Resilience and Resistance of Sagebrush Ecosystems: Implications for State and Transition Models and Management Treatments

Authors: Chambers, Jeanne C., Miller, Richard F., Board, David I., Pyke, David A., Roundy, Bruce A., et al.

Source: Rangeland Ecology and Management, 67(5) : 440-454

Published By: Society for Range Management

URL: https://doi.org/10.2111/REM-D-13-00074.1

Rangeland Ecol Manage 67:440–454 | September 2014 | DOI: 10.2111/REM-D-13-00074.1

Resilience and Resistance of Sagebrush Ecosystems: Implications for State and Transition Models and Management Treatments

Jeanne C. Chambers,[1] Richard F. Miller,[2] David I. Board,[3] David A. Pyke,[4] Bruce A. Roundy,[5] James B. Grace,[6] Eugene W. Schupp,[7] and Robin J. Tausch[8]

Authors are [1]Research Ecologist, [3]Ecologist/Data Analyst, and [8]Range Scientist, US Forest Service, Rocky Mountain Research Station, Reno, NV 89512, USA; [2]Professor, Rangeland Ecology & Management, Oregon State University, Corvallis, OR 97331, USA; [4]Research Ecologist, US Geological Survey, Forest and Rangeland Ecosystem Science Center, Corvallis, OR 97331, USA; [5]Professor, Plant and Wildlife Sciences, Brigham Young University, UT 84602, USA; [6]Research Ecologist, US Geological Survey, National Wetlands Research Center, Lafayette, LA 70506, USA; and [7]Professor, Wildland Resources, Utah State University, Logan, UT 84322, USA.

Abstract

In sagebrush ecosystems invasion of annual exotics and expansion of piñon (*Pinus monophylla* Torr. and Frem.) and juniper (*Juniperus occidentalis* Hook., *J. osteosperma* [Torr.] Little) are altering fire regimes and resulting in large-scale ecosystem transformations. Management treatments aim to increase resilience to disturbance and enhance resistance to invasive species by reducing woody fuels and increasing native perennial herbaceous species. We used Sagebrush Steppe Treatment Evaluation Project data to test predictions on effects of fire vs. mechanical treatments on resilience and resistance for three site types exhibiting cheatgrass (*Bromus tectorum* L.) invasion and/or piñon and juniper expansion: 1) warm and dry Wyoming big sagebrush (WY shrub); 2) warm and moist Wyoming big sagebrush (WY PJ); and 3) cool and moist mountain big sagebrush (Mtn PJ). Warm and dry (mesic/aridic) WY shrub sites had lower resilience to fire (less shrub recruitment and native perennial herbaceous response) than cooler and moister (frigid/xeric) WY PJ and Mtn PJ sites. Warm (mesic) WY Shrub and WY PJ sites had lower resistance to annual exotics than cool (frigid to cool frigid) Mtn PJ sites. In WY shrub, fire and sagebrush mowing had similar effects on shrub cover and, thus, on perennial native herbaceous and exotic cover. In WY PJ and Mtn PJ, effects were greater for fire than cut-and-leave treatments and with high tree cover in general because most woody vegetation was removed increasing resources for other functional groups. In WY shrub, about 20% pretreatment perennial native herb cover was necessary to prevent increases in exotics after treatment. Cooler and moister WY PJ and especially Mtn PJ were more resistant to annual exotics, but perennial native herb cover was still required for site recovery. We use our results to develop state and transition models that illustrate how resilience and resistance influence vegetation dynamics and management options.

Key Words: *Bromus tectorum* invasion, ecological sites, environmental gradients, mechanical treatments, piñon and juniper expansion, prescribed fire

INTRODUCTION

Sagebrush ecosystems are undergoing large scale transformations that are affecting a diversity of rangeland resources and influencing both management plans and actions (Knick and Connelly 2011; Miller et al. 2011). Invasion and expansion of annual invaders, especially cheatgrass (*Bromus tectorum* L.), at low to mid elevations are resulting in an annual grass fire cycle and conversion of large areas to annual weed dominance (D'Antonio and Vitousek 1992; Balch et al. 2013). Expansion and infilling of piñon and juniper trees at middle to high elevations are resulting in depletion of understory species and increased risk of large and high-severity fires (Miller et al. 2013). Many sagebrush ecosystems are fragmented and degraded, and multiple species associated with these ecosystems are of conservation concern (Wisdom et al. 2005).

Researchers and managers alike have emphasized the need to implement management actions that will increase resilience of native ecosystems to stress and disturbance and/or enhance resistance to invasion (Holling 1996; Briske et al. 2008; Brooks and Chambers 2011; Chambers et al. 2014). We define resilience as the capacity of an ecosystem to *regain* its fundamental structure, processes, and functioning when altered by stressors like drought and disturbances like overgrazing by livestock and altered fire regimes (Holling 1973; Allen et al. 2005). We define resistance as the capacity of an ecosystem to *retain* its fundamental structure, processes, and functioning despite stresses, disturbances, or invasive species (Folke et al. 2004). Resistance to invasion by nonnative plants is increasingly important in rangeland ecosystems; it is a function of the abiotic and biotic attributes and ecological processes of an ecosystem that limit the population growth of an invading species (D'Antonio and Thomsen 2004).

To increase the resilience and resistance of sagebrush ecosystems, management actions have focused on decreasing woody species (shrubs and/or trees) to 1) reduce fuel loads and continuity in order to decrease fire severity and extent, 2) lower competitive suppression of perennial herbaceous species, which

This is Contribution Number 83 of the Sagebrush Steppe Treatment Evaluation Project, funded by the Joint Fire Science Program (05-S-08), the Bureau of Land Management, the US Forest Service, the National Interagency Fire Center, and the Great Northern Land Conservation Cooperative.

Correspondence: Jeanne C. Chambers, US Forest Service, Rocky Mountain Research Station, Reno, NV 89512, USA. Email: jchambers@fs.fed.us

Manuscript received 22 May 2013; manuscript accepted 1 December 2013.

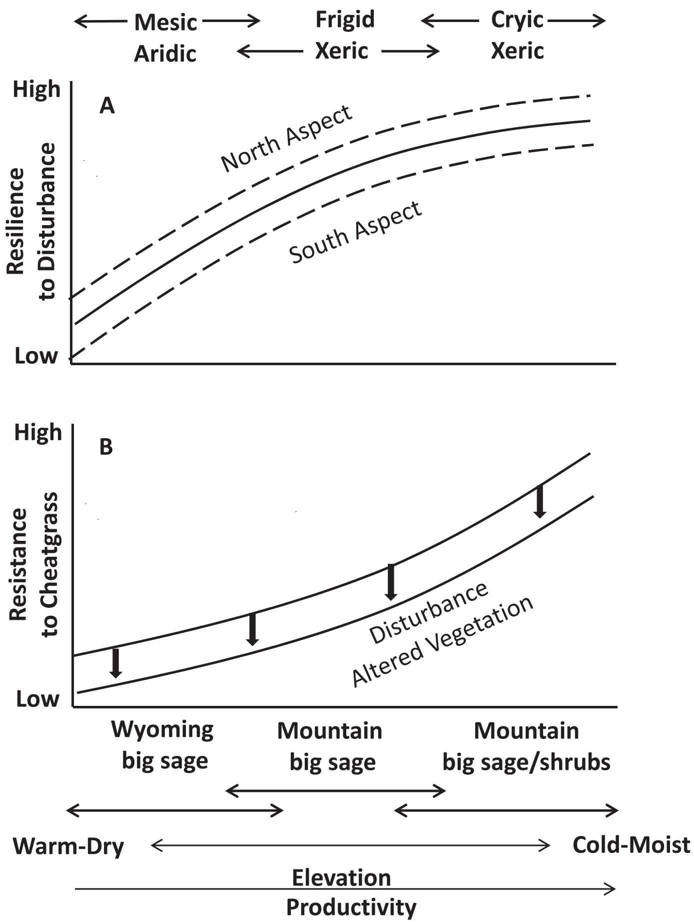

Figure 1. **A**, Resilience to disturbance and **B**, resistance to cheatgrass over a typical temperature/precipitation gradient in the Great Basin. Predominant ecological sites that occur along this continuum include Wyoming big sagebrush on mesic/aridic sites to mountain big sagebrush on frigid/xeric sites to mountain big sagebrush and root-sprouting shrubs on cryic/xeric sites. Resilience increases along the temperature/precipitation gradient and is influenced strongly by site characteristics like elevation and aspect. Resistance also increases along the temperature/precipitation gradient and is affected by disturbances and management treatments that alter vegetation structure and composition and increase resource availability. (adapted from Chambers et al. 2014)

largely determine resilience to fire and resistance to invasion, and 3) decrease longer term risk of cheatgrass dominance (Miller et al. 2013, 2014b). Responses to management treatments vary because sagebrush ecosystems occur over a broad range of abiotic and biotic conditions and differ significantly in resilience to stress and disturbance and resistance to invasion (Chambers et al. 2014; Miller et al. 2013). A stronger understanding of factors that influence resilience to management treatments and resistance to invaders could increase the ability to prioritize treatment areas and to select the most appropriate treatments for each area.

Recent research shows that resilience to disturbance changes along environmental gradients in sagebrush ecosystems (Chambers et al. 2014). Higher resilience is associated with greater resource availability and more favorable environmental conditions for plant growth and reproduction (Fig. 1A; Chambers 2005; Condon et al. 2011; Davies et al. 2012). Cooler and moister sites at higher elevations characterized by mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* [Rydb.] Beetle) and mountain brush types (i.e., mountain big sagebrush, snowberry [*Symphoricarpos* spp.], serviceberry [*Amelanchier* spp.]) typically have higher soil water and nutrient availability and, consequently, higher net productivity than warmer and drier sites at lower elevations characterized by Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) (West 1983a, 1983b; Tausch and Tueller 1990; Alexander et al. 1993; Dahlgren et al. 1997; Miller et al. 2011). These relationships are modified by effects of elevation, landform, slope, aspect, and soil characteristics, and, thus, vegetation composition and structure (Johnson and Miller 2006; Condon et al. 2011). Disturbance history differs along environmental gradients, and because cooler and moister sites with relatively high productivity had high fuel abundance and continuity, they had more frequent presettlement fires (Miller et al. 2011) and often have a greater abundance of fire-tolerant species (Pyke et al. 2010). Higher mean biomass of perennial grasses and forbs coupled with more rapid shrub recruitment on productive, higher elevation sites can result in greater resilience to disturbance through a smaller initial change in community composition and more rapid recovery following fire (Chambers 2005; Davies et al. 2012).

Research also indicates that resistance to invasive annual grasses changes along environmental gradients in sagebrush ecosystems (Fig. 1B). Resistance to an invasive species is a function of the environmental conditions that define where a species can establish and persist (i.e., fundamental niche) and of the effects of interactions with the native community on its actual occurrence (i.e., realized niche) (Chambers et al. 2014). The fundamental niche of cheatgrass is determined by soil temperature and water availability and, thus, is strongly influenced by elevation, landform, slope, and aspect (Chambers et al. 2007; Condon et al. 2011). In sagebrush ecosystems, cheatgrass germination, growth, and/or reproduction appear to be optimal in relatively warm and dry Wyoming big sagebrush communities due to high climate suitability (Chambers et al. 2007; Roundy et al. 2007; Leger et al. 2009). Low and sporadic precipitation limit cheatgrass establishment in warm and dry salt desert communities at low elevations (Meyer et al. 2001), while low soil temperatures constrain cheatgrass growth and reproduction in mountain big sagebrush and mountain brush communities at high elevations (Chambers et al. 2007). The realized niche represents a subset of the fundamental niche and is strongly mediated by resource availability and interactions with the native plant community (Chambers et al. 2014).

Disturbances and stresses, including management treatments that alter vegetation composition and/or structure, can increase resource availability and affect resilience to disturbance and resistance to invaders (Leffler and Ryel 2012). Effects of vegetation management treatments designed to decrease woody species depend on characteristics of the area to be treated, treatment severity, and relative abundance of the primary functional groups prior to treatment. For example, in wooded shrublands prescribed fire removes fire-intolerant trees and shrubs and can result in increased soil water and nutrient availability (Rau et al. 2007; Roundy et al. 2014b), slow shrub recovery, and lower resistance to cheatgrass (Miller et al. 2014b; Roundy et al. 2014a). In contrast, mechanical reduction of trees has little effect on shrubs and at low to intermediate tree covers can result in higher resistance to cheatgrass than prescribed fire (Miller et al. 2014a; Roundy et al. 2014a). Treatment outcomes are highly dependent on initial cover of native perennial herbaceous species, but mechanical removal of trees results in smaller initial change in community composition and may result in more rapid recovery compared to burns.

State and transition models (STMs) are widely used in rangeland management to describe changes in plant communities and associated soil properties, causes of change, and effects of management interventions (Stringham et al. 2003; Bestelmeyer et al. 2009). Incorporating information on the resilience of rangeland ecosystems to disturbance into STMs can improve our ability to understand and predict the outcomes of management actions (Briske et al. 2008; Bagchi et al. 2012). To date, a lack of information on the ecosystem attributes that determine resilience and the uncertainties surrounding estimates of these attributes has limited the development of STMs that address ecosystem resilience (Briske et al. 2008; Bestelmeyer et al. 2009). To our knowledge, there have been no attempts to include information specifically related to resistance to invasion in STMs. The Sagebrush Steppe Treatment Evaluation Project (SageSTEP), a collaborative research and management effort, provides the necessary data for evaluating key elements of resilience and resistance to invasion in sagebrush ecosystems (McIver et al. 2010; McIver and Brunson 2014) and incorporating this information into STMs.

Here we use SageSTEP data to examine effects of fire vs. mechanical treatments on resilience and resistance to invasion in sagebrush ecosystems. We compare sites that differ in environmental characteristics and dominant sagebrush species and that are exhibiting cheatgrass invasion and/or piñon and juniper expansion. We predict that strong differences in resilience and resistance to cheatgrass and other annual exotics exist among sites that differ in environmental characteristics and that these differences influence treatment outcomes. We ask four related questions to address this prediction: 1) How do environmental characteristics influence resilience to prescribed fire and mechanical treatments? 2) How do environmental characteristics influence resistance to cheatgrass and other annual exotics after prescribed fire and mechanical treatments? 3) How do contingency effects of weather influence perennial native herbaceous species and invaders without treatment? 4) How does pretreatment cover of perennial native herbaceous species influence resistance to invasion after prescribed fire and mechanical treatments? We use our results to develop STMs for sagebrush ecosystems that explicitly incorporate resilience and resistance information.

METHODS

Study Sites

SageSTEP sites are arrayed across a broad geographical area that encompasses a range of environmental conditions. For a map of the SageSTEP site locations and description of the overall study design, see McIver and Brunson (2014). In this study, we examine the responses of three site types with different dominant sagebrush species and soil temperature and moisture regimes to prescribed fire and mechanical treatments. We selected seven sites to examine effects of fire and mechanical treatment on a Wyoming big sagebrush type (WY shrub) exhibiting invasion by cheatgrass (Onaqui, Owyhee, Roberts, Gray Butte, Moses Coulee, Rock Creek, and Saddle Mountain) (see Pyke et al. 2014). Sites were located in five states (Idaho, Nevada, Oregon, Utah, and Washington) and six Major Land Resource Areas (Columbia Basin, Columbia Plateau, Malheur High Plateau, Owyhee High Plateau, Snake River Plains, and Great Salt Lake Area) (USDA-NRCS 2007). Subdominants on these sites were bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Love) or Thurber's needle grass (*Achnatherum thurberianum* [Piper] Barkworth), soils were loams, soil temperature regimes were mesic to frigid, and soil moisture regimes were aridic to xeric. Criteria used to select sites were 1) the dominant shrub was Wyoming big sagebrush, 2) soils were loams, and 3) cheatgrass invasion had occurred but native grasses and forbs were still present in the understory.

We selected nine sites to examine effects of fire and mechanical treatment on Wyoming big sagebrush (Marking Corral, South Ruby, Greenville Bench, Onaqui, and Scipio) and mountain big sagebrush (Blue Mountain, Devine Ridge, Walker Butte, and Seven Mile) types exhibiting piñon and juniper expansion (see Miller et al. 2014b; Roundy et al. 2014a). Sites were located in four states (Utah, Nevada, California, and Oregon) and four Major Land Resource Areas (Malheur High Plateau, Klamath Basin, Central Nevada Basin and Range, and Salt Lake Area) (USDA-NRCS 2007). The Wyoming big sagebrush type (WY PJ) had bluebunch wheatgrass and needlegrasses in the understory, loamy and typically skeletal soils, and mesic/aridic to xeric soil temperature/moisture regimes. The mountain big sagebrush type (Mtn PJ) had Idaho fescue (*Festuca idahoensis* Elmer) and bluebunch wheatgrass in the understory, loamy soils or mollic epipedons, frigid/xeric soil regimes, and little cheatgrass. Devine Ridge (DR) differed as codominants were Sandberg bluegrass (*Poa secunda* J. Presl) and Thurber needlegrass, soils were orthents, and it was on a warm, west-facing slope. Criteria used to select sites were 1) the dominant shrub was big sagebrush, 2) piñon and/or juniper was currently expanding into the site, 3) there was no evidence that stands were dominated previously by mature piñon or juniper, 4) soils were loams, 5) native grasses and forbs were present in the understory, and 6) introduced species were present but not a dominant component.

Treatments

Treatment-plot layout was a randomized complete block with each of the 16 sites representing a block. The seven sagebrush sites exhibiting cheatgrass invasion ranged in size from roughly 120 to 325 ha depending on the willingness of land managers to remove sagebrush. Three treatment plots that were 20 to 81 ha in size were established at each sagebrush site. Each treatment plot contained 6 to 9 measurement subplots that were 0.1 ha (33×30 m) in size and that were positioned to cover a range of perennial grass cover. A one-time treatment—control, prescribed fire, or mowing of sagebrush with a rotary blade to a height of $\sim$35 cm—was randomly assigned to each treatment plot in the block. Treatments were applied in 2006, 2007, and 2008 using a stagger-start design (Loughin 2006) in which all treatments at a given site were applied in the same year to form a statistical block, but start dates varied among sites. A stagger-start design alleviates effects of starting an experiment under the same set of climate conditions so that results can be applied over a broader inference space. Prescribed fire was applied in October on all sites except Moses Coulee, which received a May fire, and mowing was conducted in the same year as fire within a site. Shrub cover was reduced from 26% to 4% by fire and from 20% to 8% by mowing (Pyke et al. 2013).

For each of the nine sagebrush sites exhibiting tree expansion, three 8–20 ha treatment plots were established depending on site uniformity and topography. Each treatment plot contained 15 measurement subplots that were 0.1 ha (33×30 m) in size and that were positioned to include the range of tree covers that occurred on the site. One of three treatments was randomly assigned to each treatment plot in the block—control, cut-and-leave, and prescribed fire. In the cut-and-leave treatment, all trees > 2 m tall were cut and left on the ground. Treatments were applied in 2006, 2007, and 2009 for the piñon and juniper sites in a stagger-start design (Loughin 2006). Burning and cut-and-leave treatments were applied at each site in the same year to form a statistical block. Prescribed fire was applied between August and early November, and tree cutting was implemented between September and November. Tree canopies were reduced to < 5% in burn plots and < 1% in cut-and-leave plots (Miller et al. 2014b).

Measurements

Data were collected from each subplot on all 16 sites during the growing season immediately prior to treatment application (year 0) and for three growing seasons afterwards (Miller et al. 2014b; Pyke et al. 2014). Due to funding constraints, fewer sites were sampled in year 4 posttreatment for all site types, and the number of subplots sampled was decreased on six of the 11 sites that were sampled. Within each subplot, plant and ground surface cover were sampled using the point-intercept method at 0.5-m intervals along five, 30-m transects ($n=300$ points/subplot) (Herrick et al. 2009). Plants were recorded by life form. Native life forms included total shrubs, sagebrush (*Artemisia* L.), perennial grasses, perennial forbs, annual forbs, and soil crusts. Introduced plant life forms included exotic grasses (primarily cheatgrass) and exotic forbs. Ground surface cover consisted of bare ground and litter. Foliar cover of each life form except shrubs was recorded as a single hit at each point if the point came into contact with that life form. Shrub canopy cover was measured by recording a hit as a direct contact or the point falling within the live canopy perimeter. More than one life form or ground cover class could be recorded at a single point, but each had a maximum of one hit per point. Bare ground was recorded when it was the only hit.

Analyses

Site and Treatment Effects. To examine resilience to fire and resistance to invaders across the three site types, we performed ANOVAs using generalized linear mixed effects models. We examined fixed effects of site type, years since treatment, treatment (fire and control), and their interactions for four variables—shrub, perennial native herbaceous, all annual exotic species, and only cheatgrass cover. Based on standard graphical examinations of residuals, a negative binomial distribution fit the data best when a log link and an offset of the number of points sampled per plot was used. The overall model design was based on a BACI (Before/After Control/Impact) design in which sampling begins prior to treatment (year 0) and continues posttreatment (years 1, 2, 3, and 4). Untreated plots (controls) are sampled to evaluate effects of natural temporal variation. The spatial design of the experiment was a randomized block. Blocks (random variable) were sites in which plots (random variable represented by the interaction of site by treatment) were randomly assigned treatments. Measurements on the subplots were averaged to the plot level. A staggered start design was used in which not all sites were treated in the same year. This created the hierarchical blocking (random) factors of "year of treatment." To account for temporal variation, calendar year, and calendar year by site type were included as random effects in the model.

Because the two mechanical treatments were not equivalent in the WY shrub and piñon-juniper sites, we used the same method as above, but with two different models, to compare effects of fire and mechanical treatments. For Mtn PJ and WY PJ site types, we expanded the treatments to include cut-and-leave, fire, and control. For WY shrub, we excluded site type and included mowing, fire, and control. These and all other analyses that included WY shrub sites excluded fire plots for 1) the Roberts site due to an inadequate burn and 2) the Moses Coulee site because the fire occurred in May instead of October. As described above, year 4 posttreatment had fewer sites and lower subsample numbers.

Annual Variation in Herbaceous Response Among Controls. To evaluate the interannual variation during the period of the experiment for each site type, we conducted ANOVAs in which control plots were modeled as a function of calendar year, site type, and their interaction. Response variables used were those expected to exhibit high interannual variability: perennial native herbaceous, total annual exotic, and cheatgrass cover. Based on standard graphical examinations of residuals, a negative binomial distribution fit the data best when a log link and an offset of the number of points sampled per plot was used.

Relationship of Perennial Native Herbaceous Species to Annual Exotics and Cheatgrass. We examined relationships between perennial native herbaceous cover in the year of treatment to perennial native herbaceous, annual exotic, and cheatgrass cover 3 yr after treatment. We conducted generalized linear mixed effects ANOVAs for effects of treatment, site type, perennial native herbaceous cover in the year of treatment, and their interactions on perennial native herbaceous, total annual exotic, and cheatgrass cover 3 yr after treatment. Based on standard graphical examinations of residuals, a negative binomial distribution fit the data best when a log link and an offset of the number of points sampled per plot was used. We maintained the randomized block spatial design of the experiment and the staggered start design by including treatment year as a random factor in the model.

We used simple linear regressions to help illustrate the nature of these relationships. To take advantage of the BACI design, we also conducted ANOVAs and simple linear regressions of initial cover of perennial native herbaceous species related to

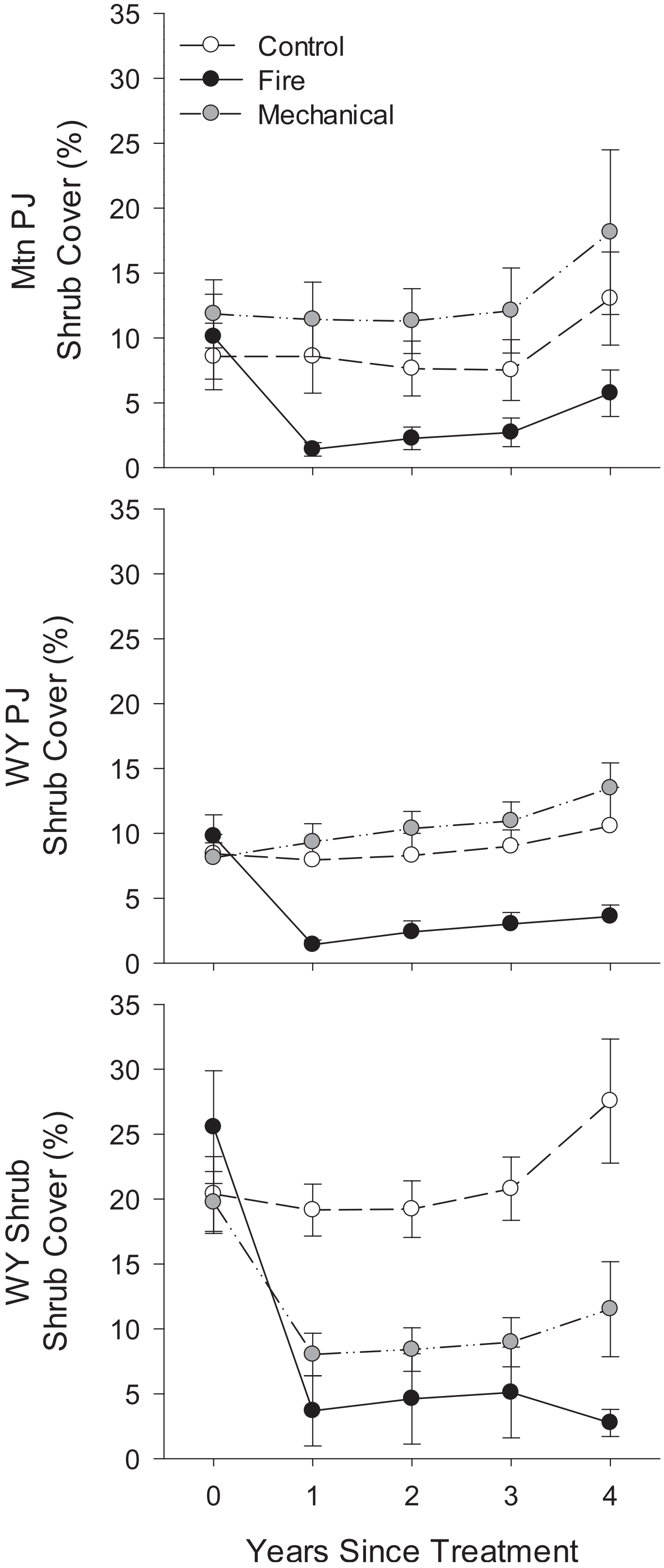

Figure 2. Shrub cover in control, fire, and mechanical plots on Mtn PJ, WY PJ, and WY shrub sites the year before treatment and the first 4 yr after treatment. Values are mean ± SE.

total annual exotics and cheatgrass prior to treatment. These analyses were based on individual subplot data.

RESULTS

Site and Treatment Effects

Shrub cover showed a three-way interaction among site type, treatment, and year of response in the overall model ($F_{8,39}$=4.01, P=0.0015). Cover of shrubs was higher pretreatment and in control plots on WY shrub sites than Mtn PJ sites, but was higher on WY shrub than WY PJ sites only on fire plots (Fig. 2; $P < 0.05$). Shrub cover did not differ between WY PJ and Mtn PJ sites prior to treatment or in control plots. Fire decreased shrub cover relative to pretreatment and to control plots on all site types in all posttreatment years ($P < 0.05$). Shrub cover increased from year 1 to years 3 and 4 in fire plots on WY PJ and Mtn PJ sites ($P < 0.05$), but did not increase posttreatment on WY shrub sites. In the model comparing fire and mowing treatments for the WY shrub site, mowing decreased shrub cover in all posttreatment years (Fig. 2; $P < 0.004$), and shrub cover did not increase on mowed plots over time. Shrub cover was lower on fire plots than mowed plots ($P < 0.004$). In the model comparing fire and cut-and-leave treatments, the WY PJ and Mtn PJ sites showed similar responses to each other (Fig. 2). Shrub cover was higher on cut-and-leave plots than pretreatment and on control plots only in year 4 ($P < 0.006$). Fire plots had lower shrub cover than cut-and-leave plots in all posttreatment years ($P < 0.001$).

Perennial native herbaceous cover showed significant differences only among treatments and years of response in the overall model due to similar responses among sites (treatment×year, $F_{4,39}$=18.30, $P < 0.0001$). Fire decreased perennial native herbaceous cover relative to pretreatment and to control plots in the first year after treatment on all sites (Fig. 3; $P < 0.002$). However, cover on fire plots was higher in years 2, 3, and 4 relative to year 1 ($P < 0.0009$). In the model comparing fire and mowing treatments for the WY shrub site, perennial native herbaceous cover was higher in years 3 and 4 than pretreatment for both fire (Fig. 3; $P < 0.03$) and mowed plots ($P < 0.06$), but did not differ for treatment and control plots in years 2, 3, and 4. Fire plots differed from mowed plots only in the first year after treatment when perennial native herbaceous cover was lower on fire plots (P=0.0001). In the model comparing fire and cut-and-leave treatments for WY PJ and Mtn PJ sites, perennial native herbaceous cover was higher in cut-and-leave plots than pretreatment or in control plots in years 2, 3, and 4 (Fig. 3; $P < 0.05$). Fire plots had lower perennial native herbaceous cover than cut-and-leave plots in years 1 and 2 ($P < 0.006$) but not in years 3 and 4.

Annual exotic cover differed among site types in the overall model (Fig. 4; $F_{2,11}$=4.46, P=0.0381). Cover of annual exotics in Mtn PJ sites was less than in WY shrub sites ($P < 0.01$). Annual exotic cover in WY PJ sites did not differ from that in WY shrub sites, but was marginally higher than in Mtn PJ sites ($P < 0.10$). A treatment by year interaction also occurred in the overall model ($F_{4,39}$=14.6, $P < 0.0001$). Fire increased annual exotic cover relative to pretreatment and to control plots in years 3 and 4 ($P < 0.01$). In the model comparing fire and mowing treatments for the WY shrub site, annual exotic cover

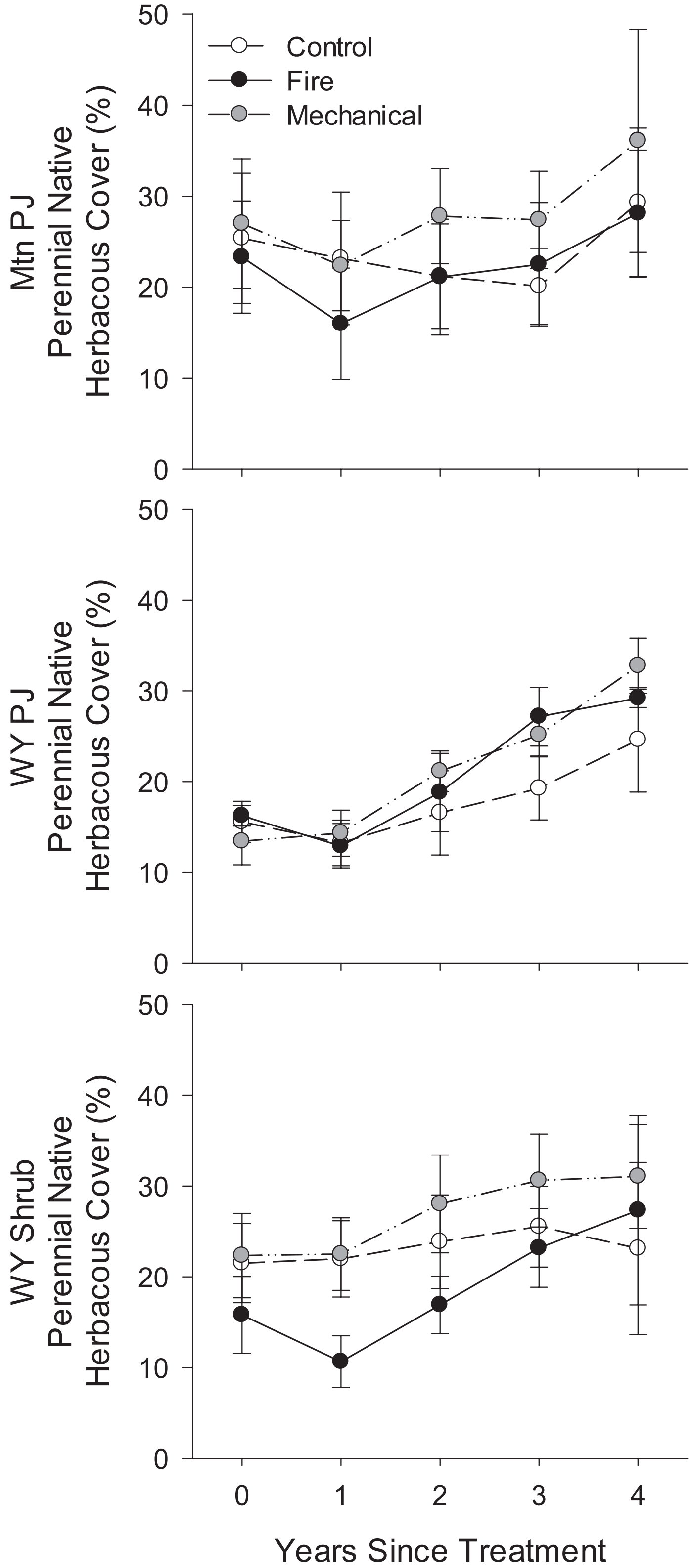

Figure 3. Perennial native herbaceous cover in control, fire, and mechanical plots on Mtn PJ, WY PJ, and WY shrub sites the year before treatment and the first 4 yr after treatment. Values are mean ± SE.

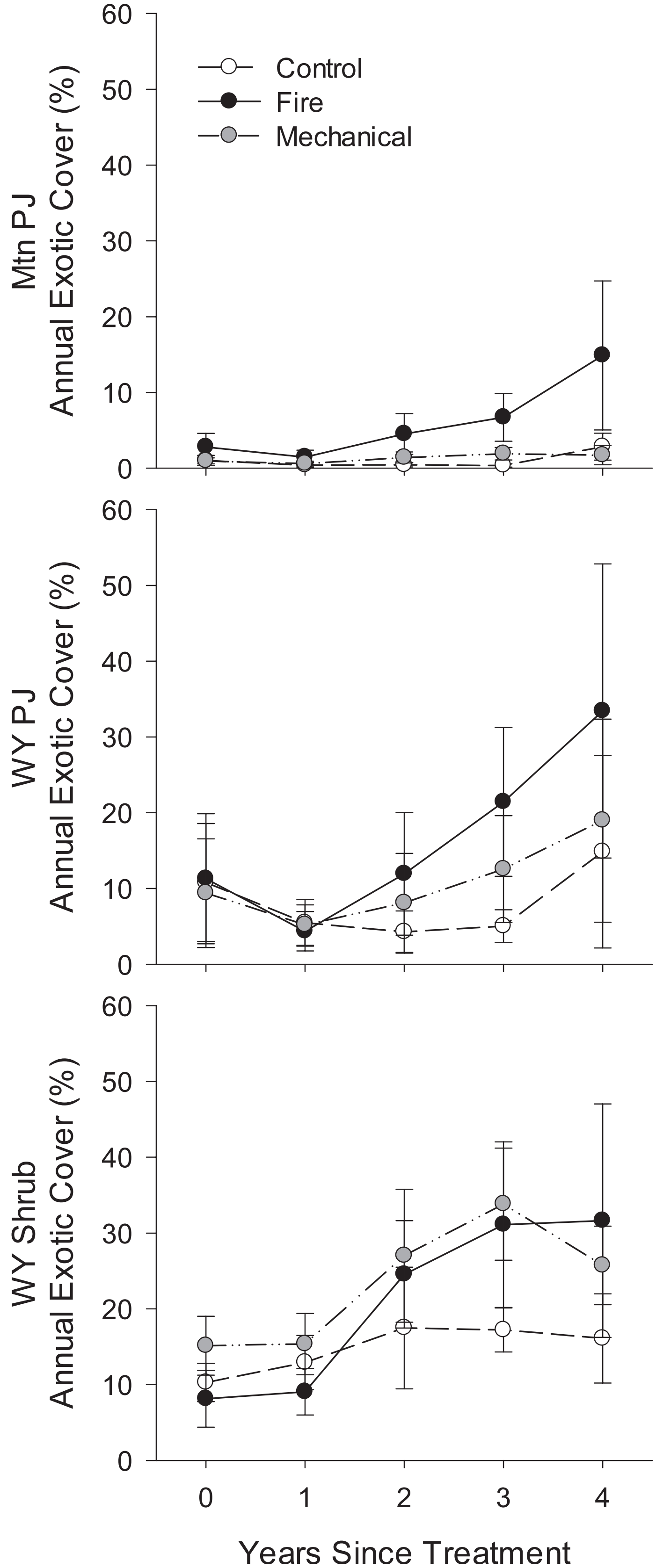

Figure 4. Annual exotic cover in control, fire, and mechanical plots on Mtn PJ, WY PJ, and WY shrub sites the year before treatment and the first 4 yr after treatment. Values are mean ± SE.

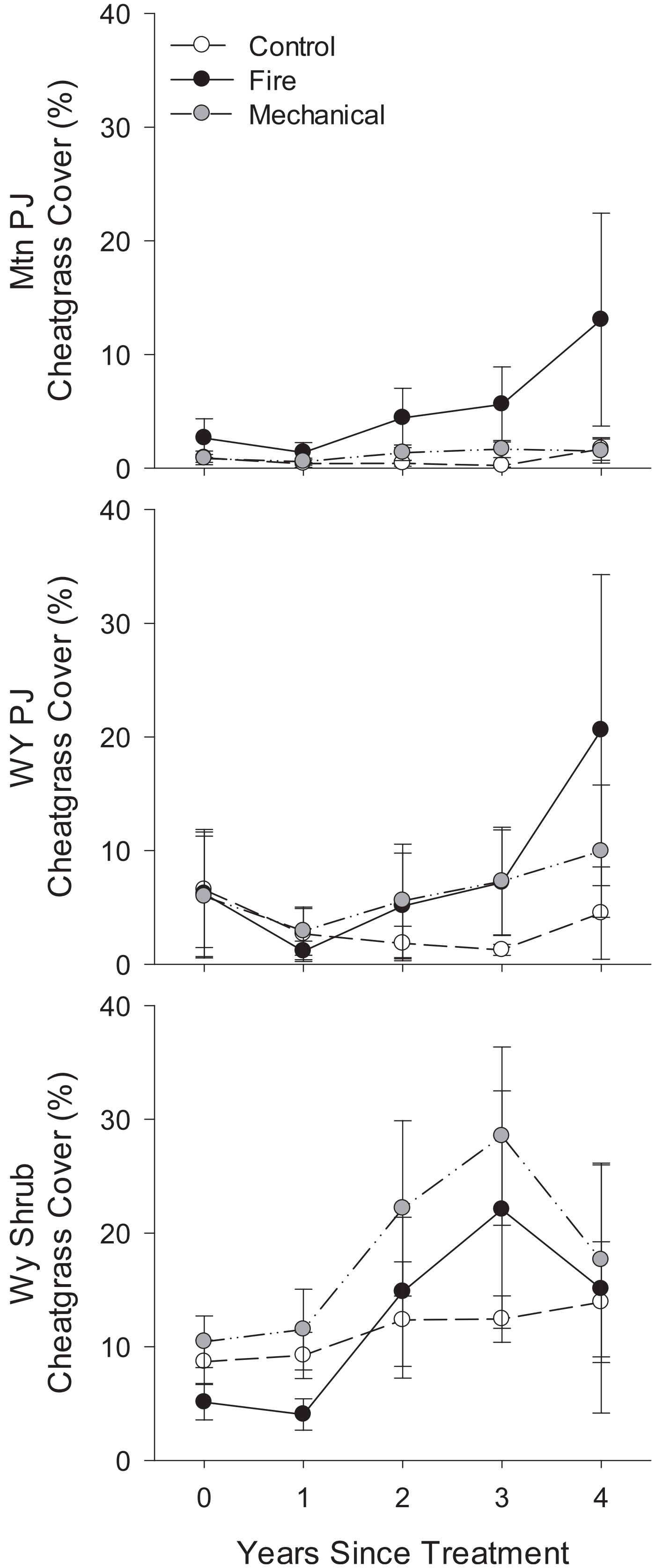

Figure 5. Cheatgrass cover in control, fire, and mechanical plots on Mtn PJ, WY PJ, and WY shrub sites the year before treatment and the first 4 yr after treatment. Values are mean ± SE.

was higher on mowed plots in years 3 and 4 compared to pretreatment (Fig. 4; $P < 0.02$), but did not differ between fire and mowed plots. In the model comparing fire and cut-and-leave treatments for WY PJ and Mtn PJ sites, annual exotic cover in years 3 and 4 was generally higher on cut-and-leave plots than pretreatment or on control plots (Fig. 4; $P < 0.06$). Annual exotic cover was marginally higher on fire plots than on cut-and-leave plots in years 3 and 4 ($P < 0.07$).

Cheatgrass cover exhibited a three-way interaction among site type, treatment, and year in the overall model (Fig. 5; $F_{8,39}=2.11$, $P=0.0501$). Cheatgrass cover was higher on fire plots in years 3 and 4 than pretreatment on WY shrub and WY PJ sites ($P < 0.03$), but only in year 3 on Mtn PJ sites ($P=0.03$). However, on WY shrub sites, control and fire plots did not differ in any year. Cheatgrass cover was higher in fire plots on WY shrub than Mtn PJ sites in all years, but it did not differ for WY shrub and WY PJ sites, and was marginally higher in WY PJ than Mtn PJ sites only in year 4 ($P < 0.08$). In the model comparing fire and mowing treatments for the WY shrub site, cheatgrass cover was higher on mowed plots in years 3 and 4 than pretreatment (Fig. 5; $P < 0.01$). Cheatgrass cover on mowed plots did not differ from that on fire plots or control plots in any year. In the model comparing fire and cut-and-leave treatments for WY PJ and Mtn PJ sites, cheatgrass cover was higher on cut-and-leave than pretreatment and control plots in years 3 and 4 (Fig. 5; $P < 0.03$). Cheatgrass cover did not differ for fire vs. cut-and-leave plots, despite apparently higher cover on fire than cut-and-leave plots in Mtn PJ.

Annual Variation in Herbaceous Cover Among Controls

Perennial native herbaceous cover differed only among years ($F_{4,52}=3.25$, $P=0.0187$) and not among site types on control plots (Fig. 6). Higher cover occurred in 2011 than all other years ($P < 0.05$) on all site types, but no other differences existed among years.

Annual exotic and cheatgrass cover showed strong differences among sites types ($F_{2,52}=28.06$, $P < 0.0001$; $F_{2,52}=27.01$, $P < 0.0001$, respectively) and weak differences among years ($F_{2,52}=2.33$, $P < 0.0685$; $F_{2,52}=2.265$, $P < 0.0751$, respectively) on control plots (Fig. 6). Cover of annual exotics and cheatgrass decreased in the order: WY shrub > WY PJ > Mtn PJ. Higher cover of annual exotics and cheatgrass occurred in 2011 than 2008 and 2010 ($P < 0.02$). Averaged over the 5 yr, cheatgrass cover comprised 74%, 43%, and 75% of annual exotic cover on WY shrub, WY PJ, and Mtn PJ control plots, respectively.

Relationship of Perennial Native Herbaceous Species to Annual Exotics and Cheatgrass

The relationship of initial perennial native herbaceous cover before treatment (year 0) to perennial native herbaceous, annual exotic, and cheatgrass cover in year 3 differed among site types. Interactions among site type and initial perennial native herbaceous cover occurred for year 3 cover of perennial native herbaceous species ($F_{2,379}=6.79$, $P=0.0013$), annual exotics ($F_{2,379}=7.28$, $P=0.0008$), and cheatgrass ($F_{2,379}=3.68$, $P < 0.0262$). Also, differences among control and fire treatments occurred in year 3 cover of perennial native herbaceous species ($F_{1,11}=5.70$, $P=0.0361$), annual exotics ($F_{1,11}=10.85$, $P=0.0071$), and cheatgrass ($F_{1,11}=4.30$, $P=0.0608$).

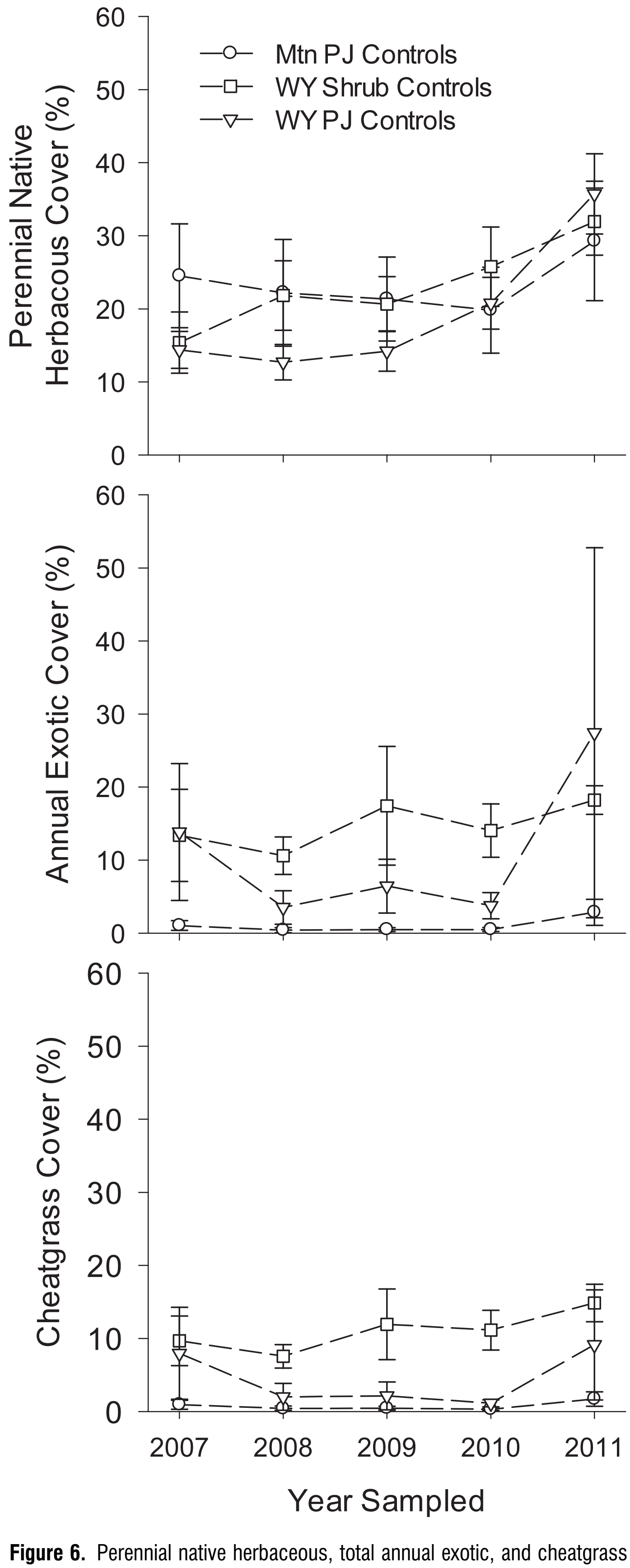

Figure 6. Perennial native herbaceous, total annual exotic, and cheatgrass cover on control plots in Mtn PJ, WY PJ, and WY shrub plots in 2007 through 2011. Values are mean ± SE.

Linear regressions illustrate the nature of these relationships for the different site types. In Mtn PJ sites, initial cover of perennial native herbaceous species was positively related to year 3 cover of these species in control ($R^2=0.77$, $P<0.0001$), fire ($R^2=0.64$, $P<0.0001$) and mechanical plots ($R^2=0.69$, $P<0.0001$). Cheatgrass cover was generally low on Mtn PJ sites and exhibited no relationship to initial perennial native herbaceous species in year 3 on control, fire, or mechanical plots. Annual exotic cover was comprised almost entirely of cheatgrass cover on Mtn PJ sites and exhibited very similar relationships to those for cheatgrass.

In WY PJ sites, cover of perennial native herbaceous species was more variable among sites and the relationship between initial and year 3 cover was not as strong as in Mtn PJ for control ($R^2=0.56$, $P<0.0001$), fire ($R^2=0.32$, $P<0.0001$), or mechanical plots ($R^2=0.54$, $P<0.0001$). Initial perennial herbaceous cover and cheatgrass cover in year 3 exhibited no relationship in control plots, a weak negative relationship in fire plots ($R^2=0.05$, $P=0.0421$), and a moderate negative relationship in mechanical plots ($R^2=0.17$, $P<0.0001$). Annual exotic cover in year 3 exhibited a weak negative relationship to initial perennial native herbaceous species in mechanical plots ($R^2=0.0821$, $P<0.01$).

In WY shrub sites, the relationship between initial and year 3 perennial native herbaceous cover was strong in control ($R^2=0.57$, $P<0.0001$), fire ($R^2=0.48$, $P<0.0001$), and mechanical plots ($R^2=0.51$, $P<0.0001$) (Fig. 7). Overall cover of cheatgrass in WY shrub sites was high, and initial perennial native herbaceous cover and year 3 cheatgrass cover were negatively related in control plots ($R^2=0.15$, $P=0.0004$). Initial perennial native herbaceous cover and year 3 cheatgrass cover also were negatively related in fire ($R^2=0.11$, $P=0.0068$) and especially mow plots ($R^2=0.54$, $P<0.0001$). When the Owyhee site, which had little to no cheatgrass cover, was excluded from analysis the relationship was stronger for fire plots ($R^2=0.49$, $P<0.0001$) and similar for mow plots ($R^2=0.39$, $P<0.0001$). Similar relationships existed for initial cover of perennial native herbaceous and year 3 cover of annual exotics in control ($R^2=0.098$, $P=0.0062$) and mow plots ($R^2=0.390$, $P<0.0001$). In fire plots initial perennial native herbaceous cover and initial cover of annual exotics were positively related ($R^2=0.3604$, $P<0.0001$). Annual exotics had generally high cover in fire plots in year 3 and showed no relationship to initial perennial native herbaceous cover.

DISCUSSION

Resilience to Fire and Mechanical Treatments

This research confirmed our prediction that differences in resilience to fire and mechanical treatments exist among site types differing in environmental characteristics and sagebrush species. We found that resilience was influenced by soil temperature/moisture regimes and generally increased from warm/dry (mesic/aridic) WY shrub to cool moist (frigid/xeric) Mtn PJ as shown previously (Fig. 1A; Chambers 2005; Condon et al. 2011; Davies et al. 2012; Chambers et al. 2014). Although WY shrub sites exhibited no increases in shrub cover after fire or mowing, WY PJ and Mtn PJ had significantly higher shrub cover 3 to 4 yr after fire and cut-and-leave

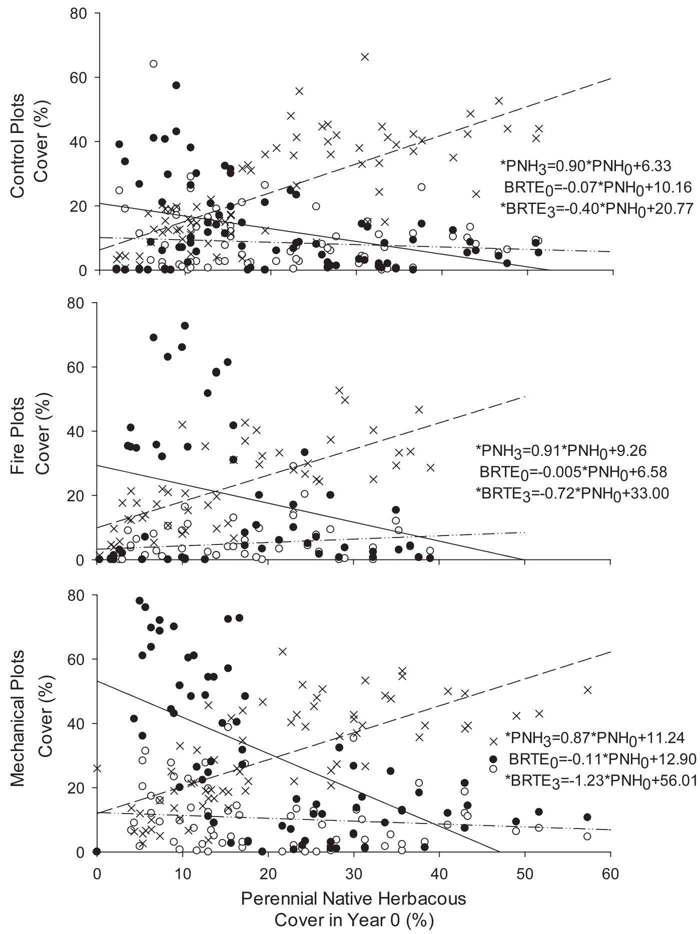

Figure 7. The relationships between perennial native herbaceous cover in year 0 (PNH_0) and perennial native herbaceous cover in year 3 (PNH_3) indicated by a dashed line, cheatgrass cover in year 0 ($BRTE_0$) indicated by a dashed and dotted line, and cheatgrass cover in year 3 ($BRTE_3$) indicated by a solid line in control, fire, and mechanical plots on WY shrub sites. PNH_3 is shown as an x (×), $BRTE_0$ as an open circle (○), and $BRTE_3$ as a closed circle (•). Significant regression equations are indicated by an asterisk.

treatments. The increases in shrub cover on WY PJ and Mtn PJ sites occurred because of higher levels of sagebrush recruitment (Miller et al. 2014b) and a greater percentage of root-sprouting shrubs such as yellow rabbitbrush (*Chrysothamnus viscidiflorus* [Hook.] Nutt.) and Saskatoon serviceberry (*Amelanchier alnifolia* [Nutt.] Nutt ex M. Roem). All site types had more perennial, native herbaceous species in years 3 and 4 after treatment than pretreatment, but fire and mow plots did not differ from control plots on WY shrub sites. The perennial, native herbaceous species that showed the greatest response were Sandberg bluegrass and squirreltail (*Elymus elymoides* [Raf.] Swezey) in WY shrub sites, bluebunch wheatgrass in WY PJ, and Idaho fescue in Mtn PJ sites. Our inability to detect larger differences among the WY PJ and Mtn PJ types was likely due to variability among individual sites in soil temperature/moisture regimes and initial levels of cheatgrass invasion and/or piñon and juniper expansion.

Resilience was influenced by treatment severity and initial abundance of plant functional groups. In WY shrub sites, fire and mowing both reduced shrub cover and had parallel effects on posttreatment shrub and perennial native herbaceous cover. An increase in soil water and nutrient availability, limited native species response, and high propagule pressure from annual exotics likely resulted in the observed increase in cheatgrass and overall annual exotic cover on treated plots (Leffler and Ryel 2012). Contingency effects of growing season conditions and competition from cheatgrass and annual exotic forbs likely caused a lack of a consistent positive response for perennial native herbaceous and shrub cover in WY shrub sites (Bakker et al. 2003; Hendrickson and Lund 2010). In WY PJ and Mtn PJ sites, shrub cover was reduced about 85% by fire, but was not reduced by the cut-and-leave treatment. Increases in perennial native herbaceous cover on these sites appeared to be proportional to available resources as greater increases occurred on high tree cover plots (Roundy et al. 2014b). However, posttreatment values reflected pretreatment values and were lower on plots with high (40–75%) than low (0–20%) initial tree cover (Roundy et al. 2014b). Also, increases in cheatgrass and other annual exotics were greater on treated plots with middle (20–40%) to high (40–75%) than low (0–20%) initial tree cover (Roundy et al. unpublished data). These results indicate that treatment severity is typically higher for 1) fire because it removes most woody vegetation and 2) high tree cover as most woody vegetation is removed regardless of treatment and little perennial native herbaceous vegetation remains to facilitate recovery. On relatively warm and dry sites, cut-and-leave treatments at low to mid tree covers likely will result in a higher probability of recovery to a desirable state than prescribed fire or treating at higher tree covers.

Resistance to Cheatgrass and Other Annual Exotics

Resistance to cheatgrass and other annual exotics was strongly influenced by soil temperature/moisture regimes in both fire and mechanical treatments and increased from warm/dry (mesic/aridic) WY shrub to cold moist (frigid to cool frigid/xeric) Mtn PJ as predicted (Fig. 1B). WY shrub sites were less resistant to cheatgrass following fire and mechanical treatment than WY PJ and Mtn PJ sites, and WY shrub sites and WY PJ sites were less resistant to annual exotic forbs than Mtn PJ sites. In WY shrub, treatment outcomes were influenced by generally greater climatic suitability to cheatgrass (Chambers et al. 2007) and annual exotic forbs and higher initial cover of exotics. In WY PJ and Mtn PJ, differences in soil temperature/moisture regimes among individual sites influenced resistance to cheatgrass and annual exotic forbs. Cheatgrass cover was generally low (< 5%) on WY PJ sites, except for Scipio which was a warm mesic/aridic site, and on Mtn PJ sites, except for Devine Ridge which was characterized as having frigid/xeric conditions but was dominated by species adapted to warmer sites like Thurber's needlegrass (Miller et al. 2014b). Annual exotic forb cover was high on only two WY PJ sites, Scipio and Onaquim which are characterized by warm mesic/aridic conditions (Miller et al. 2014b). Sites with low cheatgrass and annual exotic forb cover typically had cool mesic to cool frigid classifications. SageSTEP sites were selected to have sufficient perennial herb cover to minimize increases in annual exotics and did not cover the entire range of environmental gradients in the Great Basin, but these results are consistent with prior research in the region (Chambers et al. 2007; Condon et al. 2011; Davies et al. 2012).

Annual exotic forbs had a significant effect on treatment response in WY Shrub and WY PJ sites where they occurred. Species like desert madwort (*Alyssum desertorum* Stapf.), curveseed butterwort (*Ceratocephala testiculata* Crantz [Roth]), herb sophia (*Descurainia sophia* [L.] Webb exPrantl), and tall tumblemustard (*Sisymbrium altissimum* L.) comprised 45% and 24% of the increase in annual exotic cover on fire and mow plots in WY shrub sites, and 58% and 40% of the increase on fire and cut-and-leave plots in WY PJ sites. Annual exotic forbs including spring verba (*Draba verna* L.), herb sophia, and yellow salsify (*Tragopogon dubius* Scop.) were only 1.3% in both fire and cut-and-leave plots in frigid Mtn PJ sites. Decreased competition with cheatgrass and increased soil water availability can cause increased establishment of annual forbs (Ducas et al. 2011), and both of these conditions likely occurred in the initial years after treatment (Pyke et al. 2014; Roundy et al. 2014b). Efforts to control exotic plant species often result in secondary invasion by nontarget exotic plant species (Rinella et al. 2009; Larson and Larson 2010). On WY shrub and WY PJ sites, treatments that decrease woody species competition may release both cheatgrass and annual forbs and increase fine fuels if sites lack sufficient native, perennial herbaceous species to effectively compete for increased resources.

Contingency Effects of Weather on Herbaceous Species

Annual variation of herbaceous cover in sagebrush ecosystems closely tracks annual precipitation (West and Yorks 2002; Bradley and Mustard 2005). Annual differences in herbaceous cover in control plots generally were most pronounced on sites with high climate suitability for cheatgrass and annual exotic forbs (i.e., mesic/aridic to xeric soil temperature/moisture regime). In WY shrub sites, which had high initial cover of annual exotic species, there was a twofold difference in both annual exotic and perennial native herbaceous cover between the lowest and highest average cover. In WY PJ sites, there was a 10-fold difference between the lowest and highest average annual exotic cover and a threefold difference between the highest and lowest perennial native herbaceous cover. Longer-term monitoring will be required to determine resistance to annual exotics on these sites, but precipitation will likely interact with treatment effects to influence both native perennial and annual exotic cover over time (West and Yorks 2002).

Pretreatment Cover of Perennial Native Herbaceous Species and Resistance to Invasion

Perennial native herbaceous species are a primary determinant of site resilience to disturbance and management treatments and/or resistance to cheatgrass and annual exotic forbs (Chambers et al. 2007; Miller et al. 2014a). In WY shrub sites, perennial native herbaceous cover of about 20% appeared necessary to maintain relatively low cover of cheatgrass in control plots and prevent significant increases after fire and mowing (Fig. 7). Portions of these sites likely will exhibit increases in cheatgrass after treatment even with an average herbaceous cover of 20% due to high variation in cover across sites and the influence of distances between perennial plants and biological soil crusts on cheatgrass cover (Reisner et al. 2013). Annual exotic forbs exhibited a general increase on WY shrub sites after treatment, especially on fire plots, regardless of perennial native herbaceous cover. Previous research indicates that abundance of annual exotic forbs tends to decrease over time (Allen and Knight 1984; McLendon and Redente 1990), and annual exotic forbs may return to pretreatment values in the absence of repeated disturbance.

In WY PJ and Mtn PJ sites, perennial native herbaceous cover of 20% also appeared necessary to prevent a large increase in cheatgrass and other annual exotics (data not shown). In cooler and moister WY PJ and especially Mtn PJ sites with relatively high resistance, perennial native herbaceous cover may be less important for preventing dominance by annual invaders due to lower climate suitability (Chambers et al. 2007). However, adequate cover of perennial native herbaceous species and root-sprouting shrubs is still necessary for soil stabilization and overall site recovery (Miller et al. 2014a). Sites differ in topography, soils characteristics, and productivity as well as resistance to invaders and all of these factors should be taken into account when determining indicators of potential recovery (Miller et al. 2013).

State and Transition Models That Incorporate Resilience and Resistance Information

We use our results to expand on previously published STMs for sagebrush (Holmes and Miller 2010) and wooded shrublands (Briske et al. 2008; Peterson et al. 2009) by explicitly incorporating information on resilience to disturbance and management treatments and resistance to invasion. We use the interagency framework for developing STMs (Caudle et al. 2013). Our data show that Wyoming big sagebrush sites with warm/dry (mesic/aridic) soil temperature/moisture regimes are characterized by low to moderate resilience to fire and management treatments and low resistance to cheatgrass and other annual exotics (Fig. 8). The sagebrush mowing treatment was intended to release perennial herbaceous species and increase resistance to annual exotics (R2 and 3b in Fig. 8). Both mowing and fire resulted in slight increases in perennial native herbaceous cover in the invaded state. However, annual exotic and cheatgrass cover also tended to increase and there was no recruitment of sagebrush. Post-burn areas with low perennial native herbaceous cover were converted to an annual state (T5 and T7 in Fig. 8). The only exceptions were sites with relatively cool soil temperatures (e.g., Owyhee). Thus, management treatments are unlikely to provide a restoration pathway to the reference state once these ecosystems are invaded if insufficient perennial herbaceous species exist prior to treatment, especially on the warm end of the temperature/precipitation gradient. Recent research indicates that seeding after fire may increase perennial native grasses and sagebrush, but cheatgrass and annual exotics are likely to persist (R6, R8, and R9 in Fig. 8; Knutson et al. 2014).

We include both Wyoming and mountain big sagebrush in a big sagebrush STM with potential for piñon and juniper expansion based on the responses of our WY PJ sites and a Mtn PJ site excluded from this analysis. Mountain big sagebrush sites typically have cooler and wetter temperature/precipitation regimes than Wyoming big sagebrush sites (Miller et al. 2013b), but both species have broad ecological amplitudes

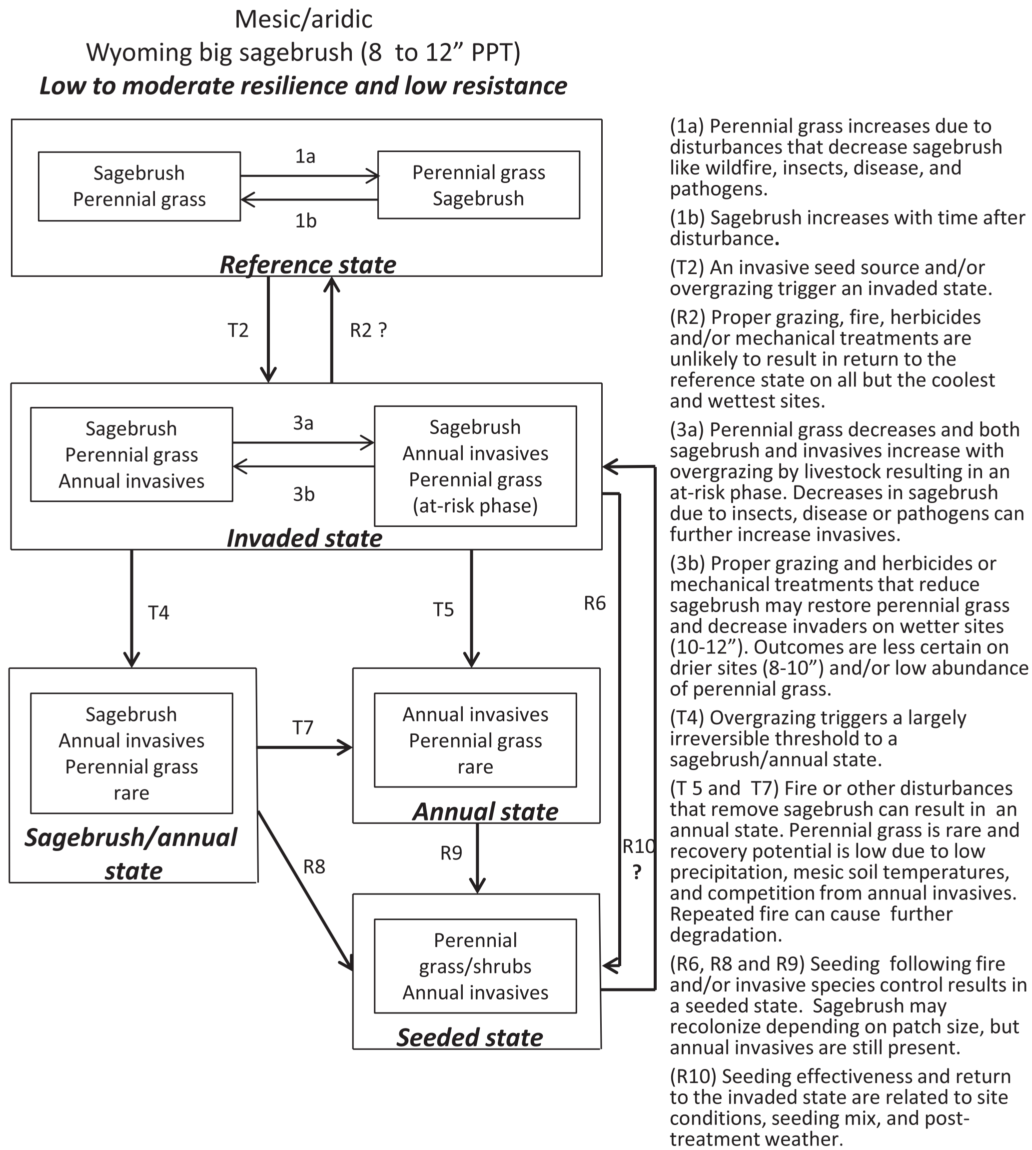

Figure 8. A state and transition model for a Wyoming big sagebrush ecosystem with a mesic/aridic soil temperature/moisture regime that is characterized by low to moderate resilience to disturbance and management treatments and low resistance to cheatgrass and other annual exotics. Large boxes illustrate states that are comprised of community phases (smaller boxes) which interact with the environment to produce a characteristic composition of plant species, functional and structural groups, soil functions, and range of variability. Transitions among states are shown with arrows starting with T; restoration pathways are shown with arrows starting with R. The "at risk" community phase is most vulnerable to transition to an alternative state.

and can overlap and even hybridize in lower elevation expansion woodland (Garrison et al. 2013) where management treatments are often conducted. Our data show that big sagebrush sites that are exhibiting piñon and juniper expansion and that have relatively warm (cool mesic to warm frigid) and moist (xeric) soil temperature/moisture regimes are characterized by moderate resilience to fire and management treatments and moderately low resistance to cheatgrass and other annual exotics (Fig. 9). Increases in perennial native herbaceous species and shrub recruitment occurred over a range of tree covers in the early to mid-phases of tree expansion (Phase I through Phase II) for both the cut-and-leave (4b in Fig. 9) and fire treatment (3 and 5 in Fig. 9). This is consistent with the community phase pathways for the reference state illustrated elsewhere for wooded shrublands (Briske et al. 2008; Peterson et al. 2009). Prior research indicates that infilling of Phase II woodlands can result in a biotic threshold to a wooded state with increased risk of high severity crown fires (T6 in Fig. 9) and, depending on soils, slope, and understory species, an abiotic threshold to an eroded state (T7 in Fig. 9; Miller et al. 2014a). We found that on relatively warm and dry sites, presence of cheatgrass and other annual exotics coupled with low cover of perennial native herbaceous species resulted in a wooded/invaded state following cut-and leave-treatments (T8 in Fig. 9) and an annual state following fire (T10 and T11 in Fig. 9). The increase in cheatgrass and other annual exotics cover was positively related to tree cover (Roundy et al. 2014a). Other research indicates that seeding can increase perennial herbaceous species and sagebrush (R12, R13, R14, and R15 in Fig. 9). Depending on seeding mix, grazing, and weather conditions, cooler and wetter sites can return to the

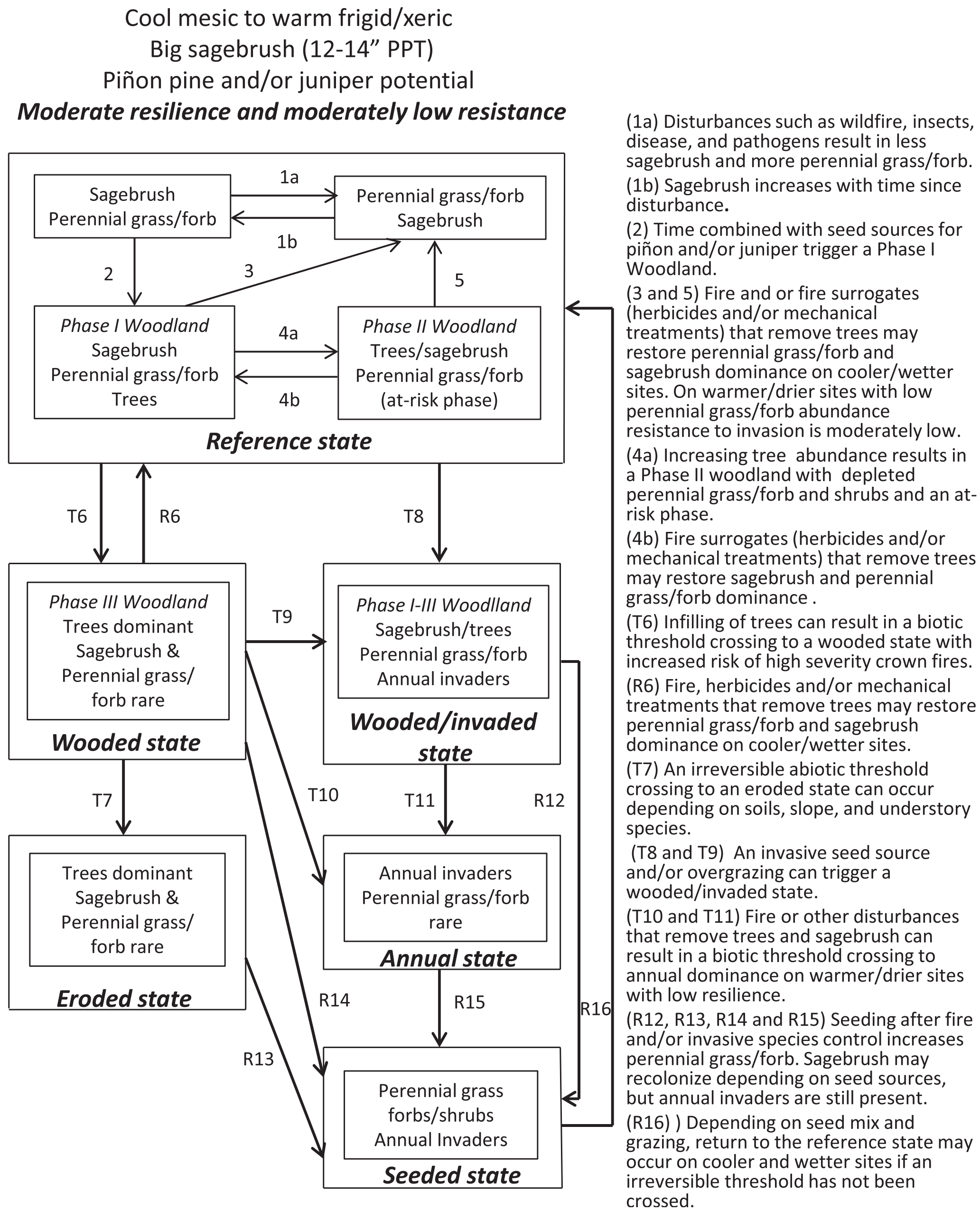

Figure 9. A state and transition model for a big sagebrush ecosystem with a cool mesic to warm frigid/xeric soil temperature/moisture regime that is exhibiting piñon and juniper expansion. This type is characterized by moderate resilience to disturbance and management treatments and moderately low resistance to cheatgrass and other annual exotics. Large boxes illustrate states that are comprised of community phases (smaller boxes) which interact with the environment to produce a characteristic composition of plant species, functional and structural groups, soil functions, and range of variability. Transitions among states are shown with arrows starting with T; restoration pathways are shown with arrows starting with R. The “at risk” community phase is most vulnerable to transition to an alternative state.

reference state if an abiotic threshold has not been crossed (R16 in Fig. 9) (Pyke 2011).

Our data show that mountain big sagebrush sites that are exhibiting piñon and juniper expansion and that have cool and moist (cool frigid/xeric) soil temperature/moisture regimes are characterized by moderately high resilience to disturbance and resistance to invasives (Fig. 10). As for the big sagebrush type, increases in perennial native herbaceous species and shrub recruitment occurred across a range of tree densities (Phase I through Phase II) for cut-and-leave (4b in Fig. 10) and fire treatments (3 and 5 in Fig. 10). Annual exotics had generally low abundance on these sites. As for WY PJ, in the absence of treatment, infilling of phase II woodlands can result in a biotic threshold to a wooded state and, depending on soils and topography, an abiotic threshold crossing to an eroded state (T7 in Fig. 10; Miller et al. 2014a). Seeding of Phase III woodlands (closed wooded shrublands) with depleted understories after fire can increase perennial herbaceous species and sagebrush (R8 and R9 in Fig. 10) (Pyke 2011). Depending on seed mix and grazing, return to the reference state may be possible if an irreversible threshold has not been crossed.

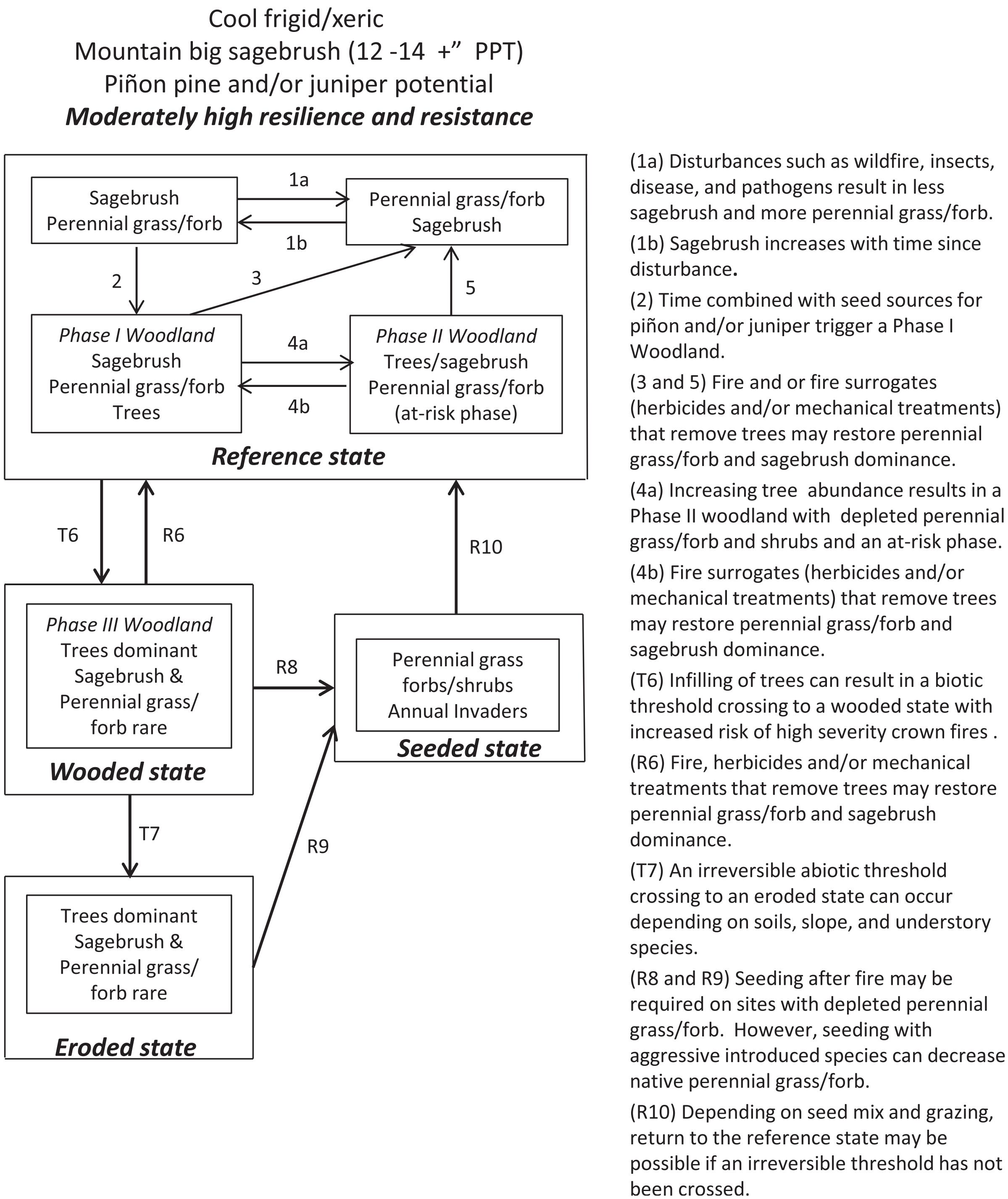

Figure 10. A state and transition model for a mountain big sagebrush ecosystem with a cool frigid/xeric soil temperature/moisture regime that is exhibiting piñon and juniper expansion. This type is characterized by moderately high resilience to disturbance and management treatments and resistance to cheatgrass and other annual exotics. Large boxes illustrate states that are comprised of community phases (smaller boxes) which interact with the environment to produce a characteristic composition of plant species, functional and structural groups, soil functions, and range of variability. Transitions among states are shown with arrows starting with T; restoration pathways are shown with arrows starting with R. The "at risk" community phase is most vulnerable to transition to an alternative state.

MANAGEMENT IMPLICATIONS

An understanding of the relative differences in resilience to disturbance and management treatments and resistance to cheatgrass and other annual exotics can be used to prioritize areas for treatment and select the most appropriate treatments. Resilience to management treatments and resistance to annual exotic species is influenced by soil temperature/moisture regimes and generally increases from warm/dry (mesic/aridic) Wyoming big sagebrush to cool/moist (frigid/xeric) mountain big sagebrush sites. We found that warm/dry Wyoming big sagebrush sites had low to moderate resilience to fire and mowing treatments and generally low resistance to annual exotics. In the first 4 yr after treatment, we found that fire and mowing resulted in only small increases in perennial native grasses and forbs, little to no shrub recruitment, and significant increases in annual exotics. Wyoming and mountain big sagebrush sites exhibiting piñon and juniper expansion with intermediate soil temperature regimes (cool mesic to warm frigid/xeric) had moderate resilience to fire and cut-and-leave treatments but moderately low resistance to annual exotics. Fire and cut-and-leave treatments increased both perennial native herbaceous species and shrub recruitment, but large increases in annual exotics occurred on some sites. In relatively warm big sagebrush sites in general (warm mesic to warm frigid), perennial native grass and forb cover of about 20% prior to treatments appeared necessary to prevent significant increases in cheatgrass and other exotic annuals posttreatment. Mountain big sagebrush with cool and moist (cool frigid/xeric) soil temperature/moisture regimes had moderately high resilience to fire and cut-and-leave treatments and resistance to annual exotics. Fire and cut-and-leave treatments increased both perennial native herbaceous species and shrub recruitment and annual exotics were a minor component of these sites. Treatment severity increased in big sagebrush sites exhibiting tree expansion with 1) fire, because it removed all woody vegetation, and 2) high tree cover, as most woody vegetation was removed regardless of treatment and little perennial native herbaceous vegetation remained to facilitate recovery. On sites with relatively low resistance to annual exotics, cut-and-leave treatments at low to middle tree covers result in a higher likelihood of recovery to a desirable state than prescribed fire. On sites with relatively high resistance to annual exotics, either fire or cut-and-leave treatments at low to middle tree covers can result in a desirable state. STMs that incorporate information on resilience to management treatments and resistance to annual exotics can be used as aids in the planning process. Sagebrush sites occur over continuums of ecological conditions, such as temperature and precipitation, and careful assessment of site conditions always will be necessary to determine the relevance of a particular STM, the suitability of a site for treatment, and the most appropriate treatment(s) (Pyke 2011; Chambers et al. 2014; Miller et al. 2013, 2014a).

ACKNOWLEDGMENTS

We thank Dave Turner for statistical advice, and Jim McIver, Peter Weisberg, Tanya Skurski, and three anonymous reviewers for helpful comments on the manuscript, and Mike Pellant for assistance with development of the STMs. We acknowledge and thank our additional SageSTEP co-PI's who contributed to the design of this study. This is Contribution Number 83 of the Sagebrush Steppe Treatment Evaluation Project, funded by the Joint Fire Science Program (05-S-08), the Bureau of Land Management, the US Forest Service, the National Interagency Fire Center, and the Great Northern Land Conservation Cooperative.

LITERATURE CITED

Alexander, E. B., J. I. Mallory, and W. L. Colwell. 1993. Soil-elevation relationships on a volcanic plateau in the southern Cascade Range, northern California, USA. *Catena* 20:113–128.

Allen, C. R., L. Gunderson, and A. R. Johnson. 2005. The use of discontinuities and functional groups to assess relative resilience in complex systems. *Ecosystems* 8:958–966.

Allen, E. B., and D. H. Knight. 1984. The effects of introduced annuals on secondary succession in sagebrush-grassland, Wyoming. *Southwestern Naturalist* 4:407–421.

Bagchi, S., D. D. Briske, X. B. Wu, M. P. McClaran, B. T. Bestelmeyer, and M. E. Fernandez-Gimenez. 2012. Empirical assessment of state-and-transition models with a long-term vegetation record from the Sonoran Desert. *Ecological Applications* 22:400–411.

Bakker, J. D., S. D. Wilson, J. M. Christian, X. Li, L. G. Ambrose, and J. Waddington. 2003. Contingency of grassland restoration on year, site, and competition from introduced grasses. *Ecological Applications* 13:137–153.

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

Bestelmeyer, B. T., A. J. Tugel, G. L. J. Peacock, D. G. Robinett, P. L. Shaver, J. R. Brown, J. E. Herrick, H. Sanchez, and K.M. Havstad. 2009. State-and transition models for heterogeneous landscapes: a strategy for development and application. *Rangeland Ecology & Management* 62:1–15.

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

Briske, D. D., B. T. Bestelmeyer, T. K. Stringham, and P. L. Shaver. 2008. Recommendations for development of resilience-based state-and-transition models. *Rangeland Ecology & Management* 61:359–367.

Brooks, M. L., and J. C. Chambers. 2011. Resistance to invasion and resilience to fire in desert shrublands of North America. *Rangeland Ecology & Management* 64:431–438.

Caudle, D., J. DiBenedetto, M. Karl, H. Sanchez, and C. Talbot. 2013. Interagency ecological site handbook for rangelands. Available at: http://jornada.nmsu.edu/sites/jornada.nmsu.edu/files/InteragencyEcolSiteHandbook.pdf. Accessed 4 October 2013.

Chambers, J. C. 2005. Fire related restoration issues in woodland and rangeland ecosystems. *In*: L. Taylor, J. Zelnik, S. Cadwallader, and B. Hughes [comps.]. Mixed fire regimes: ecology and management. Symposium Proceedings. MIXC03, Spokane, WA, USA: Association of Fire Ecologists. p. 149–160.

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

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

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

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

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

Dahlgren, R. A., J. L. Boettinger, G. L. Huntington, and R. G. Amundson. 1997. Soil development along an elevational transect in the western Sierra Nevada. *Geoderma* 78:207–236.

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

Ducas, L. P., S. B. Jones, A. J. Leffler, and R. J. Ryel. 2011. Associations of near-surface soil moisture and annual plant community dynamics. *Natural Resources and Environmental Issues* 17:75–82.

Folke C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics* 35:557–581.

Garrison, H. D., L. M. Shultz, and D. McArthur. 2013. Studies of a new hybrid taxon in the *Artemisia tridentata* (Asteraceae: Anthemideae) complex. *Western North American Naturalist* 73:1–19.

Hendrickson, J. R., and C. Lund. 2010. Plant community and target species affect responses to restoration strategies. *Rangeland Ecology & Management* 63:453–442.

Herrick, J. E., J. W. Van Zee, K. M. Havstad, L. M. Burkett, and W. G. Whitford. 2009. Monitoring manual for grassland, shrubland, and savanna ecosystems. Tucson, AZ, USA: University of Arizona Press. 36 p.

Holling, C. S. 1973. Resilience and stability in ecological systems. *Annual Review of Ecology and Systematics* 4:1–23.

Holling, C. S. 1996. Surprise for science, resilience for ecosystems, and incentives for people. *Ecological Applications* 6:733–735.

Holmes, A. A., and R. F. Miller. 2010. State-and-transition models for assessing grasshopper sparrow habitat use. *Journal of Wildlife Management* 74:1834–1840. doi:10.2193/2009-417

Johnson, D. D., and R. F. Miller. 2006. Structure and development of expanding western juniper woodlands as influenced by two topographic variables. *Forest Ecology and Management* 229:7–15.

Knick, S. T., and J. W. Connelly. 2011. Greater sage-grouse—ecology and conservation of a landscape species and its habitats. Studies in avian biology no. 38. Berkeley, CA, USA: University of California Press. 646 p.

Knutson, K. C., D. A. Pyke, T. A. Wirth, R. S. Arkle, D. S. Pilliod, M. L. Brooks, J. C. Chambers, and J. B. Grace. 2014. Long-term effects of reseeding after wildfire on vegetation composition in the Great Basin shrub steppe. *Journal of Applied Ecology*. doi:10.1111/1365-2664.12309

Larson, D. L., and J. L. Larson. 2010. Control of one invasive plant species allows exotic grasses to become dominant in northern Great Plains grasslands. *Biological Conservation* 143:1901–1910.

Leffler, A. J., and R. J. Ryel. 2012. Resource pool dynamics: conditions that regulate species interactions and dominance. *In*: T. A. Monaco and R. L. Sheley [eds.]. Invasive plant ecology and management: linking processes to practice. Cambridge, MA, USA: CAB International.p. 57–78.

Leger, E. A., E. K. Espeland, K. R. Merrill, and S. E. Meyer. 2009. Genetic variation and local adaptation at a cheatgrass (*Bromus tectorum*) invasion edge in western Nevada. *Molecular Ecology* 18:4366–4379.

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

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

McIver, J. D., M. Brunson, S. Bunting, J. Chambers, N. Devoe, P. Doescher, J. Grace, D. Johnson, S. Knick, R. Miller, M. Pellant, F. Pierson, D. Pyke, K. Rollins, B. Roundy, E. Schupp, R. Tausch, and D. Turner. 2010. The Sagebrush Steppe Treatment Evaluation Project (SageSTEP): a test of state-and-transition theory. Fort Collins, CO, USA: US Department of Agriculture, Forest Service, RMRS-GTR-237. 16 p.

McLendon, T., and E. F. Redente. 1990. Succession patterns following soil disturbance in a sagebrush steppe community. *Oecologia* 85: 293–300.

Meyer, S. E., S. C. Garvin, and J. Beckstead. 2001. Factors mediating cheatgrass invasion of intact salt desert shrubland. *In*: D. E. McArthur and D. J. Fairbanks [comps]. Shrubland ecosystem genetics and biodiversity: proceedings. Ogden UT: US Department of Agriculture, Forest Service. RMRS-P-21. p. 224–232.

Miller, R., J. Chambers, and M. Pellant. 2014a. A field guide to selecting the most appropriate treatments in sagebrush and pinyon-juniper ecosystems in the Great Basin: evaluating resilience to disturbance and resistance to invasive annual grasses and predicting vegetation response. Fort Collins, CO, USA: US Department of Agriculture, Forest Service, RMRS-GTR-322.

Miller, R. F., J. C. Chambers, D. A. Pyke, F. B. Pierson, and C. J. Williams. 2013. A review of fire effects on vegetation and soils in the Great Basin Region: response and ecological site characteristics. Fort Collins, CO: USA: Department of Agriculture, Forest Service. RMRS-GTR-308. 136 p.

Miller, R. F., S. T. Knick, D. A. Pyke, C. W. Meinke, S. E. Hanser, M. J. Wisdom, and A. L. Hild. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. *In*: Knick S. T. and J. W. Connelly [eds.] Greater sage-grouse—ecology and conservation of a landscape species and its habitats. Studies in avian biology no. 38. Berkeley, CA, USA: University of California Press. p. 145–185.

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

Peterson, S. L., T. K. Stringham, and B. K. Roundy. 2009. A process-based application of state-and-transition models: a case study of western juniper (*Juniperus occidentalis*) encroachment. *Rangeland Ecology & Management* 62:186–192.

Pyke, D. A. 2011. Restoring and rehabilitating sagebrush habitats. *In*: S. T. Knick and J. W. Connelly [eds.] Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in avian biology no. 38. Berkeley, CA, USA: University of California Press. p. 531–548.

Pyke, D. A., M. L. Brooks, and C. M. D'Antonio. 2010. Fire as a restoration tool: a decision framework for predicting the control or enhancement of plants using fire. *Restoration Ecology* 18:274–284.

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

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

Reisner, M. D., J. B. Grace, D. A. Pyke, and P. S. Doescher. 2013. Conditions favouring *Bromus tectorum* dominance of endangered sagebrush steppe ecosystems. *Journal of Applied Ecology*. doi:10.1111/1365–2664.12097

Rinella, M. J., B. D. Maxwell, P. K. Fay, T. Weaver, and R. L. Sheley. 2009. Control effort exacerbates invasive-species problem. *Ecological Applications* 19:155–162.

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

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

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

Stringham, T. K., W. C. Krueger, and P. L. Shaver. 2003. State and transition modeling: an ecological process approach. *Journal of Range Management* 56:106–113.

Tausch R. J., and P. T. Tueller. 1990. Foliage biomass and cover relationships between tree- and shrub-dominated communities in pinyon-juniper woodlands. *Great Basin Naturalist* 50:121–134.

[USDA-NRCS] US Department of Agriculture-Natural Resources Conservation Service. 2007. National Soil Survey Handbook, Title 430-VI. Available at: http://soils.usda.gov/technical/handbook/. Accessed 4 March 2011.

West, N. E. 1983a. Intermountain salt-desert shrubland. *In*: N. E. West [ed.]. Temperate deserts and semi-deserts. Amsterdam, the Netherlands: Elsevier Publishing Company. p. 375–378.

West, N. E. 1983b. Great Basin-Colorado Plateau sagebrush semi-desert. *In*: N. E. West [ed.]. Temperate deserts and semi-deserts. Amsterdam, the Netherlands: Elsevier Publishing Company. p. 331–350.

West, N. E., and T. P. Yorks. 2002. Vegetation responses following wildfire on grazed and ungrazed sagebrush semi-desert. *Rangeland Ecology & Management* 55:171–181.

Wisdom, M. J., M. M. Rowland, and L. H. Suring [eds.]. 2005. Habitat threats in the sagebrush ecosystem: methods of regional assessment and applications in the Great Basin. Lawrence, KS, USA: Alliance Communications Group, Allen Press. 301 p.