

ORIGINAL ARTICLE

Genetic architecture of adaptation to novel environmental conditions in a predominantly selfing allopolyploid plant

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Genetic architecture of adaptation is traditionally studied in the context of local adaptation, viz. spatially varying conditions experienced by the species. However, anthropogenic changes in the natural environment pose a new context to this issue, that is, adaptation to an environment that is new for the species. In this study, we used crossbreeding to analyze genetic architecture of adaptation to conditions not currently experienced by the species but with high probability of encounter in the near future due to global climate change. We performed targeted interpopulation crossing using genotypes from two core and two peripheral *Triticum dicoccoides* populations and raised the parents and three generations of hybrids in a greenhouse under simulated desert conditions to analyze the genetic architecture of adaptation to these conditions and an effect of gene flow from plants having different origin. The hybrid (F1) fitness did not differ from that of the parents in crosses where both plants originated from the species core, but in crosses involving one parent from the species core and another one from the species periphery the fitness of F1 was consistently higher than that of the periphery-originated parent. Plant fitness in the next two generations (F2 and F3) did not differ from the F1, suggesting that effects of epistatic interactions between recombining and segregating alleles of genes contributing to fitness were minor or absent. The observed low importance of epistatic gene interactions in allopolyploid *T. dicoccoides* and low probability of hybrid breakdown appear to be the result of permanent fixation of heterozygosity and lack of intergenomic recombination in this species. At the same time, predominant but not complete selfing combined with an advantage of bivalent pairing of homologous chromosomes appears to maintain high genetic variability in *T. dicoccoides*, greatly enhancing its adaptive ability.

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INTRODUCTION

Adaptive differentiation evolves as a result of spatially varying selection (Garcia-Ramos and Kirkpatrick, 1997; Kirkpatrick and Barton, 1997; Doebeli and Dieckmann, 2003) and is usually detected by cross-relocation of individuals originating in different habitats (Turesson, 1922; Clausen *et al.*, 1940; Kawecki and Ebert, 2004; Leimu and Fisher, 2008; Hereford, 2010). However, although the cross-relocation can efficiently detect adaptive differentiation, it does not allow inferences about genetic architecture of this differentiation, viz. genetic effects responsible for fitness differences. The genetic architecture of adaptation to particular environmental conditions and traits involved in adaptive population differentiation can be studied through experimental hybridization between ecotypically differentiated populations and planting of the hybrids together with parents in the common garden or reciprocal-transplant field experiments. Comparison of fitness of several generations of hybrids with parental populations is a way to elucidate the contribution of dominance, genetic linkage and pleiotropic effects of genes under selection to the phenotype (Fenster and Galloway, 2000; Erickson and Fenster, 2006; Johansen-Morris and Latta, 2006; Leinonen *et al.*, 2011; Volis, 2011).

Genetic architecture of adaptation is traditionally studied in the context of local adaptation, viz. spatially varying conditions experienced by the species. However, changes in the natural environment

due to unprecedented growth of anthropogenic pressure across the globe are posing a new context to this issue, that is, adaptation to an environment that is new for the species. This knowledge becomes extremely important for conservation decisions, for example in making choice of material for relocation, or in management of threatened and rare species. Although there is a great increase in conservation biology interest to effects of crossing between genetically divergent lineages (Hufford and Mazer, 2003; Tallmon *et al.*, 2004; Edmands, 2007; Grindeland, 2008; Frankham *et al.*, 2011), no study up-to-date used crossbreeding and analysis of progeny for species in new environmental settings.

There are several possible ways to achieve adaptation to a new environment. Some individuals can be preadapted, or, alternatively, the new combinations of traits created via hybridization can be advantageous in the new environmental settings. The latter possibility can be a result of heterosis that does not disappear after F1, for example, permanent fixation of heterozygosity in allopolyploids, or recombination in F2.

In this study, we used crossbreeding to analyze genetic architecture of adaptation to conditions not currently experienced by the species but with a high probability of encounter in the near future due to the global climate change. Global climate change is expected to strongly affect Mediterranean-type ecosystems by increasing aridity (i.e. higher

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temperatures, lower rainfall and greater potential evapotranspiration) and frequency of extreme drought conditions (Schröter *et al.*, 2005). A gradient of aridity determines distribution limits of many species in the Mediterranean basin, and populations from a species periphery in this region often occupy the extremes of such a gradient (Yom-Tov and Tchernov, 1988; Kadmon and Danin, 1997). Wild emmer wheat, *Triticum turgidum* L. ssp. *dicoccoides* (Körn. ex Asch. & Graebn.) Thell. (hereafter *T. dicoccoides*) is no exception from this general pattern. The species' northern geographic limit is determined by low winter temperatures and its southern limit by low precipitation (Willcox, 2005; Özkan *et al.*, 2011). Rapid aridification will cause the species edge populations to experience conditions more arid than in any part of the current species distribution.

Genetic population differentiation (Fahima *et al.*, 2002; Ozbek *et al.*, 2007; Özkan *et al.*, 2011) and population local adaptation (Volis *et al.*, 2014a, 2015c) have been reported in this species. Introduction beyond the current range of *T. dicoccoides*, in the Negev Desert (Beer Sheva location—Bergman Campus) having around 200 mm of annual rainfall, revealed inferiority of genotypes from the southern arid range population in spite of detected local adaptation for this population (Volis *et al.*, 2014a).

In this study, we used genotypes from two locations that differ in topography separated by about 1 km within a core *T. dicoccoides* population with moderate gene flow (Volis *et al.*, 2015b), and two populations at the opposite edges of the species range, with both highly distinct environments (semiarid and mountain) and high degree of isolation. We performed targeted interpopulation crossing and grew up the parents and three generations of hybrids in a greenhouse under simulated desert conditions to analyze the genetic architecture of adaptation to these conditions and an effect of gene flow from plants having different origin.

MATERIALS AND METHODS

Study species and sampling

Wild emmer wheat, *T. turgidum* var. *dicoccoides* (hereafter *T. dicoccoides*), is a predominantly self-pollinating tetraploid annual grass (Volis *et al.*, 2014b) that

contains two genomes ($2n=4x=28$, genome AABB) and is the tetraploid progenitor of most cultivated wheats (Feldman *et al.*, 1995). It is found in habitats with annual precipitation ranging from 300 to over 1300 mm, at altitudes between -100 and 1400 m, and in several soil types, although most populations are found on terra-rossa and basalt soils (Feldman and Sears, 1981; Feldman and Kislev, 2007). We have chosen two populations representing the species distributional core in the Upper Jordan Valley catchment area with relatively favorable conditions (Mediterranean grassland), and two populations from the two opposite edges of the species distributional range with much more extreme environmental conditions (mountain and semidesert steppe) (Figure 1).

Ammiad conservation site from which two of the populations are derived (K and N) features a typical Mediterranean climate with an average annual rainfall of 580 mm. At this location, we chose two previously identified topographically dissimilar microhabitats (Anikster and Noy-Meir, 1991; Noy-Meir *et al.*, 1991). Ammiad North (N) is located on a moderate north-facing slope at an elevation of 260–280 m with relatively low rock cover (20–60%). Ammiad Karst (K) is on a steep south-facing slope of rockier micro-relief (40–80% rock cover) at 320–340 m above sea level. Mount Hermon (MH) population is the northern-most population in Israel with more than 1300 mm of rainfall and much cooler climate than in Ammiad (the area is covered with snow during winter months). Har Amasa (HA) population is the southern-most population located on the edge of Judean desert with around 300 mm of rainfall. For detailed information about the population locations see Volis *et al.* (2015a).

Although the two populations sampled at Ammiad conservation site represented different topographic conditions (habitats), they were in close proximity to each other (about 1 km) and therefore in all the analyses are treated hereafter as HABITATS, and when pooled together are referred to as a single POPULATION called Ammiad.

Accessions of K, N, MH and HA origin used in this study came from a collection of the Institute for Cereal Crops Improvement (Tel Aviv University, Tel Aviv, Israel).

Crossing design and common garden experiment

In 2007 in a greenhouse at the Bergman Campus, Beer Sheva, Israel, we performed artificial pollination of a mother plant with pollen from plants originating from K, N, HA and MH populations/habitats. This could be done due to the large number of tillers produced by a mother plant. Crossing was done using a protocol of Florell (1934). Using this method, we crossed 17, 20,

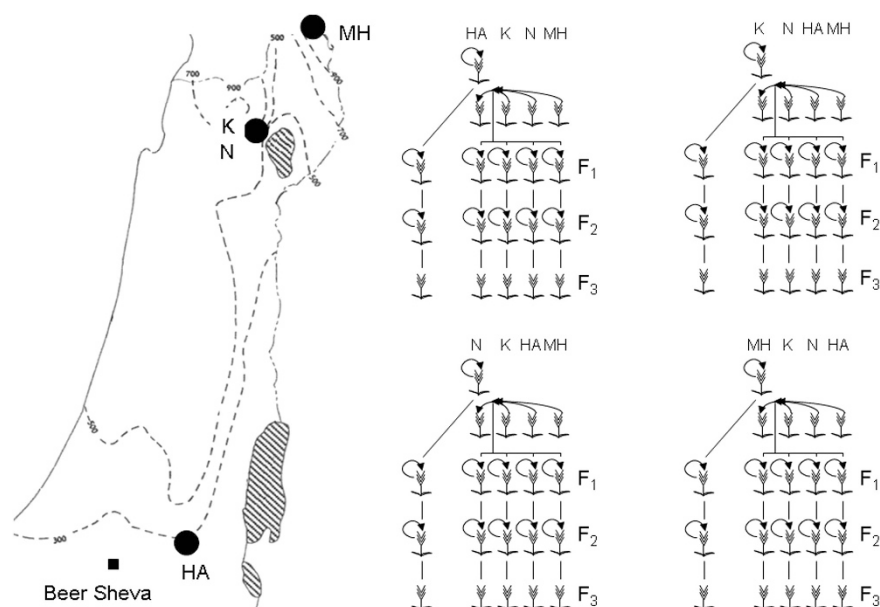


Figure 1 Left panel. Map of Israel showing isohyets of multiyear averages of annual rainfall amount (mm) and study populations. Right panel. Scheme of crossing design.

10 and 8 genetically different mother plants of K, N, HA and MH origin, respectively with plants originating in three other populations/habitats and compared the parents, produced hybrids (F1) and their self-pollinated offspring (F2 and F3) for performance (total weight of produced spikelets) and two phenotypic traits (days to awning and individual spikelet weight) in a common garden experiment in 2010–2011 (Figure 1). In this experiment, the plants were grown in a greenhouse at the Bergman Campus, Beer Sheva. Beer Sheva is located in the Northern Negev desert (annual rainfall 205 mm). Seeds were simultaneously germinated in an incubator at 24 °C and transferred into 3 l pots filled with locally collected and sieved loess soil. The experiment was conducted during the natural growing season for emmer (October–May) and was simulating the local desert conditions. The amount of water supplied to the plants was kept at the minimum necessary for plants to survive and reproduce and the plants were showing signs of suffering from drought (low turgor and wilting of leaves) during the whole experiment. However, because of a high evaporation rate in the greenhouse due to higher ambient temperatures as compared with the temperature outside the greenhouse, the amount of water supplied (equivalent to 505 mm of rainfall) was higher than naturally occurring in the Negev desert (around 200 mm). Watering was done twice a week using a drip-irrigation system. The plants were arranged using a completely randomized design. In total, 1002 plants were grown comprising two replications of 130, 160 and 156 F1, F2 and F3 hybrids, respectively, and of 55 parents. The average of the two replications was used in subsequent analyses of the measured traits.

Two putatively adaptive traits, start of awning and individual spikelet weight, were measured to examine adaptive genetic differentiation of populations/habitats and gene action (additive or dominant) in these traits. Onset of reproduction and maternal investment are the traits closely related to fitness and presumably involved in local adaptation in the studied species (Volis *et al.*, 2014a, 2015a). Traits related to the timing of life-history transitions, such as timing of reproduction, are among those that are expected to experience the strongest selection as climate changes (Bradshaw and Holzapfel, 2008). *T. dicoccoides* is an annual grass inhabiting open Mediterranean vegetation, viz. it grows in a habitat with low precipitation throughout its short growing season (October–March), and rapid development and flowering before onset of summer drought is essential for survival and reproduction in these conditions. Selection for earlier flowering was detected in winter annuals from Mediterranean climate regions in a number of studies (Stanton *et al.*, 2000; Rajakaruna *et al.*, 2003; Peleg *et al.*, 2005; Sherrard and Maherali, 2006; Volis, 2009).

Individual seed size/weight is also a trait to large extent determining plant fitness because seed size is positively related with seedling growth and establishment (reviewed in Leishman *et al.*, 2000; Moles and Westoby, 2004).

Additive vs dominant gene action in these two traits was studied by comparing F1 with each parent and the mid-parent value by a paired *t*-test.

It is known that fruit number and quality directly influence plant fitness, and a measure of fecundity must incorporate both these reproductive components. Therefore, the total weight of mature seeds produced by a plant appears to be the best estimate of its fitness (Volis *et al.*, 2004; Volis, 2009) and this trait was used in this study as the measure of plant performance. To estimate outbreeding depression or heterosis effect in hybrids, as well as the genetic mechanisms responsible for this effect (additive, dominant or epistatic), relative performance (RP) was calculated for each plant as $RP = w_i / \max(w_{PQ}, w_{P\delta}, w_{F1}, w_{F2}, w_{F3})$, where w_i is the fitness of a plant compared with maximum fitness of itself and its relatives w_{PQ} and $w_{P\delta}$ (the progeny of mother and father plant derived through selfing), and w_{F1} , w_{F2} , w_{F3} (F1, F2 and F3). Usage of the RP values that are bounded by unity allowed standardization of the data.

Analysis of genetic mechanisms of variation in performance (total seed mass per plant) of hybrids and their parents employed one-way ANOVA followed by the Newman–Keuls test for comparison of F1, P1 and P2, and one-sided *t*-test for comparison of F1 with the mid-parent value.

RESULTS

Population phenotypic differentiation

Two measured phenotypic traits, days to awning and individual spikelet weight differed among the populations, but not between the two habitats within the Ammiad population (Figure 2).

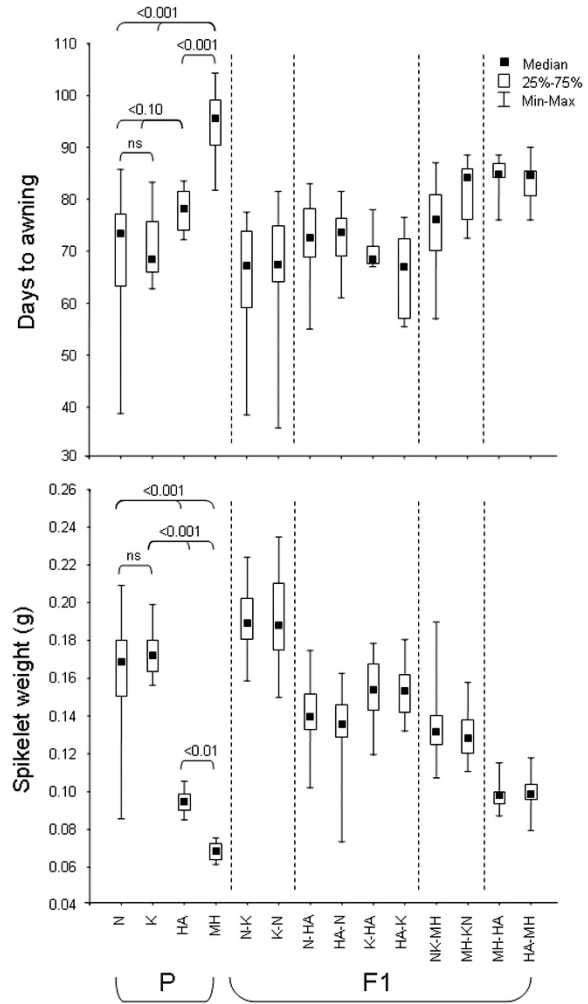


Figure 2 Box and whiskers plots for days to awning and individual spikelet weight of P and F1 plants. Significance of pair-wise differences after the Newman–Keuls test are indicated above brackets.

Days to awning was inherited as an additive trait in crosses between HA and MH plants, but showed dominance for early start of awning in crosses involving Ammiad plants and either HA or MH plants. Spikelet weight in all crosses showed dominance for heavy weight (Table 1).

Hybrid performance and its genetic basis

In pairs HA–MH and K–N parents did not differ in performance in the measured fitness estimate, total seed mass, but in other pairs they did differ (Table 2).

The hybrid phenotype was intermediate and significantly differed from both parents in only one cross, A–HA (Figure 3). In two crosses, N–K and K–N, neither the parents nor the hybrids and parents differ. And in a cross HA–MH, the hybrids were superior to both parents. In other crosses, the hybrids differed significantly from only one parent (Figure 3) indicating dominance.

In the F2 and F3, no reduction in fitness as compared with F1 was observed in any cross indicating no hybrid breakdown in later-generation hybrids (Figure 3). The results provided no evidence for underdominance or epistasis, and revealed a single case of heterosis. Dominance and additive gene action were the predominant mechanisms (Figure 3).

Table 1 Days to awning and spikelet weight mean values (\pm s.e.) of F1 and two parents in a particular cross, and results of a paired *t*-test comparing F1 with each parent and the mid-parent value

Cross	Number of crosses	Days to awning						Spikelet weight (mg)					
		♀	F1	♂	F1—♀	F1—♂	F1—MP	♀	F1	♂	F1—♀	F1—♂	F1—MP
HA×MH	13	76.5±1.2	83.0±1.1	94.0±1.9	5.1***	5.3***	1.8 NS	94.1±6.9	99.3±10.3	70.1±7.9	2.1*	15.1***	8.8***
MH×HA	7	91.4±3.7	84.2±1.5	76.7±1.7	1.6 NS	5.2**	0.1 NS	69.1±1.8	98.6±3.3	94.4±2.6	6.0***	1.5 NS	4.9**
K×N	17	71.8±1.5	66.9±3.0	71.4±3.5	1.6 NS	1.5 NS	2.2*	173.3±23	191.9±62	163.9±7.8	3.2**	2.8*	4.0**
N×K	20	68.7±2.6	65.7±2.2	72.6±1.3	2.1*	3.0*	3.8**	165.8±2.8	191.5±3.7	173.5±2.0	4.7***	4.8***	6.1***
K×HA	15	69.8±1.4	70.2±0.9	77.4±1.1	0.2 NS	4.7***	3.8**	175.4±3.2	154.2±4.5	93.0±5.3	5.5***	14.7***	5.3***
HA×K	11	78.4±1.2	65.8±2.2	71.2±1.8	4.6***	2.2*	4.0**	94.0±1.7	152.6±4.1	170.2±3.3	18.2***	3.4**	5.4***
N×HA	18	72.7±2.2	72.4±2.1	78.6±0.7	0.1 NS	2.8*	2.0 NS	159.4±8.0	141.3±4.6	92.7±0.8	2.2*	10.1***	3.3**
HA×N	11	77.8±1.0	72.9±1.7	73.1±1.4	3.0*	0.1 NS	1.5 NS	93.6±1.2	132.9±0.7	151.1±1.2	5.7***	1.7 NS	1.5 NS
NK×MH	18	70.6±2.2	75.2±1.9	88.2±1.6	2.4*	5.7***	2.5*	165.7±7.0	133.7±4.7	67.9±0.9	4.6***	13.0***	3.5**
MH×NK	13	95.6±2.1	81.7±1.5	71.0±2.0	7.0***	6.3***	1.2 NS	69.0±1.5	129.7±3.5	168.5±4.3	14.9***	11.3***	3.9**

Abbreviations: A, Ammiad; K, Ammiad Karst; HA, Har Amasa; MH, Mount Hermon; MP, Mid-parent; N, Ammiad North; NS, not significant.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table 2 Genetic mechanisms of variation in performance (total seed mass per plant) of interpopulation hybrids (F1 and F2) and their parents

Cross	Hypothesis					
	Newman-Keuls test					One-sample <i>t</i> -test
	$P1 \neq P2$ (difference in adaptive potential)	$F_1 > P1 \& P2$ (heterosis)	$F_1 = P1 \text{ or } P2$ (dominance)	$F_1 < P1 \& P2$ (underdominance)	$F_2 < F_1, P1 \& P2$ (epistasis)	$MP = F_1 = F_2$ (additive)
HA×MH	No	Yes	No	No	No	No ($t = 1.8\ddagger$)
MH×HA	No	No	No	No	No	Yes ($t = 0.1$ NS)
K×N	No	No	No	No	No	Yes ($t = 0.8$ NS)
N×K	No	No	No	No	No	Yes ($t = 0.4$ NS)
K×HA	Yes	No	Yes	No	No	Yes ($t = 0.4$ NS)
N×HA	Yes	No	No	No	No	Yes ($t = 0.1$ NS)
K×MH	Yes	No	Yes	No	No	Yes ($t = 0.4$ NS)
N×MH	Yes	No	Yes	No	No	No ($t = 4.6$ ***)
A×HA	Yes	No	No	No	No	Yes ($t = 0.3$ NS)
HA×A	Yes	No	Yes	No	No	No ($t = 2.2$ *)
A×MH	Yes	No	Yes	No	No	No ($t = 3.2$ **)
MH×A	Yes	No	Yes	No	No	No ($t = 1.9\ddagger$)

Abbreviations: A, Ammiad; HA, Har Amasa; K, Ammiad Karst; MH, Mount Hermon; MP, Mid-parent; N, Ammiad North; NS, not significant.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; $\ddagger < 0.1$.

A range of F1–F3 phenotypes in all crosses was greater than of the parent phenotypes (Figure 4).

DISCUSSION

A seed introduction experiment conducted at four locations from which the parent plants originated, revealed superiority of HA, MH and Ammiad plants in their native environments, suggesting local adaptation (Volis *et al.*, 2014a, 2015c). In contrast, no microhabitat local adaptation was found within the Ammiad location, that is, of the K and N plants (Volis *et al.*, 2015c). In the introduction of HA, MH and K genotypes into the novel climatic environment for the species, the K plants showed higher performance than plants of other origins. The superior fitness of K origin plants was evident in the number of seeds per plant 1 year after introduction and in a proportion of seeds of K origin in the total seed pool per introduction plot 4 years after introduction (Volis *et al.*, 2015c).

In the present study, ecological differentiation consistent with local adaptation was evident in two phenotypic traits, start of flowering indicated by awning and individual spikelet weight. These two traits were shown to be under selection in emmer (Volis *et al.*, 2014a), wild barley and wild oat (Volis, 2009). In the study of Volis *et al.* (2015a) under drought stress conditions simulated in the greenhouse, the K plants demonstrated the earliest onset of flowering and the highest spikelet weight among those that were introduced (*viz.* HA, MH and K). These population differences were genetically determined and were observed not only under drought stress but also under favorable conditions (Volis *et al.*, 2015a). The present study revealed that expression of genes contributing to these two traits in F1 hybrids grown under simulated desert conditions varied from additive to full dominance, with dominance for earlier flowering and larger spikelets. It does not seem to be a coincidence that plants that were superior in the novel environmental conditions possessed traits that were favored

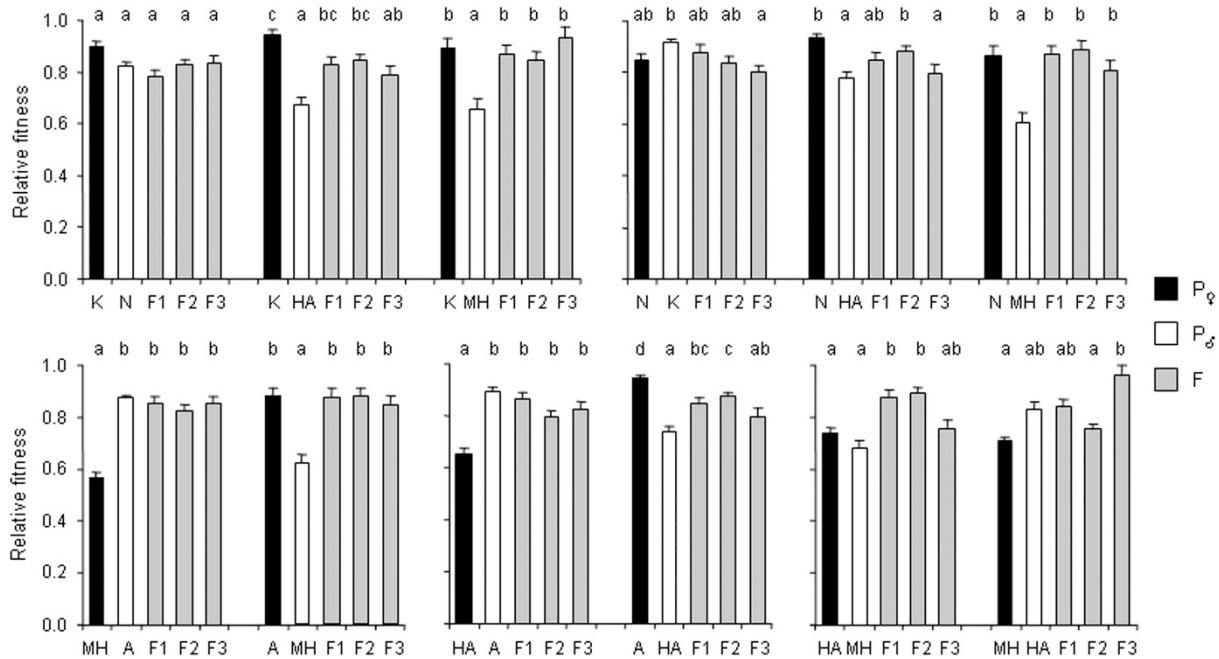


Figure 3 Relative performance in total seed mass of three generations of interpopulation hybrids (F1, F2 and F3) and their parents. Upper panel: crosses between plants from the two Ammiad habitats (N and K) and the HA and MH populations. Lower panel: crosses between all Ammiad plants (N and K combined) and plants from the HA and MH populations. Letters denote results of the Newman–Keuls test comparing plant performance within a particular interpopulation cross.

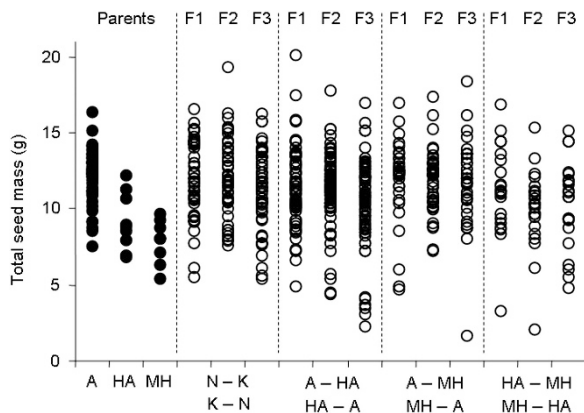


Figure 4 Performance, estimated as total seed mass, of three generations of interpopulation hybrids (F1, F2 and F3) and their parents.

under a wide range of conditions and exhibited incomplete or complete dominance.

The hybrid (F1) fitness under simulated in the greenhouse desert conditions did not differ from that of the parents in crosses of N and K plants, but was consistently higher than of either HA or MH parents in crosses involving one parent from Ammiad and one parent originating elsewhere. Similar to the two quantitative traits, the genes contributing to the total weight of seeds produced by a plant exhibited incomplete or complete dominance. It appears that Ammiad plants are closer to the optimal for the Negev desert environment phenotype than the other two ecotypes, and alleles received from HA and MH plants, inferior in this environment, diluted a set of alleles better adapted to this environment. Because of dominance, this diluting effect in most cases was negligible or absent. In contrast, hybrids that resulted from a cross between ecotypes further from the optimal for

the Negev desert environment phenotype (*viz.* HA and MH) were more fit than the either parent when the mother plant was HA and MH was a pollen donor. The reciprocal, however, was not true indicating nuclear–cytoplasmic interaction (Levin, 2003). Reciprocal differences in fitness and importance of cytoplasmic origin for F1 hybrids were reported in several inter- and intraspecific crossbreeding studies (Campbell and Waser, 2001; Galloway and Fenster, 2001; Rhode and Cruzan, 2005; Campbell *et al.*, 2008; Sambatti *et al.*, 2008).

Plant fitness in the next two generations (F2 and F3) did not differ from the F1, suggesting that effects of epistatic interactions between recombining and segregating alleles of genes contributing to fitness were minor or absent. This observed lack of hybrid breakdown in F2 disagrees with the results of a methodologically similar study in diploid wild barley (Volis, 2011) and raises a question of possible polyploidy effect because emmer wheat is a tetraploid comprising two independently inherited subgenomes. Allopolyploidy is a process of hybridization between different species followed by chromosome doubling or a result of fusion of unreduced gametes of two species. Thus allopolyploidization creates ‘doubled interspecific hybrids’, leading to permanent fixation of heterozygosity and hybrid vigor (Chen, 2010). The allopolyploidy is known to facilitate tolerance to genomic changes that are either unattainable or unfavorable at the diploid level (Feldman and Levy, 2005; Feldman and Levy, 2009). This tolerance is mostly due to prevention of segregation of new intergenomic combinations. Although several recent studies showed that chromosome substitutions and rearrangements between homologous regions do happen in the early generations postpolyploidization (Xiong *et al.*, 2011; Chester *et al.*, 2012), it does not happen in *T. dicoccoides* due to complete absence of intergenomic pairing. Thus, as a result of permanent fixation of heterozygosity and lack of intergenomic recombination, a wide range of new combinations within each of the two subgenomes in *T. dicoccoides* has fitness similar to the parent’s and therefore is maintained and not purged. If both parents have genotypes that are far

from the local optimum, the proportion of new combinations having higher fitness than any of the parents increases. This, indeed, was observed only in a cross between MH and HA ecotypes inferior in the desert environment. On the other hand, recombination in F2 and following generations within subgenomes is still possible (Feldman and Levy, 2005), and, again, its effect is more evident in a cross between genotypes that are far from the local optimum.

To summarize, analysis of genetic architecture of adaptation in allopolyploid *T. dicoccoides* revealed low importance of epistatic gene interactions and low probability of hybrid breakdown. At the same time predominant but not complete selfing combined with an advantage of bivalent pairing of homologous chromosomes appears to insure maintenance of a wealth of genetic variability in this allopolyploid species, greatly enhancing its adaptive ability.

DATA ARCHIVING

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.5d3s2>.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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