

Evolutionary ecology along invasion fronts of the annual grass *Aegilops triuncialis*

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Abstract Over the last two decades, *Aegilops triuncialis* (barbed goatgrass) has rapidly spread into many annual grassland and serpentine soil sites within California, USA. The capacity of this species to invade edaphically stressful serpentine soil is especially unusual. It is unclear whether genetic differentiation, phenotypic plasticity, or both have allowed *A. triuncialis* to invade competitive (i.e. high productivity non-serpentine annual grassland) and edaphically stressful (i.e. low productivity serpentine) environments. We used a reciprocal transplant field experiment to examine the effects of plasticity and genetic variation on *A. triuncialis* phenology and demography along invasion fronts associated with interspecific competition and edaphic gradients. We reciprocally transplanted seeds collected behind

invasion fronts (core subpopulations) and along invasion fronts (edge subpopulations). For both gradient types we measured higher reproduction and population growth at invasion front edges. This was true for both edge and core subpopulation seed sources, suggesting that phenotypic plasticity may facilitate invasive spread. Consistent planting site effects indicated that phenotypic plasticity is a primary contributor to *A. triuncialis* demographic responses along interspecific competition gradients. In contrast, significant seed source effects suggest genetic differentiation along invasion fronts in serpentine edaphic gradients. Although persistent maternal environmental effects cannot be ruled out entirely, seed source effects suggest genetic differences between serpentine subpopulations located behind and beyond the invasion fronts for plant survival, plant size, total seed production, and individual seed size. Rapid expansion of *A. triuncialis* in California may reflect an evolutionary capacity in this species for both phenotypic plasticity and genetic differentiation.

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Introduction

Although there is a long history of ecological studies of biological invasions, only recently has that research focused on the evolutionary aspects of biological

invasions (Sakai et al. 2001; Lee 2002). One particular goal is a better understanding of the relative roles of in situ genetic differentiation and phenotypic plasticity in facilitating the establishment and spread of invasive plants (Dietz and Edwards 2006). Research on mine spoils demonstrates clearly that many species, particularly grasses, are capable of rapid adaptation to localized edaphic stress gradients (reviewed in Bradshaw and Hardwick 1989). In addition, numerous studies have reported on the ability of annual species to adjust to fine-grained environmental heterogeneity through developmental plasticity (Jain 1969; Sultan and Bazzaz 1993; Dyer et al. 2010). Therefore, if genetic bottlenecks limit an invading species' ability for local adaptive genetic differentiation, then phenotypic plasticity may facilitate those invasions by buffering against environmental stress (Rice and Mack 1991a; Ghalambor et al. 2007). In addition to the more commonly considered within-generation adaptive plasticity, maternal environmental effects or trans-generational plasticity may further increase the capacity of a species to adapt to new habitats and thus facilitate invasive spread (Sultan et al. 2009; Dyer et al. 2010). Despite research focused on the role of genetic differentiation and plasticity of plant invaders at regional scales and across habitats (Rice and Mack 1991b; Sakai et al. 2001; Sexton et al. 2002), more information is needed concerning the evolutionary dynamics of invasive populations at the very local spatial scale (Parker et al. 2003; Sexton et al. 2009). In particular, post-establishment outward movement of the invasion front is likely predicated on a combination of plastic responses and adaptive genetic variation on a very local scale (Dietz and Edwards 2006).

Aegilops triuncialis L. (barbed goatgrass) is an invasive annual grass species introduced from Eurasia that is currently spreading rapidly in California. Expanding invasion fronts can be found at numerous sites in both grassland and serpentine habitats (Thomson 2007; Lyons et al. 2010) and these invasion fronts offer an excellent opportunity to examine the relative roles of genetic differentiation and plasticity in facilitating invasive spread of this species. At a local scale, invasions of *A. triuncialis* into both non-serpentine annual grasslands and serpentine soils are often characterized by a relatively distinct invasion front (Thomson 2007). For example, along the leading edge of invasion fronts into serpentine sites, the density of *A. triuncialis* often drops off sharply (<50 tillers/m²) while behind the

invasion front the density of barbed goatgrass is typically very high (>500 tillers/m²) (Thomson 2007). Dispersal of *A. triuncialis* seeds between subpopulations in core microsites (located behind the invasion front) and subpopulations in edge microsites (located at the expanding edge of the invasion front) is extremely limited (Thomson 2007). This limited dispersal, coupled with the highly selfing nature of *A. triuncialis* (van Slageren 1994), suggests that gene flow between core and edge subpopulations of *A. triuncialis* should be very low. Reduced gene flow is predicted to foster the evolution of core and edge ecotypes if adequate genetic variation is present and selective differences between core and edge microsites are sufficiently strong.

The non-serpentine annual grasslands into which *A. triuncialis* is expanding are characterized by relatively high productivity and plant density. In contrast, serpentine habitats are characterized by severe edaphic resource limitations (Kruckeberg 2004) resulting in lower productivity and plant density in comparison to grassland habitats. Therefore, the selective agents experienced by *A. triuncialis* plants in core and edge microsites within these habitats are likely to be either biotic (e.g. resource competition), abiotic (e.g. edaphic stress), or both. Although the role of facilitation in serpentine soils is not well known, it may influence emergence in *A. triuncialis* (Eviner and Chapin 2003) and survival in *Plantago erecta* (Espeland and Rice 2007) in serpentine habitats.

Within the habitats invaded by *A. triuncialis*, different competitive regimes are predicted for the subpopulations located in core and edge microsites. In California non-serpentine annual grassland habitats, intraspecific competition is a significant component of the plant-plant interactions within established core areas where densities of *A. triuncialis* are highest. In contrast, *A. triuncialis* subpopulations in the edge microsites at or near the spreading front will encounter lower densities of conspecifics and interspecific interactions will become dominant. In contrast to non-serpentine annual grasslands, serpentine habitats are characterized by edaphic stress factors such as very low macronutrient availability, low Ca to Mg ratios, reduced soil moisture, and heavy metal toxicity. Within serpentine areas invaded by *A. triuncialis*, these edaphic stressors may have a greater influence on edge subpopulations while intraspecific competition is of greater importance within established core subpopulations (Thomson 2007). For example, during

the spring growing season, soil moisture depletion occurs more rapidly in serpentine edge microsites than in core microsites primarily because of coarser soil texture and lower water holding capacity (McKay and Rice, unpublished data). If the initial invasion and establishment occurs on better soils (i.e. core microsites), then selection caused by abiotic stress may be greater in edge microsites of lower soil nutrients and reduced soil water availability.

Adaptive phenotypic plasticity may be the most likely mechanism for establishment and demographic expansion by invasive species experiencing severe genetic bottlenecks during introduction into their new range (Sexton et al. 2002; Parker et al. 2003; Richards et al. 2006). For example, a recent study compared molecular markers between 57 accessions of *A. triuncialis* from its home range and 11 invasive populations in California (Meimberg et al. 2006). The results indicated that an extreme genetic bottleneck occurred during the process of establishment of *A. triuncialis* in California. Only three multilocus genotypes were identified in *A. triuncialis* accessions in California while 36 genotypes were identified in the home range accessions. These results further indicated that a population at any given site represents a single introduction and that the amelioration of local genetic bottlenecks by multiple introductions is probably rare to non-existent. For the genetically depauperate populations of this species, the molecular evidence supports predictions that range expansion along local biotic and abiotic gradients should result primarily from phenotypically plastic responses.

Despite evidence that molecular genetic variation is extremely low, greenhouse common garden experiments indicate genetic variation in flowering time among genotypes from different serpentine sites in California (Meimberg et al. 2010). However, it is unknown whether there is significant genetic variation in quantitative traits related to survival and reproduction within *A. triuncialis* populations expanding into both non-serpentine annual grasslands and serpentine sites. Indeed, the degree to which subpopulations within an actively expanding population may diverge genetically along a selection gradient will depend on the amount of standing quantitative genetic variation, the amount of gene flow between core and edge subpopulations, and differential selection between core and edge microsites.

We used reciprocal transplant experiments between edge and core microsites to test for evidence of local

adaptation in core and edge subpopulations. To get a broader understanding of plastic and genetic responses of populations along the selection gradients associated with invasion fronts, we also compared variation in these different modes of adaptation between interspecific competition gradients in non-serpentine annual grassland habitats and edaphic stress gradients in serpentine habitats (hereafter referred to as competition and edaphic gradients, respectively). Because a large number of previous studies have indicated local adaptation to serpentine soils in native species (Brady et al. 2005), we expected that local adaptation in *A. triuncialis* edge and core subpopulations would be more likely to occur along edaphic gradients within serpentine habitats. We used field-collected seed in these experiments to capture the combined influence of genetic and plastic (i.e. within and across generation phenotypic plasticity) effects on localized adaptation and invasion as they actually occur in the field. This approach was preferred because it provided us with a realistic view of the combined effects of genetic differentiation and plasticity despite the resulting limitations on our capacity to isolate the influence of maternal environmental effects.

We also examined the potential fitness consequences of phenotypic variation in flowering time across invasion fronts in both non-serpentine annual grassland and serpentine habitats. In particular, previous studies have indicated that serpentine soils dry more quickly (Sambatti and Rice 2006) and that maternal effects may induce earlier flowering on serpentine soils (Dyer et al 2010). By using phenotypic selection analyses, we tested whether there was significant selection for earlier flowering along invasion fronts in the field. We expected that selection for earlier flowering would be most pronounced at the leading edges of invasion fronts (i.e. edge microsites) where interspecific competition might be strongest in non-serpentine annual grassland habitats and edaphic stress might be greatest within serpentine habitats.

Materials and methods

Species

Aegilops triuncialis L. is a cleistogamous annual grass with a native range throughout Europe, Asia and the Mediterranean Basin. *A. triuncialis* was first collected

in California in 1914 in an area previously grazed by Mexican cattle (Kennedy 1928). However, it was not until the 1920s that *A. triuncialis* was recorded as a significant grassland invader (Peters et al. 1996). *A. triuncialis* shares many basic characteristics with other Eurasian annual grasses in California including large seed size, distinctive adaptations to herbivory and animal dispersal, winter-annual growth habits, and invasive potential. High germination rates of *A. cylindrica* Host. seeds recovered from cattle feces suggests herbivores may be an important dispersal vector for the genus (Lyon et al. 1992). Range expansion of *A. triuncialis* has accelerated in recent years and the species is now considered a serious noxious range weed due to its poor palatability for livestock (Peters et al. 1996). In addition, the ability of *A. triuncialis* to invade edaphically stressful serpentine habitats in California (Meimberg et al. 2006; Lyons et al. 2010) makes it a significant threat to biodiversity because of the pronounced native species endemism found within serpentine sites (Kruckeberg 2004; Brady et al. 2005).

Experimental design and analyses

To conduct this experiment, it was necessary to identify field locations in which populations of *A. triuncialis* showed core and edge subpopulation structure indicative of active invasive spread across areas that could be characterized by increasing edaphic stress or increasing interspecific competition (i.e. edaphic or competition gradients). We identified competition gradients and edaphic gradients at the field sites by examining aboveground biomass (see below). We made bulk seed collections from six field locations that included core and edge microsite subpopulations along three edaphic gradients and three competition gradients. Field reciprocal transplant experiments were initiated at each of the seed collection locations at both ends (i.e. core and edge microsites) of each gradient type. We established 10 seed planting blocks within both edge and core microsite areas in each of the six gradients (Fig. 1). Planting blocks were divided into two subplots that received either edge or core subpopulation seeds. Within a subplot, seeds were sowed into the soil without removing litter at a spacing of 2 cm with nine seeds from each subpopulation in each subplot (a total of 18 seeds per block). Plastic toothpicks were used to

mark the location of each seed. To prevent the introduction of novel genotypes during the reciprocal transplant experiments at each location, only seeds collected from that location were used.

The three competition gradient locations (Biological, Watershed, and Foster) and one edaphic gradient location (Foster) were located within ungrazed ecological research areas of the University of California Hopland Field Research and Extension Center (39°00'10"N; 122°06'03"W). Of the two remaining edaphic gradient locations, one (McLaughlin) was at the University of California McLaughlin Reserve (38°51'41"N; 122°24'28"W) while the other (Snell) was at the Napa Missimer Snell Valley Reserve (38°41'56"N; 122°24'24"W).

For each subplot in a block, the demographic parameters of plant survival and net reproductive rate (i.e. seeds produced in a subplot divided by seeds initially planted into a subplot) were measured. In addition, we also measured individual plant traits such as plant flowering time, plant biomass, seeds per plant, and average individual seed weight per plant. For the *A. triuncialis* response variables described above, multivariate analysis of variance and univariate analysis of variance (GLM Procedure, SAS Institute 2011) were used to examine main and interactive effects of gradient type, seed collection location (nested within gradient type), subpopulation seed source, and planting microsite. For phenotypic variation in the traits measured, genetic contributions were estimated by subpopulation main effects while evidence for phenotypic plasticity was inferred from planting microsite main effects. Subpopulation by microsite interactions for fitness traits were examined for evidence of local adaptation. Response variables that exhibited heterogeneity of variance were natural log (ln) transformed before analysis.

To measure phenotypic selection on *A. triuncialis* phenology, flowering time was averaged across individuals within each of the two subplots in a block and regressed against individual fitness measures of seed mass per plant and the average mass of individual seeds. Average flowering time was also regressed against the population fitness index of net population growth rate. Linear and quadratic regression coefficients were examined for significance in order to test for directional, stabilizing/disruptive selection, or both.

Before setting up the field experiments, we attempted to identify competition and edaphic gradients based on

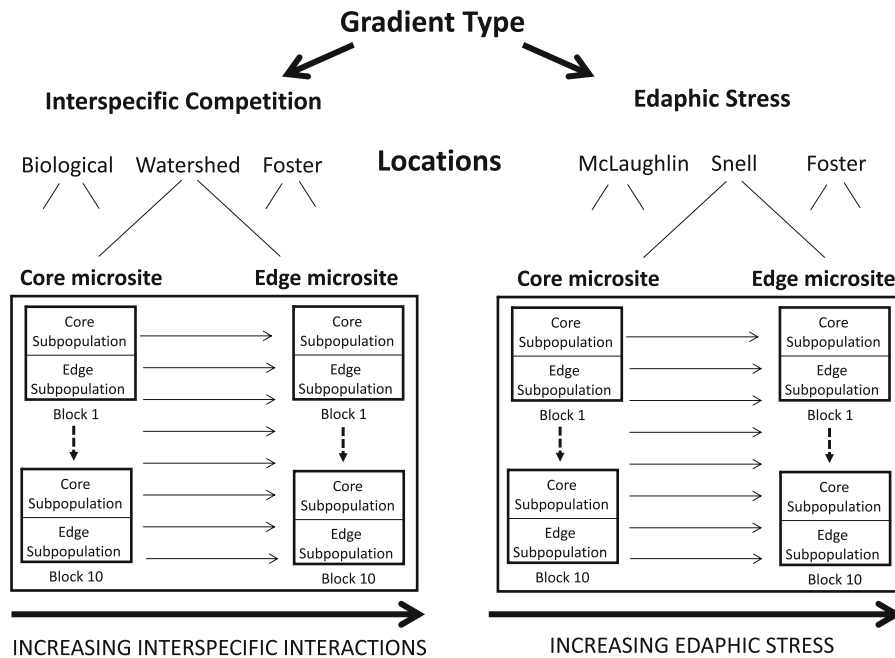


Fig. 1 Experimental design of the reciprocal transplant study of *A. triuncialis*. For both interspecific competition and edaphic stress gradient types, three locations were identified for reciprocal transplant experiments. Seeds were collected from subpopulations at the ends of the gradients at each location. At each location, core subpopulations were collected from core

habitats appearing. Our primary goal was to find locations being invaded by *A. triuncialis* that would provide reasonable replication of each gradient type. To verify perceived differences in competition between and within the competition and edaphic gradients, above-ground standing biomass samples (n = 10 quadrats per microsite type) were collected at each location. Analysis revealed that aboveground biomass (and thus the potential for either intraspecific or interspecific competition) was much higher overall ($P = 0.004$) in the competition gradient locations (Fig. 2; Appendix Table 2). In addition, within the serpentine edaphic gradient locations there was a significant drop ($P < 0.001$) in aboveground biomass between core and edge microsites (Fig. 2; Appendix Table 2); this result further supports our assumption that edaphic stressors are more important than either interspecific or intraspecific competition at the edge of invasion fronts in serpentine soils. At the competition gradient locations, aboveground biomass did not differ significantly between core and edge microsites. However, at all three competition gradient locations, the existence of a

microsites located behind the invasion front while edge subpopulations were collected from edge microsites located just beyond the leading edge of the invasion front. Nine seeds of each subpopulation seed source were reciprocally transplanted into 10 blocks within each microsite type

gradient in interspecific competition is supported by estimates indicating that relative cover of *A. triuncialis* was $>80\%$ in core microsites and $<20\%$ in edge microsites (K. Rice, unpublished data).

Results

Manova

There were significant main and interactive effects of gradient type, location, subpopulation seed source, and planting microsites on the suite of response variables measured (Appendix Table 3). Given the overall significance of the treatment factors indicated by this MANOVA, a series of protected ANOVAs were then performed on each response variable separately. Within each protected ANOVA, our primary interest was in significant main and interactive effects of gradient type, subpopulation seed source, and planting microsite treatments that would provide information on either plastic or genetic responses of *A. triuncialis* to

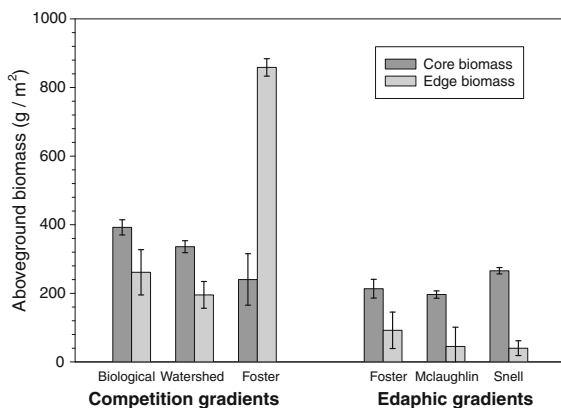


Fig. 2 Mean aboveground community biomass per m² from each of the six field locations before initiation of the reciprocal transplant experiment; error bars indicate ± 1 SE. Biomass was greater overall in competitive gradients than in edaphic gradients ($P < 0.001$). The gradient by microsite interaction was also significant ($P < 0.001$); orthogonal contrasts indicated that core microsite biomass was significantly greater than edge microsite biomass within edaphic gradients ($P < 0.001$), but was not significantly different in competitive gradients ($P = 0.203$)

the generalized growing conditions of the gradient extremes. We were less interested in main or interactive effects of location because locations were used primarily to provide replication for each gradient type.

Initial seedling survival

Initial seedling establishment indicated a gradient type by subpopulation interaction ($P = 0.0081$) such that survival of seedlings from different subpopulation seed sources differed in the edaphic gradient, but not in the competition gradient (Appendix Table 4). In the edaphic gradient, the edge subpopulation seed source exhibited higher seedling survival than the core subpopulation source but there was no significant difference in survival between edge and core subpopulation sources in the competition gradient (Fig. 3a).

Initial seedling survival also varied with gradient type and planting microsite ($P < 0.0001$). In the competition gradient, seedling survival was similar in the core and edge planting microsites while survival in core microsites in the serpentine gradient was much lower than in edge microsites (Fig. 3b). There was no indication of local adaptation to core and edge microsites because the subpopulation seed source by planting microsite interaction term was not significant along either gradient type.

Variation in flowering time

Flowering time differed significantly among locations (Appendix Table 5): the Julian date for flowering time (mean ± 1 SE) ranged from 129.5 ± 0.8 days at Watershed to 146.0 ± 1.0 days at McLaughlin. Averaged across locations, there was also a significant ($P < 0.0001$), but smaller, difference in flowering time between edaphic and competition gradients (137.3 ± 0.5 days and 132.6 ± 0.5 days, respectively). There was a small but significant ($P = 0.0234$) overall subpopulation effect because edge subpopulations flowered slightly earlier (134.2 ± 0.4 days) than core subpopulations (135.6 ± 0.5 days). Plasticity in flowering time between planting microsites varied strongly among locations ($P = 0.0152$). For example, at the Biological location, average flowering time at edge microsites was 5 days earlier than core microsites while, at the McLaughlin location, flowering in edge microsites was 3 days later than in core microsites.

Plant mass

There was an overall main effect of subpopulation seed source on plant mass ($P = 0.0053$, Appendix Table 6) because, regardless of planting microsite or location, plants from edge subpopulation seed sources were slightly larger (7 %) than plants from core subpopulations (183.2 ± 11.7 mg and 170.8 ± 12.1 mg, respectively). Plastic growth responses to core and edge planting microsites varied significantly between gradient types ($P < 0.0006$, Fig. 4). Along edaphic gradients, plants growing in edge microsites were consistently smaller than plants growing in core microsites (Fig. 4). In contrast, along competition gradients, plants growing in edge microsites were larger than plants growing in core microsites (Fig. 4).

Seed output per plant

Seed production per plant was significantly higher ($P = 0.0034$, Appendix Table 7) in the competition gradient than in the edaphic gradient (1.80 ± 0.14 seeds/plant and 0.85 ± 0.14 seeds/plant, respectively). Plants from edge subpopulation seed sources produced more seeds ($P < 0.0001$) than plants from core subpopulations (Appendix Table 7; Fig. 5a) although phenotypic expression of this possible genetic

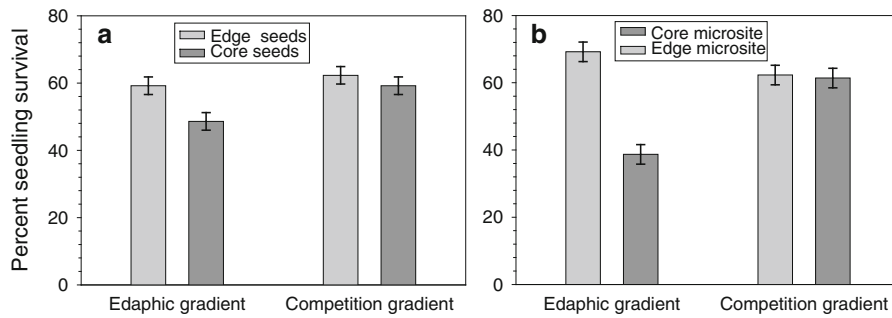


Fig. 3 Percent seedling survival of *A. triuncialis*; error bars indicate ± 1 SE. **a** Orthogonal contrasts indicate that survival of seedlings from edge subpopulation seed sources was significantly higher in edaphic gradients ($P < 0.001$) while there was no significant effect of subpopulation seed source on seedling survival in competition gradients ($P = 0.838$). **b** Orthogonal

contrasts indicate that, regardless of subpopulation seed source, survival of seedlings was significantly higher in edge microsities in edaphic gradients ($P < 0.001$) while there was no significant difference in seedling survival between edge and core microsities in the competition gradient type ($P = 0.472$)

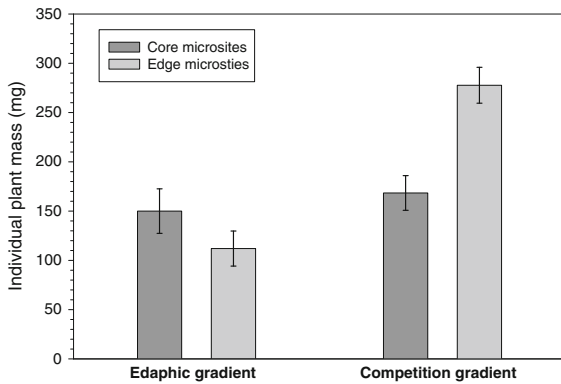


Fig. 4 *Aegilops triuncialis* individual plant mass; error bars indicate ± 1 SE. A gradient by planting microsite interaction was significant ($P < 0.0006$) such that plants in core microsities grew larger in the edaphic gradient while plants in edge microsities were larger in the competition gradient

effect on seed production did vary among locations (subpopulation by location interaction, $P = 0.0006$). Regardless of subpopulation seed source, seed production per plant was higher ($P = 0.0021$) in plants growing in edge microsities than in individuals planted into core microsities (Appendix Table 7; Fig. 5b). As indicated by the significant interaction between location and planting microsite ($P = 0.0051$), this plastic effect of greater seed production in edge microsities varied among locations within a gradient type. The relatively low average numbers of seeds per plant reflect, in part, the inclusion of plants that did not survive to reproduce (i.e. seed production in these individuals was zero).

Net reproductive rate

Using net reproduction as a measure of population growth (i.e. seed output from a plot divided by seed input), it appears that populations of *A. triuncialis* are growing more rapidly overall along competition gradients than along edaphic gradients ($P < 0.0001$, Appendix Table 8; 1.72 ± 0.14 and 0.82 ± 0.14 , respectively). Across gradient types, population growth is estimated to be faster ($P < 0.0001$) at edge microsities than in core microsities (1.59 ± 0.14 and 0.94 ± 0.14 , respectively). A possible genetic basis for differences in population growth rate (i.e. a subpopulation effect) is expressed along edaphic gradients only, where growth rates in edge subpopulation seed sources are higher ($P = 0.0442$) than in core subpopulations (Fig. 6).

Individual seed size

The significant main effect of subpopulation seed source on individual seed weight ($P = 0.0168$, Appendix Table 9) indicates that seeds produced by edge subpopulation plants (8.18 ± 0.20 mg) were consistently larger than seeds produced by core subpopulation plants (7.55 ± 0.21 mg) regardless of planting microsite or location. The fact that seeds from edge maternal plants were consistently larger across a wide range of maternal plant environments (i.e. multiple locations within a gradient type as well as edge and core planting microsities) suggests that this seed size difference represents a genetic effect of

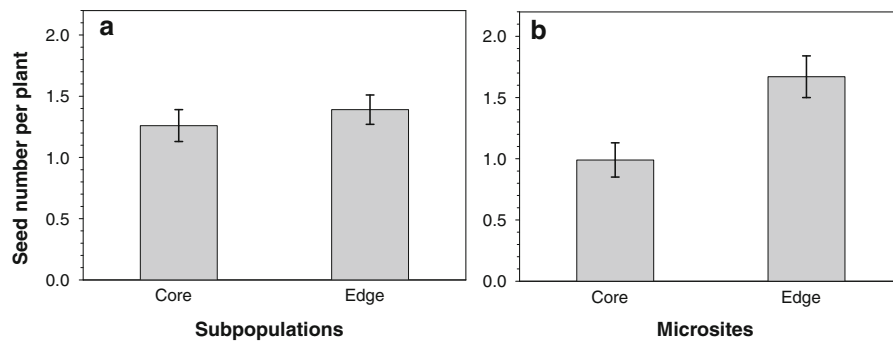


Fig. 5 Seed number per plant; error bars indicate ± 1 SE. **a** Regardless of planting microsite, plants from edge subpopulations produced more seed than plants from core

subpopulations ($P < 0.001$). **b** Regardless of subpopulation seed source, plants growing in edge microsities produced more seed than plants growing in core microsities ($P < 0.0021$)

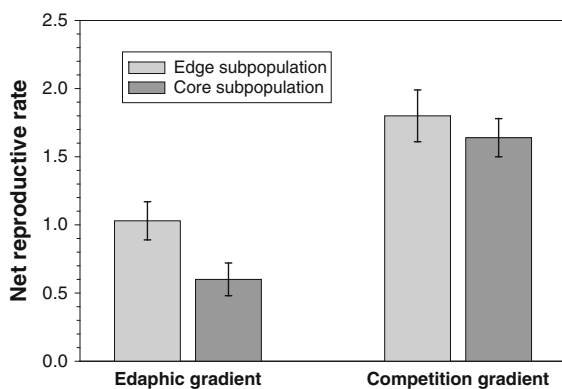


Fig. 6 Net reproductive rate (seed output per plot/seed input; error bars indicate ± 1 SE.). A gradient by subpopulations interaction was significant ($P < 0.0442$); orthogonal contrasts indicate that the net reproductive rate for edge subpopulations was greater than core subpopulations in edaphic gradients ($P < 0.0014$) but there was no significant difference in net reproduction between subpopulations in competition gradients ($P = 0.695$)

subpopulation seed source. This consistent expression of a seed source effect across a number of maternal environments significantly reduces the likelihood that maternal environmental effects alone are causing this variation in seed size. Nonetheless, there were also indications of within-generation plasticity in this trait because of the interactive effects of planting microsite and location.

Phenotypic selection analysis of flowering time

When we detected significant selection for flowering time in populations of *A. triuncialis*, it was consistently directional selection for earlier flowering

(Table 1). Quadratic regression coefficients that might indicate stabilizing or disruptive selection were never significant. Differences in the strength of directional selection between edge and core microsities were dependent on gradient type. Along competition gradients there was strong directional selection for earlier flowering in both edge and core microsities for all fitness traits.

Along edaphic gradients, the results were somewhat more complex. First the dataset was subdivided with one subset of the data including the Snell and Foster results and the second subset containing results from the McLaughlin location. This was done because all the populations at McLaughlin flowered much later and this caused non-independence among data points in overall regression analyses of the combined edaphic gradient data. Regression analyses of the Snell/Foster dataset for total seed mass per plant and net reproduction indicated directional selection for early flowering in edge microsities but no significant selection in core microsities (data not shown). Using individual seed weight as a fitness measure, there was no selection detected in either edge or core microsities in the Snell/Foster dataset. Similar results were obtained from the McLaughlin data; there was strong selection for early flowering in edge microsities (using seed mass and individual seed weight as fitness indices) while no significant selection was detected in core microsities. When net reproduction was used as a fitness measure, there was no selection detected in either edge or core microsities. Overall, selection for early flowering along edaphic gradients was relatively strong in edge microsities and statistically undetectable in core microsities.

Table 1 Phenotypic selection analyses of effects of flowering time on components of fitness in barbed goatgrass at both edge and core planting microsites within interspecific competition and edaphic stress gradients

Gradient type and planting microsite	Net reproduction			Seed mass per plant			Individual seed mass		
	β	R ²	<i>P</i> value	β	R ²	<i>P</i> value	β	R ²	<i>P</i> value
Competitive gradient and core microsite	-0.052	0.32	<0.0001	-0.117	0.55	<0.0001	-0.0003	0.57	<0.0001
Competitive gradient and edge microsite	-0.047	0.23	0.0002	-0.087	0.42	<0.0001	-0.0002	0.41	<0.0001
Serpentine gradient and core microsite (excluding McLaughlin location)	-0.025	0.12	0.1092	-0.080	0.27	0.0166	-0.0001	0.09	0.1878
Serpentine gradient and edge microsite (excluding McLaughlin location)	-0.072	0.26	0.0008	-0.192	0.30	0.0003	-0.0002	0.07	0.1135
McLaughlin location and core microsite	-0.029	0.19	0.1529	-0.040	0.06	0.4661	-0.0001	0.01	0.7806
McLaughlin location and Edge microsite	-0.112	0.42	0.0065	-0.179	0.52	0.0017	-0.0007	0.49	0.0025

The data from McLaughlin, an edaphic gradient location, were analyzed separately because flowering was much later at this location and thus created non-independence problems for an overall regression of all edaphic gradient locations. Directional selection (β) was estimated by the linear regression coefficient; quadratic coefficients that might indicate stabilizing or disruptive selection were not significant in any regression. Significant linear regressions ($P < 0.05$) for different treatments are presented in bold font

Discussion

The recent surge in the spatial spread of *A. triuncialis* in California grasslands is exceptional in both its speed and the wide range of grassland habitats that are being invaded. Our results from both interspecific competition and edaphic stress gradient reciprocal transplants suggest that this extensive and rapid spread can be viewed as resulting from a “mixed strategy” that potentially involves both phenotypically plastic and genetic responses. Plasticity responses are indicated by differences in within-population phenotypic expression among edge and core planting microsites while genetic effects are suggested by differences in response between seeds from edge and core subpopulations. As discussed below, the effect of subpopulation seed source on plant responses may also reflect maternal environmental or trans-generational plasticity effects. The relative importance of plastic and genetic effects on the capacity of *A. triuncialis* to spread depends on both the trait and the type of gradient under consideration.

Gradient type affected the expression of plastic or genetic differences for all traits examined in *A. triuncialis*. For example, both plasticity and seed source effects were detected for seedling establishment within invasion fronts along edaphic gradients but not along competition gradients. Specifically, establishment in core microsites in the edaphic gradient was significantly lower than in edge microsites; suggesting that the high density of *A. triuncialis* in these core microsites

may reduce seedling survival. A higher overall rate of establishment of seeds from the edaphic edge subpopulation suggests that larger seed size in edge subpopulations, resulting from genetic and/or maternal effects, may increase rates of seedling survival in stressful environments. In contrast, plasticity in flowering time between plants in core and edge microsites was only detected along competition gradients with flowering occurring earlier in edge microsites. Results from selection analysis of flowering time along competition gradients are consistent with this response although this analysis indicated that earlier flowering was selectively favored in both core and edge microsites. We suggest that this earlier flowering may be in response to soil water depletion under interspecific competitive conditions. *A. triuncialis* flowers relatively late compared to other winter annuals and it is possible that earlier flowering phenotypes may have a greater probability of successfully setting seed before soil water resources are depleted. Selection analysis also indicated that earlier flowering should be favored in edge microsites in edaphic gradients perhaps reflecting lower rates of soil moisture retention within the coarser soils found in edge microsites (McKay and Rice, unpublished data). However, as noted above, this selection for earlier flowering in edge microsites was not sufficient to induce a plasticity response in flowering within edaphic gradients.

A primary motivation for our study was to examine how the combination of phenotypic plasticity and genetic differentiation in *A. triuncialis* demography

might affect the capacity of *A. triuncialis* to spread along both competition and edaphic gradients. The potential role of phenotypic plasticity in promoting invasive spread of *A. triuncialis* can be examined by comparing demographic performance between core and edge microsites averaged across effects of subpopulation seed source. Results at both the population scale and individual plant level suggest that plasticity significantly facilitates *A. triuncialis* expansion along invasion fronts. Regardless of subpopulation seed source, plants growing in edge microsites in both gradient types produced more seed than plants in core microsites. This indication of greater reproductive output at the edge of the invasion front was also expressed at the population level in terms of net reproductive rate. Net reproduction, averaged across both subpopulation seed source and gradient type, was 1.6 in edge microsites and 0.9 in core microsites suggesting population expansion and spread at the invasion front with relative stasis in core sites located behind the front. Given that this higher rate of population growth occurred at the invasion fronts within both competition and edaphic gradients, we suggest that plasticity in reproductive traits may be an important factor promoting *A. triuncialis* invasions in both serpentine and non-serpentine annual grassland habitats in California.

Beginning with the introduction of the term “general-purpose genotype” to the discussion of weed evolution (Baker 1974), there has been continuing interest in the potential importance of phenotypic plasticity in plant invasions (Jain 1969; Rice and Mack 1991a; Leger and Rice 2003). In *Aegilops*, it has been noted that, even in their home range, polyploid species exhibit low ecological affinity, suggesting the general importance of plasticity in the more “weedy” species within the genus (Zohary and Feldman 1962). Analysis of molecular variation among populations of barbed goatgrass indicates minimal regional genetic structure in its native range (Meimberg et al. 2006); further supporting the idea that *A. triuncialis* may be a highly plastic colonizing species, even in its home range. In addition, a recent study on the capacity of *A. triuncialis* to grow on different soil types also suggests that the occurrence of *A. triuncialis* on serpentine soils in California may result from adaptive plastic responses (Lyons et al. 2010).

Studies on other invasive species have indicated that plasticity may be an important factor in

facilitating the expansion of range limits where reduced gene flow and demographic bottlenecks limit the amount of genetic variation within populations at a species margin (Parker et al. 2003; Leger et al. 2009). Strong genetic bottlenecks have been detected in *A. triuncialis* during its colonization of California (Meimberg et al. 2006), so its successful invasion of a range of grassland habitats in California may result, in part, from adaptive phenotypic plasticity.

Maternal environmental effects represent another potential source of adaptive plasticity that can operate across generations (i.e. transgenerational plasticity). Transgenerational plasticity may be an important mode of adaptive plastic response for invasive species with low amounts of genetic variation (Dyer et al. 2010). Previous glasshouse studies on *A. triuncialis* indicate that maternal plants grown in serpentine soils produce smaller seeds that, in turn, result in smaller plants. Individuals produced by maternal plants grown on serpentine soils also flowered earlier (Dyer et al. 2010). In the current study, seeds from each of the subpopulations were collected directly from the field and thus the size and phenology of plants produced from this seed may be influenced by the maternal environment. In particular, the subpopulation differences in seedling establishment found for edge seed sources in the serpentine gradient may be influenced by transgenerational plasticity. This expectation arises from the large amount of evidence indicating that the effects of maternal environment are most strongly expressed early in a plant’s life history (Roach and Wulff 1987). Although the influence of transgenerational plasticity is typically less in later life stages, *A. triuncialis* is rather exceptional in the persistence of these maternal environmental effects in both its growth and phenology (Dyer et al. 2010). Thus, it is quite possible that transgenerational plasticity may be an important factor creating differences in plant size, seed production and flowering time between core and edge *A. triuncialis* subpopulations, especially in serpentine habitats.

Although phenotypic plasticity is likely an important factor contributing to *A. triuncialis* invasion in California, genetic differentiation over small spatial scales may also be occurring, particularly along invasion fronts into serpentine habitats. Differences between seed sources from core and edge subpopulations were found for plant survival, plant size, and total seed production suggesting the possibility for genetic

differences in traits related to fitness. As noted above, some of these subpopulation differences may be caused by transgenerational plasticity. However, fairly strong evidence for genetic differentiation is found in the data for subpopulation variation in individual seed size. Maternal plants from edge subpopulations produced seeds that were larger than the seeds produced by mothers from core subpopulations in both gradient types. Although transgenerational plasticity effects cannot be ruled out completely, the fact that edge source maternal plants produced consistently larger seeds across all planting conditions argues for a least some genetic contribution to this phenotypic variation in seed size. The likelihood that phenotypic differences between serpentine and non-serpentine populations of *A. triuncialis* have some genetic basis is also supported by previous common garden glasshouse experiments (Lyons et al. 2010; Meimberg et al. 2010). These glasshouse studies found significant variation between serpentine and non-serpentine populations in a number of phenological and morphological traits. The observation by Lyons et al. (2010) that serpentine seed sources exhibited greater root to shoot ratios is of particular interest because it sheds some light on possible mechanisms of adaptation to the more xeric and low nutrient environment of serpentine soils.

Whether local adaptation has significantly facilitated the invasion of *A. triuncialis* into the grasslands and serpentine habitats of California is still somewhat unclear. Glasshouse studies have found that for several fitness traits, serpentine populations of *A. triuncialis* appear better adapted to serpentine soils than non-serpentine populations (Lyons et al. 2010). However, field experiments with these same populations did not provide evidence for local adaptation. Our field study indicates that edge subpopulations of *A. triuncialis* exhibit a greater rate of population increase in both edge and core microsites within serpentine habitats. Thus there is no interaction of subpopulation source and planting microsite that might indicate highly localized adaptation. Further, this subpopulation seed source effect occurs only along serpentine (edaphic) gradients and is not expressed between core and edge subpopulations in competition gradients. A factor that may further complicate interpretation is the possibility that *A. triuncialis* genotypes invading California serpentine habitats may be pre-adapted to serpentine soils (Meimberg et al. 2010). Within its broad native range in Eurasia, *A. triuncialis* has been observed to occur on

serpentine soils (H. Meimberg, pers. com.). If these serpentine adapted genotypes were introduced into California, they may have facilitated *A. triuncialis* invasion of serpentine habitats. A better understanding of the role of genetic differentiation in promoting the spread of *A. triuncialis* into serpentine habitats will require a protocol that reduces the potential of maternal environmental effects by growing field collected seed for a generation in a common garden.

Overall, our field results suggest that the likelihood for adaptive genotypic differentiation is greater along serpentine invasion fronts (i.e. edaphic gradients) while phenotypic plasticity may be the primary adaptive response along invasion fronts within non-serpentine annual grasslands (i.e. interspecific competition gradients). It appears that the current invasion success of *A. triuncialis* in a wide range of non-serpentine annual grassland and serpentine habitats in California results from a decidedly mixed strategy of phenotypic plasticity (within and across generations) and genetic differentiation. This invasive grass has just recently begun to spread rapidly in California within the last two decades and its capacity to invade serpentine habitats presents an especially worrisome challenge for the conservation of a unique endemic serpentine flora. Unfortunately, other recent studies have identified both dispersal and demographic characteristics that facilitate the movement of *A. triuncialis* and other invasive species into serpentine habitats (Thomson 2007; Baythavong et al. 2009). It seems clear that an effective strategy to slow the expansion of invasive plants into serpentine habitats will have to employ a synthetic view of both the evolutionary and ecological determinants of invasive spread (Thomson et al. 2011).

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Appendix

See Tables 2, 3, 4, 5, 6, 7, 8, and 9.

Table 2 Analysis of variance of treatment effects on aboveground biomass

Source	DF	Sum of squares	F ratio	Prob > F
Gradient type	1	17.72	40.21	0.0004
Location (gradient type)	7	2.826	5.73	<0.0001
Microsite	1	6.046	65.22	<0.0001
Block (microsite, location)	81	5.671	0.75	0.8972
Microsite × gradient type	1	3.763	40.59	<0.0001
Error	84	7.787		

Biomass data were ln transformed before analysis to reduce heterogeneity of variance. Location and interactions with location were nested within gradient type while block, as a random factor, was nested within planting microsite and location. Significant treatment effects ($P < 0.05$) are presented in bold font

Table 3 MANOVA results indicating significant effects of several experimental factors on barbed goatgrass survival, phenology, and reproduction

Source	Wilks' Lambda	Num DF	Den DF	F value	Prob > F
Gradient	0.539	5	91	15.59	<0.0001
Location (gradient)	0.138	20	302.8	12.39	<0.0001
Subpopulation	0.660	5	70	7.20	<0.0001
Microsite	0.787	5	91	4.91	0.0005
Block (gradient, location, microsite)	0.002	475	355.3	1.74	<0.0001
Gradient × subpopulation	0.872	5	70	2.05	0.0815
Gradient × microsite	0.608	5	91	11.73	<0.0001
Subpopulation × location (gradient)	0.618	20	233.1	1.82	0.0196
Microsite × location (gradient)	0.483	20	302.8	3.71	<0.0001
Microsite × subpopulation	0.921	5	70	1.20	0.3167
Gradient × microsite × subpopulation	0.934	5	70	0.98	0.4341
Microsite × subpopulation × location (gradient)	0.684	20	233.1	1.41	0.1167

Location and interactions with location were nested within gradient type while block, as a random factor, was nested within planting microsite and location. Significant treatment effects ($P < 0.05$) are presented in bold font

Table 4 Analysis of variance of treatment effects on barbed goatgrass seedling survival

Source	DF	Sum of squares	F ratio	Prob > F
Gradient	1	0.2437	5.5301	0.0206
Location (gradient)	4	1.0998	6.2395	0.0002
Microsite	1	1.2310	27.9341	<0.0001
Block (microsite, location)	113	4.6578	0.9354	0.6365
Subpopulation	1	0.4319	9.8012	0.0023
Microsite × gradient	1	1.0020	22.7381	<0.0001
Subpopulation × gradient	1	0.3216	7.2987	0.0081
Subpopulation × microsite	1	0.0354	0.8032	0.3722
Location × microsite (gradient)	4	0.1053	0.5976	0.6652
Location × subpopulation (gradient)	4	1.2961	7.3527	<0.0001
Subpopulation × microsite × gradient	1	0.0375	0.8504	0.3586
Location × microsite × subpopulation (gradient)	4	0.4482	2.5428	0.0441
Error	103	4.4390		

Location and interactions with location were nested within gradient type while block, as a random factor, was nested within planting microsite and location. Significant treatment effects ($P < 0.05$) are presented in bold font

Table 5 Analysis of variance of treatment effects on barbed goatgrass flowering time

Source	DF	Sum of squares	F ratio	Prob > F
Gradient	1	636.1846	43.2259	< 0.0001
Location (gradient)	4	2,232.6329	37.9243	< 0.0001
Microsite	1	43.6264	2.9642	0.0882
Block (microsite, location)	102	887.6714	0.5913	0.9929
Subpopulation	1	78.8597	5.3582	0.0234
Microsite × gradient	1	56.4819	3.8377	0.0539
Subpopulation × gradient	1	1.5850	0.1077	0.7437
Subpopulation × microsite	1	37.9870	2.5810	0.1125
Location × microsite (gradient)	4	194.3630	3.3015	0.0152
Location × subpopulation (gradient)	4	93.8950	1.5949	0.1848
Subpopulation × microsite × gradient	1	18.9846	1.2899	0.2598
Location × microsite × subpopulation (gradient)	4	44.3643	0.7536	0.5589
Error	73	1,074.3908		

Location and interactions with location were nested within gradient type while block, as a random factor, was nested within planting microsite and location. Significant treatment effects ($P < 0.05$) are presented in bold font

Table 6 Analysis of variance of treatment effects on barbed goatgrass individual plant mass

Source	DF	Sum of squares	F ratio	Prob > F
Gradient	1	4.5614	18.1780	< 0.0001
Location (gradient)	4	6.0891	6.0666	0.0003
Microsite	1	0.9985	3.9793	0.0487
Block (microsite, location)	102	20.5217	0.8018	0.8477
Subpopulation	1	2.0810	8.2932	0.0053
Microsite × gradient	1	3.2114	12.7981	0.0006
Subpopulation × gradient	1	0.0042	0.0167	0.8976
Subpopulation × microsite	1	0.4350	1.7337	0.1922
Location × microsite (gradient)	4	5.7014	5.6803	0.0005
Location × subpopulation (gradient)	4	2.9490	2.9381	0.0263
Subpopulation × microsite × gradient	1	0.1500	0.5977	0.4420
Location × microsite × subpopulation (gradient)	4	0.7702	0.7673	0.5501
Error	71	17.8160		

Location and interactions with location were nested within gradient type while block, as a random factor, was nested within planting microsite and location. Significant treatment effects ($P < 0.05$) are presented in bold font

Table 7 Analysis of variance of treatment effects on number of seeds per plant (ln transformed)

Source	DF	Sum of squares	F ratio	Prob > F
Gradient	1	3.6561	9.2418	0.0034
Location (gradient)	4	5.1126	3.2309	0.0173
Microsite	1	3.9530	9.9924	0.0021
Block (microsite, location)	101	55.7804	1.3960	0.0714
Subpopulation	1	6.4788	16.3770	< 0.0001
Microsite × gradient	1	0.4067	1.0281	0.3142

Table 7 continued

Source	DF	Sum of squares	F ratio	Prob > F
Subpopulation × gradient	1	0.2211	0.5590	0.4572
Subpopulation × microsite	1	0.3988	1.0080	0.3189
Location × microsite (gradient)	4	6.4446	4.0726	0.0051
Location × subpopulation (gradient)	4	8.8322	5.5815	0.0006
Subpopulation × microsite × gradient	1	0.6173	1.5604	0.2159
Location × microsite × subpopulation (gradient)	4	1.6678	1.0540	0.3861
Error	68	26.9010		

Location and interactions with location were nested within gradient type while block, as a random factor, was nested within planting microsite and location. Significant treatment effects ($P < 0.05$) are presented in bold font

Table 8 Analysis of variance of treatment effects on net reproduction (ln transformed)

Source	DF	Sum of squares	F ratio	Prob > F
Gradient	1	2.1885	19.1460	< 0.0001
Location (gradient)	4	1.7315	3.7869	0.0065
Microsite	1	1.8481	16.1676	< 0.0001
Block (microsite, location)	114	20.3909	1.5648	0.0109
Subpopulation	1	0.7683	6.7214	0.0110
Microsite × gradient	1	0.0403	0.3524	0.5540
Subpopulation × gradient	1	0.4743	4.1497	0.0442
Subpopulation × microsite	1	0.0125	0.1093	0.7416
Location × microsite (gradient)	4	1.6630	3.6371	0.0082
Location × subpopulation (gradient)	4	2.6237	5.7383	0.0003
Subpopulation × microsite × gradient	1	0.1600	1.4001	0.2395
Location × microsite × subpopulation (gradient)	4	0.1990	0.4353	0.7829
Error	102	11.6593		

Location and interactions with location were nested within gradient type while block, as a random factor, was nested within planting microsite and location. Significant treatment effects ($P < 0.05$) are presented in bold font

Table 9 Analysis of variance of treatment effects on average individual seed weight (ln transformed)

Source	DF	Sum of squares	F ratio	Prob > F
Gradient	1	0.0000001	0.0257	0.8730
Location (gradient)	4	0.0001841	16.1623	< 0.0001
Microsite	1	0.0000089	3.1386	0.0795
Block (microsite, location)	101	0.0001546	0.5374	0.9977
Subpopulation	1	0.0000171	6.0124	0.0168
Microsite × gradient	1	0.0000001	0.0005	0.9823
Subpopulation × gradient	1	0.0000021	0.7520	0.3889
Subpopulation × microsite	1	0.0000068	2.4067	0.1255
Location × microsite (gradient)	4	0.0000450	3.9540	0.0061
Location × subpopulation (gradient)	4	0.0000221	1.9381	0.1140
Subpopulation × microsite × gradient	1	0.0000021	0.7533	0.3885
Location × microsite × subpopulation (gradient)	4	0.0000106	0.9346	0.4493
Error	68	0.0001936		

Location and interactions with location were nested within gradient type while block, as a random factor, was nested within planting microsite and location. Significant treatment effects ($P < 0.05$) are presented in bold font

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