Chapter 5
Ecological Genetics, Local Adaptation, and Phenotypic Plasticity in *Bromus tectorum* in the Context of a Changing Climate

Rebecca A. Hufft and Tamara J. Zelikova

Abstract Effective management of invasive species spread requires understanding the potential of exotic species to colonize different habitat types. In the case of *Bromus tectorum*, colonization potential includes persisting in variable environments via phenotypic plasticity or via genetic variation. *Bromus tectorum* L. (cheatgrass or downy brome) is a highly invasive, self-pollinating, winter annual grass that was introduced to the intermountain region of North America around 1890 and expanded to its modern range within 40 years. Common garden studies have helped shed light on outcrossing frequency, microsite effects on establishment and growth, traits that could confer invasiveness, and variation in germination, morphology, and physiology. Here, we review the evidence for existing local adaptation and phenotypic plasticity in *B. tectorum* in its invaded range along with the potential for responses to climate change and discuss implications of both for its success as an invader and future management. All of these studies show that *B. tectorum* can tolerate a wide range of habitats as the result of genetic variation among populations, a range of locally adapted ecotypes, and phenotypic plasticity. The success of *B. tectorum* could be due to its ability to maintain fitness in both high-quality and marginal environments.

Keywords Adaptive evolution • Common garden • General-purpose genotype • Genetic variation • Phenotypic plasticity • Reciprocal transplant

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5.1 Introduction

Ecological genetics, the study of the genetic basis for traits of ecological significance, such as those related to fitness, flowering time, and drought tolerance, provides valuable information to address ecological and evolutionary questions in natural systems. Heritable traits that confer high fitness can result in the adaptation of a population to its local environment, i.e., local adaptation (e.g., Turesson 1922; Clausen et al. 1941; Hiesey and Milner 1965; Gurevitch 1992; Dudley and Schmitt 1995; Cordell et al. 1998; Huey et al. 2000; Leimu and Fischer 2008). Understanding which fitness traits are advantageous in particular environments is especially relevant for invasive species and can help target management efforts to areas where invasive species might spread (Parker et al. 2003), especially in the face of climate change.

We know that plants can evolve over relatively short time scales to adapt to environmental conditions (Franks et al. 2007) and invasive species can do so even more quickly in their introduced range (Maron et al. 2004; Colautti and Barrett 2013). Multiple introductions are common for invasive species and can increase genetic variation and thus the potential for adaptive evolution (Dlugosch and Parker 2008). We would predict that invaders likely succeed in multiple environments if they are preadapted to local conditions, locally adapted via the creation of new genotypes through gene flow among independent introductions, or present general-purpose genotypes that survive through phenotypic or developmental plasticity (Parker et al. 2003). Effective management of the spread of invasive species requires differentiating among these options by quantifying the capacity for invasive species to have general-purpose genotypes (Baker 1965) with high levels of plasticity, assessing their ability to genetically adapt to new environments via in situ evolution of novel genotypes, or determining the prominence of preadapted genotypes (Parker et al. 2003). Understanding the relative roles of phenotypic plasticity and genetic adaptation in key life history traits of invasive species can help explain their success and help guide future management efforts.

Bromus tectorum L. (cheatgrass or downy brome) is a highly invasive, self-pollinating, winter annual grass that was introduced to the intermountain region of North America around 1890 and expanded to cover the intermountain West within 40 years, occupying much of the perennial shrublands in Washington, Idaho, Oregon, Nevada, Utah, and British Columbia (Mack 1981). This species is unique as one of the few invaders for which we have a good understanding of the dispersal history (Novak and Mack 1993, 2001; Novak et al. 1993). Historical and genetic data suggest multiple introductions into North America (Novak and Mack 2015). These multiple introductions have led to higher genetic diversity than would otherwise be expected in a predominantly selfing species (Novak and Mack 2015) and provide additional mechanisms underlying the success of its invasion (i.e., the potential to have preadapted genotypes and higher diversity on which evolution could act in situ to generate novel genotypes).

In its native range, *B. tectorum* succeeds in a variety of habitats, including the arid steppe region of Europe, the Middle East, and temperate and tropical parts of Asia, and this success in diverse habitats is thought to be due to high phenotypic plasticity (Fenesi et al. 2011). *Bromus tectorum* occurs in grasslands and shrublands on a range of soil types in North America, including salt desert, semidesert shrubland, shrub-steppe, grassland, low-elevation dry forest, and mid- and high-elevation mesic forests (Rice and Mack 1991a). While it can utilize the understory of forested areas, *B. tectorum* is often at low abundance (e.g., less than 5 % cover under *Cercocarpus ledifolius* Nutt., Leger et al. 2009), and forest understory is considered marginal habitat (Rice and Mack 1991a). A generalist ecological and evolutionary strategy, along with the genetic changes that may have occurred during and after its introduction, could be the reason for the ability of *B. tectorum* to invade a range of habitats (from Mojave Desert to intermountain montane and from open to understory vegetation), leading to its ultimate success as an invader in North America (Fig. 1.1 in Germino et al. 2015; Fig. 5.1).

There are two main approaches for studying genetic variation among populations and environments: (1) direct evaluation of neutral molecular genetic variation (with unknown ecological importance) and (2) measurement of genetic variation in quantitative traits (with known ecological function but unknown genetic basis) (Via 1990). Common garden and reciprocal transplant studies have been used for the past century to answer ecological and evolutionary questions, especially those related to local adaptation (Turesson 1922; Clausen et al. 1948). Common garden studies evaluate all genotypes in a common environment and through manipulations attempt to identify causal mechanisms for variation. Reciprocal transplant studies are essentially extensions of common garden studies that allow the incorporation of all the environmental variability in the home sites to test for local adaptation but do not necessarily inform a direct causal mechanism for adaptation. Reciprocal transplant studies can provide evidence of adaptive differentiation but must be combined with other approaches to identify causes of such variation, including genetic studies to determine if results are due to in situ evolution or preadapted genotypes, the role of multigenerational effects, and an examination of traits conferring adaptation. Common garden studies can be more logistically feasible than reciprocal transplant studies and can help identify putative causes of variation when experimental manipulations are used; however, they cannot provide direct evidence of adaptation, since not all genotypes are tested in their home environments, and environmental differences between the common garden location and the site of origin can lead to differences in performance rather than directly evaluating adaptation.

Common garden studies with *B. tectorum* have helped shed light on outcrossing frequency (Meyer et al. 2013), microsite effects on establishment and growth (Hoover and Germino 2012), possession of traits that could confer invasiveness (Fenesi et al. 2011), and variation in germination, morphology, and physiology (Rice and Mack 1991a; Kao et al. 2008; Bykova and Sage 2012). All these studies

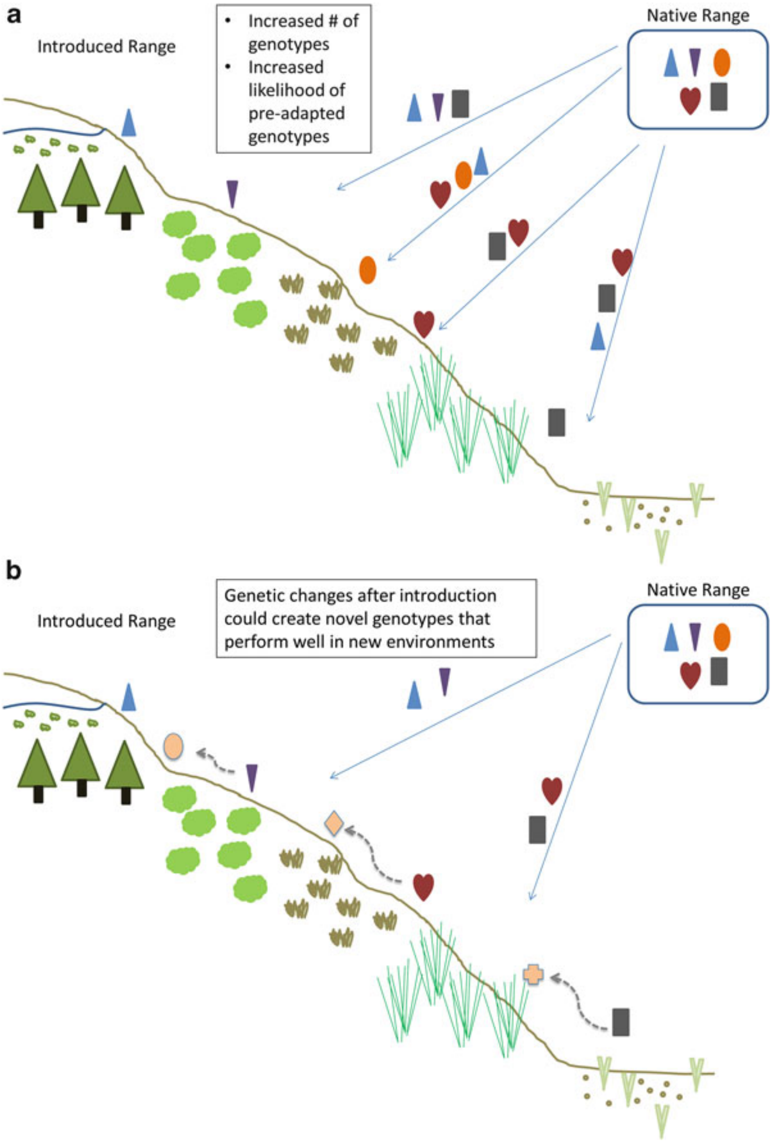

Fig. 5.1 Broad ecological tolerance in the introduced range can occur through three main processes described here. *Symbols* inside each box represent different genotypes. (**a**) Preadapted genotypes, (**b**) novel genotypes, and (**c**) phenotypic plasticity

show that *B. tectorum* can tolerate a wide range of environmental conditions as the result of genetic variation and locally adapted ecotypes. Here, we review the evidence for existing phenotypic plasticity and local adaptation in *B. tectorum* in its invaded range and discuss implications for future management in a changing climate.

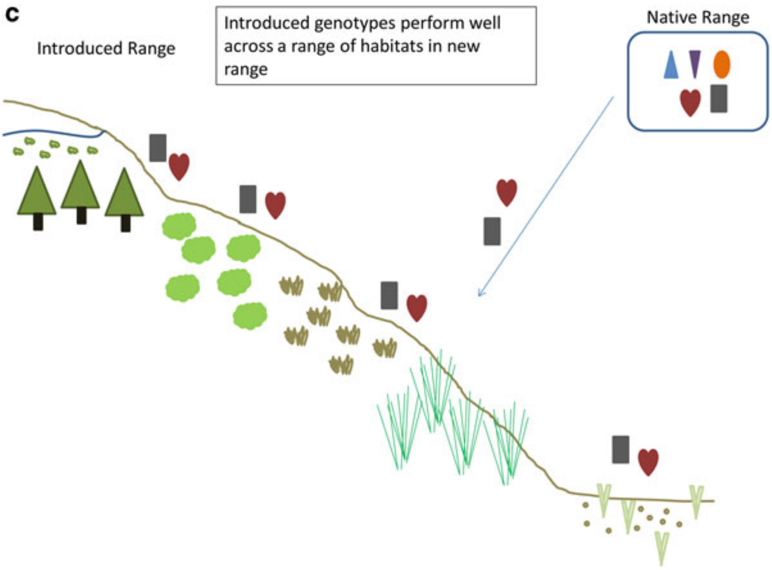

Fig. 5.1 (continued)

5.2 Evidence for Broad Environmental Tolerance

Bromus tectorum has a wide temperature tolerance that likely plays an important role in invasion success (Brooks et al. 2015), with the current northern range limit likely determined by its maximum cold tolerance (Salo 2005; Bykova and Sage 2012). *Bromus tectorum* could tolerate temperatures down to −31 °C in a greenhouse experiment and survived a sudden, severe fall freeze better than a congener (*Bromus rubens* L.) tested in the same experiment (Bykova and Sage 2012). In addition to surviving fall freezes, *B. tectorum* is able to take advantage of transient warm periods in autumn and spring with increased nitrate acquisition rates relative to native perennial grasses (Leffler et al. 2011) and greater root growth than natives at low temperatures. This ability to survive and thrive at low temperatures and take advantage of transient warm periods could give *B. tectorum* a competitive edge over native species in habitats characterized by cold winters. While *B. tectorum* can tolerate low temperature extremes, the optimal temperature range for *B. tectorum* growth is 10–20 °C, and it barely grows at or below 5 °C and above 40 °C (McCarlie et al. 2000). Thus, despite a low level of tolerance for extremes and fine-scale modeling efforts that predict an expansion of *B. tectorum* into colder habitats (West et al. 2015), a shift in temperature optima would be necessary for *B. tectorum* to continue to invade and succeed if climate extremes become the new norm as predicted (IPCC 2014).

In addition to the effects of temperature on growth and reproduction, *B. tectorum* is also responsive to other extreme growing conditions, with evidence for a genetic basis underlying the ability to tolerate such conditions. For example, there is genetic differentiation among *B. tectorum* populations growing in high and low salinity environments. A unique microsatellite genotype dominated a *B. tectorum* population in a high saline playa, but this genotype was absent in populations occurring on nonsaline soils (Scott et al. 2010). In a reciprocal transplant experiment, plants from the high salinity playa sites showed evidence of adaptation to high salinity, with larger size and seed production in high salinity treatments than individuals from less saline home sites in a greenhouse experiment (Scott et al. 2010). The same Scott et al. (2010) experiment also found that seeds from saline sites had higher germination and plant establishment rates than seeds from other sites. In addition, some seeds from the nonsaline habitat performed best at their site of origin, when compared to other reciprocal seeding transplant sites (Scott et al. 2010). Similar differences in plant performance and reproduction between home and away soils were found in a study in central Nevada (Haubensak et al. 2014). The genotypic variation and differential performance among habitats suggest local adaptation that may have resulted from selection for preadapted genotypes or the presence of novel genotypes. However, given low outcrossing rates, the creation of novel genotypes is less likely responsible for the presence of adapted genotypes on the high salinity playa sites (Scott et al. 2010).

At sites with established, high-density *B. tectorum* populations, generalist genotypes dominate. In contrast, at sites of recent expansions such as salt desert and warm desert habitats, unique genotypes dominate, suggesting they are specialist genotypes (Merrill et al. 2012). A more recent study confirms only genotypes specific to warm desert habitats (specialist genotypes) are found across a range of recently invaded warm and salt desert habitats in the Mojave Desert (Lara 2013). This suggests that while specialist genotypes may be important in the initial stages of the introduction and as populations get well established over time and reach high densities, generalist genotypes may be the force behind their long-term success.

Finally, although most *B. tectorum* seeds germinate within a year, some can remain in the seed bank for 3–5 years and germinate under more favorable environmental conditions. Variation in the timing of *B. tectorum* seed germination is under strong genetic control and likely contributes to its invasiveness (Meyer and Allen 1999). Greenhouse experiments show that the relationship between *B. tectorum* germination and temperature varies across populations (Meyer and Allen 1999), that seed dormancy is thermoregulated (Bair et al. 2006), and that the likelihood of seed dormancy appears to vary across *B. tectorum* populations (Rice and Dyer 2001; Kao et al. 2008). Comparisons of *B. tectorum* seed morphology among native and introduced populations show that North American seeds have thinner lemma and palea, morphological changes that help seeds germinate faster (Liu et al. 2013). Taken together, seed characteristics vary across *B. tectorum* populations, and this variation is genetically controlled and also influenced by the environment, with direct influence on germination timing and competitive success.

5.3 Evidence for Local Adaptation via Neutral Genetic Variation

With its annual, selfing life history, *B. tectorum* is expected to have very low levels of outcrossing and within-population genetic diversity. Indeed, outcrossing rates are low in introduced field populations in North America (Valliant et al. 2007) and even in experimentally created, high-diversity populations in a common garden study (Meyer et al. 2013). Despite low outcrossing rates, genetic diversity in its invaded range in North America seems higher than expected and sufficient to allow for adaptation into new environments (Table 5.1). Furthermore, large numbers of recombinant genotypes could be generated given the millions of plants per hectare in North America (Meyer and Leger 2010). This is largely because there is ample genetic variation within North American *B. tectorum* populations on which selection can act (Ramakrishnan et al. 2006; Ashley and Longland 2007; Valliant et al. 2007; Kao et al. 2008; Schachner et al. 2008; Huttanus et al. 2011; Avolio et al. 2012; Merrill et al. 2012). Because *B. tectorum* is a primarily selfing plant, genotypes with high fitness can be maintained, and low outcrossing rates (1 %) assure formation of novel genotypes (Meyer et al. 2013). Although some studies have concluded that the low outcrossing rates observed in *B. tectorum* are insufficient to introduce novel genotypes (0.58 %, Merrill et al. 2012), others have concluded that some populations do have outcrossing rates high enough to help create novel genotypes during range expansion into new habitats (1.62 %, Leger et al. 2009). In addition, genotypes can have variable outcrossing rates depending on the environment (Ashley and Longland 2007; Meyer et al. 2013), which means the rate of outcrossing could also change with continued range expansions and climate change. In order to better assess actual outcrossing rates and implications for the creation of novel genotypes and resultant species range expansion, a more sensitive molecular marker system, such as the previously developed SNP markers (Meyer et al. 2013), needs to be combined with a broader sample of individuals across the range of habitats (Meyer and Leger 2010).

Variation in genotypes among habitat types can indicate the presence of specialized ecotypes, and especially in *B. tectorum*, genetic markers correlate with and can be good surrogates for phenotypic traits (Ramakrishnan et al. 2004). In a microsatellite study using 21 western North American populations ranging from desert to montane from previous germination studies, genetic variation was correlated with habitat types (Meyer et al. 1997), indicating the presence of distinct *B. tectorum* ecotypes (Ramakrishnan et al. 2006). In addition, there was a genetic basis for seed germination traits that varied across populations (Ramakrishnan et al. 2006). Using two populations of *B. tectorum* in the Great Basin (one low-density population at high elevation and one high-density population at low elevation), Leger et al. (2009) used microsatellites to evaluate within-population genetic variation and a reciprocal transplant study to evaluate field performance. Within-population genetic and phenotypic variation differed between high- and low-elevation sites, suggesting a level of local adaptation to a particular set of environmental conditions that vary with elevation, namely, temperature and precipitation. This local adaptation could stem

Table 5.1 Results of genetic analyses of *Bromus tectorum*. (A) is the average number of alleles per locus, (FIS) is the inbreeding coefficient, and (H_T) is the total gene diversity

Study	Location	Marker	Sample size	Genotypes	A	FIS	H_T	Heterozygotes/%	Mean heterozygosity
Novak et al. (1991)	Western USA	Allozyme	1830		1.05	1	0.132	0	0
Bartlett et al. (2002)	Eastern USA	Allozyme	1248		1.01	1	0.075	0	0
Bartlett et al. (2002)	NV-CA	Allozyme	546		1.05	1	0.192	0	0
Bartlett et al. (2002)	Intermountain West	Allozyme	825		1.05	1	0.119	0	0
Bartlett et al. (2002)	British Colombia	Allozyme	329		1.08	1	0.261		0
Bartlett et al. (2002)	Europe	Allozyme	1242		1.02	0.98			0.0001
Bartlett et al. (2002)	Southwest Asia	Allozyme	484		1.04	0.96			0.0002
Valliant et al. (2007)	Canada	Allozyme	1892		1.04	0.9917	0.159	8/0.0042	
Schachner et al. (2008)	Midcontinent USA	Allozyme	1624	9	1.04	0.9778	0.228		0.0002
Huttanus et al. (2011)	Central USA	Allozyme	1841		1.05	0.9979	0.187	1/0.0005	
Ramakrishnan et al. (2006)	UT, ID, NV, CO	SSR	807	50	2.73	1		0	0
Ashley and Longland (2007)	NV	SSR	182	51		0.891–1	0.234	15/8.24	0.021
Kao et al. (2008)	CO	SSR	90	41	2.53	0.968–1		1/1.1	0.0002
Leger et al. (2009)	NV	SSR	185	29				3/1.62	
Scott et al. (2010)	UT	SSR	200	28				2/1	
Merrill et al. (2012)	Intermountain West	SSR	1884	131	10	0.977		11/0.58	0.0071
Meyer et al. (2013)	Intermountain West	SSR	2000			0.9851		15/0.0075	
Zelikova et al. (2013)	UT	SSR	36						0.257
Meyer et al. (2013)	Intermountain West	SNP	1429		1.70	0.97–0.99		119/8.32	0.00325

from the presence of preadapted genotypes or in situ evolution of novel genotypes, two non-mutually exclusive mechanisms that can lead to similar outcomes. The same study also found that while individuals from the high-density, low-elevation site were locally adapted as illustrated by higher germination rates and overall survival, there was still potential for adaptation at the invasion edge (high elevation) due to relatively high genetic diversity within those high-elevation sites and evidence of outcrossing. Such potential for further adaptation could mean that *B. tectorum* could continue to invade into higher elevations and additional habitats.

5.4 Evidence for Broad Environmental Tolerance via Phenotypic Plasticity

The success of species in a large range of environments suggests a high level of either genetic adaptation or phenotypic plasticity. Selection operates on phenotypic variation, and success in a broad range of environmental conditions can result from an increase in phenotypic plasticity (Bradshaw 1965). Environmental and habitat variation necessitates some level of physiological adaptation, and for *B. tectorum*, the most important physiological attributes that promote its invasiveness are (1) large temperature tolerance range, (2) early germination paired with rapid growth and high rates of water and nutrient uptake (Funk and Vitousek 2007; James et al. 2011), and (3) competitive ability in extreme environments (Chambers et al. 2015).

Invasive species generally show significantly more phenotypic plasticity than non-invasive species (Davidson et al. 2011). Because maternal effects can contribute to trans-generational plasticity (Dyer et al. 2010), the increase in phenotypic plasticity may be advantageous to invasive species (allowing them to perform well in newly invaded environments in the first generation) or may hinder local adaptation by impeding selection for locally adapted traits because phenotypes still reflect the former maternal environment (Moran and Alexander 2014 and references therein). In its native range, *B. tectorum* has exceptionally high phenotypic plasticity (Fenesi et al. 2011). Not only is this species-level plasticity beneficial to invasiveness, but it has been suggested that *B. tectorum* is even more plastic in its invasive range relative to its native range, including greater adaptive plasticity for freezing tolerance and more rapid seedling emergence in response to warm temperatures (Griffith et al. 2014), though more populations should be tested in the native range to confirm this finding.

Rice and Mack (1991b) evaluated *B. tectorum* phenotypic plasticity variation among six populations along a gradient in temperature and precipitation in habitats in its invaded range where populations were genetically differentiated (Rice and Mack 1991a). Across the range of habitats tested, phenotypic plasticity in flowering phenology and seed weight was very low, but aboveground biomass and seed number plasticity was high. Rice and Mack suggested that even when there is a genetic basis for phenological traits, *B. tectorum* fitness may still be driven by environmental factors given its high level of plasticity (Rice and Mack 1991b). High phenotypic plasticity in flowering, aboveground biomass, and seed production has been observed at these same sites over years that varied in temperature and precipitation, with plants producing few seeds in harsh years and many seeds under optimal climate conditions, attesting to the benefit of plasticity in seed production (Mack and Pyke 1983). While this is not unique to just *B. tectorum*, this does attest to the fact that although a genetic basis for many traits has been found, important fitness traits are still more likely controlled by the environment.

5.5 Implications of Local Adaptation and Phenotypic Plasticity for Invasion Success

Bromus tectorum is both phenotypically plastic and able to adapt to local conditions, traits that surely contribute to *B. tectorum* success in a wide range of habitats. This ability to maintain fitness advantages in both unfavorable and favorable environments is what Richards et al. (2006) call a Jack-and-master, a dual strategy that appears to also account for the success of another North American invader, *Tamarix ramosissima* Ledeb. (Sexton et al. 2002). Regardless of whether it results from the arrival of preadapted genotypes or in situ adaption, local adaptation may be associated with variation in phenotypic plasticity, such that populations with higher plasticity can take advantage of changing environmental conditions, while populations with lower plasticity have more fixed traits and thrive under stable conditions. In a field study monitoring *B. tectorum* phenology in response to late season moisture, mesic site plants had more phenological plasticity that allowed them to take advantage of the late season moisture, but xeric site plants had more fixed phenology and could not make use of the late season rains (Dyer et al. 2012). This is somewhat counterintuitive because xeric environments are broadly characterized by more variable precipitation regimes, and selection should favor traits that are compatible with high phenological plasticity (xeric sites, Dyer et al. 2012). However, not all traits would be expected to show increased phenological plasticity, and the timing of seed germination is generally less variable in more predictable environments (Meyer and Allen 1999).

In addition to germination, the phenology of growth and reproduction is under environmental and genetic regulation (Ball et al. 2004). In a common garden study, *B. tectorum* flowering times varied among habitat types, with shrub-steppe and semidesert shrubland ecotypes flowering the earliest and high-elevation mesic forest flowering the latest (Rice and Mack 1991a). The adaptive significance of such variation could be related to drought avoidance in semidesert shrubland and steppe habitats (Rice and Mack 1991a) but remains to be explored in other habitats. Vernalization (i.e., prechilling requirement for flowering) also varies by habitat type and appears to be adaptively significant, with warm desert populations flowering without vernalization and cooler foothills and montane sites flowering faster with increased vernalization (Meyer et al. 2004). The interaction between environmental and genetic control of phenology has implications for how *B. tectorum* will grow and reproduce under future climate conditions, with some ecotypes likely to expand, while others contract if genetic variation in traits related to phenology does not match the pace of changes in environmental conditions. Understanding the importance of phenological plasticity is especially important in light of changing climate, where higher plasticity may be associated with better ability to adapt to more unpredictable future climate.

5.6 Ecological and Evolutionary Adaptations to Climate Change

Plant evolutionary responses to climate change can be critical in determining species persistence, and this is especially true with invasive species that have higher phenotypic plasticity that can be adaptive (Davidson et al. 2011). As a result of both the potential introduction of preadapted genotypes and higher phenotypic plasticity, invasive species such as *B. tectorum* may be especially poised to show evolutionary responses to climate change, and their responses may be more rapid than those of native species (Clements and Ditommaso 2011). There are several lines of evidence to suggest that *B. tectorum*, along with other invasive grasses in the genus *Bromus*, should be capable of both ecological and evolutionary responses to climate change (Lee 2002), especially in light of its annual life cycle and primarily selfing reproduction that can maintain genotypes with high fitness (Meyer et al. 2013). As a result, *B. tectorum*'s responses to climate change could be especially rapid (Jump and Penuelas 2005; Leger et al. 2009). Furthermore, climate has a substantial influence on most aspects of *B. tectorum*'s life cycle, including seed vernalization (Meyer et al. 2004), germination (Meyer et al. 1997; Meyer and Allen 1999), establishment and growth (Bradford and Lauenroth 2006; Chambers et al. 2007), and flowering and senescence (Zelikova et al. 2013). Finally, both climate change and responses to those changes are expected to vary spatially (Bradley et al. 2009, 2015; Bradley 2010), influencing optimal *B. tectorum* growth conditions and pushing physiological limitations differentially across the invaded range. A clear understanding of which traits are under selection and how all these factors interact is necessary to model invasion potential under future climatic conditions.

Ecological responses to climate change are well documented, but there is little direct evidence for adaptation to climate change (Merila 2012), largely because documenting evolutionary responses is difficult and requires carefully designed experimental manipulations (Gienapp et al. 2008). In addition, traits under selection may be correlated or antagonistic to the direction of selection (Etterson and Shaw 2001). Finally, many other factors change along with climate, making it difficult to separate plastic and evolutionary responses. Climate change experiments are especially useful for understanding *B. tectorum* ecological and evolutionary responses to climate change, at least in part because experiments can cover *B. tectorum*'s entire life cycle. *Bromus tectorum* reproduces only by seed, facilitating measures of lifetime reproductive success (i.e., fitness) within experiments.

Ecological responses to climate change have been noted in both observational and experimental studies. Here, we summarize findings from climate manipulation experiments and discuss the evolutionary implications where possible. Although current knowledge of *B. tectorum* biology and spatial genetic variation across the western USA-invaded range is ample and growing (Ramakrishnan et al. 2006; Ashley and Longland 2007; Valliant et al. 2007; Kao et al. 2008; Schachner et al. 2008; Huttanus et al. 2011; Avolio et al. 2012; Merrill et al. 2012; Atkinson and Brown 2015; Novak and Mack 2015), few studies link genetic variation with adaptation to a changing climate, and no studies take that information into a distribution modeling framework. Thus, we present current knowledge to date and highlight knowledge gaps. In several instances, specific data on *B. tectorum* are not available. As a result, we present data from experiments on congeners and make predictions about how *B. tectorum* is likely to respond to similar stressors and environmental changes. *Bromus* species appear to respond strongly to experimental global change manipulations, including elevated CO_2, warming, altered precipitation, and N fertilization (as a proxy for N deposition) across a range of sites (discussed in detail below, see also Bradley et al. 2015; Belnap et al. 2015). Although a number of studies report ecological responses, genetic responses to climate change are rarely addressed. However, given the phenotypic variation and evidence that much of that variation can be adaptive, there is a clear potential for evolutionary responses (Clements and Ditommaso 2011) that have yet to be quantified (but see Zelikova et al. 2013; Grossman and Rice 2014). More broadly, evolutionary responses in other *Bromus* species can inform hypotheses of how *B. tectorum* might respond to elevated CO_2 in the future.

5.6.1 Elevated CO_2

Atmospheric CO_2 concentrations are predicted to reach 600 ppm by the end of the twenty-first century (IPCC 2014) and will present novel environmental conditions for plants that have not experienced such high atmospheric CO_2 concentrations for 20 million years (Pearson and Palmer 2000). Hundreds of studies have examined how elevated CO_2 affects plant development, but few studies have examined the influence of CO_2 as a selective agent, and none have examined potential evolutionary adaptation under elevated atmospheric CO_2 in *B. tectorum*. Elevated CO_2 generally increases plant water-use efficiency and, for C_3 plants, photosynthetic rates, which can translate to increases in biomass accumulation and reproduction and help facilitate biological invasions (Weltzin et al. 2003). This positive ecological effect of CO_2 enrichment has been shown for *B. tectorum* in low-elevation desert and shrubland sites and in greenhouse experiments with *B. tectorum* seeds collected from across an elevation gradient in northern Nevada (Ziska et al. 2005), for *Bromus erectus* Huds. and *B. rubens* in the Desert FACE site (Huxman et al. 1998; Smith et al. 2000; Nagel et al. 2004), and for *Bromus inermis* Leyss. in a Minnesota grassland (Lau et al. 2010; Steinger et al. 2000). In the Desert FACE experiment, *B. rubens* plants produced more seeds under elevated CO_2 conditions, but the growth rate of the resultant seedlings was lower, and it appears that the increase in seed and plant C:N ratios under elevated CO_2 reduced the seed quality and seedling performance (Huxman et al. 1998). Given the generality of the positive CO_2 enrichment effect across *Bromus* species, future atmospheric CO_2 conditions are likely to favor *B. tectorum* in certain portions of its range. Nitrogen (N) limitation may constrain the stimulatory effects of CO_2, especially in N-limited systems (Larigauderie et al. 1988; Hungate et al. 1996), and water limitation may reduce effects of CO_2 during low precipitation years and during droughts (Nowak et al. 2004).

Although largely contingent on moisture availability and N status, the general ability of plants to respond to CO_2 enrichment can be both genotype and density dependent (Bazzaz et al. 1995; Ainsworth et al. 2008), and this variation in the strength of responses has evolutionary implications. In the Mojave Desert FACE experiment, Grossman and Rice (2014) examined the physiological responses of *B. rubens* to elevated CO_2 and found evidence of evolutionary adaptation. Specifically, they reported a reduction in phenotypic plasticity and a shift toward reduced stomatal conductance in plants grown under CO_2 enrichment (Grossman and Rice 2014). Reduced stomatal conductance can conserve water and can therefore be adaptive (Drake et al. 1997; Ainsworth and Long 2005), especially in water-limited systems such as the Mojave Desert, where water availability drives most measures of plant performance. In addition, the ability to respond to changes in atmospheric CO_2 concentrations can vary across genotypes within a population (Curtis et al. 1994).

5.6.2 Warming

Along with increasing atmospheric CO_2 concentrations, air temperatures and precipitation regimes are also changing, with ecological and evolutionary consequences for plants. There is consistent evidence that warming shifts plant phenology, with earlier emergence in spring that can provide individuals with access to limited resources (Verdu and Traveset 2005). There is also a link between the timing of life history events such as emergence, growth, and flowering and plant fitness (Ellwood et al. 2013), suggesting that changes in phenology can be under selection. In manipulation experiments on the Colorado Plateau, *B. tectorum* consistently responded to warming, with earlier growth and flowering, an overall longer growing season, and increased biomass and reproductive output, but only in years with ample spring precipitation (Zelikova et al. 2013). Similar phenology results were also observed in northern Utah's Wasatch Mountains, where warming also advanced spring phenology in *B. tectorum* (Compagnoni and Adler 2014).

The experimental warming-induced changes in *B. tectorum* biomass and reproductive output reported in Zelikova et al. (2013) also influenced offspring performance in follow-up greenhouse studies, leading to higher germination rates and lower mortality for plants from warmed seed sources. Shifts in phenology associated with warming were only evident in wetter years, however, and were dependent on soil water availability. The positive effects of warming were diminished in dry years (Zelikova et al. 2013; Compagnoni and Adler 2014). Coupled with other findings that *B. tectorum* growth and reproduction increased in wet years, there is also some indication that increasing temperature may select for particular genotypes (Zelikova et al. 2013), evidenced by the reduction in genotypic diversity under warming. Selection for warming-specific genotypes could potentially increase *B. tectorum* population growth in the future if the warming trajectory continues, though the relative size of the increase depends on concomitant change in effective soil moisture, which is a function of both precipitation and evapotranspiration.

Water availability mediates *B. tectorum* responses to other factors that influence plant establishment and success, including soil texture (Miller et al. 2006; Zelikova et al. 2013) and nutrient additions (Leffler et al. 2005). Plants can be limited either by water or combination of water and N (Concilio and Loik 2013), and the frequency of rain events early in the growing season has a disproportionally large enhancement of *B. tectorum* growth, fecundity, and abundance (Prevey et al. 2010; Concilio et al. 2013; Bradley et al. 2015), suggesting that future invasion will be especially sensitive to climate change. The ecological effects of warming and N deposition on *Bromus* have been well described, but the potential for adaptive and evolutionary responses has received little attention to date and presents a knowledge gap. Taken together, the results from field climate change experiments suggest that predicted increases in temperature, shifts from snow to rain in low to mid-elevations, and increasing snow inputs at higher elevations, particularly in northern latitudes, could facilitate the expansion of *B. tectorum* northward and upward in elevation. Since drought periods may have substantial influence on the ability of *B. tectorum* to reproduce, this expansion depends on the timing of rain events and the relative abundance of preadapted genotypes or potential for the creation of novel genotypes.

Similarly, decreases in precipitation and increases in temperature at low-elevation sites, particularly in southern latitudes, may decrease *B. tectorum* invasion potential in those populations that cannot adapt and instead favor *B. rubens* (Bradley et al. 2015). If *B. tectorum* ecological responses and fitness consequences to environmental change differ among genotypes, there is a potential for climate change to impose selection that favors certain genotypes with locally adapted traits or that confers increased phenotypic plasticity. There is some preliminary data to suggest the potential for adaptive evolution to occur in response to warming in short time frames. Microsatellite data collected on genotypes from a warming experiment on the Colorado Plateau in southeastern Utah are consistent with the hypothesis that over 5 years of experimental warming, selection has reduced genetic diversity and favored particular genotypes (Zelikova et al. 2013). For populations that are relatively continuous, gene flow from warming-adapted populations could bolster adaptation. For noncontiguous populations, adaptation may have to come from within. Taken together, future global change, including increasing atmospheric CO_2 concentrations, warming, and N deposition, is expected to favor *B. tectorum*, alleviating physiological limitations on early season growth as well as enhancing growth in N-limited habitats in those areas that are increasingly water limited due to decreases in precipitation or increases in evapotranspiration. Such responses have clear implications for managing *B. tectorum* and likely other exotic annual *Bromus*.

5.7 Management Implications

Evidence for local adaptation, along with high levels of phenotypic plasticity, makes *B. tectorum* a very serious threat for continued spread into novel habitats even under current climatic conditions. The risk that this species could spread or become more dominant in areas in which it already occurs depends on the direction of the change with increased risk in areas that receive more effective precipitation and decreased risk in areas that receive less (Bradley et al. 2015). There will likely be areas of expansion and contraction, with *B. tectorum* predicted to increase in areas that receive the majority of their yearly precipitation in winter and spring and decrease in areas that receive a high proportion of precipitation in summer (Bradley et al. 2009). Management strategies that limit gene flow among populations and limit additional introductions from the native range could reduce the adaptive potential of *B. tectorum* (Schachner et al. 2008), but these strategies are unlikely to prevent the evolution of novel invasive traits (Dlugosch and Parker 2008). Thus, strategies will need to also target the creation of novel genotypes and their expansion.

A comprehensive management strategy should include protection, prevention, restoration, monitoring, and adaptive management (Chambers et al. 2014) as well as building capacity for resistance (Fig. 1.1 in Germino et al. 2015). In addition to reducing habitat disturbance in relatively intact systems, the best strategy to control *B. tectorum* might be strengthening the competitive ability of native species. Research has shown that native grass species growing in areas invaded by *B. tectorum* can adapt to have traits important for restoration (Kulpa and Leger 2013) and that the evolution of native grass species in response to *B. tectorum* can happen rapidly (Rowe and Leger 2011). Successful management practices will have to take into consideration the roles of adaptation and plasticity and how they interact to affect the spread of regional ecotypes. For example, understanding the limits to phenological or physiological plasticity to environmental factors such as temperature could allow management to direct treatments at more appropriate times. In years with high winter and spring precipitation, increased resources to battle new and low-density invasions will be crucial to limit its continued spread. Above all, the highly successful strategies of both local adaptation and phenotypic plasticity require management strategies that focus on limiting disturbance and restoring landscapes with sufficient densities of native species such that *B. tectorum* cannot establish or compete. Managing impacts of the human footprint, including transportation and utility corridors, will be important in limiting the spread into new environments (Leu et al. 2008), which is especially important given its ability to thrive in such a broad range of environments. The best strategy might be focusing on the traits of the native species used in restoration that can increase resistance to and resilience from invasion (see Sect. 5.8).

5.8 Research Needs

The variation in physiological tolerance and the genetic basis for that variation help define potential areas of *B. tectorum* expansion and could inform future management efforts. Direct field observations and collections confirm that *B. tectorum* has expanded its range into more arid salt desert and warm desert communities (Meyer et al. 2001; Ramakrishnan et al. 2006). Although higher-elevation environments have historically been relatively free from invasion (Bradley and Mustard 2006), *B. tectorum* is increasing in abundance in these habitats as well (Chambers et al. 2007; Kao et al. 2008; Leger et al. 2009; Griffith and Loik 2010; Bromberg et al. 2011). *Bromus tectorum* is also actively expanding its range in South America in habitats that are similar to the Great Basin in the USA (Biganzoli et al. 2013). Ongoing expansion of *B. tectorum* into higher elevations, such as in the Rocky Mountains (Kao et al. 2008; Bromberg et al. 2011; West et al. 2015), and into drier areas, such as in the Mojave Desert (Lara 2013), suggests that we still do not know the full ecological limits of this species and highlights the importance of understanding the genetic mechanisms responsible for its success in new areas.

Understanding and increasing resilience to disturbance and resistance to invasion are key to successfully managing *B. tectorum* (Fig. 1.1 in Germino et al. 2015; Chambers et al. 2014). Although *B. tectorum* is one of the most well-studied invasive species, several ecological and evolutionary questions remain unaddressed. Expanding the existing molecular work on *B. tectorum* to include next-generation sequencing allows researchers to evaluate gene expression across ecotypes and in different habitats to better understand the interaction between plasticity and genetic adaptation (Meyer et al. 2013). Next-generation sequencing approaches are powerful tools that allow us to better assess the actual outcrossing rates and the implications for the creation of novel genotypes and resultant species range expansion, especially when applied across a broader sample of individuals and across the range of habitats (Meyer and Leger 2010).

In the face of climate change, there is a critical need to measure the rate and magnitude of species distributional shifts, especially for policy- and management-relevant species such as *B. tectorum*. We first need to understand ecological tolerances as they relate to future range shifts and adaptations to climate change. The degree to which evolution influences responses varies spatially and across ecotypes, but we lack sufficient information to quantify this variation and its spatiotemporal variance. Field and laboratory experimental studies that manipulate climate, namely, temperature and precipitation regimes, and focus on quantifying the potential for evolution can fill current knowledge gaps. We argue that it is absolutely essential to develop the best possible case studies that target environmental gradients that encompass the local range of the species and that have conservation-relevant outcomes and incorporate evolutionary responses within a modeling framework. *Bromus tectorum* represents a superlative species for such integration.

Incorporating the current knowledge of *Bromus* responses to climate change knowledge into future distribution modeling efforts and the potential for evolutionary responses is needed. Given our knowledge about historical and ongoing invasions, *B. tectorum* presents an ideal model system for developing these modeling approaches (Parker et al. 2003). For example, developing models that incorporate the potential for *B. tectorum* to adapt to climate change in situ and extending such models across space to encompass the differential adaptation potential inherent across different ecotypes are a grand challenge. Such models will need to bring different kinds of data together, including data from studies to understand the physiological limits of adaptation across genotypes, common garden experiments with the same genotypes to link genotypic variation with phenotypic expression, and climate manipulation experiments that directly test the role of adaptation in responding to climate change under field conditions. Improving distribution modeling efforts is especially important when considering the allocation of limited management resources and focusing eradication efforts to areas where *B. tectorum* is expected to expand in the future, increasing the success of management efforts before *B. tectorum* further expands its range. In many instances, eradication or limiting range expansion may not be possible. Increasing predictive capacity and limiting impacts may be a better management option.

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