

Demography and role of the seed bank in Mediterranean and desert populations of wild barley

Sergei Volis^{1,2,*}, Samuel Mendlinger¹, David Ward²

¹ The Institutes for Applied Research, Ben-Gurion University of the Negev, Beer Sheva, Israel

² Mitrani Department for Desert Ecology, Blaustein Institute for Desert Research, Ben-Gurion University of the Negev, Sede Boqer, Israel

Received October 10, 2002 · Accepted January 30, 2003

Abstract

We compared the demography of two populations of wild barley, *Hordeum spontaneum*, that occupy environments of different aridity (desert and Mediterranean) and represent distinct parts of the species' distribution (periphery and core) in Israel. Our demographic study included a survey of survival and fecundity of adults in quadrat plots marked at two sites in natural vegetation (one site per population), and the creation of experimental seed banks examined over three years. We measured variability in population growth rate and investigated the role of the seed bank in the demography of two populations. The latter employed construction of two-stage, three age-class transition matrices and usage of elasticity analysis. At both sites, population dynamics appear to be transient with high fluctuations of population growth rate due to variability in annual rainfall and, most likely, intra- and inter-specific density dependence. The importance of the seed bank differed among two populations. Seed dormancy had almost no demographic effect on the Mediterranean population, while it was of paramount importance in the desert population. The two populations also differed in seed and seedling survival and per adult fecundity, presumably due to the difference between two sites in (i) relative impact of seed predation, (ii) effects of density dependence on population demography, and (iii) lower vigor of seeds of desert vs. Mediterranean origin. Our study highlights the importance of life history adaptations that may evolve under specific selective forces in different parts of a species' range, which, in certain circumstances, may be critical for the persistence of a species.

Wir verglichen die Demographie von zwei Populationen Wilder Gerste, *Hordeum spontaneum*, die Habitate unterschiedlicher Trockenheit (Wüste und mediterran) besetzen und die unterschiedliche Bereiche der Artenverbreitung (Peripherie und Kern) in Israel repräsentieren. Unsere demographischen Untersuchungen bestanden in einer Erfassung der Überlebensrate und der Fruchtbarkeit ausgewachsener Pflanzen in quadratischen Versuchsfeldern, die in zwei Untersuchungsflächen in der natürlichen Vegetation (eine Untersuchungsfläche pro Population) markiert wurden und in der Herstellung einer experimentellen Samenbank, die über drei Jahre beobachtet wurde. Wir erfassten die Variabilität der Populationswachstumsrate und untersuchten die Rolle der Samenbank in der Demographie der beiden Populationen. Letzteres erforderte die Konstruktion von Zwei-Stadien, Drei-Altersklassen-Transitions-Matrizen und die Verwendung einer Elastizitäts-Analyse. Die Populationsdynamiken scheinen in beiden Untersuchungsflächen kurzlebig zu sein, mit einer hohen Fluktuationsrate des Populationswachstums aufgrund der Variabilität des jährlichen Niederschlags und am wahrscheinlichsten aufgrund der intra- und interspezifischen Dichteabhängigkeit. Die Bedeutung der Samenbank unterschied sich zwischen den beiden Populationen. Die Samendormanz

*Corresponding author: Sergei Volis, The Institutes for Applied Research, Ben-Gurion University of the Negev, POB 653, Beer Sheva 84105, Israel, Phone: ++972-8-6461973, Fax: ++972-7-6472984, e-mail: volis@bgumail.bgu.ac.il

hatte bei der mediterranen Populationen nahezu keinen demographischen Effekt, während sie bei der Wüstenpopulation von herausragender Bedeutung war. Die beiden Populationen unterschieden sich auch in der Überlebensrate der Samen und Keimlinge und der Pro-Pflanzen-Fruchtbarkeit, vermutlich aufgrund der Unterschiede der beiden Untersuchungsflächen in (i) der relativen Wichtigkeit der Samenprädation, (ii) den Effekten der Dichteabhängigkeit der Populationsdemographie und (iii) der geringen Vitalität der Samen der Wüsten-Herkunft im Gegensatz zur mediterranen Herkunft. Unsere Studie hebt die Bedeutung einer Anpassung im Lebenszyklus hervor, die bei spezifischen selektiven Faktoren in den unterschiedlichen Teilen eines Verbreitungsgebietes einer Art evolviere können und die unter bestimmten Umständen wichtig für den Bestand einer Art sein können.

Key words: annual plant – aridity gradient – core and peripheral populations – elasticity – life cycle

Introduction

Variation in temporal and spatial patterns of seed germination and plant establishment among populations of an annual species may result from many factors, such as rainfall (Wagner & Spira 1994, Marone et al. 2000), local topography and soil properties (Reichman 1984, Cabin et al. 2000), availability of suitable sites (Milton 1995, Aguiar & Sala 1997), and biotic interactions (Milton 1995, Mull & MacMahon 1996). The importance of these factors in the demography of populations distributed along environmental gradients (such as aridity) is largely unknown. Because a gradient of aridity in many cases determines the limits of species distribution (Gaston 1990, Brown et al. 1996), populations from a species distributional periphery often occupy the extremes of such gradient. For example, many species reach the edge of their distribution range along a steep climatic gradient in Israel. The importance of peripheral populations in the maintenance of the entire species has been recognized by ecologists and conservation biologists (Scudder 1989, Safriel et al. 1994, Lesica & Allendorf 1995, Kark et al. 1999) and, therefore, understanding population dynamics and its causes in different parts of a species' distribution may have both theoretical and applied merits.

Compared to core populations, populations at a species' periphery tend to be more isolated and patchily distributed (Carter & Prince 1988), with lower and more fluctuating population densities (Gaston 1990, Brown et al. 1995, Holt et al. 2002). Analytical models and simulations using transition matrices predict a higher probability of extinction: 1) under higher environmental variability, and 2) in populations with lower finite rate of increase, λ and higher variation in λ (Goodman 1987, Menges 1992, Lande 1993). As a peripheral population is likely to have lower and more variable λ -values than a population from a species core, it may have a higher probability of becoming extinct. However, the assumption of lower and more variable λ -values in peripheral populations may not be

correct if sufficient evolutionary time and strong natural selection led to different plant strategies evolving in peripheral parts of the species' distribution. Plants from a less predictable periphery may have specific adaptations to temporal heterogeneity or to a complex pattern of site availability, disturbance regime, predation and competition.

Seed banks are recognized for their importance in population dynamics of plants, and, in particular, of annuals (Kalisz & McPeck 1992, Philippi 1993, Pake & Venable 1996). Delayed germination through persistence in the seed bank is considered to be an adaptive bet-hedging strategy buffering against the detrimental effects of a temporally-varying environment (Cohen 1966, Venable & Lawlor 1980, Klinkhamer et al. 1987). Therefore, we may expect, all other features being equal, that a seed bank will be more important in the population dynamics of populations occupying temporally heterogeneous and unpredictable environments.

A gradient of aridity distinguishing Mediterranean (mesic) and desert (xeric) environments in Israel parallels a concomitant gradient of environmental productivity and predictability. This phenomenon results from an inverse relationship between the variation in annual precipitation with its mean. Deserts are renowned for their highly unpredictable patterns of precipitation (Noy-Meir 1973, Ludwig 1986, Polis 1995) and overall low productivity, although patches of relatively high productivity do occur (Noy-Meir 1981). Compared to deserts, Mediterranean-climate regions are characterized by a more predictable onset of the rainy season, more reliable within-season supply of water and a longer growing season (Shmida & Burgess 1988). In 1996 we started a comparative study of two populations, Mediterranean and desert, of wild barley *Hordeum spontaneum* Koch. Several manipulative experiments with reciprocal seed and seedling introductions conducted on these two populations (Volis et al. 2002a) demonstrated higher fitness of plants in their indigenous locations suggesting local adaptation. The

desert and Mediterranean plants differed in number of traits, including phenology, reproductive allocation pattern and seed dormancy. The observed differences in seed dormancy may indicate their importance for local population persistence, as well as a difference in barley spatio-temporal population dynamics in two parts of the species distribution. The objective of present study was determining whether two populations differ in the manner expected of core and peripheral populations (as outlined above) with regard to: (1) spatio-temporal dynamics (more variable in the periphery if not compensated by local adaptation of life history); and (2) relative importance of age/stage classes, including the seed bank in their effects on population growth rate λ (seed bank more important in the periphery).

Materials and methods

The study species

Wild barley, *Hordeum spontaneum*, in Israel is one of the major annual components of open park-forests with *Quercus ithaburensis* and of Mediterranean grasslands, but also occupies ephemeral river valleys (wadis) in arid environments (the Negev and Judean deserts). The abundance of *H. spontaneum* varies greatly, with a decline in population size from mesic (Mediterranean) toward a xeric (desert) climate. However, population density within the wadis is often as high as in the more climatically favorable environments due to water accumulating from runoff from the adjoining hillsides.

Seeds are produced in spring (April–May). Dispersal of seeds is usually restricted to the radius of a mother plant, when spikelets fall and either are impaled in the dry remnants of the dead mother plant (Gutterman 1992) or penetrate into soil cracks by the combined effect of wind and gravity (Volis, personal observations), where they remain until germination in the following season. Buried seeds gain an advantage in post-dispersal predation avoidance, while those lying on the soil are intensively harvested by ants and granivorous rodents (Volis, personal observations). Some spikelet mobility also occurs by wind (a few meters) or by being entrapped in the fur of animals (long distances). Seeds are innately dormant at dispersal and require high temperature after ripening (Gutterman 1993). A specific amount of rainfall as a single rainy event (>10 mm) is needed to trigger germination in fall (Gutterman & Gozlan 1998). Seedlings emerge in November–December, grow and mature through winter–early spring and senesce before summer. Seeds that do not germinate in the autumn following dispersal either enter the seed bank or die.

The study sites

One research site was established per Mediterranean and desert climatic zone in Israel (for a detailed description see Volis et al. 2002a). The Mediterranean wild barley population (M) is in a semi-steppe batha (shrubland kind vegetation community), and the desert population (D) is in a wadi (ephemeral river valley). The D site was found to be more spatially variable in available nitrogen (Volis, unpublished data) and to be less predictable in annual rainfall amount than the M site (mean annual precipitation is 90 and 400 mm, and CV in annual rainfall over 50 years is 0.43 and 0.32 in D and M site, respectively).

In March–April 1996, four 10-m long transects distributed along a slope 20 m apart were marked in the M site. Five 1 × 1 m quadrates 1 m apart were permanently marked along each transect. At this site, the distribution of *H. spontaneum*, despite high variation in abundance, is more or less continuous. At the D site, where barley distribution is highly patchy and discontinuous, neither transects nor equidistant spacing was possible. Therefore a 1 m² permanent plot (1 × 1 m quadrate) was marked in each barley patch. Fifty plots were marked at the D site. The number of plots was double that of the number of quadrates at the M site to account for high spatial heterogeneity. In December 1996, additional two transects were marked in the M site.

Seed bank dynamics

We created two experimental seed banks and monitored the fate of the seeds during 3 consecutive years. These two seed banks were a part of a larger seed bank set of reciprocally introduced seeds of different origin (Volis et al. 2002b). Seeds of *H. spontaneum* were collected from adult plants near the plots under observation and 10 genotypes from each population were planted in 1997–1998 in a greenhouse to obtain F1 seeds. Offspring (F1) were combined into two bulk seed samples. The 1998–1999 season was extremely dry (39.6 mm versus 90 mm mean annual rainfall for the last 50 years) and there was a very low germination percentage at D site. In order to trace the inter-seasonal differences in germination and survival, the ten genotypes per population were used again to obtain F1 seeds and the experiment was repeated in 1999 at the D site. We earlier reported (Volis et al. 2002a) the results of 1998 and 1999 seed bank experiments for the first year after dispersal. In this paper, we present the results of a three-year germination survey for each experiment.

Plant demography and transition probability matrix

Plant individuals were counted at seedling and adult stage, and seed production quantified in each 1 m² plot. Emerging seedlings were censused every two weeks and marked by colored toothpicks during the first two months after germination. At maturation and prior to seed dispersal, all adult plants were counted and 12 randomly-chosen plants per plot were scored for number of spikes and number of spikelets per spike. Three stage life tables were constructed for each site and each year of observation. As monitored plots remained intact throughout the study, the number of seeds per plot was estimated from the number of mature adults multiplied by the average yield per adult. As experimental seed bank dynamics and plant demography were monitored in different years, the absence of a direct link between the two data sets prevented calculation and incorporation of the soil seed bank into year-specific life tables. Therefore, life tables assumed no seed bank. As our results show below, this assumption is not justified for years with exceptionally low rainfall only. Survival from the previous to next stage, and yield per adult were calculated for each plot and their means over plots were used for construction of the transition probability matrix.

To construct a transition probability matrix for *H. spontaneum* that accounts for seed bank we adopted a two-stage, age-structured life cycle and transition matrix from Kalisz & McPeck (1992). The life cycle on

which the *H. spontaneum* transition probability matrix was based (Fig. 1) assumed two stages: (A) for adult plants at maturation but prior to seed dispersal, and (S) for a seed in the seed bank. S₁, S₂ individuals are seeds that persisted in the seed bank for 1 and 2 years; A₁ individuals are adults developed from seeds produced in the previous season; and A₂, A₃ are plants developed from seeds that entered the seed bank two and three years ago, respectively. The adult stage encompasses the whole individual lifespan except the seed stage, i.e. seedling stage and includes reproduction as well. Vital rates (Fig. 1) were calculated following Kalisz & McPeck (1992), with the same assumptions of i) equal survival probabilities and expected fecundities of adults derived from seeds of different age; and ii) equal probability of entering seed bank in a given year for seeds produced by adults derived from seeds of different age. Seeds were found not to persist in the seed bank for more than two years. Therefore, our matrix has two seed and three adult stages with vital rates > 0. P₂₁ and P₃₂ are the probabilities of remaining dormant for seeds after being in the seed bank for one and two years, respectively. P₅₁ and P₆₂ are the probabilities of germinating for seeds that have been in the seed bank for one and two years, respectively. B₁₄ = B₁₅ = B₁₆ are the multiplicative probabilities: (probability of survival from germination to reproduction) (S) × (fecundity) (F) × (probability of a newly formed seed to enter the seed bank) (E). B₄₄ = B₄₅ = B₄₆ are the multiplicative probabilities: (probability of survival from germination to reproduction) (S) × (fecundity) (F) × (probability of a newly

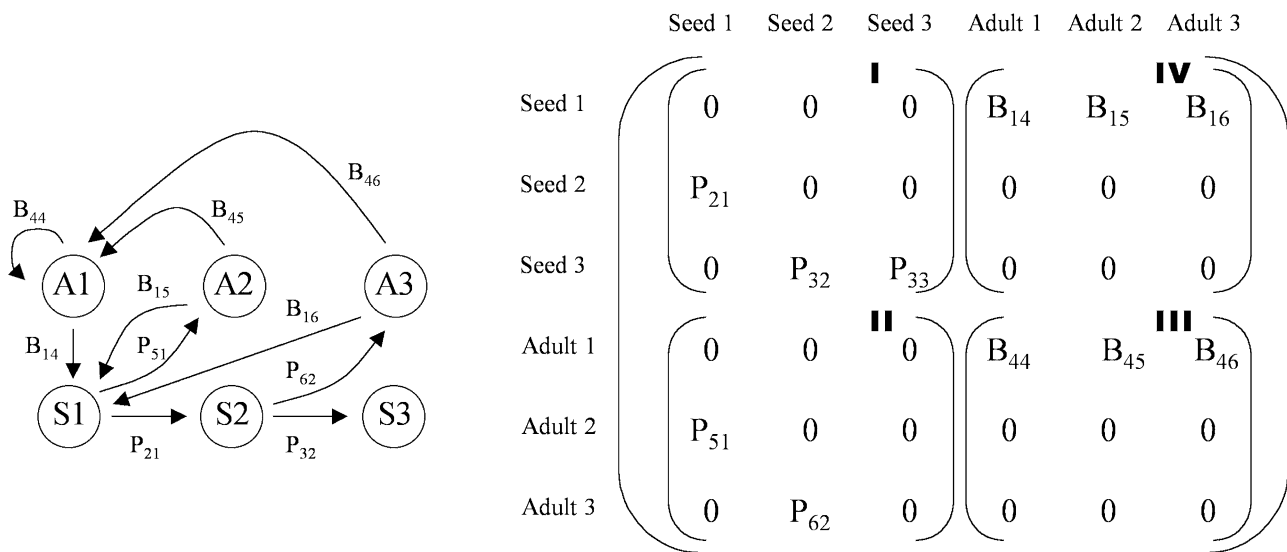


Fig. 1. Life cycle graph and transition matrix for *H. spontaneum* adopted from Kalisz & McPeck (1992) with two stages (adult and seed) and three ages-classes (from 1 to 3 years old). S₁–S₃ are seeds and A₁–A₃ are adults from 1 to 3 years old, respectively. The matrix transition

formed seed to germinate in the following fall) (G). P_{21} , P_{32} , P_{51} and P_{62} were calculated from experimental seed bank dynamics. Probabilities needed to derive other matrix elements ($B_{14} - B_{16}$ and $B_{44} - B_{46}$) were either calculated from life tables (S, F and G) or from a system of two equations (E):

$$\begin{cases} x + y + z + h = N \\ A + B + C = 1 \end{cases}$$

where N is number of seeds per plot after dispersal; x is number of germinated seeds; y is number of non-germinated dead seeds; z is the number of dormant seeds entering the seed bank; h is number of harvested or consumed seeds removed from the plot before the first rain; A , B and C are the first year fractions of germinating, dying without germination and becoming dormant seeds, respectively, determined in the experimental seed bank. We assume that $x : A = y : B = z : C$. N and x are the life table values and h is the remainder when all other parts of the equation are known. Probability E is then z/N . This was the procedure for obtaining probability E for Mediterranean (M) matrices and for desert (D) "good year" matrices (a definition of "good year" and "poor year" see below). The procedure for deriving E for desert "poor year" matrices was slightly different. For a poor year, we assumed the same probability of seed harvest and consumption as for a good year because they take place before rains start. Therefore, h was taken from a "good year", entered into equation together with N , and other values were calculated accordingly. Probability S for desert "poor year" matrices was approximated by survivorship of germinated seeds in the experimental seed bank of 1998/99 and probability G was calculated as x/N . Three transition matrices were constructed for each of two seasons, 1996/97 and 1997/98: one matrix for the M population and two matrices for the D population. These two D matrices assumed two possible scenarios of a following "good year" with relatively favorable amount of precipitation and timing during a season (at least one early, November to January, rain with ≥ 15 mm of precipitation, Aronson & Shmida 1992) (seed bank of 1999) and a "poor year" where these requirements are not met (seed bank of 1998). A distinction between "poor" and "good" year appears to be crucial for understanding seed bank dynamics and pattern of germination in wild barley, because this is a distinction between a year when triggering of mass germination occurs and a year when it does not. An effective rain (a single event with ≥ 15 mm) is such a trigger. No "poor" by this definition years happen at M site.

The 95% confidence intervals were estimated for demographic parameters by bootstrapping with random reassignment to regenerate the original sample sizes repeated 1000 times. This was done by the pro-

gram RESAMPLING STATS (Simon 1995). Demographic parameters (number of reproductive individuals within a plot) subjected to t-tests were log-transformed to meet the assumption of normality.

The relative importance of different transition matrix elements, life history stages and demographic parameters on population growth is most efficiently evaluated using elasticity analysis (de Kroon et al. 1986). Elasticity ($e_{ij} = \delta \lambda / \delta a_{ij} \cdot a_{ij} / \lambda = \delta \ln \lambda / \delta \ln a_{ij}$) measures a proportional contribution of transition matrix elements a_{ij} to λ . Since elasticities always sum up to unity, they allow inter-species or inter-population comparisons, and, because they can be summed across selected regions of the matrix, they allow complex comparisons of matrix elements (e.g. seed and adult stages). In our study we applied elasticity analysis to compare the relative importance of the seed bank among populations and years.

Results

Seed demography

The percentage of viable seeds that did not germinate in a year following dispersal was 7.6 for the M site, and 18.5 and 56.6 for the D site ("good" and "poor" years, respectively) (Fig. 2). The percentage of seeds persisting for 2 years was 0.2 of at the M site, and 0.3 and 15.1 for the D site ("good" and "poor" years, re-

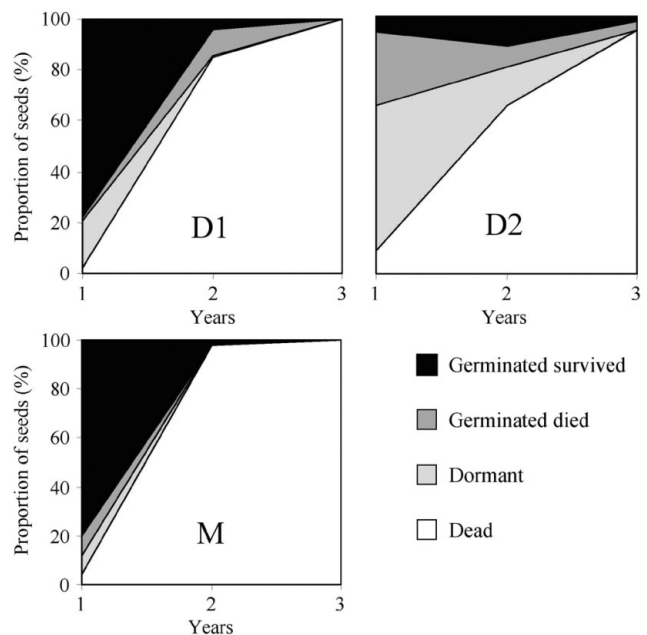


Fig. 2. The fates of seeds in experimental seed banks established at the M site in 1998, and at the D site in 1998 and 1999 over three year period. The D1 and D2 represent "good year" and "poor year", respectively.

spectively). No seeds persisted for three or more years in the experimental seed bank at any site. Percentage persistence of seeds for one year was significantly lower at the M site than at the D site in either the “good” or “poor” year ($\chi^2 = 5.2$, $p < 0.05$ and $\chi^2 = 55.0$, $p < 0.001$).

Plant abundance and patch dynamics

The spatial distribution and local abundance of wild barley was found to be very patchy at a small scale of meters, as reflected by the confidence intervals for both sites (Table 1). Average population size and number of reproductive individuals within a plot varied greatly among years at both sites but with higher abundance and lower patchiness at M as compared with D site in two of three years (Fig. 3). Only in 1996 was there no difference in the distribution of number of reproductive individuals within a plot between two sites (Kolmogorov-Smirnov $D = 0.262$, $p > 0.05$), while in 1997 and 1998 the distributions were significantly different (Kolmogorov-Smirnov $D = 0.323$ and

0.708, $p < 0.05$ and < 0.001 , respectively). Repeated measures analysis of variance with one grouping factor (sites) and one within factor (years) revealed that number of reproductive individuals within a plot differed among three years ($F_{2,130} = 24.8$, $p < 0.001$), among two sites ($F_{1,65} = 8.0$, $p < 0.01$) and in site patterns of change through time as reflected by the site by year interaction ($F_{2,130} = 18.8$, $p < 0.001$). Number of adults per plot in a given year was a strong determinant of number of adults per plot in the following year at D site (1996–97, $R^2 = 0.65$, $F = 65.8$, $p < 0.001$; 1997–98, $R^2 = 0.75$, $F = 104.0$, $p < 0.001$), while at M site, the relationship of per plot abundances in consecutive years was weaker or absent (1996–97, $R^2 = 0.06$, $F = 1.1$, $p > 0.05$; 1997–98, $R^2 = 0.59$, $F = 41.1$, $p < 0.001$; 1998–99, $r^2 = 0.38$, $F = 17.1$, $p < 0.001$).

Despite high fluctuation in number of plants per plot over time, plot occupancy remained close to 100% for the whole period of observation at both sites (D site 91.1 and 91.1 in 1997 and 1998; M site 100, 96.7, 100 in 1997, 1998 and 1999).

Table 1. Life table data for two populations, M and D, years 1996–2000 (assuming no seed bank). Means over plots (above) are presented with 95% confidence intervals.

Stage		Year				
		1996	1997	1998	1999	2000
M population	Seeds	–	736 578–1253	1346 1566–5057	2236 1520–3040	139 91–182
	Seedlings	–	195 122–284	363 241–495	–	–
	Adults	31 14.5–31.6	84 53.7–119.8	196 143–253	29 21.1–38.1	–
	Fecundity	37.2 32.9–42.3	22.5 15.1–23.0	10.5 9.0–12.1	4.7 3.6–6.1	–
	R_0	–	1.57 0.95–2.27	1.73 1.41–2.04	0.12 0.07–0.17	–
D population	Seeds	–	1190 768–1879	1505 785–2567	913 402–1638	–
	Seedlings	–	64 39.4–93.6	43 21.3–73.6	–	–
	Adults	20 13.7–30.0	39 22.9–62.0	31 14.6–56.5	0	–
	Fecundity	53.2 42.7–63.3	35.8 30.1–43.0	29.7 25.5–33.7	0	–
	R_0	–	1.07 0.80–1.38	0.77	0	–

– not estimated

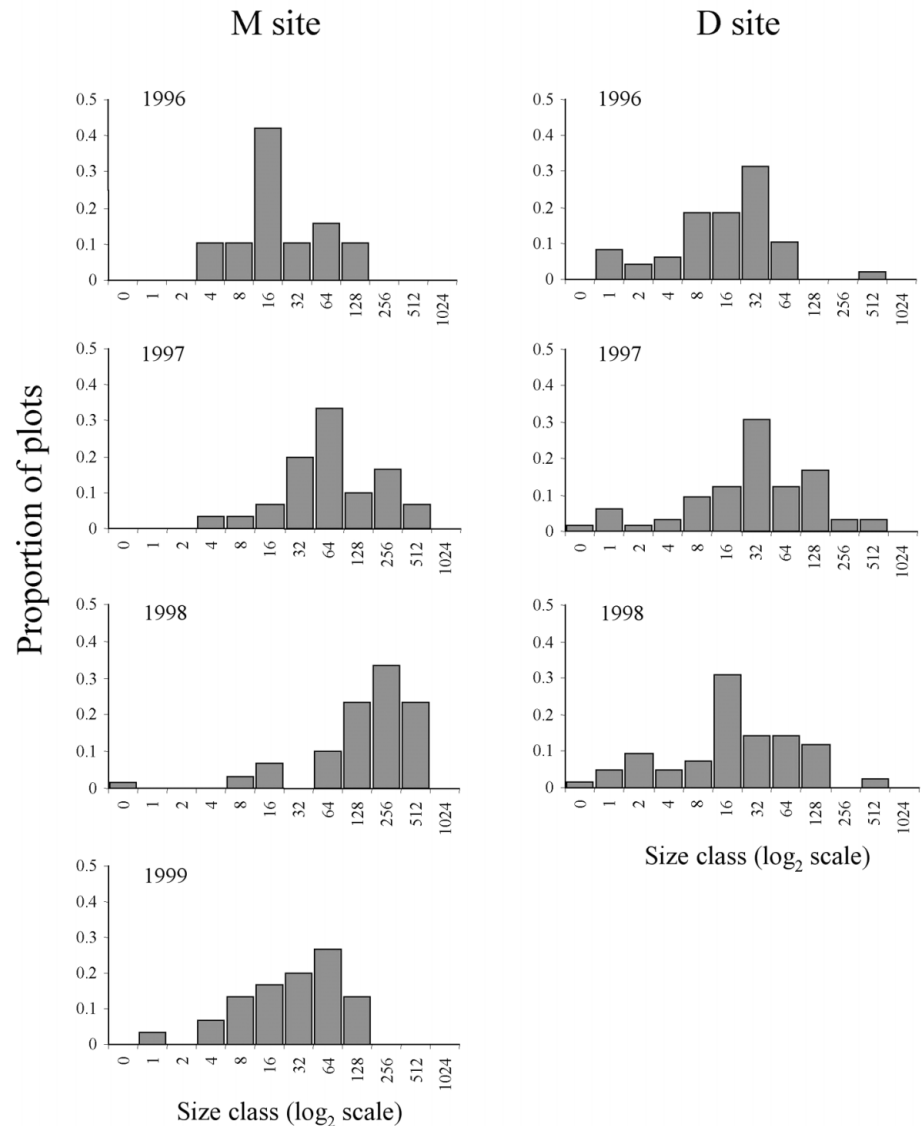


Fig. 3. Plot-size distributions (number of adult plants per 1 m²) for the desert (D) and Mediterranean (M) population of *H. spontaneum* surveyed during 1996–1999. No adults survived to maturation at the D site in 1999.

General demographic patterns

Probability of survival from seed to seedling stage in both 1997 and 1998 (Table 1) was significantly higher at the M site than at the D site (Mann-Whitney U test, χ^2 approximation = 25.5 and 47.1, both $p < 0.001$). However, the opposite was true for the probability of survival from seedling to adult (years 1997 and 1998, Mann-Whitney U test, χ^2 approximation = 7.4 and 14.8, $p < 0.01$ and < 0.001 , respectively) and per adult fecundity (years 1996, 1997 and 1998, Mann-Whitney U test, χ^2 approximation = 15.7, 9.6 and 42.6, $p < 0.001$, < 0.01 and < 0.001 , respectively).

Net reproductive rate (R_0), calculated for each plot as F_x/N_x under the assumption of no seed bank equals the finite rate of population increase, λ . The changes

in R_0 of two populations (M and D) through time correlated with annual rainfall (Pearson correlation, $r = 0.58$, $p < 0.001$ for both sites) with R_0 of the M population significantly higher than that of the D population in two seasons out of three (Mann-Whitney U test, χ^2 approximation = 1.7, 20.2 and 60.0, $p > 0.05$, < 0.001 and < 0.001 , years 1997, 1998 and 1999, respectively) (Fig. 4).

Transition matrices and elasticity analysis

The population growth rate, λ , of the M population was estimated as 2.67 and 2.05 in the years 1997 and 1998, assuming seed bank dynamics of the experimental seed bank (Table 2). Estimation of λ of the D population for the same years (1997 and 1998) accounted

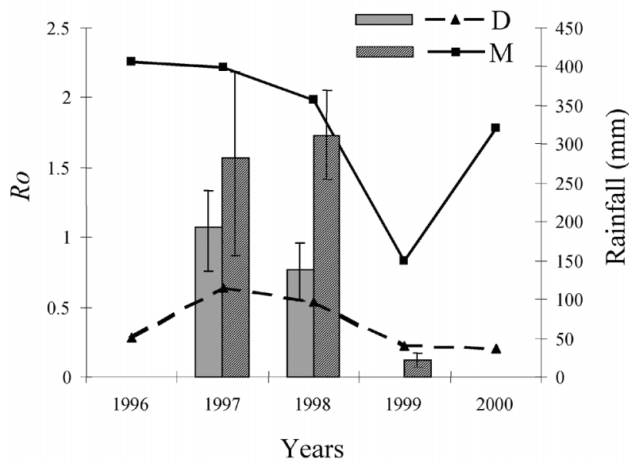


Fig. 4. Changes in net reproductive rate (R_0) over three consecutive years in the desert (D) and Mediterranean (M) population, and the amount of annual rainfall in corresponding study sites.

for two possible scenarios in the following season, being either a “good year” or “poor year”. These two scenarios predicted λ of 1.48 and 1.01 in “good” and 0.44 and 0.30 in “poor” following seasons for 1997 and 1998, respectively (Table 2). It is legitimate to compare λ of two populations calculated using data of 1997 and 1998 assuming for D population the “good year” scenario, because in both these years annual rainfall at both sites was close to the multiyear mean amount. Comparison of population λ 's shows no significant difference in inter-seasonal λ variation between the desert and Mediterranean populations (CV = 19% and 13%, $\chi^2 = 1.3$, $p > 0.05$).

Relative importance of stage/age classes in influencing population growth rate (λ) while accounting for the seed bank was investigated by elasticity analysis (Fig. 5). In the M population, elasticities of stage/age classes other than A_1 summed up to less than 2% in both 1997

Table 2. Population projection matrices and elasticities of matrix elements for two populations, M and D, in years 1997 and 1998. For the D population there are two possible scenarios of seed germination in the following year (“poor” with no single rainy event ≥ 15 mm, and “good” with at least one such event).

			Projection matrices					Elasticities				
			S1	S2	A1	A2	A3	S1	S2	A1	A2	A3
M population	1997	S1	0	0	0.351	0.351	0	0	0	0.013	0.001	0
		S2	0.031	0	0	0	0	0.001	0	0	0	0
		A1	0	0	2.636	2.636	0	0	0	0.957	0.014	0
		A2	0.281	0	0	0	0	0.014	0	0	0	0
		A3	0	0	0	0	0	0	0	0	0	0
	1998	S1	0	0	0.168	0.168	0	0	0	0.011	0.001	0
		S2	0.031	0	0	0	0	0.001	0	0	0	0
		A1	0	0	2.033	2.033	0	0	0	0.965	0.011	0
		A2	0.281	0	0	0	0	0.011	0	0	0	0
		A3	0	0	0	0	0	0	0	0	0	0
D population	1997	S1	0	0	0.232	0.232	0.232	0	0	0.113	0.146	0.090
		S2	0.276	0	0	0	0	0.135	0	0	0	0
		A1	0	0	0.141	0.141	0.141	0	0	0.052	0.069	0.043
		A2	0.347	0	0	0	0	0.217	0	0	0	0
		A3	0	0.344	0	0	0	0	0.135	0	0	0
	“good” year	S1	0	0	0.318	0.318	0	0	0	0.093	0.013	0
		S2	0.014	0	0	0	0	0.001	0	0	0	0
		A1	0	0	1.309	1.309	0	0	0	0.696	0.093	0
		A2	0.784	0	0	0	0	0.104	0	0	0	0
		A3	0	0	0	0	0	0	0	0	0	0
	1998	S1	0	0	0.106	0.106	0.106	0	0	0.078	0.148	0.135
		S2	0.276	0	0	0	0	0.175	0	0	0	0
		A1	0	0	0.065	0.065	0.065	0	0	0.021	0.041	0.036
		A2	0.347	0	0	0	0	0.191	0	0	0	0
		A3	0	0.344	0	0	0	0	0.175	0	0	0
	“good” year	S1	0	0	0.166	0.166	0	0	0	0.100	0.015	0
		S2	0.014	0	0	0	0	0.001	0	0	0	0
		A1	0	0	0.882	0.882	0	0	0	0.670	0.100	0
A2		0.784	0	0	0	0	0.114	0	0	0	0	
A3		0	0	0	0	0	0	0	0	0	0	

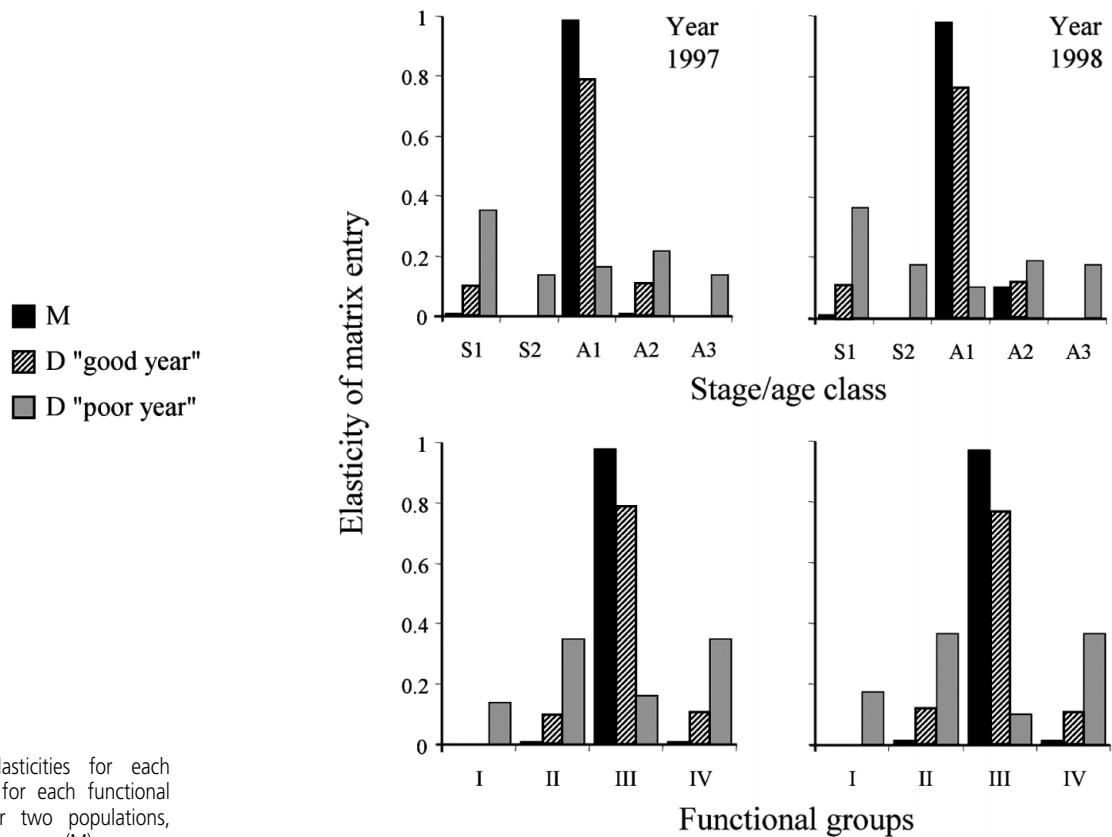


Fig. 5. Summed elasticities for each stage/age class and for each functional group calculated for two populations, desert (D) and Mediterranean (M).

and 1998. In the D population, elasticity of A_1 was also great but lower for a “good year” scenario (79% and 77%) while it was the lowest or among the lowest for a “poor year” scenario (17% and 10%). In the “poor year”, elasticities of other stage/age classes substantially increase as compared with a “good year”, and elasticity of S_1 becomes the highest (35% and 36%).

Partitioning of elasticity values into functional groups I–IV (Fig. 5) shows the following. The Group I (aging of dormant seeds in the seed bank) has elasticity of zero for both the M population and “good year” scenario for the D population, while its elasticity is 14% and 17% for the “poor year” scenario for the D population. The group II (emergence from the dormant seed bank) and the group IV (entering dormant seed bank) elasticities are low in the M population (less than 1.5% in both years), higher in the “good year” scenario for the D population (10–12%) and are the highest among other functional groups in the “poor year” scenario D population (35–37%). The group III elasticity (germination without entering the seed bank) predominates in the M population (98% in both years) and in “good year” scenario for the D population (77–79%) but becomes low in “poor year” scenario for the D population (10–16%).

Discussion

High and stable patch occupancy (despite high fluctuation in plant number) makes unlikely a metapopulation structure and dynamics for wild barley. This conclusion holds for two habitats with different climate and spatio-temporal heterogeneity, Mediterranean (mesic) and desert (xeric). Although *H. spontaneum* is a ruderal species able to occupy frequently-disturbed environments, wild barley, nevertheless, was found not to be prone to local extinction.

On the other hand, we found the lifetime of *H. spontaneum* seed in soil not to exceed 3 years, which is inconsistent with the notion that there is a long-lived and large seed bank, and it should be classified as a short-term persistent seed bank (seeds surviving 1–4 years) (Thompson et al. 1997). Seed longevity of most grassland annuals (Rice 1989, Milberg 1995, Thompson et al. 1997) and of many annuals inhabiting deserts (Kemp 1989) was reported to be low and inconsistent with a large and persistent seed bank. As wild barley is not a true desert species and occupies the most favorable microsites of relatively high water availability in arid environment, the absence of a long-term persistent seed bank in this species is not surpris-

ing. However, our study demonstrates that, in occasional extremely dry years when amount or timing of rainfall is insufficient for plants to mature or even for seeds to germinate, a short-term persistent seed bank becomes the most important demographic stage ensuring population existence. Occasional occurrence of years of annual rainfall insufficient to sustain plant growth is a distinct feature of desert environments (Inouye 1995). Relatively small changes in seed probability of becoming dormant and entering the seed bank under extremely dry conditions have the greatest consequences among transition probabilities for population growth rate. We may expect such susceptibility to induced dormancy to have evolutionary benefits and therefore to be under selection. Indeed, *H. spontaneum* seeds of desert origin had a lower germination fraction than seeds from the Mediterranean population in a year following seed dispersal and a relatively more persistent seed bank in the next two years in both native (desert) and alien (Mediterranean) introduction sites.

Spatial (between-site) and temporal (between-season) variation in percent germination exhibited by seeds of the same genetic origin and maternal environment undoubtedly shows that, in addition to innate dormancy (Gutterman 1993), wild barley possesses conditional dormancy, i.e. germination over a narrow range of conditions. *H. spontaneum* appears to exhibit a D/CD (“dormant/conditionally dormant”) annual seed dormancy cycle (*sensu* Baskin et al. 1993) in which seeds are dormant since maturity throughout summer and enter conditional dormancy in autumn. The proportion of conditionally-dormant seeds that germinate may be close to unity if conditions required for germination are met or it may be close to zero if they are far below the conditions needed. Conditional dormancy, however, does not exclude some complications like a certain degree of “coin-flipping” in germination in wild barley (Kaplan & Cooper 1984). A general rule in this species appears to be an increasing role of germination-regulating mechanisms that reduce temporal variation in population growth rate from the more predictable Mediterranean towards less predictable desert environments.

Our results suggest that, in both desert and Mediterranean populations, λ may seriously drop in unfavorable years, but with a difference in recovery in the following season. In the Mediterranean population, even in the most unfavorable years, adults are present and seeds are produced. Consequently, these seeds serve to restore initial population size. A contributing effect of the seed bank is negligible. In contrast, in the desert population, in years of insufficient rainfall a situation of no adults surviving to seed production is possible (as happened in season 1998–99).

Under these circumstances the only source of population recovery is the seed bank.

It is important to note that “good” and “poor” years in our study denote only conditions for germination (specifically, a sufficiently large first effective rain that serves as a triggering germination threshold and adequate soil moisture during the period needed for development of a seed into seedling) (Freas & Kemp 1983, Gutterman & Evenari 1994, Gutterman & Golan 1998) and are not implied to be related to environmental conditions following germination. Thus, high seed germination observed in the experimental seed bank in the “good” 1999–2000 year was accompanied by high seedling mortality in the field caused by insufficient rainfall during the rest of the season. Interestingly, the only significant difference between the two consecutive seasons 1998–1999 and 1999–2000 was in the first effective rain (10.8 mm vs. 15.3 mm). The difference of less than 5 mm resulted in a large increase in D seed percent germination and survival of seedlings. A 15 mm threshold of autumnal rainfall to trigger germination of most annual species was also reported by Pitt & Heady (1978) for California grasslands.

Survival of seeds at the desert site was found to be lower in the plots under observation as compared with the Mediterranean site but not much different in the experimental seed banks (where ant, rodent and bird foraging were excluded) in a “good” year (Fig. 2). The latter appears to reflect the high impact of seed predation on population demography at this site. In contrast, seedling survival and per adult fecundity were lower in the Mediterranean than in the desert population. Altogether these findings may indicate i) lower vigor of desert vs. Mediterranean seeds and ii) greater density dependence at Mediterranean vs. desert sites.

Unrealistically high values of λ (for a long period) calculated for the M population (2.67 and 2.05 using data of 1997 and 1998, respectively) undoubtedly suggest transient dynamics of wild barley in this habitat, which only partly is due to temporal variation in annual rainfall. Other processes at the population and community level, such as intra- and interspecific density dependence, appear to be as important in the mesic environment. The demographic dynamics of the D population also appears to be transient but the effects of temporal heterogeneity (inter-annual variation in rainfall) on population dynamics appears to be stronger, reducing population size in unfavorable years to a very low level. In these seldom and unpredictably occurring unfavorable years, a decrease in the desert population’s λ will be greater than in the Mediterranean population, but in more favorable years we may expect no significant difference in inter-seasonal λ variation between the desert and Mediterranean populations.

Our results show that, although there is strong local adaptation to the desert environment at the species periphery through conditional seed dormancy, which has a strong effect on population demography, it can not fully compensate for the difference between the species core (Mediterranean) and periphery (desert) in climatic unpredictability. However, despite a difference in the amplitude of demographic fluctuations between the Mediterranean and desert populations, they had similarly low and almost zero local extinction at a fine spatial scale of 1 m² during 3 years of observations. This implies that conditional seed dormancy and a short-term persistent seed bank ensure persistence of peripheral barley populations at a level similar to that of core populations.

Acknowledgement. We thank Ruti Soto for the assistance in the laboratory. A grant from the Israel Academy of Sciences (86293101) and a local grant of the Mitrani Department for Desert Ecology supported this study.

This is publication number 370 of the Mitrani Department for Desert Ecology.

References

- Aguiar MR, Sala OE (1997) Seed distribution constrains dynamics of the Patagonian steppe. *Ecology* 78: 93–100.
- Aronson J, Shmida A (1992) Plant species diversity along a Mediterranean-desert gradient and its correlation with interannual rainfall fluctuations. *Journal of Arid Environments* 23: 235–247.
- Baskin CC, Chesson PL, Baskin JM (1993) Annual seed dormancy cycles in two desert winter annuals. *Journal of Ecology* 71: 551–556.
- Brown JH, Mehlman DW, Stevens GC (1995) Spatial variation in abundance. *Ecology* 76: 2028–2043.
- Brown JH, Stevens GS, Kaufman DM (1996) The geographic range: size, shape, boundaries, and internal structure. *Annual Reviews of Ecology and Systematics* 27: 597–623.
- Cabin RJ, Marshall DL, Mitchell RJ (2000) The demographic role of soil seed banks. II. Investigations of the fate of experimental seeds of the desert mustard *Lesquerella fendleri*. *Journal of Ecology* 88: 293–302.
- Carter RN, Prince SD (1988) Distribution limits from a demographic viewpoint. In: Davy AJ, Hutchings MJ, Watkinson AR (eds) *Plant Population Ecology*. Blackwell Scientific Publications, Oxford, pp 165–184.
- Cohen D (1966) Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology* 12: 119–129.
- de Kroon H, Plaisier A, van Groenendael J, Caswell H (1986) Elasticity as a measure of relative contribution of demographic parameters to population growth rate. *Ecology* 67: 1427–1431.
- Freas KE, Kemp PR (1983) Some relationships between environmental reliability and seed dormancy in desert annual plants. *Journal of Ecology* 71: 211–217.
- Gaston KJ (1990) Patterns in the geographical ranges of species. *Biological Reviews of the Cambridge Philosophical Society* 65: 105–129.
- Goodman D (1987) The demography of chance extinction. In: Soulé ME (ed) *Viable Populations for Conservation*. Cambridge University Press, Cambridge, pp 11–34.
- Gutterman Y (1992) Ecophysiology of Negev upland annual grasses. In: Chapman GP (ed) *Desertified Grassland: Their Biology and Management*. Linnean Society Symposium. Series 13. Academic Press, London, pp 145–162.
- Gutterman Y (1993) Seed germination in desert plants. *Adaptation of desert organisms*. Springer Verlag, Berlin.
- Gutterman Y, the late Evenari M (1994) The influences of amounts of distribution of irrigation during the hot and dry season on emergence and survival of some desert winter annual plants in the Negev Desert of Israel. *Israel Journal of Plant Science* 42: 1–14.
- Gutterman Y, Gozlan S (1998) Amounts of winter or summer rain triggering germination and “the point of no return” of seedling desiccation tolerance, of some *Hordeum spontaneum* local ecotypes in Israel. *Plant and Soil* 204: 223–234.
- Holt AR, Gaston K J, He F (2002) Occupancy-abundance relationships and spatial distribution: A review. *Basic and Applied Ecology* 3: 1–13.
- Inouye RS (1995) Population biology of desert annual plants. In: Polis GA (ed) *The Ecology of Desert Communities*. University of Arizona Press, pp 27–54.
- Kalisz S, McPeck MA (1992) Demography of an age-structured annual: resampled projection matrices, elasticity analyses, and seed bank effects. *Ecology* 73: 1082–1093.
- Kaplan RH, Cooper WS (1984) The evolution of developmental plasticity in reproductive characteristics: an application of the adaptive coin-flip principle. *American Naturalist* 123: 393–410.
- Kark S, Alkon PU, Safriel UN, Randi E (1999) Conservation priorities for the chukar partridge in Israel based on genetic diversity across an ecological gradient. *Conservation Biology* 13: 542–552.
- Kemp PR (1989) Seed banks and vegetation processes in deserts. In: Leck MA, Parker VT, Simpson RL (eds) *Ecology of soil seed banks*. Academic Press, San Diego, pp. 257–281.
- Klinkhamer PGL, de Jong TJ, Metz JAJ, Val J (1987) Life history tactics of annual organisms: the joint effects of dispersal and delayed germination. *Theoretical Population Biology* 32: 127–156.
- Lande R (1993) Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* 142: 911–927.
- Lesica P, Allendorf FW (1995) When are peripheral populations valuable for conservation. *Conservation Biology* 9: 753–760.
- Ludwig J (1986) Primary production variability in desert ecosystems. In: Whitford W (ed) *Pattern and Process in Desert Ecosystems*. University of New Mexico Press, Albuquerque, pp 5–17.
- Marone L, Horno ME, González del Solar R (2000) Post-dispersal fate of seeds in the Monte desert of Argentina: patterns of germination in successive wet and dry year. *Journal of Ecology* 88: 940–949.

- Menges ES (1992) Stochastic modeling of extinction in plant populations. In: Fiedler PL, Jain S (eds) *Conservation Biology: The Theory and Practice of Nature Conservation, Preservation and Management*. Chapman and Hall, New York, pp 253–275.
- Milberg P (1995) Soil seed bank after eighteen years of succession from grassland to forest. *Oikos* 72: 3–13.
- Milton SJ (1995) Spatial and temporal patterns in the emergence and survival of seedlings in arid Karoo shrubland. *Journal of Applied Ecology* 32: 145–156.
- Mull JF, MacMahon JA (1996) Factors determining the spatial variability of seed densities in a shrub-steppe ecosystem: the role of harvester ants. *Journal of Arid Environments* 32: 181–192.
- Noy-Meir I (1973) Desert ecosystems: environment and producers. *Annual Reviews of Ecology and Systematics* 4: 25–41.
- Noy-Meir I (1981) Spatial effects in modelling of arid ecosystems. In: Goodall D, Perry R (eds) *Arid-Land Ecosystems: Structure, Functioning and Management*, vol. 2. Cambridge University Press, pp 411–432.
- Pake CE, Venable DL (1996) Seed banks in desert annuals: implications for persistence and coexistence in variable environments. *Ecology* 77: 1427–1435.
- Pitt MD, Heady HF (1978) Responses of annual vegetation to temperature and rainfall patterns in northern California. *Ecology* 59: 336–350.
- Philippi T (1993) Bet-hedging germination of desert annuals: beyond the first year. *American Naturalist* 142: 474–487.
- Polis GA (1995) Desert communities: an overview of patterns and processes. In: Polis GA (ed) *The ecology of desert communities*. University of Arizona Press, pp. 1–26.
- Reichman OJ (1984) Spatial and temporal variation of seed distributions in Sonoran desert soils. *Journal of Biogeography* 11: 1–11.
- Rice KJ (1989) Impacts of seed banks on grassland community structure and population dynamics. In: Leck MA, Parker VT, Simpson RL (eds), *Ecology of soil seed banks*. Academic Press, San Diego, pp 211–230.
- Safriel UN, Volis S, Kark S (1994) Core and peripheral populations, and global climate change. *Israel Journal of Plant Sciences* 42: 331–345.
- Scudder GGE (1989) The adaptive significance of marginal populations: a general perspective. In: Levings CD, Holtby LB, Henderson MA (eds) *Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks*. Canadian Special Publication in Fisheries and Aquatic Science 105, pp 180–185.
- Shmida A, Burgess T (1988) Plant growth-form strategies and vegetation types in arid environments. In: Werger MJA, van der Aart PJM, During HJ, Verhoeven JTA (eds) *Plant Form and Vegetation Structure*. SPB Academic, Hague, pp 211–242.
- Simon JL (1995) *Resampling: The New Statistics*. Julian L. Simon.
- Thompson K, Bakker JP, Bekker RM (1997) *Soil seed banks of North West Europe: Methodology, density and longevity*. Cambridge University Press, Cambridge.
- Venable DL, Lawlor L (1980) Delayed germination and dispersal in desert annuals: escape in space and time. *Oecologia* 46: 272–282.
- Volis S, Mendlinger S, Ward D (2002a) Adaptive traits of wild barley plants of Mediterranean and desert origin. *Oecologia* 133: 131–138.
- Volis S, Mendlinger S, Ward D (2002b) Differentiation in populations of *Hordeum spontaneum* Koch along a gradient of environmental productivity and predictability: life history and local adaptation. *Biological Journal of Linnean Society* 77: 479–490.
- Wagner LK, Spira TP (1994) Germination, recruitment and survival in the weedy annual *Medicago polymorpha* in successive wet and dry years. *American Midland Naturalist* 131: 98–108.
- Yom-Tov Y, Tchernov E (1988) *The zoogeography of Israel*. Dr W. Junk Publ., Dordrecht.