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Role of selection and gene flow in population differentiation at the edge vs. interior of the species range differing in climatic conditions

S. VOLIS,* D. ORMANBEKOVA† and I. SHULGINA*

*Key Laboratory of Biodiversity and Biogeography, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 650204, China, †Department of Agricultural Sciences, University of Bologna, Bologna 40127, Italy

Abstract

Evaluating the relative importance of neutral and adaptive processes as determinants of population differentiation across environments is a central theme of evolutionary biology. We applied the Q_{ST}–F_{ST} comparison flanked by a direct test for local adaptation to infer the role of climate-driven selection and gene flow in population differentiation of an annual grass *Avena sterilis* in two distinct parts of the species range, edge and interior, which represent two globally different climates, desert and Mediterranean. In a multiyear reciprocal transplant experiment, the plants of desert and Mediterranean origin demonstrated home advantage, and population differentiation in several phenotypic traits related to reproduction exceeded neutral predictions, as determined by comparisons of Q_{ST} values with theoretical F_{ST} distributions. Thus, variation in these traits likely resulted from local adaptation to desert and Mediterranean environments. The two separate common garden experiments conducted with different experimental design revealed that two population comparisons, in contrast to multipopulation comparisons, are likely to detect population differences in virtually every trait, but many of these differences reflect effects of local rather than regional environment. We detected a general reduction in neutral (SSR) genetic variation but not in adaptive quantitative trait variation in peripheral desert as compared with Mediterranean core populations. On the other hand, the molecular data indicated intensive gene flow from the Mediterranean core towards desert periphery. Although species range position in our study (edge vs. interior) was confounded with climate (desert vs. Mediterranean), the results suggest that the gene flow from the species core does not have negative consequences for either performance of the peripheral plants or their adaptive potential.

Keywords: adaptive potential, aridity, gene flow, local adaptation, peripheral populations, phenotypic variation, population differentiation, Q_{ST} vs. F_{ST}, species range

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Introduction

Widely distributed species often exhibit considerable phenotypic variation which can be either adaptive or result from nonadaptive evolutionary processes. Recognition of the adaptive significance of such differentiation and its relationship with environmental variables has been a challenging task in evolutionary biology (Endler 1977; Conover & Schultz 1995; Linhart & Grant 1996; Rasanen & Hendry 2008; Colautti *et al.* 2012). For plants, climate is among the most important environmental factors determining species ranges and phenotypic differentiation within the ranges. Such climatic variables as temperature and precipitation are critical determinants of plant developmental processes and life history that optimize individual fitness in a given environment.

A number of studies analysed population genetic pattern in xeric vs. mesic environments when the latter

Correspondence: Sergei Volis, Fax: 86 871 5223170;
E-mail volis@mail.kib.ac.cn

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represented the interior and edge conditions of the species range, respectively (Clegg & Allard 1972; Hamrick & Allard 1972; Comes & Abbott 1999; Volis *et al.* 2002a, 2014; Volis 2011). Organisms inhabiting a species' edge usually experience more extreme and less predictable environmental conditions, and lower availability of suitable habitats which results in lower and more fluctuating population densities, smaller population sizes and reduced population connectivity than in the species interior (Hengeveld & Haeck 1982; Lawton 1993; Gaston 2003; Vucetich & Waite 2003). These features make peripheral populations more prone to extinction and migration dependent. Genetically, due to small size and spatial isolation, the peripheral populations are expected to have reduced variation and higher levels of population subdivision than the core ones. Reduced genetic variation may prevent peripheral populations from adapting to their local conditions. However, under strong natural selection and given sufficient evolutionary time, plants from a stressful and less predictable xeric environments at the species range edge might have evolved specific adaptations to local conditions. There are two alternative views on predominant evolutionary factors that shape the genetic makeup of peripheral populations and determine their conservation utility. One view is that peripheral populations may lack selectively important alleles which limit their short-term persistence and long-term evolutionary potential. The alternative view is that peripheral populations, due to selection under conditions marginal for the species, possess locally adapted alleles that can be important for the species' long-term survival (Lesica & Allendorf 1995). So, what is the role of local selection in the population genetic pattern at the species edge as compared with the species interior? Answering this question requires population genetic analysis to be flanked by an explicit test of local adaptation.

Although local adaptation appears to be a common phenomenon in plant populations, experimental introductions usually produce mixed results, with home advantage detected in some but not all locations, traits or years of observations (Nagy & Rice 1997; Galloway & Fenster 2000; Joshi *et al.* 2001; Volis *et al.* 2002c, 2015; Santamaria *et al.* 2003; Etterson 2004; Volis 2009; Stanton-Geddes *et al.* 2012a,b). A failure to detect local adaptation in reciprocal transplant experiments can result from several methodological constraints. The study period of one or even 2 years may often be too short to detect home advantage if the environmental conditions at the study locations significantly fluctuate over years. Second, some important stages of the species life cycle experiencing strong local selection can be missing during the experiment (e.g. when seedlings rather than seeds are used as transplants). Finally, the experiment can ignore selection effect of local biotic environment if vegetation is removed from the transplant site.

To account for all these potential effects, we conducted a transplant experiment repeated over several years, in which seeds of different origin were reciprocally introduced into natural environments where they were exposed during the whole life cycle to local abiotic and biotic conditions. In addition, we performed a comparison of relative levels of among-population differentiation in neutral molecular markers (as measured by F_{ST}) and in quantitative traits that may be targets of selection (as measured by Q_{ST}) to discriminate between adaptive and nonadaptive processes at the two studied environments (Prout & Barker 1989, 1993; Spitze 1993). In the case of spatially varying selection favouring different genotypes in different environments, Q_{ST} is expected to be significantly higher than F_{ST}. Under the other two scenarios, Q_{ST} is either smaller than F_{ST} (convergent selection), or Q_{ST} and F_{ST} do not differ (i.e. no detectable effect of selection) (Merila & Crnokrak 2001; McKay & Latta 2002).

Soon after its introduction the Q_{ST}–F_{ST} comparison has become a routine test for adaptive population divergence (reviewed in Leinonen *et al.* 2008, 2013; De Kort *et al.* 2013) despite its recognized methodological limitations (Leinonen *et al.* 2008; Pujol *et al.* 2008; Whitlock 2008; Whitlock & Guillaume 2009; Volis & Zhang 2010; Edelaar *et al.* 2011). Several factors have been recognized as potentially violating the test assumption of genetic equilibrium such as demographic history (Miller *et al.* 2008) and presence of dominance and epistasis (Whitlock 1999; Lopez-Fanjul *et al.* 2003; Goudet & Buchi 2006; Goudet & Martin 2007). Genetic variability in quantitative traits can also depend on environmental conditions under which traits are measured (Mitchell-Olds & Rutledge 1986; Merila & Crnokrak 2001; Palo *et al.* 2003; Gomez-Mestre & Tejedo 2004).

How reliable is the Q_{ST}–F_{ST} test in detecting the effect of natural selection and what is its relative value in comparison with other techniques for studying diversifying selection? Addressing this question requires varying sampling design for the Q_{ST}–F_{ST} comparison and conducting an explicit field test of local selection effect.

Our study focused on evolutionary processes that occur in mesic vs. xeric environments representing the species distributional core and periphery, respectively. A sharp gradient of increasing aridity separates the desert and Mediterranean regions in Israel. In Israel, many species that are widespread in Mediterranean (mesic) environment reach the edge of their distribution range in harsh desert (xeric) environment (Yom-Tov & Tchernov 1988). Deserts are renowned for highly fluctu-

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ating and unpredictable precipitation from 1 year to the next (Polis 1995), while in Mediterranean-climate regions, the onset of the rainy season is more predictable, within-season supply of water is more reliable and the duration of growing season is longer than in deserts (Shmida & Burgess 1988). Under these different conditions, plants of several annual species were found to differ in phenology, reproductive allocation and morphology (Aronson *et al.* 1992, 1993; Volis *et al.* 2002b; Petru *et al.* 2006; Volis 2007; Liancourt & Tielbörger 2008). In these studies, the arid ecotypes reproduced earlier and produced more diaspores per plant biomass than conspecific plants growing under more humid conditions.

An annual grass *Avena sterilis* L. is widely and abundantly distributed in the Mediterranean climate zone of Israel but also penetrates into the desert environment where it exhibits lower abundance, higher patchiness and greater isolation as compared with the core Mediterranean environment. *A. sterilis* has been previously shown to possess high environmentally related phenotypic and life history variation (Volis 2007, 2009, 2014). In the current study, we analysed variation in quantitative traits and neutral molecular SSR markers between/among populations of *A. sterilis* from desert and Mediterranean climate zones of Israel to understand an interplay of local selection and gene flow across the species range. To do this, we measured several presumably adaptive life history and morphological traits in two common garden greenhouse experiments and surveyed six putatively neutral SSR loci. Among the specific objectives of this study were as follows: (i) to demonstrate the adaptive nature of ecotypic differences in this species between Mediterranean and desert plants by a multiyear reciprocal transplant experiment; (ii) to identify quantitative traits associated with this differentiation; (iii) to estimate the gene flow between Mediterranean and desert populations that represent the species distributional core and periphery; and (iv) to compare the extent and structure of variation in neutral (SSR) and adaptive quantitative trait variation in these two parts of the species range.

Materials and methods

Study species

Avena sterilis L. is a predominantly selfing winter annual grass. In Israel, this species is one of the major components of annual vegetation in the mesic Mediterranean including open park-forests, maquis and hemicryptophytic/dwarf shrub formations, and also penetrates into less favourable desert habitats (wadi beds and loessial depressions) (Zohary 1983).

In this species, the dispersal unit is a spikelet that usually contains several florets that differ in size and time of germination (Volis 2014). The inflorescence is a panicle with basipetal maturation of spikelets (from the periphery to the centre). Seedlings emerge in November–December, grow and mature through winter – early spring, produce seeds in April–May and senesce before summer. Seeds that do not germinate in the autumn following dispersal either die or enter the soil seedbank where they can remain dormant for several years (Sanchez Del Arco *et al.* 1995; Volis 2014).

Choice of populations

Ten locations have been chosen for this study employing nested sampling design, that is in two climatic zones (desert and Mediterranean) with five populations per zone (Fig. 1). Populations within a zone represented the same environment with respect to climate, relief, slope exposition, vegetation and soil type. All 10 populations were used in an analysis of quantitative trait and molecular (SSR) variation, and at one population location per zone, we conducted a reciprocal transplant test.

The Mediterranean research site (BG population) was in Beit Guvrin National Park located in the Shefela Hills (elevation 300 m, annual temperature 19 °C, temperature in January 9 °C, number of rainy days 37, annual precipitation 400 mm, CV in annual rainfall 0.32). The area is a semisteppe batha (a formation with dwarf shrubs of Mediterranean and steppe origin) on rendzina soil with mosaic of shrub – semishrub cover (*Sarcopo-*

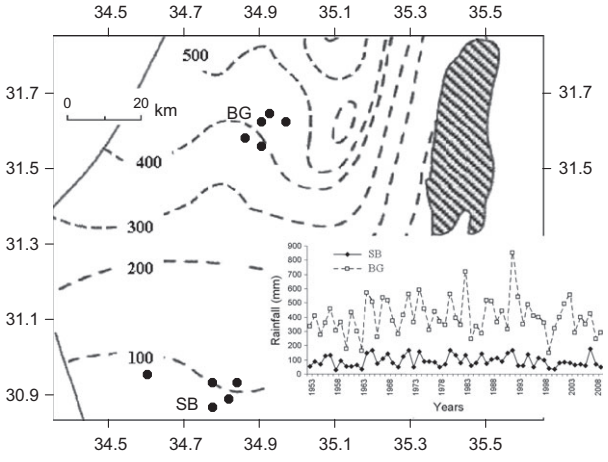

Fig. 1 Map of Israel showing isohyets of multiyear averages of annual rainfall amount (mm) and sampled localities. The two transplant localities (SB and BG) are named on the map. The inset shows annual rainfall (mm) for the SB and BG sites during 1952–2009. Meteorological data are from Israel Meteorological Service.

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terium spinosum, *Calicotome villosa*, *Cistus salvifolius*) and dense stands of *A. sterilis,* among other grasses.

The desert research site (SB population) was in a wadi in the Negev Desert (elevation 400 m, annual temperature 19 °C, temperature in January 11 °C, number of rainy days 15, annual precipitation 90 mm, CV in annual rainfall 0.44), in an experimental area of the Mitrani Department for Desert Ecology, Ben-Gurion University. There is sparse desert vegetation on loess soil (dominated by shrubs and semishrubs including *Retama raetam*, *Thymelea hirsuta*, *Zygophyllum dumosum*, *Hammada scoparia*) with patchily distributed *A. sterilis* within the wadi.

A seed collection of *A. sterilis* in ten population locations was made in 1996. Additional collections were conducted in 2001 and 2004 in SB and BG populations. The collected plants were always more than 1 m apart to increase a probability of sampling genetically unrelated individuals. The seeds were either used in the following season or stored in the refrigerator at 5 °C.

Local adaptation experiment

A genotype-by-environment interactions experiment was conducted in two locations, BG and SB during four consecutive years starting in 2005. Ten seeds collected in 2004 from the individuals separated by at least 2 m in each location were germinated and grown under greenhouse conditions in a fully randomized design. In the next winter, the self-progeny of ten mother plants composed the two seed pools. Three seeds of each origin arranged as two adjacent triangles separated by a marked rod were reciprocally introduced at randomly chosen 30 plots in the BG and SB sites. Seeds within a triangle were 10 cm from each other, half buried vertically in the soil. The soil surface within a plot and 10 cm around it was carefully scrapped to allow identification of the introduced seeds, but no weeding of non-introduced vegetation that resulted from the soil seed bank was applied during the experiment. In addition, due to the easily identifiable position of each introduced seed, visual examination was regularly conducted after seed germination to insure that only introduced and no other oat plants are present at the plot. At seed maturity, we calculated the number of panicles per introduced plant and number of spikelets in each panicle. The procedure of seed propagation in a greenhouse followed by reciprocal introduction *in situ* (except for 2005 when introduction was performed at the SB site only) was performed repeatedly during 4 years to account for interseasonal variation in amount and timing of precipitation.

To infer local adaptation, we used 'local vs. foreign' definition of Kawecki & Ebert (2004) and two statistical approaches. The General Linear Model of Statistica (StatSoft Inc. 2004) was used to analyse the plant performance, measured as the number of seeds produced per introduced seed (including zero values for nongerminated or failed to survive/reproduce individuals), in the local adaptation experiment. The model included as terms site, seed origin, year and plots nested within sites. The site, origin and year were treated as fixed effects, and plot was treated as a random effect. Only plots where at least one plant had performance above zero were included in this analysis. This analysis was carried out on the data for the 2006, 2007 and 2008 years when transplanting was carried out at both sites. In 2005, seeds were introduced to the SB site only; therefore, these data were analysed by two-way ANOVA with one fixed effect (origin) and one random effect (plot). In both analyses data were $\sqrt{}$-transformed prior to analysis.

In addition to the above analysis, the advantage of plants of local origin was tested at each location separately through aster modelling of individual lifetime fitness (Geyer *et al.* 2007; Shaw *et al.* 2008) as implemented in R (R Development Core Team 2009). Aster models are a significant improvement over previous attempts to model lifetime fitness because they allow modelling (using a likelihood approach) multiple components of life history in a single analysis, with an individual's response at each life history stage conditioned upon its response at the previous stage. The modelled life history stages and their statistical distributions were early-season seed germination (Bernoulli) and number of seeds (zero-truncated negative binomial). In each aster model comparison, Likelihood ratio test compared the fit of the full model to reduced models that sequentially dropped terms.

Quantitative trait variation

Two common garden experiments were performed to separately partition the quantitative genetic variation into between- and within-population components needed for estimation of Q_{ST}. Plants were grown under the same uniform conditions in a greenhouse at the Bergman Campus, Beer Sheva, and the same set of quantitative traits was measured. The traits included tiller height (TH), flag and penultimate leaf length and width (FLL, PLL, FLW and PLW), number of spikelets per panicle (SPP), number of days to anthesis (DAN) and individual spikelet weight (SWT). The 3 L pots filled with the commercial potting mixture and containing a single plant were arranged in a greenhouse at the Bergman Campus, Beer Sheva, using block design. Watering during the experiment was carried out regularly (twice a week) through drip-irrigation system.

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Prior to these two experiments, the mother plants representing different accessions were planted under uniform conditions in a greenhouse to minimize maternal effects and three offspring per mother plant were used in the common gardens. As *A. sterilis* is predominantly autogamous, the offspring of each mother plant can be considered as a genetically identical single genotype. In both common gardens, each of three offspring per accession (=genotype) was randomly assigned to one of three blocks.

In the first common garden conducted in 2003–2004, we used one population per climatic zone (SB and BG) represented by randomly chosen accessions (66 and 57, respectively). In the second common garden conducted in 2004–2005, we used 15 randomly chosen accessions from each of 10 populations (five populations per climatic zone).

The structure of variation in phenotypic traits for both common gardens was analysed after running nested ANOVA by partitioning the total variance into several components. In the two population common garden, two random effects were Populations and Accessions nested within Populations. In the ten population common garden, three random effects included Regions, Populations nested within regions and Accessions nested within Populations. The REML procedure was used for calculation of variance components. In addition, in the ten population common garden population comparisons were carried out in a pairwise fashion comparing each desert population with one nondesert population at a time. For each measured trait in both common gardens, we estimated broad-sense heritability, $H^2 = V_G/(V_G + V_E)$. The within-accession variance estimated the environmental variance, V_E, and the among-accession variance provided an estimate of the genetic variance, V_G.

Pairwise comparisons of total genetic variance were carried out (i) comparing two regions (desert and Mediterranean) and (ii) comparing each desert population with one Mediterranean population 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, which has a chi-square distribution. The matrices were constrained to be positive definite, so that variances were non-negative.

SSR variation

In analysis of presumably neutral molecular variation, two separate analyses using the same SSR loci were conducted. In the first one, we analysed two populations, SB and BG, represented by 75 and 53 individual samples, respectively. In the second one, we analysed ten populations each represented from 14 to 15 individuals. DNA extraction followed modified CTAB protocol (Rogers & Benedich 1985). Six polymorphic nuclear microsatellite loci, AM-1, AM-3, AM-22, KSUM176 (Fu *et al.* 2007) and MAMA-4, MAMA-6 (Wight *et al.* 2003), were amplified using primer-specific polymerase chain reaction (PCR) programme as described in Table S1 (Supporting information). The PCR products were detected and sized by the ABI PRISM 3700 DNA Analyzer at the Hebrew University, Jerusalem, Israel. The data were analysed using PEAK SCANNER™ SOFTWARE v1.0 (Applied Biosystems).

The distribution of SSR variation among regions, among populations within regions and within populations was investigated by an analysis of molecular variance (AMOVA; Excoffier *et al.* 1992) using GENALEX 6.5 (Peakall & Smouse 2006). The number of permutations for significance testing was set at 1000. We also estimated several alternative to F_{ST} estimates of population differentiation as implemented in GENALEX 6.5.

We submitted the per-locus estimates of Na, Ne and He from the two population assessment to paired *t*-test, and from the ten population assessment to ANOVA to test whether measures of population genetic diversity differed among populations of different origin. Each ANOVA model included two factors: genetic locus and geographic region (desert and Mediterranean). Na and Ne were square-root transformed to improve the homoscedasticity of residuals.

We examined asymmetric rates of immigration using the number of mutants per generation ($\theta = 4N_e\mu$), the mutation-scaled effective immigration rate ($M = m/\mu$) and their product $\theta M/4$, which is the number of immigrants entering population each generation (i.e. N_em), estimated with MIGRATE-N 3.2 (Beerli & Felsenstein 2001) assuming an infinite allele mutational model. The estimates were averaged over loci and provided with 95% CI. Each run was conducted with ten short chains of 500 and three long chains of 5000, and the burn-in at the beginning of each chain of 10 000. Ten simulations were performed and their results combined. Several separate analyses and estimations of gene flow were performed based on explicit assumptions. For the two population data, we estimated N_em assuming a unidirectional gene flow from BG to SB population due to their difference in population sizes and range position (i.e. from the species interior to edge). For the ten population data, at first we treated two sets of five populations as two gene pools assuming that interpopulation gene flow within each region exceeds gene flow between the regions, and calculated the unidirectional N_em from the Mediterranean to the desert pool, which

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represent the species interior and edge, respectively. Then, we estimated N_em from the Mediterranean gene pool to each desert population assuming that desert populations have much lower spatial connectivity and therefore lower gene flow among them than the Mediterranean populations.

Q_{ST}–F_{ST} comparison

We did not separate total genetic variance into additive and nonadditive components in calculation of Q_{ST} and used only the total genetic variation because this is the variation important to selection in selfing species (e.g. Banta *et al.* 2007). The hierarchical Q_{ST} estimates, regional (Q_{RT}) and population (Q_{SR}), were calculated for each measured trait according to Whitlock & Gilbert (2012), with a correction for self-pollination as $Q_{RT} = V_R/(V_R + V_B + V_A)$ and $Q_{SR} = V_B/(V_B + V_A)$, where V_R is the estimated variance component for the region effect, V_B is the estimated variance component for the population effect, and V_A is the estimated variance component for the accession (=genotype) effect. For each trait, we estimated Q_{ST} across all populations (overall Q_{ST}) and for traits exceeding neutral expectations (as described below) for all pairs of populations (pairwise Q_{ST}).

We also examined quantitative trait neutrality by comparing overall Q_{ST} values against a distribution of F_{ST} values following Whitlock (2008). According to Lewontin & Krakauer (1973), the distribution of F_{ST} among loci is approximated by a chi-square distribution $(n-1)F_{ST}/\bar{F}_{ST}^2$ with $(n-1)$ degrees of freedom where n is the number of populations and $\bar{F}_{ST}$ is the mean F_{ST} value. The variance of the distribution is given by $2\bar{F}_{ST}^2/(n-1)$. The value of trait overall Q_{ST} that falls outside 97.5% upper percentile value of the simulated distribution of F_{ST} is likely to indicate that the trait is under spatially varying selection (Whitlock 2008). We used the average F_{ST} value estimated by GENALEX 6.5 to calculate the upper 97.5% upper percentile value of F_{ST} expected by the Lewontin–Krakauer prediction.

Results

Local adaptation experiment

Plant performance measured as the number of spikelets/plant was affected by two main effects, year and site, but was unaffected by spikelet origin. However, all the interactions involving plant origin had a significant effect on plant performance (Table 1). Variation in plant survival and fecundity among the sites and years reflected a difference in biotic/abiotic conditions and interannual variation in rainfall. What is more important is an interaction between plant origin with site and year (Table 1). Significant origin × site interaction indicates an advantage of the native plants at their home site as compared with the aliens despite a difference in growing conditions from year to year that differentially affects plants of SB and BG origin (significant origin × year interaction) and causes in certain years inferiority of the locals (significant origin × year × site interaction) (Fig. 2). In only 1 year, 2007, characterized by unusually high precipitation in the Negev desert (Fig. 1), the BG plants were superior over SB plants at the SB site.

In 2005, seeds were introduced to the SB site only and therefore were analysed separately. The SB plants showed better performance than the BG ones (d.f. = 3, $F = 12.2$, $P < 0.01$).

Table 1 (A) Three-way mixed-model ANOVA on number of spikelets per plant; plot (nested within site) is a random effect. (B) Aster model analysis of cumulative individual fitness (germination and fecundity)

(A)

Source	d.f.	MS	*F*	*P*
Site	1	18.0	5.8	0.018
Plot(Site)	40	3.1	0.9	ns
ORIGIN	1	0.3	0.2	ns
ORIGIN*Site	1	16.6	10.4	0.002
ORIGIN*Plot(Site)	40	1.7	1.4	ns
Year	2	94.4	30.7	<0.001
Year*Site	2	88.2	28.7	<0.001
Year*Plot(Site)	57	3.1	2.5	<0.001
ORIGIN*Year	2	8.4	6.8	0.002
ORIGIN*Year*Site	2	5.9	4.7	0.012
ORIGIN*Year*Plot(Site)	57	1.2	0.8	ns
Error	412	1.6		

(B)

Model	Test d.f.	Test deviance SB site	*P*-value	Test deviance BG site	*P*-value
All years					
Block	29	644.8	<0.0001	192.7	<0.0001
Year	2	1150.6	<0.0001	4.5	0.106
Origin	2	4.9	0.085	31.3	<0.0001
2005					
Block	29	181.9	<0.0001		
Origin	1	8.8	0.003		
2006					
Block	29	256.2	<0.0001	275.0	<0.0001
Origin	1	6.4	0.011	33.6	<0.0001
2007					
Block	29	1058.3	<0.0001	100.2	<0.0001
Origin	1	18.2	<0.0001	9.9	0.002
2008					
Block	29	103.2	<0.0001	68.8	<0.0001
Origin	1	30.3	<0.0001	5.2	0.022

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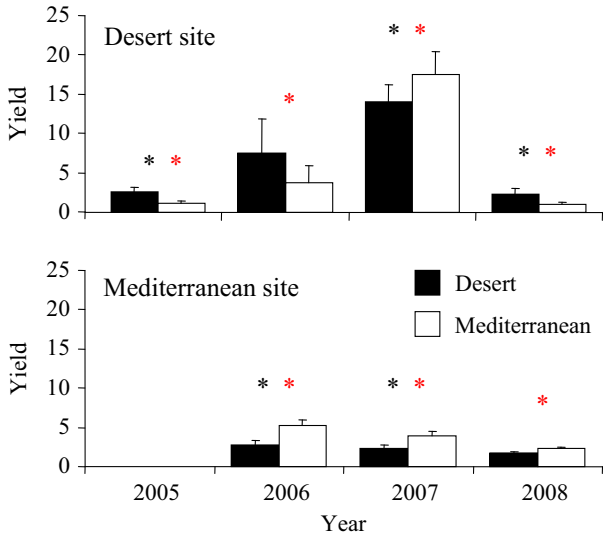

Fig. 2 Average yield (number of spikelets per individual) of plants of two origins (desert vs. Mediterranean) reciprocally introduced at two sites during 4 years (except for 2005 when plants were introduced at the desert site only). Significant difference between two origins is denoted by an asterisk as revealed by paired contrast test (in black) and by aster modelling (in red).

Aster modelling that allowed analysing simultaneously two fitness components, seed germination and conditioned on it plant fecundity, revealed superiority of locals at the SB site in years 2005, 2006 and 2008, while the aliens were superior in the very wet year 2007. At the BG site, locals were superior in all years (Table 1).

Genetic variation at SSR loci

A total of six SSR loci were scored in two separate genetic variation assessments, of the two populations (75 and 53 plants of SB and BG origin, respectively) and of the ten populations (five desert and five Mediterranean populations, from fourteen to fifteen plants per population). Number of alleles (Na), effective number of alleles (Ne) and expected heterozygosity (He) averaged over loci were relatively uniform, while observed heterozygosity (Ho) varied more substantially across the ten populations (range 0.038–0.167) (Table 2). In the two population assessment, over all loci the average population Na and Ne were 7.6 and 4.0, and Ho and He were 0.052 and 0.688, respectively. In the ten population assessment, over all loci and populations, Na and Ne were 4.6 and 3.0, and Ho and He were 0.100 and 0.565, respectively (Table 2). Consistent with known predominant self-pollination of *A. sterilis*, the inbreeding coefficient (F_{IS}) was 0.922 and 0.799 (two population and ten population assessment, respectively).

In the two population assessment, extent of genetic variation did not differ between BG and SB population (Na = 6.8 vs. 8.3, $t_5 = 1.6$; Ne = 3.7 vs. 4.2, $t_5 = 0.4$; He = 0.697 vs. 0.679, $t_5 = 0.3$, for all tests $P > 0.05$). However, in the 10 population assessment, genetic variation was significantly higher in the Mediterranean populations than in the desert populations (Na = 5.3 vs. 3.9, $F_{1,48} = 20.6$, $P < 0.001$; Ne = 2.2 vs. 1.9, $F_{1,48} = 14.1$, $P < 0.001$; He = 0.624 vs. 0.506, $F_{1,48} = 7.8$, $P < 0.01$).

In both population assessments, overall population differentiation by Weir and Cockerham *F*-statistics and AMOVA were very similar, while *D* and G''_{ST} were substantially higher (Table 3). In the two population assessment, Φ_{ST} was lower than in the ten population assessment (0.068 vs. 0.174, respectively). Partitioning of Φ_{ST} into regional and population components in the 10 population assessment revealed a predominant population effect (14%), but a regional effect was also significant (4%).

Estimation of gene flow

In two population analysis of SSR variation, we estimated a unidirectional gene flow from the species core population (BG) to the edge population (SB). The estimates of θ_{BG} and θ_{SB} were 2.56 (2.38–2.77) and 2.32 (2.13–2.56), respectively, and the mutation-scaled effective immigration rate ($M = m/\mu$) from the BG to SB population was 3.73 (3.07–4.68). As $\theta = 4N_e\mu$, the resulting estimate of gene flow N_em is 2.16.

From the ten population SSR data, we estimated a unidirectional gene flow from the Mediterranean gene pool to the desert one, assuming that interpopulation gene flow within each region exceeds gene flow between the regions. The resulting estimates θ_{Med} and θ_{Des} were 4.65 (4.34–4.97) and 1.07 (0.99–1.17), respectively, and *M* from the Mediterranean to the desert pool was 8.37 (6.91–9.98), providing N_em of 2.24. In estimating N_em from the Mediterranean gene pool to each desert population, the θ values of a recipient population ranged 0.30–0.56 and of the donor gene pool ranged 4.98–11.20. The resulting N_em ranged 0.597–0.829.

All the above estimates of gene flow from the species interior (Mediterranean part of the species range) to the species edge (desert) are number of immigrant individuals N_em and not number of gametes $4N_em$ because a gene flow through seeds should be more important in this species than through pollen.

Quantitative trait variation

Population means for the studied quantitative traits are shown in Table 2. In the two population common garden, the SB and BG populations differed in all traits

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Table 2 Population geographic coordinates, trait means (SE) for 8 quantitative traits and statistics of genetic diversity across 6 SSR loci. Letters denote the results of Tukey HSD test

	Geographic coordinates		Quantitative traits								Statistics of genetic diversity			
Populations	Lon	Lat	DAN	TH	FLL	FLW	PLL	PLW	SPP	SW	Na	Ne	Ho	He
Two population comparison														
SB*	34.76	30.85	36.9 (0.5)	—	19.4 (0.4)	9.4 (0.2)	24.8 (0.4)	11.4 (0.1)	—	80.5 (0.7)	8.3 (2.2)	4.2 (1.2)	0.044 (0.018)	0.679 (0.074)
BG*	34.89	31.60	49.8 (0.4)	—	24.7 (0.3)	11.7 (0.2)	27.6 (0.3)	13.0 (0.1)	—	95.6 (1.1)	6.8 (1.5)	3.7 (0.5)	0.060 (0.026)	0.697 (0.046)
Ten population comparison														
Desert														
SB*	34.76	30.85	25.67 (1.54)^{f}	119.8 (3.6)^{b}	25.6 (0.7)^{ab}	14.5 (0.4)^{ab}	44.6 (0.8)^{a}	18.0 (0.4)^{ab}	55.7 (2.0)^{abc}	80.1 (1.2)^{d}	4.3 (1.0)	2.8 (0.7)	0.133 (0.079)	0.542 (0.099)
ARU	34.77	30.91	30.9 (0.5)^{de}	137.0 (2.3)^{a}	22.6 (0.7)^{bcd}	12.7 (0.3)^{cd}	39.8 (0.9)^{bcd}	16.2 (0.2)^{cd}	52.2 (1.3)^{bcd}	85.4 (1.9)^{bcd}	3.7 (0.6)	2.3 (0.4)	0.111 (0.085)	0.484 (0.093)
HAT	34.84	30.92	27.5 (0.5)^{ef}	137.3 (2.4)^{a}	20.0 (0.4)^{d}	12.8 (0.3)^{cd}	33.6 (0.6)^{e}	15.5 (0.2)^{d}	48.0 (1.1)^{cd}	82.7 (1.0)^{cd}	3.8 (0.7)	2.2 (0.4)	0.167 (0.060)	0.480 (0.088)
NN	34.81	30.87	34.2 (0.7)^{cd}	132.6 (2.8)^{a}	20.8 (0.9)^{cd}	12.3 (0.3)^{cd}	37.9 (1.5)^{cde}	15.8 (0.2)^{d}	49.0 (1.1)^{cd}	80.6 (1.6)^{d}	3.8 (0.8)	2.9 (0.5)	0.093 (0.062)	0.562 (0.116)
SHZ	34.59	30.95	27.3 (0.9)^{ef}	114.1 (2.7)^{b}	15.8 (0.7)^{e}	11.9 (0.4)^{d}	35.9 (1.1)^{de}	18.6 (0.6)^{a}	61.6 (2.0)^{a}	61.6 (1.4)^{e}	3.8 (0.8)	2.2 (0.4)	0.089 (0.037)	0.464 (0.105)
Mediterranean														
BG*	34.89	31.60	34.3 (0.9)^{cd}	133.5 (2.7)^{a}	24.5 (0.6)^{ab}	13.2 (0.3)^{bcd}	40.3 (0.8)^{bcd}	16.6 (0.3)^{bcd}	47.3 (1.4)^{d}	92.4 (2.3)^{ab}	5.8 (1.2)	3.6 (0.9)	0.067 (0.030)	0.643 (0.071)
NEH	34.95	31.61	39.3 (1.1)^{ab}	142.0 (2.4)^{a}	23.6 (0.6)^{bc}	13.3 (0.3)^{abcd}	40.8 (0.7)^{abc}	16.7 (0.2)^{bcd}	47.9 (1.1)^{d}	97.5 (2.6)^{a}	4.7 (1.0)	3.1 (0.7)	0.038 (0.017)	0.595 (0.073)
AMZ	34.89	31.54	38.8 (0.8)^{ab}	135.1 (2.2)^{a}	24.6 (0.6)^{ab}	13.5 (0.3)^{abcd}	43.0 (0.9)^{ab}	16.9 (0.2)^{bcd}	50.8 (1.6)^{cd}	91.7 (2.7)^{ab}	5.3 (0.9)	3.5 (0.7)	0.156 (0.070)	0.653 (0.063)
LKH	34.85	31.57	37.2 (1.0)^{bc}	136.2 (2.6)^{a}	24.4 (0.6)^{ab}	14.8 (0.3)^{a}	41.4 (1.0)^{abc}	17.7 (0.4)^{ab}	60.2 (2.0)^{ab}	85.4 (2.0)^{bcd}	5.0 (1.1)	3.1 (0.9)	0.056 (0.032)	0.517 (0.112)
ZFR	34.92	31.63	42.0 (0.8)^{a}	142.2 (2.8)^{a}	26.6 (0.8)^{a}	13.8 (0.3)^{abc}	44.0 (0.8)^{ab}	17.8 (0.3)^{abc}	51.4 (2.0)^{cd}	91.0 (2.6)^{abc}	5.7 (1.4)	4.4 (1.0)	0.089 (0.044)	0.713 (0.053)

DAN, number of days to anthesis; TH, tiller height (cm); FLL, flag leaf length (cm); FLW, flag leaf width (mm); PLL, penultimate leaf length (cm); PLW, penultimate leaf width (mm); NSP, number of spikelets in a panicle; SWT, mean spikelet weight (mg).
*Used in transplant experiment.

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Table 3 Statistics of genetic diversity and structure for six SSR markers

Genetic parameters	AM-1	AM-3	AM-22	KSUM176	MAMA-4	MAMA-6	Locus mean (SE)
Two population comparison							
Na	5.5	11.5	5.0	4.0	15.0	4.5	7.583 (1.3)
Ne	2.0	4.8	3.9	2.9	7.4	2.7	3.966 (0.6)
Ho	0.016	0.007	0.119	0.044	0.013	0.113	0.052 (0.015)
He	0.483	0.791	0.742	0.635	0.852	0.623	0.688 (0.042)
F_{IS}	0.967	0.992	0.839	0.930	0.984	0.819	0.922 (0.031)
$F_{ST\ Weir\ and\ Cockerham}$	0.068	0.069	0.059	0.057	0.040	0.111	0.066 (0.015)
$\Phi_{ST\ AMOVA}$	0.069	0.069	0.064	0.059	0.057	0.121	0.068
D	0.067	0.305	0.191	0.114	0.271	0.213	0.164 (0.042)
G''_{ST}	0.128	0.353	0.239	0.166	0.300	0.300	0.219 (0.041)
Two population group comparison							
Na	4.0	6.9	3.6	2.6	7.4	3.1	4.6 (0.3)
Ne	2.7	4.6	2.3	1.6	4.6	2.2	3.0 (0.2)
Ho	0.007	0.014	0.238	0.109	0.096	0.134	0.100 (0.017)
He	0.588	0.716	0.548	0.321	0.718	0.501	0.565 (0.028)
F_{IS}	0.988	0.981	0.565	0.662	0.866	0.732	0.799 (0.071)
$F_{ST\ Weir\ and\ Cockerham}$	0.191	0.183	0.086	0.121	0.225	0.275	0.180 (0.028)
$\Phi_{ST\ AMOVA}$	0.154	0.147	0.054	0.120	0.195	0.329	0.174
Φ_{RT}	0.018	0.008	0.020	0.063	0.000	0.174	0.040
Φ_{SR}	0.138	0.140	0.034	0.060	0.195	0.187	0.140
D	0.302	0.545	0.061	0.045	0.780	0.383	0.274 (0.109)
G''_{ST}	0.406	0.610	0.102	0.121	0.822	0.538	0.385 (0.107)

Na, number of alleles; Ne, number of effective alleles; Ho, observed heterozygosity; He, expected heterozygosity; F_{IS}, inbreeding coefficient; D, measure of population structure by Jost (2008); G''_{ST}, measure of population structure by Meirmans & Hedrick (2011).

studied (Table 4). However, in the ten population study, the regions (desert and Mediterranean) differed only in DAN, FLL and SWT. There was a great variation among populations within regions for all the studied traits. Despite substantial among-population variation, plants of desert origin in general flowered earlier, had shorter flag leaves and smaller spikelets than Mediterranean ones (Table 2).

Trait heritability above 0.4 was detected in the two population common garden in four traits of six, while in the ten population common garden in only two traits of eight. These were the two traits with highly significant inter-regional differences, DAN and SWT. Partitioning of total phenotypic variance into genetic and environmental components and pairwise population comparison revealed higher genetic variance in SB vs. BG population in four of six measured traits, and for no trait, BG population had a superior genetic variance. In a comparison of genetic variance in two gene pools comprising five populations each (desert and Mediterranean), the desert global population had higher genetic variance in TH, FLL and PLL, and lower genetic variance in SWT than the Mediterranean one (Table 4).

In pairwise comparisons of desert vs. Mediterranean populations for the three traits that differed between the two regions (DAN, FLL and SWT), the compared populations differed in variance only in 21 of 75 comparisons. For DAN, one desert population (SB) had higher variance than four Mediterranean populations, while the two other desert populations (ARUA and HATR) had lower variance than two and three Mediterranean populations, respectively. For FLL, HATR population had lower variance than the all Mediterranean populations, but NN population had higher variance than three Mediterranean populations. And for SWT, SHIZ population had lower variance than three Mediterranean populations (Table 5).

F_{ST}–Q_{ST} comparison

All the pairwise F_{ST} and Q_{ST} were plotted against geographic distance (Fig. 3). Plants originating in different climate zones were separated by at least 60 km, while populations within the same climate zone were within 23 km from each other. The average pairwise F_{ST} for the pairs of desert populations was significantly higher than for the pairs of Mediterranean populations (0.181 ± 0.024 vs. 0.102 ± 0.024) but did not differ from the pairs of mixed desert-Mediterranean origin (0.172 ± 0.024) (Fig. 3).

The estimated overall Q_{ST} values for each trait were compared to the predicted theoretical distribution of F_{ST} (Lewontin & Krakauer 1973) to identify traits with Q_{ST} values acceding those expected under trait neutral-

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Table 4 Nested ANOVA results, broad-sense heritability (H^2), estimates of population differentiation (Q_{ST}, Q_{RT} and Q_{SR}), genetic components of variance (V_G) and results of analysis of deviance comparing pairwise genetic variance (δL) for 8 quantitative traits. For trait abbreviations, see Table 2

	Quantitative traits							
	DAN	TH	FLL	FLW	PLL	PLW	SWT	SPP
Two population comparison								
Pop d.f. = 1	128.4***	—	45.6***	51.8***	11.8***	34.9***	72.1***	—
Gen (Pop) d.f. = 121	19.2***	—	5.9***	2.3***	5.9***	2.0**	3.4***	—
H^2	0.82	—	0.62	0.31	0.62	0.26	0.44	—
Q_{ST}	0.69	—	0.47	0.59	0.18	0.52	0.60	—
$V_{G\ SB}$	54.1	—	23.0	2.3	25.9	1.6	67.3	—
$V_{G\ BG}$	18.3	—	7.0	0.8	4.2	0.4	65.3	—
δL	14.3***	—	12.8***	3.7 ns	23.7***	4.7*	0.01 ns	—
Ten population comparison								
Region d.f. = 1	21.7**	4.1 ns	5.5*	2.8 ns	3.2 ns	0.2 ns	9.0*	0.2 ns
Pop (Region) d.f. = 8	5.1***	5.4***	9.1***	5.6***	6.6***	6.8***	5.6***	5.7***
Gen (Pop, Reg) d.f. = 136	6.3***	1.9***	2.2***	1.3*	2.6***	1.9***	5.4***	3.1***
H^2	0.64	0.25	0.30	0.10	0.36	0.24	0.61	0.31
Q_{RT}	0.56	0.21	0.32	0.19	0.16	0	0.34	0
Q_{SR}	0.25	0.39	0.51	0.56	0.38	0.43	0.29	0.38
$V_{G\ desert}$	35.71	201.0	17.5	1.2	35.0	2.3	92.2	49.2
$V_{G\ Mediterranean}$	25.0	36.2	3.9	0.6	6.8	1.3	184.4	114.4
δL	1.7 ns	12.4***	14.2***	1.2 ns	18.1***	2.1 ns	6.3*	0.9 ns

Residual d.f. = 238 (two pop comparison) and d.f. = 283 (ten pop. comparison).
Likelihood ratio tests were used to compare the fit of the constrained and unconstrained models that estimated genetic variance. Analysis of deviance δL = (−2 log-likelihood) and significance of χ^2 *P*-values for each test are listed; ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, ns not significant.

ity (Whitlock 2008). For the two population comparison, the F_{ST} distribution mean was 0.068 with a predicted 97.5 percentile value of 0.260. In the two population comparison, all the traits except for PLL had Q_{ST} values exceeding this 97.5 percentile value (Table 4). However, for the ten population comparison, the F_{RT} distribution mean was 0.160, and only DAN, FLL and SWT had Q_{RT} values higher than a predicted F_{RT} 97.5 percentile value of 0.311 (Table 4 and Fig. 3). The average pairwise Q_{ST} for these three traits was higher for the pairs of desert populations than for the pairs of Mediterranean populations (0.325 ± 0.087 vs. 0.197 ± 0.065; 0.534 ± 0.122 vs. 0.147 ± 0.062; and 0.404 ± 0.135 vs. 0.067 ± 0.038; DAN, FLL and SWT, respectively).

Discussion

Local adaptation and F_{ST}–Q_{ST} comparison

Populations experiencing globally different climatic conditions usually show adaptive differentiation in life history and other traits. Amount and timing of precipitation is known to be one of the most important climatic parameters influencing the onset and duration of the growing season and, consequently, strategies for plant development and reproduction. However, differences among populations experiencing different climatic conditions can also result from adaptation to other than climate factors or nonadaptive evolutionary processes affecting gene flow (Bradshaw 1984; Loveless & Hamrick 1984; Heywood 1991).

The plants in two populations representative of two distinct environments, desert and Mediterranean, exhibited local adaptation. This adaptation was evident as a home advantage in a multiyear transplant experiment. In addition, the overall regional differentiation in several quantitative traits (Q_{RT}) acceded corresponding differentiation in neutral molecular markers (F_{RT}) and, hence, these traits are likely to be involved in local adaptation. The observed regional/population differentiation in quantitative traits (measured by Q_{ST}) and neutral differentiation at molecular markers (measured by F_{ST}) suggest that variation in these traits among the desert and Mediterranean environments is likely

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Table 5 Pairwise comparisons of genetic variance components. In each comparison, one desert population was compared with one Mediterranean population

	Mediterranean				
	BG	ZAFR	LAKH	AMAZ	NEH
DAN					
Desert					
SB	ns	9.3**,‡	4.1*,‡	8.4**,‡	4.8*,‡
ARUA	ns	ns	6.4*,†	ns	4.4*,†
HATR	ns	ns	7.6**,†	4.0*,†	5.1*,†
SHIZ	ns	ns	ns	ns	ns
NN	ns	ns	ns	ns	ns
FLL					
Desert					
SB	ns	ns	ns	ns	ns
ARUA	ns	ns	ns	ns	ns
HATR	6.1*,†	6.7**,†	8.2**,†	7.4**,†	8.5**,†
SHIZ	ns	ns	ns	ns	ns
NN	6.9**,‡	ns	4.4*,‡	4.9*,‡	5.1*,‡
SWT					
Desert					
SB	ns	ns	ns	ns	ns
ARUA	ns	ns	ns	ns	ns
HATR	ns	ns	ns	ns	ns
SHIZ	ns	7.9**,†	ns	6.8**,†	4.5*,†
NN	ns	ns	ns	ns	ns

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.

†Significantly lower variance in the desert as compared with the Mediterranean population; ‡Significantly higher variance in the desert as compared with the Mediterranean population; $^{**}P < 0.01$, $^{*}P < 0.05$, ns not significant.

maintained by a balance between gene flow and adaptation to local environment.

In our study, we used microsatellites for getting the F_{ST} values. Usage of SSRs in F_{ST}–Q_{ST} comparison has been criticized (Jost 2008; Heller & Siegismund 2009; Edelaar *et al.* 2011) because of known properties of this class of markers such as high mutation rate and, as a result, large number or alleles per locus and high expected heterozygosity. Because F_{ST}-type statistics is based on heterozygosity, the estimates of population differentiation will have a downward bias when number of alleles per locus is high. Several alternative estimates of population differentiation that correct the dependency of F_{ST} on the amount of within-population variation have been proposed such as *D* (Jost 2008) and G''_{ST} (Meirmans & Hedrick 2011). Nevertheless, we utilized the F_{ST} statistics via AMOVA, which implements a matrix of genetic distances between genotypes, for several reasons. Estimation of population differentiation with several levels of hierarchy (i.e. with regions and populations nested within regions) is straightforward in AMOVA, but is not possible with either *D* or G''_{ST}. Second, several recent reviews found no significant effect of marker type on F_{ST} (Leinonen *et al.* 2008; De Kort *et al.* 2013) justifying use of F_{ST} in analysis of SSR variation in this study.

Although the F_{ST}–Q_{ST} comparison is theoretically appealing and straightforward way of detecting local selection effect, getting an accurate estimate of Q_{ST} can be challenging because estimation of Q_{ST} is likely to be affected by the experimental design (number of populations representing a particular environment, genotypes per population and replicates) and environmental conditions under which traits are measured. In our study, we measured the same quantitative traits on plants from desert and Mediterranean environments and estimated trait Q_{ST} in two separate common garden experiments conducted with different experimental design. The results suggest that two population comparisons are likely to detect population differences in virtually every trait, especially if the number of families per population is large. The resulting Q_{ST} values in such comparisons will be biased upward. However, many of these differences will reflect effects of local rather than regional environment. The resulting outcome of $Q_{ST} > F_{ST}$ would still suggest effect of adaptation, but causes of this adaptation will be difficult to surmise.

Spatially varying selection and targets of selection

Comparison of F_{ST} and Q_{ST} allowed us to identify several quantitative traits that are likely to be involved in adaptation to spatially varying climatic conditions. Although all the studied traits demonstrated significant population differentiation, only three traits showed significant regional (i.e. desert vs. Mediterranean) differences, and were identified as exceeding neutral expectation by the Q_{ST}–F_{ST} comparison. These traits were days to anthesis, flag leaf length and individual spikelet weight. All these traits are involved in optimization of reproduction, and determine switch to reproduction (days to anthesis), grain filling (flag leaf length) and size of the propagules (spikelet weight).

Rapid development and early start of flowering are likely to be favoured in areas with less predictable climate such as deserts. Although there was a substantial interpopulation variation, plants from the desert environment flowered earlier than plants from more mesic Mediterranean populations. Increasing aridity leads to shortening of growing season and populations from arid habitats usually flower earlier than in more mesic sites (Aronson *et al.* 1992; Bennington & McGraw 1995; Del Pozo *et al.* 2002; Eckhart *et al.* 2004; Franke *et al.*

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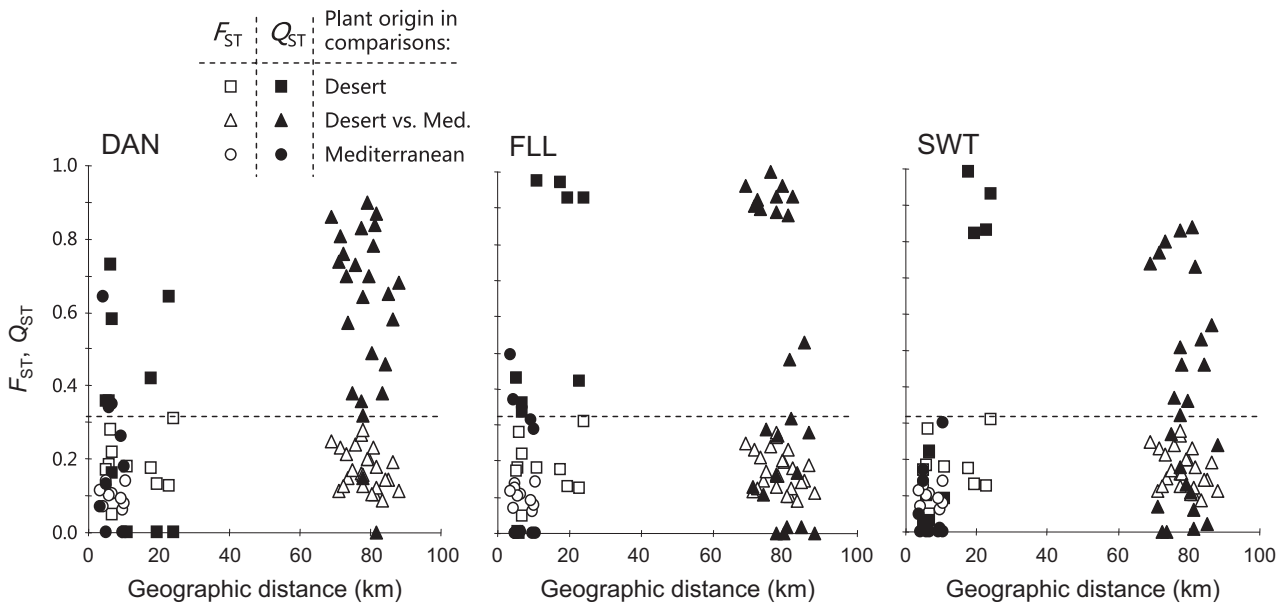

Fig. 3 F_{ST} and Q_{ST} values against geographic distance for all pairwise combinations of populations for three quantitative traits. The dashed line shows the upper 95% limit for F_{ST} values for neutral divergence.

2006; Hall & Willis 2006; Volis 2007). Early flowering, allowing escaping drought conditions is favoured under experimentally induced drought stress (Stanton *et al.* 2000; Volis *et al.* 2004; Peleg *et al.* 2005; Franks *et al.* 2007). Selection for advance of flowering was observed in *Hordeum spontaneum* in a reciprocal transplant experiment with one desert and one Mediterranean site (Volis *et al.* 2002b).

Based on previous knowledge, we expected to detect a difference in resource allocation, that is trade-off between investment in size vs. number between plants of desert and Mediterranean origin. Estimation of total seed production and seed size for several annual plants of Israel revealed differential reproductive strategies and fitness outcomes between desert and Mediterranean populations as related to seed size/number variation (Aronson *et al.* 1990, 1993; Volis 2007). A decrease in individual spikelet weight with a concomitant increase in a number of spikelets per panicle along an aridity gradient was detected earlier in *A. sterilis* (Volis 2007), but only the former was also observed in this study. A high variation in a number of spikelets per panicle among populations within each climate zone appears to reflect a prevailing importance of other than climate factors in selection on this trait. As for a difference between desert and Mediterranean populations in spikelet size, it may have several causes that only indirectly are related to climate conditions. It is known that 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 vigour and seed predation effect) (Gomez 2004).

Adaptive potential of edge populations and gene flow

In our study species, range position (edge vs. interior) was confounded with climate (desert vs. Mediterranean), and therefore, the observed local adaptation of the edge populations is not surprising. On the other hand, less favourable climatic conditions experienced by the marginal in comparison with the core populations determined their difference in size and connectivity. Genetic diversity is often reduced in marginal populations as a result of their higher spatial isolation and smaller sizes leading to greater impact of genetic drift (Eckert *et al.* 2008). Indeed, we detected a general reduction in neutral (SSR) genetic variation in peripheral desert as compared with Mediterranean core populations. On the other hand, the molecular data indicated intensive gene flow from the Mediterranean core towards desert periphery, and strong gene flow from the species core is predicted to swamp the potentially beneficial alleles and impede adaptation at the conditions at the species edge (Kirkpatrick & Barton 1997; Bridle & Vines 2007). However, although we detected a reduction in neutral (SSR) genetic variation, there was no concomitant decrease in adaptive quantitative trait variation of the desert populations. Coupled with the observed local adaptation of the desert plants, this suggests that the gene flow from the species core does not

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have negative consequences for either performance of the peripheral plants or their adaptive potential.

Few empirical studies have examined the adaptive potential of edge vs. core populations. Pujol & Pannell (2008) found a reduced potential to respond to selection after expansion and lower neutral genetic variation in edge populations. Similarly, in a study of Volis *et al.* (2014) the edge populations had inferior adaptive potential to the populations from the species core, but had comparable extent of neutral genetic variation. Several studies have shown that adaptive potential of edge populations can be improved if gene flow is occurring among them (Lavergne & Molofsky 2007; Sexton *et al.* 2011; Volis 2011). What we show is that adaptive potential of edge populations can not only be high but in some traits even exceed the adaptive potential of core populations, and that intensive gene flow from the core to periphery does not impede adaptation to the peripheral conditions. Our results provide strong support to a view that peripheral populations can maintain sufficient variation in adaptively important traits despite both low effective population size and gene flow from the species interior. This implies a crucial role of peripheral populations in species responses to rapid environmental change (Etterson & Shaw 2001; Parmesan 2006; Bell & Gonzalez 2011).

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S.V. designed research; S.V., D.O. and I.S. performed research; S.V. analyzed data and S.V. wrote the paper.

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Data accessibility

Morphological data used for analysis with Quercus: Dryad doi: 10.5061/dryad.s3d45.
Field experiment data: Dryad doi: 10.5061/dryad.5d3s2.
SSR data: Dryad doi: 10.5061/dryad.5d3s2.

Supporting information

Additional supporting information may be found in the online version of this article.

Table S1 Primer-specific PCR protocols.

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