

Effects of elevation and selective disturbance on soil climate and vegetation in big sagebrush communities

BRUCE A. ROUNDY^{1,†} AND JEANNE C. CHAMBERS²

¹Department of Plant and Wildlife Sciences, Brigham Young University, Provo, Utah 84602 USA

²USDA Forest Service, Rocky Mountain Research Station, Reno, Nevada 89509 USA

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Abstract. Changing climatic conditions prompt concerns about vegetation response to disturbance under future compared to past conditions. In this long-term study, we examined soil climate and vegetation differences at lower, mid, and upper elevations in two separate locations in the Great Basin, USA. We hypothesized that soil climate and vegetation associations across the elevational gradient could help predict responses under future warming and drying. We measured soil water availability, soil temperatures, and vegetation cover in relation to fire and perennial herb removal at each elevation for 13–17 yr after treatment. Seasonal soil water availability increased, while soil temperature-related variables decreased with increasing elevation. Soil water availability in spring was positively correlated with October through June precipitation ($r^2 = 0.53$), while water availability in spring through fall was positively correlated with perennial plant cover ($r^2 = 0.65$). Partition models separated low, mid, and high elevations by spring soil water availability and growing degree days when soil water was available ($R^2 = 0.93$). Current soil climate and vegetation conditions at lower elevations could indicate future conditions at higher elevations under a warmer and drier climate. During the first years after removal of perennial grasses and forbs, there was an increase in soil water availability in spring at 13–30 cm soil depth that was associated with sagebrush establishment, particularly at upper elevations. In subsequent years, sagebrush continued to dominate even though little difference in soil water availability existed between disturbed and undisturbed plots. This indicates that quickly establishing sagebrush preempted resources and reduced perennial herb recovery. Resource preemption after disturbance will likely be a major driver of plant succession in the future as in the past. Species that establish best under future warmer and drier conditions are most likely to dominate after disturbance. A negative correlation ($r^2 = 0.34$) between the standard deviation of annual spring soil water availability and perennial vegetation cover, which helps resist annual grass invasion, supports the hypothesis that greater resource fluctuation is associated with greater plant community invasibility. Current responses to fire and loss of native plant cover across elevational gradients can indicate future responses under a warmer and drier climate.

Key words: *Bromus tectorum*; climate change; elevation gradient; fire; herbaceous species removal; plant succession; resource growth pool; plant competition; fluctuating resource hypothesis.

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† **E-mail:** bruce_roundy@byu.edu

INTRODUCTION

Concerns about global climate change prompt increased interest in how environmental

conditions affect vegetation responses to disturbance (Kerns et al. 2018). Responses to disturbance across elevation gradients of warmer and drier to cooler and wetter conditions may

provide insights into the nature of those effects for semiarid areas of the world which are predicted to become warmer and drier (Huang et al. 2016). Space for time substitutions can allow accurate predictions in plant succession when the gradients are similarly scaled (Blois et al. 2013).

Regional climate drives large-scale vegetation patterns, but topography may greatly affect environmental conditions and vegetation responses to disturbance within a region. Sagebrush ecosystems of the Great Basin in the western United States are topographically diverse and provide an excellent study system to examine effects of local climate on vegetation response to disturbance. In the Great Basin, cool, wet winters, and warm, dry summers result in seasonal differences in resource availability and growing conditions (Schlaepfer et al. 2012a,b, Miller et al. 2013, Lauenroth et al. 2014). The rain shadow of the Sierra Nevada mountain range west of the Great Basin region results in a semiarid climate especially sensitive to climate change (Hidy and Klieforth 1990, Wharton et al. 1990). Southwest to northeast trending mountain ranges, coupled with storms that generally track from west to east, create localized climatic patterns that range from warmer and drier to cooler and wetter as elevation increases (West 1988). Analyses of recent climate change in the Great Basin indicate that seasonal soil water availability and soil temperature variables related to plant growth are already changing (Snyder et al. 2019). Climate change projections indicate that higher temperatures combined with decreases in snow-to-rain ratios are likely to accelerate current trends, resulting in decreases in depth of soil water recharge, earlier starts of the growing season, shorter duration of soil water, and ultimately longer periods of dry soil conditions (Palmquist et al. 2016a,b, Gergel et al. 2017).

Vegetation cover in sagebrush systems should increase with increasing elevation and associated increases in soil water availability. The resource growth pool concept (Ryel et al. 2008, 2010, Lefler and Ryel 2012) indicates that growth of sagebrush ecosystem plants is maximized when soil matric potential is >-1.5 MPa in the upper 30 cm of soil. In this zone, plant roots overlap with available nitrogen and soil water is sufficient for nitrogen flow to roots (see also Kulmatiski et al.

2020). Study sites arrayed along elevational gradients and monitored over time can provide empirical information on likely changes in soil climate and the resource growth pool with increased warming and decreased precipitation.

Vegetation responses to small- and large-scale disturbances such as grazing and fire are greatly affected by regional and local climatic patterns, as well as annual variability (Chambers et al. 2017, 2019). In sagebrush ecosystems, resilience to disturbance and resistance to annual plant invasion generally increase as elevation increases, because the climate is cooler and wetter and resources are more consistently available (Chambers et al. 2014a,b, 2017, 2019). Resilience, or ability to regain characteristic ecosystem structure, function, and processes, is associated with perennial plant recovery and resistance to dominance by non-native annuals such as cheatgrass (*Bromus tectorum* L.). A common disturbance is moderately severe fire that kills nonsprouting big sagebrush (*Artemisia tridentata* Nutt.), but allows perennial grasses to survive and regrow (Miller et al. 2013). Heavy spring herbivore grazing that targets perennial grasses but avoids lower palatability sagebrush can result in shrub-dominated communities (Young et al. 2002, Adler et al. 2005, Reisner et al. 2013, Chambers et al. 2017). Rangeland vegetation management and woody plant and non-native plant control are based on the idea that selective control of life forms and species considered undesirable for management goals can release resources for those considered desirable (Vallentine 1989, Krueger-Mangold et al. 2006, Archer and Predick 2014).

Resource availability and preemption by species with adaptive life-history traits have been considered major drivers of post-disturbance succession (Bazzaz 1979, 1990, D'Antonio and Chambers 2006). Initial post-disturbance succession is often dominated by shorter-lived species, which rely on rapid dispersal and growth when resources are highly available. As time since disturbance increases, longer-lived species with larger root systems and canopies result in increased resource acquisition and can preempt resources from shorter-lived life forms (Barbour et al. 1999). Species that are able to quickly colonize disturbed areas and continue to preempt resources are likely to continue to dominate (Prev  y et al. 2010).

In resource-limited environments such as sagebrush ecosystems, resource fluctuation may also affect post-disturbance succession. The fluctuating resource hypothesis suggests that high inter-annual variability in precipitation and soil water can result in periods when resource availability exceeds capacity of the native community to fully utilize those resources (Davis et al. 2000). These periods provide opportunities not only for non-native plant invasion (Davis et al. 2000), but also for establishment and growth of native species.

In 2005, we initiated a mechanistic study to determine effects of removal of perennial herbaceous species (herbicide), nonsprouting sagebrush shrubs (fire), and removal and fire combined on soil temperature and water availability as well as establishment, growth, and reproduction of cheatgrass (Chambers et al. 2007, 2017). Removal of perennial shrubs and especially perennial herbaceous species resulted in higher initial establishment and growth of cheatgrass at lower and mid elevations, but cooler soil temperatures restricted cheatgrass establishment and growth at upper elevations (Chambers et al. 2007). Perennial herbaceous removal resulted in initial increases in soil water availability and associated establishment of sagebrush. After 12–13 yr, sagebrush dominated removal plots, especially at higher elevations (Chambers et al. 2017). This experiment provides a unique opportunity to build on prior work and evaluate relationships among vegetation response to fire and plant removal and seasonal soil water availability and temperatures 13–17 yr after treatment. Study sites arrayed across low, mid, and high elevations in two separate locations allow us to examine: (1) how precipitation, soil climate, and vegetation change with increasing elevation; and (2) how disturbance affects soil climate and associated vegetation response across the elevational gradient. We discuss implications of the results for resource availability, preemption, and fluctuations over time in a warmer and drier climate.

METHODS

Study system

Our study was conducted in the states of Nevada and Utah in the western United States along elevation gradients within watersheds

characterized by big sagebrush vegetation (Chambers et al. 2007). To determine effects of selective disturbance on typical native vegetation at each elevation, we selected study sites at low, mid, and high elevation in each state (Chambers et al. 2017). To better test the fluctuating resource hypothesis of invasibility, we selected three additional sites at low elevation that represented a range of vegetation conditions. Two of these sites in each state were seeded to the introduced perennial grass, crested wheatgrass (*Agropyron cristatum* L. Gaertn.) and had varying amounts of sagebrush. One additional site in Utah was characterized by the native perennial grass, squirreltail (*Elymus elymoides* (Raf.) Swezey), Wyoming big sagebrush (*A. tridentata* Nutt. ssp. *wyomingensis* Beetle & Young), and shadscale (*Atriplex confertifolia* (Torr. & Frém.) S. Watson. In Nevada, sites were located in Underdown Canyon of the Shoshone Mountain Range on the Humboldt-Toiyabe National Forest at 39° north latitude, 117° 30' west longitude at low (1960 m), mid (2190 m), and high (2380 m) elevations. The crested wheatgrass site in Nevada was also in the Shoshone Range about 7 km southwest of the low elevation site at similar elevation (2060 m) on land managed by the Bureau of Land Management. In Utah, sites were located in the East Tintic Range on land administered by the Bureau of Land Management's Fillmore Field Office at 40° north latitude, 112° west longitude at low (1710 m), and mid (2274 m) elevations in Black Rock Canyon and at high (2274 m) elevation in nearby Mill Canyon. The crested wheatgrass (1597 m) and squirreltail (1627 m) sites in Utah were approximately 3 and 5 km north, respectively, of the low elevation site at similar elevations (Blank et al. 2007). All study sites were fenced to prevent livestock grazing prior to conducting the experiment, and the fences were maintained over time.

Study sites were semiarid with most precipitation arriving from November through May as snow or snow mixed with rain. Annual precipitation averaged across the study period (2001–2018) increased with increasing elevation in Nevada and Utah, respectively: low (202 and 301 mm), mid (321 and 445 mm), and high (459 and 521 mm). Mean annual temperatures ranged from about 9.2°C to 7.5°C and decreased with increasing elevation. In Nevada, all sites were

characterized by loam to sandy-loam soils weathered from volcanic rocks (welded-tuff; Blank et al. 2007). In Utah, soils were gravely coarse sandy loams to sandy loams weathered from alluvium and colluvium derived from limestone and volcanic rocks (USDA 2000). Herbaceous cover was generally dominated by perennial grasses on all sites and increased with elevation (Chambers et al. 2017). Low elevation sites were characterized by Wyoming big sagebrush; mid and upper elevation sites by mountain big sagebrush (*A. tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle). Annual invasive grasses were comprised solely of cheatgrass (*Bromus tectorum*).

Experimental design

Our experiment examined the response of the sites arrayed over the elevation gradient to herbaceous species removal and burning. We performed a factorial experiment to assess all combinations of two treatments: herbaceous perennial species removal (0 and 100%, referred to as “intact”, and “removed”) and burning (referred to as “unburned” and “burned”). There were three blocks of each treatment combination per site, and treatments were randomly assigned to plots (2 removal $\times$ 2 burned treatments $\times$ 3 blocks = 12 treatment plots per site). The experiment was initiated in 2001. Individual subplots (3.0 m diameter) were located within each of the shrub-dominated study sites around a focal big sagebrush shrub and were separated by 2 m or more.

Removal treatments were applied in spring of 2001 during active vegetation growth (mid-late May). Herbaceous vegetation was removed by spraying with glyphosate (Roundup, Monsanto, St. Louis, Missouri, USA), a nonspecific herbicide that has no residual activity in soil, at a dosage of 170.5 mL Roundup/4.5 L water. The removal treatment was accomplished by spraying all herbaceous vegetation in the plot.

Burning treatments were applied in 2001 in early to mid-October for Nevada and early November for Utah by USDA Forest Service and Bureau of Land Management fire management personnel. A burn barrel 3.4 m in diameter was placed around each plot, 4.5 kg of clean and weed-free dry straw was added for consistent fuel loading, and the plot was lit with a drip

torch (see Chambers et al. 2007). A portion of each plot was seeded with cheatgrass, immediately after burning to meet objectives of the initial study (Blank et al. 2007, Chambers et al. 2007).

Seedbed environmental monitoring

In summer 2001, soil temperature and matric potential sensors were buried at depths of 1–3, 13–15, and 28–30 cm in cheatgrass seeded and not seeded subplots within each treatment combination (unburned–no removal, burned–no removal, unburned–removal, burned–removal). Thermocouples to measure temperature were installed in two blocks of each treatment combination. Gypsum blocks (Delmhorst, Towaco, New Jersey, USA) were installed in all three blocks and each treatment combination. Data from sensors buried at the lower two depths were used in the current study. Thermocouple and gypsum-block outputs were read every minute and hourly averages recorded using Campbell Scientific, CR-10X microloggers and AM16/32 multiplexers. Soil water potentials down to –1.5 MPa were estimated from gypsum-block electrical resistance using a standard calibration curve (Campbell Scientific 1983). Data were recorded from fall 2002 through spring 2018. We used soil temperature and soil matric potential data to calculate seasonal variables associated with plant growth and cover (Rau et al. 2014, Roundy et al. 2014). Hourly soil water matric potential and temperature data were used to calculate soil climate variables for six seasons: early spring (March–April), late spring (May–June), spring (March–June), summer (July–August), fall (September–November), and winter (December–February). Seasonal variables included wet days, average length of wet period, number of wet periods, wet degree days, degree days, frost-free days, and average soil temperatures (Roundy et al. 2018). Soil climate variables were analyzed across the 13–15 and 28–30 cm depths to represent the resource growth pool (Leffler and Ryel 2012).

Vegetation measurements

We evaluated response of the vegetation community in 2003, 2006, 2011, and 2014, which was 13 yr after initial treatments. The exception was the Utah squirreltail site, which was not

evaluated in 2014. Each treatment plot was divided into four uniform quarters using cardinal directions and two 0.25-m² quadrats were placed within each quarter. Aerial cover was estimated ocularly, and density was counted for all plant species within quadrats. In 2006, 2011, and 2014, sagebrush seedlings (<10 cm in height) and juveniles (10–40 cm in height) were counted in each quadrat. In 2014, height, longest diameter, and diameter perpendicular to the longest diameter were measured for each sagebrush plant rooted in each treatment plot. These measurements were used to calculate individual sagebrush canopy area in m² for the entire subplot.

Statistical analyses

General mixed models were used to test elevation and treatment effects. Elevation and disturbance treatment effects on seasonal wet days and soil temperature-related variables were analyzed across years from 2004 through spring 2018 using data from low, mid, and high elevation sagebrush sites with states as random blocks (Chambers et al. 2017; Tables 1–3). Similarly, treatment effects for the crested wheatgrass sites were analyzed using states as random blocks (Table 1). Wet days from soil water matric potential measured in three complete blocks of each treatment at each study site were analyzed by site for each season across all available years. To represent changes over time, wet days in spring were calculated when data were most complete: 3 and 13 yr after treatment (2004 and 2014) for sagebrush sites at low, mid, and high elevation; 4 and 12 yr after treatment (2005 and 2013) for crested wheatgrass sites; and 3 and 10 yr after treatment (2004 and 2011) for the squirreltail site. Standard errors for these estimates used states as random variables in the elevation and crested wheatgrass analysis and blocks as random variables in the squirreltail analysis. Soil climate variables generally met the assumptions of mixed model analysis as determined by observation of residuals.

We used general mixed model analysis of vegetation cover to evaluate long-term responses to herbaceous species removal and burning for each of the study sites at 2 and 13 yr post-treatment (2014), except for the squirreltail site which was evaluated at 1 and 10 yr post-treatment (2011, Table 4). To test effects of elevation and treatment

on vegetation cover for sagebrush sites (Chambers et al. 2017) and of treatment on the two crested wheatgrass sites, removal and burn treatments were considered as fixed factors and block as random. Vegetation cover percentage was logit-transformed prior to analysis (Warton and Hui 2011). Variables included perennial grass, shrub, forb, total perennial herbaceous, and total perennial cover, as well cover of species of interest such as sagebrush and cheatgrass. Since sagebrush seedling and juvenile density varied greatly among different sites, we used the 3 blocks at each site to estimate means and standard errors by site, year (2006, 2011, 2014), and treatment.

Differences among least squares means for significant fixed effects for both vegetation and soil climate variables were evaluated using the Tukey-Kramer adjustment or pairwise *t*-tests. Effects and differences were emphasized when *P* < 0.1. All analyses were performed using JMP Pro 14 (JMP 2019).

We used decision tree partition models, in a classification tree analysis (JMP 2019, McCune and Grace 2002, Thomas et al. 2020) to predict elevation and perennial vegetation cover using only soil water availability variables or using both soil water and temperature-derived variables (Table 5). Soil water and temperature data were averaged across years 2004 through spring 2018 for low, mid, and high elevation sites for both states with treatments used as observations (2 states × 3 elevations × 4 treatments = 24 observations). Vegetation cover data were from 2014 measurements. The LogWorth statistic was used to determine independent variables and make optimal splits of groups of the dependent variable. A hierarchical tree of splits was produced which associated groups and subgroups of the dependent variable with a partition or cutoff value of an independent variable. Partition models used low, mid, and high elevation categories as dependent discrete variables or perennial vegetation cover as a continuous-dependent variable.

We used simple regression to relate soil climate variables to precipitation (PRISM 2018), elevation, and perennial vegetation cover. To relate soil climate to perennial vegetation cover, we used seasonal soil climate variables averaged across the 2003 through spring 2018 period of measurement and vegetation cover from the 2014

Table 1. *P* values for *F* significance of seasonal wet days in relation to elevation (E), perennial herb removal (R), and burning (B) implemented in 2001.

Effect	Early spring	Late spring	Spring	Summer	Fall	Winter
Sagebrush community						
E	0.9714	0.0029	0.132	0.0783	0.4044	0.9675
R	0.3364	0.6754	0.4895	0.75	0.1784	0.3634
B	0.0646	0.0756	0.02	0.2936	0.2918	0.0513
E × R	0.6103	0.6882	0.7412	0.3193	0.3607	0.4562
E × B	0.467	0.3823	0.3712	0.9708	0.8442	0.114
R × B	0.9649	0.7547	0.9812	0.9961	0.6034	0.1418
E × R × B	0.8636	0.3966	0.5976	0.4673	0.3119	0.2374
Crested wheatgrass community						
R	0.2427	0.8582	0.3455	0.8708	0.7269	0.7254
B	0.6694	0.4856	0.6453	0.886	0.8225	0.9251
R × B	0.8342	0.7393	0.6149	0.252	0.1252	0.5363
Squirreltail community						
R	0.5948	0.6139	0.67	0.142	0.9687	0.1449
B	0.4897	0.8919	0.5676	0.1955	0.6787	0.3791
R × B	0.2322	0.3303	0.2709	0.8063	0.5977	0.5218

Note: Analysis was by season and across years from 2004 through spring 2018. *P* values < 0.1 appear in boldface.

Table 2. Soil temperature-related variables (means ± SE) for sagebrush communities at different elevations and seasons averaged across 2004 through spring 2018.

Elevation	Early spring	Late spring	Spring	Summer	Fall	Winter
Wet degree days						
Low	451.3 ± 44.18 A	460.8 ± 16.24 B	912 ± 33.7 A	106.8 ± 19.95 A	240.9 ± 90.24 A	101.9 ± 22.74 A
Mid	268.5 ± 44.18 A	439.2 ± 15.43 B	701.7 ± 33.47 A	77.9 ± 19.23 A	201.1 ± 89.91 A	28.4 ± 22.74 A
High	150.5 ± 44.26 A	601.1 ± 17.39 A	760.1 ± 34.74 A	138 ± 20.69 A	212.1 ± 90.27 A	40.7 ± 22.81 A
Degree days						
Low	479.7 ± 45.56 A	1121.9 ± 57.89 A	1593.3 ± 100.71 A	1536.4 ± 69.98 A	1137.6 ± 123.66 A	127.5 ± 22.97 A
Mid	270.8 ± 45.56 AB	825.6 ± 57.83 AB	1095.8 ± 100.66 AB	1132.7 ± 69.94 B	734.6 ± 123.62 A	29 ± 22.98 A
High	151.2 ± 45.63 B	779.8 ± 57.98 B	935.9 ± 100.92 B	1168.6 ± 70.03 B	751.6 ± 123.66 A	45.8 ± 23.08 A
Frost-free days						
Low	60.5 ± 5.4 A	61 ± 0.03 A	121.5 ± 5.51 A	62 ± 0.01 A	90.2 ± 7.12 A	57 ± 18.95 A
Mid	51.4 ± 5.4 A	61 ± 0.03 A	112 ± 5.51 A	62 ± 0 A	77.2 ± 7.12 A	25.2 ± 18.96 A
High	48.9 ± 5.4 A	60.9 ± 0.03 A	109.9 ± 5.51 A	62 ± 0.01 A	86.2 ± 7.12 A	43 ± 18.97 A
Soil temperature (°C)						
Low	7.9 ± 0.93 A	18.4 ± 0.95 A	13.1 ± 0.92 A	24.8 ± 1.13 A	12.5 ± 1.62 A	0.9 ± 1.85 A
Mid	4.1 ± 0.93 A	13.5 ± 0.95 B	8.8 ± 0.92 AB	18.3 ± 1.13 B	7.6 ± 1.62 A	−3.1 ± 1.85 A
High	2.3 ± 0.93 A	12.8 ± 0.95 B	7.6 ± 0.92 B	18.8 ± 1.13 B	8.2 ± 1.62 A	−0.6 ± 1.85 A

Note: Means followed by the same letter are not significantly different at *P* < 0.05.

sampling. Treatments within each site were used as observations (9 sites × 4 treatments, *n* = 36 or 6 sites × 4 treatments, *n* = 24). To relate perennial vegetation cover to resource variability, we regressed it on the standard deviation of spring wet days for 6 yr when all sites had complete data (2003, 2004, 2005, 2007, 2008, 2009) using site by treatment data as observations (*n* = 36).

RESULTS

Elevation, seasonal, and annual effects on soil climate

Wet days.—Both mixed model and partition analysis indicated that late spring soil water availability increased with increasing elevation. When analyzed across all years (2004 through

Table 3. Mixed model *P* values for *F* significance of elevation (E) and disturbance treatments on soil temperature-related variables in sagebrush communities.

Effect	Early spring	Late spring	Spring	Summer	Fall	Winter
Wet degree days						
E	0.066	0.032	0.066	0.328		0.049
B	0.442	0.931	0.722	0.813		0.370
R	0.611	0.997	0.785	0.866		0.298
E × B	0.961	0.966	0.983	0.617		0.041
E × R	0.846	0.925	0.696	0.973		0.708
R × B	0.045	0.808	0.539	0.646		0.061
E × B × R	0.466	0.890	0.954	0.698		0.050
Degree days						
E	0.108	0.044	0.732	0.085	0.134	
B	0.299	0.057	0.035	0.595	0.136	
R	0.722	0.681	0.940	0.603	0.605	
E × B	0.990	0.153	0.153		0.363	
E × R	0.804	0.067	0.184	0.112	0.272	
R × B	0.030	0.121	0.374	0.122	0.074	
E × B × R	0.221	0.103	0.503	0.282	0.783	
Frost-free days						
E	0.312	0.538	0.329	0.591	0.468	0.404
B	0.906	0.354	0.946	0.465	0.668	0.935
R	0.472	0.507	0.561	0.466	0.536	0.942
E × B	0.611	0.612	0.607	0.515	0.555	0.553
E × R	0.342	0.404	0.436	0.515	0.275	0.322
R × B	0.525	0.262	0.331	0.436	0.816	0.770
E × B × R	0.322	0.585	0.242	0.534	0.395	0.641
Average soil temperature (°C)						
E	0.070	0.044	0.088	0.084	0.169	0.385
B	0.305	0.057	0.035	0.588	0.305	0.701
R	0.645	0.681	0.987	0.603	0.554	0.439
E × B	0.990	0.153	0.154		0.502	0.311
E × R	0.777	0.067	0.180	0.112	0.338	0.757
R × B	0.029	0.121	0.343	0.122	0.077	0.756
E × B × R	0.212	0.103	0.473	0.282	0.835	0.682

Notes: Treatments were unburned or burned (B) and perennial herbs left intact or removed (R) in 2001. Analysis across years from 2004 through spring 2018. *P* values < 0.1 appear in boldface.

spring 2018) wet days varied most by elevation in late spring (Table 1). A partition model with only seasonal available water variables included (no temperature-related variables) separated elevations by late spring water availability ($R^2 = 0.93$, $n = 6$ sites $\times$ 4 treatments = 24, averaged across all years 2004 through spring 2018; Table 5). Wet days varied seasonally with early spring > winter > late spring > fall > summer (Fig. 1; Appendix S1: Table S2). However, wet days increased with elevation most in late spring and fall (Fig. 1). October through June precipitation was positively correlated with spring wet days (Fig. 2). Seasonal wet days varied most by

year when each site was analyzed separately (Appendix S1: Tables S1, S2). The Nevada crested site had fewer wet days than the lower elevation site while the Utah crested and squirreltail sites had generally similar wet days as the Utah lower elevation site (Appendix S1: Table S2).

Soil temperature-related variables.—Soil temperature variables were generally highest for low elevation sites, and lower for mid and high elevation sites for most seasons (Table 2). Large standard errors and lack of significant differences among elevations for some variables were associated with high annual variability in seasonal temperatures. A partition model that included

Table 4. Mixed model P values for F significance for plant cover variables for sagebrush and crested wheatgrass communities in 2003 and 2014 (first and second post-treatment measurement years, respectively), and for a squirreltail community in 2002 and 2011 (first and second post-treatment measurement years, respectively) in relation to elevation (E), perennial herb removal (R), and burning (B) in 2001.

Effect	Cheatgrass cover		Perennial herb cover		Shrub cover		Total perennial cover	
	First	Second	First	Second	First	Second	First	Second
Sagebrush community								
E	0.6054	0.0232	0.3715	0.1857	0.2336	0.1521	0.2556	0.1537
R	0.0881	0.4132	0.0043	0.0046	0.1856	0.4767	0.0404	0.0253
B	0.1943	0.9123	0.0418	0.9658	0.0002	0.0061	0.0022	0.0137
E $\times$ R	0.4621	0.4942	0.179	0.2527	0.6504	0.5803	0.2782	0.7481
E $\times$ B	0.3037	0.7604	0.0473	0.3458	0.0651	0.0255	0.5408	0.1004
R $\times$ B	0.6837	0.0002	0.5712	0.2601	0.369	0.86	0.2367	0.574
E $\times$ R $\times$ B	0.3524	0.0011	0.9381	0.3851	0.6744	0.3828	0.4309	0.38
Crested wheatgrass community								
R	0.4948	0.5	0.0422	0.2335	0.3696	0.6396	0.0794	0.8778
B	0.4969	0.5	0.9668	0.6829	0.4646	0.0241	0.8703	0.1162
R $\times$ B	0.5075	0.5	0.9382	0.0202	0.8414	0.9992	0.9335	0.8713
Squirreltail community								
R	0.6992	0.1138	0.0355	0.1921	0.4226	0.332	0.0355	0.5876
B	0.7087	0.8188	0.8682	0.2395	0.4226	0.4425	0.8707	0.5497
R $\times$ B	0.1209	0.8804	0.9783	0.0606	0.4226	0.9506	0.9753	0.1338

Note: P values < 0.1 appear in boldface.

Table 5. Partition models to distinguish elevations for sagebrush communities using (1) soil temperature and water variables, (2) soil water variables only, and (3) perennial vegetation cover from both soil temperature and water variables.

Variable	Cutoff	N	Elevation	Cover (%)	SE
1. Predicts elevation from soil water and temperature variables ($R^2 = 0.93$)					
Early spring wet degree days	< 171.3	8	Upper		
Early spring wet degree days	≥ 171.3	16	Lower, mid		
Early spring wet degree days	< 426.4	8	Mid		
Early spring wet degree days	≥ 426.4	8	Lower		
2. Predicts elevation from soil water variables ($R^2 = 0.93$)					
Late spring wet days	≥ 39.7	8	Upper		
Late spring wet days	< 39.7	16	Lower, mid		
Late spring maximum dry period (days)	< 31.9	8	Mid		
Late spring maximum dry period (days)	≥ 31.9	8	Lower		
3. Predicts perennial vegetation cover from soil water and temperature variables ($R^2 = 0.81$)					
Early spring wet periods (no.)	< 1.02	6		54.9	4.45
Early spring wet periods (no.)	≥ 1.02	18		23.3	2.24
Fall average dry period (days)	< 37.7	6		31	3.17
Fall average dry period (days)	≥ 37.7	12		19.5	2.31
Fall wet periods (no.)	< 2.35	5		26	3.39
Fall wet periods (no.)	≥ 2.35	7		14.8	1.63

Notes: Soil water and temperature data are averaged across years 2004 through spring 2018, $n = 24$ (2 states $\times$ 3 elevations $\times$ 4 treatments). Vegetation cover data are from 2014.

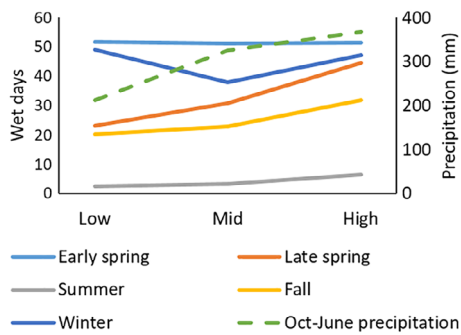


Fig. 1. Seasonal wet days and October through June precipitation for low, mid, and high elevation sagebrush sites averaged over 13–15 yr of available data from 2004 through 2017. Annual standard errors for wet days ranged from 0.67 to 4.04 for all seasons except winter, which ranged from 5.6 to 7.4. Standard errors for precipitation for elevations were low = 15.9 and mid and high = 22.9.

both seasonal available water and temperature-related variables separated low, mid, and high elevations by early spring wet degree days ($R^2 = 0.93$, $n = 6$ sites $\times$ 4 treatments = 24, averaged across all years from 2004 through spring 2018; Table 5).

Effects of disturbance

Wet days.—Disturbance effects and disturbance by year interactions were seldom significant when analyzed for each site separately (Appendix S1: Table S1), indicating that increased soil water availability after disturbance was short-lived on most sites (Fig. 3). When analyzed across years for the sagebrush community, the burn treatment had the least wet days in spring and winter (Table 1). The magnitude of the differences in spring wet days decreased within a few years after burning (Fig. 3). Analyzed across years, no disturbance effects were significant for the crested wheatgrass and squirreltail communities (Table 1).

Soil temperature-related variables.—These variables were only analyzed across years. For the low, mid, and high elevation sagebrush communities, burned plots had higher average soil temperatures (15.1 ± 0.79) in late spring than unburned plots ($P < 0.057$, 14.7 ± 0.79 ; Table 3). There were some significant interactions between fire and perennial herb removal and between disturbance treatment and elevation (Table 3).

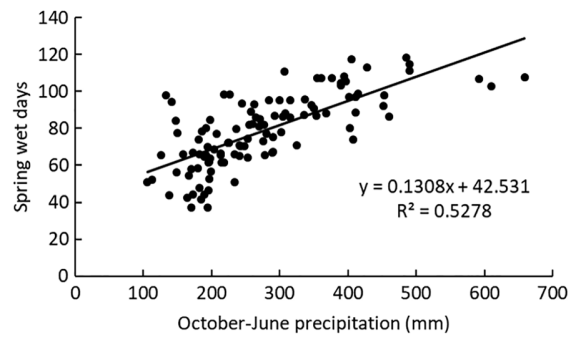


Fig. 2. Spring wet days as a function of PRISM (2018) estimated precipitation from October through June ($n = 109$). Data from one squirreltail, two crested wheatgrass, and two low, mid, and high elevation sagebrush sites from 2004 through spring 2018.

Degree days and average soil temperatures in early spring were lower on perennial herb removal than intact plots when not burned, but were higher on removal than intact plots when burned. For winter and at lower elevation, perennial herb removal plots had greater wet degree days than intact burned plots, whereas for unburned plots at lower elevation or both unburned and burned plots at other elevations, wet degree days were similar for intact and removal treatments. For the crested wheatgrass and squirreltail communities and across all years, soil temperatures and related variables did not vary significantly by disturbance treatment for most seasons.

Vegetation.—Ten years after disturbance cheatgrass cover was low at all elevations and sites and was near zero at high elevation. For the sagebrush communities, cheatgrass cover initially increased following perennial herb removal ($P < 0.09$) in 2003 (Table 4). By 2014, cheatgrass cover was less than in 2003 and the interaction of elevation, perennial herb removal, and burning was significant ($P < 0.001$). At low and mid elevations, cheatgrass cover was slightly higher on burned than unburned plots with intact perennial herbs, but higher on unburned than burned plots with perennial herbs removed (Fig. 4). Cheatgrass cover was inconsistent for treatments but was minimal by 2011 and 2014 on the squirreltail and crested wheatgrass sites.

Across all elevations for the sagebrush, crested wheatgrass, and squirreltail communities,

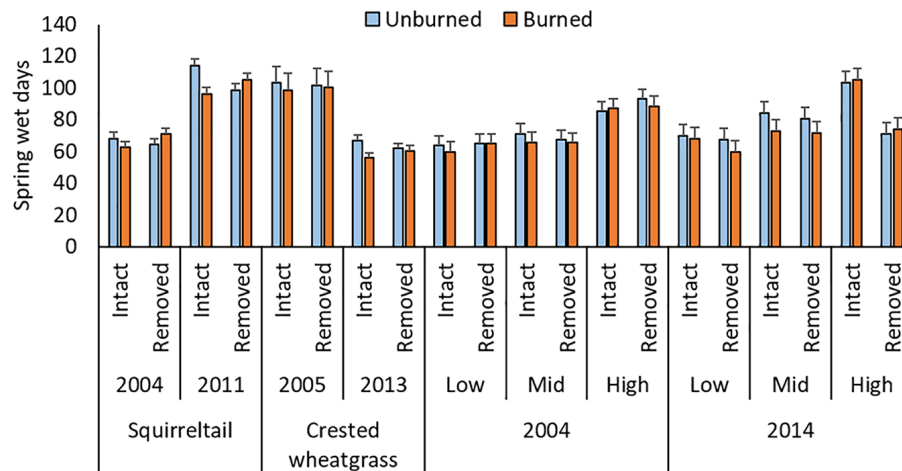


Fig. 3. Wet days in spring for low, mid, and high elevation sagebrush communities as well as squirreltail and crested wheatgrass communities 3–5 yr (2004 and 2005) and 10–13 (2011 and 2014) years after perennial herb removal (removed) and fire. Lines above bars are 1 SE.

perennial herb cover was reduced most by removal and was increasing but still recovering by 2011 or 2014 (Fig. 4). Perennial herb cover on sagebrush, crested wheatgrass, and squirreltail communities was lower on removal compared to intact plots 1–2 yr after treatment, but this effect only persisted for the sagebrush community (Table 4, Fig. 4). For the sagebrush community, removal had a long-term effect on perennial herb cover at all elevations. Intact plots and removal plots had 11.6% and 2.3% perennial herb cover in 2003 and 9.4% and 3.9% in 2014 (Fig. 4). Perennial herbs recovered best at high elevation.

In contrast, perennial herb cover was initially decreased by burning at low elevation but increased at mid and high elevation. By 2014, burning had no effect (Table 4, Fig. 4). Shrub cover was initially reduced by burning, but had recovered at high elevation in 2014 because of high sagebrush seedling establishment (Figs. 4, 5). Sagebrush seedling and juvenile density varied greatly across sites and years but where initial establishment was high, it decreased over time as recruited sagebrush plants increased in size (Fig. 5). Shrub recovery from burning was less at low and mid elevations. Effects of burning and removal on shrub cover varied between the Nevada and Utah crested wheatgrass sites. Shrub cover was increased by removal especially

on the Nevada site due to increased sagebrush establishment (Fig. 5).

Vegetation and soil climate

Total perennial cover was positively correlated with spring through fall wet days for all sites ($P < 0.0001$, $r^2 = 0.041$, $n = 9$ sites $\times$ 4 treatments = 36) and for only the sagebrush communities ($P < 0.0001$, $r^2 = 0.65$, $n = 6$ sites $\times$ 4 treatments = 24, Fig. 6). A partition model using available water and soil temperature variables from the sagebrush communities indicated that total perennial vegetation was positively associated with fewer early spring and fall wet periods ($R^2 = 0.81$, Table 5). Total perennial vegetation was greatest at high elevation where the number of early spring wet periods was < 1.02 , meaning that early spring generally had one long wet period, rather than intermittent wet and dry periods. Lowest perennial cover was associated with lower elevations and with less consistent available moisture in early spring (more wet periods, indicating intermittent wet and dry periods) and similarly less consistent wet periods and longer average dry periods in fall. The standard deviation of spring wet days across 6 yr when data were available for all sites was significantly negatively correlated with perennial vegetation cover in 2014 ($r^2 = -0.34$, $P < 0.0002$, Fig. 6).

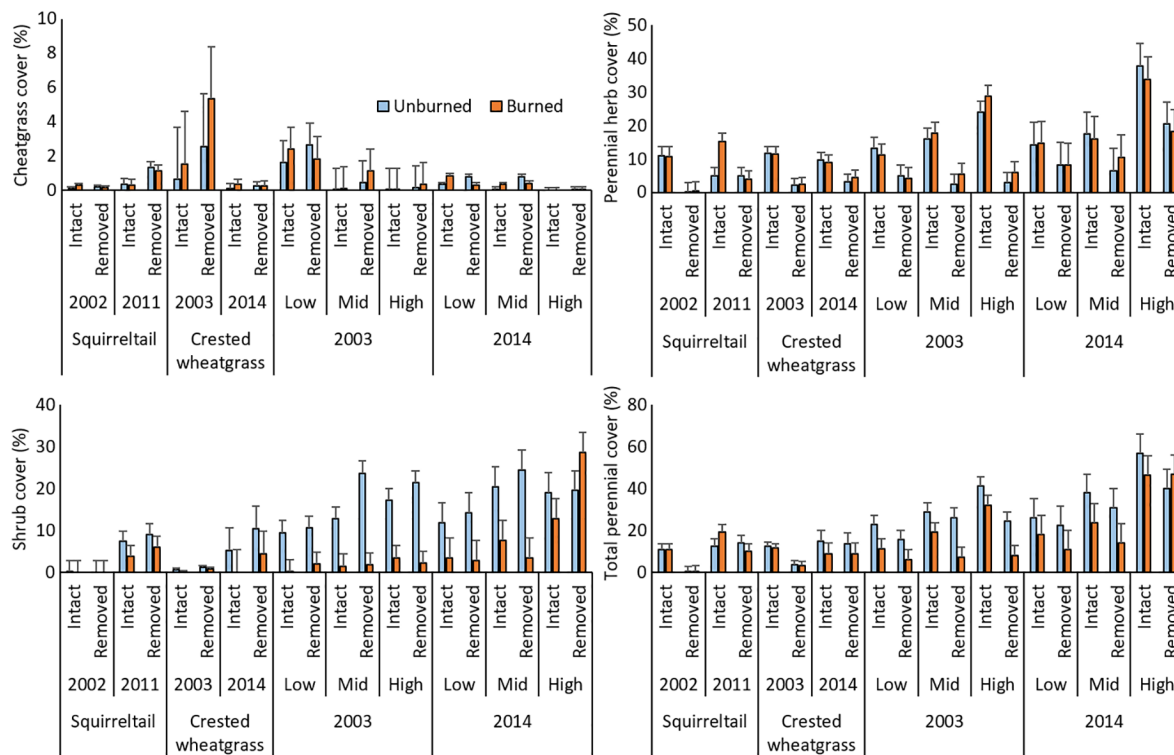


Fig. 4. Plant cover for squirreltail, crested wheatgrass, and sagebrush communities at low, mid, and high elevation after no disturbance (intact, unburned), perennial herb removal, and burning in 2001. Lines above bars are 1 SE.

DISCUSSION

Elevation effects and future changes in climate and vegetation

Our results associate soil climate and vegetation cover across an elevation gradient. We found that longer periods of soil water availability at 13–30 cm soil depth were associated with increasing elevation and greater sagebrush and perennial herb cover, indicating greater productivity (Figs. 2, 3). This supports the resource growth pool concept of Leffler and Ryel (2012) and the findings of Kulmatiski et al. (2020) that plant growth in sage-steppe systems is associated with resource availability at relatively shallow soil depths. We were also able to associate Great Basin soil climate across the elevation gradient with easily measured climate variables (Fig. 2). We were able to identify seasonal differences in soil climate across an elevation gradient. Lower elevation communities were warmer and drier, especially in late spring and fall, while upper

elevation communities were cooler and wetter (Tables 3–5). Higher elevation communities had longer periods of soil water availability than mid elevation communities in late spring and summer. These findings allow us to generally use elevation differences in soil climate and vegetation to estimate changes under a warming climate.

Species distribution model predictions for big sagebrush vary but generally indicate that warmer and drier conditions in the future could support sagebrush at northerly regions and higher elevations (Schlaepfer et al. 2012b). Our results generally support this prediction by showing that big sagebrush cover and total perennial cover currently increase at higher elevations following disturbance (Fig. 4). In big sagebrush sites across the western United States, winter and spring precipitation is projected to increase in some areas and decrease in others (Snyder et al. 2019), but late spring and summer water availability is projected to decrease due to warming effects on the hydrological cycle and increased

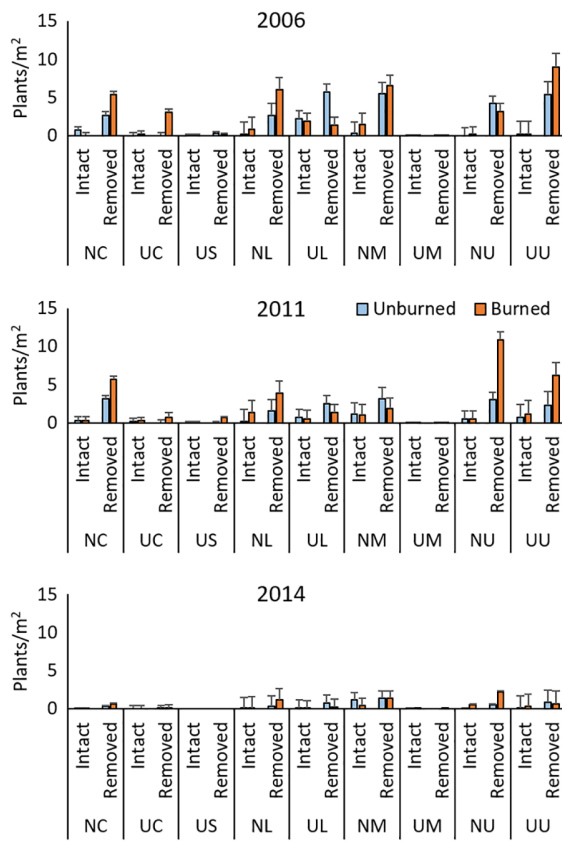


Fig. 5. Density of sagebrush seedlings and juveniles. Treatments are perennial herbs intact or removed by herbicide and unburned or burned. Lines above bars are 1 SE. Abbreviations are NC, Nevada crested wheatgrass; UC, Utah crested wheatgrass; US, Utah squirreltail; NL, NM, and NU, Nevada low, mid, and upper elevation; UL, UM, UU, Utah low, mid, and upper elevation sites.

evapotranspiration (Palmquist et al. 2016a). Drier late spring and summer conditions at mid and upper elevation in the northern distribution of sagebrush may maintain or increase suitability for big sagebrush, but those conditions may decrease suitability at lower elevations (Palmquist et al. 2016b).

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). These projections of lower water availability in late spring parallel those we found

at lower compared to higher elevations. Effects of water availability on sagebrush and perennial herb cover and of small-scale disturbance across the elevation gradient we studied may indicate response to similar disturbances under future conditions. Specifically, shrub and perennial grass responses currently observed at lower elevations after disturbance may occur at mid and upper elevations in the future. Our study indicates that where sagebrush seed availability is high and perennial grasses are reduced by inappropriate grazing, big sagebrush may increase at mid and upper elevations. Where both inappropriate grazing and fire occur, invasive annual plants will likely increase (Bradley et al. 2016, Urza et al. 2017). Where perennial grass cover remains high but big sagebrush seed availability is low after fire, resistance to invasive annuals may be high but big sagebrush establishment will likely be reduced at mid to upper elevations. Chambers et al. (2017) suggested that greater sagebrush cover and density in our study at higher elevations was due to wetter conditions that favored its establishment. Because big sagebrush establishment is episodic and limited by spring and summer drought, its establishment could be limited by future warming and drying conditions across its range of elevational adaptation (Schlaepfer et al. 2014, 2015, Shriver et al. 2018). Large-scale fire in a warmer and drier climate may become an even larger driver of decreased sagebrush and increased invasive plants at mid to upper elevations (Ford et al. 2012, Polley et al. 2017).

Perennial grasses are key to cheatgrass resistance because they draw soil water and nutrient resources from the same rooting zone (Leffler and Ryel 2012, Chambers et al. 2017, Roundy et al. 2018, Kulmatiski et al. 2020). Although there are many factors that favor or disfavor perennial grasses compared to cheatgrass (Chambers et al. 2016), environmental conditions relative to germination, establishment, growth, persistence, and seed production are of major importance (Chambers et al. 2007, Roundy et al. 2007, Bradley et al. 2016). Seasonal soil climate is a major controlling factor. Roundy et al. (2018) found that sites with warmer late springs and warmer and wetter falls had more cheatgrass cover, while sites with wetter winters and early springs had more perennial herbaceous cover. In

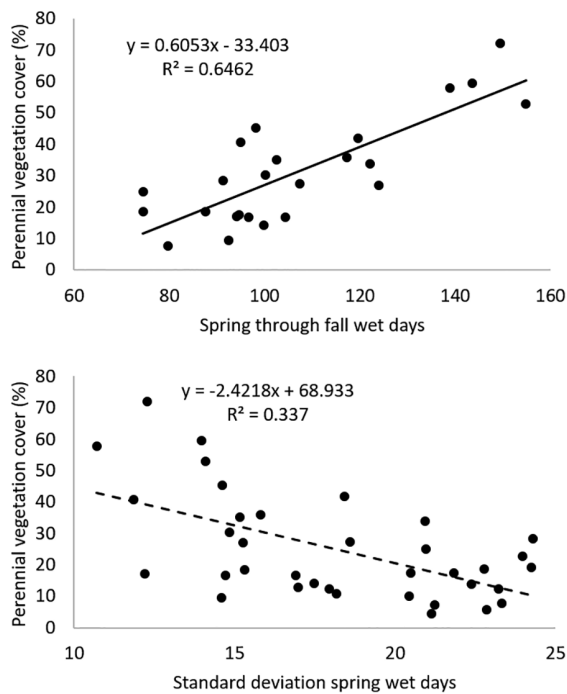


Fig. 6. Perennial vegetation cover in relation to spring through fall wet days for low, mid, and high elevation sagebrush communities (top) and to the standard deviation of annual spring wet days for squirreltail, crested wheatgrass, and low, mid, and high elevation sagebrush communities (bottom).

the current study, wet days increased with increasing elevation most in late spring (Table 5, Fig. 1) and soil-temperature-related variables decreased with increasing elevation in most seasons (Tables 2, 3). Perennial herb and total perennial cover tended to increase with increasing elevation (Fig. 4). Our study associates greater precipitation with greater spring soil water availability, cooler temperatures, and increased perennial herbaceous and total perennial cover as elevation increases. It also associates greater annual variability in spring soil water availability with decreased perennial vegetation cover as elevation decreases (Fig. 6). These associations suggest that as the climate becomes warmer and drier and precipitation is more variable, perennial grass and total perennial vegetation cover will decrease and some higher elevation sagebrush communities could become less resistant to cheatgrass dominance.

Effects of disturbance and resource preemption

Small-scale disturbances of fire and perennial herb removal had major effects on vegetation composition more than a decade later. Chambers et al. (2017) found that 12 and 13 yr after perennial herb removal, perennial herb cover was decreased across elevations while big sagebrush density and cover were increased. We found a similar trend of increased sagebrush establishment on the low, mid, and high elevation sites where perennial herbs were removed, especially at high elevations (Figs. 3, 4). Increased spring soil water availability the first few years after perennial herb removal on all sites (Chambers et al. 2007) likely facilitated sagebrush establishment and strongly influenced competitive relationships. Where sagebrush density was high, plants were generally small, indicating high intraspecific competition for soil resources; and perennial herb cover was low, indicating high interspecific competition. Surviving sagebrush plants increased in size as sagebrush density decreased by 2014 as observed elsewhere (Shriver et al. 2019). Sagebrush recruitment was lower or much less consistent at the grass-dominated squirreltail and Utah crested wheatgrass sites, even though soil water availability increased initially after perennial herb removal. A low and variable sagebrush seed source combined with generally warmer and drier conditions likely had a greater effect on establishment than the short-term resource pulse.

By 3 yr after treatment, there were few differences in seasonal soil water availability associated with either perennial herb removal or fire. This indicates a short window of resource availability following disturbance for regrowth of surviving residual plants and establishment of new individuals. It also indicates soil water use or preemption by surviving and establishing plants a few years after disturbance. Once established, sagebrush seedlings largely prevented establishment and growth by perennial grasses, especially where these grasses had been removed. Post-burn seeding of western juniper sites with few residual understory plants resulted in an average sagebrush cover of ~30% in sagebrush seeded plots compared with ~1% in unseeded plots eight years later, but total herbaceous vegetation, perennial grass, and annual forb cover were lower where sagebrush was seeded (Davies and

Bates 2019). In plots that were burned but perennial herbs left intact, sagebrush still established but remained sub or co-dominant with perennial grasses (Fig. 4). These results suggest that to restore sagebrush after wildfire or woody plant control, it is necessary to seed as soon as possible after the disturbance or treatment before understory perennial grasses and forbs increase. Where perennial herbs have been diminished by inappropriate grazing, both woody plant control and grazing management may be necessary to restore these species.

Increased soil water availability after disturbance in the Great Basin is dependent on annual inputs from winter and spring precipitation (Fig. 1), as well as transpiration outputs from residual or reestablishing vegetation and from soil water evaporation. Increased water yield after shrub reduction is most probable in winter rainfall areas, such as the Great Basin (Archer and Predick 2014). Sagebrush–bunchgrass communities typically deplete spring soil water in the upper root zone completely through transpiration and evaporation (Anderson et al. 1987). Spring wet days increased with elevation in our study, but were always fewer than the 122 days of spring (March–June), even at the highest elevations (Fig. 2). Increased soil water after shrub control is often temporary as perennial grasses increase and use the water previously used by sagebrush (Bradford et al. 2014). Our results indicate that increased soil water availability after perennial herb or shrub reduction can also be short-lived when shrubs recover through seedling establishment. Sagebrush, rather than perennial grass dominance on our perennial herb-reduced and burned plots, likely occurred because our plots were small, surrounded by living sagebrush, and presumably had high sagebrush seed availability. This response would not be expected to occur where large-scale shrub reduction results in lack of sagebrush seed availability (e.g., Germino et al. 2018).

Increased soil water after plant reduction depends on changes in associated water inputs and losses, especially lower transpiration by the species reduced and recovery of other water users in the community. For example, reduced transpiration after shrub control could increase deeper soil water, which is used by shrubs for maintenance when more shallow soils are dry

(Leffler and Ryel 2012, Germino and Reinhardt 2014, Bradford et al. 2014, Kulmatiski et al. 2020). Studies by Roundy et al. (2014, 2018, 2020) indicate that pinyon and juniper tree reduction increased spring soil water availability even 13–14 yr after disturbance, especially on drier years. Effects of sagebrush reduction (mowing) on soil water availability in non-tree communities were much less pronounced (Roundy et al. 2018). These studies included tree and shrub reduction on larger-scale plots than the current study. Additional soil water availability in spring after tree reduction was most evident where trees had high cover before removal and understory shrubs and grasses that could use the soil water following tree removal were lacking. The recovery of vegetation after disturbance and additional soil water availability were negatively associated and mediated by precipitation inputs. Removal of a major precipitation interceptors and water users, such as pinyon or juniper trees, increased time of soil water availability in spring much more in drier than wetter years (Roundy et al. 2020). Where residual or reestablishing vegetation rapidly replaces the cover removed by disturbance, additional soil water availability from disturbance may be limited.

Decreased seasonal soil temperatures and related variables with increasing elevation were a strong trend, even though annual variability limited significant differences (Table 4). Across all years and elevations, burning increased soil temperatures by 0.4°C. Burning generally increases post-fire soil temperatures in the first few years (Neary et al. 1999, Roundy et al. 2018), especially in surface soils, which can speed up germination of seeds of both invasive annual grasses and native perennial grasses (Cline et al. 2018). Our data document that for big sagebrush communities in the Great Basin, seasonal maximums for optimum establishment and growing conditions are in spring when soil water availability and warm temperatures overlap.

Invasibility and fluctuating resources

Our results lend support to the fluctuating resource hypothesis (Davis et al. 2000). According to this hypothesis, in dryland ecosystems with high inter-annual variability in precipitation and soil water, periods exist when resource availability exceeds capacity of the native

community to fully utilize those resources (Davis et al. 2000). These periods provide opportunities not only for non-native plant invasion (Davis et al. 2000), but also for establishment and growth of native species. Across the lower elevation sites, we found less perennial vegetation cover and lower soil water availability than at higher elevations. We also found fluctuations in soil water availability (standard deviation of spring wet days) to be moderately ($r^2 = 0.34$) and negatively associated with perennial vegetation cover (Fig. 6). Fluctuating resources accounted for some differences in cheatgrass invasibility (Chambers et al. 2007), but adaptation to environmental conditions and differential ability of species to acquire resources under those conditions also play a role (Pearson et al. 2018). Although cheatgrass cover was limited on the small disturbance plots in this study, it was highest at the low and mid elevation sites. Cheatgrass was also observed in fire or soil-disturbed areas near the plots at all but the high elevation sites. At the Nevada high elevation site, cheatgrass was observed on warmer south-facing slopes that were nearby. Cheatgrass dominance after disturbance is a function of both resource availability and adaptation to temperature (Chambers et al. 2007, Roundy et al. 2018). More consistently available resources that support greater perennial growth combined with cooler temperatures at higher elevations increase resistance to cheatgrass. Current projections of warmer and drier conditions at mid and high elevations indicate that big sagebrush communities at these elevations will become less resistant to invasion over time.

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