

Using germination prediction to inform seeding potential: II. comparison of germination predictions for cheatgrass and potential revegetation species in the Great Basin, USA

Nathan L. Cline^a, Bruce A. Roundy^{a,*}, Stuart Hardegee^b, William Christensen^a

^a Brigham Young University, Provo, UT 84602, USA

^b Northwest Watershed Research Center USDA-ARS, Boise, ID, USA

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ABSTRACT

Germination models predict germination timing under seedbed water potential and temperature conditions. Using a wet thermal time model for germination prediction, we estimated progress toward germination (PTG) of 31 seedlots (10 species) as a function of hourly seedbed temperature ($> 0\text{ }^{\circ}\text{C}$) when soils were above a water potential of -1.5 MPa . Seasonally-summed progress toward germination with a value > 1 indicates that germination will occur for that season. We used near surface (1–3 cm) soil water potential and temperature measurements collected at 24 sites in the Great Basin to determine effects of site, season, and year on PTG. On tree encroached sites, we also determined effects of tree infilling phase at time of tree removal, removal method, and microsite on estimated PTG. Soils were wet and warm enough in early spring, late spring, and fall for PTG > 1 indicating potential germination for most seedlots and species on most sites and years. Prescribed burning increased PTG as much as three times more than either tree cutting or mechanical shredding. Germination prediction could help to screen for plant materials adapted to specific sites or assess effects of seed additives or treatments that time germination to maximize seedling survival.

1. Introduction

Cheatgrass (*Bromus tectorum* L.) and infilling of woodlands threaten the sagebrush (*Artemisia* L.) ecosystem in the Great Basin by preemptively utilizing available resources and altering the fire cycle (Harris and Wilson, 1970; Chambers et al., 2014; Pyke et al., 2014; Roundy et al., 2014a, 2014b). Allowing sagebrush communities to naturally recover after wildfires is preferred when ecological thresholds have not been crossed (Whisenant, 1999). However, recovery fails when insufficient residual grasses and shrubs are left to resist cheatgrass (Miller et al., 2007). Another rehabilitation approach is to seed desirable species after wildfire (Whisenant, 1999; Call and Roundy, 1991) or in conjunction with controlled burning or other fuel control methods (Bybee et al., 2016). Seeding success may be increased by the selection of adapted plants for climatic conditions, seeding during specific seasons, and preparing the seedbed to maximize soil water availability (Hardegee et al., 2016; Roundy and Call, 1988). Plant materials for seeding are selected based on regional adaptation, but germination is constrained by site and year-specific soil water and temperature conditions (Rawlins et al., 2012b). Seedlings often fail when site, annual, and seasonal weather is not conducive to soil

moisture and temperature conditions that promote seedling survival (Ryel et al., 2010; Condon et al., 2011; Hardegee et al., 2016; Knutson et al., 2014). Predicting germination timing in relation to soil water availability and temperature for weeds and seeded revegetation species may help develop strategies to improve seedling survival (Call and Roundy, 1991).

Successful plant establishment in sagebrush communities of the Great Basin requires that seeds germinate and seedlings establish under a climatic context of cool wet winters and warm, dry summers (Caldwell, 1985; Donovan and Ehleringer, 1994). Germination may occur in fall when precipitation is sufficient and before temperatures are too cold, or in spring when water is available from winter and spring recharge and temperatures are favorable (Campbell and Harris, 1977; Caldwell, 1985). Rehabilitation seeding is generally done between summer and early winter after summer wildfire or before fuel control treatments such as mechanically shredding are implemented (Hardegee et al., 2016; Bybee et al., 2016). Recent research suggests that germination is generally not limiting in sagebrush communities for several Great Basin revegetation species or for competing cheatgrass (Roundy et al., 2007; James et al., 2011). However, germination timing may play an important role in seedling survival. Manipulating

* Corresponding author. Department of Plant and Wildlife Sciences, 4105 LSB Brigham Young University, Provo, UT 84602, USA.
E-mail address: bruce_roundy@byu.edu (B.A. Roundy).

germination timing to minimize competition with weeds (Hardegee and Van Vactor, 2000), frost (Boyd and Lemos, 2013; Roundy and Madsen, 2016), or drought may enhance seedling survival and revegetation success (Madsen et al., 2012). Spatial and temporal differences, rehabilitation treatment, tree infilling phase, and associated microsites affect the time of soil water availability and temperature of the seedbed environment for both cheatgrass and revegetation species (Cantón et al., 2004; Weisberg et al., 2007; Young et al., 2013; Roundy et al., 2014b). The effects of these factors on germination timing should be determined to help predict effects on seedling survival.

Thermal time models estimate potential germination timing of a seedlot, e.g. days to 50% germination of the seed sample. Potential germination models are developed by measuring percent germination over time for a range of constant incubation temperatures. The inverse of the time to germination (germination rate) for each seed sub-population at various constant temperatures are fitted to linear and non-linear regression equations for each seedlot (Roundy and Biedenbender, 1996; Hardegee et al., 1999; Rawlins et al., 2012a). Germination rate is summed as progress toward germination (PTG) and a value > 1 indicates positive germination potential for specific temperatures and water potential of the seed incubation environment. Thermal time models that characterize soil conditions as either wet or dry using a threshold water potential are referred to as wet thermal time models (Finch-Savage et al., 2001; Roundy et al., 2007; Rawlins et al., 2012b). Wet thermal time models provided accurate predictions for greater than 75% of estimations of germination of six species at two locations in Utah during late winter through early spring (Rawlins et al., 2012b).

Here we used a wet thermal model and *in situ*-measured soil water potential and temperature to determine differences in seasonal PTG for various seedlots of revegetation species and cheatgrass in Great Basin communities. We compared seasonal PTG by site, season, year, tree (*Juniperus* spp. and *Pinus* spp.) removal methods, tree infilling phase, and various microsites for multiple sites across the Great Basin region.

2. Methods

2.1. Study sites

We used soil water potential and temperature data collected at 24 sites across the Great Basin described in Cline et al. (2018). Sites were divided into four experiments and were designated (1) “sagebrush (*Artemisia* spp.) and perennial grass- NV UT”, (2) “sagebrush and perennial grass-SageSTEP” (3) “crested wheatgrass” (*Agropyron cristatum* L.), and (4) “woodland” (Cline et al., 2018). The sagebrush and perennial grass-NV UT experiment was located on six sagebrush sites with associated native bunchgrasses, two sagebrush sites seeded to crested wheatgrass and recolonized by sagebrush, and a squirrel tail (*Elymus elymoides* (Raf.) Swezy) site with scattered big sagebrush and shadscale (*Atriplex confertifolia* (Torr. & Frem.) S. Watson) shrubs, all having data from 2002 to the spring of 2011 (Chambers et al., 2007; Roundy et al., 2007; Cline et al., 2018). The sagebrush and perennial grass-SageSTEP experiment was located on three sagebrush and perennial bunchgrass sites and was measured from 2008 to the spring of 2011 (McIver et al., 2010; Cline et al., 2018). The crested wheatgrass experiment was located in two fire rehabilitation seedings that resulted in near complete crested wheatgrass dominance with data from 2006 to the spring of 2011 (Hulet et al., 2010; Rawlins et al., 2012b; Cline et al., 2018). The woodland experiment was located on three western juniper (*Juniperus occidentalis* Hook.) sites in California and Oregon, two single-leaf pinyon (*Pinus monophylla* Torr. & Frém.) and Utah juniper (*Juniperus osteosperma* Engelm.) sites in Nevada, two Utah juniper sites in Utah, and two Colorado pinyon (*Pinus edulis* Engelm.) and Utah juniper sites in Utah. Data available varied with site and years since tree reduction treatment (Cline, 2014; Roundy et al., 2014b). Woodland plots were placed across three tree infilling phases according to relative cover

(Miller et al., 2005): in Phase I the majority of cover is perennial grasses and shrubs, in Phase II the cover is shared by perennial grasses, shrubs, and trees, and in Phase III the majority of cover is trees. Plots used in the sagebrush and perennial grass-NV UT, sagebrush and perennial grass-SageSTEP, and crested wheatgrass experiments were untreated. Woodland sites had both treated and untreated plots. Woodland treatments included prescribed burning, tree cutting and mechanical shredding. Mechanical shredding was conducted only at the Utah sites and all woodland sites included untreated plots.

2.2. Thermal time analysis

Experiments were originally set up in a randomized block design to determine vegetation treatment effects (Chambers et al., 2007; Rawlins et al., 2012b; Roundy et al., 2014a, 2014b). Cline et al. (2018) described the experimental design and characterized the climate conditions and seedbed soil moisture and temperature conditions for each experiment over the same time periods as in the present study. Soil matric potential from gypsum blocks and soil temperature from thermocouples buried at 1–3 cm were read every 60 s and hourly averages recorded by Campbell Scientific, Inc. microloggers (Cline, 2014).

We compiled 31 germination prediction equations to estimate PTG. Nineteen germination prediction equations were compiled from the median germination rate of 18 seedlots from previous studies (Table 1; Roundy et al., 2007; Rawlins et al., 2012a). There were eight cheatgrass, two crested wheatgrass, one bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve), one Snake River wheatgrass (*Elymus wawawaiensis* J. Carlson & Barkworth), one squirreltail, two common yarrow (*Achillea millefolium* L.), one Lewis flax (*Linum lewisii* Pursh), one blue flax (*Linum perenne* L.), and one longspur lupine (*Lupinus arbustus* Douglas ex Lindl.) seedlots. Another 13 seedlot equations for five species were derived from constant incubation temperature data compiled from Hardegee et al. (2008, 2010). There were five squirreltail, two big squirreltail (*Elymus multisetus* M. E. Jones), two bluebunch wheatgrass, two basin wildrye (*Leymus cinereus* (Scribn & Merr.) Á.), and two Sandberg bluegrass (*Poa secunda* J. Presl.) seedlots.

Germination rate or 1/days to 50% germination of germinable seeds was regressed on constant incubation temperatures for all seedlots using a combination of best fit linear and nonlinear regression equations as derived from Tablecurve[®] 2D curve fitting software (Table 1, Roundy et al., 2007; Rawlins et al., 2012a). Linear regressions were derived from the lowest two incubation temperature rates as described by Roundy et al. (2007) and were used to estimate PTG for the lower sub-optimal temperature range (< 0–5 °C, 0–10 °C, or sometimes 0–15 °C) as described in Hardegee et al. (1999), Roundy et al. (2007), and Rawlins et al. (2012a). Best fit linear and nonlinear regressions were selected utilizing the highest R^2 and F -values with minimum residuals for incubation temperatures > 10 or sometimes 15 °C (Roundy et al., 2007; Rawlins et al., 2012a). Hourly field soil temperature average was used as the independent variable in these regression equations to calculate hourly PTG for each seedlot. Progress toward germination for a season was calculated by summing hourly PTG for each hour when soil water potential was > –1.5 MPa. When hourly PTG sums to 1, 50% of seeds are predicted to germinate for that seedlot. Sums of PTG > 1 indicate increasing potential for seeds to germinate. We report cumulative summing of PTG across intermittent wet periods as was found to be most accurate in predicting field germination by Rawlins et al. (2012a).

We used mixed model analysis of variance (Littell et al., 2006) to analyze each experiment separately. Site was considered a random block across the region for the sagebrush and perennial grass-NV UT, sagebrush and perennial grass-SageSTEP, and woodland experiments, while four replicated blocks per site were used as a random factor for the crested wheatgrass experiment. Fixed factors were seasons, years, and seedlots for all experiments. Site was a fixed factor in the crested wheatgrass experiments, while woodland experiments had additional

Table 1
Seedlots and related studies where constant temperature germination trials were conducted and thermal germination equations were developed.

Species & Seedlot	Origin or Cultivar	Constant Temperature Germination Trial	Development of Predictive Equation
Cheatgrass (<i>Bromus tectorum</i> L.)			
CC07BRTE	Cache Creek, BC	Roundy et al., 2007	Roundy et al., 2007
LPBRTE	Lookout Pass, UT	Roundy et al., 2007	Roundy et al., 2007
OD98BRTE	Odessa, WA	Roundy et al., 2007	Roundy et al., 2007
SB98BRTE	Spences Bridge, BC	Roundy et al., 2007	Roundy et al., 2007
TM97BRTE	Ten Mile, ID	Roundy et al., 2007	Roundy et al., 2007
LPRBRTE	Lookout Pass, UT	Rawlins et al., 2012a	Rawlins et al., 2012a
SFBRTE	Spanish Fork Farm, UT	Roundy et al., 2007	Roundy et al., 2007
SVBRTE	West Skull Valley, UT	Rawlins et al., 2012a	Rawlins et al., 2012a
Perennial Grass			
Crested wheatgrass (<i>Agropyron</i> ssp.)			
AGCR	Hycrest	Rawlins et al., 2012a	Rawlins et al., 2012a
AGDE	Nordan	Rawlins et al., 2012a	Rawlins et al., 2012a
Bluebunch wheatgrass (<i>Pseudoroegneria spicata</i> (Pursh) Á. Löve)			
APSSP	Anatone	Rawlins et al., 2012b	Rawlins et al., 2012a
GPSSP	Goldar	Present Study	Hardegee et al., 2010
WPSSP	Whitmar	Present Study	Hardegee et al., 2010
Snake River wheatgrass (<i>Elymus wawawaiensis</i> J. Carlson & Barkworth)			
ELWA2	Secar	Rawlins et al., 2012b	Rawlins et al., 2012a
Bottlebrush Squirreltail (<i>Elymus elymoides</i> (Raf.) Swezey)			
ELEL	Sanpete	Rawlins et al., 2012a	Rawlins et al., 2012b
T-1202	Hwy 75 X 20, ID	Hardegee et al., 2008	Present Study
T-1205-98	W. Hill City, ID 1998	Hardegee et al., 2008	Present Study
T-1205-99	W. Hill City, ID 1999	Hardegee et al., 2008	Present Study
T-1175-98	Ditto Creek Rd, ID 1998	Hardegee et al., 2008	Present Study
T-1175-99	Ditto Creek Rd, ID 1999	Hardegee et al., 2008	Present Study
Big Squirreltail (<i>Elymus multisetus</i> M. E. Jones)			
ELMU-1	Sand Hollow	Hardegee et al., 2010	Present Study
ELMU-2	Sand Hollow	Hardegee et al., 2010	Present Study
Basin wildrye (<i>Leymus cinereus</i> (Scribn & Merr.) Á. Löve)			
Magnar	LECI-1	Hardegee et al., 2010	Present Study
Trailhead	LECI-2	Hardegee et al., 2010	Present Study
Sandberg bluegrass (<i>Poa secunda</i> J. Presl.)			
POSE-1	Commercial Seed Company	Hardegee et al., 2010	Present Study
POSE-2	Commercial Seed Company	Hardegee et al., 2010	Present Study
Forbs			
Common yarrow (<i>Achillea millefolium</i> L.)			
ACMI-1	Eagle	Rawlins et al., 2012a	Rawlins et al., 2012a
ACMI-2	VNS White	Rawlins et al., 2012a	Rawlins et al., 2012a
Lewis flax (<i>Linum lewisii</i> Pursh)			
LILE	Provo, UT	Rawlins et al., 2012a	Rawlins et al., 2012a
Blue flax (<i>Linum perenne</i> L.)			
LIPE	Appar	Rawlins et al., 2012a	Rawlins et al., 2012a
Longspur lupine (<i>Lupinus arbustus</i> Douglas ex Lindl.)			
LUAR	Wells common garden	Rawlins et al., 2012a	Rawlins et al., 2012a

fixed factors of tree removal methods, tree infilling phase, and microsites of the tree mound perimeter, shrub mound, and interspace. The tree mound perimeter is defined as the extant tree or previous tree drip line, as evidenced by the edge of the tree litter mound. For the woodland experiment, site was a random factor. Seasons were early spring (1 March to 30 April), late spring (1 May to 30 June), and fall (1 September to 30 November), and winter (1 December to 28 February). Because the number of days was uneven for each season, we compared annual PTG for each season separately for all site experiments (Roundy et al., 2014b; Cline et al., 2018). Significant differences among some fixed factors were determined by the Tukey-Kramer multiple comparison test ($P < 0.05$). To compare effects of tree reduction treatment on PTG, we standardized the effects of site soil water potential and temperature by comparing the differences in PTG between treated and untreated plots at each study site. To simplify the presentation of all of our results, and because of the statistical constraints and complexity of analyzing different experiments and fixed, as well as random factors such as site we took a descriptive approach by presenting estimates and standard errors to indicate relative magnitude of PTG as a function of primary and secondary effects. We were most interested in the relative effects of different factors on whether germination was predicted or not than statistical significance of all the various interactions among the different factors.

3. Results

3.1. Season, year, and seedlot effects

Season, year, site, and seedlot all affected PTG for sagebrush and crested wheatgrass sites (Figs. 1–4). Seedbeds summed the highest PTG in early and late spring, less PTG in fall than spring, and least in winter (Figs. 1–4, Table 2). Seedbeds summed enough PTG (≥ 1) to predict 50% germination in spring (74.2–99.2% of cases), and usually in fall (38.3–95.4% of cases) (Table 2). Progress toward germination varied within season by experiment and year, with least PTG for fall in 2009, and least PTG for late spring in 2007 (Fig. 1). Although PTG was generally similar within a season for the non-woodland experiments and sites, PTG was much higher in late spring for the upper elevation than middle and lower elevation sites in the Sagebrush and Perennial Grass-NV-UT experiment (Fig. 2). Percentage of cases when germination was predicted was highest in spring, lower in fall, and least in winter (Table 2). However, these predictions varied by site. For example, some lower elevation sites such as the Nevada crested, Nevada and Utah lower elevation sites, and Utah middle elevation site had a higher percentage of cases (20.4–49.6%) where germination was predicted in winter than did the higher elevation sites (Table 2). Some sites had high germination prediction in fall ($> 75\%$ of cases) while others were much

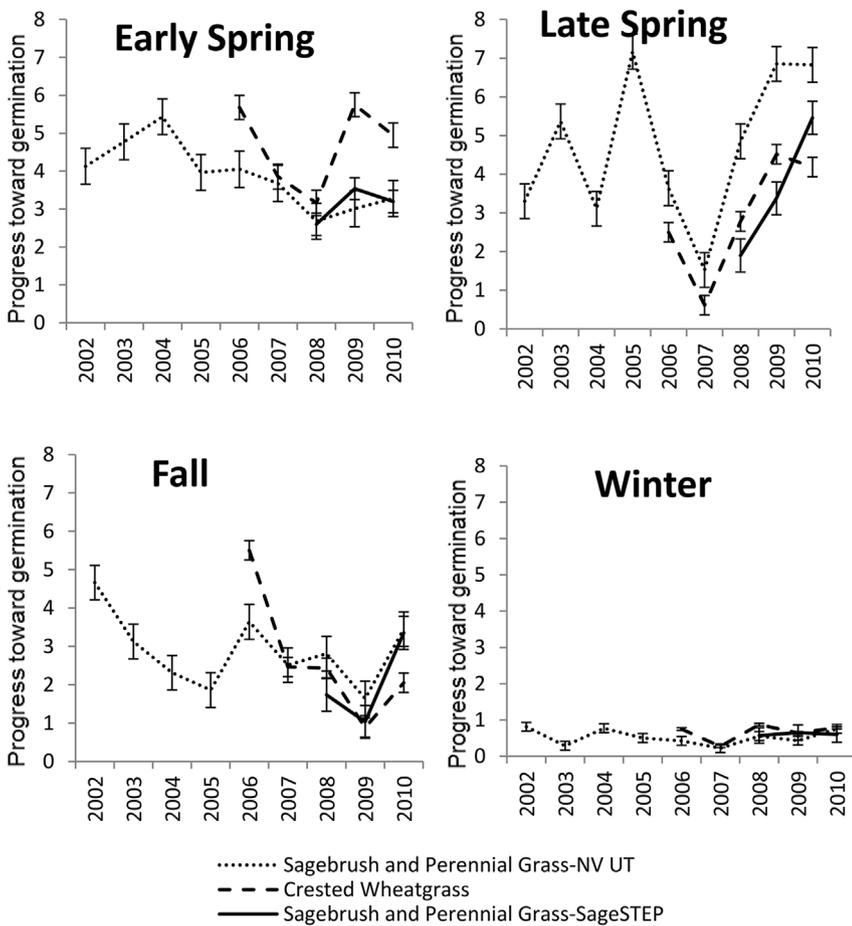


Fig. 1. Annual progress toward germination by season across all seedlots for sagebrush and perennial grass, crested wheatgrass, and sagebrush sites. Error bars are ± 1 standard error of the mean. Seasons were early spring – 1 March to 30 April, late spring – 1 May to 30 June, fall – 1 September to 31 November, and winter – 1 December to 28 February.

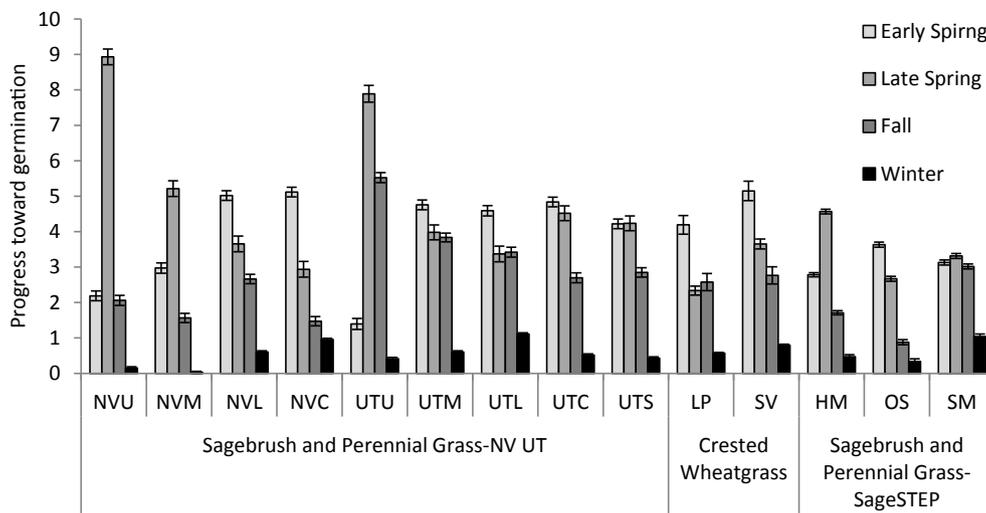


Fig. 2. Seasonal progress toward germination averaged across all seedlots by site and experiment. Error bars are ± 1 standard error of the mean. Seasons were early spring – 1 March to 30 April, late spring – 1 May to 30 June, fall – 1 September to 31 November, and winter – 1 December to 28 February. Sites are NVU = Underdown Canyon High elevation, NVM = Underdown Canyon Middle elevation, NVL = Underdown Canyon Low elevation, UTU = Mill Canyon High elevation, UTM = Black Rock Canyon Middle elevation, UTL = Black Rock Canyon Low elevation, NVC = Barrett Canyon, UTC = Boulter Creek, UTS = Boulter Creek ELEL, HM = Hart Mountain, OS = Onaqui Sagebrush, SM = Saddle Mountain, SV = Skull Valley, LP = Lookout Pass.

lower (< 38.3–64.1% of cases) (Table 2).

Woodland sites also varied in seasonal PTG (Fig. 3, Table 2). As with sites in the crested and sagebrush experiments, woodland sites summed enough PTG to predict germination most often in late spring, less in early spring and fall, and least in winter (Fig. 3, Table 2). Some sites varied substantially in PTG summation and seasonal germination prediction. For example, Bridge Creek and Stansbury summed enough PTG to predict germination in winter in 73.5 and 29.6% of cases, while other sites did so in 2.1–15.8% of cases (Table 2). Some woodland sites summed enough PTG to predict germination in fall (> 81% of cases), but South Ruby did so in only 36.8% of cases (Table 2).

Seedlots varied in PTG across a number of factors, but cheatgrass overall had higher PTG than perennial grasses or forbs, and germination was predicted for most seedlots in all seasons except winter (Fig. 4). Highest PTG was estimated for most seedlots in late spring for the two sagebrush experiments and in early spring for the crested wheatgrass experiment (Fig. 4). For these non-woodland experiments, the seedlot by year interaction was significant ($P < 0.0001$) for half of the season-experiment cases tested. Generally, this interaction was significant more often for fall, winter, and late spring than for early spring. This suggests that not only do these seasons tend to be more variable in meeting germination requirements than early spring, but that species

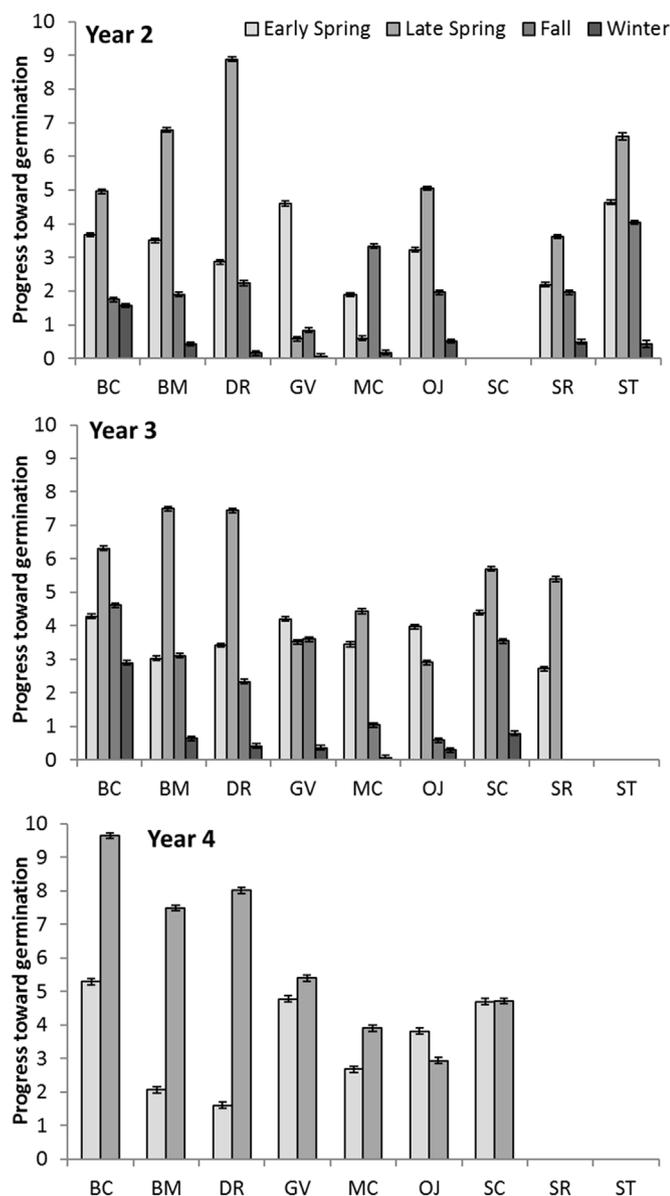


Fig. 3. Seasonal progress toward germination across treated and untreated plots for woodland sites for year 2 (top), year 3 (middle), and year 4 (bottom) since implementation of tree reduction treatments. Data are averages of untreated plots and plots where trees were reduced. Error bars are ± 1 standard error of the mean. Seasons were early spring – 1 March to 30 April, late spring – 1 May to 30 June, fall – 1 September to 31 November, and winter – 1 December to 28 February. Sites are BC – Bridge Creek, OR; BM – Blue Mountain, CA; DR – Devine Ridge, OR; GV – Greenville, UT; MC – Marking Corral, NV; OJ – Onaqui, UT; SC – Scipio, UT; SR – South Ruby, NV; ST – Stansbury, UT.

and seedlots may respond to this variability differently. For the woodland experiment, highest PTG for most seedlots was in early spring (Fig. 4). For woodlands, the seedlot by treatment interaction was most often significant ($P < 0.05$) for early spring when tested separately for each of 4 years since treatment. This seedlot by treatment interaction was significant for two of the four seasons tested for 1, 2, and 3 years since treatment. However, except for early spring, the interaction significance varied with season on a given year since treatment. This interaction demonstrates that some subtle relationships exist among annual and seasonal weather, treatment effects on seedbed microclimate, and germination potential of various species or seedlots.

3.2. Tree removal response

Because of site differences (Fig. 3), we standardized the effects of

site soil water potential and temperature by comparing the differences in PTG between treated and untreated plots at each study site. For this difference analysis, main and interaction effects on additional PTG were generally significant for tree removal methods, tree infilling phase, and microsites through the third year after treatment ($P < 0.05$). Although PTG additions varied by year since treatment, burning consistently added more PTG than cutting for most seasons (Fig. 5). Additions generally diminished with increasing year since treatment. On Utah sites, tree shredding added more PTG than cutting and slightly less than burning. Treatments generally added more PTG in spring, followed by fall, with minimal additions in winter. Implementation of tree reduction at Phase III of woodland infilling generally added more PTG than tree reduction at Phase II while implementation at Phase II generally added more PTG than implementation at Phase I (Fig. 6). In late spring, more PTG was generally added by treatments at the tree mound perimeter than at the shrub perimeter, where more PTG was generally added than in tree and shrub interspaces (Fig. 6).

4. Discussion

The use of soil climate conditions to evaluate potential germination timing in field seedbeds has been limited, but has potential for improved revegetation decision-making (Hardegreer et al., 2010, 2016). Previous studies have investigated aspects of predicting potential germination using thermal time. Roundy et al. (2007) assessed PTG using the wet thermal time model for 18 seedlots of cheatgrass across 4 yr and nine sites in Nevada and Utah. Hardegreer et al. (2008, 2010, 2013) simulated germination rate for multiple species and seedlots using a 38 yr history of soil microclimate data from a site in Idaho. Rawlins et al. (2012a) evaluated PTG for 10 species with soil microclimate data from one site in Nevada. Rawlins et al. (2012b) field verified potential germination response for five species based on soil microclimate conditions at two sites in Utah for 3 yr. Our study evaluated 31 seedlots (11 species) from previous studies (Roundy et al., 2007; Hardegreer et al., 2010; Rawlins et al., 2012a, 2012b). Further, we added several years of soil microclimate data collected at previous study sites (Chambers et al., 2007; Hardegreer et al., 2010; Rawlins et al., 2012b), added three sagebrush sites with the sagebrush and perennial grass-SageSTEP experiment, and added nine sites with the woodland experiment. Our study represents the most comprehensive study to date to investigate potential germination from such a broad range of Great Basin plant materials and site conditions.

For most of the seedlots we tested, germination was predicted in most springs and falls, but few or no winters (Fig. 4). We consider that our predictions are seasonally accurate because most PTG is summed within the temperature range where germination is highly predictable (Cline et al., 2018). However, germination timing is less predictable for cooler temperatures (0 to < 5 °C) which are most prevalent in winter (Cline et al., 2018). Rawlins et al. (2012b) found that wet thermal germination models correctly predicted germination timing in seedbags retrieved from the field 75–95% of the time during late winter to mid-spring. They attributed lower accuracy (50–71%) in fall to early winter to differences in seed and measured soil wet periods, rather than temperature. When their predictions were wrong, it was generally because they overestimated time (estimated no germination when seeds in seedbags had already germinated).

Successful seedling establishment should be associated, in part, with greater time when soil temperatures are warm and wet enough to support germination (Ryel et al., 2010; Roundy et al., 2014b; Cline et al., 2018). Though there was significant variation between sites, seasons, and years, seedbeds summed sufficient thermal time in the fall, early, and late spring to predict germination of 50% of the seed population for most of the seedlots we studied. Our findings are consistent with Roundy et al. (2007) where cheatgrass seedlots were estimated to germinate at the sagebrush and perennial grass-NV UT sites for most years during the fall and spring. Roundy et al. (2007) and our study

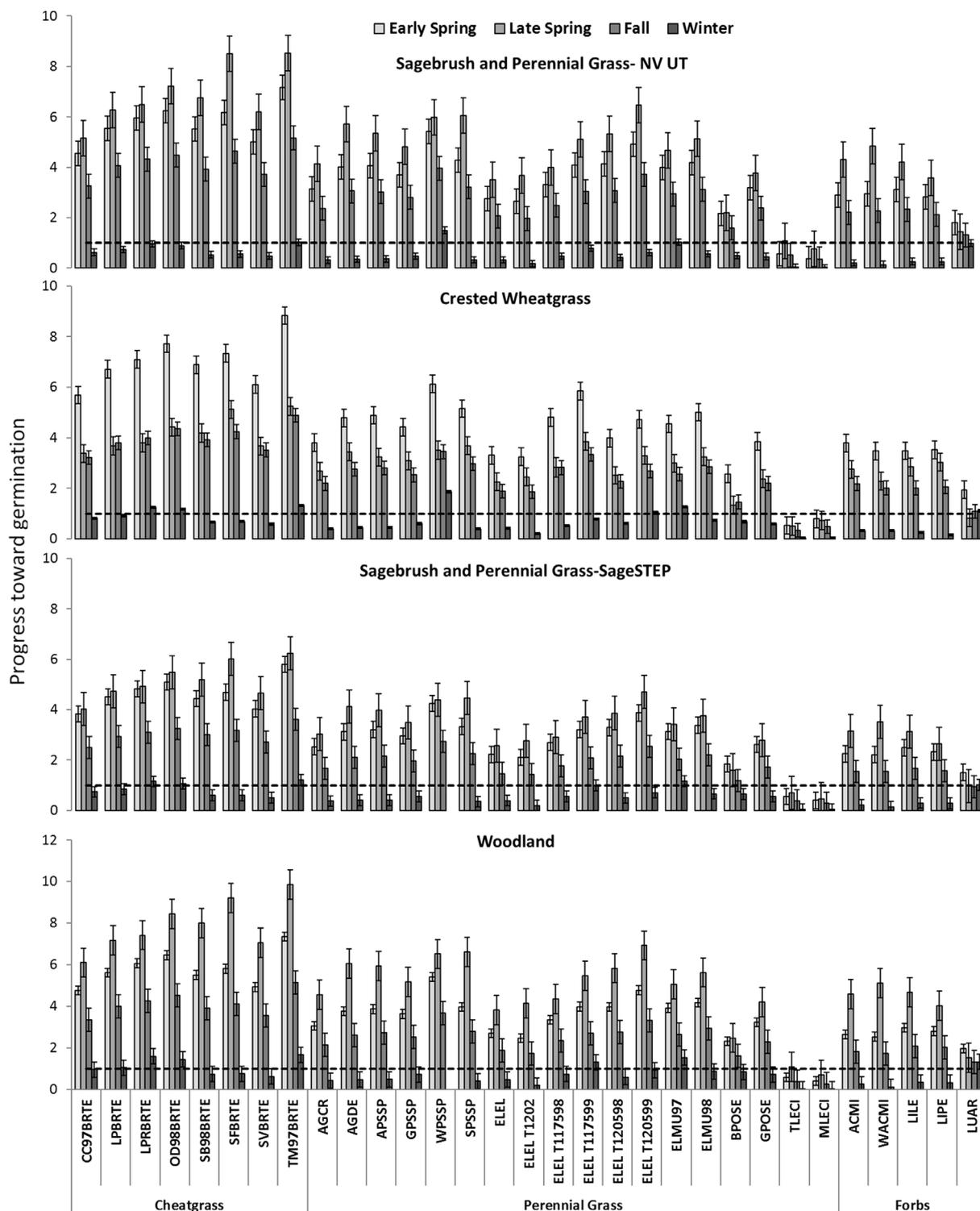


Fig. 4. Seasonal progress toward germination by seedlot and plant functional group, averaged across all sites for four experiments. Woodland includes treated and untreated sites. Error bars are ± 1 standard error of the mean. Seasons were early spring – 1 March to 30 April, late spring – 1 May to 30 June, fall – 1 September to 31 November, and winter – 1 December to 28 February. See Table 2 for species codes. Dashed horizontal line indicates a progress toward germination of 1 where at least 50% of seeds are predicted to germinate.

confirm findings of James et al. (2011) who suggest that germination does not generally limit plant establishment on Great Basin sagebrush communities on most years during the fall and spring.

Wet thermal germination models may be useful in determining seed coating treatments or optimal sowing conditions to increase post-germination survival of seedlings, as well as which plant materials are most likely to establish under specific soil moisture-temperature conditions (Madsen et al., 2012; Roundy and Madsen, 2016). Mortality in

perennial grass seedlings examined for arid grassland restoration may occur before emergence (James et al., 2011). Wilson and Briske (1979) found that seedling survival in blue grama (*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths) was greatest when adventitious root growth had successfully begun before soils dried in the summer and the next winter freeze. Boyd and Lemos (2013) found increased mortality in perennial grasses if freezing occurred during the seminal root phase of root development. These studies suggest that seedling survival increases

Table 2

Percentages of PTG estimations (SE) for seasons and sites where seedbeds accumulated enough PTG to sum to ≥ 1 . Percentages are calculated from all years measured for non-woodland sites and from all years, treatments, infilling phases, and microsites measured for woodland sites. Sites are BC = Bridge Creek, OR; BM = Blue Mountain, CA; DR = Devine Ridge, OR; GV = Greenville, UT; Marking Corral, NV; OJ = Onaqui Woodland, UT; SC = Scipio, UT; SR = South Ruby, NV; NVU = Underdown Canyon High elevation, NV; NVM = Underdown Canyon Middle elevation, NV; NVL = Underdown Canyon Low elevation, NV; UTU = Mill Canyon High elevation, UT; UTM = Black Rock Canyon Middle elevation, UT; UTL = Black Rock Canyon Low elevation, NV; NVC = Barrett Canyon, NV; UTC = Boulter Creek, UT; UTS = Boulter Creek ELEM, UT; HM = Hart Mountain, OR; OS = Onaqui Sagebrush, UT, SM = Saddle Mountain, WA; SV = Skull Valley, UT; LP = Lookout Pass, UT.

Experimental Design	Sites	Fall	Winter	Spring	Early	Late
					Spring	Spring
Sagebrush & Perennial Grass	NVC	38.3 (15.7)	38.4 (12.7)	99.2 (11.7)	94.6 (0.5)	87.5 (10.9)
	NVU	74.7 (15.5)	2.8 (1.8)	99.6 (11.7)	83.5 (5)	99.2 (11.7)
	NVM	50.4 (16.6)	0.8 (0.7)	95.6 (11.5)	90.3 (10.8)	91.5 (11.1)
	NVL	79 (14.2)	20.4 (5.7)	97.2 (11.6)	92.8 (1.6)	87.1 (11)
	UTC	82.9 (15.1)	13.3 (6.4)	98.2 (0.9)	94.6 (1.1)	73.5 (13.7)
	UTU	95.4 (15.9)	14.7 (5.1)	98.6 (16.5)	63.2 (14.1)	98.2 (16.4)
	UTM	93.9 (0.6)	22.2 (9.1)	98.6 (0.8)	94.3 (0.5)	86 (5.4)
	UTL	89.9 (15.1)	49.6 (11.3)	96 (11.5)	92.7 (11.1)	67.3 (15.1)
	UTS	83.5 (11.2)	8.9 (3.2)	97.1 (1.5)	89.6 (3.7)	81 (10.5)
	LP	76.3 (17.8)	16.3 (3.7)	95.6 (1.9)	93.5 (0.2)	83.4 (8.2)
Crested Wheatgrass	SV	79.9 (17.7)	32.3 (10.3)	98.4 (0.9)	94.9 (0.4)	94.7 (17.4)
	HM	46.6 (17.9)	20.9 (6.5)	80.5 (17.3)	70.4 (15.3)	76.7 (17.8)
Sagebrush	OS	41.6 (14.9)	5.7 (1.3)	78.7 (16.9)	74.2 (14.9)	69.7 (16.8)
	SM	64.1 (20)	35.5 (11.7)	92.6 (20.6)	85.6 (19.6)	65.1 (18.9)
Woodlands	BC	87.6 (3.8)	73.5 (4.6)	99.5 (0.1)	99.1 (0.6)	95.9 (1.3)
	BM	86.2 (2.2)	14.2 (2.6)	98.8 (0.4)	84.5 (3)	96.8 (0.6)
	DR	81.3 (7.8)	8.9 (2.9)	98.6 (0.7)	85.8 (4.8)	95.4 (2.5)
	GV	56.8 (17)	7.1 (3.8)	85.3 (10.9)	82.1 (10.4)	54.8 (15.8)
	MC	70.1 (12.7)	2.1 (1.4)	91.7 (3.3)	84.3 (3.1)	71 (14.9)
	OJ	61.7 (14.7)	13.1 (4.6)	95.1 (2.6)	87.8 (3)	77.1 (12.9)
	SC	86.4 (2.4)	15.8 (4.5)	97.5 (0.5)	91 (0.7)	90 (2.3)
	SR	36.8 (14.6)	5.9 (3.7)	95.5 (0.9)	88.2 (1.3)	86.6 (3)
	ST	90.7 (1.3)	29.6 (8.7)	98.4 (0.9)	91 (0.9)	93.1 (2.9)

if germination timing allows for roots to extend into deeper soils ahead of the soil drying front during the late spring and summer, but also increases when timing allows for seedlings to avoid frost periods (Roundy and Madsen, 2016). While seedbeds in our study generally summed more than enough PTG for potential germination during either early or late spring for most seedlots, there were some interesting interactions in seasonal germination for different sites (Figs. 2–4). For example, high PTG was predicted for Bridge Creek in winter and limited germination was predicted for South Ruby in fall (Table 2). Seasonal site differences may account for some of the differences in revegetation success. Examples of differences in seedlots are basin wildrye (*Leymus cinereus* (Scribn. & Merr.) Á. Löve) and lupine (*Lupinus arbustus* Douglas ex Lindl.). These species required the entire spring to sum sufficient PTG to germinate if planting date was on 1 March. Basin wildrye emerged much better under water additions from irrigation than with natural rainfall at a semi-arid site in Nevada (Roundy, 1985). Extending the germination period in spring by irrigation may have allowed basin wildrye to sum more PTG. Delayed germination could limit seedling survival for some species if seminal root extension is insufficient for root contact with wet soils ahead of the soil drying front (Roundy et al., 1997). However, seed treatments which delay germination until after freezing could also help avoid frost mortality for many species (Roundy and Madsen, 2016). Drought and climate change potentially decrease spring wet periods and increase freeze – thaw cycles (Abatzoglou and Kolden, 2011). Germination delay to avoid freezing mortality must be timed to also avoid seedling mortality due to desiccation as soils dry out in spring. Species with inherently delayed germination may only successfully establish in areas and on years when available soil water is extended.

Germination prediction may be useful in relating seeding potential to specific environmental conditions. Winter precipitation would be expected to play a critical role in extending the period of available water for root growth in the spring. Cline (2014) found that winter precipitation was highly correlated with increased wet degree days for early spring. We found that spring had the most PTG in comparison

with other seasons. Snow melt supports soil water recharge at deeper soil depths (Campbell and Harris, 1977) while snow insulates the soil surface and seeds from freeze – thaw cycling (Hardy et al., 2001). Insulation of the soil surface delays germination by keeping seeds cool when soils are likely to freeze and thaw too frequently (Milbau et al., 2009). Soil temperature and moisture should be measured in relation to seed germination and seedling demography studies to better understand how environmental conditions affect plant establishment. Wet thermal prediction of germination timing can play a key role in these studies by indicating when seedlings are exposed to specific environmental conditions.

4.1. Tree reduction response

Tree reduction treatments may increase cheatgrass cover by liberating previously unavailable resources along a tree cover phase gradient. Utah juniper reduction increased inorganic N fivefold (Young et al., 2014). Percent cheatgrass cover increased with increasing pre-treatment woodland infilling phase by the third and 6th years post treatment (Roundy et al., 2014a; Williams et al., 2017). Bates et al. (2014) found that cheatgrass replaced native plants after fire burned a dense western juniper woodland. Cline (2014) found an increase in wet degree days with treatment and increasing infilling phase at temperature ranges between 5 °C and 25 °C where the majority of PTG is summed. We found that tree reduction added PTG for all 31-plant materials, including cheatgrass. We also found that implementing tree reduction at infilling phase III added more PTG than implementation at lower infilling phases. While effects of woodland reduction on increasing time of available resources may be expected to diminish over time as residual understory plants grow and transpire, Roundy et al. (2014b) and Cline (2014), reported that these effects extend at least to the fourth spring since treatment.

Because tree reduction treatments provide a pulse of plant available resources in the soil, residual vegetation or seedbank should be expected to manifest an increase in vegetation cover. Miller et al. (2014)

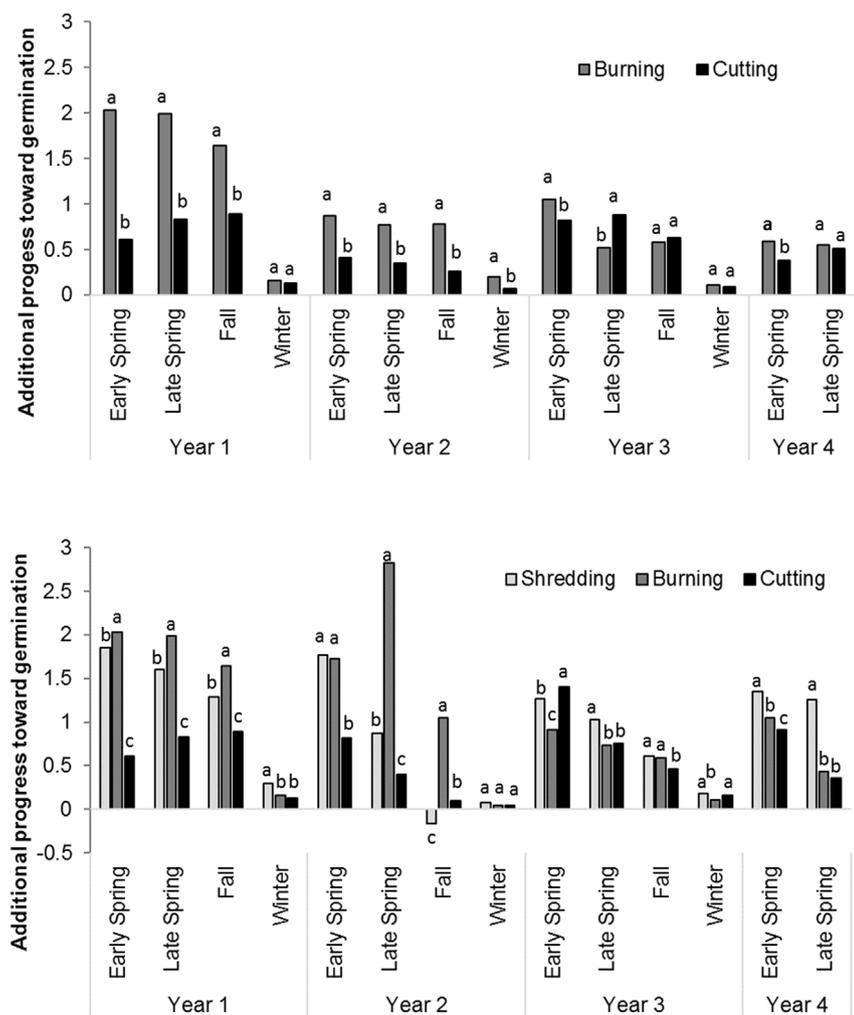


Fig. 5. Additional progress toward germination for tree removal methods by season averaged across all woodland sites (top) and Utah woodland sites (bottom) by season and year since treatment. Different letters indicate significant differences within a season ($P < 0.05$).

indicated that postburn understory vegetation recovered and surpassed preburn cover percentages by the second or third year following tree reduction treatments of wooded sagebrush lands. They also noted that perennial grass cover increased during the second year and exceeded pretreatment cover by the third year following mechanical treatments. This ongoing increase in perennial grass cover is a response to continued availability of resources resulting from treatment. However, Miller et al. (2014) noted that the increase in perennial grass cover came primarily from residual plant growth and not from new seedlings. Initially low seedling density following treatment may result from tree exclusion of understory plants and reduction of propagules. As trees infill, they decrease soil water availability for understory shrubs and herbs, which then decrease in cover and density (Miller et al., 2014; Roundy et al., 2014b). The added wet days and degree days from reducing trees (Young et al., 2013) increases PTG and improves the likelihood of germination and subsequent establishment. Seeding desirable plant materials in association with tree removal may be needed to accomplish restoration goals where desirable residual propagules are limited (Bybee et al., 2016).

Prescribed burning added more wet degree days in the seedbed than tree cutting during the spring (Cline et al., 2018). Yet we found that burning resulted in twice the additional PTG as tree cutting in comparison to untreated plots during every season at least up to the second year after treatment. By the fourth year after treatment, prescribed burn seedbeds had more additional PTG than those in cut treatments only in early spring. Tree shredding produced an intermediate effect between burning and tree cutting. During the second and into the third year shredding response varied in comparison to other treatments. By late

spring of the third year and into fourth year, shredding added more additional PTG than both burning and tree cutting (Fig. 5). Shredding reduces runoff from hill slopes and adds wet degree days to seedbeds (Cline et al., 2010, 2018). It is likely that decomposition of shredded material requires many years, leaving the soil covered and limiting plant growth where debris is deep (Young et al., 2013).

We found more PTG added by tree reduction treatments at the tree mound perimeter compared to shrub mound perimeter and interspace microsites during late spring (Fig. 6). Also, Roundy et al. (2014b) reported that tree reduction increased wet days more at the tree mound perimeter than at other microsites at 18–30 cm soil depth. Tree mounds are often covered by a litter and duff layer. Litter and duff layers likely act similar to shredded material in trapping soil moisture and increasing wet degree days in the seedbed (Cline et al., 2010, 2018; Young et al., 2013). Also, piñon and juniper tree structure filters water away from its trunk to the tree mound perimeter. Interspace microsites have been found to dry more rapidly than tree mounds (Breshears et al., 1998). In the current study, we measured soil water and temperature only on tree mound edge, interspace, and shrub mound edge microsites. In a detailed study of effects of tree shredding on soil microclimate at phase III infilling, Young et al. (2013) found that tree reduction increased soil water availability and temperature. Soil cover from shredded debris or litter also increased these factors, but to a lesser degree than tree removal. Presumably by reducing transpiration soil water loss and interception of precipitation, tree reduction increases time of available soil water more under tree litter or shredded debris than in interspaces. The increase in soil resources results in greater seeded grass seedling biomass in comparison to interspaces (Young

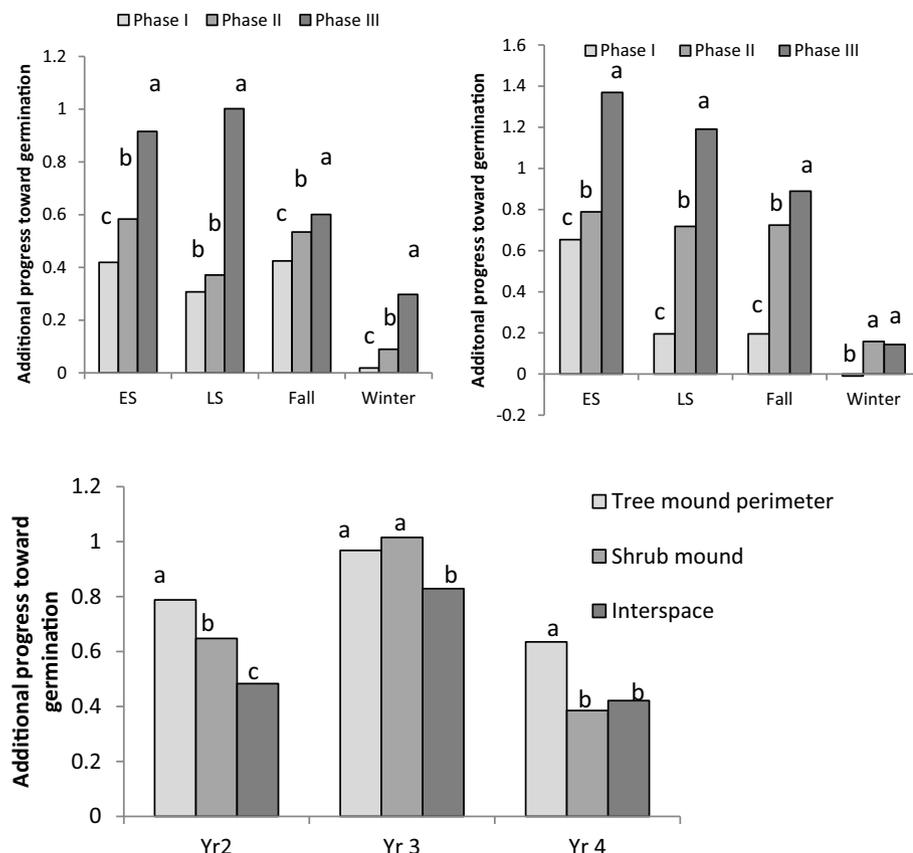


Fig. 6. Additional progress toward germination for tree reduction treatments implemented at different phases of tree infilling for the second (top left) and third (top right) year since treatment by season, averaged across all woodland sites. ES and LS = early and late spring. Additional progress toward germination for microsites by year since tree reduction treatment for late spring (1 May to 30 June) averaged across all woodland sites and tree reduction treatments (bottom). Different letters indicate significant differences within a season and year ($P < 0.05$).

et al., 2013).

4.2. Site potential and resistance to cheatgrass

Perennial herbaceous cover has been identified as an indicator of resilience to disturbance and resistance to cheatgrass invasion (Chambers et al., 2014; Pyke et al., 2014). Others have found that perennial herbaceous cover > 20% limits cheatgrass (Bybee et al., 2016; Chambers et al., 2014).

Hardegree et al. (2010), Rawlins et al. (2012a), and our study indicate that cheatgrass should germinate faster and earlier than many perennial grasses at cooler early spring temperatures. The ability to germinate at cooler temperatures when soils are wet on warmer and dryer sites may provide an advantage over revegetation species that require wet soil conditions at warmer temperatures to sum sufficient PTG for germination. Cheatgrass seedlings also have a higher nitrogen absorption rate compared to some common revegetation plant materials (e.g. *E. elymoides*, and *P. spicatum*) (Leffler et al., 2011) at temperature ranges (10–25 °C) where wet degree days are highest in the seedbed (Cline et al., 2018). Higher N absorption rates at warmer temperatures in the fall may allow cheatgrass to extend roots and preempt soil water in the spring (Leffler et al., 2011). Cheatgrass's head start may mean that soil water (Harris and Wilson, 1970) and soil inorganic nitrogen resources may become depleted at warmer and dryer sites before some revegetation plant materials can germinate and extend their roots to a sufficient depth (Leffler et al., 2011, 2013).

5. Conclusions

Development and use of wet thermal time regressions for a large number of species and seedlots provided an opportunity to predict timing of potential germination over a large network of sites where soil microclimate was measured over several years. Germination of at least

50% of the seed population was predicted to occur for most plant materials in the spring and fall, but highest PTG was predicted in the spring. While significant variation among sites, years, and tree removal treatments was found, these factors rarely influenced whether at least 50% germination will occur over the course of a season. Variation in these factors may influence germination timing, subsequent root growth timing, and probability for seedling establishment. Estimation of germination timing in conjunction with root growth timing may be used as a tool for plant material selection, characterization of site potential, and evaluation of effects of seedbed modification and additives to improve seedling survival.

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References

Abatzoglou, J.T., Kolden, C.A., 2011. Climate change in western US deserts: potential for increased wildfire and invasive annual grasses. *Rangel. Ecol. Manage.* 64, 471–478.
 Bates, J.D., Sharp, R.N., Davies, K.W., 2014. Sagebrush steppe recovery after fire varies by development phase of *Juniperus occidentalis* woodland. *Int. J. Wildland Fire* 23, 117–130.
 Boyd, C.S., Lemos, J.A., 2013. Freezing stress influences emergence of germinated perennial grass seeds. *Rangel. Ecol. Manage.* 66, 136–142.
 Breshears, D.D., Nyhan, J.W., Heil, C.E., Wilcox, B.P., 1998. Effects of woody plants on microclimate in a semi-arid woodland: soil temperature and evaporation in canopy and intercanopy patches. *Int. J. Plant Sci.* 159, 1010.
 Bybee, J., Roundy, B., Young, K., Hulet, A., Roundy, D., Crook, L., Aanderud, Z., Eggett, D., Cline, N., 2016. Vegetation response to piñon and juniper tree shredding. *Rangel. Ecol. Manage.* 69, 224–234.
 Caldwell, M.M., 1985. Cold desert. In: Chabot, H. A., B.F. (Ed.), Mooney (EDS.) *Physiological Ecology of North American Plant Communities*. Chapman & Hall, New

- York, pp. 198–212.
- Call, C.A., Roundy, B.A., 1991. Perspectives and processes in revegetation of arid and semiarid rangelands. *J. Range Manage.* 44, 543–549.
- Campbell, M.M., Harris, G.A., 1977. Water relations and water use patterns for *Artemisia tridentata* Nutt. In wet and dry years. *Ecology* 58, 652–659.
- Cantón, Y., Solé-Benet, A., Domingo, F., 2004. Temporal and spatial patterns of soil moisture in semiarid badlands of SE Spain. *J. Hydrol.* 285, 199–214.
- Chambers, J., Bradley, B., Brown, C., D'Antonio, C., Germino, M., Grace, J., Hardegee, S., Miller, R., Pyke, D., 2014. Resilience to stress and disturbance and resistance to *Bromus tectorum* L. invasion in cold desert shrublands of Western North America. *Ecosystems* 17, 360–375.
- Chambers, J.C., Roundy, B.A., Blank, R.R., Meyer, S.E., Whittaker, A., 2007. What makes Great Basin sagebrush ecosystems invulnerable to *Bromus tectorum*? *Ecol. Monogr.* 77, 117–145.
- Cline, N.L., 2014. Wet-thermal Time and Plant Available Water in Seedbeds and Root Zones across the Sagebrush Steppe Ecosystem. PhD. Dissertation. Brigham Young University, Provo, Utah, USA, pp. 139.
- Cline, N.L., Roundy, B.A., Christensen, W.F., 2018. Soil temperature and plant available water in the Great Basin: I. Temperature range validation of germination prediction models. *J. Arid. Environ.*
- Cline, N., Roundy, B., Pierson, F., Kormos, P., Williams, C.J., 2010. Hydrologic response to mechanical shredding in a juniper woodland. *Rangel. Ecol. Manage.* 63, 467–477.
- Condon, L., Weisberg, P., Chambers, J., 2011. Abiotic and biotic influences on *Bromus tectorum* invasion and *Artemisia tridentata* recovery after fire. *Int. J. Wildland Fire* 20, 597–604.
- Donovan, L.A., Ehleringer, J.R., 1994. Water stress and use of summer precipitation in a Great Basin shrub community. *Funct. Ecol.* 8, 289–297.
- Finch-Savage, W.E., Phelps, K., Steckel, J.R.A., Whalley, W.R., Rowse, H.R., 2001. Seed reserve-dependent growth responses to temperature and water potential in carrot (*Daucus carota* L.). *J. Exp. Bot.* 52, 2187–2197.
- Hardegee, S.P., Jones, T.A., Pierson, F.B., Clark, P.E., Flerchinger, G.N., 2008. Dynamic variability in thermal-germination response of squirreltail (*Elymus elymoides* and *Elymus multisetus*). *Environ. Exp. Bot.* 62, 120–128.
- Hardegee, S.P., Jones, T.A., Roundy, B.A., Shaw, N.L., Monaco, T.A., 2016. Assessment of range planting as a conservation practice. *Rangel. Ecol. Manage.* 69, 237–247.
- Hardegee, S.P., Moffet, C.A., Roundy, B.A., Jones, T.A., Novak, S.J., Clark, P.E., Pierson, F.B., Flerchinger, G.N., 2010. A comparison of cumulative-germination response of cheatgrass (*Bromus tectorum* L.) and five perennial bunchgrass species to simulated field-temperature regimes. *Environ. Exp. Bot.* 69, 320–327.
- Hardegee, S.P., Moffet, C.A., Flerchinger, G.N., Cho, J., Roundy, B.A., Jones, T.A., James, J.J., Clark, P.E., Pierson, F.B., 2013. Hydrothermal assessment of temporal variability in seedbed microclimate. *Rangel. Ecol. Manage.* 66, 127–135.
- Hardegee, S.P., Van Vactor, S.S., 2000. Germination and emergence of primed grass seeds under field and simulated-field temperature regimes. *Ann. Bot.* 85, 379–390.
- Hardegee, S.P., Van Vactor, S.S., Pierson, F.B., Palmquist, D.E., 1999. Predicting variable-temperature response of non-dormant seeds from constant-temperature germination data. *J. Range Manage.* 52, 83–91.
- Hardy, J.P., Groffman, P.M., Fitzhugh, R.D., Henry, K.S., Welman, A.T., Demers, J.D., Fahey, T.J., Driscoll, C.T., Tierney, G.L., Nolan, S., 2001. No title. *Biogeochemistry* 56, 151–174. <http://dx.doi.org/10.1023/a:1013036803050>.
- Harris, G.A., Wilson, A.M., 1970. Competition for moisture among seedlings of annual and perennial grasses as influenced by root elongation at low temperature. *Ecology* 41 (530), 534.
- Hulet, A., Roundy, B.A., Jessop, B., 2010. Crested wheatgrass control and native plant establishment in Utah. *Rangeland Ecol. Manage.* 63, 450–460.
- James, J.J., Svejcar, T.J., Rinella, M.J., 2011. Demographic processes limiting seedling recruitment in arid grassland restoration. *J. Appl. Ecol.* 48, 961–969.
- Knutson, K.C., Pyke, D.A., Wirth, T.A., Arkle, R.S., Pilliod, D.S., Brooks, M.L., Chambers, J.C., Grace, J.B., 2014. Long-term effects of seeding after wildfire on vegetation in Great Basin shrubland ecosystems. *J. Appl. Ecol.* 51, 1414–1424.
- Leffler, A.J., James, J.J., Monaco, T.A., 2013. Temperature and functional traits influence differences in nitrogen uptake capacity between native and invasive grasses. *Oecologia* 171, 51–60.
- Leffler, A.J., Monaco, T.A., James, J.J., 2011. Nitrogen acquisition by annual and perennial grass seedlings: testing the roles of performance and plasticity to explain plant invasion. *Plant Ecol.* 212, 1601–1611.
- Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., Shabenberger, O., 2006. SAS[®] for mixed models, second ed. SAS Institute, Inc., Cary, NC, USA, pp. 813.
- Madsen, M.D., Davies, K.W., Williams, C.J., Svejcar, T.J., 2012. Agglomerating seeds to enhance native seedlings emergence and growth. *J. Appl. Ecol.* 49, 431–438.
- Mclver, J., Brunson, M., Bunting, S., Chambers, J., Devoe, N., Doescher, P., Grace, J., Johnson, D., Knick, S., Miller, R., Pellant, M., Pierson, F., Pyke, D., Rollins, K., Roundy, B., Schupp, E., Tausch, R., Turner, D., 2010. The Sagebrush Steppe Treatment Evaluation Project (SageSTEP): a Test of State-and-transition Theory. Page 16. USDA Forest Service RMRS-GTR-237. Ft. Collins, CO, USA.
- Milbau, A., Graae, B.J., Shevtsova, A., Nijs, I., 2009. Effects of a warmer climate on seed germination in the subarctic. *Ann. Bot.* 104, 287–296.
- Miller, R.F., Bates, J.D., Svejcar, T.J., Pierson, F.B., Edleman, L.E., 2005. Biology, Ecology, and Management of Western Juniper (*Juniperus occidentalis*). Technical Bulletin 152. Oregon State University, Corvallis, OR, USA, pp. 82.
- Miller, R.F., Bates, J.D., Svejcar, T.J., Pierson, F.B., Edleman, L.E., 2007. Western Juniper Field Guide: Asking the Right Questions to Select Appropriate Management Actions. U.S. Geological Survey Circular 1321. pp. 26.
- Miller, R.F., Seufert, J., Roundy, B.A., Tausch, R.J., Pereira, C., Hulet, A., Chambers, J.C., 2014. Short-term response of woodlands in the Intermountain West to prescribed fire and mechanical treatments. *Rangel. Ecol. Manage.* 67, 468–481.
- Pyke, D.A., Shaff, S.E., Lindgren, A.I., Schupp, E.W., Doescher, P.S., Chambers, J.C., Burnham, J.S., Huso, M.M., 2014. Region-wide ecological responses of arid Wyoming big sagebrush communities to fuel treatments. *Rangel. Ecol. Manage.* 67, 455–467.
- Rawlins, J.K., Roundy, B.A., Davis, S.M., Egget, D., 2012a. Predicting germination in semi-arid wildland seedbeds. I. Thermal germination models. *Environ. Exp. Bot.* 76, 60–67.
- Rawlins, J.K., Roundy, B.A., Egget, D., Cline, N.L., 2012b. Predicting germination in semi-arid wildland seedbeds II. Field validation of wet thermal-time models. *Environ. Exp. Bot.* 76, 68–73.
- Roundy, B.A., 1985. Emergence and establishment of basin wildrye and tall wheatgrass in relation to moisture and salinity. *J. Range Manage.* 38, 126–131.
- Roundy, B.A., Call, C.A., 1988. Revegetation of arid and semiarid rangelands. In: Tueller, P.T. (Ed.), *Vegetation Science Applications for Rangeland Analysis and Management*. Kluwer Academic, Dordrecht, The Netherlands, pp. 607–635.
- Roundy, B.A., Biedenbender, S.H., 1996. Germination of warm-season grasses under constant and dynamic temperatures. *J. Range Manage.* 49, 425–431.
- Roundy, B.A., Abbott, L.B., Livingston, M., 1997. Surface soil water loss after summer rainfall in a semidesert grassland. *Arid. Soil Res. Manage.* 11, 145–158.
- Roundy, B.A., Hardegee, S.P., Chambers, J.C., Whittaker, A., 2007. Prediction of cheatgrass field germination potential using wet thermal accumulation. *Rangel. Ecol. Manage.* 60, 613–623.
- Roundy, B.A., Miller, R.F., Tausch, R.J., Young, K., Hulet, A., Rau, B., Jessop, B., Chambers, J.C., Eggett, D., 2014a. Understorey cover responses to piñon-juniper control across tree cover gradients in the Great Basin. *Rangel. Ecol. Manage.* 67, 482–494.
- Roundy, B.A., Young, K., Cline, N., Hulet, A., Miller, R.F., Tausch, R.J., Chambers, J.C., Rau, B., 2014b. Piñon-juniper reduction effects on soil temperature and water availability of the resource growth pool. *Rangel. Ecol. Manage.* 67, 495–505.
- Roundy, B.A., Madsen, M.D., 2016. Frost dynamics of sagebrush steppe soils. *Soil Sci. Soc. Am. J.* 80, 1403–1410.
- Ryel, R.J., Leffler, A.J., Ivans, C., Peek, M.S., Caldwell, M.M., 2010. Functional differences in water-use patterns of contrasting life forms in Great Basin steppelands. *Vadose Zone J.* 9, 548–560.
- Weisberg, P.J., Lingua, E., Pillai, R.B., 2007. Spatial patterns of piñon-juniper expansion in Central Nevada. *Rangel. Ecol. Manage.* 60, 115–124.
- Williams, R.E., Roundy, B.A., Hulet, A., Miller, R.F., Tausch, R.J., Chambers, J.C., Matthews, J., Schooley, R., Eggett, D., 2017. Pretreatment tree dominance and conifer removal treatments affect plant succession in sagebrush communities. *Rangel. Ecol. Manage.* 70, 759–773.
- Wilson, A.M., Briske, D.D., 1979. Seminal and adventitious root growth of blue grama seedlings on the Central Plains. *J. Range Manage.* 32, 209–213.
- Whisenant, S.G., 1999. *Repairing Damaged Wildlands: a Process Orientated, Landscape-scale Approach*. Cambridge University Press, New York, New York, USA, pp. 130–132.
- Young, K.R., Roundy, B.A., Eggett, D.L., 2013. Tree reduction and debris from mastication of Utah juniper alter the soil climate in sagebrush steppe. *For. Ecol. Manage.* 310, 777–785.
- Young, K.R., Roundy, B.A., Eggett, D.L., 2014. Mechanical mastication of Utah juniper encroaching sagebrush steppe increases inorganic soil N. *Appl. Environ. Soil Sci.* 2014, 10. <https://doi.org/10.1155/2014/632757>, 632757.