

ARTICLE

Special Feature: Sagebrush Steppe Treatment Evaluation Project

Ten-year ecological responses to fuel treatments within semiarid Wyoming big sagebrush ecosystems

David A. Pyke¹  | Scott E. Shaff¹  | Jeanne C. Chambers²  |
Eugene W. Schupp³  | Beth A. Newingham⁴  | Margaret L. Gray³  |
Lisa M. Ellsworth⁵ 

¹U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, Corvallis, Oregon, USA

²U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Reno, Nevada, USA

³Department of Wildland Resources/Ecology Center, Utah State University, Logan, Utah, USA

⁴U.S. Department of Agriculture, Agricultural Research Service, Great Basin Rangelands Research Unit, Reno, Nevada, USA

⁵Fisheries and Wildlife Department, Oregon State University, Corvallis, Oregon, USA

Correspondence

David A. Pyke

Email: david_a_pyke@usgs.gov

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Abstract

Sagebrush ecosystems of western North America are threatened by invasive annual grasses and wildfires that can remove fire-intolerant shrubs for decades. Fuel reduction treatments are used ostensibly to aid in fire suppression, conserve wildlife habitat, and restore historical fire regimes, but long-term ecological impacts of these treatments are not clear. In 2006, we initiated fuel reduction treatments (prescribed fire, mowing, and herbicide applications [tebuthiuron and imazapic]) in six *Artemisia tridentata* ssp. *wyomingensis* communities. We evaluated long-term effects of these fuel treatments on: (1) magnitude and longevity of fuel reduction; (2) Greater Sage-grouse habitat characteristics; and (3) ecological resilience and resistance to invasive annual grasses. Responses were analyzed using repeated-measures linear mixed models. Response variables included plant biomass, cover, density and height, distances between perennial plants, and exposed soil cover. Prescribed fire produced the greatest reduction in woody fuel over time. Mowing initially reduced woody biomass, which recovered by year 10. Tebuthiuron did not significantly reduce woody biomass compared to controls. All woody fuel treatments reduced sagebrush cover to below 15% (recommended minimum for Greater Sage-grouse habitat), but only prescribed fire reduced cover to below controls. Median mowed sagebrush height remained above the recommended 30 cm. Cheatgrass (*Bromus tectorum*) cover increased to above the recommended maximum of 10% across all treatments and controls. Ecological resilience to woody fuel treatments was lowest with fire and greatest with mowing. Low resilience over the 10 posttreatment years was identified by: (1) poor perennial plant recovery posttreatment with sustained reductions in cover and density of some perennial plant species; (2) sustained reductions in lichen and moss cover; and (3) increases in cheatgrass cover. Although 10 years is insufficient to conclusively describe final ecological responses to fuel treatments, mowing woody fuels has the greatest potential to reduce

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woody fuel, minimize shrub mortality and soil disturbance, maintain lichens and mosses, and minimize long-term negative impacts on Greater Sage-grouse habitat. However, maintaining ecological resilience and resistance to invasion may be threatened by increases in cheatgrass cover, which are occurring regionally.

KEYWORDS

biological soil crust, *Bromus tectorum*, downy brome, exposed soil, imazapic, lichen, moss, mowing, perennial plant density, prescribed fire, shrub height, Special Feature: Sagebrush Steppe Treatment Evaluation Project, tebuthiuron

INTRODUCTION

Wildfire is a common natural disturbance that may shift plant dominance between shrubs and grasses in semiarid lands worldwide, particularly in systems with sufficient fuel mass or continuity (West, 1983). Fire-tolerant or fire-resilient plant communities similar to those in Mediterranean ecosystems (Keeley et al., 2011) are dominated by woody and herbaceous plants with perennating meristems deep enough below the soil surface to insulate meristems from lethal heat and allow regrowth soon after fire (Pyke et al., 2010). These fire-resilient ecosystems may return to their prefire dominance hierarchy in a decade or two. Conversely, semiarid ecosystems dominated by fire-intolerant plants may require multiple decades to return to prefire plant communities. For example, in big sagebrush (*Artemisia tridentata*) ecosystems, fire kills big sagebrush plants because all perennating buds are located on the current year's aboveground wood (Bilbrough & Richards, 1991, 1993), whereas perennating buds on herbaceous plants are at or below the soil surface and are often insulated from lethal heat (Pyke et al., 2010; Whelan, 1995). Big sagebrush death from fire often leads to herbaceous vegetation dominating burned communities for multiple decades until shrubs can reestablish and re-exert dominance in the community (West, 1983). Fire ecology and fire management of forested and chaparral systems have been widely studied for decades (Greenberg & Collins, 2021; Keeley et al., 2011), but less is known about fire ecology and management of semiarid shrub-steppe ecosystems (Shinneman et al., 2019).

Fire managers implement fuel treatments in shrub-steppe systems based in part on their knowledge of treatments implemented in forest and chaparral systems. Managers implement fuel treatments before wildfires or during suppression operations in efforts to reduce fire size, intensity, and severity (Crist et al., 2019). Elimination or reduction of woody fuels is a common fuel treatment practice because woody fuels create more intense, difficult-to-control wildfires compared to herbaceous-

fuel-dominated systems. Woody-fuel-dominated systems produce fires with greater flame lengths and residence times than herbaceous system often creating more severe impacts on plant communities (Whelan, 1995).

In the US intermountain region, fire management is a complex problem that must contend with a series of overlapping resource issues (Boyd & Svejcar, 2009). In this region's big sagebrush ecosystems, dominance of non-native annual grasses, such as cheatgrass (*Bromus tectorum*), has dramatically changed fire regimes (Balch et al., 2013; Bradley et al., 2018; Brooks et al., 2004; D'Antonio & Vitousek, 1992; Rahlao et al., 2009) and has influenced fuel reduction or fire suppression treatments (Crist et al., 2019). Warm and dry portions of big sagebrush ecosystems are more prone (less resistant) to cheatgrass dominance than cooler and moister portions of these ecosystems (Chambers, Bradley, et al., 2014; Chambers, Miller, et al., 2014; Roundy & Chambers, 2021). Fire managers must also consider preserving and maintaining wildlife habitat, especially for species of concern, such as Greater Sage-grouse (*Centrocercus urophasianus*, hereafter called sage grouse). Nesting and brood-rearing success of sage grouse is associated with high shrub canopy cover, that is often mostly sagebrush, at or above 15% and with heights greater than 30 cm tall (Connelly et al., 2000; Lockyer et al., 2015). Fire managers are encouraged to protect sagebrush communities that meet or exceed these criteria (Crist et al., 2019), thus adding the complexity of when and where to place fuel treatments.

Fuel treatment effectiveness and longevity are much better understood in forested, compared to nonforested systems (Hudak et al., 2011; Kalies & Yocum Kent, 2016; Martinson & Omi, 2013). While Hudak et al. (2011) and Martinson and Omi (2013) examined the effectiveness of fuel treatments in nonforested systems, both reviews concluded there were insufficient data that included untreated controls to draw conclusions.

Experimental approaches examining different fuel treatments with untreated controls may help fire managers make informed decisions regarding ecological

consequences of alternative fuel treatments and the longer term effects of treatments on environmental resources (Shinneman et al., 2019). The Sagebrush Steppe Treatment Evaluation Project (SageSTEP) was initiated in 2005 to examine ecosystem responses to fuel reduction treatments in big sagebrush communities over time. Treatments were implemented at multiple sites in relatively warm and dry Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis*) communities experiencing initial invasions of non-native annual grasses, primarily cheatgrass (McIver & Brunson, 2014).

Prescribed fire, mowing, and herbicides were common fuel reduction treatments in sagebrush steppe in the early 2000s (McIver et al., 2010; Pilliod, Welty, & Toevs, 2017). Fires kill big sagebrush and will likely provide the greatest reduction in woody biomass (burnable fuel). However, sagebrush mortality leaves openings in the plant community for other species to establish. In the absence of invasion of non-native annual grasses after fire, native herbaceous perennials have the potential to expand and dominate these ecosystems postfire until shrubs reestablished (Chambers et al., 2007; Chambers, Bradley, et al., 2014). In many areas, cheatgrass now has the potential to expand and dominate burned communities, especially where native perennial herbaceous species have been depleted and shrub cover has increased (Chambers, Board, et al., 2017). As a fuel reduction treatment, mowing reduces shrub height and cover with minimal impact to the shrub population (provided the mowing height is tall enough not to kill sagebrush), perennial herbaceous plants, and soils (Hess & Beck, 2012). As with fire, mowing can create openings in the community and elevate resource availability (Rau et al., 2014) increasing annual grass growth and reproduction leading to increased interactions between cheatgrass and native perennial plants (Chambers et al., 2021). Herbicides, such as tebuthiuron or imazapic, may reduce targeted plant groups (e.g., shrubs or annual grasses, respectively) with a restoration goal of increasing perennial herbaceous plants in spaces formerly occupied by the deceased shrubs and annual grasses (Mealor et al., 2013; Olson & Whitson, 2002). Little is known, however, about the long-term impacts of herbicide treatments on fuels and big sagebrush plant communities.

We initially presented short-term (pre- and 3 years posttreatment) ecological responses to fuel treatments across the SageSTEP network of sites (Pyke et al., 2014). Woody fuel treatments varied in their impacts on shrub biomass and cover (Pyke et al., 2014). Prescribed fire removed nearly all shrub biomass and cover, while mowing reduced shrub cover below 10% and tebuthiuron had little influence on biomass and cover. Herbaceous biomass and cover declined initially with fire and mowing

but not with tebuthiuron. After those initial declines, biomass and cover of herbaceous plants recovered or increased in all treatments except in those treated with imazapic. Cheatgrass cover in woody fuel treatments did not increase in the first 3 years when compared to controls. The imazapic treatment reduced cheatgrass to near-zero cover during this period with only minor increases by year 3. The declines in sagebrush cover with fire and mowing placed these communities below the guideline for cover for successful sage grouse nesting and brood-rearing habitat, while cheatgrass remained below the maximum cover that would restrict nesting (Coates et al., 2016; Connelly et al., 2000; Lockyer et al., 2015). Since community resistance (i.e., the ability of the community to retain its structure, processes, and functioning when exposed to stressors; Chambers, Maestas, et al., 2017; Folke et al., 2004) to annual grass invasion depends on perennial grass cover being maintained or increasing with treatment (Chambers, Bradley, et al., 2014; Chambers, Miller, et al., 2014), the mixed results for perennial grass cover in the first 3 years created concerns regarding resistance to invasion and resilience of these communities (i.e., the ability for these plant communities to reorganize and regain their fundamental structure, processes, and functioning to stressors; Chambers, Board, et al., 2017; Holling, 1973) to disturbances such as fuel treatments.

This paper extends previous analyses to evaluate longer term ecological responses of sagebrush grassland communities at the same sites immediately before and at three times (years 3, 6, and 10) after applications of woody fuel and invasive annual grass treatments. We address three questions: (1) What is the magnitude and longevity of shrub and annual grass fuel reduction treatments on the biomass, density, cover, and height of Wyoming big sagebrush and other shrubs? (2) Did woody fuel treatments achieve minimum nesting habitat quality for sage grouse by year 10? and (3) Are these Wyoming big sagebrush communities resilient to fuel treatments and resistant to posttreatment cheatgrass invasion?

STUDY AREA AND METHODS

This study was conducted at six of the seven initial sites in the SageSTEP sagebrush–cheatgrass network (Figure 1; McIver & Brunson, 2014). One site was eliminated because a wildfire burned the majority of the treatments in the third year posttreatment. All sites had loamy soils ranging from coarse silt loams to loams with varying amounts of surface stones and soil depths. The soil temperature–moisture regimes (terminology follows USDA Soil Survey; Maestas et al., 2016; Soil Survey

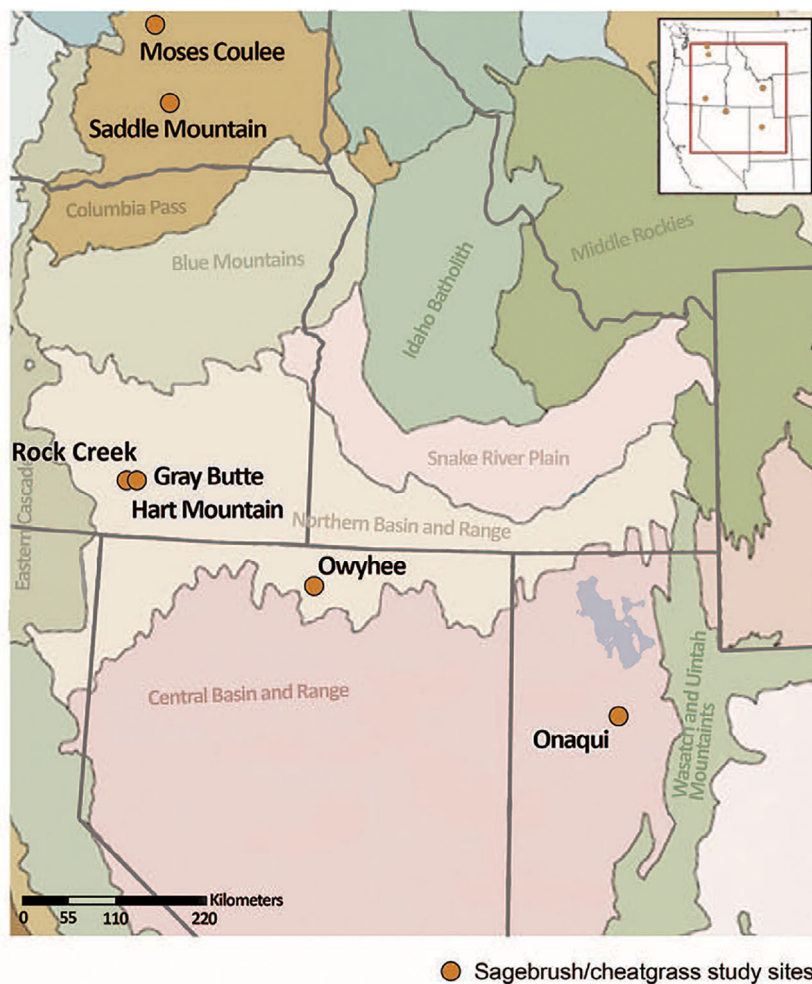


FIGURE 1 Six sites within the Sagebrush Steppe Treatment Evaluation Project in the western United States overlaid on US Environmental Protection Agency, Level III Ecoregions (Omernik & Griffith, 2014).

Staff, 2014) range from frigid-xeric (cool-winter moist) at the two Oregon sites to mesic-xeric bordering on aridic (warm-winter moist bordering on dry) at the Moses Coulee, Washington site. The other three sites are mesic-xeric (warm-winter moist). These soil temperature and moisture regimes provide an approximate indication of the site's potential resilience to disturbances; cool and winter moist sites are thought to have moderately high resilience and moderate resistance to annual grass invasion, while warm and winter dry sites are thought to have low resilience and resistance (Chambers, Maestas, et al., 2017; Maestas et al., 2016).

The 30-year average annual growing season precipitation had a range of 111 mm between the driest and wettest sites (Figure 2). The range from maximum to minimum annual precipitation during the growing season at a site was smallest (164 mm) at Saddle Mountain and largest (283 mm) at Owyhee. Precipitation in the year before treatment applications was below average at

four of the six sites and often the lowest recorded annual growing season precipitation. The largest annual precipitation in the lowest elevation sites (Saddle Mountain and Moses Coulee) occurred in years 8 and 9 posttreatment, whereas in the other sites the highest annual precipitation varied among posttreatment years (Figure 2). Finally, the high temporal and spatial variability in precipitation observed in this study is likely a major factor behind high variance for nearly all measured response variables.

Pretreatment, native vegetation at all sites was dominated by a combination of native shrubs (mostly Wyoming big sagebrush) and to a lesser extent yellow rabbitbrush (*Chrysothamnus viscidiflorus*), and of native perennial bunchgrasses (including bluebunch wheatgrass [*Pseudoroegneria spicata*], squirreltail [*Elymus elymoides*], needlegrass [*Achnatherum* sp.], and Sandberg bluegrass [*Poa secunda*]). Cheatgrass was present at all sites and occurred initially in 81% of all measurement subplots, but was subordinate to the

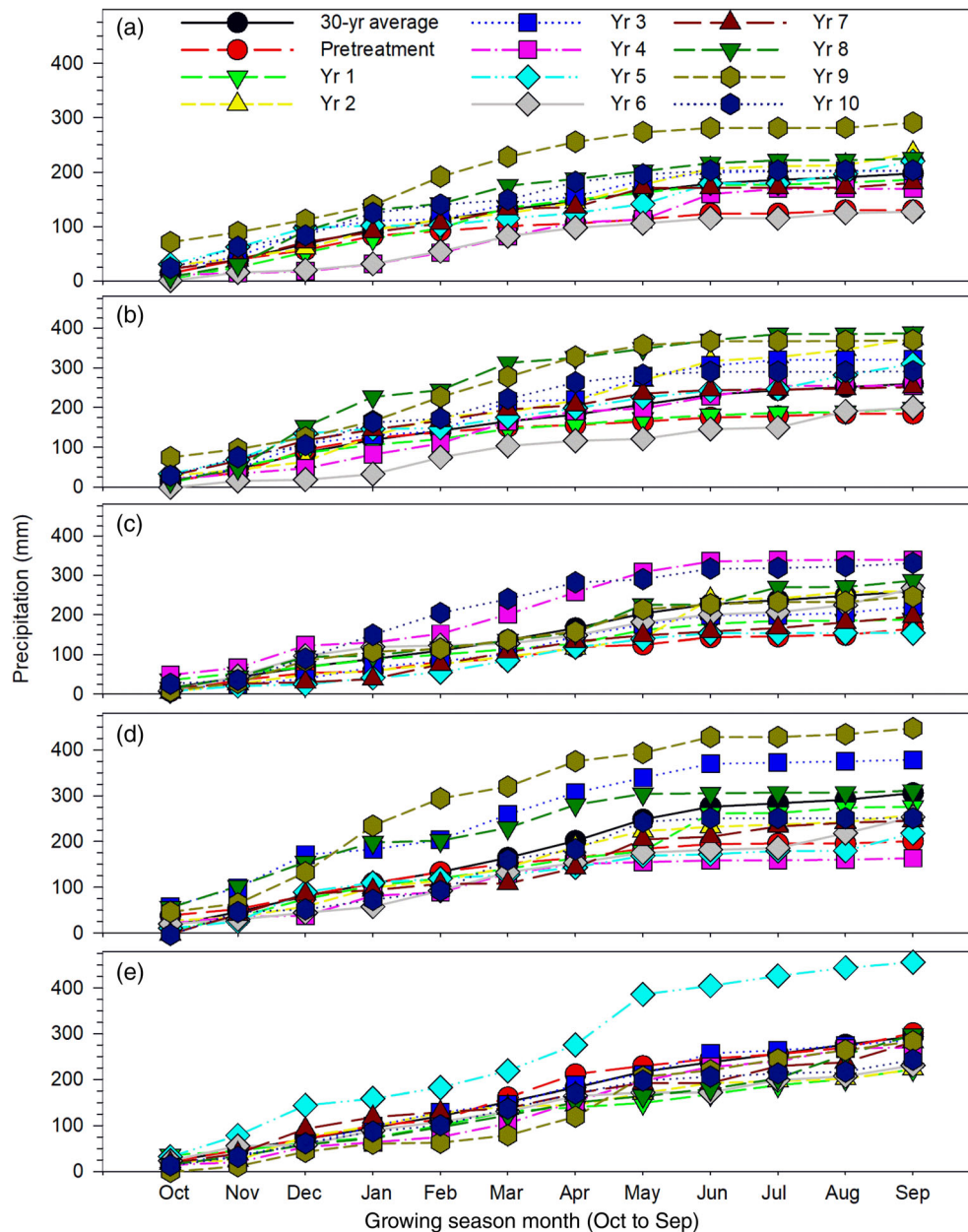


FIGURE 2 Cumulative precipitation for the 30-year (1990–2020) annual average and each annual growing season (October year, through September year_{*i*+1}), for the growing season year preceding treatment (pretreatment), and for the 10 posttreatment years at the five locations of the six Sagebrush Steppe Treatment Evaluation Project (SageSTEP) sites ordered from top to bottom by elevation (lowest to highest) (a) Saddle Mountain, Washington (270 m elevation); (b) Moses Coulee, Washington (520 m); (c) Gray Butte and Rock Creek, Oregon (1500 m); (d) Owyhee, Nevada (1630 m); (e) Onaqui, Utah (1660 m).

native vegetation before fuel treatments were applied (median perennial plant and cheatgrass cover in treatments ranged between 18% and 25% and between 5% and 8%, respectively; Pyke et al., 2014).

The experimental design was a randomized block, split-plot with repeated measures at the subplot scale. Each of the six sites was treated as a block with four whole plots that were assigned one of four woody fuel treatments (fire, mowing, tebuthiuron, or untreated

control). The size of each whole plot within a site was similar but ranged between 30 and 81 ha at different sites depending on environmental heterogeneity, land access, and land manager's willingness to set aside land for study. Prior to study initiation, livestock grazing was allowed at four of the six sites, but these sites were subsequently fenced. The other two sites (Rock Creek and Gray Butte in Oregon) had livestock removed and were fenced 10 years before the study. Fences were maintained

annually with only occasional livestock intrusion for short periods.

The initiation of fuel treatments was staggered over 3 years and the timing of the treatment implementation depended on when the local fire management officer felt it was safe to implement the prescribed fire whole-plot treatment. In addition, this person assigned where the fire treatment could be safely and logistically controlled. After the fire treatment was assigned, the control, mowing, or tebuthiuron plots were randomly assigned to the remaining whole-plot treatments. Fire conditions varied, but prescribed fires were conducted in late summer and early fall, during periods of little wind with fires burning from the exterior to the center of the plot. Prescribed fires occurred after the wildfire season with cooler temperatures, less wind, and higher humidity than when wildfires typically burn. Not all measurement subplots (described below) had all vegetation and litter consumed by fire, so fire crews spot-treated unburned portions with additional ignitions of all visible unburned shrubs.

Mowing and tebuthiuron treatments were intended to reduce shrub cover (mostly sagebrush) by 50%. Mowing was done with a wheeled-tractor pulling a rotary deck mower (~3.7 m diameter) set at a height between 30.5 and 38.1 cm depending on the site and the original shrub heights. Tebuthiuron (Spike 20P; 1.68 kg/ha) was applied aerially by fixed-wing aircraft or helicopter. Woody fuel treatments were applied in 2006 (Onaqui), 2007 (Rock Creek), and 2008 (Gray Butte, Saddle Mountain, Owyhee, Moses Coulee) giving a staggered start design (Loughin, 2006). This design alleviates effects of starting an experiment under the same set of climatic conditions so that results can be applied more broadly. Mowing and tebuthiuron application occurred within 4 months after the fire except at Moses Coulee, where the mow and tebuthiuron treatments occurred in winter and the fire occurred the following autumn. For analyses, we treated the Moses Coulee fire plot as missing data as in the short-term analysis (Pyke et al., 2014).

Each whole plot (woody fuel treatment) had 18 or 24 measurement subplots (30 × 33 m; about 0.1 ha) dispersed across the treatment area. Half of the subplots (9 or 12) were randomly selected to receive the herbicide imazapic (Plateau; 22.2% acid equivalent), intended to control invasive annual grass. We used a stratified random selection process to capture the variation in the cheatgrass-to-native perennial grass cover found in the whole plot (see Pyke et al., 2014). Imazapic was applied within a month after the fire using an all-terrain vehicle.

All subplots were permanently marked and measurements taken the year before the fuel treatments were applied, as well as in years 1, 2, 3, 6, and 10. Vegetation measurement protocols for all response variables

(Table 1) followed Herrick et al. (2005). Vascular and nonvascular plant foliar cover and soil surface cover were collected by species or plant functional group, and surface cover class near the peak of the growing season (May through July depending on site) using the line-point intercept method. Lichen and moss cover were summarized as total cover (points contacting lichen or moss as a soil surface contact whether or not plants or litter were contacted first) and exposed cover (points contacting lichen or moss without plants or litter contacted first; these can be considered as interspace lichens and moss). Exposed soil cover (also mostly interspace soil) was a contact on mineral soil without additional plant, litter, or surface cover contacts. Densities (counts per unit area) of shrubs greater than 15 cm (considered adults) were collected by species in three 2 × 30-m belt transects per measurement subplot. Densities of perennial grasses and forbs were collected in forty-five 0.25-m² frames within subsample plots. Shrub biomass (in kilograms per hectare) was estimated from allometric relationships of individual shrub canopy heights, greatest width, and greatest perpendicular width to the first width of all major shrub species, provided the shrub was greater than 15-cm tall and had at least 10% of the canopy alive. Shrubs were measured in five nested circular frames, ranging in size from 0.5- to 3-m radius, that were placed every 6 m along the central transect of the subplot. Observers selected the smallest circular frame to measure approximately a total of 15 individuals across all five circular plots within the subplot. The same frame size was used for all five circular frames within a subplot (see supplemental information in Pyke et al., 2014). Basal gaps greater than 20 cm were measured between bases of perennial plants along transects in subplots.

Each response variable (Table 1) was analyzed using separate repeated-measures linear mixed models with restricted/residual maximum likelihood (PROC MIXED; SAS 9.4, SAS Institute, 2016). Many response variables required a natural log transformation (Appendix S1: Table S1) to adhere to assumptions for parametric statistical analyses. The fixed explanatory variables included woody fuel treatment (control, prescribed fire, mowing, or tebuthiuron), imazapic, and year with their interactions. Sites ($n = 6$), plots ($n = 4$ woody fuel treatments) within sites and subplots ($n = 18$ or 24), and within plots were treated as random factors in the model with subplots as the repeated measure. If models did not converge, the three-factor interaction was dropped and models converged (Appendix S1). Lower order significant interactions or main effects were presented only if higher order interactions were not significant ($p > 0.05$). We report least-square mean estimates for significant responses and their corresponding 95% confidence limit

TABLE 1 Significance (*p*) values for each response variable given main effects (woody fuel treatment, imazapic, and year).

Response variable	Woody fuel treatment	Imazapic	Fuel-by-imazapic	Year	Year-by-fuel	Year-by-imazapic	Year-by-fuel-by-imazapic
Shrub							
Total shrub biomass	<0.001	0.342	0.961	<0.001	<0.001	0.874	0.998
Density of all shrubs >15-cm tall	0.001	0.752	0.806	<0.001	<0.001	0.770	0.894
Wyoming big sagebrush cover	<0.001	0.641	0.997	<0.001	<0.001	0.917	0.997
Wyoming big sagebrush height	0.001	0.495	0.631	<0.001	<0.001	0.204	0.862
Height of all shrubs	<0.001	0.730	0.548	<0.001	<0.001	0.160	0.914
Herbaceous							
Herbaceous and fine litter biomass	0.036	0.337	0.968	<0.001	<0.001	0.490	0.978
Perennial deep-rooted grasses							
Cover	0.399	0.625	0.944	0.188	0.072	0.784	0.999
Density	0.176	0.519	0.810	0.769	0.244	0.932	0.999
Sandberg bluegrass							
Cover	0.005	0.003	0.359	<0.001	0.589	0.011	0.994
Density	0.015	0.004	0.723	0.003	0.559	0.063	0.9523
Perennial forbs							
Cover	0.418	0.362	0.900	<0.001	<0.001	0.079	0.966
Density	0.214	0.003	0.283	<0.001	0.588	0.028	0.764
Annual plants							
Forb cover	0.425	0.322	0.607	<0.001	0.443	0.203	0.983
Cheatgrass cover	0.531	0.151	0.944	<0.001	0.004	<0.001	0.967
Lichen and moss							
Total cover	0.034	0.426	0.832	<0.001	<0.001	0.619	0.999
Exposed cover	<0.001	0.612	0.419	<0.001	<0.001	0.045	0.983
Plant spatial relationships (gaps)							
Distance between perennial plants	0.071	0.028	0.599	<0.001	0.045	0.693	0.938
Proportion of gaps >2 m	0.120	0.070	0.572	<0.001	0.541	0.554	0.988
Exposed mineral soil	0.786	0.032	0.879	<0.001	0.002	0.119	0.969

Note: Models with *p* values bolded were significant at $\alpha = 0.05$.

(LSMEANS statement) and used the pairwise two-sample *t*-test with Bonferroni adjustments associated with the LSMEANS DIFF statement to indicate significant differences at $p \leq 0.05$ (Appendix S2: Tables S1–S3). Transformed parameters were back-transformed for presentation yielding estimated medians and confidence limits.

RESULTS

Pretreatment response variables did not differ among treatment or control plots (woody fuel or imazapic) (year 0 $p > 0.05$; Appendix S2: Tables S2 and S3) except for

Sandberg bluegrass cover, where the fire treatment by chance had significantly lower cover than other treatments (tab. 3 in Pyke et al., 2014). Posttreatment, woody fuel treatments or their interactions with years significantly impacted all responses except perennial grasses, annual forbs, and proportion of gaps between perennial plants greater than 2 m (Table 1). Imazapic treatments alone or as an interaction with years significantly affected Sandberg bluegrass, perennial forbs, cheatgrass, lichens, and mosses, as well as distances between perennial plants and exposed mineral soil. Imazapic treatments never interacted with the woody fuel treatments for any response variable ($p \geq 0.28$; Table 1). Details for the major significant treatment effects follow.

Shrub responses

The three woody fuel treatments varied in total shrub biomass reductions and in their recovery over time to levels in untreated controls (Table 1, Figure 3a). Prescribed fire produced the greatest reduction in shrub biomass (<10% of untreated control) immediately after treatment and sustained that reduction for 10 years (Figure 3a; fire-years 3–6 or 6–10 $p \geq 0.68$). The mowing treatment reduced total shrub biomass to levels intermediate between prescribed fire and tebuthiuron treatments. Mowing reduced total shrub biomass immediately after treatment and through year 6 (Figure 3a; mow-years 3–6 $p = 1.00$), but a significant increase was observed between years 6 and 10 (Figure 3a; mow-years 6–10 $p < 0.01$). Although median total shrub biomass appeared lower than the control in the tebuthiuron

treatment, these reductions did not differ significantly from untreated controls during the 10 years (Figure 3a).

The density of all adult shrubs (taller than 15 cm) varied by woody fuel treatment and time since treatment (Table 1, Figure 3b). Prescribed fire reduced shrub density to 15% of the control in year 3, recovered to nearly 30% of the control levels by year 6, held constant to Year 10 (fire-years 3–6 $p < 0.001$; fire-years 6–10 $p = 1.0$), and by year 10 was still significantly less than in controls (Figure 3b). Shrub densities in mowing and control treatments in each posttreatment year did not differ significantly (control to mow-years 3, 6, 10 $p = 1.0$). Shrub densities in the tebuthiuron treatment never differed from those in controls, but their median values were reduced such that densities did not differ from burned treatments in years 6 and 10 (Figure 3b).

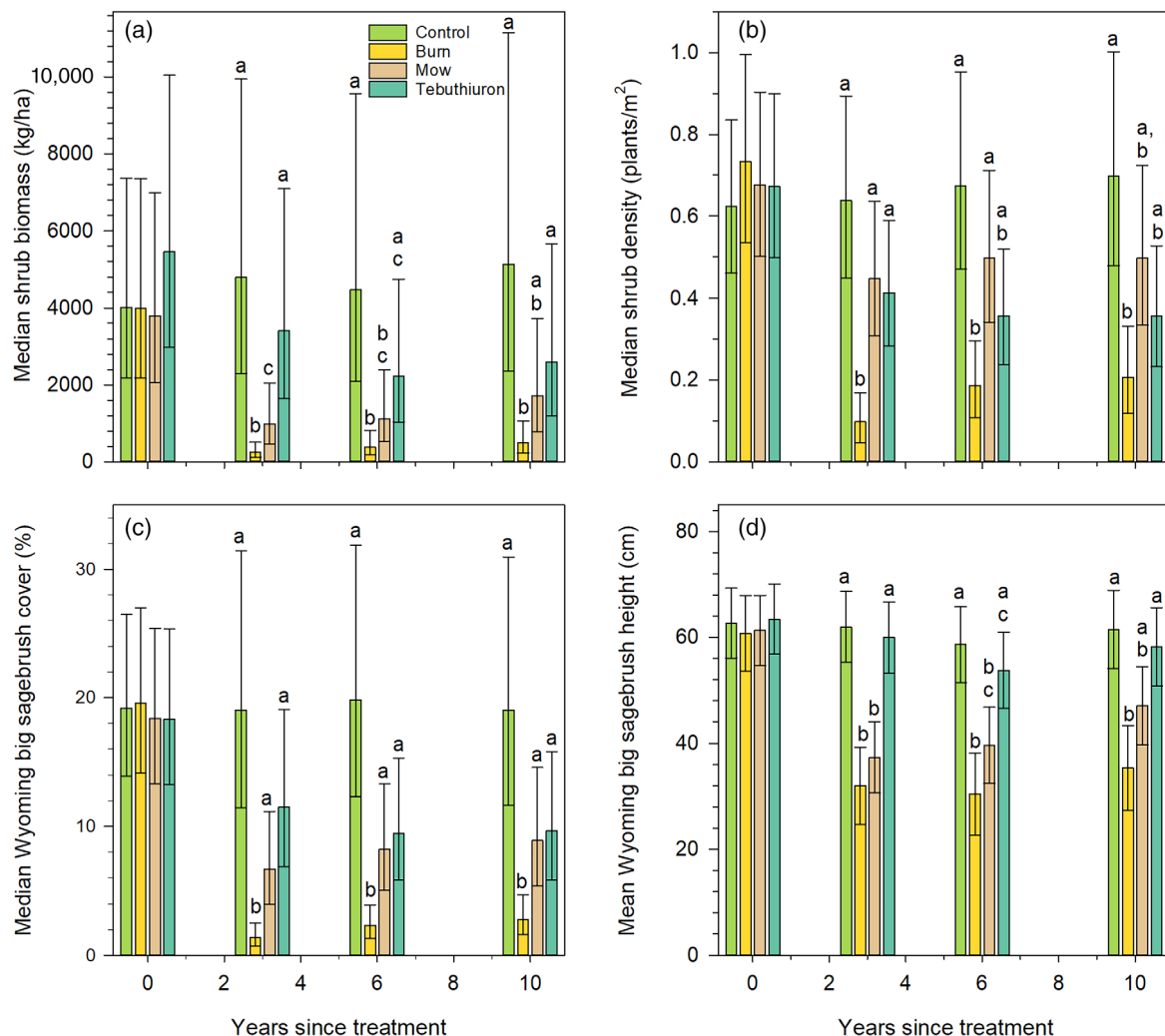


FIGURE 3 Shrub responses to woody fuel treatments measured the growing season before (year 0) and 3, 6, and 10 years after treatment application: (a) biomass of all shrubs; (b) density of all shrubs >15 cm tall; (c) Wyoming big sagebrush foliar cover; (d) Wyoming big sagebrush height. Bars indicate measures of central tendency with corresponding 95% confidence limits. Different lowercase letters indicate significant differences among fuel treatments within a year ($p \leq 0.05$).

Prescribed fire significantly reduced Wyoming big sagebrush cover relative to controls for all 10 years post-treatment (Figure 3c). Sagebrush cover in the burn treatment increased from years 3 to 6 (fire-years 3–6 $p < 0.01$), but no further significant increase in sagebrush cover occurred between years 6 and 10 (fire-years 6–10 $p = 1.00$). Wyoming big sagebrush cover in the mowing and tebuthiuron treatments appeared to have a nearly 50% reduction compared to controls, but that reduction was not significant (Figure 3c; mow-year 3 $p > 0.06$; tebuthiuron-year 6 $p > 0.77$).

Mean sagebrush height before applying woody fuel treatments was 62 cm ($CI_{95\%}$ 57 cm, 67 cm) (Figure 3d). Heights of sagebrush that survived prescribed fires were one-half the heights in the untreated controls for all years (fire-years 3, 6, and 10 $p < 0.01$) but were never shorter than 30 cm, which is the minimum recommended height for sage grouse habitat. Mowing reduced heights in year 3 to 37 cm and height did not increase again until between years 6 and 10, reaching 47 cm in year 10 (mow-years 3–10 $p < 0.01$). Sagebrush height in the tebuthiuron treatment was never reduced significantly below the height in the controls in any posttreatment year (control to tebuthiuron-years 3, 6, or 10 $p > 1.00$).

Herbaceous responses

Herbaceous biomass (live and standing dead + fine litter) increased between years 3 and 6 with prescribed fire compared to controls or other woody fuel treatments, but this difference disappeared between Years 6 and 10 (Table 1, Figure 4a). Herbaceous biomass increased significantly in the tebuthiuron and control treatments between years 6 and 10 (tebuthiuron-years 6–10 $p < 0.01$; control-years 6–10 $p < 0.05$). The cover and density of perennial deep-rooted grasses was not significantly affected by any treatment or time (Table 1, Figure 4b,c).

Sandberg bluegrass, the only shallow-rooted and early phenology perennial grass species, had unique fixed-effects compared to other herbaceous species. Sandberg bluegrass cover and density was lowest in the prescribed fire and the tebuthiuron treatments, but neither fuel treatment effect varied with time (Table 1, Figure 5a,b). Sandberg bluegrass cover and density were both significantly lower in the prescribed fire plots compared to controls, but not for tebuthiuron plots, due to high variability. It should be noted, however, that lower Sandberg bluegrass cover in posttreatment prescribed fire plots was likely due to the lower cover in these same plots before treatments were applied (Pyke et al., 2014).

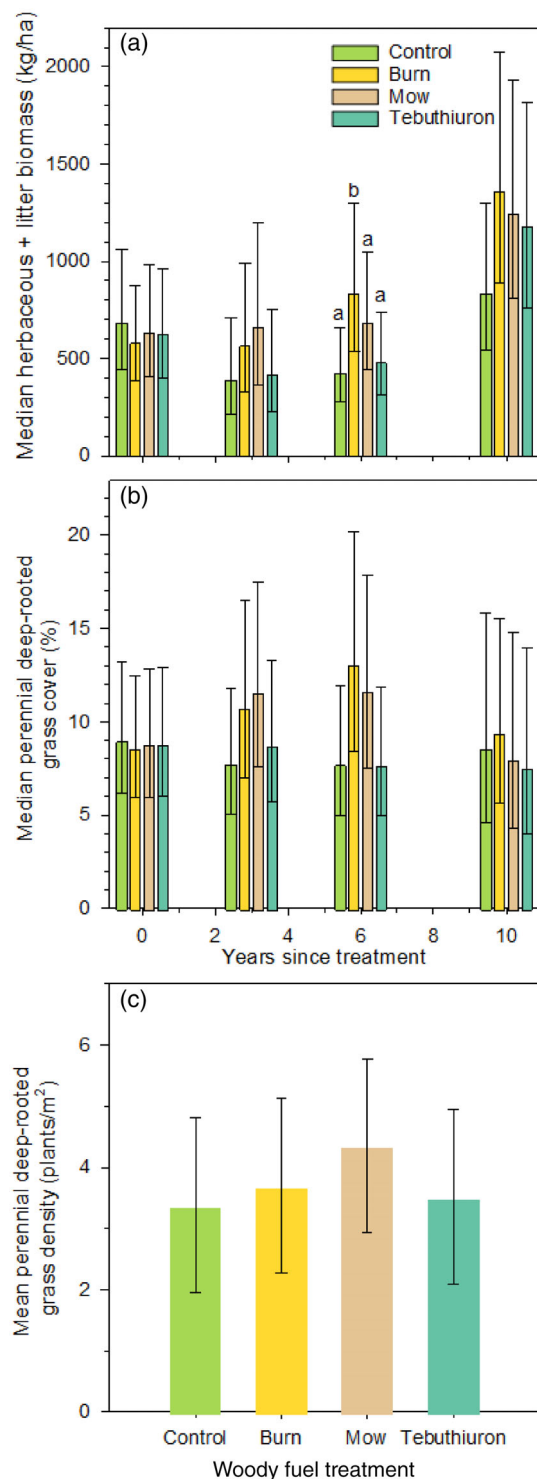
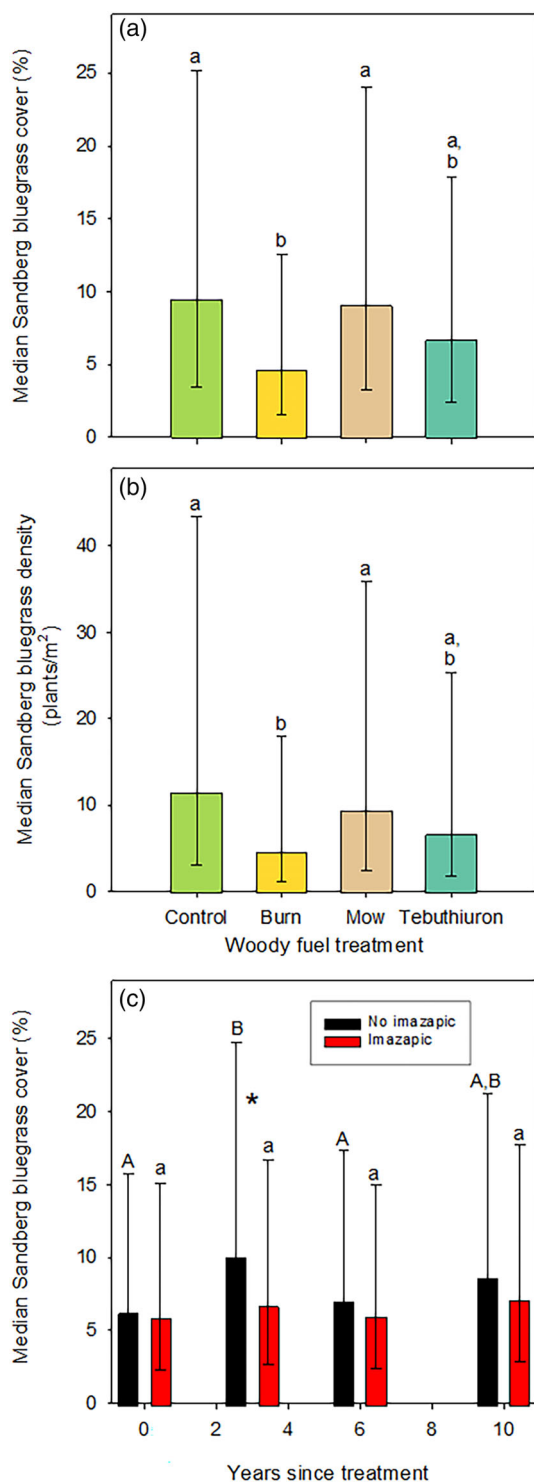


FIGURE 4 (a) Herbaceous biomass including herbaceous litter, (b) perennial deep-rooted grass cover, and (c) density of perennial deep-rooted grasses in response to woody fuel treatments measured the growing season before (year 0) and 3, 6, and 10 years after treatment application (a and b) or averaged across years (c). Bars indicate measures of central tendencies with corresponding 95% confidence limits. Different lowercase letters indicate significant differences among fuel treatments within a year ($p \leq 0.05$).

Imazapic significantly affected the cover and density of Sandberg bluegrass and responses for cover varied with time (Table 1). Woody fuel treatments with imazapic had lower Sandberg bluegrass cover compared to those without imazapic in year 3 only (Figure 5c). Sandberg bluegrass density was also significantly lower with imazapic.

Perennial forb cover response varied by woody fuel treatment and time since treatment (Table 1, Figure 6a).



Perennial forb cover increased significantly in the prescribed fire treatment only in year 3 compared to the prescribed fire treatment in other years (fire-year 3 to fire-years 0, 6, or 10 $p < 0.01$). Similar to the imazapic effect on Sandberg bluegrass, imazapic reduced perennial forb density in year 3 only (Table 1, Figure 6b). In contrast, annual forb cover was not affected by woody fuel treatments nor imazapic but varied with time since treatment, with annual forb cover highest in years 3 and 10 (Table 1, Figure 6c).

Cheatgrass cover increased fourfold in year 10 across all treatments, but did not vary among woody fuel treatments among years (Table 1, Figure 7a). Imazapic lowered cheatgrass cover in year 3 by 65% compared to controls but cheatgrass cover recovered to pretreatment (imazapic-years 0–6 $p = 0.959$) and untreated levels by year 6 (imazapic to no imazapic in years 6–10 $p = 1.00$; Figure 7b).

Lichen and moss responses

Prescribed fire reduced total and exposed lichen and moss cover in the third year posttreatment (Figure 7c,d), but by year 10, lichen and moss cover in the four treatments did not differ among treatments. Total lichen and moss cover (Figure 7c) was nearly five times greater than exposed mosses that occur in interspaces (Figure 7d) in all woody fuel treatments, indicating that most lichens and mosses were located under plants or associated with litter on the soil surface. Mowing, tebuthiuron, and imazapic did not significantly reduce lichen and moss cover compared to controls (Table 1).

Plant spatial relationships

Gap distances among perennial plants were affected by woody fuel treatments across years, but not within years

FIGURE 5 (a) Sandberg bluegrass cover and (b) density in response to woody fuel treatment as a main effect averaged over all measured years. (c) Sandberg bluegrass cover in response to imazapic treatment measured the growing season before (year 0) and 3, 6, and 10 years after treatment application. Bars are medians with their corresponding 95% confidence limits. In (a) and (b), different lowercase letters indicate significant differences among woody fuel treatments ($p \leq 0.05$). In (c), the asterisk (*) indicates a significant difference between imazapic treatments within each year, lowercase letters indicate significant differences among years for plants treated with imazapic, and uppercase letters indicate significant differences among years for plants not treated with imazapic ($p \leq 0.05$).

(Table 1, Figure 8a). For example, prescribed fire treatments had larger gaps than pretreatment prescribed fire in year 3, but did not differ from the untreated control in year 3 (Figure 8a). The imazapic treatment as a main effect (Table 1) increased gap distances from 187 to 213 cm. The proportion of gaps greater than 2 m increased with each year through year 6 but returned to

pretreatment levels by year 10 across all treatments (Figure 8b).

Exposed mineral soil

Cover of exposed mineral soil was affected by woody fuel treatments and time since treatment (Table 1, Figure 8c). Within any given year, the cover of exposed mineral soil did not significantly differ among treatments. Furthermore, untreated controls did not differ significantly in exposed mineral soil over time. But the cover of exposed mineral soil in each woody fuel treatments became lower over time, from year 3 to year 10 (Figure 8c). The prescribed fire treatment increased exposed soil in year 3, which then declined in year 6 and even further in year 10. Mowing and tebuthiuron also reduced cover of exposed soil to below pretreatment levels in year 10. Imazapic significantly increased the cover of exposed mineral soil from a median of 16% to 18% across all years and woody fuel treatments (data not shown).

Community cover dominance

Total cover of vascular plants and lichens and mosses was near 80% pretreatment and in all treatments at 3, 6, and 10 years posttreatment (Figure 9a,b). Prescribed fire decreased or had a neutral effect on various components of perennial plant cover and decreased lichens and mosses by year 10, while cheatgrass and litter cover increased (Table 2, Figure 9c,d). The combined losses of cover of Wyoming big sagebrush, Sandberg bluegrass, and lichens and mosses was replaced by cheatgrass cover in the community (Figure 9). The two less severe fuel treatments (mowing and tebuthiuron) allowed perennial plants and lichens and mosses to maintain their positions in the dominance hierarchy although with some reductions (Figure 9c,d) with increases in cheatgrass dominance in all treatments by year 10. The tebuthiuron

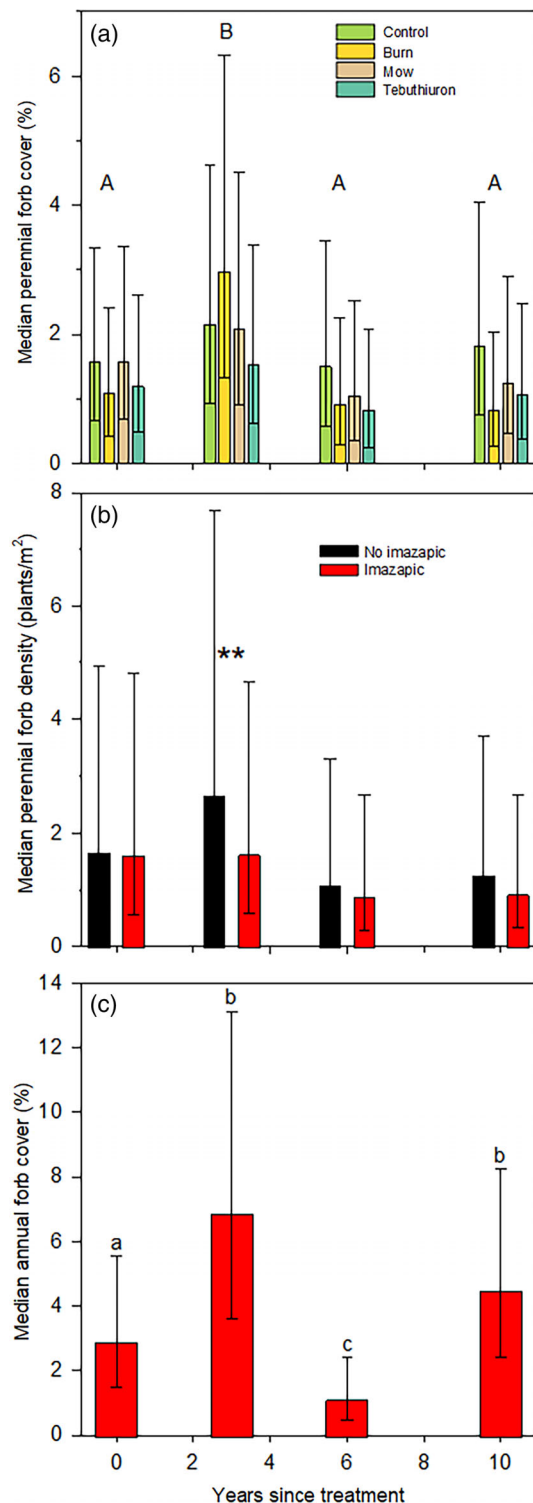


FIGURE 6 (a) Perennial forb cover in response to woody fuel treatments, (b) perennial forb density in response to imazapic treatments, and (c) annual forb cover averaged over all treatments and measured the growing season before (year 0) and 3, 6, and 10 years after treatment application. Bars are medians with their corresponding 95% confidence limits. In (a), different uppercase letters indicate significant differences among years averaged across woody fuel treatments ($p \leq 0.05$). In (b), a double asterisk (**) indicates a year when imazapic treatments differed significantly ($p \leq 0.01$). In (c), different lowercase letters indicate significant differences among years ($p \leq 0.05$).

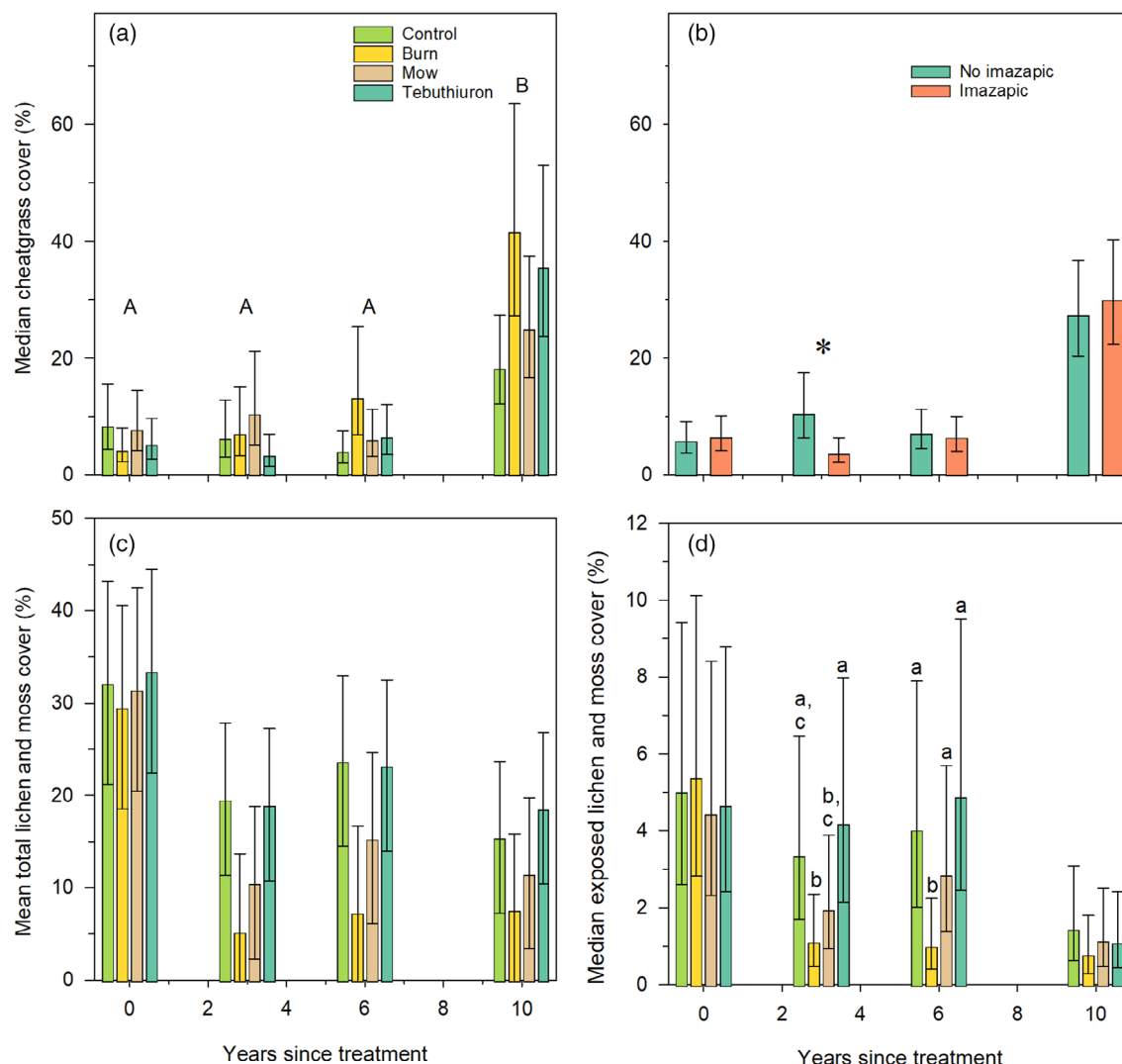


FIGURE 7 Cheatgrass cover measured in response to (a) woody fuel treatments, and (b) imazapic treatments in the growing season before (year 0) and 3, 6, and 10 years after treatment application. (c) Total lichen and moss cover and (d) exposed lichen and moss cover measured in response to woody fuel treatments in the growing season before (year 0) and 3, 6, and 10 years after treatment application. Bars indicate measures of central tendencies with corresponding 95% confidence limits. In (a), different uppercase letters indicate significant differences among years ($p \leq 0.05$). In (b), pairs of bars with an asterisk differed significantly ($p \leq 0.05$) within that year. In (c) and (d), bars with different lowercase letters among fuel treatments within a year differed significantly ($p \leq 0.05$).

treatment was the least severe disturbance with the least reductions in cover of the treatments, but also had little to no impact on woody fuel biomass (Table 2). While imazapic negatively affected Sandberg bluegrass, perennial gap distance, and exposed soil, it positively affected lichens and mosses (Table 2).

DISCUSSION

Land management actions are conducted to achieve desired outcomes within constraints set by the environment. A concomitant goal, equal in importance, is to sustain or restore resilience after disturbance and resistance to

invasive plant dominance of the community, in order to avoid community changes to less diverse and less desirable communities that may not be possible to restore to the original without large economic inputs (Monaco et al., 2016; Pyke et al., 2016). Fuel treatments are being considered and implemented worldwide, but effectiveness is generally evaluated by only examining the treatment's ability to reduce fuels, while ecological consequences are rarely examined (Argañaraz et al., 2017; Fernandes et al., 2012; Penman et al., 2014; Price & Bedward, 2020; Rahlao et al., 2009). Sagebrush ecosystem of North America is one of the largest fire-prone ecosystems on the continent and is one of the most threatened ecologically by the combination of fire, plant invasions, and climate change (Bradley et al., 2016;

Chambers, Bradley, et al., 2014; Mac et al., 1998). Woody fuel and invasive annual grass treatments are being applied more frequently than in the past (Pilliod, Welty, & Toevs, 2017), but the long-term ecological responses of plant communities to such treatments are largely unknown (Shinneman et al., 2019). This study provides a comprehensive attempt to identify the magnitude and longevity of fuel

treatments while simultaneously examining responses of plant communities and their individual components over a 10-year period after treatment. It represents the only spatially dispersed, controlled, and replicated study in semiarid big sagebrush ecosystems (McIver & Brunson, 2014) and to our knowledge the first such study that focuses on ecological impacts of fuel treatments on semiarid shrub–grassland ecosystems in the world.

A common characteristic to all responses in this study was large confidence limits. Two contributors to the size of the confidence limits were the small sample sizes ($n = 6$ sites), and these sites experience varying weather conditions in the years before and after treatment applications (Figure 2). Given this large variation in responses, we were able to provide clear differences in responses to fuel treatments. These differences provide managers with anticipated responses over a 10-year period after treatment application throughout the study region.

Magnitude and longevity of shrub and annual grass fuel reductions

Prescribed fire in arid Wyoming big sagebrush communities created the greatest reduction in woody fuel, sustained through 10 years. If fire burns all of the current year's growth on a big sagebrush plant, it dies since it is incapable of sprouting from roots or older wood (Bilbrough & Richards, 1991; Miller et al., 2013). The death of big sagebrush permits fertile voids for new plant recruitment (Davies, Bates, & James, 2009; Germino et al., 2018; Sankey et al., 2012). Wyoming big sagebrush has limited means for immediately refilling these voids, due to a limited and short-lived seed bank (Pekas & Schupp, 2013; Wijayratne & Pyke, 2012), episodic seed production, and an arid climate that often restricts germination and young

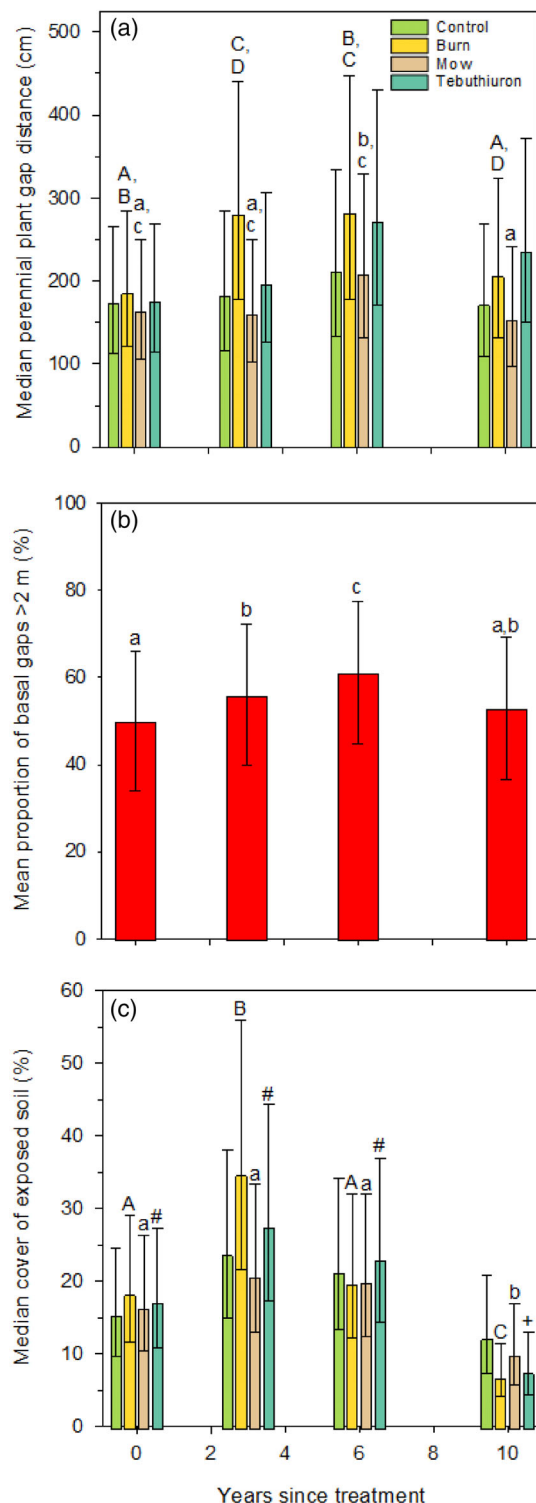


FIGURE 8 (a) Perennial plant basal gap distance measured in response to woody fuel treatments in the growing season before (year 0) and 3, 6, and 10 years after treatment application; (b) proportion of basal gaps among perennial plants that were greater than 2 m measured in the growing season before (year 0) and 3, 6, and 10 years after treatment application; and (c) the cover of exposed soil (no vegetation above) measured in response to woody fuel treatments in the growing season before (year 0) and 3, 6, and 10 years after treatment application. Bars indicate measures of central tendencies with corresponding 95% confidence limits. In (a) and (c), bars with different uppercase letters among burn treatments, with different lowercase letters among mowed treatments, and with different symbols among tebuthiuron treatments differed significantly ($p \leq 0.05$). In (b), bars with different lowercase letters differed significantly ($p \leq 0.05$) among years.

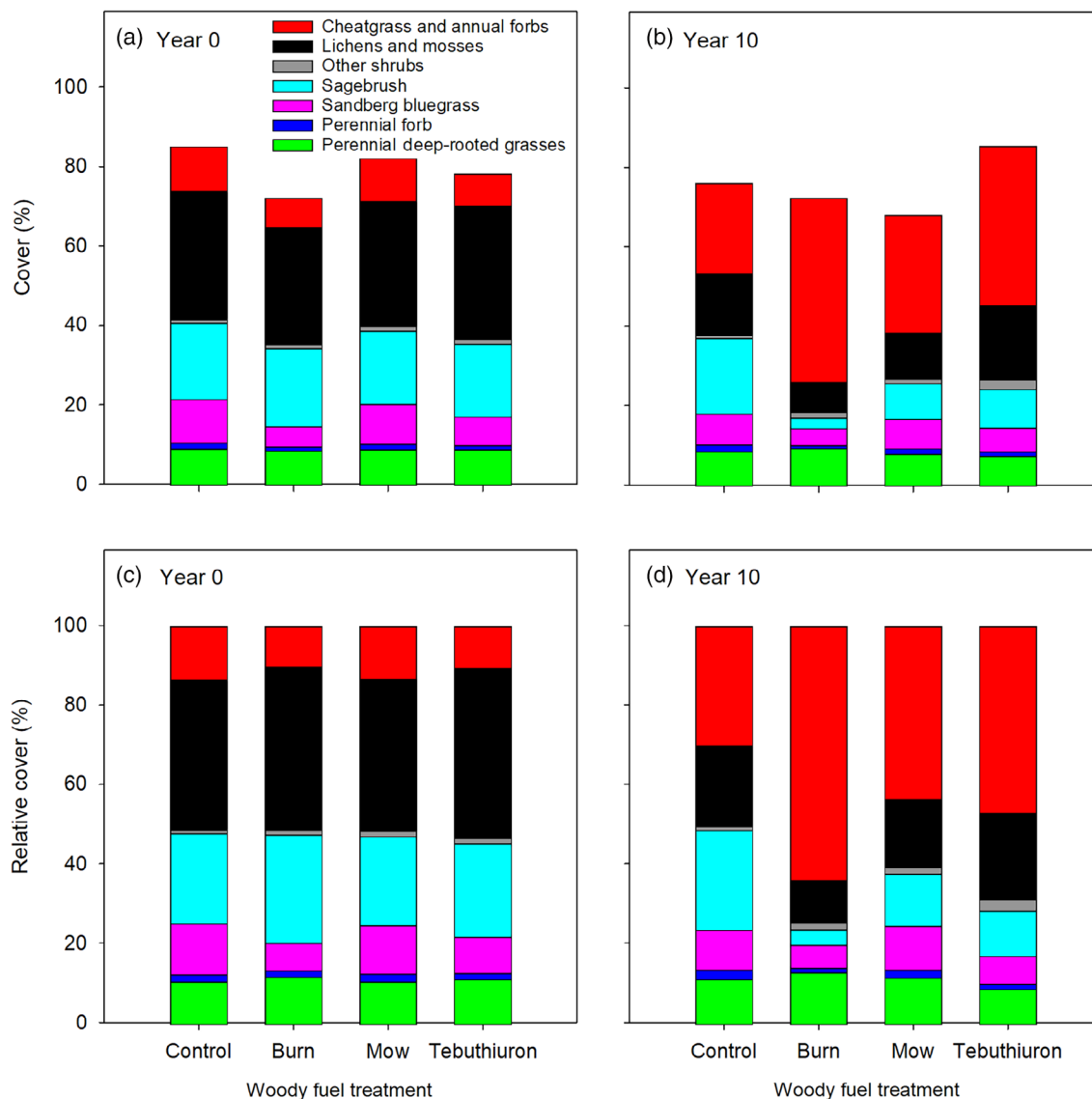


FIGURE 9 Total cover (a and b) or relative cover (c and d) and their component plant groups contributing to the total or relative cover measured in woody fuel treatments in: (a) and (c) the growing season before treatments (year 0); and (b) and (d) year 10 after treatments.

plant growth (Booth et al., 2003; Perryman et al., 2001; Shriver et al., 2018). In contrast, fire can stimulate recovery and sometimes dominance of fire-tolerant and resprouting shrubs (Miller et al., 2013; Pyke et al., 2010), such as green rabbitbrush (*Ericameria teretifolia*) (Blaisdell, 1953; Rhodes et al., 2010; Young & Evans, 1974), although we found no increase in *E. teretifolia* (Chambers et al., 2021; Reis et al., 2019) in our study.

Mowing and tebuthiuron partially reduced woody biomass, but differed in timing of these reductions. These two treatments also differed in their impacts on height of shrubs in the community, which contributed to differences in potential fire behavior (Ellsworth et al., 2022). While mowing provided an immediate reduction in biomass and height of shrubs with minor recovery by 10 years after treatment, tebuthiuron reduced shrub biomass only late in the 10-year

posttreatment period, and shrub height was not reduced, because some plants were not killed and thus retained their initial height. The combination of greater reductions in fuel load (biomass) and fuel packing (including height) by prescribed fire and mowing influenced declines in modeled fire behavior (Ellsworth et al., 2022).

The total elimination of woody fuel by prescribed fire in our subplots likely led to increases in herbaceous fuels. By year 10, all woody fuel treatments had similar increases in herbaceous and litter biomass relative to controls. Most of this biomass was likely contributed by cheatgrass since herbaceous perennial plants had the same or slightly less cover throughout the study, while cheatgrass cover increased with time. Years with high autumn precipitation and adequate precipitation for early cheatgrass cohorts to survive can increase cheatgrass seed production and population size (Mack &

TABLE 2 Summary of plant and soil responses to four fuel or restoration treatments.

Plant/soil response	Burn	Mow	Tebuthiuron	Imazapic
Total shrub biomass (Figure 3a)	↓↓↓	↓ ↓ •	• • •	• • •
Density of all shrubs >15 cm (Figure 3b)	↓↓↓	• • •	• • ↓	• • •
Wyoming big sagebrush cover (Figure 3c)	↓↓↓	↓↓↓	• ↓ ↓	• • •
Wyoming big sagebrush height (Figure 3d)	↓↓↓	↓↓↓	• • •	• • •
Herbaceous and fine litter biomass (Figure 4a)	• ↑ ↑	• • •	• • •	• • •
Perennial deep-rooted grass cover (Figure 4b)	• • •	• • •	• • •	• • •
Perennial deep-rooted grass density (Figure 4c)	• • •	• • •	• • •	• • •
Sandberg bluegrass cover (Figure 5a)	• • •	• • •	• • •	↓ • •
Sandberg bluegrass density (Figure 5b,c)	↓↓↓	• • •	• • •	↓ ↓ ↓
Perennial forb cover (Figure 6a)	↑ • •	• • •	• • •	• • •
Perennial forb density (Figure 6b)	• • •	• • •	• • •	↑ • ↓
Annual forb cover (Figure 6c)	• • •	• • •	• • •	• • •
Cheatgrass cover (Figure 7a,b)	• • •	• • •	• • •	↓ • •
Total lichen/moss cover (Figure 7c,d)	↓ ↓ •	• • •	• • •	• • •
Perennial gap distance (Figure 8a,b)	↑ • •	• • •	• • •	↑ ↑ ↑
Exposed soil cover (Figure 8c)	• • ↓	• • ↓	• • ↓	↑ ↑ ↑

Notes: The up (↑) and down (↓) arrows indicate an increase or decrease relative to controls, with boldface arrows indicating greater magnitude of change for 3, 6, and 10 years of the study and across six sites in the Great Basin. A dot indicates no effect or a neutral response relative to untreated controls. Mixtures of responses (up, down, or dot) indicate a temporal shift with time since treatment (left to right represent early to later times since treatment).

Pyke, 1983). Many of our sites met these conditions between years 5 and 10 (Figure 2), which may have contributed to the increase in cheatgrass cover and biomass in Year 10.

Finally, while cheatgrass cover was nearly eliminated with imazapic in the first 3 years posttreatment (Pyke et al., 2014), this reduction was not maintained after that time. In addition, woody fuel treatments did not appear to enhance cheatgrass cover when imazapic was applied.

Woody fuel treatments and minimum nesting and brood-rearing habitat for Greater Sage-grouse

Minimum guidelines for successful sage grouse nesting habitat in sagebrush ecosystems include big sagebrush at least 30 cm tall with sagebrush canopy cover >15%, and cheatgrass canopy cover <10% (Coates et al., 2016; Connelly et al., 2000, 2011). The big sagebrush height requirement was maintained by all woody fuel treatments. The prescribed fire treatment only maintained the minimum height because the few shrubs left after fires were able to regrow, were partially burned and survived, or never burned. Mowing heights in our study were set at or above 30 cm (Pyke et al., 2014), thus allowing mowing to maintain minimum big sagebrush heights for sage grouse. Other mowing studies have prescribed mowing heights of 20 cm (Davies et al., 2011, 2012; Davies &

Bates, 2014; Davies, Bates, Johnson, & Nafus, 2009; Hess & Beck, 2014), which impacts recovery over time because fewer big sagebrush perennating buds remain for growth (Bilbrough & Richards, 1993).

Big sagebrush cover remained below the minimum 15% recommended for sage grouse habitat for 10 years in all woody fuel treatments. Prescribed fire was the most severe treatment killing nearly all sagebrush plants within our measurement subplots by design (plants that were unburned by the carrying fire were burned by hand). Many prescribed fires only partially burn designated areas due to weather conditions and fuel distribution, but the loss of sagebrush cover, regardless of the amount, will likely be maintained for more than 10 years. Tebuthiuron was the least severe treatment because it allowed about 50% of the sagebrush to survive and those surviving plants maintained their individual canopy areas. Recovery of sagebrush cover after prescribed fire or tebuthiuron will require recruitment and growth of new plants. In addition, any sagebrush recruit would experience intense competition for resources with established native plants and invasive cheatgrass, lessening the likelihood of fast recovery (Chambers et al., 2021; Germino et al., 2018; Reichenberger & Pyke, 1990; Shriver et al., 2018; Wijayratne & Pyke, 2012). Consequently, recovery of big sagebrush cover for sage grouse habitat after fire or tebuthiuron will likely take decades (Hess & Beck, 2012) and will require sagebrush

recruitment. Although sagebrush densities when mowed were intermediate between the control and tebuthiuron treatments, they were not statistically different from either. If densities are not sufficient and recruitment remains low, then cover will likely plateau below the minimum level for sage grouse.

Perennial forb and grass cover are also important for sage grouse nesting and brood-rearing success (Connelly et al., 2011). Fuel treatments did not impact these vegetation components in a significant and long-term manner, such that they would likely impact sage grouse. Since treated areas in this study were selected because they had relatively high levels of herbaceous perennials, we hypothesized they would not require a restoration seeding and would have adequate resilience to recover from disturbance (Pyke et al., 2014). For sites that do not have adequate herbaceous perennials pretreatment, active restoration to establish herbaceous perennials after a fire is typically done to reduce the potential dominance of invasive annual grasses (Knutson et al., 2014). In our study, fire reduced perennial grass cover in the first year after treatment, but cover returned to control levels in years 2 and 3 posttreatment (Pyke et al., 2014). Our results of minimal change in cover of deep-rooted perennial grasses differed slightly from the increase in cover of all perennial grasses noted by Chambers et al. (2021), which is likely an artifact of how perennial grasses and treatments were categorized.

Lastly, successful sage grouse nesting appears to increase when cheatgrass cover remains below 10% (Connelly et al., 2000; Lockyer et al., 2015), but none of the fuel treatments in these warm-dry big sagebrush communities were able to remain below this level, including the controls. However, since it was only at year 10 posttreatment that cheatgrass cover levels exceeded 10%, we cannot conclude that cheatgrass cover will remain at these undesired levels henceforth. In any case, low resistance to cheatgrass and resilience to disturbance have been noted for warm and dry sites like these (Chambers, Miller, et al., 2014), and thus caution should be exercised when applying fuel treatments (especially prescribed fire) in sagebrush communities that support sage grouse.

Resilience and resistance of arid big sagebrush communities

Ecologically resilient ecosystems are capable of adjusting their plant composition and recovering basic structure and function following natural disturbances and management activities (e.g., wildfires and fuel treatments) (Chambers, Maestas, et al., 2017; Holling, 1973). Ideally, resilient ecosystems are also capable of resisting population growth and dominance of invasive species

(D'Antonio & Thomsen, 2004). Management of sagebrush ecosystems in the western United States is currently focused on controlling wildfires and by maintaining or restoring ecological resilience and resistance to invasive annual grasses through prewildfire management choices (Crist et al., 2019). Sites used in this study are described as ranging from moderately high resilience and moderate resistance to low resilience and resistance (Chambers, Bradley, et al., 2014; Chambers, Maestas, et al., 2017; Chambers, Miller, et al., 2014; Maestas et al., 2016; Pyke et al., 2014).

Both abiotic and biotic characteristics of big sagebrush communities determine their relative resilience and resistance before and after disturbances. Responses to disturbances, such as fuel treatments that eliminate shrubs in arid sagebrush ecosystems, are strongly influenced by pretreatment cover and density of perennial herbaceous plants that can regrow and establish in gaps created after death of the dominant shrubs (Chambers et al., 2007, 2021; Chambers, Maestas, et al., 2017; Chambers, Miller, et al., 2014). In addition, community resistance to cheatgrass invasion and expansion is aided by maintaining or increasing lichens and mosses and increasing growth and establishment of perennial grasses, which reduces distances among perennial herbaceous plants (Chambers et al., 2007; Chambers, Bradley, et al., 2014; Chambers, Miller, et al., 2014; Condon & Pyke, 2018; Reisner et al., 2013; Roundy et al., 2018). Our sites all began with moderate cover of perennial grasses and forbs, but relatively high cover of lichens and mosses before treatment (Figure 9a). However, by the 10th year posttreatment all fuel treatments had cheatgrass as either a codominant (mowing and tebuthiuron) or a clear dominant (fire), indicating limited resistance to cheatgrass even in a less severe disturbance.

Evaluation of the relationship between initial cover of perennial herbaceous species and the increase in cheatgrass cover during the first 3 years after fuel treatments on these sites indicated that about 20% perennial herbaceous cover was needed to prevent increases in cheatgrass during this time period (Chambers, Miller, et al., 2014). Relative plant covers varied among sites and subplots, but prior to treatment perennial herbaceous plant cover averaged about 20% and cheatgrass cover was about 12% (Figure 9a). Perennial herbaceous cover remained roughly the same through year 10 (Figure 9b). Wyoming big sagebrush and lichens and mosses had the greatest cover before treatments, but had the largest reductions in treated plots by year 10 (Figure 9a,b). The reduction in Wyoming big sagebrush was the focus of our woody fuel treatments, and we accomplished those reductions. The reductions of lichens and mosses with fire matches other studies (Condon & Gray, 2020),

including when wildfires are used as treatments (Condon & Pyke, 2018). Reductions in lichens and mosses after fire and other treatments are likely the result of increases in cheatgrass, which creates a dense buildup of litter that shades lichens and mosses, leading to their declines (Belnap et al., 2006; Dettweiler-Robinson et al., 2013; Hilty et al., 2004; Serpe et al., 2013). Regardless of the cause of the increase in cheatgrass, the consistently high level of cheatgrass cover that occurred between years 6 and 10 is troubling. Our sites were not resistant to increases in cheatgrass cover regardless of the fuel treatment applied, or even in the absence of treatment. Cheatgrass populations are known to fluctuate widely over years depending on weather (Mack & Pyke, 1983). Therefore, weather between posttreatment Years 6 and 10 may have been a contributing factor, but unfortunately our lack of replicated fuel treatments at the site level prevents us from being able to tease out the site-specific weather effects. Perhaps an additional study can examine the site-specific responses to weather by using only a single treatment, such as the controls, to focus on this question.

The removal of big sagebrush in woody fuel treatments did not consistently enhance perennial herbaceous plants over time, even when cheatgrass was controlled by imazapic for 3 years. Previous studies also found that imazapic reduced non-native annual grasses for a limited time, but did not lead to an increase in native perennial plant cover and density (Davies & Hamerlynck, 2019; Davies & Sheley, 2011; Davison & Smith, 2007; Elseroad & Rudd, 2011). Our results provide greater evidence that imazapic applications alone are insufficient to increase perennial herbaceous plants, and therefore seeding might be required to increase cover and density of native perennials (Monaco et al., 2017).

Fuel treatments differed in their disturbance severity and potentially in their impacts on community resilience and resistance. Prescribed fire was anticipated to be the most severe disturbance, as it burned all plants and likely changed soil microbial communities and nutrient availability (Rau et al., 2014; Stubbs & Pyke, 2005; Whelan, 1995), whereas mowing only changed shrub structure with minor impacts on other plants or soil nutrients (Rau et al., 2014), and tebuthiuron killed only a proportion of the shrubs in the community (Olson & Whitson, 2002). Most perennial grasses (e.g., bluebunch wheatgrass, needlegrasses, and squirreltail) in big sagebrush communities are relatively tolerant of fire (Miller et al., 2013) and our study results supported this expectation, by returning to prefire cover and density in 1 or 2 years postfire (Pyke et al., 2014). Yet perennial grasses never increased in cover or density during the 10 years regardless of woody fuel treatment. Additionally, it

appears that prescribed fire and imazapic may have reduced the density and potentially cover of Sandberg bluegrass, contributing to another potential loss of resistance to cheatgrass. This however was not a clear finding since our prescribed fire plots had lower Sandberg bluegrass cover before treatments (Pyke et al., 2014). Further study regarding the impacts that prescribed fire and imazapic may have on Sandberg bluegrass growth and demography is warranted.

To be effective in the long term, fuel treatments are usually intended to be applied on a regular basis to keep fire intensity and spread at a minimal level (Crist et al., 2019; Shinneman et al., 2018). Our treatments were only conducted once, providing us the opportunity to determine the time needed before retreatment (Ellsworth et al., 2022). Multiple fuel treatments over time may lead to different shifts in species groups. Shinneman et al. (2020) noted that repeated fires on the same site in big sagebrush ecosystems in the Columbia Basin may lead to greater dominance of non-native annual grasses. To our knowledge, no one has examined multiple applications of mowing or herbicides on the plant communities including lichens and mosses, but as fuel treatments are applied more regularly in the future, monitoring of plant community responses, including lichens and mosses, will aid land managers' decisions about where and when to apply these treatments.

Shorter gap distances among perennial plants and higher cover of lichens and mosses have been noted as key characteristics that lead to higher cheatgrass resistance (Condon & Pyke, 2018; Reisner et al., 2013). Gap distances between perennial plants increased in the early years after prescribed fire (Pyke et al., 2014) but returned surprisingly to pretreatment levels by year 10, especially in the fire and tebuthiuron treatments that killed sagebrush. We suspect that the long-term reduction in lichen and moss cover and low perennial native herbaceous cover with prescribed fire (and to a lesser extent mowing) were major contributors to a loss of resistance to cheatgrass.

Wildfires threaten the sustainability of native big sagebrush ecosystems with conversion to annual grass dominance (Pilliod, Welty, & Arkle, 2017). Nearly all wildfire ignitions in the United States are controlled with initial attacks and remain below 4000 ha, but the rise in megafires worldwide (e.g., de la Berrera et al., 2018; Germino et al., 2018; Wintle et al., 2020) increases the management impetus to preemptively manage fire-prone landscapes using fuel treatments (Crist et al., 2019; Gill et al., 2013). These treatments may reduce fuels, aiding fire suppression and protection of habitats, but as our study demonstrates, they also have both anticipated and unanticipated ecological consequences, resulting from

selective plant population declines, increases in resource availability (Rau et al., 2014), and shifts in dominance between plant functional groups. Implementing fuel treatments that not only reduce fuel and fire potential but also minimize impacts on wildlife habitat and maintain or increase ecosystem resilience to disturbance and resistance to non-native species will provide a more holistic approach to fuel management.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Shaff, 2020) are available from Science Base: <https://doi.org/10.5066/P90APJ96>.

ORCID

David A. Pyke  <https://orcid.org/0000-0002-4578-8335>

Scott E. Shaff  <https://orcid.org/0000-0001-8978-9260>

Jeanne C. Chambers  <https://orcid.org/0000-0002-1419-9247>

Eugene W. Schupp  <https://orcid.org/0000-0002-1258-503X>

Beth A. Newingham  <https://orcid.org/0000-0002-3324-500X>

Margaret L. Gray  <https://orcid.org/0000-0002-4810-8876>

Lisa M. Ellsworth  <https://orcid.org/0000-0001-7232-2656>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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