

# Effect of *Pseudoroegneria spicata* (bluebunch wheatgrass) Seeding Date on Establishment and Resistance to Invasion by *Bromus tectorum* (cheatgrass)

Audrey J. Harvey, Stacy C. Simanonok, Lisa J. Rew, Timothy S. Prather and Jane M. Mangold

## ABSTRACT

Rangelands degraded by non-native annual grasses are commonly restored by integrating herbicide with fall seeding of native perennial grasses. Seeds are expected to remain dormant throughout winter and emerge in spring. However, restoration often fails due to annual grass seedlings out-competing seeded grasses because they emerge sooner and grow faster. At two sites in Montana, we tested eight seeding dates of *Pseudoroegneria spicata* to determine the effect on resistance to invasion by the annual grass *Bromus tectorum*. After one growing season, fall (November) and early spring (April) seeding resulted in larger *P. spicata* than later spring seeding (May) (829–1,180 tillers per m<sup>2</sup> versus 349–561 tillers per m<sup>2</sup>) at one site, while seeding date had no effect on *P. spicata* at the second site. In the second season and after *B. tectorum* introduction, fall and early spring seeded *P. spicata* was more resistant to *B. tectorum* compared to late spring seeded. For example, *B. tectorum* was less dense (480 ± 101 tillers per m<sup>2</sup>) in *P. spicata* stands seeded 7 April than 12 May (943 ± 188 tillers per m<sup>2</sup>), and *B. tectorum* biomass was lower in fall-seeded stands (227 ± 81 g per m<sup>2</sup>) than stands seeded 12 May (533 ± 206 g per m<sup>2</sup>). Our results demonstrate that establishment and subsequent invasion resistance is enhanced by seeding native grasses from fall to early spring, presenting a wider timeframe for seeding than commonly practiced.

**Keywords:** invasive grass, seasonal priority effect, seeding timing

## 🌿 Restoration Recap 🌿

- We seeded the native perennial grass *Pseudoroegneria spicata* in November 2015 and weekly from April to early May 2016 to determine which seeding date resulted in the best stand establishment and greatest potential to resist invasion by the invasive annual grass *Bromus tectorum*.
- *Pseudoroegneria spicata* stands seeded in fall (November) and early spring (April) had higher plant density and biomass than those seeded later in spring (late April through May).
- *Bromus tectorum* was less abundant in *P. spicata* stands seeded in fall and early spring than in stands seeded in late spring, suggesting larger perennial grasses can limit invasion of annual grasses.
- Seeding *P. spicata* after 206 growing degree days (GDD, first week of May) is not advised as there was a trend of decreasing *P. spicata* and increasing *B. tectorum* abundance after this date.
- Land managers may have a wide window of opportunity for seeding native grasses, ranging from a fall dormant seeding through early spring, but care should be taken to not seed too late in spring.

Degraded range and wildlands are difficult to revegetate due to the persistence of non-native, annual grasses

or secondary invasions following control of the target annual grass (Pearson et al. 2016, Schantz et al. 2016). In habitats dominated by non-native, invasive annual grasses, their seedlings can outcompete native perennial grass seedlings due to early emergence of the annual grasses (Wainwright et al. 2012). Earlier emergence by these invasive winter annual grasses compared to native plants allows

for primary access to water and nutrients (Mangla et al. 2011a, Dickson et al. 2012). These benefits are amplified after germination and emergence because ruderal invasive annual grasses grow faster than native perennial grasses, compounding preemptive use of essential resources (Grotkopp and Rejmánek 2007, James and Drenovsky 2007, James 2008). Being the first to fill a vacant ecological niche is known as a priority effect (Wainwright et al. 2012). Seed banks of lands infested by invasive annual grasses are often dominated by those same species, limiting the recruitment of native plants.

Strategically modifying the seeding date of native plants to mitigate seasonal priority effects of invasive annual grasses during revegetation can be an ecologically-based management approach for improving native species recruitment and establishment (James et al. 2011, Farrell and Fehmi 2018). For example, the native grass *Pseudo-roegneria spicata* (bluebunch wheatgrass) suppressed the non-native, invasive annual grass *Bromus tectorum* (cheatgrass) in a greenhouse setting when seeded four weeks prior to seeding of *B. tectorum* (Orloff et al. 2013, Larson et al. 2018). Similar studies also support the effectiveness of seeding early to improve native grass establishment over invasive annual plants (Grman and Suding 2010, Boyd and James 2013). In the field, Boyd and Lemos (2015) attributed higher seedling survival of fall versus spring seeding to more established root systems from additional growing degree days (GDD). However, the success of direct seeding from fall versus spring seeding is still largely unknown in relation to its potential for resisting subsequent weed invasion.

During revegetation of invasive annual grass-infested areas in the semi-arid western United States, seeding of native perennial grasses like *P. spicata* often occurs in the fall, following a summer or fall herbicide application aimed at controlling annual grasses. Seeds are expected to remain dormant throughout winter and emerge in the spring at the earliest opportune time (Boyd and James 2013). However, fall dormant seeding has its limitations. First, fall dormant seedings expose seeds to predators and pathogens for several months before the seeds are expected to germinate, and some research suggests that seeds of native species may be more susceptible to predation than those of non-native species (Lucero and Callaway 2018). Furthermore, unanticipated germination prior to spring can put seedlings at risk of failure during winter freeze-thaw cycles (James et al. 2012). Revegetation failure can also result from the slow-growing nature of native perennial grasses, which do not typically reach reproductive maturity in the first growing season in contrast to quickly-growing annual grasses that complete their life cycle in less than a year (Schantz et al. 2016). Finally, though fall dormant seedings are common practice

(Monsen and Stevens 2004), they eliminate the option of a spring herbicide application to control spring-emerging invasive grasses because such an application would also injure seedlings of the seeded species.

Delaying seeding until spring, as an alternative to seeding in the fall, has had varied success in terms of density and biomass of seeded perennial grasses (Schantz et al. 2015, 2016). Density of surviving seedlings from spring seeding can be similar or greater than that of fall seeding (Boyd and Lemos 2015). Spring seeding on a site where annual grass propagule pressure was low (between 150–1,500 seeds per m<sup>2</sup>) and irrigation was available during the first growing season, resulted in satisfactory perennial grass establishment (Schantz et al. 2016). However, in semi-arid climates where irrigation is not available, delaying seeding until spring can be risky. Seedlings emerge, but may not grow enough, particularly in terms of root length, to survive seasonal drought (Schantz et al. 2016). Late spring-seeded perennial grasses also experience fewer GDD and accumulated precipitation than fall or early spring seedlings (Boyd and Lemos 2015). Addressing how late in the spring seeding can occur while still resulting in satisfactory native perennial grass establishment is necessary to improve revegetation of invasive annual grass-infested range and wildlands.

The first objective of this study was to examine whether fall or early to late spring seeding resulted in higher establishment of the native perennial grass *P. spicata* over two growing seasons. Consistent with previous studies (Boyd and James 2013, Boyd and Lemos 2015), we hypothesized perennial grass density and biomass to be highest for fall and early spring-seeded cohorts when compared to late spring-seeded cohorts. We used *P. spicata* for this study because it is a large-statured, native bunchgrass that is common across mountain and foothill rangelands, is valued as a forage species for livestock and wildlife (Stubbendieck et al. 1997), and in Montana it is often one of the last native perennial grasses to persist in areas invaded by non-native species (J. Mangold, Montana State University, pers. comm.). Several cultivars of *P. spicata* have demonstrated successful establishment in other studies (Sheley et al. 2001, Sheley et al. 2006, Jacobs et al. 2006, Rinella et al. 2012, Mangold et al. 2015).

The second objective addressed whether *P. spicata* seeding date affected suppression of the invasive annual grass *B. tectorum* when it was introduced to the plots at the end of *P. spicata*'s first growing season. We hypothesized *B. tectorum* biomass and density would be lowest where *P. spicata* was seeded in fall and early spring when compared to late spring seeding, due to the predicted increase in density and biomass of *P. spicata* plants during the first growing season.

## Methods

This study occurred at two field sites which were located at the Arthur H. Post Research Farm (45°40'38.01" N 111°9'19.49" W) and Fort Ellis Research Farm (45°40'13.19" N 110°58'48.13" W), hereafter referred to as Post Farm and Fort Ellis, respectively, near Bozeman, Montana. Elevation at Post Farm and Fort Ellis are 1,450 m and 1,484 m, respectively. In 2016 and 2017, the total annual precipitation at Post Farm was 32.5 cm and 37.7 cm, and annual minimum/maximum temperatures were 1.21°C/14.8°C and 0.23°C/13.8°C, respectively (Table 1, NOAA 2018). In 2016 and 2017, the total annual precipitation at Fort Ellis was 46.7 cm and 60.7 cm, and minimum/maximum temperatures were 1.06°C/13.8°C and -0.1°C/13.0°C, respectively (Table 1, Weather Underground 2018).

Prior to setting up the study, existing vegetation was manually removed, and the fallow fields were tilled. A completely randomized split-plot design was used to test eight seeding dates of *P. spicata* (whole plots, 1 m × 2 m with additional 0.5 m buffer) and two levels (absent and present) of *B. tectorum* competition (split-plots, 1 m × 1 m). Seeding treatments were replicated four times at each site for a total of 32 main plots and 64 split-plots per site.

The eight seeding date treatments were 8 November 2015 (fall) and seven weekly spring seeding dates from 1 April 2016 to 12 May 2016 (early to late spring, Table 2). Seeds of *P. spicata* (Goldar cultivar) were hand broadcasted evenly on the soil surface at 667 seeds per m<sup>2</sup> (following Orloff et al. 2013) for each treatment at each site. Seeds

were produced and obtained from Bruce Seed Farm near Townsend, Montana, approximately 100 km from the study sites. June of the first growing season was drier than the 30-year mean precipitation (Western Regional Climate Center 2019) at the Post Farm: we applied the equivalent of 1.27 cm of precipitation in June 2016 to address this deficit. All vegetation other than *P. spicata* was removed by hand throughout the first growing season. In September 2016, after the first growing season and when plants were in a reproductive state, *P. spicata* density (tillers per m<sup>2</sup>) was measured across whole plots (1 m × 2 m).

After the first growing season, *B. tectorum* seeds were sown into competition split-plots on 1 September 2016 at 1,112 seeds per m<sup>2</sup> (following Orloff et al. 2013), using seeds collected from several sites near Bozeman, Montana. In both years, only target species, *P. spicata* and *B. tectorum*, were grown and all other species were removed by hand until data were collected from 23 June 2017–10 July 2017. Three randomly-placed 50 cm × 20 cm frames (Daubenmire 1959) per split-plot were used to sample density (tillers per m<sup>2</sup>) and aboveground biomass of *P. spicata* and *B. tectorum*. Biomass was clipped to 2 cm above ground level, dried at 37°C for 48 hours, and weighed to the nearest 0.1 gram.

An analysis of variance (ANOVA) was used on a general linear model with a Quasi-Poisson distribution to detect differences in *P. spicata* density (tillers per m<sup>2</sup>) by seeding date for each site for objective one. One replication of the Spring 5 seeding data at Post Farm was removed from analysis because the plots received run-off irrigation from

**Table 1. Average spring (March–May), summer (June–August), fall (September–November), and total precipitation (cm) and average minimum and maximum temperatures (°C) for spring, summer, fall and annual at Post Farm and Fort Ellis across a 30-year period and years 2016 and 2017. \*30-year averages (1981–2010) were based on the Western Regional Climate Center (WRCC) monthly data for this region and were only available at the Post Farm site**

Site	Year	Precipitation (cm)				Temperature (°C, min/max)			
		Spring	Summer	Fall	Total	Spring	Summer	Fall	Annual
Post Farm	30 year*	4.76	4.57	3.00	41.1	-0.8/13.6	5.09/26.3	-0.5/14.3	-0.7/14.1
	2016	3.76	2.06	4.09	32.5	1.24/14.7	9.47/28.0	2.89/15.0	1.21/14.8
	2017	4.67	2.18	3.68	37.7	1.44/14.5	10.3/27.8	0.16/13.0	0.23/13.8
Fort Ellis	2016	5.35	2.57	6.30	46.7	1.25/13.1	9.45/26.4	2.66/14.3	1.06/13.8
	2017	8.08	5.02	5.13	60.7	0.85/13.3	10.2/26.5	-0.3/12.3	-0.1/13.0

**Table 2. Seeding dates and cumulative growing degree days (GDD = sum of average daily temperature °C — temperature base 4.4°C between 1 March 2016 to 12 May 2016) for *Pseudoroegneria spicata* at Post Farm (PF) and Fort Ellis (FE) sites.**

Treatment	Seeding Date	PF GDD	FE GDD	Average GDD
Fall	8 November 2015	—	—	—
Spring 1 (S1)	1 April 2016	39.5	34.4	37.0
Spring 2 (S2)	7 April 2016	70.1	58.1	64.1
Spring 3 (S3)	13 April 2016	114	93.7	104
Spring 4 (S4)	21 April 2016	142	126	134
Spring 5 (S5)	29 April 2016	172	150	161
Spring 6 (S6)	5 May 2016	217	195	206
Spring 7 (S7)	12 May 2016	261	231	246

an adjacent field and produced abnormally high *P. spicata* densities. In both years, *P. spicata* density across main plots was used to determine establishment for all seeding cohorts, whereas in the second year *P. spicata* density in the no competition plots were evaluated. Tukey pairwise comparisons were used to determine differences across seeding date treatments for each site.

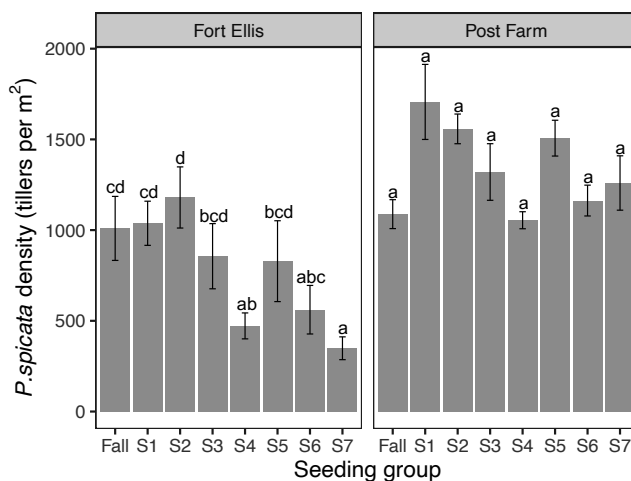
For objective two, the effect of seeding date on *P. spicata* and *B. tectorum* was analyzed using ANOVA models. Specifically, an ANOVA on a linear mixed effects model was used to determine differences in *P. spicata* density and biomass, where fixed effects were seeding and competition treatments and site, and random effects accounted for plot-to-plot variation. When analyzing *B. tectorum* density, an ANOVA was used on a general linear model to determine seeding date treatment effects across sites. Data were over-dispersed, so a Quasi-Poisson distribution was used. When analyzing *B. tectorum* biomass, an ANOVA was used on a linear model to determine seeding date treatment effects across sites. Tukey pairwise comparisons were used to determine differences between seeding groups and competition levels.

For all analyses, all models were explored for normality, independence, and constant variance assumptions and median values are shared. Graphical interpretations and analyses were conducted using R Software 3.5.1 (R Core Team 2018), specifically dplyr, lme4, emmeans, and ggplot2 packages (Bates et al. 2015, Lenth et al. 2018, Wickham 2016, Wickham et al. 2018).

## Results

### *Pseudoroegneria spicata* Density and Biomass

Seeding treatments affected *P. spicata* density after one growing season, but the effect depended on site ( $F_{7,110} = 2.759, p = 0.011$ ). At Fort Ellis, Spring 2 resulted in  $1,180 \pm 169$  tillers per  $m^2$  (estimate  $\pm$  standard error), which was similar to Fall ( $1,009 \pm 176$  tillers per  $m^2$ ), Spring 1 ( $1,038 \pm 122$  tillers per  $m^2$ ), Spring 3 ( $856 \pm 180$  tillers per  $m^2$ ), and Spring 5 ( $829 \pm 223$  tillers per  $m^2$ ) (Figure 1). Spring 4, Spring 6, and Spring 7 had similarly low densities at  $472 \pm 72$  tillers per  $m^2$ ,  $561 \pm 134$  tillers per  $m^2$ , and  $349 \pm 63$  tillers per  $m^2$ , respectively. At Post Farm, there was no



**Figure 1.** *Pseudoroegneria spicata* density (tillers per  $m^2 \pm$  SE) after one growing season (2016) at two sites in southwestern Montana. Seeding dates are Fall (11 November 2015), S1 (1 April 2016), S2 (7 April 2016), S3 (13 April 2016), S4 (21 April 2016), S5 (29 April 2016), S6 (5 May 2016), S7 (12 May 2016). Similar letters indicate no difference in density across treatments within a site ( $\alpha = 0.05$ ).

effect of seeding treatment on *P. spicata* density. Densities ranged from  $1,054 \pm 47$  tillers per  $m^2$  in Spring 4 to  $1,706 \pm 207$  tillers per  $m^2$  in Spring 1 (Figure 1).

After two growing seasons, seeding treatment affected density of *P. spicata* ( $F_{7,47} = 3.344, p = 0.005$ ) (Table 3). Spring 7, which resulted in  $1,221 \pm 158$  tillers per  $m^2$ , was lower than Spring 1 and Spring 2 ( $1,988 \pm 145$  and  $1,895 \pm 110$  tillers per  $m^2$ , respectively) (Figure 2). Density of *P. spicata* was otherwise similar across seeding treatments and ranged from 1,221 to 1,988 tillers per  $m^2$ .

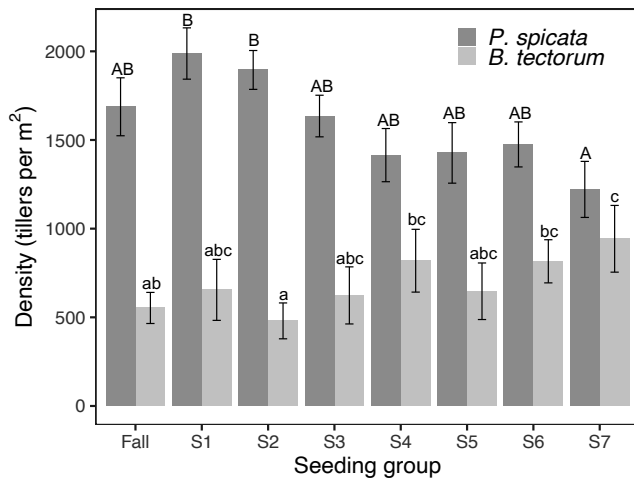
Density of *P. spicata* was also affected by competition from *B. tectorum*, where the effect varied by site ( $F_{1,54} = 23.63, p < 0.001$ ) (Table 3). At Fort Ellis, the no competition treatment (control) yielded higher density of *P. spicata* ( $1,735 \pm 122$  tillers per  $m^2$ ) than the *B. tectorum* competition treatment ( $1,161 \pm 107$  tillers per  $m^2$ ), while *B. tectorum* competition had no effect on *P. spicata* density at Post Farm (mean =  $1,748 \pm 55$  per  $m^2$ ).

After two growing seasons, biomass of *P. spicata* was affected by seeding treatment ( $F_{7,47} = 3.423, p = 0.005$ ) (Table 3). Biomass was lower in seeding treatments Spring

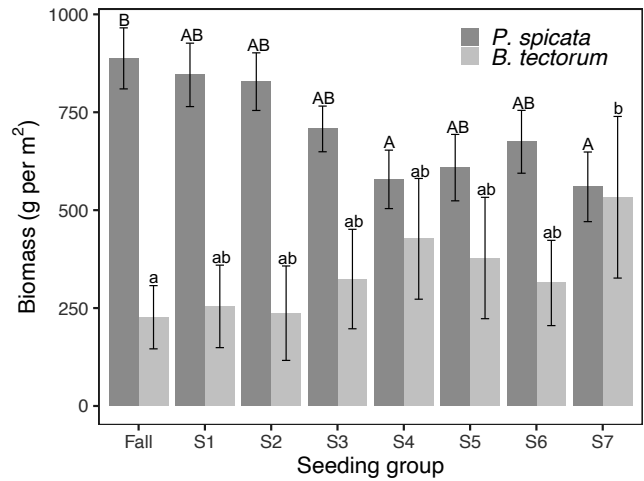
**Table 3.** Analysis of variance (ANOVA) table for *Pseudoroegneria spicata* density (tillers per  $m^2$ ) and biomass (g per  $m^2$ ) after two growing seasons (2017). Competition indicates presence or absence of *Bromus tectorum*.

Main Effects and Interactions	df	Density		Biomass	
		F-value	p-value	F-value	p-value
Seeding	7, 47	3.344	0.005	3.423	0.005
Competition	1, 54	8.706	0.005	5.139	0.027
Site	1, 47	8.944	0.004	35.31	< 0.001
Seeding*Competition	7, 54	1.416	0.218	1.234	0.301
Seeding*Site	7, 47	1.959	0.081	1.361	0.244
Competition*Site	1, 54	23.63	< 0.001	9.731	0.003





**Figure 2.** *Pseudoroegneria spicata* and *Bromus tectorum* density (tillers per m<sup>2</sup> ± SE) across seeding treatments after two growing seasons (2017) at two sites in southwestern Montana. Seeding dates are Fall (11 November 2015), S1 (1 April 2016), S2 (7 April 2016), S3 (13 April 2016), S4 (21 April 2016), S5 (29 April 2016), S6 (5 May 2016), S7 (12 May 2016). Similar letters indicate no difference in a species' density across treatments ( $\alpha = 0.05$ ).



**Figure 3.** *Pseudoroegneria spicata* and *Bromus tectorum* biomass (g per m<sup>2</sup> ± SE) across seeding treatments after two growing seasons (2017) at two sites in southwestern Montana. Seeding dates are Fall (11 November 2015), S1 (1 April 2016), S2 (7 April 2016), S3 (13 April 2016), S4 (21 April 2016), S5 (29 April 2016), S6 (5 May 2016), S7 (12 May 2016). Similar letters indicate no difference in a species' biomass across treatments ( $\alpha = 0.05$ ).

7 and Spring 4 (560 ± 88.9 g per m<sup>2</sup> and 578 ± 74.6 g per m<sup>2</sup>, respectively) compared to Fall (888 ± 77.9 g per m<sup>2</sup>) (Figure 3). Otherwise, biomass was similar across most seeding treatments (Figure 3).

Biomass of *P. spicata* was affected by competition treatment, and the effect varied by site ( $F_{1,54} = 9.731, p = 0.003$ ) (Table 3). At Fort Ellis, the no competition treatment yielded higher *P. spicata* biomass (687 ± 57.2 g per m<sup>2</sup>) than the *B. tectorum* competition treatment (455 ± 51.8 g per m<sup>2</sup>). Competition from *B. tectorum* had no effect on *P. spicata* biomass at Post Farm (mean = 859 ± 31.2 g per m<sup>2</sup>).

### **Bromus tectorum Density and Biomass**

There was a difference in *B. tectorum* density due to the main effects of site ( $F_{1,54} = 173.2, p < 0.001$ ) and seeding treatment ( $F_{7,55} = 4.500, p < 0.001$ ; Table 4). Fort Ellis had higher density of *B. tectorum* (1,019 ± 59 tillers per m<sup>2</sup>) than Post Farm (356 ± 29 tillers per m<sup>2</sup>). Averaged across sites, *B. tectorum* density was higher in Spring 7 (943 ± 188 tillers per m<sup>2</sup>) than Fall (553 ± 88 tillers per m<sup>2</sup>) and Spring 2 (480 ± 101 tillers per m<sup>2</sup>) (Figure 2). All other seeding treatments were similar to each other.

Biomass showed a similar pattern to density: there was a difference in *B. tectorum* biomass across the main effects of site ( $F_{1,47} = 158.0, p < 0.001$ ) and seeding treatment ( $F_{7,47} = 2.397, p = 0.035$ ; Table 4). Fort Ellis had higher *B. tectorum* biomass (636 ± 53.4 g per m<sup>2</sup>) than Post Farm (26.3 ± 6.0 g per m<sup>2</sup>). Averaged across sites, *B. tectorum* biomass was higher in Spring 7 (533 ± 206 g per m<sup>2</sup>) than Fall (227 ± 80.7 g per m<sup>2</sup>) (Figure 3). All other seeding treatments were similar to each other.

### **Discussion**

Fall (i.e., November) and early spring (i.e., April) seeding generally resulted in greater establishment of *P. spicata* after one and two growing seasons than late spring seeding, as has been observed in other studies (Boyd and Davies 2012, Boyd and James 2013, Rinella and James 2017). The effect of seeding date was more pronounced in the first year at Fort Ellis, with the exception of Spring 5 at both sites. We believe the Spring 5 seeding cohort benefited from 2.2 cm of snow that fell from 23 April to 28 April 2016 (NOAA 2018) across both sites. The legacy of seeding date was less pronounced in the second year, as would be expected, though greater establishment of *P. spicata* in the fall (i.e., biomass) and early spring (i.e., density) than late spring was evident across the two sites. Our results generally support the first hypothesis and previous studies, indicating fall and early spring seeding produce larger perennial grasses than late spring seeding dates (James et al. 2012, Boyd and Lemos 2015). We recognize that other native grasses may differ in optimal seeding time, but given that *P. spicata* is arguably one of the most important native grasses on western rangeland, our study provides important information on best practices for its establishment.

The second hypothesis that *B. tectorum* density and biomass was expected to be lowest where *P. spicata* was highest in fall and early spring seeding was also generally supported. In particular, the high density of *P. spicata* in the Spring 2 treatment (i.e., seeded 7 April) had the greatest competitive effect on *B. tectorum* density. *Pseudoroegneria spicata* biomass also was greatest in the Fall as compared

to late spring (i.e., seeded 21 April and 12 May) seeding which subsequently led to lower *B. tectorum* biomass. This study also indicates that seeding after the first week of May (above 206 GDD; Table 2) is not ideal as there was a trend of decreasing *P. spicata* abundance and subsequent increase in *B. tectorum* abundance at the latest spring seeding date. This trend was consistent across both sites, suggesting results found here may hold true across locations that have similar climatic conditions as southwestern Montana.

Across both sites there was no competition by seeding date interaction which suggests once *P. spicata* is established, the effect of competition from *B. tectorum* is lessened. We did not measure resource availability (e.g., soil moisture or nutrient concentrations), and we acknowledge that competition in fallow and tilled fields used in this study is not like that in impacted rangelands. Furthermore, establishment of *P. spicata* was higher than that seen in studies that occurred in range or wildlands infested with *B. tectorum* or other invasive plants (Whitson and Koch 1998, Sheley et al. 2001, Mangold et al. 2015). However, our results support that *P. spicata*, once established, can be highly competitive against secondary invasion (Rinella et al. 2012, USDA-NRCS 2012). Providing seeded species with a seasonal priority effect can shift competitive dynamics in a positive direction (Orloff et al. 2013), and along with other research suggests large and robust perennial grasses can limit invasion by annual grasses (Whitson and Koch 1998, Humphrey and Schupp 2004, James et al. 2008, Davies and Johnson 2017, Young et al. 2005).

Despite evidence suggesting precipitation is a key factor influencing revegetation success in semi-arid regions (Hardegree et al. 2013, Hardegree et al. 2016), wetter conditions at Fort Ellis compared to Post Farm did not have a substantial impact on *P. spicata* establishment and competitive dynamics with *B. tectorum*. In fact, abundance of *P. spicata* was lower at Fort Ellis than Post Farm; and, perhaps accordingly, abundance of *B. tectorum* was higher at Fort Ellis. Other revegetation studies have failed to find a beneficial effect of additional moisture on seedling success. For example, experimental observations in Oregon found no effect of additional watering on final density and biomass of *P. spicata* that was seeded fall (Boyd and James 2013) or spring (James and Svejcar 2010). However, it should be noted that in our study there was more variability at Fort Ellis in the response of *P. spicata* density to seeding date during the first year of the study, and there was an effect of the competition treatment during the second year of the study. Of further note, annual precipitation at Fort Ellis during our study was higher than the 30-year average precipitation and within the recommended precipitation zone (at least 30.5 cm) for the cultivar of *P. spicata* used in this study (USDA-NRCS 2012). Of the recommended USDA cultivars of *P. spicata*, “Goldar,” which was used in this study, is well adapted for rapid growth under dry

conditions at or above 30.5 cm of annual rainfall above 1,000 m elevation (USDA-NRCS 2012).

One of the foremost risks to seeding a degraded site with native species is competition from invasive seedlings (Ray-Mukherjee et al. 2011). Decreasing seeds of undesirable species in the seed bank to a level that allows native species to establish (less than 1,500 seeds per m<sup>2</sup>; Schantz et al. 2016) can prove difficult when natural seed rain of *B. tectorum* can be as high as 12,000 seeds per m<sup>2</sup> (Humphrey and Schupp 2001). Applying management tactics that eliminate or reduce seed production, like herbicides or targeted grazing, over multiple years or using herbicides with multiple years of annual grass control (Sebastian et al. 2016, Sebastian et al. 2017a, Sebastian et al. 2017b) can reduce the seed bank of invasive annual grasses and minimize competition with seeded species. Continued practice of fall dormant seeding at the recommended rate (approximately 17 pounds per acre for *P. spicata*) (Sheley et al. 2008) is supported by this study, but practitioners should consider early spring seeding as an option as well. Our findings suggest that land managers can delay seeding until early spring without compromising native grass establishment. Spring seeding offers the option of applying a non-selective, non-persistent herbicide like glyphosate to control *B. tectorum* seedlings that emerged over the winter and into early spring (Kyser et al. 2012, Kyser et al. 2013), eliminating competition for at least one growing season. If seeding is delayed until spring, though, seeding after the first week of May (or GDD greater than 206) is not recommended as it could result in decreased establishment.

Our results show that providing native perennial grasses with a seasonal priority effect can improve their resistance to invasion by weedy annual grasses. The success of varied seeding dates indicates a wide range of opportunity available to land managers when seeding native grasses with fall (November) and early spring (April) seeding producing favorable results. However, we also found a trend of decreasing *P. spicata*, as well as increasing *B. tectorum*, when cohorts were seeded after 206 GDD. Further studies could help consolidate the optimum range of *P. spicata* seeding dates for different regions across the West. In addition, testing the effect of seeding date for other important native grass species of mountain and foothill rangelands in the West is also encouraged.

## Acknowledgments

Funding for this project was provided by Montana Noxious Weed Trust Fund, and L.J.R. and J.M.M. are supported by NIFA-USDA Hatch MONB000363 and MONB00359, respectively.

## References

- Bates, D., M. Mächler, B.M. Bolker and S.C. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.

- Boyd, C.S. and K. Davies. 2012. Spatial variability in cost and success of revegetation in a Wyoming big sagebrush community. *Environmental Management* 50:441–450.
- Boyd, C.S. and J.J. James. 2013. Variation in timing of planting influences bluebunch wheatgrass demography in an arid system. *Rangeland Ecology and Management* 66:117–126.
- Boyd, C.S. and Lemos, J.A. 2015. Evaluating winter/spring seeding of a native perennial bunchgrass in the sagebrush steppe. *Rangeland Ecology and Management* 68:494–500.
- Daubenmire, R.F. 1959. A canopy-cover method of vegetational analysis. *Northwest Science* 33:43–64.
- Davies, K. and D. Johnson. 2017. Established perennial vegetation provides high resistance to reinvasion by exotic annual grasses. *Rangeland Ecology and Management* 70:748–754.
- Dickson, T.L., J.L. Hopwood and Wilsey, B.J. 2012. Do priority effects benefit invasive plants more than native plants? An experiment with six grassland species. *Biological Invasions* 14:2617–2624.
- Farrell, H.L. and J.S. Fehmi. 2018. Seeding alters plant community trajectory: Impacts of seeding, grazing and trampling on semi-arid re-vegetation. *Applied Vegetation Science* 21:240–249.
- Grman, E. and K.N. Suding. 2010. Within-year soil legacies contribute to strong priority effects of exotics on native California grassland communities. *Restoration Ecology* 18:664–670.
- Grotkopp, E. and M. Rejmánek. 2007. High seedling relative growth rate and specific leaf area are traits of invasive species: Phylogenetically independent contrasts of woody angiosperms. *American Journal of Botany* 94:526–532.
- Hardegree, S.P., C.A. Moffet, G.N. Flerchinger, J. Cho, B.A. Roundy, T.A. Jones and F.B. Pierson. 2013. Hydrothermal assessment of temporal variability in seedbed microclimate. *Rangeland Ecology and Management* 66:127–135.
- Hardegree, S.P., T.A. Jones, B.A. Roundy, N.L. Shaw and T.A. Monaco. 2016. Assessment of range planting as a conservation practice. *Rangeland Ecology and Management* 69:337–347.
- Humphrey, L.D. and E.W. Schupp. 2001. Seed banks of *Bromus tectorum* dominated communities in the Great Basin. *Western North American Naturalist* 61:85–92.
- Humphrey, L.D. and E.W. Schupp. 2004. Competition as a barrier to establishment of a native perennial grass (*Elymus elymoides*) in alien annual grass (*Bromus tectorum*) communities. *Journal of Arid Environments* 58:405–422.
- Jacobs, J.S., S.E. Sing and J.M. Martin. 2006. Influence of herbivory and competition on invasive weed fitness: Observed effects of *Cyphocleonus achates* (Coleoptera: Curculionidae) and grass-seeding treatments on spotted knapweed performance. *Environmental Entomology* 35:1590–1596.
- James, J.J. and R.E. Drenovsky. 2007. A basis for relative growth rate differences between native and invasive forb seedlings. *Rangeland Ecology and Management* 60:395–400.
- James, J.J. 2008. Effect of soil nitrogen stress on the relative growth rate of annual and perennial grasses in the Intermountain West. *Plant and Soil* 310:201–210.
- James, J.J., K.W. Davies, R.L. Sheley and Z.T. Aanderud. 2008. Linking nitrogen partitioning and species abundance to invasion resistance in the Great Basin. *Oecologia* 156:637–648.
- James, J.J. and T.J. Svejcar. 2010. Limitations to postfire seedling establishment: The role of seeding technology, water availability, and invasive plant abundance. *Rangeland Ecology and Management* 63:491–495.
- James, J.J., R.E. Drenovsky, T.A. Monaco and M.J. Rinella. 2011. Managing soil nitrogen to restore annual grass-infested plant communities: effective strategy or incomplete framework? *Ecological Applications* 21:490–502.
- James, J.J., M.J. Rinella and T.J. Svejcar. 2012. Grass seedling demography and sagebrush steppe restoration. *Rangeland Ecology and Management* 65:409–417.
- Kyser, G.B., J.E. Creech, J. Zhang and J.M. DiTomaso. 2012. Selective control of medusahead (*Taeniatherum caput-medusae*) in California sagebrush scrub using low rates of glyphosate. *Invasive Plant Science and Management* 5:1–8.
- Kyser, G.B., R.G. Wilson, J. Zhang and J.M. DiTomaso. 2013. Herbicide-assisted restoration of Great Basin sagebrush steppe infested with medusahead and downy brome. *Rangeland Ecology and Management* 66:588–596.
- Larson, C.D., E.A. Lehnhoff, C. Noffsinger and L.J. Rew. 2018. Competition between cheatgrass and bluebunch wheatgrass is altered by temperature, resource availability, and atmospheric CO<sub>2</sub> concentration. *Oecologia* 186:855–868.
- Lenth, R., H. Singmann, J. Love, P. Buerkner and M. Herve. 2018. Estimated marginal means, aka least-squares means. CRAN. CRAN.R-project.org/package=emmeans.
- Lucero, J.E. and R.M. Callaway. 2018. Native granivores reduce the establishment of native grasses but not invasive *Bromus tectorum*. *Biological Invasions* 20:3491–3497.
- Mangla, S., R.L. Sheley, J.J. James and S.R. Radosevich. 2011a. Intra and interspecific competition among invasive and native species during early stages of plant growth. *Plant Ecology* 212:531–542.
- Mangla, S., R.L. Sheley, J.J. James and S.R. Radosevich. 2011b. Role of competition in restoring resource poor arid systems dominated by invasive grasses. *Journal of Arid Environments* 75:487–493.
- Mangold, J.M., N. Orloff, H. Parkinson and M. Halstvedt. 2015. Integrating herbicides and re-seeding to restore rangeland infested by an invasive forb-annual grass complex. *Ecological Restoration* 33:16–19.
- Monsen, S.B. and R. Stevens. 2004. Seedbed preparation and seeding practices. Pages 121–154 in S.B. Monsen, R. Stevens and N.L. Shaw, comps. *Restoring western ranges and wildlands*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. General Technical Report RMRS-GTR-136.
- NOAA. 2018. Daily summary station details from 2017 and 2018 for station Bozeman 6 W Experimental Farm, MT US C00241047 (accessed November 24, 2018). [www.ncdc.noaa.gov/cdo-web](http://www.ncdc.noaa.gov/cdo-web).
- Orloff, N., J.M. Mangold and F.D. Menalled. 2013. Role of size and nitrogen in competition between annual and perennial grasses. *Invasive Plant Science and Management* 6:87–98.
- Pearson, D.E., Y.K. Ortega, J.B. Runyon and J.L. Butler. 2016. Secondary invasion: The bane of weed management. *Biological Conservation* 197:8–17.
- R Core Team 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [www.R-project.org](http://www.R-project.org).
- Ray-Mukherjee, J., T.A. Jones, P.B. Adler and T.A. Monaco. 2011. Immature seedling growth of two North American native perennial bunchgrasses and the invasive grass *Bromus tectorum*. *Rangeland Ecology and Management* 64:358–365.
- Rinella, M.J., J.M. Mangold, E.K. Espeland, R.L. Sheley and J.S. Jacobs. 2012. Long-term population dynamics of seeded plants in invaded grasslands. *Ecological Applications* 22:1320–1329.
- Rinella, M.J. and J.J. James. 2017. A modelling framework for improving plant establishment during ecological restoration. *Ecological Modelling* 361:177–183.



- Schantz, M.C., R.L. Sheley and J.J. James. 2015. Role of propagule pressure and priority effects on seedlings during invasion and restoration of shrub-steppe. *Biological Invasions* 17:73–85.
- Schantz, M.C., R.L. Sheley, J.J. James and E.P. Hamerlynck. 2016. Role of dispersal timing and frequency in annual grass-invaded Great Basin ecosystems: How modifying seeding strategies increases restoration success. *Western North American Naturalist* 76:36–52.
- Sebastian, D.J., J.R. Sebastian, S.J. Nissen and K.G. Beck. 2016. A potential new herbicide for invasive annual grass control on rangeland. *Rangeland Ecology and Management* 69:195–198.
- Sebastian, D.J., M.B. Fleming, E.L. Patterson, J.R. Sebastian and S.J. Nissen. 2017a. Indaziflam: a new cellulose-biosynthesis-inhibiting herbicide provides long-term control of invasive winter annual grasses. *Pest Management Science* 73:2149–2162.
- Sebastian, D.J., S.J. Nissen, J.R. Sebastian and K.G. Beck. 2017b. Seed bank depletion: The key to long-term downy brome (*Bromus tectorum* L.) management. *Rangeland Ecology and Management* 70:477–483.
- Sheley, R.L., J.S. Jacobs and D.E. Lucas. 2001. Revegetating spotted knapweed infested rangeland in a single entry. *Journal of Range Management* 54:144–151.
- Sheley, R.L., J.M. Mangold and J.L. Anderson. 2006. Potential for successional theory to guide restoration of invasive-plant-dominated rangeland. *Ecological Monographs* 76:365–379.
- Sheley, R.L., J.M. Mangold, K. Goodwin and J. Marks. 2008. Revegetation guidelines for the Great Basin: Considering invasive weeds. *USDA Agricultural Research Service*.
- Stubbendieck, J., S. Hatch and C. Butterfield. 1997. *North American Range Plants*, 5th edition. Lincoln, NE: University of Nebraska Press.
- USDA-NRCS. 2012. Release brochure for “Goldar” bluebunch wheatgrass (*Pseudoroegneria spicata*). USDA Natural Resources Conservation Service, Aberdeen Plant Materials Center. Aberdeen, Idaho.
- Wainwright, C.E., E.M. Wolkovich and E.E. Cleland. 2012. Seasonal priority effects: implications for invasion and restoration in a semi-arid system. *Journal of Applied Ecology* 49:234–241.
- Weather Underground. 2018. Weather history details from 2017 and 2018 for station one mile east of Bozeman, MT KMTBOZEM46 (accessed November 24, 2018). [www.wunderground.com/personal-weather-station/dashboard?ID=KMTBOZEM46#history](http://www.wunderground.com/personal-weather-station/dashboard?ID=KMTBOZEM46#history).
- Western Regional Climate Center. 2019. NCDC 1981–2019 Monthly Normals for station Bozeman 6 W Exp Farm, Montana (accessed June 20, 2019). [wrcc.dri.edu/cgi-bin/cliMAIN.pl?mtboz1](http://wrcc.dri.edu/cgi-bin/cliMAIN.pl?mtboz1).
- Whitson, T.D. and D.W. Koch. 1998. Control of downy brome (*Bromus tectorum*) with herbicides and perennial grass competition. *Weed Technology* 12:391–396.
- Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. New York, NY: Springer-Verlag. [ggplot2.tidyverse.org](http://ggplot2.tidyverse.org).
- Wickham, H., R. Francois, L. Henry, K. Müller and RStudio. 2018. *dplyr: A grammar of data manipulation*. CRAN. [CRAN.R-project.org/package=dplyr](http://CRAN.R-project.org/package=dplyr).
- Young, T.P., E.P. Zefferman, K.J. Vaughn and S. Fick. 2015. Initial success of native grasses is contingent on multiple interactions among exotic grass competition, temporal priority, rainfall and site effects. *AoB PLANTS* 7:1–9.

---

Audrey J. Harvey, Montana State University, College of Agriculture, Department of Land Resources and Environmental Sciences, Bozeman, MT 59717.

Stacy Simanonok, Montana State University, College of Agriculture, Department of Land Resources and Environmental Sciences, Bozeman, MT 59717.

Lisa J. Rew, Montana State University, College of Agriculture, Department of Land Resources and Environmental Sciences, Bozeman, MT 59717.

Timothy S. Prather, University of Idaho, Department of Plant Sciences, Moscow, ID 83844.

Jane Mangold, (corresponding author), Montana State University, College of Agriculture, Department of Land Resources and Environmental Sciences, Bozeman, MT 59717, [jane.mangold@montana.edu](mailto:jane.mangold@montana.edu)

---



Wood pewee. Chambers W. and R. Chambers. 1881. *Encyclopaedia - A Dictionary of Universal Knowledge for the People*. Philadelphia, PA: J.B. Lippincott & Co. The Florida Center for Instructional Technology, [fcit.usf.edu](http://fcit.usf.edu).