

**WITHIN- AND TRANS-GENERATIONAL PLASTICITY  
AFFECTS THE OPPORTUNITY FOR SELECTION IN BARBED  
GOATGRASS (*AEGILOPS TRIUNCIALIS*)<sup>1</sup>**

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- *Premise of the study:* Environments are composed of selective agents, and environments may also modify the efficacy of these agents. Environments affect the rate of maximum evolutionary change by influencing variation in relative fitness (i.e., the opportunity for selection, or *I*). Within- and transgenerational plastic environmental responses may affect *I*, speeding or slowing processes of local adaptation.
- *Methods:* We determined whether environmental factors affected the opportunity for selection (*I*) in *Aegilops triuncialis* (barbed goatgrass) by measuring *I* as a within- and transgenerational plastic response to two maternal glasshouse environments (serpentine/dry and loam/moist). We also determined whether this species' two most common genetic lineages (determined by DNA microsatellite length polymorphism) varied in response to glasshouse treatments.
- *Key Results:* Opportunity for selection was less for plants grown in the dry serpentine environment than for plants grown in the moist loam environment. This response varied between genetic lineages. The east lineage exhibited a within-generation response to the dry serpentine environment. For both seed mass and average seed weight in this lineage, the opportunity for selection was lower in dry serpentine than in moist loam. The west lineage had a transgenerational response to the dry serpentine such that the opportunity for selection for seed number and seed mass was lower for plants produced by mothers grown in dry serpentine than for plants produced by mothers in moist loam.
- *Conclusions:* Phenotypic variation in relative fitness is constrained by the dry serpentine environment, which leads to lower evolvability in this environment. Within- and transgenerational effects of the environment may slow local adaptation to serpentine soils.

**Key words:** secondary invasion; serpentine; annual grasslands; canalization; maternal effects

Phenotypic plasticity in response to the environment may generate different average responses for individual traits across environments (Sultan et al., 2009) as well as influence the magnitude of phenotypic variability within an environment (Debat and David, 2001). Thus, when fitness is the trait of interest, plasticity can both affect average fitness and the variance in fitness within populations in response to environmental factors. Under conditions of range expansion, populations encounter novel environments that amplify variation in fitness within populations (Schlichting, 2008). While environments usually contain agents of natural selection, environments may also modify the efficacy of that selection (Crow and Morton, 1955; Brodie et al., 1995; Parker et al., 2003). The opportunity for selection (*I*) is an expression of the evolvability of a particular trait within a population (Hansen et al., 2003). When *I* is small, there is less opportunity for selection to act (Crow, 1958; Brodie et al., 1995;

Debat and David, 2001; Waller et al., 2008). The response to selection is also constrained by *I* because the most that a mean can shift in response to selection is the square root of *I* (Arnold and Wade, 1984). Here, we use *I* to examine the evolvability of increased fitness within expanding populations of an invasive annual grass, barbed goatgrass (*Aegilops triuncialis* L.).

In a related study, Meimberg et al. (2006) found that *Ae. triuncialis* collections from California have higher fitness when grown in a dry, serpentine environment compared to a moist, nonserpentine (i.e., loam) environment, and thus adaptation may allow this species to further expand its range to serpentine. When adaptive phenotypes are present in a population, selection can reinforce reductions in fitness variation, leading to genetic assimilation (Eshel and Matessi, 1998; Pal and Miklos, 1999). However, decreases in phenotypic variability can also decrease the potential for a population to respond to selection (Crow and Morton, 1955; Gavrilets and Hastings, 1994; Brodie et al., 1995; Debat and David, 2001; Waller et al., 2008).

In this study, we explore within and across generation effects of the environment on fitness and ask if within- and/or transgenerational plasticity can alter rates of evolutionary change. The genotype by environment interaction is usually measured as within-generation phenotypic plasticity, but, transgenerational plasticity can affect the opportunity for selection within populations and adds a historical layer to the environmental portion of “genotype by environment” interactions (Agrawal, 2002; Galloway and Etterson, 2007; Dyer et al., 2010). Within-generation plasticity could facilitate adaptation to serpentine in this species if higher fitness in dry serpentine environment is paired with

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greater  $I$ . This process would be further accelerated if transgenerational plasticity also generates greater  $I$  in progeny from parents grown in a serpentine environment. We grew field-collected seeds from serpentine and nonserpentine habitats for two generations in the glasshouse, separating the effects of habitat seed source (habitat of field-collected seed) and our experimental glasshouse environments (dry serpentine vs. moist loam) to observe the effects of adaptation and plasticity on components of offspring fitness.

## MATERIALS AND METHODS

**Study species**—*Aegilops triuncialis*, a close relative of cultivated wheat (*Triticum aestivum*), is native to the Mediterranean basin and Middle East. Because of its morphological similarities to wheat, *A. triuncialis* may have been introduced in the mid-1800s to the western United States and California as a wheat or alfalfa seed contaminant. *Aegilops triuncialis* is a self-fertilizing annual grass and grows in dense populations on moderately fertile soils. It is a noxious weed in California and Oregon. *Aegilops triuncialis* shares basic characteristics with other invasive annual grasses in California, including large seed size, distinctive adaptations to herbivory and animal dispersal, and a winter-annual growth habit. The species has successfully invaded loam soils in north-central California, often forming large populations of high density. *Aegilops triuncialis* typically occurs as smaller populations at lower densities on serpentine soils.

**Glasshouse experiment—Maternal generation**—To examine within-generation plasticity responses to soil environment, seeds were collected from 16 *A. triuncialis* source populations (5 from serpentine habitats, 11 from nonserpentine habitats) in northern California. A previous analysis of these populations has shown that each population consists of a single lineage (determined by DNA microsatellite length polymorphism) that is uncorrelated with habitat type (Meimberg et al., 2006). We hypothesized that each lineage resulted from a different introduction event (Meimberg et al., 2006). Our experiment used the most common two lineages (east and west). The east lineage occurs east of the California central valley, and the west lineage occurs west of the valley. The experiment comprised 10 source populations of the east lineage and six source populations of the west lineage. One spike was collected from each of 15 families from each source population. Source population is the unit of replication in this experiment, with each of the 15 sampled families nested within a population serving as subsamples. Seeds used in this experiment were chosen from the midrange of seed masses of each field-collected spike. Any reduction of variability in seed mass resulting from this choice was assumed to be equal across all treatments. One seed per family was planted in each treatment: a pot filled with field-collected serpentine soil or a pot filled with field-collected loam soil. Pots were 3.8 cm in diameter and 21 cm deep (Stuewe and Sons “supercells”; Tangent, Oregon, USA). Seeds were planted on 5 February 2005 and placed outdoors at the University of California, Davis. Pots were watered daily, either by rainfall or supplemental hand watering. Germination began on 9 February. Pots were brought into the glasshouse on 5 May at the start of flowering. Starting on 24 May, serpentine soil pots received one-third the volume of water of loam soil pots to simulate the earlier dry-down of these serpentine habitats (K. Rice, unpublished data). Watering of all pots was reduced from daily to biweekly on June 6. Seeds were collected daily as they matured and were stored in the laboratory at 25°C. Strong population differentiation in response to soil type would result in a significant source habitat by maternal environment interaction in our analysis of this experiment, but it is important to note that our glasshouse maternal environments mirror source habitats only on the coarsest scale of soil chemistry and water availability and do not simulate other habitat factors.

**Progeny generation**—To examine the effect of transgenerational plasticity on plant phenotypes, seeds produced from the maternal generation experiment were used the following growing season in a progeny generation experiment. In this experiment, all progeny were planted in the same soil and received the same watering treatment. All source populations used in the maternal generation were represented in the progeny generation, and, again,

population was the unit of replication. Our subsamples comprised only 10 of the original 15 families from each population. All pots were filled with non-serpentine soil, and we kept track of both maternal environment and source habitats for each plant. Thus, although 10 source families per population were used in this experiment, seeds used were collected from 20 maternal-generation plants: 10 from dry serpentine treatment and 10 from moist loam. Three individually weighed seeds from each maternal family served as subsamples. Pots, each planted with a single seed, were watered with fertilizer prior to sowing and watered daily as germination occurred in the glasshouse. After germination was completed (23 February 2007), pots were placed outdoors. Pots were watered 3 times wk<sup>-1</sup> for the duration of the experiment, either by rainfall or by hand watering. Seedling size (i.e., number of leaves) was measured 4 wk after sowing. Pots were brought into the glasshouse at the start of flowering. Seeds were collected daily as they ripened and then stored in the laboratory at 25°C.

**Data collection and analysis**—In both the maternal and progeny generations, we recorded the number of seeds produced and total seed mass; we also calculated average seed size (total seed mass/number of seeds). To examine treatment effects on within-generation plasticity, we performed a multivariate analysis of variance (MANOVA) on the means of these traits for the maternal generation, using lineage, source habitat, maternal environment, and the source habitat  $\times$  maternal environment interaction as factors. To examine treatment effects on transgenerational plasticity, we performed a MANOVA on the mean seedling size, seed number, total seed mass, and average seed size in the progeny generation, using lineage, source habitat, maternal environment, and the source habitat  $\times$  maternal environment interaction as factors. In each case, lineage was highly significant (Table 1A), so we performed an additional MANOVA on response variables separated by lineage to determine whether treatments had an effect once lineage differences were taken into account.

Although trait means of the maternal generation experiment were analyzed in another study (Meimberg et al., 2006), only qualitative differences were reported for measured traits, with the exception of seed number. In that study, maternal plants grown in dry serpentine soil pots were found to produce 0.5 more seeds per plant than plants grown in the moist loam pots, regardless of source population. Because quantitative differences were not reported in the previous publication for other traits, we reanalyzed them and report them here, along with results on  $I$ , which have not been analyzed previously.

Because trait means were significantly different between lineages (Table 1A), we performed separate MANOVAs on the opportunity for selection ( $I$ ) for each lineage (Downhower et al., 1987), with source habitat, maternal environment, and their interaction as factors. We calculated  $I$  as the variance/mean<sup>2</sup> (Crow, 1989) of each dependent variable.  $I$  was calculated at the family level for the progeny generation (then averaged across families to get the value of  $I$  for each population) and calculated at the population level for the maternal generation.  $I$  was square-root transformed for analysis to satisfy parametric analysis assumptions. When the MANOVA showed significance for a factor, we performed follow-up single-factor ANOVAs to determine the dependent variable responding to our treatments (Scheiner and Gurevitch, 2001). Because of the selfing nature of this species, paternal and maternal environmental effects cannot be partitioned. We set our significance level at  $P = 0.05$  for all analyses. Results are presented as means  $\pm$  SE.

## RESULTS

The interaction between source habitat and maternal environment, which would indicate population differentiation by source habitat, was never significant ( $P > 0.1$ ; Table 1B). Thus, results are shown by lineage and by maternal environment (Table 2A) or by lineage and by source habitat (Table 2B). As was reported in an earlier study (Meimberg et al., 2006), maternal means for seed number and seed mass were greater in the dry serpentine maternal environment than in the moist loam environment in both lineages. This is in contrast to the effect of source habitat on maternal plants, where seed mass and average seed weight were less in plants from serpentine habitats within the east lineage (Table 2B).

TABLE 1A. Results of MANOVA: (A) means of each generation, (B) means of each generation separated by lineage, and (C) opportunity for selection (*I*) of each generation separated by lineage. SH = source habitat, ME = maternal environment.

	Maternal plants					Progeny				
	Canonical coefficient	Pillai's trace	df	<i>F</i>	<i>P</i>	Canonical coefficient	Pillai's trace	<i>F</i>	df	<i>P</i>
Lineage	0.982	0.964	3, 25	224.41	<0.0001	0.970	0.941	96.26	8, 19	<0.0001
SH	0.309	0.095	3, 25	0.88	0.4655	0.357	0.128	0.88	8, 19	0.4915
ME	0.305	0.093	3, 25	0.85	0.4777	0.143	0.020	0.12	8, 19	0.972
SH*ME	0.311	0.097	3, 25	0.89	0.4595	0.418	0.175	1.27	8, 19	0.310

TABLE 1B.

	Maternal plants					Progeny				
	Canonical coefficient	Pillai's trace	df	<i>F</i>	<i>P</i>	Canonical coefficient	Pillai's trace	df	<i>F</i>	<i>P</i>
East Mean										
SH	0.641	0.411	3, 14	3.72	0.033	0.596	0.355	8, 8	1.32	0.319
ME	0.666	0.444	3, 14	4.26	0.022	0.183	0.034	8, 8	0.08	0.994
SH * ME	0.351	0.123	3, 14	0.75	0.538	0.487	0.237	8, 8	0.75	0.605
West mean										
SH	0.781	0.611	3, 6	3.14	0.109	0.537	0.289	8, 1	0.33	0.875
ME	0.972	0.944	3, 6	34.01	< 0.001	0.529	0.280	8, 1	0.31	0.884
SH * ME	0.640	0.409	3, 6	1.39	0.335	0.541	0.293	8, 1	0.33	0.872

TABLE 1C.

	Maternal plants					Progeny				
	Canonical coefficient	Pillai's trace	df	<i>F</i>	<i>P</i>	Canonical coefficient	Pillai's trace	df	<i>F</i>	<i>P</i>
East <i>I</i>										
SH	0.534	0.290	3, 12	2.18	0.130	0.480	0.231	4, 12	0.66	0.661
ME	0.653	0.427	3, 12	3.97	0.027	0.650	0.422	4, 12	1.61	0.237
SH*ME	0.504	0.254	3, 12	1.82	0.185	0.467	0.219	4, 12	0.62	0.691
West <i>I</i>										
SH	0.383	0.146	3, 6	0.34	0.795	0.764	0.584	3, 6	1.12	0.469
ME	0.709	0.503	3, 6	2.02	0.213	0.979	0.958	3, 6	18.16	0.008
SH * ME	0.593	0.352	3, 6	1.08	0.424	0.430	0.185	3, 6	0.18	0.956

As a within-generation response, east-lineage maternal plants expressed less opportunity for selection (*I*) in seed mass ( $0.10 \pm 0.02$ ) and average seed weight ( $0.07 \pm 0.01$ ) in the dry serpentine environment compared with the moist loam ( $0.18 \pm 0.02$  and  $0.15 \pm 0.02$ , respectively;  $P < 0.03$ , Tables 1C and 2A). West-lineage maternal plants did not exhibit differences in *I* as a within-generation response to environment ( $P > 0.2$ ; Table 1C). There was a transgenerational response to maternal environment in progeny from the west lineage. For seed number and seed mass, these plants exhibited more than twice the opportunity for selection when their mothers were grown in the moist loam environment than when their mothers were grown in the dry serpentine environment ( $P < 0.01$ , Table 1C and Fig. 1).  $I_{\text{seed number}}$  was  $0.11 \pm 0.03$  for plants from dry-serpentine-grown mothers and  $0.28 \pm 0.06$  for plants from moist-loam-grown mothers (Fig. 1).  $I_{\text{seed mass}}$  was  $0.11 \pm 0.03$  for plants from dry-serpentine-grown mothers and  $0.29 \pm 0.07$  for plants from moist-loam-grown mothers (Fig. 1). Trends for all progeny (both east and west lineages) were that *I* was less in progeny from dry-serpentine-grown mothers compared with progeny from

moist-loam-grown mothers for all dependent variables (Fig. 1). Parallel trends were also observed as a within-generation response to maternal environment (Table 2A).

## DISCUSSION

The two lineages had different responses to source habitat and maternal environment, but generally the dry serpentine treatment resulted in greater fitness and decreased opportunity for selection compared with the moist loam treatment. The east lineage responded to source habitat with lower fitness when its origin was serpentine rather than nonserpentine habitat. The east lineage also responded to maternal environment with greater fitness when the maternal environment was dry serpentine rather than moist loam. The west lineage responded to maternal environment with greater fitness as a within-generation response in the dry serpentine environment compared with moist loam and showed no significant fitness response to source habitat. The opportunity for selection (*I*) was affected as a within-generation response in east-lineage plants. Plants grown in the dry serpentine environment

TABLE 2A. Means for maternal plants separated by lineage and treatment: (A) maternal environment (ME), where Serp = dry/serpentine environment and Loam = moist/loam environment; and (B) source habitat (SH), where Serp = serpentine habitat and Loam = nonserpentine habitat. Numbers in parentheses are  $\pm$ SE. Different letters or symbols indicate significant differences within lineages ( $P < 0.05$ ). Opportunity for selection ( $I$ ) was not analyzed by source habitat ( $P > 0.4$  in MANOVA; Table 1); means are shown for information only. West-lineage means were not analyzed by source habitat ( $P > 0.1$  in MANOVA; Table 1B) but are shown for information only.

Lineage	ME	<i>n</i>	# seeds	$I_{\# \text{ seeds}}$	Seed mass (mg)	$I_{\text{seed mass}}$	Avg. seed weight (mg)	$I_{\text{avg. seed weight}}$
East	Loam	10	1.7 (0.8) <sup>a</sup>	0.14 (0.02) <sup>a</sup>	23.1 (1.0) <sup>a</sup>	0.18 (0.02) <sup>a</sup>	14.6 (0.7) <sup>a</sup>	0.15 (0.02) <sup>a</sup>
East	Serp	10	2.2 (0.1) <sup>b</sup>	0.10 (0.02) <sup>a</sup>	29.9 (1.2) <sup>b</sup>	0.10 (0.02) <sup>b</sup>	14.1 (0.5) <sup>a</sup>	0.07 (0.01) <sup>b</sup>
West	Loam	6	3.0 (0.1) <sup>+</sup>	0.09 (0.02) <sup>+</sup>	26.6 (0.5) <sup>+</sup>	0.12 (0.02) <sup>+</sup>	8.9 (0.3) <sup>+</sup>	0.05 (0.01) <sup>+</sup>
West	Serp	6	3.7 (0.1) <sup>*</sup>	0.08 (0.03) <sup>+</sup>	29.6 (0.8) <sup>*</sup>	0.06 (0.01) <sup>*</sup>	8.2 (0.2) <sup>+</sup>	0.04 (0.01) <sup>+</sup>

TABLE 2B.

Lineage	SH	<i>n</i>	# seeds	$I_{\# \text{ seeds}}$	Seed mass (mg)	$I_{\text{seed mass}}$	Avg. seed weight (mg)	$I_{\text{avg. Seed weight}}$
East	Loam	8	1.9 (0.1) <sup>a</sup>	0.13 (0.02)	27.6 (1.2) <sup>a</sup>	0.14 (0.02)	14.9 (0.4) <sup>a</sup>	0.10 (0.02)
East	Serp	2	1.9 (0.1) <sup>a</sup>	0.09 (0.02)	23.6 (1.7) <sup>b</sup>	0.14 (0.05)	12.8 (0.9) <sup>b</sup>	0.15 (0.03)
West	Loam	3	3.2 (0.2)	0.07 (0.01)	27.9 (1.0)	0.09 (0.02)	8.7 (0.4)	0.04 (0.01)
West	Serp	3	3.4 (0.2)	0.09 (0.03)	28.3 (0.9)	0.09 (0.02)	8.4 (0.2)	0.01 (0.01)

resulted in an opportunity for selection about half that of plants grown in the moist loam environment. For west-lineage plants, the transgenerational response resulted in progeny from dry serpentine mothers with an opportunity for selection about one-third of that of progeny from mothers grown in moist loam.

Variability in fitness may be the end product of many contributing developmental pathways that all respond differently to environmental cues. These individual pathways may combine to stabilize fitness across different selection regimes. Alternatively, this stability in fitness may be due to a single provisioning pathway (e.g., Schlichting, 2008) that performs extremely reliably in the dry serpentine environment but exhibits more variable performance in the moist loam environment. Interactions among developmental pathways and their regulatory systems can work to produce more or less phenotypic variation in

different environments even when the genotypes are the same (Braendle and Felix, 2008). Although mechanisms for the transmission of transgenerational plasticity are not well studied or understood, there is some evidence for seed-coat influence on progeny development (Lacey et al., 1997) as well as instances of epigenetic alterations in several plant species (Feil and Fraga, 2012).

Physiological components of within-generation plasticity and their evolutionary outcomes are well studied (Schlichting and Smith, 2002) and transgenerational responses to maternal stress have been found in multiple plant species (Agrawal, 2002; Galloway and Etterson, 2007; Riginos et al., 2007; Sultan et al., 2009; Dyer et al., 2010). In another study on *A. triuncialis*, Dyer et al. (2010) showed that progeny of serpentine-grown parents have lower photosynthetic rates and higher

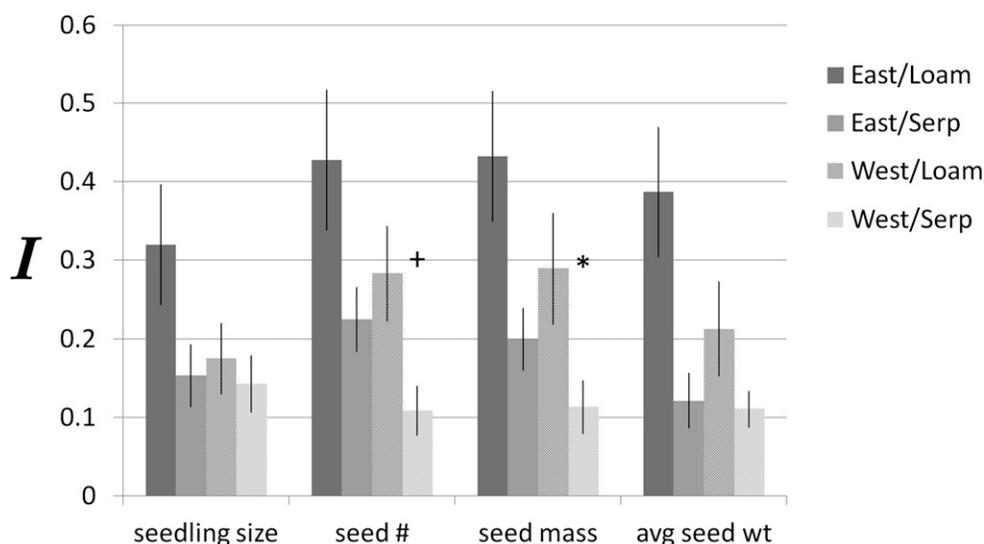


Fig. 1. Opportunity for selection ( $I$ ) for progeny traits by lineage and maternal environment (Loam = moist loam, Serp = dry serpentine). East-lineage  $I$  was not analyzed ( $P > 0.2$  in MANOVA, Table 1B) but is presented for comparison. Symbols indicate significant difference within west lineage (+  $P < 0.05$ , \*  $P = 0.05$ ).

biomass accumulation than those from nonserpentine-grown parents. In *Impatiens capensis*, drought-stressed maternal plants appeared to produce progeny with adaptive gas exchange physiology: progeny from water-stressed maternal plants lost less water to transpiration without a concomitant cost to biomass production (Riginos et al., 2007). By contrast, we found no differences in progeny means in response to different controlled maternal environments. Although the studies cited above did not analyze variation, standard deviations and standard errors appear to be similar among progeny in these studies (Agrawal, 2002; Galloway and Etterson, 2007; Riginos et al., 2007; Sultan et al., 2009; Dyer et al., 2010). Our finding of very different levels of variation among progeny may be unusual although the lack of formal studies on the effect of transgenerational plasticity on the opportunity for selection make generalizations premature.

We could not test for potential fitness effects of different environments within the progeny generation because all plants were grown in loam soil and received the same watering treatment. Given that the expression of maternal effects can vary with progeny environment and that progeny stress is often necessary for full expression of maternal effects (Miao et al., 1991; Watson and Hoffmann, 1995; Van Zandt and Mopper, 2004), our study may have underestimated the magnitude of these effects in this species.

We found greater opportunity for selection in the moist loam environment than in the dry serpentine environment, as both a within- and a trans-generational plastic response. Although the within-generation response to the dry serpentine environment was greater fitness than in the moist loam, the opportunity for selection in the dry serpentine was less, both within and across generations. This decrease in phenotypic variability in response to the dry serpentine can decrease the potential for populations in this environment to respond to selection (Crow and Morton, 1955; Gavrillets and Hastings, 1994; Brodie et al., 1995; Debat and David, 2001; Waller et al., 2008). Other researchers have shown that the magnitude and environmental dependence of fitness variation (i.e., opportunity for selection), mean fitness, and trait heritability are all important determinants of adaptive evolution (Schlichting and Smith, 2002; Ghalambor et al., 2007; Schlichting, 2008). In barbed goatgrass, there is evidence that environmental effects on fitness means and opportunity for selection may be uncorrelated and operate in confounding directions within trajectories of adaptive evolution.

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