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Variation in Timing of Planting Influences Bluebunch Wheatgrass Demography in an Arid System

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Abstract

Establishing perennial grasses from seed in postdisturbance Wyoming big sagebrush (*Artemesia tridentata* subsp. *wyomingensis* Welsh) communities is often unsuccessful, due in part to a lack of knowledge of the seedling ecology of perennial grasses. We examined the influence of planting timing on germination and seedling demography of bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Love) in the northern Great Basin. In 2008 (year 1) and 2009 (year 2) we planted seeds monthly, September–December, in 1-m^2 plots (500 seeds per plot) using a randomized block design with five replications. Germination timing was indexed using seed bags placed adjacent to 1-m^2 plots and retrieved at 2-wk intervals in fall and 1-mo intervals in spring. Seedlings were marked in March–June of the year following planting; seedlings alive in July were considered initially established. Planting in September and October had up to 80% germination prior to winter, whereas December plantings germinated mainly in spring and at reduced rates (15–35%). Seeds planted in September and October emerged approximately a month earlier than November–December plantings. The percentage of germinated seeds that emerged was highest for September–October plantings but the percentage of emergent seeds surviving to the end of the first growing season was highest for later plantings. Final seedling density was lowest for November planting in year 1 and highest for September and October planting in year 2. Our data indicate that timing of and performance at critical stages of seedling development were affected by planting month. We suggest that it may be possible to use emerging technologies (e.g., seed coatings or germplasm manipulations) to produce variable chronologies of seedling development with single plantings and allow managers to exploit multiple temporal windows of opportunity for seedling establishment.

Key Words: perennial bunchgrass, restoration, sagebrush steppe, seedling ecology

INTRODUCTION

Worldwide, arid-land plant communities are critically important for forage production and as a reservoir of biodiversity (Bedunah et al. 2006; Rosiere 2006). The integrity of these ecosystems has been increasingly compromised in association with a growing number of factors including intensive agricultural production and associated desertification, land type conversion, altered ecological processes, and invasion or expansion of nondesirable plant species (Milton et al. 1994; Greene and Stager 2001; Gisladottir and Stocking 2005; Huxman et al. 2005). Among these factors, invasive plant species, particularly annual grasses, currently threaten shrub- and grass-dominated ecosystems across North and South America, Eurasia, Africa, and Australia (D'Antonio and Vitousek 1992; Mack et al. 2000). Containing the spread of invasive plant species and restoring areas previously invaded is contingent on successful propagation and maintenance of desired species. To date, restoration attempts in arid-land plant communities have been insufficient to curtail the spread of invasive plants, and restoring desirable vegetation is limited, in part, by an insufficient understanding of the reproductive ecology of key species (James et al. 2011).

In arid and semiarid portions of the western United States, sagebrush plant communities occupy over 62 million hectares and provide a wide variety of ecological services including maintenance of plant diversity, habitat for obligate and facultative sagebrush wildlife species, and forage for livestock grazing (Küchler 1970; Miller et al. 1994; West and Young 2000). Low to mid-elevation plant communities such as those dominated by Wyoming big sagebrush (*Artemesia tridentata* subsp. *wyomingensis* Welsh) are increasingly impacted by nonnative invasive annual grasses such as cheatgrass (*Bromus tectorum* L.) and medusahead (*Taeniatherum caput-medusae* [L.] Nevski; Chambers et al. 2007). These annual grasses alter the ecology of sagebrush/perennial bunchgrass plant communities by creating a more continuous fuel bed that cures earlier in the growing season than native perennials (Brooks et al. 2004). Altered fuel bed characteristics in invaded areas have dramatically increased fire frequency resulting in reduction or elimination of perennial plant species and associated ecosystem services over millions of hectares in the Intermountain West (Melgoza et al. 1990; Whisenant 1990; D'Antonio and Vitousek 1992; Miller and Eddleman 2000; Stringham et al. 2003; Pellant et al. 2004; Davies and Svejcar 2008) and jeopardized much of the remaining intact rangeland within the region (Pellant and Hall 1994). This process has resulted in what has been characterized as the largest plant invasion in recent North American history (D'Antonio and Vitousek 1992; Chambers et al. 2007).

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Much of the management effort to stem annual grass invasion has been associated with seeding perennial grass species in the postfire environment (Eiswerth et al. 2009). Established native and nonnative perennial grasses can compete effectively with annual species (Chambers et al. 2007) and help to reduce invasion (Davies 2008). However, competition at the seedling stage strongly favors annual grasses (Young and Mangold 2008) and thus, establishment of perennial bunchgrasses from seed in postdisturbance Wyoming big sagebrush communities has met with only limited success (Pyke et al. 2003), particularly for native species (Robertson et al. 1966) despite massive capital and logistical expenditures. This lack of success is likely, in part, a function of reliance on ineffectual restoration techniques and paradigms (Boyd and Svejcar 2009), but is also related to a lack of understanding of the seedling ecology of seeded perennial grasses.

Previous work suggests that soil water content and temperature influence perennial grass germination (Hardegree 1994; Meyer et al. 2000; Hardegree et al. 2003, 2010; Hardegree and Van Vactor 2004; Rawlins et al. 2012a, 2012b) and establishment (Hironaka and Sindelar 1975). The abiotic environment of the Wyoming big sagebrush alliance is highly variable within and between years (Bates et al. 2007), and within this variable environment, most restoration/rehabilitation efforts focus on planting perennial grass seeds during the fall period; by convention, the majority of this effort is in October and November. Fall is a period of strong transition in both temperature and moisture patterns from a hot and dry summer regime to the cold temperatures and frozen soils of winter. During the fall period, the abiotic environment can vary dramatically depending on the occurrence of fall moisture and timing of seasonal air temperature changes and their effect on soil temperature. Thus, the specific timing of planting will impact the immediate seed environment and may ultimately impact degree of restoration/rehabilitation success. Traditional wisdom suggests that planting in late fall (e.g., November), when soils are at or near the freezing point, will curtail prewinter germination and prevent subsequent freeze–thaw cycles from damaging germinated seeds prior to spring emergence (Arredondo et al. 1998). However, to date there is only limited empirical work documenting the influence of planting date on seeding success or describing the chronology of seedling development in response to temporally variable environmental factors.

Bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Love) is one of the most prevalent native perennial bunchgrasses in the western United States and is found in plant communities throughout the Intermountain West (Miller et al. 1986; Pyke 1990). Seeds begin germination in fall (bluebunch wheatgrass does not require cold stratification; Link et al. 2011) and germination rate decreases as temperatures approach freezing (Kitchen and Monsen 1994). Seed production can vary widely between years (Pyke 1990) and establishment from seed following disturbance can be limited by abiotic factors (Mangla et al. 2011) and competition with exotic species (Knapp 1996).

The objectives of the current study were to determine the influence of timing of planting on germination, emergence, and initial establishment of bluebunch wheatgrass under conditions of ambient and excess soil water (to mimic a wider range of environmental conditions). We hypothesized that: 1) fall/winter germination would decrease with later planting date, 2) spring germination would result in increased emergence of germinated seedlings compared to fall/winter germination, 3) survival of emergent seedlings would increase with fall/winter germination in association with increased potential for root development and resource capture at time of spring thaw, and 4) watering would increase percentage of germination, emergence, and initial establishment.

METHODS

Our study site was located at the Northern Great Basin Experimental Range, approximately 50 km west of Burns, Oregon, at an elevation of approximately 1 400 m. Annual precipitation is highly variable, but averages 286 mm with the majority falling as rain or snow during the October to March period (data file, Eastern Oregon Agricultural Research Center, Burns, OR). 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).

To assess the influence of planting month and watering on percentage of seedling emergence and initial establishment, and seedling density and biomass, we used a randomized complete block design with five blocks, two watering levels, and four dates of planting. This design was repeated in 2008–2009 ("year 1") and 2009–2010 ("year 2"). Treatments were imposed on 1.66×0.75 m plots. Watering treatments consisted of no watering ("ambient") and ambient plus 75% of historic monthly average ("watered"). Plots in the later treatment were hand-watered from 21 September through soil freezing in early December. Watering frequency was based on historical (1937–2006) average by month (Table 1). The amount of water applied in a single watering was calculated by dividing the historical monthly average precipitation by the historical event frequency and multiplying by 0.75.

A 1.33×0.75 m section of each plot was demarcated and hand-seeded in the third week of September, October, or November or the second week of December of each year. 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, WA). Seed viability was determined in an incubation chamber by placing 50 seeds on moist filter paper (four replications) for 4 wk (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.

We began counting emergent seedlings in March of both study years; counts continued on a 2–3-wk basis thereafter until early July. Seedlings of nonseeded species were removed from plots during counts. We monitored plots for emergence in the fall/early winter but observed no emergence until March. Emergence was defined as the presence of a coleoptile or cotyledon above the soil surface. For the initial count, emergent seedlings were marked with a toothpick; for subsequent counts, toothpicks were removed for dead seedlings (desiccated seedlings that broke when touched) and added for new seedlings. Toothpick colors were unique to each count. After

Table 1. Historical precipitation amount, and frequency and watering amount for plots planted with bluebunch wheatgrass in southeast Oregon. Watering amount per plot is equal to 75% of the historical (1937–2006) monthly precipitation amount divided by historical precipitation frequency and adjusted for a 1.25-m^{-2} plot.

Planting month	Historical precipitation (cm)	Historical precipitation frequency	Precipitation per event (cm)	Water amount (ml) for 1.25-m^{-2} plot
September	1.37	4	0.34	3 210.94
October	2.18	6	0.36	3 406.25
November	2.89	9	0.32	3 010.42
December	3.27	9	0.36	3 406.25

the final seedling density count of each year (1 July 2009; 8 July 2010), we measured seedling height and harvested, oven-dried, and weighed aboveground seedling biomass. Seedlings alive in July were considered to be initially established.

Soil moisture and temperature were logged on an hourly basis using Gro-Point sensors (Environmental Sensors Inc., Sidney, BC) buried to a depth of approximately 2 cm within one ambient plot and one watered plot. Values for soil moisture and temperature were averaged within month. Current and historical precipitation and air temperature data were collected at an existing nearby (< 1 km) weather station.

To index percentage of germination of planted seeds we used a buried seed bag technique (Abbott and Roundy 2003) within the unplanted 0.33×0.75 m section of each plot. Bags were planted simultaneous with plot seeding and were prepared by filling a 10.2×15.2 cm nylon mesh bag (S-10648W, Uline, Chicago, IL) with a mix of 50 bluebunch wheatgrass seeds and sifted (6-mm mesh) soil from the study site. Bags were placed at 0–2 cm soil depth and bags were harvested twice monthly (one bag · plot^{-1} · harvest^{-1}) beginning 2 wk after planting through December and monthly in March, April, and May (year 2 only). Following harvest, materials from bags were washed over a 0.7-mm mesh screen to separate seeds from soil and seeds were classified as germinated or nongerminated. Seeds with visual radicle development were considered germinated.

Data Analysis

Data were examined for skewness and kurtosis (PROC UNIVARIATE; SAS Institute Inc. 1999). When normality or homogeneity of variance assumptions were violated, data were weighted by the inverse of the treatment variance (James and Drenovsky 2007; Neter et al. 1990). Because years had unique precipitation and temperature regimes (Fig. 1), statistical analysis was conducted within study year.

We used analysis of variance (ANOVA; PROC MIXED, SAS Institute Inc. 1999) to evaluate planting month and watering effects on percentage of germination, emergence and initial establishment, and seedling density and biomass. Block and the block by treatment interaction were considered random effects in the model. Covariance structure was determined as per Littell et al. (1996). When significant main or interactive effects were found, we used the LSMEANS procedure (SAS Institute Inc. 1999) to determine differences among treatment means.

To examine the relative performance of seedlings by life history stage, we expressed values for germination, emergence, and initial establishment within year, relative to percentage of maximum possible values. We estimated percentage of germination per plot by dividing the highest observed germination values (regardless of date) from seed retrieval bags by 50, and then adjusted these values by the estimate of seed viability percentage determined from laboratory viability tests. We then estimated the total number of seeds germinating for each plot by multiplying percentage of germination values by the number of seeds planted (i.e., 500) in each plot. Observed values for total emergent seedlings were then divided by the per-plot estimates of the number of germinated seeds to obtain estimates of percentage of emergence. Values for percentage of initial establishment were calculated by dividing the number of live seedlings at the final (July) count by the total number of emerged seedlings.

We further partitioned emergence by examining the proportion of total emergence, within year, that was recorded on each

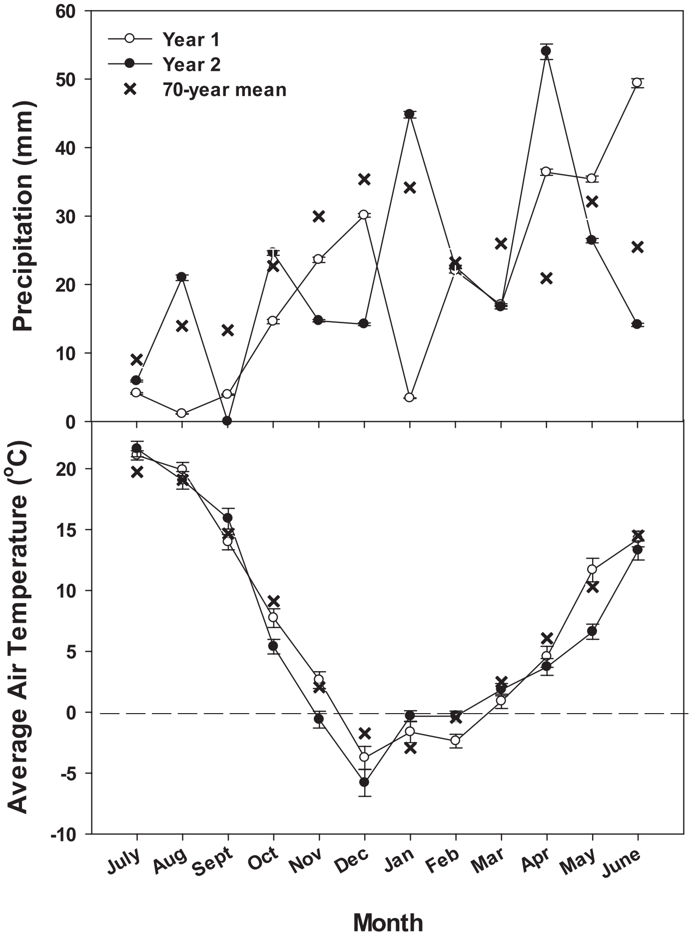

Figure 1. Monthly air temperature and precipitation at southeast Oregon study site. Data are stratified by year 1 (2008–2009), year 2 (2009–2010), and long-term mean (1936–2006). Nonhistorical means ($n = 28–31$) are plotted with associated standard errors.

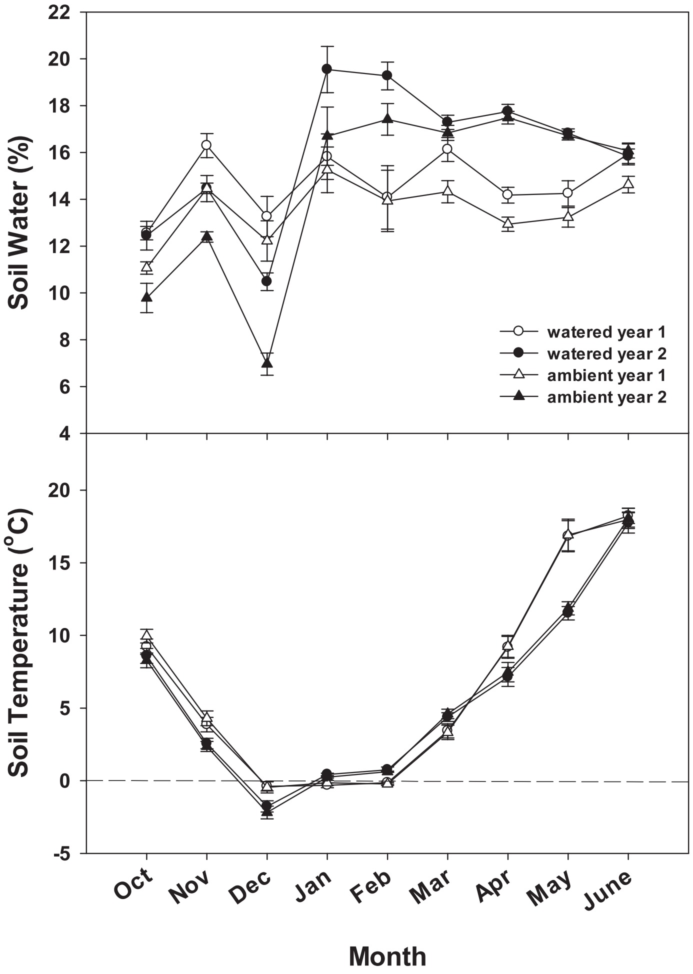

Figure 2. Surface (0–5 cm) soil water content and temperature (°C) for ambient and water-added plots in southeast Oregon. Data are stratified by year 1 (2008–2009) and year 2 (2009–2010). Means (n=28–31) are plotted with their associated standard errors.

date of data collection; we then used ANOVA to determine the effect of planting month and watering treatment on percentage of total emergence by date of data collection. Percentage of survival within these cohorts was calculated by dividing the number of initially established seedlings from each cohort by the number that emerged. We used ANOVA to determine differences in cohort survival by date of emergence. Main effects, interactions, and treatment differences were considered to be significant at α=0.05. All means are reported with their associated standard errors.

RESULTS

July through June precipitation was 241 mm in year 1 and 259 mm in year 2 compared to a 70-yr average of 286 mm (Fig. 1). Seasonality of precipitation varied strongly within study years and both years had wetter spring (April–June) periods than average (121.2 mm and 94.5 mm in years 1 and 2 compared to a 70-yr mean of 78.5 mm). June precipitation was above average in study year 1 and below average in year 2. Average monthly air temperatures closely tracked long-term averages in most months but were below normal in October and November of year 2, February of year 1 and May of year 2.

Soil water content ranged from 11.1 ± 0.26% for ambient plots in October to 16.3 ± 0.51% for November watered plots in year 1. In year 2, water content was lowest for December ambient plots (7.0 ± 0.48%) and highest for January watered plots (19.5 ± 0.99%; Fig. 2). Moisture generally declined from snowmelt (March) through June, but increased in June in year 1 due to high rainfall inputs. Soil temperatures ranged from a high of approximately 18°C in June (both years) to –2.2 ± 0.44°C in December of year 2 (Fig. 2). The first sustained (>5 d) soil freezing period was by December 3 in year 1 and by December 10 in year 2. Average monthly soil temperatures were below freezing for 3 mo in year 1 and 1 mo in year 2 (Fig. 2).

Seed viability was 99 ± 1% in year 1 and 92 ± 1% in year 2. Recovery of seeds from seed bags was 99.8% in both years. Timing of germination varied by data collection date by planting month and planting month by water treatment in both years (Table 2; Fig. 3). In both years, September- and October-

Table 2. Analysis of variance table with F statistic and P values for factors effecting different measures of seedling performance at varying demographic stages. Only significant ($P \leq 0.05$) factors are shown.

			Year 1		Year 2	
Dependent variable	Figure	Significant effects	F statistic	P value	F statistic	P value
Germination timing	3	planting month × data collection date	15.26	< 0.001	4.49	< 0.001
		planting month × water treatment	5.15	0.002	16.90	< 0.001
Germination	4	planting month	42.6	< 0.001	—	—
		planting month × water treatment	—	—	4.80	0.008
Emergence	4	planting month × water treatment	3.02	0.046	3.99	0.018
Initial establishment	4	planting month	—	—	12.42	< 0.001
		planting month × water treatment	3.28	0.035	—	—
Emergence timing	5	planting month × data collection date	5.56	< 0.001	5.69	< 0.001
Survival of emergent seedlings	5	data collection date	7.87	< 0.001	8.33	< 0.001
Seedling density (plants · m^{-2})	6	planting month	9.56	< 0.001	5.71	< 0.001
Seedling biomass (g · m^{-2})	6	planting month	9.51	< 0.001	8.46	< 0.001
Seedling biomass (g · $plant^{-1}$)	6	planting month	3.05	0.049	3.57	0.027

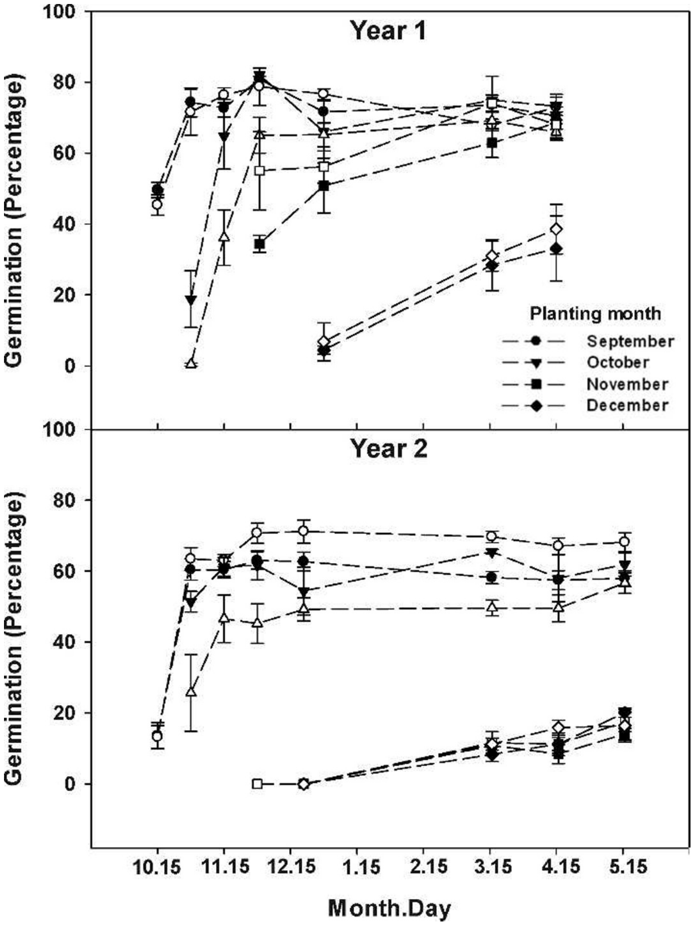

Figure 3. Timing of germination for bluebunch wheatgrass seeds by month of planting, data collection date, and water treatment for plots planted in southeast Oregon. Closed symbols indicate means for watered plots and open circles represent ambient plots. Data are stratified by year 1 (2008–2009) and year 2 (2009–2010). Means ($n=5$) are plotted with their associated standard errors.

planted plots had germination (40–80%) prior to onset of freezing soils. Elevated fall moisture in year 1 was associated with numerically higher germination for September- and October-planted plots as compared to year 2 (Fig. 3). Fall and winter germination of plots planted in November was higher in year 1 than year 2, ranging from 50.8 ± 7.74% to 56.1 ± 4.53%, for watered and ambient plots, respectively, and was 0% for year 2 (regardless of watering treatment). December-planted plots germinated mainly in the spring period with peak germination values approaching 30% and 20% for years 1 and 2, respectively. Watering was associated with increased fall and winter germination rates of October-planted plots in both years (Fig. 3).

Percentage of germination (in seed bags) differed by planting month in year 1, and planting month by water treatment in year 2 (Table 2; Fig. 4). In year 1, germination was highest for September and October plots at approximately 80% and decreased to 39.72 ± 4.59% with December planting. Both November and December plots had lower germination (approximately 20%) than earlier plantings in year 2. Percentage of emergence differed by planting month by water treatment in year 1 and year 2 (Table 2; Fig. 4). November plots had lowest percentage of emergence in year 1 (1.51 ± 0.28% and 0.76 ± 0.23% for watered and ambient plots, respectively) and watering increased emergence for October plots (from 7.36 ± 1.89% to 18.03 ± 3.43%). In year 2, September watered plots had highest percentage of emergence (watered = 19.77 ± 2.07%, ambient = 11.69 ± 2.57%); remaining planting dates had values < 7%. Percentage of initial seedling establishment was influenced by planting month by water in year 1 and planting month in year 2 (Table 2; Fig. 4). December ambient plots had highest percentage of initial establishment in year 1 (73.15 ± 13.77%). November and December plots had highest percentage of initial establishment in year 2 (approximately 73%), which was more than double that recorded for September and October Plots.

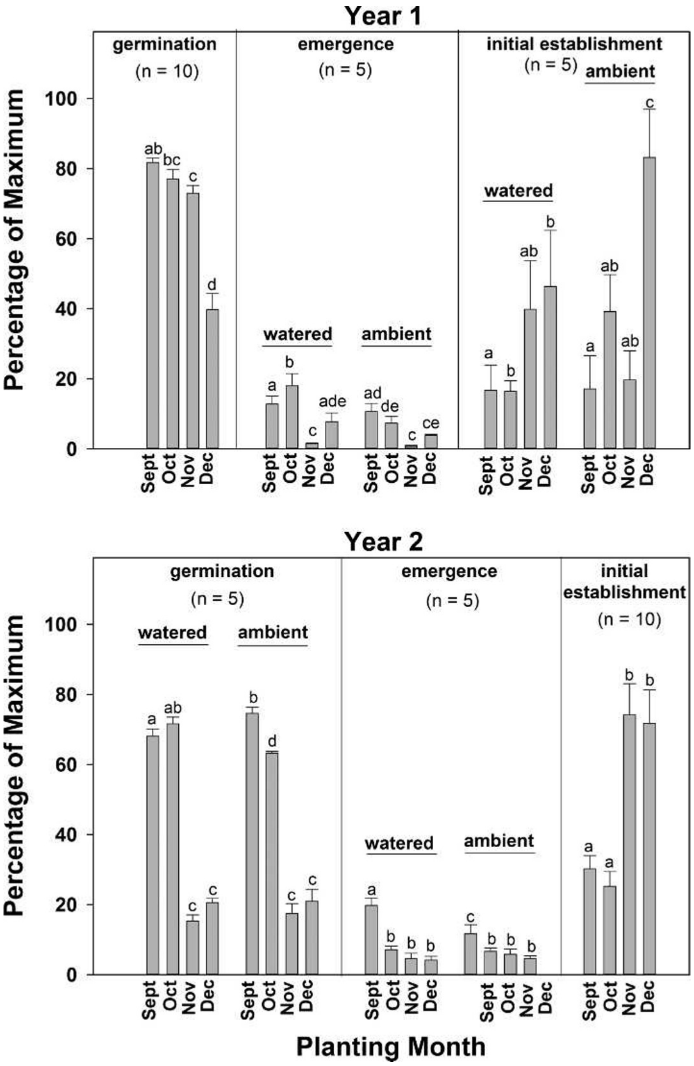

Figure 4. Percentage of germination, emergence, and initial establishment for bluebunch wheatgrass seeds as a function of planting month and watering treatment. Means within a year and panel without a common letter are different ($\alpha=0.05$). Data are stratified by year 1 (2008–2009) and year 2 (2009–2010) and only significant main effects and interactions are reported. Data indicate percentage of maximum possible score; scores for "emergence" were calculated based on the number of germinated seeds and "initial establishment" was calculated as a percentage of emergent seedlings. This differs from final seedling density as presented in Figure 6. Means are plotted with their associated standard errors.

Timing of emergence varied by planting month by date of data collection in both years (Table 2; Fig. 5). For September- and October-planted plots, emergence largely occurred by (year 1) or prior to (year 2) April 8. Emergence in these plots was more temporally dispersed in year 1 with approximately 80% of total emergence occurring from 11 March through 8 April; in year 2, September- and October-planted plots had 83.3 ± 4.22% and 74 ± 4.80% emergence, respectively, by the first data collection on 17 March (Fig. 5). Survival of emergent cohorts varied by date in both years (Table 2; Fig. 5). We found a pattern of increasing survival with later calendar date of emergence ranging from mid-March through early May. Survival then remained elevated for seedlings emerging through mid-June (Fig. 5).

Final seedling density varied by planting month in both years (Table 2; Fig. 6). In year 1 density ranged from 11.6 ± 2.38 plants · m^{-2} for October plots to a low of 1.30 ± 0.37 plants · m^{-2} for November plots (Fig. 6). September plots had highest seedling density in year 2 (17.8 ± 3.71 plants · m^{-2}) and November plots were lowest (2.5 ± 0.40 plants · m^{-2}). Seedling biomass per unit area was influenced by planting month in year 1 and year 2 (Table 2; Fig. 6). November plots had lower biomass than other planting months in year 1 (0.1 ± 0.04 g · m^{-2}) and year 2 (1.7 ± 0.18 g · m^{-2}) and September plots had highest biomass in year 2 (10.1 ± 0.18 g · m^{-2}). Planting month influenced biomass of individual seedlings in both years with no consistent between-year pattern (Table 2; Fig. 6).

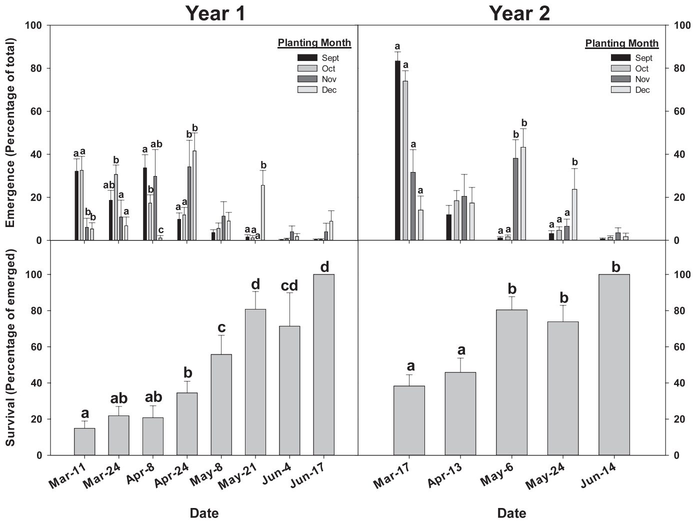

Figure 5. Emergence and survival of bluebunch wheatgrass seeds as a function of data collection date (dates describe cohort emergence rather than changes in a single cohort through time). Emergence values ($n=10$) are the percentage of seedlings (within year) that emerged on a given date. Survival values ($n=40$) are the percentage of an emergent cohort (within date and year) that survived to establishment. Means within a year, panel, and date without a common letter are different ($\alpha=0.05$). Data are stratified by year 1 (2008–2009) and year 2 (2009–2010). Means are plotted with their associated standard errors.

DISCUSSION

Seasonal patterns of temperature and soil moisture conditions across the Wyoming big sagebrush alliance provide a complex environment for germination, emergence, and establishment of perennial grasses. Seeds that germinate in fall often have high moisture availability but developing coleoptiles and radicles will be exposed to the rigors of frozen soil events during winter. Alternatively, advanced root development associated with fall germination may "prime" seedlings for increased resource capture during spring snowmelt, a life history strategy that is employed by most annual grasses resulting, at least partially, in their competitive dominance (Harris 1967). Spring germination avoids potential damage associated with soil freezing, but at the expense of delayed root development and potentially decreased survival in the ensuing summer dry period (Hardegree 1994). In our study, seedlings did not emerge prior to winter snow, regardless of planting or germination date.

Emergence and Germination vs. Planting Date

Our results clearly demonstrate variable success across life history stages and that success at a given stage is influenced by planting date. We found that emergence was the most limiting life history stage (Fig. 4), and, contrary to our hypothesis, planting dates with seeds that germinated predominately in spring did not have higher emergence. In general, less than 20% of germinated seeds emerged and for most year/treatment combinations, that number was < 10%. Previous fieldwork documenting emergence patterns for perennial grasses in sagebrush ecosystems is extremely limited. One study (James and Svejcar 2010) reported comparable emergence rates (4% of

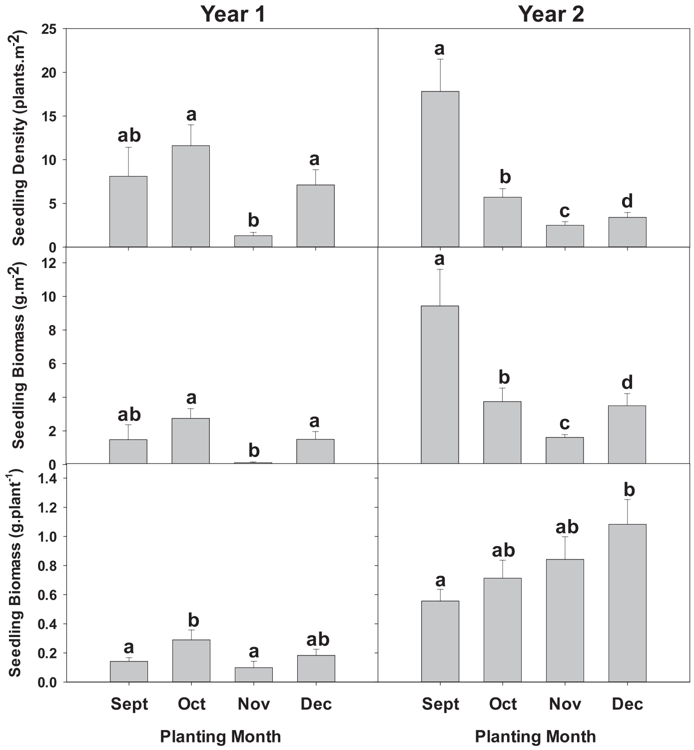

Figure 6. Final seedling density and biomass (per plant and per unit area) as a function of planting month. Means within a year and panel without a common letter are different ($\alpha=0.05$). Data are stratified by year 1 (2008–2009) and year 2 (2009–2010). Means ($n=10$) are plotted with their associated standard error.

germinated seeds) for November-planted seeds. Our decision to harvest seedlings at the time of senescence during the first growing season did not permit us to examine interannual survival of emergent seedlings. Other authors have found high grass seedling mortality during the first summer drought period (Salhi and Norton 1987; Pyke 1990). In contrast, Chambers (2000) found that once perennial grass seedlings emerged, survival in sagebrush steppe was high ($> 50\%$ over 2 yr). Similarly, Huber-Sannwald and Pyke (2005) reported 50–85% survival (20 mo) of emergent bluebunch and desert (*Agropyron desertorum* [Fisch. ex Link] Schult.) wheatgrasses. Experimental evidence from our area suggests that seedling survival to the end of the first growing season represents a major demographic milestone. James et al. (2011) reported approximately 0.70 probability of survival of bluebunch wheatgrass seedlings from the first to second growing seasons postemergence.

The degree to which emergence limited final seedling density varied by planting date with the balance of the data suggesting that emergence may be less limiting with early planting (September or October). The bulk of early-planted seed had emerged by mid-April as compared to November and December plantings that continued to show strong emergence into early to mid-May (Fig. 5). One explanation for a low percentage of emergence for November-planted plots in year 1 is that these plots initiated germination prior to winter onset (i.e., frozen soil conditions; see Fig. 3), within approximately 10 d of the first soil freezing event. Average soil temperature was below freezing for approximately 3 mo in year 1 as compared to 1 mo in year 2. Previous work with perennial grasses (Laude 1956) suggests that exposure of germinated seeds to freezing conditions can cause high levels of preemergent mortality. Slightly warmer soil temperatures and elevated soil moisture content in February (Fig. 2) may have resulted in less temporally dispersed emergence in year 2 as compared to year 1 (Fig. 5; Hardegree et al. 2010). Additional environmental correlates explaining differential emergence timing relative to planting date are unclear in our data. Such patterns may relate to timing of development of seedlings from competing species (Rummell 1946; Hironaka 1961; Mack and Pyke 1983), but competing vegetation was removed from our plots. Other authors have reported that crusting of the soil surface may decrease emergence of germinated seedlings (Wood et al. 1982; Unger 1984) by physically preventing coleoptile emergence, or indirectly by impeding water infiltration into the soil (Rapp et al. 2000). In our study, soil moisture during the emergence period was generally sufficient to prevent issues with soil crusting.

Percentage of germination was impacted by planting date. Earlier-planted (September, October, but also November in year 1) plots had up to 400% higher germination rates as compared to late-planted plots (December, but also November in year 2; Fig. 4). These data suggest that the wet-degree-day requirement for germination was met earlier, with early-planted plots (Meyer et al. 2000; Hardegree et al. 2003; Hardegree et al. 2010; Rawlins et al. 2012b). James and Svejcar (2010) found comparable rates (56–78%) of field germination to the present study for November-planted bunchgrasses using a seed bag technique. Consistent with our hypothesis, fall/winter germination decreased with later planting date, and prewinter germination of September and October plots (Fig. 3) was associated with a high percentage of seeds germinating (Fig. 4). It is interesting to note that germination of November plots was highest in year 1 (Fig. 4) and that up to 55% of these seeds had germinated by December (Fig. 3). Maximum germination of November plots was much reduced in year 2 (Fig. 4), but germination did not initiate prior to spring (Fig. 3). This differential between-year germination is associated with slightly colder soil temperatures in early winter (December) for year 2 (Fig. 2) and the first soil freezing event in year 1 falling on 12 December, approximately 1 wk later than the first event in year 2. Hardegree et al. (2003) reported that seeds exposed to 3°C vs. 9°C took almost four times the number of days (29.3 d vs. 8.1 d) to reach 50% of total germination. Additionally, decreased fall/winter germination of November- and December-planted plots in year 2 is associated with reduced soil water content, particularly in December, as compared to year 1 (Fig. 2). This explanation is consistent with empirical models linking germination with the interactive influence of temperature and moisture availability (Meyer et al. 2000; Hardegree et al. 2003; Rawlins et al. 2012a, 2012b). Because we did not attempt postretrieval germination of nongerminated seeds, our estimates of germination rate should be considered conservative. For example, if seeds were undergoing secondary dormancy, or if they germinated but died during winter, we would have recorded those seeds as nongerminated.

Previous literature (e.g., Van Mourik et al. 2005) has criticized the buried seed bag technique because loss of seeds to fungal pathogen attack (due to high seed density) can lead to overestimates of seed bank depletion, but others have found that this technique compares favorably to alternate methods (Schutte et al. 2008). Our use of the buried bag technique could lead to underestimates of germination if nongerminated seeds were actually dormant, and underestimates in the case of fungal pathogen attack. In either case, we have no reason to suspect that such inaccuracies would change relative differences noted between planting dates.

A greater understanding of the relationship between environmental factors and seedling emergence could significantly improve seeding success. However, improvements in germination and initial establishment may also be important, even with low emergence. For example, with September- and October-planted seeds, germination was relatively high but there is room for improvement in the relatively low percentage of emergent seedlings that survived to initial establishment. Conversely, late-planted seeds have a high percentage of initial establishment but low germination rates limit the potential density of established plants. Thus, low emergence could be at least partially offset by improvement in germination or establishment percentages.

Planting Date Effects on Initial Establishment and Seedling Density

Our results suggest that timing of planting and timing of germination can have a strong influence on the temporal pattern of emergence and the subsequent survival of emergent seedlings (Figs. 4 and 5). Results of this study contradict our hypothesis that survival of emergent seedlings would increase with fall/winter germination. Seedlings in plots planted in

September and October (and November in year 1) had a much lower percentage of initial establishment than plots planted in December (and November in year 2), which had up to 80% initial establishment (Fig. 4). Increased percentage of initial establishment for late-planted plots corresponded to later germination (Fig. 3) and emergence (Fig. 5) dates and may relate to resource availability at the time of germination. Our data suggest that soil water content can be higher following spring snowmelt and rainfall as compared to the fall period (e.g., year 2) but that this pattern will vary by year (Fig. 2). Soil temperature had similar variability in spring vs. fall patterns across years (Fig. 2); however, soil and air temperatures (Fig. 1) in both years were decreasing over time in fall and increasing over time in spring, which may have promoted more favorable conditions for initial establishment of spring-germinated seedlings. Most planting month/year combinations produced final (July) seedling densities that would be considered successful within a restoration context (e.g., > 5 plants $\cdot$ m^{-2}) and were comparable to other work incorporating hand-seeded plots (e.g., Eckert et al. 1986, James and Svejcar 2010).

The relative effect of planting date on seedling demography may be influenced by the potentially interactive effects of planting date and competition from nonplanted species. In our study, we removed nonplanted species (mainly cheatgrass) from plots at approximately 2-wk intervals beginning with the first seedling count in March. This strategy allowed us to more effectively isolate the influence of planting date on seedling demography, but curtailed our ability to place those results within the context of competition from nonplanted species. Competition from nonplanted annual grasses can decrease establishment of seedling perennial grasses (Rafferty and Young 2002).

Watering Effects

Evidence for our hypothesis that water additions would increase seedling performance with respect to percentages of germination, emergence, and initial establishment was not clear-cut and when watering treatment was significant it interacted with planting month and varied by year (Fig. 4). Data for most planting dates suggest that watering may increase initial germination but that over time these patterns (as compared to ambient plots) converge to similar maximum germination percentages (Fig. 3). Emergence was the only life history stage for which watering treatment was significant in both years, with limited evidence suggesting some benefit to watering for September or October planting (Fig. 4). Furthermore, the fact that seedling density and biomass did not differ by watering treatment suggests that fall watering within the bounds of the frequency and amount applied in this study has little effect. This is somewhat surprising given that both study years had below normal precipitation (Fig. 1) but is not unprecedented in the literature. James and Svejcar (2010) found that spring watering had no effect on density of seeded perennial bunchgrasses. The fact that both study years had above normal precipitation periods at or just after the time of seedling emergence (Figs. 1 and 5) may have dampened the potential magnitude of watering effects. Watering may also have an effect on survival of seedlings at time horizons beyond those examined in the current study.

Additional research is needed to test the efficacy of the findings of this study in different years and sites, given that demography of seeded perennial grasses is inherently tied to variation in both year and site conditions (Boyd and Svejcar 2009). To that end, our study took place in the mesic end of the Wyoming big sagebrush alliance and within years with precipitation slightly below that of long-term average. While we investigated planting success at the scale of 1-m^{-2} plots and 1-mo intervals, smaller-scale variation in environmental conditions (e.g., Pierson and Wight 1991) will undoubtedly have influence on seedlings. Alternatively, research to determine the mechanistic underpinnings of findings in this study may allow for prediction of seedling demography under a wide variety of abiotic conditions associated with a diversity of temporal and spatial scales.

MANAGEMENT IMPLICATIONS

Prior to European arrival, recovery of native perennial grasses following disturbance could have been through either vegetative or sexual reproduction (Ratzlaff and Anderson 1995; Liston et al. 2003). Because of strong interannual variability in the climate of sagebrush systems (Bates et al. 2007), successful reproduction of native perennial bunchgrasses from seed may have been episodic and associated with years having favorable climatic conditions. This is significant because present-day management techniques for restoring ecologically degraded Wyoming big sagebrush communities rely on successful and timely reproduction from seed, an association that may not fit with the historical ecology of native perennial grasses in these systems. If we are to use these techniques to promote the abundance of a limited number of desirable perennial species in a climatically variable environment, then we should attempt to capitalize on all available windows of opportunity in time for germination and emergence. Our data suggest that early-planted (September and October) seeds will have a high percentage of germination and emergence, but that late-planted seeds have an increased percentage of initial establishment of emergent seedlings. Because emergence is the most limiting demographic stage, September or October planting may result in highest probability of restoration success, although final plant density by planting month was not consistent between years (Fig. 6).

Our data highlight the importance of timing of key demographic stages for planted seeds. For example, our data indicate that timing of germination influences temporal emergence patterns and likelihood of initial seedling establishment. We suggest that these results could be used to guide technologies, such as seed coating, to produce variable chronologies of seedling development with single plantings that effectively allow managers to “hedge their bets” (Philippi 1993; Adondakis and Venable 2004) by exploiting multiple temporal windows of opportunity for seedling establishment. In theory, a mix of noncoated and hydrophilic and hydrophobic coated seeds (Scott 1989) could promote a diversity of germination and emergence episodes over time that increases the probability of seeding success in a temporally variable restoration environment. Previous literature (Stratton 1992; Kelly and Levin 1997) also suggests the potential for manipulating germplasm to select for variable timing of emergence to best match the constraints of a temporally and spatially variable environment. Improvements may be small, but managers should consider that small improvements can have merit. For example, only 5–10 established $\text{plants} \cdot \text{m}^{-2}$ are needed for successful restoration of Wyoming big sagebrush (Vallentine 1989); with a seeding rate for perennial bunch grasses of 10–14 $\text{kg} \cdot \text{ha}^{-1}$, or approximately 500 $\text{seeds} \cdot \text{m}^{-2}$ (Boyd and Davies 2010), a 1% increase in the number of seeds that eventually establish equates to a 5 $\text{plant} \cdot \text{m}^{-2}$ increase in seedling density. Thus, small increases in survival probabilities can equate to significant improvement in restoration success.

LITERATURE CITED

Abbott, L. B., and B. A. Roundy. 2003. Available water influences field germination and recruitment of seeded grasses. *Journal of Range Management* 56:56–64.

Adondakis, S., and D. L. Venable. 2004. Dormancy and germination in a guild of Sonoran desert annuals. *Ecology* 85:2582–2590.

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

Bates, J. D., T. Svejcar, R. F. Miller, and R. A. Angell. 2007. The effects of precipitation timing on sagebrush steppe vegetation. *Journal of Arid Environments* 64:670–697.

Bedunah, D. J., E. D. McArthur, and M. Fernandez-Gimenez [comps.].2006. Rangelands of Central Asia: Proceedings of the Conference on Transformations, Issues, and Future Challenges; 27 January 2004; Salt Lake City, UT, USA. Fort Collins, CO, USA: USDA Forest Service Rocky Mountain Research Station. Proceeding RMRS-P-39. 127 p.

Boyd, C. S., and K. W. Davies. 2010. Shrub microsite influences post-fire perennial grass establishment. *Rangeland Ecology & Management* 63:248–252.

Boyd, C. S., and T. J. Svejcar. 2009. Managing complex problems in rangeland ecosystems. *Rangeland Ecology & Management* 62:491–499.

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

Chambers, J. C. 2000. Seed movements and seedling fates in disturbed sagebrush steppe ecosystems: implications for restoration. *Ecological Applications* 10:1400–1413.

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

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

Davies, K. W. 2008. Medusahead dispersal and establishment in sagebrush steppe plant communities. *Rangeland Ecology & Management* 61:110–115.

Davies, K. W., and T. J. Svejcar. 2008. Comparison of medusahead-invaded and noninvaded Wyoming big sagebrush steppe in southeastern Oregon. *Rangeland Ecology & Management* 61:623–629.

Eckert, R. E., Jr., F. F. Peterson, M. S. Meurisse, and J. L. Stephens. 1986. Effects of soil-surface morphology on emergence and survival of seedlings in big sagebrush communities. *Journal of Range Management* 39:414–420.

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

Gisladottir, G., and M. Stocking. 2005. Land degradation control and its global environmental benefits. *Land Degradation & Development* 16:99–112.

Greene, R. P., and J. Stager. 2001. Rangeland to cropland conversions as replacement land for prime farmland lost to urban development. *The Social Science Journal* 38:543–555.

Hardegree, S. P. 1994. Matric priming increases germination rate of Great Basin native perennial grasses. *Agronomy Journal* 86:289–293.

Hardegree, S. P., G. N. Flerchinger, and S. S. Van Vactor. 2003. Hydrothermal germination response and the development of probabilistic germination profiles. *Ecological Modelling* 167:305–322.

Hardegree, S. P., C. A. Moffet, B. A. Roundy, T. A. Jones, S. J. Novak, P. E. Clark, F. B. Pierson, and G. N. Flerchinger. 2010. A comparison of cumulative-germination response of cheatgrass (*Bromus tectorum* L.) and five perennial bunchgrass species to simulated field-temperature regimes. *Environmental and Experimental Botany* 69:320–327.

Hardegree, S. P., and S. S. Van Vactor. 2004. Microclimatic constraints and revegetation planning in a variable environment. *Weed Technology* 18:1231–1215.

Harris, G. A. 1967. Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum*. *Ecological Monographs* 37:89–111.

Hironaka, M. 1961. The relative rate of root development of cheatgrass and medusahead. *Journal of Range Management* 14:263–267.

Hironaka, M., and B. W. Sindelar. 1975. Growth characteristics of squirreltail seedlings in competition with medusahead. *Journal of Range Management* 28:283–285.

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

Huxman, T. E., B. P. Wilcox, D. D. Breshears, R. L. Scott, K. A. Snyder, E. E. Small, K. Hultine, W. T. Pockman, and R. B. Jackson. 2005. Ecohydrological implications of woody plant encroachment. *Ecology* 86:308–319.

James, J. J., and R. E. Drenovsky. 2007. A basis for relative growth rate differences between native and invasive forb seedlings. *Rangeland Ecology & Management* 60:395–400.

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

James, J. J., T. J. Svejcar, and M. J. Rinella. 2011. Demographic processes limiting seedling recruitment in arid grassland restoration. *Journal of Applied Ecology* 48:961–969.

Kelly, M. G., and D. A. Levin. 1997. Fitness consequences and heritability aspects of emergence date in *Phlox drummondii*. *Journal of Ecology* 85:755–766.

Kitchen, S. G., and S. B. Monsen. 1994. Germination rate and emergence success in bluebunch wheatgrass. *Journal of Range Management* 47:145–150.

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

Küchler, A. W. 1970. Potential natural vegetation. *In:* The national atlas of U.S.A. Washington, DC, USA: Government Printing Office. p. 90–91.

Laude, H. M. 1956. The seedling emergence of grasses as affected by low temperature. *Agronomy Journal* 48:558–560.

Lentz, D. R., and G. H. Simonson. 1986. A detailed soils inventory and associated vegetation of Squaw Butte Range Experiment Station. Corvallis, OR, USA: Agricultural Experiment Station, Oregon State University. Special Report 760. 184 p.

Link, S. O., R. O. Cruz, B. L. Harper, J. D. Jones, and B. L. Penney. 2011. Shrub-steppe species survival after outplanting on bare soils. *In:* L. E. Riley, D. L. Haase, and J. R. Pinto [tech. coords]. National Proceedings: Forest and Conservation Nursery Associations—2010. Fort Collins, CO, USA: USDA Forest Service. RMRS-P-65. p. 159–167.

Liston, A., B. L. Wilson, W. A. Robinson, P. S. Doescher, N. R. Harris, and T. Svejcar. 2003. The relative importance of sexual reproduction versus clonal spread in an aridland bunchgrass. *Oecologia* 137:216–225.

Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS system for mixed models. Cary, NC, USA: SAS Institute. 656 p.

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

Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10:689–710.

Mangla, S., R. L. Sheley, J. J. James, and S. R. Radosevich. 2011. Role of competition in restoring resource poor arid systems dominated by invasive grasses. *Journal of Arid Environments* 75:487–493.

Melgoza, G., R. S. Nowak, and R. J. Tausch. 1990. Soil water exploitation after fire: competition between *Bromus tectorum* (cheatgrass) and two native species. *Oecologia* 83:7–13.

Meyer, S. E., S. B. Debaene-Gill, and P. S. Allen. 2000. Using hydrothermal time concepts to model seed germination response to temperature, dormancy loss and priming effects in *Elymus elymoides*. *Seed Science Research* 10:213–223.

Miller, R., J. Seufert, and M. Haferkamp. 1986. The ecology and management of bluebunch wheatgrass (*Agropyron spicatum*): a review. Corvallis, OR, USA: Oregon State University Agricultural Research Station. Bulletin No. 669. 39 p.

Miller, R. F., and L. L. Eddleman. 2000. Spatial and temporal changes of sage grouse habitat in the sagebrush biome. Corvallis, OR, USA: Oregon State University Agricultural Experiment Station. Technical Bulletin 151. 35 p.

Miller, R. F., T. J. Svejcar, and N. E. West. 1994. Implications of livestock grazing in the Intermountain sagebrush region: plant composition. *In:* M. Vavra, W. A. Laycock, and R. D. Pieper [eds.]. Ecological implications of livestock herbivory in the West. Denver, CO, USA: Society for Range Management. p. 101–146.

Milton, S. J., R. J. Dean, M. A. du Plessis, and W. R. Siegfried. 1994. A conceptual model of arid rangeland degradation. *Bioscience* 44:70–76.

Neter, J., W. Wasserman, and M. H. Kutner. 1990. Applied linear statistical models: regression, analysis of variance and experimental design. 3rd ed. Homewood, IL, USA: Irwin. 1408 p.

Pellant, M., B. Abbey, and S. Karl. 2004. Restoring the Great Basin desert, USA: integrating science, management and people. *Environmental Monitoring and Assessment* 99:169–179.

Pellant, M., and C. Hall. 1994. Distribution of two exotic grasses on public lands in the Great Basin: status in 1992. *In:* S. B. Monsen and S. G. Kitchen. [comps.]. Proceedings—Ecology and Management of Annual Rangelands; 18–22 May 1992; Boise ID, USA. Ogden, UT, USA: USDA Forest Service Intermountain Research Station. General Technical Report INT-GTR-313. p. 109–112.

Philippi, T. 1993. Bet-hedging germination of desert annuals: variation among populations and maternal effects in *Lepidium lasiocarpum*. *American Naturalist* 142:488–507.

Pierson, F. B., and J. R. Wight. 1991. Variability of near-surface soil temperature on sagebrush rangeland. *Journal of Range Management* 44:491–497.

Pyke, D. A. 1990. Comparative demography of co-occurring introduced and native tussock grasses: persistence and potential expansion. *Oecologia* 82:537–543.

Pyke, D. A., T. O. McArthur, K. S. Harrison, and M. Pellant. 2003. Coordinated Intermountain restoration project—fire, decomposition and restoration. *In:* N. Allsopp, A. R. Palmer, S. J. Milton, K. P. Kirkman, G. I. H. Kerley, C. R. Hurt, and C. J. Brown [eds.]. Proceedings of the VIIth International Rangelands Congress; 26 July–1 August 2003; Durban, South Africa. Hilton, South Africa: Grassland Society of South Africa. p. 1116–1124.

Rafferty, D. L., and J. A. Young. 2002. Cheatgrass competition and establishment of desert needlegrass seedlings. *Journal of Range Management* 55:70–72.

Rapp, I., I. Shainberg, and A. Bannin. 2000. Evaporation and crust impedance role in seedling emergence. *Soil Science* 165:354–364.

Ratzlaff, T. D., and J. E. Anderson. 1995. Vegetal recovery following wildfire in seeded and unseeded sagebrush steppe. *Journal of Range Management* 48:386–391.

Rawlins, J. K., B. A. Roundy, and S. Davis. 2012a. Predicting germination in semi-arid wildland seedbeds I. Thermal germination models. *Environmental and Experimental Botany* 76:60–67.

Rawlins, J. K., B. A. Roundy, D. Egget, and N. Cline. 2012b. Predicting germination in semi-arid wildland seedbeds II. Field validation of wet thermal-time models. *Environmental and Experimental Botany* 76:88–73.

Robertson, J. H., R. E. Eckert, Jr., and A. T. Bleak. 1966. Responses of grasses seeded in an *Artemisia tridentata* habitat in Nevada. *Ecology* 47:187–194.

Rosiere, R. E. 2006. Sagebrush shrub steppe. *In:* Range Types of North America. Stephenville, TX, USA: Tarleton State University. Available at: http://www.tarleton.edu/%7Erange/. Accessed 12 October 2012.

Rummell, R. S. 1946. Some effects of competition from cheatgrass brome on crested wheatgrass and bluestem wheatgrass. *Ecology* 27:159–167.

Salhi, D. O., and B. E. Norton. 1987. Survival of perennial grass seedlings under intensive grazing in semi-arid rangelands. *Journal of Applied Ecology* 24:145–151.

SAS Institute Inc. 1999. SAS procedures guide, release 8.0. Cary, NC, USA: SAS Institute. 1624 p.

Schutte, B. J., A. S. Davis, K. A. Renner, and J. Cardina. 2008. Maternal and burial environment effects on seed mortality of velvetleaf (*Abutilon theophrasti*) and giant foxtail (*Setaria faberi*). *Weed Science* 56:834–840.

Scott, J. M. 1989. Seed coatings and treatments and their effects on plant establishment. *Advances in Agronomy* 42:43–83.

Stratton, D. A. 1992. Life-cycle components of selection in *Erigeron annuus*: I. phenotypic selection. *Evolution* 46:92–106.

Stringham, T. K., W. C. Krueger, and P. L. Shaver. 2003. State and transition modeling: an ecological process approach. *Journal of Range Management* 56:106–113.

Unger, P. W. 1984. Tillage effects on surface soil physical conditions and sorghum emergence. *Soil Science Society of America Journal* 48:1423–1432.

Vallentine, J. F. 1989. Range developments and improvements. San Diego, CA, USA: Academic Press. 524 p.

Van Mourik, T. A., T. J. Stomph, and A. J. Murdoch. 2005. Why high seed densities within buried mesh bags may overestimate depletion rates of soil seed banks. *Journal of Applied Ecology* 42:299–305.

West, N. E., and J. A. Young. 2000. Intermountain valleys and lower mountain slopes. *In:* M. A. Barbour and W. D. Billings [eds.]. North American terrestrial vegetation. 2nd ed. New York, NY, USA: Cambridge University Press. p. 255–284.

Whisenant, S. G. 1990. Changing fire frequencies in Idaho's Snake River Plains: ecological and management implications. *In:* E. D. McArthur, E. M. Romney, S. D. Smith, and P. T. Tueller [eds.]. Symposium on Cheatgrass Invasion, Shrub Die-Off, and Other Aspects of Shrub Biology and Management; 5–7 April 1990; Las Vegas, NV, USA. Ogden, UT, USA: USDA Forest Service. p. 4–10.

Wood, K. M., R. E. Eckert, W. H. Blackburn, Jr., and F. F. Peterson. 1982. Influence of crusting soil surfaces on emergence and establishment of crested wheatgrass, squirreltail, Thurber needlegrass, and fourwing saltbush. *Journal of Range Management* 35:282–287.

Young, K., and J. Mangold. 2008. Medusahead outperforms squirreltail through interference and growth rate. *Invasive Plant Science and Management* 1:73–81.