Interaction of historical and nonhistorical disturbances maintains native plant communities

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Abstract. Historical disturbance regimes are often considered a critical element in maintaining native plant communities. However, the response of plant communities to disturbance may be fundamentally altered as a consequence of invasive plants, climate change, or prior disturbances. The appropriateness of historical disturbance patterns under modern conditions and the interactions among disturbances are issues that ecologists must address to protect and restore native plant communities. We evaluated the response of *Artemisia tridentata* ssp. *wyomingensis* (Beetle & A. Young) S.L. Welsh plant communities to their historical disturbance regime compared to other disturbance regimes. The historical disturbance regime of these plant communities was periodic fires with minimal grazing by large herbivores. We also investigated the influence of prior disturbance (grazing) on the response of these communities to subsequent disturbance (burning). Treatments were: (1) ungrazed (livestock grazing excluded since 1936) and unburned, (2) grazed and unburned, (3) ungrazed and burned (burned in 1993), and (4) grazed and burned. The ungrazed–burned treatment emulated the historical disturbance regime. Vegetation cover, density, and biomass production were measured the 12th, 13th, and 14th year post-burning. Prior to burning the presence of *Bromus tectorum* L., an exotic annual grass, was minimal (<0.5% cover), and vegetation characteristics were similar between grazed and ungrazed treatments. However, litter accumulation was almost twofold greater in ungrazed than in grazed treatments. Long-term grazing exclusion followed by burning resulted in a substantial *B. tectorum* invasion, but burning the grazed areas did not produce an invasion. The ungrazed–burned treatment also had less perennial vegetation than other treatments. The accumulation of litter (fuel) in ungrazed treatments may have resulted in greater fire-induced mortality of perennial vegetation in ungrazed compared to grazed treatments. Our results demonstrate that prior disturbances exert a strong influence on the response of plant communities to subsequent disturbances and suggest that low-severity disturbances may be needed in some plant communities to increase their resilience to more severe disturbances. Modern deviations from historical conditions can alter ecosystem response to disturbances, thus restoring the historical disturbance regime may not be an appropriate strategy for all ecosystems.

Key words: Artemisia tridentata; Bromus tectorum; *cheatgrass; ecosystem management; fire; grazing; historical conditions; invasive plants; Northern Great Basin Experimental Range, Oregon, USA; prior disturbance; sagebrush.*

INTRODUCTION

Historical disturbances are often considered a requirement to maintain native plant communities, and this has resulted in the reconstruction of historical disturbance regimes to direct ecosystem management. The best management of ecosystems has been assumed to be accomplished by reestablishing historical disturbance regimes (Baker 1994, Cissel et al. 1999, Suding et al. 2004, Wright and Agee 2004). Generally, it is believed that the greater the deviation from past disturbance patterns, the more negative the ecosystem impacts. Restoration of ecosystems can often be accomplished by reinstating historical disturbance re-

gimes (Baker 1993, 1994, Suding et al. 2004). However, some ecosystems have experienced irrevocable changes in environmental conditions and biotic potentials that could potentially alter the response of the plant community to disturbance (Suding et al. 2004). For example, climate change or invasive plants may result in a different plant community response to disturbance than expected under historical conditions (Millar and Woolfenden 1999, Suding et al. 2004).

Another possible deviation from historical conditions that could have profound implications to reinstating historical disturbance regimes is previous disturbances. Prior disturbances have been associated with an increasing severity of subsequent disturbances (Platt et al. 2002, Kulakowski and Veblen 2007), and successive disturbances may have compounding negative effects (Paine et al. 1998). However, interactions among

different disturbances have seldom been empirically tested. To protect and restore native plant communities, it is critical to understand the influence of prior disturbances on subsequent disturbances and to determine if successive disturbances have a compounding effect. The outcome of reintroducing historical disturbances is not clear, especially with the threat of invasive plants and other deviations from past conditions.

Deviations from historical disturbance regimes, such as livestock grazing of plant communities that did not evolve with large numbers of large herbivores, are generally considered negative. Plant communities that did not evolve with large herbivore pressure are not expected to be able to tolerate livestock grazing (Fleischner 1994, Noss 1994, Belsky and Blumenthal 1997, Jones 2000). In a review of the literature without differentiating between grazing utilization levels, Jones (2000) suggested that livestock grazing has detrimental effects on arid ecosystems of North American that evolved with few large herbivores. However, there is some disagreement on the effects of livestock grazing of these plant communities depending on level of utilization (e.g., Rice and Westoby 1978, West et al. 1984, Rickard 1985, Eckert and Spencer 1986, 1987, Courtois et al. 2004, Manier and Hobbs 2006). Currently, many of these plant communities that did not evolve with large herbivores are grazed by domestic livestock and have the potential to burn, thus a better understanding of the effects of interactions between historical and nonhistorical disturbances is critical. Returning plant communities to their historical disturbance regime would involve prescribed burning of some plant communities and potentially removing domestic livestock. The impact of returning the historical disturbance regime remains uncertain under current conditions. For example, the response of *Artemisia tridentata* ssp. *wyomingensis* (Beetle & A. Young) S.L. Welsh plant communities to their historical disturbance regime of periodic fire without domestic livestock grazing is unknown under modern conditions.

Artemisia tridentata ssp. *wyomingensis* (hereafter "*A. tridentata*") plant communities of the Great Basin and Intermountain West (USA) are estimated to have a historical fire-return interval of 50 to >100 years (Wright and Bailey 1982, Mensing et al. 2006). The plant communities of the Great Basin and Intermountain West evolved with few large herbivores, and thus domestic livestock use of these plant communities is considered a deviation from the historical disturbance regime (Mack and Thompson 1982). The historical disturbance regime for these communities would have been periodic fires without domestic livestock grazing. European settlement of western Northern America has generally elongated fire-return interval in late seral *A. tridentata* plant communities (Davies et al. 2008) and introduced domestic livestock to this region in large numbers in the mid-to-late 1800s (Oliphant 1968).

In many ecosystems there is a threat of invasion by exotic species following disturbance, which represents a risk not present during much of the past. Reinstatement of the historical disturbance regime in *A. tridentata* plant communities raises some concerns because of the threat of invasion by *Bromus tectorum* L., an exotic annual grass, following fire. *B. tectorum* invasion can promote fires that are too frequent for the reestablishment of *A. tridentata* and detrimental to native herbaceous vegetation (Stewart and Hull 1949, Whisenant 1990). Modern-day burning may promote the invasion of these communities by *B. tectorum* (Stewart and Hull 1949, Young and Allen 1997). The initial increase in resources with burning (Hobbs and Schimel 1984, Young and Allen 1997, Davies et al. 2007a) would favor *B. tectorum* invasion (Young and Allen 1997). However, Davies et al. (2007a) demonstrated that prescribed fall burning of late seral *A. tridentata* plant communities could be accomplished without promoting *B. tectorum* invasion. Burned *A. tridentata* communities were more resistant to *B. tectorum* invasion than unburned communities in the fourth growing season post-burn (Davies et al. 2008). Similar to fire, grazing by domestic livestock has been identified as a causal agent of *B. tectorum* invasion by reducing the ability of the native plant communities to resist invasion and by dispersing *B. tectorum* seeds (Daubenmire 1970, Mack 1981, Knapp 1996). However, *B. tectorum* has been found in plant communities that have experienced minimal or no domestic livestock grazing (Svejcar and Tausch 1991, Davies et al. 2006).

To evaluate the response of native plant communities to their historical disturbance regimes under modern conditions and to determine the influence of prior disturbances on subsequent disturbances, we investigated the effects of historical and nonhistorical disturbance patterns to *A. tridentata* plant communities in the northern Great Basin. Management directed by the historical disturbance regime would exclude livestock grazing and periodically apply prescribed fire to late seral *A. tridentata* plant communities. We speculated that burning of plant communities grazed by livestock would have more negative impacts on desirable vegetation than would burning of plant communities protected from livestock use, because large herbivore grazing is a deviation from the historical disturbance regime of these communities. Thus, we expected to see a compounding effect (Paine et al. 1998) when fire follows long-term use by large herbivores. We also speculated that the ungrazed compared to the grazed treatment would have greater cover, density, and biomass production of native grasses and forbs. We hypothesized that (1) deviations from historical disturbance regimes would negatively impact native plant communities, (2) prior disturbances would significantly impact subsequent disturbances, and (3) successive disturbances, i.e., long-term grazing followed by fire, would have compounding negative effects on native plant communities.

METHODS

Study area

The study was conducted at the Northern Great Basin Experimental Range (NGBER) in southeastern Oregon (43°29′ N, 119°43′ W) about 56 km west of Burns, Oregon, USA. Climate is typical of the northern Great Basin with cool, wet winters and hot, dry summers. The NGBER received on average 300 mm of precipitation annually during the past 50 years (1956–2005). Precipitation during the sampling years was 117%, 115%, and 70% of the long-term average in 2004–2005, 2005–2006, and 2006–2007, respectively. Elevation at the study sites is ~1400 m above sea level and topography is generally flat (slopes 0–3°). Soils at the study sites are coarse-loamy, mixed frigid, Orthidic Durixerolls, loamy mixed, frigid, shallow Aridic Durixerolls, and coarse-loamy Aridic Duric Haploxerolls. *Artemisia tridentata* ssp. *wyomingensis* is the dominant shrub at all sites and dominant bunchgrass species varies by site. *Achnatherum thurberianum* (Piper) Barkworth (Thurber's needlegrass), *Festuca idahoensis* Elmer (Idaho fescue), *Koeleria macrantha* (Ledeb.) J.A. Schultes (prairie junegrass), *Pseudoroegeria spicata* (Pursh) A. Löve (bluebunch wheatgrass), and *Elymus elymoides* (Raf.) Swezey (squirreltail) are common large perennial bunchgrasses on the study sites.

Experimental design

To determine the effects of grazing and fire on vegetation, a randomized block with a complete two-by-two factorial design was used. Treatments were applied at three different sites with different herbaceous species composition and soil characteristics. Treatments were the factorial combinations of burned or unburned and grazed or ungrazed: (1) ungrazed and unburned, (2) ungrazed and burned, (3) grazed and unburned, and (4) grazed and burned. Ungrazed treatments were 2-ha livestock-grazing exclosures established in 1936. Thus, prior to 1936 they experienced livestock grazing. Native herbivores had access to vegetation inside the exclosures. The grazed treatment plots were located, in 1936, adjacent to the exclosures and on the same soil type as the exclosures. Density data collected in 1937 revealed no differences in the densities of *Poa secunda* J. Presl, large perennial grasses, annual grasses, perennial forbs, and annual forbs between inside and outside the exclosures ($P > 0.05$). *Bromus tectorum* was not present inside or outside the exclosures in 1937. The grazed treatments adjacent to the exclosures were grazed by cattle until 1990. Livestock grazing pressure was moderate, 30–40% use of available forage. From 1938 to 1949 livestock use was rotation grazing with stocking rates determined from range surveys conducted in 1938 and 1944. From 1949 to 1990, the grazing program was a deferred-rotation system with occasional years of complete rest. Grazing treatments were not identical among sites because the sites were in three different

65-ha pastures. In 1992 and 1993 the cover, density, and biomass production of herbaceous species were not statistically different between the ungrazed and grazed treatments (Rose et al. 1994). However, in both years litter biomass was almost two-fold higher in the exclosures compared to outside (Rose et al. 1994). No fires occurred at the study sites during the study (1936–2007), except for the prescribed burn treatments. In late September of 1993, prescribed burning treatments were applied as strip-head fires using drip torches to ungrazed and grazed 0.4-ha plots at each site. Air temperature was between 20° and 27°C, wind speeds varied from 6 to 21 km/hr, and relative humidity was between 8% and 22% during the prescribed burns. Fine fuel loads (standing biomass and litter) averaged across all sites was 689 kg/ha in grazed treatments and 793 kg/ha in ungrazed treatments prior to the burning (Rose et al. 1994). Fine fuel loads prior to burning were measured using 30, 0.2-m^2 frames per treatment.

Measurements

Vegetation characteristics were sampled in 2005, 2006, and 2007, the 12th, 13th, and 14th years post-burning, respectively. Sample sizes were optimized through the use of previous data from this ecosystem (Davies et al. 2006, 2007a, Bates et al. 2009). Each treatment replicate was sampled using a 30×60 m plot centered in the treatment area to limit edge effects. Five 30-m transects, spaced at 15-m intervals, were established in the 30×60 m plot. Herbaceous canopy cover was estimated and density was measured by species inside 40×50 cm frames (0.2 m^2) located at 3-m intervals on each transect line, resulting in 10 frames per transect and 50 frames per plot. Bare ground, moss, and litter cover were also measured in the 40×50 cm frames. Shrub cover by species was measured by line-intercept method (Canfield 1941) along the five 30-m transect lines per plot. Shrub density by species was measured by counting all individuals rooted in five 2×30 m belt transects. Herbaceous biomass by functional group was determined in late June in each year by clipping, oven drying, and then weighing the current year's growth from 25 randomly located 1-m^2 frames per treatment replicate.

Statistical analysis

Repeated-measures analysis of variances (ANOVA) using the Proc Mix procedure in SAS version 9.1 (SAS Institute 2002) were used to determine the influence of grazing and fire on vegetation characteristics. Fixed variables were grazed and burned treatments and their interaction. Random variables were sites and site-by-treatment interactions. Covariance structures were determined using the Akaike's information criterion (Littell et al. 1996). Data were tested for normality using the univariate procedure in SAS version 9.1 (SAS Institute 2002). Data that violated assumptions of normality were log-transformed. Response variable means are reported with standard errors (mean ± SE).
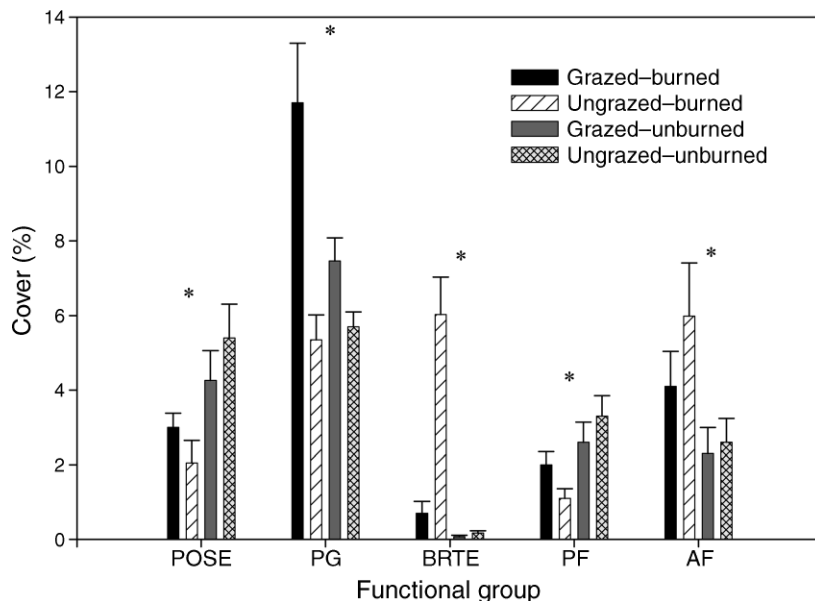
FIG. 1. Functional-group cover of the four treatments averaged over 2005, 2006, and 2007 at the Northern Great Basin Experimental Range, Oregon, USA. Vegetation key: POSE = *Poa secunda*, PG = tall perennial bunchgrass, BRTE = *Bromus tectorum*, PF = perennial forb, and AF = annual forb. Treatment key: ungrazed = livestock excluded since 1936, grazed = moderately grazed by livestock until 1990, burned = prescribed fall burned in 1993, and unburned = no prescribed burning. Data are means + SE; an asterisk (*) indicates significant interaction between grazing and burning treatments for that functional group ($P < 0.05$).

For these analyses, herbaceous cover, density, and biomass production were grouped into five functional groups: *P. secunda*, large native perennial grasses, *B. tectorum* (only annual grass present), perennial forbs, and annual forbs. *P. secunda* was treated as a separate perennial-grass functional group because of its smaller stature and relatively rapid phenological development compared to other perennial grasses in this ecosystem (Davies 2008, James et al. 2008). Functional groups are a common classification of plants based on physiological and morphological characteristics (Lauenroth et al. 1978). Plant functional groups are an important and useful classification for management (Davies et al. 2007b), also facilitate comparisons among sites with varying species composition, and simplify analysis (Boyd and Bidwell 2002).

RESULTS

Cover

The interaction between burning and grazing treatments influenced cover of all herbaceous functional groups ($P < 0.01$) (Fig. 1). *Poa secunda* cover was decreased with burning and protection from grazing prior to burning amplified this decrease ($P < 0.01$). *Poa secunda* cover was highest in the ungrazed–unburned treatment and lowest in the ungrazed–burned treatment. The responses of large perennial bunchgrass cover to burning varied by grazing treatment ($P < 0.01$). Large perennial bunchgrass cover increased with burning in the grazed treatments, while it was not affected by

burning in ungrazed treatments. Large perennial bunchgrass cover was greatest in the grazed burned treatment and lowest in the ungrazed–burned treatment. *Bromus tectorum* cover appears to generally increase with burning; however, the magnitude of the increase was larger in ungrazed compared to grazed treatments ($P < 0.01$). *Bromus tectorum* cover was 8.6-fold greater in the ungrazed–burned treatment than in any of the other treatments. Similarly, annual forb cover generally increased with burning and its greatest increase was in the ungrazed burned treatment ($P < 0.01$). Annual forb cover was dominated by introduced annual forbs. Perennial forb cover was lower with grazing in the unburned treatment; however, the situation was reversed in the burned treatments with more perennial forb cover in the grazed compared to ungrazed plots ($P < 0.01$). The interaction between burning and grazing treatments influenced cover of moss and bare ground ($P < 0.01$), but not *Artemesia tridentata* ssp. *wyomingensis* or *Chrysothamnus viscidiflorus* (Hook.) Nutt. (green rabbitbrush) cover ($P = 0.34$ and 0.77, respectively) (Fig. 2). Grazing, burning, and their interaction did not influence litter cover ($P > 0.05$). Though differences in bare ground were small, burning increased bare ground more than grazing and the grazed treatments had higher bare ground compared to ungrazed treatments ($P < 0.01$). Moss cover decreased with burning, but its decrease was greater in ungrazed treatments ($P < 0.01$). Burning decreased *A. tridentata* cover and increased *C. viscidiflorus* cover ($P = 0.04$ and <0.01, respectively). Grazing
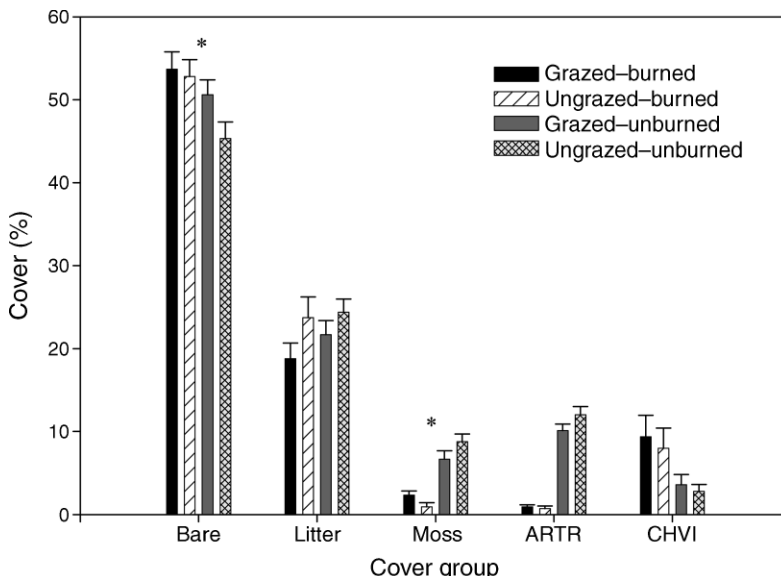
FIG. 2. Shrub species, litter, and moss cover, and bare ground of the four treatments averaged over 2005, 2006, and 2007 at the Northern Great Basin Experimental Range. Cover types: Bare = bare ground, ARTR = *Artemisia tridentata* ssp. *wyomingensis*, and CHVI = *Chrysothamnus viscidiflorus*. Treatment key: Ungrazed = livestock excluded since 1936, Grazed = moderately grazed by livestock until 1990, Burned = prescribed fall burned in 1993, and Unburned = no prescribed burning. Data are means + SE; an asterisk (*) indicates significant interaction between grazing and burning treatments for that cover group (*P* < 0.05).

did not influence *A. tridentata* cover (*P* = 0.43), but slightly increased *C. viscidiflorus* cover (*P* = 0.05). No interactions existed between year and treatment for any of the functional groups, litter, or bare ground cover values (*P* > 0.05).

Density

Large perennial bunchgrass and *B. tectorum* densities were influenced by the interaction of burning and grazing (*P* < 0.01) (Fig. 3). *Chrysothamnus viscidiflorus* density was also influenced by the interaction between burning and grazing (*P* < 0.01). *Poa secunda*, perennial forb, annual forb, and *A. tridentata* ssp. *wyomingensis* densities were not influenced by the interaction between burning and grazing treatments (*P* > 0.05). Burning decreased perennial bunchgrass density in the ungrazed treatment, but did not influence bunchgrass density in the grazed treatment (*P* < 0.01). Large perennial
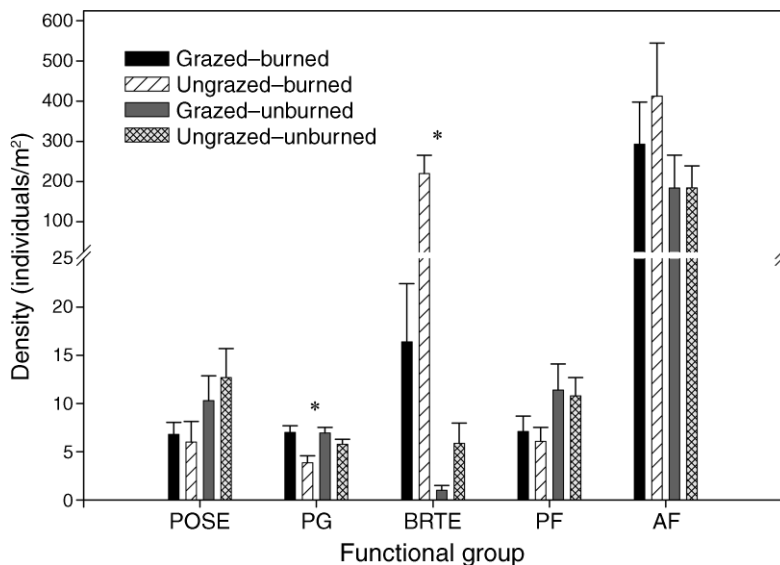

FIG. 3. Functional-group density of the four treatments averaged over 2005, 2006, and 2007 at the Northern Great Basin Experimental Range. Functional groups and treatments are as in Fig. 1. Data are means + SE; an asterisk (*) indicates significant interaction between grazing and burning treatments for that functional group (*P* < 0.05).
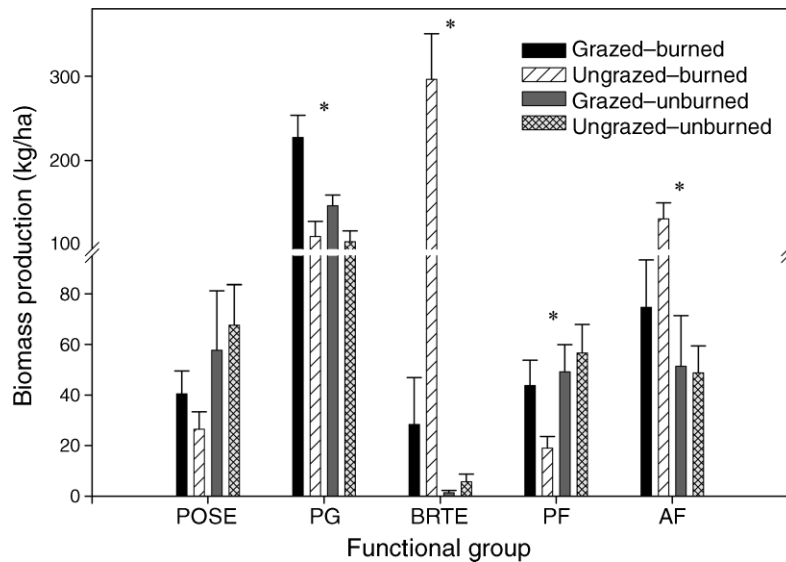
FIG. 4. Functional-group biomass production of the four treatments averaged over 2005, 2006, and 2007 at the Northern Great Basin Experimental Range. Functional groups and treatments are as in Fig. 1. Data are means + SE; an asterisk (*) indicates significant interaction between grazing and burning treatments for that functional group ($P < 0.05$).

bunchgrass density was approximately 1.9-fold greater in the grazed–burned compared to the ungrazed–burned treatment. Burning appears to increase *B. tectorum* density; however, this was magnified when applied to ungrazed treatments ($P < 0.01$). *B. tectorum* density was more than 15-fold greater in the ungrazed burn treatment than any of the other treatments. Burning generally increased *C. viscidiflorus* density; however, the increase in *C. viscidiflorus* density was largest in the ungrazed–treatment ($P < 0.01$). *C. viscidiflorus* density was lowest in ungrazed–unburned (0.25 ± 0.08 individuals/m^2 [mean ± SE]), followed by grazed–unburned (0.31 ± 0.10 individuals/m^2), grazed–burned (0.45 ± 0.12 individuals/m^2), and ungrazed–burned (0.54 ± 0.14 individuals/m^2) treatment. Burning decreased *P. secunda* and perennial forb density ($P < 0.01$), but their densities were not influenced by grazing ($P > 0.05$). In general, annual forb density increased with burning ($P = 0.02$), but was not influenced by grazing ($P = 0.36$). Annual forb density was dominated by introduced species. *Artemisia tridentata* density was 6.8-fold greater in the unburned (0.34 ± 0.03 individuals/m^2) compared to the burned (0.05 ± 0.01 individuals/m^2) treatments ($P = 0.04$), but did not differ by grazing treatment ($P = 0.98$). Year by treatment interactions did not influence density of any of the functional groups ($P > 0.05$).

Biomass

Biomass production of large perennial bunchgrass, *B. tectorum*, perennial forb, and annual forb were influenced by the interaction of burning and grazing ($P < 0.01$) (Fig. 4). The interaction between grazing and burning was not significant for *P. secunda* biomass production ($P = 0.22$). Large perennial bunchgrass

production increased with burning in the grazed treatment, but did not increase with burning in the ungrazed treatment ($P < 0.01$). Burning the grazed treatment increased perennial bunchgrass production 1.6-fold. Burning generally increased *B. tectorum* biomass production; however the magnitude was larger in the ungrazed treatments ($P < 0.01$). *Bromus tectorum* biomass production increased more than 49-fold with burning in the ungrazed treatment. Perennial forb biomass production decreased when the ungrazed treatment was burned, but was not influenced by burning in the grazed treatment ($P < 0.01$). Perennial forb biomass decreased three-fold when the ungrazed treatment was burned. Biomass production of annual forbs, mainly comprised of introduced species, increased with burning; however, the increase was magnified when burning ungrazed treatments ($P < 0.01$). Annual forb production increased 2.7-fold with burning in the ungrazed treatment and 1.5-fold with burning in the grazed treatment. The ungrazed–burned treatment was the only treatment to produce more annual than perennial herbaceous vegetation biomass. Biomass of the functional groups was not influenced by interactions between year and treatment ($P > 0.05$).

DISCUSSION

Individual circumstances will dictate the value of emulating historical disturbance regimes for maintaining native plant communities. Disturbance impacts may be altered by changes in climatic conditions and/or anthropogenic impacts. Further complicating the issue of reinstating historical disturbance regimes are invasive species. In our specific example, the historical disturbance regime of *Artemesia tridentata* ssp. *wyomingensis*

Fig. 5. Photograph of the grazed and burned treatment on the left and the ungrazed and burned treatment on right, in 2007, 14 years post-fire. Treatments are adjacent to each other (note the similar ridge in the background of the photographs). Native perennial bunchgrass and the exotic annual-grass *Bromus tectorum* are dominating the grazed–burned and the ungrazed–burned treatments, respectively. Note the continuity of fine fuels (mainly previous year's *B. tectorum* tillers) in the ungrazed–burned compared to the grazed–burned treatment. Photo credit: K. W. Davies.

plant communities is estimated to have consisted of a 50- to >100-year fire-return interval (Wright and Bailey 1982, Mensing et al. 2006) and a lack of large-herbivore grazing pressure (Mack and Thompson 1982). Emulating this disturbance regime for *A. tridentata* ssp. *wyomingensis* plant communities did not produce the expected effect of shifting the dominance from shrubs to native forbs and perennial grasses. Long-term protection from livestock grazing followed by fire resulted in a substantial *Bromus tectorum* invasion (Fig. 5) and a large increase in nonnative annual forbs. In the ungrazed treatment, herbaceous dominance shifted from perennial vegetation to annual vegetation with burning. The ungrazed–burned treatment was the only treatment to have a substantial invasion of *B. tectorum*. Invasions by annual grasses are especially problematic because exotic annual-grass invasions can degrade wildlife habitat, reduce biodiversity, and potentially alter ecosystem functions (Davies and Svejcar 2008). This is especially concerning because the *B. tectorum* invasion does not appear to be a short-term response to burning, but is evident approximately a decade and a half post-fire and does not appear to be dissipating.

Though herbivory at the levels domestic livestock graze these landscapes is not considered part of the historical disturbance regime in the Intermountain West and Great Basin (USA) (Mack and Thompson 1982) and has been reported as a causal agent of *B. tectorum* invasion (Daubenmire 1970, Mack 1981, Knapp 1996), our results suggest that under current conditions light to moderate livestock grazing, as a disturbance to reduce litter accumulation, may indirectly prevent *B. tectorum* invasion. The level of grazing pressure is critical, because heavy grazing would facilitate *B. tectorum* invasion by decreasing native plant species (Daubenmire 1970, Mack 1981, Knapp 1996). However, in our study long-term livestock-grazing exclusion decreases the ability of the native herbaceous community to tolerate fire, thereby creating safe sites and allowing *B. tectorum* an opportunity to invade. Lack of grazing allows fine fuels to accumulate, potentially resulting in greater mortality of desirable vegetation from fire in ungrazed compared to grazed treatments. Grazing has been demonstrated to reduce the accumulation of fine fuels, while protection from grazing allows accumulation of fine fuels (Belsky and Blumenthal 1997). The exclosures in our study had almost double the amount of litter compared to the grazed treatment, containing 105 kg/ha more fine fuel prior to burning (Rose et al. 1994). Though the accumulation of fuels does not appear to be dramatic, the spatial distribution of the fine fuels is probably critical. Most of the fine fuels appear to be accumulating around and in the crown areas of the native perennial grasses, probably increasing the likelihood of fire-induced mortality. Odion and Davis (2000) found that increases in soil heating from micro-site fuel accumulations increased the vulnerability of perennial grasses to fire.

The nonhistorical disturbance regime maintained the native plant community, while emulating the historical disturbance regime appeared to facilitate the decline of the native plant community. An understanding of ecological relationships among disturbances and plant community dynamics is critical, as historical disturbance regimes may not always be appropriate to maintain native plant communities under current conditions. Other authors have also suggested that invasive species and changes in other factors may alter the relationships among disturbance patterns and plant communities (Millar and Woolfenden 1999, Suding et al. 2004). Our results run counter to the intuitively appealing assumption that the best management of ecosystems can be accomplished by mimicking historical disturbance regimes (Baker 1993, Baker 1994, Cissel et al. 1999,

Mortiz and Odion 2004, Wright and Agee 2004). Ecologists must also consider that changing biotic and abiotic factors may influence the composition of plant communities relative to historical conditions. Millar et al. (2007) suggested that current and future forest management cannot be adequately directed by past forest conditions.

The shift of our plant community from native perennial species to exotic annual species with long-term grazing exclusion followed by fire supports theories of alternative or multiple steady states (Westoby et al. 1989, Friedel 1991, Laycock 1991, Suding et al. 2004). The increase in exotic annuals and decrease in perennials over the 14-year period suggests that this is not a transitional vegetation state. Codominance by exotic annual grasses increases the risk of frequent fires that would be detrimental to remaining native vegetation (Whisenant 1990, D'Antonio and Vitousek 1992). The historical disturbance regime facilitated the onset of a new disturbance regime that would probably have very negative impacts on native flora and fauna. The effects of exotic-plant invasions are probably especially destructive when they increase fire frequency (Vitousek 1990, D'Antonio and Vitousek 1992). However, the similarity in vegetation characteristics between the grazed–unburned and the ungrazed–unburned treatments would not suggest that the unburned–ungrazed treatment was approaching a transition to a different state that could be induced by one disturbance (Figs. 1–4). The lack of obvious differences between the grazed–unburned and the ungrazed–unburned treatments supports previous reports of minor differences between ungrazed and light to moderately grazed treatments (West et al. 1984, Rickard 1985, Courtois et al. 2004, Manier and Hobbs 2006); however, comparing the grazed–burned and the ungrazed–burned treatments suggests there were substantial functional or structural differences between grazed and ungrazed plant communities. This stresses the importance of understanding the relationships among community structure, ecological processes (such as colonization), and disturbances.

Our results demonstrate that prior disturbance history can have a substantial influence on the response and recovery of plant communities to individual disturbances. The effects of different prior disturbance history were evident almost a decade and half post-fire and do not appear to be dissipating. Prior disturbances have been reported to be associated with fire severity and extent (Kulakowski and Veblen 2007) and susceptibility to wind damage (Kulakowski and Veblen 2002) in subalpine forests. Stand age and increases in fuel loads as controlled by prior disturbances were suggested as the major factors explaining the severity and extent of disturbances (Kulakowski and Veblen 2002, 2007). Our study illustrates that prior disturbances can influence the response of plant communities to subsequent disturbances by reducing and influencing distribution of fuel loads. The prior disturbance history was critical in determining post-fire susceptibility to exotic-plant invasion and, thus, if the plant community could recover. This supports previous assertions that prior land-use activities influence ecosystem function and structure (Foster et al. 2003). Because grazing and fire occur across the majority of wildlands around the globe, grazing, as a disturbance that modifies fuel loads prior to fire, is probably having substantial influence on plant communities and, subsequently, fauna dependent upon those plant communities.

Forests are traditionally thought of as the vegetation type requiring fuel reductions to facilitate desired responses to fire (Dodge 1972, Allen et al. 2002). Given the potential for forests to accumulate high fuel loads due to fire suppression (Dodge 1972, Allen et al. 2002), it is not a surprise that they have been the primary focus for fuel-reducing research and management. However, our results suggest that plant communities with much lower fuel loads may also need fuel-reducing disturbances to prevent negative community shifts following fire. Invasive species and probably climate change have produced conditions where fuel loads within the natural range of variability can result in severe negative responses to fire. Continued climate change and the introduction of new invasive species will probably exacerbate this situation. This also suggests that plant communities with excessive fuel loads may be at greater risk than previously identified. Climate change, anthropogenic stressors, and invasive species have created situations where management strategies need to focus on promoting ecosystem resistance and resilience (Millar et al. 2007). Thus, nonhistorical disturbances may be needed to promote community resistance and resilience in the face of changing environments and land uses.

Multiple disturbances that occur in short succession have been identified as having greater effects than the same disturbances either individually or with greater temporal separation (Paine et al. 1998). However, grazing prior to fire reduced the negative effects of fire on plant communities. Thus, successive disturbances may either compound (Paine et al. 1998, Kulakowski and Veblen 2007) or mediate their effects. The effects of successive disturbances depend upon the impact of the preceding disturbance on the community. Paine et al. (1998) summarized studies where an initial disturbance produced a negative effect and amplified the negative impact of a subsequent disturbance. Kulakowski and Veblen (2007) reported that increases in fuels from prior disturbances increased fire severity. Long-term grazing reduced fine-fuel loads and thus decreased the negative effects of fire. Low-severity disturbances may mediate the effects of potentially more severe disturbances, even without altering species composition. Thinning and low-severity fires have been suggested to increase resilience of forested systems to more severe disturbances (Allen et al. 2002). Our results caution against assuming disturbances that have limited temporal separation will have greater influence on communities than disturbances separated by

a greater amount of time or single disturbances. A better understanding of the interactions between disturbances and ecological processes will be necessary to predict the impacts of multiple disturbances, regardless of historical knowledge.

Conclusions

One of the goals of ecosystem management is to restore historical disturbance regimes (Grumbine 1994). However, our results indicate that deviations from historical conditions have the potential to alter ecosystem response to disturbances, suggesting historical disturbance regimes may not be an appropriate model for current management. Recognizing that because modern conditions differ from historical conditions, the response of ecosystems to historical disturbance regimes may have also been altered is a critical element to understanding the interactions between disturbance and ecosystem dynamics. Returning ecosystems to "historical" or "pre-European settlement" conditions by reintroducing historical disturbance is probably a simplistic view of ecosystem dynamics. The effects of the prior disturbance on plant communities will determine if the successive disturbance effects are compounded or mediated. Even plant communities that are not accumulating fuels beyond historical conditions may need low-severity fuel-reducing disturbances to improve their resilience to more-severe disturbances. Objectives for ecosystem management probably need to be focused on specific measurable goals that society has determined are valuable (soil stability, biodiversity, wildlife habitat, forage production, etc.) instead of trying to emulate historical disturbance regimes and conditions. A more mechanistic view of disturbances will become even more critical with the continued global spread of organisms and global climate change.

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