

Effects of precipitation change and neighboring plants on population dynamics of *Bromus tectorum*

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Abstract Shifting precipitation patterns resulting from global climate change will influence the success of invasive plant species. In the Front Range of Colorado, *Bromus tectorum* (cheatgrass) and other non-native winter annuals have invaded grassland communities and are becoming more abundant. As the global climate warms, more precipitation may fall as rain rather than snow in winter, and an increase in winter rain could benefit early-growing winter annuals, such as *B. tectorum*, to the detriment of native species. In this study we measured the effects of simulated changes in seasonal precipitation and presence of other plant species on population growth of *B. tectorum* in a grassland ecosystem near Boulder, Colorado, USA. We also performed elasticity analyses to identify life transitions that were most sensitive to precipitation differences. In both study years, population growth rates were highest for *B. tectorum* growing in treatments receiving supplemental winter precipitation and lowest for those receiving the summer drought treatment. Survival of seedlings to flowering and seed production contributed most to population growth in all treatments. Biomass of neighboring native plants was positively correlated with reduced population growth

rates of *B. tectorum*. However, exotic plant biomass had no effect on population growth rates. This study demonstrates how interacting effects of climate change and presence of native plants can influence the population growth of an invasive species. Overall, our results suggest that *B. tectorum* will become more invasive in grasslands if the seasonality of precipitation shifts towards wetter winters and allows *B. tectorum* to grow when competition from native species is low.

Keywords *Bromus tectorum* · Demography · Climate change · Invasive species · Semi-arid grassland

Introduction

Climate change is expected to shift the distribution of plant species (Walther et al. 2002; Parmesan and Yohe 2003). Invasive species, in particular, may have traits that will allow them to benefit from climate change (Dukes and Mooney 1999; Thuiller et al. 2007; Hellmann et al. 2008). Accurately predicting how invasion risk will change as the climate changes is important for effective management and restoration strategies (Dukes and Mooney 1999; Bradley et al. 2009). Additionally, climate change will affect entire communities, not single species living in isolation, and research needs to address how changes in climate will affect interactions between biotic elements in an ecosystem to understand how any one species will be affected (Suttle et al. 2007; Adler et al. 2012). In this study we sought to examine how precipitation change associated with climate change may impact the invasive grass *Bromus tectorum*, one of the most ubiquitous non-native species in the Intermountain West, using a unique combination of empirical studies and demographic analyses.

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Bromus tectorum has invaded a large portion of rangelands in the Intermountain West since its introduction to the USA from Eurasia in the late 1800s (Mack 1981). *Bromus tectorum* can impact ecosystems by preempting soil resources before native plants are active, reducing plant diversity, altering nutrient cycling, and altering fire frequencies (Melgoza et al. 1990; D'Antonio and Vitousek 1992; Concilio et al. 2013). The success of this invasive grass is partially attributed to its plastic growth responses to changing conditions (Mack and Pyke 1983; Griffith et al. 2014). While *B. tectorum* has historically been a very successful invader in areas with winter-wet climate regimes, it is not as widespread in areas with more spring and summer precipitation (Mack 1989). However, some evidence indicates that *B. tectorum* and other winter-active non-native species are becoming more common in areas along the Front Range of Colorado (Bromberg et al. 2011; Bush et al. 2007) that historically received the majority of annual precipitation in spring and summer.

Climate predictions differ on exactly how precipitation will change in the future (IPCC 2013), but there is general agreement that as temperatures warm, more precipitation will fall as rain rather than snow in the winter in the eastern foothills of the Rockies (Ray et al. 2008; IPCC 2013). There has already been an increase in the fraction of winter precipitation falling as rain rather than snow along the Front Range of Colorado from 1949 through to 2004 (Knowles et al. 2006). Bioclimatic envelope analyses and results from manipulative experiments suggest that *B. tectorum* may respond positively to increased winter precipitation (Bradley 2009; Concilio et al. 2013; Zelikova et al. 2013), so understanding how shifting precipitation patterns associated with climate change affect this species will be important for management considerations.

Other factors may influence the success of *B. tectorum* in the foothills of Colorado. Competition from resident species can affect resource availability and contribute to the invasion resistance of ecosystems (e.g., Tilman 1997; Naeem et al. 2000; Corbin and D'Antonio 2004). Competition from established species may limit the ability of new species to invade (Kennedy et al. 2002) or, alternatively, neighboring plant species may have no effect, or even facilitate the establishment of new species (Bulleri et al. 2008; Griffith 2010). The outcomes of interactions between species may also shift under a changing climate (Dormann 2007; Concilio et al. 2013). On the other hand, competing species may not capitalize on changing precipitation patterns, and allow for an increase in unused resources available for invasive species (Davis et al. 2000). Species whose niches overlap with *B. tectorum* may experience stronger interactions with *B. tectorum* and climate change than species with large niche differences (MacDougall et al. 2009; Adler et al. 2012).

This study combines population matrix models and measures of neighboring plant species to obtain a more informed picture of how *B. tectorum* will respond to changing climatic conditions and also to changes in competition resulting from climate change. Specifically, we used a demographic approach to examine how population growth and transitions to different life stages respond to changes in precipitation. At the start of the study, we hypothesized that *B. tectorum* would have higher rates of population growth in plots receiving supplemental winter precipitation and that *B. tectorum* would be less successful in plots with greater biomass of neighboring plants. Finally, we predicted that increased winter precipitation would increase the biomass of other winter-active exotic plants at our site.

Materials and methods

Field site

The field site is in a mixed-grass prairie located approximately 15 km northwest of Boulder, Colorado, USA (40°07'N, 105°18'W) at an elevation of 1798 m a.s.l. Average annual precipitation is 475 mm year⁻¹, and average annual temperature is 10.5 °C (WRCC 2014). The site has a continental climate, with most precipitation falling in spring and early summer. Soils at the field site are well drained, colluvial, sandy loams (USDA 2001). The site has been impacted by cattle grazing in the past and has now been substantially invaded by *Bromus tectorum*.

The plant community at the site is composed of a mix of winter-active exotic plant species and later-growing native plant species (Knochel 2009). The most common exotic species are *B. tectorum*, *Bromus japonicus*, *Poa compressa*, *Erodium cicutatum*, *Alyssum parviflorum*, and *Sisymbrium altissimum*. The most common native species are *Pascopyrum smithii*, *Sporobolus cryptandrus*, *Psoralidium tenuiflorum*, *Ambrosia artemisiifolia*, and *Erigeron flagellaris*.

Experimental design

In June 2010, we established a precipitation manipulation experiment at the site. Precipitation manipulations were based on information from global climate circulation models (GCMs) and preliminary climate analyses of historical data from climate stations along the Front Range of Colorado (Prevéy 2014). GCMs disagree on how precipitation will change along the Colorado Front Range (IPCC 2013), but most models show increases in winter precipitation, and some show decreases in summer precipitation (Weltzin et al. 2003; IPCC 2013). To address this uncertainty in precipitation change, we established five precipitation treatments based on IPCC climate model predictions: control,

winter-wet, winter-wet/summer-wet, winter-wet/summer-dry, and winter-dry/summer-wet. We allocated each treatment to ten 2×2 -m plots spread over an area of approximately 1 ha, for a total of 50 plots, from 01 June 2010 through to 30 September 2013. Treatments were randomly assigned to ten spatially aggregated blocks to account for heterogeneity across the site. To increase precipitation in the winter-wet and summer-wet precipitation treatments, we added water to plots during the periods October–March or June–September, respectively, using well water that is available at the study site. We added an amount of water to each plot that would increase total precipitation by approximately 50 % above ambient precipitation in either season. Water was added to plots slowly with a sprinkler once or twice per week in 1–2 cm precipitation events during either the summer or winter (summer-wet or winter-wet treatment, respectively). Our aim was to specifically test the effects of increased liquid precipitation that may be received in warmer years in the future. Thus, we only added water to plots on days that were above freezing. To decrease summer or winter precipitation in the summer and winter-dry treatments, we used passive deflection rain-out shelters that blocked 50 % of incoming precipitation, based on the design of Yahdjian and Sala (2002). These rain-out shelters were designed to have minimal effects on wind speed, temperature, or incoming light (Yahdjian and Sala 2002). For this study, we excluded the winter-wet/summer-wet treatments because *B. tectorum* senesces before we began with the summer precipitation additions, and abundance results for *B. tectorum* from the winter-wet/summer-wet treatment were similar to those from other winter-wet treatments (Prevéy and Seastedt 2014). The exact amount

of water added or withheld from each treatment is provided in Table 1.

Demographic measurements

We began demographic measurements of *B. tectorum* in November 2011, 1 year after initiation of the larger precipitation manipulation experiment. For this study, we first created one disturbed and seeded subplot within each of the ten plots in the four selected precipitation treatments. On 15 November 2011, half of each 2×2 -m plot was disturbed to remove surface vegetation. We then monitored the demography of *B. tectorum* in a 0.1-m^2 subplot centered within the disturbed section of each plot [Electronic Supplementary Material (ESM) Fig. A1]. We removed all vegetation and litter from these subplots to create similar conditions between different plots and to enable us only to examine competition of plants growing at the same time as *B. tectorum*. Removing litter and vegetation also allowed us to better observe the germination and survival of *B. tectorum* individuals that would be otherwise difficult to detect in thatch and litter layers. Fifty *B. tectorum* seeds were sown in each subplot. Prior to sowing, soil samples (volume 141.4 cm^3) were collected from the center of each subplot to a soil depth of 5 cm to estimate pre-existing seedbank size and seed viability. Soil samples were sieved to isolate *B. tectorum* seeds, and these seeds were counted and then placed between wet filter papers in petri dishes to test seed viability. The filter paper was kept moist over a 3-week period, and all seeds that germinated were counted and used to estimate the existing seedbank size in each plot. Every 2 weeks after sowing, from 25 November

Table 1 Precipitation and temperatures of the different treatment regimes over the study period (October 2011–August 2013)

Dates	Precipitation treatments				Average precipitation (mm) ^a	Temperature (°C) ^a
	Control (mm)	Winter-wet (mm)	Winter-wet/summer-dry (mm)	Winter-dry/summer-wet (mm)		
Winter 2011/2012 (Oct–Mar)	123.21	237.21	237.21	61.61	160.78	5.31
Spring 2012 (April–May)	74.93	74.93	37.47	74.93	142.49	14.03
Summer 2012 (June–Sept.)	168.25	168.25	84.13	277.00	171.70	22.25
Winter 2012/2013 (Oct–Mar)	134.10	209.10	209.10	67.05	160.78	4.09
Spring 2013 (April–May)	162.31	162.31	81.15	162.31	142.49	10.42
Summer 2013 (June–Aug)	59.39	59.39	41.20	139.39	133.35	21.91

^a ‘Average precipitation.’ is the long-term (1950–2000) average precipitation received in Boulder, CO, over the listed dates. Temperature and average precipitation data were obtained from the Boulder COOP weather station (WRCC 2014). Temperature values are average temperatures over the listed dates

2011 through to 19 June 2011, we recorded the germination and survival of all *B. tectorum* individuals growing in the subplots; each individual was classified as a new seedling (1–2 leaves, height <1 cm) or as a surviving seedling (≥ 3 leaves, height >1 cm, or formation of a basal rosette). On 20 June 2012, following the senescence of all *B. tectorum* in the subplots, we harvested all aboveground biomass in each subplot. The biomass of *B. tectorum* and all other plant species was sorted by species, then dried, and weighed. We also counted the number of seeds produced by each *B. tectorum* plant. Beginning in October 2012, we repeated the demographic censuses for another year. On 18 October 2012, we planted another 50 seeds in each subplot and monitored subplots every 2 weeks from 24 October 2012 through to 25 June 2013. In addition, to test seedbank viability, we placed 30 *B. tectorum* seeds in mesh bags and buried the mesh bags at a soil depth of 5 cm below each subplot on 18 October 2012 (ESM Fig. A1). The mesh bags were harvested in May 2013, after all germination had occurred. Seeds in mesh bags were classified as germinated or ungerminated. All ungerminated seeds were placed in petri dishes with moist filter paper for 3 weeks to test for viability. On 26 June 2013, we harvested all aboveground biomass in each subplot and counted seeds using the same methods described above for 2012.

In 2012 and 2013, we also recorded infection of *B. tectorum* with the fungal pathogen *Ustilago bullata* to examine whether pathogen infection impacted seed production and population growth (Prevéy and Seastedt 2015). *Ustilago bullata* systematically infects *B. tectorum* as a seedling and then entirely co-opts seed production of the plant, causing the grass to produce spores of the fungus instead of viable seeds (Alexopoulos et al. 1996). To quantify the effects of the pathogen, we harvested six *B. tectorum* individuals per plot in June 2012 and eight individuals per plot in June 2013 at evenly spaced marked locations along a transect running through the middle of each plot. Individuals were dried, weighed, and inspected for *U. bullata* infection, and all viable seeds produced per individual were counted.

Demographic analysis and model parameterization

To determine how precipitation treatments affected population growth and the importance of different life stages of *B. tectorum*, we used information from demographic censuses to create population matrix models. We utilized stage-classified matrix models with a projection interval of one season (Fig. 1) and established five life stages for *B. tectorum* (Fig. 1). Probabilities of transitioning between life stages (e.g., S_1 , G_3) were calculated using information from demographic censuses from fall 2011 to summer 2012, and from fall 2012 to summer 2013. Fecundity (F_1) was calculated using the average seed production of *B. tectorum* in each

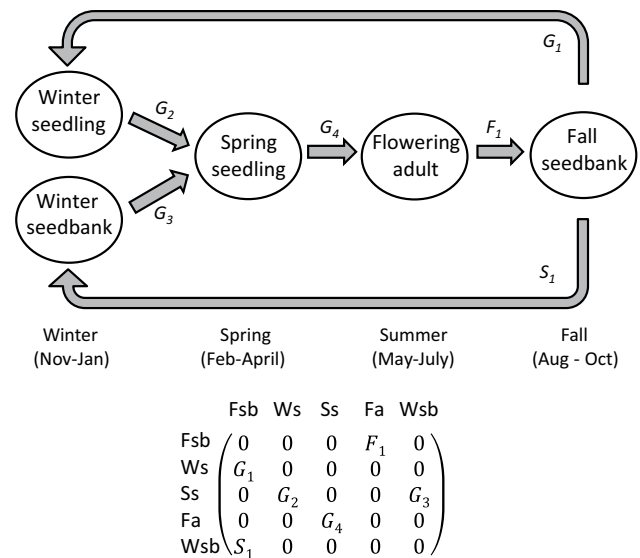


Fig. 1 Life cycles and stage-classified matrix population model for *Bromus tectorum*. The five stages in the model are winter seedbank (Wsb), fall seedbank (Fsb), winter seedlings (Ws), spring seedlings (Ss), and flowering adults (Fa). Arrows indicate transition between life stages (S_1 , G_1 – G_4 , F_1) with a probability of transition. The time scale for each transition is one season

plot. We decided not to include a seedbank that persisted for >1 year based on results from seed viability tests on the seeds in the mesh bags. There were no plots where we observed >5 % of seeds in the mesh bags that were ungerminated but were still viable after 1 year in the soil.

We calculated population growth rates separately for *B. tectorum* in each plot in each year as the dominant eigenvalues of the population matrix models (λ , Caswell 2001). To examine how important transitions from different life stages were to population growth, we also performed elasticity analyses on average matrices from each treatment. All analyses were conducted using the popbio package in R (Stubben and Milligan 2007).

Statistical analyses

We modeled the following response variables separately using linear mixed-effects models: population growth rate of *B. tectorum*, seed production, percentage cover of *B. tectorum* in undisturbed plots, aboveground biomass of *B. tectorum*, and over-winter survival of *B. tectorum*. For each response we examined the additive and interactive effects of year, precipitation manipulations, competitor biomass, and pathogen infection. Plot and block were considered to be random effects in the models. We used the “step” function in the lmerTest package in R (Kuznetsova et al. 2014) to drop predictor variables that did not account for significant variation in the response variable from the final model. Linear mixed-effects models were also used to examine

how precipitation treatments affected the biomass of native and exotic species growing in subplots. We analyzed the biomass of native and exotic plants separately because the two groups differ in their timing of active growth and therefore may be differentially affected by seasonal precipitation treatments, as well as differentially affect the population growth of *B. tectorum*. Percentage cover of *B. tectorum* and all aboveground biomass variables were square-root transformed before analysis to help meet assumptions of homogeneity of residuals. Significant differences between treatments and years at the $p < 0.05$ level were calculated from F statistics based on Satterthwaite's approximations of degrees of freedom for linear mixed-effects models (Kuznetsova et al. 2014). Data were analyzed using the lme4 package (Bates et al. 2011) and the lmerTest package (Kuznetsova et al. 2014) in the statistical program R (R Development Core Team 2012).

To examine possible competitive relationships in more detail, we used *B. tectorum* population growth rate as a response variable in a number of simple linear regressions. Predictor variables were: total neighbor biomass (native and exotic species), biomass of native species, and biomass of exotic species in each plot in 2012 and 2013. All biomass variables were square-root transformed before analysis. We used linear models to calculate R^2 and p values for correlations of all biomass variables in 2012, as well as of total and exotic competitor biomass in 2013. Square-root transformed native biomass in 2013 did not fit assumptions of normality, so we used a Spearman's rank correlation to calculate correlation coefficients and p values for the relationship between native biomass and population growth rates in 2013. The Spearman's rank correlation was performed using the Hmisc package in R (Harrell et al. 2012).

Results

Ambient precipitation received during spring over the 2 years of the experiment varied greatly. The spring of 2012 was very dry, whereas that of 2013 was wetter than average (Table 1). Results from linear-mixed models revealed that precipitation treatment, year, and biomass of adjacent native plants significantly affected the population growth rates of *B. tectorum* over the study period (Table 2; Fig. 2a). Total biomass of neighboring plants and abundance of the pathogen *U. bullata* did not influence population growth rates in either year (all $p > 0.44$). Population growth rates of *B. tectorum* were lower overall in 2012 than in 2013 and lowest in the winter-dry/summer-wet treatment in both years (Table 2; Fig. 2a).

Seed production of *B. tectorum* differed significantly between 2012 and 2013 (Table 2; Fig. 2b). Seed production was lowest in the winter-dry treatment in 2012, but highest

in the winter-dry treatment in 2013 ($p = 0.006$). Cover of *B. tectorum* was significantly lower in the winter-dry treatment than in winter-wet treatments in both years ($p = 0.0005$; Fig. 2c). Aboveground biomass of *B. tectorum* was lower in all treatments in 2012 than in 2013 ($p < 0.0001$).

Native plant biomass was highest in the winter-dry treatment in 2013 (Fig. 3a), and exotic plant biomass was highest in the winter-wet/summer-dry treatment in 2012, and higher overall in 2013 than in 2012 (Table 2; Fig. 3b). There were no significant correlations between total competitor biomass and population growth rates of *B. tectorum* in either 2012 or 2013 (all $R^2 < 0.09$, $p > 0.07$). However, there were negative correlations between native plant biomass and population growth rates of *B. tectorum* in both years (Fig. 3c, e). There was a positive correlation between exotic plant biomass and population growth rates in 2012 (Fig. 3d), but no significant correlation in 2013 (Fig. 3f).

In 2012, results of the elasticity analyses revealed that survival of spring seedlings to flowering and seed production contributed more to population growth than other transitions in all treatments (Fig. 4). In 2013, however, elasticities for the winter-dry treatment differed from those of the other treatments. In the winter-dry treatment, survival of spring seedlings to flowering and seed production were the most important contributors to population growth, similar to elasticities of all treatments in 2012. In the winter-wet and control treatments in 2013, the entire life history pathway for fall-emerging seedlings (germinating in fall, surviving over winter and spring, and producing seeds) contributed more to population growth rates than the life history pathway of seeds overwintering in the seedbank and germinating in the spring (Fig. 4).

Discussion

Changes in precipitation patterns resulting from climate change have the potential to impact population dynamics of invasive species. The results of this study show that increased winter precipitation benefitted population growth of *B. tectorum*, especially when the biomass of nearby native plants was low. Spring precipitation was also a large driver of differences in population growth rates, and population growth rates were higher for all treatments in 2013 after an unusually wet spring. Productivity, seed production, abundance, and overwinter survival all varied between treatments and years, demonstrating the sensitivity of *B. tectorum* to precipitation timing. The most important stages for population growth of *B. tectorum* were survival from seedling to flowering plant and seed production. Elasticity values also varied with precipitation treatments, showing that changes in precipitation can alter the most important life transitions for *B. tectorum*.

Table 2 Results of linear mixed-effects models of demographic measurements of *Bromus tectorum* and aboveground biomass of neighboring plants in response to precipitation treatments^a

Response variable	Predictor variable	Parameter estimate ^b	df	t	p (>t)	Variance ^c		
						Block	Plot	Residual
λ^d of <i>Bromus tectorum</i>	Intercept	1.46 ± 0.19	3, 27.3	7.50	<0.0001	0.07 ± 0.25	0.07 ± 0.28	0.11 ± 0.34
	Winter-wet/summer-dry	0.17 ± 0.17		1.01	0.30			
	Winter-wet	0.20 ± 0.17	3, 27.3	1.22	0.23			
	Winter-dry/summer-wet	-0.32 ± 0.17	3, 27.3	-1.95	0.06			
	Year	0.17 ± 0.14	1, 44.1	1.23	0.22			
	Native biomass	-0.21 ± 0.09	1, 67	-2.51	0.01			
	Year × native biomass	0.22 ± 0.08	1, 45.1	2.72	0.009			
Seed production	Intercept	5.23 ± 0.46		11.47	<0.0001	0.08 ± 0.28	0	1.1 ± 1.41
	Winter-wet/summer-dry	1.84 ± 0.63	3, 63	2.91	0.005			
	Winter-wet	0.03 ± 0.63	3, 63	0.04	0.97			
	Winter-dry/summer-wet	-1.78 ± 0.63	3, 63	-2.81	0.007			
	Year	1.67 ± 0.63	1, 63	2.66	0.01			
	Year × summer dry	-1.70 ± 0.89	3, 63	-1.90	0.06			
	Year × winter wet	-0.45 ± 0.89	3, 63	-0.50	0.62			
	Year × winter dry	2.54 ± 0.89	3, 63	2.85	0.006			
Cover of <i>B. tectorum</i>	Intercept	5.64 ± 0.68		8.36	<0.0001	2.03 ± 1.42	1.87 ± 1.37	1.32 ± 1.16
	Winter-wet/summer-dry	1.97 ± 0.71	3, 27	2.76	0.01			
	Winter-wet	0.82 ± 0.71	3, 27	1.16	0.26			
	Winter-dry/summer-wet	-2.84 ± 0.71	3, 27	-3.99	0.0005			
<i>B. tectorum</i> biomass	Intercept	0.27 ± 0.02		16.56	<0.0001	0.01 ± 0.02	0	0.01 ± 0.09
	Year	0.15 ± 0.02	1, 62.7	7.07	<0.0001			
Native plant biomass	Intercept	1.38 ± 0.24		5.75	0.0003	0.42 ± 0.65	0.45 ± 0.67	0.40 ± 0.64
Exotic plant biomass	Intercept	1.54 ± 0.24		6.37	<0.0001	0.06 ± 0.25	0	0.84 ± 0.92
	Winter-wet/summer-dry	0.61 ± 0.29	3, 66	2.11	0.04			
	Winter-wet	0.19 ± 0.29	3, 66	0.67	0.51			
	Winter-dry/summer-wet	-0.03 ± 0.29	3, 66	-0.10	0.92			
	Year	1.07 ± 0.20	1, 66	5.23	<0.0001			

^a Only predictor variables that accounted for significant variation in the response variables were included in final analyses. All treatment estimates are compared to the control treatment. *P* values and degrees of freedom (*df*) were calculated using the Satterthwaite approximation. All variables other than λ of *B. tectorum* were square-root transformed before analysis

^b Parameter estimate data are presented ± standard error (SE)

^c Variance data are presented ± standard deviation (SD)

^d λ , Eigenvalue of the respective population matrix model

Our results suggest that *B. tectorum* may become increasingly invasive in Colorado if the climate shifts to a more winter-wet regime. Consistent with our hypotheses, population growth increased in all treatments with increased winter precipitation. In 2012, winter drought led to decreasing population growth of *B. tectorum*, indicating that drier winters could decrease invasion success. However, in 2013, after an unusually wet spring, even *B. tectorum* in the winter-dry treatment had a high population growth rate, and population growth in all treatments was higher than those in 2012. These findings indicate that both winter and spring precipitation contribute to the success of *B. tectorum*. As such, they agree with those from

bioclimatic envelope models showing winter and spring precipitation to be strong predictors of *B. tectorum* dominance throughout the Intermountain West (Bradley 2009). Plasticity in the timing of growth allows cheatgrass to take advantage of either ample winter or spring precipitation (Harris 1967; Mack and Pyke 1983; Concilio et al. 2013), increasing its probability of success in variable climates.

At our field site, a seedbank does not seem to play a large role in population dynamics of *B. tectorum*. We found little evidence of a seedbank that lasts for >1 year. Studies in other invaded areas have found a similar lack of dormancy over multiple years in *B. tectorum* seeds (Hulbert 1955; Griffith 2010), although some studies have found

Fig. 2 Responses of *B. tectorum* to the four precipitation manipulations in 2012 and 2013. **a** Average population growth rates (λ), **b** numbers of seeds produced per individual, **c** percentage cover, **d** above-ground biomass per individual of *B. tectorum*. Bars Means of the untransformed data, whiskers standard error (SE). Bars with different lowercase letters are significantly different from each other at the $p < 0.05$ level. Significant differences were calculated from F statistics based on the Satterthwate’s approximations of degrees of freedom

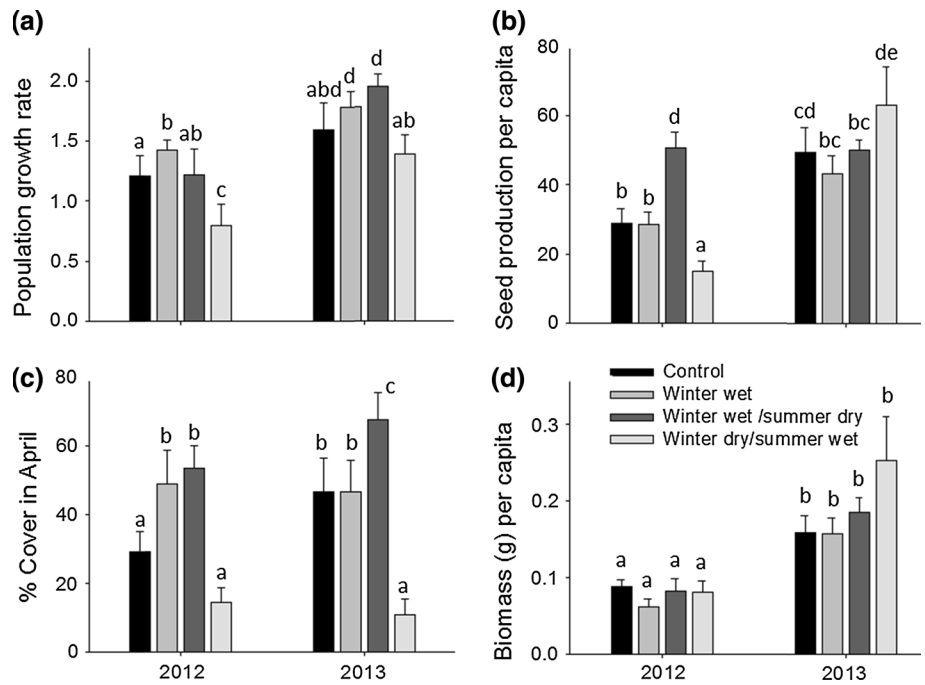
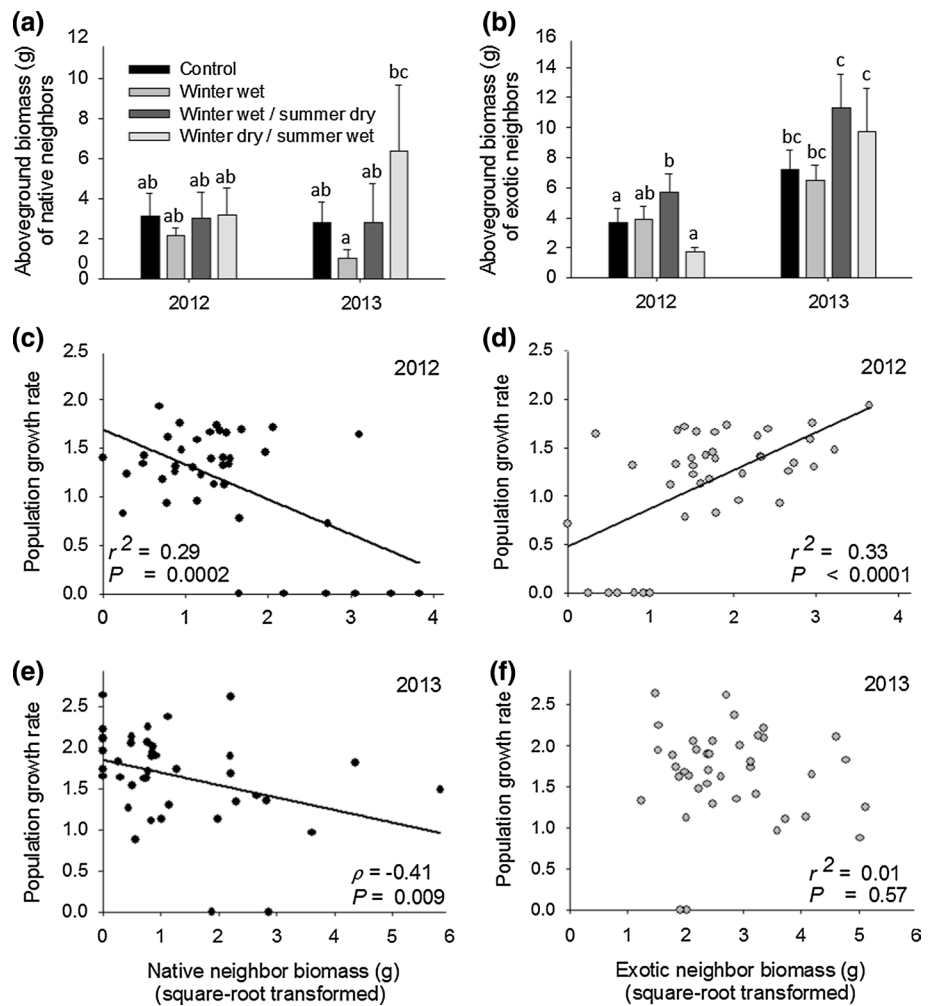


Fig. 3 Top row Responses of neighboring plant biomass to the four precipitation manipulations in 2012 and 2013. **a** Average aboveground biomass of native plants, **b** average aboveground biomass of exotic plants growing in subplots in each treatment in 2012 and 2013. Bars Means of the untransformed data, whiskers SE. Bars with different lowercase letters are significantly different from each other at the $p < 0.05$ level. Middle and bottom rows Correlations of aboveground biomass of square-root transformed native plant neighbors (**c, e**) and square-root transformed exotic plant neighbors (**d, f**) to population growth rates of *B. tectorum* in 2012 (**c, d**), and 2013 (**e, f**)



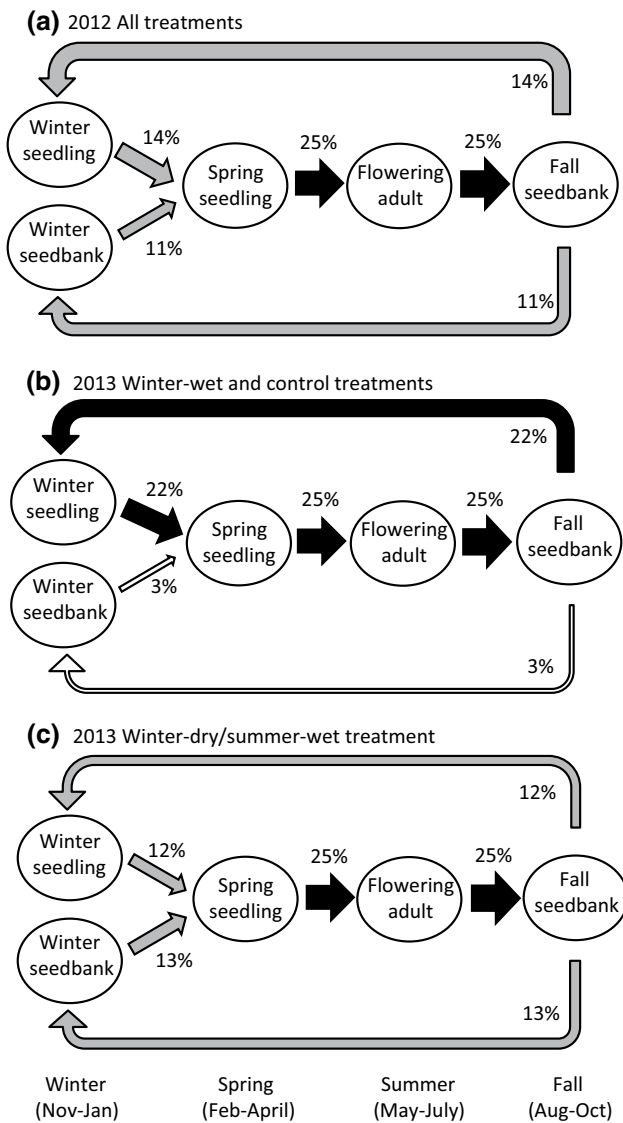


Fig. 4 Elasticities of population growth rates of *B. tectorum* in response to precipitation manipulations in 2012 and 2013. In 2012, all treatments had similar elasticities. In 2013, elasticities in the winter-dry/summer-wet treatment differed from those of the other treatments. Wider arrows with darker shading indicate transition probabilities that contribute most to population growth

viable seed that can last for ≥ 2 years in litter layers and maintain *B. tectorum* populations after years of low seed production (Young et al. 1969; Young and Evans 1975). Since we removed litter from the subplots where we measured germination, we were unable to measure the longevity of seeds suspended in litter at our field site. Evidence from a California grassland suggests that other non-native annual grasses do not form long-lived seedbanks (Faist et al. 2013). These results are promising for control measures in ecosystems invaded by exotic annual grasses. If *B. tectorum* populations decline over a few years with dry winters and springs, it may be possible to eradicate—or at

least significantly further reduce—this species from an area if management applications are timed accordingly (Prev y et al. 2014).

There was a negative correlation between native plant biomass and population growth rates of *B. tectorum*. While our study did not directly manipulate the competitive environment, this negative correlation agrees with findings from previous research. At local scales, other studies have found similar associations between native and exotic species (Tilman 1997; Naeem et al. 2000), and several studies show that established native vegetation has the ability to limit the growth of *B. tectorum* (Chambers et al. 2014; Ponzetti et al. 2007; Reisner et al. 2013; Leger et al. 2014). In 2013, native species biomass was lower in the winter-wet treatment than in the winter-dry treatment, indicating that increased winter precipitation may lead to a reduction in native plants, which could further facilitate invasion of *B. tectorum*.

Interestingly, exotic competitor biomass did not reduce the population growth of *B. tectorum*, even though the biomass of other exotic species was often greater than that of native species in subplots. In 2012, exotic plant biomass was correlated with greater population growth rates of *B. tectorum*. All exotic species at the field site are winter-active annuals or perennials, and most are growing during the same time period as *B. tectorum*, so one might assume there would be greater competitive pressure because the species are occupying similar temporal niches (Adler et al. 2012). However, many of the other exotic species are taprooted forbs that are possibly using resources from different depths in the soil than *B. tectorum*. The positive association of exotic species has been observed multiple times in more heavily invaded areas (Piemeisel 1951; Kulmatiski 2006), but mechanisms driving these positive associations between exotic species remain unclear. Communities composed entirely of exotic species may remain in this alternative state for long periods and prevent the re-establishment of more diverse native communities (Simberloff and Von Holle 1999; Kulmatiski 2006).

The survival of *B. tectorum* seedlings in spring to flowering plants and seed production were the two most important transitions contributing to the population growth of *B. tectorum* in both years. This is logical, as seed production of an annual plant without a substantial seedbank determines the number of individuals in the next generation (Watkinson et al. 1989). Other studies have shown that even when there is a low density of *B. tectorum* individuals, if those individuals produce a large quantity of seeds, then populations can remain viable (Hulbert 1955). In 2013, the overwinter survival of seedlings that germinated in fall of 2012 was also very important to population growth, but only in the control and winter-wet treatments. Elasticity values in the winter-dry treatment were higher for seeds remaining viable in the seedbank until spring and for spring germination. Fall

germination was low in the winter-dry treatment, with comparatively greater spring germination after a wet-up in the spring, making spring seedling germination a more important contributor to population growth after winter drought. Altering the timing of precipitation not only affected abundance and seed production of *B. tectorum*, it also changed the timing and relative importance of different life stages to population growth. Our elasticity analyses provide new information on how *B. tectorum* can adjust growth strategies to match the environment and further illustrate the ability of this species to alter its phenology to match climatic conditions (Beckstead et al. 1996). Management applications aimed to reduce spring seedling survival and seed production, such as spring grazing or burning, may be effective at reducing the population growth of *B. tectorum*.

This study has important implications for the management of disturbed or invaded ecosystems in a changing climate. Currently, climate and land use change are creating disturbances that can reduce competition from the resident community and increase the success of colonizing invasive plant species (Hobbs and Huenneke 1992; Dukes and Mooney 1999). Invasive species, such as *B. tectorum*, may be able to exploit changes in precipitation patterns that natives cannot. However, the findings of our study support the results of others showing that competition from native species is important and can deter invasion. Management actions that favor natives need to be considered along with management actions that directly reduce *B. tectorum* populations. Future invasibility of plant communities will not only be a function of changing climate, but also of levels of disturbance and the resilience of the existing plant community to climate change (Chambers et al. 2014; Reisner et al. 2013). Our research highlights the importance of considering the strong interactive effects that climate change and biotic change can have on the success of invasive species.

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Author contribution statement JSP and TRS conceived and designed the experiments. JSP performed the experiments, analyzed the data, and wrote the manuscript. TRS provided extensive editorial advice.

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