by the semi-deciduous, dimorphic shrub *S. spinosum* (L.) Sp. at the three northern sites, and by the semi-deciduous shrub *Z. dumosum* Boiss. at the southernmost site, with interspersed ephemeral herbaceous patches (for details, see Fleischer & Sternberg 2006; Holzapfel et al. 2006). The probability of drought periods (rainfall inter-space events) and inter-annual precipitation variability increases from the mesic to the arid end of the gradient (see rainfall coefficient of variance (CV), Table 1) and rainfall unpredictability therefore is highest at the arid end of the range. Previous studies at the sites have shown that the risk of reproductive failure is high at the arid station, low at the semi-arid and negligible at the two Mediterranean stations (Petru & Tielbörger 2008).

Soil seed bank sampling

Soil seed bank samples were collected at the end of the summer drought and before the onset of fall rains and ensuing germination during three consecutive years (late September 2001, 2002 and 2003). The late collection date ensured that seeds present in these soil samples were exposed for at least five months to local natural climatic conditions after seed set and shedding (March/April). This period of field exposure may be important for breaking seed dormancy in some species. Moreover, since major losses due to granivory also occur in this period (mainly by ants and rodents), sampling at this late date ensures that the number of seeds in the soil samples represents a more accurate representation of the potential seedling germination at each station. Each study site was sampled in two representative habitats: (a) open gaps between shrubs dominated by herbaceous vegetation and (b) shrub understory. In each study site we randomly collected a total of 50 soil seed bank samples (25 samples for each habitat). Each sample measured 5 × 5 cm to a depth of 5 cm, and included seeds on the surface and plant litter. Each soil sample was thoroughly mixed, and stones and coarse roots were removed. These samples were later spread in plastic trays (12 × 14 cm, 6.5 cm depth, with

drainage holes) on a gauze sheet placed on top of a 3 cm-thick layer of perlite. The thickness of the soil layer was between 0.75 and 1 cm. The trays were irrigated during winter (early October) in a nethouse at the Botanical Gardens of Tel Aviv University, Israel. Emerging seedlings were identified, counted and continuously removed until no further emergence was observed (mid-March). The overall seed germinability in each soil sample was determined by replicating the above procedure for each tray for three consecutive germination seasons (winters). During summer, seed bank trays were not watered and naturally dried in the nethouse in order to mimic typical dry and hot field conditions during this period. At the end of the third germination season, soils were passed through 5 and 0.35 mm sieves, to retrieve non-germinated seeds that were then counted under a 80× magnification microscope. As the counting of retrieved seeds per sample was very time-consuming and their numbers were very low (<1% of total number of seedlings emerged), this fraction was not considered in the analysis. Seeds smaller than 0.35 mm were not considered due to work load issues. According to our knowledge of the seed bank flora (unpublished database), the number of species with seeds smaller than 0.35 mm that remained non-germinated was not important. They reflected only 5% of the total species considered in the present study.

The described method has three important advantages over the frequently used filtering technique as described by Pake and Venable (1996): (1) very small seeds can be easily quantified, (2) species with similar seeds but different seedlings can be more readily identified, and (3) cumulative seed bank depletion over several years can be assessed. Seed bank depletion over time is rarely considered in studies similar to the present one.

$$PT(sm) = \sum \frac{\text{seed density of a given species } [SD_{i,\dots,n}]}{\text{total seed density at the site } [SD_t]} \times \text{seed mass of the specific species } [SM_{i,\dots,n}]$$

Germination fraction and seed density calculation

We refer to seeds that germinated during the first watering season as non-dormant. All seeds that germinated only during the second and the third consecutive seasons were regarded as dormant, as they did not germinate under the initial optimal watering and temperature conditions. The germination fraction of each species for each season (G_s) was calculated as follows: number of seeds that germinated during germination season x (1st, 2nd or 3rd)/total number of all seeds that germinated during the three seasons. Seed densities refer to the number of seeds per sample/tray (see Appendix A).

Seed mass

We use the term “seeds” throughout the study to refer to seeds in their simplest form (seeds without inclusive structures – *sensu* Bekker et al. 1998). Newly produced seeds were randomly collected in late spring of 2002, 2003 and 2004. We collected a total of 158 species representing the most abundant species at the respective study sites. Seeds were air-dried and seed mass of 10 seeds from 10 individuals was weighed to an accuracy of 0.1 mg. For almost all species seeds were collected from the experimental site where the species reached its maximal abundance along the aridity gradient. Seed mass was averaged for five species with equal densities across sites. Seeds mass data for five additional species were not collected at the study sites but were obtained from Azcárate, Sánchez, Arqueros, and Peco (2002). A table of seed mass and relative frequency for the species considered in this study is provided in Appendix A.

Seed traits weighted by seed density

To understand the seed trait function in a particular habitat in terms of its relationship to plant abundance (a measure of ecological success), trait data were weighted by the relative density of the species within the community (Pakeman et al. 2008). Proportional seed Traits (PT) values were calculated to consider the relative density of the seeds at the different study sites. PT values were taken into account as follows:

$$PT_{sm} = \sum_{i=1}^n \left[\left(\frac{SD_{i,\dots,n}}{SD_t} \right) \times SM_{i,\dots,n} \right]$$

For *seed mass*:

seed density of a given species [$SD_{i,\dots,n}$]

Statistical analysis

Analysis of variance (ANOVA) was used to test for differences in seed mass and seed density. Data for seed mass, density, and derived PT values were log-transformed prior to the analyses (Sokal & Rohlf 1995). The Tukey HSD test was used to compare differences of means among seed traits for all paired combinations (Tukey 1953). Correlations were performed to observe the relationship between seed mass and germination fractions. Multiple analysis of variance (MANOVA) was used to evaluate differences in germination dynamics between sites. Multiple analysis of covariance (MANCOVA) was applied to test for differences in germination dynamics among populations of each detected species (main effect: site, covariance: rain in previous year, when seeds were created). All analyses were conducted using the statistical package JMP 7 (SAS Institute Inc., Cary, USA).

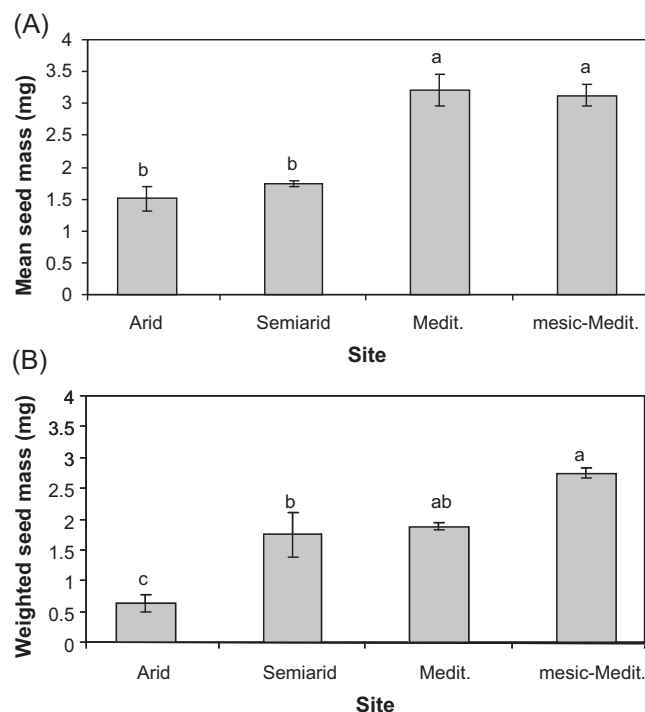


Fig. 1. Seed mass along the aridity gradient: (A) data representing mean seed mass (\pm S.E.) of 158 annual species from four communities along the gradient; (B) proportional changes in seed mass weighted by the relative abundance in each community at the respective study site (PT value). One-way ANOVA was used to test differences in seed mass between populations ($P=0.0083$ (A); and $P=0.0009$ (B)). Different letters indicate significant differences between sites (Tukey HSD test $\alpha=0.005$).

Results

Community level seed mass variation along the aridity gradient

Mean seed mass increased with increasing rainfall along the aridity gradient. Significant differences (One-way ANOVA main factor = site, $df=3$, $F=6.3$, $P=0.017$) were found between seed mass from the arid and semiarid sites and those from the Mediterranean and mesic Mediterranean sites (Fig. 1A). The increase in seed mass with increasing rainfall was even more pronounced when seed mass was weighted by the relative seed density of the populations along the gradient (One-way ANOVA main factor = site, $df=3$, $F=16.2$, $P=0.0009$, Fig. 1B). Following the weighting, the arid site was significantly different from all other sites, indicative of a larger component of annuals with smaller seeds in this plant community. Significant differences in seed mass were also noted between the semiarid and mesic Mediterranean sites, indicating increasing seed mass with increasing rainfall.

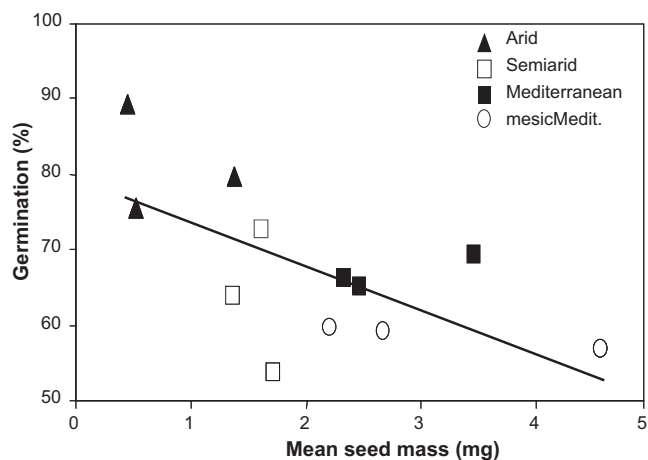


Fig. 2. Relationship between seed mass and germination fraction of annual species. Each point represents the mean seed mass and mean germination fraction for each sampling year (2001, 2002 and 2003) and site. Regression equation: $y = 2.1816x^2 - 15.96x + 88.44$; $R^2 = 0.5068$; $F = 4.625$, $P = 0.0415$.

Population level seed mass variation along the aridity gradient

Seed mass differences in the 15 most abundant species from at least two populations along the aridity gradient were examined (Table 2). Of these, nine species showed significant differences in seed mass between populations. In most of them, seed mass increased with decreasing aridity (*Brachypodium distachyon*, *Crithopsis delileana*, *Hippocrepis unisiliquosa*, *Onobrychis squarrosa*, *Plantago cretica*, *Pteroccephalus brevis*, and *Rhagadiolus stellatus*). The exception to this trend was noted in populations of *Avena sterilis* and *Lolium rigidum*, which showed significantly higher seed mass with increasing aridity (Table 2). The remaining six species showed no significant differences among populations.

Community level seed mass and germination fractions

A significant negative relationship was found between seed mass and mean germination fraction (Fig. 2). Seeds of arid communities were smaller and showed a higher germination fraction than seeds from more mesic communities. Means of total germination rates of soil seed banks that were collected in the years 2001–2003 (three consecutive years) at the study sites along the aridity gradient are presented in Fig. 3. Each seed bank sample was monitored for three consecutive germination seasons. The results showed significantly higher germination (by 17%) in the arid community compared to all other sites during the first germination season (MANOVA main factor = site, $df=3$, $F=5.441$, $P=0.0006$). Significant differences were noted during the second and third germination season,

Table 2. Seed mass of populations of 13 annual species present at the study sites along the aridity gradient. Within a species, one-way ANOVA was used to test for differences in seed mass among populations. Means with shared letters do not differ from each other (Tukey HSD tests, $P > 0.05$).

| Species | Family | Site along aridity gradient | Mean seed mass (mg) | StdErr | F ratio | prob > F |
|---------------------------------|----------------|-----------------------------|---------------------|---------|---------|-------------------|
| <i>Aegilops peregrina</i> | Poaceae | Mesic. Medit. | 12.553 | 1.007 | 1.634 | 0.2713 |
| <i>Aegilops peregrina</i> | | Medit. | 10.283 | 0.876 | | |
| <i>Aegilops peregrina</i> | | Semiarid | 11.317 | 0.773 | | |
| <i>Anagalis arvensis</i> | Primulaceae | Mesic. Medit. | 0.414 | 0.006 | 0.733 | 0.5192 |
| <i>Anagalis arvensis</i> | | Medit. | 0.433 | 0.026 | | |
| <i>Anagalis arvensis</i> | | Semiarid | 0.377 | 0.053 | | |
| <i>Avena sterilis</i> | Foaceae | Mesic. Medit. | 8.337 | 0.285b | 60.52 | 0.0001 |
| <i>Avena sterilis</i> | | Medit. | 9.160 | 0.336b | | |
| <i>Avena sterilis</i> | | Semiarid | 12.980 | 0.150a | | |
| <i>Brachypodium distachyon</i> | Foaceae | Mesic. Medit. | 3.330 | 0.231a | 41.21 | 0.0003 |
| <i>Brachypodium distachyon</i> | | Medit. | 3.693 | 0.028a | | |
| <i>Brachypodium distachyon</i> | | Semiarid | 2.233 | 0.033b | | |
| <i>Catapodium rigidum</i> | Poaceae | Mesic. Medit. | 0.194 | 0.020 | 4 | 0.72 |
| <i>Catapodium rigidum</i> | | Medit. | 0.184 | 0.009 | | |
| <i>Crithopsis delileana</i> | Foaceae | Mesic. Medit. | 4.293 | 0.168a | 4.072 | 0.0152 |
| <i>Crithopsis delileana</i> | | Semiarid | 3.003 | 0.246b | | |
| <i>Hedypnois rhagadioloides</i> | Asteraceae | Mesic. Medit. | 2.427 | 0.238 | 1.055 | 0.405 |
| <i>Hedypnois rhagadioloides</i> | | Medit. | 2.083 | 0.075 | | |
| <i>Hedypnois rhagadioloides</i> | | Semiarid | 2.250 | 0.123 | | |
| <i>Hippocrepis unisiliquosa</i> | Fabaceae | Mesic. Medit. | 3.657 | 0.035a | 721.2 | <0.0001 |
| <i>Hippocrepis unisiliquosa</i> | | Medit. | 3.677 | 0.055a | | |
| <i>Hippocrepis unisiliquosa</i> | | Semiarid | 1.850 | 0.020b | | |
| <i>Hippocrepis unisiliquosa</i> | | Arid | 1.803 | 0.039b | | |
| <i>Lolium rigidum</i> | Foaceae | Mesic. Medit. | 1.340 | 0.091a | 5.029 | 0.0073 |
| <i>Lolium rigidum</i> | | Medit. | 1.937 | 0.052b | | |
| <i>Onobrychis squarrosa</i> | Fabaceae | Mesic. Medit. | 21.300 | 1.584a | 30.04 | 0.0007 |
| <i>Onobrychis squarrosa</i> | | Medit. | 20.903 | 1.896a | | |
| <i>Onobrychis squarrosa</i> | | Semiarid | 10.777 | 0.223b | | |
| <i>Plantago cretica</i> | Plantaginaceae | Mesic. Medit. | 1.699 | 0.073a | 79.37 | <0.0001 |
| <i>Plantago cretica</i> | | Medit. | 1.238 | 0.020b | | |
| <i>Plantago cretica</i> | | Semiarid | 0.994 | 0.024c | | |
| <i>Pterocephalus brevis</i> | Dipsacaceae | Medit. | 1.860 | 0.087a | 11.1 | 0.0004 |
| <i>Pterocephalus brevis</i> | | Semiarid | 0.580 | 0.055b | | |
| <i>Rhagadiolus stellatus</i> | Asteraceae | Mesic. Medit. | 6.160 | 0.307a | 10.56 | 0.0108 |
| <i>Rhagadiolus stellatus</i> | | Medit. | 4.663 | 0.263ab | | |
| <i>Rhagadiolus stellatus</i> | | Semiarid | 4.096 | 0.333c | | |
| <i>Stipa capensis</i> | Foaceae | Medit. | 1.480 | 0.021 | 2.808 | 0.1378 |
| <i>Stipa capensis</i> | | Semiarid | 1.703 | 0.092 | | |
| <i>Stipa capensis</i> | | Arid | 1.593 | 0.070 | | |
| <i>Trifolium stellatum</i> | Fabaceae | Mesic. Medit. | 3.363 | 0.132 | 3.028 | 0.1233 |
| <i>Trifolium stellatum</i> | | Medit. | 3.010 | 0.118 | | |
| <i>Tri folium stellatum</i> | | Semiarid | 3.240 | 0.036 | | |

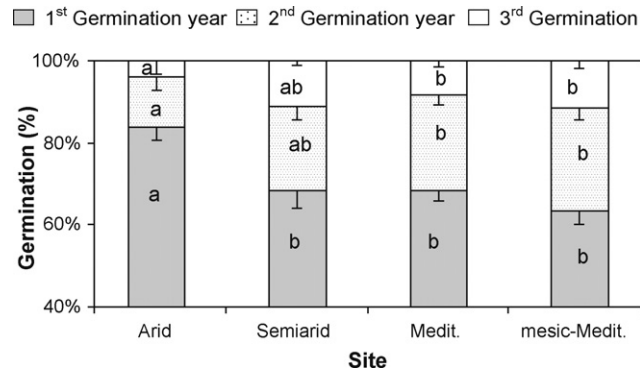


Fig. 3. Community level description of soil seed bank germination dynamics in four different communities along the aridity gradient. Rare species with less than 10 seeds per site were omitted from calculation. Each column describes germination fraction during three seasons after seed shedding for one site. MANOVA test was used to test for differences in germination dynamics between sites (Main effect: Site ($P=0.0006$)). Different letters indicate significant differences between sites (Univar H-F tests, $P=0.05$).

particularly between the arid and the Mediterranean sites, as the Mediterranean sites showed higher germination fractions during these germination events (Fig. 3). The semiarid site showed intermediate germination fractions compared to the arid and Mediterranean sites in these seasons.

Germination fractions at the population level

Different germination strategies were noted among populations of selected abundant species spanning across the gradient from arid to mesic Mediterranean sites (Fig. 4, Table 3). It is important to mention that only one of the studied species (*H. unisiliquosa*) was present at all four sites, but most species had representatives in up to three neighboring sites. The annual forb, *Anagallis arvensis*, showed relatively low germination fractions during the first germination season (Fig. 4A). This phenomenon was noted for all its populations along the aridity gradient. We found significant differences in germination fractions among populations of this species. Specifically, the semiarid population displayed highest dormancy as peak germination fractions were

Table 3. Comparison between soil seed bank germination dynamics of nine dominant annuals species from different population along the aridity gradient. MANCOVA test was used to test for differences in germination dynamics among populations (e.g. germination fraction during three consecutive seasons as described in Fig. 4). Main effect: Site, covariate: rain in previous year, when seeds were produced. Means with different letters are significantly different from each other (Univar H-F tests, $P>0.05$).

| Species | Model | | Main effect | | | | Covariate | |
|---------------------------------|----------------|-----------------|-------------------------------------|----------------------|----------------|-----------------|----------------|-----------------|
| | <i>F</i> value | Prob > <i>F</i> | Site | Group | <i>F</i> value | Prob > <i>F</i> | <i>F</i> value | Prob > <i>F</i> |
| <i>Anagallis arvensis</i> | 14.741 | <0.0001 | Mesic. Medit. Medit. Semiarid | a a c | 14.556 | <0.0001 | 27.888 | <0.0001 |
| <i>Plantago cretica</i> | 6.010 | <0.0001 | Mesic. Medit. Medit. Semiarid | a b ab | 3.648 | 0.0162 | 14.063 | <0.0001 |
| <i>Brachypodium distachyon</i> | 3.337 | 0.0099 | Mesic. Medit. Medit. Semiarid | ab a b | 3.337 | 0.0099 | 0.503 | 0.5338 |
| <i>Catapodium rigidum</i> | 0.940 | 0.4475 | Mesic. Medit. Medit. Semiarid | n.s. n.s. n.s. | 1.011 | 0.3874 | 2.134 | 0.1329 |
| <i>Lolium rigidum</i> | 0.669 | 0.0103 | Mesic. Medit. Medit. Semiarid | ab a b | 4.975 | 0.0031 | 4.827 | 0.0189 |
| <i>Stipa capensis</i> | 0.689 | 0.7069 | Medit. Semiarid Arid | n.s. n.s. n.s. | 0.355 | 0.355 | 0.203 | 0.7322 |
| <i>Hedypnois rhagadioloides</i> | 0.561 | 0.7212 | Mesic. Medit. Medit. Semiarid | n.s. n.s. n.s. | 0.724 | 0.5457 | 1.130 | 0.3145 |
| <i>Rhagadiolus stellatus</i> | 1.964 | 0.0981 | Mesic. Medit. Medit. Semiarid | a b ab | 2.855 | 0.0417 | 1.227 | 0.286 |
| <i>Filago desertorum</i> | 0.914 | 0.0026 | Semiarid Semiarid Arid | a a b | 5.285 | 0.007 | 3.894 | 0.0246 |

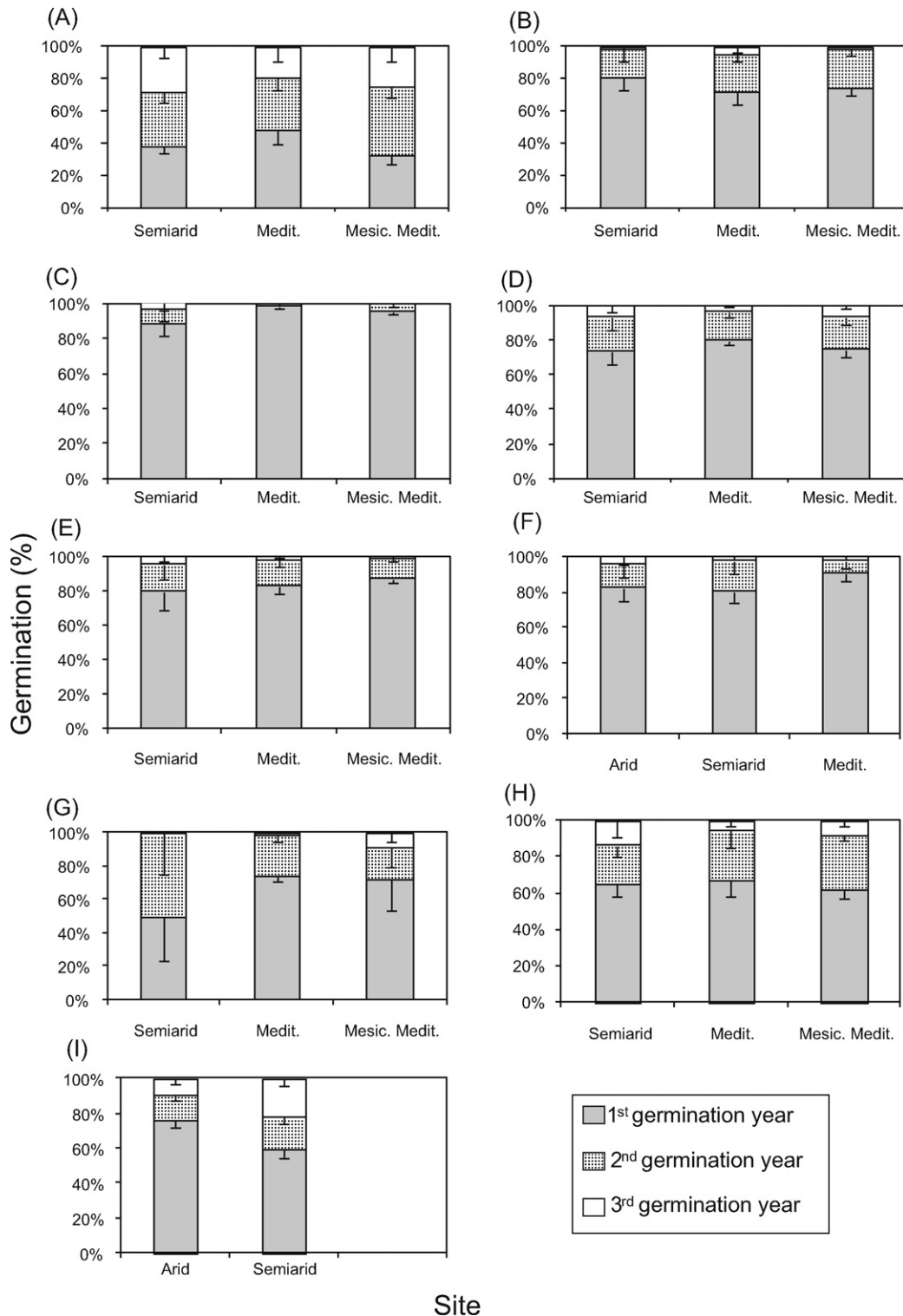


Fig. 4. Population level description of soil seed bank germination dynamics of nine annual species, each from different populations along the aridity gradient. Each column describes germination fraction during three seasons after seed shedding for one site. (A) *Anagallis arvensis*, (B) *Plantago cretica*, (C) *Brachypodium distachyon*, (D) *Catapodium rigidum*, (E) *Lolium rigidum*, (F) *Stipa capensis*, (G) *Rhagadiolus stellatus*, (H) *Hedypnois rhagadioloides*, and (I) *Filago desertorum*.

noted during the third germination season (Fig. 4A). The MANCOVA analysis showed that rainfall in the previous year was a main explanatory factor of significant differences in germination between populations (Table 3). *P. cretica*, an abundant annual forb (Fig. 4B, Table 3), showed a significant difference between populations but no clear trend in relation to site differences. Rainfall from the previous year had a significant effect on germination in each site indicating potential maternal effects on germination fractions. *B. distachyon*, a common annual grass, showed a high germination fraction in the first germination season in all stations (Fig. 4C). This high germination strategy is shared by almost all studied grass populations. Similarly, populations of *L. rigidum* and *Catapodium rigidum*, two common annual grasses, showed relative high germination fractions during the first germination season, although a proportion (ranging 25–15%) of seeds remained dormant and germinated during the two following germination seasons (Fig. 4D and E). A significant difference was found among the *L. rigidum* populations, while the *C. rigidum* populations could not be differentiated (Table 3). *Stipa capensis* (Fig. 4F), an abundant annual grass at the arid sites, showed high germination rates in the first season after seed shedding with no significant difference among populations (Table 3). Among the two abundant annual composites, *R. stellatus* and *Hedypnois rhagadioloides* (Fig. 4G and H), only the latter showed a significant difference among populations (Table 3). The two examined populations of *Filago desertorum* (Fig. 4I), a common annual composite at the xeric sites of the gradient, significantly differed from each other (Table 3), with the arid site population being less dormant in comparison to the semiarid population.

Discussion

The body of theoretical ecological literature predicts that the fraction of dormant seeds in the soil and seed mass increases with increasing climatic variability and aridity (Cohen 1966, 1967; Venable & Brown 1988). These authors in general agree on the notion that increased dormancy evolved as a bet-hedging strategy in reaction to marked environmental stochasticity typical for arid regions.

However, our data do not follow these expectations. Instead, soil seed banks at the arid site, where climate is highly variable and unpredictable, were characterized by the highest germination fractions and lowest seed mass. Similar trends were found in a study on annual communities in a coastal sand dune system in Israel (Yu, Sternberg, Kutiel, & Chen 2007). In that study, seed dormancy and size were compared among three micro-habitats, which differed in soil moisture conditions and habitat predictability. Seeds in drier and more unstable micro-habitats (open sand trails) were less dormant and smaller than those in more humid sites (shrub understory) (Yu et al. 2007). Similarly, Rees

(1996) found for a British grassland community that dormancy was negatively related to seed size and states that this is consistent with heavy seeds having better establishment success and suffering higher levels of herbivory. In our study, potentially selective granivory of larger seeds by desert rodents and harvester ants (Inouye, Byers, & Brown 1980) may have an important effect in determining the average seed size found in the communities along the gradient. Furthermore, soil seed banks from the arid and semiarid sites were experimentally exposed to extremely good conditions that are hardly ever present in nature. It is known that under such good rainfall conditions, species from desert ecosystems show very high germination rates (Volis 2009) as have been observed for desert samples in our study.

At the mesic end of the gradient, above-ground competition is likely to be a dominant factor shaping life history traits (Petrů, Tielbörger, Belkin, Sternberg, & Jeltsch 2006; Schifffers & Tielbörger 2006). Larger seeds may better able to support seedling establishment under such competitive conditions (Coomes & Grubb 2003) creating a selective force that favors larger seeds at the mesic end of the gradient. Disturbance agents such as fire and grazing are also key drivers in Mediterranean ecosystems. The relative higher dormancy observed in the more mesic ecosystems probably buffers against these common disturbance agents in these systems, while dormancy in arid ecosystems acts against climatic unpredictability. This hypothesis is confirmed by our data that showed relatively lower germination fraction and higher seed mass of the annual plant communities at more mesic sites. In addition, Baskin and Baskin (2001) indicated that seed dormancy may act not only as an adaptation to unpredictable environments, but also as a guarantee for long-term survival under high plant densities. For example in the Mediterranean region, climatic constraints are less pronounced but biotic effects due to high neighbor densities and/or grazing are likely to be important factors structuring herbaceous plant communities (Sternberg et al. 2003; Holzapfel et al. 2006). Therefore, the main environmental constraint in the Mediterranean ecosystems appears to be intense competition by neighboring plants and disturbance agents. These ecosystems are characterized by higher seed densities, and are consequently expected to be highly competitive environments that potentially favor larger seed size (Walters & Reich 2000; Turnbull, Coomes, Hector, & Rees 2004; Schifffers & Tielbörger 2006). Moreover, at the mesic end of the gradient, biomass production is higher (Holzapfel et al. 2006); this increase in productivity may favor higher resource allocation to seed mass compared to the less productive ecosystems in the arid sites. Similar relationships between seed size and habitat productivity were found in other Mediterranean and semiarid regions (Fernandez Ales, Laffarga, & Ortega 1993; Osem et al. 2006), although these findings are in contrast to other studies that have shown that larger seeds are often more abundant under drier conditions (Wright & Westoby 1999). The analysis of dormancy and

seed mass traits at the population level along the aridity gradient (Fig. 4, Table 2) can contribute to understanding the differences between arid sites and mesic sites at the community level. Typical species of arid origin such as *S. capensis* and *F. desertorum* showed different germination strategies. *S. capensis* (Fig. 4F), the most abundant grass species in the arid habitat, showed high germination fraction in all populations along the gradient, while *F. desertorum* showed higher germination fraction in the arid site in comparison to the semiarid site (Fig. 4I). For species originating in more mesic habitats there was no clear effect of the aridity gradient even when significant differences were found among populations. We believe that the highly diverse germination strategies of populations at the more mesic sites may buffer against any significant clear germination trend of these communities as expected by the original hypothesis.

In contrast to seed dormancy, seed mass exhibited clear differences between populations. There was a significant decrease in seed mass with increasing aridity in seven out of fifteen examined species. Four other species showed similar yet not significant trends. Abiotic stress factors at the arid end and biotic stresses at the mesic end of the gradient may be the driving evolutionary forces leading to the selection of different life traits in plant populations that form these communities along the aridity gradient. On the regional scale, we conclude that the ecological conditions typical of arid regions in Israel favor species with lighter seed mass that have either conditional or only little dormancy. This preferential life trait combination might be the result of evolutionary favored wind-dispersal abilities (Greene & Johnson 1993) that are favored in sparse desert vegetation and by short period pulses when adequate amounts of water and other resources are available for germination (Guterman 2002). In contrast, the mesic end of the gradient showed that competition for resources (e.g. light, space, etc.) is likely to be a dominant factor shaping life history traits (Petru et al. 2006; Schiffers & Tielbörger 2006). This is supported by the relatively high seed dormancy and higher seed mass in annual plant communities in the mesic sites.

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Appendix A. Supplementary Material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.baae.2011.09.003.

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