ORIGINAL ARTICLE

Introduction beyond a species range: a relationship between population origin, adaptive potential and plant performance

S Volis[1], D Ormanbekova[2], K Yermekbayev[2], M Song[1] and I Shulgina[1]

The adaptive potential of a population defines its importance for species survival in changing environmental conditions such as global climate change. Very few empirical studies have examined adaptive potential across species' ranges, namely, of edge vs core populations, and we are unaware of a study that has tested adaptive potential (namely, variation in adaptive traits) and measured performance of such populations in conditions not currently experienced by the species but expected in the future. Here we report the results of a *Triticum dicoccoides* population study that employed transplant experiments and analysis of quantitative trait variation. Two populations at the opposite edges of the species range (1) were locally adapted; (2) had lower adaptive potential (inferred from the extent of genetic quantitative trait variation) than the two core populations; and (3) were outperformed by the plants from the core population in the novel environment. The fact that plants from the species arid edge performed worse than plants from the more mesic core in extreme drought conditions beyond the present climatic envelope of the species implies that usage of peripheral populations for conservation purposes must be based on intensive sampling of among-population variation.

Heredity (2014) **113**, 268–276; doi:10.1038/hdy.2014.25; published online 2 April 2014

INTRODUCTION

Plant performance and adaptive potential across species range

The 'abundant center' model (Sagarin and Gaines, 2002) predicts a decrease in population size toward the species distributional periphery that implies that evolutionarily stable limits of species geographic distributions are shaped by two genetic parameters, effective population size and the amount of gene flow, and that these two parameters are higher at the range center and lower at range margins. According to this concept, species do not expand beyond range edges and plants fail to adapt to local conditions there because of lower genetic diversity and higher genetic differentiation in geographically peripheral as compared with core populations and therefore limited availability of locally beneficial alleles in these populations (Mayr, 1963; Hoffmann and Blows, 1994; Hoffmann and Parsons, 1997; Lennon et al., 1997; Holt and Keitt, 2000, 2005; Blows and Hoffmann, 2005; Alleaume-Benharira et al., 2006).

The 'abundant center' model also has implications for a question of how population position within a species range affects its evolutionary potential, namely, its ability to adapt to changing environmental conditions. If peripheral populations have lower genetic variation in potentially adaptive traits than populations at the species core because of strong genetic drift, as predicted by the 'abundant center' model, then their potential for evolutionary adaptation to future changes will be low. On the other hand, if peripheral populations maintain substantial genetic variation in traits conferring adaptation to the specific range conditions, then their evolutionary potential and hence conservation value will be high. In the latter case, peripheral populations can facilitate shifts in species'

geographical distributions in response to rapid environmental change (Etterson and Shaw, 2001; Parmesan, 2006; Bell and Gonzalez, 2011).

Tests of theoretical predictions about evolution of range boundaries and adaptive potential of populations having different positions within a species range require analysis of species' response to environments at the center, margin and beyond the range edge by transplant experiments (Sexton et al., 2009). Unfortunately, only few reciprocal transplant studies assessing local adaptation and ecotypic differentiation have included both the range boundary and conditions beyond the current niche space (but see Geber and Eckhart, 2005; Griffith and Watson, 2006; Angert et al., 2008; Stanton-Geddes et al., 2012a, b).

Population response to climate change

The effects of global climate change are predicted to be especially severe for Mediterranean-type ecosystems as a consequence of the intensification of their already limiting conditions for plant regeneration (Schröter et al., 2005; Giorgi and Lionello, 2008). Predicted climate change in the Mediterranean basin includes both increasing aridity and greater frequency of extreme drought conditions. It is expected that by the end of the twenty-first century, the Mediterranean region including the Middle East coastal regions will experience a substantial increase and northward extension of arid regimes (Gao and Giorgi, 2008), and an analysis of the impact of these climate changes on natural vegetation predicts a transition of many grass-covered areas to bare ground conditions (Zeng and Yoon, 2009; Anav and Mariotti, 2011).

Because a gradient of aridity determines distribution limits of many species in the Mediterranean basin, populations from a species periphery in this region often occupy the extremes of such gradient. Wild emmer wheat, *Triticum turgidum* L. ssp. *dicoccoides* (hereafter *T. dicoccoides*) is no exception to this pattern with its northern geographic limit determined by low winter temperatures and its southern limit by low precipitation (Willcox, 2005; Özkan *et al.*, 2011). *T. dicoccoides* is an annual grass with a mainly Eastern Mediterranean distribution, extending into southeastern Turkey, Iraq and Iran. Under the predicted scenario of rapid aridization, the species edge populations will experience conditions more arid than in any part of the current species distribution. Will edge populations exhibit better performance under these conditions than core populations and how can this be connected with their adaptive potential (namely, extent of quantitative trait genetic variation)? To answer these questions, we selected two core populations (Ammiad Karst (K) and Ammiad North (N)) in close proximity so that extensive gene flow between them is likely, and two edge populations isolated from the core and from each other: Har Amasa (HA) from the edge determined by low precipitation and drought, and Mount Hernon (MH) from the edge determined by low temperature. Our study included (1) a local adaptation test through a 4-year reciprocal transplant experiment; (2) the analysis of population genetic variation in quantitative traits; and (3) the selection analysis of experimentally induced drought effects on phenotypic traits. These experiments were planned to provide an explanation for results of the experimental introduction of plants of peripheral and core origin into conditions beyond the boundary, into the desert environment.

MATERIALS AND METHODS
Study species and sampling locations
T. dicoccoides is a predominantly self-pollinating (>95% for the whole *Triticum–Aegilops* group; Mendlinger and Zohary, 1995) annual grass (for details about species ecology see Supplementary Material). Its distribution is in the 'Fertile Crescent', an area comprising hilly and mountainous parts of southeastern Turkey, northeastern Iraq and southwestern Iran and continuing southwestward into Syria, Jordan and Israel (Zohary and Hopf, 2000; Feldman and Kislev, 2007; Özkan *et al.*, 2011). The dense natural populations are frequent in the Upper Jordan Valley catchment area, whereas elsewhere in the Fertile Crescent, populations are small, isolated and patchily distributed (Feldman and Kislev, 2007; Özkan *et al.*, 2011) (Figure 1). The distribution of this species is known in great detail (Özkan *et al.*, 2011), and all populations known to-date in Israel are depicted on Figure 1.

We sampled two populations representing the species distributional core in the Upper Jordan Valley catchment area (K and N), and two populations from the two opposite edges of species distributional range (cold edge MH and hot edge HA) (Figure 1; see Supplementary Methods for details on sampling locations). Sampling was done in 2007. From each sampled plant we took a separately bagged spike and precise GIS (geographic information system) coordinates of its location. The number of sampled plants was 70, 68, 57 and 94 for K, N, MH and HA locations, respectively.

We are fully aware of the drawbacks of a sampling design with no replication. However, there is only population of wild emmer wheat in a location with <400 mm rainfall (true species periphery), making replicated sampling design impossible. The hot edge HA population is distributed over a very limited area of <1 ha and comprises several hundred individuals. Despite fluctuating demography (S Volis, personal observations) typical for an annual species inhabiting arid environment with unpredictable amount and timing of rainfall, the population does not appear to be prone to extinction because of the presence of a soil seed bank for the species and the location micro-relief with soil pockets among large rocks serving as refuges in years with heavy grazing. The other three sampled populations comprise thousands of plants.

As our study included several methodologically different experiments, we provide a general scheme of the study design in Figure 2.

Transplant experiment
We designed our transplant experiment to test for relative performance (RP) of (1) planted individuals and (2) their progeny (that is, population size over generations). The latter is possible if the origin of the plants in the experimental population is identified and relative fitness is estimated as the proportion of plants/seeds of particular origin in the total number of plants/seeds. For this purpose we selected four simple sequence repeat markers for the molecular genotype identification. As soon as four markers allowing easy identification of the accession origin to one of the four populations were chosen, we randomly chose five accessions per population for which unequivocal population origin identification with these markers was proved. These accessions were planted before experiment in a greenhouse to obtain the necessary amount of seeds and to remove/reduce maternal effects. These seeds were genetically identical to the mother plant. The propagated seeds were used for creation of random combinations of accessions to be reciprocally transplanted.

In the transplant experiment, randomly located replicated plots contained 36 seeds arranged equidistantly in six 50 cm long strips spaced 10 cm apart. In each strip, six seeds individually placed in Eppendorf tubes open from both sides and filled with the soil from the burial site were buried at 10 cm intervals so that tube edge was at ground level. Each plot comprised a set of either 4 accessions representing populations HA, K, N and MH replicated 9 times, or 3 accessions (populations HA, K and MH replicated 12 times) arranged regularly as in a checkerboard (Figure 2). In November 2007, sets of three accessions were planted at the MH and HA sites and sets of four accessions were planted at the K and N sites. The vegetation and litter within plots plus 30 cm around was carefully removed. Each tube was tagged with a wire attached to the tube and painted with a fluorescent paint to allow subsequent detection. Ten plots were established at the MH and HA sites and nine plots at the K and N sites. In addition, five plots (that is, five sets of three accessions) were established beyond the current range of *T. dicoccoides*, in the Negev desert (Beer Sheva location–Bergman Campus) with ∼200 mm of annual rainfall. Plant fate was followed throughout the season and seed germination, plant mortality and number of seeds produced were recorded. The seeds were counted on a plant before shattering, allowed to fall and left untouched. This procedure made possible (1) the estimation of such fitness components as survival, fecundity and the overall fitness for each introduced seed at the end of the first season; and (2) the estimation of accession success over time using genotyping with simple sequence repeat markers.

As seeds of *T. dicoccoides* possess dormancy and can stay viable in the soil for at least 1 year, in the introduction year only fitness of germinated seeds was assessed using $RP = (w_a - w_l)/max(w_a, w_l)$, where w_l was the fecundity of plants of local origin, and w_a was the fecundity of plants of nonlocal origin (aliens). The RP values were calculated for each accession within a plot within a transplant site. The fitness of plants of different origins at 4 years after transplantation was estimated as number of seeds relative to the total seed pool. The RP values of plants of different origins in the introduction year were analyzed over plots by one-sample *t*-test. Similarly, the observed proportions of seeds of different origins in plots at 4 years after introduction were at first subtracted from those expected under no selective advantage (that is, equal for all accessions) and then analyzed over plots by one-sample *t*-test.

The performance of plants of different origins at Beer Sheva location was compared using aster modeling of individual and group lifetime fitness (Geyer *et al.*, 2007; Shaw *et al.*, 2008) as implemented in R (R Development Core Team, 2009). The life-history stages that we modeled, and their statistical distributions, for the first year assessment were early-season seed germination (Bernoulli), whether a plant reproduced or not (Bernoulli) and total seeds per plant (Poisson). For the fourth year assessment, we had to reshape data for analysis following Stanton-Geddes *et al.* (2012a, b) because it was not an individual-based but a group-level aster analysis that starts with a 'root' of 12 as the number of seeds of particular origin sown in first year. The life-history stages that we modeled, and their statistical distributions, were number of plants (Poisson) and number of seeds (zero-truncated negative binomial). As the current aster package automatically accommodates only single-parameter exponential family distributions, the size parameters for the negative binomial distributions were chosen by fitting that distribution (fitdistr function in library MASS; Venables and Ripley, 2002 in R) to the conditional distribution of seeds counted. For each pair-wise population comparison, a likelihood ratio
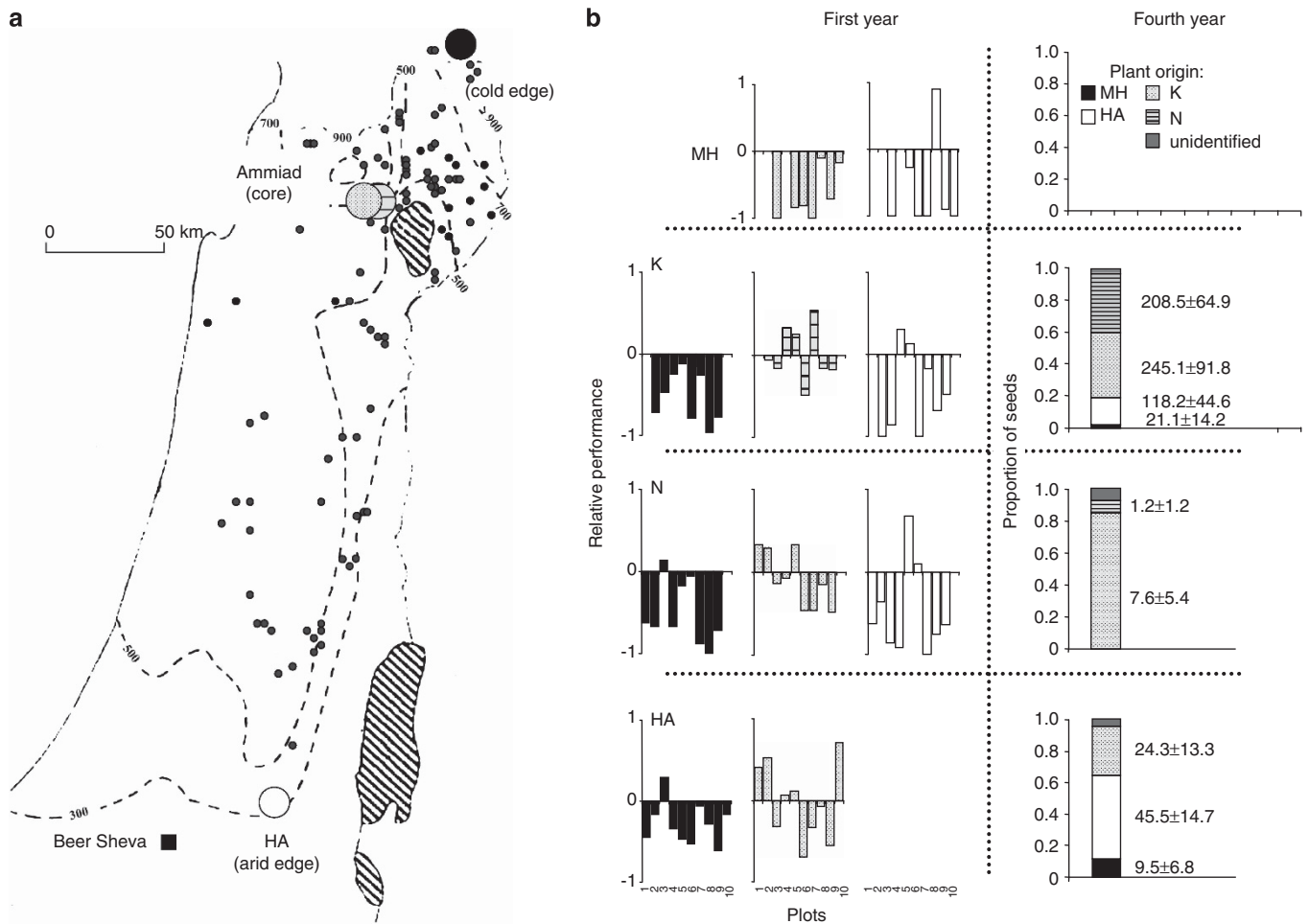
Figure 1 (**a**) Map of Israel showing isohyets of multiyear averages of annual rainfall amount (mm), distribution of *T. dicoccoides*, study populations and transplant locations. Dots mark known populations of *T. dicoccoides* based on data of the Institute for Cereal Improvement (Israel). (**b**) Performance of alien plants relative to the natives in the year of planting (left) and proportions of seeds of different origins at 4 years after planting (right) in each of the four locations in the reciprocal transplant experiment. No plants survived after 4 years at the MH location. Numbers next to the bars denote average number of seeds (±s.e.) of particular origin per plot.

Figure 2 Scheme of the study design and the addressed scientific questions.

Table 1 Summary of results from aster model comparisons testing the effect of population origin on individual (first year) and group (fourth year) fitness at Beer Sheva transplant location

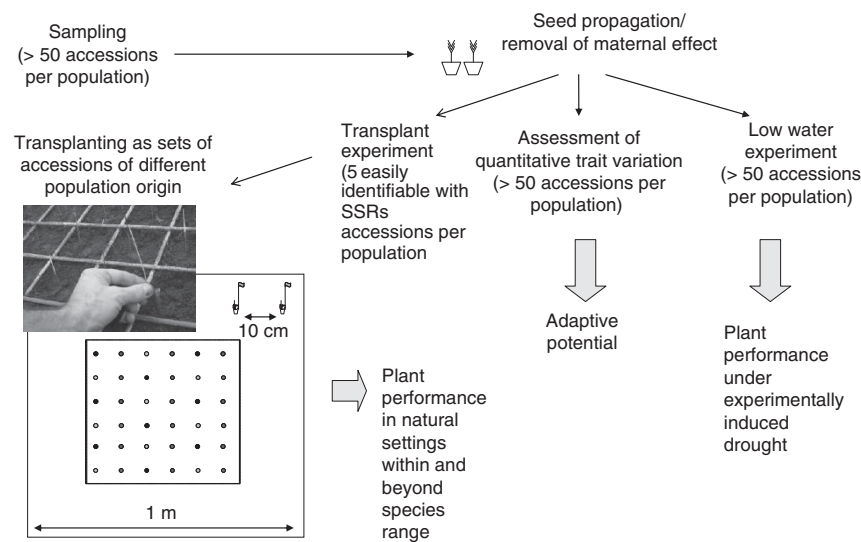| Model	Model d.f.	Test d.f.	Test deviance	P-value	Model d.f.	Test d.f.	Test deviance	P-value
First year (3 pop.)					*Fourth year (3 pop.)*			
Full	3				2			
Block	7	4	39.3	<0.0001	4	2	3.0	0.23
Population	9	2	56.5	<0.0001	6	2	63.1	<0.0001
First year (HA vs *MH)*					*Fourth year (HA* vs *MH)*			
Full	3				2			
Block	7	4	47.7	<0.0001	4	2	0.9	0.62
Population	8	1	3.0	0.08	5	1	0.1	0.73
First year (HA vs *K)*					*Fourth year (HA* vs *K)*			
Full	3				2			
Block	7	4	37.7	<0.0001	4	2	10.6	<0.0001
Population	8	1	46.7	<0.0001	5	1	64.5	<0.0001
First year (K vs *MH)*					*Fourth year (K* vs *MH)*			
Full	3				2			
Block	7	4	28.6	<0.0001	4	2	0.5	0.90
Population	8	1	33.3	<0.0001	5	1	44.4	<0.0001

Abbreviations: HA, Har Amasa; K, Ammiad Karst; MH, Mount Hernon.
Likelihood ratio tests were used to compare the fit of the full model with reduced models that sequentially dropped terms. Analysis of deviance (-2 log likelihood) and χ^2 P-values for each model test are listed.

test compared the fit of the full model with reduced models that sequentially dropped terms.

Assessment of quantitative trait variation

Seeds from the plants separated by >1 m in each of the four populations were used for analysis of extent and structure of genetic variation in 11 quantitative traits. Sample sizes are given in Table 2. Seeds were simultaneously germinated at 24 °C and transferred into 3-l pots arranged in a greenhouse at the Bergman Campus, Beer Sheva, using a block design. The 54–65 accessions (= families) were sown for each source population and each accession was represented by three individually planted seeds. The pots were filled with commercial potting mixture. During the experiment, the plants received amount of water equivalent to 1058 mm of rainfall. Watering was done twice a week through a drip-irrigation system. The measured quantitative traits included tiller height (TH), flag and penultimate leaf length and width (FLL, PLL, FLW and PLW), spike length (SPL), awn length (AWL), number of spikelets in a spike (NSP), number of days to awning (DAW) and seed maturation (DMT). At senescence, mean spikelet weight (SWT) was obtained from the total number of spikelets and total seed mass per plant.

As *T. dicoccoides* is highly selfing, we did not separate total genetic variance into additive and nonadditive components and used only the total genetic variation because this is the variation important to selection in selfing species (see, for example, Banta *et al.*, 2007). Population pairwise comparisons of genetic variance were done using the program pcrf1, part of the software Quercus (Shaw, 1991). The estimates of population genetic and environmental variance were made with and without the pair of variance–covariance matrices constrained to be the same, and the fit of the models compared using two times the difference in log-likelihood that has χ^2 distribution. The matrices were constrained to be positive definite, so that variances were nonnegative. The estimated variance components were then used to calculate the broad-sense heritability H^2.

Low water experiment

Simultaneously with the common garden experiment and at the same location, we conducted another experiment in a greenhouse to study selective responses of accessions from the four populations to simulated drought stress conditions in an extremely arid environment. The 3-l pots were filled with commercial potting mixture. The amount of water supplied to the plants was kept at minimum necessary for plants to survive and reproduce. Because of the high evaporation rate in the greenhouse because of different soil and ambient temperatures as compared with natural conditions, the amount of water supplied (equivalent to 460 mm of rainfall) is impossible to convert into naturally occurring precipitation, but plants were showing signs of suffering from drought (low turgor and wilting of leaves) during the whole experiment. The same accessions with those in the common garden experiment were used: 56, 52, 52 and 64 accessions for population (MH, K, N and HA, respectively). The accessions were not replicated. The same traits as in the common garden experiment were measured. The trait selection effects were calculated using data on all measured plants (that is, 227 plants). The effect of population origin on plant performance (total weight of mature spikelets produced by a plant) was tested by one-way analysis of variance. Relative fitness was estimated as the total weight of mature spikelets produced by a plant relative to the maximum observed total weight of mature spikelets per plant. This measure of fitness is preferred over the total number of spikelets per plant as spikelet weight varies greatly among populations and individuals with a tradeoff between number of spikelets and individual spikelet weight. Selection differentials (α) were calculated as a covariance of relative fitness with the standardized traits. As effects of traits on fitness could be indirect and mediated by other traits, we estimated the direct effects by linear selection gradients. To obtain selection gradients, before the analysis the highly inter-correlated variables (those with correlation coefficient >0.7) were subjected to factor analysis to avoid multicollinearity (see Supplementary Table 1). The derived variables (rotated factors) can be called leaf size (FLL, PLL, FLW and PLW), reproductive structure size (SPL and AWL) and phenology (DAW and DMT). The derived variables and original variables TH, NSP and SWT were regressed on the relative fitness. To account for the effect of population origin, the categorical variable ORIGIN was added as a predictor variable to the analysis done using General Linear Model of Statistica (StatSoft Inc., 2004). Predicted population evolutionary change in response to increasing aridity was calculated using the breeders equation $R = H^2 \alpha$.

RESULTS

Plant performance in reciprocal transplant experiment

In the reciprocal transplant experiment, in the year of planting, the average RP of plants of nonlocal origin analyzed over plots by

Table 2 Population mean ± s.e., genetic variance component (in parentheses) and broad-sense heritability (in bold) for 11 quantitative traits in the common garden experiment; and selection differentials and linear selection gradients (± s.e.) in the low water experiment

Population	n	TH	DAW	DMT	NSP	SWT	SPL	AWL	FLL	FLW	PLL	PLW
Common garden experiment												
HA	65	67.1 ± (16.9) 0.8b **0.23**	141.3 ± (39) 0.8c **0.62**	173.5 ± (11) 0.5b **0.47**	20.5 ± (4.80) 0.3b **0.69**	87.4 ± (156) 1.9b **0.46**	25.7 ± (2.85) 0.2b **0.50**	15.0 ± (3.18) 0.2b **0.66**	14.2 ± (1.30) 0.3b **0.13**	0.96 ± (0.08) 0.01b **0.05**	20.3 ± (5.15) 0.4b **0.25**	1.01 ± (0.46) 0.01b **0.19**
K	54	76.9 ± (40.0) 1.0c **0.44**	127.1 ± (181) 1.9a **0.76**	162.3 ± (146) 1.7a **0.74**	16.9 ± (3.24) 0.3a **0.45**	154.7 ± (106) 2.2d **0.22**	26.3 ± (4.84) 0.3c **0.65**	16.5 ± (6.73) 0.4c **0.83**	21.1 ± (47.2) 1.0c **0.75**	1.41 ± (5.74) 0.04c **0.61**	28.5 ± (29.1) 0.8c **0.61**	1.43 ± (3.86) 0.03c **0.59**
N	56	70.3 ± (26.3) 0.9b **0.30**	134.5 ± (155) 1.7b **0.87**	170.0 ± (129) 1.5b **0.89**	16.5 ± (4.43) 0.3a **0.72**	139.2 ± (425) 3.3c **0.62**	26.6 ± (2.72) 0.2c **0.52**	16.9 ± (2.70) 0.2c **0.63**	13.7 ± (5.67) 0.4b **0.43**	1.00 ± (0.92) 0.02b **0.23**	21.7 ± (7.85) 0.5b **0.30**	1.06 ± (1.16) 0.02b **0.44**
MH	56	62.0 ± (9.9) 0.8a **0.10**	155.6 ± (11) 0.6d **0.41**	182.9 ± (8) 0.5c **0.46**	21.9 ± (6.39) 0.4c **0.73**	55.3 ± (42) 1.3a **0.34**	22.6 ± (1.94) 0.2a **0.32**	12.4 ± (2.47) 0.2a **0.58**	9.2 ± (2.42) 00.3a **0.37**	0.67 ± (0.34) 0.01a **0.24**	13.5 ± (5.46) 0.4a **0.37**	0.75 ± (0.13) 0.01a **0.13**
Low water experiment												
Selection differential (α)		0.51***	−0.53***	−0.49***	−0.29**	0.70**	0.51***	0.50***	0.40***	0.56**	0.50***	0.55**
Selection gradient (β)		0.03 ± 0.06 NS	0.05 ± 0.06 NS	0.05 ± 0.08 NS	0.24 ± 0.06***	0.74 ± 0.11***	0.16 ± 0.08*	0.16 ± 0.08*		0.16 ± 0.06*		

Abbreviations: AWL, awn length; DAW, number of days to awning; DMT, number of days to seed maturation; FLL, flag leaf length; FLW, flag leaf width; HA, Har Amasa; K, Ammiad Karst; MH, Mount Hernon; N, Ammiad North; n, number of accessions; NS, not significant; NSP, number of spikelets in a spike; PLL, penultimate leaf length; PLW, penultimate leaf width; SPL, spike length; TH, tiller height. For highly intercorrelated variables, selection gradients were calculated for derived variables (rotated factors). Letters denote the results of Tukey's honest significant difference (HSD) test.
*P<0.05; **P<0.01 and ***P<0.001.

Figure 3 (**a**) Annual precipitation at Beer Sheva transplant location over the past half century. The solid line is the multiyear average. Broken lines indicate the period of transplant experiment. (**b**) Performance of plants (means and s.e. of total number of seeds produced) in the year of planting and proportions of seeds of different origins at 4 years after planting at Beer Sheva transplant location. Numbers next to the bars denote average number of seeds (± s.e.) of particular origin per plot.

one-sided *t*-test was significantly or marginally significantly different from zero for HA and K origin at MH site (−0.61 ± 0.27 and −0.70 ± 0.14, t_6 = 2.2 and 4.7, P<0.10 and <0.01), MH origin at HA site (−0.28 ± 0.09, t_9 = 3.3, P<0.01), MH and HA origin at K site (−0.55 ± 0.11 and −0.47 ± 0.18, t_7 = 5.0 and 2.6, P<0.01 and <0.05) and MH and HA origin at N site (−0.52 ± 0.13 and −0.49 ± 0.18, t_8 = 3.4 and 2.3, P<0.05 and <0.10).

In neither of the two core populations (K and N) were the locals superior over plants from the second population (0.01 ± 0.12 and −0.08 ± 0.13, t_7 = 0.1 and t_8 = 1.0, P>0.10 at K and N sites, respectively).

At 4 years after transplantation, the RP of plants of different origins was estimated as either number of seeds relative to the total seed pool or plants relative to the total number of plants per plot (because of high similarity of these results, only the proportion of seeds over all plots per site are shown in Figure 1). The proportion of seeds and plants of native origin was significantly higher than expected under no local selection at HA site (expected value for HA = 0.333, t_8 = 2.4 and 2.3, P<0.05) and at K and N sites when expected proportions of both K and N were pooled (that is, treating K and N as identical origin (expected value for K + N = 0.5; K site t_8 = 4.2 and 5.3, P<0.01; N site t_3 = 41.0 and 15.0, P<0.001 and <0.01). No germinated seeds were observed at MH site from 1 year after transplantation.

The proportion of seeds and plants of K and N origins did not differ from expected under no local selection at K site (t_7 = 1.7 and 1.9, P>0.10), whereas the proportion of K plants was higher than expected at N site (t_3 = 9.5, P<0.05).

At Beer Sheva location, the K accessions were superior over both HA and MH accessions in the year of transplanting and 4 years after transplanting in aster modeling analysis (Table 1 and Figure 3).

Table 3 Overall quantitative trait differences among the four populations

Population	$F_{33, 647}$	Population			
	60.8^{***}	HA	K	N	MH
HA		—	72.9***	30.4***	21.4***
K	3.70	—		24.7***	143.4***
N	1.54	1.25	—		81.0***
MH	1.08	7.27	4.05	—	

Abbreviations: HA, Har Amasa; K, Ammiad Karst; MH, Mount Hernon; N, Ammiad North. The results of pairwise contrasts in MANOVA are shown as Hotelling–Lawley trace (below diagonal) and approximate $F_{11, 217}$ with a significance after sequential Bonferroni adjustment (above diagonal).
***$P < 0.001$.

Extent and structure of phenotypic variation

Population means and genetic variance for 11 quantitative traits measured in the greenhouse are shown in Table 2. The four populations differed over all traits analyzed simultaneously in each pairwise comparison (Table 3). Plants from K and N flowered earlier, had smaller number but heavier spikelets in a spike and larger spikes with longer awns than HA and MH accessions. The K and N plants differed from each other in size of flag and penultimate leaf, spikelet weight, time to flowering and maturation and TH. The MH plants differed from plants of other origin in all the traits measured. Plants from HA had values intermediate between MH and the other two origins (K and N) in DAW, NSP, SWT, SPL and AWL, but resembled plants of N origin in TH, DMT and all the leaf size traits (Table 2).

Partitioning of total phenotypic variance into genetic and environmental components and pairwise population comparisons revealed higher genetic variance in K vs HA and MH (6 and 10 traits, respectively) and N vs HA and MH (5 and 5 traits, respectively). For no trait K and N populations had lower genetic variance than either HA or MH population (Table 4). Multivariate population pairwise comparison of genetic variance for three groups of traits detected higher genetic variance in K vs HA and MH in all three groups of traits and in N vs HA and MH in three and two groups of traits, respectively (Table 4). Trait heritability and response to selection varied among populations with no consistent differences between the core and peripheral populations (Table 2 and Figure 4).

Plant performance under drought

Under drought, population origin had a significant effect on plant performance ($F_{3, 129} = 20.6$, $P < 0.001$, one-way analysis of variance). The K and N plants had higher total seed weight (8.1 ± 0.4 and 6.7 ± 0.5 g, respectively) than the HA and MH plants (5.3 ± 0.3 and 3.7 ± 0.3 g, respectively). This order followed the order observed under favorable conditions in the common garden experiment (17.7 ± 0.4, 17.5 ± 0.3, 13.6 ± 0.3 and 6.6 ± 0.3 g for K, N, HA and MH plants, respectively).

There was a directional negative selection on DAW, DMT and NSP, and positive selection on all other traits for relative fitness estimated by total weight of fertile spikelets per plant (Table 2). A significant positive selection gradient was detected for SPW and NSP and for the derived from SPL and AWL variable (Reproductive structure size) (Table 2). All the other variables had no direct effect on relative fitness.

Table 4 Pairwise population comparison of genetic variance components for single traits and three trait groups, phenology (DAW, DMT), leaf size (FLL, FLW, PLL, PLW) and reproduction (NSP, SWT, SPL, AWL)

Traits	d.f.	HA–K	HA–N	HA–MH	MH–K	MH–N	K–N
TH	1	3.1 NS	0.8 NS	0.4 NS	4.5*	1.7 NS	0.8 NS
DAW	1	23.8***	21.3***	11.7***	60.2***	57.2***	0.3 NS
DMT	1	54.6***	57.4***	1.0 NS	64.8***	62.9***	0.2 NS
NSP	1	1.2 NS	0.1 NS	0.9 NS	3.6 NS	1.4 NS	0.7 NS
SWT	1	0.5 NS	8.4**	30.5***	119.8***	43.0***	10.2**
SPL	1	2.4 NS	0.1 NS	0.9 NS	5.4*	0.7 NS	2.7 NS
AWL	1	6.1*	0.2 NS	0.6 NS	9.9**	0.1 NS	8.5**
FLL	1	67.0***	6.6*	0.8 NS	63.8***	3.9*	36.6***
FLW	1	47.1***	5.1*	1.6 NS	42.0***	2.3 NS	18.1***
PLL	1	17.6***	0.6 NS	0.1 NS	18.5***	0.5 NS	10.5**
PLW	1	22.9***	3.4 NS	2.3 NS	41.8***	15.1***	10.4**
Phenology	3	67.6***	65.6***	14.3**	72.3***	76.7***	4.9 NS
Leaf size	10	126.8***	29.7***	10.6 NS	133.4***	0.1 NS	98.1***
Reproduction	10	46.8***	40.0***	37.6***	58.1***	76.4***	50.0***

Abbreviations: AWL, awn length; DAW, number of days to awning; DMT, number of days to seed maturation; FLL, flag leaf length; FLW, flag leaf width; HA, Har Amasa; K, Ammiad Karst; MH, Mount Hernon; N, Ammiad North; NS, not significant; NSP, number of spikelets in a spike; PLL, penultimate leaf length; PLW, penultimate leaf width; SPL, spike length; TH, tiller height. Likelihood ratio tests were used to compare the fit of the constrained and unconstrained models that estimated genetic variance. Analysis of deviance (-2 log likelihood) and significance of χ^2 P-values for each test are listed.
*$P < 0.05$, **$P < 0.01$ and ***$P < 0.001$.

DISCUSSION

The transplant experiment provided a convincing evidence of local adaptation in *T. dicoccoides* that resulted from divergent selection across the species range. In the three macroenvironments that corresponded to the species cold range edge, core and arid range edge, local accessions exhibited a home advantage. At the species core, the N and K accessions did not differ in performance across the two microhabitats, suggesting no difference in local selection between the two habitats. However, the local conditions at the two core locations were clearly different as evident in very different survival and sizes of experimental populations after 4 years. These differences are most likely to be the result of fine-scale topographic differences and associated biotic interactions (grazing, competition).

The fact that no plants survived at the cold range edge transplant location after four generations suggests a stronger local selection and much steeper gradient of the major distribution limiting factor (cold) in this part of the species range. In contrast, at the arid range edge and beyond it, effect of insufficient rainfall and associated drought may not be evident within a relatively short time spell of several years. As seeds of *T. dicoccoides* can stay dormant in the soil seed bank for 1 year (Horovitz, 1998), a population can survive a year with an amount of rainfall below a threshold for plant survival and reproduction. However, two consecutive drought years will drive a population to extinction. This can explain why the experimental population at Beer Sheva survived after 4 years, but no population of *T. dicoccoides* is found in an area with < 300 mm of rainfall.

Beside strength of divergent selection, evolution across species ranges depends on extent of among-population gene flow and differences in effective population sizes (Turelli, 1997; Leimu et al., 2006; Kawecki, 2008). It is often assumed, in accord with the abundant center hypothesis, that effective population sizes are larger and genetic drift is smaller at the range center as compared with the range periphery, and hence genetic diversity and adaptive genetic potential in central populations is higher than in peripheral
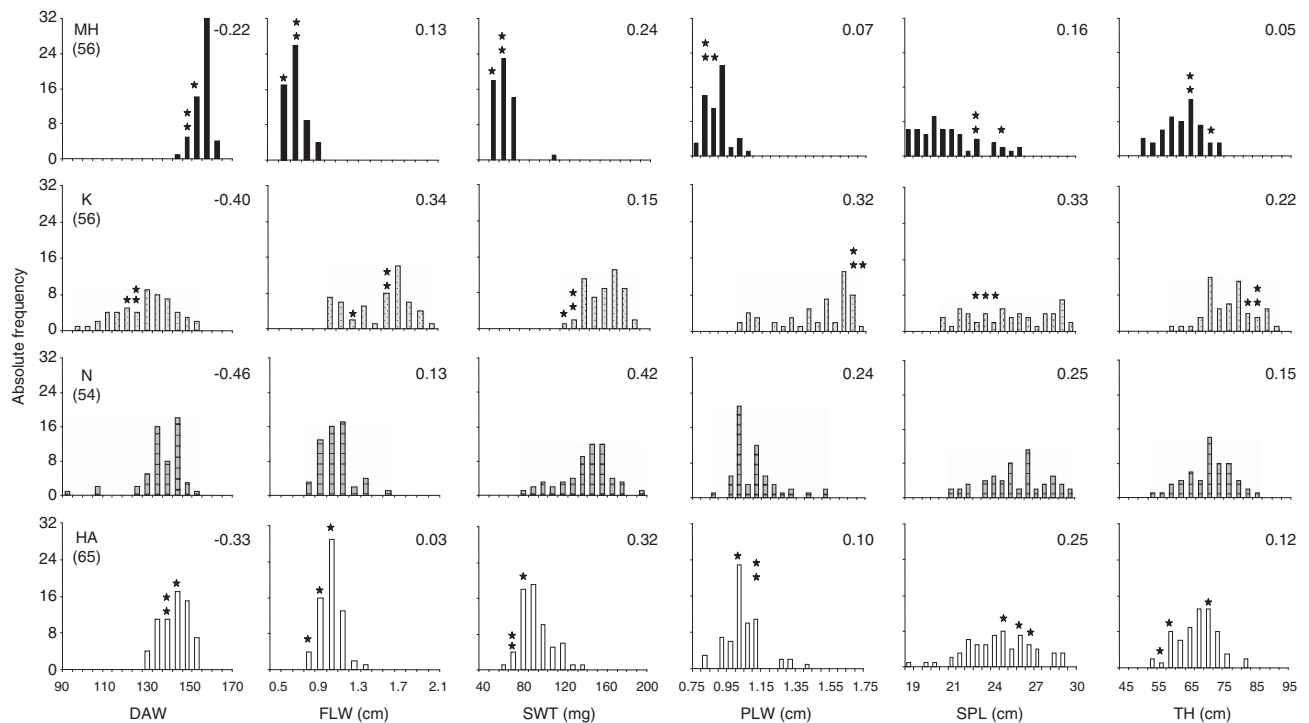
Figure 4 Population/habitat frequency distribution and response to selection calculated as R = H²α of the traits measured in the common garden experiment with selection differential (α) >0.5, and the number of accessions per population/habitat (in parenthesis). Accessions introduced at Beer Sheva location are denoted with an asterisk.

populations. This is a common explanation to why peripheral populations do not expand beyond range edges.

Analysis of quantitative trait variation revealed lower genetic variation in the two peripheral as compared with the two core populations for some although not all analyzed traits, and in no trait any peripheral population have had higher variation than any of the two core populations. This indicates a lower adaptive potential of the two peripheral as compared with the two core populations. Our next step was to compare performance of the plants having different population origins in the novel, but anticipated, environmental conditions. By introducing plants beyond the current species range, namely, into the desert location, we tested whether the adaptive potential, inferred from the genetic variation in important for adaptation quantitative traits, will be related to plant performance in novel conditions.

The transplant experiments conducted at two temporal scales and organization levels (one-generation individual and four-generation population) revealed that both edge populations were locally adapted to their marginal conditions as indicated by a home advantage (Figure 1). We therefore expected that the plants from the HA edge population would outperform plants of the other populations when transplanted to the Negev desert site with extremely arid conditions. Surprisingly, the opposite was the case, and plants from the core population K outperformed plants from the arid edge population HA in the year of transplanting and over both MH and HA genotypes 4 years after transplanting (Figure 3). Better performance under novel conditions of plants from core populations is usually explained by reduced adaptive potential of the edge populations (Stanton and Galen, 1997; Helenurm, 1998; Geber and Eckhart, 2005; Emery et al., 2010), inferred from a general reduction in genetic variation in these populations (see, for example, Moeller et al., 2011). However, our study is the first that experimentally demonstrated a relationship

between these two population properties, namely, variation in quantitative traits and plant performance in natural conditions beyond the current species range.

To understand the counterintuitive inferior performance of the HA plants originating from the most arid for *T. dicoccoides* environment in the more arid Negev desert test site, we conducted a selection experiment. The selection analysis of experimentally induced drought effect indicates that the poorer performance of the HA plants outside the species range is directly related to their poorer adaptation to drought than the Ammiad (that is, K and N) plants. If we (1) consider the involvement of the measured quantitative traits in selection to drought stress (Table 2); (2) compare population/habitat frequency distributions of these traits and finally (3) mark the frequency distribution location of each accession planted at Beer Sheva location (Figure 4), we can see a clear pattern of selective advantage of the three accessions (those from the plots where introduced populations did not get extinct after 4 years) from the Ammiad population over accessions from MH and HA. Thus, inferiority of HA phenotypes appears to come from lower selective value in traits that are involved in adaptation to drought (start of flowering, leaf and seed sizes). As for superior fitness of HA plants in their own environment, it appears to be because of involvement of currently unknown abiotic and/or biotic interactions beside the effect of aridity.

Increasing aridity leads to shortening of growing season, and populations from arid habitats were found to flower earlier than in more mesic sites in many annual and perennial species (Aronson et al., 1992; Bennington and McGraw, 1995; Del Pozo et al., 2002; Eckhart et al., 2004; Franke et al., 2006; Hall and Willis, 2006; Volis, 2007). Selection for advance of flowering was found in several studies with experimentally induced drought stress (Stanton et al., 2000; Volis et al., 2004; Franks et al., 2007) and in a reciprocal transplant experiment with one desert and one Mediterranean site (Volis et al.,

2002). Although effects of flowering and maturation time on fitness in our study were found to be indirect and mediated by other traits, under drought, plants that flowered and set seeds earlier had higher fitness. Similarly, early flowering was associated with higher fitness under experimentally induced drought stress in the study by Peleg et al. (2005). Surprisingly, in our study, plants from arid range location HA flowered and produced seeds later than the plants from the two more mesic core locations (Table 2 and Figure 4). This means that plants from the species core were preadapted better to extremely arid Beer Sheva location.

Negative selection on days to flowering and positive selection on individual spikelet weight under water stress was also observed in a methodologically similar study done on wild barley (Volis et al., 2004). Selection on seed size is complex, and optimal seed size appears to be a compromise between two selective forces acting in opposite directions (selection for seedling vigor and seed predation effect) (Gomez, 2004). The latter effect was absent in our introduction experiment at Beer Sheva location, whereas the first one was definitely present.

Few empirical studies have examined the adaptive potential of edge vs core populations. Pujol and Pannell (2008) found a reduced potential to respond to selection after expansion and lower neutral genetic variation in edge populations. However, peripheral populations demonstrated improved adaptive potential if gene flow was occurring between differentiated peripheral populations (Lavergne and Molofsky, 2007; Sexton et al., 2011; Volis, 2011). Potential positive effects of gene flow among peripheral populations include creation of new combinations of alleles with enhanced fitness (Volis, 2011) and purging of deleterious mutations that lead to inbreeding depression (Pujol et al., 2009; Facon et al., 2011). Thus, the reduced adaptive potential of the HA population appears to be a result of its extreme isolation from other peripheral population. As for the reduced adaptive potential of the MH population, it is most probably because of isolation from core and other peripheral populations and fixation of favorable alleles under strong local selection.

An important conclusion having conservation implications is that plants from the species extreme periphery with conditions seemingly closest to those in the new environment may have in this environment poorer fit than plants from much more favorable conditions of the species distributional core. This does not mean that peripheral populations in general have lower potential to adapt to changing environmental conditions than core populations. However, because peripheral populations are smaller, more isolated and often experience stronger local selection than core populations, usage of peripheral populations must be based on more intensive sampling of among-population variation.

DATA ARCHIVING
Data available from the Dryad Digital Repository: doi:10.5061/dryad.b59v1.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

Alleaume-Benharira M, Pen IR, Ronce O (2006). Geographical patterns of adaptation within a species' range: interactions between drift and gene flow. J Evol Biol 19: 203–215.
Anav A, Mariotti A (2011). Sensitivity of natural vegetation to climate change in the Euro-Mediterranean area. Climate Res 46: 277–292.
Angert AL, Bradshaw AD, Schemske DW (2008). Using experimental evolution to investigate geographic range limits in monkeyflowers. Evolution 62: 2660–2675.
Anikster Y, Noy-Meir I (1991). The wild-wheat field laboratory at Ammiad. Isr J Bot 40: 351–362.
Aronson J, Kigel J, Shmida A, Klein J (1992). Adaptive phenology of desert and Mediterranean populations of annual plants grown with and without water stress. Oecologia 89: 17–26.
Banta JA, Dole J, Cruzan MB, Pigliucci M (2007). Evidence of local adaptation to coarse-grained environmental variation in Arabidopsis thaliana. Evolution 61: 2419–2432.
Bell G, Gonzalez A (2011). Adaptation and evolutionary rescue in metapopulations experiencing environmental deterioration. Science 332: 1327–1329.
Bennington CC, McGraw JB (1995). Natural selection and ecotypic differentiation in Impatiens pallida. Ecol Monogr 65: 303–323.
Blows MW, Hoffmann AA (2005). A reassessment of limits to evolutionary change. Ecology 86: 1371–1384.
Del Pozo A, Ovalle C, Aronson J, Avendano J (2002). Ecotypic differentiation in Medicago polymorpha L. along an environmental gradient in central Chile. I. Phenology, biomass production and reproductive patterns. Plant Ecol 159: 119–130.
Eckhart VM, Geber MA, McGuire CM (2004). Experimental studies of adaptation in Clarkia xantiana. I. Sources of trait variation across a subspecies border. Evolution 58: 59–70.
Emery NC, Rice KJ, Stanton ML (2010). Fitness variation and local distribution limits in an annual plant population. Evolution 65: 1011–1020.
Etterson JR, Shaw RG (2001). Constraint to adaptive evolution in response to global warming. Science 294: 151–154.
Facon B, Hufbauer RA, Tayeh A, Loiseau A, Lombaert E, Vitalis R et al. (2011). Inbreeding depression is purged in the invasive insect Harmonia axyridis. Curr Biol 21: 424–427.
Feldman M, Kislev ME (2007). Domestication of emmer wheat and evolution of free-threshing tetraploid wheat. Isr J Plant Sci 55: 207–221.
Franke DM, Ellis AG, Dharjwa M, Freshwater M, Fujikawa M, Padron A et al. (2006). A steep cline in flowering time for Brassica rapa in southern California: population-level variation in the field and the greenhouse. Int J Plant Sci 167: 83–92.
Franks SJ, Sim S, Weis AE (2007). Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. Proc Natl Acad Sci USA 104:4 1278–1282.
Fritz SE, Lukaszewski AJ (1989). Pollen longevity in wheat, rye and triticale. Plant Breed 102: 31–34.
Gao X, Giorgi F (2008). Increased aridity in the Mediterranean region under greenhouse gas forcing estimated from high resolution simulations with a regional climate model. Global Planet Change 62: 195–209.
Geber MA, Eckhart VM (2005). Experimental studies of adaptation in Clarkia xantiana. II. Fitness variation across a subspecies border. Evolution 59: 521–531.
Geyer CJ, Wagenius S, Shaw RG (2007). Aster models for life history analysis. Biometrika 94: 415–426.
Giorgi F, Lionello P (2008). Climate change projections for the Mediterranean region. Glob Planet Change 63: 90–104.
Golenberg EM (1987). Estimation of gene flow and genetic neighborhood size by indirect methods in a selfing annual, Triticum dicoccoides. Evolution 41: 1326–1334.
Gomez JM (2004). Bigger is not always better: conflicting selective pressures on seed size in Quercus ilex. Evolution 58: 71–80.
Griffith TM, Watson MA (2006). Is evolution necessary for range expansion? Manipulating reproductive timing of a weedy annual transplanted beyond its range. Am Nat 167: 153–164.
Hall MC, Willis JH (2006). Divergent selection on flowering time contributes to local adaptation in Mimulus guttatus populations. Evolution 60: 2466–2477.
Helenurm K (1998). Outplanting and differential source population success in Lupinus guadalupensis. Conserv Biol 12: 118–127.
Hoffmann AA, Blows MW (1994). Species borders: ecological and evolutionary perspectives. Trends Ecol Evol 9: 223–227.
Holt RD, Keitt TH (2000). Alternative causes for range limits: a metapopulation perspective. Biol Lett 3: 41–47.
Holt RD, Keitt TH (2005). Species' borders: a unifying theory in ecology. Oikos 108: 18–27.
Horovitz A (1998). In Zencirci N, Kaya Z, Anikster Y, Adams WT (eds) Proceedings of International Symposium on In Situ Conservation of Plant Genetic Diversity. Central Research Institute for Field Crops: Ankara, Turkey, pp 185–188.
Kawecki TJ (2008). Adaptation to marginal habitats. Ann Rev Ecol Syst 39: 321–342.
Lavergne S, Molofsky J (2007). Increased genetic variation and evolutionary potential drive the success of an invasive grass. Proc Natl Acad Sci USA 104: 3883–3888.
Leimu R, Mutikainen P, Koricheva J, Fischer M (2006). How general are positive relationships between plant population size, fitness and genetic variation? J Ecol 94: 942–952.
Lennon JJ, Turner JRG, Connell D (1997). A metapopulation model of species boundaries. Oikos 78: 486–502.

Mayr E (1963). *Animal Species and Evolution*. Harvard University Press: Cambridge, MA.

Mendlinger S, Zohary D (1995). The extent and structure of genetic variation in species of the Sitopsis group of *Aegilops*. *Heredity* **74**: 616–627.

Moeller DA, Geber MA, Tiffin P (2011). Population genetics and the evolution of geographic range limits in an annual plant. *Am Nat* **178**: S44–S57.

Özkan H, Willcox G, Graner A, Salamini F, Kilian B (2011). Geographic distribution and domestication of wild emmer wheat (*Triticum dicoccoides*). *Genet Res Crop Evol* **58**: 11–53.

Parmesan C (2006). Ecological and evolutionary responses to recent climate change. *Ann Rev Ecol Evol Syst* **37**: 637–669.

Peleg Z, Fahima T, Abbo S, Krugman T, Nevo E, Yakir D *et al.* (2005). Genetic diversity for drought resistance in wild emmer wheat and its ecogeographical associations. *Plant Cell Environ* **28**: 176–191.

Pujol B, Pannell JR (2008). Reduced responses to selection after species range expansion. *Science* **321**: 96.

Pujol B, Zhou SR, Sanchez Vilas J, Pannell JR (2009). Reduced inbreeding depression after species range expansion. *Proc Natl Acad Sci USA* **106**: 15379–15383.

R Development Core Team (2009). R Foundation for Statistical Computing: Vienna, Austria.

Sagarin RD, Gaines SD (2002). The 'abundant centre' distribution: to what extent is it a biogeographical rule? *Ecol Lett* **5**: 137–147.

Schröter D, Cramer W, Leemans R, Prentice IC, Araújo MB, Arnell NW *et al.* (2005). Ecosystem service supply and vulnerability to global change in Europe. *Science* **310**: 1333–1337.

Sexton JP, McIntyre PJ, Angert AL, Rice KJ (2009). Evolution and ecology of species range limits. *Annu Rev Ecol Evol Syst* **40**: 415–436.

Sexton JP, Strauss SY, Rice KJ (2011). Gene flow increases fitness at the warm edge of a species range. *Proc Natl Acad Sci USA* **108**: 11704–11709.

Shaw RG, Geyer CJ, Wagenius S, Hangelbroek HH, Etterson JR (2008). Unifying life-history analyses for inference of fitness and population growth. *Am Nat* **172**: E35–E47.

Stanton-Geddes J, Shaw RG, Tiffin P (2012a). Interactions between soil habitat and geographic range location affect plant fitness. *PLoS One* **7**: e36015.

Stanton-Geddes J, Tiffin P, Shaw RG (2012b). Role of climate and competitors in limiting fitness across range edges of an annual plant. *Ecology* **93**: 1604–1613.

Stanton ML, Galen C (1997). Life on the edge: adaptation versus environmentally mediated gene flow in the snow buttercup, *Ranunculus adoneus*. *Am Nat* **150**: 143–178.

Stanton ML, Roy BA, Thiede DA (2000). Evolution in stressful environments. I. Phenotypic variability, phenotypic selection, and response to selection in five distinct environmental stresses. *Evolution* **54**: 93–111.

Turelli M (1997). Environmental heterogeneity, maternal effects and spatial patterns of genetic variation. *Evolution* **51**: 93–94.

Volis S (2007). Correlated patterns of variation in phenology and seed production in populations of two annual grasses along an aridity gradient. *Evol Ecol* **21**: 381–393.

Volis S (2011). Adaptive genetic differentiation in a predominantly self-pollinating species analyzed by transplanting into natural environment, crossbreeding and Q_{ST}–F_{ST} test. *New Phytol* **192**: 237–248.

Volis S, Mendlinger S, Ward D (2002). Adaptive traits of wild barley plants of Mediterranean and desert origin. *Oecologia* **133**: 131–138.

Volis S, Verhoeven K, Mendlinger S, Ward D (2004). Phenotypic selection and regulation of reproduction in different environments in wild barley. *J Evol Biol* **17**: 1121–1131.

Willcox G (2005). The distribution, natural habitats and availability of wild cereals in relation to their domestication in the Near East: multiple events, multiple centres. *Veg Hist Archaeobot* **14**: 534–541.

Zeng N, Yoon J (2009). Expansion of the world's deserts due to vegetation–albedo feedback under global warming. *Geophys Res Lett* **36**: L17401.

Zohary D, Hopf M (2000). *Domestication of Plants in the Old World: The Origin and Spread of Cultivated Plants in West Asia, Europe, and the Nile Valley*. Oxford University Press: Oxford.

Supplementary Information accompanies this paper on Heredity website (http://www.nature.com/hdy)