

## Life history variation in an annual plant under two opposing environmental constraints along an aridity gradient

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Petrů, M., Tielbörger, K., Belkin, R., Sternberg, M. and Jeltsch, F. 2006. Life history variation in an annual plant under two opposing environmental constraints along an aridity gradient. – *Ecography* 29: 000–000.

Environmental gradients represent an ideal framework for studying adaptive variation in the life history of plant species. However, on very steep gradients, largely contrasting conditions at the two gradient ends often limit the distribution of the same species across the whole range of environmental conditions. Here, we study phenotypic variation in a winter annual crucifer *Biscutella didyma* persisting along a steep gradient of increasing rainfall in Israel. In particular, we explored whether the life history at the arid end of the gradient indicates adaptations to drought and unpredictable conditions, while adaptations to the highly competitive environment prevail at the mesic Mediterranean end. We examined several morphological and reproductive traits in four natural populations and in populations cultivated in standard common environment. Plants from arid environments were faster in phenological development, more branched in architecture and tended to maximize reproduction, while the Mediterranean plants invested mainly in vertical vegetative growth. Differences between cultivation and field in diaspore production were very large for arid populations as opposed to Mediterranean ones, indicating a larger potential to increase reproduction under favorable conditions. Our overall findings indicate two strongly opposing selective forces at the two extremes of the aridity gradient, which result in contrasting strategies within the studied annual plant species.

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Widely distributed plant species are often exposed to a broad range of environmental conditions (Joshi et al. 2001). In order to persist in different environments, plants often vary considerably in their life history and the expression of morphological traits. This phenotypic variation may be due to plasticity, or genetically determined ecotypic differentiation (Clausen et al. 1940, Schilchting 1986, Dudley and Schmitt 1995).

Environmental gradients provide a useful framework for evaluating the relative importance of differential selection for adaptive traits maximizing species fitness (Lande 1977, Endler 1986). For example, extensive

work has been done along environmental gradients looking at shifts in phenology, growth and sexual reproduction (Hauser and Weidema 2000, Olsson and Agren 2002, Stinson 2004), reproductive allocation (Callahan and Waller 2000, Sugiyama 2003), and phenotypic plasticity and genetic variation (Fritsche and Kaltz 2000, Galloway and Fenster 2000, Joshi et al. 2001, Volis et al. 2001, 2002a, b, c, d, Santamaria et al. 2003, Casler et al. 2004). These studies covered a wide range of spatial scales (from local and regional to a global scale) and a range of environmental conditions.

Accepted 17 June 2005

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ISSN 0906-7590

Optimally, the environmental gradients should include a wide range of conditions in order to allow the detection of clear patterns of phenotypic or genetic differentiation. Therefore, many previous studies have been conducted across relatively large spatial scales (Hauser and Weidema 2000, Galloway and Fenster 2000, Santamaria et al. 2003, Casler et al. 2004). However, if the gradient is too steep, studies of trait variation may be hampered by the fact that only few species may persist along the whole spectrum of environmental conditions. Another shortcoming of large-scale gradient studies is that habitat conditions are very likely to differ in many different aspects, and confounding of the environmental factor of interest with other factors becomes more likely (Sugiyama 2003, Santamaria et al. 2003, Casler et al. 2004).

Several studies, so far, have focused on climatic gradients (Volis et al. 2001, 2002a, b, c, d, Olsson and Agren 2002, Del Pozo et al. 2002a, b, Sugiyama 2003, Santamaria et al. 2003). Yet, only scarce data exist on climatic gradients, which occur over a relatively short geographic distance. This is unfortunate, since first, climate is one of the most important factors determining the geographical distribution and abundance of plant species (Woodward 1987), and secondly, such gradients represent an ideal case for studying adaptive shifts in traits within a given species. In particular, rainfall gradients have only been investigated by a limited number of researchers (Aronson et al. 1990, 1992, 1993, Volis et al. 2001, 2002a, b, c, d, Del Pozo et al. 2002a, b). Climate gradient studies further increase in significance as the degree of local adaptation of plants to climatic conditions may determine the vulnerability of species to climate change (Rehfeldt et al. 2002).

In summary, the above studies emphasize the need for studying adaptive variation in plant life history traits to a variety of climatic conditions. Here, we evaluate the phenotypic performance of an abundant eastern Mediterranean annual plant species along a steep climatic gradient, which varies both in amount as well as predictability of water availability. The abiotic conditions represent two opposing environmental constraints at the two extremes of the gradient, which should generate distinct plant responses. Specifically, at the arid end of the precipitation gradient, rainfall events are highly fluctuating and unpredictable from one year to the next. Adaptation to such conditions results often in great plasticity in plant size and phenological development (Went 1949, Lewontin 1957, Levins 1963, Jain 1978, Evenari et al. 1982, Aronson et al. 1990). For example, it has been found that arid ecotypes reproduce earlier and produce more diaspores per plant biomass than conspecific plants growing under more humid conditions (Aronson et al. 1990, Volis et al. 2002a), since the shorter growing season and the unpredictability of environmental conditions requires fast development

and rapid response to episodic rainfall. At the Mediterranean end of the gradient, climatic constraints are less prominent but neighbor densities are much higher (Holzapfel et al. pers. comm.). Therefore, the main environmental constraint is most likely the density of neighboring plants, and shifts in plant life history traits towards the wet end of the gradient should reflect competitive ability. This expectation is in concordance with the theory of Grime (1973a, b, 1977), who predicted dominance of superior competitors at the favorable end of productivity gradients. Specifically, plants growing under more productive conditions should invest more into survival under intense neighbor competition rather than to fast reproduction and allocate more biomass into vegetative growth (Aronson et al. 1993, Nachreiner 2005). According to Newman (1973) and Tilman (1988), it is mainly above-ground competition intensity which increases along productivity gradients. Therefore, vegetative investment at the wet end should be predominantly into shoot mass and height, rather than into below-ground biomass.

Morphological, phenological and reproductive traits have been previously compared between two contrasting extremes – arid and humid – on Eastern Mediterranean climatic gradients for a number of species (Aronson et al. 1990, 1992, 1993). However, little is known whether the observed differences between the studied populations change gradually along the gradient. Such gradual and directional change would be a strong indication for adaptive variation. In the notable exception, where rigorous tests were done on adaptive plant trait variation across a steep climatic gradient, the rainfall differences were confounded with between-site differences in presence of frost, topographic position, and bedrock (Volis et al. 2001, 2002a, b, c, d).

Here, we explore variation in phenotypic traits of an annual plant species, the crucifer *Biscutella didyma*. Specifically, we search for trends in trait variation reflecting the changes of rainfall along a steep climatic gradient in Israel. These trends are studied both under natural conditions as well as in a standard environment, for evaluating natural (i.e. in situ) vs genetically based differences between the climatic populations (see Clausen et al. 1940, Hauser and Weidema 2000). We focus on growth morphology and architectural traits, phenological shifts and changes in allocation patterns, and their relation to the opposing environmental conditions along the gradient.

In particular, we test the following hypotheses: 1) Plant morphology shifts from small, dense plants in the arid region to tall, loosely branched plants in the Mediterranean region. 2) Reproductive allocation decreases from the arid to the Mediterranean populations. 3) Onset of flowering and completion of the life cycle is faster for arid than for Mediterranean populations. 4) Differences between optimal conditions in cultivation

and conditions in the field result in large positive response of desert populations to the cultivation and small response of Mediterranean populations.

## Methods

### Study species

*Biscutella didyma* (further referred to as *Biscutella*) is a winter annual crucifer. Under natural conditions, the plant grows 15–50 cm high and it has 5–10 radical leaves and several fruiting branches. Fruits are double silicles fragmenting easily, and dispersing when ripe (further referred to as diaspores). The species has a Mediterranean and Irano-Turanian distribution and occurs in a wide range of habitats from dwarf shrublands, fallow fields, steppes and deserts (Zohary 1966).

### Study system

We studied *Biscutella* populations from four stations on similar bedrock and exposition, located along a S–N oriented gradient of increasing rainfall in Israel (further referred to as an arid, semi-arid, Mediterranean and mesic Mediterranean, Table 1). In these stations, the growing season responds to the distribution of rainfall, and germination of annuals and re-growth of most perennials occurs in October–November, soon after first major rains (ca 10–20 mm). The length of the rainy season increases from the desert (December–March) to the Mediterranean (October–May).

### Plant cultivation

In June 2002, we collected ripe *Biscutella* diaspores from ca 300 randomly selected individuals in each of the natural populations. Previous trials have indicated that oversummering in the field is the optimal method for naturally breaking seed dormancy. Therefore, we stored the fresh diaspores from May to September 2002 in the respective field stations, in bags made from organza (light transparent synthetic fabric), which we attached to the ground surface. In September 2002, we collected the bags in the field and transferred them to a laboratory for counting diaspores into equal portions. At the end of November 2002, we planted the diaspores in pots (7 × 7 cm × 15 cm deep) filled with a mixture of garden soil and sand (2:1) with added one handful of Osmocot Scott® fertilizer (15% N, 9% P<sub>2</sub>O<sub>5</sub>, 9% K<sub>2</sub>O) per 15 l soil mixture. We planted ca 30 diaspores in each pot to assure substantial germination. A week after the bulk germination, we thinned seedlings randomly to one seedling per pot. We placed the pots in a screen-house at the Botanical Garden at Tel Aviv Univ. (further referred

Table 1. Environmental conditions at four stations with *Biscutella* populations on a S–N oriented rainfall gradient in Israel.

Station	Latitude	Longitude	Location	Altitude (m)	Avg temp (°C)	Geology and soil	Avg rainfall (mm)	Rainfall 2001/2002 (mm)	Rainfall 2002/2003 (mm)	Vegetation description
Arid	30°52'N	34°46'E	north of Sde Boger (central Negev)	470	19.1	limestone and desert Lithosol	90	100	86	annuals and small shrubs: <i>Zygophyllum dumosum</i> , <i>Artemisia sieberi</i>
Semi-arid	31°23'N	34°54'E	northeast of Lahav (northern Negev)	590	18.4	limestone and Brown Rendzina	300	305	342	dwarf shrubland: <i>Sarcopoterium spinosum</i> , <i>Thymelea hirsuta</i> , <i>Coridothymus capitatus</i> and annuals
Mediterranean	31°42'N	35°03'E	south of Mattia (Jerusalem Mts) east of Ein Ya'akov (northern Galilee)	620	17.7	limestone, hard chalk and Terra Rossa	540	736	795	dwarf shrublands: <i>S. spinosum</i> and annuals
Mesic Mediterranean	33°00'N	35°14'E		500	18.1	limestone, hard chalk and Terra Rossa	780	905	1031	Mediterranean maquis to garrigue: <i>Calicotome villosa</i> and annuals

to as cultivation) under identical light and water regime, where we kept them until the end of the experiment, randomizing the pot position three times during the course of the experiment. Except for rainy days, plants got irrigated daily with an automatic irrigation system, so that growth was unlikely to be water-limited. Shortly before the onset of flowering, we prevented cross-pollination by fully isolating the populations in organza enclosures constructed around the flowering plants grouped by station (all plants from one station under one enclosure). We hand-pollinated flowers within each station to standardize pollination success and to maximize diaspore production, and kept plants in cultivation irrigated until all plants from all the stations finished completely with flowering and produced ripe (brown) diaspores.

### Morphological traits

We quantified growth morphology and plant architecture of 24 individuals per *Biscutella* population both in the field and under cultivation (also referred to as field and cultivated groups). In the field, we randomly marked 24 individuals from the wild populations; in cultivation we used all potted plants. Due to plant loss and damage (especially in cultivation), and due to early diaspore dispersal, sample sizes were not equal for all parameters (see Table 2). We measured plant height during diaspore maturation when the first diaspores on a given plant began drying out and we evaluated plant growth by using plant height as a nondestructive measure for biomass. Parallel trials indicated that height is highly correlated with total plant biomass (Schiffers 2003). We used these nondestructive measurements since we harvested the ripe diaspores and therefore, could not harvest the plants. We further counted number of fruiting stems (the main stem bearing fruits and all branches with fruits) during diaspore maturation. We defined plant “growth architecture” as number of fruiting stems per plant height, with many branches per height reflecting a more compact architecture and few branches defining a loose shape.

Table 2. Results of ANOVAs for parameters of plant performance in cultivation and in the field (separate ANOVAs) comparing the four populations (A = arid, SA = semi-arid, M = Mediterranean and MM = mesic Mediterranean). Note the different sample sizes (=N) within groups for the various parameters and the unbalanced design for ANOVAs in few groups.

Parameters	Conditions N	Cultivation (DF = 3)		Field (DF = 3)	
		F	p	F	p
Height	24	65.2	<0.001	22.8	<0.001
Fruiting stems	20	18.8	<0.001	0.3	0.787
Fruiting stems/height	16	1.5	0.229	32.6	<0.001
Number of diaspores	f: 8, c: 7 A; 8 SA, M; 5 MM	6.2	0.003	3.4	0.032
Diaspore diameter	20	37.2	<0.001	11.3	<0.001
Diaspores/height	f: 8, c: 7 A, M, MM; 6 SA	17.2	<0.001	0.7	0.556

### Fitness-related traits

To evaluate reproductive output in cultivated and field groups, we counted number of diaspores per plant prior to dispersal, i.e. when fruit maturation began and all diaspores were still attached to the fruiting stems. We harvested all ripe brown diaspores from plants both in cultivation and in the field and measured the diaspore diameter of a subset of plants in both growth conditions. A previous study has indicated that diaspore diameter and weight are good surrogates for diaspore quality (Schiffers 2003). We estimated reproductive allocation as the number of diaspores produced per unit plant height. We further documented phenology (dates of first flowering and end of fruiting) in cultivation and in the field.

### Data analyses

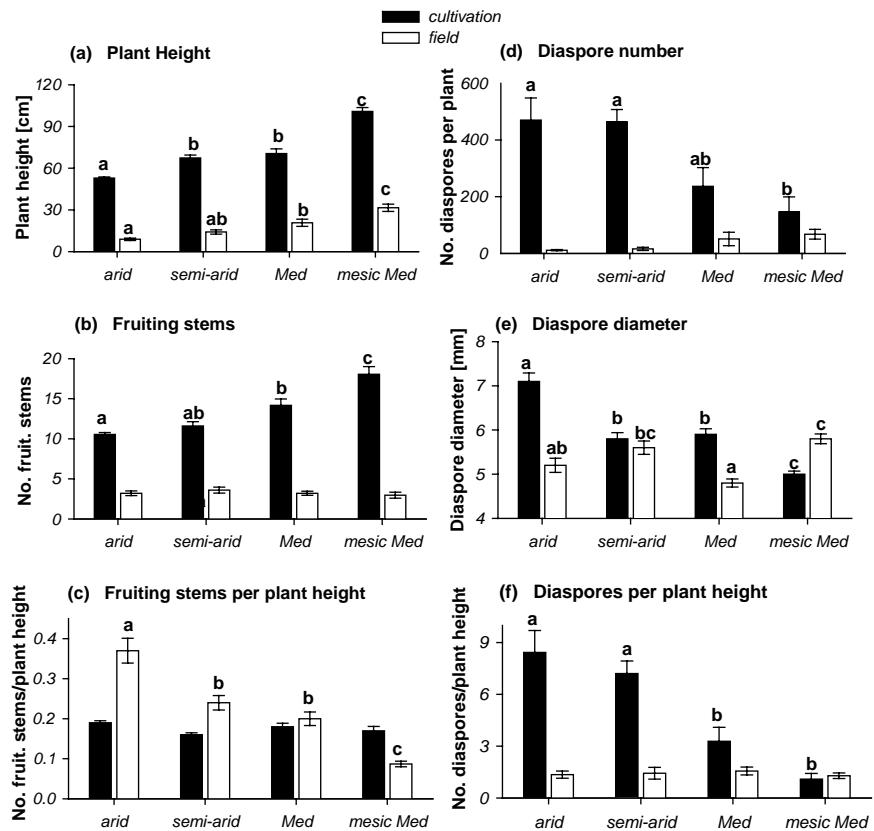
We analyzed the differences between populations for all parameters using one-way ANOVAs separately for the populations in cultivation and in the field. Due to plant loss and damage in cultivation and due to time constraints, our sample sizes for number of diaspores and diaspores per plant height were unbalanced. We run unbalanced design ANOVAs with small sample sizes including all available data (see Underwood 1997). Tukey's post-hoc tests compared pairwise differences in population means within the cultivated and field groups. All data conformed to the assumptions of ANOVA without transformation. We further compared the parameters of plant performance in single populations under cultivation vs. in the field pairwise using separate t-tests with Bonferroni adjusted significance level to 0.0125 (Sokal and Rohlf 2000).

## Results

### Growth and plant architecture

Both field and cultivated populations showed a clear and significant trend of gradually increasing plant sizes along the gradient (Fig. 1a, Table 2). The cultivated plants in

Fig. 1. Architectural and fitness parameters of four populations of *Biscutella didyma* under common (cultivation) and field conditions (arid, semi-arid, Mediterranean (Med) and mesic Mediterranean (mesic Med); (a) plant height, (b) number of fruiting stems, (c) number of fruiting stems per plant height, (d) diaspore number, (e) diaspore diameter, and (f) diaspore number per plant height. Mean values  $\pm 1$  SE. Different letters above error bars indicate significant differences among populations within a given treatment (cultivation vs field, Tukey's test,  $p < 0.05$ ).



all populations were 2 to 3 times larger than the plants in the field (Fig. 1a). The relative increase in plant size from arid to mesic Mediterranean was greater in the field (3-fold) than in cultivation (Fig. 1a). Cultivated plants produced significantly more fruiting stems in cultivation compared to the field in all populations (Fig. 1b, Table 3), with an increase towards the wet end of the gradient, while field populations did not differ in their number of fruiting stems (Fig. 1b, Table 2). The growth architecture, i.e. the number of fruiting stems per plant height, showed divergent patterns in the different growth conditions (Fig. 1c, Table 2, 3). Field plants had significantly more fruiting stems per plant height (i.e. a

more tight architecture) in the arid region, declining towards mesic Mediterranean (Fig. 1c, Table 2). This morphological difference disappeared under common growth conditions in cultivation (Fig. 1c, Table 2). Note that the field populations showed a similar number of fruiting stems (Fig. 1b, Table 2) and the differences in fruiting stems per plant height among the field populations were mainly correlated with plant height (Fig. 1a). In the cultivated plants, the fruiting stem number and plant height increased proportionally and the fruiting stem per plant height was constant across the different populations (Fig. 1c).

Table 3. Results of t-tests for parameters of plant performance comparing single populations in cultivation vs in the field. Pairwise difference tested with Bonferroni adjusted significance level (0.0125). Note the different sample sizes within populations for the various parameters.

Population	Arid			Semi-arid			Mediterranean			Mesic Mediterranean		
	DF	t	p	DF	t	p	DF	t	p	DF	t	p
Height	46	35.7	<0.001	46	20.9	<0.001	46	11.6	<0.001	46	18.0	<0.001
Fruiting stems	38	17.0	<0.001	38	12.5	<0.001	38	12.0	<0.001	38	12.6	<0.001
Fruiting stems/height	30	5.4	<0.001	30	3.8	<0.001	30	1.0	0.320	30	6.5	<0.001
Number of diaspores	13	6.3	<0.001	14	10.3	<0.001	14	2.7	0.019	11	1.7	0.117
Diaspore diameter	38	7.7	<0.001	38	0.7	0.447	38	6.6	<0.001	38	5.5	<0.001
Diaspores/height	13	5.9	<0.001	12	7.8	<0.001	13	1.8	0.090	13	2.0	0.063

## Fitness-related traits

Diaspore number was significantly higher in the cultivated plants compared to the field in the arid and semi-arid regions (Fig. 1d, Table 2, 3). Diaspore number of cultivated plants declined significantly from the arid towards the mesic Mediterranean (Fig. 1d, Table 2), but increased the opposite direction in the field. Despite the overall significant population difference, there were no pairwise significant differences among the field populations (Fig. 1d). Cultivated plants produced larger diaspores than plants in the field, except the semi-arid population (Fig. 1e, Table 2, 3) and diaspore diameter followed a declining trend from the arid towards the mesic Mediterranean. In field populations, diaspore diameter varied non-directionally (Fig. 1e, Table 2). The diaspore number per plant height showed a sharp decline from the arid towards the mesic Mediterranean in cultivation, but was indifferent in the field (Fig. 1f, Table 2, 3).

## Phenology

There were marked phenological shifts in timing of flowering along the climatic gradient. Arid populations both in the field and in cultivation began flowering earlier in the season both in the field as well as under common growth conditions. Onset of flowering gradually progressed to semi-arid, Mediterranean and mesic Mediterranean populations (Table 4). In the cultivated plants, first flowering occurred with intervals of 8–10 d between each of two neighboring populations along the gradient (Table 4). The favorable conditions in the cultivation extended the length of the reproductive period (from the first flowering until no more flowering occurred and all diaspores were set) compared to the field, and the reproductive period prolonged from the arid towards the mesic Mediterranean region, especially in the cultivation (Table 4). In the field this period lasted 40, 62, 56 and 54 d (arid – mesic Mediterranean respectively), while in the cultivation it was 63, 92, 98 and 99 d, Table 4).

## Discussion

In this study, we found distinct directional trends in growth morphology, architecture, and fitness-related traits across four populations of the winter annual crucifer *Biscutella didyma* growing along a steep rainfall gradient in Israel. Based on our comparison of trait variation between field and common environments, we suggest that these trends may be genetically based (Turesson 1922, Clements et al. 1950, Langlet 1971, Rehfeldt et al. 1999, 2002 and Hauser and Weidema 2000). Our findings confirm recent findings on directional phenotypic variation of multiple plant species in the same system (Nachreiner 2005) and complement Aronson et al.'s findings (1990, 1992, 1993) of contrasting trait values on the two extreme edges of a different rainfall gradient in the region. We thus empirically support previous theoretical work suggesting that life history traits should vary in a clinal fashion along continuous gradients with gradually changing environmental factors (Cooper 1963, Weber and Schmid 1998, Li et al. 1998, Rehfeldt et al. 1999).

Selective forces for traits maximizing species fitness have been documented to change along gradients (Hickman 1975, Aronson et al. 1992, 1993). Our findings indicate that in our system, there are two major selective forces which are negatively correlated and which shift simultaneously and steadily along the climatic gradient. The first force, which apparently dominates the wet end of the gradient, is competition. The second force, which prevails at the arid end, is scarcity and unpredictability of rain. In the following, we discuss how our results relate to our hypotheses of these two opposing forces.

## Competition

There has been an intensive debate about whether competition intensity increases along productivity gradients (Grime 1973a) or whether it stays constant (Newman 1973, Tilman 1988). Though this so-called Grime-Tilman conflict is far from being resolved, both theories agree that above-ground competition is more intense at the favorable end of a resource gradient. Therefore, we hypothesized that shifts in traits towards

Table 4. Dates of the first flowering and dates of the end of fruiting (no more flowering and all diaspores set) of *Biscutella didyma* from the four stations Arid (Sde Boqer), Semi-arid (Lahav), Mediterranean (Matta) and Mesic Mediterranean (Ein Ya'akov) in the cultivated and field groups (data from field stations according to Holzapfel and Parag pers. comm.). Plants in cultivation were irrigated from 20 November 2002. First effective rain in the field (ca 10 mm), after which germination occurred.

Plant population	First flowering in cultivation	End of fruiting in cultivation	First flowering in the field	End of fruiting in the field	First rain in the field
Arid	19 Jan 2003	24 Mar 2003	4 Feb 2003	16 Mar 2003	9 Dec 2002
Semi-arid	27 Jan 2003	29 Apr 2003	8 Feb 2003	11 Apr 2003	31 Oct 2002
Mediterranean	6 Feb 2003	15 May 2003	18 Feb 2003	15 Apr 2003	9 Dec 2002
Mesic Mediterranean	17 Feb 2003	27 May 2003	2 Mar 2003	25 Apr 2003	12 Nov 2002

the Mediterranean should reflect adaptations to above-ground competition. Our findings corroborate this hypothesis in two aspects. First, plant architecture changed from small, compact plants in the arid regions to tall, loosely branched plants in the Mediterranean region, where biomass, height and density of neighbors are relatively high (Holzapfel et al. pers. comm.). Secondly, there were differences in reproductive allocation, which can be related to changes in competition intensity. It has been suggested that Mediterranean plants should be selected to cope with competition with neighbor plants (Shmida et al. 1986, Shmida and Burgess 1988) and consequently, are “programmed” for relatively greater allocation to vegetative growth at the expense of lower reproductive output (Weiner 1988). Results of our study fully support this prediction, as our cultivated plants exhibited a dramatic decrease in reproductive allocation from the arid to the Mediterranean.

## Climate

Climatic differences between the arid and the humid end of the gradient do not only include the average amount of annual rainfall but more important, the rainy season is much shorter in the arid region and availability of water is highly variable and unpredictable between years.

Adaptive shifts in timing of flowering are known to occur in annuals along longitudinal and altitudinal climatic gradients and have been related to the length of the growing season (Turesson 1922, Ray and Alexander 1966, Lacey 1986, Li et al. 1998, Callahan and Waller 2000, Olsson and Agren 2002). In our system, rains start usually later and finish earlier in the arid region compared to the Mediterranean (Shmida and Burgess 1988), resulting in a much shorter growing season. Therefore, we hypothesized that desert annuals would flower earlier and accomplish their life cycle faster, according to the “living fast and dying young” principle (Aronson et al. 1990, 1993). The flowering schedule observed in our study confirmed this hypothesis: plants began flowering earlier in the arid region and progressed towards the Mediterranean. Interestingly, this pattern was stable even under varying onset of rain. Flowering phenology was similar across populations both in cultivation as well as in the field, indicating that this behavior may be genetically determined (Turesson 1922, Clements et al. 1950, Langlet 1971, Hauser and Weidema 2000).

The largest constraint on long-term persistence of plants in the desert is the high and unpredictable variation in resource availability (water). A major mechanism which allows annual plants to persist even after years with no reproduction is the maintenance of a persistent seed bank (Cohen 1966). In addition, plants

may develop strategies, which enable them to maximize the fitness gain from an occasional favorable season. For example, theory predicts that in low-density areas, such as our arid site, plants should allocate much more to reproduction in order to be able to maximize reproductive output as soon as the environment allows it (Levins 1963, Jain 1978). Therefore, the pattern we have found here, with high reproductive allocation towards the arid populations, may be explained similarly by the two selective forces competition and climate.

Another strategy which helps to cope with the unpredictability of favorable years is to maximize reproduction during good years and to “store” these fitness gains in the between-year seed bank during unfavorable years. Therefore, we would expect that desert populations would exhibit a larger potential to rapidly respond to varying rainfall conditions than Mediterranean ones. In order to test this prediction, we need to compare our findings from the field and the cultivation: here, large differences between cultivation and field would suggest a large environmental component in trait expression, since in the field, plant performance is not only determined by genetic effects but by actual climatic, edaphic and biotic conditions. One of our most intriguing findings is that under cultivation (i.e. optimal conditions), desert plants produced almost three times as many seeds as plants from the mesic Mediterranean, while in the field, the opposite pattern was found. This suggests that desert plants have a much higher potential to respond plastically to differing rainfall conditions. Support for this observation also stems from a recent study which showed higher *Biscutella* seed production in the arid than in the semi-arid populations during a relatively rainy season (Nachreiner 2005). Clearly, this ability to “bet” on favorable years represents an advantage in habitats, where such years occur only very rarely.

In addition to maximizing seed number under optimal conditions, desert plants also showed an increase in diaspore size, when irrigated. It is clear that this pattern may be similarly advantageous as increasing the number of offspring. However, this finding contradicts one of the fundamental principles of life history theory: the seed size – seed number trade-off. In cultivation, diaspore number and size were positively correlated and decreased markedly from the arid towards the Mediterranean. This trend has found support in parallel studies on additional annual species in our system (Nachreiner 2005), while another study in the region has indicated that the annual grass *Stipa capensis* produced higher number of smaller diaspores in arid populations compared to the Mediterranean ones (Aronson 1990). In the same study, diaspore size of another annual grass, *Brachypodium distachyon*, were significantly larger than the Mediterranean, but their number did not differ between the two populations. In our study, diaspores

of desert annuals were – unexpectedly – either much larger than (cultivation) or similar in size to those of plants growing at the humid end of the gradient.

In summary, our findings suggest that the observed clinal trends in life history traits along the climatic gradients indicate the response of plants to two opposing selective forces at the two climatic extremes. Above-ground competition intensity at the wet end apparently favors taller plants, which invest more into vegetative growth. On the other hand, low resource availability and highly pulsed resources at the arid end select for rapid development, high reproductive allocation and high plasticity in seed production with respect to water availability. An intriguing consequence of our study is that although basic plant strategy theory has been developed for explaining between-species differences in habitat-trait relationships (Grime 1973b, 1977, Harper 1977), our findings suggest that largely opposing strategies may be found even within a single species.

*Acknowledgements* – We would like to thank Jaime Kigel for logistical and technical support, Yoni Hartmann, Nina Hobbahn and Yael Mutsafi for assistance, and Clara Ariza, Deborah Goldberg, Claus Holzapfel, Jaime Kigel, Hadas Parag, Ilana Stheim and Vigdis Vandvik for motivating discussions and helpful comments to the manuscript drafts. We thank the Botanical Gardens of Tel Aviv Univ. for technical support during the cultivation experiment and staff of the Univ. of Michigan Biological Station for logistic support to MP. This study is part of the GLOWA Jordan River project funded by the German Federal Ministry of Education and Research (BMBF).

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*Subject Editor: Francisco Pugnaire.*