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Bromus tectorum Response to Fire Varies with Climate Conditions

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ABSTRACT

The invasive annual grass *Bromus tectorum* (cheatgrass) forms a positive feedback with fire in some areas of western North America's sagebrush biome by increasing fire frequency and size, which then increases *B. tectorum* abundance post-fire and dramatically alters ecosystem structure and processes. However, this positive response to fire is not consistent across the sagebrush steppe. Here, we ask whether different climate conditions across the sagebrush biome can explain *B. tectorum*'s variable response to fire. We found that climate variables differed significantly between 18 sites where *B. tectorum* does and does not respond positively to fire. A positive response was most likely in areas with higher annual temperatures and lower summer precipitation. We then chose a climatically intermediate site, with intact sage-brush vegetation, to evaluate whether a positive feedback had formed between *B. tectorum* and fire. A chronosequence of recent fires (1–15 years) at the site created a natural replicated experiment to assess abundance of *B. tectorum* and native plants. *B. tectorum* cover did not differ between burned and unburned plots but native grass cover was higher in recently burned plots. Therefore, we found no evidence for a positive feedback between *B. tectorum* and fire at the study site. Our results suggest that formation of a positive *B. tectorum*-fire feedback depends on climate; however, other drivers such as disturbance and native plant cover are likely to further influence local responses of *B. tectorum*. The dependence of *B. tectorum*'s response to fire on climate suggests that climate change may expand *B. tectorum*'s role as a transformative invasive species within the sage-brush biome.

INTRODUCTION

Invasive plant species can cause distinct and long-lasting changes to community structure and function (Levine and others 2003). A fundamental shift in ecosystem function can occur where invasive plant species alter fire regimes resulting in negative consequences for native communities (Brooks and others 2004). *Bromus tectorum* (cheatgrass), an invasive annual grass, is often cited as a quintessential example of a species that has ecosystem level impacts by altering the pre-invasion fire regime

in the western USA sagebrush biome (Pellant 1990; D'Antonio and Vitousek 1992; Brooks and others 2004; Mack 2011). *B. tectorum* senesces early in the summer and increases fine fuel load and continuity, which can lead to more frequent and larger fires (Whisenant 1990; Link and others 2006; Balch and others 2013). Many studies have found an increase in *B. tectorum* abundance, biomass or seed production following fire, particularly in the Great Basin and south-central Washington (West and Hassan 1985; Billings 1994; Chambers and others 2007; Davies and others 2009, 2012a), creating a positive feedback between fire and *B. tectorum*. This feedback has resulted in dense stands of *B. tectorum* in many areas of the western USA (Mack 2011). Some have suggested that fire in certain sagebrush steppe and grassland communities can result in a transition to an annual-dominated alternative state (Young and Evans 1973; Davies and others 2009, 2012a; Mack 2011). However, others have found that the response of *B. tectorum* to fire is ephemeral (Christensen 1964; Hosten and West 1994; West and Yorks 2002; Mata-Gonzalez and others 2007). Furthermore, in the eastern or northeastern part of the sagebrush biome (parts of Idaho, Wyoming and Montana) studies have found no response of *B. tectorum* to fire (Blaisdell 1953; Antos and others 1983; Humphrey 1984; Cook and others 1994; Seefeldt and McCoy 2003; Menke and Muir 2004). In addition, *B. tectorum* invasion or transitions to *B. tectorum*-dominated vegetation states can occur without fire (Bangert and Huntly 2010; Bagchi and others 2013).

Clearly ecosystem level impacts due to *B. tectorum* invasion after fire are strong in some regions, such as many parts of the Great Basin, but nonexistent in others. There are several alternative hypotheses to explain *B. tectorum*'s differential response to fire across its invaded range in the western USA. Prior disturbance, such as grazing or previous fires, has been suggested as a potential driver; however, grazing has been an inconsistent predictor of post-fire invasion (Seefeldt and McCoy 2003; Davies and others 2009, 2012a; Rew and Johnson 2010). Fire severity has also been implicated as a mechanism that can alter *B. tectorum* response to fire with higher *B. tectorum* abundance in more severely burned areas (Keeley and others 2003; Davies and others 2009). It has been shown that *B. tectorum* distribution depends on climatic variables (Bradley 2009; Bradley and Wilcove 2009) and it follows logically that its response to fire and tendency to form a positive feedback may be associated with climate, though this has yet to be formally tested. Biotic mechanisms are also suggested to be impor-

tant, as greater native vegetation cover is associated with lower *B. tectorum* invasion (Chambers and others 2007; Condon and others 2011). Thus, interactions between climate, native vegetation, and *B. tectorum* may modify the magnitude of *B. tectorum* post-fire abundance and subsequent impact. Understanding the importance and nature of how climate may affect this particularly detrimental invasion is critical as areas that currently do not experience high levels of *B. tectorum* invasion after fire may become more climatically suitable for *B. tectorum* invasion with climate change (Bradley 2009; Bradley and Wilcove 2009). In addition, fire activity in the West is predicted to increase with climate change (Westerling and others 2006). Therefore it is increasingly important to recognize the role that climate plays in the variable response to fire.

Although the differences in response of *B. tectorum* to fire at a local scale have been the focus of most studies (for example, Blank and others 2007; Chambers and others 2007; Shinneman and Baker 2009; Condon and others 2011), the mechanisms that may be driving differences in response to fire at the regional scale have not been addressed. Therefore, the first goal of this study was to determine if climate differences explain the variation seen in *B. tectorum* response to fire at the regional scale. A review of the literature yielded 18 study sites where the response of *B. tectorum* to fire was recorded. We expected that regional temperature and precipitation gradients would be associated with differences in *B. tectorum* response to fire.

The second goal of this study was to determine if a positive feedback between *B. tectorum* and fire existed at a site with little anthropogenic disturbance in southeastern Idaho [Idaho National Laboratory (INL)]. The climate at the INL is intermediate between the areas that do, and do not, experience a positive *B. tectorum* response to fire. The INL provided an ideal location for studying the response of *B. tectorum* to fire because a chronosequence of recent fires created a natural experiment. Recent studies of vegetation at the INL suggest that although *B. tectorum* is present throughout the site, it is not a large component of the overall vegetation (Brummer and others 2013; Lavin and others 2013). However, another recent study of a long-term data set at this site revealed that *B. tectorum* populations increased in the late 1980s and have remained at moderate densities since then (Bagchi and others 2013). Therefore, the INL represents a site that has been invaded by *B. tectorum*, with an intermediate climate that may or may not be conducive to formation of a positive

feedback with fire. Thus, we recorded *B. tectorum*, native perennial grass, and shrub abundance across the chronosequence of fires to determine if fire, independent of physical disturbance, could increase the degree of invasion at this site and facilitate an eventual transition to an annual-dominated state.

METHODS

Relationship Between Climate and Regional Patterns of *B. tectorum* Response to Fire

To examine our hypothesis that climate patterns may determine *B. tectorum* response to fire at a regional scale, we used empirical studies that examined *B. tectorum* abundance or biomass before and after a fire, or in paired burned and unburned plots in western USA sagebrush steppe and grass-dominated communities (see Appendix A in Supplementary Material for details). We found a total of 18 study sites, six of which recorded no response (short or long term) of *B. tectorum* to fire (Antos and others 1983; Humphrey 1984; Cook and others 1994; Seefeldt and McCoy 2003; Menke and Muir 2004; Davies and others 2012b) and 12 of which recorded increases in *B. tectorum* density, seed production, or biomass in burned plots (Pickford 1932; Christensen 1964; Young and Evans 1978; West and Hassan 1985; McArthur and others 1990; Whisenant 1990; Hunter 1991; Billings 1994; Chambers and others 2007; Davies and others 2009; Davies and others 2012a). Nineteen bioclimatic variables, monthly precipitation, monthly minimum temperatures, and monthly maximum temperatures from WorldClim 1.4 data layers (Hijmans and others 2005) were extracted for each study site using the coordinates reported in the respective study (or the best estimates given site descriptions).

We tested if climate variables previously found to be important for describing *B. tectorum* occurrence (Bradley 2009) were different between sites with and without a positive *B. tectorum* response to fire with Welch's two-sample *t* tests. These climate variables which included summer (June–September) precipitation, average annual precipitation, spring (April and May) precipitation, and winter (December–February) maximum temperature were derived from the monthly precipitation, minimum temperatures, and maximum temperatures extracted from WorldClim.

A principle coordinates (PCO) analysis of the 18 study sites was performed on standardized data that included the 19 bioclimatic variables, monthly

precipitation, monthly minimum temperatures, and monthly maximum temperatures, as well as elevation, longitude, and latitude. General linear models were then used to assess the strength and direction of the relationship between PCO axes 1 and 2 and each of the variables used to ordinate the 18 study sites. Individual variables, climate and otherwise, having the strongest relationship with PCO axes 1 and 2 were also evaluated for differences between sites with and without a positive *B. tectorum* response to fire with Welch's *t* tests. All statistical analyses (including those described below) were performed in the program R version 2.15.1 (R Development Core Team 2012). The PCO analysis was performed with labdsv (Roberts 2012) and vegan (Oksanen and others 2012).

Finally, we made a predictive map of *B. tectorum* response to fire under current and future climate scenarios at a regional extent and coarser grain. We used the five bioclimatic variables most correlated with PCO axis 1 (Table 1) from the 18 study sites as predictor variables and *B. tectorum* as the response in a logistic regression. Highly collinear variables were eliminated using analysis of variance inflation values (using a VIF = 3 cutoff value). Corrected Akaike's Information Criterion (AICc) was used to select the best model. The equation from the selected model was then used to create a predictive map displaying the probability of a positive *B. tectorum* response to fire under current and future climate conditions in the western USA. The current temperature scenario was obtained from the 2.5 min spatial resolution WorldClim data (Hijmans and others 2005). The future climate scenario represents downscaled IPPC₅ data extracted from the NASA GISS-E2-R general circulation model under the IPPC representative concentration pathway RCP4.5.

Upper Snake River Plain Study Site

Our site-specific observations were from the INL in southeastern Idaho, USA. The area is approximately 490 km² with an elevation range from 1,461 to 1,638 m and dominated by an *Artemisia tridentata* ssp. *wyomingensis* (Wyoming big sagebrush) steppe community. The 30-year average summer (July–September) precipitation is 4.3 cm, fall precipitation (October–December) is 5.19 cm, winter precipitation (January–March) is 4.49 cm, and spring precipitation (April–June) is 7.87 cm. Precipitation in the summer, fall, winter, and spring previous to sampling was 2.93, 8.53, 2.96, and 6.49 cm, respectively. The INL site is unique in that it has not been grazed by livestock since the

Table 1. Results from the General Linear Models Used to Assess the Strength and Direction of the Relationship Between PCO Axis 1 and Each of the Variables Used to Ordinate the 18 Study Sites

Variable	Coefficient	SE	P value	R ²
Annual mean temp.	0.21076	0.01549	<0.0001	0.91
Precip. of warmest quarter	−0.17011	0.02067	<0.0001	0.79
Max. temp. warmest month	0.181	0.02391	<0.0001	0.76
Mean temp. of coldest quarter	0.17158	0.02377	<0.0001	0.74
Mean temp. of warmest quarter	0.17288	0.02412	<0.0001	0.74
Precip. of driest month	−0.5914	0.09	<0.0001	0.7
Precip. of driest quarter	−0.1882	0.0292	<0.0001	0.69
Min. temp. of coldest month	0.1399	0.0276	<0.0001	0.58
Spring precip. (April–June)	−0.1329	0.03353	0.001	0.45
Mean temp. of driest quarter	0.0405	0.0112	0.00212	0.4

Results for the ten climate variables that were most correlated with PCO 1 are shown in declining order of importance. temp. Temperature, precip. precipitation, min. minimum, max. maximum.

1940s and access to the site is highly restricted, thus disturbance due to human land-use is relatively low. A study of *B. tectorum* occupancy at the site from 2009 through 2011 estimated that the species occupied 82% of sampled plots (Brummer and others 2013) but with low overall cover (for example, our plot subset had a mean *B. tectorum* cover of 3.95%; Anderson and Inouye (2001) found mean *B. tectorum* cover of 2.28% in 1995 at the site). Starting in 1994, a series of fires burned roughly half of the previously intact sagebrush communities creating a natural experiment. The ignitions were primarily of human origin. The average fine fuel load in unburned areas, as determined for 64, 0.25 m² random plots using the photoload sampling technique (Keane and Dickinson 2007), was 376.8 kg/ha and primarily consisted of standing dead herbaceous cover and small amounts of herbaceous and *Artemisia tridentata* litter.

Plant Species Abundance Data

The positive feedback between *B. tectorum* and fire depends on two steps: increased abundance of *B. tectorum* post-fire and increased frequency and size of fires, due largely to increases in fine fuel loads and continuity. *B. tectorum* cover was recorded in plots across a fire chronosequence to determine if abundance increased post-fire at the INL. Stratified random transects 10 m wide beginning at random points along roads and continuing for 2 km perpendicular to the road were delineated (described in more detail in Brummer and others 2013). The transects were stratified by five fire categories: twice burned (10–15 years and 1-year post-fire), 1-year post-fire, 3–4 years post-fire, 11–15 years post-fire, and not recorded as burned. Ten 100 m²

plots were selected at random distances along each transect for the purpose of this study. Within each plot the aerial percent cover of *B. tectorum*, aerial percent cover and identity of the four most dominant vascular plants (excluding *B. tectorum*), and percent cover of litter were recorded. All cover data were collected by the first author to ensure consistency across plots. Twenty-three transects were sampled for a total of 216 plots. Sampling took place in June 2011.

Data Analysis

Hurdle models (Carlevaro and others 2012) were used to predict response of three grass types (*B. tectorum*, native bunch grasses, and native rhizomatous grasses) to fire category due to the highly skewed distribution of the native grass cover data. Hurdle models first model the presence and absence of the species using logistic regression and then, where the species is present, model the logarithm of the percent cover of that species. Presence and absence were modeled as a function of time since fire divided into three categories: recently burned (1-year post-fire, 3–4 years post-fire, and burned twice), burned 11–15 years ago, and unburned. Three categories were used instead of all five because some of the smaller categories contained all presence points for each grass group and thus could not be modeled with logistic regression. Both cover and relative cover (percent cover of plant type of interest divided by total plant cover in the plot) were used as response variables to years since fire. Relative cover was analyzed in addition to cover because recently burned areas had lower overall vegetation cover. Therefore, analyzing only cover could miss changes in relative abundance of plant types. The only native rhizomatous grass

observed was *Agropyron dasystachyum*. Native bunch grasses were more diverse and included, in decreasing order of frequency: *Poa secunda*, *Elymus elymoides*, *Agropyron spicatum*, *Stipa comata*, *Oryzopsis hymenoides*, and *Elymus cinereus* (taxonomic nomenclature follows Cronquist and others (1977)). Shrub cover and relative cover was log transformed (+0.1% was added to all data) and modeled with a linear regression. A hurdle model was not used for shrub cover because all unburned plots contained shrubs and thus a logistic model was not appropriate. Native shrubs observed in decreasing order of frequency included: *Chrysothamnus viscidiflorus*, *A. tridentata*, *Ericameria nauseosa*, *Tetradymia canescens*, *Grayia spinosa*, *Krascheninnikovia lanata*, and *Tetradymia spinosa*. *B. tectorum* was present in 93%, native rhizomatous grasses in 33%, native bunch grasses in 73%, and shrubs in 76% of sampled plots.

To examine whether *B. tectorum* was associated with higher levels of litter cover, and thus contributed to the buildup of fine fuels, litter was modeled as a function of both *B. tectorum* and native plant cover. Due to the highly skewed distribution, a hurdle model was also used to model percent litter cover as a function of cover of the four vegetation types (*B. tectorum*, native bunch grasses, native rhizomatous grasses, and shrubs).

Multiple linear regression was used to determine if any correlations existed between *B. tectorum* and native vegetation. *B. tectorum* cover and relative cover (*B. tectorum* cover divided by total plant cover) were log transformed (+0.1% was added to all data) to achieve normality, and each response variable was analyzed with multiple linear regression with time since fire, aspect, native bunch grass cover, native rhizomatous grass cover and shrub cover as explanatory variables. Aspect was derived in ArcGIS from a 30 m DEM and was included in the model to account for differences in cover due to topographic position. A semivariogram was constructed for each model to test for residual spatial autocorrelation of the cover data and no significant autocorrelation was evident.

RESULTS

Relationship Between Regional Patterns of *B. tectorum* Response to Fire and Climate

We found significant differences in climate between study sites in which *B. tectorum* responded positively to fire and those in which it did not (Figures 1, 2). Sites where *B. tectorum* did not respond to fire had

on average 54.1 mm more summer precipitation (95% CI 17.4–90.7, $t = 3.4$, $df = 8.7$, $P = 0.009$), and mean maximum winter temperatures that were 15.4°C colder (95% CI –24.6 to –6.3, $t = -3.7$, $df = 11.1$, $P = 0.004$) than sites with a positive response (Figure 1). There was marginal support for higher spring precipitation in no response sites (95% CI 1.9–51.3, $t = 2.0$, $df = 13.9$, $P = 0.067$) but no significant difference in annual precipitation (95% CI –28.6 to 210.9, $t = 1.7$, $df = 10.3$, $P = 0.12$) between sites (Figure 1). Mean annual temperature, winter maximum temperature, and spring precipitation at the INL suggest that *B. tectorum* is unlikely to respond to fire, whereas the values for annual precipitation, summer precipitation, and mean maximum temperature of the warmest month at the site suggest that *B. tectorum* there could have a positive response to fire (Figure 1).

PCO analysis showed that climate factors did separate sites by *B. tectorum*'s response to fire along PCO axis 1 (Figure 2). PCO axis 1 explained 53% and PCO axis 2 explained 21% of the variation. Eight climate variables were highly correlated ($R^2 > 0.5$) with PCO axis 1 (Table 1). More temperature variables were highly correlated with PCO axis 1 than precipitation variables. The top two variables that were not tested above (mean annual temperature and maximum temperature of warmest month) are different between sites that do and do not have a positive *B. tectorum* response to fire (Mean annual temperature: 95% CI –5.6 to –2.2, $t = -5.0$, $df = 13.3$, $P = 0.0002$; Maximum temperature of warmest month: 95% CI –6.4 to –2.1, $t = -4.4$, $df = 9.8$, $P = 0.001$; Figure 1). The INL fell at an intermediate point along PCO axis 1 between sites that do and do not have a positive *B. tectorum* response to fire (Figure 2).

After identifying the climate variables that differed most between sites with alternative post-fire responses (Table 1) and then eliminating collinear variables, the best logistic model for *B. tectorum* response to fire included only mean annual temperature (Bio1) and precipitation of the warmest quarter (Bio18; Figure 3).

Response to Fire on the Upper Snake River Plain

B. tectorum Response to Fire

The incidence and cover of *B. tectorum* did not increase in burned areas of the INL (Figure 4A). The probability of occurrence of *B. tectorum* was not higher in recently burned plots (1-year post-fire, 3–4 years post-fire, and twice burned) than in

Figure 1. Boxplots showing the climate variables that best explain *B. tectorum* occurrence (A–D) and other important climate variables for explaining *B. tectorum* response to fire (E, F) at sites where there is no *B. tectorum* response to fire (none) and sites where there is a positive response to fire (positive). The values for the INL are marked on each plot with a dashed line. Climate variables shown include summer precipitation (precip) (A), annual precipitation (B), spring precipitation (C), winter maximum temperature (temp) (D), annual mean temperature (E), and maximum temperature in the warmest month (F). All temperatures are in degrees Celsius and precipitation is in millimeters. Climate data were extracted from WorldClim 1.4 data layers (Hijmans and others 2005).

unburned plots ($P = 0.26$; for detailed statistical results from all hurdle models see Appendix B in Supplementary Material). Indeed, in plots that burned 11–15 years prior to our observations, *B. tectorum* probability of occurrence (probability = 0.70) was an estimated 15% lower than in unburned sites (probability = 0.82, $P = 0.04$).

When present, cover of *B. tectorum* was not higher in 1-year post-fire plots ($P = 0.44$), in 11–15 years post-fire plots ($P = 0.89$) or in the twice burned plots ($P = 0.58$) compared to unburned plots (Figure 4A). In 3–4 years post-fire plots, the median *B. tectorum* cover was one-fifth of the median *B. tectorum* cover in unburned plots ($P = 0.002$;

Figure 2. Plot of PCO axes 1 and 2 from the PCO performed on Euclidean distances among the 18 study sites based on climate variables, elevation, longitude and latitude. Filled circles are study sites where there was a positive *B. tectorum* response to fire and hollow circles are sites where there was no *B. tectorum* response to fire. The INL site is marked with an asterisk.

Figure 4A). The results for relative cover (*B. tectorum* cover divided by total plant cover) were similar except that the relative *B. tectorum* cover in plots burned 1 year prior to sampling was higher than in unburned plots ($P = 0.009$; Figure 4B).

Bromus tectorum cover and relative cover were negatively correlated with native bunch grass cover after accounting for time since fire, aspect, shrub cover, and rhizomatous grass cover (cover: $\beta_{\text{bunch}} = -0.12$, $F_{1,207} = 18.36$, $P < 0.0001$; cover model $F_{8,207} = 6.14$, $P < 0.0001$, adjusted $R^2 = 0.16$; relative cover: $\beta_{\text{bunch}} = -0.030$, $F_{1,207} = 29.61$, $P < 0.0001$; relative cover model $F_{8,207} = 15.6$, $P < 0.0001$, adjusted $R^2 = 0.35$). *B. tectorum* cover and relative cover were also negatively correlated with rhizomatous grass cover after accounting for time since fire, aspect, shrub cover, and bunch grass cover ($\beta_{\text{rhizom}} = -0.047$, $F_{1,207} = 3.61$, $P = 0.059$ and $\beta_{\text{rhizom}} = -0.037$, $F_{1,207} = 45.18$, $P < 0.0001$, respectively). Finally, *B. tectorum* cover and relative cover were also negatively correlated with shrub cover after accounting for time since fire, aspect, and grass cover ($\beta_{\text{shrub}} = -0.060$, $F_{1,207} = 9.58$, $P = 0.002$ and $\beta_{\text{shrub}} = -0.073$, $F_{1,207} = 30.48$, $P < 0.0001$, respectively).

Native Bunch Grass Response to Fire

Native bunch grass cover showed the strongest response to fire between 3 and 15 years after burn-

ing. Native bunch grass probability of occurrence in plots burned 11–15 years prior to sampling (probability = 0.88) was an estimated 30% higher than in unburned plots (probability = 0.62; $P = 0.001$). There was no difference in native bunch grass probability of occurrence between unburned and recently burned plots (1-year post-fire, $P = 0.08$; 3–4 years post-fire, $P = 0.98$; burned twice, $P = 0.52$). However, where bunch grasses were present, their median cover was an estimated 4.2 times higher in 3–4 years post-fire plots and 1.7 times higher in 11–15 years post-fire plots than in unburned plots ($P < 0.0001$; $P = 0.009$, respectively). Where present, bunch grass cover did not differ between unburned plots and plots burned 1 year earlier ($P = 0.16$) or plots burned twice ($P = 0.09$).

Native bunch grasses had higher relative cover in all four time-since-burn categories than in the unburned plots (1 year, $P < 0.0001$; 3–4 years, $P < 0.0001$; 11–15 years, $P = 0.057$; burned twice, $P < 0.0001$; Figure 5A). However, the greatest difference between bunch grass relative cover in unburned and burned plots occurred 3–4 years after fire indicating a potential spike in native perennial bunch grasses 3–4 years post-fire until shrubs begin to dominate again 11–15 years post-fire (Figure 5C).

Native Rhizomatous Grass Response to Fire

Overall rhizomatous grass (*A. dasystachyum*) cover and occurrence were higher in recently burned areas (Figure 5B). The probability of occurrence of native rhizomatous grass in recently burned plots (probability = 0.48) was an estimated 22% higher than in unburned plots (probability = 0.37; $P = 0.03$) but did not differ between unburned plots and plots burned 11–15 years prior to sampling ($P = 0.14$). No rhizomatous grass was present in the 3–4 years post-fire plots.

Where rhizomatous grass was present, the median cover was an estimated 1.91 times higher in plots burned twice than in unburned plots ($P = 0.046$; Figure 5B), although no difference was detected between unburned plots and plots burned 1 or 11–15 years before sampling ($P = 0.09$ and $P = 0.61$, respectively). However, the median relative cover in plots burned both twice and 1 year prior to sampling was more than three times the median relative cover in unburned plots ($P < 0.0001$; Figure 5B).

Native Shrub Response to Fire

Time since fire was a significant predictor of shrub cover ($F_{4,211} = 67.975$, $P < 0.001$, adjusted

Figure 3. Map of the probability of a positive *B. tectorum* response to fire across the western USA under current (**A**) and future (**B**) climate scenarios. Probabilities are based on the best model (as determined by corrected AIC) of presence and absence of a positive *B. tectorum* response to fire estimated with logistic regression. The model contained average annual temperature (Bio1) and precipitation of the warmest quarter (Bio18) as predictors. The equation for the model of probability of a positive *B. tectorum* response to fire is as follows: $\text{Probability} = \exp(-14.41 + 3.47 \times \text{Bio1} - 0.14 \times \text{Bio18}) / (1 + \exp(-14.41 + 3.47 \times \text{Bio1} - 0.14 \times \text{Bio18}))$. Climate data were obtained from WorldClim at 2.5 minutes spatial resolution (Hijmans and others 2005). The future climate data represent downscaled IPCC₅ data from the NASA GISS-E2-R general circulation model under the IPCC representative concentration pathway RCP4.5. The *blue circles* represent study sites where no *B. tectorum* response to fire was observed and the *red crosses* represent study sites where a positive *B. tectorum* response to fire was recorded. Lowest probabilities are represented with *white*, graduating through *gray* to *black*, the highest probability.

Figure 4. *B. tectorum* cover (**A**) and relative cover (**B**) for each fire category. Cover was estimated in plots where *B. tectorum* was present (that is, no plots scored for zero were included so that the figure matches the results from the second part of the hurdle models). Plots burned twice were burned both 1-year ago and 11–15 years ago.

$R^2 = 0.55$) and relative cover ($F_{4,211} = 40.82$, $P < 0.001$, adjusted $R^2 = 0.45$). Shrub cover and relative cover were both significantly lower in recently burned than in unburned plots ($P < 0.0001$ to $P = 0.0064$ for all pairwise comparisons; Figure 5C; Appendix B in Supplementary Material). However, there was no difference in shrub cover or relative cover between plots burned between 11 and 15 years prior to sampling and unburned plots ($P = 0.20$ and $P = 0.24$, respectively). In plots burned between 1 and 4 years prior to sampling, the median shrub cover and relative shrub cover were only an estimated 0.5–11% (for all pairwise comparisons) of the median shrub cover and relative shrub cover in unburned plots. *C. viscidiflorus* was the most frequent shrub found in recently burned areas due to its ability to resprout post-fire.

Relationship Between Litter and Vegetation Type on the Upper Snake River Plain

Cover of the different vegetation types was a significant predictor of litter cover ($F_{4,211} = 25.63$, $P < 0.001$, adjusted $R^2 = 0.31$). Litter percent cover was positively correlated with shrub cover ($\beta = 0.16$, $F_{1,211} = 81.38$, $P < 0.0001$) and bunch grass cover ($\beta = 0.13$, $F_{1,211} = 17.48$, $P < 0.0001$) after accounting for the other vegetation types. There was no significant relationship between litter

Figure 5. Relative native bunch grass (**A**), relative native rhizomatous grass (**B**), and relative shrub (**C**) cover for each fire category. Cover was estimated in plots where that growth form was present (that is, no plots scored for zero were included so that the figures match the results from the second part of the hurdle models). Plots burned twice were burned both 1-year ago and 11–15 years ago.

cover and native rhizomatous grass cover ($F_{1,211} = 0.00$, $P = 0.99$) or *B. tectorum* cover ($F_{1,211} = 3.07$, $P = 0.08$) after accounting for the other vegetation types.

DISCUSSION

Factors Affecting Regional Differences in the *B. tectorum* Fire-Feedback

Our first objective was to evaluate if climate was associated with a positive feedback between *B. tectorum* and fire as observed in the sagebrush biome of western USA. We found that climate variables are important predictors of where, geographically, *B. tectorum* may have a positive response to fire and therefore could initiate a positive feedback. This result is not unexpected given that climate has been found to be an important factor in *B. tectorum* establishment and distribution regionally (Bradford and Lauenroth 2006; Bradley 2009). We found that several of the climatic predictors of *B. tectorum* distribution (Bradley 2009) are also important in predicting its response to fire. However, temperature seems to play a more important role in predicting response to fire than it does in predicting distribution. The winter annual life history strategy

allows *B. tectorum* to take advantage of late fall and early spring moisture when other plants (for example, native grasses and forbs) are dormant. *B. tectorum* roots can grow until temperatures drop below 3°C, whereas the roots of many wheatgrasses cannot grow below 7–8°C (Upadhyaya and others 1986). Therefore, the time period over which *B. tectorum* could be growing, may be longer than for other plants where winter temperatures are warmer.

Precipitation in the summer was found to be important for predicting both *B. tectorum* response to fire (this study) and *B. tectorum* distribution (Bradley 2009). *B. tectorum* is more successful in areas with lower summer precipitation. Lower summer precipitation could either favor *B. tectorum* by decreasing the competitiveness of native perennials or by increasing fire frequency (Bradley 2009). Our study suggests that even after fire *B. tectorum* will not increase in abundance in areas with certain climates, potentially because competitiveness of native perennials may be higher than *B. tectorum* in these areas. Higher spring and summer precipitation would negate the benefit of a winter annual life history because water is readily available throughout the growing season, not just in the early spring when *B. tectorum* is photosynthesizing and growing before other species. *B. tectorum* may be more competitive in areas with less precipitation because its morphology, featuring a highly branched diffuse, shallow root system, takes advantage of small amounts of rain, where more deeply rooted perennial bunchgrasses cannot (Upadhyaya and others 1986). Fire may only accelerate the transition to an annual-dominated state in areas that are climatically favorable to *B. tectorum*'s life history strategy, suggesting that climate rather than fire may be the primary factor mediating *B. tectorum* impact regionally.

In the future, if climate change causes a reduction in spring or summer precipitation and an increase in temperatures, *B. tectorum* could have a positive response to fire in areas of the sagebrush biome where it currently does not respond. Bradley's (2009) bioclimatic envelope model suggested that the border between Idaho and Montana, as well as sections of Wyoming, is most likely to experience increases in *B. tectorum* climate suitability under multiple climate scenarios. If a fundamental shift in climate patterns occurs that asymmetrically favors winter annuals, *B. tectorum* is likely to become more dominant and fire is likely to exacerbate the rate of ecosystem structural and functional changes under new climate conditions (Figure 3).

B. tectorum Response to Fire at a Climatically Intermediate Site

The second objective of this study was to use a natural fire chronosequence to determine whether fire, in the absence of strong physical disturbance, leads to increased *B. tectorum* abundance. The results from our climate analysis suggested that the INL was intermediate in climate to areas where *B. tectorum* did and did not increase post-fire. We examined *B. tectorum* cover across a 15-year post-fire chronosequence and found no evidence that *B. tectorum* had increased in response to fire in this native-dominated sagebrush steppe plant community.

Fire in combination with *B. tectorum* is reported to cause an ecosystem transition in some cases (Billings 1994; Mack 2011), an assertion derived from studies in the Great Basin rather than throughout the sagebrush biome. Our results, in the northeast region of the biome, suggest that *B. tectorum*'s response to fire can be very ephemeral, and much less pronounced than the response of native perennial bunch and rhizomatous grasses. Native rhizomatous grass exhibited the largest difference in relative abundance between burned and unburned areas 1 year after fire, although bunchgrasses also had significantly higher relative abundances in recently burned plots than unburned plots, likely due to the release from competition with shrubs. *B. tectorum* had the least difference in relative abundance between burned and unburned plots. These results suggest that fire did not cause a transition to an alternate annual-dominated state. Instead, native perennial grasses responded more positively to fire than *B. tectorum*. Furthermore, increased fire frequency did not necessarily result in *B. tectorum* invasion, as evidenced by the lack of difference in *B. tectorum* abundance between unburned and twice burned plots.

If a positive feedback between *B. tectorum* and fire was to form, we would expect that *B. tectorum* would produce most of the litter (and thus fine fuel) in an area. However, at the INL there was no significant relationship between *B. tectorum* cover and litter cover, suggesting that *B. tectorum* was likely not responsible for the majority of the litter at the INL site. In fact, fine fuel loads at the INL were half that of the fuel loads where a positive feedback response of *B. tectorum* to fire was found (Davies and others 2009). Both native shrub and bunch grass cover were significantly positively correlated with litter cover and thus likely more responsible for the buildup of litter fuels than *B. tectorum*. *B. tectorum* made up only a small percent of the plant

cover (3.95 and 1% mean and median of abundance plots, respectively) and thus was not present in high enough abundance to have a major impact on fine fuel loads or continuity. These results suggest no positive feedback between fire and *B. tectorum* at the INL.

Factors Driving the Response of *B. tectorum* to Fire Throughout the Sagebrush Biome

Our climate meta-analysis suggested that climate has a significant effect on *B. tectorum*'s response to fire. Other factors that have also been hypothesized to effect *B. tectorum*'s fire response include pre-fire disturbance history and fire severity.

The INL study site has low physical disturbance (for example, grazing, anthropogenic activities) and the site has had approximately 70 years to recover from livestock grazing (Anderson and Inouye 2001; Lavin and others 2013). The sagebrush community is relatively intact and presumably native plant propagules are abundant. In contrast, many sagebrush communities in the Great Basin, including southern Idaho, have a long and continuous history of intense grazing or cropping. We found a negative relationship between native plant cover and *B. tectorum* cover, suggesting that lower levels of invasion were associated with higher native plant cover. A long-term study at the same site also found a negative correlation between abundance of nonnative species and native plant cover (Anderson and Inouye 2001), which agrees with the finding of a negative relationship of nonnative species diversity and native species diversity in unburned sagebrush steppe of the INL (Lavin and others 2013). Other sites with intact sagebrush, high perennial native cover, or less physical disturbance have also been found to be more resistant to *B. tectorum* and invasion of exotic species (Daubenmire 1942; Seefeldt and McCoy 2003; Chambers and others 2007; Prevy and others 2010; Condon and others 2011; Davies and others 2012a).

Although previous disturbances may reduce the resilience of the system to perturbations such as fire, areas that were burned twice (high-frequency disturbance) at the INL site did not show an increase in *B. tectorum* abundance post-fire. Physical disturbance versus fire can have different effects on plant communities (Lavin and others 2013). However, a stronger positive post-fire response of *B. tectorum* has been found on sites not grazed by domestic livestock than on grazed sites, which was attributed to buildup of fine fuels (Davies and

others 2009). Thus, prior physical disturbance, including grazing, is not always the single factor driving post-fire *B. tectorum* invasion, suggesting other interacting factors may be important.

Variability in fire severity between sites may also explain the inconsistent development of a positive *B. tectorum*-fire feedback. More severe fires may result in a more rapid invasion of *B. tectorum* due to increased mortality of native grasses (Davies and others 2009) and may explain the contrasting responses between our results and those of Davies and others (2009) who found a positive response in ungrazed sagebrush steppe. We found no increase in *B. tectorum* relative cover in the twice burned areas relative to unburned areas but did find a slight, transient increase in *B. tectorum* in the more severely burned 1-year post-fire plots, suggesting that fire severity may have an effect. However, that effect was smaller in magnitude and duration (2-fold vs 8-fold difference in cover) than that found by Davies and others (2009). This suggests that fires are not as severe in our system or that there is a driver of greater relative importance. The structure of the vegetation at our site was similar to that of Davies and others (2009) and most fires at the INL burned naturally (that is, not prescribed burns on days selected for control of the fires) through dense stands of old-growth *A. tridentata* in mid-summer providing a fuel load and weather conditions that would likely maximize fire severity. Thus our results, compared to those of Davies and others (2009), lead us to believe that factors other than fire severity play a critical role in determining post-fire *B. tectorum* response.

Although prior disturbances and fire severity can explain differences in *B. tectorum* abundance post-fire (Keeley and others 2003; Davies and others 2009, 2012a), our assertion that fire severity and prior disturbance may not always be the most important determinant of post-fire cheatgrass response is supported by other studies in which different sequences and intensities of the same disturbances resulted in drastically different outcomes (see Rew and Johnson 2010 for review). Therefore, we assert that climate has greater relative importance for forecasting whether a positive feedback is observed between *B. tectorum* and fire at the regional scale. We recognize, however, the local importance of physical disturbance history and fire severity in determining the post-fire *B. tectorum* abundance within sagebrush steppe communities. In addition, interactions between climate, fire, and *B. tectorum* are likely, given the impact of climate on fire activity in the western USA (Littell and others 2009; Abatzoglou and Kolden 2013).

Although the climate at the INL is intermediate to climate in areas that do and do not experience increased *B. tectorum* post-fire, we believe that climate, in combination with other factors, plays a leading role in explaining the lack of a positive *B. tectorum* response to fire at the INL site. Although summer precipitation at the INL is low, spring precipitation is high which may allow native perennial grasses to be more competitive (as suggested by their high post-fire abundances and the negative correlation between them and *B. tectorum*). In addition, winter temperatures at the INL are low, which would limit the advantage *B. tectorum* has as a winter annual. The INL may have the right combination of low disturbance levels and sufficient climate limitations to prevent the formation of a positive feedback between *B. tectorum* and fire. However, it is possible that in other areas that are also climatically intermediate there may be a more positive *B. tectorum* response to fire if disturbance levels are higher.

CONCLUSIONS

The positive feedback between fire and *B. tectorum* abundance is not consistent across the introduced range of *B. tectorum* in western North America because climate may be interacting with fire to mediate the invasiveness of this winter annual across the sagebrush biome. Although *B. tectorum* may be an aggressive and transformative invader in the Great Basin and south-central Washington, this response is not universal. Our study suggests that the lack of consistent response and ecosystem impact by *B. tectorum* is associated with differences in climate. In areas of the sagebrush biome that experience cold winters and wet summers, *B. tectorum* is not likely to develop annual-dominated states, even if fire severity is high. However, it is possible that in such areas local factors such as native plant cover and disturbance level may shift the balance in determining *B. tectorum* response to fire. In the future, climate change could cause *B. tectorum* to become more problematic and form positive feedbacks throughout the northeast part of the sagebrush biome where it historically has not responded positively to fire.

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