esa ECOSPHERE

Resilience and resistance in sagebrush ecosystems are associated with seasonal soil temperature and water availability

Bruce A. Roundy,[1,]† Jeanne C. Chambers,[2] David A. Pyke,[3] Richard F. Miller,[4] Robin J. Tausch,[2] Eugene W. Schupp,[5] Ben Rau,[6] and Trevor Gruell[1]

[1]Plant and Wildlife Science Department, Brigham Young University, Provo, Utah 84602 USA
[2]Rocky Mountain Research Station, United States Forest Service, Reno, Nevada 89512 USA
[3]Forest and Rangeland Ecosystem Science Center, United States Geological Survey, Corvallis, Oregon 97331 USA
[4]Eastern Oregon Agricultural Research Center, Oregon State University, Corvallis, Oregon 97331 USA
[5]Wildland Resources/Ecology Center, Utah State University, Logan, Utah 84322-5230 USA
[6]Pisgah National Forest, United States Department of Agriculture, Forest Service, North Carolina 28768 USA

Citation: Roundy, B. A., J. C. Chambers, D. A. Pyke, R. F. Miller, R. J. Tausch, E. W. Schupp, B. Rau, and T. Gruell. 2018. Resilience and resistance in sagebrush ecosystems are associated with seasonal soil temperature and water availability. Ecosphere 9(9):e02417. 10.1002/ecs2.2417

Abstract. Invasion and dominance of exotic grasses and increased fire frequency threaten native ecosystems worldwide. In the Great Basin region of the western United States, woody and herbaceous fuel treatments are implemented to decrease the effects of wildfire and increase sagebrush (*Artemisia* spp.) ecosystem resilience to disturbance and resistance to exotic annual grasses. High cover of the exotic annual cheatgrass (*Bromus tectorum*) after treatments increases fine fuels, which in turn increases the risk of passing over a biotic threshold to a state of increased wildfire frequency and conversion to cheatgrass dominance. Sagebrush ecosystem resilience to wildfire and resistance to cheatgrass depend on climatic conditions and abundance of perennial herbaceous species that compete with cheatgrass. In this study, we used longer-term data to evaluate the relationships among soil climate conditions, perennial herbaceous cover, and cheatgrass cover following fuel management treatments across the environmental gradients that characterize sagebrush ecosystems in the Great Basin. We examined the effects of woody and herbaceous fuel treatments on soil temperature, soil water availability (13–30 and 50 cm depths), and native and exotic plant cover on six sagebrush sites lacking piñon (*Pinus* spp.) or juniper (*Juniperus* spp.) tree expansion and 11 sagebrush sites with tree expansion. Both prescribed fire and mechanical treatments increased soil water availability on woodland sites and perennial herbaceous cover on some woodland and sagebrush sites. Prescribed fire also slightly increased soil temperatures and especially increased cheatgrass cover compared to no treatment and mechanical treatments on most sites. Non-metric dimensional scaling ordination and decision tree partition analysis indicated that sites with warmer late springs and warmer and wetter falls had higher cover of cheatgrass. Sites with wetter winters and early springs (March–April) had higher cover of perennial herbs. Our findings suggest that site resistance to cheatgrass after fire and fuel control treatments decreases with a warmer and drier climate. This emphasizes the need for management actions to maintain and enhance perennial herb cover, such as implementing appropriate grazing management, and revegetating sites that have low abundance of perennial herbs in conjunction with fuel control treatments.

Key words: *Bromus tectorum;* climate change; mechanical fuel treatments; plant invasions; prescribed fire.

Received 28 June 2018; accepted 23 July 2018. Corresponding Editor: Michael C. Duniway.

† **E-mail:** bruce_roundy@byu.edu

Introduction

Invasions by exotic grasses and the grass/fire cycles that they initiate represent increasing threats to native ecosystems around the globe (D'Antonio and Vitousek 1992, Rossiter et al. 2003, Brooks et al. 2004, Balch et al. 2013, Germino et al. 2016). A diverse array of vegetation management treatments is used in ecosystems experiencing annual grass invasions to (1) reduce or modify fuels and thus decrease wildfire extent, severity, and frequency, and (2) increase the resilience or recovery potential of ecosystems to wildfire and other disturbances that increase susceptibility to exotic grass invasion (Chambers et al. 2014*a*, *b*). However, use of vegetation management treatments (e.g., prescribed fire, mechanical treatments such as cut-and-leave and mastication, and herbicide applications) to modify fuels and increase ecosystem resilience to future disturbances has mixed results in forests (Reinhardt et al. 2008) and various shrublands, including chaparral (Keeley and Fotheringham 2006) and sagebrush (Bates et al. 2000, 2005, 2013, 2014, 2017, Bates and Svejcar 2009, Davies et al. 2012*a*, *b*, O'Connor et al. 2013, Bristow et al. 2014, Pyke et al. 2014, Roundy et al. 2014*a*, *b*, Williams et al. 2017). Recent research indicates that successful use of these treatments requires an understanding of the underlying factors that influence ecosystem resilience to disturbance, or capacity to reorganize and regain characteristic structure and function (Chambers et al. 2014*a*, *b*, 2017*a*, Urza et al. 2017) and resistance to invasive plant species, or capacity to prevent the population growth of the invader (D'Antonio and Thomsen 2004).

The sagebrush biome in the western United States is an area comprising >500,000 km^2 (Miller et al. 2011) that is exhibiting rapid conversion to exotic annual grasses, such as cheatgrass (*Bromus tectorum* L.), particularly in warmer and drier ecological types (Balch et al. 2013, Brooks et al. 2016, Brummer et al. 2016, Chambers et al. 2016). Across much of the biome, factors such as improper grazing, fire exclusion, and climate change have caused increases in woody fuels characterized by fire-intolerant species, such as sagebrush, piñon pine, and juniper (Burkhardt and Tisdale 1976, Miller and Wigand 1994, Miller et al. 2008, Romme et al. 2009, Davies et al. 2011, Summers and Roundy 2018). These changes have resulted in decreases in fine fuels characterized by perennial grasses and forbs (Miller et al. 2013). The introduction of exotic annual grasses has resulted in increases in the amount and continuity of fine fuel in areas with depleted perennial grasses and forbs and consequently more frequent and extensive fires (Brooks et al. 2004, Balch et al. 2013). Exotic annual grasses typically increase following fire and, once dominant, have significant impacts on ecosystem structure and function (Germino et al. 2016). Vegetation management treatments are widely used to reduce woody fuels, increase fire-tolerant perennial herbaceous species, and control fine fuels resulting from exotic annual grasses (Miller et al. 2011, 2013, 2017).

In sagebrush ecosystems, resilience to disturbances, such as inappropriate livestock grazing and wildfire, and resistance to exotic annual grasses are largely a function of abiotic ecosystem attributes such as temperature and precipitation regimes and biotic ecosystem attributes, such as fire-tolerant perennial herbaceous species (Chambers et al. 2007, 2014*a*, *b*, Condon et al. 2011, Davies et al. 2012*a*). Soil properties related to resource availability, such as texture, water-holding capacity, and nutrient availability, are associated with resilience and resistance before and after disturbance (Rau et al. 2007, 2008, 2011, 2014, Sankey et al. 2012, Young et al. 2013*a*, *b*, 2014, Aanderud et al. 2017). Soil hydrologic properties that influence infiltration and sediment movement are associated with abiotic resilience (Williams et al. 2016). More favorable environmental conditions for native plant establishment and growth and greater productivity of perennial herbaceous species due to higher precipitation and cooler temperatures typically equate to greater resilience at higher than lower elevations (Condon et al. 2011, Davies et al. 2012*a*, Chambers et al. 2014*a*, *b*, Knutson et al. 2014). Also, climate suitability to exotic annual grasses decreases as soil temperatures become colder resulting in greater resistance to these grasses at higher than lower elevations (Chambers et al. 2007, 2014*a*, *b*, Condon et al. 2011, Brooks et al. 2016). On climatically suitable sites, resistance is highly dependent on the abundance of perennial herbaceous species (Chambers et al. 2007, 2014*a*). Although soil temperature and water availability and the relative abundance of perennial herbaceous species are key attributes of ecosystem resilience to disturbance and resistance to exotic annual grasses, studies are needed to quantify the influence of these attributes on resilience and resistance following vegetation management treatments over the environmental gradients that characterize these ecosystems.

Perennial herbaceous species, especially deep-rooted grasses, play important roles in ecosystem resilience or recovery following both disturbances and vegetation management treatments that result in elevated resource availability (Chambers et al. 2007, 2014*a*, 2017*a*, Roundy et al. 2014*b*). Perennial native grasses are highly competitive for available resources and are a strong indicator of resilience to disturbances including fuel control treatments that remove fire-intolerant shrubs and trees (Davies and Svejcar 2008, Condon et al. 2011, Davies et al. 2012*b*, Chambers et al. 2014*b*, Roundy et al. 2014*a*). These grasses typically survive both wildfire and prescribed fire, regrow once conditions are suitable, and stabilize hydrologic and biogeochemical processes if they are sufficiently abundant (Leffler and Ryel 2012, Miller et al. 2013). They also are highly effective competitors with widespread exotic annual grasses, such as cheatgrass (Chambers et al. 2007, Davies and Svejcar 2008, Blank and Morgan 2012). Their abundance has been greatly reduced in many sagebrush–bunchgrass communities by heavy and recurrent grazing during the growing season, which has allowed ungrazed shrubs like sagebrush to increase in abundance (Young et al. 1979, Adler et al. 2005, Miller et al. 2010, Reisner et al. 2013, 2015, Chambers et al. 2017*a*). Following either wildfire, prescribed fire, or mechanical treatments that remove sagebrush, piñon pine, or juniper, cheatgrass often increases initially or in areas where perennial native grasses have been depleted (Miller et al. 2005, 2013, 2014*a*, *b*, Chambers et al. 2007, 2014*b*, Bates et al. 2011, 2013, 2014, Davies et al. 2012*b*, Pyke et al. 2014, Roundy et al. 2014*a*, Williams et al. 2017). However, increases in cheatgrass cover are typically less following mechanical treatments than prescribed fire in part due to more rapid growth of perennial grasses in the first few years after treatment (Bates et al. 2005, 2007, Davies et al. 2011, Chambers et al. 2014*b*, Miller et al. 2014*a*, *b*, Pyke et al. 2014, 2017, Rau et al. 2014, Roundy et al. 2014*a*, Bybee et al. 2016, Williams et al. 2017).

Understanding how different climatic conditions as indicated by soil moisture and temperature affect responses to vegetation treatments can help natural resource managers predict where additional weed control and revegetation may be needed. It can also help managers predict how ecosystems and their responses to treatments may vary in response to climate change (Bradley et al. 2016). This information can be useful for selecting species to use in restoration for projected climates (Butterfield et al. 2016). The Sagebrush Treatment and Evaluation project (SageSTEP) is a multistate, multidisciplinary study to determine the effects of fuel control treatments for sagebrush ecosystems across the Great Basin region, USA (McIver and Brunson 2014). Initial results indicate that while region-wide responses to treatments exist, some responses vary across the environmental gradients that characterize the sites (Miller et al. 2014*b*, Pyke et al. 2014, Roundy et al. 2014*a*, Williams et al. 2017). On four sagebrush SageSTEP sites, Rau et al. (2014) found that sites that were drier due to lower precipitation or had sandy soils with lower water-holding capacity had more cheatgrass cover after treatment. Chambers et al. (2014*b*) associated differences in vegetation response after treatment with soil temperature and moisture regimes across 16 SageSTEP sagebrush and tree-expansion sites and found that the warmest and driest sites were least resistant to increases in cheatgrass, while the coolest and wettest sites were most resistant to cheatgrass. These studies indicate that pretreatment differences in abiotic variables, such as soil temperature, soil water availability, and soil texture, as well as differences in biotic variables, such as tree, shrub, and perennial and annual grass cover, could be used to predict outcomes of vegetation treatments.

In this study, we used data from 17 of the long-term SageSTEP sites to critically evaluate the relationships among soil climate conditions, perennial herbaceous cover, and cheatgrass cover following fuel management treatments across the environmental gradients that characterize sagebrush ecosystems in the Great Basin. Our intent was to identify soil climate conditions and vegetation attributes that indicate resilience to disturbance and resistance to exotic annual grasses. The study had the following components. First, we determined the vegetation variables that best represented plant community responses to treatments. Second, we evaluated how vegetation and soil climate responses to treatments varied across and among study sites. Third, we related vegetation and soil climate responses to each other to quantify soil climate and vegetation indicators of resilience and resistance.

Methods

Vegetation treatments and measurements

We measured plant cover, soil temperature, and soil water availability on 17 sites across the semi-arid Great Basin of the western United States, including six Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) sites (SB) without woodland (WL) expansion and eleven big sagebrush sites with Wyoming and mountain big sagebrush subspecies (*A. t.* ssp. *vaseyana* (Rydb.) Beetle) in various stages of WL expansion as described in McIver and Brunson (2014). There were no seeding treatments applied on any of the sites. On the SB sites, treatments included untreated, burned, mowed, and tebuthiuron (Spike 20P) herbicide application as described in Pyke et al. (2014). Prescribed fire was implemented in late summer and fall and was followed by spot burning to blacken all shrubs. In the mow treatment, shrubs were mowed to a height of 30–38 cm in the fall. Tebuthiuron was applied at 1.68 kg/ha. Mowing and tebuthiuron treatments were intended to reduce woody plant cover by 50% (Pyke et al. 2014). In addition, all of these whole-plot treatments and controls were divided into split plots that either received or did not receive a pre-emergent herbicide (imazapic) application to reduce cheatgrass. Imazapic (Plateau, 22.2% acid equivalent) was applied at 105 g/ha within about a month after prescribed fire (Pyke et al. 2014).

On the WL sites, we measured plant cover on untreated, burned, tree cut-and-leave, and tree-masticated (four Utah sites only) plots as described in Miller et al. (2014*b*), Roundy et al. (2014*a*), and Williams et al. (2017). Prescribed fire was conducted in late summer and fall, with follow-up spot fires to completely burn all measurement subplots. Mechanical tree reduction consisted of cut-and-leave treatment plots on all WL sites and, on the four Utah sites, an additional tree mastication plot. On the mechanical treatment plots, all trees >2 m in height were cut by chain saw or masticated with a Fecon Bull Hog attachment (Fecon, Lebanon, Ohio, USA). Tree canopy cover was reduced to <5% in the burn plots and <1% in the mechanically treated plots. For our current analysis, we averaged vegetation cover and soil data across cut and masticated plots for the Utah sites. Tree mastication has generally produced similar understory responses as tree cutting (Roundy et al. 2014*a*, Bybee et al. 2016).

Because plots could not all be burned in the same year (Miller et al. 2014*b*), all treatments on a site for both SB and WL experiments were applied in 2006, 2007, and 2009 in a stagger start design (Loughlin 2006). This design avoids potential for restricted inferences associated with implementing all treatments under the same set of climatic conditions. Vegetation data used in this study were from measurements made prior to treatment and 6 yr after treatment, except for the Stansbury and Roberts sites. The Stansbury WL site was burned by a wildfire in 2009, 2 yr after treatment, while the Roberts SB site was burned by a wildfire in 2010, 4 yr after treatment. Vegetation data used for these sites were from measurements made on the Stansbury site 2 yr after treatment and on the Roberts site 3 yr after treatment.

For measurement of plant cover, we randomly established 0.1-ha (30 × 33 m) subplots within each treatment and untreated control plot (McIver and Brunson 2014, Miller et al. 2014*b*, Pyke et al. 2014, Roundy et al. 2014*a*, Williams et al. 2017). For SB sites, there were 18–24 subplots per whole-plot treatment (9–12 subplots per imazapic split plot) and subplots spanned a range of perennial grass cover (Pyke et al. 2014). For WL sites, there were 15 subplots that spanned a gradient of pretreatment tree cover (Roundy et al. 2014*a*, Williams et al. 2017). For both site types, subplots were chosen randomly within categories of perennial grass (SB) and tree (WL) cover to allow sampling to cover a gradient of these functional groups. For each subplot, we established a 30-m baseline with five permanent transects placed at 2, 7, 15, 23, and 28 m. We used the line-point intercept method (Herrick et al. 2009) to sample plant cover by species and ground cover groups every 0.5 m along each transect for a total of 300 points for each subplot. We then categorized cover data as follows: shrub; tall grass (deep-rooted); short grass (shallow-rooted; only Sandberg bluegrass (*Poa secunda* J. Presl) was considered a short grass in this study); perennial, annual, and exotic forb; cheatgrass; and bare ground. We recorded foliar cover for each functional group as a single hit for each point if the point contacted any member of that functional group. More than one functional group could be recorded at a single point. Bare ground was only recorded if it was the first and only hit at a point. We calculated percent cover for each subplot for each variable from these data.

Soil climate data collection

We collected soil temperature and water availability data on each of the treatment plots at each SB site. We placed two measurement stations within each treatment plot—one on a subplot with relatively low perennial grass cover and one on a subplot with relatively high perennial grass cover. For untreated and burn treatment plots, we additionally placed stations on subplots of low and high perennial grass cover within no imazapic and imazapic-treated plots. At each station, soil temperatures and soil water matric potential were measured in four microsites: shrub canopy edge, adjacent to tall perennial grass, adjacent to short perennial grass, and interspace between shrubs and grasses. Sensors adjacent to grasses were approximately 10 cm from the nearest tiller. For each microsite, we buried soil temperature and matric potential sensors at 1–3, 13–15, 18–20, and 28–30 cm deep. For the WL sites, we placed three stations within each treatment plot, corresponding to three phases of tree infilling (Miller et al. 2005) as described in Roundy et al. (2014*b*). We buried sensors at each of the four microsites: tree canopy edge, shrub canopy edge, and two interspaces between shrubs within interspaces between trees. We buried sensors at the same depths as those for the SB sites. The Natural Resources Conservation Service classifies rangeland ecological sites based on soil temperatures and water availability at a depth of 50 cm (Caudle et al. 2013). To better relate our measurements to their classification system, in 2011 we installed soil temperature and matric potential sensors at 50 cm deep in one interspace at each station located on untreated and burned plots for both SB and WL.

Soil temperature and water availability stations were each equipped with Campbell Scientific (Logan, Utah, USA) CR10X or CR1000 microloggers and multiplexers connected to soil temperature and soil water matric potential sensors as described in Roundy et al. (2014*b*). Thermocouples were used to measure temperature and gypsum blocks (Delmhorst Instrument Company, Towaco, New Jersey, USA) were used to measure soil water matric potential at each microsite and depth. The microloggers were programmed to read sensors every 60 s and to store hourly averages. Gypsum block resistance data were converted to water potential using standard calibration curves (Campbell Scientific, 1983). Although some error may be introduced by not individually calibrating each gypsum block, blocks calibrated with standard equations were relatively consistent and sensitive to soil drying in a growth chamber study (Taylor et al. 2007). Plants typical of sagebrush ecosystems can extract soil water at depths >30 cm and below the -1.5 MPa matric potential limit of measurement for gypsum blocks. However, soil water in the upper 30 cm of soil that is held at matric potentials >-1.5 MPa is critical for growth of shrub and herbaceous species in these systems (Leffler and Ryel 2012). The upper 30-cm depth interval has the highest concentration of nutrients, and matric potentials >-1.5 MPa are necessary for nutrients to flow to roots (Ryel et al. 2010, Leffler and Ryel 2012). We used soil temperature and soil matric potential data to calculate seasonal variables that we expected would be associated with plant growth and cover (Rau et al. 2014, Roundy et al. 2014*b*, Table 1). We calculated soil temperature and soil water availability variables (Table 1) for six seasons: early spring (March–April), late spring (May–June), spring (March–June), summer (July–August), fall (September–November), and winter (December–February). Treatments were implemented and soil measurement equipment was installed on different years for some of the sites. To analyze data for as many sites as possible and to relate the measurements to the vegetation data, we selected the four years of highest data availability. These years were 2012 through spring of 2016 and were generally 6–11 yr after treatment for most sites. We calculated averages of seasonal soil climate variables (Table 1) across these years, across the lower three depths (13–15, 18–20, and 28–30 cm), across four microsites, and within each treatment and perennial grass condition (SB) or infilling phase (WL). For the Stansbury and

Table 1. Seasonal soil temperature and soil water availability variables.

Variable	Units and explanation
Soil temperature	
Maximum	°C
Minimum	°C
Mean	°C
Degree-days	Sum of hourly temperatures >0°C/24
Frost-free days	Sum of hours when hourly soil temperature was >0°C/24
Wet degree-days	Sum of hourly temperatures >0°C for each hour that soil matric potential >−1.5 MPa/24
Maximum wet degree-day period	Sum of wet degree-days for the period with maximum continuous hourly temperatures >0°C and soil matric potentials >−1.5 MPa
Wet days	Sum of hours when soil matric potential >−1.5 MPa/24
Wet periods (no.)	Number of times that soil matric potential >−1.5 MPa, before or after being <−1.5 MPa
Average wet period (d)	Average length in days of all wet periods
Maximum wet period (d)	Sum of wet days for the longest period that soil was continuously wet (>−1.5 MPa matric potential)
Dry days	Sum of hours when soil matric potential <−1.5 MPa/24
Dry periods (no.)	Number of times that soil matric potential <−1.5 MPa, before or after being >−1.5 MPa
Average dry period (d)	Average length in days of all dry periods
Maximum dry period (d)	Sum of dry days for the longest period that soil was continuously dry (<−1.5 MPa matric potential)

Roberts sites, we averaged soil responses for 2 and 3 yr prior to the wildfire for untreated and treated plots. For burn treatments on these sites, we also averaged data from stations on wildfire-burned plots for 2012 through spring 2016.

We also measured air temperature and precipitation (1–1.5 m height) on one station at each site (untreated high perennial grass for SB, untreated Phase III infilling for WL). Precipitation was measured with an electronic tipping bucket rain gage (Texas Electronics, Dallas, Texas, USA) and removable precipitation adapter for snowfall (Campbell Scientific). We measured air temperature in a Gill shield using a Campbell Scientific Model 107 temperature probe.

Analysis

Analyses were structured to (1) identify community composition patterns across the sites, (2) determine the effects of treatments on vegetation and soil climate variables, and (3) determine the effects of climate variables on vegetation patterns. To first determine vegetation variables which best represented plant community responses to vegetation treatments, we used non-metric dimensional scaling (NMS) to ordinate plant cover variables across sites and treatments (Peck 2016). Data for SB treatments and WL treatments were initially analyzed separately because some of the treatments were not the same. For example, SB herbicide and mow treatments had no equivalence for the WL sites and mechanical tree removal on the WL sites did not have an equivalent treatment for the SB sites. We analyzed the site types separately to determine non-confounded treatment trends within the site types. A randomization test was applied to determine significance of the ordinations and a stress test to determine the number of axes for the final solution. Once the number of axes was determined, NMS was conducted at least twice more using 250 iterations to check for consistency in the output. The iteration with the lowest stress was chosen. After rotating the axes so that variables associated with perennial native herbaceous cover were on the primary axis, we calculated the Pierson correlation of vegetation cover variables in relation to axis scores. A second NMS analysis used data from burn plots from both the SB and WL sites together to best represent the gradient in vegetation across all study sites. Prescribed fire was the one treatment that was similar for both site types because all vegetation was ignited in this treatment. Thus, we analyzed composition across both site types on the burn treatment in order to identify patterns of vegetation response to fire that were similar across both site types. As with the first NMS, axes were rotated to represent variables associated with perennial herbaceous cover on the primary axis and Pierson correlations were calculated for vegetation cover variables with axis scores. Non-metric dimensional scaling analyses were conducted in PC-ORD v. 6

and 7 (MjM Software Design, Gleneden Beach, Oregon, USA).

Second, we determined variation in treatment response across, among, and within study sites. To determine vegetation cover and soil climate responses across study sites, we used mixed model analysis. Because some treatments were not equivalent, we analyzed vegetation cover data and soil climate variables separately for SB and WL sites. Site was considered a random effect and treatment was considered fixed. For the vegetation cover analysis, measurement time was also included as a fixed variable. The measurement times were (1) pretreatment, (2) 2 yr post-treatment for the Stansbury site, 3 yr post-treatment for the Roberts site, and 6 yr post-treatment for all other sites. We had to use earlier post-treatment data for the Stansbury and Roberts sites because they were burned in wildfires in 2009 and 2010, respectively. Percent cover was logit-transformed prior to analysis (Warton and Hui 2011), while soil climate variables were not transformed because their residuals were generally normally distributed. The Tukey test was used to determine significant differences ($P < 0.05$) among treatment means across sites. To determine variation in vegetation cover for treatments among and within study sites, we calculated and graphed means and standard errors across subplots for each treatment at each study site for both pre- and post-treatment. To determine biotic constraints on annual grass cover both across and within study sites, we conducted simple linear regression across study sites and by treatment, and then within each study site and treatment. For these regressions, we used post-treatment subplot data with cheatgrass cover as the dependent variable and perennial herbaceous cover as the independent variable. Finally, to determine the effects of treatments on soil climate variables both across and within study sites, we compared cross-site treatment means and standard deviations with those calculated for each site and across treatments within site using subplot data.

Our third set of analyses related vegetation response to site and soil climate conditions. To characterize the climate of our sites, we separately graphed SB and WL site October –June precipitation and mean annual air temperature for 2012 through June 2016 using data collected on-site, and 30-yr means (PRISM 2017). We then tested the effects of October–June precipitation and mean annual temperature (independent variables) on perennial herbaceous and cheatgrass cover on the burn treatment (dependent variables) using simple and multiple regression. To determine vegetation associations with soil climate responses, we used two analyses. First, we calculated Pierson correlations of soil climate variables with vegetation axes scores from our NMS ordinations described above. Second, we used decision tree partition analysis in JMP v 12.1.0 statistical analysis software to analyze data from SB and WL burn plots combined (SAS Institute 2015). Partition analysis finds independent variables that best predict groups of a dependent variable. We primarily used data from burn plots because the burn treatment was most similar across both SB and WL sites and because annual plants and cheatgrass are most likely to dominate after fire. That makes burn treatment analysis our best indicator of climate effects on annual plant response. In decision tree analysis, the LogWorth statistic is used to determine the independent variables that make the optimal splits of groups of the dependent variable. A hierarchical tree of splits is produced which associates groups and subgroups of the dependent variable with a partition or cutoff value of an independent variable. In our partition analyses, the dependent variable was either perennial native herbaceous or cheatgrass cover, and the independent variables were seasonal soil climate variables. A second partition analysis was also run to determine how soil climate variables on untreated plots associated with perennial herbaceous and cheatgrass cover on burn plots. A final partition analysis was conducted to determine associations of perennial grass and cheatgrass cover with soil variables measured at 50 cm deep.

Results

Plant community patterns indicated by NMS axes

Ordination results indicated that annual and perennial herb cover represented major gradients from low to high cover across our sites and treatments. Near-perpendicular axes of annual and perennial herbaceous cover of all ordinations confirmed a negative relationship between these variables. All NMS ordinations were significant ($P < 0.01$), as determined by randomization tests

(Peck 2016). Ordination of SB vegetation using data from untreated, burned, mowed, and tebuthiuron-treated plots indicated that three axes explained 84.3% of the variability with axes 1, 2, and 3 accounting for 55.8%, 26.8%, and 1.7% of the variation (stress = 7.98; Fig. 1). Axis 1 depicted a gradient from more shrub (lower scores) to more perennial herbaceous dominance (higher scores) as indicated by correlation of vegetation functional groups with axis scores (Table 2). Axis 2 represented a gradient from more bare ground (higher scores) to more annual forb and cheatgrass cover (lower scores). Axis 3 represented a gradient from more bare ground (higher scores) to more short grass cover (lower scores). Treatment centroids indicated that the burn and mow treatments were associated with more perennial herbaceous and annual cover, with no treatment and tebuthiuron treatment being associated with more bare ground and less annual and perennial herbaceous cover (Fig. 2).

Ordination of WL vegetation indicated that two axes explained 93.6% of the variability with axes 1 and 2 accounting for 62% and 31.6% of the variation (stress = 13.8; Fig. 2). Axis 1 represented a gradient from low to high perennial herbaceous cover, as indicated by vegetation functional group correlations with NMS scores (Table 2). Axis 2 represented a gradient from low to high annual forb and cheatgrass cover. The

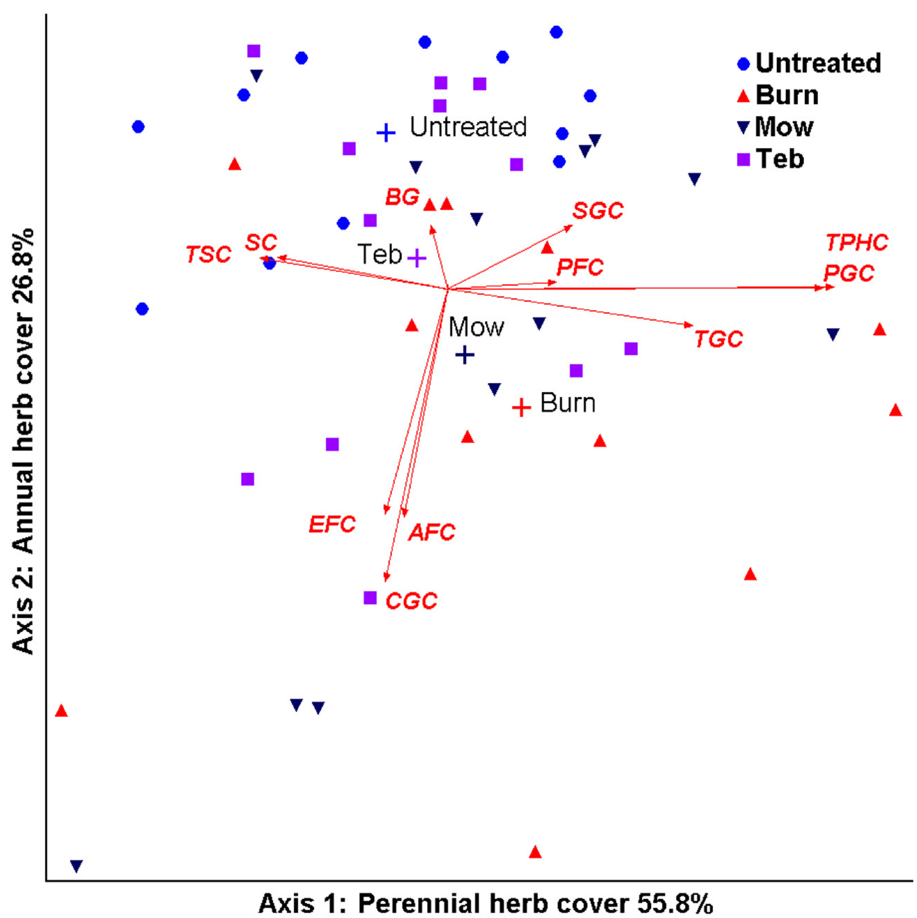


Fig. 1. Non-metric dimensional scaling ordination of vegetation cover on six sagebrush sites and four fuel control treatments. Teb, tebuthiuron treatment; BG, bare ground; AFC, annual forb; CGC, cheatgrass; EFC, exotic forb; TSC, shrub; SC, sagebrush; SGC, short grass (Sandberg blue grass); TGC, tall grass; PGC, perennial grass; PFC, perennial forb; TPHC, perennial herbaceous. Length of red lines for these variables indicates correlation with axis scores.

Table 2. Correlation statistics of vegetation cover variables with non-metric dimension scaling ordination axes for sagebrush and woodland sites and fuel control treatments and for prescribed burn treatments on all sites.

		Axis 1		Axis 2		Axis 3	
Site type or treatment	Vegetation	r	r^2	r	r^2	r	r^2
Sagebrush	Sagebrush	−0.638	0.407	0.277	0.077	−0.355	0.126
	Shrub	−0.671	0.45	0.272	0.074	−0.309	0.096
	Perennial forb	0.511	0.261	0.13	0.017	−0.095	0.009
	Tall grass	0.766	0.587	−0.297	0.088	0.183	0.034
	Short grass	0.546	0.298	0.391	0.153	−0.575	0.331
	Perennial grass	0.949	0.901	0.036	0.001	−0.127	0.016
	Perennial herbaceous	0.963	0.926	0.06	0.004	−0.135	0.018
	Cheatgrass	−0.389	0.151	−0.837	0.701	−0.339	0.115
	Annual forb	−0.324	0.105	−0.739	0.546	0.33	0.109
	Exotic forb	−0.389	0.151	−0.734	0.539	0.287	0.083
	Bare ground	−0.204	0.041	0.39	0.152	0.656	0.43
Woodland	Sagebrush	0.138	0.019	−0.191	0.036	–	–
	Shrub	0.315	0.099	−0.184	0.034	–	–
	Perennial forb	0.252	0.063	0.244	0.06	–	–
	Tall grass	0.879	0.773	−0.059	0.003	–	–
	Short grass	0.534	0.285	0.309	0.096	–	–
	Perennial grass	0.966	0.933	0.05	0.002	–	–
	Perennial herbaceous	0.968	0.938	0.13	0.017	–	–
	Cheatgrass	0.408	0.166	0.869	0.754	–	–
	Annual forb	0.241	0.058	0.822	0.675	–	–
	Exotic forb	0.26	0.068	0.82	0.672	–	–
	Bare ground	−0.87	0.757	−0.477	0.227	–	–
Sagebrush and woodland burn plots	Sagebrush	−0.48	0.23	−0.18	0.032	–	–
	Shrub	−0.406	0.165	−0.114	0.013	–	–
	Perennial forb	0.246	0.061	−0.171	0.029	–	–
	Tall grass	0.907	0.823	−0.018	0	–	–
	Short grass	0.525	0.276	−0.086	0.007	–	–
	Perennial grass	0.956	0.914	−0.021	0	–	–
	Perennial herbaceous	0.97	0.941	−0.086	0.007	–	–
	Cheatgrass	0.099	0.01	−0.865	0.748	–	–
	Annual forb	0.159	0.025	−0.842	0.709	–	–
	Exotic forb	0.192	0.037	−0.88	0.775	–	–
	Bare ground	−0.719	0.517	0.624	0.39	–	–

Note: "–" indicates a blank space because the Woodland and Sagebrush and Woodland burn plot models had no axis 3 and therefore no correlation statistics for that axis.

mechanical treatment centroid indicated an association with more perennial herbaceous cover, while the burn treatment centroid indicated an association with more annual forb and cheatgrass cover.

Ordination of SB and WL vegetation combined on burned plots indicated that two axes explained 95.1% of the variation (stress = 10.8, Fig. 3). Axis 1 accounted for 46.8% of the variation and was associated with perennial herbaceous cover (Table 2). Axis 2 accounted for 48.3% of the variation and was associated with annual forb and cheatgrass cover. Based on these NMS results, we choose cheatgrass cover to represent resistance and perennial herbaceous cover to represent resilience in our subsequent analyses. Lower cheatgrass cover indicates more resistance to population growth of annual invasive grasses (D'Antonio and Thomsen 2004). More perennial herb cover indicates greater resilience because it represents greater potential of the site to return to a predisturbance state where native bunchgrasses were a key lifeform (Miller et al. 2011).

Vegetation responses to treatments and sites

For the SB sites, only analyses across the imazapic treatments within the untreated and burned plots revealed higher cheatgrass cover

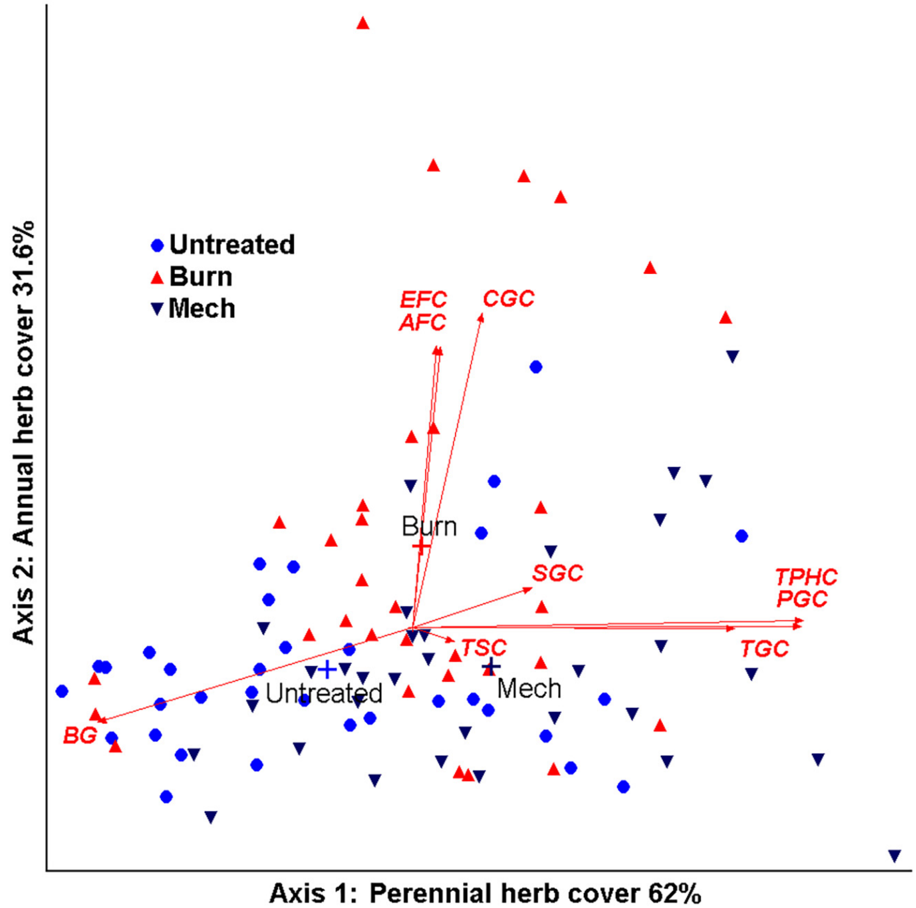


Fig. 2. Non-metric dimensional scaling ordination of vegetation cover on eleven woodland sites and four fuel control treatments. Mech is mechanical tree reduction. See Fig. 1 for abbreviations. Length of red lines for these variables indicates correlation with axis scores.

($P < 0.05$) on burned (15.4% ± 2.3%) than untreated plots (7.5% ± 2.3%; Appendix S1: Table S1). Burning increased ($P < 0.05$) tall grass cover (18.5% ± 2.4%) compared to no treatment (9.1% ± 2.4%) across both no imazapic and imazapic-treated plots, while imazapic decreased short grass cover (8.9% ± 2.2%) compared to no imazapic (10.9% ± 2.2%) across both untreated and burn treatments ($P < 0.05$). Lack of statistically significant differences in treatments across the region was associated with substantial variation in response to treatments at different sites (Fig. 4). For example, burning increased cheatgrass cover compared to pretreatment at the Owyhee, Roberts, and Onaqui sites, while mowing and tebuthiuron increased it at the Owyhee and Roberts sites (Fig. 4). In contrast, burning increased perennial herb cover compared to pretreatment at the Moses Coulee, Saddle Mountain, and Roberts sites; mowing increased it on the Rock Creek, Saddle Mountain, and Owyhee sites; and tebuthiuron increased it somewhat at the Owyhee and Roberts sites (Fig. 4). Owyhee and Roberts had much higher cheatgrass cover than the other sites, while Moses Coulee had higher perennial herb cover than the other sites.

For the WL sites, treatment, time of measurement, and their interaction were significant ($P < 0.05$) for both cheatgrass and perennial herbaceous cover (Appendix S1: Table S1). For WL sites, burning resulted in the highest cheatgrass cover (18.8% ± 3.1%, 6 yr since treatment for all sites except Stansbury which was 2 yr since treatment), while mechanical treatments resulted

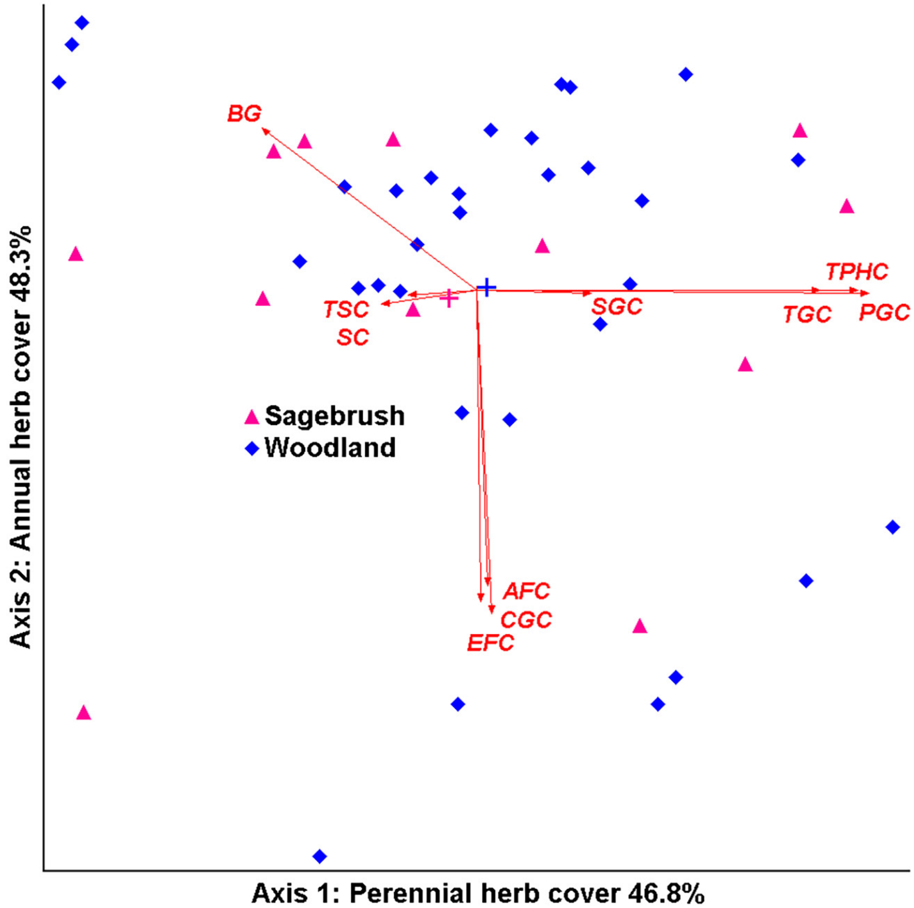


Fig. 3. Non-metric dimensional scaling ordination of vegetation cover on prescribed burn plots for 17 sagebrush and woodland sites. See Fig. 1 for abbreviations. Length of red lines for these variables indicates correlation with axis scores.

in the highest perennial herbaceous cover (31.5% ± 3.4%). As with the SB sites, there was high variation in cover among WL sites (Fig. 4). Burn plots had the highest cheatgrass cover on all sites, but cover varied greatly among the sites from <5% at Walker Butte and Seven Mile to >30% at Stansbury, Scipio, and Greenville (Fig. 4). Mechanical tree reduction produced the highest perennial herbaceous cover on seven of eleven sites, but it varied from <20% at Seven Mile to >30% on mechanical plots at most other sites.

Relationship of cheatgrass cover to perennial herbaceous cover for treatments and sites

We found high variation in cheatgrass and perennial herbaceous cover for both SB and WL subplots across sites. Regressions of cheatgrass cover on perennial herb cover across all sites and by treatment generally had significant intercepts and slopes. However, regression fit varied greatly for SB and WL sites with r^2 values ranging from near zero to 0.89 across the separate sites and treatments, indicating large site-specific differences in cheatgrass and perennial herb cover among subplots across sites for the six years of the study (Appendix S1: Tables S2, S3). Regressions varied in intercepts, slopes, and significance among treatments and sites, indicating site-specific relationships between cheatgrass and perennial herbaceous cover. In general, the ability to detect significant negative effects of perennial herb cover on cheatgrass cover ($P < 0.05$), as indicated by more negative slopes within the treatments, was greater with higher

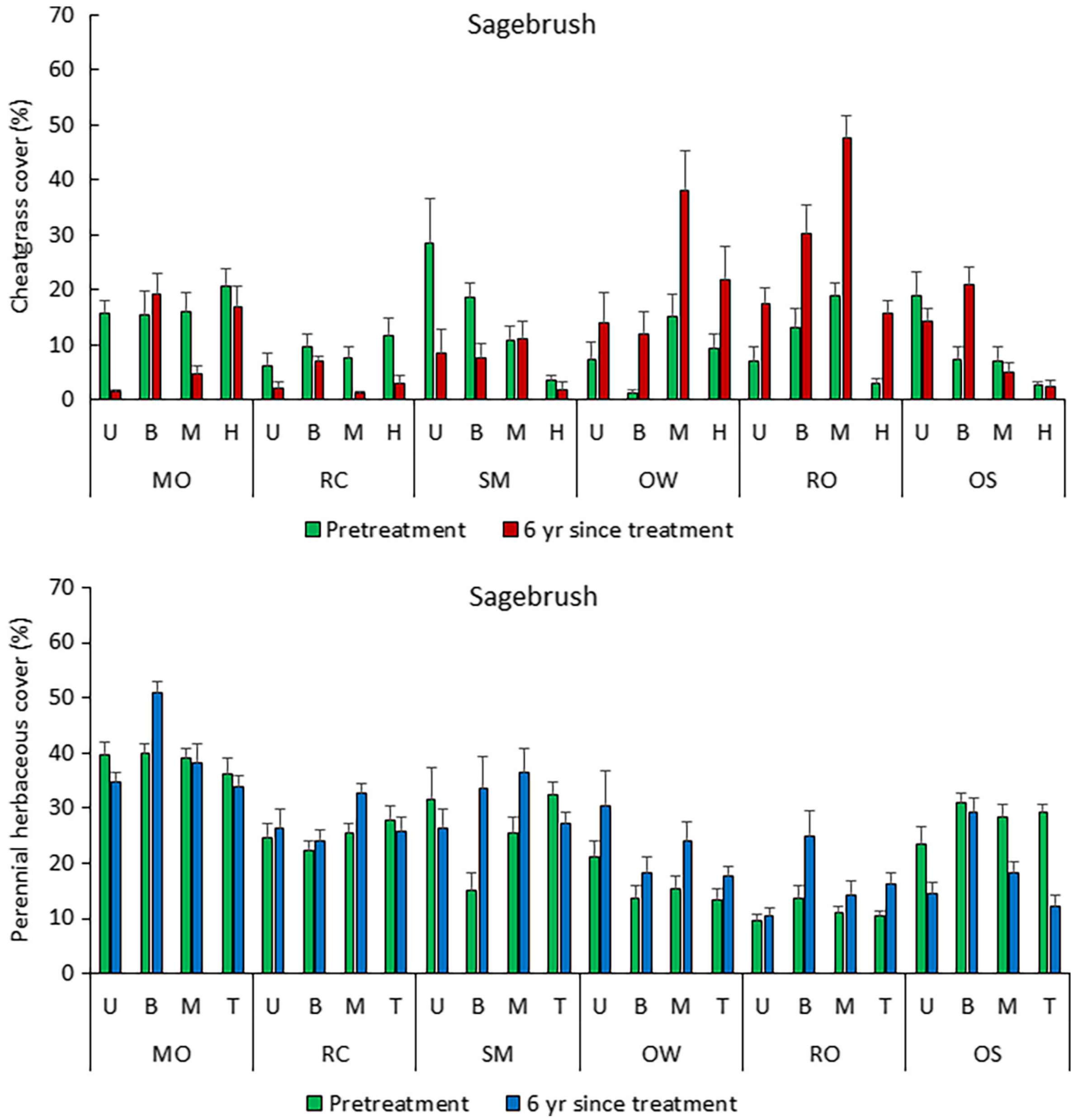
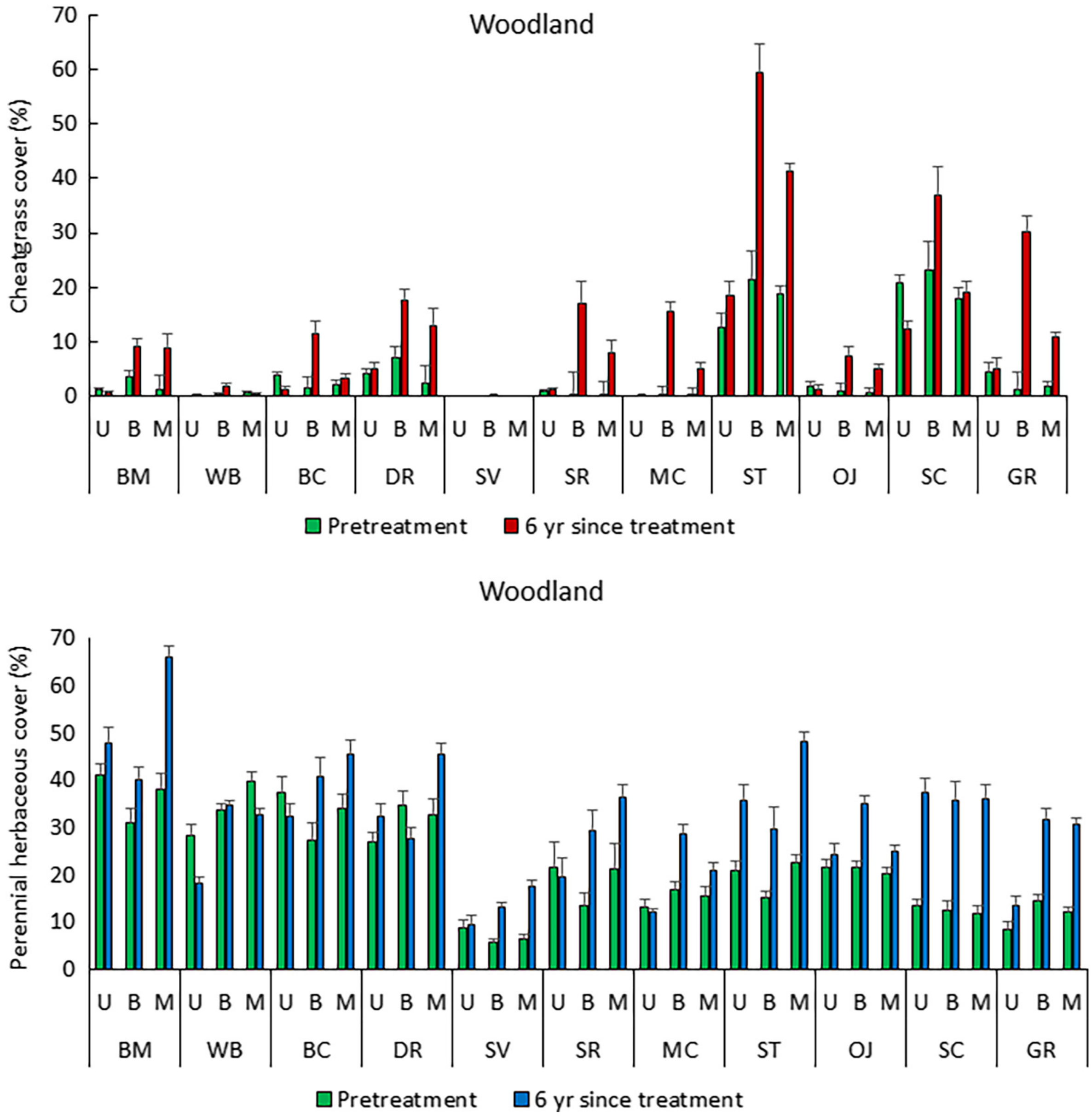


Fig. 4. Pretreatment and post-treatment cover + 1 standard error of cheatgrass and perennial herbs on sagebrush and woodland sites in the Great Basin. Post-treatment is 2 and 3 yr since treatment for the ST and RO sites, and 6 yr after treatment for all other sites. UT, untreated; B, burned; M, mechanical treatment; T, tebuthiuron treatment; and from roughly west to east, sagebrush sites were MO, Moses Coulee Washington; RC, Rock Creek Oregon; SM, Saddle Mountain Washington; OW, Owyhee Nevada; RO, Roberts Idaho; OS, Onaqui sage Utah; and from west to east, woodland sites were BM, Blue Mountain California; WB, Walker Butte, BC, Bridge Creek, and DR, Devine Ridge Oregon; SV, Seven Mile; SR, South Ruby; and MC, Marking Corral Nevada; ST, Stansbury; OJ, Onaqui juniper; SC, Scipio; GR, Greenville Bench Utah.



(Fig. 4. *Continued*)

cover of both cheatgrass and perennial herbaceous species for SB sites when perennial herb cover was greater than that of cheatgrass (Appendix S1: Tables S2, S3). For regressions of separate SB and WL sites and treatments, intercepts were significant ($P < 0.05$) for most treatments within sites, except for no treatment and where cheatgrass cover was less than about 8%. Two relatively warm and dry WL sites, including Stansbury and Scipio, had significant slopes for the burn treatment with cheatgrass cover as high as or higher than perennial herb cover.

Precipitation and air temperature among sites

The SB and WL sites occurred along a gradient of mean annual air temperature and precipitation (Fig. 5). Variation among sites was more pronounced for the relatively warm 2012–2016 study period than the 30-yr mean (PRISM 2017; Fig. 1). For the 2012–2016 period of soil measurements,

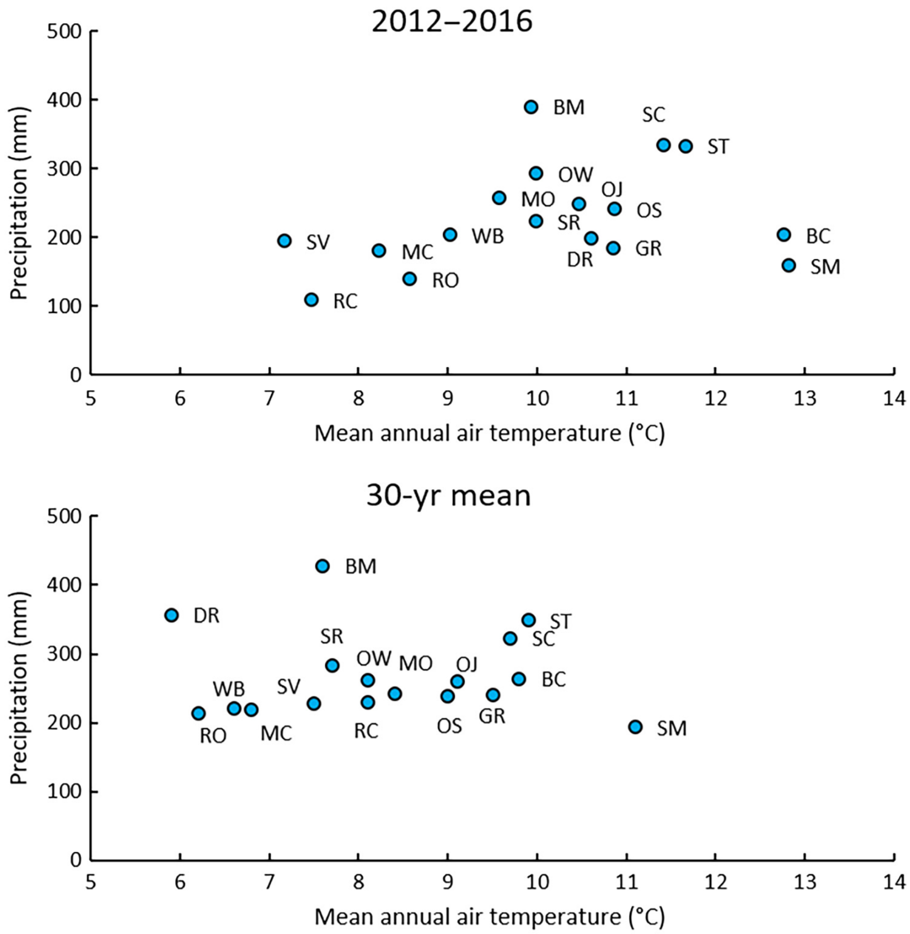


Fig. 5. October–June precipitation and mean annual air temperature for sagebrush and woodland sites from 2012 through June 2016 and 30-yr averages (PRISM 2017). See Fig. 4 caption for site abbreviations.

mean annual air temperatures were 9.9°C and 10.2°C for the SB and WL sites, respectively. Those means were 1.4°C and 2.0°C higher than the 30-yr mean. For the 2012–2016 period of soil measurements, mean October–June precipitation was 200 mm for the SB sites and 245 mm for the WL sites. These amounts were 30 and 43 mm less than the 30-yr average for the SB and WL sites, respectively. The Saddle Mountain SB site was warm and dry, the Stansbury and Scipio WL sites were warm and wet, and the Seven Mile and Marking Corral WL sites and the Roberts SB site were cooler and drier.

Soil climate responses to treatments and sites

Soil climate variables were highly variable among seasons (Appendix S1: Tables S4, S5). Wet degree-days (Table 1), a useful measure of both favorable soil temperatures and water availability for plant growth, was highest in spring. Across SB sites, fall wet days were greater for burn (14.4 ± 1.4) than untreated (11.1 ± 1.4) plots across imazapic treatments and were greater for no imazapic (14.2 ± 1.4) than imazapic plots (11.4 ± 1.4) across untreated and burn treatments ($P < 0.05$). Average soil temperatures were about 1°C higher for burn than untreated plots in early spring, summer, and fall. Degree-days were slightly higher for burn than untreated plots in late spring, but the reverse was true in fall. Standard deviations of soil climate variables for treatments across sites were higher than within sites and across treatments (Appendix S1: Table S4).

Analyzing across all WL sites as blocks, burning increased ($P < 0.05$) mean soil temperatures compared to untreated and mechanical plots for most seasons (Appendix S1: Table S5). Degree-days followed a similar pattern, except that mechanical plots had fewer degree-days than untreated and burn plots in spring. Burning and mechanical tree reduction increased soil temperature and water availability variables compared to no treatment in fall and spring. As with the SB sites, larger standard deviations among WL sites within a treatment than among treatments within a site indicated more effect of site than treatment on soil climate variability (Appendix S1: Table S5).

Correlation of precipitation and air temperature with vegetation cover

For SB and WL sites, October–June precipitation and annual average temperatures either for the 2012 to spring 2016 or the 30-yr means were not significantly correlated alone or together in multiple regression with annual or perennial herbaceous cover on burn plots ($P > 0.05$), which exhibited the largest increases in annual plant cover in response to treatment.

Correlation of vegetation gradients displayed by NMS axes with soil climate variables

For the SB NMS ordination using data for all treatments (Fig. 1), soil climate variables were moderately correlated with vegetation ordination axes (Table 3). Variables associated with warmer and wetter winters and early springs were positively correlated with axis 1 (higher perennial herbaceous cover and lower sagebrush and total shrub cover). Variables with negative correlations with this axis such as average dry period were associated with decreasing perennial herbaceous cover. Soil variables associated with warmer falls, winters, and springs were positively correlated with axis 2, representing cheatgrass and other annual plant cover (Table 3). Variables associated with wetter springs and falls were correlated with axis 3, which represented more short grass cover and lower bare ground.

For the WL ordination (Fig. 2), soil climate variables associated with wetter winters and early springs were positively correlated with axis 1 or perennial herb cover (Table 3). These variables were negatively correlated with bare ground. Variables associated with warmer springs, summers, and falls were most positively correlated with axis 2 or more annual forb and cheatgrass cover (Table 3). We focused much of the remainder of our analysis on the burn treatment because it was the most similar treatment for both SB and WL areas, and because it was most likely to be dominated by cheatgrass. For the ordination of SB and WL burn plots combined (Fig. 3), variables correlated with axis 1 or perennial herbaceous cover indicated positive associations with warmer and wetter winters and warmer springs (Table 3). Although correlations of soil temperature and some soil water availability variables with axis 2 or annual cover were significant ($P < 0.05$) for the burn treatment, they were not very high ($r^2 \leq 0.16$) (Table 3). Because axis 2 scores were more negative as annual forb and cheatgrass cover increased (Fig. 3), negative correlation of soil climate variables with axis 2 scores (Table 3) indicates a positive association between soil climate variables and annual plant cover. Variables representing warmer late springs, summers, and falls were most correlated with increasing cheatgrass cover for SB and WL sites and for burn treatments (Table 3).

Partition analysis of vegetation cover and soil climate variables

Decision tree partition analysis of SB and WL together was used to associate seasonal soil climate variables with either total perennial herbaceous or cheatgrass cover for burned plots. When the decision tree analysis was run for cheatgrass cover as the dependent variable and included all seasonal soil climate variables, summer wet degree-days was selected as the first partition or split. The R^2 for this model was 0.70, and higher cheatgrass cover was associated with warmer and wetter summers, winters, and late springs. However, because summer wet days were very limited on most of our sites (Appendix S1: Tables S4, S5), we reran the partition analysis omitting summer soil climate variables to better see how perennial herbaceous and cheatgrass cover were associated with soil climate for the other seasons. The decision tree model for cheatgrass cover with summer soil climate variables omitted had an R^2 of 0.69 (Table 4). High cheatgrass cover was associated with warmer late springs and warmer and wetter falls (Table 4). If late springs were cooler, higher cheatgrass cover was associated with warmer falls. With this analysis, the model for predicting

Table 3. Correlation statistics for soil temperature and water variables with vegetation cover non-metric dimensional scaling ordination axes for sagebrush and woodlands sites and fuel control treatments and for prescribed burn treatments on all sites.

Site type or treatment	Variable	r	r^2
Axis 1—Perennial herbaceous			
Sagebrush			
Winter	Maximum wet degree-day period	0.57	0.33
	Wet days	0.56	0.32
	Maximum wet day period	0.56	0.31
	Maximum dry day period	−0.54	0.29
	Wet degree-days	0.54	0.29
	Average wet period	0.53	0.28
	Frost-free days	0.50	0.25
Early spring	Mean soil temperature	0.54	0.29
	Minimum soil temperature	0.54	0.29
	Degree-days	0.54	0.29
	Frost-free days	0.50	0.25
Woodland			
Winter	Average wet period	0.58	0.34
	Maximum wet day period	0.54	0.29
	Wet days	0.49	0.24
	Maximum dry day period	−0.45	0.20
	Frost-free days	0.45	0.20
Early spring	Maximum wet day period	0.50	0.25
	Average wet period	0.48	0.23
	Wet days	0.48	0.23
	Maximum dry day period	−0.45	0.20
Sagebrush and woodland burn plots			
Winter	Frost-free days	0.46	0.21
	Dry periods	−0.46	0.21
	Wet periods	−0.42	0.18
	Average wet period	0.39	0.15
Early spring	Wet degree-days	0.41	0.17
	Maximum wet degree-day period	0.40	0.16
	Minimum soil temperature	0.38	0.14
Late spring	Minimum soil temperature	0.44	0.19
	Maximum dry day period	−0.35	0.12
Summer	Minimum soil temperature	0.42	0.18
Axis 2—Annual herbaceous			
Sagebrush			
Winter	Minimum soil temperature	0.61	0.37
	Mean soil temperature	0.58	0.34
	Frost-free days	0.57	0.33
	Maximum dry day period	−0.54	0.29
	Wet degree-days	0.51	0.26
Early spring	Frost-free days	0.60	0.36
Spring	Frost-free days	0.60	0.36
Fall	Frost-free days	0.58	0.34
	Minimum soil temperature	0.56	0.32
	Maximum dry day period	0.46	0.22

(Table 3. Continued.)

Site type or treatment	Variable	r	r^2
Woodland			
Summer	Degree-days	0.57	0.33
	Mean soil temperature	0.57	0.33
	Minimum soil temperature	0.41	0.17
Fall	Degree-days	0.60	0.36
	Mean soil temperature	0.59	0.35
	Wet degree-days	0.30	0.09
Late spring	Mean soil temperature	0.42	0.18
	Wet degree-days	0.42	0.17
Spring	Mean soil temperature	0.37	0.14
Sagebrush and woodland burn plots			
Summer	Degree-days	−0.35	0.12
	Mean soil temperature	−0.35	0.12
	Maximum dry day period	0.29	0.09
	Minimum soil temperature	−0.29	0.08
Fall	Degree-days	−0.39	0.16
	Mean soil temperature	−0.38	0.14
	Minimum soil temperature	−0.29	0.09
Late spring	Degree-days	−0.29	0.08
	Mean soil temperature	−0.29	0.08

perennial herbaceous cover had an R^2 of 0.71 and included six partitions or splits (Table 4). Higher perennial herbaceous cover was associated with fewer winter dry periods, wetter and warmer springs, and cooler falls. For sites with drier winters, more perennial herbaceous cover was associated with wetter and warmer early springs.

We also conducted decision tree analysis of post-fire cheatgrass cover on burn plots using untreated plot soil climate variables as independent variables to estimate how preburn soil conditions associated with post-burn perennial herbaceous and cheatgrass cover. For that analysis, the model R^2 was 0.70 for cheatgrass cover and 0.77 for perennial herbaceous cover (Appendix S1: Table S6). Wetter falls, or if drier, warmer late springs, were associated with more cheatgrass cover while drier falls and cooler late springs were associated with less cheatgrass cover. Warmer and wetter springs were associated with more perennial herbaceous cover, while cooler springs were associated with lower cover.

Partition analysis of cheatgrass and perennial herbaceous cover was also conducted using annual seasonal soil climate variables measured at 50 cm soil depth. Although there was little difference in soil temperatures at this depth between untreated and burned plots, there was a large difference in cheatgrass cover. Therefore, we only used data from burned plots in the analysis. The decision tree model for cheatgrass cover had an R^2 of 0.62 and four splits (Table 5). Greater cheatgrass cover was associated with an average soil temperature at 50 cm ≥12.3°C, as well as a greater maximum dry period, and maximum soil temperatures at 50 cm ≥23.8°C. The model for perennial herbaceous cover had an R^2 of 0.62 and had five splits (Table 5). Greater perennial herbaceous cover was associated with longer average wet periods, an earlier start to the maximum wet period (earlier than 15 April, but later than 28 January), and cooler minimum soil temperatures.

Discussion

Ordination by functional groups indicated that both annual and perennial herbaceous plant cover represented major gradients in pre- and post-treatment plant communities. Because they are directly related to resilience to disturbance and resistance to exotic annual grasses in sagebrush ecosystems (Chambers et al. 2014*a*, *b*), we chose cheatgrass and perennial herbaceous cover as biotic variables to compare plant cover responses after vegetation management treatments to decrease fuels. We found that prescribed fire was the treatment that most increased cheatgrass cover. This result is typical for sagebrush

Table 4. Partition model decision tree estimates of perennial herbaceous and cheatgrass cover for burned sagebrush and woodland plots associated with different ranges of soil variables (13–30 cm soil depth).

Soil variable	Cutoff	Cover (%)	SE	N
Perennial herbaceous cover model R^2 = 0.71				
Winter dry periods (no.)	<2.5	35.2	1.78	34
Spring average wet period (d)	≥50.5	41.7	2.87	12
Early spring wet periods (no.)	≥1.6	48.7	4.08	5
Early spring wet periods (no.)	<1.6	36.7	2.84	7
Spring average wet period (d)	<50.5	31.7	1.91	22
Spring frost-free days	122	41.2	4.2	5
Spring frost-free days	<122	28.9	1.65	17
Fall maximum soil temperature (°C)	<26.1	32.8	2.06	8
Fall maximum soil temperature (°C)	≥26.1	25.4	1.96	9
Winter dry periods (no.)	≥2.5	20.6	3.04	10
Early spring wet degree-days	≥330.3	28.6	2.89	5
Early spring wet degree-days	<330.3	12.6	1.16	5
Cheatgrass cover model R^2 = 0.69				
Late spring degree-days	≥1132.5	25.9	3.37	20
Fall maximum dry day period (d)	<67.2	34.3	4.3	11
Fall frost-free days	≥90.9	41.9	7.25	5
Fall frost-free days	<90.9	27.9	3.91	6
Fall maximum dry day period (d)	≥67.2	15.6	2.77	9
Late spring degree-days	<1132.5	10	1.86	24
Fall minimum soil temperature (°C)	≥1.7	20.2	5.22	5
Fall minimum soil temperature (°C)	<1.7	7.3	1.44	19
Fall minimum soil temperature (°C)	≥−0.82	9.8	1.45	14
Fall average wet period (d)	≥14.7	14.3	2.43	5
Fall average wet period (d)	<14.7	7.2	1.2	9
Fall minimum soil temperature (°C)	<−0.82	0.4	0.32	5

Note: SE, standard error of mean; N, number of observations for each perennial herbaceous or cheatgrass cover group.

ecosystems in the Great Basin region where, depending on severity, fire reduces woody plant cover and may temporarily reduce perennial grass cover, thereby creating high resource availability for exotic annuals such as cheatgrass (Miller et al. 2013). Perennial herbaceous cover typically increases after mechanical tree reduction (Bates et al. 2000, 2005, 2007, Roundy et al. 2014*a*, Bybee et al. 2016, Williams et al. 2017) and over time after fire (Miller et al. 2013, 2014*b*). However, as the current and previous studies found, the effects of both fire and mechanical woody plant reduction on both cheatgrass and perennial herbaceous vegetation can be highly variable across the environmental gradients and site types that characterize these ecosystems (Davis 1979, Bates and Svejcar 2009, Bates et al. 2011, 2013, 2017, Davies et al. 2012*a*, *b*, Miller et al. 2013, 2014*a*, *b*, Chambers et al. 2014*b*, Davies and Bates 2014, Pyke et al. 2014, Roundy et al. 2014*a*, Taylor et al. 2014, Bybee et al. 2016, Havrilla et al. 2017, Williams et al. 2017). Previous studies also found that much of that variability can generally be explained by climate, pretreatment abundance of annual and perennial species prior to treatment, and soil conditions (Chambers et al. 2007, 2014*b*, 2017*a*, Davies and Svejcar 2008, Sankey et al. 2012, Rau et al. 2014).

Environmental conditions such as soil water and temperature have major effects on climate suitability for individual species as well as on interactions between invasive brome grasses and perennial species, especially perennial grasses (Chambers et al. 2016). We found that treatment effects on environmental conditions, as well as background site environmental conditions, influenced vegetation response. Increases in soil temperatures and water availability after fire and mechanical treatments have been associated with greater biomass or cover of both cheatgrass and perennial herbs (Bates et al. 2000, 2002, Blank et al. 2007, Chambers et al. 2007, 2017*a*, Keeley and McGinnis 2007, Rau et al. 2007, 2008, 2014, Allen et al. 2011, Miller et al. 2013, Young et al. 2013*a*, *b*, 2014, Roundy et al. 2014*b*, Aanderud et al. 2017). Tree reduction can greatly increase the time of available water in spring, especially on areas with advanced expansion (Young et al. 2013*b*, Roundy et al. 2014*b*). We found a greater effect of treatments on soil climate variables for tree-expansion (WL) than non-expansion (SB) sites (Appendix S1: Tables S4, S5). Warmer soil and air temperatures are associated with higher seed germination, seed production, and population growth of cheatgrass (Chambers et al. 2007, Roundy et al. 2007, Compagnoni and Adler 2014, Blumenthal et al. 2016). Increased soil temperatures on burned plots and greater wet degree

Table 5. Partition model decision tree estimates of perennial herbaceous and cheatgrass cover (%) for prescribed burn treatments on sagebrush and woodland sites associated with different ranges of soil variables measured at 50 cm soil depth.

Soil variable	Cutoff	Mean	SE	N
Perennial herbaceous cover (%) model R^2 = 0.62				
Average wet period (d)	<24	16	1.54	6
Average wet period (d)	≥24	33.3	1.79	30
Start maximum wet period	≥106.2 (15 April)	24.1	0.87	5
Start maximum wet period	<106.2 (15 April)	34.9	1.75	30
Maximum dry period (d)	<161.5	24.4	1.69	5
Maximum dry period (d)	≥161.5	37	1.56	25
Minimum soil temperature (°C)	<−0.042	43.6	1.49	6
Minimum soil temperature (°C)	≥−0.042	34.9	1.47	19
Start maximum wet period	<28 (28 January)	28.9	1.55	6
Start maximum wet period	≥28 (28 January)	37.6	1.23	13
Cheatgrass cover (%) model R^2 = 0.62				
Average soil temperature (°C)	≥12.3	26.9	4.23	15
Maximum dry day period (d)	≥197.1	39	7.07	6
Maximum dry day period (d)	<197.1	18.1	3.29	9
Average soil temperature (°C)	<12.3	9.5	1.83	26
Maximum soil temperature (°C)	≥23.8	21.1	3.82	8
Maximum soil temperature (°C)	<23.8	6.5	1.29	18
Number of wet periods	≥1.25	10.9	1.47	8
Number of wet periods	<1.25	2.9	1.08	10

Note: SE, standard error of mean; N, number of observations for each cover group.

days on mechanical plots likely stimulated cheatgrass growth (Appendix S1: Tables S4, S5). We did not measure soil climate at seedbed depths in our current analysis. However, Cline et al. (2018*a*, *b*) analyzed seedbed temperature and water potential of our woodland sites and found that burning increased predicted germination of both cheatgrass and perennial grasses. In our current analysis, and except for tree reduction treatments at mid to advanced expansion, variation of soil climate variables among sites and within a treatment was greater than their variation among treatments within a site. Our current analysis shows that soil temperature-related variables measured in the root zone below the seedbed are affected more by site differences than those due to vegetation treatments within a site. This indicates that site environmental conditions influence vegetation treatment responses.

Our results linking warmer and drier soil climate conditions with cheatgrass occurrence and dominance are generally consistent with both survey and experimental approaches that have associated cheatgrass with environmental conditions. Bradford and Lauenroth (2006), Bradley (2009), and Taylor et al. (2014) found that areas with increased summer precipitation were most resistant to cheatgrass due to less favorable conditions for cheatgrass establishment and stronger competition from perennial grasses (Chambers et al. 2016). Warmer temperatures favor cheatgrass, but its primary limitation is growing-season precipitation (Bradley and Mustard 2005, Bradley 2009). Surveys of Condon et al. (2011) and Brummer et al. (2016) and experimental studies of Chambers et al. (2007) confirm that cheatgrass is best adapted to warmer conditions within the Wyoming big sagebrush type where summer precipitation is limited and plants mainly depend on winter and spring soil moisture. Precipitation is also more variable in the Wyoming than mountain big sagebrush zone, resulting in less perennial plant abundance to resist cheatgrass dominance after disturbance (Davis et al. 2000, Chambers et al. 2007). However, Brummer et al. (2016) note that there are areas within the Wyoming big sagebrush type that are not dominated by cheatgrass, even after fire. Other experimental studies have shown that induced warmer temperatures increase cheatgrass cover at higher elevations, depending on water availability as associated with more or less snowpack (Griffith and Loik 2010, Concilio et al. 2013, Compagnoni and Adler 2014). Cheatgrass is projected to spread and dominate where it is already well adapted and where climate changes could increase fire frequency (Abatzoglou and Kolden 2011, Boyte et al. 2016, Coates et al. 2016). It may also expand its range upward in elevation and to the north as temperatures warm and to the east in areas where summer precipitation decreases (Bradley et al. 2016). The range of cheatgrass may contract in warmer and drier areas, but increases in other annual grasses, such as *B. rubens*, may negate any restoration opportunities (Bradley et al. 2016).

Our results generally support these conclusions and emphasize the importance of seasonal climate effects on vegetation trajectories after disturbance. We observed consistent patterns from partition analysis not only for cheatgrass cover, but also for perennial herbaceous cover. Specific independent variables, break points, and groups varied among the three sets of partition models we ran, so we caution about making highly specific inferences about site groupings. However, perennial herbaceous cover was positively associated with wetter soils, specifically wetter winters and early springs (Tables 4, 5). Cheatgrass cover was positively associated with warmer and drier sites, specifically sites with warmer late springs and falls. On sites with cooler late springs, those with warmer falls supported higher cheatgrass cover (Tables 4, 5). Sites with dry or cold falls had less cheatgrass cover. These associations for both perennial herbaceous and cheatgrass cover were also consistent with NMS plant cover score correlations with soil variables (Table 3).

Cheatgrass is most competitive in semi-arid areas like the Great Basin where its life cycle matches the cool-wet winters, and warm, dry summers (Bradford and Lauenroth 2006). Its ability to germinate in many falls (Bradford and Lauenroth 2006, Roundy et al. 2007, Cline et al. 2018*b*) and grow roots through the winter (Harris 1977, Aguirre and Johnson 1991, Nasri and Doescher 1995) makes it competitive with perennial bunchgrasses during the short period in spring and early summer when soil water is available and temperatures are warm enough for rapid growth (Leffler and Ryel 2012). Our results specifically indicate the positive association of warm late springs and warm and wet falls with cheatgrass cover and suggest that sites most prone to fall germination of cheatgrass may be least resistant to its dominance. The ability to germinate in spring (Roundy et al. 2007) supports cheatgrass persistence, but fall-germinated cheatgrass may produce more tillers and seeds than germinants from other seasons (Mack and Pyke 1983, Griffith and Loik 2010). Cheatgrass has relatively high frost tolerance (Bykova and Sage 2012), but fall germination could result in cheatgrass seedling frost mortality (Bradley et al. 2016) because multiple freeze–thaw cycles are common during the winter in the sagebrush steppe where cheatgrass is adapted (Roundy and Madsen 2016). Fall germination could also result in mortality associated with snow cover (Griffith and Loik 2010, Compagnoni and Adler 2014). Cooler temperatures and fewer degree-days at higher elevations are associated with reduced cheatgrass emergence, growth, and seed production (Chambers et al. 2007). On climatically suitable sites, cheatgrass may also be constrained at higher elevations by greater competition from more abundant perennial grasses sustained by more consistent precipitation and soil water availability (Chambers et al. 2007, Roundy et al. 2014*b*). Our results indicate that perennial herbaceous cover is highest on sites with greater availability of soil water in winter and early spring.

While treatments in the sagebrush zone may increase soil water availability and even soil temperatures, response by perennial or annual plants will be heavily influenced by site seasonal soil temperature and water availability. From our partition analysis results, we depict abiotic conditions influencing perennial herbs and cheatgrass in a simple key that shows estimates of relative cheatgrass resistance (Table 6). Sites with the lowest or intermediate abiotic cheatgrass resistance due to soil climate will be most sensitive to treatments that reduce biotic resistance or cover of perennial herbs, such as severe fire or heavy spring grazing. Sites that are more abiotically resistant to cheatgrass are most likely to retain or recover perennial herb cover and resist cheatgrass dominance after disturbance. Uncertainty in seasonal climate projections and highly variable microclimates associated with topographic variability makes projections of cheatgrass–perennial herbaceous dominance difficult, but examining seasonal relationships allows some general predictions (Bradley et al. 2016).

Table 6. Seasonal climatic conditions associated with abiotic resistance to cheatgrass.

Seasonal climatic conditions	Effects on		Resistance to cheatgrass
	Perennial herbs	Cheatgrass	
Wetter winters and early springs	+		
Cooler springs, cool, dry falls		–	Highest
Warm late springs, warm, wet falls		+	Intermediate
Drier winters and early springs	–		
Cooler springs, cool, dry falls		–	Intermediate
Warm late springs, warm, wet falls		+	Lowest

For the northern Great Basin, climate change models predict lower precipitation in October, April, and May, while projecting higher precipitation for winter and early spring and warmer temperatures for fall, winter, and spring (Boyte et al. 2016). Based on these projections and the associations in Table 6, we expect that some sites will move from higher to intermediate cheatgrass resistance due to warmer springs or drier winters and early springs. On the other hand, a decrease in October precipitation could reduce fall cheatgrass germination for some sites and make them slightly more resistant to cheatgrass. While warming trends are expected to increase cheatgrass cover at higher elevations (Bromberg et al. 2011, Compagnoni and Adler 2014), the increase may be geographically small (Boyte et al. 2016). Our results suggest that these increases could be offset by increased winter and early spring precipitation which favors perennial herbs.

Our results generally support the soil temperature/moisture model of sagebrush steppe ecosystem resilience and resistance proposed by Chambers et al. (2014*a*), supported by Chambers et al. (2014*b*), and established into a management framework by Miller et al. (2014*a*), Chambers et al. (2017*b*), and Pyke et al. (2017). This model associates cooler soil temperature and wetter soil moisture regimes with greater resilience and resistance of sagebrush ecosystems. The Chambers et al. (2014*a*) model encompasses warmer-drier (salt desert shrub) and cooler-wetter (mountain brush zone) sites than most of the sites we analyzed in this SageSTEP study. In the Chambers et al. (2014*b*) analysis of 16 SageSTEP sites, Wyoming big sagebrush sites were associated with warmer-drier soil temperature and moisture regimes and lower resilience and resistance than cooler and wetter mountain big sagebrush tree-expansion sites. Wyoming big sagebrush tree-expansion sites fell in the middle of these two and were not as easily categorized as more or less resilient and resistant.

Our analysis of 17 SageSTEP sites indicates that favorable growth conditions in one season may compensate for less favorable conditions in another season for both cheatgrass and perennial herbs. Also, higher perennial herb cover can resist cheatgrass on sites where it is climatically adapted. The Onaqui juniper burn plot is an example of where soil temperature and moisture favor perennial herbs and slightly disfavor cheatgrass, although cheatgrass is definitely adapted, as seen in some dense patches on the site. From the partition analysis (Table 4), the burn plot classified as moderate-to-high potential for perennial herbs associated with wetter winters and lower potential for cheatgrass associated with cooler and drier falls. It had high perennial grass cover, limited cheatgrass cover, and a marginally significant ($P = 0.06$) negative slope between the two (Appendix S1: Table S3). On this site, abiotic conditions and site history support high cover of perennial grasses, which are resisting cheatgrass, even though it is adapted to the site. Many of our other sites are similar to this where cheatgrass is adapted but held more or less in check by perennial herb cover. The two sites with the least cheatgrass cover on burn plots were Walker Butte and Seven Mile. The Walker Butte burn plot had much higher perennial herb cover and associated wetter winters and early springs than Seven Mile (Appendix S1: Table S3). Both sites had cooler late springs and cooler falls and were associated with less cheatgrass potential (Table 4). Slopes of cheatgrass as a function of perennial herb cover were not significant for either of these sites, suggesting that cheatgrass may be climatically controlled on both of these sites, but especially on the Seven Mile site where there is limited perennial herb cover.

Site history and pretreatment perennial herb abundance can interact with climatic conditions and result in more or less perennial herb cover and biotic resistance to cheatgrass. This can make associations of soil climate and vegetation composition and subsequent prediction of resistance and resilience difficult for a specific site. The Stansbury burn plot had the highest cheatgrass cover of all of our sites. According to our partition analysis (Table 4), it has high potential for perennial herbs associated with wetter winters and springs and moderate potential for cheatgrass associated with warmer falls. Perennial herb cover had a significant ($P < 0.0001$) negative association with cheatgrass on this site (Appendix S1: Table S3), and we have observed limited cheatgrass cover on this site where perennial grass cover is high. Higher biotic control of cheatgrass across this site may be limited by the amount of perennial herb cover prior to burning. In contrast, the Saddle Mountain site is the warmest and driest of our sites and classifies as having lower resilience due to drier winters and early springs (Table 4). It is moderately resistant to cheatgrass because it has dry falls (Table 4). However, both cheatgrass and perennial grasses grow well on this site during the warm winters when soil moisture is available. This allows higher cover of perennial grass to resist cheatgrass cover, as indicated by the significant ($P = 0.029$) negative relationship between the two (Appendix S1: Table S2). This example illustrates that even warmer and drier sites can have high resistance to cheatgrass if high perennial herb cover is maintained.

While our results confirm that resistance to cheatgrass and resilience to disturbance are associated with seasonal soil temperatures and water availability in the sagebrush zone, many of our sites were susceptible to increases in cheatgrass cover, especially after fire (Fig. 4), and had soil climate conditions where cheatgrass is adapted. These sites appear to be representative of major areas in the sagebrush biome where cheatgrass is expected to increase in abundance with warming seasonal temperatures (Boyte et al. 2016, Bradley et al. 2016, Coates et al. 2016). We conclude that managing grazing and implementing vegetation treatments in these areas to support the highest potential cover of desirable perennial herbaceous species will best support resilience to wildfire and resistance to cheatgrass. This may include revegetation on sites which lack perennial herb cover.

Acknowledgments

Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. This is contribution number 120 of the Sagebrush Steppe Evaluation Project (SageSTEP) funded by the U.S. Joint Fire Science Program, Bureau of Land Management, National Interagency Fire Center, Great Basin Landscape Conservation Cooperative, and Brigham Young University. The authors thank the many students who collected field data and helped install equipment.

Literature Cited

Aanderud, Z. T., D. R. Schoolmaster, D. Rigby, J. Bybee, T. Campbell, and B. A. Roundy. 2017. Soils mediate the impact of fine woody debris on invasive and native grasses as whole trees are mechanically shredded into fuel breaks in piñon-juniper woodlands. Journal of Arid Environments 137:60–68.

Abatzoglou, J. T., and C. A. Kolden. 2011. Climate change in western US Deserts: potential for increased wildfire and invasive annual grasses. Rangeland Ecology & Management 64:471–478.

Adler, P. B., D. G. Milchunas, O. E. Sala, I. C. Burke, and W. K. Laurenroth. 2005. Plant traits and ecosystem grazing effects: comparison of U.S. sagebrush steppe and Patagonia steppe. Ecological Applications 15:774–792.

Aguirre, L., and D. A. Johnson. 1991. Influence of temperature and cheatgrass competition on seedling development of two bunchgrasses. Journal of Range Management 44:347–354.

Allen, E. B., R. J. Steers, and S. Dickens. 2011. Impacts of fire and invasive species on desert soil ecology. Rangeland Ecology & Management 64:450–462.

Balch, J. K., B. A. Bradley, D. M. D'Antonio, and J. Gómez-Dans. 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980-2009). Global Change Biology 19:173–183.

Bates, J. D., K. W. Davies, A. Hulet, R. F. Miller, and B. A. Roundy. 2017. Sage grouse groceries: forb response to piñon-juniper treatments. Rangeland Ecology & Management 70:106–115.

Bates, J. D., K. W. Davies, and R. N. Sharp. 2011. Shrub-steppe early succession following juniper cutting and prescribed fire. Environmental Management 47:468–481.

Bates, J. D., R. F. Miller, and T. J. Svejcar. 2000. Understory dynamics in cut and uncut western juniper woodlands. Journal of Range Management 53:119–126.

Bates, J. D., R. F. Miller, and T. Svejcar. 2005. Long-term successional trends following western juniper cutting. Rangeland Ecology & Management 58:533–541.

Bates, J. D., R. F. Miller, and T. Svejcar. 2007. Long-term vegetation dynamics in a cut western juniper woodland. Western North American Naturalist 67:549–561.

Bates, J. D., R. O'Connor, and K. W. Davies. 2014. Vegetation recovery and fuel reduction after seasonal burning of western juniper. Fire Ecology 10:27–48.

Bates, J. D., R. N. Sharp, and K. W. Davies. 2013. Sagebrush steppe recovery after fire varies by development phase of *Juniperus occidentalis* woodland. International Journal of Wildland Fire. https://doi.org/10.1071/WF12206

Bates, J. D., and T. J. Svejcar. 2009. Herbaceous succession after burning of cut western juniper trees. Western North American Naturalist 69:9–25.

Bates, J. D., T. J. Svejcar, and R. F. Miller. 2002. Effects of juniper cutting on nitrogen mineralization. Journal of Arid Environments 51:221–234.

Blank, R. R., J. Chambers, B. Roundy, and A. Whittaker. 2007. Nutrient availability in rangeland soils: influence of prescribed burning, herbaceous vegetation removal, overseeding with *Bromus tectorum*, season, and elevation. Rangeland Ecology & Management 60:544–655.

Blank, R. R., and T. Morgan. 2012. Suppression of *Bromus tectorum* L. by established perennial grasses: potential mechanism – part one. Applied and Environmental Soil Science 2012:Article ID 632172. https://doi.org/10.1155/2012/632172

Blumenthal, D. M., J. A. Kray, W. Ortmans, L. H. Ziska, and E. Pendall. 2016. Cheatgrass is favored by warming but not CO_2 enrichment in a semi-arid grassland. Global Change Biology. https://doi.org/10.111/gcb.13278

Boyte, S. P., B. K. Wylie, and D. J. Major. 2016. Cheatgrass percent cover change: comparing recent estimates to climate change-driven prediction in the Northern Great Basin. Rangeland Ecology & Management 69:265–279.

Bradford, J. B., and W. K. Lauenroth. 2006. Controls over invasion of *Bromus tectorum*: the importance of climate, soil, disturbance, and seed availability. Journal of Vegetation Science 17:693–704.

Bradley, B. A. 2009. Regional analysis of the impacts of climate change on cheatgrass invasion shows potential risk and opportunity. Global Change Biology 15:196–208.

Bradley, B. A., C. A. Curtis, and J. C. Chambers. 2016. *Bromus* response to climate and projected changes with climate change. Pages 257–274 *in* M. J. Germino, J. C. Chambers, and C. S. Brown, editors. Exotic brome grasses in arid and semiarid ecosystems of the western US. Causes, consequences, and management implications. Springer Series on Environmental management. Springer International Publishing, Basel, Switzerland.

Bradley, B. A., and J. F. Mustard. 2005. Identifying land cover variability distinct from land cover change: cheatgrass in the Great Basin. Remote Sensing of Environment 94:204–213.

Bristow, N. A., P. J. Weisberg, and R. J. Tausch. 2014. A 40-year record of tree establishment following chaining and prescribed fire treatments in singleleaf pinyon (*Pinus monophylla*) and Utah juniper (*Juniperus osteosperma*) woodlands. Rangeland Ecology & Management 67:389–396.

Bromberg, J. E., S. Kumar, C. S. Brown, and T. J. Stohlgren. 2011. Distributional changes and range predictions of downy brome (*Bromus tectorum*) in Rocky Mountain National Park. Invasive Plant Science and Management 4:173–182.

Brooks, M. L., C. S. Brown, J. C. Chambers, C. M. D'Antonio, J. E. Keely, and J. Belnap. 2016. Exotic annual *Bromus* invasions: comparisons among species and ecoregions in the western United States. Pages 11–60 *in* M. J. Germino, J. C. Chambers, and C. S. Brown, editors. Exotic brome grasses in arid and semiarid ecosystems of the western US. Causes, consequences, and management implications. Springer Series on Environmental management. Springer International Publishing, Basel, Switzerland.

Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. BioScience 54:677–688.

Brummer, T. J., K. T. Taylor, J. Rotella, B. D. Maxwell, L. J. Rew, and M. Lavin. 2016. Drivers of *Bromus tectorum* abundance in the western North American sagebrush steppe. Ecosystems 19:986–1000.

Burkhardt, J. W., and E. W. Tisdale. 1976. Causes of juniper invasion in southwestern Idaho. Ecology 57:472–484.

Butterfield, B. J., S. M. Copeland, S. M. Munson, C. M. Roybal, and T. E. Wood. 2016. Prestoration: using species in restoration that will persist now and in the future. Restoration Ecology. https://doi.org/10.1111/rec.12381

Bybee, J., B. A. Roundy, K. R. Young, A. Hulet, D. B. Roundy, L. Crook, Z. Aanderud, D. L. Eggett, and N. L. Cline. 2016. Vegetation response to piñon and juniper tree shredding. Rangeland Ecology & Management 69:224–234.

Bykova, O., and R. F. Sage. 2012. Winter cold tolerance and geographic range separation of *Bromus tectorum* and *Bromus rubens*, two severe invasive species in North America. Global Change Biology 18:3654–3663.

Campbell Scientific. 1983. Model 227 Delmhorst cylindrical soil moisture block manual. Campbell Scientific, Logan, Utah, USA.

Caudle, D., J. DiBenedetto, M. Karl, H. Sanchez, and C. Talbot. 2013. Interagency ecological site handbook for rangelands. http://jornada.nmsu.edu/sites/jornada.nmsu.edu/files/InteragencyEcolSiteHandbook.pf

Chambers, J. C., D. A. Board, B. A. Roundy, and P. J. Weisberg. 2017*a*. Removal of perennial herbaceous species affects response of cold desert shrublands to fire. Journal of Vegetation Science. https://doi.org/10.111/jvs.12548

Chambers, J. C., J. D. Maestas, D. A. Pyke, C. S. Boyd, M. Pellant, and A. Wuenschel. 2017*b*. Using resilience and resistance concepts to manage persistent threats to sagebrush ecosystems and greater sage-grouse. Rangeland Ecology & Management 70:149–164.

Chambers, J. C., B. A. Bradley, C. A. Brown, C. D'Antonio, M. J. Germino, S. P. Hardegree, J. B. Grace, R. F. Miller, and D. A. Pyke. 2014*a*. Resilience to stress and disturbance, and resistance to *Bromus tectorum* L. invasion in the cold desert shrublands of western North America. Ecosystems 17:360–375.

Chambers, J. C., R. F. Miller, D. I. Board, J. B. Grace, D. A. Pyke, B. A. Roundy, E. W. Schupp, and R. J. Tausch. 2014*b*. Resilience and resistance of sagebrush ecosystems: implications for state and transition models and management treatments. Rangeland Ecology & Management 67:440–454.

Chambers, J. C., M. J. Germino, J. Belnap, C. S. Brown, E. W. Schupp, and S. B. St. Clair. 2016. Plant community resistance to invasion by *Bromus* species: the roles of community attributes, *Bromus* interactions with plant communities and *Bromus* traits. Pages 275–304 *in* M. J. Germino, J. C. Chambers, and C. S. Brown, editors. Exotic brome grasses in arid and semiarid ecosystems of the western US. Causes, consequences, and management implications. Springer Series on Environmental management. Springer International Publishing, Basel, Switzerland.

Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Whittaker. 2007. What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? Ecological Monographs 77:117–145.

Cline, N. L., B. A. Roundy, and W. F. Christensen. 2018*a*. Using germination prediction to inform seeding potential: I. temperature range validation of germination prediction models for the Great Basin, USA. Journal of Arid Environments 150:71–81.

Cline, N. L., B. A. Roundy, S. Hardegree, and W. Christensen. 2018*b*. Using germination prediction to inform seeding potential: II. comparison of germination predictions for cheatgrass and potential revegetation species in the Great Basin, USA. Journal of Arid Environments 150:82–91.

Coates, P. S., M. A. Ricca, B. G. Prochazka, M. L. Brooks, K. E. Doherty, T. Kroger, E. J. Blomberg, C. A. Hagen, and M. L. Casazza. 2016. Wildfire, climate, and invasive grass interactions negatively impact an indicator species by reshaping sagebrush ecosystems. Proceedings of the National Academy of Sciences USA 113:12745–12750.

Compagnoni, A., and P. B. Adler. 2014. Warming, competition, and *Bromus tectorum* population growth across an elevation gradient. Ecosphere 5:Article 121. https://doi.org/10.1890/es14-00047.1

Concilio, A. L., M. E. Loik, and J. Belnap. 2013. Global change effects on *Bromus tectorum* L. (Poaceae) at its high-elevation range margin. Global Change Biology 19:161–172.

Condon, L., P. L. Weisberg, and J. C. Chambers. 2011. Abiotic and biotic influences on *Bromus tectorum* invasion and *Artemisia tridentata* recovery after fire. International Journal of Wildland Fire 20:1–8.

D'Antonio, C. M., and M. Thomsen. 2004. Ecological resistance in theory and practice. Weed Technology 18:1572–1577.

D'Antonio, C. M., and P. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23:63–87.

Davies, G. M., J. D. Bakker, E. Dettweiler-Robinson, P. W. Dunwiddie, S. A. Hall, J. Downs, and J. Evans. 2012*a*. Trajectories of change in sagebrush steppe vegetation communities in relation to multiple wildfires. Ecological Applications 22:1562–1577.

Davies, K. W., J. D. Bates, and A. M. Nafus. 2012*b*. Mowing Wyoming big sagebrush communities with degraded herbaceous understories: Has a threshold been crossed? Rangeland Ecology & Management 65:498–505.

Davies, K. W., and J. D. Bates. 2014. Attempting to restore herbaceous understories in Wyoming big sagebrush communities with mowing and seeding. Restoration Ecology 22:608–615.

Davies, K. M., C. S. Boyd, J. L. Beck, J. D. Bates, T. J. Svejcar, and M. Gregg. 2011. Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush plant communities. Biological Conservation 144:2573–2584.

Davies, K. W., and T. J. Svejcar. 2008. Comparison of medusahead-invaded and noninvaded Wyoming big sagebrush steppe in southeastern Oregon. Rangeland Ecology & Management 61:623–629.

Davis, W. F. 1979. Mechanical control of sagebrush. Pages 49–53 *in* The Sagebrush Ecosystem: A Symposium. April 1978. Utah State University, Logan, Utah, USA.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88:528–534.

Germino, M. J., J. C. Chambers, and C. S. Brown, editors. 2016. Exotic brome grasses in arid and semiarid ecosystems of the western US. Causes, consequences, and management implications. Springer Series on Environmental management. Springer International Publishing, Basel, Switzerland.

Griffith, A. B., and M. E. Loik. 2010. Effects of climate and snow depth on *Bromus tectorum* population dynamics at high elevation. Oecologia 164:821–832.

Harris, G. 1977. Root phenology as a factor of competition among grass seedlings. Journal of Range Management 30:172–177.

Havrilla, C. A., A. M. Faist, and N. N. Barger. 2017. Understory plant community responses to fuel-reduction treatments and seeding in an upland piñon-juniper woodland. Rangeland Ecology & Management 70:609–620.

Herrick, J. E., J. W. Van Zee, K. M. Havstad, L. M. Burkett, and W. G. Whitford. 2009. Monitoring manual for grassland, shrubland, and savannah ecosystems. University of Arizona Press, Tucson, Arizona, USA.

Keeley, J. E., and C. J. Fotheringham. 2006. Wildfire management on a human dominated landscape: California chaparral wildfires. Pages 69–75 *in* G. Wuerthner, editor. Wildfire – A century of failed forest policy. Island Press, Covelo, California, USA.

Keeley, J. E., and T. W. McGinnis. 2007. Impact of fire and other factors on cheatgrass persistence in a Sierra Nevada ponderosa pine forest. International Journal of Wildland Fire 16:96–106.

Knutson, K. C., D. A. Pyke, T. A. Wirth, R. S. Arkle, D. S. Pilliod, M. L. Brooks, J. C. Chambers, and J. B. Grace. 2014. Long-term effects of seeding after wildfire on vegetation in Great Basin shrubland ecosystems. Journal of Applied Ecology 51:1414–1424.

Leffler, A. J., and R. J. Ryel. 2012. Resource pool dynamics: conditions that regulate species interactions and dominance. Pages 57–78 *in* T. A. Monaco and R. L. Sheley, editors. Invasive plant ecology and management. Linking processes to practice. CAB International, Cambridge, Massachusetts, USA.

Loughlin, T. 2006. Improved experimental design and analysis for long-term experiments. Crop Science 46:2492–2506.

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

McIver, J., and M. Brunson. 2014. Multidisciplinary, multisite evaluation of alternative sagebrush steppe restoration treatments: the SageSTEP project. Rangeland Ecology & Management 67:435–439.

Miller, R. F., J. D. Bates, T. J. Svejcar, F. B. Pierson, and L. E. Eddleman. 2005. Biology, ecology, and management of western juniper (*Juniperus occidentalis*). Technical Bulletin 152, Oregon State University Agricultural Experiment Station, Corvallis, Oregon, USA.

Miller, R. F., J. C. Chambers, and M. Pellant. 2014*a*. A field guide to selecting the most appropriate treatments in sagebrush and pinyon-juniper ecosystems in the Great Basin: evaluating resilience to disturbance and resistance to invasive annual grasses and predicting vegetation response. Gen. Tech. Rep. RMRS-GTR-322. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Miller, R. F., J. Ratchford, B. A. Roundy, R. J. Tausch, A. Hulet, and J. Chambers. 2014*b*. Response of conifer-encroached shrublands in the Great Basin to prescribed fire and mechanical treatments. Rangeland Ecology & Management 67:468–481.

Miller, R. F., J. C. Chambers, D. A. Pyke, F. B. Pierson, and C. J. Williams. 2013. A review of fire effects on vegetation and soils in the Great Basin Region: response and ecological site characteristics. Gen. Tech. Rep. RMRS-GTR-308. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Miller, R. F., R. J. Tausch, E. D. McArthur, D. D. Johnson, and S. C. Sanderson. 2008. Age structure and expansion of piñon-juniper woodlands: a regional perspective in the Intermountain West. Research Paper Report RMRS-RP-69. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Miller, R. F., S. T. Knick, D. A. Pyke, C. W. Meinke, S. E. Hanser, M. J. Wisdom, and A. L. Hild. 2010. Characteristics of sagebrush habitats and limitations to long-term conservation. Studies in Avian Biology. http://sagemap.wr.usgs.-gov/monograph.aspx

Miller, R. F., S. T. Knick, D. A. Pyke, C. W. Meinke, S. E. Hanser, M. J. Wisdom, and A. L. Hild. 2011. Characteristics of sagebrush habitats and limits to long-term conservation. Pages 145–184 *in* S. T.

Knick and J. W. Connelly, editors. Greater sage-grouse – Ecology and conservation of a landscape species and its habitats. University of California Press, Berkeley, California, USA.

Miller, R. F., D. E. Naugle, J. D. Maestas, C. A. Hagen, and G. Hall. 2017. Targeted woodland removal to recover at-risk grouse and their sagebrush-steppe and prairie ecosystems. Rangeland Ecology & Management 70:108.

Miller, R. F., and P. E. Wigand. 1994. Holocene changes in semiarid pinyon-juniper woodlands: response to climate, fire, and human activities in the US Great Basin. BioScience 44:465–474.

Nasri, M., and P. S. Doescher. 1995. Effect of temperature on growth of cheatgrass and Idaho fescue. Journal of Range Management 48:406–409.

O'Connor, C., R. Miller, and J. D. Bates. 2013. Vegetation response to western juniper slash treatments. Environmental Management 52:553–566.

Peck, J. E. 2016. Multivariate analysis for community ecologists: step-by-step. Second edition. MJM Software Design, Gleneden Beach, Oregon, USA.

PRISM climate data. 2017. PRISM climate data. http://prism.oregonstate.edu

Pyke, D. A., S. E. Shaff, A. I. Lindgren, E. W. Schupp, P. S. Doescher, J. C. Chambers, J. S. Burnham, and M. M. Huso. 2014. Region-wide ecological responses of arid Wyoming big sagebrush communities to fuel treatments. Rangeland Ecology & Management 67:455–467.

Pyke, D. A., et al. 2017. Restoration handbook for sagebrush steppe ecosystems with emphasis on greater sage-grouse habitat- Part 3. Site level restoration decisions. U.S. Geological Survey Circular 1426. https://doi.org/10.3133/cir1426

Rau, B. M., R. R. Blank, J. C. Chambers, and D. W. Johnson. 2007. Prescribed fire in a Great Basin sagebrush ecosystem: dynamics of soil extractable nitrogen and phosphorus. Journal of Arid Environments 71:362–375.

Rau, B. M., J. C. Chambers, R. R. Blank, and D. W. Johnson. 2008. Prescribed fire, soil, and plants: burn effects and interactions in the central Great Basin. Rangeland Ecology & Management 61:169–181.

Rau, B. M., J. C. Chambers, D. A. Pyke, B. A. Roundy, E. W. Schupp, P. Doescher, and T. G. Caldwell. 2014. Soil resources influence vegetation and response to fire and fire-surrogate treatments in sagebrush-steppe ecosystems. Rangeland Ecology & Management 67:506–521.

Rau, B. M., D. W. Johnson, R. R. Blank, R. J. Tausch, B. A. Roundy, R. F. Miller, T. G. Caldwell, and A. Lucchesi. 2011. Woodland expansion's influence on belowground carbon and nitrogen in the Great Basin US. Journal of Arid Environments 75:827–835.

Reinhardt, E. D., R. E. Keane, D. E. Calkin, and J. D. Cohen. 2008. Objectives and considerations for wildland fuel treatment in forested ecosystems of the interior western United States. Forest Ecology and Management 256:1997–2006.

Reisner, M. D., P. S. Doescher, and D. A. Pyke. 2015. Stress-gradient hypothesis explains susceptibility to *Bromus tectorum* invasion and community stability in North America's semi-arid *Artemisia tridentata wyomingensis* ecosystems. Journal of Vegetation Science. https://doi.org/10.1111/jvs.12327

Reisner, M. R., J. B. Grace, D. A. Pyke and P. S. Doescher. 2013. Conditions favoring *Bromus tectorum* dominance of endangered sagebrush steppe ecosystems. Journal of Applied Ecology 50:1039–1049.

Romme, W. H., et al. 2009. Historical and modern disturbance regimes, stand structures, and landscape dynamics in piñon-juniper vegetation of the Western United States. Rangeland Ecology & Management 62:203–222.

Rossiter, N. A., S. A. Setterfield, M. M. Douglas, and L. B. Hutley. 2003. Testing the grass-fire cycle: alien grass invasion in the tropical savannahs of northern Australia. Diversity and Distributions 9:169–176.

Roundy, B. A., S. P. Hardegree, J. C. Chambers, and A. Whittaker. 2007. Prediction of cheatgrass field germination potential using thermal accumulation. Rangeland Ecology & Management 60:613–623.

Roundy, B. A., and M. D. Madsen. 2016. Frost dynamics of sagebrush steppe soils. Soil Science Society of America Journal 80:1403–1410.

Roundy, B. A., R. F. Miller, R. J. Tausch, K. Young, A. Hulet, B. Rau, B. Jessop, J. C. Chambers, and D. Eggett. 2014*a*. Understory cover responses to piñon–juniper treatments across tree dominance gradients in the Great Basin. Rangeland Ecology and Management 67:482–494.

Roundy, B. A., K. Young, N. Cline, A. Hulet, R. F. Miller, R. J. Tausch, J. C. Chambers, and B. Rau. 2014*b*. Piñon-juniper reduction increases soil water availability of the resource growth pool. Rangeland Ecology & Management 67:495–505.

Ryel, R. J., A. J. Leffler, C. Ivans, M. S. Peek, and M. M. Caldwell. 2010. Functional differences in water-use patterns of contrasting life forms in Great Basin steppelands. Vadose Zone Journal 9:548–560.

Sankey, J. B., M. J. Germino, T. T. Sankey, and A. N. Hoover. 2012. Fire effects on the spatial patterning of soil properties in sagebrush steppe, USA: a meta-analysis. International Journal of Wildland Fire 21:545–556.

SAS Institute Inc. 2015. JMP 12 specialized models. SAS Institute Inc., Cary, North Carolina, USA.

Summers, D. D., and B. A. Roundy. 2018. Evaluating mechanical treatments and seeding of a Wyoming big sagebrush community 10 yr post treatment. Rangeland Ecology & Management 71:298–308.

Taylor, K., T. Brummer, L. J. Rew, M. Lavin, and B. D. Maxwell. 2014. *Bromus tectorum* response to fire varies with climatic conditions. Ecosystems 17:960–973.

Taylor, J. R., B. A. Roundy, and P. S. Allen. 2007. Soil water sensor accuracy for predicting seedling emergence using a hydrothermal time model. Arid Land Research and Management 21:229–243.

Urza, A. K., P. J. Wesiberg, J. C. Chambers, J. M. Dhaemers, and D. Board. 2017. Post-fire vegetation response at the woodland-shrubland interface is mediated by the pre-fire community. Ecosphere 8: Article e01851.

Warton, D., and F. K. Hui. 2011. The arcsine is asinine: the analysis of proportions in ecology. Ecology 92:3–10.

Williams, C. J., F. B. Pierson, K. E. Spaeth, J. R. Brown, O. Z. Al-Hamdan, M. A. Weltz, and M. H. Nichols. 2016. Incorporating hydrologic data and ecohydrologic relationships into ecological site descriptions. Rangeland Ecology & Management 69:4–19.

Williams, R. E., B. A. Roundy, A. Hulet, R. F. Miller, R. J. Tausch, J. C. Chambers, J. Matthews, R. Schooley, and D. L. Eggett. 2017. Pretreatment tree dominance and conifer removal treatment affect plant succession in sagebrush communities. Rangeland Ecology & Management 70:759–773.

Young, J. A., R. E. Eckert Jr., and R. A. Evans. 1979. Historical perspectives regarding the sagebrush ecosystem. Pages 1–13 *in* The Sagebrush Ecosystem: A Symposium. April 1978. Utah State University, Logan, Utah, USA.

Young, K. R., B. A. Roundy, and D. L. Eggett. 2013*a*. Plant establishment in masticated Utah juniper woodlands. Rangeland Ecology & Management 66:597–607.

Young, K. R., B. A. Roundy, and D. L. Eggett. 2013*b*. Tree reduction and debris from mastication of Utah juniper alter the soil climate in sagebrush steppe. Forest Ecology and Management 310:777–785.

Young, K. R., B. A. Roundy, and D. L. Eggett. 2014. Mechanical mastication of Utah juniper encroaching sagebrush steppe increases inorganic soil N. Applied and Environmental Soil Science. http://dx.doi.org.10.1155/2014/632757

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2417/full