

Sergei Volis · Samuel Mendlinger · David Ward

Adaptive traits of wild barley plants of Mediterranean and desert origin

Received: 14 August 2001 / Accepted: 13 June 2002 / Published online: 21 August 2002
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Abstract Reciprocal introduction of seeds and seedlings was used to test for local adaptation and to identify a set of co-adapted traits of Mediterranean and desert ecotypes of wild barley *Hordeum spontaneum*. Evidence for local adaptation was found in seedling introductions into intact environments and from ecotype colonization success in the first generation after seed dispersal. Estimates of fitness were obtained at particular stages of the life cycle (seed, seedling and adult). Experiments that manipulated the environment (vegetation removal, different plant density) demonstrated the intensity and direction of natural selection in different life history episodes, but there was no strong evidence for local adaptation under these circumstances. The observed genetically determined differences between Mediterranean and desert ecotypes can be summarized as the following: reproductive output was higher in desert plants, with smaller seeds than in Mediterranean plants. There was a higher competitive ability of Mediterranean than desert plants. Plants of desert origin had significant reductions in yield when grown in mixed stands with Mediterranean plants; no such effect was observed for plants of Mediterranean origin. Seed germination and seedling survival was lower in seeds of desert origin. This was due to both: genetically determined higher dormancy of desert seeds and a trade-off between no. of seeds and their size (directly related to seed/seedling vigour).

Keywords Ecotype · Life history · Reciprocal transplant

Introduction

Genetic differentiation of plants occupying a range of environments is a common phenomenon arising from the interplay of selection and gene flow (Jain and Bradshaw 1966; Levin 1988). Ecotypic differentiation is a result of habitat-specific natural selection strong enough to override the effect of gene flow. The net effect of selection is a multiplicative function of selection episodes at different stages of life history. Therefore both the absolute differences in abiotic effects among environments and the selection effects they produce in different life history stages are important factors influencing ecotypic differentiation. In addition, the abiotic effects varying across environments can be accompanied by concomitant biotic effects including competition. A gradient of environmental productivity determined by soil properties and moisture availability can create contrasting selective pressures of intra- and inter-specific competition (Fowler 1986; Linhart 1988). Ecotypes, differentially adapted to an array of competitive regimes were reported in a number of studies (Davies and Snaydon 1976; Martin and Harding 1981; Schoener 1983; Turkington and Aarssen 1984; Miller and Fowler 1993).

Two globally important vegetation types, desert and Mediterranean, differ considerably in environmental productivity and predictability. Because annual variation in precipitation is an inverse function of the mean annual precipitation, patterns of precipitation in deserts are highly unpredictable (Polis 1995). Moreover, because the variation in the timing of rainfall is the major stochastic factor influencing productivity (Noy-Meir 1973; Ludwig 1986, 1987), deserts are characterized by low productivity although patches of relatively high productivity do occur (Noy-Meir 1981). Such a spatial differentiation into patches of good and poor quality is much stronger in deserts than in Mediterranean environments (Shmida et al. 1986; Polis 1995). The intensity of biological interactions, and competition in particular, has been hypothesized to decrease towards more extreme desert environmental conditions (Noy-Meir 1973; Grime 1977;

S. Volis (✉) · S. Mendlinger
The Institutes for Applied Research,
Ben-Gurion University of the Negev, POB 653,
Beer Sheva 84105, Israel
e-mail: volis@bgumail.bgu.ac.il

S. Volis · D. Ward
Mitrani Department for Desert Ecology,
Blaustein Institute for Desert Research,
Ben-Gurion University of the Negev,
Sede Boqer 84990, Israel

Shmida et al. 1986) although direct experimental support for this hypothesis is lacking. In Mediterranean-climate regions, the onset of the rainy season is more predictable, within-season supply of water is more reliable and the duration of the growing season is longer than in deserts (Shmida and Burgess 1988). Some differences in phenology and reproductive allocation between plants of the same species originating from desert and Mediterranean regions were found in a few studies (Aronson et al. 1992, 1993). However, these studies did not involve either tests of local adaptation or analyses of important life cycle stages and fitness components (i.e. seed and seedling survival).

The main objective of this study was to test the adaptive nature of ecotypic differences between Mediterranean and desert plants of *Hordeum spontaneum* Koch. Snow and Brody (1984) reported the existence of different ecotypes of *H. spontaneum* in Israel, but no rigorous test of local adaptation of these ecotypes has ever been undertaken. Another objective was to determine abiotic and biotic selection forces at different stages of the life cycle including competition in both environments. We predicted that desert plants will differ from Mediterranean plants in the traits that enable adaptation to a harsher and less predictable environment: (1) size and no. of seeds produced by a plant, (2) seed dormancy, (3) seed and seedling survival. We also expected to find a difference in ecotype responses to the effects of competition, which might arise due to the differences in (1) and (3).

Materials and methods

Study species and choice of populations

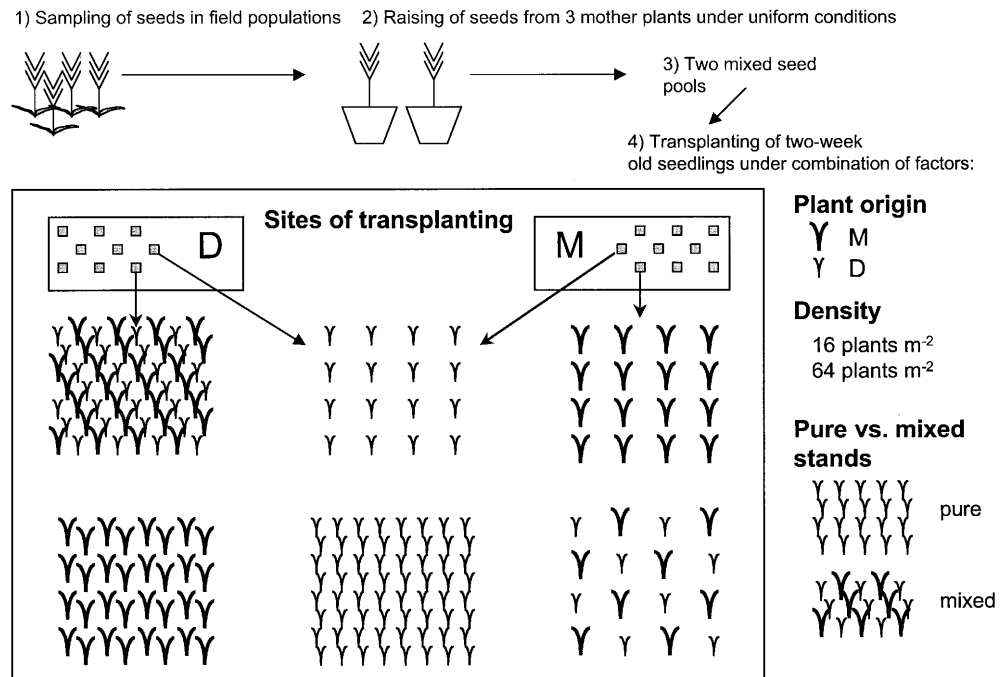
H. spontaneum is a predominantly selfing annual grass of Mediterranean and Irano-Turanian distribution (Harlan and Zohary 1966). It is well adapted to a Mediterranean-type climate with short warm winters and long dry summers. Despite its predominantly Mediterranean and Irano-Turanian distribution, wild barley penetrates into desert environments where it maintains stable populations. Seed collection was conducted in 1996 in one Mediterranean and one desert location in Israel. The Mediterranean wild barley population (M) is in Beit Guvrin National Park located in the Shefela Hills (elevation 300 m, annual precipitation around 400 mm, coefficient of variation in annual precipitation over 49 years 32%). The area is a semi-steppe batha on rendzina soil with mosaic of shrub-semi-shrub cover (*Sarcopoterium spinosum*, *Calicotome villosa*, *Cistus salvifolius*) and dense stands of *H. spontaneum*, among other grasses. This is a typical large and dense population of *H. spontaneum* for central and northern Israel.

The desert population (D) is in a wadi (Arabic for ephemeral river valley) in the Negev Desert (elevation 400 m, annual precipitation around 100 mm, coefficient of variation in annual precipitation over 49 years 43%), fenced off as an experimental area of the Mitrani Department for Desert Ecology, Ben-Gurion University. There is sparse desert vegetation on loess soil (dominated by shrubs and semi-shrubs *Retama raetam*, *Thymelea hirsuta*, *Zygophyllum dumosum*, *Hammada scoparia*) with patchily distributed *H. spontaneum*. A small barley population representative of the Negev Desert is isolated by hills surrounding the wadi.

Experimental design

Two sites (D and M) were tested for available soil nitrogen (NO_3^-) using a nested design. The sample cores were taken from the microsites occupied by *H. spontaneum*. It was not possible to place transects equidistant from one another because of the patchy distribution of *H. spontaneum* in both areas. Therefore, the soil cores were taken 1 m apart in four linear transects randomly located along the wadi (D) or along the slope (M). The soil was sieved and 10 g (fresh weight) was processed according to standard protocols (Mulvaney 1996).

Fig. 1 A scheme of experimental design for transplant experiment with removal of vegetation. *M* Mediterranean-origin population, *D* desert-origin population



Several experiments with reciprocal transplants were conducted during 1996/7. In these studies, 2-week-old plants from indigenous and alien environments were reciprocally transplanted at both the D and M sites.

The design of the first study is presented in Fig. 1. Full-sibs of three mother plants from each of two habitats were mixed and used as the seed pool. In order to facilitate identification, we used seeds of easily distinguishable spikelet morphs from each population: black morphs from D and yellow morphs from M. A spikelet colour in barley is determined by a single gene, and no pleiotropic association between spikelet colour and other plant parameters have been observed. In particular we found no significant differences in yield and survival of colour morphs of desert origin (the black morphs have never been found in a Mediterranean part of Israel) (unpublished data). The difference in spikelet colour allowed us to estimate the reproductive success of two populations over time when grown in mixed stands. In this study all vegetation was cleared from the plots and each plot was fenced off. Colonizing areas in these environments were established using a completely randomized design with two plant densities (16 and 64 plants m^{-2}) and two planting treatments: (1) pure stands (only D or M), and (2) 50:50 mixed stands. At the end of the 1997/1998 field season between 500 and 1,000 seeds were collected after seed maturation from each mixed stand plot with high plant density (64 plants m^{-2}), brought to the laboratory and identified as either D (black) or M (yellow).

In the second study of genotype-by-environment interactions we have used the full-sibs of ten mother plants from each of the two habitats without colour distinction. One hundred 2-week-old D and M seedlings were reciprocally transplanted into plots of approximately 100 m^2 where the indigenous vegetation had not been removed. Thus, the transplanted plants were exposed to the abiotic and biotic interactions that plants encounter in the field. In each environment, we used two plots (sub-sites): (1) in D one site was at the beginning of a wadi and another in a wadi depression, (2) in M the two sites were at different positions along a slope. The D site 1 (wadi depression) contained a small but very dense stand of barley while site 2 (beginning of the wadi) had almost no vegetation cover. The two M sites did not differ vegetatively. In this study, survival during the season and fecundity of D and M plants at senescence were obtained and compared.

In addition to the transplanting of seedlings, trays filled with soil of the site of transplanting and containing spikelets of each D and M origin were buried at each transplant site in 1998–1999. Two trays per ecotype per site were buried with 400 spikelets per ecotype per site. Two months after seed germination the trays were removed, brought to the laboratory and seeds classified as: (1) germinated and survived, (2) germinated and died, (3) non-germinated. A fine metal net over the trays prevented seed predation by ants, rodents and birds. However, this net could not exclude seed infestation by soil arthropods and infection by fungi. Therefore, a fraction of non-germinated seeds represents two effects that can be disentangled only in a long-term experiment – seed infestation/infection in the soil and dormancy. In this paper we present the results of short-term germination experiments. The 1998–1999 season was extremely dry at the D site (39.6 mm versus 90 mm mean annual rainfall for the last 49 years) and there was a very low germination percentage. In order to trace the inter-seasonal differences in germination and survival the experiment was repeated in 1999–2000 at the D site.

Data analysis

To determine the possible interactions between origin of seeds, site of transplanting, type of competition (intra- vs. inter-specific) and intensity of competition [low (16 plants m^{-2}) vs. high (64 plants m^{-2}) density] we used a fully factorial ANOVA conducted on the log-transformed no. of spikes and total no. of seeds/per plant. Ratio and percentage data were arcsin $\sqrt{}$ transformed and tested for normal distribution prior to ANOVA. The effects of interspecific competition on yield (no. of spikelets/plant) of M and D plants under different combinations of site and density effects were tested by χ^2 -test.

Results

Transplanting with removal of vegetation

All four main effects strongly affected plant fecundity (no. of seeds/plant) (Tables 1, 2). The site effect appears to be

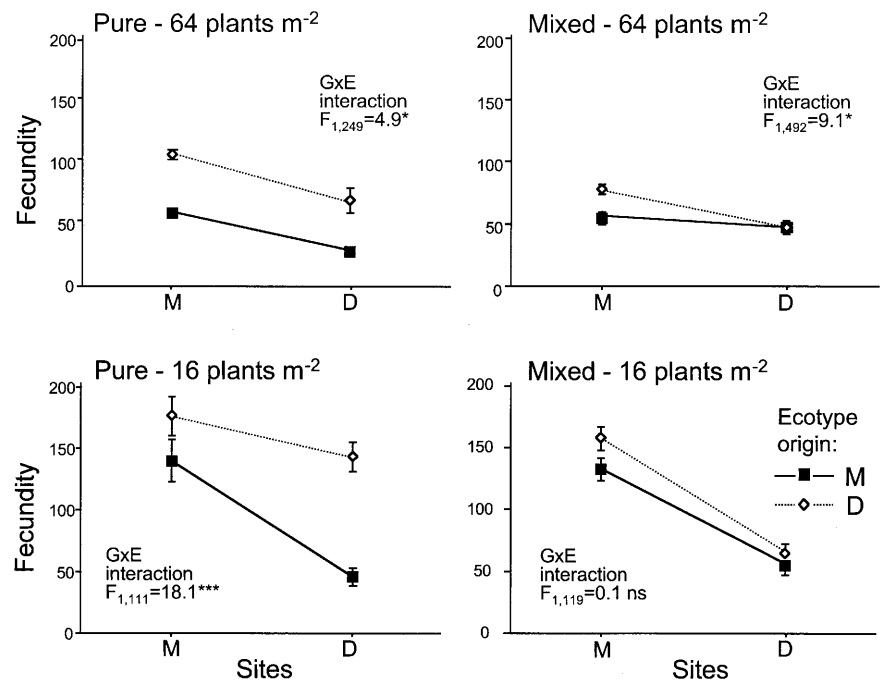
Table 1 ANOVA of four fixed effects and their interactions in three reproductive traits. In all analyses, $df=1$ for the main effects and each of the interactions, error $df=1,133$ for no. of spikes/plant, and $df=975$ for no. of seeds/spike and no. of seeds/plant

| Source | No. of spikes/plant | | No. of seeds/spike | | No. of seeds/plant | |
|-------------------------------|---------------------|----------|--------------------|----------|--------------------|----------|
| | <i>F</i> | <i>P</i> | <i>F</i> | <i>P</i> | <i>F</i> | <i>P</i> |
| Main effects | | | | | | |
| Site (S) | 216.5 | *** | 78.5 | *** | 208.3 | *** |
| Origin (O) | 86.0 | *** | 76.1 | *** | 98.9 | *** |
| Competition (C) | 17.7 | *** | 2.7 | NS | 11.4 | *** |
| Density (D) | 178.7 | *** | 71.1 | *** | 173.3 | *** |
| Two-way interactions | | | | | | |
| S×O | 0.9 | NS | 11.5 | *** | 4.6 | * |
| S×C | 0.0 | NS | 0.2 | NS | 0.0 | NS |
| S×D | 28.9 | *** | 4.2 | * | 11.0 | *** |
| O×C | 29.1 | *** | 37.1 | *** | 37.9 | *** |
| O×D | 2.1 | NS | 0.4 | NS | 0.7 | NS |
| C×D | 0.0 | NS | 1.8 | NS | 0.1 | NS |
| Three-way interactions | | | | | | |
| S×O×C | 7.5 | ** | 24.4 | *** | 16.9 | *** |
| S×O×D | 3.7 | NS | 24.8 | *** | 7.1 | ** |
| S×C×D | 19.7 | *** | 12.7 | *** | 20.1 | *** |
| O×C×D | 1.5 | NS | 2.0 | NS | 0.1 | NS |
| Four-way interaction | | | | | | |
| S×O×C×D | 0.1 | NS | 11.5 | *** | 0.6 | NS |

* $P<0.05$, ** $P<0.01$, *** $P<0.001$, NS not significant ($P>0.05$)

Table 2 Least square means and SE (*in parentheses*) of the main effects in six reproductive traits. Significantly different pairs are denoted by an asterisk

| Source | No. of spikes/plant | No. of seeds/spike | No. of seeds/plant | Spikelet weight (mg) | Caryopsis weight (mg) | Ratio caryopsis: spikelet weight |
|--------------------|---------------------|--------------------|--------------------|----------------------|-----------------------|----------------------------------|
| Site | | | | | | |
| M | 7.0 (0.1) | 15.9 (0.1) | 113.1 (2.3) | 54.7 (1.0) | 25.6 (0.5) | 45.8 (0.7) |
| D | 4.1 (0.1)* | 14.1 (0.1)* | 63.6 (2.3)* | 62.5 (0.9)* | 27.5 (0.5)* | 43.2 (0.7)* |
| Origin | | | | | | |
| Mediterranean | 4.7 (0.1) | 14.1 (0.1) | 70.9 (2.3) | 68.9 (0.9) | 33.8 (0.5) | 48.9 (0.7) |
| Desert | 6.3 (0.1)* | 15.9 (0.1)* | 105.7 (2.4)* | 48.4 (1.0)* | 19.3 (0.5)* | 40.1 (0.7)* |
| Competition | | | | | | |
| Intrapopulation | 6.0 (0.1) | 15.2 (0.1) | 96.8 (2.5) | 60.6 (0.8) | 26.8 (0.4) | 45.6 (0.6) |
| Interpopulation | 5.1 (0.1)* | 14.8 (0.2)* | 79.8 (2.2)* | 56.6 (0.8)* | 26.8 (0.5) | 43.3 (0.8)* |
| Density | | | | | | |
| Low | 6.9 (0.1) | 15.9 (0.2) | 114.3 (2.8) | 58.7 (0.9) | 26.7 (0.5) | 44.6 (0.7) |
| High | 4.1 (0.1)* | 14.2 (0.1)* | 62.3 (1.7)* | 58.5 (1.0) | 26.4 (0.5) | 44.4 (0.7) |

* $P < 0.05$ **Fig. 2** Genotype-by-environment interactions ($G \times E$) of the D and M plants under combinations of competition and density effects. For other abbreviations, see Fig. 1

a result of higher precipitation at M as compared with the D environment (408 ± 22 mm vs. 94 ± 6 mm average annual rainfall over last 40 years, respectively, $t = 14.8$, $P < 0.001$, t -test) and not because of soil fertility (2.0 ± 0.2 p.p.m. vs. 6.6 ± 0.7 p.p.m. of organic nitrogen, respectively, $t = 5.7$, $P < 0.001$, t -test). Plants of desert origin had higher reproductive outputs than plants of Mediterranean origin at both sites, while yield was higher in pure than in mixed stands and under low density vs. high density (Table 2).

Both transplant site and population origin significantly affected reproductive output, but the interaction effect was marginally significant ($F_{1,975} = 4.6$, $P = 0.032$) [the Site \times Origin ($S \times O$) interactions under all combinations of

effects are shown in Fig. 2]. The most important $S \times O$ interaction was that found at the lowest plant density (density 16 plants/m²) in pure stands. This interaction was highly significant ($F_{1,111} = 18.1$, $P < 0.001$) and demonstrated a steeper decline in fecundity for M as compared with D plants in the D site. There was no difference in the response of D and M plants to density, but there was a differential response to mixed vs. pure stand planting (Table 1). However, three-way interactions involving site and origin effects [$S \times O \times$ Competition ($S \times O \times C$) and $S \times O \times$ Density ($S \times O \times D$)] were both significant (Table 1).

Similarly, the two other reproductive traits (no. of spikes/plant and no. of seeds/spike) were strongly affect-

Table 3 Effect of competition between two ecotypes on yield (no. of spikelets/plant) of Mediterranean-population (*M*) and desert-population (*D*) plants under different combinations of site and

density effects. Significance of M-D differences under particular combination of effects is tested by χ^2 -test

| Type of competition | M site | | | | D site | | | |
|------------------------|-------------|-------|--------------|-------|-------------|-------|--------------|------|
| | Low density | | High density | | Low density | | High density | |
| | M | D | M | D | M | D | M | D |
| Intrapopulation | 140.1 | 176.2 | 60.3 | 105.6 | 45.7 | 142.8 | 29.3 | 74.5 |
| Interpopulation | 132.0 | 156.7 | 56.5 | 77.3 | 55.9 | 65.2 | 47.8 | 47.5 |
| Reduction in yield (%) | 5.7 | 10.8 | 5.0 | 27.3 | -21.7 | 54.5 | -65.5 | 36.0 |
| χ^2 | 0.1 NS | | 1.1 NS | | 16.1*** | | 10.1*** | |

*** $P < 0.001$, NS $P > 0.05$

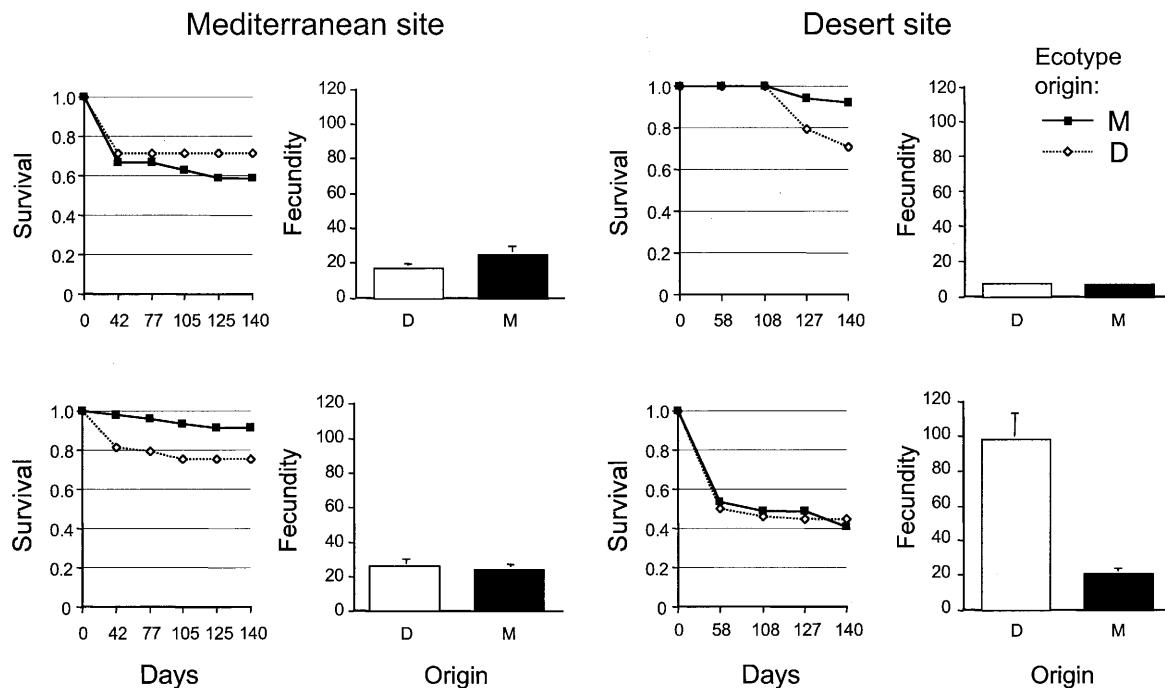


Fig. 3 Plant survival and fecundity at two sites of transplanting with intact vegetation. One hundred 2-week-old seedlings were transplanted in each of two sub-sites at each site. For abbreviations, see Fig. 1

ed by all four main effects (with the exception of the effect of competition on seeds/spike). There was also a significant two-way origin-by-competition interaction but not of origin-by-density, and a three-way $S \times O \times C$ interaction. The $S \times O \times D$ interaction was significant for the no. of seeds/spike only (Table 1). There was a strong interaction effect of transplant site and population origin on no. of seeds/spike ($F_{1,975} = 11.5$, $P < 0.001$), but not on no. of spikes/plant ($F_{1,975} = 0.9$, $P > 0.05$).

Population origin and transplant site had opposite effects on the weight of the kernel (caryopsis) and the spikelet (dispersal unit). Plants of Mediterranean origin, *M*, produced heavier caryopses and spikelets than plants of desert origin, *D* (35.0, 32.4 mg vs. 20.0, 18.4 mg, and 71.7, 64.7 mg vs. 51.6, 43.9 mg for *D* and *M* sites, respectively). However, caryopsis and spikelet weights of

both ecotypes were larger at *D* than at the *M* site (Table 2). The ratio caryopsis:spikelet weight was higher in Mediterranean than in desert plants and in *M* than in *D* transplant sites.

A direct comparison of the two ecotypes' competitive abilities in indigenous and alien environments revealed the superiority of the *M* ecotype in mixed stands at the *D* site (Table 3). At this site, the total yield of plants of Mediterranean origin significantly increased and plants of desert origin decreased in mixed stands as compared with pure stands. This change in reproductive output was observed under both planting densities.

Transplanting into intact environments

A comparison of the adaptive ability of *D* and *M* plants when transplanted into intact indigenous and alien environments revealed no difference in survival between ecotypes (Fig. 3). There was also no difference in plant fecundity at both *M* sub-sites, and at one *D* sub-site. In the

other D sub-site (beginning of a wadi), indigenous transplants had superior fecundity ($F_{1,41}=22.5, P<0.001$).

Success over time

The colonizing success of the two populations over time when grown in mixed stands was a short-term phenomenon. After 1 year, the proportion of seeds from the indigenous ecotype in the total seed pool was higher than that of the alien ecotype in all the experimental plots (test of independence of mean site-by-ecotype frequencies, $\chi^2_1=53.7, P<0.001$) (Fig. 4).

Introduction of seeds

No significant site-by-origin interaction was found for percentage of germinated seeds and surviving seedlings. However, effects of site and origin were substantial on both fitness components, seed germination and seedling survival (Table 4). A higher percentage of seeds germinated and more seedlings survived at the M site than at the D site. Similarly, there was a higher percentage of germinated seeds and more seedlings of Mediterranean origin than of desert origin (Fig. 5).

Table 4 ANOVA of two fixed effects and their interaction on seed germination and seedling survival tested by reciprocal introduction of two seed ecotypes into Mediterranean and desert sites during one season (1998–1999), introduction of two seed ecotypes into the desert site during two seasons (1998–1999 and 1999–2000). In both analyses, $df=1$ for the main effects and the interaction; error $df=4$

| Source | Germination (%) | | Seedling survival (%) | |
|--|-----------------|----------|-----------------------|----------|
| | <i>F</i> | <i>P</i> | <i>F</i> | <i>P</i> |
| Reciprocal introduction | | | | |
| Site (S) | 15.3 | 0.017 | 38.3 | 0.003 |
| Origin (O) | 4.4 | 0.102 | 5.6 | 0.077 |
| S×O | 0.4 | 0.573 | 0.4 | 0.579 |
| Introduction of two seed ecotypes | | | | |
| Season (Sn) | 29.0 | 0.006 | 73.7 | 0.001 |
| O | 9.6 | 0.037 | 6.8 | 0.060 |
| Sn×O | 0.1 | 0.968 | 0.6 | 0.465 |

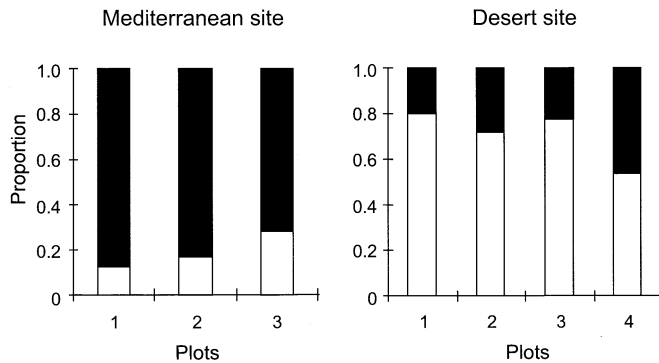
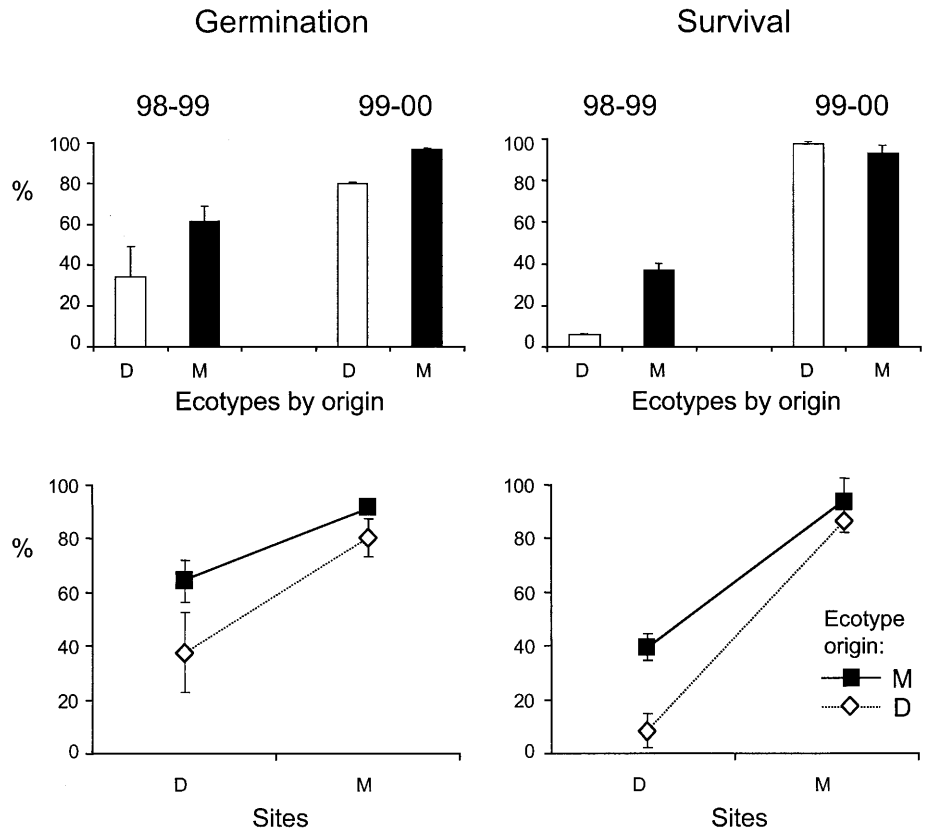


Fig. 4 Contribution of desert (white area of rectangle) and Mediterranean (black area of rectangle) genotypes to the total seed pool 1 year after transplanting in mixed stands at a density of 64 plants m⁻²

Fig. 5 Germination of seeds and survival of seedlings of two ecotypes in 1998–1999 and 1999–2000 seed introductions at the desert site (top) and at the two sites in a reciprocal seed introduction (1998–1999) (bottom). Bars indicate 1 SE. For abbreviations, see Fig. 1



The difference in seed germination between the two ecotypes was not influenced by inter-seasonal rainfall variation at the D site. Seedling survival in the 1999–2000 season did not differ between the two genotypes while the season-by-origin interaction was significant (Table 4), indicating the poorer ability of D-origin seedlings (as compared with M-origin seedlings) to survive in a poor season (Fig. 5). Interestingly, the only significant difference between two consecutive seasons was in the first effective rainfall (10.8 mm vs. 15.3 mm). The difference of <5 mm resulted in a large increase in the survival of D-origin seedlings.

Discussion

Most of the fitness components tested in the present study were found to be genetically determined rather than environmental, and can be ascribed to population origin. The variation in reproductive output (a measure of individual fitness at the adult stage) had a substantial environmental component (which included abiotic environment, competition type and intensity). Nonetheless, in each environment, plant fecundities were sharply differentiated by plant origin. Plants of desert origin had higher yield than plants of Mediterranean origin, which was due both to greater production of reproductive tillers and more seeds per spike. When 2-week-old seedlings were transplanted with or without removal of other vegetation, variation in another fitness component, seedling survival, was found to be entirely environmental (mortality was negligibly small in the experiment with vegetation removal). However, survival of seedlings that developed from reciprocally introduced seeds had a genetic component, with seedlings of Mediterranean origin surviving better than seedlings of desert origin in a year with poorer rainfall. Variation in germination percentage in the season following dispersal also had a genetic component. A smaller proportion of seeds of desert origin germinated regardless of introduction site. This difference was due to both higher seed dormancy and higher mortality of desert than Mediterranean seeds (unpublished data). The higher mortality of seeds and seedlings of desert origin seems to be a result of smaller seed size as compared with the Mediterranean ecotype [see Baskin and Baskin (1998) and references therein for the association of seed size with seed germination and seedling vigour].

We found two opposite effects of xeric vs. mesic environments on seed weight: (1) an increase in weight, which was a short-term effect induced during plant growth, and (2) a decrease in weight, which was a genetically determined, long-term evolutionary effect. Apparently, these two antagonistic effects represent acclimation and adaptation mechanisms adjusting species to environment. The advantage of large seed size in xeric environments accrues due to the higher vigour of seedlings, which may trade-off with lower persistence in the seed bank (Gross and Smith 1991; Baskin and Baskin 1998).

Seed traits characteristic of a persistent seed bank are small seed size and hard seed coats, which decrease vulnerability to predation (Silvertown 1981). Both these features differentiated seeds of desert and Mediterranean origin, with the former being smaller and having a higher proportion of spikelet mass devoted to kernel defence than the latter.

A highly significant S×O interaction ($F_{1,111}=18.1$, $P<0.001$) expressed under low plant density in pure stands strongly suggests that there has been adaptation of D and M plants to their local environments. However, the advantage of indigenous genotype in a particular fitness component is misleading if the net effect of selection (i.e. fitness over all selection episodes of the life history) is unmeasured. Relative ecotype fitness, measured at the population level in the first generation after simulated colonization of two environments clearly showed the adaptive superiority of native ecotypes. Although plants of desert origin produced more seeds in both environments, differential survival at the seed and seedling stage, and a different response to the effects of competition resulted in a higher proportion of indigenous vs. alien seed ecotypes in both environments in the season after transplanting. Therefore, the genetic differences we found between two ecotypes cannot be attributed to random genetic factors (drift and gene flow), but are evolutionary consequences of local selection processes.

Together, these results demonstrate not only the local adaptation of Mediterranean and desert ecotypes, but also the existence of adaptive life history differences in Mediterranean and desert plants. Mediterranean plants, occupying a more favourable and predictable environment, produced larger seeds than plants of desert origin. The advantage of large seed size is that it provides for better growth and establishment of a seedling and consequently of an adult, often with competitive superiority over smaller-seeded forms (Black 1956; Stanton 1984). Higher competitive ability, according to Grime (1977), is a characteristic of plants originating from productive and predictable environments. We found a decrease in the fecundity of desert plants when grown together with Mediterranean plants, especially at high density (64 plants/m²), suggesting greater competitive ability of the latter. The desert ecotype produced smaller but more numerous seeds, and had lower percent germination in the season following dispersal than the Mediterranean ecotype. Additionally, the desert ecotype was found to be more sensitive to environmental cues for the initiation of germination, such as first effective rainfall. The last-mentioned trait is one of the most conspicuous features of desert annual plants (Freas and Kemp 1983; Gutterman and Evenari 1994) and was found to differentiate desert and Mediterranean barley ecotypes (Gutterman and Gozlan 1998). Our findings are consistent with those reported by Schmidt and Levin (1985) for *Phlox drummondii* of lower germination rate and higher dormancy in xeric vs. mesic populations. The higher reproductive output of a xeric than a mesic population was found in *Anthoxanthum odoratum* but with little inter-population variation in seed

germination and establishment (Platenkamp 1990). Higher seed production of plants from a more xeric site was also found in *Poa annua* (Law et al. 1977), although higher aridity in this study was confounded with higher disturbance. In our opinion, the most important traits that differentiated the two ecotypes at the seed stage (start of germination, dormancy), seedling stage (survival) and adults (onset of seed production and senescence, size and no. of produced seeds) demonstrate the directions of natural selection in Mediterranean vs. desert environments. However, the direct causes of the evolutionary processes in these environments (e.g. drought per se, unpredictability of rainfall, spatial heterogeneity, competition etc.) are still to be investigated.

Acknowledgements 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 no. 360 of the Mitrani Department for Desert Ecology.

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