

Phenological sensitivity of *Bromus tectorum* genotypes depends on current and source environments

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Abstract

Plants respond to their environment with both short-term, within-generation trait plasticity, and long-term, between-generation evolutionary changes. However, the relative magnitude of plant responses to short- and long-term changes in the environment remains poorly understood. Shifts in phenological traits can serve as harbingers for responses to environmental change, and both a plant's current and source (i.e., genotype origin) environment can affect plant phenology via plasticity and local adaptation, respectively. To assess the role of current and source environments in explaining variation in flowering phenology of *Bromus tectorum*, an invasive annual grass, we conducted a replicated common garden experiment using 92 genotypes collected across western North America. Replicates of each genotype were planted in two densities (low = 100 seeds/1 m², high = 100 seeds/0.04 m²) under two different temperature treatments (low = white gravel; high = black gravel; 2.1°C average difference) in a factorial design, replicated across four common garden locations in Idaho and Wyoming, USA. We tested for the effect of current environment (i.e., density treatment, temperature treatment, and common garden location), source environment (i.e., genotype source climate), and their interaction on each plant's flowering phenology. Flowering timing was strongly influenced by a plant's current environment, with plants that experienced warmer current climates and higher densities flowering earlier than those that experienced cooler current climates and lower densities. Genotypes from hot and dry source climates flowered consistently earlier than those from cool and wet source climates, even after accounting for genotype relatedness, suggesting that this genetically based climate cline is a product of natural selection. We found minimal evidence of interactions between current and source environments or genotype-by-environment interactions. Phenology was more sensitive to variation in the current climate than to variation in source climate. These

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results indicate that cheatgrass phenology reflects high levels of plasticity as well as rapid local adaptation. Both processes likely contribute to its current success as a biological invader and its capacity to respond to future environmental change.

KEY WORDS

Bromus tectorum, climate change, local adaptation, phenology, plasticity

INTRODUCTION

Predicting the effect of rapid environmental change on plants requires understanding the multiple mechanisms by which individual plants and their populations respond to shifts in their environment (Anderson et al., 2012; Ensing & Eckert, 2019; Hamann et al., 2021; Ramirez-Parada et al., 2024; Richardson et al., 2017). Under increased temperatures, plants can shift their phenology via plasticity, resulting in earlier spring flowering or delayed autumn flowering, for example (Anderson et al., 2012; Ramirez-Parada et al., 2024). Plastic responses to biotic interactions can also affect the timing of germination, growth, and flowering (Elzinga et al., 2007). For example, intraspecific competition has both been shown to hasten (Antonovics & Levin, 1980; Lyons & Mully, 1992; Rice & Mack, 1991b; Schmitt et al., 1987; Vermeulen, 2015; Willenborg et al., 2009) and delay (Antonovics & Levin, 1980; Linhart, 1988) flowering time. However, the effect of biotic interactions, such as density dependence, on flowering phenology is generally understudied (Wolf et al., 2017).

Genetically based clines across broad environmental gradients (Alberto et al., 2013; Franke et al., 2006; McGahey et al., 2020) demonstrate that flowering phenology may be under strong selection (Colautti et al., 2017; Franks et al., 2007). This is, in part, because flowering phenology is highly heritable as it has direct links to plant fitness at the end of the growing season (Nicotra et al., 2010; Revolinski et al., 2023). Plasticity may also be under selection (Nicotra et al., 2010). The effect of a plant's current environment (abiotic and biotic) on its traits can be mediated by genotype such that the underlying genetics and current environment interact (Bradshaw, 1965). Given sufficient variation in these effects (i.e., genotype-by-environment interactions) and the reliability of environmental signals, theory predicts that plant populations may evolve increased sensitivity to their current environment (i.e., plasticity) in response to the increasingly variable environmental conditions predicted under climate change (Chevin & Hoffmann, 2017; Nicotra et al., 2010).

Forecasting phenological responses to climate change will require understanding both the short- and long-term effects of the environment (Toftegaard et al., 2016).

Plasticity may allow plants to respond to the increased interannual variability expected under climate change, while directional evolutionary change may be necessary to maintain fitness in the face of long-term climate trends (Merilä & Hendry, 2014; Toftegaard et al., 2016). But despite recognition that plant responses to both short- and long-term shifts in the environment are important, the contributions of a genotype's current and source environment to phenological shifts remain poorly understood (Anderson et al., 2012; Ensing & Eckert, 2019; Ramirez-Parada et al., 2024; Richardson et al., 2017).

Understanding how short- and long-term environmental change stimulates phenological responses is particularly important for the management of invasive species because shifts in their range can have large ecological and economic implications (Clements & Jones, 2021; Hodgins et al., 2018; Zettlemoyer et al., 2019). The success of invasive species may reflect wider phenological niches than co-occurring native species (Wolkovich & Cleland, 2011) or a superior ability to phenologically track interannual fluctuations in temperature (Willis et al., 2010; Wolkovich et al., 2013; Wolkovich & Cleland, 2014; Zettlemoyer et al., 2019). Further, if biotic interactions influence phenology as evidenced by previous work (Lyons & Mully, 1992; Schmitt et al., 1987; Willenborg et al., 2009), flowering phenology may vary across an invasive species' expansion front, which could accelerate or slow spread at the range edge.

Increased genetic variation from multiple introduction events can enhance the ability of invasive populations to adapt to novel environmental conditions (Clements & Jones, 2021; Hodgins et al., 2018; Leger et al., 2009; Oduor et al., 2016). Indeed, the spread of invasive species can be facilitated by local adaptation via selection on flowering timing to best match the climate in the introduced range (Clements & Jones, 2021; Colautti & Barrett, 2010). Quantifying both plastic and fixed effects on phenology may be important for predicting population persistence under climate change (Anderson et al., 2012), and thus the future distributions of invasive species (Wolkovich & Cleland, 2011).

We conducted a replicated common garden experiment to assess the role of current and source

environments in regulating flowering time of *Bromus tectorum* (cheatgrass or downy brome)—an annual invasive grass dominant in western North America (Figure 1a). We grew replicates of 92 genotypes of *B. tectorum* at high and low densities, under high and low soil surface temperature, and across four common garden sites chosen to capture variation in climatic conditions across western North America. Understanding the effects of genetics and environment on flowering time in this species is crucial because *B. tectorum*'s invasiveness partly stems from its advanced phenology compared with native species, which allows it to establish and reproduce with minimal competition. If *B. tectorum* can effectively phenologically track environmental change, even at the edges of its range (i.e., in low-density areas), this could further enhance its competitive advantage over native species.

Our first objective was to characterize how the current and source environments of *B. tectorum* genotypes explained variation in flowering phenology. Variation in flowering phenology in response to the current environment (i.e., temperature treatment, density treatment, common garden location) provides evidence for

plasticity. To characterize the potential for fixed evolutionary shifts to explain variation in phenology, we studied the relationship between genotypes' source climate and variation in flowering time observed in the common gardens. Trait-environment correlations provide evidence of local adaptation when they align with reasonable evolutionary hypotheses of how plants respond to changes in their environment (Endler, 1986; Montague et al., 2008). We also assessed how accounting for genetic relatedness influenced the relationship between source climate and flowering time, which can provide additional evidence that natural selection maintains genetically based clines (Gamba et al., 2024). Our second objective was to test for genotype-by-environment interactions (i.e., differential responses of genotypes to current environmental conditions) and explore whether the phenological response of *B. tectorum* to its current environment depended on the genotype's source environment. Our final objective was to compare phenological sensitivities (i.e., shifts in flowering time per unit change in climate; Suonan et al., 2019; Thackeray et al., 2016) of *B. tectorum* plants to their current (Figure 1b; orange line) and source environments (Figure 1b; blue line). This analysis

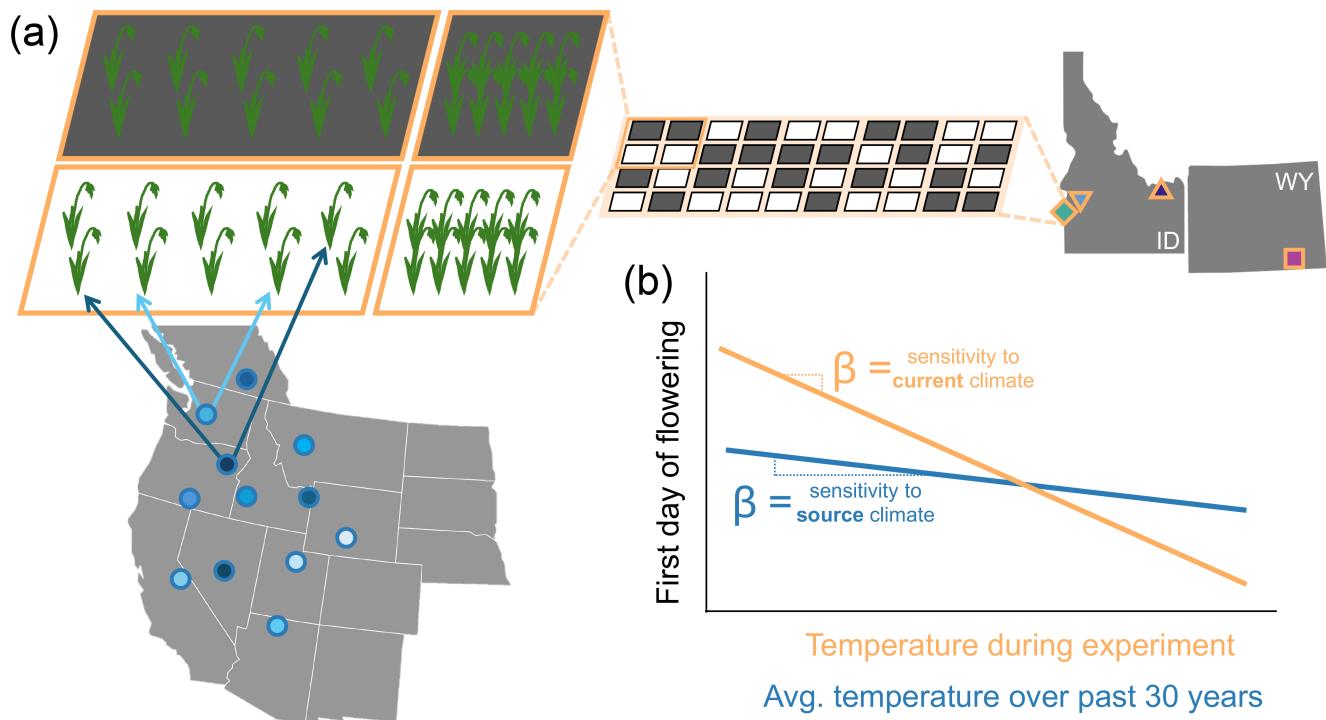


FIGURE 1 Simplified depiction of the replicated common garden experiment (a) and graphical representation of testing the roles of phenological sensitivities to current climate (orange) and source climate (blue) (b). (a) Genotypes of *Bromus tectorum* were collected across western North America and, after a generation in the greenhouse, were planted in a replicated common garden experiment. In each common garden, we manipulated soil surface temperature using two different colored gravel coverings (black = warmer, white = cooler) and intraspecific densities, factorially. The common garden experiment was replicated in four locations across Idaho (ID) and Wyoming (WY), USA that varied in their regional climatic conditions. (b) Hypothetical illustration of flowering phenology being more sensitive to current climate (i.e., evidence for plasticity) than to source climate (i.e., evidence for local adaptation).

allowed us to directly compare *B. tectorum* responses to current and source environments while controlling for differences in the range of temperatures observed in each type of environment.

While there is extensive literature on how flowering timing will shift under climate change (e.g., Badeck et al., 2004; Craufurd & Wheeler, 2009; Parmesan, 2006), our study offers a comprehensive and robust assessment of how plasticity and local adaptation can independently and interactively influence phenology. By conducting a replicated, multifactorial experiment we can directly assess environmental, genetic, and genotype-by-environment effects. Additionally, our study uses 92 *B. tectorum* genotypes collected across a broad geographical range, capturing much of the genetic variability in the species' invasive range (Gamba et al., 2024) as well as the variability in genotype-specific responses to environmental change (i.e., GxE effects). Finally, our use of genomic data allows us to more rigorously test whether observed flowering time clines suggest spatially varying selection.

METHODS

Study system

B. tectorum is an invasive annual grass, now dominant across many areas of western North America, that was introduced in the late 19th century and has been of ecological and economic concern for several decades (D'Antonio & Vitousek, 1992; Germino et al., 2016; Hulbert, 1955; Knapp, 1996; Mack, 1981). *B. tectorum* exhibits considerable phenotypic plasticity, allowing it to acclimate to short-term shifts in its environment, and substantial genetic and phenotypic variation both within and across its introduced populations (reviewed in Hufft & Zelikova, 2016; Leger et al., 2009; Rice & Mack, 1991a), despite primarily self-pollinating (Novak et al., 1991). Previous work on *B. tectorum* phenology suggests that flowering timing has a strong genetic component (Revolinski et al., 2023; Rice & Mack, 1991b), and also that flowering time can meaningfully shift in response to warming over the course of a year to a decade (Howell et al., 2020; Maxwell et al., 2023; Prevéy et al., 2024).

Common garden experiment

We conducted a replicated common garden experiment with *B. tectorum* genotypes across four sites: Sheep Station, ID ("SS"; 44.2456, -112.2144); Baltzor, ID ("BA"; 43.2085, -116.9952); Wildcat, ID ("WI"; 43.4744,

-116.9018); and Cheyenne, WY ("CH"; 41.2121, -104.8525) (Figures 1 and 2). We characterized these sites qualitatively by their average climate as follows: Sheep Station (SS) = Cold, aseasonal; Cheyenne (CH) = Cool, seasonal; Baltzor (BA) = Cool, aseasonal; and Wildcat (WI) = Hot, seasonal. We established the common garden experiment with 92 *B. tectorum* genotypes collected from across the western half of the United States and in British Columbia, Canada (Figures 1a and 2a,b). Seeds were collected from each source location in 2020 by harvesting the inflorescence of three mature *B. tectorum* individuals. Seeds from each individual were stored separately. Before initiating the common garden experiment, we grew seeds collected from the field in controlled greenhouse conditions at the University of Nevada, Reno in 2020 and Utah State University in 2021. This single generation seed bulking and selfing served to reduce the effect of maternal effects on measured traits in the common garden experiment (Roach & Wulff, 1987) and reduce the already low heterozygosity in cheatgrass genotypes. We considered seed produced from plants grown in the greenhouse that originated from a single field-collected plant as genotype replicates.

At each common garden site in fall 2021, we planted seeds 1 cm below the soil surface in a gridded design in two density treatments (low-density treatment = 100 seeds planted in a grid across a 1-m² area; high-density treatment = 100 seeds planted in a grid across a 0.04-m² area; Figure 1a) and under two temperature treatments (black gravel = higher soil surface temperature; white gravel = lower soil surface temperature; Figure 1a; Appendix S1: Table S1, Figure S2). We note that our study design follows that of Maxwell et al. (2023) closely, which was a pilot study that used similar gravel and seeding techniques to manipulate surface albedo and intraspecific density but was limited in replication and geographic scope and did not include multiple genotypes. The gravel treatments used here meaningfully alter soil surface temperatures in this system (refer to Boyd et al., 2017; Maxwell et al., 2023 for details) and in this experiment, resulted in a 2.1°C difference between treatments on average (range across common garden sites = [1.5–2.8°C]). To track individual seed planting locations, we glued each seed to a 6-inch-long toothpick using water soluble Elmer's glue, placing the lemma on the toothpick to allow for proper extension of leaves and roots (Leger et al., 2009). Within each common garden site, we replicated each density and gravel treatment combination 10 times using a randomized block design, for a total of 4000 plants in each common garden site, and 16,000 plants total (2 density treatments × 2 gravel treatments × 10 blocks × 100 plants × 4 common garden sites = 16,000 total plants; Figure 1a).

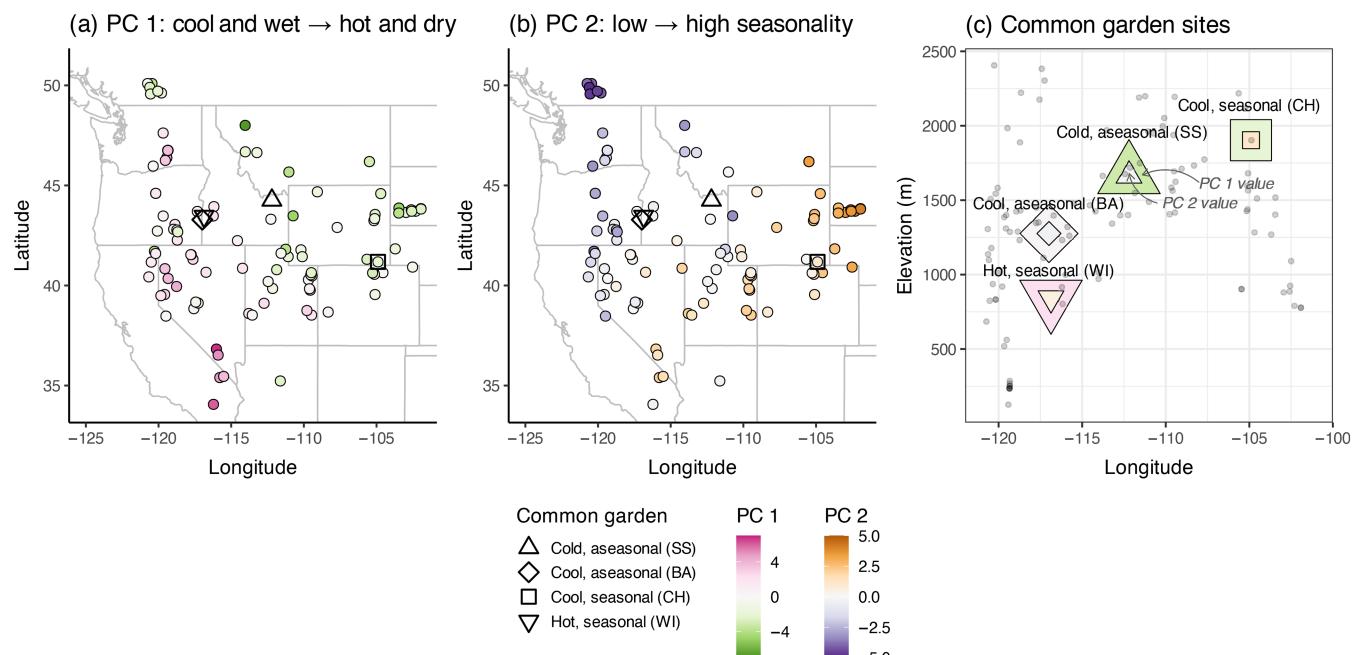


FIGURE 2 Climatic characterization of *Bromus tectorum* genotype source collection sites ($n = 92$) and common garden sites ($n = 4$). (a) Genotype source locations colored by their value along the principal component (PC) 1 climate axis, where high values of PC 1 = hot and dry, and low levels of PC 1 = cool and wet. Common garden sites are denoted as unfilled, larger shapes. (b) Genotype source locations colored by their value along the PC 2 climate axis, where high values of PC 2 = more pronounced temperature seasonality, and lower values of PC 2 = less pronounced seasonality. (c) Common garden sites classified by their longitude (x-axis), elevation (y-axis), value along the PC 1 axis (outer color) and PC 2 axis (inner color). Genotype source locations are overlaid as small gray points. BA, Baltzor; CH, Cheyenne; SS, Sheep Station; WI, Wildcat.

We collected individual plant emergence data in winter 2021 (starting dates: CH = November 10, SS = November 11, WI = December 7, BA = December 10) and collected data on individual plant growing stage starting in spring 2022 (starting dates: WI = February 24, CH = March 14, SS = March 28, BA = April 6). We aimed to conduct the phenology surveys on a biweekly basis, but the actual schedule varied across the growing season and sites due to site accessibility and personnel availability (Appendix S1: Figure S3). We recorded the following stages of *B. tectorum* phenology at each survey: V0 = single leaf visible but not fully developed, V1 = one fully developed leaf, V2 = two fully developed leaves, V3 = three fully developed leaves, V3+ = more than three fully developed leaves, BS = florets are visible in the sheath but are not fully developed, FG = florets have emerged and are green in color, FP = florets have emerged and are purple in color, FB = florets have emerged and are brown in color. We considered the date of first flowering to be the date for which a particular plant was first observed to be at least “florets green” (the FG stage). Across the phenology surveys, we also recorded herbivory, frost-heaving, and other disturbances that could affect plant growth and phenology measurements. Our analysis of flowering time includes only plants that

survived and flowered by the end of the growing season ($n = 7973$).

We recognize that several recent studies have used growing degree days rather than day of year as a metric for capturing phenological response because it more directly characterizes the biological mechanism of heat accumulation (e.g., Ensing & Eckert, 2019). However, we opted to use day of year as the response variable in our study because it affords us the ability to characterize phenology consistently across current and source environments, allowing a direct comparison of phenological sensitivities across short- and long-term shifts in climate (detailed below).

Characterizing source climate

To test for the role of source environment in regulating flowering time, we first characterized each genotype’s source climate using 19 bioclimatic variables derived from CHELSA 30-year (1981–2010) climate average data at ~1-km resolution (Karger et al., 2017). We conducted a principal components analysis in R (version 4.3.2; R Core Team, 2023) using the function *prcomp* with centered and scaled bioclimatic variables to reduce climate

variation into two main axes, where principal component (hereafter, “PC”) 1 represents a continuum from cool and wet climates to hot and dry climates (Figure 2a; Appendix S1: Table S2) and PC 2 represents a continuum from low- to high-temperature seasonality (Figure 2b; Appendix S1: Table S2). Together, these two axes explained 61% of the variation (PC 1 = 37.0%, PC 2 = 24.2%) in the 19 bioclimatic variables across our 92 genotype source climates.

Statistical analysis

We fit a linear mixed model with a Gaussian data distribution and identity-link to the first flowering date data using Bayesian inference in Stan (via *brms* version 2.19.0; Bürkner, 2017, 2018, 2021). In our linear mixed model, we included fixed effects of density treatment (categorical; two levels), gravel treatment (categorical; two levels), PC 1 value (continuous; centered and scaled), PC 2 value (continuous; centered and scaled), and common garden site (categorical; four levels). We included up to three-way interactions between density treatment, gravel treatment, and the PC 1 axis as well as interactions between density treatment, gravel treatment, and the PC 2 axis to assess if responses to the current environment depended upon the genotypes’ source environment. We included two-way interactions between common garden site and PC 1, as well as common garden site and PC 2 to address the same question.

To assess how genotype identity explains variation in flowering time, we included a random intercept of genotype in our model. We included random slopes for density treatment, gravel treatment, and common garden site across genotypes to assess the strength of genotype-by-environment interactions. Finally, we included random intercepts for plots (nested within sites and blocks) to account for exogenous variation related to experimental setting.

We fit the linear mixed model to the flowering time data with summed contrasts using a Hamiltonian Monte Carlo algorithm with three chains, each with 7500 burn-in iterations and 7500 sample iterations. Our posterior inference is based on the output from all three chains. We informed the regression and variance parameters with the default priors in the function “*brm*” (i.e., for all β : improper flat priors over all real numbers; for all σ : Student *t* [$df = 3$, $\mu = 0$, $\sigma = 17.8$]). We visually assessed the trace and density plots for each parameter and ensured that all potential scale reduction factors were less than 1.01, indicating convergence (Gelman & Rubin, 1992). We assessed model fit by plotting the posterior predictive distributions for each observation against its true observed value (Appendix S1: Figure S4a;

$R^2 = 0.748$), as well as conducting posterior predictive checks on the mean and SD of the observed data (Appendix S1: Figure S4b,c). We quantified the effect sizes of fixed-effect model terms using credible intervals and pseudo- R^2 values (where $R^2 = 1 - [\text{residual SS of the full model}/\text{total SS of a reduced model without the effect(s) of interest}]$). For each fixed effect (i.e., density, gravel, site, PC 1, and PC 2), we calculated the conditional pseudo- R^2 (accounting for random effects) both considering only the main effect, as well as considering the both the main effect and any interactions including that main effect. We calculated the pseudo- R^2 values as derived quantities from the posterior distribution, and for simplicity, report the mean of the derived quantity in text.

We structured the above linear mixed model with genotypes as random intercepts which allowed us to assess the long-term outcome of differences among source locations (i.e., source environments) and, with the inclusion of PC 1 and PC 2, to ask whether these differences among locations were related to a genetically based environmental cline. However, evidence of strong genotypic differences in phenology that can be explained by source environment (i.e., PC axes) cannot provide unequivocal evidence that the observed gradient is due to natural selection (Montague et al., 2008), because genetic drift and limited gene flow can cause geographic trait variation that may be spuriously associated with spatially autocorrelated environments. Therefore, in addition to testing for trait-environment relationships consistent with local adaptation, we fit the same model as described above with an additional covariance structure informed by a kinship matrix. The kinship matrix allows for genotypes to be correlated but does not introduce any additional parameters into the model, such that the effect α_g for each genotype g is drawn from a normal distribution following

$$\boldsymbol{\alpha} \sim N(\mathbf{0}, \sigma_{\text{gen}}^2 \mathbf{K}),$$

where $\boldsymbol{\alpha} = [\alpha_1, \alpha_2, \dots, \alpha_{n_g}]$, σ_{gen}^2 is between-genotype variance, and K is the kinship matrix. The kinship matrix was based on 266,504 genome-wide unlinked single-nucleotide-polymorphisms (genetic data in Gamba et al., 2024) and estimated with *PCAngsd* (version 0.99) using the “-kinship” option (Meisner & Albrechtsen, 2018). This software implements the PC-Relate method of Conomos et al. (2016), which estimates recent identity-by-descent relationships while accounting for population structure. We then created a positive definite transformation of this kinship matrix (92×92) to account for genetic relatedness (Jorjani et al., 2003; Thompson, 2013). If the effects of the source climate

clines are similar between the models with and without the kinship matrix, this would suggest that selection maintains the observed cline.

To provide a standardized comparison of the effects of current and source environments on flowering phenology, we calculated phenological sensitivities post hoc using predicted values from the linear mixed model for both common garden \times gravel treatment combinations and genotypes, respectively. To do this for the current climate (i.e., evidence supporting plasticity; Figure 1b, orange line), we regressed the average first flowering time predicted from the linear mixed model (without the kinship matrix) against maximum daily air temperature in all common garden and gravel treatment combinations from January through April 2022 (Appendix S1: Figure S2). We measured soil temperatures for gravel treatments at each common garden site at 0–5 cm depth every 15 min using EM50 dataloggers (Decagon, Pullman, WA) equipped with a temperature probe (model 5TM). We then estimated maximum air temperatures from measured soil temperatures using a temperature calibration derived from Petrie et al. (2020), such that $T_{\text{air}} = 0.916 \times T_{\text{soil}} + 8.838$. The slope of the regression between average maximum daily air temperature and predicted flowering day represents the phenological sensitivity to current climate. To calculate phenological sensitivity for the source climate (i.e., evidence for local adaptation via fixed traits; Figure 1b, blue line), we regressed the average first flowering time for each genotype as predicted from the linear mixed model against the average maximum daily temperature in January through April from a 30-year climate normal derived from PRISM climate data (4-km resolution; PRISM Climate Group, 2023), for which there are data that cover the timeframe of this experiment, unlike for the CHELSA climate data. The slope of this regression represents the phenological sensitivity to source climate.

We fit these two regressions within the same linear model and accounted for an interaction between type of climate (current vs. source) and maximum temperature to test for differences in phenological sensitivities. To account for variation in our predictions from the linear mixed model, we used weights in this linear model (using the “weights” argument in the R function *lm*), which were equal to the inverse variance of the estimate of predicted average flowering time from the linear mixed model for each genotype and site \times gravel combination. Our use of a simplified conversion of soil temperature to air temperature should likely not have a drastic effect on the inference from this analysis because we are interested in comparing sensitivities (i.e., slopes) rather than differences in absolute values between current and source

climates. However, to assess the sensitivity of our results to this assumption, we conducted a similar weighted regression comparing the phenological sensitivities using PRISM mean temperature data from the growing season (October 2021–June 2022) at each site, using only air temperatures and not converting from soil to air temperature ($n = 4$; current environment) and PRISM mean temperature data across a 30-year climate norm in growing season months for each genotype ($n_g = 92$; source environment).

RESULTS

Flowering phenology was strongly influenced by both the main effects of current and source environment of *B. tectorum* genotypes (Figure 3; Appendix S1: Tables S3 and S4). Across common garden sites, flowering time varied, on average, up to 25.0 days [95% credible interval: 23.3, 26.7], with plants at the hot, seasonal site flowering considerably earlier than those at the other sites (Figure 3a; Appendix S1: Figure S5; $\beta_{\text{site}W1} = -18.80$ [$-19.82, -17.79$], $R^2 = 0.65$). On average, *B. tectorum* plants in the high temperature, black gravel treatment flowered 10.3 days [9.1, 11.5] earlier than plants in the low temperature, white gravel treatment (Figure 3b; Appendix S1: Figure S5; $\beta_{\text{gravel}} = -5.14$ [$-5.74, -4.53$], $R^2 = 0.26$), and plants in the high-density treatment flowered 5.8 days earlier [4.6, 7.0] than plants in the low-density treatment (Figure 3b; Appendix S1: Figure S5; $\beta_{\text{density}} = -2.89$ [$-3.48, -2.31$], $R^2 = 0.10$). The effect of density treatment did not depend on gravel treatment (Appendix S1: Figure S5; $\beta_{\text{density:gravel}} = 0.36$ [$-0.22, 0.92$]).

Genotype source climate explained considerable variation in flowering time (Appendix S1: Table S4). Specifically, genotypes from hot and dry climates flowered earlier than those from cool and wet climates (Figure 3b; $\beta_{\text{PC1}} = -2.80$ [$-3.81, -1.77$], $R^2 = 0.10$), and genotypes from climates with greater temperature seasonality flowered earlier than those from climates with less temperature seasonality (Figure 3b; $\beta_{\text{PC2}} = -2.06$ [$-3.01, -1.08$], $R^2 = 0.06$). The effect of source climate on flowering time was similar when comparing the statistical models with and without a kinship matrix (Appendix S1: Table S4 vs. S5), which provides evidence that natural selection maintains the observed clines and that *B. tectorum* populations are locally adapted to their source climates.

We found some evidence of interactive effects between source and current environments on flowering phenology. For example, the marginal effect of density treatment varied across the PC 1 axis when plants were

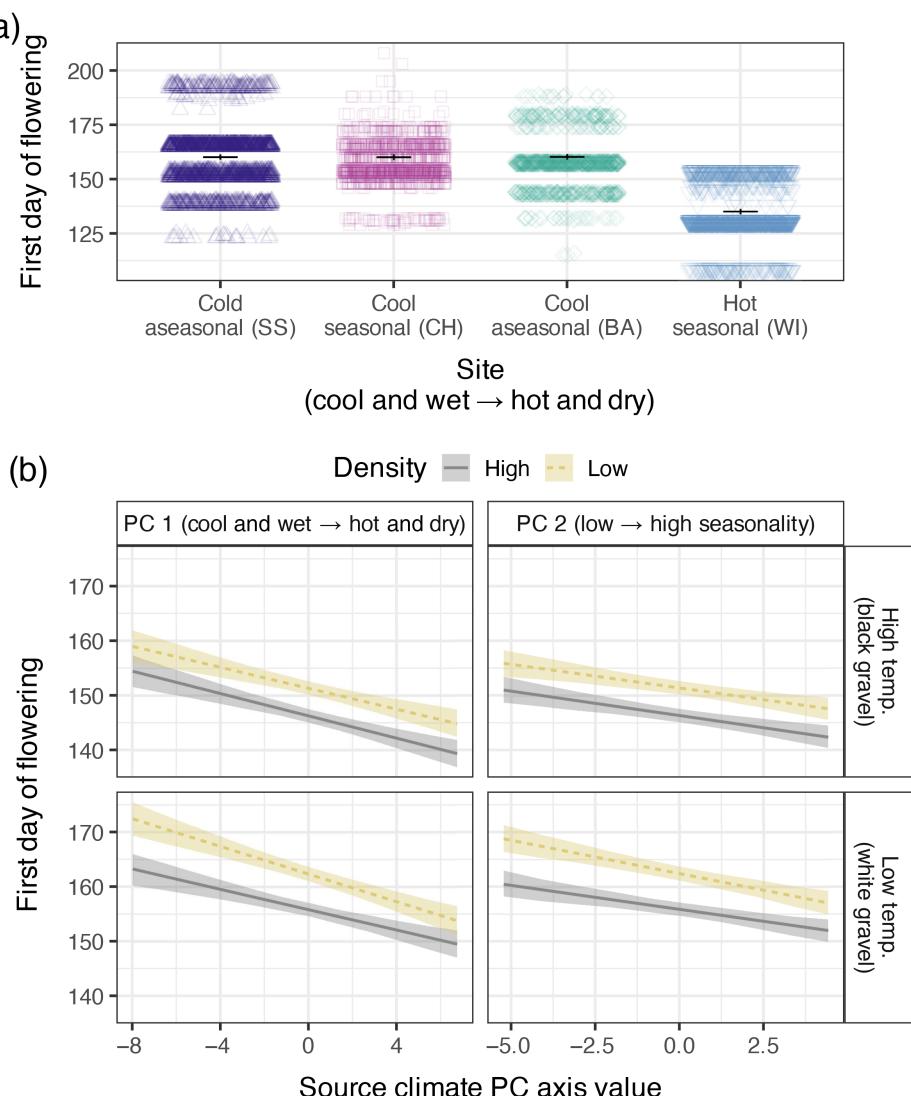


FIGURE 3 (a) Date of *Bromus tectorum* first flowering at each common garden site. Black horizontal lines with error bars represent model predicted means and 95% credible intervals, respectively. Colored points in background represent the raw data. (b) Date of first flowering for plants on high-temperature (black gravel) and low-temperature (white gravel) treatments (top and bottom panels), planted at low density (yellow) and high density (gray), across a gradient of source climate as represented by the first and second axes of a principal components (PC) analysis using climate averages for the genotypes used in the experiment (left and right panels). Predicted means averaged across other model terms are shown with the bolded lines and the shaded bands represent the 95% quantiles of the highest posterior density interval. The four common garden sites in Wyoming and Idaho, USA, were Baltzor (BA), Cheyenne (CH), Sheep Station (SS), and Wildcat (WI).

grown at lower temperatures (white gravel): the density effects were the weakest for genotypes from hot and dry climates. However, density effects did not vary with PC 1 for plants grown at high temperatures (black gravel) (Figure 3b; $\beta_{\text{density:gravel:PC1}}: -0.27 [-0.46, -0.07]$). Additionally, the strength of the PC 1 and PC 2 axes in explaining variation in flowering time varied by common garden site (Appendix S1: Figure S6), but the effect of these interactions was small compared with the additive effects of current climate and source climate (Appendix S1: Tables S3 and S4).

B. tectorum flowering time was conserved within genotypes (Figure 4; $\sigma_{\text{genotype}}: 4.64$ [95% credible interval: 3.98,

5.43]). The most extreme differences in flowering time across genotypes (averaged across sites) was 28.6 days [25.9, 31.2], with genotypes collected near the Mojave National Preserve, CA, flowering the earliest and genotypes collected near the south end of Okanagan Lake, BC, flowering the latest. Much of the genotypic variation in flowering time could be explained by genotypes' source climate (Figure 4; Appendix S1: Table S3). The effect of genotype identity on flowering time was not strongly mediated by common garden site, density treatment, and temperature treatment, suggesting weak genotype-by-environment interactions in flowering time (Figure 5). These results indicate that while current environment can affect the

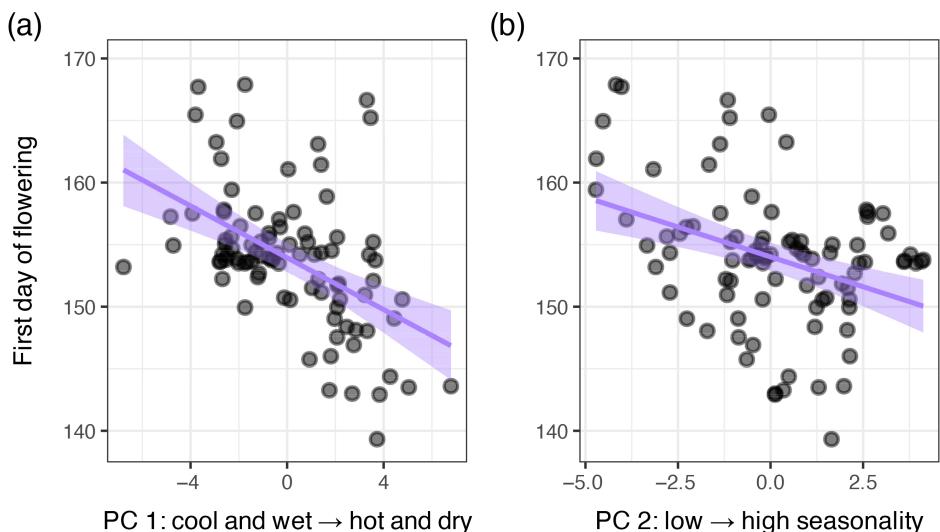


FIGURE 4 The effects of genotype and source climate on *Bromus tectorum* flowering time averaged across four common garden sites in Wyoming and Idaho, USA. Predicted average flowering times were earlier for (a) genotypes from hot and dry climates than for those from cool and wet climates, and for (b) genotypes from climates with more pronounced temperature seasonality than those from climates with less-pronounced seasonality. Points represent predicted average flowering time for each genotype ($n = 92$). Solid lines represent predicted means from the model and shaded regions represent 95% credible intervals. PC, principal component.

absolute day of flowering, the order of flowering among genotypes is best predicted by source climate and remains relatively constant across current environments (Figure 5; Spearman rank correlation coefficients for genotype order across environments: $\rho_{\text{gravel}} = 0.989$, $\rho_{\text{density}} = 0.997$, mean $\rho_{\text{site}} = 0.989$ [$\text{SD} = 0.01$]).

We calculated phenological sensitivities post hoc using model predictions and average maximum temperature values from the temperature (gravel) treatments in each common garden site, and source climate for each genotype. Across both source and current climates, flowering was consistently earlier as temperature increased, however flowering time was more sensitive to current climate (Figure 6; $\beta_{\text{env,current}} = -5.29$ [-6.32, -4.25]) compared with source climate (Figure 6; Appendix S1: Table S6; $\beta_{\text{env,source}} = -1.03$ [-1.39, -0.67]; $\beta_{\text{temp:env}} = 4.26$ [3.16, 5.36]). This finding was corroborated with a supplementary analysis comparing the phenological sensitivities of source and current climate using PRISM mean temperature data at the site level (Appendix S1: Figure S7; $\beta_{\text{temp:env}} = 5.84$ [2.95, 8.72]).

DISCUSSION

We found that flowering phenology in *B. tectorum* genotypes is sensitive to both abiotic and biotic short-term shifts in current environment and long-term shifts in source climate. Genetic and environmental cues combined additively (i.e., significant main effects) to

determine flowering time with a high degree of plasticity across genotypes: neither genotype-by-environment interactions nor interactions between current and source climate explained substantial variation in flowering time. These results suggest that predicting advances in cheatgrass phenology under climate change will require sufficient estimates of both short-term, plastic, and long-term, evolutionary responses, but not of complex interactions.

All our manipulations of the current environment—common garden site, gravel treatment, and density treatment—had significant, additive effects on flowering. Plants experiencing warmer temperatures across the growing season, either at the hot, seasonal site (Figure 3a) or in the high-temperature treatment (Figure 3b; Appendix S1: Figure S5) exhibited earlier flowering phenology. The magnitude of phenological responses to shifts in the current environment was impressive: flowering time differed across sites by almost a month and across temperature (gravel) treatments by over a week (Figure 3). This result agrees with those of other studies that found *B. tectorum* flowered earlier under experimentally manipulated, warmer conditions (Howell et al., 2020; Maxwell et al., 2023) and agree with a broader swath of literature that has shown this shift across other taxa (e.g., Anderson et al., 2012; Collins et al., 2024; Ehrlén & Valdés, 2020; Richardson et al., 2017; Wadgymar et al., 2018).

Our finding that plants in high-density plots flowered earlier than those in lower density plots is also consistent with previous studies that manipulated plant densities

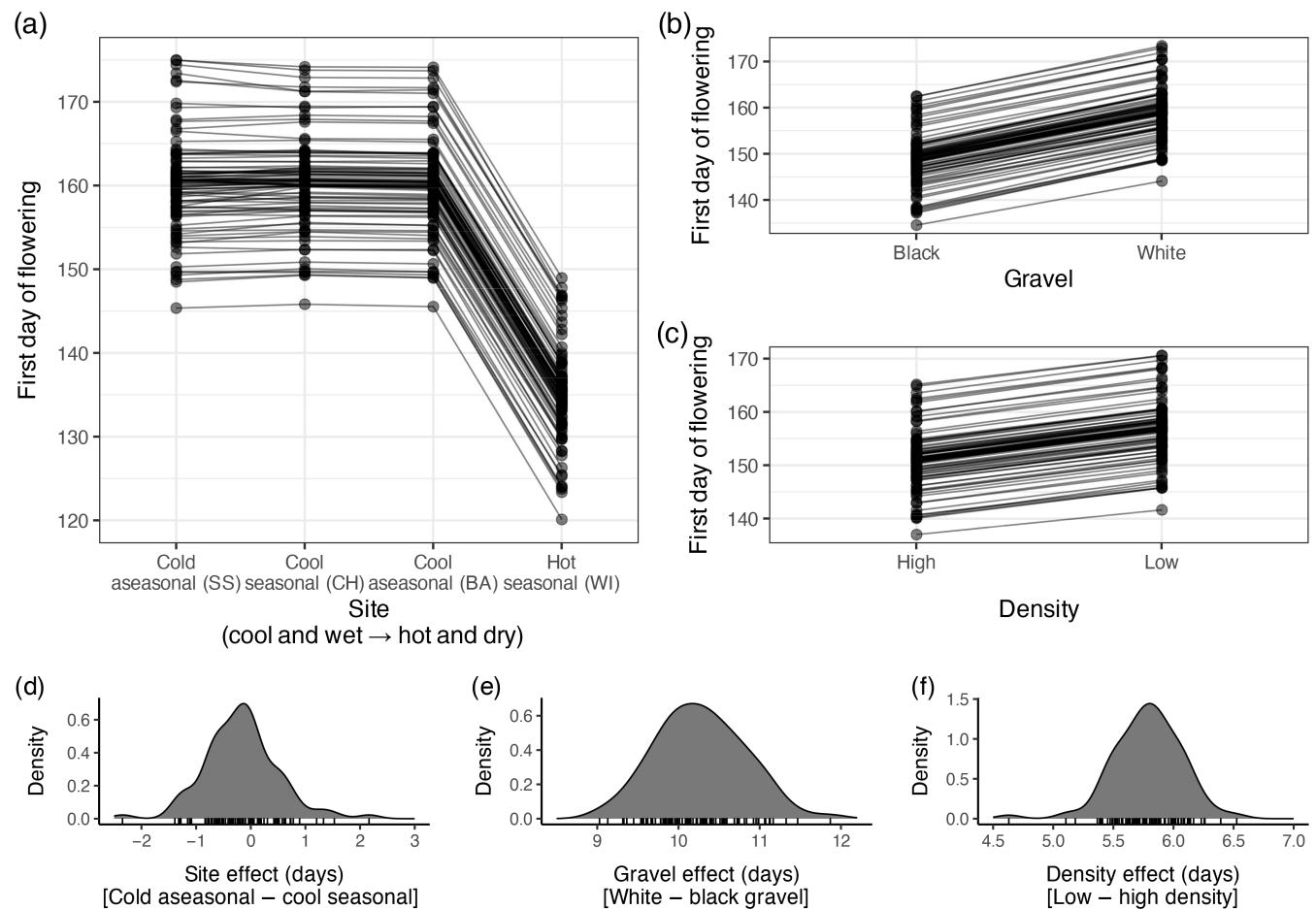


FIGURE 5 Predicted average flowering times for each *Bromus tectorum* genotype across (a) four common garden sites in Wyoming and Idaho, USA, (b) gravel treatments, and (c) density treatments. Each genotype is represented by points connected by a line. Note that the scales of the y-axes vary between plots (a) and (b), (c). Predicted differences in flowering time between (d) the cold aseasonal and cool seasonal sites (as an example of between-site comparison), (e) gravel treatments, and (f) density treatments across genotypes. Distributions in (d)–(f) characterize average genotype responses to current environment, where the vertical lines under each distribution (rug) depicts each genotype's predicted value.

experimentally (Lyons & Mully, 1992; Maxwell et al., 2023; Rice & Mack, 1991b; Schmitt et al., 1987; Willenborg et al., 2009). Several biologically relevant mechanisms have been proposed to explain why plants at higher densities flower earlier than those at lower densities. Competition for resources early in the growing season can expedite flowering (Willenborg et al., 2009) and slow juvenile growth at high densities can promote earlier flowering (Schmitt et al., 1987). High annual plant densities can also have indirect effects on phenology by changing surface soil temperature via mediating heat exchange and fluxes (Goldberg et al., 2001; Maxwell et al., 2023). However, there is a surprising paucity of recent literature investigating the importance of density on flowering time compared with climate warming, and only a few studies that manipulate these abiotic and biotic environments simultaneously (e.g., Taylor et al., 2019). While the effects of density in our experiment were modest compared with

temperature effects, they are still important to consider for predicting future shifts in phenology, especially given that cheatgrass can reach densities much higher than the high-density treatment in this experiment (Stewart & Hull, 1949; Young & Evans, 1978).

Consistent with other studies, we found that flowering time was under strong genetic control (Anderson et al., 2012; Revolinski et al., 2023; Rice & Mack, 1991a, 1991b; Vitasse et al., 2009), with *B. tectorum* genotypes varying in average flowering time up to nearly 1 month. Climate, as characterized by two PCs, explained much of the variation in the predicted mean flowering times for genotypes (Figure 4). Our results contribute to the growing evidence that *B. tectorum* genotypes in the invaded range exhibit genetically based climate clines (Gamba et al., 2024; Hufft & Zelikova, 2016; Leger et al., 2009) and, with the inclusion of a kinship matrix (Appendix S1: Table S5), substantiate this as a response to selection.

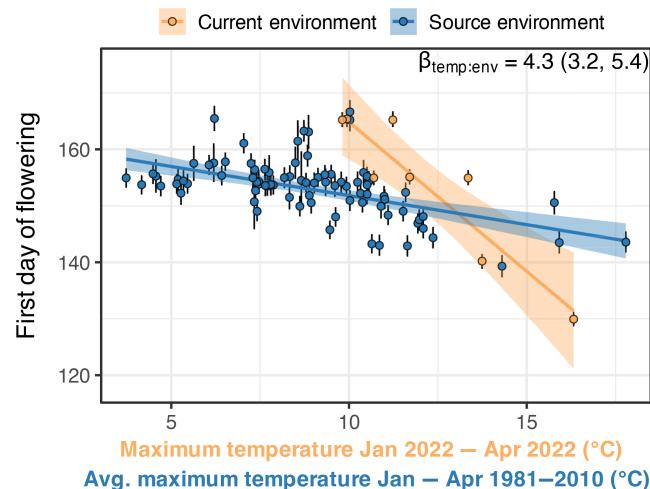


FIGURE 6 Predicted average first day of flowering for *Bromus tectorum* genotypes (“source environment”; blue points with 95% credible intervals) and current environments (orange points with 95% credible intervals) as a function of average maximum temperature from January through April across a 30-year climate norm ($n = 92$ genotypes) or from January–April 2022 ($n = 8$ common garden sites \times gravel treatments), respectively. Predicted mean flowering times as a function of maximum temperature for each environment type from a weighted regression are represented with lines and shaded 95% CIs.

We also found that local adaptation in response to temperature was in a direction consistent with phenological plasticity (Figure 6), a phenomenon referred to as co-gradient plasticity (Albecker et al., 2022; Eckhart et al., 2004; Ensing & Eckert, 2019; Vander Mijnsbrugge et al., 2016). Co-gradient plasticity is a critical mechanism by which plants can adapt to novel environments because colonizers can quickly adjust their phenotypes to match those of locally adapted residents (Ensing & Eckert, 2019). However, there is still not a consensus as to whether plant populations will exhibit co-gradient or countergradient plasticity (i.e., plasticity in response to temperature is in the opposite direction of local adaptation), as there is strong empirical support for both mechanisms across taxa (Ehrlén & Valdés, 2020; Ensing & Eckert, 2019; Toftegaard et al., 2016). For example, Toftegaard et al. (2016) found evidence of both co-gradient and counter-gradient plasticity among five *Brassicaceae* species in response to warming within the same experiment. Resolving what determines the direction of plasticity relative to local adaptation will be critical for making predictions of shifting phenology that span from short- to long-term timescales.

Despite evidence for strong plastic and evolutionary phenological responses, we found little evidence of genotype-by-environment interactions (Figure 5), indicating a similar degree of phenotypic plasticity among

genotypes. While this nearly complete lack of GxE interactions was somewhat surprising given previous work (Richardson et al., 2017), a similar lack of GxE response to experimentally manipulated temperature was recently found for a variety of traits including flowering timing in the alpine herb *Wahlenbergia ceracea* (Arnold et al., 2024). Variability in genotypes’ response to their current environment (i.e., genotype-by-environment interactions) serves as the material for which selection acts upon for the evolution of plasticity and is a precursor to adaptive plasticity (Josephs, 2018). Thus, this result has implications for the ability of plant populations to shift their plasticity under different climate regimes, as theory predicts that increased plasticity will evolve under increasingly variable environments (Chevin & Hoffmann, 2017).

While we did find some evidence for interactions between source and current environments (Figure 3b; Appendix S1: Figure S6), these interactions had considerably smaller effect sizes compared with the main effects. Nevertheless, these interactive effects may shed light on mechanisms. For example, the fact that the effect of density on flowering time in the lower temperature treatment depended on the PC 1 axis (Figure 3b) may indicate that the strength of intraspecific interactions depends on abiotic conditions (García-Cervigón et al., 2013). Specifically, plants from cool, wet environments were able to delay flowering under the current conditions in which this might be most advantageous (i.e., low density and lower temperature), but plants from hotter, drier environments displayed less plasticity in response to current conditions. Significant interactions between common garden location and both PC 1 and PC 2 suggest that the effect of source environment on phenology may depend on current environmental conditions (Appendix S1: Figure S6). Variation in the strength of genetically based clines has been shown for other invasive species, specifically that clines can weaken in the invasive range compared with the native range, allowing for high invader performance regardless of local environmental conditions (Endriss et al., 2018).

Our post hoc analysis showed strong phenological sensitivity of *B. tectorum* to source climate and an even stronger response to current climate (Figure 6). Other studies that compared plastic responses to current climate with evidence for adaptation to source climate in flowering phenology also found that both processes are important, but that plasticity was stronger (Arnold et al., 2024; Ensing & Eckert, 2019; Ramirez-Parada et al., 2024). In our study, a 1°C increase in mean maximum temperature over the growing season would immediately cause flowers to emerge 6 days earlier on average (Figure 6). Given sufficient time for long-term,

evolutionary processes to occur, this 1°C temperature increase would result in an additional 1 day earlier flowering time on average (responses to current + source environments = 7 days earlier; Figure 6). However, our estimates are based on relatively few common garden location × gravel treatment combinations ($n = 8$); further work is needed to improve this estimate for the *B. tectorum* system.

Both plastic and evolutionarily fixed responses to the environment likely contribute to the invasion success of *B. tectorum* (Dukes & Mooney, 1999) and we provide robust evidence across a diverse set of genotypes and environments to support this claim. We found that *B. tectorum* populations exhibit strong genetically based clines in its introduced range—a quick evolutionary response for a highly self-pollinating plant, as *B. tectorum* did not establish in western North America until at least the late 19th century (Mack, 1981). High plasticity in flowering time may help explain how cheatgrass has historically been able to thrive in temporally variable environments and can colonize in climatically heterogeneous, montane habitats (Bromberg et al., 2011; Smith et al., 2022). Strong shifts in flowering phenology in response to changes in soil surface temperature suggests that cheatgrass may be able to acclimate to future climate warming easily (Howell et al., 2020) and take advantage of an expansion of its phenological niche (Blumenthal et al., 2016). *B. tectorum*'s ability to shift flowering phenology suggests it will likely be adept at responding to increasing interannual fluctuations predicted under climate change (Salinger, 2005). Given evidence of co-gradient plasticity from our study, cheatgrass phenology may be shifting via plasticity in novel environments in ways that bring plants closer to the optimal, locally adapted phenotype (Ensing & Eckert, 2019), promoting its success. While flowering phenology does not fully capture *B. tectorum*'s invasion syndrome, advanced phenology is likely a critical mechanism by which *B. tectorum* outcompetes native vegetation (Blumenthal et al., 2016; Chambers et al., 2016; Howell et al., 2020). Work investigating the contributions of short- and long-term climate responses to *B. tectorum* fitness will be critical to testing this hypothesis and predicting the effect of climate change on the trajectory of the invasion.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Vahsen & Maxwell, 2024) are available in Zenodo at <https://doi.org/10.5281/zenodo.14417844>.

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