

Differentiation in populations of *Hordeum spontaneum* along a gradient of environmental productivity and predictability: life history and local adaptation

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Received 22 July 2002; accepted for publication 1 August 2002

Reciprocal introduction of seeds and seedlings of wild barley, *Hordeum spontaneum*, originating in four different environments of Israel was used to: (1) test for local adaptation, (2) make inferences about environmental effects on life-history and reproductive traits, and (3) identify trait combinations with recognizable 'strategies'. The four populations examined represented the following environments: (1) desert – low productivity and predictability, drought stress; (2) semi-steppe batha – moderate productivity and predictability; (3) grassland – high productivity and predictability; and (4) mountain – high productivity and predictability but with severe frost stress. Significant genotype-by-environment interactions were observed for yield and reproductive biomass, seedling biomass and percentage germinated and survived seeds, suggesting local ecotype adaptation. Increasing productivity and predictability of environment in respect to rainfall, without concomitant frost stress, was found to select for high reproductive biomass and large seeds, a high fraction of germinating seeds and high vigour of seedlings. The optimal strategy changes with increasing productivity and predictability and involves a trade-off between seed size and number, with reduced yield but increased seed mass, consistent with competition selection (or K-selection *sensu* MacArthur & Wilson (1967)) type. No specific life-history adaptations to predictable frost stress were detected for the mountain ecotype, but there was higher survival of seedlings in their indigenous (mountain) environment compared with other ecotypes. The latter appears to be a physiological adaptation to frost, which is consistent with selection for stress tolerance (or S-selection *sensu* Grime (1977)) type. The other stress factor, drought, which is very unpredictable in deserts, was associated with high seed dormancy, small seed size and low vigour of seedlings, but relatively high yield, which is consistent with a stress-escape bet-hedging strategy. © 2002 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2002, 77, 479–490.

ADDITIONAL KEYWORDS: aridity gradient – ecotype – reciprocal transplant – plant strategy – wild barley.

INTRODUCTION

Plants distributed along broad environmental gradients often differ in morphological or life-history traits, a pattern consistent with environmentally induced ecotypic differentiation (Chapin & Chapin, 1981;

Grant & Wilken, 1988; Macdonald & Chinnappa, 1989). Since the classical studies of Turesson (1922) and Clausen *et al.* (1940, 1948), this assumption has usually been verified by tests of local adaptation conducted as reciprocal introductions of seeds or seedlings. The selective advantage of local genotypes has been revealed in some studies (Davies & Snaydon, 1976; Chapin & Chapin, 1981; Schmidt & Levin, 1985; Waser & Price, 1985; Jordan, 1992; Nagy & Rice, 1997), but not in others (Fowler & Antonovics, 1981; Antonovics & Primack, 1982; Platencamp, 1990). The

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latter could be due either to prevalence of stochastic over deterministic environmental effects or because only a part of the plant's life history was analysed. The net effect of selection is a multiplicative function of selection episodes at different stages of the life history. Therefore, both the absolute differences in abiotic or biotic effects among environments and the selection effects they produce in different life-history stages are important factors influencing ecotypic differentiation.

Delayed germination through persistence in the seed bank is considered to be an adaptive bet-hedging strategy buffering against detrimental effects of a temporally varying environment (Cohen, 1966; Venable & Lawlor, 1980; Brown & Venable, 1986; Klinkhamer *et al.*, 1987). Several empirical studies investigating environmental causes and evolutionary consequences of delayed germination, in contrast to theoretical predictions, found no obvious association of the fraction of newly produced seeds entering the seed bank and a climatic or altitudinal gradient (Jain, 1982; Platencamp, 1991; Philippi, 1993; Kigel, 1995; Clauss & Venable, 2000; Cavieres & Arroyo, 2001). Most of these studies compared xeric vs. mesic conditions without explicit regard to the environmental predictability associated with aridity or the scale of this unpredictability. However, when aridity is investigated at an inappropriate (too fine) scale the differences in amount and predictability of rainfall between study sites may not impose selection regimes distinct enough to evolve different germination strategies. Another common feature of these experiments was the determination of germination fractions under controlled conditions of a greenhouse or growth chamber and using seeds collected *in situ*, i.e. without elimination of maternal effects during seed development, and without accounting for environmental effects during seed germination and genotype–environment interactions. In studies where at least some of these effects were accounted for (e.g. maternal effects), ecotypes from high rainfall regions had a shorter dormancy period than ecotypes from drier regions (Hacker, 1984; Hacker & Ratcliff, 1989).

A powerful approach to eliminate all effects except genetically determined interpopulation differences in germination pattern is: (1) to plant seeds collected in natural populations under controlled conditions to exclude maternal effects; and (2) to conduct a reciprocal introduction of F1 seeds into an array of native and alien conditions corresponding to seed origin.

The study of conspecific populations distributed along clear environmental gradients, e.g. soil nutrients and water gradients, can elucidate phenotypic effects of natural selection and reveal adaptive plant strategies. Technical problems associated with this task include: (1) the difficulty in disentangling effects of habitat-specific natural selection and stochastic

genetic processes such as gene flow and random genetic drift; (2) variation in gene flow and selection with life-cycle stages; and (3) inter-annual environmental variation. In order to overcome these problems, we tested for local adaptation with reciprocal seed and seedling introductions and by measuring stage-specific fitness differences. This approach allowed us to identify a set of 'coadapted traits designed by natural selection, to solve particular ecological problems' (Stearns, 1976) in wild barley, *Hordeum spontaneum* Koch. *Hordeum spontaneum* was a good study system as it grows naturally over a wide range of environments in Israel, including such extremes as deserts and mountains.

We had the following objectives in this study: (1) to test the adaptive nature of ecotypic differences between plants of *H. spontaneum*; (2) to identify main selection forces at different stages of the life cycle; and (3) to identify resulting plant strategies in four distinct environments along the gradients of productivity and predictability.

MATERIAL AND METHODS

STUDY SPECIES AND CHOICE OF POPULATIONS

In Israel, the aridity gradient creates steep climatic and ecological clines (from xeric desert to mesic Mediterranean) over relatively short distances (Bitan & Ruben, 1991; Aronson *et al.*, 1992; Kadmon & Danin, 1997). While the mean annual rainfall in the Mediterranean Galilee is around 600–800 mm, the mean annual rainfall in the southern part of the Negev desert, situated only 200 km to the south, is below 100 mm and is highly variable from year to year (Bitan & Ruben, 1991) (Fig. 1). Water is the main limiting and fluctuating resource that creates this severe north–south productivity gradient (Aronson *et al.*, 1992).

Wild barley, *Hordeum spontaneum*, is a winter annual, and a predominantly selfing grass. In Israel, despite its main occurrence in steppe-like formations and park forests (Harlan & Zohary, 1966), wild barley penetrates into desert (<200 mm annual rainfall) and mountain environments (up to 1600 m elevation) where it has stable populations.

Seed collections of *H. spontaneum* were made in 1996 from 20 locations employing a cluster sampling design. Each cluster, which consisted of five populations, was representative of one of the following environments/vegetative communities: desert, semi-steppe batha (open Mediterranean vegetative community dominated by subshrubs), Mediterranean grassland, and mountain. Relief, slope exposition, vegetation and soil type were kept constant in sampling locations within a cluster. Populations comprising a

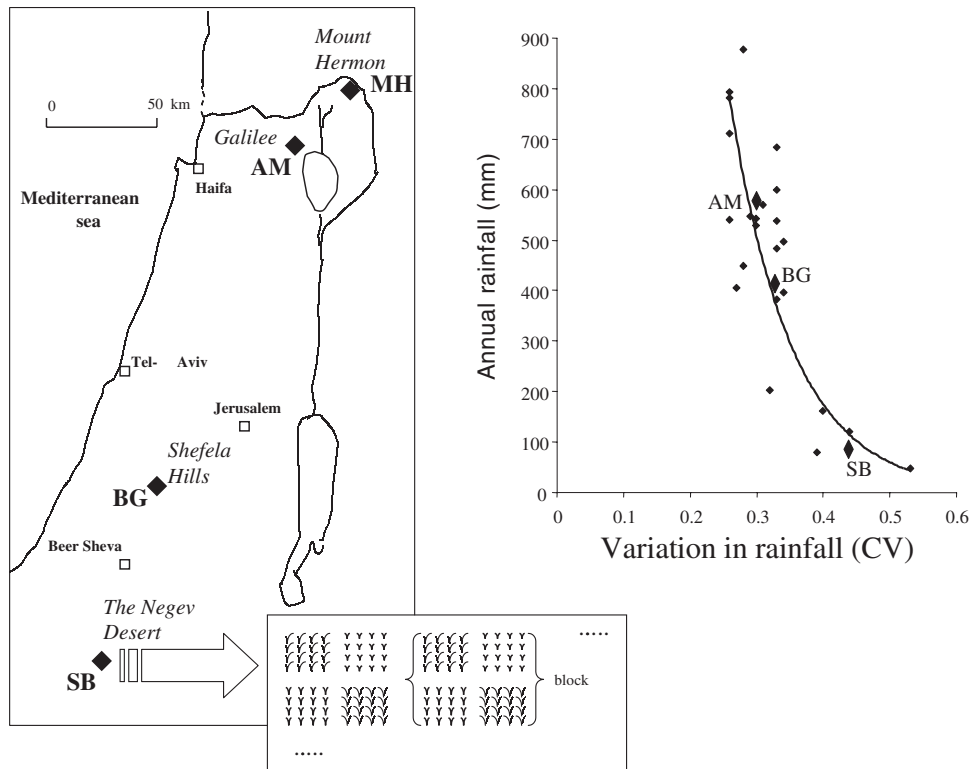


Figure 1. Distribution of four localities and a relationship between annual rainfall and its year to year variation (CV) ($R^2 = 0.65$, $P < 0.001$). The meteorological stations closest to three localities (all within 3-km distance) among 25 meteorological stations of Israel are designated. The MH locality is not shown due to lack of reliable data.

cluster were ≤ 5 km (mountain) or ≤ 20 km (other three groups) from each other. All 20 populations were used in a study of population genetic structure (Volis *et al.*, 2001), and one population from each cluster was used for a comparative study of plant phenotypic plasticity in response to experimentally manipulated water and nutrient stress (Volis, Mendlinger & Ward, 2002a), multi-level selection analysis (Volis *et al.*, 2002b), and life histories and test of local adaptation (present paper). Representative populations of each cluster were chosen for this study based on the feasibility of conducting the transplant experiments (protection from grazing, proximity to roads, etc.).

The locations of populations representing each habitat type are listed from south to north (Fig. 1):

1 SB location. Wadi (= Arabic for ephemeral river valley) in the Negev Desert, 3 km south-west of Sede Boqer fenced as an experimental area of the Mitrani Department for Desert Ecology. Sparse desert vegetation (dominated by the shrubs and semi-shrubs *Retama raetam*, *Thymelaea hirsuta*, *Zygophyllum dumosum* and *Hammada scoparia*) with patchily distributed *H. spontaneum*.

2 BG location. North-facing slope in the Shefela Hills in the Beit Guvrin National Park. Semi-steppe batha

with mosaic of shrub–semi-shrub cover (*Sarcopoterium spinosum*, *Calicotome villosa*, *Cistus salviifolius* and *C. creticus*) and dense stands of *H. spontaneum* among other grasses.

3 AM location. North-facing slope in the Upper Galilee, 1 km west of Ammiad. Mediterranean grassland without strong dominance of any species.

4 MH location. South-facing slope on Mount Hermon (Hermon Nature Reserve). Mountain forest with deciduous *Quercus boissieri*, *Q. libani* and few Rosaceae tree species accompanied by mainly perennial grasses and other herbaceous plants. The populations are within the snow line and experience severe frosts every year. *Hordeum spontaneum* has a patchy distribution with small populations which end abruptly at 1700 m altitude.

The four locations represent different environmental conditions with respect to: (1) the amount of precipitation during a rainy season (a primary factor that limits productivity), (2) predictability of amount and timing of rainy events, and (3) environmental stress (drought in desert and frosts in mountain) (Table 1). As all precipitation in Israel takes place during winter, the annual rainfall is also the amount of rainfall received by wild barley plants during a growing sea-

Table 1. Ecogeographical data for the four study populations obtained from multiple-year records of Israeli Meteorological Service

Population	Lon.	Lat.	Environment/ vegetation	Region	Soil	Altitude (m)	Climatic parameters							n
							Tm	Ta	Tj	Hu	Rd	Rn	CV	
SB	34.47	30.51	Desert	Negev Desert	Loess	470	19	26	9	36	15	90	43	49
BG	34.53	31.36	Semi-steppe batha	Shefela Hills	Rendzina	270	19	26	11	47	37	408	32	49
AM	35.33	32.57	Grassland	Upper Galilee	Terra Rossa	300	19	26	10	48	50	580	29	42
MH	35.75	33.30	Mountain	Mount Hermon	Terra Rossa	1500	11	20	1	52	70	1600	-	-

Abbreviations: Tm, mean annual temperature; Ta, mean August temperature; Tj, mean January temperature; Hu, mean humidity at 14:00; Rn, mean annual rainfall (mm); Rd, mean number of rainy days; CV, coefficient of variation in Rn (%); n, years of observation (for Rn and CV); -, no reliable data

son. The three locations (SB, BG and AM) fall along a south to north gradient with increasing amounts and predictability of precipitation, as reflected in long-term observation data (Table 1). The MH location receives the highest amount of rainfall and is very predictable in both rainfall and also frost occurrence (no reliable data available, pers. observ.). These four environments represent both clinal (aridity) and discrete (frost) environmental effects that should be reflected in life-history differentiation if populations have evolved in their environments for sufficient time.

EXPERIMENTAL DESIGN

SEEDLING TRANSPLANT EXPERIMENT

An experiment to elucidate genotype-by-environment interactions was conducted in four locations during two consecutive years (1997/98 and 1998/99). Unfortunately, for the two extreme environments, MH and SB, we only have data from one year. The site on Mount Hermon (MH) was destroyed in 1997–98 by grazing cows and the Sede Boqer plot (SB) received too little rain in 1998–99 to let barley plants mature and produce seeds. At each site a 50–100 m² plot was fenced and cleared of vegetation either where the original population was collected (BG and MH) or in close proximity (500 m away at SB; 3 km away at AM). To minimize the effects of maternal and paternal environmental variation, we used the following method to generate seeds for this study: (1) seeds were collected from all field sites in a single year; (2) ten randomly selected field-collected seeds were germinated and grown under greenhouse conditions in a fully randomized design; (3) the 2-week-old self-progeny of ten mother plants composed the seedling pools that were transplanted in each environment within 2 weeks of the first 'effective' rain (>10 mm of rain). A randomized block design was established with each block containing plants from all four populations arranged as a lattice pattern of 4 × 4 plants, with 10 cm spacing. At seed maturity, we calculated the number of spikes per plant and number of spikelets (= seeds) in each spike. From this we estimated the total number of seeds per plant. We also collected 100–200 spikelets from each population/block and estimated the average spikelet weight per population/block, and the average plant reproductive biomass per population/block.

SEED INTRODUCTION EXPERIMENT

In addition to the seedling transplant experiment, in 1998/99, 400 barley spikelets collected from greenhouse-grown mother plants from each of the four populations were buried at each transplant site. A spikelet was placed in a separated cell of a plastic tray

filled with soil of the transplant environment. Two months after the first effective rains the trays were removed, brought to the laboratory and seeds classified as: (1) germinated and survived, (2) germinated and died, and (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, the fraction of non-germinated seeds represented two effects, infestation/infection of seeds and dormancy, that could be disentangled only in a long-term experiment. For this purpose, in 1999/2000 the non-germinated spikelets were buried again at the respective transplant sites and the procedure was repeated; this was repeated again in 2000/2001. The 2-month-old plants which developed from introduced seeds were dried and weighed.

DATA ANALYSIS

To determine the possible interactions between origin of seeds, site of transplanting and year (all fixed effects) we used a 3-way mixed-model ANOVA (BG and AM sites only), and the origin-by-transplant site interaction (both fixed effects) was analysed by a 2-way mixed-model ANOVA (all four sites). Block nested within site was added as a random effect to both models. This design generally followed that of Nagy & Rice (1997). Data required no transformation to satisfy the assumptions of normality and homoscedasticity. The Tukey–Kramer test was used for multiple comparisons across sites and populations.

The differences in germination and survival among populations within and across introduction sites in each of three consecutive years were tested by a χ^2

test. The association of site and origin was analysed by a test of independence.

To illustrate the ecotype fitness reaction norms, the corresponding fitness estimates (number of spikelets per plant, reproductive biomass, seed survival and mass of 2-month-old-plants) were standardized as relative performance. This was done by dividing each source population's mean response within each site by the maximum mean response seen for the plants from that population across any of the sites.

RESULTS

SEEDLING TRANSPLANT EXPERIMENT

All three main effects strongly affected plant fitness as estimated by yield (number of spikelets per plant) and reproductive biomass. They also had a highly significant impact on contributing to reproductive biomass spikelet weight (Table 2). Year of transplanting and its interaction with transplanting site, were important (Table 2). In AM and BG, the amount of rainfall was substantially higher in 1997/98 than in 1998/99 (657 and 357 vs. 348 and 149 mm, respectively), as was the yield and reproductive biomass of plants (Fig. 2).

The gradient of increasing mean annual rainfall from desert (SB) to batha (BG) and grassland (AM) environments was reflected in a significant increase in reproductive biomass (Fig. 2). A significant increase in yield and spikelet weight was observed from BG to AM. In all cases, the direction of change in trait values was an unambiguous increase from SB to AM. At MH, both fitness estimates were significantly different from SB and BG and similar to AM (Fig. 2).

Plant origin was the prevailing determinant of spikelet weight (as reflected in proportion of SS

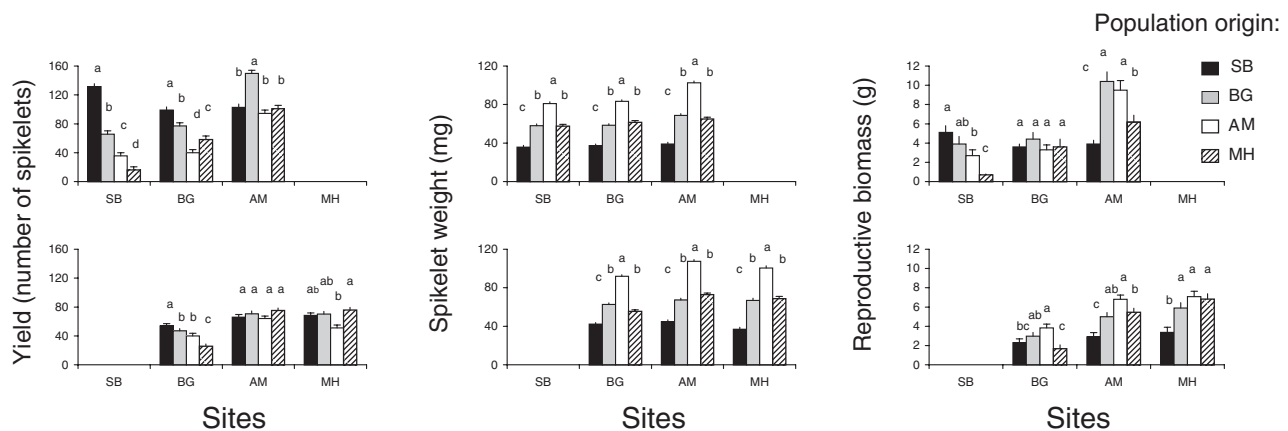


Figure 2. Major reproductive traits (means + SE) in each of four populations of wild barley reciprocally transplanted at four sites during season 1997/98 (above) and 1998/99 (below). Letters denote the results of Tukey–Kramer test comparing population values at each site.

Table 2. Three-way mixed-model ANOVA on the reproductive traits at the (a) BG and AM sites only, and (b) two-way mixed-model ANOVA on the reproductive traits at all four sites; block (nested within site) is a random effect. Average values for seed pools over 16 plants per population per block were used for spikelet weight and reproductive biomass, and individual plant values for number of spikelets per plant

Source	Number of spikelets per plant		Spikelet weight (mg)		Reproductive biomass (g)
	d.f.	F	d.f.	F	F
(a)					
Year	1	344.1***	1	10.0**	37.3***
Site	1	341.1***	1	45.7***	62.8***
Origin	3	50.7***	3	415.2***	20.6***
Year × site	1	20.0***	1	0.1 NS	9.9**
Year × origin	3	19.5***	3	1.9 NS	3.6*
Site × origin	3	30.6***	3	8.4***	10.0***
Block (site)	17	12.4***	16	1.6 NS	1.6 NS
Error	1994		101		
(b)					
Year 1997–98					
Site	2	15.4***	3	13.0***	40.0***
Origin	3	131.6***	3	516.5***	10.9***
Site × origin	6	48.3***	6	7.9***	10.9***
Block (site)	25	11.3***	20	4.1***	1.5 NS
Error	1614		59		
Year 1998–99					
Site	2	7.2**	2	10.6***	27.2***
Origin	3	6.3***	3	453.8***	21.9***
Site × origin	6	9.2***	6	6.7***	4.4**
Block (site)	24	11.8***	20	3.2***	2.0*
Error	1353		59		

Level of significance: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$; NS, not significant

explained) (Table 2). In all traits the effect of origin was highly significant suggesting that the variation in plant traits among sites had a substantial genetic component.

There were significant site-by-origin interactions in all traits studied (Table 2). The nature of these interactions can be observed in the norms of reaction for each population across environments (Fig. 2). In the 1997/98 season, the highest trait values for plants from BG, AM and MH populations were associated with the most productive and predictable environment (AM), and for plants from the SB population highest trait values were associated with its indigenous environment (SB) (Fig. 2). In 1998/99, plants of BG, AM and MH origin had similarly high trait values at AM and MH transplanting sites, but significantly smaller values at the BG site. SB plants exhibited this pattern in number of spikelets per spike and yield.

Although there was a strong origin-by-site interac-

tion for spikelet weight (Table 2), the differences between spikelets of different origin were consistent across transplant sites (i.e. reaction norms were not parallel but did not cross). In all transplant sites, AM plants had the heaviest spikelets, those of BG and MH plants were intermediate and spikelets from SB plants were the lightest (Fig. 2).

In summary, the following differences in fitness estimated by yield (number of spikelets per plant) were seen in plants of different origin over the 2 years among transplant sites: SB (desert) plants had the highest yield in the native environment and relatively high yield in the other three environments. MH (mountain) plants had the lowest yield in the SB environment, intermediate in BG and the highest yield in AM and their indigenous environment. Both BG and AM plants had their maximum fitness in AM and MH, decreasing through BG to SB (Fig. 2). The differences between plants from the extreme environments, SB

and MH, and plants from the most productive and predictable environments, BG and AM, became clear when fitness was estimated as reproductive biomass per plant: BG and AM did not differ from each other in any environment and were superior to the other two populations in the AM site in one year (Fig. 2).

SEED INTRODUCTION EXPERIMENT

Effects of origin and introduction site were substantial for both fitness components, viz. seed germination and seedling survival (Table 3). In the first year after introduction, the lowest percentage of seeds germinated and generally low survival of seedlings was observed at the SB site (range 6.1–36.0%). At the MH site, seedling survival dramatically decreased from MH to SB plants (range 5.1–74.6%). In contrast, at the BG and AM sites, seedling survival was uniformly high (range 83.0–99.7%). In the second year after introduction, the number of seeds germinated from those dormant in the previous season was high at the SB and AM sites compared with BG and MH, but this

difference was solely due to seeds of SB origin (19.7% and 13.0%, respectively).

There were also distinct differences in germination and survival pattern between seeds of different origin irrespective of introduction site. Among the four ecotypes, seeds of SB origin had the lowest fraction of germinated seeds in the first year after introduction. SB seeds had very low survival in the first year after introduction under conditions of low and unpredictable precipitation (SB) 17.1% and frosts (MH) (5.1%). In the other three ecotypes, percentage germination was higher and seedling mortality lower than in the SB ecotype. Two clear trends, possibly indicative of clinal differences, were observed at the MH site in the first year after introduction: an increase in germination fraction and a decrease in the mortality of germinated seeds from SB to MH ecotypes (Table 3).

The association of site and origin, analysed by a test of independence, was not significant for germination fraction in either the first or the second year after introduction ($\chi^2_{(9)} = 7.8$ and 17.3 , $P > 0.05$, respectively), but was highly significant for seedling survival in the

Table 3. Germination fractions and survival of germinated seeds (in percentage) over 3 years following reciprocal seed introduction and results of the χ^2 test of effect of origin for each site

Site/population	Germination fraction (%)			Survival of germinated seeds (%)		
	1998/99	1999/00	2000/01	1998/99	1999/00	2000/01
SB site						
SB	34.6	19.7	5.2	17.1	60.2	40.9
BG	61.6	3.7	0.2	36.0	71.4	0
AM	45.4	1.3	0	6.1	60.0	–
MH	64.7	0.8	0	35.7	100	–
χ^2	24.0***	40.5***	14.6**	35.8***	53.9***	202.8***
BG site						
SB	77.4	2.0	1.0	83.0	100	100
BG	86.3	2.1	0	90.3	100	–
AM	93.2	3.8	0	87.2	100	–
MH	89.2	0.9	0	83.1	100	–
χ^2	11.5*	1.9 NS	3.0 NS	3.1 NS		
AM site						
SB	78.7	13.0	0.2	98.2	100	100
BG	92.4	5.0	0	99.7	100	–
AM	88.2	5.7	0	98.7	100	–
MH	93.6	2.8	0.7	99.5	91.7	100
χ^2	13.3**	9.6*	1.4 NS	1.5 NS	25.4***	
MH site						
SB	73.1	1.3	1.3	5.1	0	0
BG	76.9	1.0	0	37.2	0	–
AM	87.2	0.9	0	60.2	0	–
MH	91.0	2.6	0	74.6	0	–
χ^2	14.2**	1.2 NS	3.4 NS	111.8***		

Level of significance: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$; NS, not significant

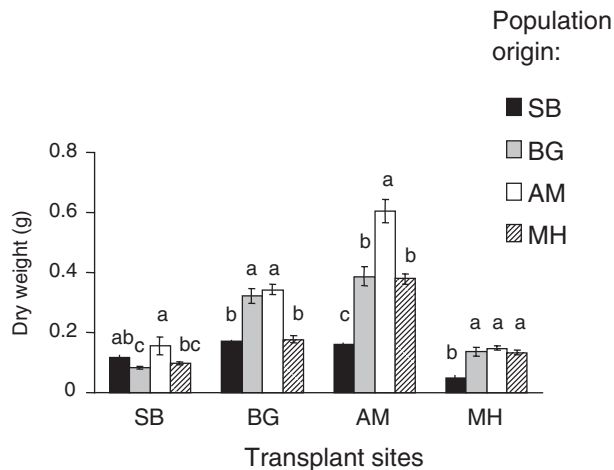


Figure 3. Weight of 2-month-old plants of different origin compared in each transplant site by Tukey–Kramer test.

first year after introduction ($\chi^2_{(9)} = 94.9$, $P < 0.001$) (Table 3).

Comparison of the dry weight of 2-month-old plants showed highly significant variation among introduction sites ($F_{3,2830} = 43.2$, $P < 0.001$) and less dramatic but significant effects of origin and origin-by-site interaction ($F_{3,2830} = 6.3$, $P < 0.001$ and $F_{9,2830} = 6.7$, $P < 0.001$, respectively). In the extreme environments, i.e. SB and MH sites, the biomass of plants was substantially lower than in the less stressful environments (BG and AM) (Fig. 3). SB plants had significantly lower biomass than plants from the other populations in all introduction sites except the SB site (Fig. 4). AM plants had higher biomass than other plants in the AM site; BG and AM plants had the highest biomass in the BG site. Three populations (BG, AM and MH) exhibited similar reaction norms in weights of young plants across four environments (Fig. 3). Plants of SB origin had low biomass irrespective of introduction site.

DISCUSSION

LOCAL ADAPTATION

We observed significant genotype-by-environment interactions for two measures of *H. spontaneum* fitness (yield and reproductive biomass). Plants originating in the two environmental extremes (SB and MH) clearly exhibited an increase in both yield and reproductive biomass in their own environments. A significant increase in both fitness traits in the most favourable environment (AM) was detected for plants originating in the two productive habitats with no obvious abiotic stress present (BG and AM). These trends, pronounced in the season 1997/98, were blurred somewhat in the extremely dry 1998/99 years

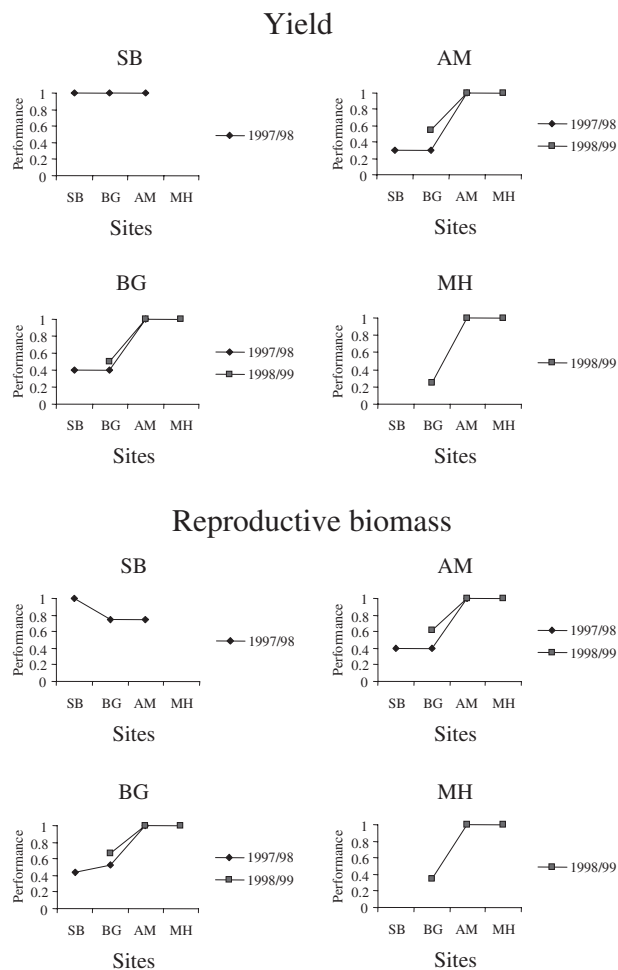


Figure 4. Standardized fitness reaction norms of four ecotypes across environments assessed by yield and reproductive biomass. Steepness of the slope shows the magnitude of ecotype plasticity.

when differences in productivity among sites became reduced.

Another fitness component, seedling survival, also showed dependence on both origin and locality. The superiority of the local ecotype and decreasing fitness rank from indigenous mountain ecotype towards the environmentally dissimilar desert ecotype was observed at the MH site (Table 3).

There was also a significant genotype-by-environment interaction for weight of young (2-month-old) plants. Plants originating from non-stressed favourable environments (BG and AM) had a significant decrease in biomass in both stressed environments (SB and MH) compared with their indigenous environments.

The observed pattern of ecotype fitness reaction norms across environments provides strong support for the specialization hypothesis for phenotypic plas-

ticity in plants (Taylor & Aarssen, 1988) as expanded by Lortie & Aarssen (1996). These authors distinguished character plasticity (i.e. plasticity for physiological, morphological or resource allocation traits) from fitness plasticity (i.e. plasticity for traits estimating fitness such as plant size, reproductive biomass or fecundity). In Lortie and Aarssen's view, plasticity in the latter traits represents not an 'adaptive alternative to specialization but rather, a product of specialization'. This means that the apparent lack of cost of specialization (i.e. when an ecotype does not exhibit poorer performance in an alien habitat), does not negate specialization itself (i.e. relatively good performance in its indigenous habitat). Moreover, Lortie & Aarssen (1996) proposed that in the process of adaptation to the more favourable end of an environmental gradient, selection should foster an increase in fitness plasticity across habitats, whereas specialization to the less favourable end would decrease this plasticity. Both predictions were supported in our study when yield or biomass estimated fitness. The ecotype from the poorest environment (desert) showed phenotypic stability in yield (Fig. 4) and lowest plasticity in reproductive biomass and total weight of juveniles among other ecotypes (Figs 4 and 5). In contrast, the fitness reaction norm of the desert ecotype was the most plastic among ecotypes when estimated in terms of survival of seeds after dispersal (Fig. 5). Low seed survival appears to be a cost by which relatively high yield is achieved under less favourable conditions (fitness trade-off), and constitutes a part of an adaptive strategy.

PLANT STRATEGIES AS DETECTED BY RECIPROCAL INTRODUCTIONS

The effectiveness of reciprocal introduction studies in detecting local adaptation has been well documented (Turesson, 1922; Clausen *et al.*, 1940, 1948; Davies & Snaydon, 1976; McGraw & Antonovics, 1983; Schmidt & Levin, 1985; Nagy & Rice, 1997; Wang *et al.*, 1997). However, the use of reciprocal introductions to generalize the observed intra-environmental variation into sets of coadapted traits (strategies) is limited because of the following:

1 The inter-environmental variation (reaction norm) may have a genetic component due to both the evolution of macro-environmental population differences, and also micro-environmental selection within local populations (Turkington & Harper, 1979; Fowler & Antonovics, 1981; Linhart, 1988).

2 The large number of selective forces, their different combinations and interactions in each local environment may obscure the general trends in trait changes along environmental gradients (Schlichting & Pigliucci, 1998).

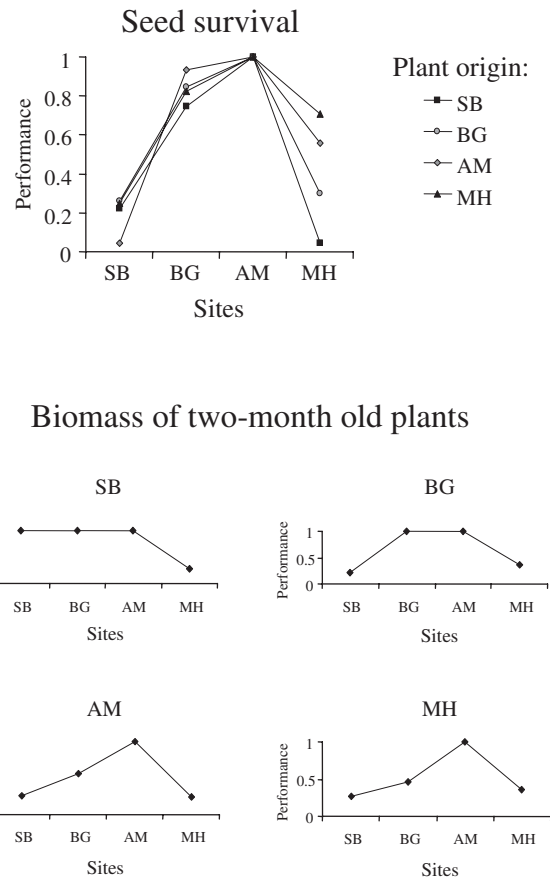


Figure 5. Standardized fitness reaction norms of four ecotypes across environments assessed by survival of seeds over a 3-year period after dispersal (upper figure) and total biomass of 2-month-old plants (lower figures). Steepness of the slope shows the magnitude of ecotype plasticity.

Nevertheless, the results of reciprocal seed and seedling introductions across four environments allow us not only to make certain inferences about specific environmental effects on life-history and reproductive traits, but also to draw parallels with previously recognized selection types and resulting plant 'strategies'. High environmental productivity and predictability without the concomitant frost stress effect (AM and BG sites) was found to select for high reproductive biomass and large seeds, high fraction of germinating seeds and high vigour of seedlings, consistent with a K-selection type (*sensu* MacArthur & Wilson, 1967). At the MH site, frost is a predictable and inescapable stress factor on *H. spontaneum*. Such stress was hypothesized to select for a stress-tolerant strategy (Grime, 1977; Greenslade, 1983). No specific life-history adaptations of the mountain ecotype were detected in our study. However, higher survival of MH seedlings in their indigenous environment compared with other ecotypes appears to be the result of a phys-

iological adaptation to frost. This is consistent with the stress (S-) (*sensu* Grime, 1977) or adversity (A-) (*sensu* Greenslade, 1983) selection type.

Another stress factor, drought, is very unpredictable in deserts and depends on both total amount of rainfall in a season and on the distribution of rain events during a season. An escape, or stress avoidance, strategy is described in 'bet-hedging' and similar concepts (Cohen, 1966; Stearns, 1976; Seger & Brockmann, 1987). The main feature of this strategy is delayed germination of some seeds in order to reduce temporal variance in individual fitness of plants. We found the fraction of seeds germinated in the second year after plant maturation to be significantly higher for the desert ecotype compared with the other three ecotypes. Other features found in this study associated with this strategy are small seed size and low vigour of seedlings, but relatively high yield. Cavieres & Arroyo (2001) reported an increasing proportion of seeds remaining dormant after dispersal as environmental unpredictability increased for populations of the perennial *Phacelia secunda* in the Mediterranean Andes of Chile. The fact that the gradient of climate unpredictability in the Andes increases with altitude towards the alpine environment (the opposite direction to that of elevated areas of Israel) enhances our conclusion of a selective role of unpredictability *per se*. Our findings are also consistent with those reported by Nardini *et al.* (2000) for two populations of *Quercus ilex* exposed to drought (Sicily) and freezing stress (Venezia Giulia). In that study, *Q. ilex* was found to exhibit two different resistance strategies, viz. tolerance of freezing stress and avoidance of drought stress.

It is interesting to trace the changes in fitness and fitness-related traits along the two inverse gradients of environmental productivity (amount of annual rainfall) and unpredictability (inter- and intra-seasonal variation in rainfall) without considering MH. Environmental productivity and unpredictability seem to induce two alternative evolutionary pathways evolving: (1) seed size and, as a result, survival and vigour of seedlings, and (2) the number of seeds produced. The SB and AM populations are representative of these two pathways, with numerous small seeds vs. few large seeds, respectively. BG plants, originating in an environment intermediate between SB and AM with respect to productivity and unpredictability, are between these two extremes. The same pattern was observed in an annual grass *Avena sterilis* sampled in the same four environments and studied using the same methodology (S. Volis, unpubl. data). The similarity in the observed pattern strongly suggests generality of the pathways detected.

A negative correlation between seed mass and number is not a new phenomenon (see van Groenendaal,

1985; Lalonde & Roitberg, 1989; McGinley, 1989), although it is only one of many choices for resource allocation in plants (Harper, Lovell & Moore, 1970; Harper, 1977; Bazzaz *et al.*, 1987). However, our study describes the dynamics of this relationship across an environmental gradient of productivity–unpredictability as a part of plant strategies. An optimal strategy with increasing productivity and predictability is reduced yield but increased seed mass, while an optimal strategy with decreasing productivity and predictability is increased yield and decreased seed mass.

These findings emphasize the importance of seed size as a part of a plant's strategy. The advantage of large seed size is that it provides for high seedling vigour, higher probability of seedling establishment and transition to adulthood, often with competitive superiority over smaller-seeded forms (Gross, 1984; Stanton, 1984a,b; Foster, 1986; Choe *et al.*, 1988). However, large seed size may trade-off with lower persistence in the seed bank (Gross & Smith, 1991; Baskin & Baskin, 1998). This trade-off can be explained by the opposing directions of selection for optimal seed size in predictable and productive vs. unpredictable and unproductive environments.

ACKNOWLEDGEMENTS

We thank Mark Rubin and Rina Offenbach for help with establishing transplant sites, Asya Ostrovsky, Eugene Dreyer, Vladimir Faitelson, Konstantin Vofsi and Leonid Strelko for field work, and Ruti Soto for 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 357 of the Mitrani Department for Desert Ecology.

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