

RESEARCH ARTICLE

Plant Recruitment and Soil Microbial Characteristics of Rehabilitation Seedings Following Wildfire in Northern Utah

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Abstract

One goal of post-fire native species seeding is to increase plant community resistance to exotic weed invasions, yet few studies address the impacts of seeding on exotic annual establishment and persistence. In 2010 and 2011, we investigated the influence of seedings on exotic annuals and the underlying microbial communities. The wildfire site in northern Utah was formerly dominated by *Artemisia tridentata* ssp. *wyomingensis*, but burned in September 2008. Experimental seeding treatments were installed in November 2008 to examine strategies for establishing native species using two drills, hand broadcasts and different timing of seed applications (resulting in 13 seeding treatments). We collected aboveground biomass of invasive annuals (*Halogeton glomeratus*, *Salsola kali*, and *Bromus tectorum*), other volunteer plants from the extant seed bank, and seeded species from all treatments in the second and third years

after fire. We sampled soils within microsites beneath native perennial bunchgrass and exotic annuals to characterize underlying soil microbial communities. High precipitation following seeding led to strong seedling establishment and we found few differences between seeding treatments established with either drill. All seeded treatments reduced exotic biomass by at least 90% relative to unseeded controls. Soil microbial communities (phospholipid fatty acid analysis), beneath *B. tectorum*, *Poa secunda*, and *Pseudoroegneria spicata* microsites differed little 3 years after fire. However, microbial abundance beneath *P. spicata* increased from June to July, suggesting that microbial communities beneath successful seedings can vary greatly within a single growing season.

Key words: *Artemisia tridentata*, *Bromus tectorum*, Great Basin, minimum-till drill, phospholipid fatty acid analysis, PLFA, rangeland drill, *Salsola kali*.

Introduction

Altered wildfire regimes resulting from exotic plant invasions are powerful agents of vegetation change in semiarid and arid regions of Australia and the Western Hemisphere (D'Antonio & Vitousek 1992). Exotic annual grasses are particularly problematic as they augment fuel loads, recover rapidly post-fire and diminish community functioning and diversity (Balch et al. 2013). In semiarid landscapes of the Intermountain West, shortened fire return intervals resulting from invasions by *Bromus tectorum* L. (cheatgrass; Balch et al. 2013) drive *Artemisia tridentata* Nutt. (big sagebrush) communities to alternate states (Chambers et al. 2007) and hinder the reestablishment of native species (Eiswerth et al. 2009). Exotic annual forbs such as

Salsola kali L. (Russian thistle) can rapidly invade disturbed sites, are especially competitive during drought, and produce many seeds (Brandt & Rickard 1994). However, *S. kali* can facilitate native perennial grasses by creating favorable microenvironments (Allen & Allen 1988). *Halogeton glomeratus* (M. Bieb.) C.A. Mey. (halogeton), another ruderal species, can inhibit native species through elemental allelopathy (Morris et al. 2009) by increasing soil salinity (Duda et al. 2003). Both *S. kali* and *H. glomeratus* can initially invade and dominate disturbed *A. tridentata* sites, but may be replaced by *B. tectorum* (Piemeisel 1951). *Bromus tectorum* facultatively fall-germinates and its rapid growth (Mack & Pyke 1983) permits early access to soil moisture (Piemeisel 1951), and allows *B. tectorum* to respond to increases in nutrients more quickly than native perennial grasses (D'Antonio & Vitousek 1992; Vasquez et al. 2008), thereby limiting root density of native seedlings (Melgoza & Nowak 1991). Reestablishment of the native cover is especially difficult in the presence of exotic annuals (Eiswerth et al. 2009; Pyke et al. 2013).

Historically, post-fire seeding relied on exotic perennial grasses to rapidly return perennial vegetation to burned areas and stabilize soils following wildfire, in order to lower costs (Hardegree et al. 2012). However, use of native species on

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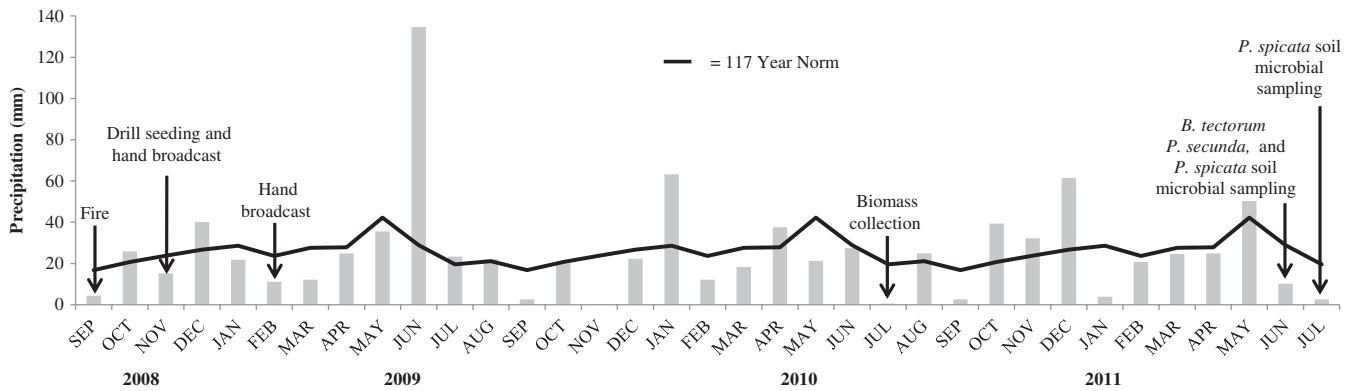


Figure 1. Monthly and long-term precipitation for the Scooby Fire site (WRCC 2012). Monthly data from Rosette, UT (1,735 m), located approximately 32 km west of the study site. The long-term norm (solid line) is the average from Rosette and Snowville, UT stations (1,396 m and 31 km northeast of the study site). Several months contain missing days. The dataset is available online at <http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?ut7408>. Last accessed August 2013.

post-wildfire sites is encouraged to maintain native genetic diversity, ecological integrity and to meet federal regulations on public lands, even though their effectiveness has been questioned (Pyke et al. 2013). Failures of native seedings have been attributed to adverse weather conditions (Chambers et al. 2007), use of maladapted seed sources (Kulpa & Leger 2013), inappropriate seeding methods (James & Svejcar 2010), and competition with exotics (Eiswerth et al. 2009). The efficacy of native seedings for excluding exotic annuals has received little documentation (Blank & Morgan 2012; Boyd & Davies 2012) and native seedings are generally less successful when exotic annuals are present (Eiswerth et al. 2009).

Links between establishment of perennial natives, exotic annuals, and soil microbial communities are seldom considered even though soil microorganisms are closely tied to plant communities via nutrient cycling and mutualistic and pathogenic associations (Wolfe & Klironomos 2005; Batten et al. 2006). The role of soil microbiota in facilitating or hindering exotic plants is ambiguous (Belnap & Phillips 2001; Wolfe & Klironomos 2005). For example, the exotic annual *H. glomeratus* may accumulate soil pathogens that hinder native species (Mangla et al. 2008).

Although soil microbial communities beneath exotic annuals should differ from those beneath native plants, rates of development are not clear. Soil microbes respond rapidly to root exudates and *B. tectorum* can alter soil communities within 3 years of invasion (Belnap & Phillips 2001). Long-term dominance of annual grass (50+ years) can shift abundance and richness of soil biota (Belnap et al. 2005). Additional shifts occur with wildfire (by damaging fungi, which are less heat resistant than bacteria; Dangi et al. 2010) and the impacts of soil disturbance by seed drills may also reduce fungi presence (Allison et al. 2005).

We investigated the impact of post-wildfire seedings on the presence of exotic annuals on an *A. tridentata* Nutt. ssp. *wyomingensis* Beetle & Young (Wyoming big sagebrush), site in northern Utah. We hypothesized that presence of exotic annuals (*B. tectorum*, *H. glomeratus*, and *S. kali*) would vary between drill types because of differences in soil disturbance.

We also hypothesized that soil microbial communities would differ within microsites beneath *Pseudoroegneria spicata* Á. Löve (bluebunch wheatgrass), *Poa secunda* J. Presl (Sandberg bluegrass), and the exotic annual *B. tectorum*. We anticipated that total soil microbial abundance should be greater under perennial bunchgrasses than under exotic annuals because perennial bunchgrasses allocate more resources to root development (Seabloom et al. 2003).

Methods

Study Site

The 2008 Scooby Fire site is located in the Wildcat Hills (41°51'16"N, 113°2'46"W), approximately 32 km southwest of Snowville, Utah in the Great Salt Lake Major Land Resource Area (028A; NRCS 2010). Elevation at the site ranges from 1,420 to 1,450 m on fan terraces and alluvial plains, with slope gradients of less than 5%. Annual air temperature means fluctuate between 7.2 and 10°C, the frost-free period ranges from 116 to 140 days, and annual precipitation varies from 200 to 300 mm (NRCS 2010). Precipitation data was gathered from Rosette, Utah, which is approximately 32 km west of the study site (1,735 m, Fig. 1). The area received above average precipitation in June 2009 after seeding. Xeric Haplocalcids (Hiko Peak, gravelly loam) and Xeric Torriorthents (Sheeprock, gravelly coarse sand) dominate the site located in Semidesert Gravelly Loam, ecological site R028AY215UT (NRCS 2010). Both soils are deep (≥ 60 cm) and well-to-excessively drained (Soil Survey Staff 2012). Current and historic land use patterns involve livestock grazing, and big game and sagebrush-obligate species such as *Centrocercus urophasianus* (greater sage-grouse) depend on the area for winter range (NRCS 2010).

In September 2008 a wildfire burned 1.54 km² of lands managed by the USDI Bureau of Land Management (BLM). Pre-burn vegetation at the site was dominated by *Artemisia tridentata* ssp. *wyomingensis*, *Poa secunda*, *Achnatherum hymenoides* (Roem. & Schult.) Barkworth (Indian ricegrass),

Table 1. Seeding treatments installed at the Scooby Fire rehabilitation site in 2008 (Shaw et al. 2011).

Drill	Drill Seed Mix Application	Broadcast Seed Mix Application (Sagebrush Rate) ^a	Treatment Symbol
No drill	No seed	No seed	C
Rangeland ^b	No seed	No seed	R0
	Drill	Drill (1x) ^a	R1x
	Drill	Drill (5x) ^a	R5x
	Drill	Drill (10x) ^a	R10x
	Drill	Hand broadcast, fall (5x)	RBC5x
	Drill	Hand broadcast, winter (5x)	RwBC5x
Minimum-till ^c	No seed	No seed	M0
	Drill	Drill (1x) ^a	M1x
	Drill	Drill (5x) ^a	M5x
	Drill	Drill (10x) ^a	M10x
	Drill	Hand broadcast, fall (5x)	MBC5x
	Drill	Hand broadcast, winter (5x)	MwBC5x

PLS = Purple live seed.

^a1x, 5x, and 10x *Artemisia tridentata* ssp. *wyomingensis* (Wyoming big sagebrush) seeding rates, 1x = 52 PLS/m². For total seed in each treatment see Table 2.

^bBroadcast seed planted through the drill was covered by dragging a chain behind the drill. Hand broadcast seed was not covered.

^cBroadcast seed was pressed into the soil surface with an imprinter unit. Hand broadcast seed was not covered.

Pseudoroegneria spicata, and *Elymus elymoides* (Raf.) Swezey (squirreltail; NRCS 2010) with some exotic annuals growing in the interspaces. Although the fire removed most of the site's vegetation and litter, a few isolated pockets remained.

Seeding Treatments

The study was conducted in 2010 and 2011 on research plots established in 2008 by Shaw et al. (2011) to investigate the response of (1) native grasses (both volunteer and seeded), (2) *Bromus tectorum*, (3) *Halogeton glomeratus*, (4) *Salsola kali*, (5) seeded forbs, and (6) other native nonseeded and exotic forbs to post-fire seeding treatments established by Shaw et al. (2011). Thirteen treatments were applied to 30-m by 70-m plots (52 plots within four blocks; Table 1). A 10-m buffer was seeded around all blocks and between plot rows (*A. hymenoides* and *P. spicata*) to reduce weed encroachment. Treatments included the use of a standard rangeland drill (P&F Services, Kemmerer, WY) or a minimum-till drill (Truax Co., Inc., New Hope, MN) to apply a large-seeded species mix, and either the two drills or hand broadcasting to apply a small-seeded species mix containing one of three rates of *A. tridentata* ssp. *wyomingensis* in November 2008 (Tables 1 and 2). More detailed seeding and vegetative outcomes are reported elsewhere (Shaw et al. 2011; Taylor et al. 2013). At the initiation of our study in 2010, seeded species provided 44% cover and did not vary among the seeded treatments. Three seeded bunchgrasses provided more than 90% of the relative cover: *P. spicata* (42.9%), *A. hymenoides* (27.9%), and *E. elymoides* (20.6%). None of the other seeded species provided more than 5% relative

cover. *Artemisia tridentata* ssp. *wyomingensis* relative cover was 0.07% and shrub density was 0.152 shrubs/m² across all seeded treatments. Three types of controls were included in the experimental design: (1) undrilled, unseeded, (2) rangeland drilled, unseeded, and (3) minimum-till drilled, unseeded. The latter two treatments simulated failed seedings.

Plant Aboveground Production Collections within Treatments

In July 2010, we initiated clipping to document biomass production. In each plot, we permanently established two 20-m long transects, 20 m apart and 10 m from the center of the longest dimension and perpendicular to the drill rows. We collected aboveground herbaceous biomass samples from two quadrats (0.25 m²) that were placed at randomly selected points 2 m away from, and on the southeast side of the transects (a total of four quadrats per plot). Sampling in 2011 was identical except that we avoided areas clipped in 2010. Within each quadrat, we clipped biomass to 2.5 cm above ground and separated it into groups. The exotic annual grass *B. tectorum* (the only nonseeded grass species found in the plots) was clipped separately. All native grasses were clipped as a group and were not separated by species, because they were very tightly inter-mixed within the drill rows. The exotic annual forbs *H. glomeratus* and *S. kali*, and the four seeded forbs, were clipped by species. Remaining forbs, a mix of other exotic and native nonseeded species, were clipped as a group and designated as "other" forbs. A few *Achillea millefolium* L. var. *occidentalis* DC. (western yarrow) were found in control plots in 2011 (4.6 g/m² in R0 plots) and although clipped by species were ultimately combined with "other forbs" as they were not seeded into the controls. Plant materials were oven-dried at 60°C for 48 hours, and dry biomass was recorded to the nearest 0.01 g. When samples weighed less than 0.01 g, even though biomass was present, we recorded 0.01 g to denote the presence of that species or plant group.

Soil Microsite Collections

In June and July 2011, we collected soil samples for phospholipid fatty acid (PLFA) analysis of microbial communities. We targeted three vegetative microsites: *P. secunda* and *B. tectorum* sampled in June, and *P. spicata* sampled in June and July. We used 0.2 m² circular plots surrounding each targeted plant for soil collection within 5 of 13 treatments (C, R0, M0, R5x, and M5x; Table 1). Selected microsites were dominated by the target species (50% or greater cover). Five *P. secunda* and five *B. tectorum* microsite samples were retrieved within each of the five treatment plots in each of the four blocks. *Pseudoroegneria spicata* microsites were sampled in June (40 samples) and July (40 samples) in only the R5x and M5x treatments with five samples taken from the two treatments in each of the four blocks (totaling 280 samples from all microsites). Approximately 15 g of soil was collected from 0–5 cm below the litter layer and within the rooting zone of the targeted grass. In some cases, *B. tectorum* was present in *P. secunda* microsites, but we selected sites that minimized its presence. One *B. tectorum* microsite contained a small amount of *P. secunda* (0.44 g) and four microsites

Table 2. Species seeded at the Scooby Fire rehabilitation site in northern Utah in 2009.

Scooby Seed Mix Species	Seeding Rate (PLS/m ²)		
	1x	5x	10x
Broadcast mix			
<i>Artemisia tridentata</i> ssp. <i>wyomingensis</i> (Wyoming big sagebrush)	52	234	495
<i>Ericameria nauseosa</i> (Rubber rabbitbrush)	86	86	86
<i>Poa secunda</i> (Sandberg bluegrass Mt. Home Germplasm)	91	91	91
<i>Achillea millefolium</i> var. <i>occidentalis</i> (Western yarrow Eagle Germplasm)	100	100	100
<i>Penstemon cyaneus</i> (Blue penstemon)	76	76	76
Total broadcast	405	587	848
Drill mix			
<i>Pseudoroegneria spicata</i> (Bluebunch wheatgrass Anatone Germplasm)	67	67	67
<i>Achnatherum hymenoides</i> ('Rimrock' Indian ricegrass)	51	51	51
<i>Elymus elymoides</i> (Squirreltail Toe Jam Creek Germplasm)	47	47	47
<i>Sphaeralcea munroana</i> (Munro's globemallow)	93	93	93
<i>Eriogonum umbellatum</i> (Sulphur-flower buckwheat)	11	11	11
Total drill	269	269	269
Total broadcast + drill	674	856	1,117

(*B. tectorum* M5x, *B. tectorum* R0, and two *P. secunda* R5x) contained small amounts of *A. millefolium* (<0.4 g). Soil samples were stored in sealed plastic bags placed on dry ice immediately after collection, then moved to a -20°C freezer at the University of Wyoming Soil Testing Laboratory until analyzed. Gravimetric soil water content was determined using the same soil collected for microbial community analysis by weighing soil before and after lyophilization. Separate soil samples (physiochemical samples) for documenting pH, electrical conductivity (EC), and texture were collected adjacent to soil microbial sampling areas within *B. tectorum* and *P. secunda* microsites. Approximately 150 g of soil was collected below the litter layer to a 5 cm depth within the rooting zone of each targeted grass in all five treatments and four replicate blocks (200 samples). Samples were allowed to air dry before being passed through a 2 mm sieve. Soils were hand-textured and analyzed for pH and EC at the University of Wyoming Soil Testing Laboratory.

Aboveground Plant Production within Microsites

After collecting soil for microbial community, pH, EC, and texture analyses, we clipped all biomass at 2.5 cm above ground within the 0.2 m² circular microsite (three of five *B. tectorum* and *P. secunda* microsites in five treatments and four blocks). *Poa secunda* (both volunteer and seeded) was clipped and bagged together. All volunteer annuals were clipped and bagged as a group. Plant materials were oven-dried at 60°C for 48 hours and dry weight recorded to the nearest 0.01 g. Very small samples (<0.01 g) were recorded as 0.01 g to denote presence of that species or plant group.

Experimental Design and Statistical Analysis

Plant Aboveground Production within Treatments

Biomass data (total, species groups, and exotic annual species) were analyzed as a randomized complete block design with four

blocks using a repeated measures (sampling year) analysis of variance (ANOVA) with JMP 10 software (SAS Institute Inc. 2012). Biomass from four quadrats in each plot was summed as g/m². Standard errors of means for each species or plant group were calculated using the four replicate blocks. When the year by treatment interaction term was significant for a species or plant group, we ran ANOVAs separately by year. Mean separation of total biomass was calculated using least significant difference (LSD). Biomass within all seeded rangeland drill treatments was combined, as was biomass collected within all seeded minimum-till drill treatments, separating the three controls for analysis using linear contrasts to compare the two drills across years. Mean separation for individual species and species groups was calculated only when treatments differed using linear contrasts to compare treatments within a drill type. We tested for sphericity and when violated, weighted the mixed model to assess impacts of unequal variances on our results. In no case did weights alter the significance of the original ANOVAs; thus, nonweighted results are presented here.

Microbial Community Analysis

Soil microbial community analysis was conducted using a modified Bligh–Dyer PLFA extraction assay (Buyer et al. 2002), which estimates the relative biomass of several microbial taxonomic groups present in the soil. We extracted fatty acids from 5 g of lyophilized, sieved (2 mm) soil using a chloroform:methanol:phosphate buffer (1:2:0.8) solvent. Phospholipids were separated from the neutral lipids and glycolipids through chromatography, subjected to mild alkaline methanolysis, and analyzed on a gas chromatograph (Agilent 6890, Agilent Technologies, Palo Alto, CA, U.S.A.) using Sherlock software (MIDI, Inc., Newark, NJ, U.S.A.). Soil microbial groups (% of total) were converted into µg fatty acid/g soil using the response of the 20:0 EE internal standard. Individual PLFA signatures were assigned to the following taxonomic groups through the use of recognized biomarkers: Gram-negative bacteria,

Gram-positive bacteria, arbuscular mycorrhizal (AM) fungi, non-AM fungi, protozoans, and total bacteria (sum of Gram- and Gram+ bacteria). We also calculated the fungi:bacteria ratio (F:B), a commonly reported indicator.

Plant Aboveground Production within Microsites

Plant biomass within the two microsites (*P. secunda* and *B. tectorum*) was summed within treatment yielding g/m² values. Plant biomass within each microsite was grouped as either volunteer annuals (primarily *B. tectorum* and the non-native forb *Sisymbrium altissimum* L., tall tumblemustard) or *P. secunda*, and analyzed using an ANOVA for a randomized complete block design. Because volunteer annuals could not be eliminated from *P. secunda* microsites, we also analyzed biomass in *P. secunda* microsites with a mixed model analysis of covariance (ANCOVA), using volunteer annuals as a covariate. In no case did the covariates alter significance, thus results from the ANOVAs are reported here. We report LSD mean separation and standard errors of means from the four replicates.

Results

Aboveground Production

In 2010, total biomass did not differ among the 13 treatments ($p = 0.0957$) and ranged from 122 g/m² (C) to 247 g/m² (R10x). In 2011, production was less in the three controls ($p = 0.0054$) than in the seeded treatments with the exception of the RBC5x, M10x, and MwBC5x treatments, which were intermediate (Fig. 2).

When combined by drill type (rangeland or minimum-till), native grass production (seeded and volunteer) was greater in drilled treatments than in any of the unseeded controls (Fig. 3a; $p = 0.0032$). Native grass production, when averaged across all treatments to evaluate the effect of year, increased ($p = 0.0239$) from 2010 to 2011 (125 to 157.1 g/m²). Other native non-seeded and exotic forbs, primarily the non-native forb *Sisymbrium altissimum*, were more productive in the controls (Fig. 3b; $p = 0.0395$) and least in the seeded rangeland and minimum-till drill treatments. Among the three controls, other forb production was greatest in the R0 and least in the C; the M0 was intermediate and did not differ from the R0 or the C. Seeded forbs, both drilled and broadcast, contributed little to total biomass production in 2010 and 2011, and did not differ among seeded treatments or controls ($p = 0.0672$), or between years ($p = 0.1373$; data not shown). Averaged across both years, seeded forbs produced 14.2 g/m² in rangeland drill seeded treatments and 19 g/m² in minimum-till drill seeded treatments.

Targeted Exotic Annuals

The three exotic annuals (combined biomass of *Bromus tectorum*, *Salsola kali*, and *Halogeton glomeratus*) produced the most biomass in the controls ($p = 0.0006$) and the least in the seeded treatments when averaged across years (Fig. 3c). In 2010, *B. tectorum* production was greatest in the undrilled

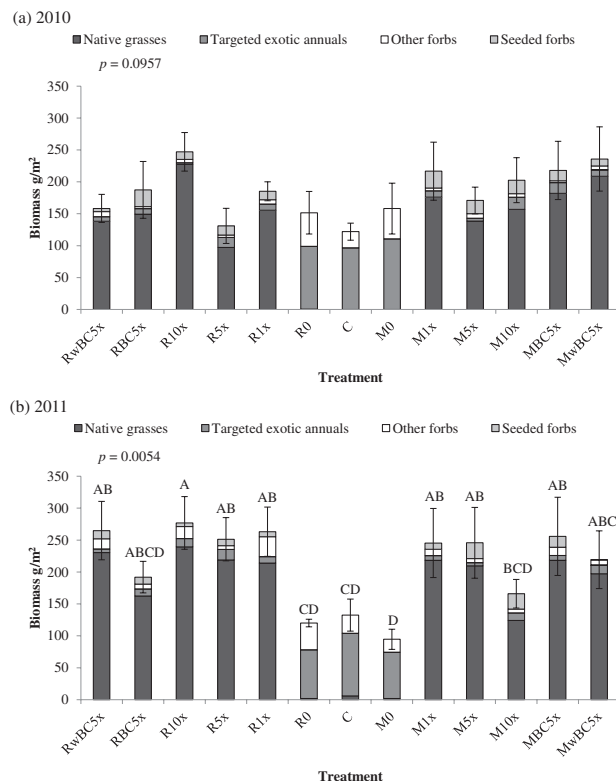


Figure 2. Aboveground production by plant groups for 13 treatments in July 2010 (a) and 2011 (b). Bars are standard errors of means for cumulative biomass. Treatment applications and seeding rates are detailed in Tables 1 and 2. Means with the same letter do not differ ($p > 0.05$, LSD).

control (C) and the M0, and least in the R0 and all seeded treatments ($p < 0.0001$; Fig. 4a). In 2011, *B. tectorum* increased across all treatments irrespective of drill type; its biomass was greatest in unseeded treatments and least in seeded treatments ($p < 0.0001$). *Salsola kali* differed among the treatments only in 2010 ($p < 0.0001$; Fig. 4b), when it was more productive in unseeded, drilled controls (R0 and M0) than in the unseeded and undrilled control (C), or any of the seeded treatments. In 2011, *S. kali* was nearly absent from the study plots and did not differ among the treatments. *Halogeton glomeratus* production was greater in 2010 (11 g/m²; $p = 0.0013$; Fig. 4c) than in 2011 (0.02 g/m²) across all treatments, and was the least productive of the three exotic annuals in 2011.

Soil Microsite Study

Aboveground Plant Biomass within Microsites

Volunteer annual biomass (*Sisymbrium altissimum* and *Bromus tectorum*) within *B. tectorum* microsites was most productive in C and M0 treatments and least in the R0 and seeded (R5x and M5x) treatments ($p = 0.0023$). Volunteer annuals collected from *Poa secunda* microsites followed a similar trend, and were most abundant in the control and M0 treatments ($p = 0.0003$). Within *P. secunda* microsites, *P. secunda* production was similar across all treatments ($p = 0.2824$).

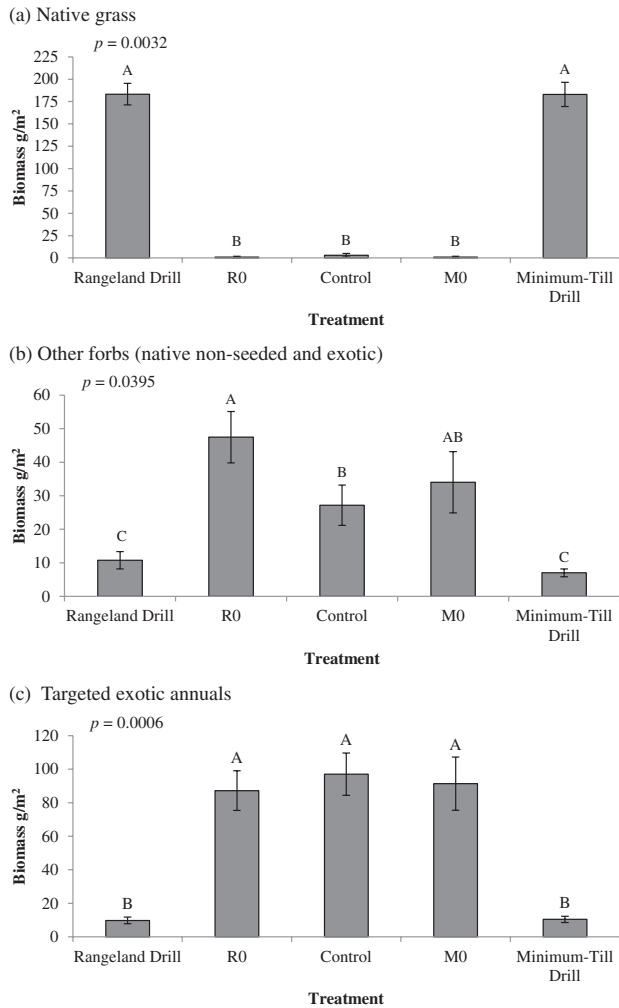


Figure 3. Production of native grasses, other native nonseeded and exotic forbs, and targeted exotic annuals in seeded and control treatments averaged across 2 years (2010 and 2011). Unseeded treatments include the control (C, no drill and unseeded), drilled with rangeland drill and unseeded (R0) and drilled with minimum-till drill and unseeded (M0; see Table 1). The drill seeded treatments (rangeland drill and minimum-till drill) are combinations of the five seeding treatments described in Table 1. Bars are standard errors of means. Within each plant group, means with the same letters do not differ ($p > 0.05$, LSMeans Contrast).

Soil Physiochemical Properties

Soil physical and chemical properties were similar across microsites and treatments. Soil textures were sandy loam or loamy sand with 12% clay, 7.7 pH, and 0.73 EC (ds/m). Soils sampled in June under *P. spicata* contained less water than soils collected from *B. tectorum* and *P. secunda* microsites ($p < 0.0001$). Soil water within *P. spicata* microsites decreased from June to July ($p = 0.0088$).

Soil Microbial Community

Microbial biomass in soils collected in June beneath *B. tectorum*, *P. secunda*, and *P. spicata* microsites did not differ

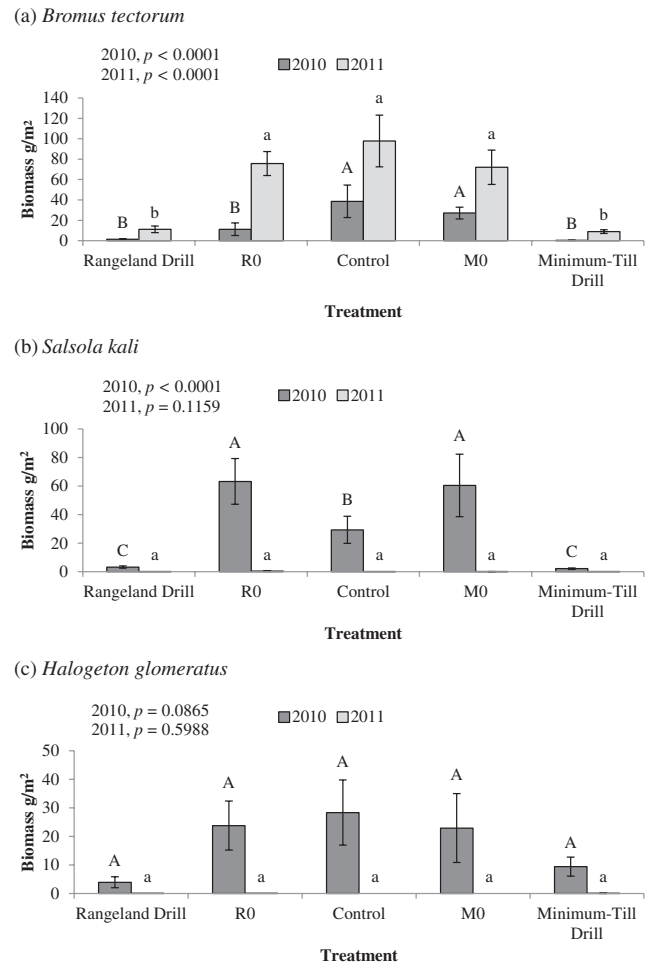


Figure 4. Production of *Bromus tectorum*, *Salsola kali*, and *Halogeton glomeratus* in rangeland and minimum-till drill seeded treatments and controls (C, R0, and M0) in July 2010 and 2011. Treatment applications and seeding rates are detailed in Tables 1 and 2. Bars are standard errors of means. Upper case letters separate 2010 means and lower case letters separate 2011 means within a species (LSMeans Contrast at $p = 0.05$).

among plant species or treatments. The F:B ratio and abundance of all soil microbial components (μg fatty acid/g soil of Gram+ bacteria, Gram- bacteria, AMF, and protozoans) were similar across all three grass microsites and treatments (Fig. 5). When *P. secunda* and *B. tectorum* microsites were compared, non-AM fungi differed in the M0 control; *P. secunda* microsites contained more fungal biomass than *B. tectorum* microsites ($p = 0.0404$; Fig. 5c). Among the *P. spicata* microsites sampled in both June and July, soil microbial communities differed between months. Microbial biomass in R5x and M5x treatments was lower in June than in July ($p = 0.0002$; Fig. 6). Gram positive ($p = 0.0057$) and Gram negative ($p = 0.0011$) bacteria, fungi ($p = 0.0224$), AMF ($p = 0.0205$), and protozoans ($p = 0.0118$) were all less abundant in June than in July within *P. spicata* microsites (Fig. 6). However, the F:B ratio did not change significantly from June to July (Fig. 6h).

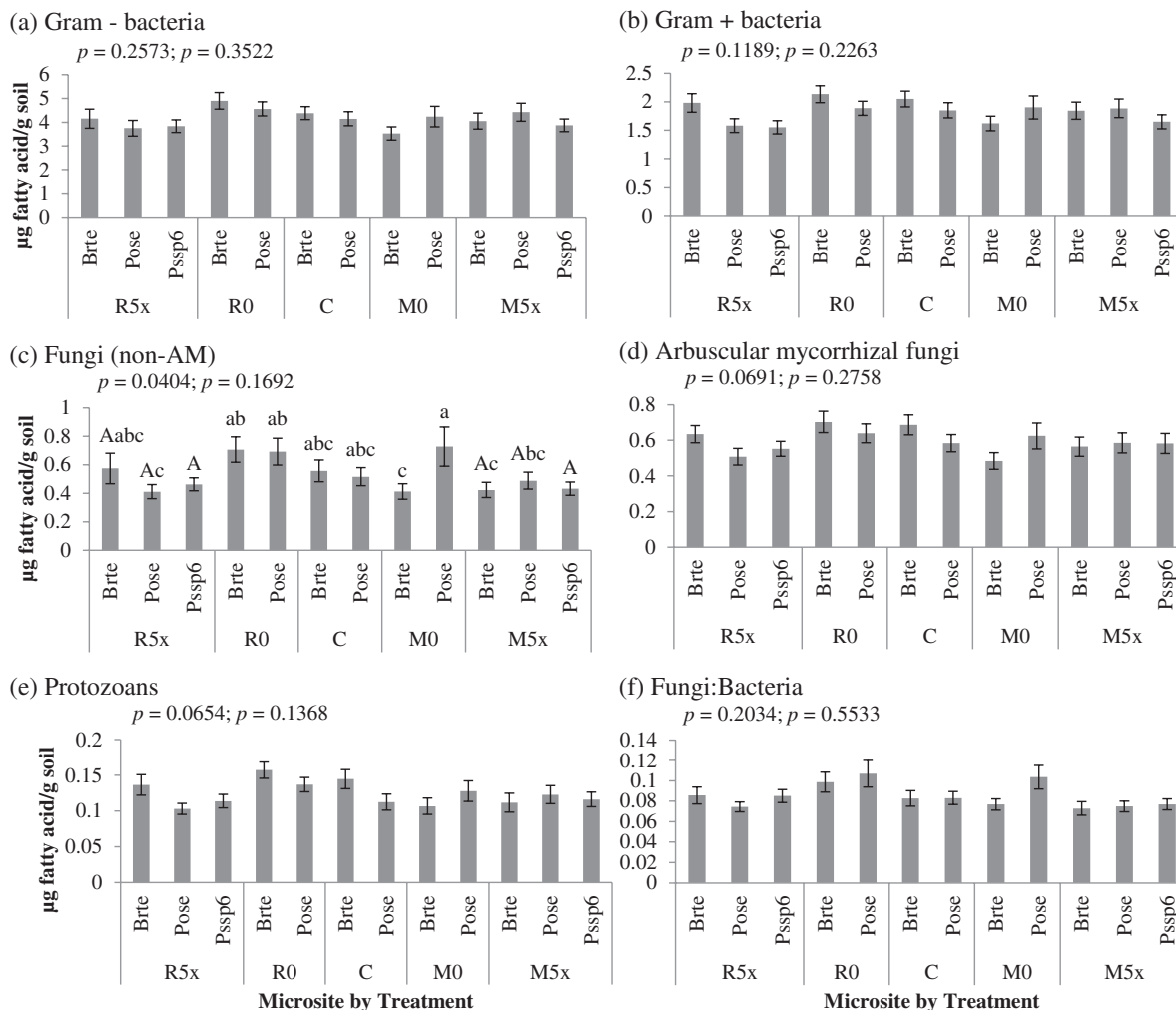


Figure 5. Soil microbial content in three microsites across five seeding treatments. Microsites are *Bromus tectorum* ($n = 100$), *Poa secunda* ($n = 100$), and *Pseudoroegneria spicata* ($n = 80$). Probability values (p) represent comparison across five treatments by microsite interaction (first value) and comparison of only the two seeded treatments (R5x and M5x) by microsite interaction (second value). *Pseudoroegneria spicata* was sampled only in R5x and M5x treatments, in both June and July (see Fig. 6). Treatment applications and seeding rates are described in Tables 1 and 2. Bars are standard errors of the means. Means with the same letter do not differ ($p > 0.05$, LSD). Upper case letters compare three microsites; lower case letters compare *B. tectorum* and *P. secunda* microsites only.

Discussion

Our results support the findings of others (Thompson et al. 2006; Boyd & Davies 2012), who demonstrate that native species can reduce dominance of exotic annuals following wild-fire. At our study site, dominance of *Bromus tectorum* in the controls suggests that rehabilitation seeding provided resistance to exotics. Similar results have been reported in this system (Blank & Morgan 2012) and in other semi-arid and arid systems where exotic annual grasses occur (Seabloom et al. 2003; Davies 2010). Our results support the efficacy of native seeding in limiting exotic annuals, even though the strong establishment of seeded species on our site may have been enhanced by above-average precipitation. We found few differences in native production between drills, but drill and treatment differences may be more pronounced in drier conditions.

Failed rehabilitation seedings are common in the Great Basin. In our study, drilling alone initially enhanced the presence of *Salsola kali* in the first year, but the effect was short-lived. *Bromus tectorum* superseded *S. kali* in the second year. *Salsola kali* responded favorably to soil disturbance as demonstrated elsewhere (Brandt & Rickard 1994). The delayed entry of *B. tectorum* in drilled but nonseeded treatments is not apparent but may be related to initially low levels of *B. tectorum* on the study site.

While invasive annuals may alter soil microbial communities through litter deposition, root exudation, and altered nutrient availability (Batten et al. 2006), few studies record soil microbial communities over time to clarify the rate of soil microbial shifts associated with invasion (Wolfe & Klironomos 2005). Belnap and Phillips (2001) compared recent *B. tectorum* invasions (2–3 years) with 50-year-old invasions on unburned sites

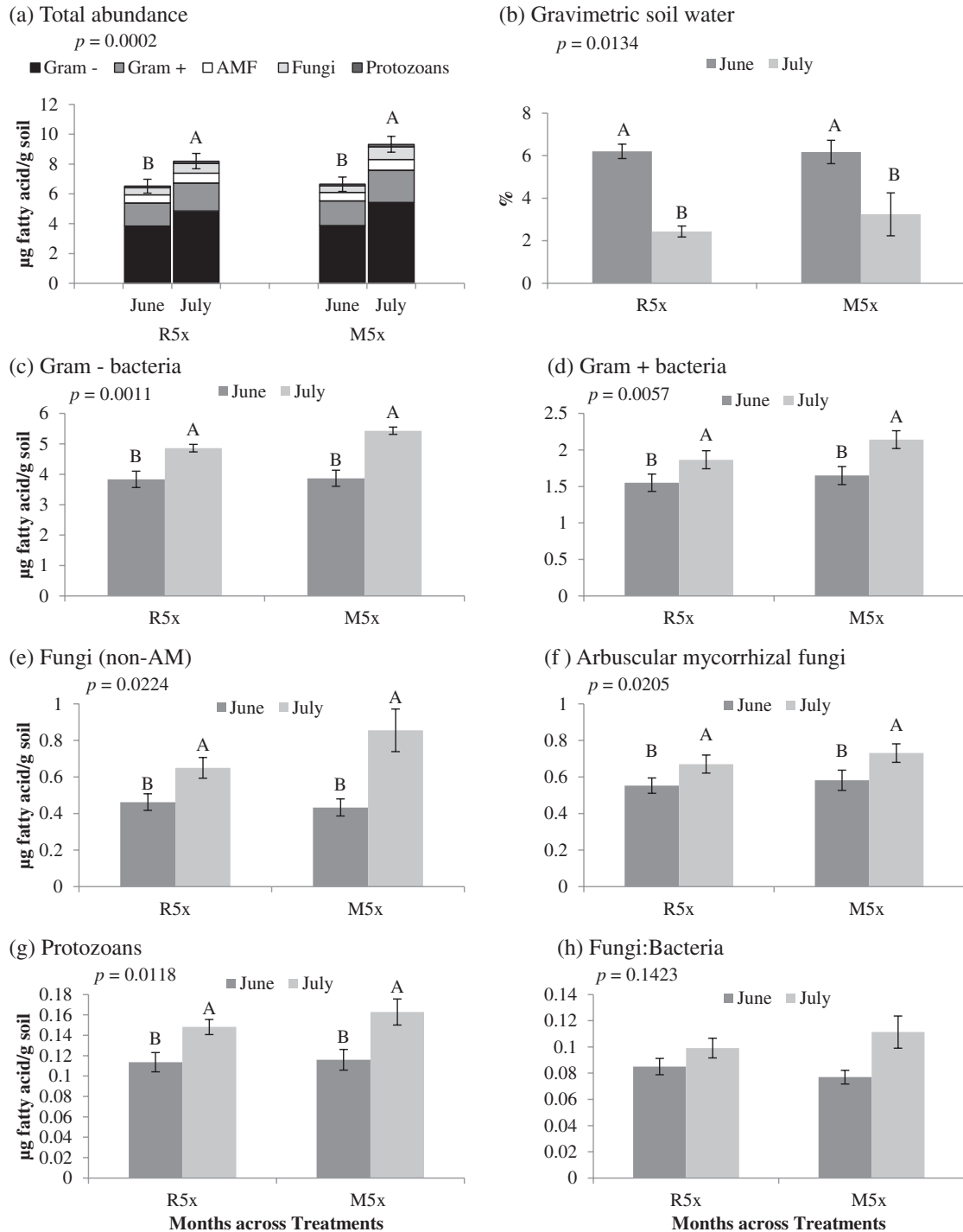


Figure 6. Soil microbial and moisture content in *Pseudoroegneria spicata* microsites in the R5x and M5x seeded treatments ($n = 80$) in June and July 2011. Seeding treatments and seeding rates are detailed in Tables 1 and 2. Bars are standard errors of means. Within each microbial taxonomic group, means with the same letter do not differ ($p > 0.05$, LSD). F -test probabilities (p values) are reported for the effect of month.

in Utah. They documented decreased species richness, fewer fungi, but similar bacteria and fungi species on recently invaded sites relative to older invasions (Belnap & Phillips 2001). Rowe and Brown (2008) propose that microbial communities do not facilitate *B. tectorum* and our results record no clear patterns in

soil conditioning beneath *B. tectorum* relative to native seeded species 3 years after seeding.

Other research suggests that soil biotic communities in mature stands of *Artemisia tridentata* are dominated by fungi, and that full recovery of the microbial community following fire

can take 3–7 years (Dangi et al. 2010). On our site, the F:B ratio was much lower than those documented in undisturbed stands of *A. tridentata* (Mummey et al. 2002). Slight shifts in non-AM fungi at our site suggest that species-specific microbial communities may eventually develop. Within-season increases in microbial abundance beneath *Pseudoroegneria spicata* despite low soil moisture suggest that water extraction by robust perennial grasses may have dried drill row soils and contributed to root turnover that stimulated microbial activity (Cotrufo et al. 2011). Because soil biota beneath drill rows varied temporally, microbial communities should be sampled often within a growing season to more clearly understand soil biotic development.

Implications for Practice

- Seeded native bunchgrasses can limit return of exotic annuals such as *Bromus tectorum*, *Salsola kali*, and *Halogeton glomeratus* for 3 years after wildfire.
- In years of favorable precipitation when wildfire rehabilitation seedings establish well, type of drill seems to have little influence on the presence of exotic annuals.
- Soil biota vary greatly within-season beneath *Pseudoroegneria spicata*, making it critical to collect repeated within-season samples to adequately characterize soil biotic communities.

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