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Response variation across a strong rainfall gradient in two naturalized annual grass species

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Abstract Non-native annual grasses in California are a functional group based on taxonomic similarity, but they may be dissimilar in terms of evolutionary potential and capacity for plastic response. The ecological character of each species is conditioned by their evolutionary history, the genetic circumstances of their introduction, and their subsequent interactions with the selective pressures in their new ranges. Early population ecology studies revealed regional monomorphism and population genetic uniformity as well as strong patterns of local adaptation. Recent studies have both challenged and verified those conclusions, and have also contributed useful new information regarding the genetic makeup of these non-native grasses. We used two very abundant and widespread species to test the prediction that non-native annual grasses would show similar adaptive responses under the same environmental conditions. Using six populations of two naturalized annual grass species collected from identical locations across a strong south-to-north rainfall gradient, we manipulated soil quality and soil moisture to test response in growth, reproduction, and phenology. *Avena barbata* populations showed strong response conditioned by resource availability and with a correlated shift in flowering phenology. In contrast, *Hordeum murinum* populations showed very uniform responses to changes in resource availability independent of their position on the rainfall gradient and with no correlated phenological shifts. Several genetic and historical factors may contribute to idiosyncratic responses and general adaptive patterns in these and other non-native species, and a better understanding of these factors will help us understand their current distributions.

Keywords Genetic variation · Invasive species · Population ecology · Plasticity · Selection

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Introduction

Plant population biology has long been focused on patterns of genetic variation in non-native annual grass species in the western US and with particular emphasis on responses to abiotic gradients. An impressive body of literature helped develop the field of population biology ("ecogenetics," Jain 1969) by documenting quantitative and qualitative measures of genetic variation in populations of annual grasses across habitats and climatic zones [e.g., Clegg and Allard (1972); Hamrick and Allard (1972); Jain (1969); Jain and Marshall (1967); Rai and Jain (1982); (1991a, b, c)]. Specific goals of many studies were to correlate plant

traits to particular habitats and to reach conclusions concerning adaptability of the populations [e.g., Clegg and Allard (1972); Rai and Jain (1982); Rice and Mack (1991a, c)]. Another objective was to investigate the rate of adaptation of invasive species in new habitats and several annual grass and forb species were useful because of their introduction to California during the Spanish mission period about 200 years earlier (Burcham 1957; Spira and Wagner 1983; Garcia et al. 1989).

The study of population range expansion in non-native species has proven to be tremendously useful for identifying and testing particular plant traits that underlie invasiveness (Sakai et al. 2001; Rice et al. 2013) and have improved our understanding of mechanisms and processes that influence population structure [e.g., Marrs et al. (2008); Meimberg et al. (2009)]. Once established, invasive species are expected to adapt to local conditions over time, but the rate of adaptation is likely dependent on initial genetic composition of the population (Sakai et al. 2001; Meyer and Leger 2010). Most invasive species are genetically depauperate in comparison to their ancestral populations as a result of genetic bottleneck effects (Meimberg et al. 2006; Dlugosch and Parker 2008). Adaptation in new environments is therefore dependent on existing genetic variation, subsequent in situ mutations, or post-invasion genetic recombination, which increases in likelihood with serial introductions (Rai 1974; Bossdorf et al. 2005; Latta 2009; Novak and Mack 2016). Existing genetic variation also includes the capacity for phenotypic plasticity, which is predicted to play an important role in the initial stages of establishment and invasion as it acts as a buffer against the selection pressures encountered in new environments (Dietz and Edwards 2006; Galloway 2005). Indeed, it is possible that plasticity and selection for local adaptation are counteracting processes (Dietz and Edwards 2006), but plasticity is predicted to play an important adaptive role in the post-invasion environment (Jain 1969; Galloway 2005; Dyer et al. 2010).

There is no a priori reason why one particular genetic characteristic should govern the process of invasion and post-invasion population structure is probably dependent on environmental conditions and genetic status at the time of introduction and spread. As noted by Jain and Bradshaw (1966), selection pressures may be responsible for local patterns in

variation, but under natural conditions the interactions between environmental and genetic factors will result in complex outcomes that may even counteract the importance of gene flow. Their paper even anticipated site-specific plastic responses or maternal effects ("conditioning") as a mechanism producing genetic differentiation. Similarly, Turkington and Harper (1979) and many of their subsequent papers showed that a variety of mechanisms are potentially responsible for structuring local population genetics.

Once a species is established and naturalized, in situ mutations and local selection pressures are predicted to tailor the invasive population to the local growing conditions, particularly with respect to rainfall, temperature, and edaphic conditions. In this way, invasive species become naturalized members of the local or regional flora and subsequently differentiate genetically from their invasive progenitors and source populations (Sakai et al. 2001; Bossdorf et al. 2005). If so, adaptive potential may not be dependent on the gradual increase of genetic variation as much as certain, perhaps novel, alleles are favored, others are lost, and the result is a better correspondence between the local conditions and the genetic makeup of the population (Latta 2009). If the selection regime is severe, non-adaptive genotypic variation should be lost as a population becomes narrowly adapted to local conditions. Under such conditions, one might predict a loss of some original genetic variation and perhaps even a loss of capacity for phenotypic plasticity as certain adaptive traits become fixed in the population. In contrast, adaptive responses may be conditioned by transgenerational plasticity (TGP), which may buffer the species from the need to adapt, and this may be sufficient for establishment and persistence (Galloway 2005; Dyer et al. 2010).

Native species with long evolutionary histories in situ are expected to show strong adaptations to local selection gradients. For example, Petru et al. (2006) showed faster phenological development in the crucifer *Biscutella didyma* at the extreme dry end of a rainfall gradient and a more competition-oriented strategy at the more productive mesic end of the gradient. One also expects trade-offs between suites of traits that together provide an adaptive strategy appropriate to the environmental conditions (Chapin et al. 1993; Sandquist and Ehleringer 1997). Such suites of traits might predict a reduction in genetic variation as selection narrows adaptive allelic

variation (Dobzhansky 1970). These patterns of local adaptation have shaped the theoretical predictions for the behavior of invasive species. For example, growing seasons of unpredictable length should favor rapid and fixed developmental strategies with a reduced range of plasticity to ensure contributions to the soil seed bank (Cohen 1967; Alpert and Simms 2002). However, such developmental strategies will have been shaped over long periods of time and our view of invasive species is one of rapid adaptation over a short period of time (Maron et al. 2004). Certainly, invasive species offer a multitude of opportunities to test a range of hypotheses regarding the importance of genetic transformation for establishment and spread across novel environmental conditions (Sakai et al. 2001).

Non-native annual grasses in California were introduced over 200 years (generations) ago and have become nearly ubiquitous across a very wide range of habitats and climate zones and are therefore ideal species for testing population-level responses to environmental conditions. We used two common annual grasses to test three hypotheses. First, naturalized annual grasses will show growth and phenology responses correlated with local climatic conditions. Specifically, we predict relatively fixed growth and phenology responses to the long-term precipitation regime at the collection site. Second, from more xeric to mesic conditions, plants will show variation in phenology that is correlated to the length of the growing season. Specifically, we predict that populations from the more xeric conditions will show rapid and fixed phenology in comparison to those from more mesic conditions. Third, along the rainfall gradient, populations from the xeric end will show a reduced capacity for plastic response compared to those at the mesic end of the gradient. Our expectation was that co-occurring populations of the two species would show similar responses given the identical growing conditions at each sample location.

Methods

We collected co-occurring populations of *Avena barbata* Link and *Hordeum murinum* L. along a south-to-north transect in California from Pyramid Lake (Los Angeles County) to Redding (Shasta County). Roadside collections were made about 80 km apart along several state highways on the eastern Central Valley and low elevation Sierra Nevada foothills to sample each species repeatedly along a south-to-north rainfall gradient. We intentionally sampled from stands of annual vegetation adjacent to the roadbed and exposure to local abiotic stressors in the disturbed roadside soils was assumed to be identical for both species. Each collection was a bulked sample of senescent spikes or florets from numerous plants and both species were collected at each location. Eleven populations were used to assess early season phenology under greenhouse conditions and to correlate phenology with mean rainfall and latitude of the collection sites. Six populations spanning the rainfall gradient were chosen for a larger greenhouse experiment that incorporated soil and water treatments (Table 1). Mean precipitation for each sample location was collected from the nearest NOAA Cooperative weather station (western regional climate center) and spanned a sixfold range in annual mean rainfall from 15.8 cm at Bakersfield to 100 cm at Redding.

The six populations of both species were grown in four environments in a full-factorial design with two types of soil and two watering treatments with 15 replicates per environment ($2 \times 6 \times 2 \times 2 \times \times 15 = 720$ pots). The two soils used were commercially available low-nutrient, coarse-textured, bagged soils that are different in organic content (OC) and gravimetric water holding capacity (WHC). Soil 1 contained ~ 13 % OC and had ~ 24 % WHC; Soil 2 contained ~ 26 % OC and had ~ 38 % WHC. The two watering treatments were low (every 3 days) and high (daily). These treatments did not mimic California rainfall patterns, but were intended to create high and low water stress on the plants over the course of the growing season. Pots were watered from the top and the amount was not sufficient for drainage from the pots. All plants were grown in a greenhouse with temperature moderated by an evaporative cooling system.

Seeds were sown in late January and plants grown singly in $10 \times 10 \times 10$ cm pots. The pots were arranged in 15 blocks on trays with one of each of the 24 treatment combinations on either low water or

Table 1 Locations ordered by latitude of the 11 sample populations of *Avena barbata* and *Hordeum murinum* in California

Location	County	Latitude	Elevation	Rainfall
Pyramid	**Los Angeles**	**34.66N**	**838 m**	**33.4 cm**
Famoso	**Kern**	**35.60N**	**128 m**	**15.8 cm**
Strathmore	Tulare	36.15N	146 m	27.9 cm
Friant	**Fresno**	**37.01N**	**159 m**	**36.4 cm**
Youd	Merced	37.46N	77 m	31.7 cm
Tullock	Calaveras	37.90N	185 m	31.6 cm
Mokelumne	**Calaveras**	**38.30N**	**466 m**	**97.9 cm**
Beale	Yuba	39.03 N	102 m	56.4 cm
Vina	**Tehama**	**39.91N**	**104 m**	**65.6 cm**
Dye	Tehama	40.10N	112 m	58.6 cm
Redding	**Shasta**	**40.60N**	**174 m**	**100.0 cm**

Mean annual rainfall data from western regional climate center (http://www.wrcc.dri.edu/). All populations were used to assess early phenology; the six populations in bold were used in the main experiment

high water trays in a split-block arrangement to facilitate watering and to avoid water movement from high to low treatment pots. The experiment was analyzed as a three-way ANOVA in a complete block design with soil as a fixed factor, water as a fixed split-block factor, and population as a random factor.

Seedlings were allowed to establish for 15 days after sowing before the water treatments began. Senescent plants were harvested in five bi-weekly harvests (10 May, 24 May, 7 June, 21 June, 5 July). Caryopses (seeds) and spikelets were collected to avoid losses as they matured throughout the study. Because of differing rates of maturation and senescence, all *Avena* were harvested in the first four harvests and the majority of *Hordeum* plants were collected in the fifth harvest. Five quantitative characteristics were recorded for each plant: aboveground plant mass (excluding seeds), flowering culm number, seed mass, seed number, and total aboveground biomass.

To facilitate presentation of the treatment interactions, population means of the biomass, culm and seed variables were expressed as ratios of the response in high to low watering treatments within each soil type. In this way, the baseline response was the response under low water, and the high water value represented the response to changes in resource availability within soil types of differing quality. The test for phenotypic plasticity required a significant three-way interaction between water, soil, and population, which would indicate that populations across the rainfall gradient were responding in a linear pattern to simultaneous changes in both soil and water resource availability.

Results

Avena barbata

Early phenology

Under greenhouse conditions, the timing of flowering of *A. barbata* populations was correlated with local rainfall patterns ($P < 0.05$, $r = -0.68$, slope $= -0.52$, $n = 11$). Populations at the xeric end of the rainfall gradient flowered earlier and at a higher percentage than populations collected from more mesic conditions (Fig. 1). This relationship was nearly identical when latitude was substituted for rainfall ($P < 0.05$, $r = -0.67$, slope $= -0.03$, $n = 11$).

Treatment response

The three-way soil x water x population interactions were significant for stem mass, seed number, seed mass, and total biomass, but not for culm number (Table 2). Each population was expressed as the ratio of the high to low water treatment means and then plotted as a response to soil treatment across the rainfall gradient (Fig. 2). For all variables, the plants growing in Soil 1 did not respond strongly to an increase in water availability and showed a less than twofold mean increase in high water treatment. In contrast, the plants in Soil 2 increased significantly from low to high water and the magnitude of the response corresponded with position on the rainfall gradient. Stem biomass and total biomass increased from threefold to fivefold from the low to
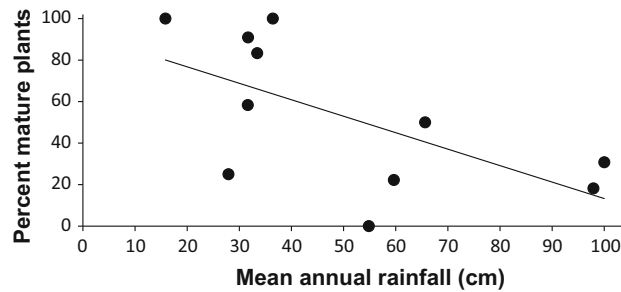
Fig. 1 Correlation of percent flowering (as of 25 April) among 11 populations of *Avena barbata* to mean annual rainfall across a south-to-north rainfall gradient. Mean annual rainfall data are shown in Table 1. Populations from the xeric sites flowered more quickly than populations from more mesic sites. The correlation is significant at $P < 0.025$

Table 2 Three-way ANOVA results of biomass and count data collected after plants reached senescence

a. *Avena barbata*							**b. *Hordeum murinum***		
Factors	df	Stem mass	Culm no	Seed mass	Seed no	Total mass	df	Stem mass	Total mass
Block	14	0.0220	0.2964	0.2203	0.0209	0.0049	14	0.0001	0.0001
Water	1	0.0001	0.0001	0.0001	0.0001	0.0001	1	0.0001	0.0001
Soil	1	0.0001	0.7505	0.0001	0.0082	0.0001	1	0.0001	0.0001
W*S	1	0.0001	**0.0001**	0.0001	0.0001	0.0001	1	**0.0001**	**0.0001**
Population	5	0.8505	0.0018	0.6537	0.0440	0.7946	5	0.9952	0.9952
W*P	5	0.0001	0.0760	0.0618	0.0001	0.0001	5	0.2294	0.4935
S*P	5	0.6099	0.0863	0.2834	0.1350	0.7225	5	0.9929	0.9927
W*S*P	5	**0.0013**	0.0516	**0.0379**	**0.0001**	**0.0009**	5	0.2229	0.4350
Model $F_{(37, 300)}$		20.51	8.05	14.18	21.85	25.90	$F_{(37,264)}$	28.79	28.51

a. *Avena barbata*. All 3-way interactions are significant except culm number. b. *Hordeum murinum*. The 2-way water x soil interactions are significant. Only factors with sufficient data for full analysis are shown. *P* values in bold are represented in Figs. 2 and 3

high end of the rainfall gradient. Culm number and seed number increased about sixfold and tenfold, respectively.

Plasticity

Populations of *A. barbata* from the mesic end of the rainfall gradient showed greater response to changes in resource availability compared to populations from the xeric end (Table 2; Fig. 2). The response of xeric populations was not strongly affected by the water treatment or by the influence of soil quality, whereas the response of mesic populations corresponded to their position on the rainfall gradient and this response was significant for four of the five variables tested.

Hordeum murinum

Phenology

Under greenhouse conditions, early season phenology of *H. murinum* showed no significant variation in time of flowering among populations or across the precipitation gradient.

Treatment response

The two-way interactions for water and soil were significant for aboveground biomass and total biomass, but no significant interactions were detected for seed traits. No treatment interactions with population were detected, nor were any main effects of
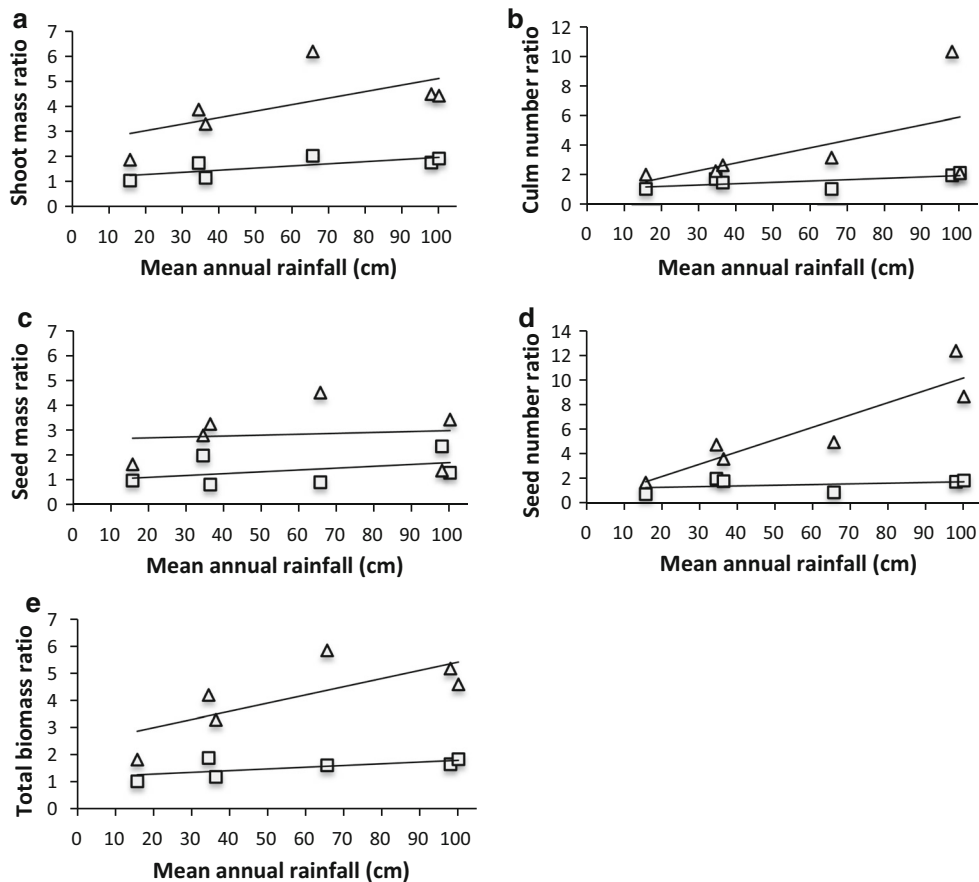
Fig. 2 Response of six populations *Avena barbata* to water and soil treatments across a south-to-north rainfall gradient. Variables measured were: **a** shoot mass ratio, **b** culm number ratio, **c** seed mass ratio, **d** seed number ratio, **e** total biomass ratio. Data points are the ratio of the response in high water to low water treatments for a given population. In Soil 1 (*squares*), plants showed no significant response to water treatment across the six populations on the rainfall gradient. In Soil 2 (*triangles*), mesic populations showed a greater response than xeric populations for all variables although the response was weak for culm number and seed mass. Water × soil × population interactions were significant for all variables except culm number ratio (see Table 2)

population detected. As water availability increased, mean biomass increased about twofold in the lower quality soil (Soil 1) and about fourfold in better soil (Soil 2).

Plasticity

No three-way soil x water x population interactions were significant indicating that populations from the xeric end of the rainfall gradient responded similarly to those from the mesic end of the gradient. There was no evidence of variation in plasticity among populations across the precipitation gradient either in response to soil quality or water availability.

Discussion

We predicted that the populations of two annual grasses used in this experiment would show similar responses to soil and water treatments because of their long history and similar distributions in California, but we observed very dissimilar responses. Both species showed restricted growth responses to the lower quality soil even when water was not limiting. This response was not unexpected: plants growing in habitats with low and unpredictable resource availability are predicted to show rapid and fixed developmental patterns (Alpert and Simms 2002). However, in the higher quality soil, the responses of the two species were very different. *Avena barbata* showed a limited
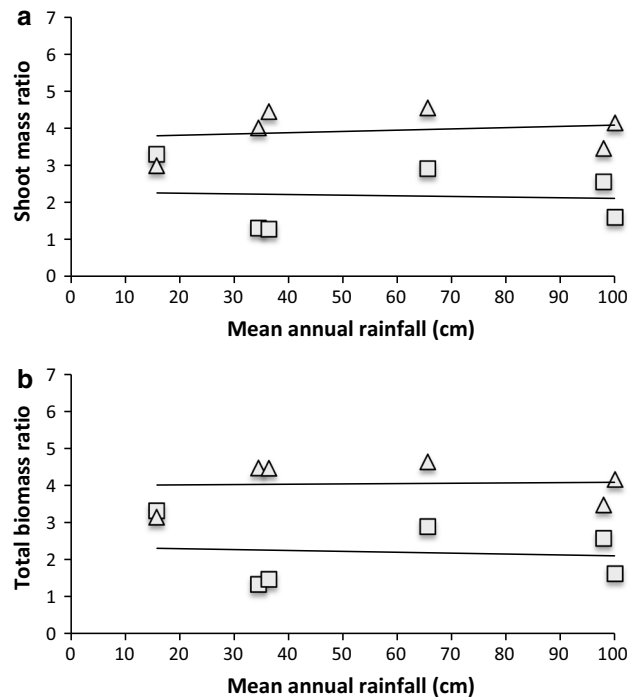
Fig. 3 Response of six populations of *Hordeum murinum* to water and soil treatments across a south-to-north rainfall gradient. Significant water × soil interactions were detected for **a** shoot mass ratio and **b** total biomass ratio. Data points are the ratio of the response in high water to low water treatments. Plants in both Soil 1 (*triangles*) and Soil 2 (*squares*) showed no significant response to water treatment across the six populations on the rainfall gradient. However, the response to the watering treatment was significantly higher in Soil 2, where biomass was about fourfold greater, than in Soil 1 where the biomass increase was about twofold. No three-way treatment interactions were significant (see Table 2)

response in xeric populations, but a response that corresponded with position along the annual rainfall gradient, and with significant variation among populations in early season phenology. In contrast, *H. murinum* showed an elevated response to the higher quality soil for all populations, but with no response corresponding to the annual rainfall gradient, and no significant variation in growth or phenology among the six populations tested. Thus, these two naturalized species of annual grass, introduced more than two centuries ago, and with similar habitat preferences throughout California, showed very different patterns of growth and phenology along a rainfall gradient.

These contrasting results challenge at least one assumption that strong population-level differentiation is more likely to be found in populations from more stable environments with low genetic mixing than from the highly disturbed soils of road verges [e.g., England et al. (2003)]. Woodland and rangeland environments, while often heavily grazed, are assumed to be less affected by the potential for genetic mixing through human movement of

propagules. Our sampling protocol (a 950 km latitudinal transect) attempted to avoid the complication of local genetic mixing and we had no a priori reasons to expect either genetic uniformity or similarity of population-level response across such a distance.

Avena barbata met our predictions that populations should show differential responses along the rainfall gradient, a high degree of phenological matching to climate, and that populations at the mesic end of the gradient would show higher capacity for plastic response. *Hordeum murinum*, in contrast, displayed a uniform response to low soil quality with an elevated but similar response in higher soil quality and with no detectable variation in trait expression or flowering phenology among populations.

Genetic patterns in non-native annual species

The population-level patterns of genetic variation in these and other non-native annual species are likely conditioned by the breeding systems of the species as

well as selection pressures within the habitat. Allard et al. (1968) concluded that inbreeding (selfing) species should show greater intra-population vs. inter-population genetic variation and greater overall genetic variation than outbreeding species. Inter-population gene flow is reduced in selfing species and local selection pressures can work only on the existing genetic variation and genotypes. Most non-native annual grasses in the western United States are primarily selfing although this propensity may also be subject to local selection pressures that can increase the potential for recombination (Kahler et al. 1975). Whether the proportion of selfing within annual grass populations shifts as a response to local conditions is unknown as is any measure of differential response among different species.

Jain and colleagues (Jain and Marshall 1967; Marshall and Jain 1969; Rai and Jain 1982; Singh and Jain 1971) found distinct patterns of monomorphism and polymorphism in regionally distributed populations of *A. barbata* and reported interactions between the population genetic structure, phenotypic plasticity, and interspecific competition. The history of the invasive genotypes or of the genetic diversity at the time of population spread could not be known and they attributed the presence of certain genotypes to selection related to regional rainfall patterns and correlated abiotic stresses.

Clegg and Allard (1972) and Hamrick and Holden (1979) showed very specific patterns of genetic differentiation over very short distances in *A. barbata* and credited those differences to site-specific selection pressure, especially to competitive interactions and water availability, over very small spatial scales. In particular, Allard et al. (1972) concluded that genotypes occupying specific microhabitats represented co-adapted gene complexes. Latta (2009) tested the same populations and locations and found evidence for genotypic selection when a particular allele was present and suggested local selection for specific alleles rather than population-wide adaptive genotypes.

Thus, there appears to be a greater importance of local genetic variation than regional genetic variation for ecotype formation in non-native annual grasses in California and the western US even 100–200 generations after introduction. A regional pattern of variation would imply recombination prior to spread as a likely mechanism, while small-scale patterns of variation would imply a response to local selection pressures and potentially a greater importance of in situ mutation. For example, Rice and Mack (1991a, b, c) found significant amounts of quantitative genetic variation many decades after post-invasion expansion in seven populations of *Bromus tectorum*, but this variation was largely within families or populations and significantly correlated with local abiotic conditions. Novak et al. (1991) examined 60 populations of *B. tectorum* and found very low electrophoretic variability across the entire North American range. Thus, invasion success is not clearly associated with genetic variation per se and may depend on phenotypic plasticity. However, the instances of apparent maladaptation (Rice and Mack 1991a, b, c) may reflect an inability to make adaptive adjustments to local conditions because of genetic constraints [e.g., Novak et al. (1991)] on phenological response (Dyer et al. 2012).

Similarly, Meimberg et al. (2006, 2009) found that the widespread and rapid invasion of *Aegilops triuncialis* in California is restricted to two of the seven known genotypes with no evidence of post-invasion recombination prior to population expansion, but with some novel variation within populations. This lack of within- and among-population genetic diversity coupled with strong response variation appears to show an overriding importance of phenotypic plasticity (Rice et al. 2013). In contrast, Volis (2007) studied the responses of two co-occurring annual grasses, *H. spontaneum* and *A. sterilis*, along a precipitation gradient within their sympatric home ranges in Israel and found consistent shifts in phenology and reproductive output as conditions became more severe, but within-population genetic variation remained very high.

Mechanisms influencing patterns of response

There are several possible mechanisms whereby naturalized species of annual grasses in California could differ in their responses to long-term local and regional climate patterns. Given the number of variables influencing the genetic structure of invasive plant populations, it is impossible to identify the exact mechanism, if there is only one, that might cause dissimilar responses in different species of annual grasses occupying the same habitats.

First, it is possible that the two species we studied experience the same selection pressures but at different intensities. Although appearing to grow and mature nearly synchronously in the field, our data suggested that *H. murinum* was more tolerant of water and temperature stress and matured more slowly and uniformly than *A. barbata*. In this study, all individuals of *A. barbata* had reached senescence before the final harvest when the majority of *H. murinum* were collected. Thus, the phenological response of *H. murinum* across this particular range may be relatively fixed compared to *A. barbata* and not subject to selection for variation.

Second, the two species were introduced to California about the same time by Spanish explorers and colonists (Spira and Wagner 1983; Garcia et al. 1989), but sample sizes, sample genetic variation, and subsequent reintroductions may have varied greatly and with different genetic consequences. Because these and other annual grass species in California show very low levels of outcrossing (Stebbins 1957; Allard et al. 1968; Giles 1984), it is possible that introductions of particularly aggressive genotypes may have resulted in very different long-term genetic structure statewide. Hamrick and Allard (1972) estimated the outcrossing rate of *A. barbata* at <3 % and also concluded that this species is subject to intense micro-geographical selection pressure that structures local populations [see also Latta (2009)]. Such structuring of local populations cannot occur without a variable gene pool, which Garcia et al. (1989) confirmed, but one that is also very well mixed, which we can only assume. *Hordeum murinum* has been studied much less than *A. barbata* with respect to regional genetic patterns although Sharifi-Rigi et al. (2014) found very strong regional segregation among the polyploids in the species and Giles (1984) reported very little genetic differentiation across a wide sampling of populations.

Third, long-term population-level response variation may also be a function of inherently different genetic structure. If the ploidy, meiotic mechanisms, or history of genetic restructuring differs among species, then the species may have very different capacities for responding to selection pressures. *Avena barbata* is $2N = 28$ and a tetraploid (Garcia et al. 1991) *Hordeum murinum* (ssp. *leporinum*) is $2N = 28, 42$ and therefore may be tetraploid or hexaploid across much of its

natural range (Sharifi-Rigi et al. 2014; Giles 1984). However, the potential for a larger and more redundant genome in *H. murinum* would be predicted to increase rather than decrease the capacity for trait expression. This potential was noted by Giles (1984) who found both genetic uniformity in the species and significant heritable variation in quantitative characters.

Fourth, each species may have a different inherent capacity for plastic expression and this certainly may be influenced by its historical changes in ploidy. However, in situ mutation over 200 years post-invasion would also argue for an increase in response capacity over time although it is possible that the mutation rates among annual grass species could vary considerably. Rai (1974) and Rai and Jain (1982) reported that polymorphisms resulting from in situ mutation in *A. barbata* were closely correlated with climate, which suggests that *A. barbata* populations are structured locally by climate variables and, as mentioned above, could be influenced by shifts in outcrossing rates. Giles (1984) examined 58 populations of *H. murinum* and found a high degree of genetic monomorphism, but a significant amount of morphological variation both within and among populations, which suggests a high level of plastic response to local conditions despite high genetic uniformity.

Fifth, successful generalist invasive species are predicted to possess a high adaptive potential, but this potential may be predicated on poorly understood genetic processes such as epigenetic transformations leading to strong maternal or transgenerational effects (Richards et al. 2006). Different species may have very different capacities in that regard. Indeed, invasive plant species may be more successful invaders precisely because of the highly variable trait expression afforded by polyploidy that buffers them from selection and this expression may be under the control of epigenetic mechanisms that activate and regulate that trait variation. If so, traits characteristic of successful invaders such as competitive superiority, allelopathy, high phenotypic plasticity, and transgenerational plasticity may be expressions of a general genetic mechanism that allows a greater range of expression based on a genome structure such as that found in polyploid species. Such species would enjoy greater buffering from selection pressure and a greater range of trait expression as growing conditions change despite having low genetic variation.

Although non-native annual grasses in the western United States are similar in appearance and ecological function, a growing number of studies indicate a diversity of variables affecting population-level genetic structure. Whether idiosyncratic, historical accident, or the result of unpredictable genetic events, the population genetic architecture of annual grass species in their non-native ranges appears highly variable. These annual grass species appear to exhibit a range of genetic responses to environmental conditions within what appear to be distinct grassland and woodland ecosystems. These responses are likely predicated on the initial genetic status of the population in the post-invasion environment and this suggests that long-term changes to population genetic structure may be difficult to predict despite self-compatibility as the predominant breeding pattern. As a consequence, despite a large literature on invasive annual grass genetics, there remains great opportunity to expand our knowledge of invasion genetics using these species.

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