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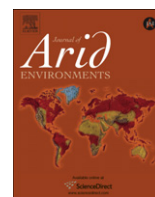
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journal homepage: www.elsevier.com/locate/jaridenvThe influence of plant removal on succession in Wyoming big sagebrush[☆]C.S. Boyd^{*}, T.J. SvejcarUSDA-Agricultural Research Service, Eastern Oregon Agricultural Research Center (EOARC), 67826-A Hwy 205, Burns, OR 97720, United States¹

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ABSTRACT

Restoration treatments are based on the largely untested notion that desired recovery of plant communities following disturbance wouldn't occur in the absence of active intervention. We identified rate of short-term (10 year) floristic changes following removal of plant functional groups in Wyoming big sagebrush plant communities in 1999–2005 and 2008. Treatments imposed on 6 × 6 m plots were: 1) removal of all plant functional groups, 2) perennial grass removal, 3) shrub removal and 4) control. Our data suggest recovery of the shrub component on shrub removal plots could take decades. Similarly, perennial grass cover and density on perennial grass removal plots was less than half that of unaltered plots 10 years after treatment. When all functional groups were removed, cover of annual forbs, annual grasses, and shrubs returned to unaltered levels within ten years or less. Perennial forbs were unaffected ($p > 0.05$) by treatment. The fact that natural recovery of some components occurred within a relatively short post-disturbance time interval (i.e. <10 years) suggests that intervention may not be necessary for some functional groups. Restoring shrubs in areas dominated by perennial grasses may require targeted reductions of competing perennial grasses. Conversely, shrub dominance may limit perennial grass re-establishment.

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1. Introduction

Much of the Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* (Beetle and A. Young) S.L. Welsh) Alliance has been modified from historical plant composition (Miller and Eddleman, 2000; Wisdom et al., 2005). The spatial magnitude of these modifications has created a large and growing need for restoration of native plant communities. For example, invasive annual grasses are currently impacting millions of hectares of Great Basin rangeland (Pellant et al., 2004) and much of the remaining intact rangeland is in danger of transition to annual grass dominance (Pellant and Hall 1994a,b). Sagebrush control projects have impacted over 2 million ha with prescribed fire, mechanical, or herbicide treatments (Crawford et al., 2004), while the direct and indirect impacts of past heavy livestock use may cause increased woody plant composition and decreased herbaceous perennial vegetation (Miller et al., 1994) on an untold number of hectares. These disturbances have, in turn, resulted in a variety of different plant communities needing restoration, ranging from annual grass-dominated to predominately

woody vegetation, to perennial grass-dominated communities with a minimal shrub component. When plant communities are dominated by one functional group, restoring them can be difficult due to reduced species performance (Pickett et al., 1987) associated with competitive interactions between seeded and existing vegetation.

Evaluating the success of restoration in the Wyoming big sagebrush alliance has been complicated by the lack of reporting of “natural recovery”, which we define as the establishment of desired species in the absence of restoration activities. Without knowledge of natural recovery, it is impossible to gauge the amount of floristic change associated with restoration practices (Eiswerth and Shonkwiler, 2006), leaving the effectiveness of restoration efforts open to question. Limited evidence suggests the proportion of restoration success attributable to natural recovery may be substantial (Pyke et al., 2003). Additionally, limitations on restoration capital (both financial and logistical) dictate that we specifically define conservation/restoration priorities (Wisdom et al., 2005). To accomplish this we need a baseline understanding of the extent to which a problem may recover “on its own”; the latter being predicated on a knowledge base sufficient to understand natural recovery trajectories over time for differing pre-restoration species composition. Defining rates of natural recovery for different pre-restoration plant communities would aid in prioritizing restoration activities by delineating those areas most likely to recover without intervention.

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The objective of our study was to identify the nature and rate of short-term (10 years) floristic changes following removal of plant functional groups in Wyoming big sagebrush plant communities. These patterns of change could be used as an index to natural recovery for a variety of restoration scenarios. We hypothesized that post-treatment succession would be characterized by a dominance of those functional groups initially remaining after treatment and that site availability would favor non-native annual grasses in cases of perennial grass or complete vegetation removal.

2. Methods

2.1. Study site

Our study site was located within a Wyoming big sagebrush community at the Northern Great Basin Experimental Range, approximately 72 km west of Burns, Ore. (43.48 N, 119.72 W). The elevation was approximately 1500 m and slope $\leq 1\%$. Annual precipitation is highly variable, but crop year inputs (September–June) average 25.7 cm with the majority falling as rain or snow during the October to March period (long term dataset, Eastern Oregon Agricultural Research Center, Burns, Oregon). Soils were well drained and classified as a Holtle–Milican complex with a surface horizon of loamy alluvium underlain by duripan at approximately 30–50 cm (Lentz and Simonson, 1986). Wyoming big sagebrush was the dominant shrub (about 98% of shrub canopy cover) with limited amounts of rabbitbrush (*Chrysothamnus nauseosus* (Pall.) and Britt.). The dominant perennial grass at the site was bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Love), with lesser amounts of Thurber's needlegrass (*Achnatherum thurberiana* (Piper) Barkworth), Idaho fescue (*Festuca idahoensis* Elmer) and Sandberg's bluegrass (*Poa secunda* J. Presl). Prominent perennial forbs included western yarrow (*Achillea millefolium* DC.), milk vetch (*Astragalus curvicaulus*) and tailcup lupine (*Lupinus caudatus* Kellogg). Annual forbs included pale alyssum (*Alyssum alyssoides* Stapf), fireweed (*Epilobium paniculatum*, Nutt.) and maiden blue-eyed Mary (*Collinsia parviflora* Lindl.). The non-native cheatgrass (*Bromus tectorum* L.) was the only annual grass present at the site. Precipitation data were collected at an existing nearby (<1 km) weather station. Data were summarized by crop year (September–June) as this time period has been shown to strongly influence production at the study site (Sneva, 1982).

2.2. Experimental design

We used a randomized complete block, repeated measures design with 4 treatments and 5 blocks. Response data were collected in 1999 through 2005 and 2008. Treatments were imposed on 6 × 6 m plots beginning in spring and as needed during the growing season of 1998 and in the spring of 1999; treatments consisted of: 1) complete removal (CR) of all plant functional groups, 2) perennial grass removal (PGR), 3) shrub removal (SR) and 4) control (no functional groups removed). A 2 m buffer was mowed between individual plots. Removal of functional groups was accomplished by hand application of glyphosate herbicide (10:1 mix with water) formulated with polyethoxylated tallowamine (Roundup®, MONSANTO Company, St. Louis, MO) to the functional group targeted for elimination.

2.3. Soil nitrogen

Availability of soil nutrients can alter successional patterns in shrub-dominated ecosystems (James et al., 2006). To document short-term changes in soil nutrient availability associated with functional group removal we measured soil nitrogen in August of 1998 and 1999 by collecting two soil cores (0–15 cm) in each plot.

Samples were homogenized and the nitrogen fraction extracted using 2 N KCl solution within 24 h of removal from the field. Prior to extraction, soils were sieved through a 2-mm mesh screen to remove rocks, roots and other large organic material. The extraction technique consisted of shaking 10g of soil with 50 ml of 2 N KCl solution for 1 h. Extracts were allowed to settle for 30 min and then filtered through #42 Whatman filter paper. Extracts were frozen in 20 ml scintillation vials until analyzed for nitrate (NO₃⁻) and ammonium (NH₄⁺) content at the Oregon State University Central Analytical Lab.

2.4. Plant abundance

Cover/density estimates were made by species in late June or early July of each year along three 5 m permanent transects in each plot. For herbaceous vegetation, bare ground, and litter, five 50 × 40 cm quadrats were placed systematically along each permanent transect and cover and density were estimated by species. Shrub density was estimated by counting the number of shrubs, by species, rooted within a 1 m belt centered over each 5 m permanent transect. Shrub cover, by species, was estimated by measuring 2 diagonals on all shrub canopies within the belt transect. To estimate shrub canopy cover within a plot we used the 2 diagonals to calculate the elliptical crown area for each shrub, summed these areas across transects, and divided the resulting value by the area of the belt transects. For cover estimates, all shrub material within the belt transect was measured, regardless of whether the parent shrub was rooted within the belt. Shrub canopy cover was not estimated in 2004. Herbaceous species cover and density data were collated by functional group to simplify analysis and interpretation (Boyd and Bidwell, 2002; Davies et al., 2007a); functional groups included: 1) perennial grasses, 2) annual grasses, 3) perennial forbs and 4) annual forbs.

2.5. Data analysis

Data were examined for skewness and kurtosis (PROC UNIVARIATE, SAS, 1999). When normality or homogeneity of variance assumptions were violated, data were weighted by the inverse of the treatment variance (James and Drenovsky, 2007; Neter et al., 1990). Canopy cover and soil nutrient data were analyzed using repeated measures analysis of variance (PROC MIXED, Littell et al., 1996) with repeated years ($n = 7$ for canopy cover, $n = 2$ for soil nutrients), 5 blocks and 4 treatments. When significant time × treatment interactions were detected, we used the LSMEANS procedure (SAS, 1999) to determine treatment differences within year. Covariance structure was determined using the Akaike's Information Criterion (Littell et al., 1996). Block and the block × treatment interaction were considered random effects in the model. Main effects, interactions and treatment differences were considered to be significant at $\alpha = 0.05$. All means are reported with their associated standard errors.

3. Results

3.1. Precipitation

Crop year precipitation varied strongly over time and all but two years were below normal (Fig. 1). Values ranged from a high of 37.1 cm (144% of normal) in 2006 to a low of 11.7 cm (46% of normal) in 2002.

3.2. Soil nitrogen

Soil ammonium values varied with year ($P = 0.043$), treatment ($P = 0.012$) and year × treatment ($P = 0.002$). In 1998, NH₄⁺

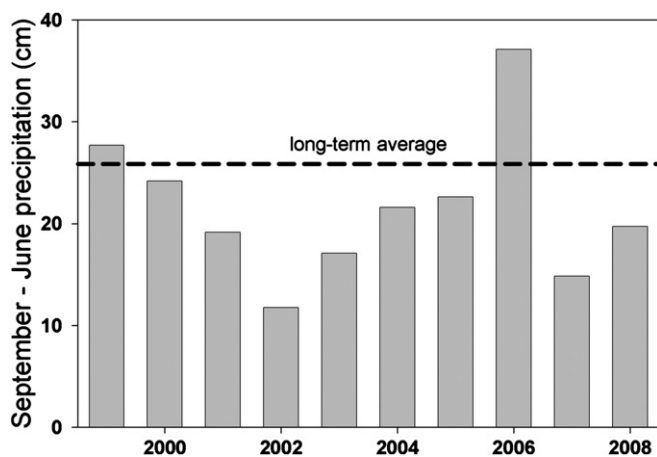


Fig. 1. Crop year precipitation values for study site at the Northern Great Basin Experimental Range in Harney County, Oregon. Values are the summed totals from September of the calendar year prior through June of the indicated year. Long-term average is 25.7 cm.

decreased ($P \leq 0.05$) by about 35% with perennial grass removal to $1.03 \mu\text{g/g}$ (± 0.01) and did not vary among remaining treatments (Fig. 2A). In 1999, NH_4^+ was lower ($P \leq 0.05$) in the CR treatment ($\bar{X} = 1.00 \mu\text{g/g}$ ± 0.02) compared to control and PGR treatments (Fig. 2A). Nitrate levels varied by year ($P < 0.001$), treatment ($P < 0.001$) and the year \times treatment interaction ($P = 0.003$). For the CR treatment, values for NO_3^- were more than 300% higher

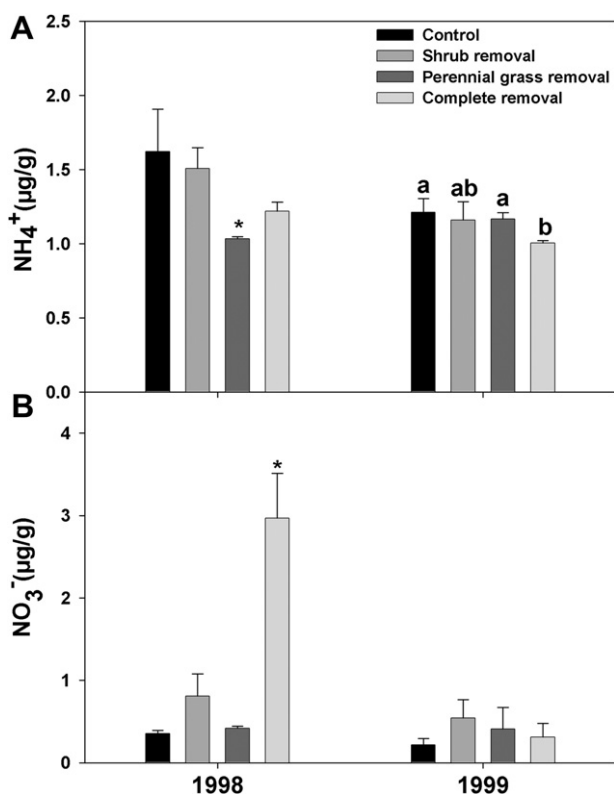


Fig. 2. Soil NH_4^+ (A) and NO_3^- (B) values by treatment and year. Within a graph and year, means without a common letter are different ($\alpha = 0.05$); an asterisk is used to denote one mean that differs from the remaining within a year. Treatments included removal of shrubs, perennial grasses, all vegetation ("complete removal") and no treatment ("Control"). Treatments were initiated in spring of 1998, measurements were taken in August of each year.

($\bar{X} = 2.97 \mu\text{g/g}$ ± 0.55 , $P \leq 0.05$) than remaining treatments in 1998; treatments were invariant in 1999 (Fig. 2B).

3.3. Functional group responses

3.3.1. Perennial grasses

Perennial grass canopy cover varied by year ($P < 0.001$), treatment ($P < 0.001$) and year \times treatment ($P < 0.001$) (Here and elsewhere, main effect differences within year are noted within Figs. 3 and 4). The PGR and CR treatments had lowest ($P \leq 0.05$) perennial grass cover and CR was generally lower than PGR (Fig. 3). Cover was highest ($P \leq 0.05$) for SR plots, which exceeded control plot values in most years. By ten years post-treatment cover values for CR and PGR plots were 39% and 48%, respectively, of control plots. Perennial grass density varied by year ($P < 0.001$) and treatment ($P < 0.001$) but not year \times treatment ($P = 0.16$, Fig. 3). Control ($\bar{X} = 27.8 \text{ plants/m}^2 \pm 2.2$) and SR ($\bar{X} = 29.9 \text{ plants/m}^2 \pm 1.6$) treatments had greater density than PGR ($\bar{X} = 7.0 \text{ plants/m}^2 \pm 0.5$) and CR plots ($\bar{X} = 2.8 \text{ plants/m}^2 \pm 0.45$, $P \leq 0.05$) and by ten years post-treatment values for PGR and CR plots were less than 30% of control and SR plots (Fig. 3).

3.3.2. Annual grasses

Annual grass cover and density were impacted by year ($P < 0.001$), treatment ($P \leq 0.001$) and the year \times treatment interaction ($P < 0.001$). By year 3 following treatment application (2001) canopy cover and density of annual grasses increased ($P \leq 0.05$) in CR plots compared to all other treatments; in year 10, control plots had lowest annual grass cover and density ($P \leq 0.05$, Fig. 3). At maximum values, annual grass canopy cover (2001) and density (2003) in the CR treatment were 285 and 43-fold greater than controls plots.

3.3.3. Annual forbs

Annual forb cover and density varied by year ($P < 0.001$), treatment ($P \leq 0.001$) and year \times treatment ($P < 0.001$). The year after initial treatment (1999) cover of annual forbs increased ($P \leq 0.05$) about 7-fold in the PGR treatment and 20-fold in the CR treatment relative to control plots (Fig. 3). Cover values generally remained higher for the CR treatment until year seven (2005) when values equalized ($P > 0.05$) across treatments. From year two (2000) through year six (2004) density values were highest ($P \leq 0.05$) for the CR treatment (Fig. 3).

3.3.4. Perennial forbs

Canopy cover of perennial forbs was influenced by year ($P = 0.018$), but not by treatment ($P = 0.10$); density was invariant across treatment ($P = 0.348$) but varied by year ($P = 0.004$). Cover values were lowest ($P \leq 0.05$) in 1999 and 2000 with no discernable pattern of change over time (Fig. 3). Similarly, density had no discernable pattern and was highest in 2005 ($\bar{X} = 3.84 \text{ plants/m}^2 \pm 0.48$) and lowest in 2003 ($\bar{X} = 1.87 \text{ plants/m}^2 \pm 0.33$, Fig. 3).

3.3.5. Shrubs

Shrub cover and density differed by year ($P < 0.001$), treatment ($P < 0.001$), and year \times treatment ($P < 0.001$). In the year following treatment (1999), cover values were highest ($P \leq 0.05$) for the PGR and control treatments and lowest for the CR and SR treatments (Fig. 4A). By year seven (2005) cover values were similar ($P > 0.05$) between control and CR treatments and both were higher ($P \leq 0.05$) than the SR treatment. Initial post-treatment shrub density was highest ($P \leq 0.05$) for control and PGR treatments, which exceeded the initial density of the SR treatment by 4–5x. For the remainder of the study, the SR treatment had the lowest

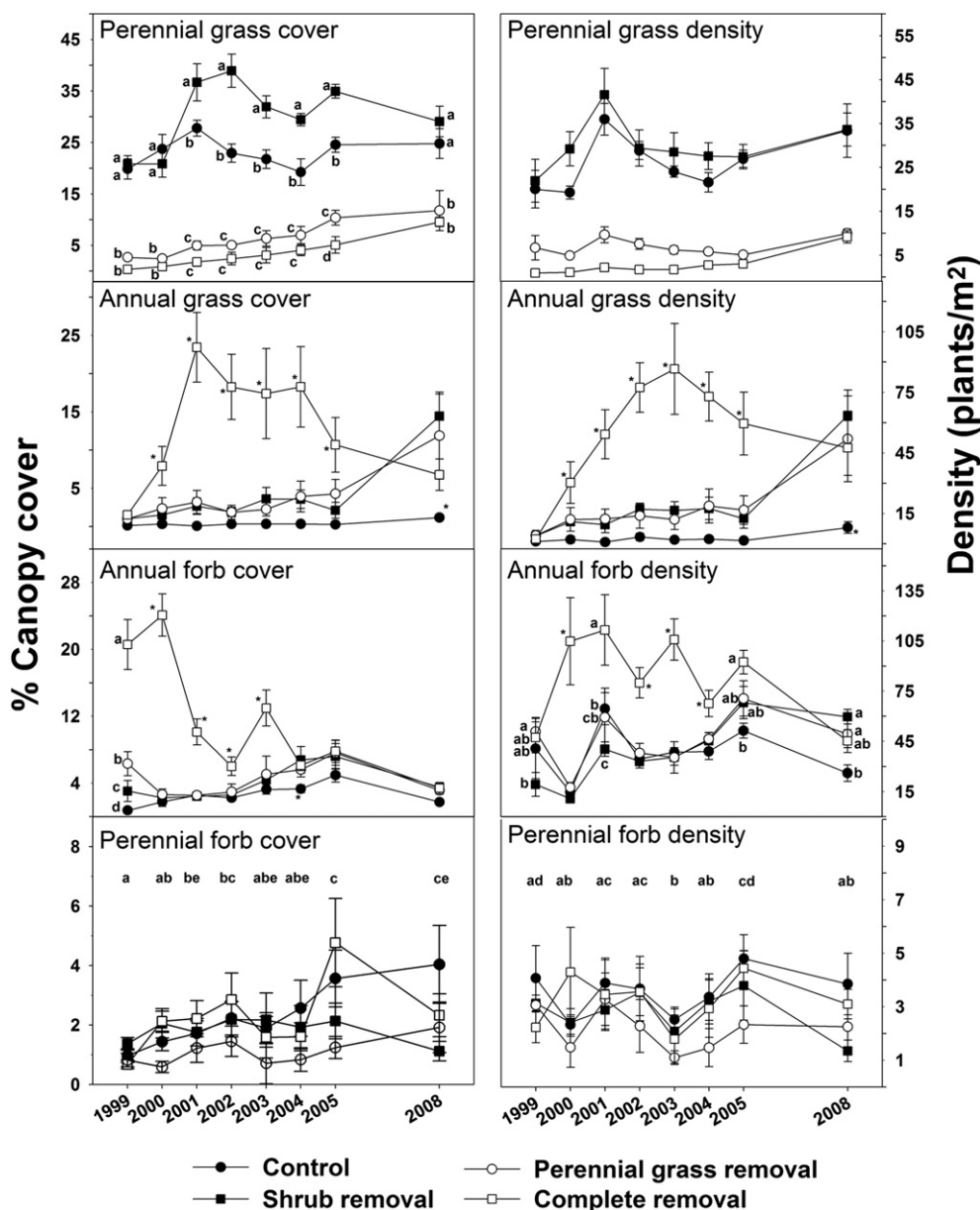


Fig. 3. Canopy cover and density values by treatment and year for functional groups. Within a graph and year, means without a common letter are different ($\alpha = 0.05$); an asterisk is used to denote one mean that differs from the remaining within a year. Perennial grass density differed only by treatment and mean separations are not included in this figure. Perennial forb cover and density mean separations were by year. Treatments were initiated in spring of 1998 and included removal of shrubs, perennial grasses, all vegetation (“complete removal”) and no treatment (“Control”).

($P \leq 0.05$) density values and there were few differences ($P > 0.05$) between any of the remaining treatments (Fig. 4B).

4. Discussion

4.1. The restoration context

Millions of hectares of lower elevation sagebrush steppe are in need of restoration (Miller and Eddleman, 2000). In most cases the plant communities targeted for restoration are missing or have a greatly diminished major functional group (e.g., shrubs or perennial grasses), or have too high a composition of invasive annual grasses. As a group, forbs (at least native forbs) are generally considered desirable, but there is only limited information on the factors which control their abundance. Unfortunately, there is

relatively little scientific information on how the various functional groups interact to influence site recovery. Such information should help managers make decisions about restoration strategies for a given site. We found that initial functional group composition does influence recovery of shrubs and grasses, but generally not forbs.

There are many anthropogenic or natural disturbances which remove one functional group but not others. For example, fire (either natural or prescribed) generally removes shrubs (West and Hassan, 1985; Wroblewski and Kauffman, 2003), but can remove both shrubs and perennial grasses depending on circumstances (Davies et al., 2009). Various shrub removal treatments (e.g., brush-beating and herbicides) have been applied over the years to increase forage production (Schneeegas, 1967; Vale, 1974). There are also natural factors which can cause shrub mortality, such as

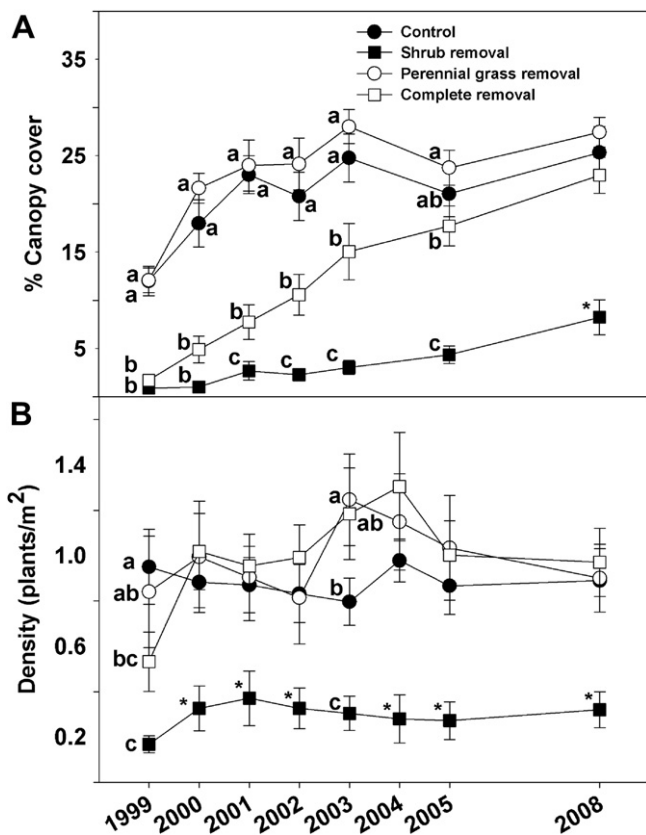


Fig. 4. Shrub canopy cover (A) and density (B) values by treatment and year. Within a graph and year, means with differing letters are different ($\alpha = 0.05$); an asterisk is used to denote one mean that differs from the remaining within a year. Treatments included removal of shrubs, perennial grasses, all vegetation (“complete removal”) and no treatment (“Control”). Treatments were imposed during the growing season in 1998 and spring of 1999.

outbreaks of aroga moth (*Aroga websteri*, Gates, 1964). Conversely, long-term overuse by livestock may deplete perennial grasses, but have minimal effect on shrub abundance (Crawford et al., 2004; Miller et al., 1994). We suggest that a fundamental understanding of functional group interactions will be critical to predicting successional patterns following such disturbances.

4.2. Functional group responses

Prior research has examined competitive relationships within and successional patterns of sagebrush plant communities. Chambers et al. (2007) reported that cheatgrass biomass increased two to three times following removal of perennial grasses in sagebrush communities of the northern Great Basin. In this study the magnitude of cheatgrass increase was 5-fold greater in burned plots with perennial grasses removed. Similarly, James et al. (2008) found removal of perennial grasses alone (compared to factorial removal with perennial and annual forbs, but not shrubs) was sufficient to promote increased exotic annual grass abundance in Oregon sagebrush steppe. In contrast, we found that removal of perennial grasses alone did not stimulate an increase in annual grass abundance over time and that complete removal of vegetation was necessary to stimulate this response (Fig. 3).

Other authors have reported an initial spike in nutrients following severe disturbance such as fire (Davies et al., 2007b; Rau et al., 2007). This spike can create an environment that increases competitive fitness of annual species (Bechtold and Inouye, 2007;

Mclendon and Redente, 1991). Our finding that complete removal of vegetation was necessary to increase annual grass abundance may be related to the fact that only the CR treatment had in initial spike in nitrogen (NO_3^-) availability following treatment; NH_4^+ actually decreased in PGR plots in the year of treatment (Fig. 2). However, in our study, treatment-associated increases in soil nitrogen dissipated within a year of initial treatment (Fig. 2) and annual grass cover/density in the CR treatment did not begin to increase until two years following initial treatment (Fig. 3). This suggests that the post-treatment spike in annual grasses that occurred for the CR treatment was probably associated less with enhanced nutrient availability, and more with increased site availability (Krueger-Mangold et al., 2006; Pickett et al., 1987) and removal of competing vegetation since no other treatments had a strong initial increase in annual species.

Our study site was located near the mesic end of the Wyoming big sagebrush Alliance, and the initial abundance of cheatgrass (see “control” treatment in Fig. 3) was within the range reported for high ecological condition Wyoming big sagebrush communities (Davies et al., 2006). These factors may have combined to create a higher threshold of disturbance for establishment and proliferation of annual grasses in the SR and PGR treatments. Propagule availability was probably similar for all plots, given the small size of the plots and their proximity to surrounding intact shrub/grass communities. Other authors (e.g., Boyd and Davies, 2010; Eiswerth et al., 2008) found that presence of shrubs in the pre-disturbance environment was associated with decreased annual grass abundance and increased establishment of seeded perennial grasses post-disturbance, even if the shrubs were removed by disturbance. This role of shrubs in reducing annual grasses was not evident in the present study under conditions of natural recovery as evidenced by the high level of cheatgrass abundance in the CR treatment (which had previously contained shrubs). Readers should also consider that the immediate nature of our herbicide-induced removal may be more severe than chronic disturbances such as grazing that reduce functional group abundance over time but may not result in complete removal. Additionally, grazing, along with more acute disturbances such as fire will allow for regrowth of some top-killed species such as rabbit brush (Davies et al., 2007b), whereas herbicide application results in death of above and below-ground portions of the plant.

Our data suggest that annual grasses in the CR treatment were declining and cover of perennial grasses was increasing over a 10-year post-treatment time horizon (Fig. 3). This differs from other published reports (e.g., West and Young, 2000; Whisenant, 1990) indicating change to a new annual grass-dominated state following severe disturbance such as fire. However, our findings largely agree with those of West and Yorks (2002) who found that initial dominance of cheatgrass eventually gave way to perennial grass re-establishment in burned Wyoming big sagebrush in Utah. More arid sites may shift to annual dominance, whereas slightly more mesic sites (such as ours) may, over time, allow for perennial grass recovery (Tausch et al., 1994). The slow natural recovery of perennial grasses in the PGR and CR treatments (Fig. 3) suggests that managers should consider active management practices to augment succession (Sheley et al., 2009). These practices could include decreasing competition through targeted shrub reduction and/or increasing seed availability through drilling or broadcast seeding applications. Perennial grasses have been shown to increase the resistance of plant communities to invasion by exotic annual grasses (Robertson et al., 1966; Chambers et al., 2007; Davies, 2008) and prolonged recovery periods may elevate the chance of annual grass invasion.

Removal of shrubs in Idaho (Bechtold and Inouye, 2007) and Oregon (Hedrick et al., 1966) promoted increased perennial grass

cover and biomass to at least 7 years post-treatment. We found that canopy cover of perennial grasses following shrub removal increased relative to control plots (Fig. 3). One explanation for this result would be enhanced perennial grass density associated with increased site availability in the absence of shrubs. However, we failed to find substantive differences in perennial grass density between control and SR plots (Fig. 3), suggesting that existing plants increased growth in response to shrub removal, perhaps as a result of decreased competition for available water (Inouye, 2006) or increased nutrient availability in interspace locations following shrub removal (Bechtold and Inouye, 2007). The lack of recovery of perennial grass cover and density in the CR treatment was associated with strong increases in annual grass cover and density (Figs. 3 and 4), while poor recovery of perennial grasses in the PGR treatment correlated with high shrub abundance (Fig. 3). This latter finding suggests that restoring perennial grasses in shrub-dominated systems may benefit from targeted thinning of shrubs to increase establishment of perennial grass seedlings. It is unlikely that limitations in seed availability negatively influenced recovery of perennial grasses given the small size of our plots and the surrounding intact sagebrush/bunchgrass vegetation. Abundance of perennial forbs was not associated with treatment, but canopy cover varied strongly across years (by almost 300%, Fig. 3). Annual forbs increased in the CR but displayed high between-year variability (Fig. 3), suggesting that gauging forb recovery trajectories will require monitoring over large time horizons (Bates, 2004).

To our knowledge this is the first study to document changes in shrub abundance directly associated with perennial grass removal. Thus, comparable literature is limited to studies involving heavy or severe utilization of perennial grasses by herbivores grazing in sagebrush/bunchgrass vegetation. Previous work in sagebrush steppe has suggested increased abundance of sagebrush with spring utilization of perennial grasses by a variety of domestic herbivores (Austin and Urness, 1995; Jensen et al., 1972; Urness, 1990). In one study, heavy utilization of perennial grasses by horses in spring increased sagebrush production by 83% compared to protected plots (Austin et al., 1994). Our data indicate that removal of perennial grasses numerically increased canopy cover (Fig. 4A) of shrubs relative to control plots, however this increase was not statistically significant. The slow recovery of shrubs in SR plots suggests that a reduction in perennial grasses may benefit shrub restoration in communities with abundant perennial grasses and little to no shrub presence. In our study shrub recovery was faster when all vegetation was removed compared to shrub removal alone (Fig. 4). Recovery of shrubs in the CR plots took place within the context of relatively high cover and density of annual grasses, suggesting resource partitioning between these two functional groups. It should be noted that while our study indicated that shrubs can increase in the presence of invasive annual grasses, this effect may be scale dependent in that: A) the small size of our plots probably didn't limit sagebrush seed availability, and B) at larger spatial scales annual grass invasion can result in increased fire frequency which can reduce or eliminate shrubs (Brooks et al., 2004). The initially increasing trend in sagebrush cover in our control treatment (1999–2001, Fig. 4A) was likely associated with continuing recovery from an arora moth infestation (Gates, 1964) that ended in 1994. Additionally our sampling methodology incorporated a 15 cm gap rule (Boyd et al., 2007), so as a given sagebrush canopy "filled in" measurements of that plants' canopy could increase dramatically as previously distinct patches (i.e., ≥ 15 cm distant) coalesced.

Shrub recovery trajectories (for SR and CR) are in agreement with published estimates for recovery of Wyoming big sagebrush following herbicide treatment (2,4-D) or rotocutting (Davies et al. 2009; Hedrick et al., 1966; Wambolt and Payne, 1986). However

published recovery data following burning (e.g. Baker, 2006; Beck et al., 2009; Wambolt and Payne, 1986) suggest a much longer recovery period than for the CR treatment in our study. Ziegenhagen (2003) noted that precipitation conditions in the initial establishment year following fire had a large impact on subsequent recruitment of sagebrush seedlings. In our study, precipitation was slightly above average in the growing season following treatment, which could have bolstered recruitment of seedlings and ultimately shortened recovery time. In our small plots, recovery was not likely hampered by seed availability (given the presence of mature sagebrush in neighboring plots and surrounding vegetation) whereas in large disturbances such as wildfires, seed availability in the interior portions of the burn will be limited to soil seed pools and rodent caches (Ziegenhagen, 2003) and shrub re-establishment may be impaired (Blaisdell, 1953). Shrub cover increased slower in SR compared to CR treatments (Fig. 4), with CR reaching control levels by six years post-treatment. Assuming equal shrub seed availability in both treatments, the dominant presence of perennial grasses in the SR treatment may have slowed shrub recovery. Other authors have found that competition from perennial grasses limits shrub production (Ganskopp et al., 2004; Hedrick et al., 1966; Urness, 1981) and that livestock grazing of perennial grasses can shorten recovery periods for shrubs (Pechanec and Stewart, 1944; Ganskopp et al., 2004). In our study, plots were not grazed and the SR treatment had the highest cover of perennial grasses (Fig. 3).

Perennial forbs were not strongly influenced by treatment, while annual forbs were largely invariant to SR or PGR treatments and increased with complete removal. In our study, the annual forb functional group was dominated by the non-native pale alyssum and native fireweed, both of which have no reported value to wildlife or livestock species. Other forb genera (perennial and annual) in this study, including *Crepis*, *Collinsia*, *Astragalus* and *Agoseris* have been reported to be of importance in the diet of sagegrouse (*Centrocercus urophasianus*, Barnett and Crawford, 1994; Drut et al., 1994). Our work suggests that active restoration of forb species is not a management concern within the site and climatic conditions encountered in this study. Information on forb response to functional group removal is generally lacking in the literature but others have reported that forb diversity and abundance are invariant to fire (Fischer et al., 1996; Nelle et al., 2000). In contrast, Wroblewski and Kauffman (2003) found that crown volume of *Crepis* and *Astragalus* increased in the first growing season post-fire.

5. Conclusions

Our results can be used to guide and prioritize restoration activities in Wyoming big sagebrush communities. Consistent with our initial hypothesis, we found that post-disturbance functional group composition was strongly biased toward initial functional group dominance. Contrary to our expectations, exotic annual grasses did not increase with removal of perennial grasses alone, perhaps due to the relatively mesic nature of our study area and low initial seed availability for annual grasses. The fact that natural recovery of some functional groups occurred within a relatively short post-disturbance time interval (i.e. <10 years) underscores the need for practitioners to consider natural recovery of desired species before undertaking extensive restoration/rehabilitation projects. Our understanding of natural recovery could be significantly improved if practitioners monitored natural recovery rates in conjunction with restoration/rehabilitation efforts. Such monitoring does not have to be logistically taxing and could be as simple as leaving unseeded areas within larger re-seeding projects and conducting surveys of desired vegetation within seeded and non-

seeded areas. Our estimates of recovery time took place within the context of sufficient propagule availability from surrounding seed sources. In situations where propagule availability may be limited, our estimates should be considered conservative. Results from this study suggest that in some cases, successful restoration of shrubs or perennial grasses may benefit from targeted thinning of the opposing functional group (i.e. thin grasses to get shrubs and vice versa). In the case of shrub abundance, prior research has demonstrated the value of targeted grazing of bunchgrasses. Research aimed at determining the necessary magnitude (i.e. threshold) for such reductions could greatly enhance restoration efforts in sagebrush-bunchgrass plant communities. In low elevation sagebrush communities, reductions in competing perennial vegetation should be approached cautiously to avoid potential increases in exotic annual grasses. Additional research is needed to explore the influence of ecological site on natural recovery dynamics.

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