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Taylor, Megan, M., Exotic, native and seeded species and soil biotic community response to post-fire seedings in northern Utah, M.S., Department of Ecosystem Science and Management, May 2013.

Post-fire seeding of native species is intended to reduce weed entry, yet few studies have addressed the impacts of seeding methods on the establishment and persistence of exotic annuals. In summers of 2010 and 2011, we investigated productivity of exotic annuals across rehabilitation seedings that were established on the Scooby Wildfire site in northern Utah. The site, which was formerly dominated by *Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young (Wyoming big sagebrush), burned in September 2008. Experimental treatments were applied in November 2008 and February 2009 to compare rangeland drill and minimum-till drill seedings of native grasses, forbs, and shrubs. We sampled soils under native perennial bunchgrass and associated exotic annuals to characterize soil physical, chemical, and biological properties three years after wildfire and rehabilitation seeding. We also collected aboveground biomass samples of invasive annual species (*Halogeton glomeratus* (M. Bieb.) C.A. Mey. [halogeton], *Salsola kali* L. [Russian thistle], and *Bromus tectorum* L. [cheatgrass]), volunteer (plants that established after the fire from the extant seed bank) and seeded native grasses, native and exotic volunteer forbs (excluding the three mentioned above), and seeded native forbs in four replicate blocks of 13 seeding treatments two and three years post-fire. Three years after seeding, production within the documented plant groups (excluding shrubs) did not differ between the two drill types. Rehabilitation seeding limited the biomass of annual exotics in both years, demonstrating that seeding with native species can effectively curtail the productivity of exotic annuals. We documented minor drill differences because of above-average precipitation received the spring following rehabilitation seeding which resulted in high native seeded species establishment. Different

results might be expected during years of less favorable precipitation. We did not detect differences in soil microbial communities among plant microsites three years after wildfire, but within the same microsite temporal changes in microbial abundance were documented. Individual plant species may influence microbial communities over time and trends in microbial communities should be monitored regularly and over longer time periods than are often reported.

EXOTIC, NATIVE AND SEEDED SPECIES AND SOIL BIOTIC COMMUNITY RESPONSE TO POST-FIRE SEEDINGS IN NORTHERN UTAH

By

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CHAPTER I

Introduction

The sagebrush ecosystem is one of the most imperiled in the United States (Noss et al. 1995; Davies et al. 2011). Once occupying over 620,000 km^2 in the western United States and southwestern Canada (McArthur & Plummer 1978; West & Young 2000; Davies et al. 2011), it currently covers only 56% of its historic range (Knick et al. 2003; Davies et al. 2011). Several threats have degraded sagebrush ecosystems in the Great Basin, including: livestock overgrazing, agricultural conversion, urbanization, energy development, mineral extraction, climate change, conifer encroachment, exotic annual grass and forb invasion, and altered fire regimes (McArthur & Goodrich 2004; Pellant et al. 2004; Bradley 2010; Rowland et al. 2010; Davies et al. 2011).

Invasion by exotic annuals has changed the character of sagebrush-perennial bunchgrass communities in the Great Basin. *Bromus tectorum* L. (Poaceae, cheatgrass), *Salsola kali* L. (Chenopodiaceae, Russian thistle), and *Halogeton glomeratus* (M. Bieb.) C.A. Mey. (Chenopodiaceae, halogeton) are ruderal species that can rapidly colonize disturbed sites, potentially preempting establishment by native species. *Salsola kali* may expedite revegetation success on disturbed sites by acting as a nurse plant for native seedlings (protection from the wind and retaining snow [Allen & Allen 1988; Howard 1992]). However, *S. kali* is successional to *B. tectorum* and its litter deposits can create microenvironments favorable to *B. tectorum* germination and establishment (Piemeisel 1951; Evans & Young 1983).

Bromus tectorum produces fine fuels which can reduce fire return intervals and increase fire intensity, resulting in the replacement of native plant communities by near monotypic stands of invasive species (Young et al. 1987; D'Antonio & Vitousek 1992; Knapp 1996; Brooks &

Chambers 2011). Additionally, *B. tectorum, S. kali*, and *H. glomeratus* are prolific seed producers and quickly generate large seed banks, allowing these species to maintain stable populations in arid and semiarid environments (Hassan & West 1986; Brandt & Rickard 1994; West & Young 2000; Kitchen & Jorgensen 2001).

While the consequences of exotic plant invasion on the aboveground plant community are well documented (Mack 2011; Vilà et al. 2011), the impacts of exotics on soil microbial communities and soil physiochemical properties escape generalization. Changes in fire regimes, root exudation, root turnover and decomposition, and the quantity and quality of litter inputs associated with exotic invasion may alter soil rhizosphere environments (Eckert & Kinsinger 1960; Harper et al. 1996; Belnap & Phillips 2001; Duda et al. 2003; Blank & Morgan 2011). Both *H. glomeratus* and *S. kali* increase soil surface salinity by incorporating sodium from the soil profile in plant tissues which is then leached into the soil from litter after senescence (Harper et al. 1996; Duda et al. 2003). Soil salinization is linked to the inhibition of microbial activity (Eckert & Kinsinger 1960). *Halogeton glomeratus* may also increase pH, exchangeable sodium, and electrical conductivity (Duda et al. 2003) and can accumulate pathogenic fungi within its rhizosphere that are fatal to native seedlings (Harper et al. 1996). *Bromus tectorum* may influence nitrogen availability (Blank & Morgan 2011), disrupt soil food webs, decrease populations of soil fungi, and lower microbial species diversity (Belnap & Phillips 2001). However, the temporal rate of impact on soil biology and whether exotic annual-associated microbial communities promote invasion and inhibit the successful establishment of native species is unclear (Belnap & Phillips 2001; Wolfe & Klironomos 2005; Batten et al. 2006).

Preventing the spread of exotic annuals and reinstating historic fire regimes are integral to the conservation of sagebrush communities. One method to curtail invasion by exotic annuals

is to revegetate wildfire-impacted sites. However, wildfire rehabilitation is difficult in areas of sporadic precipitation (Chambers et al. 2007). Restoration of low- to mid-elevation (800 to 2200 m), xeric sagebrush communities has often met with failure because of improper seed bed preparation and inadequate seeding technology (James & Svejcar 2010), and competition with exotics annuals (Eiswerth et al. 2009). In addition, rehabilitation failure can occur because of herbivory, disease, other disturbances, and lapses in post-fire seeding management (Monsen & Stevens 2004).

We examined an *Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young (Asteraceae, Wyoming big sagebrush) site in northern Utah that burned in September 2008. We investigated the impact of native seeding on productivity of 1) seeded forbs; 2) native and exotic volunteer (plants that established after the fire from the extant seed bank) forbs; 3) native grasses (both volunteer and seeded); 4) *B. tectorum*; 5) *H. glomeratus*; and 6) *S. kali* two and three years following wildfire. We also characterized the structure of soil microbial communities associated with two native perennial bunchgrasses, *Pseudoroegneria spicata* (Pursh) Á. Löve (bluebunch wheatgrass) and *Poa secunda* J. Presl (Sandberg bluegrass), and associated annual exotics (*B. tectorum* and *H. glomeratus*). We asked: 1) How does seeding methodology influence productivity of native speeded species, volunteer native and exotic forbs, and volunteer *B. tectorum*, *S. kali*, and *H. glomeratus*? 2) How do soil physical, chemical, and biological properties differ under native perennial bunchgrasses and exotic annual grasses? 3) How quickly do soil physical, chemical, and biological properties change within one growing season? and 4) What is the relationship of aboveground biomass production to belowground microbial production?

Aboveground production of native seeded species and native and exotic volunteer species in seeding treatments is presented in Chapter II. Chapter III characterizes soil physical and chemical properties and microbial communities under native grass, exotic grass, and exotic forb microsites within a subset of the seeding treatments. Conclusions, research implications, and management considerations are discussed in Chapter IV.

LITERATURE CITED

Allen, E. B., and M. F. Allen. 1988. Facilitation of succession by the nonmycotrophic colonizer *Salsola kali* (Chenopodiaceae) on a harsh site: effects of mycorrhizal fungi. American Journal of Botany **75**:257-266.

Batten, K. M., K. M. Scow, K. F. Davies, and S. P. Harrison. 2006. Two invasive plants alter soil microbial community composition in serpentine grasslands. Biological Invasions **8**:217-230.

Belnap, J., and S. L. Phillips. 2001. Soil biota in an ungrazed grassland: response to annual grass (*Bromus tectorum*) invasion. Ecological Applications **11**:1261-1275.

Blank, R. R., and T. Morgan. 2011. Evidence that invasion by cheatgrass alters soil nitrogen availability. Natural Resources and Environmental Issues **17**:1-4.

Bradley, B. A. 2010. Assessing ecosystem threats from global and regional change: hierarchical modeling of risk to sagebrush ecosystems from climate change, land use and invasive species in Nevada, USA. Ecography **33**:198-208.

Brandt, C. A., and W. H. Rickard. 1994. Alien taxa in the North American shrub-steppe four decades after cessation of livestock grazing and cultivation agriculture. Biological Conservation **68**:95-105.

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

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

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

Davies, K. W., C. S. Boyd, J. L. Beck, J. D. Bates, T. J. Svejcar, and M. A. Gregg. 2011. Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush plant communities. Biological Conservation **144**:2573-2584.

Duda, J. J., D. C. Freeman, J. M. Emlen, J. Belnap, S. G. Kitchen, J. C. Zak, E. Sobek, M. Tracy, and J. Montante. 2003. Differences in native soil ecology associated with invasion of the exotic annual chenopod, *Halogeton glomeratus*. Biology and Fertility of Soils **38**:72-77.

Eckert, R. E. Jr., and F. E. Kinsinger. 1960. Effects of *Halogeton glomeratus* leachate on chemical and physical characteristics of soils. Ecology **41**:764-772.

Eiswerth, M. E., K. Krauter, S. R. Swanson, and M. Zielinski. 2009. Post-fire seeding on Wyoming big sagebrush ecological sites: regression analyses of seeded nonnative and native species densities. Journal of Environmental Management **90**:1320-1325.

Evans, R. A., and J. A. Young. 1983. Microsite requirements for downy brome (*Bromus tectorum*) infestation and control on sagebrush rangelands. Weed Science **32**:13-17.

Harper, K. T., R. Van Buren, and S. G. Kitchen. 1996. Invasion of alien annuals and ecological consequences in salt desert shrublands of western Utah. Pages 58-65 in J. R. Barrow, E. D. McArthur, R. E. Sorebee, and R. J. Tausch, editors. Proceedings. Symposium on shrubland ecosystem dynamics in a changing climate. INT-GTR-319. U.S. Department of Agriculture, Forest Service, Ogden, Utah.

Hassan, M. A., and N. E. West. 1986. Dynamics of soil seed pools in burned and unburned sagebrush semi-deserts. Ecology **67**:269-272.

Howard, J. L. 1992. *Salsola kali*. Fire Effects Information System. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Missoula, Montana. (available from http://www.fs.fed.us/database/feis/).

James, J. J., and T. Svejcar. 2010. Limitations to postfire seedling establishment: the role of seeding technology, water availability, and invasive plant abundance. Rangeland Ecology and Management **63:**491-495.

Kitchen, S. G., and G. L. Jorgensen. 2001. Winterfat decline and halogeton spread in the Great Basin. Pages 200-203 in E.D. McArthur, and D. J. Fairbanks, compilers. 2001. Shrubland ecosystem genetics and biodiversity: proceedings. RMRS-P-21. U.S. Department of Agriculture, Forest Service, Fort Collins, Colorado.

Knapp, P. A. 1996. Cheatgrass (*Bromus tectorum* L.) dominance in the Great Basin desert: history, persistence, and influences to human activities. Global Environmental Change **6**:37-52.

Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. V. Riper. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. The Condor **105**:611–634.

Mack, R. N. 2011. Fifty years of "Waging war on cheatgrass": research advances, while meaningful control languishes. Pages 253-265 in D. Richardson, editor. Fifty years of invasion ecology. Wiley-Blackwell Press, Oxford, United Kingdom.

McArthur, E. D., and A. P. Plummer. 1978. Biogeography and management of western native shrubs: a case study, section Tridentatae of *Artemisia*. Great Basin Naturalist Memoirs **2**:229-243.

McArthur, E. D., and S. K. Goodrich. 2004. Chapter 2. The Intermountain setting. Pages 7-14 in S. B. Monsen, R. Stevens, and N. L. Shaw, compilers. Restoring western ranges and wildlands, vol. 1. RMRS-GTR-136. U.S. Department of Agriculture, Forest Service, Fort Collins, Colorado.

Monsen, S. B., and R. Stevens. 2004. Chapter 12. Seedbed preparation and seeding practices. Pages 121-154 in S. B. Monsen, R. Stevens, and N. L. Shaw, compilers. Restoring western ranges and wildlands, vol. 1. RMRS-GTR-136. U.S. Department of Agriculture, Forest Service, Fort Collins, Colorado.

Noss, R. F., E. T. LaRoe III, and J. M. Scott. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. National Biological Service Biological Report 28, Washington, D.C.

Pellant, M., B. Abbey, and S. Karl. 2004. Restoring the Great Basin desert, U.S.A: integrating science, management, and people. Environmental Monitoring and Assessment **99**:169-79.

Piemeisel, R. L. 1951. Causes affecting change and rate of change in a vegetation of annuals in Idaho. Ecology **32:**53-72.

Rowland, M. M., L. H. Suring, and M. J. Wisdom. 2010. Assessment of habitat threats to shrublands in the Great Basin: a case study. Pages 673-685 in J. M. Pye, H. M. Rauscher, Y. Sands, D. C. Lee, J. S. Beatty, editors. Advances in threat assessment and their application to forest and rangeland management. PNW-GTR-802. U.S. Department of Agriculture, Forest Service, Portland, Oregon.

Vilà, M., J. L. Espinar, M. Hejda, P. E. Hulme, V. Jarošík, J. L. Maron, J. Pergl, U. Schaffner, Y. Sun, and P. Pyšek. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecology Letters **14**:702-708.

West, N. E., and J. A. Young. 2000. Intermountain valleys and lower mountain slopes. Pages 255-284 in M. B. Barbour and W. D. Billings, editors. North American Terrestrial Vegetation. Cambridge University Press, Cambridge, United Kingdom.

Wolfe, B. E., and J. N. Klironomos. 2005. Breaking new ground: soil communities and exotic plant invasion **55**:477-487.

Young, J. A., R. A. Evans, R. E. Eckert Jr., and B. L. Kay. 1987. Cheatgrass. Rangelands **9**:266-270.

CHAPTER II

Invasive Species Production Following Post-wildfire Rehabilitation of an *Artemisia tridentata* ssp. *wyomingensis* Community

Research Paper

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Key words: *Artemisia tridentata* ssp. *wyomingensis*, *Bromus tectorum*, Great Basin, minimum-till drill, rangeland drill, *Salsola kali*, semiarid rangelands

Introduction

Wildfire is a significant agent of community turnover and disturbance on arid and semiarid landscapes of the Intermountain West (Bainbridge 2007). Shortened fire return intervals resulting from invasions of exotic annual grasses and forbs, such as *Bromus tectorum* L. (Poaceae, cheatgrass; Young et al. 1987), *Salsola kali* L. (Chenopodiaceae, Russian thistle; Smith 2005), and *Halogeton glomeratus* (M. Bieb.) C.A. Mey. (Chenopodiaceae, halogeton; Pavek 1992) can drive *Artemisia tridentata* Nutt. (Asteraceae, big sagebrush) communities to alternate states dominated by exotic annual species (Ziegenhagen & Miller 2009). Entry of exotic annuals into semiarid *A. tridentata* communities can hinder the establishment of native species after wildfire. *Salsola kali*, *H. glomeratus*, and *B. tectorum* are disturbance dependent and highly successful competitors in semiarid ecosystems. The warm season (C4) annual forb, *S. kali*, can rapidly invade disturbed sites and is especially competitive during times of drought (Allen 1982). *Salsola kali* is a prolific seed producer and has extensive seed dispersal (Brandt & Rickard 1994). However, it may also facilitate the growth of native perennial grasses by creating favorable microenvironments (Allen & Allen 1988). *Salsola kali* is an early successional species that can later be dislodged by *B. tectorum* (Piemeisel 1951). *Halogeton glomeratus*, another warm season (C4) succulent annual forb, is of particular concern because it accumulates toxic oxalates in its tissues which are fatal when ingested by livestock, especially sheep (Cronin & Coburn 1965). *Halogeton glomeratus* may also inhibit the germination and establishment of native species through elemental allelopathy (hyper-accumulation of an element within the rhizosphere which may inhibit the growth of neighboring plants, Morris et al. 2009) by increasing soil salinity (Duda et al. 2003). *Halogeton glomeratus* produces two different types of seeds, black seeds which germinate rapidly and brown seeds which can remain viable in the seed

bank for 10 years, extending seed bank longevity and allowing the species to reestablish following extended drought (Williams 1960). Similar to *S. kali*, *H. glomeratus* is also an early successional species that is later displaced by *B. tectorum*. *Bromus tectorum*, a cool season (C3) annual graminoid, rapidly accumulates a very large seed bank, a fraction of which can remain viable after wildfire (Hassan & West 1986; West & Young 2000; Chambers et al. 2007; Beckstead et al. 2011). Wildfires occurring in monotypic *B. tectorum* stands do not generate enough radiant heat to destroy *B. tectorum* seeds and most seed morality occurs through direct contact with flames (Beckstead et al. 2011). However, large amounts of standing dead biomass (Humphrey & Schupp 2001) and the presence of woody species (Brooks 2002) can produce hotter fires (> 148ºC) which are fatal to *B. tectorum* seed (Beckstead et al. 2011).

Bromus tectorum is a facultative winter annual that can germinate in either fall or early spring before native perennial bunchgrasses. Its ability to germinate quickly when conditions are favorable and its rapid growth (Mack & Pyke 1983; Knapp 1996; Arredondo et al. 1998) permit earlier access to soil moisture (Knapp 1996), decrease root length density of native seedlings (Melgoza & Nowak 1991), and allow *B. tectorum* to respond to increases in nutrients, especially nitrogen, more quickly than native perennial grasses (Link et al. 1995; Monaco et al. 2003). *Bromus tectorum* can also outperform *Pseudoroegneria spicata* (Pursh) Á. Löve (Poaceae, bluebunch wheatgrass) and *Elymus elymoides* (Raf.) Swezey (Poaceae, squirreltail) in the seedling stage by appropriating nutrients from within the rooting zone of these native perennial bunchgrasses (Blank 2010). *Salsola kali*, *H. glomeratus*, and *B. tectorum* are successful competitors in semiarid shrublands because of their ability to invade sites and establish before native seedlings. As these invasive species supplant the native vegetation, forage production and quality, soil chemistry, and biodiversity are altered.

Post-wildfire seeding is often used to mitigate the effects of wildfire and limit invasion of exotic annuals. Historically, the prevailing paradigm has been to combat the invasion by exotic annuals by seeding exotic perennials because they rapidly colonize sites and are available and inexpensive (Richards et al. 1998). However, recent evidence suggests that sites rehabilitated with perennial exotics like *Agropyron cristatum* (L.) Gaertn. (Poaceae, crested wheatgrass) are just as susceptible to invasion by *B. tectorum* and other exotic annuals as native *A. tridentata* sites (Chambers et al. 2007). Using native species to rehabilitate post-wildfire sites is also preferable given concerns over maintaining genetic diversity and ecological integrity. Executive Order No. 11987 (1977) signed by President Jimmy Carter and later revised by President William Clinton, Executive Order No. 13112 (1999), mandate federal agencies to prevent the spread of introduced species and encourage the use of natives. The use of native species for rehabilitation projects and restoration efforts was reaffirmed in 2001 with the creation of the Native Plant Material Development Program by Congress (USDI & USDA 2002) to be administered by the Bureau of Land Management (BLM), and again with the issuance of policies FSM 2070 by the U.S. Forest Service (2008) and H-1470-2 by the BLM (2008). Both FSM 2070 and H-1470-2 require that native plant materials be the first choice for revegetation efforts (BLM 2008; USFS 2008).

The efficacy of post-fire native seedings in excluding exotic species is largely undocumented. Native seeding failures have been attributed to a myriad of variables including erratic precipitation (Chambers et al. 2007), use of inappropriate species and seed sources (Monsen & Stevens 2004), improper site preparation and inadequate seeding method (James & Svejcar 2010), and competition with exotics (Eiswerth et al. 2009). Although seed bank response is highly dependent upon fire intensity and severity, rehabilitation seedings are less successful if

the site was previously dominated by exotic annuals before wildfire (Kotanen 1997; Eiswerth et al. 2009). However, many authors suggest that successful post-fire seedings that reach maturity can effectively curtail invasion by exotic annuals (Hunter et al. 2006; Thompson et al. 2006; Blank & Morgan 2012; Boyd & Davies 2012).

We investigate the potential for limiting exotics in a variety of seeding treatments. Equipment selection and seeding technology are important to revegetation success. Seeds of grasses, forbs, and shrubs differ greatly in size, shape, and texture, and so require different seeding methods, seeding rates, and planting depths (Monsen & Stevens 2004). Standard rangeland drills have not been effective for seeding small-seeded species, even when broadcast in alternate rows, as the disks and chains tend to bury the small seeds too deep (Monsen & Stevens 2004). To circumvent these problems, a triple seedbox system with the ability to regulate seeding rates and seed delivery for grains, small seeds, and fluffy seeds was developed specifically for wild-land seeding. More recently, a minimum-till drill was designed to reduce soil disturbance and provide increased control of seed placement. Soil disturbance can facilitate invasion by exotic annuals like *S. kali and H. glomeratus* (Piemeisel 1951; Hobbs & Huenneke 1992; Pavek 1992; Brandt & Rickard 1994; Kotanen 1997). Conversely, the disking action of rangeland drills can also bury seeds too deeply, hindering their germination and emergence as has been shown to be the case with *B. tectorum* (Piemeisel 1951; Young et al. 1969). However, much of the evidence concerning appropriate seeding methodology and technology is anecdotal (Montalvo et al. 2002), and research that compares the standard rangeland drill to the minimum-till drill is lacking.

We investigated the impact of native seeding treatments on productivity of 1) seeded forbs; 2) native and exotic volunteer (plants that established after the fire from the extant seed

bank) forbs; 3) native grasses (both volunteer and seeded); 4) *B. tectorum*; 5) *H. glomeratus*; and 6) *S. kali* two and three years following wildfire on an *Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young (Asteraceae, Wyoming big sagebrush) site in northern Utah. Because of the minimum-till drill's ability to control for seeding depth and minimize soil disturbance, we hypothesize that productivity of natives will be greater and exotic annual abundance lower in minimum-till drilled treatments.

Materials and Methods

Study Site

The study area (2008 Scooby Fire), located in the Wildcat Hills (41°51'16"N, 113°2'46"W), was approximately 32 km southwest of Snowville, Box Elder County, Utah in the Great Salt Lake Major Land Resource Area (028A). Elevation at the site ranges from 1,420-1,450 m on fan terraces and alluvial plains, with slope gradients of less than 5%. Mean annual air temperature fluctuates between 7.2–10°C, the frost-free period ranges from 116–140 days, and mean annual precipitation varies from 200–300 mm (NRCS 2010). The study area received above average precipitation in June 2009 following rehabilitation seeding. Precipitation data was gathered from Rosette, Utah which is approximately 32 km west of the study site (1,735 m, Fig. 2.1). Xeric Haplocalcids (Hiko Peak, gravelly loam) and Xeric Torriorthents (Sheeprock, gravelly coarse sand) dominate the site. Both soils are characterized as deep (≥ 60 cm) and well to somewhat excessively drained (Soil Survey Staff 2012). The site is located in Semidesert Gravelly Loam ecological site R028AY215UT (NRCS 2010). Current and historic land management focuses on livestock grazing with use during fall, winter, and spring (Stettler 2009). Big game and sagebrush-obligate species such as *Centrocercus urophasianus* (Phasianidae, greater sage-grouse) depend on the area for critical winter range (NRCS 2010).

Treatment Installation

The fire burned 1.54 km^2 of *A. tridentata* ssp. *wyomingensis* vegetation on lands managed by the U.S. Department of the Interior, Bureau of Land Management (BLM) in September 2008. Vegetation at the site included *A. tridentata* ssp. *wyomingensis*, *Achnatherum hymenoides* (Roem. & Schult.) Barkworth (Poaceae, Indian ricegrass), *P. spicata*, and *E. elymoides* (NRCS 2010), with some exotic annuals growing in the interspaces. Although a few isolated pockets of vegetation remained, the fire removed most of the site's plant cover and litter.

The study was conducted in 2010 and 2011 on a research site established in 2008 to investigate the effects of drill type on the productivity of 1) seeded forbs; 2) native and exotic volunteer forbs; 3) native grasses (both volunteer and seeded); 4) *B. tectorum*; 5) *H. glomeratus*; and 6) *S. kali*. The impacts of failed seedings were also explored by passing the drills over the site without seed. Shaw et al. (2011) examined seeding strategies for applying small-seeded native species, which included: timing of hand broadcast seeding (fall versus winter broadcast intended to mimic aerial seeding) and drill application of *A. tridentata* ssp. *wyomingensis* seeding rates (1x, 5x, and 10x the standard rate). They included *A. tridentata* ssp. *wyomingensis* seeding rate differences within the drilled treatments to determine the most effective rates for obtaining shrub density targets. *Artemisia tridentata* ssp. *wyomingensis* and other seeded shrub results are not reported here.

Within the study area, five replicate blocks (each block contains approximately 0.028 km^2) were established to examine 13 seeding treatments (65 plots total, Fig. 2.3). The 13 seeding treatments (Table 2.1) were assigned randomly by plot (30-m x 70-m) and re-randomized among blocks. A 10-meter buffer was seeded using *A. hymenoides* and *P. spicata* to reduce weed

encroachment around the perimeter of all blocks and between plot rows. The blocks were surrounded by a perimeter fence to deter grazing by livestock, but did not exclude big game.

Seeding Method

Two drills (standard rangeland [P&F Services, Kemmerer, WY] and minimum-till [Truax Co., Inc., New Hope, MN]) were used to apply a large-seeded species mix (drill mix) and a small-seeded species mix (broadcast mix) to the study area in November 2008. The rangeland drill (R) is best suited for seeding large-seeded species which are drilled into the soil (Fig. 2.2). To broadcast small seeds, the disk assemblies were removed from alternate seed drops and replaced with pipes allowing the broadcast mix to drop onto the soil surface. All seeded rows (drilled and broadcast) were covered by dragging chains behind the drill. Plots were also seeded using a minimum-till drill (M) which dropped small seed on the soil surface in alternate rows and firmed the seed into the soil with an imprinter unit. Large-seeded species (drill mix) were drilled into narrow furrows created by hydraulic disk assemblies. Three controls, 1) undrilled, unseeded; 2) rangeland drilled with no seed; and 3) minimum-till drilled with no seed, were also included.

The drill seed mixture consisted of three perennial grasses and two perennial forbs (Table 2.2) and was seeded in alternate rows through each drill. The broadcast mixture included two perennial shrubs, two perennial forbs, and one perennial grass (Table 2.2). The broadcast mix was 1) mechanically surface seeded in the rows between the drill rows and covered with a chain (R) or imprinter unit (M); 2) hand broadcast immediately after drill seeding in November 2008; or 3) hand broadcast over snow in February 2009. Hand broadcasts were intended to simulate aerial seeding. Three *A. tridentata* ssp. *wyomingensis* seeding rates were included in the broadcast mix applied by the drills (seeding rate differences not included in the hand broadcast mix): 1x, 5x, and 10x the standard rate recommended by the BLM for post-fire seedings (Table

2.2). Rates for native grasses and shrubs approximated those used by the BLM, while forb rates were largely dependent on seed availability. Although all seeding treatments were installed on five replicate blocks at the site, based on initial transect data from 2010, we omitted one block because a portion of the block was dominated by volunteer *Pascopyrum smithii* (Rydb.) Á. Löve (western wheatgrass), which was largely absent from the remainder of block 3 and other blocks.

Biomass Collection

Initial monitoring in June 2009 and 2010 documented plant cover, density, and species richness along five permanently established 20-m transects in each plot using line-point intercept, basal gap measurements, and 0.5 m^2 quadrats (modified from Herrick et al. 2005; Shaw et al. 2011). In July 2010, we initiated biomass clipping studies to document invasive species production. In each plot, we collected aboveground herbaceous biomass samples adjacent to the 25-m and 45-m transects (Fig. 2.3) established along the 70-m plot edge, perpendicular to the drill-seeded rows. Two quadrats (0.25 m^2) were placed at randomly selected points 2 m away from, and on the southeast side of the two transects (a total of four quadrats per plot). Sampling in 2011 was identical except that quadrats were placed to avoid areas that were clipped in 2010. Within each quadrat, we clipped biomass to 2.5 cm above ground. Species and plant groups clipped included: 1) seeded forbs; 2) native and exotic volunteer forbs (in some instances volunteer forbs overlapped with seeded forb species and we were forced to assume that all forbs found within controls were volunteer); 3) native grasses (both volunteer and seeded); 4) *B. tectorum*; 5) *H. glomeratus*; and 6) *S. kali*. Plant materials were oven dried at 60°C for 48 hours (Bonham 1989), and dry biomass was recorded to the nearest 0.01 g. When samples did not register on the scale (< 0.01 g) even though biomass was present, we recorded 0.01 g to denote the presence of that species or plant group.

Experimental Design and Statistical Analysis

Biomass data (total, species groups, and exotic annual species) were analyzed as a randomized complete block design with four blocks using a mixed model analysis of variance (ANOVA) with JMP 10 software produced by the SAS Institute Inc. (2012). Biomass from the four quadrats in each plot was summed and production presented as g/m^2. Standard errors of the mean for each species or plant group were calculated using the four replicate blocks. Sampling year was included as the repeated measure. When the year by treatment interaction term was significant for a species or plant group, ANOVA's were run separately by year to determine treatment differences within years. Mean separation of total biomass was calculated using Least Significant Difference (LSD). Mean separation for individual species and species groups was calculated only when treatments differed using linear contrasts to compare treatments within a drill type (Table 2.3). Results are reported as seeded treatments combined by drill type (rangeland versus minimum-till), leaving all three controls separate using linear contrasts. We tested the sphericity assumption and when violated we added weights to the mixed model to assess the impact of unequal variance on ANOVAs. In no case did this step alter significance of the original ANOVAs, thus non-weighted results are presented here.

Results

Plant Production (total)

In 2010, total production did not differ among the 13 treatments ($p = 0.0957$) and ranged from 122 g/m^2 (C) to 247 g/m^2 (R10x). In 2011, production was less in the three controls ($p = 0.0054$) than in seeded treatments with the exception of the RBC5x and M10x treatments which were intermediate (Fig. 2.4). When averaged across both years, production did not differ among treatments ($p = 0.1060$).

Native Grasses and Volunteer and Seeded Forbs

When treatments were combined to compare the two drills across years (all seeded rangeland drill treatments combined, all seeded minimum-till drill treatments combined, and the three controls remaining separate in linear contrasts; Fig. 2.5a), native grass production (seeded and volunteer) was greater in drilled treatments than in unseeded controls (Fig. 2.5a; $p = 0.0032$). Native grass production, when averaged across all treatments to test the simple effect of year, increased ($p = 0.0239$) from 2010 (125 g/m^2) to 2011 (157.1 g/m^2). Volunteer (native and exotic) forbs, primarily the non-native forb *Sisymbrium altissimum* L. (Brassicaceae, tumble mustard), were most abundant in the controls (Fig. 2.5b; $p = 0.0395$) and least in the seeded rangeland and minimum-till drilled treatments. Among the three controls, volunteer 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 ($p = 0.1373$, Table 2.4). Averaged across both years, seeded forb production was 14.2 g/m^2 in rangeland drill seeded treatments and 19 g/m^2 in minimum-till drill seeded treatments.

Targeted Exotic Annuals

Targeted exotic annuals (total biomass of *B. tectorum, S. kali*, and *H. glomeratus* combined) were greatest in the controls ($p = 0.0006$) and least in the seeded treatments, when averaged across years (Fig. 2.5c). In 2010, *B. tectorum* production was greatest in the undrilled control (C) and the M0, and least in the R0 and all seeded treatments ($p < 0.0001$, Fig. 2.6a). In 2011, *B. tectorum* increased across all treatments irrespective of drill type and was most abundant in unseeded treatments and least in seeded treatments ($p < 0.0001$). *Salsola kali* differed among treatments only in 2010 ($p < 0.0001$, Fig. 2.6b) when it was more abundant in

unseeded, drilled controls (R0 and M0), than in the unseeded and undrilled control (C), or in any seeded treatments. In 2011, *S. kali* was nearly absent from the study plots and did not differ among treatments. *Halogeton glomeratus* production was greater in 2010 (11 g/m^2 across all treatments, $p = 0.0013$; Fig. 2.6c) than in 2011 (0.02 g/m^2) across all treatments. *Halogeton glomeratus* was the least productive of the three exotic annual species in 2011.

Discussion

Chambers et al. (2007) argue that many Great Basin *A. tridentata* communities are susceptible to invasion by exotic annuals because of fluctuations that occur in the availability of soil moisture. Establishment of exotic species, like *B. tectorum* (Humphrey & Schupp 2004), and native species, especially ones that have been seeded (Monsen & Stevens 2004), are reliant upon precipitation and the plant's ability to access limited supplies of soil moisture (Chambers et al. 2007). This study documented few differences in native species production between the two drills by the second and third years after seeding. Considering the water-limited character of our study site and the above-average precipitation received the spring following rehabilitation seeding, our results may be limited in demonstrating drill differences because of high native species establishment. It is possible that drill differences may be more pronounced during very dry years of less favorable precipitation. Because seedling establishment was high, we were able to document the potential for successful native seedings to limit the presence of exotic annuals.

Historically, introduced grasses were used in restoring degraded rangelands (Hafenrichter 1958; Hull 1974; Richards et al. 1998) and more recent research suggests they can act as a barrier to invasion by exotic annual grasses (Davies et al. 2010). However, many non-native restoration species have become invasive and therefore undermine rehabilitation efforts (Henderson & Naeth 2005; Fansler & Mangold 2010; Hulet et al. 2010). Native perennial grasses

are viable options for restoration, matching traditional exotic seeded species in establishment, survival, and growth (Huber-Sannwald & Pyke 2005; Thompson et al. 2006), and limiting exotic annual production following wildfire (Jessop & Anderson 2007). Established native perennial grasses hinder the growth of exotic annuals through root competition. Root systems of established perennial grasses (*Elymus wawawaiensis* J. Carlson & Barkworth (Poaceaa, Snake River wheatgrass); *Leymus triticoides* (Buckley) Pilg. (Poaceae, creeping wild rye); and *A. hymenoides*) can deplete soil nitrogen (Blank & Morgan 2012). *Bromus tectorum* is more competitive with higher nitrogen availability (Blank & Morgan 2012). Our results support post-fire seeding as an effective means to limit the production of exotic annuals, even though exotic invasives have not been eliminated from the site. Exotic species usually remain within seeded treatments and it may require many years for seeded species to dominate drill row interspaces. It would be interesting to follow native seedling recruitment between drill rows in the coming years.

High productivity of *B. tectorum* and subsequent accumulation of biomass and litter within controls will contribute to the site's susceptibility to future wildfire. *Bromus tectorum* invasion in the Great Basin can increase fire intensity (Knapp 1996) and reduce fire return intervals in *A. tridentata* ssp. *wyomingensis* communities from 50-100 years (Mensing et al. 2006) to 3-5 years (Whisenant 1990). However, *P. spicata*, *E. elymoides*, and *P. secunda* are fire-adapted species which can survive and reestablish following a burn and, depending on fire conditions, may experience increased flowering and growth following fire (Ellsworth & Kauffman 2010). Sites not previously dominated by exotic annuals may experience autogenic regeneration of native perennial bunchgrasses, which will compete with seeded species (Boyd & Davies 2012). However, sites with a significant exotic annual component will most likely be

dominated by exotic annuals following fire (Eiswerth et al. 2009) if seeding of native species is not initiated. Given that the controls at our site became dominated by *B. tectorum*, rehabilitation seeding was necessary to curtail the spread of exotic annuals.

The competitive interactions between *S. kali* and *B. tectorum* should be examined more closely in future research. In our study, *S. kali* declined in treatments where *B. tectorum* increased, and Piemeisel (1951) documented a similar progression from *S. kali* to *S. altissimum* to *B. tectorum* on sites in south central Idaho. When considering drill differences in the absence of seeding, we provide some evidence that drilling alone may initially enhance the presence of *S. kali*, although this difference was short-lived. While *S. kali* responds favorably to soil disturbance (Brandt & Rickard 1994), germination of *B. tectorum* can be initially hampered by drills that bury its seed bank too deeply (Piemeisel 1951; Young et al. 1969). As drilling disturbance became less pronounced and litter accumulated on the soil surface, *B. tectorum* was able to supersede *S. kali* (Piemeisel 1951; Evans & Young 1970). Piemeisel (1951) suggests that *B. tectorum* draws upon soil moisture in fall and early spring, and matures before late summer, just as *S. kali* is beginning to establish and grow. Accessing soil water early in the growing season and maturing before other annual exotics allows *B. tectorum* to overwhelm other annual invasives (Brandt & Rickard 1994).

The short duration of this study (two and three years after seeding) coupled with the volatile nature of exotics provide a brief estimation of potential long-term trajectories of post-wildfire rehabilitation seedings. Once native species successfully establish in post-fire sites, they should effectively limit the production of exotic annuals. Although non-native perennials can limit exotic annual invasion on wildfire rehabilitation sites (Eiswerth et al. 2009; Davies et al.

2010), our study demonstrates that native species are also effective in limiting exotic annuals following wildfire.

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LITERATURE CITED

Allen, E. B. 1982. Water and nutrient competition between *Salsola kali* and two native grass species (*Agropyron smithii* and *Bouteloua gracilis*). Ecology **63**:732-741.

Allen, E. B., and M. F. Allen. 1988. Facilitation of succession by the nonmycotrophic colonizer *Salsola kali* (Chenopodiaceae) on a harsh site: effects of mycorrhizal fungi. American Journal of Botany **75**:257-266.

Arredondo, J. T., T. A. Jones, and D. A. Johnson. 1998. Seedling growth of Intermountain perennial and weedy annual grasses. Journal of Range Management **51**:584-589.

Bainbridge, D. A. 2007. A guide for desert and dryland restoration: new hope for arid lands. Island Press, Washington, D.C.

Beckstead, J., L. E. Street, S. E. Meyer, and P. S. Allen. 2011. Fire effects on the cheatgrass seed bank pathogen *Pyrenophora semeniperda*. Rangeland Ecology & Management **64**:148-157.

Blank, R. 2010. Intraspecific and interspecific pair-wise seedling competition between exotic annual grasses and native perennials: plant-soil relationships. Plant Soil **326:**331-343.

Blank, R., and T. Morgan. 2012. Suppression of *Bromus tectorum* L. by established perennial grasses: potential mechanisms—part one. Applied and Environmental Soil Science. Article ID 632172. 9 pages. doi:10.1155/2012/63212

BLM (Bureau of Land Management). 2008. Integrated vegetation management handbook H-1740-2. Chapter 8 using native plant materials. U.S. Department of the Interior, Washington, D.C. 8 p.

Bonham, C. D. 1989. Measurements for terrestrial vegetation. John Wiley & Sons, Inc., New York.

Boyd, C. S., and K. W. Davies. 2012. Spatial variability in cost and success of revegetation in a Wyoming big sagebrush community. Environmental Management **50**:441-450.

Brandt, C. A., and W. H. Rickard. 1994. Alien taxa in the North American shrub-steppe four decades after cessation of livestock grazing and cultivation agriculture. Biological Conservation **68**:95-105.

Brooks, M. L. 2002. Peak fire temperatures and effects on annual plants in the Mojave desert. Ecological Applications **12**:1088-1102.

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

Cronin, E. H., and W. M. Coburn. 1965. Principles for managing ranges infested with halogeton. Journal of Range Management **19**:226-227.

Davies, K. W., A. M. Nafus, and R. L. Sheley. 2010. Non-native competitive perennial grass impedes the spread of an invasive annual grass. Biological Invasions **12:**3187-3194.

Duda, J. J., D. C. Freeman, J. M. Emlen, J. Belnap, S. G. Kitchen, J. C. Zak, E. Sobek, M. Tracy, and J. Montante. 2003. Differences in native soil ecology associated with invasion of the exotic annual chenopod, *Halogeton glomeratus*. Biology and. Fertility of Soils **38**:72-77.

Eiswerth, M. E., K. Krauter, S. R. Swanson, and M. Zielinski. 2009. Post-fire seeding on Wyoming big sagebrush ecological sites: regression analyses of seeded nonnative and native species densities. Journal of Environmental Management **90**:1320-1325.

Ellsworth, L. M., and J. B. Kauffman. 2010. Native bunchgrass response to prescribed fire in ungrazed mountain big sagebrush ecosystems. Fire Ecology **6**:86-96.

Evans, R. A., and J. A. Young. 1970. Plant litter and establishment of alien annual weed species in rangeland communities. Weed Science **18**:697-703.

Fansler, V. A., and J. M. Mangold. 2010. Restoring native plants to crested wheatgrass stands. Restoration Ecology **19:**16-23.

Hafenrichter, A. L. 1958. New grasses and legumes for soil and water conservation. Pages 349-406 in A. G. Norman, editor. Advances in Agronomy, Volume X. Academic Press. Inc., New York.

Hassan, M. A., and N. E. West. 1986. Dynamics of soil seeds pools in burned and unburned sagebrush semi-deserts. Ecology **67**:269-272.

Henderson, D. C., and M. A. Naeth. 2005. Multi-scale impacts of crested wheatgrass invasion in mixed-grass prairie. Biological Invasions **7:**639-650.

Herrick, J. E., J. W. Van Zee, K. M Havstad, L. M. Burkett, and W. G. Whitford. 2005. Monitoring manual for grassland, shrubland and savanna ecosystems, Volume 1 Quickstart. Pages 1-42. USDA-ARS Jornada Experimental Range, Las Cruces, New Mexico.

Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasions: implications for conservation. Conservation Biology **6:**324-337.

Huber-Sannwald, E., and D. A. Pyke. 2005. Establishing native grasses in a big sagebrush dominated site: an intermediate restoration step. Restoration Ecology **13:**292-301.

Hulet, A., B. A. Roundy, and B. Jessop. 2010. Crested wheatgrass control and native plant establishment in Utah. Rangeland Ecology and Management **63:**450-460.

Hull, A. C. Jr. 1974. Species for seeding arid rangeland in southern Idaho. Journal of Range Management **27:**216-218.

Humphrey, L. D., and E. W. Schupp. 2001. Seed banks of *Bromus tectorum*-dominated communities in the Great Basin. Western North American Naturalist **61**:85-92.

Humphrey, L. D., and E. W. Schupp. 2004. Competition and other barriers to establishment of a native perennial grass (*Elymus elymoides*) in alien annual grass (*Bromus tectorum*) communities. Journal of Arid Environments **58**:405-422.

Hunter, M. E., P. N. Omi, E. J. Martinson, and G. W. Chong. 2006. Establishment of non-native plant species after wildfires: effects of fuel treatments, abiotic and biotic factors, and post-fire grass seeding treatments. International Journal of Wildland Fire **15:**271-281.

James, J. J., and T. Svejacr. 2010. Limitations to postfire seedling establishment: the role of seeding technology, water availability, and invasive plant abundance. Rangeland Ecology and Management **63:**491-495.

Jessop, B. D., and V. J. Anderson. 2007. Cheatgrass invasion in salt desert shrublands: benefits of postfire reclamation. Rangeland Ecology and Management **60:**235-243.

Knapp, P. A. 1996. Cheatgrass (*Bromus tectorum* L.) dominance in the Great Basin desert: history, persistence, and influences to human activities. Global Environmental Change **6**:37-52.

Kotanen, P. M. 1997. Effects of experimental soil disturbance on revegetation by natives and exotics in coastal Californian meadows. Journal of Applied Ecology **34:**631-644.

JMP, Version 10. 2012. SAS Institute Inc., Cary, North Carolina.

Link, S. O., H. Bolton Jr., M. E. Theide, and W. H. Rickard. 1995. Responses of downy brome to nitrogen and water. Journal of Range Management **48**:290-297.

Mack, R. N., and D. A. Pyke. 1983. The demography of *Bromus tectorum*: variation in time and space. Journal of Ecology **71**:69-93.

Melgoza, G., and R. S. Nowak. 1991. Competition between cheatgrass and two native species after fire: implications from observations and measurements of root distributions. Journal of Range Management **44**:27-33.

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

Monaco, T. A., D. A. Johnson, J. M. Norton, T. A. Jones, K. J. Connors, J. B. Norton, and M. B. Redinbaugh. 2003. Contrasting responses of intermountain west grasses to soil nitrogen. Journal of Range Management **56**:282-290.

Monsen, S. B., and R. Stevens. 2004. Chapter 12. Seedbed preparation and seeding practices. Pages 121-154 in S. B. Monsen, R. Stevens, and N. L. Shaw, compilers. Restoring western ranges and wildlands, vol. 1. RMRS-GTR-136. U.S. Department of Agriculture, Forest Service, Fort Collins, Colorado.

Montalvo, A. M., P. A. McMillan, and E. B. Allen. 2002. The relative importance of seeding method, soil ripping, and soil variables on seeding success. Restoration Ecology **10:**52-67.

Morris, C., P. R. Grossl, and C. A. Call. 2009. Elemental allelopathy: processes, progress, and pitfalls. Plant Ecology **202**:1-11.

NRCS (U.S. Department of Agriculture, Natural Resources Conservation Service). 2010. Ecological Site Descriptions. (available from http://esis.sc.egov.usda.gov/Welcome/pgESDWelcome.aspx).

Pavek, D. S. 1992. *Halogeton glomeratus*. Fire Effects Information System. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Missoula, Montana. (available from http://www.fs.fed.us/database/feis/).

Piemeisel, R. L. 1951. Causes affecting change and rate of change in a vegetation of annuals in Idaho. Ecology **32:**53-72.

Richards, R. T., J. C. Chambers, and C. Ross. 1998. Use of native plants on federal lands: policy and practice. Journal of Range Management **51**:625-632.

Shaw, N., R. D. Cox, A. C. Ganguli, A. L. Hild, B. Newingham, M. Pellant, D. Pyke, and J. Truax. 2011. Final report: equipment and strategies to enhance the post-wildfire establishment and persistence of Great Basin native plants. Joint Fire Science Program Project Number 07-1-3-12. 30 p.

Smith, L. 2005. Host plant specificity and potential impact of *Aceria salsolae* (Acari: Eriophyidae), an agent proposed for biological control of Russian thistle (*Salsola tragus*). Biological Control **34**:83-92.

Soil Survey Staff. 2012. Official soil series descriptions. U.S. Department of Agriculture, Natural Resources Conservation Service. (available from http://soils.usda.gov/technical/classification/osd/index.html).

Stettler, H. 2009. Cultural resource inventory of 70 acres of the Scooby Fire area, Box Elder County, Utah. Pages 1-41. Utah State Antiquities Project No. U-08-ST-1063b. SWCA Environmental Consultants, Salt Lake City, Utah.

Thompson, T. W., B. A. Roundy, E. D. McArthur, B. D. Jessop, B. Waldron, and J. N. Davis. 2006. Fire rehabilitation using native and introduced species: a landscape trial. Rangeland Ecology & Management **59:**237-248.

USDI & USDA (U.S. Department of the Interior & U.S. Department of Agriculture). 2002. Report to the Congress. Interagency program to supply and manage native plant materials for restoration and rehabilitation on Federal lands. U.S. Department of the Interior & U.S. Department of Agriculture, Washington, D.C. 17 p.

USFS (U.S. Forest Service). 2008. Forest service manual, FSM 2000 national forest resource management. Chapter 2070 vegetation ecology. U.S. Department of the Interior, Washington, D.C. 12 p.

West, N. E., and J. A. Young. 2000. Intermountain valleys and lower mountain slopes. Pages 255-284 in M. B. Barbour and W. D. Billings, editors. North American terrestrial vegetation. Cambridge University Press, Cambridge, United Kingdom.

WRCC (Western Regional Climate Center). Desert Research Institute. 2012. Reno, Nevada. (available from http://www.wrcc.dri.edu/).

Whisenant, S.G. 1990. Changing fire frequencies of Idaho's Snake River Plains: ecological and management implications. Pages 4–10 in E.D. McArthur, E.M. Romney, D. Stanley, and P.T. Tueller, compilers. Proceedings of the symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management. GTR INT-276. U.S. Department of Agriculture, Forest Service, Ogden, Utah.

Williams, M. C. 1960. Biochemical analyses, germination, and production of black and brown seeds of *Halogeton glomeratus.* Weeds **8**:452-461.

Young, J. A., R. A. Evans, and R. E. Eckert Jr. 1969. Population dynamics of downy brome. Weed Science **17:**20-26.

Young, J. A., R. A. Evans, R. E. Eckert, Jr., and B. L. Kay. 1987. Cheatgrass. Rangelands **9**:266-270.

Ziegenhagen L. L., and Miller R. F. 2009. Postfire recovery of two shrubs in the interiors of large burns in the Intermountain West, USA. Western North American Naturalist **69:**195-205.

Table 2.1. 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)*	Treatment Symbol
No Drill	No Seed	No Seed	C
Rangeland**	No Seed	No Seed	R0
	Drill	Drill (1x)*	R1x
	Drill	Drill (5x)*	R5x
	Drill	Drill (10x)*	R10x
	Drill	Hand broadcast, fall (5x)	RBC5x
	Drill	Hand broadcast, winter (5x)	RwBC5x
Minimum-till***	No Seed	No Seed	M0
	Drill	Drill (1x)	M1x
	Drill	Drill (5x)	M5x
	Drill	Drill (10x)	M10x
	Drill	Hand broadcast, fall (5x)	MBC5x
	Drill	Hand broadcast, winter (5x)	MwBC5x

*1x, 5x, and 10x *Artemisia tridentata* ssp. *wyomingensis* (Wyoming big sagebrush) seeding rates, 1x = 52 PLS/m^2. For total seed in each treatment see Table 2.2.

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

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

Table 2.2. Species seeded at the Scooby Fire rehabilitation site (Shaw et al. 2011).

Scooby Seed Mix Species	**Seeding Rate (PLS/m^2)**		
	1x	**5x**	**10x**
Broadcast Mix			
Artemisia tridentata ssp. *wyomingensis* (Wyoming big sagebrush)	52	234	495
Ericameria nauseosa (Rubber rabbitbrush)	86	86	86
Poa secunda (Sandberg bluegrass Mt. Home Germplasm)	91	91	91
Achillea millefolium var. *occidentalis* (Western yarrow Eagle Germplasm)	100	100	100
Penstemon cyaneus (Blue penstemon)	76	76	76
Total Broadcast	405	587	848
Drill Mix			
Pseudoroegneria spicata (Bluebunch wheatgrass Anatone Germplasm)	67	67	67
Achnatherum hymenoides ('Rimrock' Indian ricegrass)	51	51	51
Elymus elymoides (Squirreltail Toe Jam Creek Germplasm)	47	47	47
Sphaeralcea munroana (Munro's globemallow)	93	93	93
Eriogonum umbellatum (Sulphur-flower buckwheat)	11	11	11
Total Drill	269	269	269
Total Broadcast + Drill	**674**	**856**	**1117**

Table 2.3. Conceptual questions, treatment comparisons, and datasets used in LSMeans Contrast.

Conceptual Question	**Treatments Compared**	**Datasets Used**
Do seeded treatments differ from the controls? (all 13 treatments)	C, R0, R1x, R5x, R10x, RBC5x, RwBC5x, M0, M1x, M5x, M10x, MBC5x, MwBC5x	Native grasses, exotic annuals (*H. glomeratus*, *S. kali*, *B. tectorum*), volunteer forbs, seeded forbs (*E. umbellatum*, *S. munroana*, *A. millefolium* var. *occidentalis*, *P. cyaneus*)
Does rangeland drill seeded and minimum-till drill seeded treatments differ? (10 treatments without controls)	R1x, R5x, R10x, RBC5x, RwBC5x, M1x, M5x, M10x, MBC5x, MwBC5x	Native grasses, exotic annuals (*H. glomeratus*, *S. kali*, *B. tectorum*), volunteer forbs, seeded forbs (*E. umbellatum*, *S. munroana*, *A. millefolium* var. *occidentalis*, *P. cyaneus*)
Does drill disturbance favor or limit the presence of volunteer species? (3 controls only)	C, R0, M0	Exotic annuals (*H. glomeratus*, *S. kali*, *B. tectorum*), volunteer forbs
Does machine broadcasting differ from hand broadcasting? (10 treatments without controls)	R1x, R5x, R10x, RBC5x, RwBC5x, M1x, M5x, M10x, MBC5x, MwBC5x	*A. millefolium* var. *occidentalis* and *P. cyaneus*
Does season of hand broadcast (fall vs. winter) enhance the presence of broadcast species? (2 fall and 2 winter hand broadcast treatments)	RBC5x, RwBC5x, MBC5x, MwBC5x	*A. millefolium* var. *occidentalis* and *P. cyaneus*

Table 2.4. Broadcast and drilled forb species biomass (g/m^2) in seeded treatments averaged across July 2010 and 2011. Within individual species and averaged across seed mixture (broadcast and drill), drills and seasons did not differ, LSMeans Contrast.

	Hand broadcast (season) and machine drilled in fall				**Machine broadcast and drilled in fall**	
Forb Biomass (g/m^2)	Rangeland Drill (fall)	Rangeland Drill (winter)	Minimum-till Drill (fall)	Minimum-till Drill (winter)	Rangeland Drill	Minimum-till Drill
Broadcast Mix						
Achillea millefolium var. *occidentalis*	14.43	8.80	12.80	3.00	7.30	18.50
Penstemon cyaneus	0.41	0.00	0.520	0.00	0.02	0.02
Drill Mix						
Sphaeralcea munroana	3.80	0.15	3.31	2.67	3.18	2.60
Eriogonum umbellatum	0.00	0.00	0.00	0.00	0.03	0.03
Total	**18.64**	**8.95**	**16.63**	**5.67**	**10.53**	**21.15**

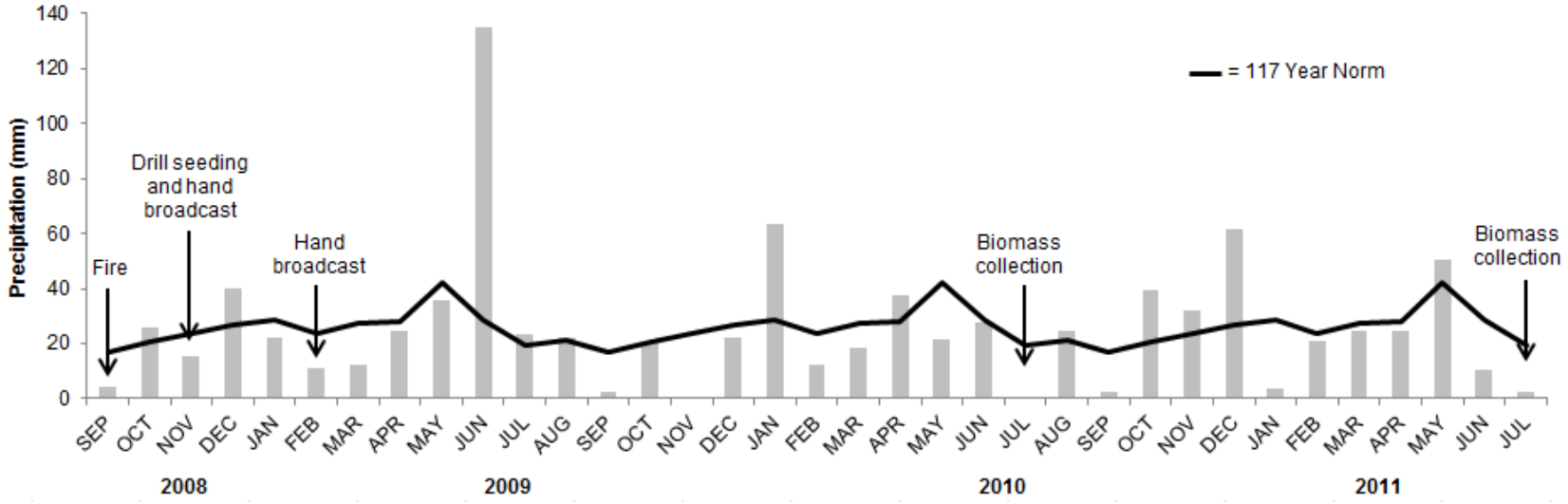


Figure 2.1. Monthly and long-term precipitation for the Scooby Fire site (WRCC 2012). Monthly data from Rosette, UT (1735 m) located approximately 32 km west of the study site. The solid line represents the 117 year norm which is an average of precipitation data from Rosette and Snowville, UT (1396 m), located approximately 31 km northeast of the study site. Some days are missing from the available dataset in 2009, 2010, and 2011. In 2009 both October and November are missing 2 days, in 2010 days missing in any month < 3, and in 2011 2-6 days are missing from January to July. Data last examined on 5 February 2013 at http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?ut7408.

Figure 2.2. A rangeland drill (A) used chains to cover seed and left deep furrows for the drill mix. The broadcast mix was applied using pipes which dropped seed onto the soil surface (B). A minimum-till drill (C) pressed broadcast seed into the soil with an imprinter unit and used hydraulic disk assemblies which left much narrower furrows for the drill mix (D, Shaw et al. 2011).

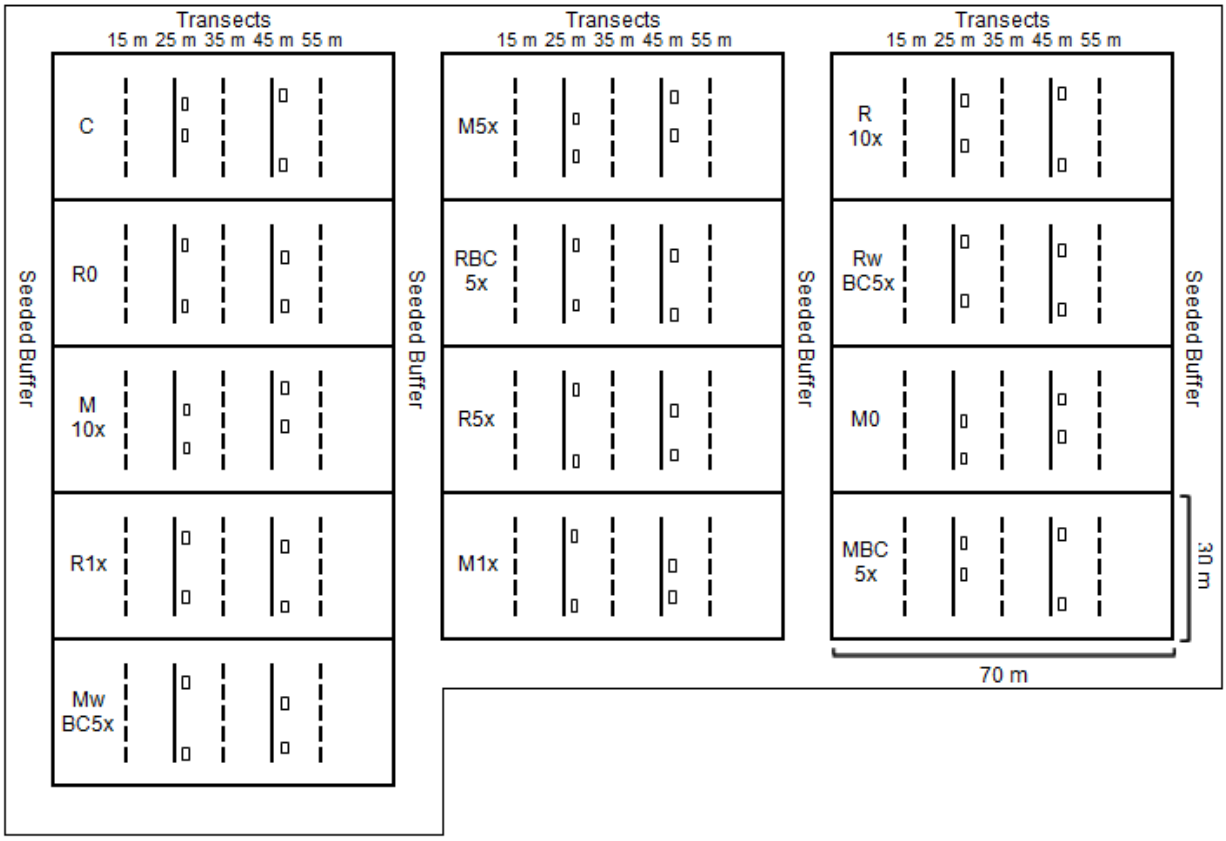


Figure 2.3. Layout of one block containing 13 30-m x70-m plots. Each plot was assigned to one of the 13 seeding treatments. Five transects (20 m long) were arranged perpendicular to seeded drill rows, but only the 25-m and 45-m transects were used in this study. Four quadrats (0.25 m^2) were placed 2 m from transects. Plot rows were separated by 10 m seeded buffers. Open boxes (□) are 0.25 m^2 quadrats and solid lines are biomass sampling transects.

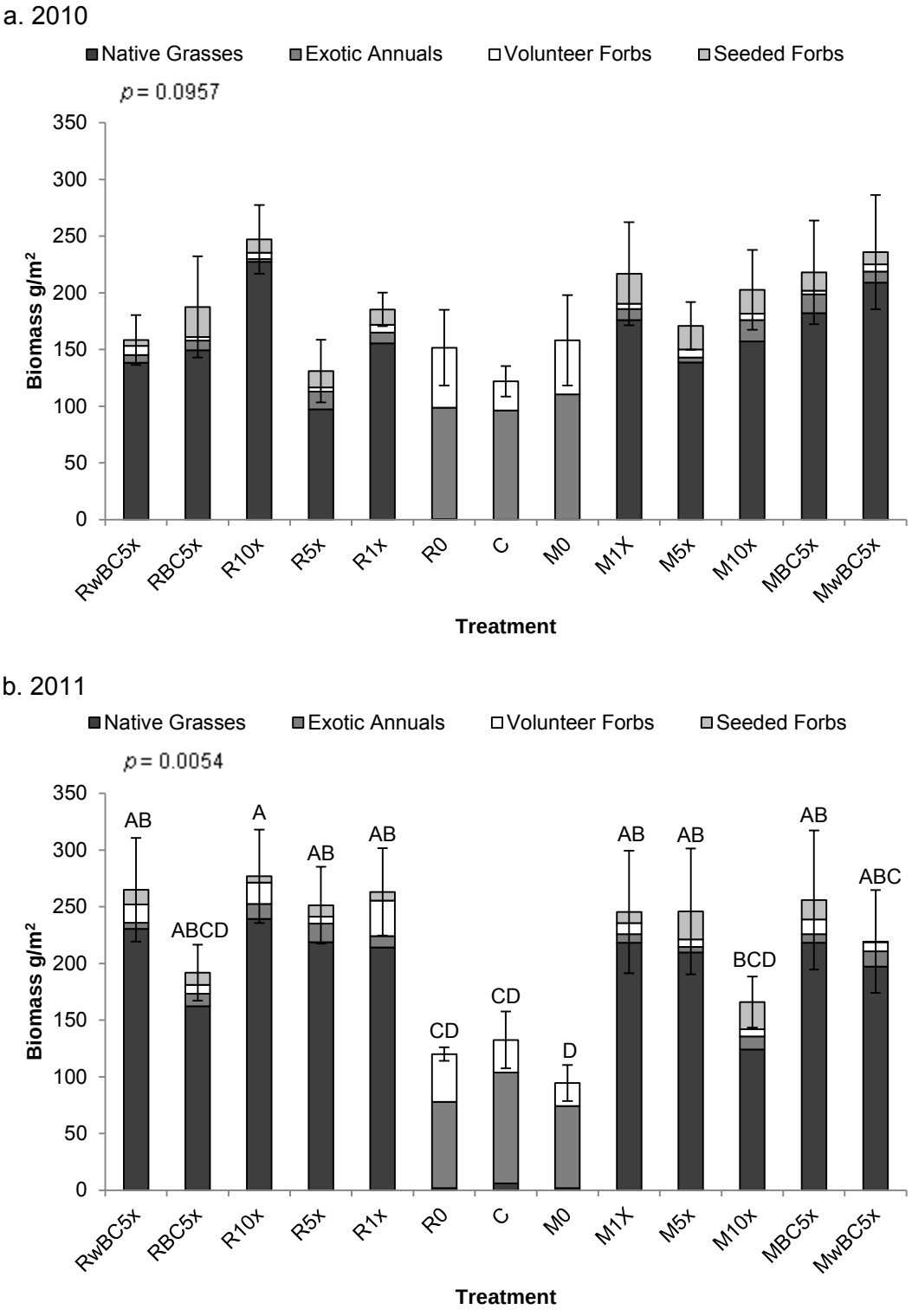


Figure 2.4. Biomass production by plant group within all 13 treatments in July 2010 (A) and July 2011 (B). Bars are standard errors of means for cumulative biomass. Means with the same letter do not differ ($p > 0.05$, LSD).

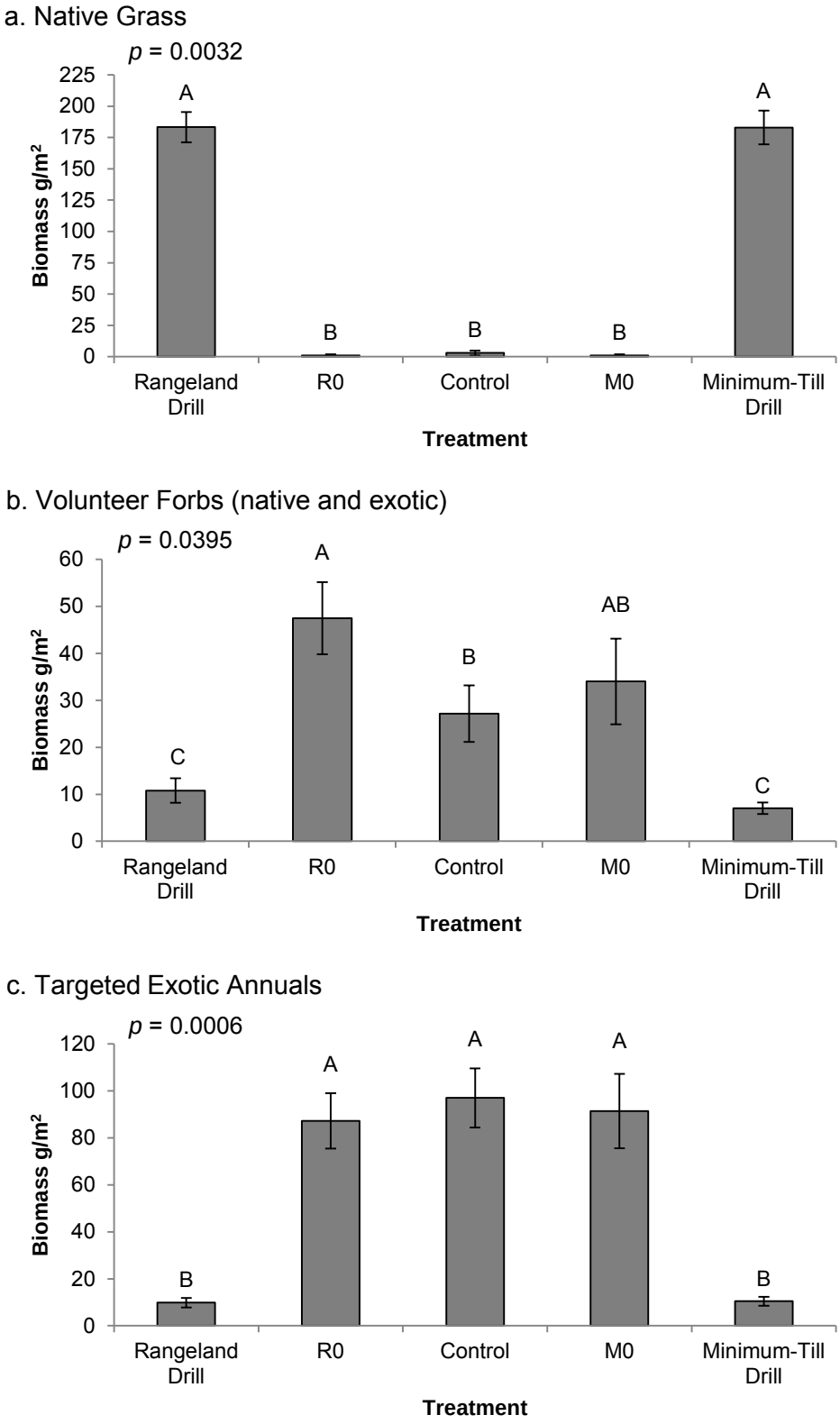
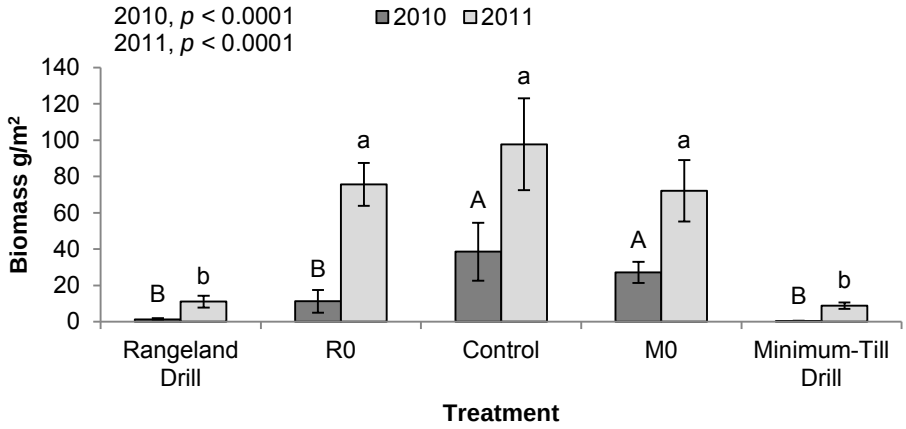
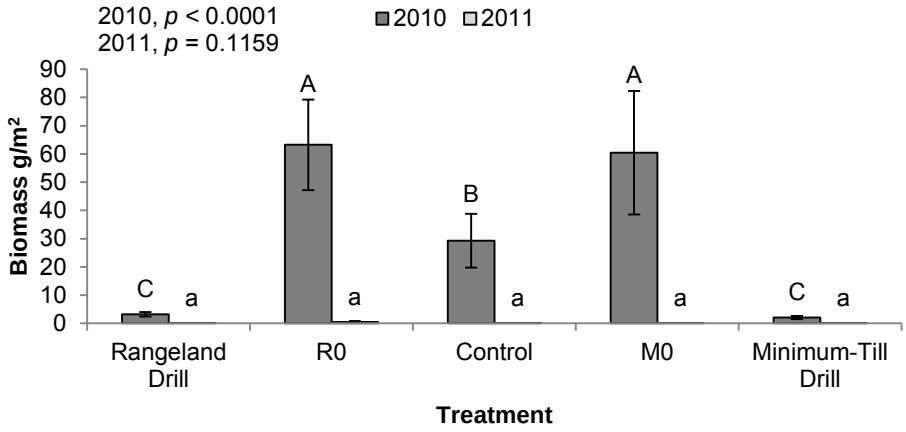


Figure 2.5. Native grasses, volunteer native and exotic forbs, and targeted exotic annuals in seeded (rangeland drill, minimum-till drill) and control treatments (R0, control, M0) averaged across 2010 and 2011. Bars are standard errors of means. Within each plant group, means with the same letters do not differ ($p > 0.05$, LSMeans Contrast).

a. *Bromus tectorum*



b. *Salsola kali*



c. *Halogeton glomeratus*

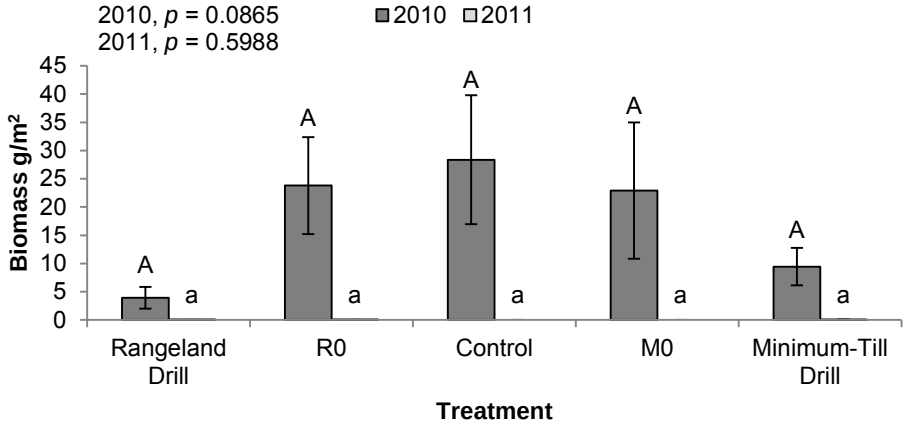


Figure 2.6. *Bromus tectorum*, *Salsola kali*, and *Halogeton glomeratus* biomass in seeded (rangeland drill, minimum-till drill) and control (R0, control, M0) treatments in July 2010 and July 2011 at the Scooby site. Bars are standard errors. Mean separation, LSMeans Contrast, was calculated within year; capital letters represent 2010 and lowercase letters represent 2011.

CHAPTER III

Soil Microbial Communities beneath Native Perennial Bunchgrasses and Exotic Annuals on a Seeded Sagebrush Site Following Wildfire

Research Paper

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Introduction

Across the Great Basin disturbed sagebrush communities contain increasing presence of invasive annuals (Howard 1992; Pavek 1992; Chambers et al. 2007; Davies et al. 2011). *Halogeton glomeratus* (M. Bieb.) C.A. Mey. (Chenopodiaceae, halogeton), *Salsola kali* L. (Chenopodiaceae, Russian thistle), and *Bromus tectorum* L. (Poaceae, cheatgrass) are three common exotics entering sagebrush landscapes. Soil microorganisms are essential to ecosystem function and are closely linked to aboveground plant community structure through nutrient cycling, decomposition, mutualistic associations, and deleterious impacts of soil pathogens and herbivores (Wolfe & Klironomos 2005; Batten et al. 2006). However, the role of soil microbiota in facilitating or hindering exotic plant invasion is not clear (Belnap & Phillips 2001; Wolfe & Klironomos 2005). Some invasive species (i.e. *H. glomeratus* and *Chromolaena odorata* (L.) King & H. Rob. [Asteraceae, Jack in the bush]) may accumulate pathogens within the rhizosphere that hinder the growth and development of native species, but have little effect on the invading species (Harper et al. 1996; Mangla et al. 2008). Exotic invasives may also benefit from below-ground enemy release. For example, Klironomos (2002) documented that while rare native plants accumulate species-specific pathogens which reduce plant growth, exotic species grown in foreign soils benefit from mycorrhizal associations and accumulate pathogens more slowly. *Centaurea maculosa* Lam. (Asteraceae, spotted knapweed), a mycorrhizal forb, can displace North American native plant communities, at least in part, by releasing toxic compounds into the soil which alter bacterial communities and reduce arbuscular mycorrhizal diversity and abundance (Bais et al. 2002; Mummey & Rillig 2006). Invasive species can self-perpetuate by altering soil physiochemical properties (Duda et al. 2003; Wolfe & Klironomos 2005). Conversely, the success of another invasive species, *Solidago gigantea* Aiton (Asteraceae,

giant goldenrod) was not dependent on altered soil biotic communities (decrease in bacteria and an increase in fungi). Productivity of *S. gigantea* was reduced when grown in *S. gigantea* invaded soil (Scharfy et al. 2010). The mixed response of invasives to plant-soil feedback mechanisms via the soil microbial community escapes generalization (Wolfe & Klironomos 2005).

Halogeton glomeratus, a warm season (C4) succulent annual forb, increases pH, exchangeable sodium, electrical conductivity, and surface soil salt content by incorporating sodium from the soil profile in plant tissues which is then leached into the soil from litter after senescence (Duda et al. 2003). *Halogeton glomeratus* does not readily form mycorrhizal associations and performs well in soils where arbuscular mycorrhizal (AM) fungi are depauperate (Allen & Allen 1988). However, Duda et al. (2003) posit that effects of *H. glomeratus* on soil chemistry may increase the pathogenic quality of the soil for other species. Harper et al. (1996) determined that fungi collected from soils under *H. glomeratus* were fatal to seedlings of *Krascheninnikovia lanata* (Pursh) A. Meeuse & Smit (Chenopodiaceae, winterfat), a native perennial shrub. Eckert and Kinsinger (1960) reported that soil salinization caused by *H. glomeratus* may inhibit the activity of nitrifying bacteria, which can reduce native plant growth. Although the changes in the soil Eckert and Kinsnger (1960) documented were evident after seven years, they did not adversely affect native plant growth. *Salsola kali*, another warm season (C4) annual forb, can also increase surface soil salinity (Harper et al. 1996) and does not form mycorrhizal associations (Allen & Allen 1988). Abundance of *S. kali* decreases when mycorrhizal fungi are present in the soil via fatal root infections. Microbial-induced mortality of *S. kali* may accelerate site colonization by mycorrhizal native species (Allen & Allen 1988). However, *S. kali* can also facilitate revegetation on disturbed sites by acting as nurse plant for

native seedlings, providing protection from the wind and retaining snow (Allen & Allen 1988; Howard 1992).

Bromus tectorum is a cool season (C3) annual graminoid originating from Eurasia, and a common exotic invasive species of sagebrush systems. *Bromus tectorum* alters fungal community composition by limiting mycorrhizal fungi, increasing abundance of generalist saprophytic fungal species, and decreasing abundance of specialized pathogens, perhaps facilitating *B. tectorum* dominance over native species (Belnap & Phillips 2001). *Bromus tectorum* also disrupts soil food webs, decreases soil fungal abundance, and lowers soil microbial species diversity (Belnap & Phillips 2001) by changing the quantity and quality of litter inputs (Hooker et al. 2008), accelerating rates of decomposition, decreasing nutrient transfer (Hawkes et al. 2006), and altering nitrogen availability (Blank & Morgan 2011). *Bromus tectorum*'s impacts on fire frequency are well documented (Young et al. 1987; D'Antonio & Vitousek 1992; Brooks & Chambers 2011; Mack 2011). Blank and Morgan (2011) and Duda et al. (2003) describe *B. tectorum* and *H. glomeratus* as soil engineers (ecosystem transformers) that alter the structure and abundance of soil microbial communities, and modify physiochemical characteristics that may have landscape-scale impacts on rehabilitation efforts and impede site restoration.

While the literature suggests that soil microbial communities should look different under exotic annual dominated sites, time needed for these shifts to occur is unclear. Soil microbes can respond rapidly to root exudates (Bever et al. 2012) and a variety of environmental stimuli. *Bromus tectorum* can alter soil communities in as little as two to three years post-invasion (Belnap & Phillips 2001). Long-term dominance (50+ years) of *B. tectorum* decreases abundance and richness of soil biota (Belnap et al. 2005), even though soil nutrient changes were variable

and transient in arid and semiarid grasslands (Evans et al. 2001; Ehrenfeld 2003; Belnap et al. 2005).

We investigated the structure of soil microbial communities associated with two native C3 perennial bunchgrasses, *Pseudoroegneria spicata* (Pursh) Á. Löve (Poaceae, bluebunch wheatgrass) and *Poa secunda* J. Presl (Poaceae, Sandberg bluegrass), and two annual exotics (*B. tectorum* and *H. glomeratus*) in post-fire rehabilitation treatments applied to a former *Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young (Asteraceae, Wyoming big sagebrush) community. We asked whether the makeup of soil microbial communities depends upon plant species-specific microsites, and compare microbial community composition and abundance under exotic annuals with that of native grasses three years after rehabilitation seeding. We characterize soil microbiota found under drill seeded (*P. spicata*) and broadcast and volunteer (*P. secunda*) grasses to understand how the presence of native grasses and exotic annuals influence soil biotic communities. Given that perennial bunchgrasses occupy the same soil space temporally and allocate more resources to root development than annual exotics, we hypothesize that total soil microbial abundance should be greater under native perennial bunchgrasses than under exotic annuals.

Materials and Methods

Study Site

The study area (2008 Scooby Fire), located in the Wildcat Hills (41°51’16”N, 113°2’46”W), was approximately 32 km southwest of Snowville, Box Elder County, Utah in the Great Salt Lake Major Land Resource Area (028A). Elevation at the site ranges from 1,420-1,450 m on fan terraces and alluvial plains, with slope gradients of less than 5%. Mean annual air temperature fluctuates between 7.2–10°C, the frost-free period ranges from 116–140 days, and

mean annual precipitation varies from 200–300 mm (NRCS 2010). The study area received above average precipitation in June 2009 following rehabilitation seeding. Precipitation data was gathered from Rosette, Utah which is approximately 32 km west of the study site (1,735 m, Fig. 3.1). Xeric Haplocalcids (Hiko Peak, gravelly loam) and Xeric Torriorthents (Sheeprock, gravelly coarse sand) dominate the site. Both soils are characterized as deep (≥ 60 cm) and well to somewhat excessively drained (Soil Survey Staff 2012). The site is located in Semidesert Gravelly Loam ecological site R028AY215UT (NRCS 2010). Current and historic land management focuses on livestock grazing with use during fall, winter, and spring (Stettler 2009). Big game and sagebrush-obligate species such as *Centrocercus urophasianus* (Phasianidae, greater sage-grouse) depend on the area for critical winter range (NRCS 2010).

Treatment Installation

The fire burned 1.54 km^2 of *A. tridentata* ssp. *wyomingensis* vegetation on lands managed by the U.S. Department of the Interior, Bureau of Land Management (BLM) in September 2008. Vegetation at the site included *A. tridentata* ssp. *wyomingensis*, *Achnatherum hymenoides* (Roem. & Schult.) Barkworth (Poaceae, Indian ricegrass), *P. spicata*, and *E. elymoides* (NRCS 2010), with some exotic annuals growing in the interspaces. Although a few isolated pockets of vegetation remained, the fire removed most of the site's plant cover and litter.

The study was conducted in 2010 and 2011 on a research site established in 2008 to investigate the effects of drill type on the productivity of 1) seeded forbs; 2) native and exotic volunteer forbs; 3) native grasses (both volunteer and seeded); 4) *B. tectorum*; 5) *H. glomeratus*; and 6) *S. kali*. The impacts of failed seedings were also explored by passing the drills over the site without seed. Shaw et al. (2011) examined seeding strategies for applying small-seeded native species, which included: timing of hand broadcast seeding (fall versus winter broadcast

intended to mimic aerial seeding) and drill application of *A. tridentata* ssp. *wyomingensis* seeding rates (1x, 5x, and 10x the standard rate). They included *Artemisia tridentata* ssp. *wyomingensis* seeding rate differences within the drilled treatments to determine the most effective rates for obtaining shrub density targets. *Artemisia tridentata* ssp. *wyomingensis* and other seeded shrub results are not reported here.

Within the study area, five replicate blocks (each block contains approximately 0.028 km^2) were established to examine 13 seeding treatments (65 plots total, Fig. 2.3 in Chapter II). The 13 seeding treatments (Table 2.1 in Chapter II) were assigned randomly by plot (30-m x 70-m) and re-randomized among blocks. A 10-meter buffer was seeded using *A. hymenoides* and *P. spicata* to reduce weed encroachment around the perimeter of all blocks and between plot rows. The blocks were surrounded by a perimeter fence to deter grazing by livestock, but did not exclude big game.

Seeding Method

Two drills (standard rangeland [P&F Services, Kemmerer, WY] and minimum-till [Truax Co., Inc., New Hope, MN]) were used to apply a large-seeded species mix (drill mix) and a small-seeded species mix (broadcast mix) to the study area in November 2008. The rangeland drill (R) is best suited for seeding large-seeded species which are drilled into the soil (Fig. 2.2 in Chapter II). To broadcast small seeds, the disk assemblies were removed from alternate seed drops and replaced with pipes allowing the broadcast mix to drop onto the soil surface. All seeded rows (drilled and broadcast) were covered by dragging chains behind the drill. Plots were also seeded using a minimum-till drill (M) which dropped small seed on the soil surface in alternate rows and firmed the seed into the soil with an imprinter unit. Large-seeded species (drill mix) were drilled into narrow furrows created by hydraulic disk assemblies. Three controls, 1)

undrilled, unseeded; 2) rangeland drilled with no seed; and 3) minimum-till drilled with no seed, were also included.

The drill seed mixture consisted of three perennial grasses and two perennial forbs (Table 2.2 in Chapter II) and was seeded in alternate rows through each drill. The broadcast mixture included two perennial shrubs, two perennial forbs, and one perennial grass (Table 2.2 in Chapter II). The broadcast mix was 1) mechanically surface seeded in the rows between the drill rows and covered with a chain (R) or imprinter unit (M); 2) hand broadcast immediately after drill seeding in November 2008; or 3) hand broadcast over snow in February 2009. Hand broadcasts were intended to simulate aerial seeding. Three *A. tridentata* ssp. *wyomingensis* seeding rates were included in the broadcast mix applied by the drills (seeding rate differences not included in the hand broadcast mix): 1x, 5x, and 10x the standard rate recommended by the BLM for post-fire seedings (Table 2.2 in Chapter II). Rates for native grasses and shrubs approximated those used by the BLM, while forb rates were largely dependent on seed availability. Although all seeding treatments were installed on five replicate blocks at the site, based on initial transect data from 2010, we omitted one block because a portion of the block was dominated by volunteer *Pascopyrum smithii* (Rydb.) Á. Löve (western wheatgrass), which was largely absent from the remainder of block 3 and other blocks.

Soil Collection

In June and July 2011, we collected soil samples for microbial community analysis (phospholipid fatty acid analysis, PLFA). We targeted four vegetative microsites (*P. secunda*, *P. spicata*, *B. tectorum*, and *H. glomeratus*) using 0.2 m^2 circular plots surrounding each targeted plant (Fig. 3.2) for soil collection within five of the thirteen treatments (C, R0, M0, R5x and M5x; Table 2.1 in Chapter II). Selected microsites were dominated by the targeted species (50%

or more cover). Five samples were retrieved for each microsite within each of the five treatments, except *P. spicata* and *H. glomeratus*. *Pseudoroegneria spicata* microsites were sampled in June (40 samples) and July (40 samples) in only the R5x and M5x treatments. *Halogeton glomeratus* was difficult to find in 2011 and only 10 total samples were retrieved from study plots. Samples were taken from four replicate blocks, resulting in a total of 290 samples (Table 3.1). *Salsola kali* was not sampled and few *H. glomeratus* microsites were located, because both species had diminished in abundance over the sampling period. Approximately 15 g of soil was collected from 0-5 cm below the litter layer and within the rooting zone of the targeted grass or forb using a hand trowel. In some cases, *B. tectorum* was present in *P. secunda* microsites, but we attempted to minimize its presence when selecting sample sites. One *B. tectorum* R5x microsite contained a small amount of *P. secunda* (0.44 g) and four microsites (*B. tectorum* M5x, *B. tectorum* R0, and two *P. secunda* R5x microsites) contained small amounts of *Achillea millefolium* L. var. *occidentalis* DC. (western yarrow, < 0.4 g). Soil samples were stored in sealed plastic bags placed on dry ice immediately after collection, then moved to the University of Wyoming soils lab and placed in a -20°C freezer until analyzed. Gravimetric soil water content (Gardner 1986) was determined using the same soil collected for microbial community analysis by weighing soil before and after lyophilization.

Separate soil samples (physiochemical samples) were collected to document pH, electrical conductivity (EC), and texture adjacent to soil microbial sampling areas within a 0.2 m^2 area surrounding *B. tectorum* and *P. secunda* microsites. Physiochemical samples were taken from these two microsites in all five treatments and four replicate blocks. Approximately 150 g of soil was collected below the litter layer to a 5 cm depth within the rooting zone. Samples were stored in plastic bags and allowed to air dry before being passed through a 2 mm sieve. Soils

were hand-textured at the University of Wyoming and then sent to the University of Wyoming Soils Testing Lab for pH and EC analysis.

Biomass Collection

After collecting soil for microbial community, pH, EC, and texture analyses, we clipped all biomass present within a 0.2 m^2 circular area centered on the targeted plant. Clipping was completed in three of the five *B. tectorum* and *P. secunda* microsites in all five treatments. We clipped biomass at 2.5 cm above ground. *Poa secunda* (both volunteer and seeded) was clipped and bagged separately by species. All volunteer (plants that established after the fire from the extant seed bank) annuals were clipped and bagged as a group, including *B. tectorum* found in *P. secunda* microsites. Plant materials were oven dried at 60°C for 48 hours (Bonham 1989) and recorded to the nearest 0.01 g. When samples did not register on the scale (< 0.01 g) even though biomass was present in the bag we recorded 0.01 g to denote the presence of that species or plant group.

Experimental Design and Statistical Analysis

Microbial Community Analysis

Soil microbial community analysis was conducted using a modified version of the Bligh-Dyer phospholipid fatty acid (PLFA) extraction assay (Bligh & Dyer 1959; Frostegård et al. 1991; Buyer et al. 2002), which estimates the relative biomass of 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) and Sherlock® software (MIDI, Inc., Newark, NJ). Soil microbial groups (as a percent 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 the following taxonomic groups through the use of recognized biomarkers: Gram – bacteria, Gram + bacteria, arbuscular mycorrhizal (AM) fungi, fungi (non-AM), protozoans, and total bacteria (sum of Gram – and Gram + bacteria). Total microbial abundance included all taxonomic groups. A fungi:bacteria ratio, which is a commonly reported indicator of substrate use (Bardgett & McAlister 1999), was also calculated by dividing fungi (non-AM) by total bacteria. This ratio represents the amount of fungi relative to bacteria. If the fungi:bacteria ratio equals one, bacteria and fungi are equally abundant; a ratio of less than one means that bacteria are more abundant than fungi.

PLFA data (total and within taxonomic groups) and gravimetric soil water were analyzed using a mixed model ANOVA for a randomized complete block design (four blocks using JMP 10 software, SAS Institute Inc., 2012). Treatment effects were microsite (*B. tectorum*, *P. secunda*, and *P. spicata*), treatment (C, R0, M0, R5x, and M5x), and their interaction. *Bromus tectorum* and *P. secunda* soil samples collected in June 2011 were analyzed using a split-plot in space design and five treatments. To locate extreme values, we plotted the residuals using a histogram with an outlier box plot to determine the shape of the distribution of the residuals. One data point (Block 4, R0 treatment, *P. secunda* microsite) was omitted from this model because microbial biomass was found to be abnormally high. *Bromus tectorum*, *P. secunda*, and *P. spicata* soil samples collected in June 2011 were analyzed in the same manner to compare only the R5x and M5x treatments. *Pseudoroegneria spicata* soil samples were analyzed using a split-plot in time design to compare months (June and July) within the R5x and M5x treatments. Standard errors were calculated using the four replicate blocks and mean separation was calculated using Least Significant Difference (Student's t). Total microbial abundance and

abundance of taxonomic groups within *B. tectorum, P. secunda*, and *P. spicata* microsites were also regressed against gravimetric soil water content.

Plant Production (aboveground biomass)

Plant production from two microsites (*P. secunda* and *B. tectorum*) was summed to obtain results in g/m^2 by treatment. Plant production was grouped as either volunteer annuals (primarily the non-native forb, *Sisymbrium altissimum* L. (Brassicaceae, tall tumblemustard) and *B. tectorum*) or *P. secunda*, analyzed in a mixed model ANOVA for a randomized complete block design (four blocks) with JMP 10 software (SAS Institute Inc., 2012). Because volunteer annuals could not be eliminated from *P. secunda* microsites, we originally analyzed biomass data collected from *P. secunda* microsites with a mixed model ANCOVA, using all volunteer annuals as a covariate. In no case did the addition of covariates alter significance, thus results from the ANOVAs are reported here. Standard errors of the mean were calculated using the four replicate blocks. Mean separation was calculated using Least Significant Difference (Student's t).

Results

Aboveground Plant Biomass within Microsites

Volunteer annuals (*S. altissimum* and *B. tectorum)* within *B. tectorum* microsites were most abundant in C and M0 treatments and least in the R0 and seeded (R5x and M5x) treatments (p = 0.0023; Table 3.2). Volunteer annuals collected from *P. secunda* microsites followed a similar trend, and were most abundant in the control and M0 treatments (p = 0.0003; Table 3.2). Within *P. secunda* microsites, *P. secunda* production was similar across all treatments (p = 0.2824).

Soil Physiochemical Properties

Soil physical and chemical properties were similar across microsites and treatments (Table 3.3). Soil textures were sandy loam or loamy sand with 12% clay, 7.7 pH, and 0.73 electrical conductivity (ds/m).

Soils sampled in June under *B. tectorum* and *P. secunda* microsites contained more water than soils collected under *P. spicata* microsites ($p < 0.0001$; Fig. 3.3). Soil water also decreased from June to July within *P. spicata* microsites ($p = 0.0088$; Fig 3.9b). Within *B. tectorum* microsites, total microbial abundance increased with greater soil moisture ($p < 0.0001$; Fig 3.4). Each component of the microbial community (Gram – and Gram + bacteria, fungi (non-AM), AMF, and protozoans) followed the same trend (Fig. 3.5). Within *P. spicata* microsites, total microbial abundance decreased with greater soil moisture ($p = 0.0202$; Fig. 3.4), as did Gram – bacteria, fungi (non-AM), and protozoans (Fig. 3.6). The relationship between total microbial abundance and gravimetric soil water was not significant within *P. secunda* microsites.

Soil Microbial Community

Total microbial biomass in soils collected within *B. tectorum*, *P. secunda*, and *P. spicata* microsites did not differ in June (Fig. 3.7a). The fungi:bacteria ratio (Fig. 3.7b) 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 (Fig. 3.8). When only *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. 3.8c).

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 (6.58 µg fatty acid/g soil) than in July (8.76 µg fatty acid/ g soil; $p = 0.0002$, Fig. 3.9).

Gram + (p = 0.0057*)* and Gram – (p = 0.0011) bacteria, fungi (p = 0.0224), AMF (p = 0.0205), and protozoans (p = 0.0118) were all more abundant in July within *P. spicata* microsites (Fig. 3.9). However, the fungi to bacteria (F:B) ratio did not change significantly from June to July (Fig. 3.9h). Soil microbial communities under *B. tectorum* and *H. glomeratus* appear to be similar on our site (Fig. 3.10). However, we were only able to collect 10 samples from *H. glomeratus* microsites, and *B. tectorum* samples were collected in June, while *H. glomeratus* soils were sampled in July the same year.

Discussion

Our study characterized soil microbial communities associated with four plant microsites, *P. spicata*, *P. secunda*, *B. tectorum*, and *H. glomeratus*. Our results did not reveal differences in soil microbial communities by microsite three years after fire and rehabilitation seeding. Exotic annual presence, density, and abundance can vary both temporally and spatially, while perennial grasses occupy the same soil space year to year. It is difficult to predict how long it may take for microsite differences to appear, but we did detect treatment by microsite effects and temporal differences in soil microbial communities, which suggest that we should have been able to identify microsite effects unless they develop much more slowly.

Invasive plant species have the potential to alter the composition, structure, and function of soil microbial communities through differential root exudation and turnover, altering the quantity and quality of litter inputs, and influencing nutrient availability (Batten et al. 2006; Westover et al. 1997). Few studies conduct assessments of soil microbial communities using repeated measures so it is difficult to find agreement on the rate of soil microbial response to plant invasion (Wolfe & Klironomos 2005). Batten et al. (2006) demonstrated that *Aegilops triuncialis* L. (Poaceae, barbed goatgrass), an annual C3 grass, can influence the soil microbial

community more quickly than *Centaurea solstitialis* L. (Asteraceae, yellow starthistle), an annual C3 forb. However, soil microbial communities under *B. tectorum* and *H. glomeratus* appear to be similar on our site, despite soils being collected in different months. Greenhouse experiments have shown that an invasive annual grass, *A. triuncialis* can change the soil microbial community in as little as two months, negatively affecting the growth and vigor of a native plant (*Lasthenia californica* DC. ex Lindl. [Asteraceae, California goldfields]) after five months (Batten et al. 2008). However, plant-associated soil microbial communities may develop more rapidly in greenhouse settings than under the same species in field settings (Batten et al. 2008; Ibekwe & Kennedy 1998). Belnap and Phillips (2001) conducted field studies in Utah to compare sites recently invaded by *B. tectorum* (within two to three years of sampling) with 50 year old invaded sites. They documented decreases in species richness and absolute numbers of fungi associated with a transition from mycorrhizal to saprophytic fungi, increases in active bacteria, and similar species of bacteria and fungi on recently invaded sites as on older invasions (Belnap & Phillips 2001). However, they collected soil samples irrespective of microsite, from a greater depth (0-10 cm), and combined samples across sites. Belnap and Phillips (2001) collected soils in fall and spring, which captured seasonal, but not necessarily monthly changes. Their study site had not recently been burned (Belnap & Phillips 2001) while microbial communities at our site were definitely impacted by wildfire. We detected few differences in soil microbiota between *B. tectorum* and perennial bunchgrass soils three years after rehabilitation seeding, with non-AM fungi being the exception.

Fire can have a more devastating impact on fungi than on bacteria, because fungi are less heat resistant (Dangi et al. 2010; Pietikäinen & Fritze 1995). Full recovery of the microbial community (i.e. having soil biotic communities dominated by fungi similar to a mature *A.*

tridentata community), can take three to seven years (Dangi et al. 2010). It is possible that our site was dominated by bacteria and not fungi because insufficient recovery has occurred three years following fire. Our microsites may currently contain microbial communities impacted by wildfire, more than the short-term influence of the seeded plant composition (Kulmatiski & Beard 2011). As *A. tridentata* ssp. *wyomingensis* becomes more abundant on the site, we would anticipate increased spatial heterogeneity of soil nutrient and water distribution (Norton et al. 2012) as the presence of *A. tridentata* often supports "islands of fertility" (Charley & West 1975; Bolton et al. 1990). Soil beneath native *A. tridentata* ssp. *wyomingensis* communities have also been described as being dominated by fungi (Dangi et al. 2010), which suggests that as *A. tridentata* ssp. *wyomingensis* presence increases it could shift the soil community to increased fungi:bacteria ratios. It would be intriguing to document the progression of soil biotic community development in seeded and non-seeded rehabilitation treatments over the next 40 years.

While soil tillage can reduce the presence of fungi (Allison et al. 2005), we did not anticipate that the effects of drilling on our site would be large because the two drills we used minimized soil disturbance. Aboveground plant biomass is also a potential driver of microbial communities (Hawkes et al. 2006). However, differential biomass production on our site did not appear to be tied to soil microbial abundance.

Microbes respond rapidly to environmental stimuli, including availability of soil moisture. Contrary to previous research (Schnürer et al. 1986; Voroney 2007) which links increases in available soil moisture to an increase in soil microbiota, primarily bacteria, we documented month to month shifts in the total abundance of soil microbes with decreased soil moisture within *P. spicata* microsites. Norton et al. (2012) also document greater soil moisture under *B. tectorum* when compared to a perennial bunchgrass (*Agropyron cristatum* (L.) Gaertn.

[crested wheatgrass]). In our study, soil microbial communities were similar across all three grass microsites despite variable soil moisture availability between grasses in drill rows versus between rows. Greater water extraction by *P. spicata* may have led to drier soil which slows decomposition rates (Van Veen & Kuikman 1990). Increased water use may have increased carbon accrual through root-derived organic matter contributions to the soil (root exudates, turnover, and decomposition; Cotrufo et al. 2011). Root inputs into the soil would be anticipated to stimulate microbial activity, which may explain the greater microbial abundance under drill rows in drier months. Many studies document seasonal changes within soil microbial communities (Bardgett et al. 1997; Bardgett et al. 1999; Schmidt et al. 2007), but few reveal changes within one season and microsite.

Our study did not allow comparison to microbial communities under *A. tridentata* ssp. *wyomingensis*, either intact stands or burned stumps. This comparison to native communities would be helpful in the future to determine trajectories and potentially indicate time needed to attain post-fire communities of soil biota. Increased sampling of the same microsite in all seeding treatments, over multiple months would have told a more complete story. Given the logistic and fiscal constraints of our study, it is informative that we captured the short-term temporal changes that can occur within the same microsite. We believe our results offer some optimism for restoration of sagebrush communities. Since the influence of *B. tectorum* on soil microbes is not apparent in the first three years, there is opportunity for restoration before positive feedbacks in the soil community facilitate *B. tectorum* recruitment and limit successful rehabilitation. However, *B. tectorum* abundance was relatively low on our site the first two years, and this window of opportunity may not be present on sites dominated by *B. tectorum* and with high *B. tectorum* recruitment.

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LITERATURE CITED

Allen, E. B., and M. F. Allen. 1988. Facilitation of succession by the nonmycotrophic colonizer *Salsola kali* (Chenopodiaceae) on a harsh site: effects of mycorrhizal fungi. American Journal of Botany **75**:257-266.

Allison, V. J., R. M. Miller, J. D. Jastrow, R. Matamala, and D. R. Zak. 2005. Changes in soil microbial community structure in a tallgrass prairie chronosequence. Soil Science Society of America Journal **69**:1412-1421.

Bais, H. P., T. S. Walker, F. R. Stermitz, R. A. Hufbauer, and J. M. Vivanco. 2002. Enantiomeric dependent phytotoxic and antimicrobial activity of (±)-catechin; a rhizosecreted racemic mixture from Centaurea maculosa (spotted knapweed). Plant Physiology **128**:1173–1179.

Bardgett, R. D., and E. McAlister. 1999. The measurement of soil fungal:bacterial biomass ratios as an indicator of ecosystem self-regulation in temperate meadow grasslands. Biology and Fertility of Soil **29**:282-290.

Bardgett, R. D., D. K. Leemans, R. Cook, and P. J. Hobbs. 1997. Seasonality of the soil biota of grazed and ungrazed hill grasslands. Soil Biology and Biogeochemistry **29**:1285-1294.

Bardgett, R. D., R. D. Lovell, P. J. Hobbs, and S. C. Jarvis. 1999. Seasonal changes in soil microbial communities along a fertility gradient of temperate grasslands. Soil Biology and Biochemistry **31**:1021-1030.

Batten, K. M., K. M. Scow, and E. K. Espeland. 2008. Soil microbial community associated with an invasive grass differentially impacts native plant performance. Microbial Ecology **55**:220-228.

Batten, K. M., K. M. Scow, K. F. Davies, and S. P. Harrison. 2006. Two invasive plants alter soil microbial community composition in serpentine grasslands. Biological Invasions **8**:217-230.

Belnap, J., and S. L. Phillips. 2001. Soil biota in an ungrazed grassland: response to annual grass (*Bromus tectorum*) invasion. Ecological Applications **11**:1261-1275.

Belnap, J., S. L. Phillips, S. K. Sherrod, and A. Moldenke. 2005. Soil biota can change after exotic plant invasion: does this affect ecosystem processes? Ecology **86**:3007-3017.

Bever, J. D., T. G. Platt, and E. R. Morton. 2012. Microbial population and community dynamics on plant roots and their feedbacks on plant communities. Annual Review of Microbiology **66**:265-283.

Blank, R., and T. Morgan. 2011. Evidence that invasion by cheatgrass alters soil nitrogen availability. Natural Resources and Environmental Issues **17**:1-4.

Bligh, E. G., and W. J. Dyer. 1959. A rapid method of total lipid extraction and purification. Canadian Journal of Biochemistry and Physiology **37**:911-917.

Bolton, H., R. E. Wildung, and J. L. Smith. 1990. Nitrogen mineralization potentials of shrub-steppe soils with different disturbance histories. Soil Science of American Journal **54**:887-891.

Bonham, C. D. 1989. Measurements for terrestrial vegetation. John Wiley & Sons, Inc., New York.

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

Buyer, J. S., D. P. Roberts, and E. Russek-Cohen. 2002. Soil and plant effects on microbial community structure. Canadian Journal of Microbiology **48**:955-964.

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

Charley, J. L., and N. E. West. 1975. Plant-induced soil chemical patterns in some shrub-dominated semi-desert ecosystems of Utah. Journal of Ecology **63**:945-964.

Cotrufo, M. F., G. Alberti, I. Inglima, H. Marjanovic, D. LeCain, A. Zaldei, A. Peressotti, and F. Miglietta. 2011. Decreased summer drought affects plant productivity and soil carbon dynamics in a Mediterranean woodland. Biogeosciences **8**:2729-2739.

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

Dangi, S. R., P. D. Stahl, E. Pendall, M. B. Cleary, and J. S. Buyer. 2010. Recovery of soil microbial community structure after fire in a sagebrush-grassland ecosystem. Land Degradation and Development **21**:423-432.

Davies, K. W., C. S. Boyd, J. L. Beck, J. D. Bates, T. J. Svejcar, and M. A. Gregg. 2011. Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush plant communities. Biological Conservation **144**:2573-2584.

Duda, J. J., D. C. Freeman, J. M. Emlen, J. Belnap, S. G. Kitchen, J. C. Zak, E. Sobek, M. Tracy, and J. Montante. 2003. Differences in native soil ecology associated with invasion of the exotic annual chenopod, *Halogeton glomeratus*. Biology and Fertility of Soils **38**:72-77.

Eckert, R. E. Jr., and F. E. Kinsinger. 1960. Effects of *Halogeton glomeratus* leachate on chemical and physical characteristics of soils. Ecology **41**:764-772.

Ehrenfeld, J. G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems **6**:503-523.

Evans, R. D., R. Rimer, L. Sperry, and J. Belnap. 2001. Exotic plant invasion alters nitrogen dynamics in an arid grassland. Ecological Applications **11**:1301-1310.

Frostegård, A., A. Tunlid, and E. Bååth. 1991. Microbial biomass measured as total lipid phosphate in soils of different organic content. Journal of Microbiological Methods **14**:151-163.

Gardner, W. H. 1986. Chapter 21. Water Content. Pages 493-541 in E. A. Klute, editor. Methods of soil analysis: part 1 physical and mineralogical methods. American Society of Agronomy, Inc. and Soil Science Society of America, Inc., Madison, Wisconsin.

Harper, K. T., R. Van Buren, and S. G. Kitchen. 1996. Invasion of alien annuals and ecological consequences in salt desert shrublands of western Utah. Pages 58-65 in J. R. Barrow, E. D. McArthur, R. E. Sosebee, and R. J. Tausch, editors. Proceedings: symposium on shrubland ecosystem dynamics in a changing climate. INT-GTR-319. U.S. Department of Agriculture, Forest Service, Ogden, Utah.

Hawkes, C. V., J. Belnap, C. D'Antonio, and M. K. Firestone. 2006. Arbuscular mycorrhizal assemblages in native plant roots change in the presence of invasive exotic grasses. Plant and Soil **281**:369-380.

Hooker, T. D., J. M. Stark, U. Norton, A. J. Leffler, M. Peek, and R. Ryel. 2008. Distribution of ecosystem C and N within contrasting vegetation types in a semiarid rangeland in the Great Basin, USA. Biogeochemistry **90**:291-308.

Howard, J. L. 1992. *Salsola kali*. Fire Effects Information System. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Missoula, Montana. (available from http://www.fs.fed.us/database/feis/).

Ibekwe, A. M., and A. C. Kennedy. 1998. Phospholipid fatty acid profiles and carbon utilization patterns for analysis of microbial community structure under field and greenhouse conditions. FEMS Microbiology Ecology **26**:151-163.

JMP, Version 10. 2012. SAS Institute Inc., Cary, North Carolina.

Klironomos, J. N. 2002. Feedback with soil biota contributes to plant rarity and invasiveness in communities. Nature **417**:67-70.

Kulmatiski, A., and K. H. Beard. 2011. Long-term plant growth legacies overwhelm short-term plant growth effects on soil microbial community structure. Soil Biology and Biochemistry **43**:823-830.

Mack, R. N. 2011. Fifty years of "Waging war on cheatgrass": research advances, while meaningful control languishes. Pages 253-265 in D. Richardson, editor. Fifty years of invasion ecology. Wiley-Blackwell Press, Oxford, United Kingdom.

Mangla, S., Inderjit, and R. M. Callaway. 2008. Exotic invasive plant accumulates native soil pathogens which inhibit native plants. Journal of Ecology **96**:58-67.

Mummey, D. L., and M. C. Rillig. 2006. The invasive plant species *Centaurea maculosa* alters arbuscular mycorrhizal fungal communities in the field. Plant and Soil **288**:81-90.

Norton, U., P. Saetre, T. D. Hooker, and J. M. Stark. 2012. Vegetation and moisture controls on soil carbon mineralization in semiarid environments. Soil Science Society of American Journal **76**:1038-1047.

NRCS (U. S. Department of Agriculture, Natural Resources Conservation Service). 2010. Ecological Site Descriptions. (available from http://esis.sc.egov.usda.gov/Welcome/pgESDWelcome.aspx).

Pavek, D. S. 1992. *Halogeton glomeratus*. Fire Effects Information System. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Missoula, Montana. (available from http://www.fs.fed.us/database/feis/).

Pietikäinen, J. and H. Fritze. 1995. Clear-cutting and prescribed burning in coniferous forest: comparison of effects on soil fungal and total microbial biomass, respiration activity and nitrification. Soil Biology and Biochemistry **27**:101-109.

Scharfy, D., S. Güsewell, M. O. Gessner, and H. O. Venterink. 2010. Invasion of *Solidago gigantea* in contrasting experimental plant communities: effects on soil microbes, nutrients and plant-soil feedbacks. Journal of Ecology **98**:1379-1388.

Schmidt, S. K., E. K. Costello, D. R. Nemergut, C. C. Cleveland, S. C. Reed, M. N. Weintraub, A. F. Meyer, and A. M. Martin. 2007. Biogeochemical consequences of rapid microbial turnover and seasonal succession in soil. Ecology **88**:1379-1385.

Schnürer, J., M. Clarholm, S. Boström, and T. Rosswall. 1986. Effects of moisture on soil microorganisms and nematodes: a field experiment. Microbial Ecology **12**:217-230.

Shaw, N., R. D. Cox, A. C. Ganguli, A. L. Hild, B. Newingham, M. Pellant, D. Pyke, and J. Truax. 2011. Final report: equipment and strategies to enhance the post-wildfire establishment and persistence of Great Basin native plants. Joint Fire Science Program Project Number 07-1-3-12. 30 p.

Soil Survey Staff. 2012. Official Soil Series Descriptions. U.S. Department of Agriculture, Natural Resources Conservation Service. (available from http://soils.usda.gov/technical/classification/osd/index.html).

Stettler, H. 2009. Cultural resource inventory of 70 acres of the Scooby Fire area, Box Elder County, Utah. Pages 1-41. Utah State Antiquities Project No. U-08-ST-1063b. SWCA Environmental Consultants, Salt Lake City, Utah.

Van Veen, J. A., and P. J. Kuikman. 1990. Soil structural aspects of decomposition of organic matter by micro-organisms. Biogeochemistry **11**:213-233.

Voroney, R. P. 2007. The soil habitat. Pages 25-49 in E. A. Paul, editor. Soil Microbiology and Biochemistry, 3rd ed. Academic Press, Elsevier, Inc., Burlington, Massachusetts.

WRCC (Western Regional Climate Center). Desert Research Institute. 2012. Reno, Nevada. (available from http://www.wrcc.dri.edu/).

Westover K. M., A. C. Kennedy, and S. E. Kelley. 1997. Patterns of rhizosphere microbial community structure associated with co-occurring plant species. Journal of Ecology **85**:863‑873.

Wolfe, B. E., and J. N. Klironomos. 2005. Breaking new ground: soil communities and exotic plant invasion **55**:477-487.

Young, J. A., R. A. Evans, R. E. Eckert Jr., and B. L. Kay. 1987. Cheatgrass. Rangelands **9**:266-270.

Table 3.1. Soil samples taken from *Poa secunda*, *Pseudoroegneria spicata*, *Bromus tectorum*, and *Halogeton glomeratus* microsites in June and July 2011 for PLFA and physiochemical analyses.

Targeted Species (microsite)	**Month**	**R5x**	**R0**	**C**	**M0**	**M5x**	**Total**
		Samples taken (no.)					
P. secunda	June	20	20	20	20	20	100
P. spicata	June	20	---	---	---	20	40
	July	20	---	---	---	20	40
B. tectorum	June	20	20	20	20	20	100
*H. glomeratus**	July	---	---	---	---	---	10
							290

**Halogeton glomeratus* was collected where found in the following treatments: MBC5x (7 samples), M10x, M1x, and M0 (1 sample each).

Table 3.2. Aboveground biomass in *Poa secunda* and *Bromus tectorum* microsites in treatments sampled for soil microbial analysis, n=20 for each microsite. Lower case letters separate treatments within a single microsite. Means with the same letter do not differ.

Microsite	Treatment	Biomass (g/m^2)			
		All Volunteer Annuals		*Poa secunda*	
Poa secunda	R5x	14.02	c	59.02	a
	R0	53.87	b	79.23	a
	C	96.48	a	83.44	a
	M0	90.02	a	56.87	a
	M5x	21.74	bc	28.09	a
	Mean	55.23		61.33	
Bromus tectorum	R5x	114.63	b	0.18	
	R0	141.09	b	0.00	
	C	228.27	a	0.00	
	M0	203.54	a	0.00	
	M5x	123.38	b	0.00	
	Mean	162.18		0.04	

Table 3.3. Soil physiochemical properties under *Poa secunda* (n = 100) and *Bromus tectorum* (n = 100) microsites in five seeding treatments.

Microsite	Treatment		pH	EC (ds/m)	Clay (%)
P. secunda	R5x		7.7	0.64	12
	R0		7.7	0.77	13
	C		7.8	0.69	13
	M0		7.6	0.75	11
	M5x		7.6	0.66	12
		Mean	7.7	0.70	12
B. tectorum	R5x		7.7	0.77	13
	R0		7.6	0.81	13
	C		7.8	0.73	13
	M0		7.6	0.78	11
	M5x		7.7	0.71	12
		Mean	7.7	0.76	12

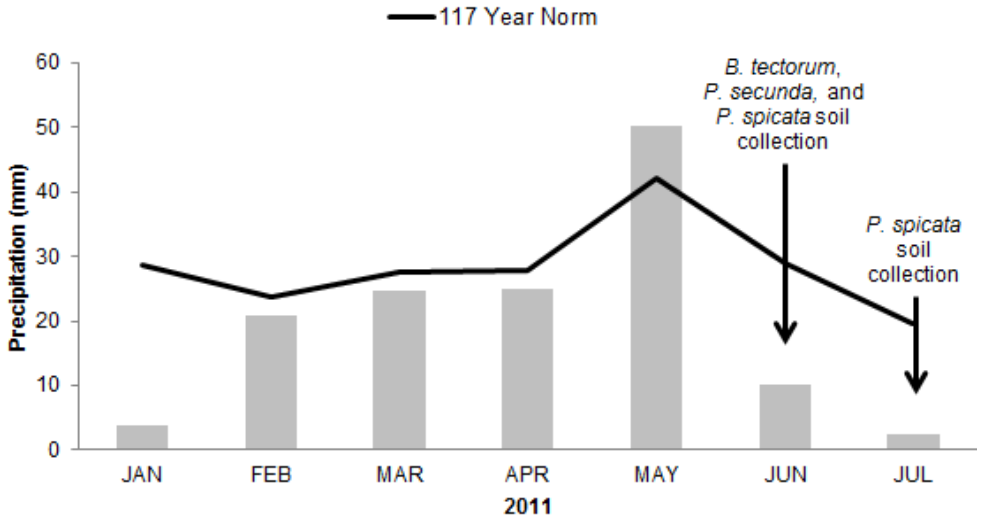

Figure 3.1. Monthly and long-term precipitation for the Scooby Fire site in 2011 (WRCC 2012). Monthly data gathered from Rosette, UT (1735 m) located approximately 32 km west of the study site. The solid line represents the 117 year norm which is an average of precipitation from Rosette and Snowville, UT (1396 m), located approximately 31 km northeast of the study site. Some days are missing from the available dataset. In 2011 2-6 days are missing from January to July. Data last examined on 5 February 2013 at http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?ut7408.

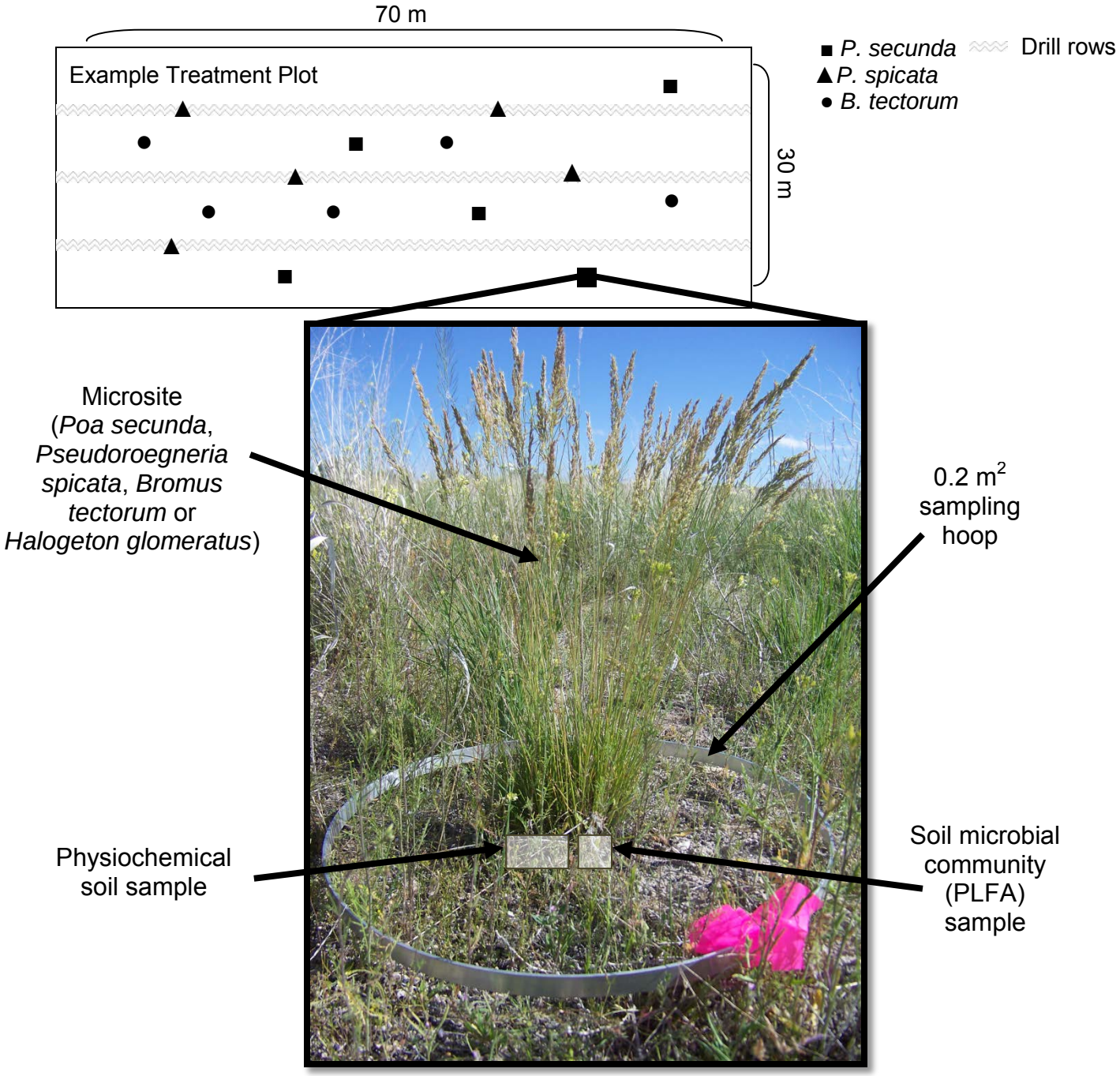

Figure 3.2. Field placement of soil samples within one 30-m x 70-m treatment plot with drill rows and interspaces. Within each of the controls (R0, C, M0), five 0.2 m^2 samples were collected within each *B. tectorum* and *P. secunda* microsite. In the R5x and M5x treatments, five 0.2 m^2 microsites were sampled in each of the three microsites (*B. tectorum*, *P. secunda*, and *P. spicata*). Ten random *H. glomeratus* samples were also collected where found, across multiple treatments and blocks. Revegetation treatments were installed at the Scooby Fire rehabilitation site in fall 2008.

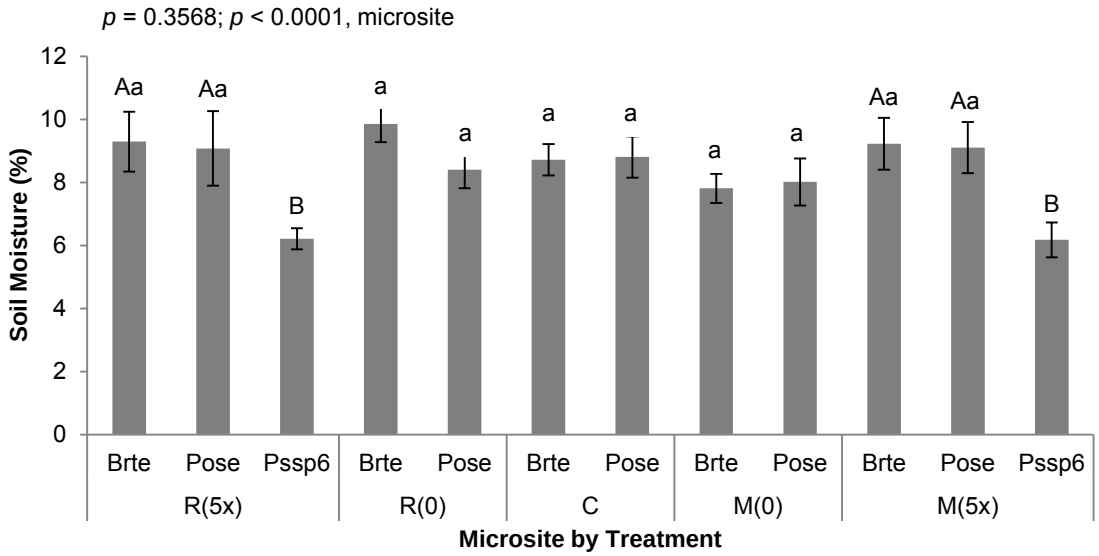

Figure 3.3. Gravimetric soil water for *Bromus tectorum* (Brte, n = 100) and *Poa secunda* (Pose, n = 100) microsites across five seeding treatments (R5x, R0, C, M0, M5x, $p = 0.3568$) and *B. tectorum, P. secunda*, and *Pseudoroegneria spicata* (Pssp6, n = 80) across drill seeded treatments (R5x, M5x, $p < 0.0001$). Bars are standard errors of means. Only when three microsites were considered (R5x, M5x treatments) did gravimetric soil water differ. Means with the same letter do not differ ($p > 0.05$, LSD). Capital letters are mean separation for all three microsites, and lower case letters are mean separation for *B. tectorum* and *P. secunda* microsites only. F-test probabilities (p values) are reported for microsite.

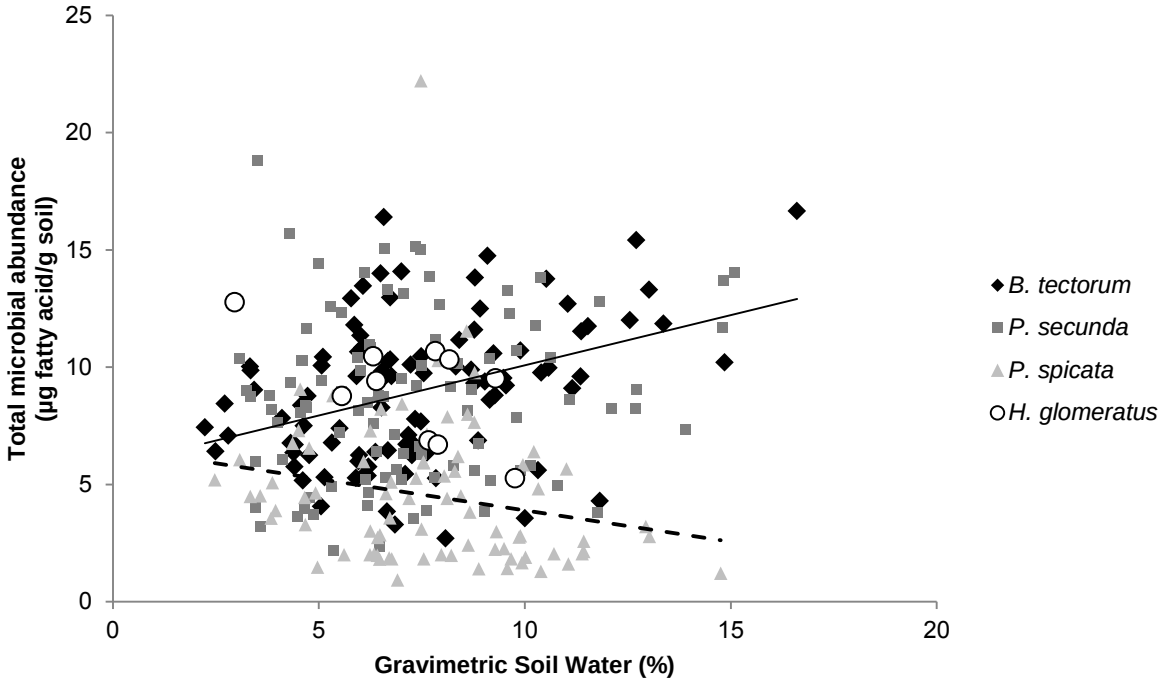

Figure 3.4. Total microbial abundance regressed against gravimetric soil water for *Bromus tectorum, Poa secunda, Pseudoroegneria spicata*, and *Halogeton glomeratus* microsites. *Bromus tectorum* (solid line) microsites yielded a positive relationship ($p < 0.0001$). *Pseudoroegneria spicata* (dotted line) microsites yielded a negative relationship ($p = 0.0202$).

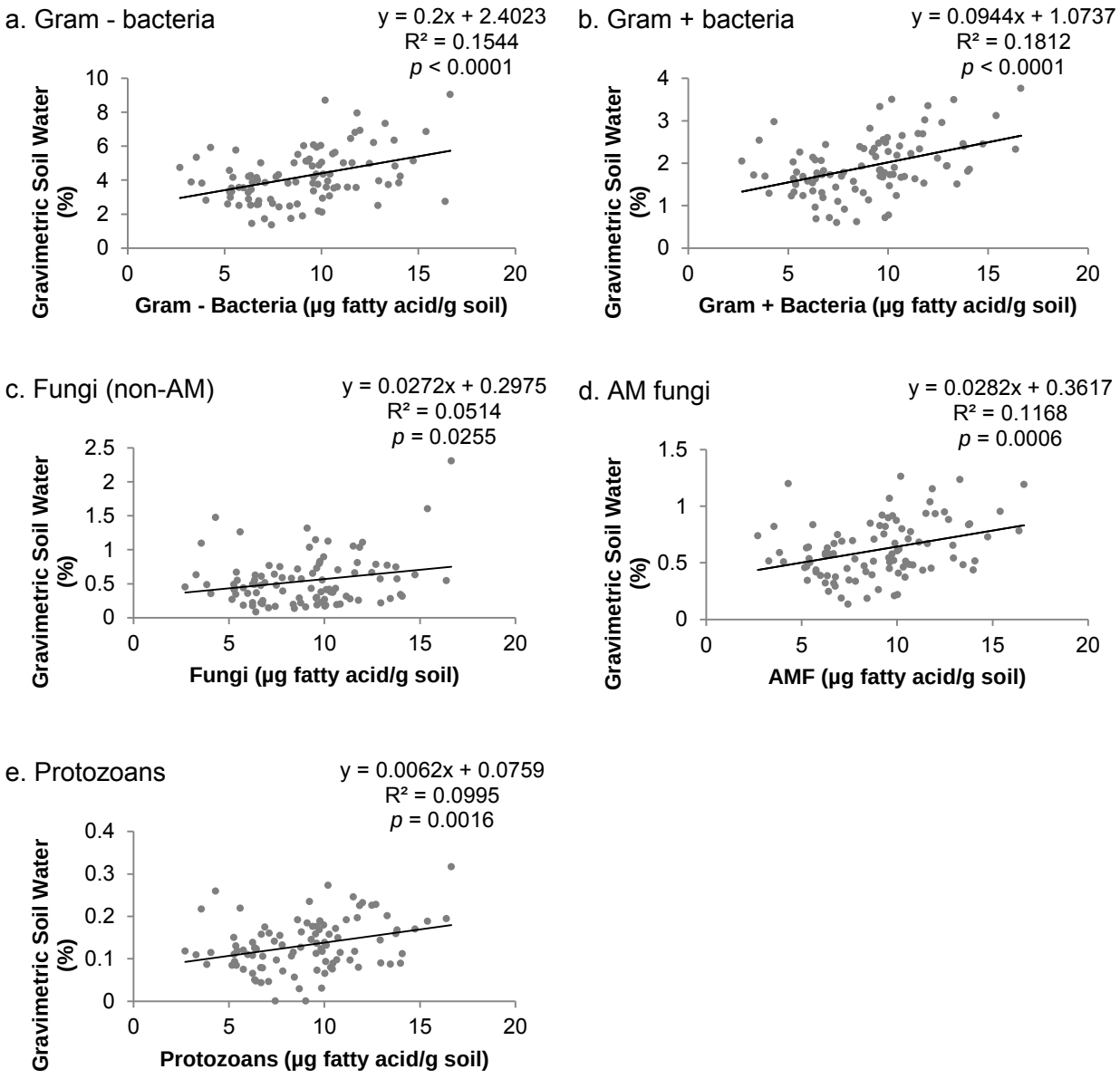

Figure 3.5. Soil biotic community composition (a-e) within *Bromus tectorum* microsites regressed against gravimetric soil water.

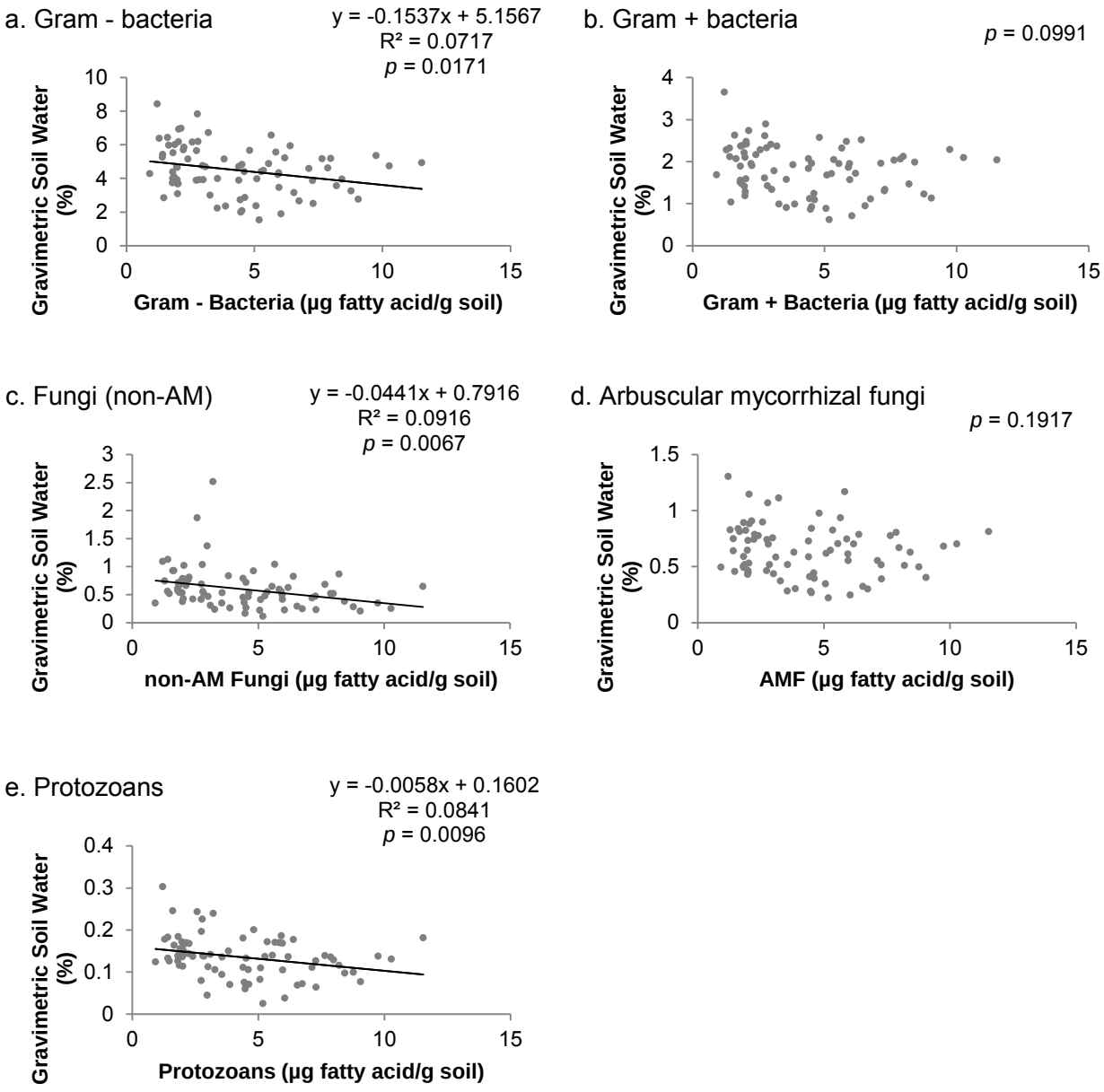

Figure 3.6. Soil biotic community composition (a-e) within *Pseudoroegneria spicata* microsites regressed against gravimetric soil water.

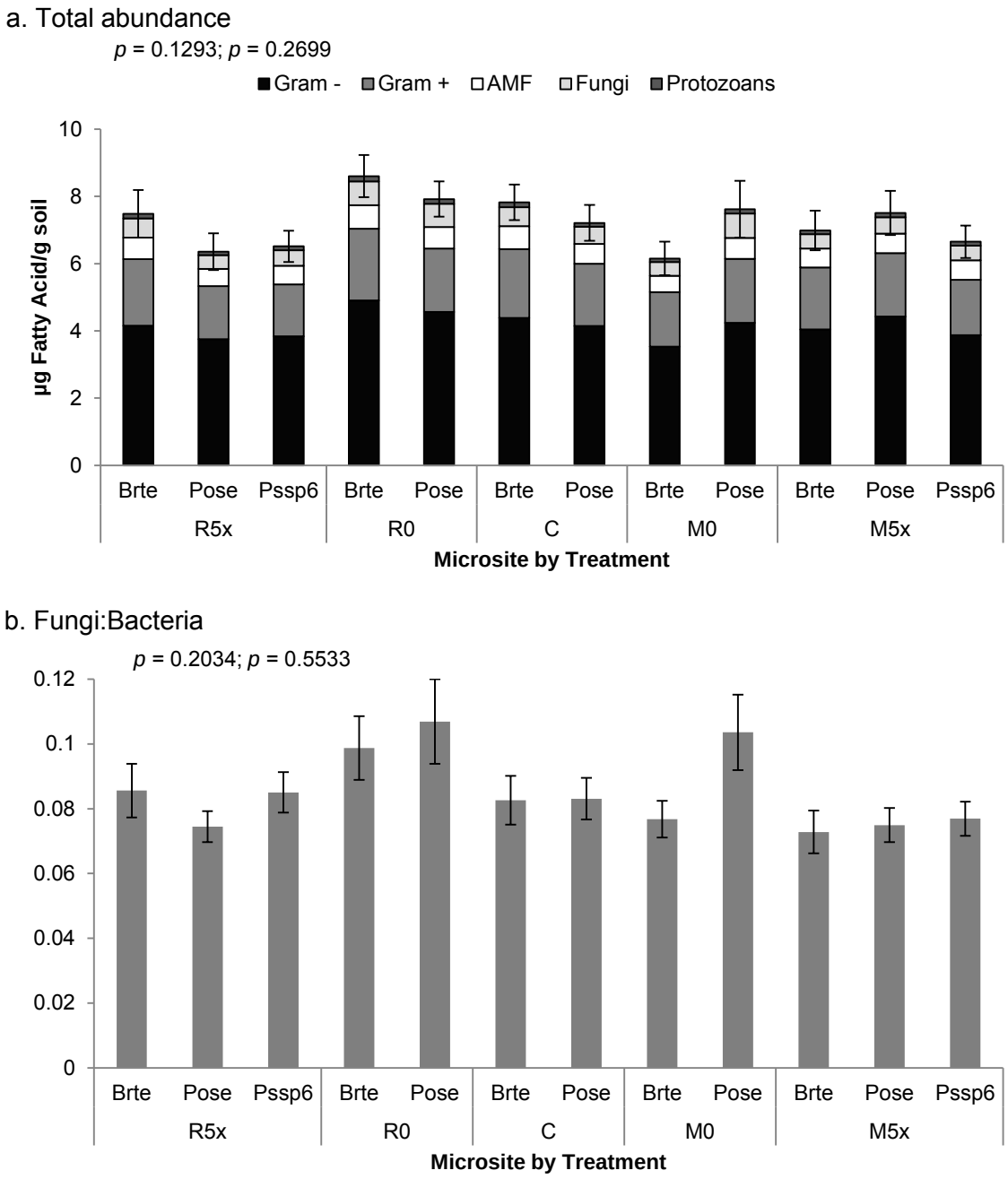

Figure 3.7. Microbial biomass production in *Bromus tectorum* (Brte, n = 100) and *Poa secunda* (Pose, n = 100) microsites across five seeding treatments (R5x, R0, C, M0, M5x, first *p* value) and *B. tectorum, P. secunda*, and *Pseudoroegneria spicata* (Pssp6, n = 80) across drill seeded treatments (R5x, M5x, second *p* value). Bars are standard errors of means. Means with the same letter do not differ ($p > 0.05$, LSD). F-test probabilities (*p* values) are reported for the microsite by treatment interaction.

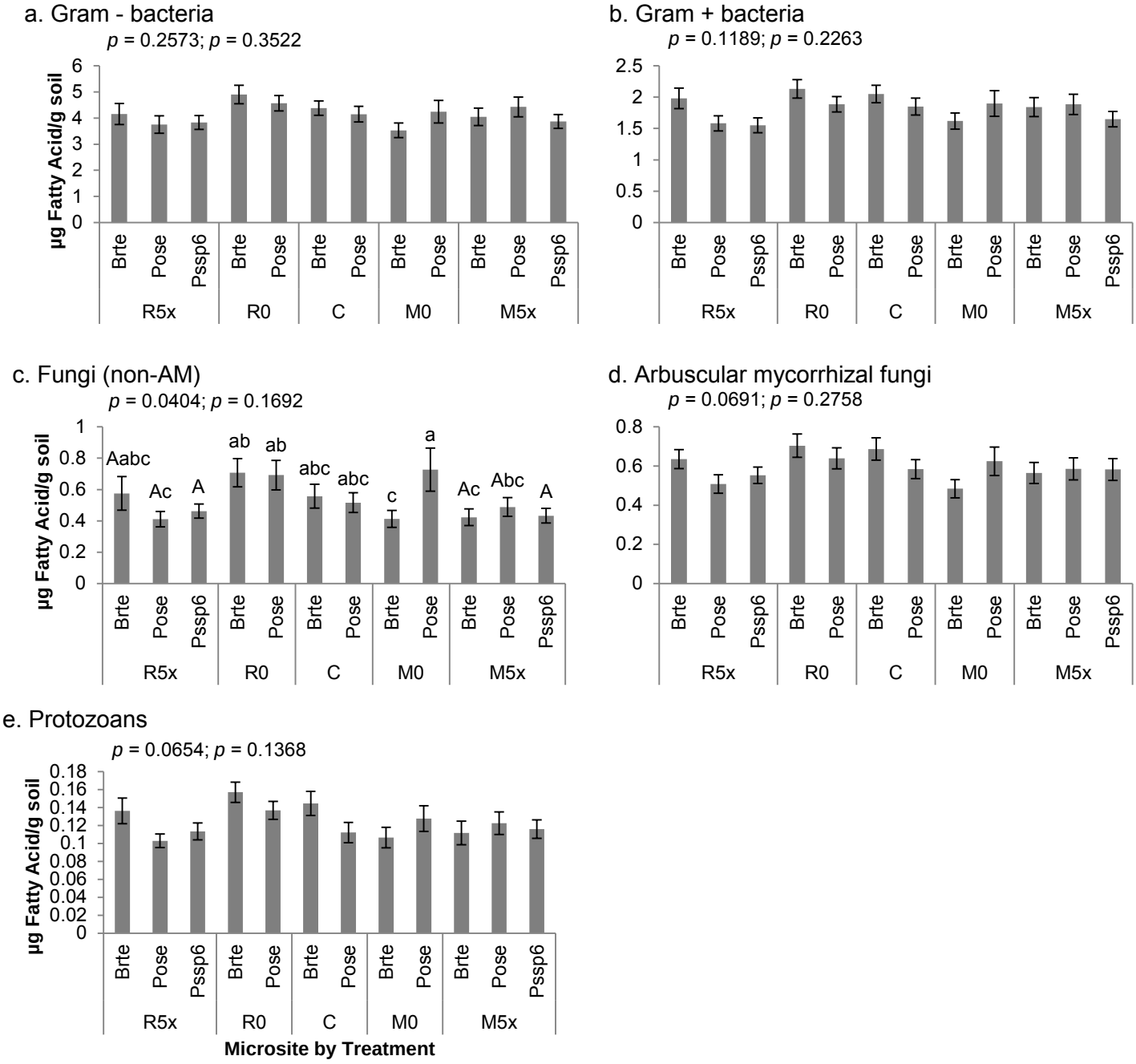

Figure 3.8. Soil microbial production for *Bromus tectorum* (Brte, n =100) and *Poa secunda* (Pose, n = 100) microsites across five seeding treatments (R5x, R0, C, M0, M5x, first *p* value) and *B. tectorum, P. secunda*, and *Pseudoroegneria spicata* (Pssp6, n =80) across drill seeded treatments (R5x, M5x, second *p* value). Bars are standard errors of means. Fungi only differed when two microsites were considered (all 5 treatments); *P. spicata*, sampled only in R5x and M5x treatments, shown for visual comparison. Means with the same letter do not differ ($p > 0.05$, LSD). Capital letters are mean separation for all three microsites, and lower case letters are mean separation for *B. tectorum* and *P. secunda* microsites only. F-test probabilities (*p* values) are reported for the microsite by treatment interaction.

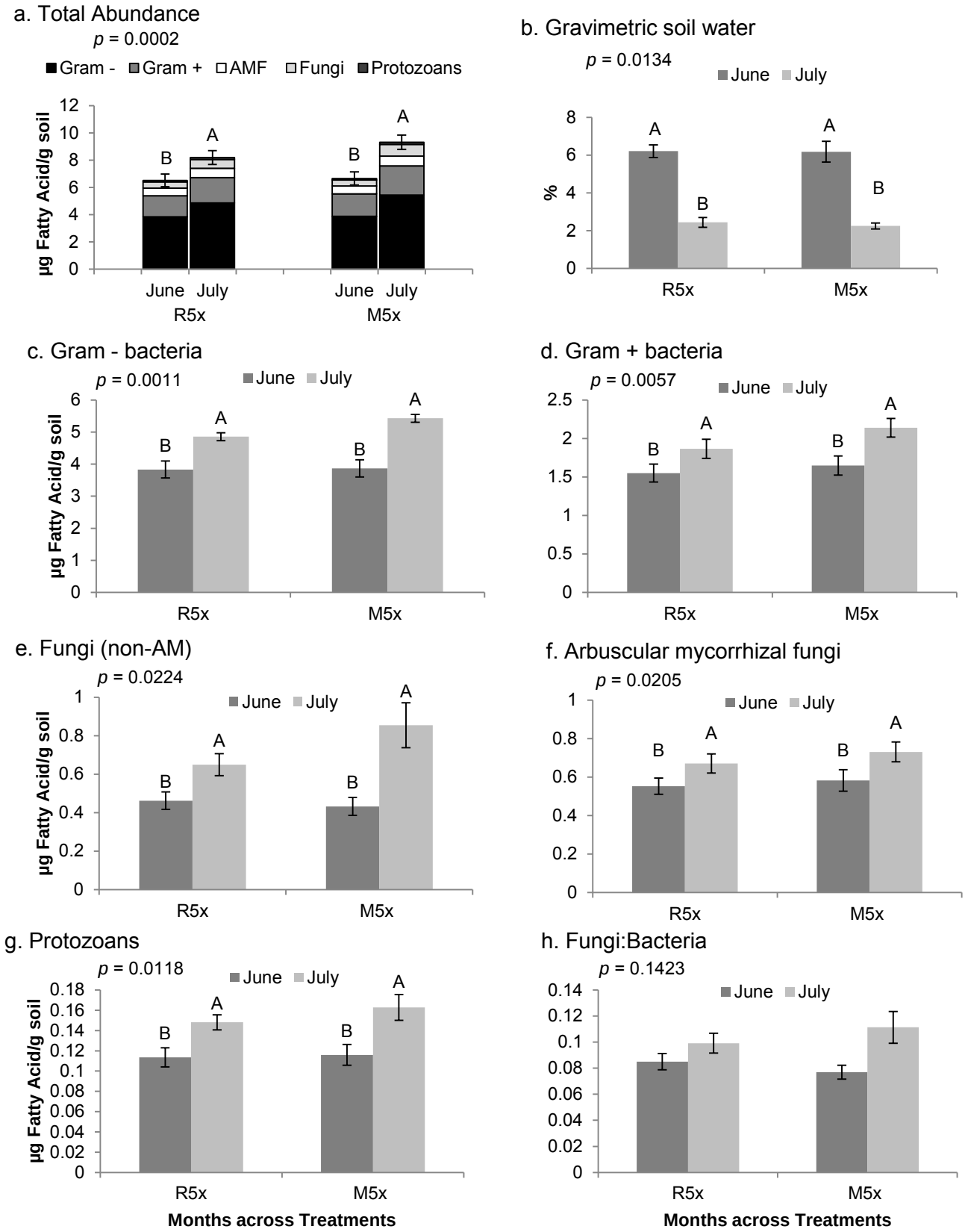

Figure 3.9. Comparison of June and July 2011 microbial biomass production and gravimetric soil water in *Pseudoroegneria spicata* microsites in the R5x and M5x treatments (n = 80). Bars are standard errors of means. Within each microbial taxonomic group means with the same letter do not differ ($p > 0.05$, LSD). F-test probabilities (p values) are reported for month.

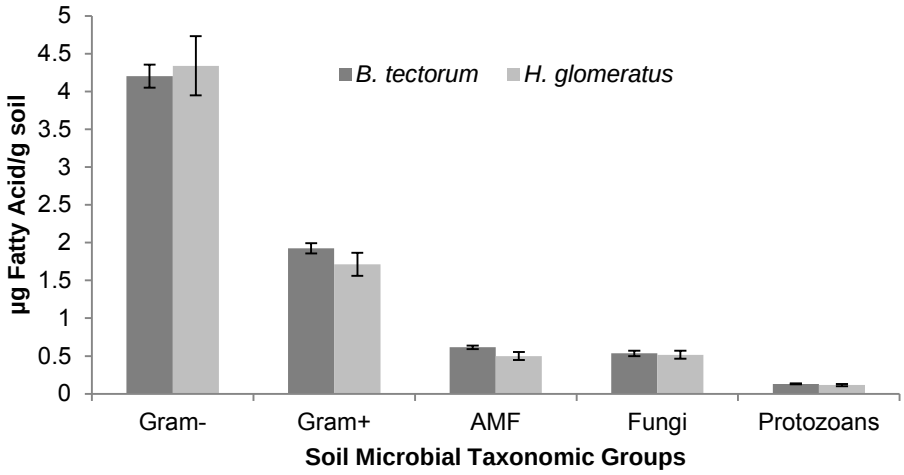

Figure 3.10. Microbial biomass production in *Bromus tectorum* microsites sampled in June 2011 and *Halogeton glomeratus* microsites sampled in July 2011, three years after wildfire rehabilitation seeding. *Bromus tectorum* samples (n = 100) were taken from five treatments (R5x, R0, C, M0, M5x). *Halogeton glomeratus* samples (n = 10) were collected from the MBC5x, M10x, M1x and R0 treatments.

CHAPTER IV

Conclusions

Invasive annuals have significantly impacted native sagebrush communities in the Great Basin by shortening fire return intervals (Young et al. 1987; Pavek 1992; Brooks et al. 2004; Smith 2005; Chambers 2008; Brooks & Chambers 2011). A growing body of evidence suggests that exotic annuals can capitalize on post-fire nutrient availability and engineer soil properties initiating positive feedbacks that favor their growth (Young & Evans 1978; Belnap & Phillips 2001; West & York 2002; Belnap et al. 2005; Batten et al. 2006; Hawkes et al. 2006; Batten et al. 2008).

Post-fire rehabilitation seedings are initiated to limit exotic annual encroachment, in addition to stabilizing soils and returning ecosystem function. However, rehabilitation efforts may fail because of variable precipitation on arid sites (Chambers et al. 2007), improper seed bed preparation and inadequate seeding technology (James & Svejcar 2010), competition from exotic annuals (Eiswerth et al. 2009), and altered soil properties. Rehabilitation efforts should follow a more holistic approach to consider the entire ecosystem (Davies et al. 2011) relative to the impacts of invasive species on both the plant community and soil biota.

Our study investigated the establishment of native seeded species and the return of volunteer plant species following wildfire rehabilitation seedings on a former *Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young (Asteraceae, Wyoming big sagebrush) site in northern Utah. Our study demonstrated that successful establishment of rehabilitation seedings can limit the presence of exotic annuals three years post-fire on lower elevation sagebrush sites. Our own results agree with other research which demonstrates that native perennial bunchgrasses

can inhibit the growth and spread of exotic annuals, such as *Bromus tectorum* L. (Poaceae, cheatgrass) by depleting soil nitrogen (Blank & Morgan 2012). At our site, native seedlings emerged and established well. Favorable precipitation the summer after rehabilitation seeding may have contributed to the high germination and establishment of natives recorded on our site. Other studies suggest that seeding method (e.g. ability to place seed at an exact depth) may be the determining factor of successful seedling establishment (James & Svejcar 2010). We detected no effects of drill type in production of native seeded species, volunteer forbs, or targeted exotic annuals three years after rehabilitation seeding. Drill differences may be more apparent when precipitation is less than ideal for seedling establishment.

Temporal differences in soil microbial presence within drill rows beneath *Pseudoroegneria spicata* (Pursh) Á. Löve (Poaceae, bluebunch wheatgrass) suggest that soil microbial abundance can fluctuate greatly within a single season. This result suggests that repeated sampling within the same season and microsite is important to refining our understanding of temporal shifts in microbial communities (Wolfe & Klironomos 2005). As we have demonstrated, microbial abundance can vary dramatically in microsites under a single plant species over one month. Few studies document soil microbial abundance within reseeded sites on a monthly basis or at small spatial scales (microsite). Soil microbial communities associated with exotic grass and forb microsites were very similar to native perennial grass microsites three years after wildfire and rehabilitation seeding. Because we recorded monthly differences beneath drill rows, we should have been able to detect microsite effects had they been present. Belnap and Phillips (2001) suggest two to three years is sufficient for *B. tectorum* to influence soil microbiota. We did not see this effect in our study where conditions were moister and the site

had recently burned. We did not document nutrient availability, but suspect that wildfire may have increased nitrogen availability.

Our results seem to support those of Rowe and Brown (2008) which suggest that soil microbial communities do not facilitate *B. tectorum* invasion. *Bromus tectorum* influenced soils did not inhibit the growth of native plants (Rowe & Brown 2008) and *B. tectorum* did not benefit from its own soil conditioning (species-specific alterations of the soil environment, Perkins & Nowak 2012). Regardless of an exotic annual's ability to alter soil properties and biotic communities, it is unclear whether these changes confer competitive benefits (Batten et al. 2006; Belnap & Phillips 2001) or at what stage of invasion soil microbes may be most beneficial or harmful (Wolfe & Klironomos 2005). In the case of *B. tectorum,* it may be that altered fire regimes (D'Antonio & Vitousek 1992), rapid response to nitrogen availability (Link et al. 1995; Monaco et al. 2003), and early germination before native perennial bunchgrasses (Mack & Pyke 1983; Knapp 1996; Arredondo et al. 1998) are more important than initiating plant-soil feedbacks in maintaining site dominance.

When restoring native plant communities, the biological properties of the soil may be integral to native plant reestablishment (Mummey & Rillig 2006). When native species are seeded immediately after wildfire, natives can quickly establish allowing them to compete with prolific and fast-spreading exotic annuals. In the short-term, native seeding does reduce production of exotic annuals. However, failed rehabilitation seedings are a common occurrence in the Great Basin. Two of our treatments were designed to replicate failed seedings and provide evidence that drilling alone may initially enhance the presence of *S. kali*, although this difference was short-lived. While *S. kali* can expedite revegetation on disturbed sites by acting as nurse plant for native seedlings (Allen & Allen 1988; Howard 1992), *S. kali* may also facilitate

invasion by *B. tectorum* (Piemeisel 1951; Evans and Young 1983). In contrast, *B. tectorum* emergence can be initially hampered by drills that bury its seed bank too deeply (Piemeisel 1951; Young et al. 1969), and perhaps provide an opportunity to reseed again before *B. tectorum* becomes fully established.

Sites not previously dominated by exotic annuals may experience autogenic regeneration of native perennial bunchgrasses which will compete with seeded species (Boyd & Davies 2012). However, if a significant exotic annual component is present prior to wildfire the site will likely be dominated by exotic annuals following fire (Eiswerth et al. 2009) in the absence of seeding. Given that the controls at our site became dominated by *B. tectorum*, rehabilitation seeding was necessary to curtail the spread of exotic annuals. It will be interesting to document the trajectory of seeded and exotic species over a longer period of time.

LITERATURE CITED

Allen, E. B., and M. F. Allen. 1988. Facilitation of succession by the nonmycotrophic colonizer *Salsola kali* (Chenopodiaceae) on a harsh site: effects of mycorrhizal fungi. American Journal of Botany **75**:257-266.

Arredondo, J. T., T. A. Jones, and D. A. Johnson. 1998. Seedling growth of Intermountain perennial and weedy annual grasses. Journal of Range Management **51**:584-589.

Batten, K. M., K. M. Scow, and E. K. Espeland. 2008. Soil microbial community associated with an invasive grass differentially impacts native plant performance. Microbial Ecology **55**:220-228.

Batten, K. M., K. M. Scow, K. F. Davies, and S. P. Harrison. 2006. Two invasive plants alter soil microbial community composition in serpentine grasslands. Biological Invasions **8**:217-230.

Belnap, J., and S. L. Phillips. 2001. Soil biota in an ungrazed grassland: response to annual grass (*Bromus tectorum*) invasion. Ecological Applications **11**:1261-1275.

Belnap, J., S. L. Phillips, S. K. Sherrod, and A. Moldenke. 2005. Soil biota can change after exotic plant invasion: does this affect ecosystem processes? Ecology **86**:3007-3017.

Blank, R., and T. Morgan. 2012. Suppression of *Bromus tectorum* L. by established perennial grasses: potential mechanisms—part one. Applied and Environmental Soil Science. Article ID 632172. 9 pages. doi:10.1155/2012/63212.

Boyd, C. S., and K. W. Davies. 2012. Spatial variability in cost and success of revegetation in a Wyoming big sagebrush community. Environmental Management **50**:441-450.

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

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

Chambers, J. C. 2008. Invasive plant species and the Great Basin. Pages 38-41 in J. C. Chambers, N. Devoe, and A. Evenden, editors. Collaborative management and research in the Great Basin—examining the issues and developing a framework for action. GTR-RMRS-204. U.S. Department of Agriculture, Forest Service, Fort Collins, Colorado.

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

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

Davies, K. W., C. S. Boyd, J. L. Beck, J. D. Bates, T. J. Svejcar, and M. A. Gregg. 2011. Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush plant communities. Biological Conservation **144**: 2573-2584.

Eiswerth, M. E., K. Krauter, S. R. Swanson, and M. Zielinski. 2009. Post-fire seeding on Wyoming big sagebrush ecological sites: regression analyses of seeded nonnative and native species densities. Journal of Environmental Management **90**:1320-1325.

Evans, R. A.; and J. A. Young. 1983. Microsite requirements for downy brome (*Bromus tectorum*) infestation and control on sagebrush rangelands. Weed Science **32**:13-17.

Hawkes, C. V., J. Belnap, C. D'Antonio, and M. K. Firestone. 2006. Arbuscular mycorrhizal assemblages in native plant roots change in the presence of invasive exotic grasses. Plant and Soil **281**:369-380.

Howard, J. L. 1992. *Salsola kali*. Fire Effects Information System, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Missoula, Montana. (available from http://www.fs.fed.us/database/feis/).

James, J. J., and T. Svejcar. 2010. Limitations to postfire seedling establishment: the role of seeding technology, water availability, and invasive plant abundance. Rangeland Ecology and Management **63:**491-495.

Knapp, P. A. 1996. Cheatgrass (*Bromus tectorum* L.) dominance in the Great Basin desert: history, persistence, and influences to human activities. Global Environmental Change **6**:37-52.

Link, S. O., H. Bolton Jr., M. E. Theide, and W. H. Rickard. 1995. Responses of downy brome to nitrogen and water. Journal of Range Management **48**:290-297.

Mack, R. N., and D. A. Pyke. 1983. The demography of *Bromus tectorum*: variation in time and space. Journal of Ecology **71**:69-93.

Monaco, T. A., D. A. Johnson, J. M. Norton, T. A. Jones, K. J. Connors, J. B. Norton, and M. B. Redinbaugh. 2003. Contrasting responses of intermountain west grasses to soil nitrogen. Journal of Range Management **56**:282-290.

Mummey, D. L., and M. C. Rillig. 2006. The invasive plant species *Centaurea maculosa* alters arbuscular mycorrhizal fungal communities in the field. Plant and Soil **288**:81-90.

Pavek, D. S. 1992. *Halogeton glomeratus*. Fire Effects Information System, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Missoula, Montana. (available from http://www.fs.fed.us/database/feis/).

Perkins, L. B., and R. S. Nowak. 2012. Soil conditioning and plant-soil feedbacks affect competitive relationships between native and invasive grass. Plant Ecology **213**:1337-1334.

Piemeisel, R. L. 1951. Causes affecting change and rate of change in a vegetation of annuals in Idaho. Ecology **32:**53-72.

Rowe, H. I., and C. S. Brown. 2008. Native plant growth and seedling establishment in soils influenced by *Bromus tectorum*. Rangeland Ecology and Management **61**:630-639.

Smith, L. 2005. Host plant specificity and potential impact of *Aceria salsolae* (Acari: Eriophyidae), an agent proposed for biological control of Russian thistle (*Salsola tragus*). Biological Control **34**:83-92.

West, N. E., and T. P. York. 2002. Vegetation responses to wildfire on grazed and ungrazed sagebrush semi-desert. Journal of Range Management **55**:171-181.

Wolfe, B. E., and J. N. Klironomos. 2005. Breaking new ground: soil communities and exotic plant invasion **55**:477-487.

Young, J. A., R. A. Evans, and R. E. Eckert Jr. 1969. Population dynamics of downy brome. Weed Science **17:**20-26.

Young, J. A., R. A. Evans, R. E. Eckert, Jr., and B. L. Kay. 1987. Cheatgrass. Rangelands **9**:266-270.

Young, J. A., and R. A. Evans. 1978. Population dynamics after wildfires in sagebrush grasslands. Journal of Range Management **31**:283-289.

APPENDIX A. ANOVA TABLES FOR BIOMASS AND SOIL MICROBIAL COMMUNITY (PLFA) ANALYSIS

Table A.1. Plant biomass averaged across 2010 and 2011 (sampling year) and Analysis of Variance F-test probabilities.

Source	DF	Total Biomass	Native Grasses	Volunteer Forbs	Exotic Annuals	*Salsola kali*	*Bromus tectorum*	*Halogeton glomeratus*
		----------g/m^2----------						
Block	3	---	---	---	---	---	---	---
Treatment	12	0.1060	0.0032	0.0395	0.0006	0.4819	0.0107	0.4551
Error a	36	---	---	---	---	---	---	---
Year	1	0.1187	0.0239	0.4471	0.2102	0.0473	0.0055	0.0013
Year*Treatment	12	0.2779	0.6397	0.3850	0.7277	<0.0001	<0.0001	0.1563
Error b	39	---	---	---	---	---	---	---
Total	103	---	---	---	---	---	---	---

Table A. 2. Total biomass and biomass of *S. kali* and *B. tectorum* analyzed separately by sampling year and Analysis of Variance F-test probabilities.

Source	DF	Total Biomass		*Salsola kali*		*Bromus tectorum*	
		----------g/m^2----------					
		2010	2011	2010	2011	2010	2011
Block	3	---	---	---	---	---	---
Treatment	12	0.0957	0.0054	<0.0001	0.1159	<0.0001	<0.0001
Error	36	---	---	---	---	---	---
Total	51	---	---	---	---	---	---

Table A.3. Drill seeded, machine broadcast, and hand broadcast forb biomass averaged across both sampling years and Analysis of Variance F-test probabilities.

Source	DF	Seeded Forbs	Drill Seeded Forbs	*Sphaeralcea munroana*	*Eriogonum umbellatum*	Broadcast Forbs	*Achillea millefolium*	*Penstemon cyaneus*
		----------g/m^2----------						
Block	3	---	---	---	---	---	---	---
Treatment	12	0.0672	0.4179	0.4316	0.6282	0.0936	0.0964	0.5078
Error a	36	---	---	---	---	---	---	---
Year	1	0.1373	0.1937	0.1941	0.8716	0.2262	0.2555	0.1741
Year*Treatment	12	0.8783	0.9033	0.9028	0.4018	0.9837	0.9846	0.5343
Error b	39	---	---	---	---	---	---	---
Total	103	---	---	---	---	---	---	---

Table A.4. Microbial biomass associated with *B. tectorum* and *P. secunda* microsites across all five treatments (R5x, R0, C, M0, M5x) and Analysis of Variance F-test probabilities, split-plot in space design.

Source	DF	Total Abundance	Total Bacteria	Gram +	Gram -	Fungi	AMF	Protozoans	Fungi:Bacteria Ratio	Soil Water*
		----------µg fatty acid/g soil----------								%
Block	3	---	---	---	---	---	---	---	---	---
Treatment	4	0.6071	0.6402	0.7552	0.5861	0.3447	0.5485	0.1697	0.2043	0.7940
Error a	12	---	---	---	---	---	---	---	---	---
Microsite	1	0.7808	0.7473	0.2278	0.9311	0.5573	0.4007	0.1474	0.3252	0.3568
Treatment*Microsite	4	0.1293	0.2006	0.1189	0.2573	0.0404	0.0691	0.0654	0.2034	0.2325
Error b	174	---	---	---	---	---	---	---	---	---
Total	198	---	---	---	---	---	---	---	---	---

*DF = 193 due to missing values

Table A.5. Microbial biomass associated with *B. tectorum*, *P. secunda*, and *P. spicata* microsites across two treatments (R5x, M5x) and Analysis of Variance F-test probabilities, split-plot in space design.

Source	DF	Total Abundance	Total Bacteria	Gram +	Gram -	Fungi	AMF	Protozoans	Fungi:Bacteria Ratio	Soil Water*
		----------µg fatty acid/g soil----------								%
Block	3	---	---	---	---	---	---	---	---	---
Treatment	1	0.6847	0.5838	0.5610	0.6014	0.6635	0.8255	0.9100	0.3059	0.9519
Error a	3	---	---	---	---	---	---	---	---	---
Microsite	2	0.4436	0.3836	0.0524	0.6243	0.6322	0.5273	0.5580	0.5779	<0.0001
Treatment*Microsite	2	0.2699	0.3140	0.2263	0.3522	0.1692	0.2758	0.1368	0.5533	0.9443
Error b	108	---	---	---	---	---	---	---	---	---
Total	119	---	---	---	---	---	---	---	---	---

*DF = 115 due to missing values

Table A.6. Microbial biomass associated with *P. spicata* microsites sampled in two treatments (R5x, M5x) over two months (June, July) and Analysis of Variance F-test probabilities, split-plot in space design.

Source	DF	Total Abundance	Total Bacteria	Gram +	Gram -	Fungi	AMF	Protozoans	Fungi:Bacteria Ratio	Soil Water*
		----------µg fatty acid/g soil----------								%
Block	3	---	---	---	---	---	---	---	---	---
Treatment	1	0.2447	0.2205	0.1814	0.2474	0.3970	0.4190	0.0520	0.7974	0.8517
Error a	3	---	---	---	---	---	---	---	---	---
Month	1	0.0002	0.0011	0.0057	0.0011	0.0224	0.0205	0.0118	0.1423	0.0088
Treatment*Month	1	0.2533	0.2883	0.3967	0.2589	0.1082	0.7247	0.5412	0.2034	0.6998
Error b	3	---	---	---	---	---	---	---	---	---
Error c	67	---	---	---	---	---	---	---	---	---
Total	79	---	---	---	---	---	---	---	---	---

*DF = 78 due to a missing value

APPENDIX B. BIOMARKERS USED IN PLFA ANALYSIS

Table B.1. Microbial taxonomic groups and their associated biomarkers used in PLFA analysis.

Taxonomic Group	**Biomarker**
Gram + bacteria	i14:0, a15:0, i15:0, i16:0, a17:0, i17:0,
Gram – bacteria	cy17:0, cy19:0, 16:1w7c, 16:1w9c, 18:1w9c
Fungi (non-AM)	18:2w6c
Arbuscular mycorrhizal fungi (AMF)	16:1w5c
Protozoans	20:3w6c, 20:4w6c