



Evaluating Winter/Spring Seeding of a Native Perennial Bunchgrass in the Sagebrush Steppe[☆]



Chad S. Boyd^{a,*}, Jarod A. Lemos^b

^a Research Scientist at the U.S. Department of Agriculture (USDA)–Agricultural Research Service, Eastern Oregon Agricultural Research Center (EOARC), Burns, OR 97720, USA

^b Research Technician at the U.S. Department of Agriculture (USDA)–Agricultural Research Service, Eastern Oregon Agricultural Research Center (EOARC), Burns, OR 97720, USA

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ABSTRACT

Sagebrush (*Artemisia tridentata* Nutt.) plant communities in the Great Basin region are being severely impacted by increasingly frequent wildfires in association with the expansion of exotic annual grasses. Maintaining native perennial bunchgrasses is key to controlling annual grass expansion, but postfire restoration of these species has proven difficult with traditional fall drill-seeding. We investigated the potential for winter/spring seeding bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Love) in southeast Oregon. In 2011–2013, 500 seeds were planted in fall, or weekly from March through early May in $1 \cdot \text{m}^{-2}$ plots using a randomized block design with 5 replications. Germination was estimated using buried bags, and emergent seedlings were counted weekly from March to June. Germination and emergence varied strongly between years and by within-year timing of planting. With adequate precipitation, percent germination was high (up to 100%) regardless of timing of planting and emergence density decreased ($P \leq 0.05$) with advancing winter/spring planting date in drier years. Emergence density was high (approaching 300 plants/ m^{-2}) with adequate precipitation but varied strongly across planting weeks for winter/spring plantings. Percent survival of emergent seedlings to harvest (July) was approximately 25–50% lower ($P \leq 0.05$) for fall-planted seeds in all years; survival of winter/spring seedlings was 80–100% with no discernable pattern between planting weeks. Our results indicate that winter/spring seeding of perennial bunchgrasses is biologically feasible in years with adequate precipitation but fall seeding was more consistently successful. Additional research is needed to determine environmental factors driving within-year variation in demographics for winter/spring planted seeds.

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Introduction

The spread of exotic annual grasses is fundamentally disrupting ecosystem processes across millions of hectares of sagebrush (*Artemisia tridentata* Nutt.) rangeland in the western United States (Meinke et al., 2009; Davies et al., 2011). Annual grasses such as cheatgrass (*Bromus tectorum* L.) and medusahead (*Taeniatherum caput-medusae* [L.] Nevski) form dense mats of fine fuels that promote frequent fire to the detriment of native plant communities, resulting in not only impaired ecological processes but also a loss or reduction in ecosystem services including carbon storage, grazing, and wildlife habitat (Melgoza et al., 1990; Whisenant, 1990; D'Antonio and Vitousek, 1992; Miller and Eddleman, 2000; Stringham et al., 2003; Davies and Svejcar, 2008). Key to reducing the impact of these species is maintenance of large perennial bunchgrasses. Perennial bunchgrasses are poor competitors with invasive annual grasses at the seedling stage; however, adult bunchgrasses can limit expression of these exotic species in sagebrush

plant communities (Humphrey and Schupp, 2004; Chambers et al., 2007; Davies, 2008).

Maintaining perennial bunchgrass populations, particularly in lower-elevation sagebrush plant communities typified by Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Beetle & Young) is increasingly difficult in association with the expanding footprint of wildfires at large spatial scales. For example, in the past 15 years 7 of the 11 western U.S. states have experienced their largest wildfires since European arrival (NOAA, 2012). In response, land management agencies have put forth significant effort to re-establish perennial grasses and shrubs following wildfire. Recent U.S. Department of Interior budgets for postfire restoration have ranged from 14 to 90 million dollars annually (USDOL, 2012). However, restoring perennial bunchgrasses from seed has proven difficult, particularly at low elevations and with native seed (Robertson et al., 1966), and efforts are often unsuccessful (Pyke et al., 2003). This lack of success may relate to ineffective restoration technologies (James and Svejcar, 2010) but is also associated with our incomplete understanding of the seedling ecology of perennial bunchgrasses and how that ecology interacts with method and timing of planting (Boyd and James, 2013).

Previous research has suggested that timing of planting has critical influence on key demographic processes (germination, emergence, and establishment) of seeded native perennial bunchgrasses. In the

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* Correspondence: Chad Boyd, USDA-ARS, EOARC, 67826-A Hwy. 205, Burns, OR 97720, USA. Tel.: +1 541 573 8939; fax: +1 541 573 3042.

E-mail address: chad.boyd@oregonstate.edu (C.S. Boyd).

northern Great Basin of the United States, [Boyd and James \(2013\)](#) reported that the most limiting demographic stage for seedlings was contingent on month of planting for fall sown seeds, but most seeds planted before December germinated but did not emerge before frozen soil conditions in winter. In a related effort, [Boyd and Lemos \(2013\)](#) found that frozen soil conditions are associated with high levels of mortality for germinated but nonemergent seedlings under laboratory conditions. The preceding suggests that a reasonable alternative to fall seeding may be planting in late winter or spring when frozen soil conditions are less likely. However, the late winter/spring period is an exceptionally variable season in the sagebrush steppe with respect to soil temperature and moisture conditions and their variation in association with snowmelt and spring weather events ([Boyd and James, 2013](#)). This suggests that a thorough evaluation of the potential for winter/spring seeding of perennial bunchgrasses should include plantings interspersed throughout this climatically dynamic period.

The objectives of the present study were to determine the efficacy of seeding bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Love) along a within-season temporal gradient of winter/spring planting and to compare the success of winter/spring plantings to a traditional fall planting. Bluebunch wheatgrass is a common native perennial bunchgrass in the Intermountain Region of the western United States and is often used in postfire rehabilitation of sagebrush rangeland ([Miller et al., 1986](#); [Pyke, 1990](#)). Seed production in this species varies strongly between years ([Pyke, 1990](#)) with germination occurring in fall, depending on soil temperature and moisture conditions ([Kitchen and Monsen, 1994](#)), followed by late winter or spring emergence. We hypothesized that seedling density resulting from winter/spring planting would be comparable with or greater than fall planting.

Methods

Study Area

Our study site was located at the Northern Great Basin Experimental Range, approximately 50 km west of Burns, Oregon (43.48 N, 119.72 W) at an elevation of approximately 1400 m. Annual precipitation is highly variable but averages 286 mm with the majority falling as rain or snow during the October to May period (data file, Eastern Oregon Agricultural Research Center, Burns, Oregon). Soils at the study site were classified as a well-drained, Derallo Variant-Pernty complex with a surface horizon of fine sandy loam underlain by bedrock at approximately 75 cm ([Lentz and Simonson, 1986](#)). Study plots were excluded from herbivory for the duration of the study using wire mesh fencing.

Plot Layout and Data Collection

We used a randomized complete block design with 11 planting dates replicated over five blocks in each of 3 years. Planting dates included fall (second week of November) and weekly, for 10 weeks, beginning the first week after snowmelt (2011–2012 = second week of March, 2013 = first week of March). In fall of 2010, we installed permanently marked $1 \cdot \text{m}^{-2}$ (67×150 cm) plots in a 5×11 grid pattern. On the assigned date, plots were raked and hand-seeded with 500 viable Anatone bluebunch wheatgrass seeds (Lot LHS1D3-445-1; L&H Seeds, Inc.; Connell, Washington). Seed viability was determined in an incubation chamber by placing 50 seeds on moist filter paper (four replications) for 4 weeks (21°C, 12 h light/12 h dark); seeds with a visible radicle were considered viable. Planted seeds were covered with approximately 1 cm of soil that had been sifted through a 6-mm mesh screen. In September of each year, we rototilled all plots and randomly assigned treatments for the next year.

We used a buried seed bag technique ([Abbott and Roundy, 2003](#)) to estimate germination of planted seeds. One bag per plot was planted within plots at 0- to 2-cm soil depth at the same time plots were seeded. Bags were constructed by filling a 10.2×15.2 cm nylon mesh bag

(#S-10648W, Uline, Chicago, Illinois) with a mix of 50 viable bluebunch wheatgrass seeds and sifted (6-mm mesh) soil taken from the study site. In 2011, bags for all plots were harvested in the last week of May. In 2012–2013, fall-planted plots were harvested coincident with the first winter/spring planting of each year and bags for winter/spring-planted plots were harvested 4 weeks post planting. Following harvest, contents of bags were washed over a 0.7-mm mesh screen to separate seeds from soil and seeds classified as germinated or nongerminated. Seeds with visual radical development were considered germinated. Percent germination was calculated by dividing the number of germinated seeds by 50 and then multiplying by 100.

For fall-planted seeds, we began counting emerging seedlings coincident with the first winter/spring planting (2011 and 2012 = second week of March, 2013 = first week of March). For winter/spring-planted plots, we began counting emerging seedlings 2 weeks after planting; emergence was defined as the presence of a coleoptile or cotyledon above the soil surface. Following the initial emergent seedling count, counts were made on a weekly basis through the second week of July. Seedlings of nonseeded species were removed from plots during counts. For the initial count, emergent seedlings were marked with a toothpick (uniquely colored by week). For subsequent counts, toothpicks were removed for dead seedlings and added for new seedlings. After the final count in 2011 and 2013, we measured seedling biomass by clipping seedlings within a plot to ground level and weighing them following oven-drying. Current and historical precipitation and temperature data were collected at an existing nearby (<2 km) weather station (data file, Eastern Oregon Agricultural Research Center, Burns, Oregon).

Data Analysis

Hourly values for temperature and precipitation were averaged within day and month for each year. We collated these monthly values by water year (from October of the year prior to emergence to September of the year of emergence). For example, the values for “2011” reflect monthly averages from October 2010 through September 2011. We summed precipitation values within water year for the March to June (“spring”) period, which has been shown to be critical for seedling emergence and survival ([Boyd and James, 2013](#)).

Data for seedling counts were summarized within year, treatment, and block according to emergent seedling density (total number of seedlings that emerged for a plot) and surviving seedling density (the number of seedlings that survived to the last count date). We also calculated the percent of emergent seedlings surviving until the final count by dividing surviving seedling density by emergent seedling density and then multiplying by 100. We used analysis of variance (PROC MIXED; SAS Institute Inc., Cary, North Carolina) to evaluate the effect of planting date on percent germination, emergent seedling density, surviving seedling density, percent of seedlings surviving, and seedling biomass. Block and the block \times treatment interaction were included in models as random effects. When significant effects were found we used the LSMEANS procedure to determine differences among treatment means. The critical value for statistical significance was set at $\alpha = 0.05$. All models were constructed within a year due to variation in environmental conditions (temperature, precipitation, and timing of snowmelt) between years. Data not meeting ANOVA assumptions were weighted by the inverse of the treatment variance ([Neter et al., 1990](#); [James and Drenovsky, 2007](#)). Means are reported with their associated standard errors.

Results

Yearly precipitation was 116%, 55%, and 82% of the long-term (70-year) mean (286 mm) for 2011, 2012, and 2013, respectively ([Fig. 1](#)). Spring precipitation was 146% of the long-term average in 2011 and 79% and 57% of the average for 2012 and 2013, respectively. Air temperatures closely tracked long-term means with the notable exception of

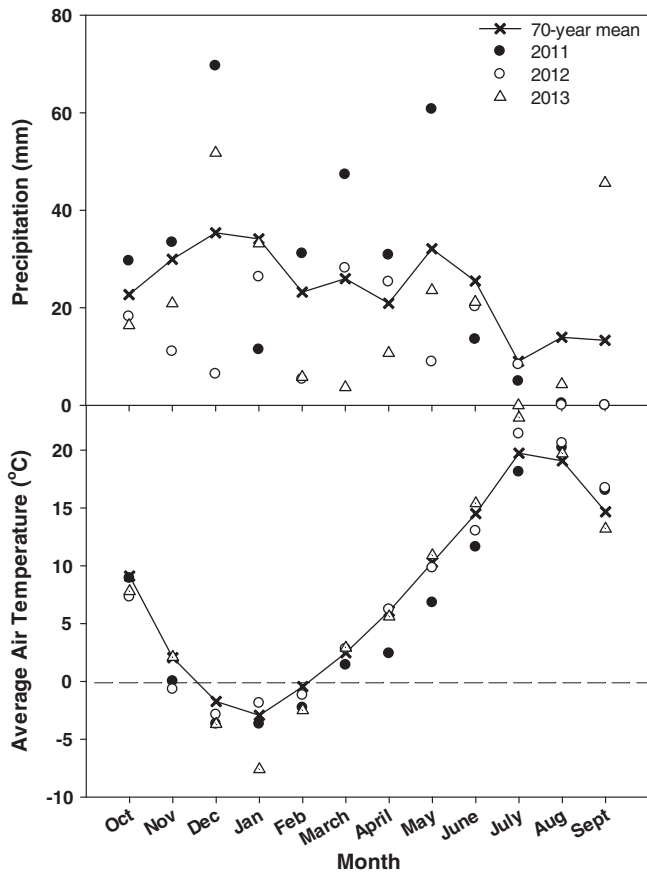


Fig. 1. Monthly average air temperature and precipitation (total by month) for plots in southeastern Oregon for 2011–2013 and 70-year mean values.

January 2013, when temperatures were almost 5°C lower than average (see Fig. 1).

Seed viability was 94.0%, 92.5%, and 90.9% in 2011, 2012, and 2013, respectively. Percent germination showed strong between-year variability and varied by planting date within all years ($P < 0.001$, Fig. 2). In 2011 germination values were similar between fall (5 November) and winter/spring planting dates ($P \leq 0.05$). Values for 2011 were relatively high compared with 2012 and 2013 and ranged from 97.6% \pm 5.0 for plots planted on April 28 to 102.9% (± 0.5) for 5 May-planted plots. Germination values in excess of 100% were possible because initial seed numbers in germination bags were adjusted on the basis of estimated seed viability. For 2012, germination was highest for 9 April-planted plots and dropped ($P \leq 0.05$) sharply for the last two spring plantings (April 30 = 23.2% \pm 7.7 and May 7 = 13.2% \pm 4.1). Germination values were relatively low in 2013. Highest ($P \leq 0.05$) germination was for fall, 14 March, or 28 March-planted plots ($\geq 73\%$) while seeds planted on 18 April and 25 April failed to germinate.

Seedling emergence was generally highest in 2011, intermediate in 2012, and lowest in 2013 (Fig. 3). Values for seedling emergence varied by planting date within all years ($p < 0.001$). In 2011, emergence was highest ($P \leq 0.05$) for plots planted on 10 March, 24 March, or 5 May (≥ 267 plants \cdot m $^{-2}$) and lowest for planting in fall, on 3 March, or 7 April (≤ 155 plants \cdot m $^{-2}$); values for winter/spring plantings were variable over time but with no discernible pattern. For 2012, emergence generally decreased over time with winter/spring plantings to a low of 19.4 plants \cdot m $^{-2}$ (± 2.5) for 16 April-planted plots but rose ($P \leq 0.05$) sharply to 190 plants \cdot m $^{-2}$ (± 29.9) for plots planted the following week. In 2013, emergence was highest ($P \leq 0.05$) for fall (14 November) and 14 March plantings (≥ 21 plants \cdot m $^{-2}$); emergent seedlings were not recorded for plots planted in April or May.

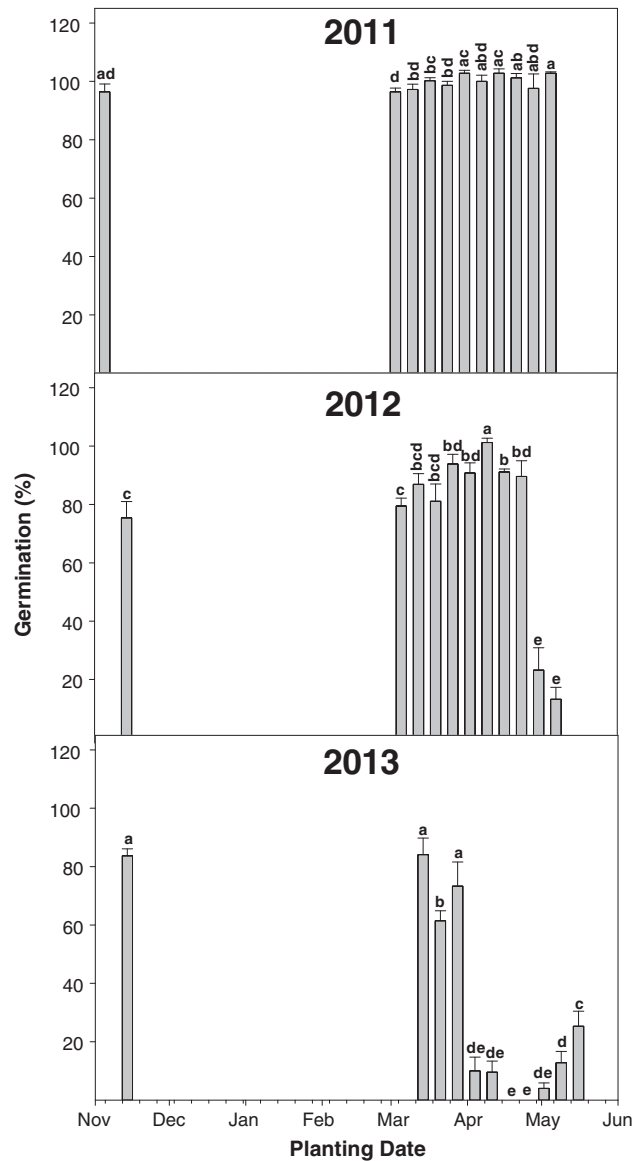


Fig. 2. Percent germination for bluebunch wheatgrass seeds as a function of planting date for plots planted in southeast Oregon. Means within a year without a common letter are different ($\alpha = 0.05$).

Surviving seedling density was variable across years in a pattern similar to emergence, with decreasing values from 2011–2013 (Fig. 4). Density varied by planting date within all years ($P < 0.001$). In 2011 density was lowest ($P \leq 0.05$) for fall-planted plots (54.4 plants \cdot m $^{-2}$ \pm 16.6) and highest for plots planted on 10 March, 31 March, and 5 May (> 240 plants \cdot m $^{-2}$). For 2012, density values were highest ($P \leq 0.05$) for 23 April-planted plots (184 plants \cdot m $^{-2}$ \pm 29.7) and lowest for plots planted 16 April (16.2 plants \cdot m $^{-2}$ \pm 1.2). In 2013, surviving seedling density was highest ($P \leq 0.05$) for fall planting and planting 14 March; seedlings were not recorded for plantings in April or May. Percent survival for winter/spring-planted plots was high in all years, varied by planting date in all years ($P < 0.001$), and ranged from a high of 100% for plots planted on 7 May, 2012 to a low of 80.3% (± 4.7) for 21 April-planted plots in 2011 (Fig. 5). In all years, survival for fall-planted plots was lower ($P \leq 0.05$) than within-year values for winter/spring plantings. Survival for fall plots across years ranged from 36.8% (± 8.4) in 2011 to 62.4% (± 0.1) in 2012.

Biomass values were generally lower in 2013 than 2011 (Fig. 6). Biomass per seedling varied by planting date in both years ($P < 0.001$). It was highest ($P \leq 0.05$) in 2011 for fall-planted plots or plots planted

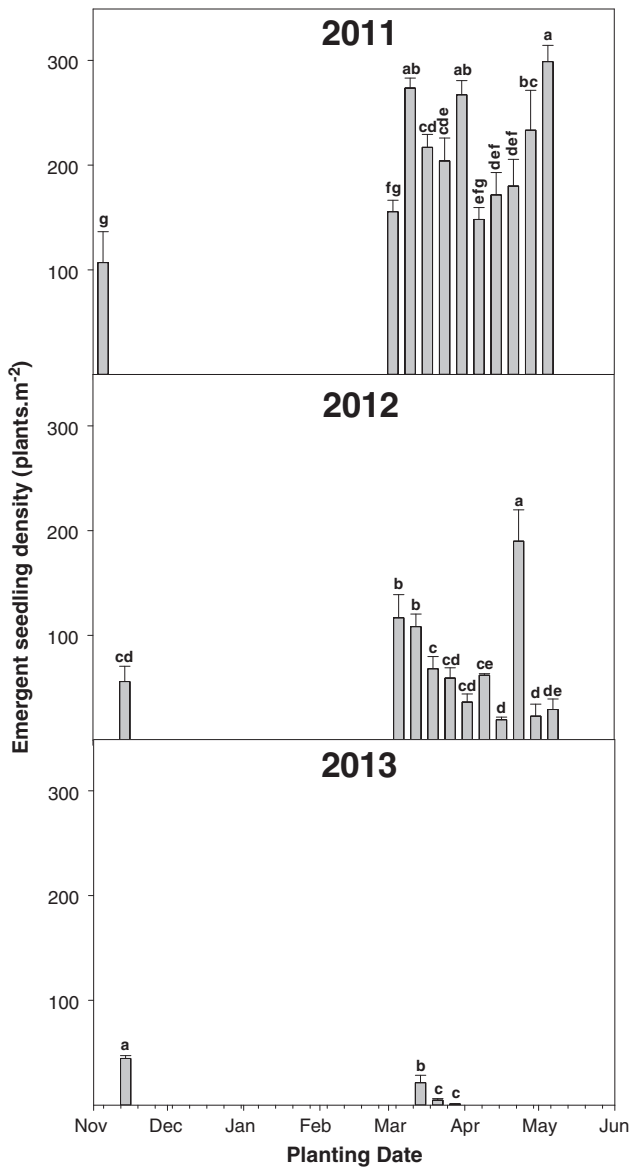


Fig. 3. Density of emergent bluebunch wheatgrass seedlings as a function of planting date for plots planted in southeast Oregon. Means within a year without a common letter are different ($\alpha = 0.05$). For winter/spring plantings, values represent the total number of seedlings that emerged (regardless of survival status) as determined by weekly counts that began 2 weeks after planting and ended in mid-July. For the fall planting, counts began coincident with the first winter/spring planting and continued until mid-July. All plots were planted with 500 viable seeds.

before April 14 ($\geq 0.23 \text{ g} \cdot \text{plant}^{-1}$) and lowest for planting on April 21 or later ($\leq 0.08 \text{ g} \cdot \text{plant}^{-1}$, Fig. 6). Values in 2013 were highest for fall planting or planting on 14 March and 21 March ($\geq 0.4 \text{ g} \cdot \text{plant}^{-1}$) and lowest for planting on 28 March ($0.2 \text{ g} \cdot \text{plant}^{-1} \pm 0.2$, Fig. 6).

Discussion

Planting Date Effects on Surviving Seedling Density and Biomass

We found strong support for the hypothesis that establishment density of winter/spring-seeded grasses was comparable with that of fall planting in most years. Surviving seedling density (see Fig. 4) for winter/spring-planted plots was equal to or greater than fall planting in 2 of 3 years of our study, and in 2011, all winter/spring planting dates were higher than fall. However, the surviving density of fall-planted seeds was more consistent across years as compared with

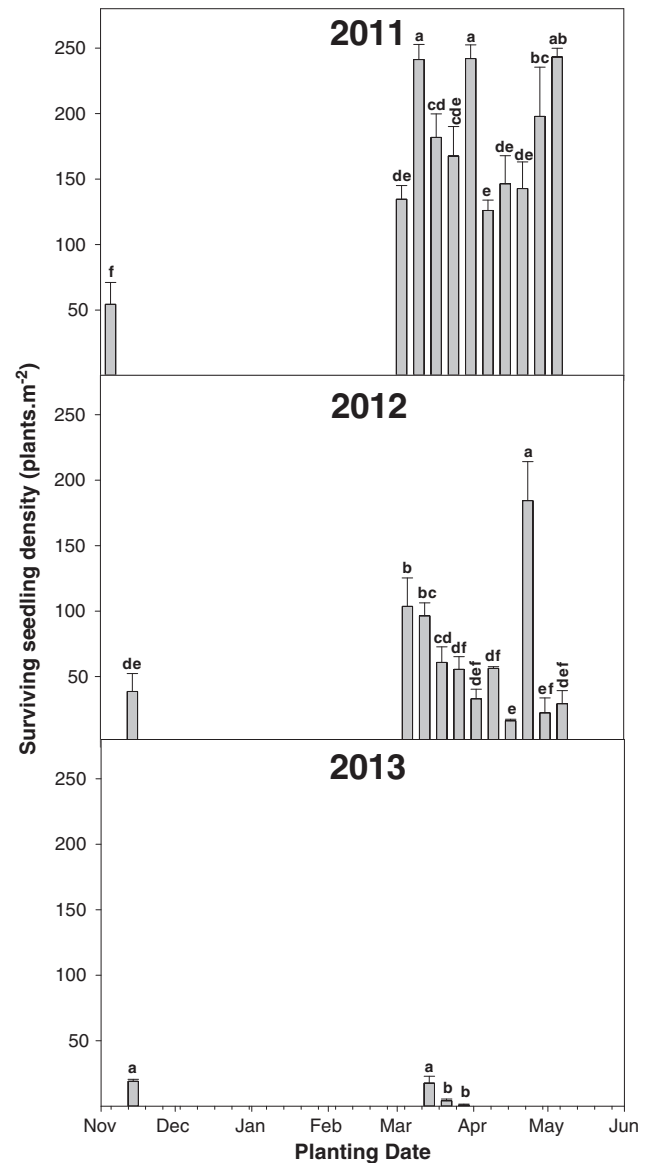


Fig. 4. Density of surviving bluebunch wheatgrass seedlings as a function of planting date for plots planted in southeast Oregon. Means within a year without a common letter are different ($\alpha = 0.05$). For all plots, data represent the density of seedlings present at the end of the first growing season (mid-July) following planting. All plots were planted with 500 viable seeds.

most winter/spring planting dates, suggesting fall planting is less sensitive to interannual variation in environmental conditions. Most winter/spring and fall planting date/year combinations that produced emergent seedlings had a seedling density by the end of the first growing season that would be in excess of long-term capacity. The maximum sustainable density of perennial grasses will vary by species and site conditions, but density values of ≥ 5 adult plants $\cdot \text{m}^{-2}$ are often considered successful within a restoration context (Eckert et al., 1986; James and Svejcar, 2010). Interannual survival of emergent seedlings was beyond the scope of the present study. That said, dramatic reductions in biomass per seedling for plots planted in late April and May of 2011 (Fig. 6a) suggest long-term fitness could be impaired relative to planting earlier in the winter/spring period or in fall. This effect would be amplified if aboveground biomass was reflective of belowground biomass given that less developed root systems may lead to decreased seedling survival during the summer dry period (Hardegreer, 1994). Our data also support the hypothesis that optimal planting time for maximum seedling establishment of winter/spring-planted seeds is variable

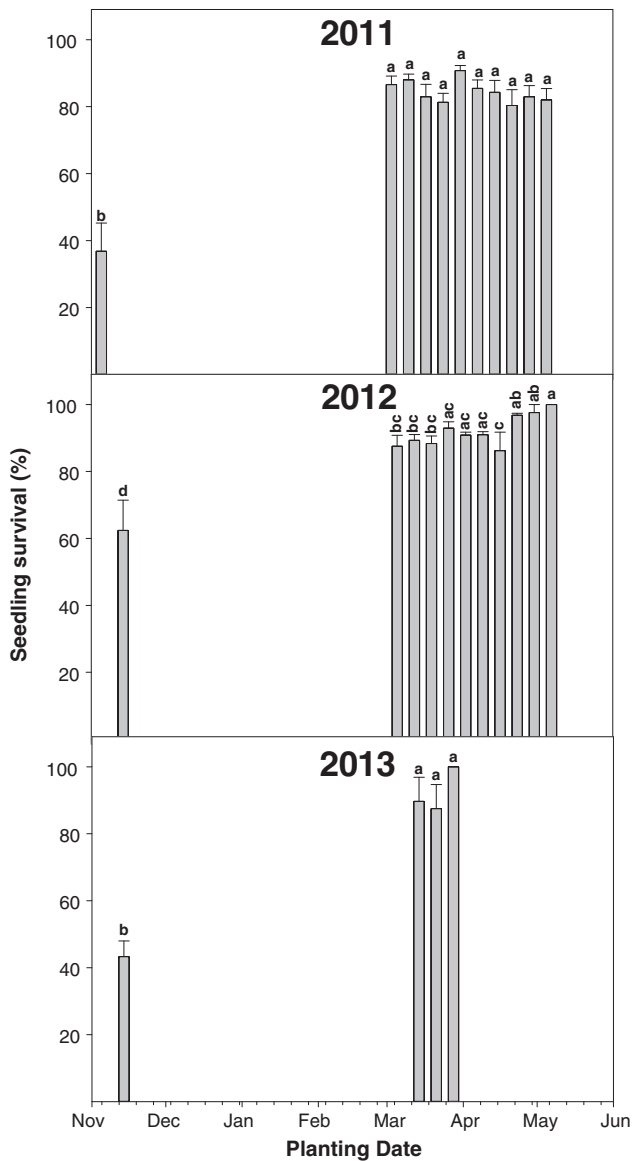


Fig. 5. Percent survival of emergent bluebunch wheatgrass seedlings as a function of planting date for plots planted in southeast Oregon. Means within a year without a common letter are different ($\alpha = 0.05$). Data represent the percent of emergent seedlings (see Fig. 3) that survived until the end of the first growing season (mid-July, see Fig. 4).

between years. We found that optimal winter/spring planting date based on surviving seedling density was different in each of the 3 study years.

In our study, precipitation varied strongly between years, particularly during the spring period, and surviving seedling density was associated positively with spring precipitation. In 2011, when spring precipitation was 146% of the long-term average, we recorded high densities (> 100 seedlings $\cdot m^{-2}$) of surviving seedlings for all winter/spring-planted treatments. In contrast, spring precipitation in 2013 was 57% of average. Seedlings were only recorded for 3 of the 10 winter/spring planting dates, and densities were less than 25 plants $\cdot m^{-2}$. Variability in optimal planting date (based on surviving seedling density) between years indicates that yearly environmental conditions play a large role in impacting winter/spring-planted seedling performance.

Planting Date Effects on Germination, Emergence, and Survival

Planting in late fall is thought to decrease the probability of germination before winter and, by extension, the probability of freeze damage to

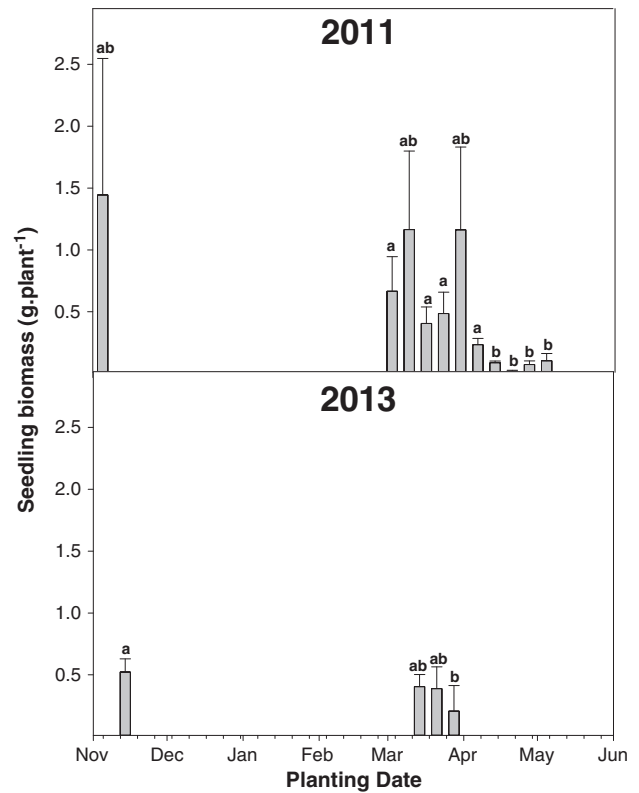


Fig. 6. End-of-growing season (mid-July) biomass of bluebunch wheatgrass seedlings as a function of planting date for plots planted in southeast Oregon. Means within a year without a common letter are different ($\alpha = 0.05$).

germinated seedlings (Arredondo et al., 1998; Boyd and Lemos, 2013). Boyd and Lemos (2013) reported laboratory research suggesting from 75% to 100% mortality (depending on germination stage) of germinated but nonemergent seedlings exposed to 30 days of frozen soil conditions and indicated that maximum mortality could occur in as little as 4 days of freezing soil. In the current study, we found that $\geq 75\%$ of fall-planted seeds had germinated at or near the time of spring snowmelt (see Fig. 2), which suggests either a mass germination event coincident with snowmelt, or that at least a portion of seeds that germinated did so before winter onset. Boyd and James (2013) reported up to 50% germination of November-planted seeds before the onset of frozen soil conditions in winter. Collectively, these data indicate that late fall planting (e.g., November) may not be effective in minimizing prewinter germination. In 2011 and 2012 germination rates for winter/spring-planted plots suggest that germination for winter/spring-planted seeds can be equal to or greater than fall planted (see Fig. 2). However, data for 2012 and 2013 indicate the potential for decreasing germination (see Fig. 2) with advancing winter/spring planting date as soils desiccate in association with below-average precipitation (see Fig. 1).

Emergent seedling density in winter/spring-planted plots was equal to or higher than fall planting in 2011 and 2012 (see Fig. 3), but emergence was greatly reduced in 2013 when spring precipitation was only 57% of the long-term average. As with surviving seedling density, within-year emergence for winter/spring-planted plots was highly variable between planting weeks. In contrast to winter/spring planting, emergence for fall-planted plots was less variable across years. This may be related to the fact that fall-planted seeds were in place from late fall through spring, which exposed them to all moisture pulses during that time frame. Seeds planted in winter/spring, particularly in late spring, would have had fewer growing degree days to germinate and emerge before seasonal soil desiccation (Meyer et al., 2000; Rawlins et al., 2012).

Our data are in agreement with previous work suggesting that emergence is the limiting developmental stage for perennial bunchgrass

seedlings (James and Svejcar, 2010; Boyd and James, 2013) and that emergence is strongly tied to precipitation. For example, in 2013, when spring precipitation was > 40% below the long-term average, germination was recorded for 8 out of 10 winter/spring planting dates but emergent seedlings were present for only the first three planting dates. We suspect that continued soil desiccation reduced emergence for subsequent planting dates. The percent of emergent seedlings that survived ranged from 87.5 ± 7.2 to 100% for these planting dates (see Fig. 5), further reinforcing the notion that emergence was the limiting demographic stage in our study. Germination fluctuated across years in association with annual precipitation (particularly spring precipitation), but the degree of variability was much less than that observed for emergence.

Compared with germination and emergence, survival of emergent seedlings was the least limiting demographic stage for winter/spring-planted plots within the time frame of our study (see Fig. 5). This finding is consistent with previous field research comparing seedling performance at similar demographic stages (James and Svejcar, 2010; Boyd and James, 2013). Our experimental design did not account for interannual seedling survival, and previous work indicates the potential for significant grass seedling mortality during the summer dry period following emergence (Salhi and Norton, 1987; Pyke, 1990). However, other research suggests that seedlings surviving to the end of the first growing season (i.e., when we harvested seedlings) are likely to survive to the subsequent growing season (Chambers, 2000; Huber-Sannwald and Pyke, 2005). High (approaching 100%) percent survival of seedlings in our study may also be associated with a lack of competition. Emergent cheatgrass was common within our plots but was removed as soon as phenological development was advanced enough to facilitate identification. Previous work has shown that competition from annual grasses can reduce establishment of seedling perennial grasses (e.g., Rafferty and Young, 2002) and expedite soil desiccation (Melgoza et al., 1990). In a field restoration context, competition with annual grasses could be particularly intense for winter/spring-seeded perennials given that exotic annual grasses often germinate in fall (Hull and Hansen, 1974). Interestingly, survival of winter/spring-planted seedlings was higher than the fall planting in all 3 years of the current study. Boyd and James (2013) found that seedlings germinating in the winter/spring period had higher postemergent survival than counterparts germinating during fall and attributed the difference to the fact that fall-germinated seedlings were developing during a time of decreasing soil temperature. We did not monitor fall germination but suspect that similar processes may have been operant in the current study.

One of the deficiencies in the present study is a lack of multiple planting dates for fall-planted seeds. The variability in seedling performance that we found in association with weekly winter/spring planting may also occur with fall planting. Previous research has noted variable seedling performance in association with summer/fall planting dates spaced at monthly intervals (Boyd and James, 2013); however, the magnitude of the timing effect was much less than observed in the current study. That said, the single fall planting date we used is representative of traditional single-entry postfire restoration in fall as currently practiced. A practical concern with winter/spring seeding is the potential for logistically unfavorable conditions during the late winter/spring period. Abundant moisture associated with snowmelt or ongoing precipitation could make drill seeding difficult and could result in high levels of ground disturbance relative to seeding under drier conditions. Additionally, our plots were hand-seeded, and when compared with drill-seeding typical of restoration and rehabilitation efforts on sagebrush rangeland, hand-seeded plots may result in significantly higher seedling density (James and Svejcar, 2010).

Management Implications

Reestablishing large perennial bunchgrass species following disturbance is critical in low-elevation sagebrush communities that are

prone to invasion by exotic annual grass species (Davies, 2008). At present, postdisturbance reestablishment of these species from seed has met with limited success at lower elevations, particularly when native species are seeded (Knutson et al., 2014). To some extent, these failures can be associated with ineffective restoration techniques that have not sufficiently evolved from their agronomic origins to effectively deal with the challenges of seeding in the rangeland context (James and Svejcar, 2010). However, major deficiencies in our knowledge of the seeding ecology of native perennial bunchgrasses accentuate issues with reseeding techniques and create a negative synergy that culminates in low probabilities of perennial bunchgrass reestablishment (Boyd and James, 2013). Currently, most perennial grass seeding takes place during the fall and overwinter mortality of seedlings could significantly decrease establishment of seeded species (Boyd and Lemos, 2013). Our data indicate that seeding during the winter/spring period may represent a viable alternative to traditional fall treatments. High variability between seeding weeks, within year, suggests that environmental conditions at or near the time of seeding will play a significant role in ultimate success. Additionally, surviving seedling density varied strongly between years in association with spring (March to May) precipitation with higher precipitation years having highest seedling density.

Our data indicate that fall seeding may be more reliable than winter/spring planting in years with very low spring precipitation (e.g., compare the relative change in surviving seedling density for fall vs. winter/spring-planted plots between an above [2011] vs. below [2012 or 2013] average year; see Fig. 4). In such years, fall-planted seedlings could have the advantage of increased time for root development before entering a prolonged dry period. However, the high within-year variability we found between weeks of winter/spring planting suggests that gross characterizations of “winter/spring” versus “fall” planting may overlook critical climate-driven micro-temporal windows of opportunity for emergence and establishment. Capitalizing on these windows of opportunity could be bolstered by linking seeding date to short-term meteorological forecasts (Hardegee et al., 2011) or by developing seed enhancement technologies that allow critical seedling demographic events to take place coincident with optimal soil temperature and moisture conditions (Madsen et al., 2013). Additional research is necessary to determine specific environmental conditions driving within-year variation in demographics for winter/spring-planted seeds. Winter/spring seeding may require development of new or altered seed planting technologies to overcome logistical issues associated with wet soil conditions at the time of seeding.

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