

IMPACTS OF NATIVE GRASSES AND CHEATGRASS ON
GREAT BASIN FORB DEVELOPMENT

by

Hilary Ann Parkinson

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Dr. Catherine Zabinski

Approved for the Department Land Resources and Environmental

Dr. Bruce Maxwell

Approved for the Division of Graduate Education

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ABSTRACT

Land managers need more information on native forb growth and interactions between forbs and grasses to improve degraded sagebrush steppe habitats in the Great Basin, and to increase the diversity of revegetation seed mixes. This is especially important in areas infested with *Bromus tectorum* (cheatgrass), an annual grass present in more than 100 million acres of the Great Basin. To gather information on forb growth and measure the effects of both native grasses and *B. tectorum* on forbs, I conducted a greenhouse experiment with 5 native forbs: *Lomatium* sp., *Eriogonum umbellatum*, *Machaeranthera canescens*, *Penstemon speciosus*, *Sphaeralcea munroana*; two native grasses: *Elymus elymoides* and *Poa sandbergii*; and *B. tectorum*. Forbs were grown alone or with a grass, and were harvested after 6, 9 or 12 weeks of growth. Excluding *Lomatium*, which became dormant before week 12, forbs did not differ in shoot relative growth rate when growing alone, but the root relative growth rate of *P. speciosus* was 50% greater. Neither native grass reduced the biomass of any forb, but growth rate was reduced for two forbs. In contrast, *B. tectorum* reduced the biomass and growth rates of all forbs, between 50 and 96%. In a second experiment, to test the ability of native forbs to establish and grow with *B. tectorum*, 4 forb species were grown in plots seeded with densities ranging from 45-360 *B. tectorum* plants m⁻² at two locations in the Snake River Plain. Water content declined with increasing densities of *B. tectorum* and forb seedling survival was reduced for 2 species when *B. tectorum* densities were greater than 150 plants m⁻². Reductions in forb biomass greater than 90% occurred for three species when *B. tectorum* densities were less than 100 plants m⁻². This study demonstrated that sites with low expected densities of *B. tectorum* should be selected when seeding forbs, but that native forbs can establish in sites with *B. tectorum* densities less than 150 plants m⁻², that native grasses and forbs can be used together in seed mixes, and that phenological and morphological characteristics can be used to optimize the diversity of seed mixes.

INTRODUCTION

Intact sagebrush-steppe habitat in the arid, interior portion of the northwest has decreased to a fraction of its original size (Noss 1995). The reduction and fragmentation of this habitat type began in the 1860s from overgrazing, followed by chaining of shrubs to increase forage for livestock, reseeding with aggressive non-native grasses, agricultural development and the introduction of exotic species (Mack 1981, Knapp 1996). The rate of habitat loss appears to far exceed the rate of natural recovery, raising concern for sagebrush-steppe obligates like Greater Sage-Grouse (*Centrocercus urophasianus*), pygmy rabbit (*Brachylagus idahoensis*), brewer's sparrow (*Spizella breweri*) and others (Connelly *et al.* 2000, Shipley *et al.* 2006). Following the fires in 1999 and 2000 that burned 2.7 million acres, land managers, including the USDI Bureau of Land Management and USFS Rocky Mountain Research Station initiated a large scale research program to improve restoration methods and develop native plant materials to increase the rate of habitat recovery and species diversity in impoverished areas (Shaw *et al.* 2005).

Restoration in this harsh arid environment faces many challenges. First is the climate in the Great Basin which has extremes in temperature with limited precipitation. The Great Basin is bordered by the Columbia Plateau to the north, the Colorado Plateau to the east, the Mojave Desert to the south and the Sierra Nevada mountains to the west (Cronquist *et al.* 1986). The aridity of this area is attributed to the Sierra Nevada Mountains and the Cascades that block storm fronts moving from the Pacific Ocean. The

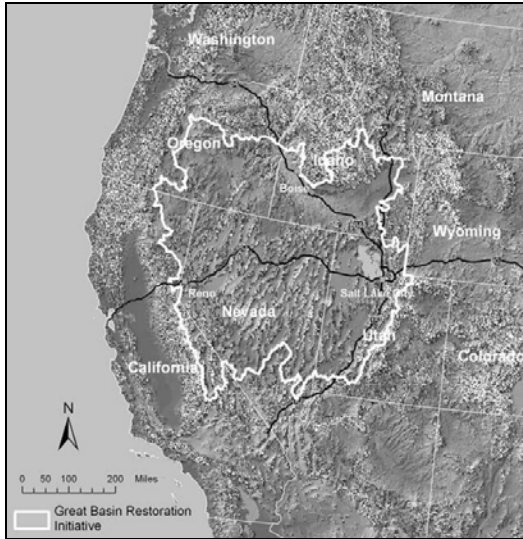


Figure 1. Map of the Great Basin.

majority of precipitation that reaches the Great Basin comes as snow, which varies greatly over short distances and increases with elevation (Knapp 1996).

There are two generalized life history strategies for plants to survive in this climate, where precipitation events are concentrated in the coldest months, followed by negligible amounts during the hot months of summer

(Dyer & Rice 1999). The first is the slow growing perennial species that efficiently allocates resources belowground, and can continue growth during prolonged periods of heat and drought. These are the plants that provide cover and forage year round and are critical for sagebrush-steppe obligates or species that depend on sagebrush and associated plants during a part of their life cycle. The second life history strategy is the cool season annual that grows rapidly when precipitation is most available, produces seed, and senesces with the onset of summer heat. They provide forage for a limited time in early spring, and no structure or cover relative to communities of sagebrush, bunchgrasses and forbs.

Perhaps the second largest barrier to the restoration of sagebrush steppe habitats is a plant with this second life history strategy, *Bromus tectorum* L., (cheatgrass, Mack 1981). Following a disturbance such as fire or overgrazing, populations of *B. tectorum* establish and increase rapidly (Billings 1990). It typically germinates in the fall,

continues root growth throughout the winter, initiates shoot growth in the late winter or early spring, and has a higher relative growth rate compared to native plants (Arredondo *et al.* 1998). These advantages over native plants, especially seedlings, make *B. tectorum* highly competitive for water.

There are two inter-related, but potentially opposing goals involved in restoring sagebrush-steppe habitats. The first goal is to reintroduce forbs, grasses and shrubs to areas where the native seed bank has been reduced to such low levels that natural recovery would be unlikely. The second goal is to quickly reestablish native communities to reduce the invasion of *B. tectorum* and other exotics which are known to inhibit population establishment. Research has demonstrated that intact communities, particularly the presence of native grasses, can reduce invasion of *B. tectorum* (Booth *et al.* 2003, Beckstead & Augspurger 2004). This suggests that rapid establishment of a native plant community to reduce *B. tectorum* would likely best be achieved by seeding dense quantities of the most rapidly growing species. The folly of this strategy is evidenced by the research now involved in reducing populations of crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.), a non-native species that has proven to be as competitive as cheatgrass. While it may limit *B. tectorum*, the monocultures are of no greater value to wildlife than *B. tectorum*. The goal of restoration of Great Basin sites is to re-establish diverse assemblages of species by limiting negative interactions among seeded species, and so creating communities resistant to *B. tectorum* invasion.

Along with the challenges of a harsh climate and the exotic species like *B. tectorum*, restoration programs are limited by a lack of information on the biology of

seeded species. Grasses and shrubs have been used since the 1970s, but the use of forbs is new, yet forbs are a critical component of sagebrush-steppe ecosystems. For example, in quality sagebrush habitat they form 80% of the diet of the threatened sage-grouse (Drut *et al.* 1994). There are three areas needing further research. First, more information is needed on the growth patterns of native forbs to limit inter-specific competition among seeded species and rapidly establish diverse communities. Second, more information is needed on native grass-forb interactions to maximize the potential for native grasses to limit *B. tectorum*, but not at the expense of forb growth. Third, information is needed on how forbs respond to *B. tectorum* and if the response varies among forb species to improve our understanding of the factors that limit forb establishment and growth.

To address these three objectives, I conducted greenhouse and field experiments. The greenhouse experiment, described in Chapter 2, was designed to obtain general information on forb growth when growing alone, including relative growth rates, and root mass ratios; to measure the effect of a native grass neighbor on forb growth; and to measure the effect of growth with *B. tectorum*. The information on forb growth characteristics can be used to design native plant communities that should maximize species richness and limit inter-specific competition. Comparing forb growth alone, to growth with native grasses will identify potential negative or positive interactions between native forbs and native grasses, suggesting modification of seeding mixtures. Comparing the relative effect of *B. tectorum* versus native grasses on forbs will help us understand the impact of this exotic grass on native forb seedling establishment.

The second experiment, described in Chapter 3, was done at two locations in the Snake River Plain of southern Idaho to measure the effects of *B. tectorum* on forb biomass and soil water. Native forbs were grown in plots with varying density of *B. tectorum*. By identifying whether species differ in their response to *B. tectorum*, land managers can choose species based on expected densities of *B. tectorum*, and reduce wasting valuable seed.

The greenhouse experiment allowed me to study belowground characteristics of native grasses and forbs in a way that is difficult in field settings. Belowground plant traits are often overlooked because of the difficulty of harvesting root tissues in field settings. The field experiment enables a more realistic approach to species interactions relative to differences in phenology, and with a realistic climatic regime.

ANALYSIS OF FORB GROWTH WITH AND WITHOUT GRASS NEIGHBORS

Introduction

Plant materials used to restore burned or degraded areas in the Great Basin have expanded from primarily grasses and shrubs to include native forbs (Shaw *et al.* 2005). Shrubs, grasses and forbs provide important forage and cover for many organisms throughout the Great Basin. For example, in healthy sagebrush steppe communities, forbs provide 80% of the diet for sagegrouse (*Centrocercus urophasianus*) during the spring and summer (Drut *et al.* 1980). Because literature and practical experience pertaining to native forbs is scant, additional information on species phenology, relative growth rate and root morphology will improve our understanding of how these species utilize resources in time and space. This will aid in selecting species and designing seedlings so that partitioning of limited resources is enhanced, while negative forb-forb interactions are reduced (Pyke & Archer 1991, Schwinning & Ehleringer 2001).

The first objective of this experiment was to gain autecological information for five commonly occurring Great Basin forbs selected for restoration projects, specifically total biomass after twelve weeks of growth, relative growth rates, and root mass ratios. The emphasis is on the early stages of growth because the seedling stage is the most critical for establishment (Cline *et al.* 1977, Aguirre & Johnson 1991). The second objective was to determine whether forbs differed in their response to growing with the invasive annual grass, *Bromus tectorum* L. (cheatgrass, downy brome). Competitive response is the “ability of an organism to avoid being suppressed by their companions”

(Goldberg & Landa 1991). *Bromus tectorum* is an aggressive colonizer and limits native plant establishment after disturbances such as fire (Mack 1981). It uses more water earlier in the growing season compared to native plants by initiating root and shoot growth at lower temperatures (Arredondo *et al.* 1998) and has a higher root and shoot relative growth rate (Cline *et al.* 1977, Aguirre & Johnson 1991). Identifying forbs that respond well or poorly to *B. tectorum* will improve the selection of forbs when paired with information on site conditions (expected *B. tectorum* densities).

Along with creating diverse plant communities to enhance habitat for wildlife, land managers are trying to identify species traits, or qualities of species assemblages, that limit the invasion and spread of *B. tectorum* (Mack & Pyke 1983, Pyke & Archer 1991, James & Drenovsky 2007). Once established, native grasses may resist invasion by or reduce spread of *B. tectorum* (Booth *et al.* 2003, Beckstead & Augspurger 2004, Getz & Baker 2008). For example, Booth *et al.* (2003) showed that *E. elymoides* reduced the competitive effects of *B. tectorum*, while having minimal effects on *Artemisia tridentata*.

To maximize this potential, but ensure that grasses are not limiting forbs, more information is needed on forb-native grass interactions, but no studies have examined effects of native grasses on native forbs. If negative interactions are identified, this information will suggest separating grasses from certain forbs (seeding in alternate rows), or seeding grasses at lower densities with certain forbs.

I tested three hypotheses: (1) forb growth will be affected by a grass neighbor; (2) a native grass neighbor will have the same effect on forb growth as *B. tectorum*, and (3) forb species will not differ in their response to growing with grass neighbors.

Materials and Methods

Plant Materials

The five native forb species were *Eriogonum umbellatum* Torr.; *Lomatium* sp.; *Machaeranthera canescens* (Pursh) A. Gray; *Penstemon speciosus* Douglas ex Lindl.; and *Sphaeralcea munroana* (Douglas) Spach. (Table 1). Identity of the *Lomatium* species is pending, but is likely *L. ambiguum*. The native grasses were *Elymus elymoides* (Raf.) Swezey and *Poa sandbergii* (Vasey), and the exotic annual was *Bromus tectorum* L.. Forb seed was collected in 2005 at wildland sites at elevations less than 1524 m (5,000') from the Snake River Plain of southern Idaho, except for *S. munroana* which was collected in Utah.

Experimental Design

Using a completely randomized experimental design, forbs were either grown alone, or with one of the following grass neighbors: *Bromus tectorum*, *Elymus elymoides*, and *Poa sanbergii*. With 5 forb species and 4 neighbor treatments, and 18 replicates of each neighbor treatment there were 360 total sampling units. After 6, 9 and 12 weeks of growth, 6 containers of each treatment were destructively harvested to obtain root and shoot biomass.

Methods

Stratification procedures were done 2-12 weeks in advance so species with physiological dormancy would emerge at the same time (Appendix A, Table 13). In mid-March, 2007, forb and grass seed were placed in a growth chamber at 24° C in Petri dishes on moistened blotter paper and sealed with Parafilm® with 14 hours of light and 10 hours of darkness. All forb seed except *M. canescens* began to germinate within 5-8 days in the growth chamber and were planted in containers in the greenhouse within 2 days of each other. The majority of *M. canescens* seedlings emerged 5-6 days after the other forbs, so they were planted in the greenhouse 7 days later than the other forbs, and were harvested 7 days later as well. The experiment began in the greenhouse the third week of March, 2007 when there was approximately 12 hours of natural sunlight, and artificial lights were on for 14 hours per day. Greenhouse temperatures were between 18 and 24 °C. Containers were randomly located in the greenhouse after 2½ weeks of growth, and moved every two weeks thereafter to minimize effects of environmental gradients.

Table 1. Plant materials, seed characteristics and location of seed collection sites.

Forbs	Common name, plant family	Seed/gram	Location and elevation of collection site*
<i>Lomatium</i> sp.	Desert parsley, Apiaceae	99.2	43.5132 N, -116.1319 W 945.49 m
<i>Eriogonum umbellatum</i>	Sulfur flower buckwheat, Polygonaceae	328.4	43.4683 N, -116.0895 W 1,032.40 m
<i>Machaeranthera canescens</i>	Hoary Aster, Asteraceae	1818	43.2332 N, -115.9148 W 958 m
<i>Penstemon speciosus</i>	Showy penstemon, Scrophulariaceae	686.5	43.3870 N, -116.0204 W 1,012.85 m
<i>Sphaeralcea munroana</i>	Munrow's globemallow, Malvaceae	300	Collected in Utah at elevation less than 1,524 m

*All forbs collected in Snake River Plain of southern Idaho except *S. munroana*

Containers were 45 cm deep and 16 cm wide (11.5 liters). Forbs were spaced 8 cm from a neighboring grass. In all containers, an additional 1-3 germinants were planted in each container to account for mortality, but plants were thinned to one forb and one grass after 10 days. Plants were misted daily during the initial establishment, watered daily from days 7 to 14; and watered every 2-3 days after that. Growing media was 1/3 top soil (silt loam), 1/3 washed concrete sand, and 1/3 peat moss. After 6, 9 and 12 weeks of growth, plants were harvested by carefully separating forb and grass root material, and cleaning roots. Plant material was dried at 65 °C for 2 days.

Data Analysis: Differences among species in forb size after 6, 9, and 12 weeks of growth were analyzed with three one-way analysis of variance (ANOVA) models on log transformed total biomass (SPSS versions 15). Model assumptions regarding normality were tested using Shapiro-Wilkes test and homogeneity of variance was assessed using Levene's test. To determine which species were different, the Tukey multiple comparison test was used at 6 weeks, and the Games-Howell post-hoc test was used at 9 and 12 weeks because the data did not meet the homogeneity of variance assumption ($p=0.026$ and $p=0.006$ respectively). An ANOVA among species was used to determine whether there were differences in root mass ratios at 6, 9, and 12 weeks.

Differences in instantaneous relative growth rates (RGR) were analyzed for all forbs except *Lomatium*. Consistent with growth patterns in a natural environment where *Lomatium* becomes dormant by early summer, *Lomatium* shoots began to senesce between weeks 9 and 12 in the greenhouse, hence it was not appropriate to measure RGR.

Instantaneous relative growth rate was computed as the slope of the natural log of forb biomass regressed on weeks of growth (destructively harvested after 6, 9 and 12 weeks). Forbs were ranked based on total biomass at each harvest (from one to six) and paired with plants of equivalent rank from harvests 9 and 12 to obtain six RGR's for each forb. I used a one-way ANOVA to determine whether instantaneous RGR fit to each size rank over weeks differed among forbs, and the Tukey multiple comparison test to determine which forbs were significantly different from one other. The RGR of shoot and root material was analyzed separately. Additionally, to avoid the bias associated with pairing plants of similar size rank across harvest periods (Poorter 1989), differences in RGR among species were tested using an ANCOVA of log transformed biomass with harvest week as the covariate (SPSS version 15). The same RGR values were obtained as using the method above (ranking and pairing). Significant differences in RGR were identified by testing for an interaction between harvest week and species. A significant interaction term indicated at least one of the species differed in relative growth rate.

Growth with Grass Neighbors: The effect of a grass neighbor on total biomass and relative growth rate of each forb was tested using five one-way ANOVA models among neighbor treatments (alone, with *B. tectorum*, *E. elymoides*, or *P. sandbergii*). The Tukey multiple comparison test was used to determine which treatments were significantly different. An ANOVA of RGR among neighbor treatments was done for all forbs except *Lomatium*. Tests of the effects of neighbor treatments on RGR were also done for root and shoot material separately.

Results

Forb Biomass without Grass Neighbors

Large differences among forbs in total biomass occurred after only 6 weeks of growth (Table 2). While relative ranking based on size was consistent throughout the experiment, *E. umbellatum* was intermediate in size between *Lomatium* and *P. speciosus* at weeks 6 and 9, but was significantly larger than *Lomatium* and smaller than *P. speciosus* by week 12.

Table 2. Total biomass (g \pm 1 SE) of forbs when growing alone after 6, 9 or 12 weeks of growth. F and p values are from a one-way ANOVA among species on the natural log of total forb biomass at each harvest. Numerator degrees of freedom for all F values = 4, denominator degrees of freedom = 25. Letters indicate significant differences at each harvest week (within a column) based on Tukey's multiple comparison test ($p < 0.05$).

Species	Total biomass (g)		
	6 weeks	9 weeks	12 weeks
<i>Lomatium</i>	0.022 \pm 0.006 a	0.07 \pm 0.003 a	0.08 \pm 0.003 a
<i>E. umbellatum</i>	0.038 \pm 0.006 ab	0.16 \pm 0.04 ab	0.46 \pm 0.12 b
<i>P. speciosus</i>	0.067 \pm 0.004 b	0.42 \pm 0.10 b	1.5 \pm 0.33 c
<i>M. canescens</i>	0.395 \pm 0.12 c	1.1 \pm 0.09 c	3.38 \pm 0.50 d
<i>S. munroana</i>	1.987 \pm 0.35 d	8.75 \pm 0.92 d	24.09 \pm 2.02 e
F	72.4**	139.40**	145.62**

** $p < 0.0001$

Forb Relative Growth Rates without Grass Neighbors

Except for *Lomatium*, which had limited growth between weeks 9 and 12, the slopes of the natural log of total forb biomass by harvest time are relatively parallel, suggesting no obvious differences in RGR by species (Figure 2). A one-way ANOVA

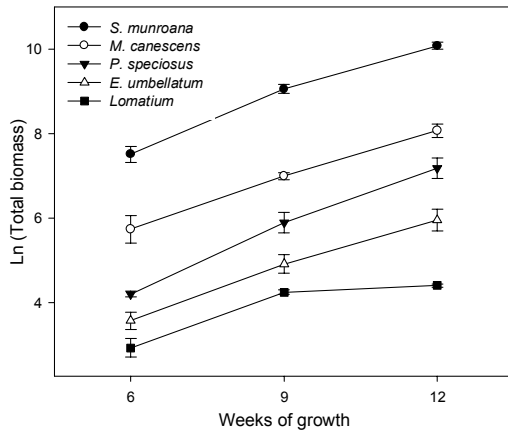


Figure 2. Natural log of total forb biomass (± 1 SE) when growing alone.

showed that total RGRs differed by forb species, but based on the Tukey multiple comparison test, only *P. speciosus* had a greater RGR than *M. canescens*, with the other forbs intermediate and not significantly different from one another (Table 3).

Table 3. Total (root and shoot) relative growth rates (RGR) (± 1 SE). All F and p values are from one-way ANOVA comparing RGR among species. Numerator degrees of freedom for all F values = 3, denominator degrees of freedom = 20. Letters indicate differences (within columns) based on Tukey's multiple comparison test ($p < 0.05$).

Species	RGR ($\text{mg mg}^{-1} \text{ week}^{-1}$)		
	Total	Shoot	Root
<i>P. speciosus</i>	0.50 \pm 0.03 a	0.41 \pm 0.08	0.72 \pm 0.06 a
<i>S. munroana</i>	0.43 \pm 0.02 ab	0.41 \pm 0.05	0.53 \pm 0.06 b
<i>E. umbellatum</i>	0.40 \pm 0.03 ab	0.38 \pm 0.06	0.48 \pm 0.08 b
<i>M. canescens</i>	0.39 \pm 0.03 b	0.36 \pm 0.07	0.48 \pm 0.10 b
F	3.34*	0.60	11.42**

* $p < 0.05$, ** $p < 0.0001$

Relative growth rate of shoot material did not differ by species (Table 3). In contrast, the root RGR of *P. speciosus* was greater than the other forbs, which were not different from each other.

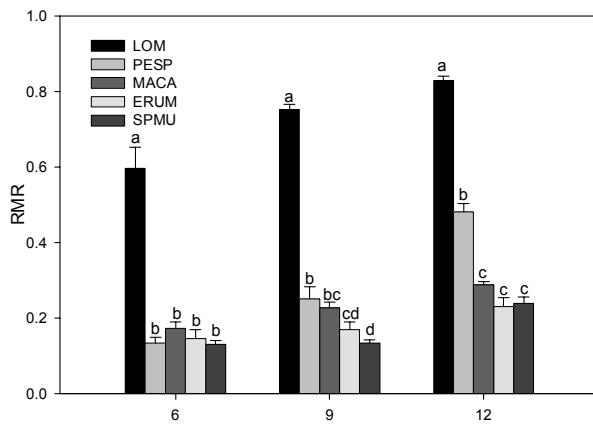


Figure 3. Root mass ratio (RMR) when growing alone after 6, 9 and 12 weeks of growth (± 1 SE). Different letters indicate significant differences among species at each harvest based on Tukey multiple comparison tests ($p < 0.05$).

($p < 0.05$, Figure 3). By week 12, the RMR of *Lomatium* was 0.83. *Penstemon speciosus* was not different than the other three forbs after six weeks of growth, but by week 12, its RMR was 0.48, the second largest of all forb species (Figure 3). The RMR of the other three forbs did not differ from each other at week 12, and averaged 0.25.

Considerable differences in root morphology were observed. The tap-rooted *Lomatium* had no lateral branches off the main root after 12 weeks of growth. In the first 6 weeks, *M. canescens* was nearly tap-rooted, and only developed lateral shoots between weeks 6 and 12. While *E. umbellatum* roots cannot be considered tap-rooted because they were so thin (< 0.1 cm), they also had minimal branching (less than 2 to 3 divisions) with nearly vertical growth; roots did not grow laterally beyond the perimeter of the crown (shoot material). In contrast, roots of *P. speciosus* and *S. munroana* were

Root Mass Ratio: Root mass ratio (RMR) was compared among species for each harvest time. Differences in RMR occurred after 6 weeks of growth ($F_{4,25} = 46.4$, $p < 0.0001$) and were maintained at weeks 9 and 12 ($F_{4,25} = 174.15$, $p < 0.001$ and $F_{4,25} = 198.16$, $p < 0.001$ respectively). The tap-rooted *Lomatium* had the largest RMR

flabelliform (fan-shaped). They were distributed laterally as much as vertically, with considerable branching near the soil surface, and throughout the depth of the container.

Forb Growth with Grass Neighbors

Effects of Grasses on Forb Biomass: The effect of a grass neighbor on forb growth could depend on both the identity of the grass and its total biomass. Grass biomass after 12 weeks of growth varied by species. Grass means averaged across all forb neighbors were 1.8 g (± 0.22) for *Poa sandbergii*; 7.3 g (± 0.54) for *E. elymoides*; and 24.0 g (± 0.52) for *B. tectorum*.

After 12 weeks of growth, there was not a significant reduction in total biomass for any of the five forbs when growing with a native grass compared to growth alone (Table 4). In contrast the total biomass of all forbs was reduced when growing with *B. tectorum*. Compared to growth alone, reductions in biomass ranged from 50% for *Lomatium* to 91% for *P. speciosus*.

Table 4. Forb total biomass (g \pm 1 SE) among neighbor treatment after 12 weeks of growth. F and p values are from one-way ANOVAs comparing forb biomass among neighbor treatments. Numerator degrees of freedom for all F values = 3, denominator degrees of freedom = 20. Letters indicate significant differences within a column ($p < 0.05$) based on the Tukey multiple comparison test. Raw/non-transformed data is presented here, log transformed data was used for analysis.

Neighbor Treatments	Forb species				
	<i>Lomatium</i>	<i>E. umbellatum</i>	<i>P. speciosus</i>	<i>M. canescens</i>	<i>S. munroana</i>
Alone	0.08 \pm 0.003 a	0.46 \pm 0.12 a	1.49 \pm 0.33 a	3.38 \pm 0.50 a	24.09 \pm 2.02 a
<i>P. sandbergii</i>	0.06 \pm 0.01 ab	0.51 \pm 0.09 a	0.70 \pm 0.08 a	5.30 \pm 1.26 a	22.13 \pm 2.38 a
<i>E. elymoides</i>	0.05 \pm 0.01 ab	0.29 \pm 0.11 ab	0.78 \pm 0.23 a	5.50 \pm 0.40 a	23.77 \pm 2.51 a
<i>B. tectorum</i>	0.04 \pm 0.01 b	0.10 \pm 0.02 b	0.13 \pm 0.02 b	0.75 \pm 0.17 b	8.76 \pm 1.44 b
F	3.03	6.24	21.59	20.13	20.59
p	0.05	0.004	<0.001	<0.001	<0.001

Effects of Grasses on Forb Relative Growth Rates: The neighbor treatment had a significant effect on the total RGR of the four forb species (Table 5). In contrast to total biomass, total RGR (roots and shoots) with a native grass was reduced for two of the forbs. The RGR of *P. speciosus* was reduced by both native grasses (average reduction was 25%) and *S. munroana* was reduced by *E. elymoides* (18% reduction). For *E. umbellatum* and *M. canescens*, there was no effect of native grasses on RGR. The RGR of all forbs was reduced by *B. tectorum* (Table 5).

Table 5. Forb total RGR (mg/mg/week \pm 1 SE) among neighbor treatments. All F and p values are from a one-way ANOVA comparing the natural log of total forb biomass among neighbor treatments. Numerator degrees of freedom for all F values = 3, denominator degrees of freedom = 20. Letters indicate significant differences (within columns) based on Tukey's multiple comparison test ($p < 0.05$).

Neighbor	Forbs							
	<i>E. umbellatum</i>		<i>P. speciosus</i>		<i>M. canescens</i>		<i>S. munroana</i>	
Alone	0.40	± 0.03 a	0.50	± 0.03 a	0.39	± 0.03 a	0.43	± 0.02 a
<i>P. sandbergii</i>	0.46	± 0.02 a	0.39	± 0.01 b	0.37	± 0.03 a	0.37	± 0.02 ab
<i>E. elymoides</i>	0.37	± 0.05 a	0.36	± 0.03 b	0.47	± 0.04 a	0.35	± 0.02 bc
<i>B. tectorum</i>	0.19	± 0.03 b	0.10	± 0.02 c	0.17	± 0.02 b	0.27	± 0.02 c
F	12.24**		46.61**		14.68**		11.91**	

** $p < 0.001$

Penstemon speciosus was the only forb for which root RGR was reduced with both native grasses (Figure 4). Additionally, the RGR of root material, but not shoot material was reduced with *P. sandbergii*. For the other species, reductions in RGR (compared to growth alone) were more common in shoot material rather than root material (Figures 4). The root RGR of *E. umbellatum* decreased only with *B. tectorum* as a neighbor, but shoot RGR of *E. umbellatum* differed with each neighbor. The root RGR of *M. canescens* and *S. munroana* was constant across neighbor treatments, whereas the

shoot RGR of both species was reduced when growing with *B. tectorum* and the shoot RGR of *S. munroana* was lower with *E. elymoides*, compared to growth alone.

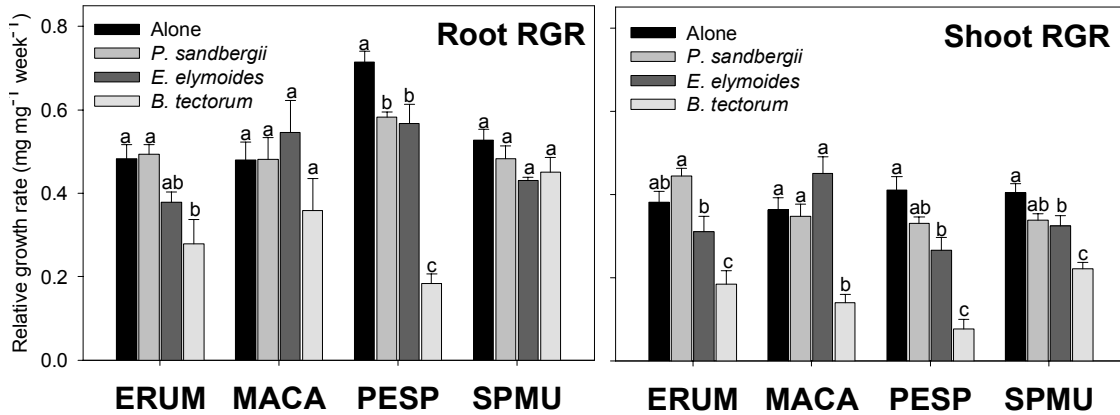


Figure 4. Forb root and shoot RGR ($\text{mg mg}^{-1} \text{ week}^{-1} \pm 1 \text{ SE}$) among neighbor treatments. Different letters indicate significant differences within forb species based on Tukey multiple comparison tests ($p < 0.05$).

Discussion

Forb Growth without Grass Neighbors

Rapid establishment of native plants following disturbance is a top priority for land managers. Because forbs are considered the most vulnerable to competition as seedlings (Cline *et al.* 1977, Aguirre & Johnson 1991), it is important to identify negative interactions between forb seedlings and other seeded species. My first research objective was to determine whether there were large differences in forb size and growth rates after 12 weeks of growth. Under the ideal conditions of the greenhouse, the biomass of *S. munroana* was an order of magnitude greater than the biomass of *M. canescens* and *P. speciosus*, two orders of magnitude greater than *E. umbellatum* and three orders of magnitude greater than *Lomatium* (Table 2). While the assumption that larger biomass

confers greater competitive effect must be tested in the field, where differences in phenology and resource levels may change outcomes, it is reasonable to assume that larger species use more resources than smaller ones, and likely deplete them at a faster rate than smaller or slower growing species (Goldberg & Landa 1991, Goldberg 1996). If total biomass is a good predictor of a plant's ability to deplete resources at the expense of neighboring plants, this data suggests *S. munroana* may reduce the biomass of other seeded forbs. To account for that in the design of restoration communities, *S. munroana* could be separated spatially from other forbs to limit negative interactions.

In the arid Great Basin where resources come in pulses, primarily in the spring, relative phenology may be as important as relative biomass in determining the outcome of competitive interactions. While *Lomatium* was the smallest, its early phenology—typically germinating 4-8 weeks prior to other forbs followed by dormancy, is likely to limit negative interactions with other forbs.

The other four forbs germinate within 3-4 weeks of each other (personal observation). Along with biomass and phenology, differences among forbs were also observed in root morphology and relative growth rate of root material. The differences in root morphology between these forbs may be a way to further limit negative interactions. The contrasting root morphologies were flabelliform (*P. speciosus*, and *S. munroana*) and tap-rooted or columnar (like *E. umbellatum* and *M. canescens*). Future studies, with a larger sample size for each root type, could seed species in rows with the same or contrasting root morphologies to measure differences in germination and biomass when growing with neighbors with similar versus contrasting root morphologies.

Attempting to maximize belowground resource partitioning spatially may be particularly important for *P. speciosus*. Relative growth rates of shoot material did not differ among species, but the RGR of *P. speciosus* root material was 50% greater compared to the other forbs. While negative interactions will depend upon the relative phenologies of species in the mixtures, and their tolerance for low resource levels, this high root RGR is likely to increase negative interactions with other forbs and should be considered when constructing seed mixtures.

Forb and Native Grass Interactions

Research has shown that intact sagebrush-steppe communities, with high percentage cover of native perennial vegetation, particularly grasses, are more resistant to invasion by *B. tectorum* (Beckstead & Augspurger 2004, Chambers *et al.* 2007, Getz & Baker 2008). My study paired native grasses with native forbs to measure the effects of growing with a native grass. *Poa sandbergii* did not reduce the biomass or RGR of any of the forbs, except *P. speciosus*. When growing with *Poa sandbergii*, *Penstemon speciosus* had the same reduction in total RGR as when growing with the much larger *E. elymoides* (average reduction in total RGR with native grasses was 25%).

The second native grass used in this study, *E. elymoides*, is of particular interest to restoration ecologists. *Elymus elymoides* is one of the few native plants that can invade existing stands of *B. tectorum* (Arredondo *et al.* 1998). *Elymus elymoides* did not reduce the total biomass of any of the species, nor relative growth rates of *E. umbellatum* or *M. canescens*, but it did reduce the relative growth rates of *P. speciosus* and *S. munroana*. This is particularly notable for *P. speciosus*, as both its root and shoot RGRs were

reduced by *E. elymoides* (Figure 4). Considering the effect of both native grasses on *P. speciosus*, future studies are needed to determine how this species responds to competition in the field from both grasses and forbs. Until this research can be completed, it may be appropriate to reduce densities of native grasses in mixtures with *P. speciosus*.

Differences in root morphology may explain why the RGR of two of the forbs was reduced by native grasses, while the other two were not. *Eriogonum umbellatum* and *M. canescens*, both with columnar, almost tap-root-like growth (minimal lateral branching, none beyond root crown), were not reduced by either native grass. The root morphologies of *P. speciosus* and *S. munroana* were flabelliform, similar to the root morphology of the grasses. Both were reduced by *E. elymoides*, and *P. speciosus* by *P. sandbergii*. Root morphology may be an important criterion when selecting species to maximize richness.

Temporal resource partitioning is likely to modify competitive interactions as well, but these effects were obscured in my study by planting forb and grass seedlings within 2-3 days of each other. In the study that found *E. elymoides* reduced *B. tectorum* without affecting *Artemisia tridentata* seedlings, the presumed mechanism was overlapping resource use between *E. elymoides* and *B. tectorum*, but non-overlapping resource use between *E. elymoides* and *A. tridentata* (Booth *et al.* 2003). This suggests that the negative interactions that occurred in the greenhouse between forbs and native grasses may not represent outcomes in the field.

Forb and *B. tectorum* Interactions

Bromus tectorum now covers more than 100 million acres of sagebrush steppe in the Great Basin and in 1996, an estimated 20% of sagebrush steppe habitat was dominated by cheatgrass densities at levels high enough to preclude natural recovery of native plants (Knapp 1996). Identifying species that can establish and grow in the presence of *B. tectorum* will help land managers improve restoration mixtures based on expected *B. tectorum* densities. This data shows that some forb species when grown with *B. tectorum* are likely to have greater reductions in biomass or RGR compared to others. The smallest forb, *Lomatium*, and largest, *S. munroana*, had the lowest mean percent reduction in biomass (51% and 64%). *Penstemon speciosus* had the greatest reduction at 92%. *Eriogonum umbellatum* and *M. canescens* were intermediate (both 78%).

This suggests that *Sphaeralcea* and *Lomatium* can be seeded with fewer restrictions, or across a greater range of expected *B. tectorum* densities compared to *P. speciosus*. However, the greenhouse study does not account for differences in phenology, which is especially relevant for *B. tectorum*. The ability of *B. tectorum* to germinate in the fall, continue root growth throughout the winter, and initiate shoot growth at lower temperatures than native plants in the spring gives it a large size advantage over spring emerging forb seedlings (Arredondo *et al.* 1998), suggesting this study underestimated the effects and the relative effects of *B. tectorum* on forb species. For example, the difference in the percentage reduction in biomass between *Lomatium* and *S. munroana* when growing with *B. tectorum* (50% and 64%) would likely become larger in the field. While both forbs will be at a size disadvantage growing with *B.*

tectorum, that disadvantage will be much larger for *S. munroana*, which germinates 1-2 months after *Lomatium*.

Few field studies investigate root biomass because of the difficulty separating root material of neighboring species, and the time consuming nature compared to measuring above ground growth. While root growth patterns will vary in the field based on resource levels and interactions with other species, the data on differences in root morphology may be used in future studies to investigate the potential for resource partitioning.

With a more complete understanding of grass-forb interactions, managers can more efficiently design seed mixes. Combining the information on root morphology with observations on relative emergence dates and periods of primary growth among forbs and native grasses will likely increase resource partitioning to minimize negative interactions among seeded species, while allowing for the development of plant communities more resistant to invasion by *B. tectorum*.

EFFECTS OF CHEATGRASS DENSITY ON FORB GROWTH AND SOIL WATER CONTENT

Introduction

Over the course of nearly 150 years, sagebrush-steppe habitat in the Great Basin has been reduced to a fraction of its original size by overgrazing, seeding with non-native species, invasion of exotic species, fire and agricultural development (Mack 1981, Knapp 1996). Concern has risen for sagebrush steppe-obligates like sage-grouse, brewer's sparrow and other animals as quality habitat diminishes and become more fragmented (Oyler-McCance *et al.* 2001, Schroeder *et al.* 2004). Large fires in 1999 and 2000 that burned 2.7 million acres initiated a large scale research effort funded by federal and state governments to improve restoration methods in disturbed sagebrush-steppe habitats and to increase the availability of native plant seed for these projects (Shaw *et al.* 2005). One of the unique objectives in the research projects started in 2000 was the imperative to use native forbs in the restoration seed mixtures. Land managers have been reseeded disturbed rangelands with native grasses and shrubs to improve forage and cover for big game in the Great Basin since the 1970s (Plummer *et al.* 1968). In the last decade, policies have changed to provide funding for research on and use of Great Basin forbs in restoration mixtures.

Establishment and survival of seeded species in the Great Basin faces many challenges. Climate is one of the largest barriers; some areas receive less than 26 cm of rain annually. Establishment and survival is further complicated by the presence of exotic species. Competition for water between native and exotic plant species is believed

to be one of the main mechanisms limiting establishment of native plants after disturbances such as fire (Harris 1967, Melgoza *et al.* 1990). The goal of my research was to improve our understanding of the effects of one of the most ubiquitous exotic species in the Great Basin, *Bromus tectorum* L. (cheatgrass, downy brome), on the growth of native forbs.

Compared to Great Basin shrubs and grasses, our understanding of factors that limit or enhance the establishment of Great Basin forbs is in an early stage. To date, research on the effects of *B. tectorum* on forbs has focused only on the most common species such, as *A. millefolium*. If species vary in their response to *B. tectorum*, then species that respond well can be recommended for a range of conditions, while those that respond poorly can be designated for only high quality sites.

The objectives of my research were (1) to identify the density of *B. tectorum* at which significant declines in native forb establishment and growth occur; (2) to determine whether effects of *B. tectorum* density vary based on the identity of the native forb; and (3) to determine when and at what depths differences in water content occur with increasing densities of *B. tectorum*.

Materials and Methods

Site Descriptions

Research was conducted at two locations in the Snake River Plain of southern Idaho, the Lucky Peak Nursery and Orchard Training Grounds. The Lucky Peak Nursery (945 m elevation) is on a leveled plateau that has been used by the U.S. Forest Service to

grow plant materials since 1959. The soils are a sandy loam derived from decomposed granite, but have been repeatedly tilled so classification is difficult. Average annual precipitation is 350 mm, the majority falling as snow and spring rain (Figure 5). The native plant community in undisturbed surrounding areas is dominated by bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A Love), squirreltail (*Elymus elymoides* (Raf.) Swezey), basin big sagebrush (*Artemisia tridentata* Nutt. ssp. *tridentata*) and rabbitbrush (*Ericameria nauseosa* (Pall. ex Pursh) G.L. Nesom & Baird).

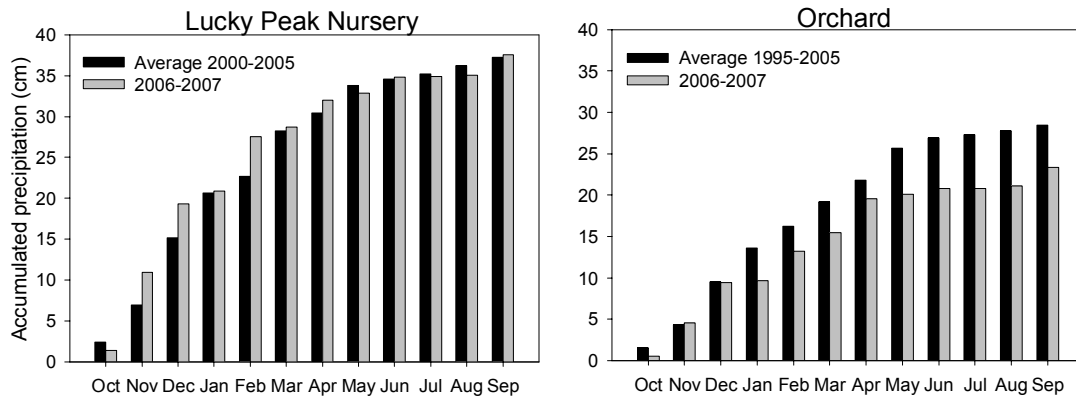


Figure 5. Average accumulated and accumulated precipitation from October 2006-September 2007 for Lucky Peak Nursery and Orchard Training Ground. Lucky Peak Data from RAWS (Western Regional Climate Center), Orchard data from Snotel (Natural Resource Conservation Service).

The Orchard site (914 m elevation) is 20 miles east, south-east of Boise, ID on land managed by the USDI Bureau of Land Management. It has been used for research on native plants since 1988 and is enclosed by an electric fence to prevent livestock grazing, and chicken wire buried to a depth of approximately 10 cm to reduce herbivory by ground squirrels and badgers. The soils are classified as a Lankbush-Tindahay sandy loam and the pH is 6.6-7.3. The native plant community is dominated by bluebunch

wheatgrass (*Pseudoroegneria spicata*), Thurber's needlegrass (*Achnatherum thurberianum* (Piper) Barkworth), and basin big sagebrush (*Artemisia tridentata*).

Experimental Design

To test the effects of *B. tectorum* density on seedling establishment and growth, the study was set up as a split-plot design. The five *B. tectorum* seeding levels were randomly assigned to main plots and the four forb species and the control were randomly assigned within each main plot (Figure 6). Main plots were 6.75 m², and single-species sub-plots were 1.35 m². In each sub-plot, forb seeds were planted in two rows of four spots, each planting spot separated by 30 cm. The treatments, *B. tectorum* seeding levels and species, were repeated in three complete blocks at Lucky Peak and five at Orchard. While both field sites were relatively homogenous, three blocks were established at Lucky Peak perpendicular to a slight slope and five blocks were established at Orchard at increasing distances from an established stand of sagebrush and rabbitbrush. The greater number of blocks at Orchard was to account for an expected increase in mortality due to the harsher site conditions.

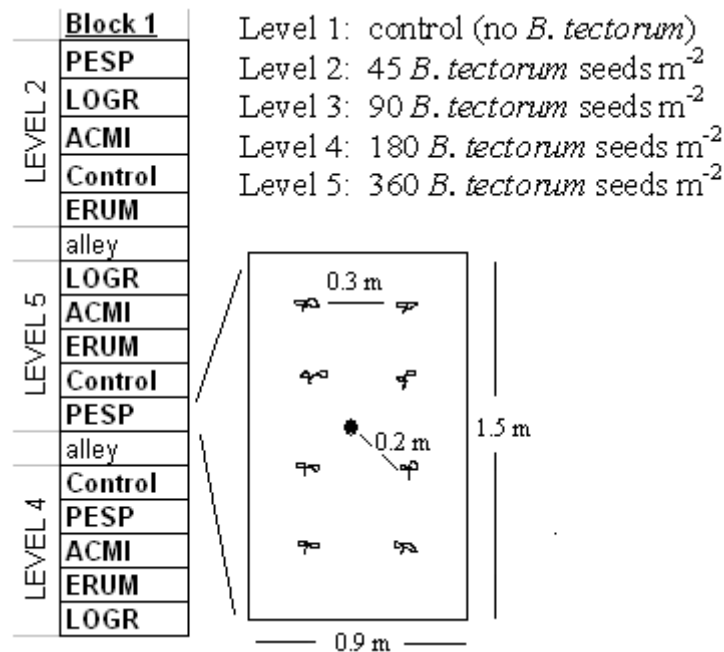


Figure 6. Main plot and sub-plot diagram. A complete block consisted of *B. tectorum* seeding levels 1-5. Levels were randomly assigned to plots. Subplots of species were nested within levels (and randomly assigned). Access tubes to measure volumetric water content were installed in the center of subplots in levels 1, 4 and 5.

Plant Materials

The four forb species used in the study were *Achillea millefolium* L. (common yarrow); *Eriogonum umbellatum* Torr. (sulfur-flower buckwheat); *Lomatium grayi* (J.M. Coult. & Rose) (Gray's biscuitroot); and *Penstemon speciosus* Douglas ex Lindl. (Royal Penstemon, Table 6). All plant material including *B. tectorum* seed was collected in the Snake River Plain of southern Idaho in the summer of 2005 at elevations less than 1,525 m (5,000').

Bromus tectorum was seeded in late September, 2006. The top 2-3 cm of soil from each sub-plot was scraped off and set aside. Pre-weighed packets of seed were scattered evenly across the sub-plot by hand, and then covered with collected soil.

Germination tests were done for *B. tectorum* by placing 50 seeds (separated into 5 sets of 10 seeds) on moistened filter paper in Petri dishes at ambient temperature. Four 1-cup samples were taken from the seed lot, weighed and cleaned to determine percent inert matter. Germination and purity were multiplied to determine pure live seed (PLS). Seed was weighed and adjusted based on PLS to contain the appropriate amount of seed for each seeding level (45, 90, 180 and 360 plants m⁻²). An additional 10% of the total was added to account for seed getting blown away or buried too deeply.

Forb seed was planted in late October, 2006. Planting depths ranged from 0.5 to 2 cm depending on species (Table 6). Ten live forb seeds were planted in each planting spot (seed packets were weighed and adjusted based on the PLS of each seed, Table 6). The PLS was determined by testing viability and estimating percent inert matter in four subsamples. Forb seed viability was determined using Tetrazolium tests developed by staff at the Rocky Mountain Research Station, Boise, ID, for all species except *A. millefolium*, which was tested at the Idaho State Seed Laboratory.

Table 6. Seed collection sites, seed characteristics and planting depths.

Species	Latitude/ Longitude	Elevation (m)	Seeds g ⁻¹	Pure Live Seed	Planting depth (cm)
<i>Achillea</i>	N 43.90045	854.05	6172.9	78%	0.5
<i>millefolium</i>	W -116.8029				
<i>Eriogonum</i>	N 43.46383	1032.36	328.41	56%	1
<i>umbellatum</i>	W -116.0895				
<i>Lomatium</i>	N 43.51325	945.49	99.2	40%	2
<i>grayi</i>	W -116.13197				
<i>Penstemon</i>	N 43.38702	1012.85	686.5	80%	0.5
<i>speciosus</i>	W -116.02043				
<i>Sphaeralcea</i>	N 43.2822	753.47	684.46	50%	1
<i>munroana</i>	W -116.574				
<i>Bromus</i>	N 43.19225	1052.47	298.5	70%	1
<i>tectorum</i>	W -116.6310				

In the spring, 7-10 days after the first seedlings emerged, empty planting spots were replanted to ensure an adequate number of plants for the study. Based on differences in phenology, replanting began in mid-March for *L. grayi*, late-March for *E. umbellatum* and early-April for *A. millefolium* and *P. speciosus*. Replanting was done twice for each species at 2-week intervals. Seeds with physiological dormancy, all but *A. millefolium*, were treated with appropriate stratification methods (Appendix A) over the winter or early spring so that 2-3 live germinants (radical, but not cotyledon leaves emerged) would be available for replanting in each empty spot. *Achillea millefolium* seed does not exhibit dormancy, so untreated seed was added to empty spots.

Materials for Measuring Soil Water

Neutron moisture meter (503DR, CPN. Corp. Martinez, CA) access tubes, 3.9 cm in diameter and 124 cm in length, were installed to a depth of 112 cm in all sub-plots without *B. tectorum* and in sub-plots seeded with densities of 180 and 360 *B. tectorum* plants m⁻² in January of 2008. A motorized soil auger, 5 cm in diameter, was used to penetrate the top 50 cm of frozen soil, and then a 5 cm bucket auger was used to excavate the remainder. As soil was removed, it was collected in a bucket, sifted, and then carefully poured back to fill voids between the access tube and surrounding soil.

Data Collection

Forbs: Presence or absence of all plants in each plot was recorded in mid-April, mid-June and late July at both sites. Length, width, and height of *A. millefolium*, *E. umbellatum* and *P. speciosus* shoot material were measured in mid-May at both sites. For

L. grayi, the total number of shoots (leaves), and the height and shoot width were also recorded in mid-May. Except for *L. grayi* at both sites and *P. speciosus* at Orchard, forbs were measured again in late-July and within 2 to 3 days of those measurements, shoot biomass was clipped at ground level, dried at 60 °C to obtain a constant biomass and weighed. *Penstemon speciosus* at Orchard was consumed by ground squirrels beginning in mid-May. By late July, all plants were gone or only small stubs remained. At Lucky Peak, *L. grayi* plants were harvested, dried and weighed as they senesced, which ranged from late May to early July. Attempts were made to measure shoot material of *L. grayi* before they were harvested, but plants were contorted, and measurements did not correspond well with plant size. At Orchard, *L. grayi* plants were consumed by ground squirrels beginning in late May and no plants were available to collect for biomass. For *A. millefolium*, the only plant that flowered, the number of flowering stalks, whether in bud or bloom, was recorded in late-June and mid-July. Reproductive biomass of the whole flowering stalk clipped just above the base, as well as just the corymbs, clipped just below where pedicels meet peduncle/flowering stalk were weighed.

Penstemon speciosus plants at Orchard were not consumed by ground squirrels until later in the summer, but some herbivory had occurred when non-destructive measurements were made in mid-May. The total number of leaves and number of leaves with herbivory were recorded to estimate percentage present in mid-May. The percent lost was added to the total size to account for herbivory. One-third of the plants had no herbivory; more than one-third had between 13-43% of leaves missing; and less than one-third had 50% of the leaves missing.

Bromus tectorum: At Lucky Peak in mid-May, *B. tectorum* densities were recorded within a 30-cm diameter frame (0.071 m²) centered on three randomly selected forbs per subplot. *Bromus tectorum* biomass was harvested at peak standing biomass beginning 23 May at Lucky Peak. The biomass within the 30-cm diameter frame around three randomly selected forbs per plot was bagged separately to determine whether biomass or density was a better predictor variable of forb growth. Plant material was clipped at ground level, dried to a constant biomass, and weighed.

At Orchard, ground squirrel herbivory reduced the size of *B. tectorum* plants. In early and mid-April several techniques (smoke bombs, bait and a kite falcon) were used to reduce ground squirrel populations within the enclosure. In late April, some leaf blades were only 3-5 cm long and prostrate in comparison to plants at Lucky Peak which were 25-40 cm tall, and in the boot stage or flowering. While mortality from herbivory was not observed and re-growth occurred, small plants are likely to have less effect on forb growth compared to large plants. Size differences were recorded by tracing the area of *B. tectorum* crowns on clear tissue paper (30 cm in diameter) centered on three randomly selected forbs per plot. *Bromus tectorum* plants were categorized as small or recently consumed if the crowns were less than or equal to 2.5 cm in diameter, and relatively intact if the crown was greater than 2.5 cm in diameter. Information was also recorded on whether plants were flowering, or had flowering stalks as an additional indicator of herbivory. Step-wise linear regression was used to determine whether all plants (large plus small), large plants only, or large plants plus a certain percentage of

small plants was the best indicator variable to predict the natural log of each forb's biomass.

While herbivory was not uniform in any of the blocks, it was heaviest in block 1 adjacent to stands of wildland shrubs (*Artemesia tridentata* and *Ericameria nauseosa*), which likely provided good cover for birds-of-prey frequently observed in the area. Similarly, in block 5, which bordered a barren field without any plant cover, herbivory was the lightest, but it varied in consistency. Only the interior blocks (2, 3 and 4) were used, hence the total number of plots was the same at both Orchard and Lucky Peak.

Soil Water Content: Soil water content was first measured on 15 March at Orchard, and on 30 March at Lucky Peak, and thereafter weekly to early-June, and then at 2- and 3-week intervals until 30 July. Soil water content was measured in the control (subplots of forbs only and subplots without any plants), and subplots seeded with 180 and 360 *B. tectorum* plants m⁻² at 20-, 40-, 60-, and 80-cm depths. *Bromus tectorum* densities around the neutron access tubes were recorded using a 40 cm diameter frame.

To calibrate the neutron probe for the soils at each site to express measured slow neutron count ratios as volumetric water content, access tubes were installed and count ratios were collected in two dry and two wet soil areas at each site (Appendix B). Three soil cores within 20-cm of each access tube were removed with a truck-mounted motorized soil corer and oven dried at 105 °C to measure gravimetric water content. Calibration relationships for each site were determined with linear regression of slow neutron count ratios against volumetric soil water content.

Data Analysis

Effects of *B. tectorum* on Forb Survival: Chi-square tests were used to determine whether there was a difference in the total number of live plants among *B. tectorum* seeding levels. Chi-square tests among *B. tectorum* seeding levels were done for *L. grayi* in mid-April and mid-May, but plants began to senesce in mid-May and were harvested as they senesced from mid-May to early July. During this period, senescence of *L. grayi* plants was monitored weekly to avoid losing biomass and to determine whether the date of senescence was related to *B. tectorum* density.

Effects of *B. tectorum* on Forb Growth: The effect of *B. tectorum* density on forb biomass at Lucky Peak was analyzed with linear regression (least squares) with forb biomass ln transformed (SPSS version 15). The confidence intervals of these slopes were used to determine whether forbs differed in response to increasing densities of *B. tectorum*. An additional analysis was done using a one-way ANOVA among *B. tectorum* density categories (0, 1-40, 41-80, 81-140, 141-200, 200-260, and > 260 plants m⁻²) to determine at what densities decreases in biomass occurred compared to the control, and whether this critical density differed among forb species. These intervals were selected to be used for all species to include an approximately equal number of samples within each category, and meet assumptions of normality and homogeneity of variance. For the two surviving forbs at Orchard, *A. millefolium* and *E. umbellatum*, data was analyzed with regression and ANOVA, in the same way as the analysis of forb data from the Lucky Peak site.

Non-destructive measurements of forb shoots in mid-May permitted the analysis of all forbs at both sites. The formula used to convert height, length, and width to plant volume is in Appendix C. Similar to the analyses done on biomass, confidence intervals on the slopes from the ln of forb volume by increasing densities of *B. tectorum* were used to determine whether response differed by species.

Effects of *B. tectorum* on Water Content: A two-way repeated measures ANOVA was used to analyze the effects of *B. tectorum* density and forb species on volumetric water content at each sampling date. If interactions were not significant ($\alpha > 0.05$), the Tukey multiple comparison test was used to determine which main effects differed from each other.

Actual *B. tectorum* densities at Lucky Peak ranged from 150 to 420 plants m⁻². The density recorded within a 40 cm diameter frame centered on each access tube was recorded and densities were categorized into three intervals: 0, 150-300 and >300 (a break in densities from 280 to 320 created these distinct categories). At Orchard, *B. tectorum* densities ranged from 150 to 567 plants m⁻². Despite the larger range in densities, there was not a significant difference in water content by adding another category (301-450), so categories at Orchard are the same as at Lucky Peak.

Results

Forb Seedling Emergence and Survival in Relation to *B. tectorum*

There was a large difference among species in the total number of seedlings observed on the three sampling dates (Table 7). Of a maximum of 120 plants, *P. speciosus* had the fewest plants at both sites, and *L. grayi* had the greatest. *Eriogonum umbellatum* and *A. millefolium* differed greatly between sites; there were 31 *A. millefolium* plants at Lucky Peak, and three times that amount at Orchard. There were 85 *E. umbellatum* plants alive at Lucky Peak in mid-May and nearly half as many at Orchard.

The total number of forb seedlings alive in mid-April was not different among *B. tectorum* seeding levels for any species at either site (Table 7). In mid-May, *Bromus tectorum* affected survival of *A. millefolium* seedlings at the Lucky Peak site where there was a lower than expected number of plants in plots seeded with 180 *B. tectorum* plants m⁻², and no *A. millefolium* plants in plots seeded with 360 *B. tectorum* plants m⁻².

For the other species at Lucky Peak, and for *E. umbellatum* and *A. millefolium* at Orchard, there was a trend of decreases in germination and increases in mortality at the higher *B. tectorum* seeding levels, but the effect was not significant. For *P. speciosus* and *L. grayi* at Orchard, there was no pattern in forb emergence or survival in relation to *B. tectorum* density.

Table 7. Total number of live forb plants among *B. tectorum* seeding levels at Lucky Peak and Orchard. The df for all chi-square tests was 4. Expected values were totals on the census date divided by 5 (for each *B. tectorum* seeding level).

Species	Location	Census Date	<i>B. tectorum</i> m ⁻²					Total	p
			0	45	90	180	360		
<i>Achillea millefolium</i>	Lucky Peak	15-Apr	4	7	7	5	2	25	0.46
		17-May	8	8	10	5	0	31	0.04
		30-Jul	8	8	10	5	0	31	0.04
	Orchard	14-Apr	12	16	18	14	18	78	0.78
		15-May	16	19	21	16	18	90	0.91
		28-Jul	16	19	21	15	14	85	0.74
<i>Eriogonum umbellatum</i>	Lucky Peak	15-Apr	12	22	22	15	15	86	0.31
		17-May	19	19	21	13	13	85	0.51
		30-Jul	19	18	19	9	11	76	0.19
	Orchard	14-Apr	8	9	8	8	11	44	0.94
		15-May	10	10	8	8	10	46	0.98
		28-Jul	9	10	7	4	6	36	0.53
<i>Lomatium grayi</i>	Lucky Peak	15-Apr	19	22	22	17	17	97	0.86
		17-May	18	22	19	17	15	91	0.83
		30-Jul	*						
	Orchard	14-Apr	16	20	16	16	15	83	0.92
		15-May	13	17	13	14	18	75	0.83
		28-Jul	**						
<i>Penstemon speciosus</i>	Lucky Peak	15-Apr	2	4	4	5	3	18	0.84
		17-May	2	7	4	7	1	21	0.12
		30-Jul	2	7	4	3	1	17	0.18
	Orchard	14-Apr	3	3	7	2	6	21	0.35
		15-May	7	5	6	7	7	32	0.97
		28-Jul	**						

*Plants were collected as they senesced

**Biomass not available, consumed by ground squirrels

The date *L. grayi* plants senesced was affected by *B. tectorum* density (Table 8). In plots seeded at the highest *B. tectorum* seeding level (360 plants m⁻²), 15 of 16 plants senesced prior to 26 May. In plots seeded at 180 plants m⁻², nearly half senesced prior to

26 May, and all by 10 June. More than half the plants in plots seeded with 90 *B. tectorum* m⁻² senesced between 27 May and 10 June. For plants in plots seeded with 45 *B. tectorum* plants m⁻², more than half senesced after 11 June. All of the *L. grayi* plants in the control senesced after 26 June, 2007. Plants that senesced prior to 26 May were one third the size of those harvested between 11 June and 25 June, and nearly one fifth the size of plants harvested after 26 June (Table 8).

Table 8. Harvest dates of *L. grayi* by *B. tectorum* seeding level (m⁻²) and average biomass by harvest date, Lucky Peak.

Harvest Date	<i>B. tectorum</i> seeding level (m ⁻²)					Total	Biomass by harvest period (± 1 SE)
	0	45	90	180	360		
Prior to 5/26*	0	4	3	8	15	30	6.70 a 0.84
5/27-6/10	0	4	10	9	1	24	10.59 a 1.60
6/11-6/25	0	8	6	0	0	14	19.35 b 1.98
After 6/26**	18	6	0	0	0	24	29.31 b 3.18
Total	18	22	19	17	16	92	

*Earliest harvest date was 5/22

**Last harvest was 7/10

Effects of *B. tectorum* on Forb Growth

The biomass of all forbs decreased with increasing densities of *B. tectorum* at Lucky Peak and Orchard (Figure 7, 8). At Lucky Peak, the biomass of all forbs except *Lomatium grayi*, declined abruptly at densities less than 100 plants m⁻² (Figure 7). For *A. millefolium*, all plants in plots with densities greater than 70 *B. tectorum* plant m⁻² were reduced by 90-99% compared to plants growing in the control plots. The biomass of all *P. speciosus* growing with *B. tectorum* was reduced by 90-99% compared to plants in the control, even where densities were as low as 14 or 28 *B. tectorum* plants m⁻². The majority of *E. umbellatum* plants were reduced by 90-99% at densities greater than 85 *B. tectorum* plants m⁻². In contrast to these species, the biomass of *L. grayi* declined more

gradually with increasing densities of *B. tectorum* (Figure 7). Not until densities were greater than 200 *B. tectorum* plants m^{-2} was there large reductions in *L. grayi* biomass (biomass was reduced by 82% compared to the control).

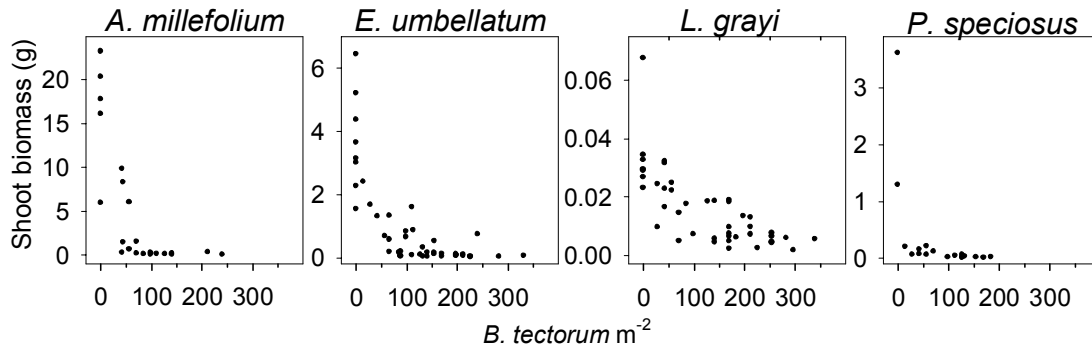


Figure 7. Forb biomass (g) by *B. tectorum* plants m^{-2} at Lucky Peak. Note different y-axes.

At Orchard, the drop in biomass for *A. millefolium* and *E. umbellatum* with increasing densities of *B. tectorum* was not as distinct, likely due to the herbivory on *B. tectorum*. However, plants in the control plots were much smaller at Orchard relative to Lucky Peak (Figures 7, 8), which may have reduced competitive interactions.

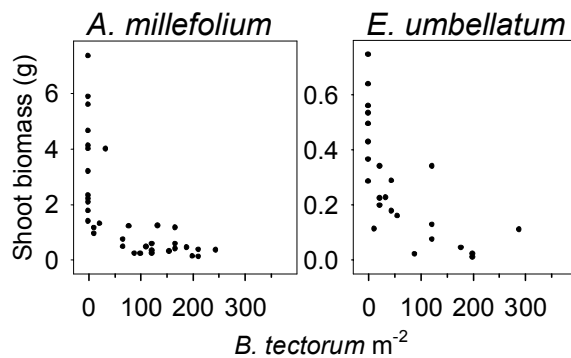


Figure 8. Forb biomass (g) by *B. tectorum* plants m^{-2} at Orchard. Note different y-axes.

Based on linear regression, forb response to *B. tectorum* was not the same among the four species. *Lomatium grayi* had the least negative slope compared to all other forbs. The slope of *Eriogonum umbellatum* was less negative than *A. millefolium*, but not different than *Penstemon speciosus* (Table 9).

Table 9. Slope (± 1 SE), confidence intervals, and regression statistics for the natural log of forb biomass by *B. tectorum* m^{-2} , Lucky Peak, late July, 2007. Letters indicate significant differences based on confidence intervals, $\alpha < 0.05$.

Species	Slope	Confidence Interval		Adjusted R-squared	F	df	p
		Lower	Upper				
<i>L. grayi</i>	-0.005 a	-0.006	-0.003	0.46	37.77	1, 43	<0.001
<i>E. umbellatum</i>	-0.017 b	-0.021	-0.013	0.62	74.39	1, 44	<0.001
<i>P. speciosus</i>	-0.025 bc	-0.033	-0.016	0.67	35.88	1, 16	<0.001
<i>A. millefolium</i>	-0.033 c	-0.043	-0.022	0.63	38.30	1, 21	<0.001

At Orchard, differences in response between *A. millefolium* and *E. umbellatum* shoot biomass to *B. tectorum* were not as clear. The herbivory on *B. tectorum* plants and the high variation within *E. umbellatum* biomass in response to *B. tectorum* complicated the analysis (Table 10). Based on overlapping confidence intervals, the responses of *A. millefolium* and *E. umbellatum* to *B. tectorum* were not different.

Table 10. Slope (± 1 SE), confidence intervals, and regression statistics for the natural log of forb biomass by *B. tectorum* m^{-2} , Orchard, late July, 2007. Letters indicate significant differences based on confidence intervals.

Species	Slope	Confidence Interval		Adjusted R ²	F	df	p
		Lower	Upper				
<i>A. millefolium</i>	-0.012	-0.015	-0.009	0.63	59.408	1, 33	<0.001
<i>E. umbellatum</i>	-0.006	-0.010	-0.001	0.16	7.22	1, 25	0.013
<i>L. grayi</i>	*						
<i>P. speciosus</i>	*						

*Biomass consumed by ground squirrels.

Achillea millefolium reproduction was affected by *B. tectorum* at both sites. At Lucky Peak, all *A. millefolium* plants in the control plots flowered, but none flowered

when growing with *B. tectorum*. At Orchard, 9 of the 11 plants that flowered were in control plots. The 2 that flowered in plots with *B. tectorum* were growing in plots with *B. tectorum* densities less than 150 plants m⁻² (122 and 133 plants m⁻²). The other forbs in this study do not typically flower in the first growing season.

The last analysis was on plant size measured in mid-May, which allowed all species to be considered at both sites. At Lucky Peak, *P. speciosus* size decreased at a greater rate with increasing densities of *B. tectorum* compared to *L. grayi* (Table 11). *Achillea millefolium* and *E. umbellatum* were intermediate in rank between *P. speciosus* and *L. grayi*, but they were not different than other forbs.

Table 11. Slope (± 1 SE), confidence intervals, and regression statistics for the natural log of forb volume

	Slope	Confidence Interval Lower
<i>P. speciosus</i>	-0.022 a	-0.033
<i>A. millefolium</i>	-0.018 ab	-0.029
<i>E. umbellatum</i>	-0.008 ab	-0.012
<i>L. grayi</i>	-0.005 b	-0.007

At Orchard in mid-May, *P. speciosus* size decreased at a greater rate compared to *L. grayi*, and the response of *A. millefolium* was intermediate, similar to results at Lucky Peak. In contrast to Lucky Peak, there was not a significant relationship between the size of *E. umbellatum* plants and density of *B. tectorum* at Orchard in mid-May (Table 12).

Table 12. Slope (± 1 SE), confidence intervals, and regression statistics for the natural log of forb volume by *B. tectorum* m⁻², Orchard mid-May, 2007. Letters indicate significant differences (based on confidence intervals).

	Slope	Confidence Interval		Adjusted R ²	F	df	p
		Lower	Upper				
<i>P. speciosus</i>	-0.037 a	-0.062	-0.012	0.33	10.00	1, 17	0.006
<i>A. millefolium</i>	-0.008 ab	-0.012	-0.005	0.36	21.39	1, 35	<0.001
<i>L. grayi</i>	-0.004 b	-0.007	-0.001	0.20	9.24	1, 33	0.005
<i>E. umbellatum</i>	-0.003 b	-0.009	0.002	0.03	1.87	1, 24	0.183

Effects of Plant Density on Soil Water Content

Soil water content in plots with forbs only was not different among forb species. It was also not different from the plots without any plants, meaning forb seedlings consumed about the same amount of water, and the water use was not large enough to be different from plots without any plants, which lost water only through direct soil evaporation.

Water content decreased with increasing amounts of *B. tectorum* at both sites (Figure 9), with the largest differences occurring at the shallowest sampling depth. At Lucky Peak on the first and second sampling dates, 31 March and 5 April, water content at 20-cm depths in plots with densities of 150-300 *B. tectorum* plants m⁻² was not different than the control (Appendix D, Table 14). At all subsequent sampling dates soil water content at the 20-cm depths in plots with 150-300 *B. tectorum* plants m⁻² was different than the control and ranged from 9% lower on 13 April to 60% lower on 22 May.

Bromus tectorum densities >300 plants m⁻² were not different than the control until the second sampling date, 5 April (Appendix D, Table 14). Water content in the highest density plots ranged from 10% lower on 5 April to 65% lower on 22 May compared to the control. Plots with *B. tectorum* densities >300 plants m⁻² were 12% lower than densities of 150-300 plants m⁻² on 13 April, and 14% lower on 27 April. At subsequent sampling dates, there were no significant differences between these two density levels.

At Orchard, there were no significant differences in soil water content at 20-cm depths between plots with *B. tectorum* densities of 150-300 and >300 plants m⁻² on any of the sampling dates (Table 15, Appendix D). There was not a significant difference in water content at 20-cm between the control and plots with *B. tectorum* until the second sampling date at Orchard, 23 March, when water content in the control was 21% lower than plots with *B. tectorum*. The difference between these two density levels and the control increased until 27 April. On 27 April, approximately 10 days after herbivory was observed at Orchard, water content in the control plots was not significantly greater than water in *B. tectorum* plots. In mid-April, repairs were made at Orchard to the enclosure fencing, deterrents were used to reduce ground squirrel populations within the enclosure, and in early May *B. tectorum* plants were observed to be recovering. On 9 May, water content was still not significantly different among *B. tectorum* levels, but on 15 May, water content in the highest level was lower than the control by 34% and the difference continued to increase.

At sampling depths below 20 cm, differences in soil water content at Lucky Peak between the control and plots with *B. tectorum* occurred later in the growing season and the magnitude of the differences decreased with depth. At 40 cm, there was no difference between the control and plots with *B. tectorum* until 7 May when soil water content at densities >300 plants m⁻² was 20% lower than the control and densities between 150-300 plants m⁻² was 27% lower than the control. At subsequent sampling dates, the density levels were not different from each other, but were 30-40% lower than the control. At 60 cm, the *B. tectorum* density levels were not different from each other, but were lower

than the control on 7, 13 and 22 of May by 10-20%. Between late March and late May, there were no differences in soil water content among *B. tectorum* treatments at the 80-cm depth.

At Orchard, the 40-cm sampling depth was different than the control on 23 May when soil water content in plots with *B. tectorum* densities >300 plants m^{-2} was 26% lower than the control. At 60 cm, soil water content in plots with densities >300 plants m^{-2} was 20% lower than control on 19 April.

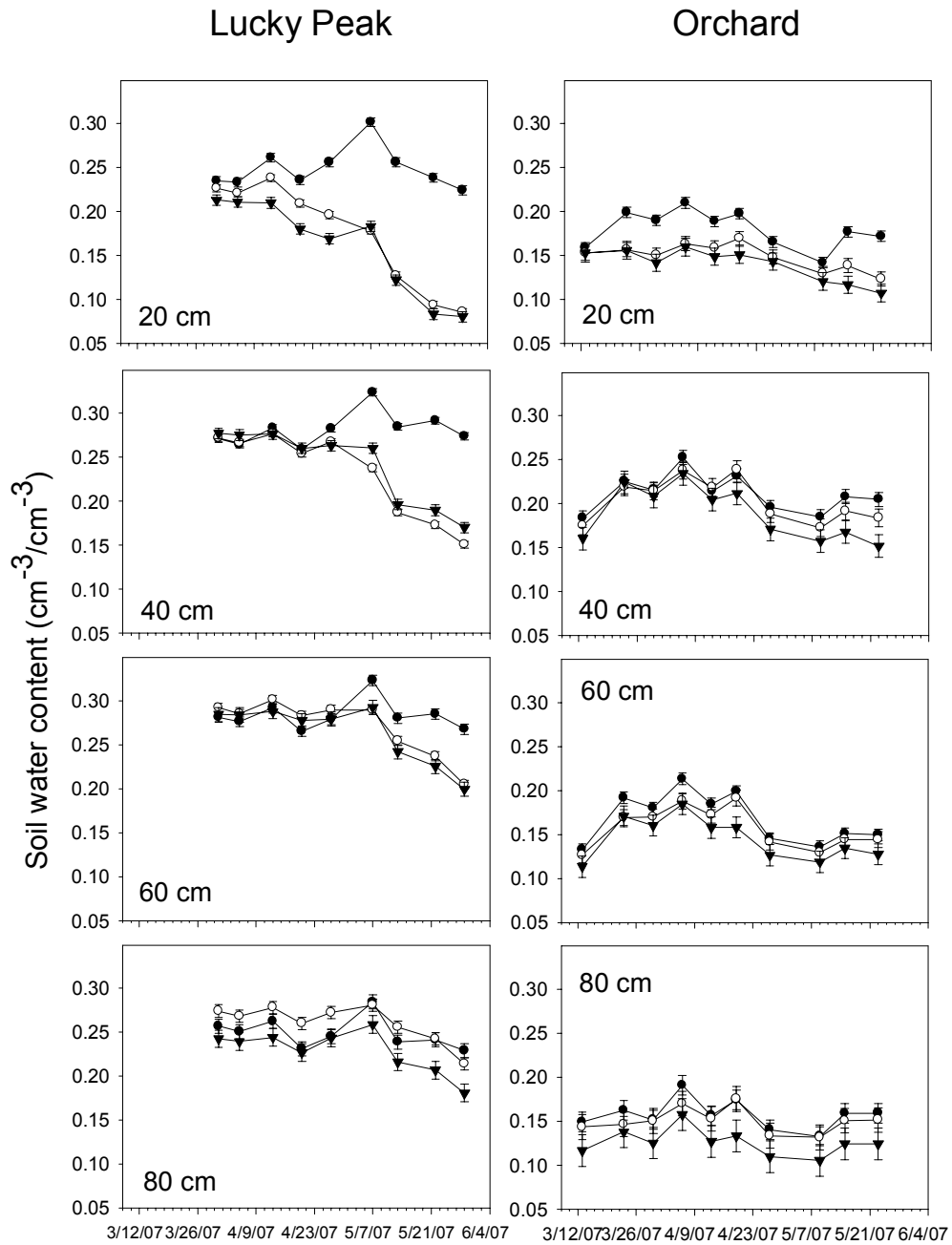


Figure 9. Volumetric soil water content in plots without *B. tectorum* (forbs only, closed circles), with *B. tectorum* densities of 150-300 plants m⁻² (open circles), and *B. tectorum* densities >300 plants m⁻² (closed triangles). Error bars ± 1 SE.

Discussion

To improve the success of restoration projects, land managers must be able to identify limiting conditions of seeded species and estimate plant performance, including survival and reproductive capacity under field conditions. Research has demonstrated that *B. tectorum* reduces the biomass and survival of grasses and shrubs (Booth *et al.* 2003, Humphrey & Schupp 2004), yet research on the competitive affects of *B. tectorum* on forbs is limited. *Bromus tectorum* densities in a burned area can be estimated based on observations prior to the fire, GIS layers, weather records and in some areas, ecological site descriptions. Identifying forb species that respond well given a background *B. tectorum* density will aid land managers in selecting species for revegetation, or even precluding some sites from restoration with forbs.

Effects of *B. tectorum* on Forb Survival

While *B. tectorum* affects mature plants, its biggest impact is on seedlings (Melgoza *et al.* 1990, Rafferty & Young 2002). The outcome of competition between *B. tectorum* and forbs may be forb mortality, reduction in biomass, or delay in years before reproductive maturity. My data showed that at Lucky Peak, mortality increased for only two of the forb species, *A. millefolium* and *L. grayi*, but only at the two highest *B. tectorum* seeding levels. If the *L. grayi* plants that senesced prior to May 26th actually died rather than entered dormancy early, then seedling mortality of these two species was near 100% at densities greater than 360 plants m⁻² (no *A. millefolium* were alive at the highest seedling level, and 15 of 16 *L. grayi* in the highest seeding level senesced prior to

May 26th) and survival was approximately 50% lower in plots seeded with 180 *B. tectorum* plants m⁻² compared to the control. In contrast to these two forbs, the total number of *E. umbellatum* and *P. speciosus* plants was not different among *B. tectorum* seeding levels at Lucky Peak. However, the small sample size of *P. speciosus* plants limits the power of these results. At the field site with high herbivory levels, plant totals among *B. tectorum* seeding levels were not different for *A. millefolium* or any of the other forbs.

This data on the effects of *B. tectorum* on forb seedling survival would be much stronger if the Orchard data was not confounded by herbivory. By late July, the Lucky Peak site received 10 cm more of precipitation relative to Orchard (Figure 5). As drought years increase in frequency, understanding whether competition from *B. tectorum* on seedlings tends to be more or less intense at lower water levels will be important information. However, considering Lucky Peak alone, it is encouraging that significant reductions in survival, or time until senescence for *L. grayi*, occurred for only two of the four forbs and only at *B. tectorum* densities well above 100 plants m⁻².

Effects of Plant Density on Soil Water Content

To increase spatial and temporal resource partitioning among native species, soil water content was measured in plots without *B. tectorum* to determine whether there were differences among forbs in water use by depth or during the growing season. The small size of forb seedlings and lack of resolution within the neutron moisture meter may have limited the ability to detect any differences among forbs. Future studies should focus on

more mature plants, or more precise measuring tools that can record soil water content closer to the surface, like time-domain reflectometry.

Fall germinating *B. tectorum* can maintain root growth throughout the winter, suggesting there could be differences in soil water content when forb seeds begin to germinate, thereby inhibiting germination or survival of forb seedlings. *Bromus tectorum* did not reduce germination (or the total number of plants among *B. tectorum* seeding levels) in mid-April at either site. At Lucky Peak, the majority of plants germinated prior to measured significant differences in soil water content at the 20 cm depth (Table 7, Table 14). At Orchard, soil water content was lower in the higher seeding levels on March 23rd by 23%, but this difference was not large enough to have a significant effect on forb seedling totals among *B. tectorum* seeding levels in mid-April.

Bromus tectorum did reduce survival of *A. millefolium* seedlings at Lucky Peak, and the water content data suggests it likely would have affected survival at Orchard in the absence of herbivory. On April 20th water content at the highest seeding level was lower than the control by 23% at both sites. Between late April and mid-May at Lucky Peak, water content declined sharply in plots with the highest levels of *B. tectorum* and by mid-May, the difference had increased to 52%. In contrast, herbivory at Orchard in mid to late April corresponded with a decline in the differences between water content among *B. tectorum* densities and the control, with no significant differences on 27 April 27 or 9 May. While *B. tectorum* plants recovered, water content in the higher *B. tectorum* seeding levels was only 34% lower than the control on 15 May 15. This temporary reprieve from reduced water availability likely coincided with the period when

A. millefolium and other forb seedlings were quite vulnerable. While ground squirrels consumed all the *L. grayi* and *P. speciosus* plants at Orchard later in the growing season, their preference for *B. tectorum* plants in mid-April appears to have had a positive effect on *A. millefolium* survival.

The spring of 2007 was unusually dry at Orchard and unusually hot at both sites compared to site averages (Figure 6). This would favor species with early phenology that germinated prior to the onset of hot weather when moisture was more available. *Lomatium grayi* was the first to germinate in mid-February, and had the highest total number of live plants when averaged at both sites (91 of 120 at Lucky Peak and 75 of 120 at Orchard, an average of 75% live between sites). *Penstemon speciosus*, along with *A. millefolium*, germinated 6-10 weeks later than *L. grayi*, and only 21 plants were alive in mid-May at Lucky Peak and only 32 at Orchard for an average of 22%. The germination of *E. umbellatum* and *A. millefolium* at Lucky Peak further supports the hypothesis that plants which germinate early in the growing season have a competitive advantage. They can access deeper layers of the soil profile before competition from *B. tectorum* limits their growth.

At depths greater than 20-cm, differences between the control and plots with *B. tectorum* were smaller in size and occurred 4-5 weeks later in the growing season compared to differences at 20-cm. This supports previous research that *B. tectorum* has the largest impact on seedlings relative to intact communities with mature plants since seedlings will have most of their root mass in the upper 20 cm (Melgoza *et al.* 1990).

The unusually dry, hot weather at Orchard that would have coincided with the period when the majority of *E. umbellatum* plants were germinating may explain the low total number of *E. umbellatum* at Orchard relative to Lucky Peak. Water content averaged across the control and all *B. tectorum* treatment levels was 20% lower in mid-March compared to mid-April At Orchard. This low water level in mid-March would correspond with the period when the majority of *E. umbellatum* plants were germinating and the higher water level in mid-April coincided with the period when *A. millefolium* was germinating. While this information is purely speculative, it suggests how inter-annual variations in climate may favor some species over others, depending on the timing of major precipitation events relative to species phenology or periods of primary growth.

Applications of Results

Lomatium grayi responded consistently better to *B. tectorum* than the other forbs at Lucky Peak, and while herbivory limits interpretation at Orchard, the trend was similar to Lucky Peak. The early phenology of *L. grayi*, followed by dormancy; its small biomass relative to the other forb species; and tap-root morphology likely contributed to it being less affected. The response of *E. umbellatum* to *B. tectorum* was better than *A. millefolium* based on regression, but this difference is not large enough to encourage *E. umbellatum* over *A. millefolium* in seed mixtures, particularly because *A. millefolium* seed is one of the least expensive and most available. However, the reason for the difference in response between *A. millefolium* and *E. umbellatum* may be similar to differences between *L. grayi* and the other forbs. *Eriogonum umbellatum* was the second forb to germinate in the spring, meaning it had a size advantage relative to *A. millefolium*.

Additionally, while it is not tap-rooted, roots grew vertically with minimal lateral branching. This may have reduced competitive interactions with the more shallow, and fibrous rooted *B. tectorum*.

Except for *P. speciosus*, it is difficult to claim the difference among species in response to *B. tectorum* were large enough to justify promoting one species over another. At densities greater than 70 to 80 *B. tectorum* plants m⁻², the biomass of *A. millefolium* and *E. umbellatum* was reduced by more than 90% compared. At densities greater than 200 plants m⁻², *L. grayi* was reduced and by an average of 82%. Additional growing seasons would be necessary to determine whether the reduction in biomass is likely to decrease the probability of survival, as well as delay the years before reproductive maturity.

Understanding the effect of *B. tectorum* on the growth and survival of *P. speciosus* is difficult because of the low number of plants at Lucky Peak and the herbivory at Orchard. However, *P. speciosus* had the largest and most consistent reduction in biomass at the lowest densities at Lucky Peak, and it responded very poorly to *B. tectorum* relative to the other species based on size in mid-May at Orchard. *Penstemon speciosus* is one of seven *Penstemon* species being grown for restoration use in the Great Basin (Shaw & Pellant 2008). Future studies with larger sample sizes and with more than one site are needed to determine whether biomass is consistently reduced by low densities of *B. tectorum* and whether other *Lomatium* species respond similarly.

My research suggests that native forbs can get established on sites with low expected densities of *B. tectorum*. However, there were large decreases in biomass at

densities less than 100 plants m^{-2} for three of four species. Many of the revegetation projects take place in the fall following fire. *Bromus tectorum* densities are typically at their lowest (around 10 plants m^{-2}) the first spring following a fire, but densities can increase to 10,000 plants m^{-2} within three years (Young & Evans 1985). While current management practices do not include reseeding native plants into dense existing stands of *B. tectorum*, sites should be selected carefully based on information on expected densities of *B. tectorum*.

CONCLUSIONS

Competition studies are typically designed in two ways, to measure “competitive effect or ability to suppress other individuals and competitive response or ability to avoid being suppressed” (Goldberg & Landa 1991). Some competition studies between *B. tectorum* and native plants have attempted to identify plants and associated traits that suppress the growth of *B. tectorum* (Humphrey & Schupp 2004, Drenovsky *et al.* 2008). My study was designed to address the latter, to understand how forbs respond to *B. tectorum*, and whether response differs among forb species. The other studies that have examined both the effect of and response to *B. tectorum* on native plants show that there is a decrease in *B. tectorum* density or growth only at very high densities of neighboring plants (Humphrey & Schupp 2004).

While reducing *B. tectorum* is an obvious goal for land managers, the cost and availability of native forb seed, along with the relatively slow growth of native forbs, reduces the likelihood that native forb establishment will be an important factor in suppressing *B. tectorum*. Alternatively, intact native plant communities are the best tool to reduce invasibility of *B. tectorum*, and as noted earlier, the presence of native grasses may be a key component.

To maximize the potential for native grasses to limit *B. tectorum*, but not native forbs, my greenhouse study demonstrated that after 12 weeks in the greenhouse, the native grass *E. elymoides* did not reduce the biomass of any of the forbs, but it did reduce the relative growth rate of *P. speciosus* and *S. munroana*. In contrast, the reduction of *P. speciosus* and *S. munroana* may suggest separating these forbs spatially, for example

seeding in different rows from *E. elymoides*. Additionally, *P. speciosus* responded very poorly to competition from both *E. elymoides* and the much smaller *Poa sandbergii*, suggesting it be spatially separated from both these native grasses to reduce negative interactions.

The goal of identifying forbs that can establish and grow with *B. tectorum* is to improve the selection of species based on expected site conditions. To reduce wasting valuable seed, species that cannot grow well with *B. tectorum* would be designated for sites expected to be in the best condition, in relation to *B. tectorum* invasion. However, the range in response to *B. tectorum* among forbs was lower than expected. In the greenhouse study, biomass was reduced by a minimum of 50% with *B. tectorum* compared to the control, while in the field study the biomass of three of four forbs was reduced by roughly 90% at *B. tectorum* densities less than 100 plants m⁻². While the range in response was relatively small in both the field study and the greenhouse study, the largest and most consistent difference among species was between *Lomatium* and *P. speciosus*.

In the greenhouse study, *Lomatium* had the smallest reduction in biomass compared to growth alone when growing with *B. tectorum*. In the field study, *L. grayi* had the best response to *B. tectorum* relative to three other forbs and was not reduced until densities were greater than 140 plants m⁻². While the species identity of the *Lomatium* in the greenhouse study is still pending, it is reasonable to assume its response to grasses is similar to the other three *Lomatium* species (*L. dissectum*, *L. grayi*, and *L. triternatum*) currently being tested and grown for restoration use in the Great Basin

(Shaw & Pellant 2008). It was collected at the same location, and seed was mature at the same time as *L. dissectum* and *L. grayi* (personal observation, spring 2005, 2006).

Additionally, root morphology is similar amongst the *Lomatium* species (personal observation). This is promising for the use of *Lomatium* in restoration projects.

In contrast, the biomass of *P. speciosus* was reduced by 98% in the greenhouse. At densities of *B. tectorum* less than 40 plants m⁻², biomass was reduced by 95% at the Lucky Peak site. In regards to designing seed mixtures, it may be an appropriate precautionary measure to separate it spatially from *E. elymoides* and *P. sandbergii*. This is one of seven *Penstemon* species being used for restoration in the Great Basin (Shaw & Pellant 2008). Until seed is both more available and less expensive, this data suggests that sites be selected very carefully before seeding *P. speciosus*, and research address whether other members of this genus respond similarly.

Achillea millefolium was used only in the field study. Like *P. speciosus*, it responded poorly to increasing densities of *B. tectorum* relative to *L. grayi*. Unlike *P. speciosus*, its greater availability, lower cost, and its potential to flower in the first year may be enough to offset its poor response. The lack of palatability of this plant is also a desirable quality. *Achillea millefolium* is often designated as a colonizer in restoration manuals. While grasses may be the best defense against *B. tectorum*, forbs with similar phenology and root structure may be able to reduce the biomass, or establishment of *B. tectorum*. Species that respond poorly are likely competing for the same resources as their neighbor, potentially reducing their neighbor's growth. This data demonstrated it had one of the largest reductions in biomass with increasing densities of *B. tectorum*.

With rapid establishment of native plant communities being one of the top objectives, and given the greater availability of *A. millefolium* seed compared to other forbs, future studies should investigate the use of this species as a nurse plant, or transition species, and measure interactions among *A. millefolium* and other forbs.

In the greenhouse, *E. umbellatum* was not reduced by either native grass. In the field study, it responded better to *B. tectorum* relative to *A. millefolium*, but the difference was not large enough to suggest promoting it over *A. millefolium*. Like *A. millefolium*, it was not palatable to ground squirrels. From the perspective of the ground squirrel, this is not a desirable characteristic, nor from the perspective of other organisms farther up in the food chain that may prey on ground squirrels. From the perspective of rapidly establishing diverse plant communities, this is a notable characteristic. Combining data from the greenhouse and field studies, *E. umbellatum* is an adaptable species, likely to respond well to competition from grasses, and based on both root morphology and small biomass, it is unlikely to affect other seeded species.

The last two species, *M. canescens* and *S. munroana*, were used in the greenhouse study only. *Machaeranthera canescens* has a number of qualities to recommend its use in restoration projects in the Great Basin. While the importance of root morphologies is purely speculative and must be tested in the field, its nearly tap-rooted morphology may minimize negative interactions with other desirable species with different root morphologies. In relation to encouraging rapid establishment, this species is especially desirable because it typically reproduces in the first growing season. It began to bolt and

form buds in the greenhouse between weeks 11 and 12. Many other native forb species require two to three years before flowering (personal observation).

The large seedling biomass of *S. munroana*, combined with its ability to flower in the first year, means this species ranks high in regards to ability to rapidly establish. However, its large biomass might cause negative interactions with other forbs. Additionally, its reduction in RGR with *E. elymoides* suggests it be separated from this native grass. Regarding response to *B. tectorum*, reduction in biomass was only 64% compared to growth alone, meaning its response was closer to *Lomatium* than *P. speciosus*. While these results are quite favorable for this species for restoration, a similar species, *S. grossulariifolia* (Hook. & Arn.) Rydb. was seeded in the field study, but less than 10 plants emerged and, in stark contrast to the greenhouse study, they were all smaller than *E. umbellatum* or *P. speciosus*. This may be due to poor seed quality; differences between these two *Sphaerolacea* species; or because *Sphaerolacea* (either species) does exceptionally well in the greenhouse under optimal conditions, but is more limited by conditions in the field. Both *S. munroana* and *S. grossulariifolia* are used in revegetation projects in the Great Basin and further information is needed on this genus.

While this experiment was not originally designed to investigate root architecture/root morphology, these characteristics, along with differences in phenology, may be an important characteristic to limit negative interactions. Future studies to identify negative interactions could explore seeding species with either the same or contrasting root morphologies to determine whether differences in root morphology limit negative interactions. The forbs with flabelliform root morphology were *A. millefolium*,

P. speciosus, and *S. munroana* and forbs with tap-rooted or columnar root morphologies were *Lomatium grayi*, *E. umbellatum* and *M. canescens*.

The identification of differences in root morphology and the observation that two forbs with flabelliform root morphology were negatively affected by a native grass, while the two with more tap-rooted or columnar root morphology were not, suggests that differences in root morphology may be a potential mechanism to reduce negative interactions. The relative importance of differences in root morphology, and whether they can increase resource partitioning spatially and temporally to increase diversity and reduce community invasibility is highly debatable. While resource partitioning spatially or temporally may not be the critical factor driving species assemblages in undisturbed communities in the Great Basin, as restoration ecologists, it is a potential tool that we should seek to maximize.

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APPENDICES

APPENDIX A

FORB SEED STRATIFICATION PROCEDURES

Table 13. Seed stratification methods for forb species in the greenhouse and field experiments. CM stands for cold moist treatment, and included storing seeds between moistened filter paper at 4.4 °C

Species	Experiment	Seed treatment
<i>A. millefolium</i>	Field	No treatments
<i>E. umbellatum</i>	Greenhouse and field	CM treatment for 2 weeks prior to expected emergence date
<i>Lomatium sp.</i> and <i>L. grayi</i>	Greenhouse/field	Soaked in water for 24 hours, CM treatments for 12 weeks prior to expected emergence date (mid December)
<i>M. canescens</i>	Greenhouse	1 day CM
<i>P. speciosus</i>	Greenhouse and field	Soaked in 500 ppm gibberellic acid for 24 hours, CM treatment for 8 weeks prior to expected emergence date (mid-January)
<i>S. munroana</i>	Greenhouse	1 week CM

APPENDIX B

CALIBRATION OF NEUTRON MOISTURE METER

In late July, the neutron probe was calibrated at each site to convert neutron probe ratios into volumetric water content. Eight access tubes were installed and neutron counts taken in two wet and two dry soil areas at each site. To obtain the wet soil samples, a 1-m² and 30-cm tall metal frame was pounded into the soil, filled with water, allowed to drain, and filled again. After a minimum of 60 hours to allow for internal redistribution of water, neutron probe count ratios were taken in the wet and dry soils. After the neutron counts were recorded, a total of three cores within 20 cm of each access tube were removed with a truck mounted, motorized soil corer. The cores were divided into sections corresponding to the depths at which neutron probe measurements were taken (0-30 for the 20-cm depth, 30-50 for the 40-cm depth etc.). The cores were immediately sealed tightly to prevent water loss and taken to the lab and weighed. They were dried at 105 °C for 24 hours and weighed again to allow calculation of mass water content. These were multiplied by the calculated soil bulk densities to obtain volumetric water contents.

At Lucky Peak, the corer could not access depths below 80 cm, and at Orchard, the corer could not access depths below 55 cm. Differences in structure and texture sometimes mean a different calibration equation is used for depths above the top 30 cm, but one equation for all depths provided the best fit at Lucky Peak. At Orchard, there was a separate equation for water content at 20 cm depths, and for depths below that.

APPENDIX C

RELATIONSHIPS BETWEEN FORB BIOMASS AND
NON-DESTRUCTIVE PLANT MEASUREMENTS

To convert size measurements to volume as a surrogate for biomass, the equation for the volume of a pyramid ($1/3 * \text{length} * \text{width} * \text{height}$) produced the best fit for all forbs (step-wise linear regression was used to test volumetric equations for a pyramid, cone, and sphere). The slopes from the natural log of biomass by *B. tectorum* density (left column) and the natural log of volume against density (right column) at Lucky Peak produced slopes that were very close. Compared to biomass, volume underestimated the affect of *B. tectorum* by 0.003 hundredths for *A. millefolium*, by 0.002 for *E. umbellatum*, and was identical for *P. speciosus*.

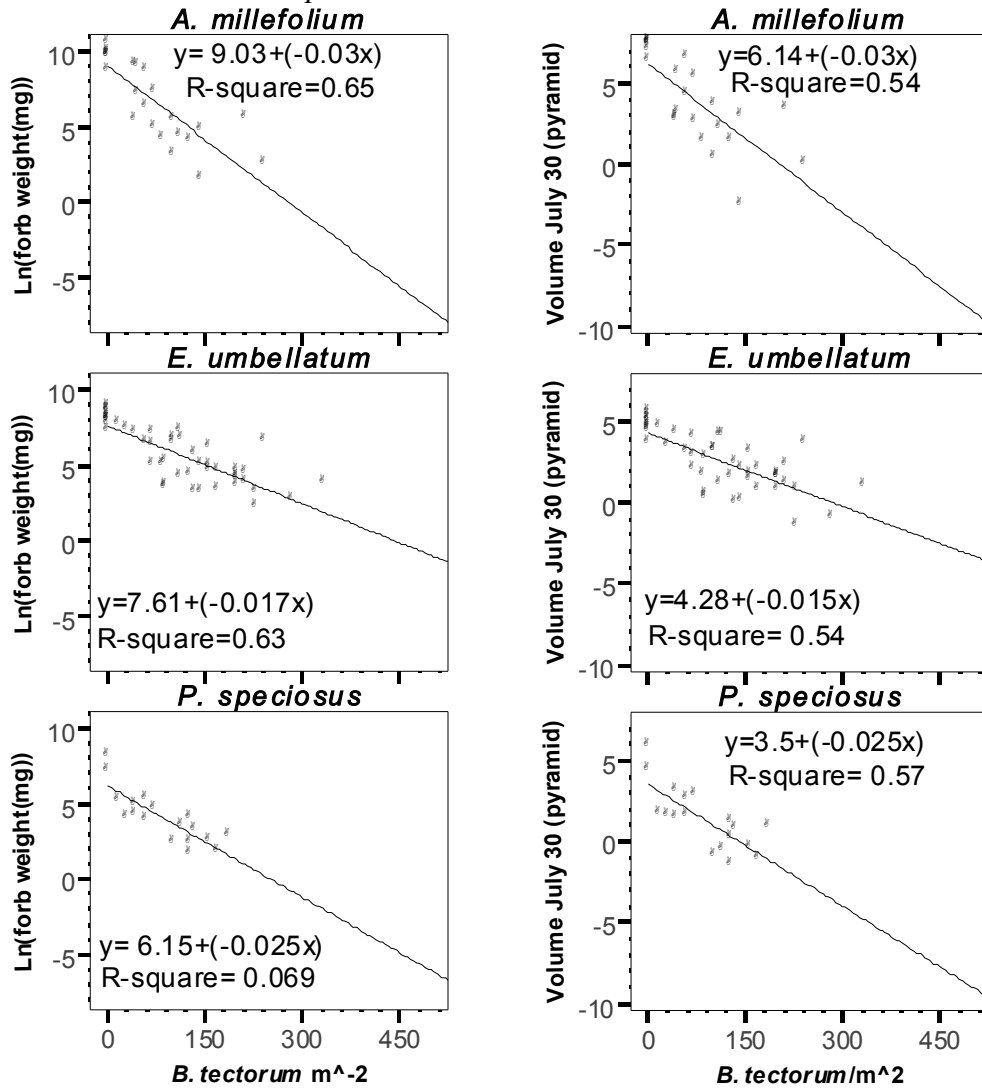


Figure 10. The natural log of biomass by *B. tectorum* (left column) and natural log of volume by *B. tectorum* (Lucky Peak)

Slopes were very similar at Orchard as well. Compared to biomass, volume overestimated the effect by 0.003 for *A. millefolium* and was the same for *E. umbellatum*.

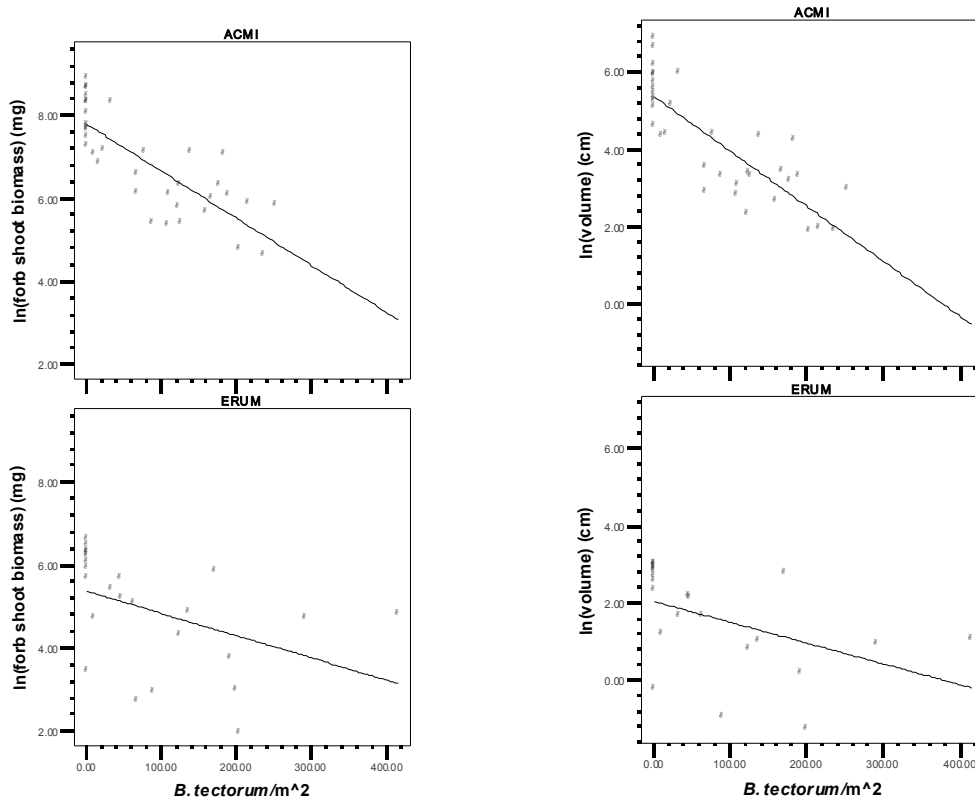


Figure 11. Natural log of *A. millefolium* and *E. umbellatum* biomass (left column) and volume (right column), by *B. tectorum* m^{-2} at Orchard.

APPENDIX D

SOIL WATER CONTENT MEASUREMENTS
AT LUCKY PEAK AND ORCHARD

Table 14. Volumetric soil water content (± 1 SE) at 20, 40, 60 and 80-cm depths among *B. tectorum* density levels at Lucky Peak, 2007. A split-plot ANOVA with time and blocks was used to analyze differences among *B. tectorum* density levels and account for repeated measures. Letters indicate significant differences at each sampling date among *B. tectorum* treatments at each depth. Numerator df were 78, and denominator df were 237.

Depth	Date	<i>B. tectorum</i> m ²											
		Control (0)			150-300			>300					
20	3/31	0.235	\pm	0.005		0.226	\pm	0.004		0.213	\pm	0.006	
20	4/5	0.233	\pm	0.005	a	0.221	\pm	0.004	ab	0.211	\pm	0.006	b
20	4/13	0.261	\pm	0.005	a	0.238	\pm	0.004	b	0.210	\pm	0.006	c
20	4/20	0.236	\pm	0.005	a	0.209	\pm	0.004	ab	0.180	\pm	0.006	b
20	4/27	0.256	\pm	0.005	a	0.196	\pm	0.004	b	0.169	\pm	0.006	c
20	5/7	0.301	\pm	0.005	a	0.178	\pm	0.004	b	0.183	\pm	0.006	b
20	5/13	0.256	\pm	0.005	a	0.127	\pm	0.004	b	0.122	\pm	0.006	b
20	5/22	0.238	\pm	0.005	a	0.094	\pm	0.004	b	0.083	\pm	0.006	b
40	3/31	0.271	\pm	0.004		0.272	\pm	0.004		0.277	\pm	0.006	
40	4/5	0.265	\pm	0.004		0.266	\pm	0.004		0.275	\pm	0.006	
40	4/13	0.283	\pm	0.004		0.277	\pm	0.004		0.276	\pm	0.006	
40	4/20	0.259	\pm	0.004		0.254	\pm	0.004		0.260	\pm	0.006	
40	4/27	0.283	\pm	0.004		0.267	\pm	0.004		0.263	\pm	0.006	
40	5/7	0.324	\pm	0.004	a	0.237	\pm	0.004	c	0.260	\pm	0.006	b
40	5/13	0.285	\pm	0.004	a	0.187	\pm	0.004	b	0.197	\pm	0.006	b
40	5/22	0.292	\pm	0.004	a	0.173	\pm	0.004	b	0.190	\pm	0.006	b
60	3/31	0.281	\pm	0.006		0.292	\pm	0.005		0.284	\pm	0.008	
60	4/5	0.276	\pm	0.006		0.285	\pm	0.005		0.284	\pm	0.008	
60	4/13	0.292	\pm	0.006		0.301	\pm	0.005		0.288	\pm	0.008	
60	4/20	0.265	\pm	0.006		0.283	\pm	0.005		0.278	\pm	0.008	
60	4/27	0.279	\pm	0.006		0.290	\pm	0.005		0.279	\pm	0.008	
60	5/7	0.323	\pm	0.006	a	0.290	\pm	0.005	b	0.292	\pm	0.008	b
60	5/13	0.280	\pm	0.006	a	0.254	\pm	0.005	b	0.242	\pm	0.008	b
60	5/22	0.285	\pm	0.006	a	0.237	\pm	0.005	b	0.225	\pm	0.008	b
80	3/31	0.257	\pm	0.008		0.274	\pm	0.007		0.242	\pm	0.010	
80	4/5	0.250	\pm	0.008		0.268	\pm	0.007		0.239	\pm	0.010	
80	4/13	0.262	\pm	0.008		0.278	\pm	0.007		0.244	\pm	0.010	
80	4/20	0.231	\pm	0.008		0.260	\pm	0.007		0.227	\pm	0.010	
80	4/27	0.245	\pm	0.008		0.272	\pm	0.007		0.243	\pm	0.010	
80	5/7	0.284	\pm	0.008		0.281	\pm	0.007		0.259	\pm	0.010	
80	5/13	0.239	\pm	0.008		0.256	\pm	0.007		0.216	\pm	0.010	
80	5/22	0.241	\pm	0.008		0.242	\pm	0.007		0.207	\pm	0.010	

Table 15. Volumetric water content (± 1 SE) at 20, 40, 60 and 80-cm depths among *B. tectorum* density levels at Orchard, 2007. A split-plot ANOVA with time and blocks was used to analyze differences among *B. tectorum* density levels and account for repeated measures. Letters indicate significant differences at each sampling date (within rows), among *B. tectorum* treatments. Numerator df were 92, and denominator df were 256.

Depth	Date	<i>B. tectorum</i> m ⁻²											
		Control (0)			150-300			>300					
20	3/13	0.159	±	0.006		0.153	±	0.008		0.153	±	0.010	
20	3/23	0.199	±	0.006	a	0.157	±	0.008	b	0.156	±	0.010	b
20	3/30	0.190	±	0.006	a	0.150	±	0.008	b	0.142	±	0.010	b
20	4/6	0.210	±	0.006	a	0.164	±	0.008	b	0.160	±	0.010	b
20	4/13	0.189	±	0.006	a	0.159	±	0.008	b	0.149	±	0.010	b
20	4/19	0.198	±	0.006	a	0.170	±	0.008	b	0.151	±	0.010	b
20	4/27	0.166	±	0.006		0.148	±	0.008		0.143	±	0.010	
20	5/9	0.142	±	0.006		0.130	±	0.008		0.121	±	0.010	
20	5/15	0.177	±	0.006	a	0.139	±	0.008	b	0.117	±	0.010	b
20	5/23	0.172	±	0.006	a	0.124	±	0.008	b	0.108	±	0.010	b
40	3/13	0.184	±	0.008		0.175	±	0.010		0.160	±	0.013	
40	3/23	0.225	±	0.008		0.219	±	0.010		0.224	±	0.013	
40	3/30	0.216	±	0.008		0.215	±	0.010		0.208	±	0.013	
40	4/6	0.253	±	0.008		0.238	±	0.010		0.234	±	0.013	
40	4/13	0.214	±	0.008		0.218	±	0.010		0.205	±	0.013	
40	4/19	0.232	±	0.008		0.239	±	0.010		0.212	±	0.013	
40	4/27	0.196	±	0.008		0.188	±	0.010		0.171	±	0.013	
40	5/9	0.185	±	0.008		0.173	±	0.010		0.158	±	0.013	
40	5/15	0.208	±	0.008		0.192	±	0.010		0.168	±	0.013	
40	5/23	0.205	±	0.008	a	0.184	±	0.010	ab	0.152	±	0.013	b
60	3/13	0.133	±	0.007		0.127	±	0.009		0.113	±	0.012	
60	3/23	0.192	±	0.007		0.169	±	0.009		0.171	±	0.012	
60	3/30	0.180	±	0.007		0.170	±	0.009		0.160	±	0.012	
60	4/6	0.213	±	0.007		0.188	±	0.009		0.184	±	0.012	
60	4/13	0.185	±	0.007		0.172	±	0.009		0.158	±	0.012	
60	4/19	0.199	±	0.007	a	0.191	±	0.009	ab	0.158	±	0.012	b
60	4/27	0.145	±	0.007		0.141	±	0.009		0.126	±	0.012	
60	5/9	0.136	±	0.007		0.129	±	0.009		0.119	±	0.012	
60	5/15	0.151	±	0.007		0.144	±	0.009		0.134	±	0.012	
60	5/23	0.149	±	0.007		0.144	±	0.009		0.127	±	0.012	
80	3/13	0.149	±	0.011		0.143	±	0.014		0.116	±	0.018	
80	3/23	0.162	±	0.011		0.146	±	0.014		0.138	±	0.018	
80	3/30	0.151	±	0.011		0.150	±	0.014		0.125	±	0.018	
80	4/6	0.191	±	0.011		0.170	±	0.014		0.157	±	0.018	
80	4/13	0.156	±	0.011		0.153	±	0.014		0.127	±	0.018	
80	4/19	0.174	±	0.011		0.175	±	0.014		0.133	±	0.018	

Table 15 (continued)

80	4/27	0.140 ± 0.011	0.133 ± 0.014	0.109 ± 0.018
80	5/9	0.133 ± 0.011	0.131 ± 0.014	0.105 ± 0.018
80	5/15	0.159 ± 0.011	0.150 ± 0.014	0.124 ± 0.018
80	5/23	0.159 ± 0.011	0.151 ± 0.014	0.124 ± 0.018