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Patterns in Cheatgrass Abundance in Foothills Grasslands in Montana

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Abstract

Cheatgrass (*Bromus tectorum* L.) is an invasive, exotic annual grass that exerts substantial negative ecological and economic influence in many of the ecosystems it invades. Cheatgrass has been extensively studied in the Great Basin region of North America where most precipitation comes in winter and early spring and the vegetation consists primarily of cool-season species and cespitose graminoid growth forms. However, much less research has been performed in the northern Great Plains region where precipitation comes primarily in spring and summer, supporting a mixture of cool and warm season plant species and both sod-forming and cespitose graminoid growth forms. In order to better understand cheatgrass ecology in the northern Great Plains region, we modeled cheatgrass abundance in relation to disturbance, vegetation, and site characteristics in two grassland locations in Montana. Multimodel inferences based on large generalized linear mixed-effects regression were used to identify variables important in predicting cheatgrass abundance. Our results suggest that cheatgrass appears to favor droughty site conditions associated with either coarser soil textures, shallower soils, or south-facing aspects. However, cheatgrass can exhibit extremely high abundances on more productive sites if disturbance creates an opportunity for invasion. Across all sites, it appears that soil disturbance can generate increased cheatgrass abundance and land management that promotes robust and vigorous vegetation and maximizes spatial and temporal niche occupancy should be encouraged to limit cheatgrass invasion and expansion.

Keywords: cheatgrass, *Bromus tectorum*, Montana, northern Great Plains, invasive, disturbance, rangeland, grassland

1. Introduction

In western North America, the cool season annual grass, cheatgrass (*Bromus tectorum* L.) is a highly invasive species exhibiting negative ecological and economic impacts in both cropland and rangeland ecosystems (Menalled et al., 2008; Young et al., 1987). Cheatgrass was first documented in Montana in approximately 1900 (Hull & Pechanec, 1947) and has since spread to every county in the state (Menalled et al., 2008). Under future climate scenarios, including warmer and wetter winters and drier summers (Bradley, 2009; Polley et al., 2013) cheatgrass may have the potential to expand its range in Montana (Bradley, 2009).

Cheatgrass can alter ecological dynamics and negatively impact biodiversity, wildlife habitat, and forage quality and quantity through its impacts on fire regimes and its invasions have initiated an ecological threshold breach in many rangeland systems (Davies et al., 2012) where natural ecosystem recovery is not possible (Briske et al., 2005). Cheatgrass alters fuel conditions and decreases fire return intervals (Whisenant, 1990) which precludes native species re-colonization. Cheatgrass can dominate a site within eight years after a wildfire (Diamond et al., 2009; Shinneman & Baker, 2009) and abundant cheatgrass tends to increase fire frequency and intensity (Billings, 1994; Young et al., 1987). Frequent wildfires present a major challenge to cheatgrass-invaded landscapes, some regions now experience major fires every five years or less but previously had fire return intervals of up to 100 years (Whisenant, 1990). This fire feedback, however, may be limited in areas where the summers are cooler and wetter (Bradley, 2009; Brummer et al., 2016; Taylor et al., 2014).

Cheatgrass is common in many plant communities but it may rely on disturbances such as fire or heavy grazing to become highly abundant (Brummer et al., 2016; Hulbert, 1955; Stewart & Hull, 1949). High native plant density and cover can increase community resistance to cheatgrass invasion and minimize cheatgrass productivity (Beckstead & Augspurger, 2004; Reisner et al., 2013) and disturbances that increase bare ground or reduce desired plant vigor and competitiveness such as grazing (Reisner et al., 2013), burrowing (Hulbert, 1955; Young et al., 1987), or fire (Whisenant, 1990), can facilitate cheatgrass invasion.

Cheatgrass has had a significant impact on ecosystems in the Great Basin of the United States and much of the research on cheatgrass invasion has occurred in this environment. The Great Basin is has a winter precipitation regime and the vegetation is primarily sagebrush steppe plant communities with cool season (C3) bunchgrasses as the dominant understory (Holechek et al., 2004). In contrast, the northern Great Plains exhibits a predominantly summer precipitation pattern and the vegetation includes a preponderance of both cool and warm (C4) season species and both sod forming and cespitose graminoid growth forms (Holechek et al., 2004). These differences in climate and pre-existing vegetation may be associated with a similarly different pattern and consequence to cheatgrass presence and invasion and an understanding of these patterns will be crucial to successfully managing landscapes and natural resources in the northern Great Plains both presently and into the future. Thus, we initiated a study to evaluate the patterns and processes associated with cheatgrass abundance in southwest and northcentral Montana. The specific objectives of this study were: 1) to quantify biotic and abiotic site characteristics including vegetation, disturbance history, and climate that are found in cheatgrass-invaded locations in southwestern and northcentral Montana; and 2) to identify and describe correlations (risk factors) between these site characteristics and cheatgrass presence and abundance in these locations.

2. Methods

2.1 Site Description and Study Design

Study locations were established in 2014 and 2015 at Red Bluff Ranch (45° 35’ 14” N, 111° 37’ 11” W), east of Norris, MT, and Thackeray Ranch (48° 22’ 7” N, 109° 35’ 39” W), southeast of Havre, MT (Figure 1). Both ranches are owned and operated by Montana State University. Red Bluff Ranch is in the foothills of the Madison and Gallatin ranges of the Rocky Mountains. The substrate of Red Bluff is characterized by sandy-skeletal to fine-loamy soils, with gravelly to coarse-sandy loam surface horizons derived from gneiss, schist, and granite (Vuke et al., 2014); some soils are very shallow, and there are occasional rocky outcrops (USDA-NRCS, 2013). The 30 year average annual precipitation at Red Bluff is 405 mm, mostly as rain in spring and autumn (PRISM Climate Group, 2016). The 30-year average minimum and maximum temperatures are -9°C and 28°C, respectively, with a range from -17.5°C to 32.8°C (PRISM Climate Group, 2016). The vegetation at Red Bluff is comprised primarily of Idaho fescue (*Festuca idahoensis* Elmer), bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A.Love), Sandburg bluegrass (*Poa secunda* J. Presl), spikemoss (*Selaginella* spp.) and fringed sagebrush (*Artemisia frigida* Willd.) with some patches of big sagebrush (*Artemisia tridentata* Nutt.).

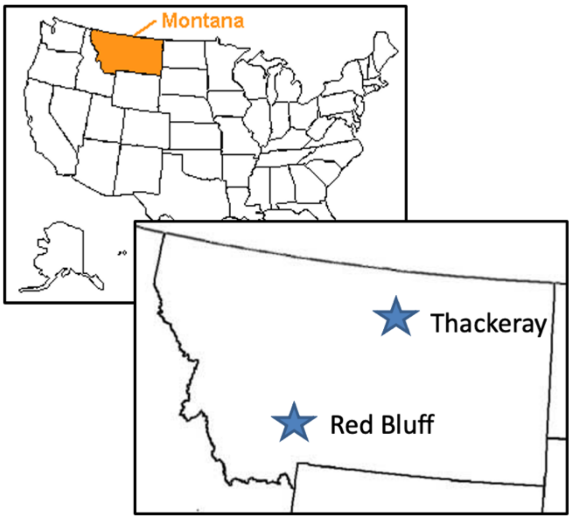

Figure 1. Study locations

Thackeray Ranch has fine- to coarse-loamy soils developed from igneous alluvial materials and/or glacial till (Bergantino et al., 2002) and is in the foothills of the Bears Paw Mountains (USDA-NRCS, 2013). Average precipitation at Thackeray is 438 mm annually, the majority coming as rain in the late spring and early summer months (PRISM Climate Group, 2016). The 30-year average minimum and maximum temperatures at Thackeray are -10°C and 26°C, respectively, with a range of -18°C to 30°C (PRISM Climate Group, 2016). Common vegetation observed at Thackeray included rough fescue (*Festuca campestris* Rydb.), bluebunch wheatgrass, and Kentucky bluegrass (*Poa pratensis* L.) along with western yarrow (*Achillea millefolium* L.), goldenpea (*Thermopsis* spp.), lupine (*Lupinus* spp.), and snowberry (*Symphoricarpos occidentalis* Hook.).

In 2014, 15 plots were randomly selected at each location from potential plots that were identified *a priori* as cheatgrass occupied sites. Seventy-four potential plots were identified at Red Bluff and 64 were identified at Thackeray. In 2015, five additional plots were randomly selected at each location from 20 *a priori* potential plot locations that met a cheatgrass free criteria. During field sampling in 2015 we detected cheatgrass in two of the uninvaded plots at Red Bluff, thus we randomly selected two additional cheatgrass free plots from the remaining list of potential plot locations and the two additional cheatgrass invaded plots were retained in the study.

At each selected plot location a 100 m^2 plot (13m x 7.7 m) was established and four 13 m parallel transects were placed within each plot and served as the framework for our field sampling. Plant cover by species was sampled using the line point intercept method (Herrick et al., 2005) every 25 cm along each transect for a total of 208 points per plot. Data from each transect were aggregated into a plot level mean value for analyses. Relative cheatgrass cover (hereafter, cheatgrass abundance) was calculated as the proportion of total vegetative cover contributed by cheatgrass. Livestock presence was approximated by counting fecal deposits within the plot (cow pies and sheep pellet clusters). Rodent burrow mounds were measured by line intercept, however these were only measured where upturned soil was easily moved by hand, with no apparent crust or compaction and no vegetation rooted in the mound. Older, hardened burrows were difficult to identify and quantify due to rooted vegetation and similarity to other bare soil patches.

Two, 5 cm diameter soil cores were removed along each transect (8 cores per plot) to a maximum depth of 10 cm and soil samples composited at the plot level and air dried for at least one month. Soil particle size analyses were performed using the hydrometer method (Gee & Bauder, 1986) on 30 – 80 g subsamples taken from the plot-level composited soil sample. Soil depth was measured from the soil surface to a depth of at least 50 cm or bedrock, which ever was shallower. Deep soils were considered 50 cm or deeper while shallow soils were < 50 cm in depth. Aspect and slope were measured *in situ* with a handheld compass and clinometer, respectively, while elevation was taken from a handheld GPS unit. Fire history was obtained from ranch records at Thackeray Ranch (D. Boss, personal communication.) and from fire maps and ranch records at Red Bluff (Becker et al., 2013; C. Marlow, personal communication). Plot locations were compared to known burns and each plot was recorded as burned or unburned. The most recent burn for all burned plots was in 2012, an no other fires were recorded at out plots in the preceding 20 years.

2.2 Data Analyses

Simpsons diversity index (Simpson, 1949) and species richness were generated from our data prior to analyses and we incorporated a sine and cosine transformations of aspect to reflect north-south (cosine of aspect) and east-west (sine of aspect) gradients. Cheatgrass abundance was logit transformed to better meet assumptions of constant variance and linearity while numerical explanatory variables were relativized by dividing the residuals by the standard deviation ensuring variable values were on comparable scales during model selection. Relationships among cheatgrass abundance and the site and disturbance characteristics were evaluated using generalized linear mixed effects regression models with a binomial distribution. Plot was included as a random effect to account for the repeated measures on cheatgrass invaded plots. The data were analyzed separately for Red Bluff and Thackeray ranches. All analyses were performed in R (R Core Team, 2021).

We used the dredge function in the MuMin R package (Bartón, 2016) to perform stepwise model selection, identifying top predictive models and the most important variables based on Akaike's Information Criterion (AIC; Akaike, 1987). To reduce redundancies among variables and maximize power in our analyses, we performed a pairwise evaluation of all explanatory variables and cheatgrass abundance and eliminated from model selection any variables that were strongly correlated to another explanatory variable but not strongly correlated to cheatgrass abundance. We ran the model selection procedure for both years combined and for each year separately. Variables that were consistently included in strong models were considered important variables. Importance values for each variable were calculated by summing the model weight for all models that included the variable and models with low AIC have high weight. Importance scores have a maximum value of 1.00 because all model weights sum to 1 (Bartón, 2016; Mazerolle, 2004). The most important variables from our modeling process were the basis for our assessment of risk factors for cheatgrass invasion.

3. Results

3.1 Red Bluff

In our exploratory evaluation of explanatory variables, cosine of aspect was not strongly related to cheatgrass abundance, so sine of aspect was the only aspect variable included in these analyses. The best predictors associated with our full model (both years) were year, burrow cover and sine of aspect (Table 1; Table 2). The year 2015 exhibited a higher cheatgrass abundance than 2014, while burrow cover was positively associated with cheatgrass (Figure 2). The positive relationship between sine of aspect and cheatgrass abundance indicated that cheatgrass had higher abundance on east-facing slopes than west-facing slopes.

When the full Red Bluff model was subdivided into 2014 and 2015 models, a different set of variables was important (Table 2). Sine of aspect was not important in either year-specific model, and burrows were only important in 2015. Perennial basal cover was important and negatively related to cheatgrass abundance in both years, but the relationship was not important in the full model. Simpson diversity and burn history were important only in 2014. Cheatgrass abundance was negatively associated to a plot having burned. Diversity was likely not important in 2015 because most of the zero plots had relatively low diversity (Figure 2) and their low values neutralize the otherwise strongly negative correlation between cheatgrass abundance and diversity, and probably drive the relative unimportance of diversity in the full model. Litter cover, fecal counts, and burrow cover were only important in 2015, and all three variables positively related to cheatgrass abundance.

3.2 Thackeray

High-ranked models from the analyses of Thackeray Ranch data indicated that cosine of aspect, sand content, soil depth, and burrow cover were the most important variables for predicting cheatgrass abundance (Table 2,3). The negative association with cosine of aspect indicates that there is likely to be more cheatgrass on south-facing slopes (Figure 3). High sand content was also associated with high cheatgrass abundance while shallow soil profiles were associated with lower cheatgrass abundances (Figure 3). Unlike at Red Bluff, burrows were negatively associated to cheatgrass abundance at Thackeray (Figure 3), likely a result of the extreme change in burrow cover of two plots, from over 20% cover in 2014 to less than 5% cover in 2015.

Table 1. Estimated coefficients from the top ten models derived from the Red Bluff initial models. Blanks in columns indicate that the variable was not included in the model. Burrow, sand, Simp Diver and Shallow Soil represent burrow cover, percent sand content, Simpson’s diversity index, and soil < 50cm in depth, respectively.

		Red Bluff Explanatory Variables										
Model	**AIC**	**Year**	**Burrow**	**Sine Aspect**	**Burn**	**Slope**	**Sand**	**Litter**	**Fecal Count**	**Basal Cover**	**Simp Diver**	**Shallow Soil**
1	369.3	.475	.173	1.594	-	-	-	-	-	-	-	-
2	370	.474	.171	1.548	-	-	.587	-	-	-	-	-
3	370	.439	.162	1.603	-	-	-	-	-	-	-.140	-
4	370	.482	.163	1.527	-	-	-	.114	-	-	-	-
5	370.6	.475	.173	1.485	-	-.428	-	-	-	-	-	-
6	370.7	.475	.172	1.479	-	-	-	-	-	-	-	-.881
7	370.9	.475	.172	1.604	1.163	-	-	-	-	-	-	-
8	371.2	.468	.171	1.647	-	-	-	-	-	.0665	-	-
9	371.3	.485	.169	1.594	-	-	-	-	.0143	-	-	-
10	370.3	.474	.171	1.369	-	-.648	.750	-	-	-	-	-

Table 2. Importance values for explanatory variables associated with cheatgrass abundance. Importance values are calculated as the sum of the Akaike weights over all models that include the explanatory variable. The maximum importance value is 1.0. Table includes results for models including both years and models for years run separately.

Red Bluff		**Thackeray**	
Variable	Importance	Variable	Importance
Full Model		Full Model	
Year	1.00	Cosine Aspect	1.000
Burrow Cover	1.00	Sand	0.89
Sine Aspect	0.93	Shallow Soil	0.76
		Burrow Cover	0.74
2014		2014	
Simpsons Diversity	0.81	Cosine Aspect	0.81
Perennial Basal Cover	0.74	Sand	0.74
		Bare Soil	0.64
2015		2015	
Litter Cover	0.74	Cosine Aspect	0.74
Fecal Density	0.61	Sand	0.34
Perennial Basal Cover	0.55	Bare Soil	0.50

When we re-fit the initial Thackeray model as separate 2014 and 2015 models, cosine of aspect, bare soil cover, and sand content were the most important variables in both sub-models (Table 2). Cosine of aspect related high cheatgrass abundance to south-facing slopes; high bare soil cover related to low cheatgrass abundance; and high sand content related to high cheatgrass abundance in both models (Figure 3).

4. Discussion

4.1 Red Bluff

At Red Bluff, three variables were the most important from our full model: year, burrow cover, and sine of aspect (degree to which a slope faces east or west). The positive association between year and cheatgrass abundance was a result of more abundant cheatgrass in 2015 than 2014, and could be associated with higher spring precipitation received in 2015 (191 mm, March to May) than in 2014 (176 mm, March to May; PRISM Climate Group, 2016). Although others have suggested spring precipitation is strongly related to cheatgrass abundance (Bradley, 2009; Taylor et al., 2014), additional years of data at Red Bluff would help explore this relationship further as cheatgrass cover could also fluctuate based on other factors such as grazing patterns and seed predation**.** Regardless cheatgrass was a larger part of the vegetation in 2015 than it was in 2014.

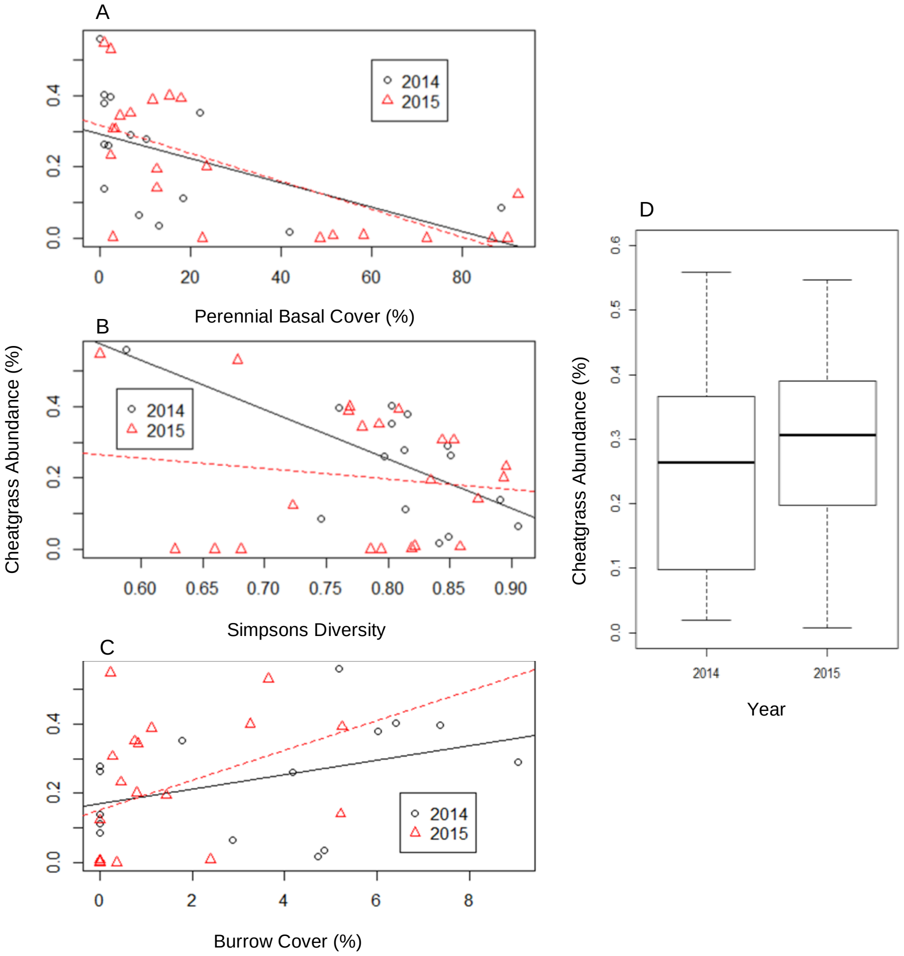

Figure 2. Relationships among cheatgrass abundance and A) perennial basal cover, B) Simpsons Diversity Index, C) ground squire burrow cover, and D) year, at Red Bluff ranch. Black symbols and lines represent 2014 data while red symbols and lines represent 2015 data.

The positive association we found at Red Bluff between rodent burrows and cheatgrass abundance could be explained by several factors. It is not clear if cheatgrass attracts rodents, rodent burrows provide sites for cheatgrass establishment, or if both organisms simply co-occur in certain habitats. The most common rodents at Red Bluff during this study were Richardson's ground squirrels (*Spermophilus richardsonii* Sabine), a diurnal species of ground squirrel which creates extensive burrows in easily dug (i.e., sandy) soil on flat to gently sloped sites (Bailey, 1893; Quanstrom, 1971). Cheatgrass was somewhat more abundant on flatter slopes and sandier soils at Red Bluff (Ozeran, 2016), so rodents and cheatgrass may be positively related because of co-occurrence on gentle slopes and coarse soil substrates.

Table 3. Estimated coefficients from the top ten models derived from the Thackeray initial models. Blanks in columns indicate that the variable was not included in the model.

		Thackeray Explanatory Variables							
Model	**AIC**	**Cosine Aspect**	**Sand**	**Shallow Soil**	**Burrow**	**Bare Soil**	**Burn**	**Litter**	**Slope**
1	275.9	-1.744	.942	-1.214	-.135	-.160	-1.006	-	-
2	277.4	-1.794	.849	-1.286	-.135	-.169	-	-	-
3	277.9	-1.769	.924	-1.324	-.159	-	-1.137	-	-
4	277.1	-1.812	.868	-1.459	-.123	-	-1.185	-.151	-
5	279.8	-1.829	.817	-1.418	-.160	-	-	-	-
6	279.1	-1.872	.754	-1.555	-.124	-	-	-.151	-
7	276.2	-1.855	.866	-1.362	-.135	-.168	-1.245	-	.296
8	280.5	-1.460	1.103	-	-.134	-.174	-	-	-
9	278	-1.828	.798	-1.402	-.112	-.147	-	-.111	-
10	276.4	-1.778	.896	-1.328	-.111	-.137	-1.059	-.114	-

Regardless of soil texture, Richardson's ground squirrels prefer habitats with short, uniform vegetation presumably to maintain an unobstructed space to watch for predators in the area (Bailey, 1893; Gilmer & Stewart, 1983). Cheatgrass grows to heights below 60 cm (Stubbendieck et al., 2011; Warg, 1938) and it senesces early in the season, so any visual obstruction created would be short-lived. In contrast, a mosaic of sagebrush and bunchgrasses could easily obscure aerial predators from a ground squirrel perspective. Further, Richardson’s ground squirrels rely on graminoids for nesting material (Quanstrom, 1971) and a plant community dominated by an annual grass such as cheatgrass could be preferable habitat for ground squirrels.

Voles are the most common rodent mentioned in Great Basin research on cheatgrass, and no strong relationships to cheatgrass have been described (Mack & Pyke, 1983; Piemeisel, 1951, 1954). At Red Bluff, voles were occasionally seen on and around our study plots, but their burrow entrances were never associated with mounds of disturbed soil. Rodent burrowing in general is perceived to be sufficient disturbance to facilitate cheatgrass dominance (Young et al., 1987). However, Richardson’s ground squirrels and larger burrowing animals are more likely to encourage cheatgrass than voles are, based on the greater aboveground disturbance associated with the ground squirrels’ burrow entrances (Mack & Pyke, 1983; Quanstrom, 1971). Because cheatgrass seeds have poor soil contact on flat surfaces (Beckstead &

Augspurger, 2004; Kelrick, 1991), freshly disturbed soil, such as a new burrow mound, provides better sites for cheatgrass establishment.

From the top models, sine of aspect indicates that east-facing slopes had higher cheatgrass abundance than west-facing slopes. Moreover, when we first located study plots, very few cheatgrass invaded sites at Red Bluff faced in westerly directions. This observed pattern suggests that cheatgrass may be more likely to invade east-facing slopes than west-facing slopes. Hanna et al. (1982) observed east-facing slopes with limited soil moisture availability, but this is an uncommon result. More often, south- and southwest-facing slopes are the driest in the northern hemisphere because they receive the highest heat load (Buffo et al., 1972; Hanna et al., 1982; McCune & Keon, 2002). Indeed, aspect was not important in either of the year sub-models and we expect that there were other factors influencing this relationship. The positive correlation between sine of aspect and litter cover and the negative correlation between sine of aspect and perennial basal cover may both contribute to higher cheatgrass abundance on east-facing plots, more litter and less basal cover are both factors that facilitate cheatgrass establishment. Data from additional west-facing plots could more thoroughly describe the relationship of cheatgrass abundance to aspect at Red Bluff.

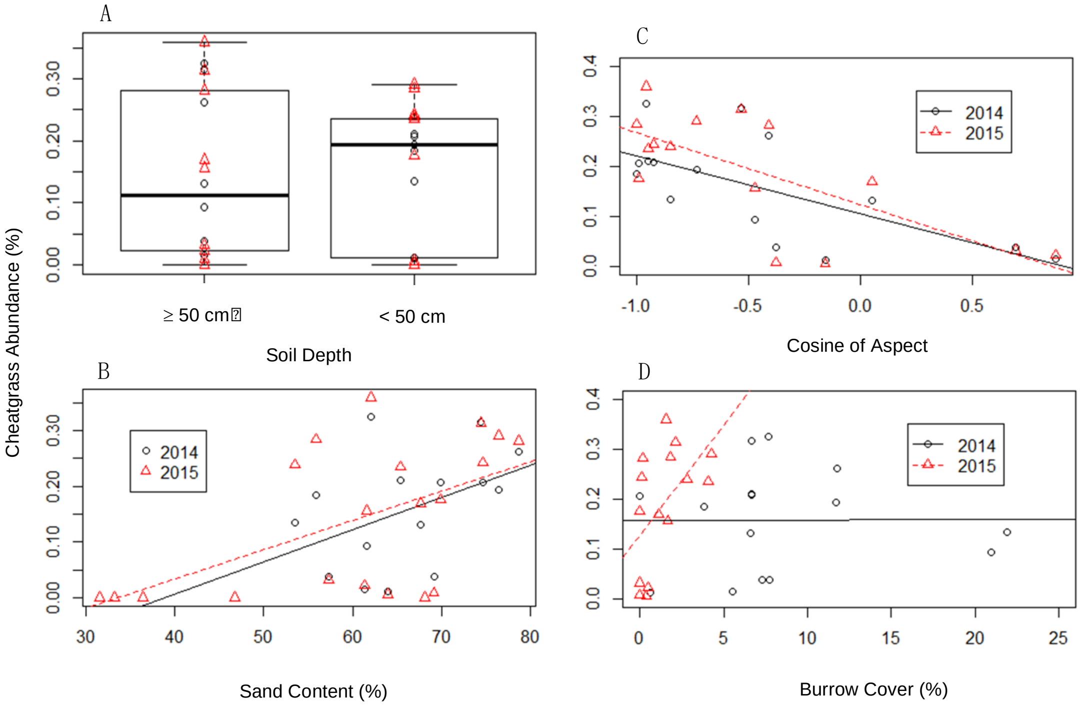

Figure 3. Relationships among cheatgrass abundance and (A) soil depth, (B) aspect, (C) soil sand content, and (D) ground squirrel burrow cover at Thackeray ranch. Black symbols and lines represent 2014 data while red symbols and line represent 2015 data.

While not important in our full Red Bluff model, diversity was important in the 2014 sub-model and the negative relationship between cheatgrass abundance and species diversity corroborates the findings of other research (Metlen, 2010; Shinneman & Baker, 2009).

Although some studies described inconsistent relationships between diversity and cheatgrass cover (e.g., Gelbard & Belnap, 2003) cheatgrass can establish low diversity monocultures that would exhibit a logical inverse relationship to cheatgrass abundance and dominance. It is unclear whether cheatgrass displaces diverse native communities or simply enters though existing niches on the landscape, however, greater diversity in time and space could hinder cheatgrass invasion and abundance by precluding it from most sites with adequate resources.

Perennial basal cover was also important in both year sub-models. Perennials provide competition for space, sunlight, and soil resources and reduced cheatgrass abundance is associated with elevated perennial density and cover (Rayburn et al., 2014; Reisner et al., 2013). In arid and semiarid ecosystems competition among plants is greater for belowground resources than for sunlight (Reichenberger & Pyke, 1990) and aboveground biomass often represents less than half of a plants total biomass (Caldwell et al., 1998). Thus, communities with higher perennial plant abundance are likely to have more extensive root systems and may be better suited to exclude cheatgrass from occupying niches within the community. In the full model, perennial basal cover was not identified as an important variable primarily due to the skewed distribution of basal cover values across plots; most plots had less than 40% perennial basal cover while a few had cover values that exceeded 40%. The few plots that exhibited high perennial basal cover reflected the high cover of spikemoss, a low growing mat forming forb (Lesica et al., 2012). Across the range of observed basal cover values (0% -92%), cheatgrass abundance varied greatly which limited the strength of the relationship. The relationship between basal cover and cheatgrass abundance would have been better defined if we had additional plots with the intermediate basal cover values between the extremes.

Although litter cover was positively correlated to cheatgrass abundance in previous studies (e.g., Bates et al., 2004; Beckstead & Augspurger, 2004), it was not an important risk factor at Red Bluff. Litter cover was only important in the 2015 model, which may reflect the influence of non-invaded plots on this variable. Non-invaded plots had low litter cover, while all invaded plots had high litter cover, skewing the slight positive relationship between litter and cheatgrass abundance to a steeper and stronger relationship. The absence of litter as a variable in most top models from the full model suggests that once other variables were included, litter was not a particularly strong associate to cheatgrass abundance at these plots. Litter cover was quite high at all invaded plots in both years, while cheatgrass abundance had a wide amplitude. The narrow range of litter cover across most levels of cheatgrass abundance at our plots reduced the likelihood of a strong relationship to cheatgrass. When it was included as a variable in our models, litter was positively associated to cheatgrass abundance. As a result, the absence of litter importance at our plots does not disagree with studies from the Great Basin which found strong relationships between cheatgrass presence and litter (Bates et al., 2004; Beckstead & Augspurger, 2004; Evans & Young, 1970; Kelrick, 1991). Additionally, most of these studies recorded litter presence or absence which does not correlate directly to litter cover, so our results may not be directly comparable to those studies’ results.

Livestock fecal count, our proxy variable for livestock presence and abundance, was not strongly related to cheatgrass abundance. Fecal count was important only in the 2015 sub-model. The positive relationship to fecal count in 2015 would indicate a positive relationship between livestock presence and cheatgrass abundance, which is suggested by many Great Basin studies (Billings, 1994; Harris, 1967; Reisner et al., 2013; Young et al., 1987). However, the trend in our data was highly influenced by one plot that had both high fecal density and cheatgrass abundance. More years of data at our plots could further clarify whether this relationship holds true at Red Bluff as livestock presence and cheatgrass abundance fluctuate over time. Moreover, livestock presence alone may not generate an increase in cheatgrass abundance, rather some level of grazing intensity or other related soil disturbance may be needed to generate opportunities for cheatgrass to capitalize on available resources.

Fire was not a strong predictor at Red Bluff in the full model, and when it was included in models, the estimated relationship between burning and cheatgrass abundance was negative. This weak relationship to cheatgrass abundance corroborates previous findings at the same ranches, in which cheatgrass levels did not differ on burned and unburned sides of a fireline (Tulganyam, 2015). Taylor et al. (2014) also suggested that regions with summer precipitation patterns tend not to have a positive relationship between cheatgrass and fire. Red Bluff receives most precipitation in the late spring/early summer, and our results and those of Tulganyam (2015) suggest that fire itself may not promote increased cheatgrass abundance. Additional study with greater variability in the fire regime would assist in clarifying this relationship.

4.2 Thackeray

At Thackeray Ranch, burrow cover, soil sand content, and aspect were identified as important variables. Unlike at Red Bluff, burrow cover was negatively related to cheatgrass abundance at Thackeray. This relationship may reflect the concurrent increase in average cheatgrass abundance and decrease in burrow cover between years. Because burrows were only measured if they were fresh, these large changes could have occurred if rodents abandoned the burrows on these plots. Nevertheless, burrows were not important in either Thackeray sub-model. The difference between years is a more reasonable explanation than burrowing being negatively associated with cheatgrass abundance, given the previous discussion about rodent burrows and cheatgrass at Red Bluff (Mack & Pyke, 1983; Piemeisel, 1951, 1954; Quanstrom, 1971; Young et al., 1987). The year effect also makes more sense given that there appears to be a positive relationship to burrows in 2015, while the apparent negative relationship in 2014 is largely a result of two plots with high burrow cover values and low cheatgrass abundance. While it is possible that large rodent populations consumed cheatgrass and drove the negative association, there is no literature to support that ground squirrels consume significant amounts of cheatgrass foliage or seeds. The positive relationship in 2015 may simply be a result of the zero plots having negligible burrow cover.

The negative relationship of cheatgrass abundance to bare soil may also have emerged from the influence of unique plots and year differences. Cheatgrass abundance at all plots was slightly higher in 2015 than 2014 while bare soil was lower, creating an apparent negative association between cheatgrass abundance and bare soil. Research from the Great Basin has described similar relationships between cheatgrass and bare ground. Undisturbed bare ground is not be an ideal site for cheatgrass establishment (Bates et al., 2004; Evans & Young, 1970) and this may be caused by low seed-soil contact between cheatgrass seeds and a relatively flat soil surface (Beckstead & Augspurger, 2004; Kelrick, 1991). Litter increases moisture retention in the surface soil and moderates soil temperature (Evans & Young, 1970), creating a more suitable microenvironment for cheatgrass germination and establishment (Beckstead & Augspurger, 2004).

Cheatgrass abundance was negatively associated to shallow soils at Thackeray, although a more complicated relationship appeared likely. Shallow soils can restrict cheatgrass abundance as indicated in by Hulbert (1955) who reported that cheatgrass grew taller and more densely on deep soils than on shallow soils in rocky areas, where perennial vegetation was also limited. Cheatgrass root mass primarily occupies the top 20-30 cm of the soil profile (Hulbert, 1955) thus cheatgrass can outcompete perennial grasses for near-surface soil moisture which would be available early in the spring and immediately after precipitation events during the growing season (Melgoza et al., 1990). By depleting surface water, cheatgrass could slow perennial growth unless the soil profile below the zone of cheatgrass root domination had adequate water for perennials. On a shallow site, it is unlikely that there would be much soil moisture available below the cheatgrass rooting zone. The same competition could occur on deeper sites, particularly in dry years, in which cheatgrass could occupy a greater proportion of the community composition of deeper sites by outcompeting perennials for shallow soil moisture where there is little or no deeper soil water. Although deep sites supported the highest cheatgrass abundance, shallow sites more commonly had moderate cheatgrass abundance, and non-invaded plots were usually on deeper sites. The overall pattern appeared to indicate that cheatgrass was frequently abundant on shallow soils and infrequently so on deep soils. Cheatgrass abundance may depend on other site characteristics to be successful on deeper and more productive sites. Of the deep sites with high cheatgrass abundance, most sites also had high fecal densities and/or high burrow cover, which indicated disturbance of vegetation or soils. Non-invaded plots, two of which were deep and four of which had fine-textured soils, had low fecal counts and nearly no burrow cover. It may be that the disturbance is necessary to open a niche for cheatgrass on deeper sites. Once cheatgrass is established it can then successfully compete for resources.

Sandy textured soils were positively associated to cheatgrass abundance but was only important in the sub-models for Thackeray. Research in other parts of the western US have mixed results about the relationship between cheatgrass and sandy soils. One study found that cheatgrass establishment and growth rates on sandy versus loamy soils depend on the season (Miller et al., 2006); another found that sandy sites generally had no cheatgrass (Brummer et al., 2016). Compaction, which is less likely in sandy soils, resulted in lower cheatgrass density and biomass production in the Great Basin (Beckstead & Augspurger, 2004). Rapidly draining, sandy soil may also be a greater stressor on native perennial growth than on cheatgrass growth. Under experimentally imposed dry conditions, native bluebunch wheatgrass seedlings senesced one to two weeks earlier than cheatgrass seedlings did, although seedlings of the introduced perennial desert wheatgrass (*Agropyron desertorum* [Fisch. ex Link] Schult.) persisted even after cheatgrass senesced (Harris & Wilson, 1970). If cheatgrass seedlings consistently outlast native perennials under drought conditions, cheatgrass could become abundant on sandy sites with native perennial grasses that then fail to recruit new plants. This phenomenon may also explain why crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.), a close relative of desert wheatgrass, is one of few perennials that can establish when planted in cheatgrass stands (Jessop & Anderson, 2007; Stewart & Hull, 1949).

Research has repeatedly described abundant cheatgrass on south-facing slopes (Billings, 1994; Metlen, 2010; Platt & Jackman, 1946), and our results suggest the same relationship to aspect. Because south aspects in the Northern Hemisphere receive more incident solar radiation year-round, they tend to be warmer and drier than north aspects under otherwise equal climatic conditions (McCune & Keon, 2002). Cheatgrass may be more competitive than native perennials on these dry slopes due to its winter annual life history. Cheatgrass grows its roots during autumn and winter, and as soon as environmental conditions are amenable to aboveground growth it can access moisture from snowmelt and precipitation before natives are fully out of their winter dormancy (Melgoza et al., 1990; Stewart & Hull, 1949). In addition, because cheatgrass is capable of setting seed on even very short tillers (e.g. 10-12 cm), it can take advantage of early season moisture and nutrient availability and produce seed before conditions are excessively warm or dry (Hulbert, 1955; Warg, 1938), and this could also explain the abundance of cheatgrass on sandy sites.

5. Conclusion

The differences between Red Bluff and Thackeray ranches influenced what factors were associated with cheatgrass abundance. Red Bluff's relatively uniform, coarse substrate and shallow soils reduced the likelihood that soil characteristics were clearly related to cheatgrass abundance. Red Bluff encompassed only seven unique ecological sites across the 22 plots, whereas Thackeray had 13 unique ecological sites across the 20 plots (Ozeran, 2016). Thus, vegetation and disturbance variables were more important than soil characteristics for predicting cheatgrass abundance at Red Bluff in our study. Disturbance at Red Bluff was from rodent burrowing, livestock grazing, and the occasional wildfire. Wildfire data on these plots were minimal, and livestock presence as quantified by fecal counts was not a strong predictor in our models. The lack of livestock relationship with cheatgrass abundance may reflect that the grazing intensity on our plots was not enough to directly encourage cheatgrass establishment through either reduced vegetation abundance and vigor or direct soil disturbance.

In contrast, disturbance at Thackeray often came from cattle rather than from rodents and several plots at Thackeray had high fecal densities which were rare at Red Bluff plots. Cattle use, although not an important variable itself at Thackeray, contributed to the unusually high cheatgrass abundance on a few of the more productive sites at this location. Three plots, all with productive, deep soils, had high fecal density and among the highest cheatgrass abundance. In comparison, most of the uninvaded plots at Thackeray had low fecal counts.

Although only two of the non-invaded plots were on deep soils, four of the five non-invaded plots had fine-textured soils. We speculate that the more productive sites, associated with deeper or finer textured soils, were more resistant to cheatgrass invasion but have the potential for very high cheatgrass abundance when disturbed.

Spikemoss appeared to be the main driver of the negative relationship between cheatgrass and perennial basal cover in Red Bluff sub-models. In general, spikemoss was the dominant source of basal cover and provided up to 90% basal cover in some plots, where cheatgrass abundance was low or zero. Few plots had very high basal cover, so the modelled relationship between cheatgrass abundance and basal cover was weak. Though we did not test the specific relationship between cheatgrass abundance and spikemoss cover, spikemoss may have some utility in competing with cheatgrass, however spikemoss is not a preferred species from a livestock production perspective.

Spikemoss was rare at Thackeray and provided little cover even when present. Although not common, there were more warm-season grasses (e.g. little bluestem (*Schizachyrium scoparium* (Michx.) Nash), red threeawn (*Aristida purpurea* Nutt.), and blue grama (*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths)) at Thackeray than at Red Bluff (blue grama only), which may increase Thackeray community resistance to invasion by having vegetation that occupies more temporal niches. Kentucky bluegrass also provided dense vegetation on several plots with low cheatgrass at Thackeray, and it may be a valuable competitor with cheatgrass. Areas with abundant Kentucky bluegrass tended to be moist sites and there may be some synergies among site and vegetation characteristics on these productive locations that limit cheatgrass invasion when the vegetation is intact.

5.1 Management Implications

The apparent phenotypic plasticity of cheatgrass (Harris, 1967) presents great challenges to reduction or elimination of the species once it is present on a site. Young et al. (1987) described a vast range of cheatgrass populations, from single, heavily seed-bearing individuals, to extremely dense stands of plants bearing few seeds. Mack and Pyke (1983) observed populations in a single location with three different phenologies exhibited – fall emergence, late winter emergence, and summer emergence. With cheatgrass so adaptable, it is likely to reestablish even after major restoration inputs have been made to invaded ecosystems. As such, it seems imperative to identify risks of cheatgrass invasion and monitor sites with the highest risks.

Despite the differences between the two ranches incorporated in this study, some constructive patterns in cheatgrass presence emerged. In our study areas, cheatgrass appears to favor droughty site conditions associated either with coarser soil textures, shallower soils, or south facing slopes and monitoring for cheatgrass presence should focus in these areas. In some cases, more productive sites (i.e., deeper soils) can promote very high abundance cheatgrass stands, however it appears that soil disturbance may facilitate the initial cheatgrass establishment. Soil disturbance may also play a role in increasing cheatgrass abundance on droughty sites, thus minimizing soil disturbance and monitoring sites that have experienced soil disturbance should be incorporated into land management activities. In addition, management that promotes robust and vigorous vegetation and maximizes spatial and temporal niche occupancy appears to be beneficial in limiting cheatgrass invasion.

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References

Akaike, H. (1987). Factor analysis and AIC. *Psychometrika*, *52*(3), 317-332.

Bailey, V. (1893). *The prairie ground squirrels or spermophiles of the Mississippi Valley*. Washington, DC, USA: Government Printing Office. USDA Bulletin No. 4.

Bartón, K. (2016). Multimodel inference. R Package MuMIn 67.

Bates, J., Svejcar, T., & Miller, R. (2004). Forage production in a cut juniper woodland. In T. Svejcar & J. Bates (Eds.), *Range Field Day Report 2004: Current forage and livestock production research* (pp. 24-31). Oregon State University Agricultural Experiment Station. Special Report 1052.

Becker, K., Clancy, E., Szypulski, J., & Three Irons, E. (2013). *Red Bluff*. Bozeman, MT, Montana State University.

Beckstead, J., & Augspurger, C. K. (2004). An experimental test of resistance to cheatgrass invasion: limiting resources at different life stages. *Biological Invasions*, *6*(4), 417-432.

Bergantino, R. N., Porter, K. W., & Hearn, B. C., Jr. (2002). *Geologic map of the Rocky Boy 30' x 60' quadrangle, north-central Montana*. Montana Bureau of Mines and Geology.

Billings, W. (1994). Ecological impacts of cheatgrass and resultant fire on ecosystems in the western Great Basin. In S. B. Monsen & S. G. Kitchen (Eds.), *Ecology and Management of Annual Rangelands* (pp. 22-30). US Forest Service Intermountain Research Station INT-GTR-313, Ogden, UT.

Bradley, B. A. (2009). Regional analysis of the impacts of climate change on cheatgrass invasion shows potential risk and opportunity. *Global Change Biology*, *15*(1), 196-208.

Briske, D. D., Fuhlendorf, S. D., & Smeins, F. (2005). State-and-transition models, thresholds, and rangeland health: a synthesis of ecological concepts and perspectives. *Rangeland Ecology & Management*, *58*(1), 1-10.

Brummer, T. J., Taylor, K. T., Rotella, J., Maxwell, B. D., Rew, L. J., & Lavin, M. (2016). Drivers of Bromus tectorum Abundance in the Western North American Sagebrush Steppe. *Ecosystems*, *19*, 986-1000.

Buffo, J. M., Fritschen, L., & Murphy, J. L. (1972). *Direct solar radiation on various slopes from 0 to 60 degrees north latitude*. USDA Forest Service, Pacific Northwest Research Station PNW-RP-142, Portland, OR USA.

Caldwell, M. M., Dawson, T. E., & Richards, J. H. (1998). Hydraulic lift: consequences of water efflux from the roots of plants. *Oecologia*, *113*(2), 151-161.

Davies, G., Bakker, J., Dettweiler-Robinson, E., Dunwiddie, P. W., Hall, S., Downs, J., & Evans, J. (2012). Trajectories of change in sagebrush steppe vegetation communities in relation to multiple wildfires. *Ecological Applications*, *22*(5), 1562-1577.

Diamond, J. M., Call, C. A., & Devoe, N. (2009). Effects of targeted cattle grazing on fire behavior of cheatgrass-dominated rangeland in the northern Great Basin, USA. *International Journal of Wildland Fire*, *18*(8), 944-950.

Evans, R. A., & Young, J. A. (1970). Plant litter and establishment of alien annual weed species in rangeland communities. *Weed science*, *18*, 697-703.

Gee, G. W., & Bauder, J. W. (1986). Particle-size analysis. In A. Klute (Ed.), *Methods of soil analysis. Part 1. Physical and mineralogical methods* (pp. 383-411). Soil Science Society of America.

Gelbard, J. L., & Belnap, J. (2003). Roads as conduits for exotic plant invasions in a semiarid landscape. *Conservation Biology*, *17*(2), 420-432.

Gilmer, D. S., & Stewart, R. E. (1983). Ferruginous Hawk populations and habitat use in North Dakota. *The Journal of Wildlife Management*, *47*, 146-157.

Hanna, A., Harlan, P., & Lewis, D. (1982). Soil available water as influenced by landscape position and aspect. *Agronomy Journal*, *74*(6), 999-1004.

Harris, G. A. (1967). Some competitive relationships between Agropyron spicatum and Bromus tectorum. *Ecological Monographs*, *37*(2), 89-111.

Harris, G. A., & Wilson, A. (1970). Competition for moisture among seedlings of annual and perennial grasses as influenced by root elongation at low temperature. *Ecology*, *51*(3), 530-534.

Herrick, J., Van Zee, J., Havstad, K., Burkett, L., & Whitford, W. (2005). *Monitoring manual for grassland, shrubland and savanna ecosystems, volume I: Quick start*. USDA-ARS Jornada Experimental Range.

Holechek, J., Pieper, R., & Herbel, C. (2004). Range management: principles and practices. Pearson Education. *Inc., Upper Saddle River, NJ*.

Hulbert, L. C. (1955). Ecological studies of Bromus tectorum and other annual bromegrasses. *Ecological Monographs*, *25*(2), 181-213.

Hull, A., & Pechanec, J. F. (1947). Cheatgrass--a challenge to range research. *Journal of Forestry*, *45*(8), 555-564.

Jessop, B. D., & Anderson, V. J. (2007). Cheatgrass invasion in salt desert shrublands: benefits of postfire reclamation. *Rangeland Ecology & Management*, *60*(3), 235-243.

Kelrick, M. I. (1991). *Factors affecting seeds in a sagebrush-steppe ecosystem and implications for the dispersion of an annual plant species, cheatgrass (Bromus tectorum L.)* Utah State University]. Logan, UT, USA.

Lesica, P., Lavin, M., & Stickney, P. F. (2012). *Manual of Montana Vascular Plants*. BRIT Press.

Mack, R. N., & Pyke, D. A. (1983). The demography of Bromus tectorum: variation in time and space. *The Journal of Ecology*, *71*, 69-93.

Mazerolle, M. J. (2004). *Mouvements et Reproduction des Amphibiens en Tourbières Perturbées* [Dissertation, Université Laval]. Ville de Québec, Québec, Canada.

McCune, B., & Keon, D. (2002). Equations for potential annual direct incident radiation and heat load. *Journal of Vegetation Science*, *13*(4), 603-606.

Melgoza, G., Nowak, R. S., & Tausch, R. J. (1990). Soil water exploitation after fire: competition between Bromus tectorum (cheatgrass) and two native species. *Oecologia*, *83*(1), 7-13.

Menalled, F., Mangold, J., & Davis, E. (2008). *Cheatgrass: identification, biology and integrated management*. Bozeman, MT, USA: Montana State University Extension. MontGuide MT200811AG.

Metlen, K. L. (2010). *Using patchy plant invasions to understand how diffuse interactions modify facilitation and competition* [Dissertation, University of Montana]. Missoula, MT, USA.

Miller, M. E., Belnap, J., Beatty, S. W., & Reynolds, R. L. (2006). Performance of Bromus tectorum L. in relation to soil properties, water additions, and chemical amendments in calcareous soils of southeastern Utah, USA. *Plant and Soil*, *288*, 1-18.

Ozeran, R. K. (2016). *Disturbance and site characteristics relate to cheatgrass (Bromus tectorum) abundance on ranches in Montana foothills ecosystems* [Thesis, Montana State University]. Bozeman, MT USA.

Piemeisel, R. L. (1951). Causes affecting change and rate of change in a vegetation of annuals in Idaho. *Ecology*, *32*(1), 53-72.

Piemeisel, R. L. (1954). Replacement control: changes in vegetation in relation to control of pests and diseases. *The Botanical Review*, *20*(1), 1-32.

Platt, K., & Jackman, E. R. (1946). *The cheatgrass problem in Oregon*. Corvallis, OR, USA: Federal Cooperative Extension Service, Oregon State College. Extension Bulletin 668.

Polley, H. W., Briske, D. D., Morgan, J. A., Wolter, K., Bailey, D. W., & Brown, J. R. (2013). Climate change and North American rangelands: trends, projections, and implications. *Rangeland Ecology & Management*, *66*(5), 493-511.

PRISM Climate Group. (2016). *Data explorer: time series values for individual locations*

Quanstrom, W. R. (1971). Behaviour of Richardson's ground squirrel Spermophilus richardsonii richardsonii. *Animal Behaviour*, *19*(4), 646-652.

R Core Team. (2021). *R: A language and environment for statistical computing*. In R Foundation for Statistical Computing. https://www.R-project.org/

Rayburn, A. P., Schupp, E. W., & Kay, S. (2014). Effects of perennial semi-arid bunchgrass spatial patterns on performance of the invasive annual cheatgrass (Bromus tectorum L.). *Plant Ecology*, *215*(2), 247-251.

Reichenberger, G., & Pyke, D. A. (1990). Impact of early root competition on fitness components of four semiarid species. *Oecologia*, *85*(2), 159-166.

Reisner, M. D., Grace, J. B., Pyke, D. A., & Doescher, P. S. (2013). Conditions favouring *Bromus tectorum* dominance of endangered sagebrush steppe ecosystems. *Journal of Applied Ecology*, *50*(4), 1039-1049.

Shinneman, D. J., & Baker, W. L. (2009). Environmental and climatic variables as potential drivers of post-fire cover of cheatgrass (Bromus tectorum) in seeded and unseeded semiarid ecosystems. *International Journal of Wildland Fire*, *18*(2), 191-202.

Simpson, E. H. (1949). Measurement of diversity. *Nature*, *163*, 688.

Stewart, G., & Hull, A. (1949). Cheatgrass (Bromus Tectorum L.) - An Ecologic Intruder in Southern Idaho. *Ecology*, *30*(1), 58-74.

Stubbendieck, J., Hatch, S. L., & Bryan, N. M. (2011). *North American Wildland Plants: A Field Guide* (2nd Edition ed.). University of Nebraska Press.

Taylor, K., Brummer, T., Rew, L. J., Lavin, M., & Maxwell, B. D. (2014). Bromus tectorum response to fire varies with climate conditions. *Ecosystems*, *17*(6), 960-973.

Tulganyam, S. (2015). *Short-term changes in vegetation and soil in response to a bulldozed fireline in northern great plains grasslands* [Thesis, Montana State University-Bozeman]. Bozeman, MT, USA.

USDA-NRCS. (2013). *Web Soil Survey* http://websoilsurvey.sc.egov.usda.gov/App/HomePage.htm

Vuke, S. M., Lonn, J. D., Berg, R. B., & Schmidt, C. J. (2014). *Geologic map of the Bozeman 30' x 60' quadrangle, southwestern Montana*. Montana Bureau of Mines and Geology. http://www.mbmg.mtech.edu/mbmgcat/public/FileDirector.asp?fn=1482&

Warg, S. A. (1938). *Life history and economic studies on Bromus tectorum* [Thesis, University of Montana]. Missoula, MT, USA.

Whisenant, S. G. (1990). Changing fire frequencies on Idaho’s Snake River Plains: ecological and management implications. In E. D. McArthur, E. M. Romney, S. D. Smith, & P. T. Tueller (Eds.), *Symposium on Cheatgrass Invasion, Shrub Die-Off, and Other Aspects of Shrub Biology and Management* (pp. 4-10). Intermountain Research Station INT-GTR-276.

Young, J. A., Evans, R. A., Eckert Jr, R. E., & Kay, B. L. (1987). Cheatgrass. *Rangelands*, *9*, 266-270.

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