

Phenotypic variation and stress resistance in core and peripheral populations of *Hordeum spontaneum*

SERGEI VOLIS* and SAMUEL MENDLINGER

The Institutes for Applied Research, Ben-Gurion University of the Negev, POB 653, Beer Sheva 84105, Israel

LINDA OLSVIG-WHITTAKER

Nature Reserves Authority, 78 Yirmiyahu St., Jerusalem 94467, Israel

URIEL N. SAFRIEL

The Mitrani Center for Desert Ecology, Ben-Gurion University of the Negev, Sede Boqer 84993, Israel, and Department of Evolution, Systematics and Ecology, Alexander Silberman Institute of Life Sciences, The Hebrew University of Jerusalem, Jerusalem 91904, Israel

NIKOLAY ORLOVSKY

The Institute for Desert Research, Ashgabat 744000, Turkmenistan

Received 6 November 1996; revised and accepted 2 February 1997

The phenotypic variation and response of plants to water stress were studied in a field trial in populations of wild barley, *Hordeum spontaneum* Koch. from Israel and Turkmenistan. Populations from the species distributional core and periphery were compared and contrasted for phenotypic variation in 16 phenological and morphological traits. The peripheral populations (six) were found to be phenotypically more variable and more resistant to water stress than core populations (12). The association of water-stress resistance with high phenotypic variability gives support to the hypothesis that populations that are genetically more variable are better adapted or pre-adapted to environmental changes and are thus valuable for conservation.

Keywords: phenotypic variation; core and peripheral populations; wild barley.

Introduction

Rapid environmental changes/deterioration occurring, either as a result of human activity or natural causes, pose the population biology question of whether populations of the same species may differ in their persistence to such changes.

If an area is undergoing an environmental change and its indigenous plant population therefore becomes extinct, the populations from the areas that have already undergone this or a similar stress should be better candidates for recolonization in this stressed area. As many aspects of plant physiology and ecology differ across a species' distribution (Parsons, 1980, 1991; Antonovics, 1994; Trevis, 1994) it is unlikely that the persistence of populations under environmental changes will be uniform regardless of a population's position in a species range. Persistence of a population under environmental stress can be attained either by the stress resistance of specific genotypes or by high phenotypic

plasticity. Genetic variability in such populations may be either low (most individuals are resistant or phenotypically plastic) or high (resistant and non-resistant genotypes are common). A combined genetic–demographic mathematical model predicts enhanced population persistence with an increase in overall genetic variance (Pease *et al.*, 1989). As individuals may vary in their persistence, either through adaptation or through phenotypic plasticity, to conditions that can never occur within most of the species range, it is plausible that genetic variability with respect to resistance and plasticity varies across the range of species distribution.

It has been shown that the genetic structure of populations from the boundary of the species distribution ('peripheral' sensu Brussard, 1984) and those away from the boundary ('core' populations) may differ (Soule, 1973; Brussard, 1984; Parsons, 1991). Three hypotheses have been developed to explain potential differences in selection processes and genetic variation patterns between peripheral and core populations and are discussed elsewhere (Safriel *et al.*, 1994). They can be briefly described as the following:

The 'Carson hypothesis'. Core populations undergo balancing selection and have high genetic variation, whereas in peripheral areas with fewer suitable ecological niches populations are adapted to a narrower range of ecological conditions and hence are less genetically variable than core populations (da Cunha and Dobzhansky, 1954; Carson, 1959);

The 'Fisher hypothesis'. Core populations undergo stabilizing selection and therefore within-population genetic variability is low, whereas peripheral populations constantly undergo fluctuating selection, induced by variable and unstable environmental conditions, and consequently have high within-population genetic variability (Fisher, 1930);

The 'Mayr hypothesis'. Gene flow from the core to the periphery is stronger than selection in the periphery, hence genetic variability is homogeneous throughout the range (Mayr, 1965, 1970).

Each hypothesis has different implications for conservation strategy and emphasizes a different allocation strategy for conservation in respect to a species core and periphery.

In this study we compared the genetic variation and phenotypic plasticity in core and peripheral populations of *Hordeum spontaneum* Koch. and asked two questions: (i) are there differences in the response to environmental changes between peripheral and core populations, and (ii) are these differences associated with differences in genetic (phenotypic) variability? Genetic variability in *H. spontaneum* across its distributional range was intensively studied for many characteristics, including disease resistance, isozymes and DNA sequences (Brown *et al.*, 1978; Nevo *et al.*, 1986; Jana and Pietrzak, 1988; Saghai Maroof and Allard, 1990; Chalmers *et al.*, 1992), but surprisingly few studies were devoted to variability in phenotypic traits (Nevo *et al.*, 1984; Snow and Brody, 1984). Study of phenotypic variability representing the whole plant level of genetic variability has an advantage over study of enzymatic and DNA variability as a study of adaptive variation while enzymatic and DNA polymorphism in many cases is selectively neutral.

Materials and methods

Species studied

Hordeum spontaneum Koch. is a morphologically diverse, widespread annual grass species with ecotypic differentiation (Snow and Brody, 1984). It is abundantly distributed in open park forests and herbaceous formations of the Near East, Turkey, western Iran, Af-

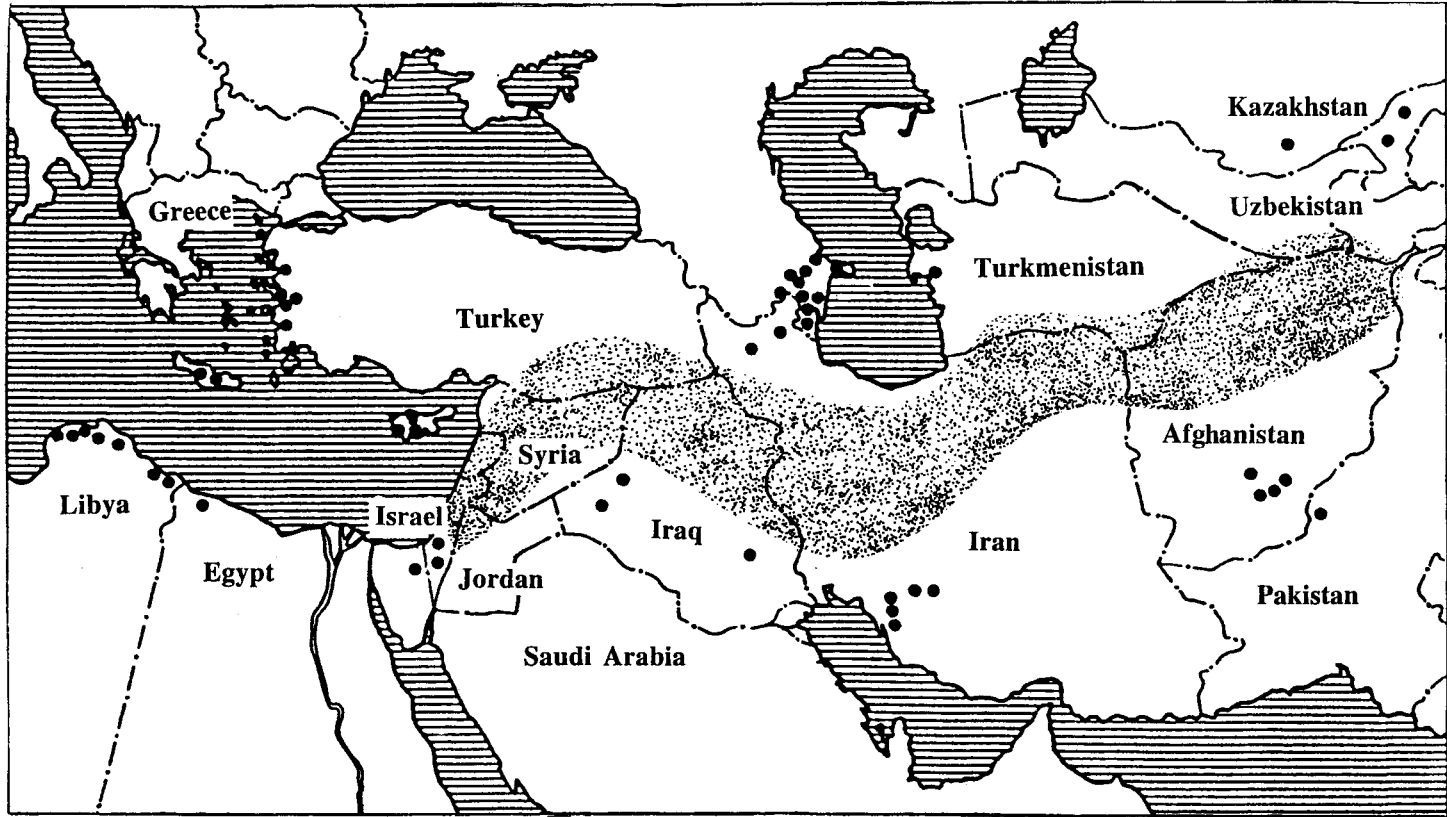


Figure 1. Distribution of wild barley, *Hordeum spontaneum*. An assumed core, where *H. spontaneum* is represented by massive stands in fairly primary habitats is shown as a dotted area. The areas with patchy and sporadic distribution of wild barley are denoted by solid circles.

ghanistan and Turkmenistan, and reaches its distributional boundary in patchy and sporadic formations in southern Israel, the Aegean region, the Egyptian coast, eastern Iran, India, Kazakstan and China (Harlan and Zohary, 1966; Zohary, 1973; personal observations) (Fig. 1).

Experimental methods

Between 30 and 50 plants each from 23 Turkmenian and seven Israeli populations were collected during two expeditions in Turkmenistan (May 1992 and 1993) and in central and southern Israel (April–May 1992 and 1993). From these, 12 Turkmenian and six Israeli populations representing the different environmental conditions of their countries were chosen for this study. We used the degree of aridity to differentiate populations into core and peripheral, which was similar to differentiation of Israeli populations into mesic and xeric ones, an approach used by Nevo *et al.* (1984) for *H. spontaneum* and by Mendlinger and Zohary for *Aegilops* species (1995). In this study, five Israeli populations were from the southern periphery (The Negev and Judean Deserts), and one Turkmenian population was from the northern periphery of the species distribution (annual rainfall 100–150 mm). The other eleven Turkmenian populations (foothills of Kopet-Dag mountain chain and Badhis Highland) and one Israeli population from the Mediterranean coast represent the species core (200–500 mm rainfall) (Table 1). Thus, the segregation of populations into core and peripheral ones employed two criteria: (i) population position in a species range (at the

Table 1. Ecogeographical data for 18 populations of *H. spontaneum* sampled in Turkmenistan and Israel in 1992–1993 and used in a field trial at Sede Boqer (1993/1994)

Population site	Country	Latitude	January temperature (t° C)	Annual temperature (t° C)	Annual rainfall (mm)
<i>Core</i>					
1	Turkmenistan	37.85	0.7	15.4	383
2	Turkmenistan	38.65	0.0	14.4	295
3	Turkmenistan	38.25	1.0	12.9	457
4	Turkmenistan	38.80	3.2	16.0	238
5	Turkmenistan	38.00	0.9	16.1	220
6	Turkmenistan	37.80	0.9	16.1	220
7	Turkmenistan	37.40	1.4	16.3	245
8	Turkmenistan	36.85	1.8	16.7	205
9	Turkmenistan	36.50	3.0	16.6	225
10	Turkmenistan	35.95	2.4	14.5	290
11	Turkmenistan	35.80	2.4	14.5	285
12	Israel	31.90	14.0	21.0	400
<i>Periphery</i>					
13	Israel	30.90	10.0	21.0	100
14	Israel	30.80	10.0	21.0	90
15	Israel	30.95	10.0	21.0	105
16	Israel	31.80	14.0	23.0	150
17	Israel	31.60	14.0	23.0	100
18	Turkmenistan	40.00	1.7	14.2	150

border of species distribution and away from it), and (ii) aridity with annual rainfall of 200 mm as the cut-off point. Plants from each population were collected along a transect(s) with the collected plants spaced between 1 and 3 m apart and one spike per plant harvested and separately bagged (Marshall and Brown, 1975; Mendlinger and Zohary, 1995).

One seed per mother plant was sown in a greenhouse on November 1, 1993, and the plantlets were transplanted into an experimental sand garden at the Institute of Desert Research in Sede Boqer on November 15. Each plantlet was transplanted into a 1/4 m² framed plot, placed in the ground and filled with sterile sand to a depth of 1 m. A complete randomized block design was used with 6–10 plants per treatment per population.

Two water treatments were examined: low (LW) and high (HW) irrigation. In addition to 14.5 litres/plant of rainfall (58 mm rainfall fell during the growing season), the plants in the low-water treatment received 9.25 litres and in the high 18.5 litres of irrigation water during the season. The amount of water supplied was calculated using the PanA transpiration rate during the season, with the low treatment representing a water stress (i.e. drought conditions) and high treatment relatively favourable conditions. Irrigation was done by hand-watering twice a week. The fertilizer NPK 20:20:20 was supplied at each irrigation, with each plant receiving the same amount of fertilizer.

After establishment, the number of days to appearance of the second vegetative tiller was recorded and the number of tillers per individual plant and tiller height were counted and measured respectively every 10 days until the plants initiated bolting. After the appearance of reproductive tillers, the first three reproductive tillers of each plant were tagged with coloured tags representing the first, second and third tiller in order of awn appearance, and each tiller was measured for culm length, flag and penultimate leaf length, spike length, awn length, number of nodes, internode length and total tiller height, and the number of days to anthesis and awning were recorded. At senescence, all spikes were harvested and the total number of reproductive tillers was counted. After harvest the number of spikelets per spike and the average spikelet and seen weight were measured.

Statistical analysis

A nested analysis of variance (ANOVA) on the morphological characters was used to partition the total variance between population groups (i.e. species core and periphery), between populations of a group and between individuals within a population. A 2-way ANOVA was carried out for all phenological and morphological traits between population groups and water treatment (HW and LW). A significant interaction between population groups and treatments was presumed to reflect the different amount of phenotypic plasticity between groups of populations. The relationship of found population plasticity with environmental factors (climatic and geographic) was studied by multiple regression analysis. Using the coefficient of variation, CV, comparison of variation in phenotypic traits between population groups was carried out using the Wilcoxon matched-pairs signed-ranks test for each trait. Principal component analysis (PCA) using the program 'CANOCO' (Ter Braak, 1987) was done to determine the pattern of interpopulation variation in phenotypic traits.

Results

Trait values

In both irrigation treatments peripheral populations started reproduction (days to anthesis and days to awn appearance) significantly earlier than core ones (Table 2). Under both

Table 2. The means of 18 phenotypic traits in two groups of populations of *H. spontaneum* (core and periphery) grown under high (HW) and low (LW) water treatments and compared by an orthogonal polynomial test. Differences between population groups are shown with corresponding levels of significance. Lengths are in cm

Traits	LW			HW		
	Core	Periphery		Core	Periphery	
<i>I. Phenological</i>						
Days till tillering	23.7	22.6	ns	24.3	22.7	ns
Days to awn appearance	161.0	149.4 ^a		160.9	150.1 ^a	
Days to anthesis	167.6	158.2 ^a		167.4	158.9 ^a	
<i>II. Morphological</i>						
<i>Vegetative</i>						
Vegetative tillers	28.8	26.8	ns	27.2	25.8	ns
Height of veg. tillers	29.3	31.8	ns	27.7	29.5	ns
<i>Reproductive</i>						
Total height	49.4	51.4	ns	68.8	60.8 ^a	
Spike length	16.5	18.1 ^a		19.5	19.2	ns
Awn length	7.4	8.1 ^a		8.3	8.5	ns
Culm length	32.9	33.2	ns	49.2	41.5 ^a	
Number of nodes	4.5	3.9 ^a		4.6	3.7 ^a	
Internode length	7.4	8.6 ^a		10.8	11.1	ns
Flag leaf length	5.0	6.4 ^a		7.4	7.5	ns
Penultimate leaf length	10.6	13.4 ^a		14.4	14.8	ns
Spikelets in a spike	25.4	24.3 ^c		29.6	24.6 ^a	
Spike weight (g)	0.89	0.94	ns	1.25	1.20	ns
Spikelet weight (mg)	34.1	39.1 ^a		41.9	49.2 ^a	
Number of rep. tillers	10.9	12.9	ns	18.5	21.5	ns
Seed weight (mg)	21.2	16.0 ^a		22.7	19.1 ^a	

Levels of significance: ^a $P < 0.001$; ^b $P < 0.01$; ^c $P < 0.05$; ns = not significant.

treatments plants from peripheral populations had significantly fewer nodes and spikelets per spike and lighter seeds but heavier spikelets than core populations. Spike and awn length, flag and penultimate leaf length and internode length did not differ between the two population groups under HW but were significantly different under LW, with all reproductive traits being smaller in core than in peripheral populations.

Days to awn appearance and days to anthesis, the phenological traits associated with the start of reproduction, were not affected by irrigation but depended upon each population's original location, i.e. Turkmenistan or Israel (Table 3). The number of days until tillering was not affected by water treatment or by the origin of the populations. The interaction between treatment and population group was not significant in any phenological trait, indicating that the phenotypic plasticity of phenological traits did not differ in populations of *H. spontaneum*. Vegetative traits were not affected by any factor.

All reproductive traits except number of nodes and spike weight were strongly affected by both water treatment and the origin of populations. Interaction between the two factors were significant in eight of the 13 traits related to plant reproduction and grain

Table 3. Two-way ANOVA for phenotypic traits in two groups of populations of *H. spontaneum* (core-periphery) grown under high (HW) and low (LW) water treatments. Differences between treatments, population groups and their interactions are shown with corresponding levels of significance

Traits	Irrigation treatment		Population groups		Interaction treatment * groups	
	F		F		F	
<i>I. Phenological</i>						
Days till tillering	0.1	ns	1.8	ns	0.1	ns
Days to awn appearance	0.1	ns	117.3 ^a		0.1	ns
Days to anthesis	0.1	ns	80.9 ^a		0.2	ns
<i>II. Morphological</i>						
<i>Vegetative</i>						
Vegetative tillers	1.2	ns	2.1	ns	0.1	ns
Height of veg. tillers	2.3	ns	2.9	ns	0.1	ns
<i>Reproductive</i>						
Total height	164.0 ^a		7.2 ^b		19.8 ^a	
Spike length	102.7 ^a		9.9 ^b		2.3 ^a	
Awn length	15.1 ^a		7.7 ^b		2.5	ns
Culm length	153.8 ^a		13.5 ^a		16.4 ^a	
Number of nodes	0.2	ns	177.7 ^a		5.2 ^c	
Internode length	188.7 ^a		14.2 ^a		4.6 ^c	
Flag leaf length	70.2 ^a		12.9 ^a		9.3 ^b	
Penultimate leaf length	58.6 ^a		22.6 ^a		12.9 ^a	
Spikelets in a spike	33.7 ^a		66.8 ^a		26.9 ^a	
Spike weight	120.4 ^a		0	ns	3.1	ns
Spikelet weight	115.4 ^a		54.6 ^a		1.8	ns
Reproductive tillers	42.2 ^a		3.9 ^c		0.2	ns
Seed weight	9.9 ^b		34.9 ^a		1.2	ns

Levels of significance: ^a $P < 0.001$; ^b $P < 0.01$; ^c $P < 0.05$; ns = not significant.

filling (Table 3). A plant's relative response to water stress as expressed in reduction in size (in total height, spike length, internode length etc.) or number (in number of nodes and number of spikelets in a spike) was greater in core than peripheral populations (22.6% versus 10.3%, $P < 0.01$, Wilcoxon signed-ranks test) (Table 4).

Regression analysis revealed that phenotypic plasticity in populations was negatively related to annual and January temperature and positively related to annual rainfall and latitude (which is negatively correlated with annual temperature, $R^2 = 0.86$, $P < 0.001$). As wild barley's environmental favorability decreases with a decrease in annual rainfall or an increase in temperature, the latter suggests a negative relationship of plasticity with environmental severity (Table 5).

Trait variability expressed as CV

Phenotypic variability, expressed as the coefficient of variation (CV), was calculated and compared and contrasted in the two water treatments (HW and LW) for each trait in the

Table 4. Means of morphological traits of *H. spontaneum* population groups and the effect of experimental water stress. The traits shown are those demonstrating significant interaction between population groups and treatment (2-way ANOVA), arranged in a decreasing order of % reduction in core populations. Lengths are in cm

Traits	Population groups					
	Core			Peripheral		
	Mean value		red.	Mean value		red.
	HW	LW	(%)	HW	LW	(%)
Culm length	49.2	32.9	33	41.6	33.3	20
Flag leaf length	7.4	5.0	32	7.5	6.4	15
Internode length	10.8	7.4	32	11.1	8.6	22
Total height	68.8	49.4	28	60.8	51.4	15
Penultimate leaf length	14.4	10.6	26	14.8	13.5	9
Spike length	19.6	16.5	15	19.2	18.1	6
Number of spikelets in a spike	29.6	25.5	14	24.6	24.3	1
Number of nodes	4.6	4.5	2	3.7	3.9	-4
Wilcoxon matched-pairs signed-ranks test:						
	Ts	n		$P < 0.01$		
	0	8				

two population groups (Table 6). Group CVs (variation in trait values over all populations of a group) ranged between 4% (days to awn appearance in core populations grown under conditions of high water availability) to 74% (number of reproductive tillers in

Table 5. Coefficients of multiple determination (R^2) employing as dependent variable the amount of a population's relative response to water stress, expressed as percentage of reduction in trait size or number in 12 Turkmenian and six Israeli populations of *H. spontaneum* grown under two water treatments (HW and LW, respectively). Independent variables were climatic and geographic factors^d. Slope is represented for regression line of the factor contributed the most to the total explained variance

Trait	$X_1X_2X_3$	R^2_1	R^2_{12}	R^2_{123}	Slope
Spike length	TjLt	0.46 ^b	0.47 ^b		-1.0
Total height	Tm	0.33 ^c			-2.8
Internode length	Tm	0.24 ^c			-2.5
Culm length	Tm	0.29 ^c			-3.2
Flag leaf length	RnLt	0.27 ^c	0.36 ^c		0.1
Penultimate leaf length	LtRnTm	0.41 ^c	0.50 ^c	0.52 ^c	2.3
Spikelets in a spike	Tm	0.51 ^a			-2.3

Levels of significance: ^a $P < 0.001$; ^b $P < 0.01$; ^c $P < 0.05$.

^d Climatic values were taken from the Atlas of Israel (1970), the USSR climate reference book, Part 30, Turkmenistan, vols 2, 4 and 5 (1967, 1968, 1969), and from multiple-year records of the Meteorological Service of Turkmenistan.

Symbols of variables: Lt = latitude; Tm = mean annual temperature; Tj = mean January temperature; Rn = mean annual rainfall.

Table 6. Variation in phenotypic traits in *H. spontaneum* population groups for two water treatments (HW and LW, respectively), expressed through coefficient of variation (CV), and the periphery/core ratio of coefficients of variation

Traits	HW			LW		
	Periphery	Core	Ratio	Periphery	Core	Ratio
<i>I. Phenological</i>						
Days till tillering	33.5	33.7	0.99	35.5	37.1	0.96
Days to awn appearance	6.7	3.9	1.70	8.4	4.8	1.74
Days to anthesis	5.2	4.0	1.29	6.9	4.6	1.48
<i>II. Morphological</i>						
<i>Vegetative</i>						
Number of vegetative tillers	39.1	37.5	1.04	45.4	29.5	1.54
Height of vegetative tillers	42.0	33.9	1.24	41.0	32.5	1.26
<i>Reproductive</i>						
Total height	31.9	23.1	1.38	25.9	31.4	0.83
Spike length	18.2	12.8	1.42	15.5	17.6	0.88
Awn length	40.0	22.9	1.75	37.0	24.3	1.52
Culm length	41.2	29.1	1.42	36.7	40.4	0.91
Number of nodes	24.3	15.2	1.60	23.1	17.8	1.30
Internode length	33.3	27.8	1.20	33.7	37.8	0.89
Flag leaf length	45.3	43.2	1.05	51.6	44.0	1.17
Penultimate leaf length	39.2	29.2	1.34	50.0	35.8	1.39
Number of spikelets in a spike	23.6	16.6	1.42	19.8	22.4	0.88
Number of reproductive tillers	70.7	57.3	1.23	74.1	66.7	1.11
Spike weight	29.1	35.2	0.83	28.7	48.3	0.59
Spikelet weight	21.5	28.6	0.75	26.7	37.1	0.72
Seed weight	28.8	29.1	0.99	26.3	31.1	0.84
Wilcoxon matched-pairs signed-ranks test:						
	Ts	$P < 0.01$		Ts	$P = ns$	
	17			70		

Levels of significance: ^a $P < 0.01$; ^b $P < 0.05$; ns = not significant.

peripheral populations grown under conditions of water stress). Core and peripheral populations were significantly different in HW treatment with more phenotypic variation in peripheral than in core populations ($P < 0.01$, Wilcoxon signed-ranks test). Variability increased with stress (LW treatment) in core populations in all traits except the number and height of vegetative tillers, whereas in peripheral populations variability increased in nine and decreased in nine traits (Table 6).

Partitioning of variation

In all traits examined, the within population component of variation was larger than the other two components (mean values 66 versus 25% and 9%) (Table 7). Population groups contributed the least to the total variance (9%) except in number of days to awn appearance and anthesis and the number of nodes. However, there was a relatively high percentage of between population groups variance for days to awn appearance and days to

Table 7. Variance components (in percentage) between population groups (core and periphery), between populations within a group and within populations for phenotypic traits in populations of *H. spontaneum* grown in a field trial at Sede Boqer (1993/1994)

Traits	Variance components		
	Between groups	Between populations	Within populations
<i>I. Phenological</i>			
Days till tillering	0	16	84
Days to awn appearance	36	21	42
Days to anthesis	33	25	43
Mean	23	21	56
<i>II. Morphological</i>			
<i>Vegetative</i>			
Number of vegetative tillers	0	16	84
Height of veg. tillers	0	28	72
Mean	0	22	78
<i>Reproductive</i>			
Total height	3	30	67
Spike length	3	21	76
Awn length	0	30	70
Culm length	3	30	66
Number of nodes	26	23	51
Internode length	2	19	79
Flag leaf length	7	15	79
Penultimate leaf length	2	24	73
Number of spikelets in a spike	15	27	58
Spike weight	0	25	75
Spikelet weight	9	27	65
Number of reproductive tillers	0	25	75
Seed weight	26	30	44
Mean	7	25	67
Total mean	9	25	66

anthesis (36.3 and 32.8%) which even exceeded the within population group component (21.2 and 24.6%, respectively). The substantial amount of between populations/population groups component of variation (together about 50% of total variation) in such traits as days to awn appearance and days to anthesis, the number of nodes and seed weight suggests their importance in *H. spontaneum* population differentiation.

Trait complexes

Principal component analysis (PCA) was performed to analyse the pattern of phenotypic variation between populations. The data matrices for HW and LW treatments contained identical variables and comprised only the traits with total between populations and population group variation exceeding 40% (days to awn appearance, number of nodes, number of spikelets in a spike and seed weight). (Days to anthesis was not used as it was

Table 8. Phenotypic traits as variables with their contribution to the three principal components for two water treatments (HW and LW, respectively)

Component contribution variable	HW			LW		
	1st	2nd	3rd	1st	2nd	3rd
Number of nodes	0.95	-0.01	-0.35	0.96	-0.11	-0.09
Number of spikelets in a spike	0.73	-0.51	-0.40	0.60	0.75	-0.26
Days to awn appearance	0.86	0.22	0.48	0.41	-0.81	-0.37
Seed weight	0.53	0.77	-0.32	0.78	-0.12	0.59
Total variance explained (%)	0.65	0.18	0.12	0.53	0.31	0.13
Accumulated variance (%)	0.65	0.83	0.95	0.53	0.84	0.97

highly intercorrelated with days to awn appearance.) The trait that contributed the most to PC I under both HW and LW treatments was number of nodes (Table 8). The first principal component explained 65 and 53% of trait variation of HW and LW, respectively.

The scattergram of population means on the first two principal components appears to group plant ecotypes by their core or peripheral position in a species distribution (Fig. 2). In both HW and LW treatments core and peripheral populations are skewed to opposite sites of the PC I. Under HW treatment there is a trend for core populations to clump together whereas peripheral populations are rather scattered. Under LW treatment this pattern is less pronounced.

Discussion

Phenotypic differentiation of *H. spontaneum* within a species range was detected for plant phenology, with 36.3 and 32.8% of the total phenotypic variation contributed to the variation between populations from the species core and periphery (in days to awn appearance and anthesis, respectively). At the same time, plant morphology was less important for determining this differentiation as only two traits, seed weight and number of nodes (25.8 and 26.5% of the population groups contribution to the total variance, respectively), were important. Thus, core and peripheral populations differed with respect to the onset of reproduction (days to anthesis and awning), in traits related to plant growth (number of nodes) and plant fecundity (seed weight). This suggests a difference between core and peripheral population strategies with plants from peripheral populations starting reproduction earlier, growing faster and having lighter seeds than from core populations. In addition, since there were fewer spikelets per spike in peripheral than in core populations, but no significant difference between population groups in the number of spikes per plant, the decrease in seed weight is not compensated for by an increase in the number of seeds produced. Hence, fast plant growth in peripheral populations appears to have a lower reproductive allocation as a trade-off. This strategy is what one would expect as the result of an unpredictable and unstable climate in peripheral areas requiring a high correlation of reproduction with stochastic weather patterns and a shortening of the vegetation period.

In most traits there was some contribution of the between-population group component to the total variance with peripheral populations harbouring significantly more variation than core ones (inter- and intrapopulation phenotypic variation were pooled). In addition,

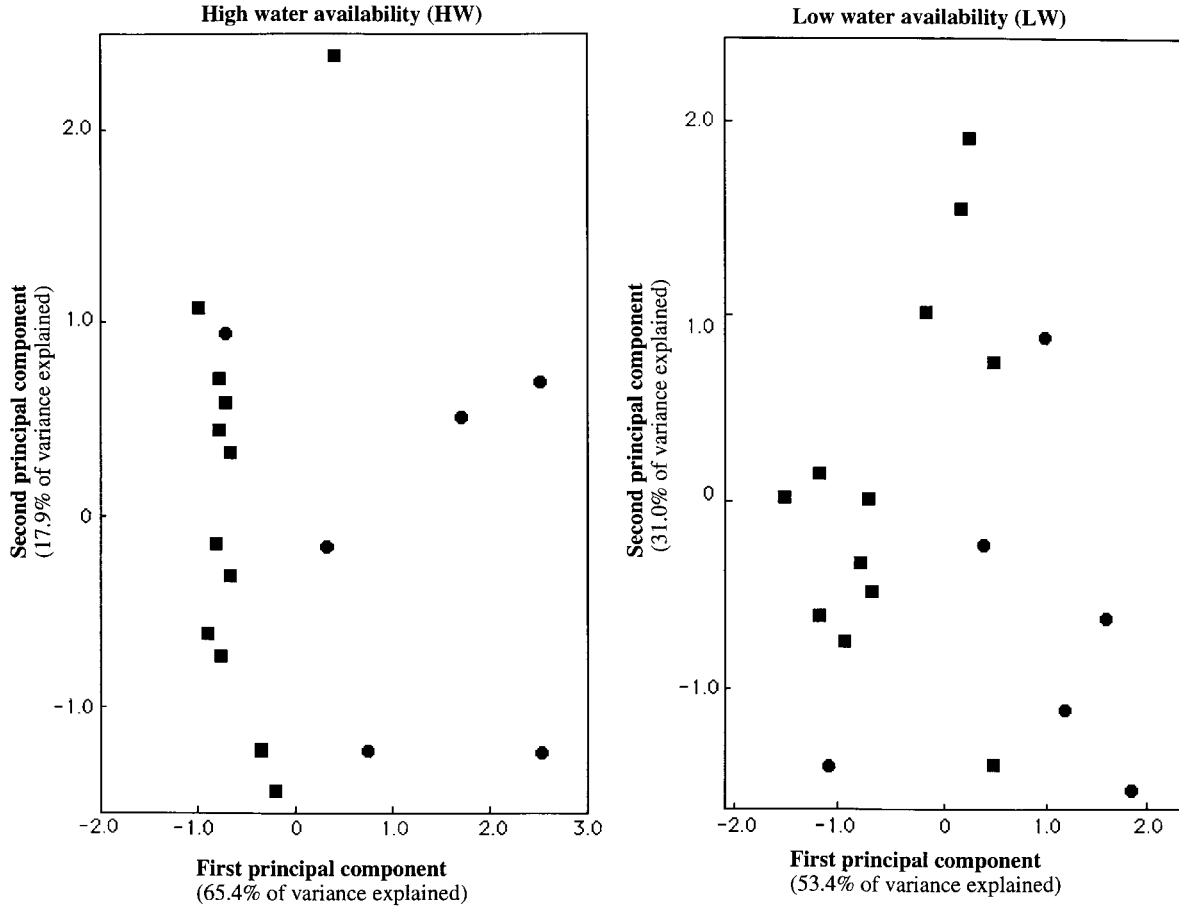


Figure 2. Principal component analysis of four morphological and phenological traits in 18 populations of *H. spontaneum* (HW and LW treatments, respectively). ■ = core populations; ● = peripheral populations.

PCA revealed a trend of interpopulation variation to be higher in peripheral versus core populations as expressed in the clumping of populations in the scattergrams. As phenotypic variability under conditions of water stress increased much more in core than in peripheral populations, this may indicate that peripheral populations are not only phenotypically more diverse, but are also less affected by stress.

Phenotypic plasticity significantly differed between core and peripheral populations in eight traits and was positively related with favourability of a population's local environment (i.e. annual rainfall and temperature) in seven of these traits. The consistency of these results points to aridity changing from a species core to its periphery as a factor in determining the level of plasticity in barley populations. This also may mean that not only significant difference in aridity between core and periphery, but also relatively small differences between population localities may play an important role in determining the population's level of phenotypic plasticity.

As the phenotypic variability, which is at least partly genetic, is shown to be higher in peripheral than in core populations, the results best fit the 'Fisher hypothesis', although an estimation of intrapopulation variation is lacking. Higher plasticity of core versus peripheral populations would initially appear to favour the 'Carson hypothesis', but as it is associated with greater decreases in fitness of core versus peripheral populations (reflected in number of reproductive tillers and spikelets in a spike) the 'Carson hypothesis' is not supported. The inequality of the total population group variation goes against the 'Mayr hypothesis'.

Persistence of populations under conditions of water stress resulted not from high phenotypic plasticity but from genetically fixed drought resistance. This suggests that in new and stressful environmental conditions which a population may face in the case of rapid environmental change/deterioration, the population persistence will be achieved not by acclimatization but by adaptation or pre-adaptation.

Higher resistance to water stress of peripheral populations was associated with their higher phenotypic variation as compared with core populations. The lower amount of phenotypic plasticity in peripheral versus core populations supports the hypothesis of antagonistic selection for phenotypic flexibility and genetic diversity (Lewontin, 1957; Bradshaw, 1965; Marshall and Jain, 1968). It is plausible that the higher plasticity found in core populations is the result of limited genetic diversity due to stabilizing selection. Another explanation may employ the hypothesis of Grime, Crick and Rincon (1986) that morphological plasticity in plants from productive and unproductive habitats have different patterns. According to Grime *et al.* (1986), high plasticity associated with high competitive ability will be favoured in productive habitats as it enables plants to escape from depletion zones and to utilize resources fast and efficient. Unproductive and stressed habitats will require conservative strategy of resource utilization with good synchronization of life cycle with seasonality and low morphological plasticity. Thus, core populations from more productive environments are expected to have higher plasticity than populations from species periphery exposed to severe stresses and resource deficiency. A test of this hypothesis is underway.

Acknowledgement

We would like to thank Ruti Soto for the assistance in the laboratory and Marc Goldberg, Azat Nurberdiev, Haim Kuperman and Natali Umansky for their help with the field work.

This study was supported by the Israel Ministry of Science and Technology programme for scientific collaboration with states of the former Soviet Union, by a grant of the Mitrani Fund for the Mitrani Center Global Climate Change Ecology Program, and by a grant from US AID-CDR for scientific collaboration of the states of the former Soviet Union with Israel (CA-13-057).

References

- Antonovics, J. (1994) Ecological genetics of metapopulations: the *Silene-Ustilago* Plant-Pathogen System. In *Ecological Genetics* (L. A. Real, ed.), pp. 146–70. New Jersey: Princeton University Press.
- Bradshaw, A.D. (1965) Evolutionary significance of phenotypic plasticity in plants. *Adv. Genetics* **13**, 115–55.
- Brown, A.H.D., Nevo, E., Zohary, D. and Dagan, O. (1978) Genetic variation in natural populations of wild barley (*Hordeum spontaneum*). *Genetica* **49**, 97–108.
- Brussard, P. (1984) Geographic patterns and environmental gradients: the central-marginal model in *Drosophila* revisited. *Annu. Rev. Ecol. Syst.* **15**, 25–64.
- Carson, H.L. (1959) Genetic conditions that promote or retard the formation of species. *Cold Spring Harbor Symp. Quant. Biol.* **24**, 87–103.
- Chalmers, K.J., Waugh, R., Watters, J., Foster, B.P., Nevo, E., Abbott, R.J. and Powell, W. (1992) Grain isozyme and ribosomal DNA variability in *Hordeum spontaneum* populations from Israel. *Theoret. Appl. Genetics* **84**, 313–22.
- da Cunha, A.B. and Dobzhansky, T. (1954) A further study of chromosomal polymorphism in *Drosophila willistoni* in relation to environment. *Evolution* **8**, 119–34.
- Fisher, R.A. (1930) *The General Theory of Natural Selection*. Oxford: Clarendon Press.
- Grime, J.P., Crick, J.C. and Rincon, E. (1986) The ecological significance of plasticity. In *Plasticity in Plants* (D.H. Jennings and A.J. Trewavas, eds), pp. 5–29. Cambridge: Company of Biologists.
- Harlan, R.J. and Zohary, D. (1966) Distribution of wild wheats and barley. *Science* **153**, 1074–80.
- Jana, S. and Pietrzak, L.N. (1988) Comparative assessment of genetic diversity in wild and primitive cultivated barley in a center of diversity. *Genetics* **119**, 981–90.
- Lewontin, R.C. (1957) The adaptations of populations to varying environments. *Cold Spring Harbor Symp. Quant. Biol.* **22**, 395–408.
- Marshall, D.R. and Brown, A.H.D. (1975) Optimum sampling strategies in genetic conservation. In *Crop Genetic Resources for Today and Tomorrow* (O.H. Frankel and J.G. Hawks, eds), pp. 53–80. Cambridge: Cambridge University Press.
- Marshall, D.M. and Jain, S.K. (1968) Phenotypic plasticity of *Avena fatua* and *A. barbata*. *Am. Nat.* **102**, 457–67.
- Mayr, E. (1965) *Animal Species and Evolution*. Cambridge, MA: Belknap Press.
- Mayr, E. (1970) *Populations, Species, and Evolution*. Cambridge, MA: Belknap Press.
- Mendlinger, S. and Zohary, D. (1995) The extent and structure of genetic variation in species of the Sitopsis group of *Aegilops*. *Heredity* **74**, 616–27.
- Nevo, E., Beiles, A., Gutterman, Y., Storch, N. and Kaplan, D. (1984) Genetic resources of wild cereals in Israel and vicinity. II. Phenotypic variation within and between populations of wild barley, *Hordeum spontaneum*. *Euphytica* **33**, 737–56.
- Nevo, E., Beiles, A. and Zohary, D. (1986) Genetic resources of wild barley in the Near East: structure, evolution and application in breeding. *Biol. J. Linnean Soc.* **27**, 355–80.
- Parsons, P.A. (1980) Adaptive strategies in natural populations of *Drosophila*: ethanol tolerance, desiccation resistance, and development times in climatically optimal and extreme environments. *Theoret. Appl. Genetics* **57**, 257–66.

- Parsons, P.A. (1991) Evolutionary rates: stress and species boundaries. *Annu. Rev. Ecol. Syst.* **22**, 1–18.
- Pease, C.M., Lande, R. and Bull, J.J. (1989) A model of population growth, dispersal and evolution in a changing environment. *Ecology* **70**, 1657–64.
- Safriel, U.N., Volis, S. and Kark, S. (1994) Core and peripheral populations and global climate change. *Israeli J. Plant Sci.* **42**, 331–45.
- Saghai Maroof, M.A. and Allard, R.W. (1990) Genetic diversity and ecogeographical differentiation among ribosomal DNA alleles in wild and cultivated barley. *Proc. Natl. Acad. Sci. USA* **87**, 8486–90.
- Snow, L. and Brody, T. (1984) Genetic variation of *Hordeum spontaneum* in Israel: eco-geographical races, detected by trait measurements. *Plant Syst. Evol.* **145**, 15–28.
- Soule, M. (1973) The epistasis cycle: a theory of marginal populations. *Annu. Rev. Ecol. Syst.* **4**, 165–87.
- Ter Braak, C.J.F. (1987) Canoco – a Fortran Program for Canonical Community Ordination by (Partial) (Detrended) (Canonical) Correspondence Analysis, Principal Component Analysis and Redundancy Analysis. TNO Institute of Applied Computer Science, Wageningen.
- Trevis, J. (1994) Ecological genetics of life-history traits: variation and its evolutionary significance. In *Ecological Genetics* (L.A. Real, ed.) pp. 171–204. New Jersey: Princeton University Press.
- Zohary, D. (1973) *Geobotanical Foundations to the Middle East*, vols 1 and 2. Stuttgart: G. Fisher, and Amsterdam: Swets and Zeitlinger.