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Repeated fire altered succession and increased fire behavior in basin big sagebrush–native perennial grasslands

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Abstract. The structure and composition of sagebrush-dominated ecosystems have been altered by changes in fire regimes, land use, invasive species, and climate change. This often decreases resilience to disturbance and degrades critical habitat for species of conservation concern. Basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*) ecosystems, in particular, are greatly reduced in distribution as land has been converted to agriculture and other land uses. The fire regime, relative proportions of shrub and grassland patches, and the effects of repeated burns in this ecosystem are poorly understood. We quantified postfire patterns of vegetation accumulation and modeled potential fire behavior on sites that were burned and first measured in the late 1980s at John Day Fossil Beds National Monument, Oregon, USA. The area partially reburned 11 yr after the initial fire, allowing a comparison of one vs. two fires. Repeated burns shifted composition from shrub-dominated to prolonged native herbaceous dominance. Fifteen years following one fire, the native-dominated herbaceous component was 44% and live shrubs were 39% of total aboveground biomass. Aboveground biomass of twice-burned sites (2xB; burned 26 and 15 yr prior) was 71% herbaceous and 12% shrub. Twenty-six years after fire, total aboveground biomass was 113–209% of preburn levels, suggesting a fire-return interval of 15–25 yr. Frequency and density of *Pseudoroegneria spicata* and *Festuca idahoensis* were not modified by fire history, but *Poa secunda* was reduced by repeated fire, occurring in 84% of plots burned 26 yr prior, 72% of plots burned 15 yr prior, and 49% in 2xB plots. Nonnative annual *Bromus tectorum* occurred at a frequency of 74%, but at low density with no differences due to fire history. Altered vegetation structure modified fire behavior, with modeled rates of fire spread in 2xB sites double that of once-burned sites. This suggests that these systems likely were historically composed of a mosaic of shrub and grassland. However, contemporary increases in fire frequency will likely create positive feedbacks of more intense fire behavior and prolonged periods of early-successional vegetation in basin big sagebrush communities.

Key words: fuel characteristic classification system; fire behavior model; Fuel Fire Tools; native bunchgrass; reburn; sagebrush fire regime; sagebrush fuels; sagebrush steppe.

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Introduction

Historically, fire was a primary disturbance in sagebrush-dominated ecosystems. Both naturally ignited fires (Houston 1973) and anthropogenic fires (McAdoo et al. 2013) influenced plant community succession (Houston 1973), increasing the diversity and heterogeneity of the landscape

(McAdoo et al. 2013) and creating a mosaic of early-successional grassland intermixed with later-successional shrub-dominated patches. Our understanding of fire effects in these systems is heavily weighted toward the early recovery period following a single fire (Miller et al. 2013). Fire effects in the widespread Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) and mountain big sagebrush (*A. tridentata* ssp. *vaseyana*) ecosystems are well-documented, but are complicated by a legacy of livestock grazing, introduction and spread of invasive species, and altered patterns of ignition (Miller et al. 1994, 2013, Brooks et al. 2004). It is estimated that fire historically occurred in xeric Wyoming big sagebrush communities every 50–100 yr or more (Wright and Bailey 1982, Baker 2006, Mensing et al. 2006), and in mesic, more productive mountain big sagebrush as frequently as every 15–25 yr (Burkhardt and Tisdale 1976, Miller and Heyerdahl 2008). The role of fire in basin big sagebrush (*A. tridentata* spp. *tridentata*) ecosystems is less understood, the few existing studies provide insight to only a short time period following fire (Sapsis and Kauffman 1991), and no state and transition models that help us understand successional dynamics exist for this system, as they do for the more common types of sagebrush (Hemstrom et al. 2002, Chambers et al. 2014*a*).

Basin big sagebrush historically occupied the most fertile and productive areas of the sagebrush steppe (e.g., alluvial flood plains, areas of deep well-drained soils; Shultz 2012). Its distribution is from 600 to 2100 m in elevation where precipitation is 200–400 mm (USDA 2019). Euro-American colonizers converted many areas once dominated by basin big sagebrush to agricultural land uses by the early twentieth century (Lesica and Cooper 1997, Shultz 2012). In many areas, basin big sagebrush is now most often found in pockets of fertile deep soil on mountain slopes and along roadways and fencerows (Shultz 2009). It has been proposed that due to relatively rapid primary productivity (Sapsis 1990) and sagebrush canopy recovery, basin big sagebrush may have historic fire-return intervals that are intermediate (Sapsis 1990) between mountain big sagebrush and Wyoming big sagebrush, or more frequent than both other subspecies (Lesica et al. 2007). Long-term successional dynamics in basin big sage ecosystems are almost completely unknown (Miller et al., 2013, Mata-Gonzalez et al. 2018).

State and transition models are often used on rangelands to characterize vegetation and surface soils on an ecological site in order to identify where management options are likely to facilitate persistence of desirable vegetation as well as to elucidate conditions that put the integrity of the system at risk of transition to a degraded state (Stringham et al. 2003, Bestelmeyer et al. 2009, 2010). There have been many state and transition models that describe disturbance and successional dynamics in Wyoming big sagebrush and mountain big sagebrush community types (i.e., Chambers et al. 2014*a*), but we are unaware of any to date that describe the less-common basin big sagebrush ecosystems.

The patterns of vegetation dominance and biomass accumulation (i.e., fuels) on the landscape through the successional trajectory are strong determinants of the behavior of wildland fires. Fuels are defined as the living and dead vegetation (biomass) that burns in a wildland fire (Pyne 1984) including organic horizons, grass, herbaceous plants, downed wood, shrubs, and trees (Byram 1959). Early-successional communities are usually dominated by herbaceous species that are readily burned when dry. When those fine herbaceous fuels are continuous, such as occurs in invasive annual-dominated communities, a positive feedback loop between increased fire and invasion often becomes established (Brooks et al. 2004, Chambers et al. 2014*b*), resulting in increases in fire probability (Westoby et al. 1989, Miller et al., 2013). Where native herbaceous plants still dominate early succession though, it is unknown whether fire risk is elevated, or whether there is potential conversion to a native grass-dominated alternative stable state (Laycock 1991). The objectives of this study were (1) to quantify patterns of postfire vegetation and biomass accumulation and the resultant potential future fire behavior in basin big sagebrush communities, (2) to understand how repeated burns affect this successional trajectory, and (3) to use this information to develop a state and transition model describing basin big sagebrush ecosystems. To address these objectives, we quantified long-term postfire vegetation composition and biomass accumulation at the John Day Fossil

Beds National Monument (JODA), on the Columbia Plateau in North-Central Oregon. We hypothesized that (1) due to the relatively rapid recovery of basin big sagebrush, biomass at sites >25 yr postfire will be similar to prefire biomass, with woody plants composing the majority of the total biomass; (2) repeated fires will alter composition, such that sites that are twice-burned will have less total biomass accumulation but a greater dominance of herbaceous vegetation compared with sites that only burned once; and (3) increased dominance by herbaceous vegetation in twice-burned plots will result in more extreme potential fire behavior compared with plots burned only once.

Materials and Methods

Study area

This research was done at John Day Fossil Beds National Monument (JODA), at sites where prescribed fires preceded the collection of plant composition and fuel data in the late 1980s in basin big sagebrush communities (Sapsis 1990). The study site was located within the Sheep Rock Unit, ~12 km NW of Dayville, Oregon, USA (44°31′ N, 119°38′ W). Domestic grazing has been excluded from the Monument since 1973. All plots were dominated by basin big sagebrush prior to burns, with Idaho fescue (*Festuca idahoensis*) and bluebunch wheat grass (*Pseudoroegneria spicata*) dominating the understory. All plots have a north-facing aspect with slopes ranging from 20% to 65% and elevations ranging from 700 to 869 m. The average annual precipitation from 1989 to 2015 was 29 cm (Prism Climate Group 2019). Soils are of the Simas–Tub association of very stony clay loam soils (USDA SCS 1981). Plots (≥0.15 ha in size) were initially burned in September 1987 (n = 4) and May 1988 (n = 5). Three additional (n = 3) plots were established as unburned controls (Sapsis 1990). Plots were previously sampled in 1987 and 1988 (prefire), in 1987 and 1988 (postfire; Sapsis 1990), and remeasured for this study in May–June 2015 (25 yr postfire [YPF] for fall burns, and 26YPF for spring burns, all referred to hereafter as 26YPF). The September 1999 700-ha Windy Point prescribed fire reburned five previously burned plots and all previously unburned controls. Plots that only burned once in 1987 or 1988 are referred to in this paper as 26YPF (n = 4), plots that only burned once in 1999 are referred to as 15YPF (n = 3), and plots that burned in both 1987 or 1988 and 1999 are called twice-burned (2xB; n = 5).

Field sampling

*Vegetation composition and structure.—*To quantify the impacts of fire on plant community composition and structure, we measured frequency at the subplot level for each herbaceous and woody species, density of each graminoid and woody species, and canopy cover and height of shrubs for each treatment plot (15YPF, 26YPF, 2xB). From these data, we calculated plant community diversity (Shannon 1948). The researchers who did the original 1987–1988 sampling were on site during the 2015 resampling to ensure continuity of methods. Nomenclature and native distribution of all plants follow the USDA Plants Database (USDA and NRCS 2019).

Frequency of herbaceous species was measured as present or absent in 10 evenly placed 0.18-m^{-2} quadrats along each of three 10-m parallel transects (30 subsamples per treatment plot). Transects were oriented systematically, with the first transect starting from a random origin in the northeast quadrant of each plot. Each transect was oriented upslope parallel to and offset 7 m from the initial transect. Density of perennial grasses was counted in the same 0.18 m^{-2} quadrats, and density of annual grasses was counted in .0025 m^{-2} nested sub-quadrats.

To determine shrub cover, first shrub density was determined in counts within five 15 × 1 meter permanent belt transects. Density per transect was then multiplied by the average crown area for basin big sagebrush for each transect, and data were then averaged across transects and scaled to get a plot-level cover estimate.

*Biomass.—*Aboveground biomass was partitioned into the following components: shrub, downed wood (DWD), live herbaceous understory, standing dead herbaceous understory, grass litter, and shrub litter. Species, crown area, and height of each shrub were measured along five 15 × 1 meter permanent belt transects per treatment plot. These transects included and extended 5 m upslope beyond the vegetation composition transects (above), with two additional perpendicular transects oriented above and below the three parallel transects. Shrub biomass was determined using previously developed allometric equations (Champlin 1982, Kauffman and Cummings 1989) using *in situ* crown area and height measurements. Downed wood was measured along each permanent transect (15 m) following methods described in Brown et al. (1982). Understory biomass was clipped to bare mineral soil in ten 0.18-m^{-2} quadrats per plot. Clipped biomass was subdivided into the following categories: (1) live and (2) dead standing biomass, (3) detached grass and forb litter, and (4) organic duff layer, composed of detached shrub material, mosses, and lichens. Samples were taken to a laboratory where they were oven-dried at 70°C to a constant mass and then weighed.

Fire behavior modeling

To quantify the impact that previous fire histories and successional stage had on potential future fire behavior, we parameterized the fire behavior modeling system fuel characteristic classification system (FCCS) in the Fuel and Fire Tool (FFT; USDA FS 2016) using *in situ* biomass data collected on all 15YPF, 26YPF, and 2xB plots. FCCS predicts surface fire behavior using ecosystem-specific biomass data and localized environmental scenarios (i.e., moisture content through the typical fire season). For each site, fuelbeds (the arrangement of biomass components) were initialized using the standard fuelbed 56: Sagebrush shrubland, and then, fuel parameters were customized to represent the quantity and arrangement of fuels collected *in situ*. Environmental scenarios were chosen to represent the range of moisture expected as vegetation phenology progresses from the active growing season (fully green scenario; D2L4 scenario in FFT), through partially curing stages (1/3 cured and 2/3 cured scenarios; D2L3 and D2L2, respectively), to late in the summer, when biomass is completely dry and risk of high-intensity fire is greatest (fully cured scenario; D2L1). Independent model runs were done for each plot at each environmental scenario. Model outputs chosen to characterize potential behavior included rate of spread (ROS; m/sec), flame length (FL; m), reaction intensity (RI; the rate of heat release per unit area of the flaming front; $kW \cdot m^{-2} \cdot min^{-1}$), and fireline intensity (FI; the rate of heat transfer per unit length of the fire front; kW m^{-1}; Byram 1959, Keeley 2009).

Data analysis

Analysis of variance (ANOVA) was used to test for differences between vegetation, biomass, and potential fire behavior (dependent variables). Fire treatment (26YPF, 15YPF, 2xB) was the independent variable. For fire behavior analyses, environmental scenario was an additional predictor variable. Significant differences between groups were determined using Tukey-Kramer honest significant difference (HSD) post hoc analysis. To test proportional biomass (percent of total biomass) by category, each category of biomass was relativized by the total biomass at the subplot level. Analyses were performed with RStudio version 0.98.1091 (RStudio Team 2015) and IBM SPSS 24 (IBM 2016).

Results

Vegetation composition and structure

Prior to burning in 1987 and 1988, the mean cover of sagebrush was 7.5–15% (Sapsis 1990). Fires initially shifted composition from shrub-dominated (prefire) to native herbaceous-dominated (1% mean shrub cover) in the first postfire year (Sapsis 1990). At 26 yr postfire, shrub cover was 18 ± 2%, higher than prefire cover. In the 15YPF and 2xB plots, shrub cover was significantly lower, at 4 ± 2% and 0.9 ± 0.6%, respectively ($P < 0.001$). Similarly, mean density of sagebrush in 26YPF sites was 3028 ± 534 sagebrush/ha, significantly higher than that of either plot that burned 15 yr ago ($P < 0.01$). Density of sagebrush at 15YPF plots was 1200 ± 601 sagebrush/ha, and in 2xB plots, it was further reduced to 160 ± 106/ha. Height of mature sagebrush was 0.76 ± 0.14 m across all fire histories ($P = 0.25$).

The fire-adapted native deep-rooted perennial bunchgrasses in this ecosystem showed stability across burn histories, with Idaho fescue occurring in every plot and 30–57% of all subplots ($P = 0.45$) and bluebunch wheat grass occurring in all plots and 60–63% of subplots ($P = 0.99$). Frequency of Idaho fescue was consistent with prefire (28–58%) and early post-first fire (23–46%) levels (Sapsis 1990). Frequency of bluebunch wheat grass exceeded prefire (23–31%) and immediate post-first fire (21–31%) levels (Sapsis 1990). Density of Idaho fescue was variable, ranging from 1.3 to 27.0 individuals per m^2, with no differences across fire histories ($P = 0.22$), and density of bluebunch wheat grass was 1.5–14.3/m^2, with no treatment differences ($P = 0.74$). Native, shallow-rooted Sandberg bluegrass was the only bunchgrass reduced by repeated fire, occurring in 84% of 26YPF subplots, 72% of 15YPF subplots, and 49% of 2xB plots ($P = 0.03$). The only nonnative bunchgrass in the plots was bulbous bluegrass (*Poa bulbosa*), which occurred in 25% of subplots, with no treatment differences ($P = 0.99$).

Cheatgrass (*Bromus tectorum*) occurred in 73–89% of subplots in the previous study (Sapsis 1990), with no change in abundance or distribution due to fire. We observed cheatgrass in 59–89% of subplots, at a mean density of 602 per square meter, with no differences between fire histories (frequency, $P = 0.35$; density, $P = 0.55$). Soft brome (*Bromus hordeaceus*) occurred in 0–27% of subplots before fires, and persisted in the same frequency (2–37%) 26 yr later, with no treatment differences ($P = 0.32$). Medusahead (*Taeniatherum caput-medusae* (L.) Nevski) did not occur prior to fire, or in the early postfire years (Sapsis 1990), but occurred in 6–13% of subplots 26 yr later at a mean density of 22/m^2, with no differences in frequency ($P = 0.30$) or density ($P = 0.35$) across fire histories.

Frequently occurring native perennial forbs included *Nothocalais troximoides* (A. Gray) Greene, *Calochortus macrocarpus* Douglas, *Asclepias fascicularis* Decne, and *Achillea millefolium* L. The only commonly occurring native annual forb was *Epilobium minutum* Lindl. ex Lehm. *Draba verna* L., *Holosteum umbellatum* L., and *Sisymbrium altissimum* L. were frequently occurring nonnative annual forbs. There were no treatment differences observed for any commonly occurring native or invasive annual or perennial forbs ($P > 0.05$). Plant community diversity (H') ranged from 1.50 to 2.25 and did not differ by fire history ($P = 0.27$).

Aboveground biomass

Prefire total aboveground biomass (TAGB) ranged from 5.5 to 11.7 Mg/ha (Sapsis 1990). The first prescribed fire consumed approximately 90% of all biomass (Sapsis and Kauffman 1991). At 26YPF, TAGB averaged 8.2 ± 1 Mg/ha, higher than biomass in any of the plots that burned 15 yr prior ($P < 0.01$; Fig. 1). The 15YPF sites had TAGB at 4.4 ± 0.5 Mg/ha, and in 2xB sites averaged 4.6 ± 0.8 Mg/ha (Fig. 1). Shrub biomass at 26YPF exceeded that of more recently burned plots ($P < 0.01$), at 3.8 ± 1.5 Mg/ha and 43% of total biomass (Figs. 2–3). In the 15YPF plots, shrub biomass was 1.7 ± 0.3 Mg/ha, comprising 38% of biomass, and in the 2xB plots, shrub biomass was 1.2 ± 0.7 Mg/ha and 19% of TAGB. Downed wood mass ranged from 0.1 to 0.6 Mg/ha across fire histories ($P = 0.10$) and comprised 2–8% of the total biomass ($P = 0.38$; Figs. 2–3).

Herbaceous biomass was higher in 2xB plots (2.6 ± 0.4 Mg/ha) than in 15YPF (2.0 ± 0.3 Mg/ha) or 26YPF (1.7 ± 0.4 Mg/ha) plots ($P < 0.01$). Similarly, herbaceous biomass made up the largest proportion of total mass in 2xB plots (64%). 15YPF plots had 45% of mass partitioned as herbaceous vegetation, higher than that seen in 26YPF plots (24%; $P < 0.01$). Organic horizons largely composed of sagebrush litter and mosses

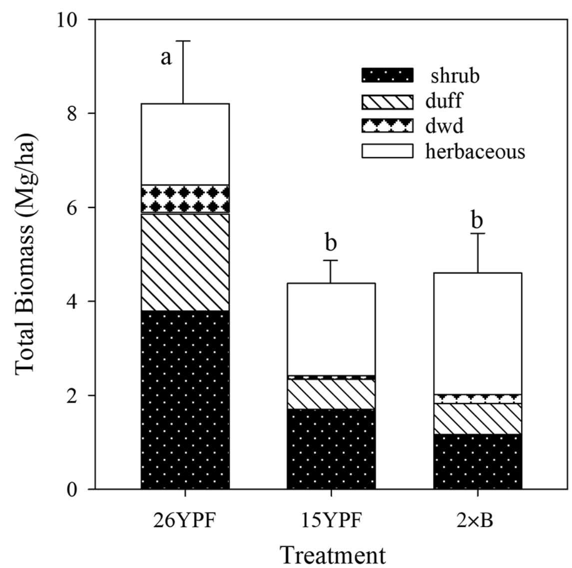

Fig. 1. Biomass composition (Mg/ha) at John Day Fossil Beds, Sheep Rock Unit, Oregon, USA, for plots with various fire histories: twenty-six years since fire (26YPF, $n = 4$), fifteen years postfire (15YPF, $n = 3$), and twice-burned (both 15 and 26 yr ago; 2xB, $n = 5$).

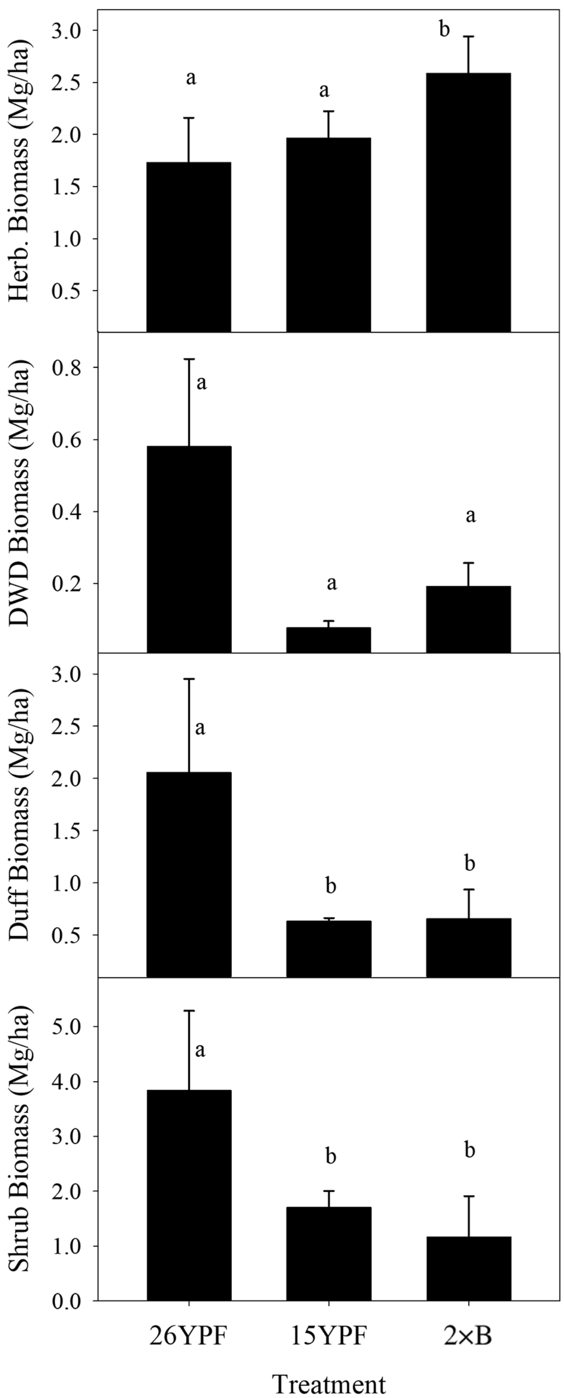

Fig. 2. Biomass by category for all three fire histories at John Day Fossil Beds, Sheep Rock Unit, Oregon, USA. The same letters over bars signify no significant difference.

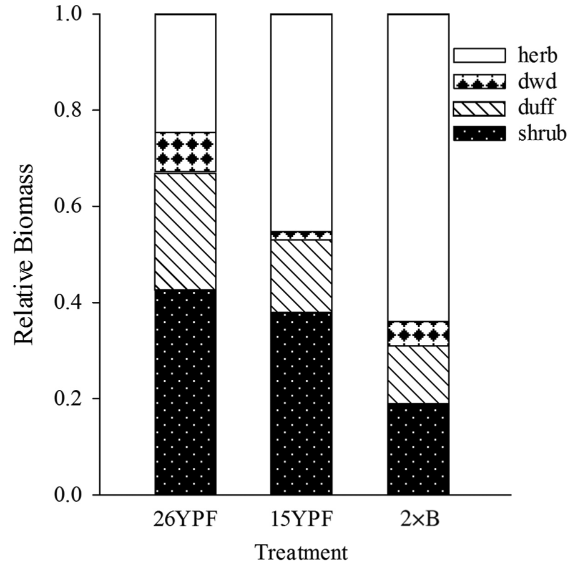

Fig. 3. Relative biomass of herbaceous, downed woody debris (dwd), duff (including detached shrub leaves and bryophytic material), and shrub vegetation in basin big sagebrush ecosystems at John Day Fossil Beds, Oregon, USA, for plots with various fire histories: twenty-six years postfire (26YPF, n = 4), fifteen years postfire (15YPF, n = 3), and twice-burned (2xB, n = 5).

(Duff) were higher in 26YPF plots (2.1 ± 0.9 Mg/ha) than in either 2xB (0.7 ± 0.2 Mg/ha) or 15YPF plots (0.6 ± 0.03 Mg/ha; P = 0.04), and relative duff mass ranged from 12% to 24% with no differences between fire histories (P = 0.19; Fig. 2–3).

Fire behavior

Changes in the plant community and fuel structure following repeated fire in basin big sagebrush communities created the potential for higher intensity fire behavior in the 2xB plots compared with once-burned plots. Predicted rate of spread (ROS) in 26YPF plots ranged from 3.0 ± 1.9 m/min under a fully green environmental scenario to 6.0 ± 4.3 m/min when vegetation was fully cured. In 15YPF plots, ROS ranged from 3.6 ± 2.6 m/min when fully green to 6.8 ± 3.6 m/min when fully cured. Dominance of herbaceous biomass in 2xB plots led to higher rates of spread, at 6.7 ± 5.5 m/min to

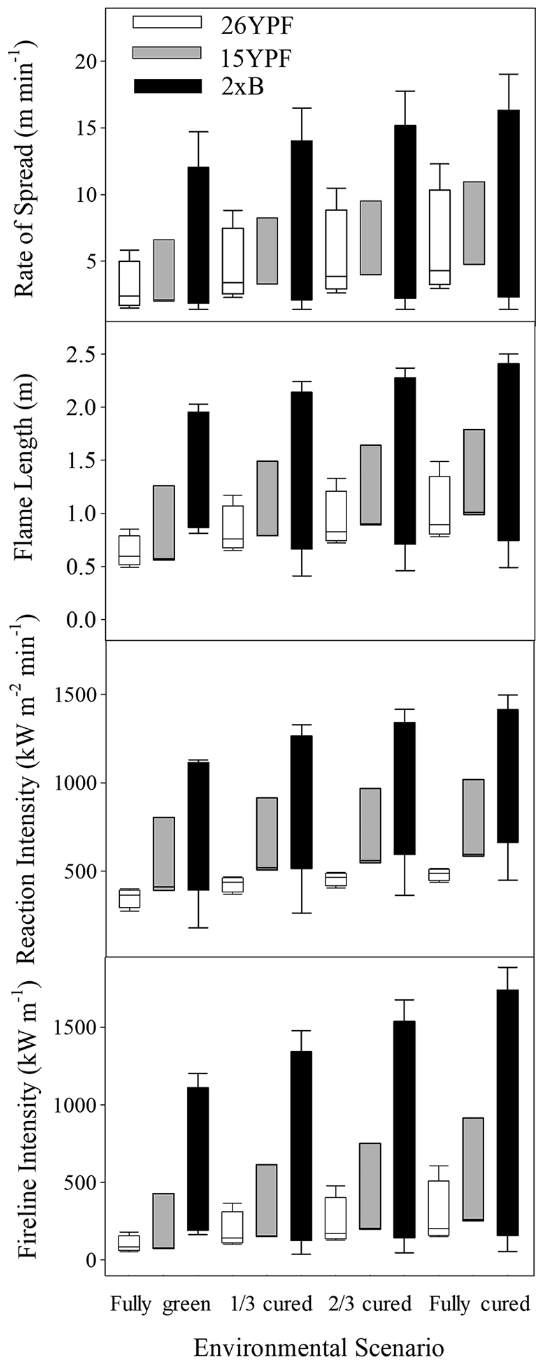

Fig. 4. Fire behavior (from top to bottom: rate of spread; flame length; reaction intensity; and fireline intensity) of a potential fire in areas that previously burned once 26 (26YPF) and 15 (15YPF) years ago, and in fires that burned twice, both 15 and 26 yr ago (2xB) in basin big sagebrush ecosystem at John Day Fossil Beds, Sheep Rock Unit, Oregon, USA.

9.5 ± 7.3 m/min under the same environmental conditions (Fig. 4). Similarly, flame lengths in 2xB plots averaged 1.4 m, which was higher than the 0.9 m flame lengths in 26YPF plots ($P = 0.01$), but not different from 15YPF plots ($P = 0.18$), which averaged 1.1 m. There was no significant increase in flame length over the range of environmental conditions ($P = 0.26$). Reaction intensity did not change over the range of environmental conditions ($P = 0.28$). 2xB plots had more variable and higher reaction intensity (885 ± 66 $kW \cdot m^{-2} \cdot min^{-1}$) than either 15YPF or 26YPF plots ($P < 0.05$). More recently burned 15YPF plots had marginally higher reaction intensity (652 ± 86 $kW \cdot m^{-2} \cdot min^{-1}$) than plots burned 26 previous (430 ± 74 kW/m^2; $P = 0.06$; Fig. 4). Fireline intensity did not change over the range of environmental conditions ($P = 0.52$). 2xB plots had higher fireline intensity (717 ± 107 kW/m) than either 15YPF or 26YPF plots ($P < 0.05$). There was no difference in fireline intensity between 15YPF plots (340 ± 138 kW/m) and 26YPF plots (204 ± 120 kW/m; $P = 0.46$; Fig. 4).

Discussion

Repeated fire in basin big sagebrush altered composition and structure, leading to a prolonged period of native herbaceous dominance and reduced shrub recovery, consistent with our hypotheses. While this is a pattern well-documented in areas where fire shifts composition from native shrub to invasive annual grass (D'Antonio and Vitousek 1992, Pilliod et al. 2017), the native deep-rooted perennial herbaceous response documented here is poorly described for the sagebrush steppe. This area is thought to have historically burned at fire-return intervals between 10 and 50 yr (Sapsis 1990, Lesica et al. 2007), but these estimates do not always take into account frequent indigenous burning for grassland management (Shinn 1980, McAdoo et al. 2013), and the high end of this range is inconsistent with the data collected in this study. Sagebrush landscapes historically were likely dominated by heterogeneous mosaics of continuous areas of late-successional sagebrush with earlier successional grasslands perforating the shrub cover (Laycock 1991, Bukowski and Baker 2013, Pennington et al. 2019). The favorable native recovery that we observed and the presence of native bunchgrasses that are adapted to survive and rapidly regrow following periodic fire (Fellows et al. 2018) indicate that the period between fires observed at these sites is likely within the range of variability that maintains the system in a mosaic of native shrub and grassland. In this study, native species dominated all sites and the area did not appear to be at risk of transition to an alternative stable state of invasive grass dominance (Fig. 5), as is often seen throughout the sagebrush steppe in areas that were subject to intensive domestic grazing or other anthropogenic disturbance (Daubenmire 1940, Seipel et al. 2018), that are dominated by invasives before fire (Ellsworth and Kauffman 2017), that have crossed an ecological threshold (Fig. 5; Davies et al. 2016), and/or that inherently lack postfire resilience (Chambers et al. 2007) due to site potential. It is likely, however, that additional fires at frequent intervals would increase invasive cover and prolong herbaceous dominance (Fig. 5; Mahood and Balch 2019).

Sagebrush individuals are killed by fire and have short-range seed dispersal distances, thus are dependent on a viable seed source and favorable climatic conditions (Maier et al. 2001, Nelson et al. 2013, Shinneman and McIlroy 2016) to regenerate in the postfire environment (Hanna and Fulgham 2015, Ellsworth et al. 2016). In areas where there have been large, continuous fires, seed source is often limited, slowing recovery of the shrub component. Further, arid conditions can limit germination and seedling survival if precipitation is not well-timed with regeneration (Nelson et al. 2013). However, when there are unburned islands remaining within the fire perimeter, shrub recovery is expedited, as these islands act as nodes for regeneration (Ellsworth and Kauffman 2017, Germino et al. 2018). The fires in this study were small prescribed burns that were done within a matrix of late-succession sagebrush canopy, providing ample seed source. Further, these fires were all located on north-facing slopes, which typically have increased resilience to fire relative to hotter, drier south slopes (Miller et al. 2013, Morris and Ledger 2016, Mata-Gonzalez et al. 2018). While seed source is often a limiting factor in sagebrush recovery (Longland and Bateman 2002), there is some evidence that this may not be the case for basin big sagebrush (Owens and Norton 1992), which

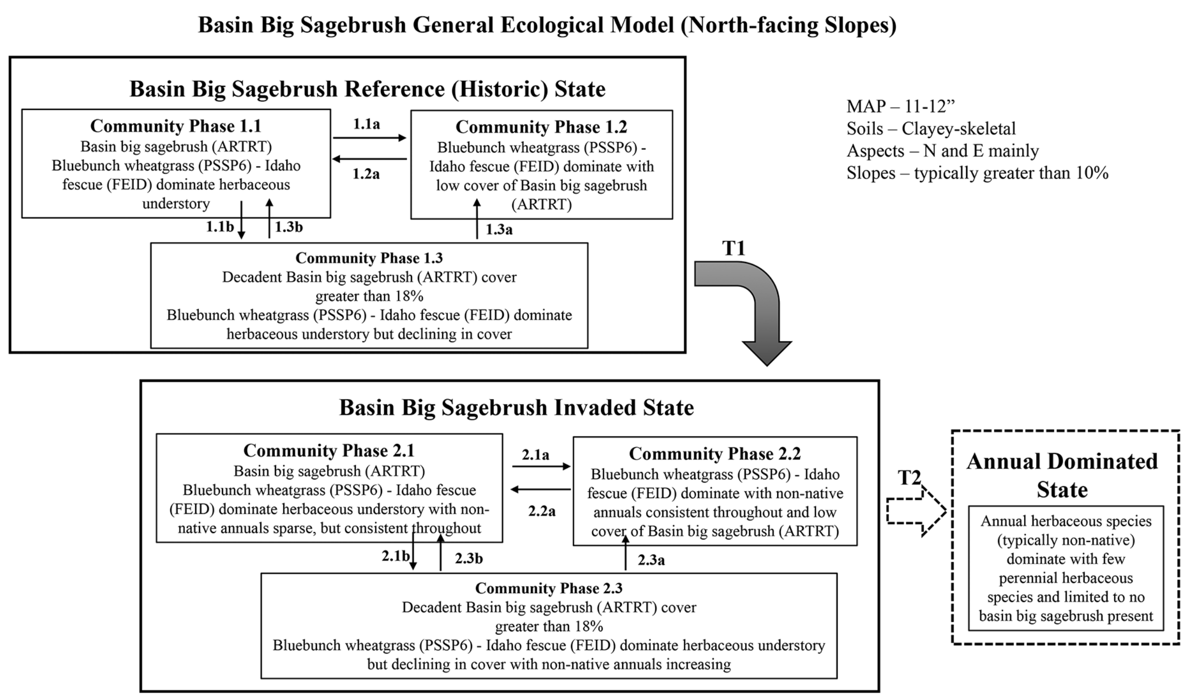

Fig. 5. State and transition model describing disturbance and succession dynamics in basin big sagebrush

(Fig. 5. *Continued*)

ecosystems. *Basin Big Sagebrush Reference (Historic) State*. This state represents the reference state that existed prior to the introduction of nonnative annuals that now dominate much of the western United States. The resistance of this state to nonnative annuals is/was relatively low; however, its existence on more north-facing slopes allows this site to be much more resilient to disturbance than similar sites on south-facing slopes. The dynamics and species composition would be similar to those described in the Basin Big Sagebrush Invaded State, without the presence of nonnative annuals. *Transition T1.*—This transition occurred due to the introduction of nonnative annual species to the site. Droughts, fires, wildlife grazing, and human settlement and recreation in the area all played a role in this introduction. Once the nonnative annuals become a consistent part of the herbaceous layer of this site, it has crossed an ecological threshold where these nonnative annuals begin to capitalize on some of the resources of the site, changing the overall ecological integrity in ways that facilitate the consistent presence of these species. *Basin Big Sagebrush Invaded State*. This state represents the long-term data collected on the plant communities for a north-facing basin big sagebrush ecosystem within John Day Fossil Beds National Park, suggesting a fire-return interval between 15 and 20 yr. Despite the presence of nonnative annuals, resistance to disturbance pressures is moderate and resilience is relatively high due to its existence on more north-facing soils. While in some similar sites, one large fire can transition this state across a threshold into an annual-dominated state, this north-facing site has higher resilience to this disturbance and is capable of recovering without crossing a threshold. All community phases are at risk of crossing a threshold, however, if the fire frequency becomes too frequent or there are additional pressures on the site such as livestock grazing, long-term drought, or pests/disease that an additional stress to the ecological integrity. *Community Phase 2.1.*—Compositionally, this community is similar to the historic reference conditions prior to invasion by nonnatives. While the dominant structural components remain, there is now a sparse, but consistent component of nonnative species in the understory. Ecological processes (infiltration, nutrient cycling, energy capture) have not been significantly compromised at this time; however, ecological resilience is reduced by the presence of nonnatives. Basin big sagebrush is a consistent part of the canopy composition and structure through reestablishment by seed and relatively rapid growth and productivity. Bluebunch wheat grass and Idaho fescue dominate the herbaceous layer, comprising the bulk of the canopy cover and biomass. Nonnative annual grasses contribute to fine fuel loading and will increase the risk of recurrent wildfires. Repeated fires (more than one fire within 15–20 yr) will send this community to CP 2.2 and potentially maintain the CP in 2.2 for an extended period of time, while also reducing the amount of acreage of this community phase and altering the natural fire regime and increasing the extent of CP 2.2. *2.1a.*—Wildfire between 15 and 20 yr, hot enough to burn out most of the woody species. *2.1b.*—Fire intervals longer than 20 yr that allow time for basin big sagebrush to dominate a greater amount of the site's resources and begin to shade out the herbaceous understory. *Community Phase 2.2.*—This community is characteristic of an early seral plant community shortly after fire, dominated by native perennial bunchgrasses and forbs. Early-successional, postfire plant communities in the invaded state will still have a significant portion of native bunchgrasses dominating the composition; however, nonnative annual grasses will also be a significant component. Native perennial bunchgrasses respond favorably to fire and experience an increase in cover and vigor. Nonnative annual grasses contribute to fine fuel loading and will increase the risk of recurrent wildfires. Repeated fires will extend the length of time and acreage of this community phase, by removing more basin big sagebrush seedlings and seeds from the site, limiting their ability to naturally reestablish into the community. *2.2a.*—Absence from natural disturbance (fire, insect attack, disease) and natural regeneration over time. In general, 15–20 yr is required for basin big sagebrush to reach prefire conditions. Length of time for sagebrush communities to fully recover is dependent on ecological variables such as springtime precipitation, proximity of nearest, seed source. *Community Phase 2.3.*—This community is characterized by a decadent basin big sagebrush overstory (18 + % canopy cover) and a reduction in the perennial herbaceous understory. In the absence of the natural fire disturbance, this sagebrush community turns into a more monotypic stands of late-successional shrubs and native bunchgrasses. This results in reduced quantity and diversity of plant species, reduced sagebrush vigor, and seed production. Overmature sagebrush plants are competitive for light, water, and nutrients, preventing recruitment and establishment of other vegetation, and increasing the amount of bare ground. Nonnative annuals persist in the understory and may increase following decrease or loss of other functional and structural groups. Loss of deep-rooted perennial bunchgrasses results in

(Fig. 5. *Continued*)

reduced infiltration, water holding, nutrient cycling, and energy capture. Contributing to the overall reduced ecological resilience of this community phase. *2.3a.*—Wildfire hot enough to remove most or all of the woody species. *2.3b.*—Patchy, low-intensity fire that does not remove most or all of the woody species and reopens the canopy. *Transition T2 (dashed—not seen at this site).* This transition occurs due to fires that occur too frequently (<10 yr between fires) that deplete the soil seedbank of most of, if not all, the native species typical of this site and all that is left are opportunistic annuals and invasive species. While this basin big sagebrush site has proven to be resilient to fire disturbance, it can cross an ecological threshold when the fire cycle becomes too frequent to allow the site time to repair itself naturally. Soil and ecological processes are changed, reducing water infiltration rates into the soil, organic matter turnover is reduced in the topsoil, and biotic integrity and diversity are lost. While we did not see this type conversion in the study plots, similar areas near our sites have seen this type conversion; thus, we believe that repeated fires with little recovery time would start to favor invasives. *Annual-Dominated State (dashed—not seen at this site).* This state represents the variation in nonnative annuals that now dominate this site. The resistance and resilience of this annual-dominated state and the community phases that may be present are very high, withstanding repeated fires and adapting yearly to climatic variations such as short- and long-term droughts. While we did not see this state in our study area, there is a risk of type conversion to this state with increased fire and invasion.

produces seed in its second year and can generate 50 million seeds/ha annually (Young et al. 1989). Collectively, these factors likely contributed to rapid postfire recovery and native dominance and caution is advised in extrapolating our results to drier, less productive, or highly disturbed sites. Further, some historic basin big sagebrush stands occurred along mesic floodplain channels and had individual shrubs reaching heights of 3 m (USDA 2019). Our upland site was far less productive, with smaller individuals, thus may have fire regimes and successional patterns that differ from those expected in lowland areas.

Biomass in sagebrush-dominated ecosystems has been described to accumulate along a sigmoidal pathway (Watts and Wambolt 1996) with mass of herbaceous and woody plant components having an inverse proportional relationship due to limited space and resources (Fig. 6; Miller et al., 2013, Pennington et al. 2019). In the initial postfire landscape, biomass is often limited, as much of the biomass is consumed by fire. Immediately after the first fire at our site, residual fine fuel biomass was 0.23 Mg/ha (Sapsis 1990), too sparse to sustain a repeat fire. In sagebrush ecosystems, threshold fuel loads for sustained ignition and spread of fire have been reported to range from 0.7 to 0.8 Mg/ha of herbaceous fuel (Beardall and Sylvester 1976) or a minimum of 20% sagebrush canopy cover (Pechanec et al. 1954). Britton and Clark (1985) similarly

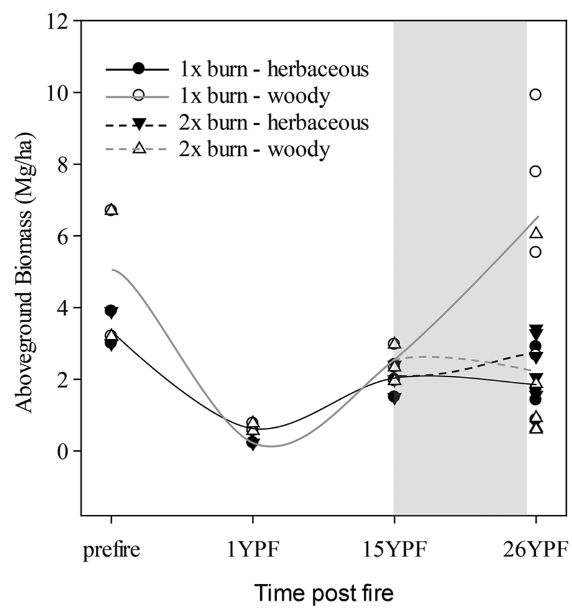

Fig. 6. Conceptual diagram showing recovery following fire in basin big sagebrush ecosystems based on data collected at John Day Fossil Beds National Monument, Oregon, USA. Dark lines show herbaceous vegetation recovery in once-burned (solid) and twice-burned (dashed) sites. Lighter gray is woody vegetation succession in once-burned (solid) and twice-burned (dashed) sites. The gray shading in from years 15 to 25 shows the resultant proposed fire-return interval for basin big sagebrush.

found that a minimum of 20% sagebrush canopy cover but only 0.30 Mg/ha herbaceous fuel would carry fire under moderate weather conditions. In all cases, by 15YPF our plots were well over these biomass thresholds for sustained surface fire spread through herbaceous fuels, and similar mesic sagebrush systems have shown adequate postfire herbaceous biomass accumulation for repeat fire spread within 5 yr postfire (Fellows et al. 2018).

This study provides evidence that burning twice within 26 yr arrested succession and modified rates and types of biomass accumulation (Fig. 6). When we compare biomass composition and sagebrush cover in the 26YPF treatment plots and prefire data collected by Sapsis (1990), it appears that the 26YPF plots now are advanced in succession compared with preburn (i.e., had a higher sagebrush cover and biomass, and lower herbaceous biomass), though climate and precipitation variability could affect inter-year herbaceous biomass (Sala et al. 2015). This suggests that the fire-return interval of basin big sagebrush is considerably lower than that of Wyoming big sagebrush and even more frequent than that of many mountain big sagebrush communities. This knowledge is critical for our understanding of succession, fuel accumulation, and resultant potential fire behavior in a little-described but imperiled subspecies of sagebrush and its associated plant communities.

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Literature Cited

Baker, W. L. 2006. Fire and restoration of sagebrush ecosystems. Wildlife Society Bulletin 34:177–185.

Beardall, L. E., and V. E. Sylvester. 1976. Spring burning for removal of sagebrush competition in Nevada. Tall Timbers Fire Ecology Conference Proceedings 14:539–547.

Bestelmeyer, B. T., K. Moseley, P. L. Shaver, H. Sanchez, D. D. Briske, and M. E. Fernandez-Gimenez. 2010. Practical guidance for developing state-and-transition models. Rangelands 32:23–30.

Bestelmeyer, B. T., A. J. Tugel, G. L. 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.

Britton, C. M., and R. G. Clark. 1985. Effects of fire on sagebrush and bitterbrush. Pages 22–26 *in* K. Sanders, J. Durham, and various agency, editors. Rangeland Fire Effects: A Symposium: Proceedings. Idaho State Office, USDI-Bureau of Land Management Boise, Idaho, USA.

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

Brown, J. K., R. D. Oberheu, and C. M. Johnston. 1982. Handbook for inventorying surface fuels and biomass in the Interior West. USDA Forest Service General Technical Report INT-GTR-129.

Bukowski, B. E., and W. L. Baker. 2013. Historical fire regimes, reconstructed from land-survey data, led to complexity and fluctuation in sagebrush landscapes. Ecological Applications 23:546–564.

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

Byram, G. 1959. Combustion of forest fuels in forest fire: control and use. McGraw-Hill, New York, New York, USA.

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

Chambers, J. C., D. A. Pyke, J. D. Maestas, M. Pellant, C. S. Boyd, S. B. Campbell, S. Espinosa, D. W. Havlina, K. E. Mayer, and A. Wuenschel. 2014*b*. Using resistance and resilience concepts to reduce impacts of invasive annual grasses and altered fire regimes on the sagebrush ecosystem and greater sage-grouse: a strategic multi-scale approach. General Technical Report. RMRS-GTR-326. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

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

Champlin, M. R. 1982. Big sagebrush (*Artemisia tridentata*) ecology and management with emphasis on prescribed burning. Dissertation. Oregon State University, Corvallis, Oregon, USA.

D'Antonio, C. M., and P. Vitousek. 1992. Biological invasions by exotic grasses, the grass-fire cycle and global change. Annual Review of Ecology and Systematics 23:63–88.

Daubenmire, R. F. 1940. Plant succession due to overgrazing in the *Agropyron* bunchgrass prairie of southeastern Washington. Ecology 21:55–64.

Davies, K. W., J. D. Bates, and C. S. Boyd. 2016. Effects of intermediate-term grazing rest on sagebrush communities with depleted understories: evidence of a threshold. Rangeland Ecology and Management 69:173–178.

Ellsworth, L. M., and J. B. Kauffman. 2017. Plant community response to prescribed fire varies by prefire condition and season of burn in mountain big sagebrush ecosystems. Journal of Arid Environments 144:74–80.

Ellsworth, L. M., D. W. Wrobleski, J. B. Kauffman, and S. A. Reis. 2016. Ecosystem resilience is evident 17 years after fire in Wyoming big sagebrush ecosystems. Ecosphere 7:e01618.

Fellows, A. W., G. N. Flerchinger, K. A. Lohse, and M. S. Seyfried. 2018. Rapid recovery of gross production and respiration in a mesic mountain big sagebrush ecosystem following prescribed fire. Ecosystems 21:1283–1294.

Germino, M. J., D. M. Barnard, B. E. Davidson, R. S. Arkle, D. S. Pilliod, M. R. Fish, and C. Applestein. 2018. Thresholds and hotspots for shrub restoration following a heterogeneous megafire. Landscape Ecology 33:1177–1194.

Hanna, S. K., and K. O. Fulgham. 2015. Post-fire vegetation dynamics of a sagebrush steppe community change significantly over time. California Agriculture 69:36–42.

Hemstrom, M. A., M. J. Wisdom, W. J. Hann, M. M. Rowland, B. C. Wales, and R. A. Gravenmier. 2002. Sagebrush-steppe vegetation dynamics and restoration potential in the Interior Columbia basin, USA. Conservation Biology 16:1243–1255.

Houston, D. B. 1973. Wildfires in northern Yellowstone National Park. Ecology 54:1111–1117.

IBM Corp. Released. 2016. IBM SPSS Statistics for Windows, Version 24.0. IBM Corp. Released, Armonk, New York, USA.

Kauffman, J. B., and D. L. Cummings. 1989. Fuel loads and biomass consumption during spring and fall prescribed fires in central Oregon rangeland ecosystems. General Technical Report. USDA Forest Service PNW research station, Seattle, Washington, USA.

Keeley, J. E. 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. International Journal of Wildland Fire 18:116–126.

Laycock, W. A. 1991. Stable states and thresholds of range condition on North American rangelands: a viewpoint. Journal of Range Management 44:427–433.

Lesica, P., and S. V. Cooper. 1997. Presettlement vegetation of southern Beaverhead County, Montana. Montana Natural Heritage Program, Helena, Montana, USA.

Lesica, P., S. V. Cooper, and G. Kudray. 2007. Recovery of big sagebrush following fire in Southwest Montana. Rangeland Ecology & Management 60:261–269.

Longland, W. S., and S. L. Bateman. 2002. Viewpoint: the ecological value of shrub islands on disturbed sagebrush rangelands. Journal of Range Management 55:571–575.

Mahood, A. L., and J. K. Balch. 2019. Repeated fires reduce plant diversity in low-elevation Wyoming big sagebrush ecosystems (1984–2014). Ecosphere 10:e2591.

Maier, A. M., B. L. Perryman, R. A. Olson, and A. L. Hild. 2001. Climatic influences on recruitment of 3 subspecies of *Artemisia tridentata*. Journal of Range Management 54:699–703.

Mata-Gonzalez, R., C. M. Reed-Dustin, and T. J. Rodhouse. 2018. Contrasting effects of long-term fire on sagebrush steppe shrubs mediated by topography and plant community. Rangeland Ecology and Management 71:336–344. https://doi.org/10.1016/j.rama.2017.12.007

McAdoo, J. K., B. W. Schultz, and S. R. Swanson. 2013. Aboriginal precedent for active management of sagebrush-perennial grass communities in the Great Basin. Rangeland Ecology & Management 66:241–253. https://doi.org/10.2111/REM-D-11-00231.1

Mensing, S., S. Livingston, and P. Barker. 2006. Long-term fire history in great basin sagebrush reconstructed from macroscopic charcoal in spring sediments, Newark Valley, Nevada. Western North American Naturalist 66:64–77.

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. General Technical Report RMRS-GTR-308. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Miller, R. F., and E. K. Heyerdahl. 2008. Fine-scale variation of historical fire regimes in sagebrush-steppe and juniper woodland: an example from

California, USA. International Journal of Wildland Fire 17:245–254.

Miller, R. F., T. J. Svejcar, and N. E. West. 1994. Implications of livestock grazing in the Intermountain sagebrush region: plant composition. Pages 100–146 *in* M. Vavra, W. A. Laycock, and R. D. Pieper, editors. Ecological implications of livestock herbivory in the west. Society for Range Management, Denver, Colorado, USA.

Morris, L. R., and E. A. Leger. 2016. Secondary succession in the sagebrush semi-desert 66 years after fire in the Great Basin, USA. Natural Areas Journal 36:187–193.

Nelson, Z. J., P. J. Weisberg, and S. G. Kitchen. 2013. Influence of climate and environment on post-fire recovery of mountain big sagebrush. International Journal of Wildland Fire 23:131–142.

Owens, M. K., and B. E. Norton. 1992. Interactions of grazing and plant protection on basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*) seedling survival. Journal of Range Management 45:257–262.

Pechanec, J. F., G. Stewart, and J. P. Blaisdell.1954. Sagebrush burning-good and bad. U.S. Department of Agriculture Farmers' Bulletin 148.

Pennington, V. E., J. B. Bradford, K. A. Palmquist, R. R. Renne, and W. K. Lauenroth. 2019. Patterns of big sagebrush plant community composition and stand structure in the western United States. Rangeland Ecology and Management 72:505–514.

Pilliod, D. S., J. L. Welty, and R. S. Arkle 2017. Refining the cheatgrass–fire cycle in the Great Basin: Precipitation timing and fine fuel composition predict wildfire trends. Ecology and Evolution 7:8126–8151.

PRISM Climate Group. 2019. Oregon State University. http://prism.oregonstate.edu

Pyne, S. J. 1984. Introduction to wildland fire: fire management in the United States. Wiley Press, New York, New York, USA.

RStudio Team. 2015. RStudio: integrated Development for R. RStudio, Boston, Massachusetts, USA.

Sala, O. E., L. A. Gherardi, and D. P. C. Peters 2015. Enhanced precipitation variability effects on water losses and ecosystem functioning: differential response of arid and mesic regions. Climatic Change 131:213–227.

Sapsis, D. B. 1990. Ecological effects of spring and fall prescribed burning on basin big sagebrush: Idaho fescue–bluebunch wheatgrass communities. Thesis. Oregon State University, Corvallis, Oregon, USA.

Sapsis, D. B., and J. B. Kauffman. 1991. Fuel consumption and fire behavior associated with prescribed fires in sagebrush ecosystems. Northwest Science 65:173–179.

Seipel, T., L. J. Rew, K. T. Taylor, B. D. Maxwell, and E. A. Lehnhoff 2018. Disturbance type influences plant community resilience and resistance to *Bromus tectorum* invasion in the sagebrush steppe. Applied Vegetation Science 21:385–394.

Shannon, C. E. 1948. A mathematical theory of communication. Bell System Technical Journal 27:379–423.

Shinn, D. A. 1980. Historical perspectives on range burning in the inland Pacific Northwest. Journal of Range Management 33:415–422.

Shinneman, D. J., and S. K. McIlroy 2016. Identifying key climate and environmental factors affecting rates of post-fire big sagebrush (*Artemisia tridentata*) recovery in the northern Columbia Basin, USA. International Journal of Wildland Fire 25:933–945.

Shultz, L. M. 2009. Monograph of *Artemisia* subgenus *tridentata* (Asteraceae-Anthemideae). Systematic Botany Monographs 89:1–131.

Shultz, L. M. 2012. Pocket guide to sagebrush. Point Reyes Bird Observatory Conservation Science Publication, Petaluma, California, USA. Pages 85.

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.

USDA, Forest Service. 2016. Fuel and fire tools. Pacific Northwest Research Station, Seattle, Washington, USA. https://www.fs.fed.us/pnw/fera/fft/index.shtml

USDA, Natural Resources Conservation Service 2019. The plants database. National Plant Data Team, Greensboro, North Carolina, USA.

USDA, Soil Conservation Service. 1981. Soil Survey of Grant County, Oregon, Central Part. https://www.nrcs.usda.gov/Internet/FSE_MANUSCRIPTS/oregon/grantOR1981/Grant.pdf

Watts, M. J., and C. L. Wambolt. 1996. Long-term recovery of Wyoming big sagebrush after four treatments. Journal of Environmental Management 46:95–102.

Westoby, M., B. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. Journal of Range Management 42:266–274.

Wright, H. A., and A. W. Bailey. 1982. Fire ecology: United States and southern Canada. John Wiley and Sons, New York, New York, USA.

Young, J. A., R. A. Evans, and D. E. Palmquist. s1989. Big sagebrush (*Artemisia tridentata*) seed production. Weed Science 37:47–53.