



Theses and Dissertations

2014-03-01

Wet-Thermal Time and Plant Available Water in the Seedbeds and Root Zones Across the Sagebrush Steppe Ecosystem of the Great Basin

Nathan Lyle Cline
Brigham Young University - Provo

Follow this and additional works at: <https://scholarsarchive.byu.edu/etd>



Part of the [Animal Sciences Commons](#)

BYU ScholarsArchive Citation

Cline, Nathan Lyle, "Wet-Thermal Time and Plant Available Water in the Seedbeds and Root Zones Across the Sagebrush Steppe Ecosystem of the Great Basin" (2014). *Theses and Dissertations*. 4384.
<https://scholarsarchive.byu.edu/etd/4384>

This Dissertation is brought to you for free and open access by BYU ScholarsArchive. It has been accepted for inclusion in Theses and Dissertations by an authorized administrator of BYU ScholarsArchive. For more information, please contact scholarsarchive@byu.edu, ellen_amatangelo@byu.edu.

Wet-Thermal Time and Plant Available Water in the Seedbeds
and Root Zones Across the Sagebrush Steppe Ecosystem
of the Great Basin

Nathan L. Cline

A dissertation submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirements for the degree of
Doctor of Philosophy

Bruce A. Roundy, Chair
Richard Gill
Stuart Hardegree
Bryan Hopkins
Samuel St.Clair

Department of Plant and Wildlife Sciences
Brigham Young University

March 2014

Copyright © 2014 Nathan L. Cline

All Rights Reserved

ABSTRACT

Wet-Thermal Time and Plant Available Water in the Seedbeds and Root Zones Across the Sagebrush Steppe Ecosystem of the Great Basin

Nathan L. Cline
Department of Plant and Wildlife Sciences, BYU
Doctor of Philosophy

Following wildfires, plant materials are direct-seeded to limit erosion and annual weed invasion. Seedlings often fail to establish because selected plant materials are not always well adapted to local soil moisture and temperature conditions. In an effort to help improve plant materials selection and to evaluate sites potential revegetation, we have worked toward developing methodology to predict germination and root growth based on site specific soil moisture and temperature conditions. First, we characterized the seedbed environment of 24 sagebrush (*Artemisia* spp.) steppe sites throughout the Intermountain West to determine the wet-thermal time of five temperature ranges relevant to germination response and thermal-time model accuracy (Chapter 1). Second, we predicted potential germination for 31 plant materials at those same sites (Chapter 2). Third, in preparation to predict root growth at multiple sites, we characterized the drying patterns and the associated plant-available water for in the seedling root zone across nine woodland (*Juniperus* spp. and *Pinus* spp.) sites (Chapter 3). For all of these studies, we determined the effects of tree reduction and tree infilling phase at time of tree reduction. Our key findings are that seedbeds generally sum most wet-thermal time at temperature ranges where the germination rates fit thermal accumulation models quite well ($R^2 \geq 0.7$). The majority of plant materials summed enough wet-thermal time for a potential germination at most sites during the fall, early spring, and late spring. Soil drying primarily occurs from the soil surface downward. Drying rates and Plant available water associated with the first drying event increase with increasing soil depth. Root zone (1-30 cm) plant-available water increases before and decreases after the first spring drying event with increasing soil depth. Tree removal with increasing pretreatment tree infilling phase generally added progress toward germination, plant available water, and wet-thermal time in the seedbed and root zones of the sagebrush steppe in the Great Basin. Because soil moisture and temperature does not appear to be limiting for potential germination, combining germination and root growth models to create a more comprehensive model may allow for a more robust prediction for seedling survival. For either root growth or combined germination and root growth models, plant available water and wet-thermal time before the first spring drying period hold the most potential for successfully predicting seedling survival.

Keywords: thermal time, germination, root growth, soil temperature, soil moisture, tree cutting, prescribed fire, mechanical shredding, SageSTEP, cheatgrass, wet days, wet degree days, woodland, seedbed

ACKNOWLEDGEMENTS

I express sincere appreciation to Dr. Bruce Roundy for providing the opportunity to conduct and report on my doctoral research. I am sincerely grateful to him and my advisory committee for their suggestions, support, and encouragement. I also express appreciation to my dear wife Hyla and my children, Elizabeth and Charles, who sacrificed so much as I completed this project. I would also like to thank Hyla and my father, Morris Cline, for reviewing the early drafts of this dissertation. I appreciate the use of the data provided by the SageSTEP project and funding provided by The Great Basin Plant Project. Finally and perhaps most importantly, I would like to thank God, our Father, and his Son, Jesus Christ, for ultimately making this experience possible.

TABLE OF CONTENTS

Title Page	i
Abstract	ii
Acknowledgements	iii
Table of Contents	iv
List of Tables	viii
List of figures	x
Chapter 1: Wet Thermal Time at Five Temperature Ranges in Seedbeds of the Sagebrush Steppe Ecosystem	
Abstract	2
Introduction	4
Methods	7
Study Sites	7
Experimental Design and Analysis	7
Results	11
Sites Characteristics	11
Temperature Range Distribution and Variation for Sagebrush and Perennial grass, Sagebrush, and Crested Wheatgrass Sites	11
Woodland Removal Response	12
Additional Wet-Degree Days in Response to Woodland Tree Removal Treatments and Infilling Phases	13

Influence of Climate and Site Physical Characteristics.....	15
Discussion	15
Seasonal Wet Thermal Time	15
Woodland Removal Response.....	17
Influence of Site Physical Characteristics	20
Management Implications	21
Literature Cited	22
Tables	30
Figures.....	33
Chapter 2: Germination Prediction of 30 Plant Materials using Soil Water Potential and	
Temperature at 24 Great Basin Sites	47
Abstract	48
Introduction.....	50
Methods.....	52
Study Sites.....	52
Thermal Time Analysis.....	53
Results	55
Sagebrush and Grasslands	56
Tree Removal Response	56
Discussion	59

Influence of Site Characteristics	63
Conclusions	64
Literature Cited	66
Tables	73
Figures	81
Chapter 3: Spring drying and wetting for seedling root zones in the Great Basin	94
Abstract	95
Introduction	96
Methods	99
Study Sites	99
Study Design and Tree Removal	99
Root Zone Conditions and Analysis	100
Results	102
Effect of Soil Depth	103
Tree Removal Response	104
Additional Wet days and Wet Degree Days Before and After the First Spring Drying Period	105
Winter versus spring precipitation	107
Discussion	107
Tree removal response	110

Literature Cited	113
Tables	121
Figures.....	125

LIST OF TABLES

Table 1-1. Site location information	30
Table 1-2. List of woodland sites, year of treatment, and years of soil moisture and temperature year data used for post treatment and woodland infilling phase analysis	31
Table 1-3. Seasonal wet degree days (\pm SE) by temperature range ($^{\circ}$ C) for year since treatment in woodlands	32
Table 2-1. List of woodland sites, year of treatment, and years of soil moisture and temperature year data used for post treatment and woodland infilling phase analysis	73
Table 2-2. Seedlots and related studies where constant temperature germination trials were conducted and thermal germination equations were developed	74
Table 2-3. Percentage of tested instances that at least 50% germination was predicted for different experimental sites in the Great Basin	76
Table 2-4. Fixed effects on progress toward germination from mixed model analysis for sagebrush and perennial grass, crested wheatgrass, and sagebrush experiments	77
Table 2-5. Progress toward germination (\pm SE) for 31 seedlots at woodland sites for each year since tree reduction treatment	78
Table 2-6. Fixed effects on PTG from mixed model analysis for different years since tree reduction for woodland sites	79
Table 2-7. Fixed effects on additional progress toward germination for tree reduction treatments compared to no tree reduction 3 yr after treatment	81

Table 3-1. List of woodland sites, year of treatment, and years of soil moisture and temperature year data used for post treatment and woodland infilling phase analysis121

Table 3-2. Percentage of time that soils dried at shallower soils before deeper soils (down), soils dried occurred at deeper soils before shallower soils (up), or both shallow and deep soils dried at the same time (even) during spring (1 March to 30 June) for the first and last drying periods of the season across treated and untreated plots122

Table 3-3. Site drying and wetting conditions (\pm standard error and \pm confidence intervals) across treated and untreated sites123

LIST OF FIGURES

Figure 1-1. Typical thermal time model illustrating days ⁻¹ to germination of a seed subpopulation as a function of incubation temperature	33
Figure 1-2. Precipitation and air temperature for sites	34
Figure 1-3. Average precipitation and air temperature by season for each experiment	36
Figure 1-4. Wet degree days by five temperature ranges and seasons for sagebrush and perennial grass, crested wheatgrass, and sagebrush sites	37
Figure 1-5. Average annual wet degree days by season and temperature range	38
Figure 1-6. Wet degree day estimates by site, season and temperature range	39
Figure 1-7. Site averages of wet degree days for second, third, and fourth years since tree reduction treatments for seedbed temperature ranges in early spring	41
Figure 1-8. Seasonal additional wet degree days by treatment for non-optimal (top) and optimal (bottom) temperature ranges	43
Figure 1-9. Additional wet degree days (tree treatment wet degree days-untreated wet degree days) for three woodland infilling phases at temperature ranges of 5 to < 10° C and 10 to < 25° C	44
Figure 1-10. The distribution of wet degree days for 19 sagebrush steppe sites in the Great Basin as explained by six site physical characteristics	45
Figure 2-1. Seasonal progress towards germination	81

Figure 2-2. Annual progress toward germination by season	82
Figure 2-3. Seasonal progress toward germination by site and experiment	83
Figure 2-4. Seasonal progress toward germination by seedlot and plant functional group for sagebrush and perennial grass (top), crested wheatgrass (middle), and sagebrush (bottom) experimental sites	84
Figure 2-5. Seasonal progress toward germination by seedlot and functional group for the woodland experiment	86
Figure 2-6. Seasonal progress toward germination across all seedlots by woodland site for year 2 (top), year 3 (middle), and year 4 (bottom) since implementation of tree reduction treatments...	87
Figure 2-7. Additional progress toward germination across all seedlots for tree removal methods by season for all woodland sites (left) and Utah sites (right) for the second (top) and fourth (bottom) years since treatment	89
Figure 2-8. Additional progress toward germination across all seedlots for tree reduction treatments implemented at different phases of tree infilling for the second (left) and third (right) year since treatment by season	90
Figure 2-9. Additional progress toward germination across all seedlots for each microsite by year since tree reduction treatment for late spring (1 May to 30 June)	91
Figure 2-10. Canonical correspondence analysis (CCA) associating site progress toward germination with early spring (1 March to 30 June) (top) and 1 September to 30 June (bottom) precipitation	92

Figure 3-1. Winter precipitation (top), spring precipitation (middle), and average spring temperature (bottom) for four years since tree reduction treatments	125
Figure 3-2. Date of the first spring drying period by soil depth across treated and untreated plots. Year 1 (Top) is represented by two Utah sites, Years 2-4 (bottom) are represented by six to eight sites each	127
Figure 3-3. Spring wet period frequency (number of wet periods from 1 March to 30 June) after the first drying period at four soil depths for 4 yr since tree reduction treatments across treated and untreated plots	128
Figure 3-4. Spring wet days (1 March to 30 June) before (top) and after (bottom) the first spring drying period at four soil depths for 4 yr since tree reduction treatments across treated and untreated plots	129
Figure 3-5. Spring (1 March to 30 June) wet degree days before and after first spring drying period at four soil depths for 4 yr since tree reduction treatments across treated and untreated plots	130
Figure 3-6. Drying rates for the first spring (1 March to 30 June) drying period between soil depths for 4 yr since tree reduction treatments across treated and untreated plots	131
Figure 3-7. Wet degree days in spring (1 March to 30 June) at four temperature ranges for four soil depths and 4 yr since tree reduction treatments across treated and untreated plots	132
Figure 3-8. Spring wet degree days for 4 yr since tree reduction treatments at the 10 to 25° C temperature range at four soil depths across treated and untreated plots	133

Figure 3-9. Additional wet days (top) and wet degree days (bottom) for soil depth, tree removal methods, microsites, and tree infilling phases the first year after tree reduction	134
Figure 3-10. Additional wet days (top) and wet degree days (bottom) before (left) and after (right) the first spring (1 March to 30 June) drying period by soil depth	135
Figure 3-11. Additional wet days (top) and wet degree days (bottom) after prescribed burning and tree cutting before (right) and after (left) the first spring (1 March to 30 June) drying period	136
Figure 3-12. Additional wet days (top) and wet degree days (bottom) for the before (right) and after (left) the first spring (1 March to 30 June) drying period when trees were reduced by prescribed burning or cutting at different phases of tree infilling	137
Figure 3-13. Additional wet days (top) and wet degree days (bottom) for before (right) and after (left) the first spring (1 March to 30 June) drying period for different microsites and after tree reduction treatments	138
Figure 3-14. Canonical correspondence analysis (CCA) associating initial spring soil drying rate for nine Great Basin woodland sites with winter (1 December to 28 February) and spring (1 March to 30 June) precipitation	139

CHAPTER 1: WET THERMAL TIME AT FIVE TEMPERATURE RANGES IN SEEDBEDS
OF THE SAGEBRUSH STEPPE ECOSYSTEM

Nathan L. Cline¹, Bruce A. Roundy², and William F. Christensen³

Authors are ¹Research Associate, Brigham Young University, Provo, UT, USA 84602,

²Professor Range Science, Brigham Young University, Provo, UT, USA 84602, ³Professor
Statistics, Brigham Young University, Provo, UT, USA 84602.

This is Contribution Number 96 of the Sagebrush Steppe Treatment Evaluation Project
(SageSTEP), funded by the U.S. Joint Fire Science Program and The Great Basin Native Plant
Project.

Correspondence: Bruce A. Roundy, Department of Plant and Wildlife Sciences, 275 WIDB,
Brigham Young University, Provo, UT 84602.

Proposed Journal: Rangeland Ecology and Management

ABSTRACT

Wet thermal germination prediction models have been developed to improve plant material selection for rangeland revegetation. These models predict when the fastest germinating subpopulations of seeds will germinate and are based on summation of thermal time when seedbed soil water matric potential > -1.5 MPa. Models are developed by fitting germination rates to incubation temperatures using linear and non-linear regression. However, germination rates can be highly variable at temperatures less than 5° C and greater than 25° C and only loosely fit regression models. Previous research has assumed that a minority of thermal time is spent in the seedbed at these temperature ranges. We tested this hypothesis by quantifying and comparing seasonal wet degree days (WDD – a measure of thermal time) of sagebrush (*Artemisia* L.) -steppe seedbeds at five temperature ranges for up to 9 yr across 24 sites. Effects of three piñon and juniper (*Pinus* spp. and *Juniperus* spp.) tree removal treatments and three woodland infilling phases at time of tree reduction were also compared. We summarized the influence of site physical characteristics on WDD. We found that seedbeds sum a majority of WDD between 5° C and 25° C, indicating that thermal models should work well for predicting field germination in most cases. Seedbeds summed enough WDD for potential germination of some species at 0 to 5° C (42.5 ± 3.89 WDD in March-April) and at 25 to $< 30^{\circ}$ C (52.9 ± 6.37 WDD in May-June) on some years and sites. However, these exceptions amount to a relatively small percentage (12-20%) of total WDD for these seasons. Tree infilling or removal added WDD at 0 to $< 5^{\circ}$ C and 25 to $< 30^{\circ}$ C on a few sites, but germination models should still be accurate enough to predict effects of vegetation manipulations on germination potential. Winter

precipitation, early spring precipitation, air temperature, and elevation were positively associated with higher early spring WDD.

INTRODUCTION

Researchers use thermal-time models to predict post-dormancy germination in range weed and revegetation species to help predict seedling establishment for rangeland revegetation (Hardegree et al., 1999; 2002). Thermal-time models estimate germination timing by summing progress toward germination as a function of degree-days above a base temperature when seeds are imbibed (Garcia-Huidobro et al., 1982a; Jordan and Haferkamp, 1989; Roundy and Biedenbender, 1996; Hardegree et al., 2002; McDonald, 2002; Bradford, 2002). Thermal-time models are developed by measuring percent germination over time for a range of constant temperatures. Germination rate (quantified as days⁻¹ to a given germination percentage) is modeled as a function of incubation temperature using linear and non-linear regression for temperature ranges that are optimal (temperatures where the germination rate is highest), sub-optimal, or supra-optimal (Fig. 1) (Garcia-Huidobro et al., 1982a; 1982b; 1985; Covell et al., 1986; Roundy and Biedenbender, 1996; Hardegree and Van Vactor, 1999; Hardegree et al., 1999; Alvarado and Bradford, 2002; Hardegree, 2006; Roundy et al., 2007; Rawlins et al., 2012a). These temperature ranges vary by species and even populations or collections of populations of different species. Generally, for upper sub-optimal and optimal temperatures of 5 to 25° C, thermal-time models fit constant temperature germination data well ($R^2 > 0.7$) (Roundy et al., 2007), whereas lower sub-optimal temperatures <5 ° C and supra-optimal temperatures >25° C have a more variable germination time response (Hardegree et al., 1999; Hardegree and Winstral, 2006; Rawlins et al., 2012a). If sagebrush (*Artemisia* spp.) steppe seedbeds spend a substantial amount of thermal time when wet (soil matric potential > - 1.5 MPa) within the lower sub-optimal and supraoptimal temperature ranges, the models may have reduced reliability.

Roundy et al. (2007) defined wet thermal time as the sum of hourly soil temperatures $> 0^{\circ}\text{C}$ or some other base temperature for each hour that the seedbed has a soil matric potential $> -1.5\text{ MPa}$ or some other base water potential over a period time. Hours are converted to days and referred to as wet degree days (WDD) (Roundy et al., 2007). Some plant materials, such as cheatgrass (*Bromus tectorum* L.), germinate with 36 to 50 wet degree days (WDD) (Hardegree 1994, Trudgill et al. 2000). Common revegetation plant materials, such as bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) Á. Löve) and squirreltail (*Elymus elymoides* (Raf.) Swezey) require an estimated 60 to 80 and 130 to 150 WDD for 50% of seeds to germinate, respectively (Hardegree 1994).

Previous characterizations of WDD at lower suboptimal and supraoptimal temperature ranges are limited (Hardegree, 2006; Rawlins et al., 2012b). Identifying site physical characteristics that most influence WDD across the sagebrush steppe may allow for future development of methods for predicting germination where soil moisture and temperature data are not available.

Sagebrush steppe climate in the Great Basin is typically characterized as having hot, dry summers and cold, wet winters. During the hot and cold periods, there is evidence that seedbeds of the sagebrush steppe may spend time at lower sub-optimal and supra optimal temperature ranges of below 5°C and above 25°C . Seedbeds at two crested wheatgrass sites (*Agropyron cristatum* (L.) Gaertn.) in Utah spent 22% of the fall to spring wet days between 0°C and 5°C (Rawlins et al., 2012b). Hardegree et al. (1999) indicated that night temperatures in April and into May often reached below 5°C and 10°C at one site in Idaho. Prediction of germination in seedbeds that spend a significant amount of time at non-optimal temperatures will require

thermal-time models that represent accurate germination timing at those temperatures, or prediction may be limited if germination is highly variable at these ranges.

Site, season, or annual variations in localized climate or alterations to vegetation structure such as fire or fuel-control treatments may change seedbed WDD by altering soil temperatures and evapotranspiration (ET) (Gifford and Shaw, 1973; Gifford, 1975; 1982; Everett and Sharrow, 1985; Davies et al., 2007; Whittaker et al., 2008). Roundy et al. (2007) found that for cheatgrass (*Bromus tectorum* L.), differences between seasons had the greatest effect on predicted potential germination, followed by site and year, while disturbance treatments had small but significant effects on predicted potential germination ($P < 0.05$). Prater and DeLucia (2006) found that ET and soil-heat flux were higher on post-fire plots than on adjacent native sagebrush plots. They concluded that the differences were due to increased soil-water content and incident solar radiation on the post-fire plots. Treatments that reduce canopy cover and transpiration may reduce soil-water loss, especially as the woodland infilling increases (Roundy et al., 2014b; Young et al., 2013). However, the effects of infilling on seedbed water and temperature dynamics are not well understood (Breshears et al., 1998).

Climatic factors such as the timing and amount of seasonal precipitation strongly affect seedbed water dynamics (Ogle and Reynolds, 2004; Bates et al., 2006; 2007). Site physical factors such as slope and elevation should likewise be strongly associated with seedbed temperature and moisture conditions (Reid, 1973; Cantón et al., 2004; Weisberg et al., 2007; Bochet et al., 2007). Determination of site characteristics, such as solar radiation, slope, precipitation, and temperature, which affect seedbed conditions and germination prediction may allow us to better select plant materials for establishment. Although site characteristics in the

Great Basin have been associated with soil water and temperatures at depths below the seedbed (Jensen et al., 1989; Ryel et al., 2010), seedbeds have not been similarly characterized.

Here, we address two questions regarding seasonal WDD at optimal and non-optimal temperature ranges. First, in sagebrush steppe communities, what effect do site, season, year, woodland removal treatment, and woodland infilling phase have on seasonal WDD at optimal and non-optimal temperature ranges? Second, which site characteristics influence seedbed WDD? We quantified WDD at temperature ranges relevant to wet thermal-time models for predicting potential germination rates. Also, we compared WDD by seasons, sites, years, tree removal treatments, and tree infilling phases. Further, we determined which climate and site characteristics were associated with seedbed WDD.

METHODS

Study Sites

We used soil water potential and temperature data collected from soil monitoring stations installed across the Great Basin. Experiments are designated “sagebrush and perennial grass”, “crested wheatgrass” (*Agropyron cristatum* (L.) Gaertn.), “sagebrush”, and “woodlands” (*Piñus spp.* and *Juniperus spp.*) (Table 1). The nine sagebrush and perennial grass sites are described in Roundy et al. (2007), Chambers et al. (2007) and Blank et al. (2007). The two crested wheatgrass sites are described in Hulet et al. (2010) and Rawlins et al. (2012b). Sagebrush and woodland site experiments included three and nine sites, respectively, and are described in McIver et al. (2010). Data from the Stansbury site were not included in analyses from summer 2009 to 2011 due to a wildfire.

Experimental Design and Analysis

Each experiment was a randomized block and mixed model analysis of variance (SAS® Institute, Inc.) was used to estimate seasonal WDD by temperature range and to determine effects of specific factors for each experiment. At each site of the sagebrush and perennial grass experiment, hourly averages were recorded at two soil water matric potential and three soil temperature plots that were replicated and untreated. We averaged replicated hourly measurements of soil water matric potential and temperature by site as was done by Roundy et al. (2007). Sites were considered random blocks across the region. Fixed factors were season and year.

At the crested wheatgrass experiment, soil monitoring stations were installed in four replicate blocks at each of two sites as described in Rawlins et al. (2012b). Soil water matric potential and temperature were measured and averaged across three untreated replicate plots in each of four blocks at each site. Block was considered random, while site, season, and year were considered fixed factors.

The sagebrush experiment was set up across the region with each of the three sites considered a random block as described in McIver et al. (2010). At each site, monitoring stations were installed within a plot (ranging from 30 to 81 ha) where perennial grass cover was greater than other areas within the plot). Soil water matric potential and soil temperature were measured under a shrub canopy, or adjacent to a tall perennial grass, a short perennial grass, and within an interspace. Season and year were considered fixed factors.

The woodland treatments were applied across the region as described in Miller et al. (2014) and Roundy et al. (2014a). Each of nine sites was considered a random block. At each site, three tree removal treatments were applied to 8-20 ha plots: prescribed burning, tree felling (also known as “cut and drop” in place), and untreated. Also, a mechanical shred or mastication

treatment was applied to the four Utah sites as described in Roundy et al. (2014a; 2014b), Young et al. (2013), and Cline et al. (2010). Within each treatment, monitoring stations were installed in each of three woodland infilling phases (Miller et al., 2007). The three phases of tree infilling are: Phase 1 represents a community where understory vegetation is dominant with trees present. Phase 2 represents a community where understory vegetation and trees co-dominate. Phase 3 represents a community where trees are dominant. Near (< 3 m) each monitoring station, soil water potential and temperature were measured at a tree drip line, shrub, and interspace. Fixed factors were season, year, tree removal treatment, and tree infilling phase.

We measured seedbed soil water potential and temperature using gypsum blocks (Delmhorst, Inc., Towaco, NJ) and thermocouples at 1-3 cm soil depth. Gypsum blocks electrical resistance estimated soil water potentials down to -1.5 MPa using a standard calibration curve (Campbell Scientific, Inc. 1983). Measurements were made every minute and hourly averages were recorded on Campbell Scientific® (Logan, UT), Inc. CR10X and CR1000 microloggers. We measured precipitation and ambient air temperature with a Texas Electronics®, Inc. (Dallas, TX) tipping-bucket rain gauge and a thermistor from Campbell Scientific®, Inc. (107 temperature probe with gill shield) at each site. Complete precipitation and ambient air temperature data were not available for sagebrush and perennial grass sites from 2002 to 2005. Also, daily maximum and minimum air temperatures were measured at sagebrush and woodland sites only.

We summed WDD for five temperature ranges for each season. Temperature ranges were: 0° C to less than 5° C (0 to < 5° C), 5° C to less than 10° C (5 to < 10° C), 10° C to less than 25° C (10 to < 25° C), 25° C to less than 30° C (25 to < 30° C), and 30° C to less than 35° C (30 to < 35° C). We did not include temperature ranges above 35° C because preliminary

analyses indicated that soils were rarely wet and therefore WDD almost always summed to zero at that temperature range. Hardegree et al. (2002) and Hardegree (2006) reported increased statistical error in seed germination trials at temperature ranges below 5° C and above 25° C. Seasons were defined as: Early spring – 1 March through 31 April, late spring-1 May through 30 June; summer – 1 July through 31 August; fall – 1 September through 30 November; winter – 1 December through 28 February. Data generally had a normal distribution and statistical outliers were removed. Significant differences among fixed factors were determined by the Tukey-Kramer significance test ($P < 0.05$). For site analysis at sagebrush and perennial grass, sagebrush, and woodland sites, we used Best Unbiased Linear Predictors (BLUPs) (Littell et al., 1996) to estimate average WDD by temperature range.

We summarized the influence of five site characteristics on WDD using a Canonical Correspondence Analysis for early spring (March-April) and fall through spring (1 September through 30 June) (PC-ORD v. 6.0, McCune and Mefford, 2010). We only used data from untreated plots and data for early spring included years 2008 through 2011, while data for fall through spring included years 2008 through 2010. The site characteristic matrices included summed solar radiation (WH/m²), elevation (m), and slope (degrees) derived from a Digital Elevation Model (DEM) (ArcGIS® v. 9.3.1 Spatial Analyst Tool). Sites with missing data were excluded from the final ordination. Row and column scores were standardized by using the centering and normalizing option (Peck, 2010). Ordination significance was determined by randomization and Monte Carlo tests ($P < 0.05$).

RESULTS

Sites Characteristics

Precipitation and temperature varied by site, season, and year during the study for all experiments (Figs. 2-3). Highest precipitation was measured in winter for sagebrush and perennial grass, sagebrush, and woodland sites in 2008, 2009, and 2010, as well as in woodlands in 2007. On crested wheatgrass sites, precipitation averaged highest in early and late spring. Highest temperatures were in summer, followed by late spring, fall, early spring, and winter.

Temperature Range Distribution and Variation for Sagebrush and Perennial grass, Sagebrush, and Crested Wheatgrass Sites

Generally, WDD averaged highest for 10 to < 25° C and second highest for the upper sub-optimal range of 5 to < 10° C for early spring, late spring, and fall (Fig. 4). As expected, the lower range of 0 to < 5° C had most WDD in winter. The 0 to < 5° C range during the early spring averaged as high as 42.6 ± 3.89 WDD at crested wheatgrass sites and 42.1 ± 6.12 WDD at sagebrush and perennial grass sites. The 25 to < 30° C temperature range averaged as high as 52.9 ± 6.37 WDD at sagebrush and perennial grass sites during late spring. Because of large differences in summed WDD between the 10 to < 25° C temperature range and the other temperature ranges, we separately analyzed interactions between temperature range and year.

For non-optimal temperature ranges, the interaction between seasonal WDD and year was significant for all seasons within sagebrush and perennial grass (early spring, $F_{24,241}=2.02$, $P = 0.0043$), sagebrush (early spring, $F_{6,265}=2.83$, $P = 0.0043$), and crested wheatgrass (early spring, $F_{4,92}=4.66$, $P = 0.0018$) sites. Annual WDD varied by season and temperature range (Figs. 4-6). The annual WDD at 0 to < 5° C averaged as high as 52.5 ± 3.97 WDD during the early spring,

49.2 ± 7.57 during the fall, and 52.2 ± 1.31 during the winter, all during 2010. The 25 to < 30° C range exceeded an average 50 WDD for three of the nine sagebrush and perennial grass sites, while all other estimates did not exceed 35 WDD. Wet degree days for the optimal temperature range of 10 to < 25° C varied every year at all three sets of sites (early spring, sagebrush and perennial grass $F_{4,21}=2.02$, $P = 0.0043$, sagebrush $F_{2,61.2}=4.04$, $P = 0.0225$, crested wheatgrass $F_{4,21}=7.82$, $P = 0.0005$). WDD averaged as high as 235.1 ± 31.3 in the early spring, 413.59 ± 39.9 WDD during late spring, 58.7 ± 6.09 WDD during the summer, and 232.3 ± 12.9 WDD during the fall. WDD did not generally exceed 10 during the winter. In general, WDD varied by site more at 5 to < 10° C and 10 to < 25° C during most seasons than at 0 to < 5° C, 25 to < 30° C, and 30 to < 35° C (Fig. 5).

Woodland Removal Response

Average annual WDD were 116.3 ± 13.6, 210.0 ± 13.6, 469.7 ± 13.7, 57.0 ± 13.6, and 29.0 ± 13.7 for the 0 to < 5° C, 5 to < 10° C, 10 to < 25° C, 25 to < 30° C, and 30 to < 35° C temperature ranges. Generally, average WDD increased by the third year post treatment for the 0 to < 5° C, 5 to < 10° C, 10 to < 25° C temperature ranges, while WDD for the 25 to < 30° C and 30 to < 35° C temperature ranges did not change (Table 3). Because the treatment year varied by sites and most seasons had an unequal number of days, we separately estimated average WDD for each season by year-since-treatment (Roundy et al., 2014b). As with the non-woodland experiments, we also separately analyzed non-optimal temperature ranges from the optimal temperature range.

Burning and tree felling treatment comparisons at non-optimal and optimal temperature ranges were significantly different for 11 of 17 seasons since treatment (3 yr, early spring,

$F_{2,247}=28.15, P < 0.0001$). Treatment plots were generally different from untreated plots at 0 to < 5° C. Where there were significant differences at 5 to < 10° C, treated plots generally had more WDD than untreated plots during early spring and fall. Also, burned plots occasionally had more WDD than untreated plots at 25 to < 30° C and 30 to < 35° C during the late spring and summer. At 10 to < 25° C, treated plots had more WDD than untreated plots during the first year after treatment and for early and late spring for the second through fourth year after treatment ($P < 0.05$). Also at 10 to < 25° C, tree felled plots had more WDD than untreated plots, but often had less WDD than burned plots. Due to WDD variation among sites (Fig. 7), we determined the average change in WDD in seedbeds as a result of treatment by comparing the difference between treated and untreated plots at each site (Roundy et al., 2014b).

Additional Wet-Degree Days in Response to Woodland Tree Removal Treatments and Infilling Phases

Treatment Response. Temperature range was significant for 12 of 17 seasons since treatment when comparing non-optimal temperature ranges ($P < 0.05$). The interaction between temperature range and tree removal treatment was significant for 8 of 17 seasons including early spring (yr 4, $F_{2,651}=6.25, P = 0.0066$), late spring (yr 4, $F_{3,613}=2.9, P = 0.0343$), summer (yr 1, $F_{3,561}=9.81, P < 0.0001$), and fall (yr 2, $F_{3,587}=3.52, P = 0.015$). Where significant, tree removal treatments generally added WDD. Most increases were observed at the upper sub-optimal range of 5 to < 10° C and the optimal range of 10 to < 25° C. Also, additional WDD tended to diminish with year since treatment (Fig. 8).

Where there were significant differences between burning and mechanical treatments, burning usually added more WDD than cutting ($P < 0.05$). Most differences were found during

early and late spring at 5 to < 10° C and 10 to < 25° C. However, during the late spring of the third and fourth year post-treatment, cutting added 10 and 14 more WDD than burning at 5 to < 10° C ($P < 0.05$). Where mechanical shredding was compared to burning and cutting at Utah sites, burned and shredded plots at 5 to < 10° C and 10 to < 25° C had up to 20 and 70 more WDD than cut plots during early spring. Also, burned plots had approximately 32 more WDD than shredded plots during late spring of the second year at 25 to < 30° C. Burning also added between 5 and 32 more WDD than shredding in the fall and winter at 0 to < 5° C and 5 to < 10° C, on average ($P < 0.05$).

Woodland Infilling Phase. At non-optimal temperature ranges, the interaction of temperature range with tree infilling phase at time of treatment was significant for early spring ($F_{6,156} = 5.15, P < 0.0001$) and late spring ($F_{6,133} = 11.77, P < 0.0001$) of the first year after treatment and during early spring of the third and fourth years after treatment across tree removal methods. During early spring of the second year, effects of woodland infilling phase were marginally significant ($F_{6,651} = 2.01, P = 0.0625$). At the optimal temperature range of 10 to < 25° C, WDD for tree infilling phases were significantly different during early spring and late spring of the third year (ES, $F_{2,130} = 5.72, P = 0.0042$; LS, $F_{2,135} = 4.85, P = 0.0093$) and early spring of the fourth year (ES, $F_{2,115} = 6.85, P = 0.0015$). Similar to non-optimal comparisons, early spring of the second year was marginal, but not significant ($P > 0.05$). Generally, increased tree infilling added WDD at 5 to < 10° C and 10 to < 25° C during the early spring (Fig. 9), but only occasionally during other seasons or at other temperature ranges ($P < 0.05$).

Influence of Climate and Site Physical Characteristics

The CCA indicated that early spring WDD was associated most with early spring and winter precipitation, elevation, and ambient air temperature. The resulting ordination was significant (Fig. 10, $P = 0.008$). Also, the association between these variables and the variation among sites for early spring WDD (axis 1 $R^2 = 0.834$, axis 2 $R^2 = 0.678$, axis 3 $R^2 = 0.420$) was also significant ($P = 0.018$). The first axis explained 44.6 % of the variability in WDD, while all three axes explained 49.9% of the variability. Because axis 1 accounted for most of the variation explained by the model, we focus our discussion on its elements. Winter precipitation, spring precipitation, and elevation were positively correlated with axis 1, while ambient air temperature was negatively correlated with axis 1. Except for Bridge Creek, Scipio, and the Boulter Creek *Elymus* sites, WDD of woodland and sagebrush and perennial grass sites were associated with increasing elevation, increasing spring and winter precipitation, and decreasing ambient air temperature. For Scipio and Boulter Creek *Elymus*, as well as sagebrush and crested wheatgrass sites, WDD were more strongly associated with increasing ambient air temperature, decreasing elevation, and decreasing spring and winter precipitation. For Mill Canyon High, WDD were strongly associated with increasing winter precipitation and elevation, as well as decreasing ambient air temperature. Association of site climate and physical characteristics with WDD for September through June was not significant ($P = 0.104$).

DISCUSSION

Seasonal Wet Thermal Time

The accuracy of thermal-time models for estimating germination in field seedbeds depends on whether or not the majority of summed WDD is within the temperature range where

variation in germination rate is minimal relative to incubation temperature. Hardegree et al. (2002) reported increased standard error in the total germination percentage at below 5° C and above 25° C. We found minimal WDD at 5 to < 10° C and 10 to < 25° C temperature ranges where variability in the germination response has been found to be minimal, averaged the most WDD days in early spring, late spring, and fall (Fig. 4). These findings are consistent with the assumption made by Rawlins et al. (2012b) that non-optimal temperature ranges sum a small percentage of thermal time compared to more optimal temperature ranges.

Despite the fact that most WDD were summed where variation in germination rate is minimal, seed beds occasionally summed sufficient WDD from 0 to < 5° C and 25 to < 30° C for potential germination prediction. All four sites averaged between 36 and 52 WDD during early spring at 0 to < 5° C. Also at 25 to < 30° C, late spring averaged up to 52.4 ± 6.37 WDD (Fig. 6). With cheatgrass needing approximately 40 to 50 WDD for potential germination prediction, wet thermal time models may overestimate the time to cheatgrass germination as a result of underestimating progress toward germination at these temperature ranges (Rawlins et al., 2012a; 2012b).

Additionally, fluctuation in wet days (> 1.5 MPa) among sites and years in the top 30 cm of the soil profile have been found (Jensen et al., 1989; Roundy et al., 2014b). In our study, differences between seasons, sites, and years were generally at the upper sub-optimal and optimal temperature ranges. However, there were occasions where WDD at non-optimal temperature ranges were sufficient for a potential germination as a result of these fluctuations. For example, some sites during the winter of 2010 averaged as high as 45 WDD (Fig. 6). The year 2010 had greater precipitation during fall and winter compared to the previous few years

during the same seasons. This increase in precipitation likely allowed for the increased summation of WDD.

Potential-germination predictions may be less accurate when sufficient WDD are summed at the lower sub-optimal range of 0 to $< 5^{\circ}$ C or at the supra optimal ranges above 25° C. However, Rawlins et al. (2012b) found that wet thermal time models were most accurate (75% to 95%) in predicting potential germination between late winter (21 Feb) and mid spring (10 May), a period where 26% of wet days were at 0 to $< 5^{\circ}$ C. A possible explanation for this apparent inconsistency may be that base temperatures (the temperature where the germination rate is zero) for many plant materials are above 0° C and, therefore there is minimal summed wet thermal time at 0 to $< 5^{\circ}$ C. Cheatgrass, bluebunch wheatgrass, and squirreltail have base temperatures at approximately 1.5° to 2° C (Hardegree, 1994; Hardegree et al., 1999; 2008). Another explanation might be that as day-time temperatures increase through the early spring, the amount of wet thermal time the seedbed spends at warmer temperatures produces a potential germination response well before sufficient wet thermal time is summed at 0 to $< 5^{\circ}$ C (Hardegree, 1994; Hardegree et al., 2008).

Woodland Removal Response

Changes in plant community structure like woodland tree removal treatments implemented at different tree infilling phases may influence soil moisture and temperature dynamics. Tree reduction has been reported to increase time of plant-available water during the spring by as much as 26 days to six weeks (Bates et al., 2000; Roundy et al., 2014b; Young et al., 2013). Also, Roundy et al (2014b) reported an additional 332.1 WDD during the spring at 13 to 30 cm soil depth compared to untreated plots. Similarly, we found that tree reduction added WDD in the seedbed generally at temperature ranges where WDD summation is highest for each

season. In general, these additions are at temperature ranges where germination variability is low. However, temperature ranges with more variability in germination response do occasionally show increased WDD as a result of treatment (Fig. 8). For example, as much as 12.1 ± 2.88 WDD and 18.2 ± 6.67 WDD was added in fall and winter at 0 to $< 5^\circ \text{C}$ as a result of treatment. These additions are still relatively small and are not likely to be sufficient to influence potential germination predictions. However, in conjunction with site and annual fluctuations, treatments may result in situations where potential germination predictions may be influenced at some non-optimal temperature ranges.

Roundy et al. (2014b) found that there was little difference in plant available water between burning and mechanical treatments at 13-30 cm soil depth the first 4 yr after treatment. For the seedbed, we found differences in WDD during some early springs, late springs, falls, and one winter for most measured temperature ranges (Fig. 8). However, these differences were generally sporadic and often inconsistent.

Where differences between tree removal treatments occurred, altering the plant community structure may have influenced the summation of WDD by changing ET dynamics. Burning removes tree and understory vegetation which allows for more incident solar radiation (Prater and DeLucia, 2006). Increased solar radiation could result in early post-winter thaw and warming of the soil surface at least until the understory vegetation recovers and may explain why burned plots often had higher additional WDD than at shredded and cut plots.

Mechanical treatments likely buffer the seedbed to changes in climate by shielding the soil surface with tree skeleton (cutting), shredded residue (mechanical shredding), and residual understory vegetation. Shredded residue has been found to decrease soil water loss from ET and runoff (Chung and Horton, 1987; Enrique et al., 1999; Cline et al., 2010). Shielding of the soil

surface during short duration precipitation events may result in precipitation interception. Further, any decomposition as a result of available nitrogen during the first few years following treatment may occur when soil moisture is high (Buggeln and Rynk, 2002; Rau et al., 2007; Young et al., 2013). The resulting positive thermodynamic condition, as well as effects resulting from changes in community structure, may explain why shredding often has more additional WDD than cutting during early spring. In any case, differences between treatments tend to diminish by the fourth year after treatment.

Roundy et al. (2014b) found that tree reduction by fire or mechanical methods resulted in increased WDD where pretreatment woodland infilling was higher at 13-30 cm soil depth. Generally, our analysis of woodland infilling phase for the seedbed was similar to their findings at the sub optimal and optimal temperature ranges. Often phase 3 had significantly more WDD than phase 1 ($P < 0.05$) where trees were reduced. Because trees are assumed to be using the majority of plant available water, phase 3 tree removal would represent a larger resource pulse (a temporary increase in available resources) than at lower infilling phases (Ryel et al., 2010; Roundy et al., 2014b; Young et al., 2013). This resource pulse may facilitate weed invasion (Chambers et al., 2007; Roundy et al., 2014b). Weed cover has been found to increase after treatment where tree infilling was greater before treatment (Roundy et al., 2014a)

Although the summation of WDD at non-optimal temperature ranges was usually small, the potential for overestimating the timing of potential germination remains a concern. Rawlins et al. (2012a) found that thermal-time models frequently overestimate germination timing. Hardegree et al. (1999) suggested that overestimation in thermal time models may be a result of germination rate sensitivity near base temperatures. Rawlins et al. (2012a) also stated that

progress toward germination may be underestimated as a result of summing WDD at non-optimal temperature ranges where germination response is not well understood (Rawlins et al., 2012a). Consequently, when climate conditions allow for a summation of WDD at the lower sub-optimal or supra optimal temperature ranges, more investigation into germination response may improve accuracy of potential germination predictions in some plant materials.

Influence of Site Physical Characteristics

Bates et al. (2006) found a reduction in plant productivity and an increase in bare ground at a Great Basin sagebrush site as a result of applying a majority of seasonal water between April and July as compared to between October and March. This indicates that sites with high winter precipitation may have more WDD during the early spring than sites with low winter precipitation. Our CCA analyses across all temperature ranges and 19 sites indicated that both early spring and winter precipitation, as well as elevation and ambient air temperature, influence early spring WDD in the seedbed. Wet degree days at wetter, cooler sites like Underdown Canyon High and Mill Canyon High tend to be positively influenced by increasing winter precipitation, increasing elevation, and decreasing ambient air temperature. On warmer, drier sites like Skull Valley, Lookout Pass, and Scipio WDD tend to be influenced with decreasing early spring precipitation, decreasing elevation, and increasing ambient air temperature. Wetter, cooler sites have more plant cover than the warmer, drier sites (Chambers et al., 2013). Plant production relies on sufficient WDD in both the seedbed for germination and in the root zone for root growth. However, frequent rewetting of the seedbed may promote germination and lengthen wet periods in the deeper root zone soil depths.

One opportunity to make thermal time models more practical in application to revegetation projects in the Great Basin is to model WDD using site characteristics. We have

identified site characteristics associated with early spring WDD across a broad range of conditions in the Great Basin. However, our analysis was not sufficient to estimate WDD at sites where soil moisture and temperature conditions are not known. An analysis of site characteristics at a finer scale may increase the percent variability explained by the CCA and may reveal other important predictors of WDD.

Management Implications

On average, WDD at lower sub-optimal and supra-optimal temperature ranges are not likely to be sufficient to influence germination as predicted by wet thermal time models during the early spring. Where germination response for individual plant materials has a relatively good fit to estimated response between 5 and 25° C, wet thermal time models may be sufficiently precise to determine the site potential for revegetation using site specific soil climate conditions. These models may also improve plant material selection for rangeland revegetation projects for the sagebrush steppe ecosystem. Tree removal treatments should not greatly influence results of model precision as it relates to wet thermal time.

LITERATURE CITED

- Alvarado, V., and K. J. Bradford. 2002. A hydrothermal time model explains the cardinal temperatures for seed germination. *Plant, Cell Environ.* 25:1061–1069.
- Bates, J. D., R. F. Miller, and T. J. Svejcar. 2000. Understory dynamics in cut and uncut western juniper woodlands. *J. Range Manage.* 53:119–126.
- Bates, J. D., R. F. Miller, and T. J. Svejcar. 2007. Long-term vegetation dynamics in a cut western juniper woodland. *Western North Am. Nat.* 67:549–561.
- Bates, J. D., T. J. Svejcar, R. F. Miller, and R. A. Angell. 2006. The effects of precipitation timing on sagebrush steppe vegetation. *J. Arid Environ.* 64:670–697.
- Blank, R. R., J. C. Chambers, B. A. Roundy, and A. Whittaker. 2007. Nutrient availability in rangeland soils: influence of prescribed burning, herbaceous vegetation removal, overseeding with *Bromus tectorum*, season, and elevation. *Rangeland Ecol. Manage.* 60:644–655.
- Bochet, E., P. García-Fayos, B. Alborch, and J. Tormo. 2007. Soil water availability effects on seed germination account for species segregation in semiarid roadslopes. *Plant Soil* 295:179–191.
- Bradford, K. J. 2002. Applications of hydrothermal time to quantifying and modeling seed germination and dormancy. *Weed Sci.* 50:248–260.

- Breshears, D. D., J. W. Nyhan, C. E. Heil, and B. P. Wilcox. 1998. Effects of woody plants on microclimate in a semiarid woodland: Soil temperature and evaporation in canopy and intercanopy patches. *Int. J. Plant Sci.* 159:1010–1017.
- Buggelnl, R., and R. Rynk. 2002. Self-heating in yard trimmings: Conditions leading to spontaneous combustion. *Compost Sci. Util.* 10:162–182.
- Campbell Scientific, Inc. 1983. Model 227 Delmhorst cylindrical soil moisture block instruction manual. Logan, UT: Campbell Scientific. 5 p.
- Cantón, Y., A. Solé-Benet, and F. Domingo. 2004. Temporal and spatial patterns of soil moisture in semiarid badlands of SE Spain. *J. Hydrol.* 285:199–214.
- 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*? *Ecol. Monogr.* 77:117–145.
- Chung, S. O., and R. Horton. 1987. Soil heat and water flow with a partial surface mulch. *Water Resour. Res.* 23:2175–2186.
- Cline, N., B. Roundy, F. Pierson, P. Kormos, and C. J. Williams. 2010. Hydrologic response to mechanical shredding in a juniper woodland. *Rangeland Ecol. Manage.* 63:467–477.
- Covell, S., R. H. Ellis, E. H. Roberts, and R. J. Summerfield. 1986. The influence of temperature on seed germination rate in grain legumes. *J. Exp. Bot.* 37:705–715.

- Davies, K. W., J. D. Bates, and R. F. Miller. 2007. Short-term effects of burning Wyoming big sagebrush steppe in southeast Oregon. *Rangeland Ecol. Manage.* 60:515–522.
- Enrique, G., I. Braud, T. Jean-Louis, V. Michel, B. Pierre, and C. Jean-Christophe. 1999. Modelling heat and water exchanges of fallow land covered with plant-residue mulch. *Ag. Forest Meteorol.* 97:151–169.
- Everett, R. L., and S. H. Sharrow. 1985. Soil water and temperature in harvested and nonharvested pinyon-juniper stands soil water and harvested and nonharvested stands. USDA For Ser IMRS-INT-342:1–4.
- Garcia-Huidobro, J., J. L. Monteith, and G. R. Squire. 1982a. Time, temperature and germination of pearl millet (*Pennisetum typhoides* s. & h.) I. Constant temperature. *Journal of Experimental Botany* 33:288–296.
- Garcia-Huidobro, J., J. L. Monteith, and G. R. Squire. 1982b. Time, temperature and germination of pearl millet (*Pennisetum typhoides* S. & H.) II. Alternating temperature. *J. Exp. Bot.* 33:297–302.
- Garcia-Huidobro, J., J. L. Monteith, and G. R. Squire. 1985. Time, temperature and germination of pearl millet (*Pennisetum typhoides* S. & H.) III. Inhibition of germination by short exposure to high temperature. *J. Exp. Bot.* 36:338–343.
- Gifford, G. F. 1975. Approximate annual water budgets of two chained pinyon-juniper sites. *J. Range Manage.* 28:73–74.

- Gifford, G. F. 1982. Impact water of burning in patterns the and grazing soil on type. *J. Range Manage.* 35:697–699.
- Gifford, G. F., and C. B. Shaw. 1973. Soil moisture patterns on two chained pinyon-juniper sites in Utah. *J. Range Manage.* 26:436–440.
- Hardegree, S. P. 1994. Matric priming increases germination rate of Great Basin native perennial grasses. *Agron. J.* 86:289–293.
- Hardegree, S. P. 2006. Predicting germination response to temperature. I. Cardinal-temperature models and subpopulation-specific regression. *Ann. Bot.* 97:1115–1125.
- Hardegree, S. P., T. A. Jones, F. B. Pierson, P. E. Clark, and G. N. Flerchinger. 2008. Dynamic variability in thermal-germination response of squirreltail (*Elymus elymoides* and *Elymus multisetus*). *Environ. Exp. Bot.* 62:120–128.
- Hardegree, S. P., T. A. Jones, and S. S. Van Vactor. 2002. Variability in thermal response of primed and non-primed seeds of squirreltail [*Elymus elymoides* (Raf.) Swezey and *Elymus multisetus* (J. G. Smith) M. E. Jones]. *Ann. Bot.* 89:311–319.
- Hardegree, S. P., and S. S. Van Vactor. 1999. Predicting germination response of four cool-season range grasses to field-variable temperature regimes. *Environ. Exp. Bot.* 41:209–217.
- Hardegree, S. P., S. S. Van Vactor, F. B. Pierson, and D. E. Palmquist. 1999. Predicting variable-temperature response of non-dormant seeds from constant-temperature germination data. *J. Range Manage.* 52:83–91.

- Hardegee, S. P., and A. H. Winstral. 2006. Predicting germination response to temperature. II. three-dimensional regression, statistical gridding and iterative-probit optimization using measured and interpolated-subpopulation data. *Ann. Bot.* 98:403–410.
- Hulet, A., B. a. Roundy, and B. Jessop. 2010. Crested wheatgrass control and native plant establishment in utah. *Rangeland Ecol. Manage.* 63:450–460.
- Jensen, M. E., G. H. Simonson, and R. E. Keane. 1989. Soil temperature and moisture regime relationships within some rangelands of the Great Basin. *Soil Sci.* 147:134–139.
- Jordan, G. L., and M. R. Haferkamp. 1989. Temperature responses and calculated heat units for germination of several range grasses and shrubs. *J. Range Manage.* 42:41–45.
- Littell, R. C., G. A. Milliken, W. W. Siroup, and R. D. Wolfinger. 1996. SAS system for mixed models. Cary NC. P. 633
- McDonald, C. K. 2002. Germination response to temperature in tropical and subtropical pasture legumes. 1. Constant temperature. *Australian J. Exp. Ag.* 42:407–419.
- McIver, J., M. Brunson, S. Bunting, J. Chambers, N. Devoe, P. Doescher, J. Grace, D. Johnson, S. Knick, R. Miller, M. Pellant, F. Pierson, D. Pyke, K. Rollins, B. Roundy, E. Schupp, R. Tausch, and D. Turner. 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.

- Miller, R. F., J. D. Bates, T. J. Svejcar, F. B. Pierson, and L. E. Eddleman. 2007. Western juniper field guide: Asking the right questions to select appropriate management actions. U.S. Geological Survey Circular 1321, 26 p.
- Ogle, K., and J. F. Reynolds. 2004. Plant responses to precipitation in desert ecosystems: Integrating functional types, pulses, thresholds, and delays. *Oecologia* 141:282–94.
- Peck, J. E. 2010. Multivariate analysis for community ecologists: Step by step using pc-ord. Glenden Beach, OR, USA.
- Prater, M. R., and E. H. DeLucia. 2006. Non-native grasses alter evapotranspiration and energy balance in great basin sagebrush communities. *Ag. For. Meteorology* 139:154–163.
- Rau, B. M., R. R. Blank, J. C. Chambers, and D. W. Johnson. 2007. Prescribed fire in a Great Basin sagebrush ecosystem: Dynamics of soil extractable nitrogen and phosphorus. *J. Arid Environ.* 71:362–375.
- Rawlins, J. K., B. A. Roundy, S. M. Davis, and D. Egget. 2012a. Predicting germination in semi-arid wildland seedbeds. I. Thermal germination models. *Environ. Exp. Bot.* 76:60–67.
- Rawlins, J. K., B. A. Roundy, D. Egget, and N. L. Cline. 2012b. Predicting germination in semi-arid wildland seedbeds II. Field validation of wet thermal-time models. *Environ. Exp. Bot.* 76:68–73.
- Reid, I. 1973. The influence of slope orientation upon the soil moisture regime and its hydrogeomorphological significance. *J. Hydrol.* 19:309–321.

- Roundy, B. A., and S. H. Biedenbender. 1996. Germination of warm-season grasses under constant and dynamic temperatures. *J. Range Manage.* 49:425–431.
- Roundy, B. A., S. P. Hardegree, J. C. Chambers, and A. Whittaker. 2007. Prediction of cheatgrass field germination potential using wet thermal accumulation. *Rangeland Ecol. Manage.* 60:613–623.
- Roundy, B. A., R. F. Miller, R. J. Tausch, K. Young, A. Hulet, B. Rau, B. Jessop, J. C. Chambers, and D. Eggett. 2014a. Understory cover responses to piñon-juniper control across tree cover gradients in the Great Basin. *Rangeland Ecol. Manage.* x:xx–xx.
- Roundy, B. A., K. Young, N. Cline, A. Hulet, R. F. Miller, R. J. Tausch, J. C. Chambers, and B. Rau. 2014b. Piñon-juniper reduction effects on soil temperature and water availability of the resource growth pool. *Rangeland Ecol. Manage.* xx:xx-xx.
- Ryel, R. J., A. J. Leffler, C. Ivans, M. S. Peek, and M. M. Caldwell. 2010. Functional differences in water-use patterns of contrasting life forms in Great Basin steppelands. *Vadose Zone J.* 9:548–560.
- Weisberg, P. J., E. Lingua, and R. B. Pillai. 2007. Spatial patterns of pinyon-juniper expansion in Central Nevada. *Rangeland Ecol. Manage* 60:115–124.
- Whittaker, A., B. A. Roundy, J. C. Chambers, S. E. Meyer, R. R. Blank, S. G. Kitchen, and J. Korfmacher. 2008. The effects of herbaceous species removal, fire, and cheatgrass (*Bromus tectorum*) on soil water availability in sagebrush steppe. Pages 49–56 in S. Kitchen, R. L. Pendleton, T. A. Monaco, and J. Vernon, editors. *Shrublands under fire: Disturbance and*

recovery in a changing world Cedar City. U. S. Department of Agriculture Forest Service
Rocky Mountain Research Station, Fort Collins, CO.

Young, K. R., B. a. Roundy, and D. L. Eggett. 2013. Tree reduction and debris from mastication
of Utah juniper alter the soil climate in sagebrush steppe. *For. Ecol. Manage.* 310:777–785.

TABLES

Table 1-1. Site location information. Community types: Mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. vaseyana (Rydb.) Beetle), Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young), crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.), squirreltail (*Elymus elymoides* (Raf.) Swezey), western juniper (*Juniperus occidentalis* Hook.), pinyon-juniper (*Pinus edulis* Engelm. - *Juniperus osteosperma* (Torr.) Little), Utah juniper (*Juniperus osteosperma* (Torr.) Little), cheatgrass (*Bromus tectorum* L.).

Site	Community Type	State	Coordinance	Elev (m)	Soil classification
Sagebrush & Perennial Grass Sites (Described in Chambers et al. 2007, Roundy et al. 2007, Blank et al. 2007)					
Underdown Canyon High (NVU)	Mountain Big Sagebrush	NV	39° N, 117°30' W	2380	Fine-loamy and loamy-skeletal, frigid Typic Haploxerolls
Underdown Canyon Mid (NVM)	Mountain Big Sagebrush	NV	39° N, 117°30' W	2190	Loamy-skeletal, mesic, Xeric Haplodurids
Underdown Canyon Low (NVL)	Wyoming Big Sagebrush	NV	39° N, 117°30' W	1960	Loamy-skeletal, mesic, Typic Haploxerolls
Mill Canyon High (UTU)	Mountain Big Sagebrush	UT	40° N, 112° W	2274	Loamy-skeletal, carbonatic, mesic, frigid, Lithic Calcixerolls
Black Rock Canyon Mid (UTM)	Mountain Big Sagebrush	UT	40° N, 112° W	2085	Loamy-skeletal, carbonatic, mesic, Lithic, Calcixerolls
Black Rock Canyon Low (UTL)	Wyoming Big Sagebrush	UT	40° N, 112° W	1710	Loamy-skeletal, carbonatic, mesic, shallow, Petrocalcic Palexerolls
Barrett Canyon (NVC)	Crested Wheatgrass	NV	39° N, 117°30' W	2065	Loamy-skeletal, mesic, Xereptic Haplodurids
Boulter Creek (UTC)	Crested Wheatgrass	UT	40° N, 112° W	1628	Fine-loamy to loamy-skeletal, mesic, Xeric Haplocalcids
Boulter Creek ELEL (UTS)	Squirreltail grass	UT	40° N, 112° W	1597	Fine-loamy to loamy-skeletal, mesic, Xeric Haplocalcids
Sagebrush Sites (Described in McIver et al. 2010)					
Hart Mountain (HM)	Wyoming Big Sagebrush	OR	42° 43' N, 119° 29' W	1510	Loamy, mixed, superactive, frigid, shallow Xeric Haplodurids
Onaqui Sagebrush (OS)	Wyoming Big Sagebrush	UT	40° 11' N, 112° 27' W	1675	Loamy-skeletal, mixed, active, mesic Xeric Haplocalcids
Saddle Mountain (SM)	Wyoming Big Sagebrush	WA	46° 45' N, 119° 21' W	1510	Coarse-silty, mixed, superactive, mesic Xeric Haplocambids
Crested Wheatgrass Sites (Described in Rawlins 2012 and Hulet et al. 2010)					
Skull Valley (SV)	Crested Wheatgrass	UT	40°18' N, 112°51' W	1524	Sandy loam, mixed (Calcareous) mesic, and xeric Torriorthents
Lookout Pass (LP)	Crested Wheatgrass	UT	40°09' N, 112°28' W	1676	Taylorflat fine -loamy, mixed, mesic, xerolic Calciorthids
Woodland Sites (Described in McIver et al. 2010)					
Blue Mountain (BM)	Western Juniper	CA	41° 49' N, 120° 50' W	1510	Loamy, mixed, superactive, mesic Lithic Haploxerolls
Bridge Creek (BC)	Western Juniper	OR	44° 36' N, 120° 9' W	840	Sandy loam, frigid Typic Haploxerolls to frigid Torriorthents
Devine Ridge (DR)	Western Juniper	OR	43° 43' N, 118° 56' W	1510	Loamy-skeletal, mixed, superactive, frigid Lithic Haploxerolls
Marking Corral (MC)	Pinyon-juniper	NV	39° 25' N, 115° 7' W	1730	Loamy-skeletal, mixed, superactive, mesic Argidic Durixerolls
South Ruby (SR)	Pinyon-juniper	NV	40° 40' N, 109° 46' W	2005	Loamy, mixed, superactive, mesic, shallow Haploduridic Durixerolls
Greenville Bench (GV)	Pinyon-juniper	UT	38° 12' N, 112° 47' W	1800	Loamy-skeletal, carbonatic, mesic Typic Calcixerolls
Scipio (SC)	Pinyon-juniper	UT	39° 16' N, 112° 4' W	1755	Loamy-skeletal, mixed, superactive, mesic, shallow Calcic Petrocalcids
Onaqui woodland (OJ)	Utah Juniper	UT	40° 13' N, 112° 28' W	1705	Loamy-skeletal, carbonatic, mesic, shallow Petrocalcic Palexerolls
Stansbury (ST)	Utah Juniper	UT	40° 35' N, 112° 39' W	1740	Loamy-skeletal, mixed, active, frigid Pachic Haploxerolls

Table 1-2. List of woodland sites, year of treatment, and years of soil moisture and temperature year data used for post treatment and woodland infilling phase analysis. * Years where only early spring and late spring data was used.

Site	Treatment and phase comparison				
	Year treated	Year data used for year since treatment			
	Year 1	Year 2	Year 3	Year 4*	
Blue Mountain	2007		2009	2010	2011
Bridge Creek	2006		2008	2009	2010
Devine Ridge	2007		2009	2010	2011
Marking Corral	2006		2008	2009	2010
South Ruby	2008		2010	2011*	
Stansbury	2007	2008	2009*		
Onaqui	2006	2007	2008	2009	2010
Scipio	2007			2010	2011
Greenville	2007		2009	2010	2011
Total number of sites		2	7	7	7

Table 1-3. Seasonal wet degree days (\pm SE) by temperature range ($^{\circ}$ C) for year since treatment in woodlands. Dash marks (-) indicate temperature ranges that had little or no wet degree days.

Season	Year Since Treatment	Wet Degree Days for a Temperature Range				
		0 to $< 5^{\circ}$ C	5 to $< 10^{\circ}$ C	10 to $< 25^{\circ}$ C	25 to $< 30^{\circ}$ C	30 to $< 35^{\circ}$ C
Early Spring	Year 1	40.9 \pm 12.9	82.7 \pm 12.9	140.4 \pm 12.9	1.46 \pm 12.9	0.1 \pm 12.9
	Year 2	45.2 \pm 5.3	79.5 \pm 5.3	113.4 \pm 5.3	4.4 \pm 5.3	0.8 \pm 5.3
	Year 3	51.7 \pm 2.7	87.0 \pm 2.7	128.9 \pm 2.7	4.3 \pm 2.6	0.4 \pm 2.6
	Year 4	44.4 \pm 6.4	79.3 \pm 6.4	116.8 \pm 6.4	3.9 \pm 6.4	0.5 \pm 6.4
Late Spring	Year 1	3.0 \pm 45.0	32.0 \pm 45.0	189.8 \pm 45.0	28.3 \pm 45.0	3.0 \pm 45.0
	Year 2	7.9 \pm 16.1	40.1 \pm 16.2	227.6 \pm 16.2	29.1 \pm 16.2	13.3 \pm 16.1
	Year 3	9.4 \pm 8.9	63.5 \pm 8.9	274.0 \pm 8.9	32.2 \pm 8.9	12.0 \pm 8.9
	Year 4	8.9 \pm 16.9	72.9 \pm 16.9	324.2 \pm 16.9	16.3 \pm 16.9	8.9 \pm 16.9
Summer	Year 1	-	-	48.8 \pm 5.9	15.0 \pm 5.9	11.7 \pm 5.9
	Year 2	-	-	15.9 \pm 2.7	4.2 \pm 2.7	3.7 \pm 2.7
	Year 3	-	-	67.0 \pm 8.5	22.7 \pm 8.5	16.1 \pm 8.5
Fall	Year 1	30.8 \pm 5.5	62.1 \pm 5.5	71.7 \pm 5.5	8.8 \pm 5.5	6.0 \pm 5.5
	Year 2	26.2 \pm 4.7	54.5 \pm 4.7	64.8 \pm 4.7	3.7 \pm 4.7	1.7 \pm 4.7
	Year 3	33.9 \pm 8.9	24.7 \pm 8.5	88.1 \pm 8.5	1.9 \pm 8.5	0.7 \pm 8.5
Winter	Year 1	23.8 \pm 5.6	10.8 \pm 6.0	3.4 \pm 5.6	-	-
	Year 2	21.5 \pm 5.8	12.2 \pm 5.8	2.2 \pm 5.8	-	-
	Year 3	42.2 \pm 10.6	21.4 \pm 10.6	2.1 \pm 10.6	-	-

FIGURES

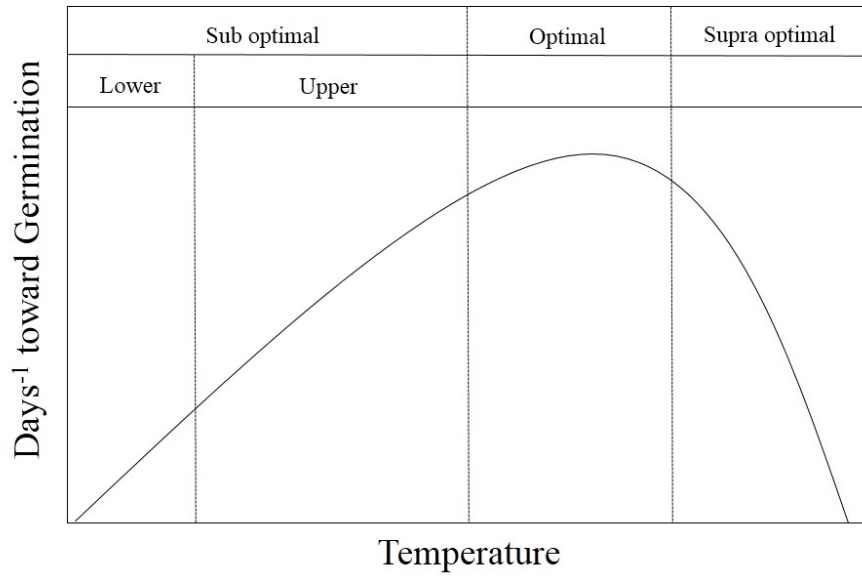


Figure 1-1. Typical thermal time model illustrating days-1 to germination of a seed subpopulation as a function of incubation temperature (Rawlins et al., 2012a). These nonlinear curves vary by subpopulations of seeds. Temperature is divided up into generalized ranges based on optimal germination rate.

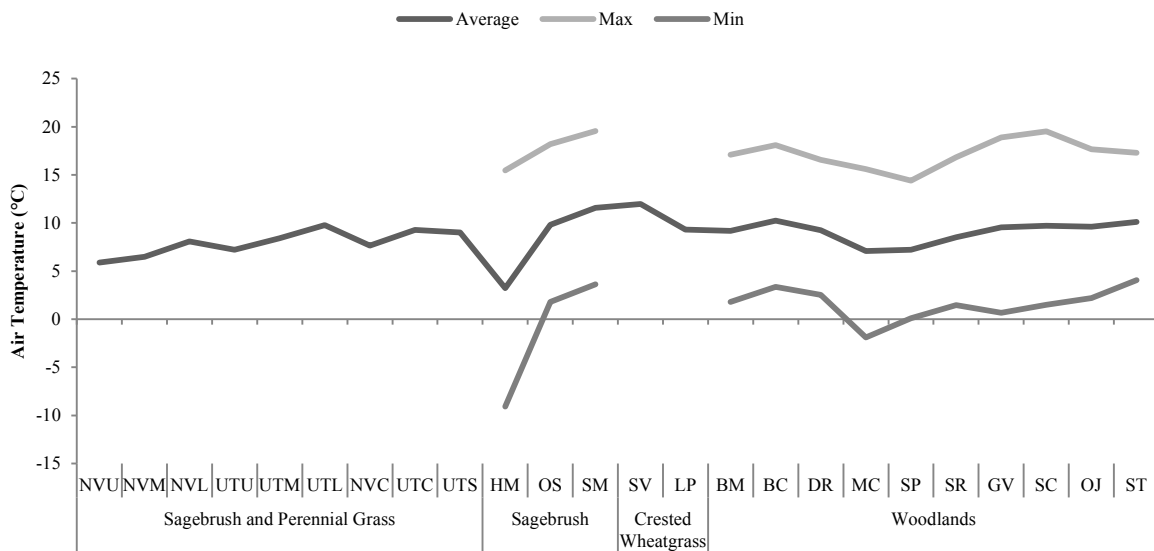
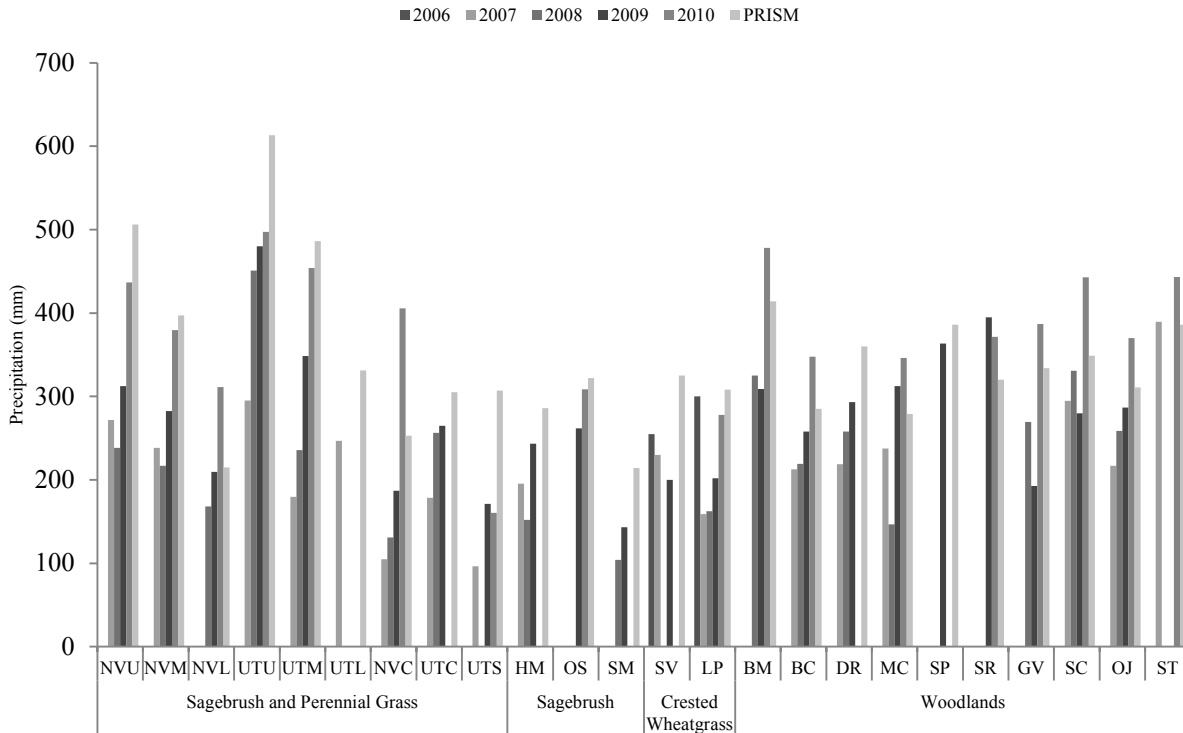


Figure 1-2. Precipitation and air temperature for sites. NVU = Underdown Canyon High elevation, NVM = Underdown Canyon Middle elevation, NVL = Underdown Canyon Low elevation, UTU = Mill Canyon High elevation, UTM = Black Rock Canyon Middle elevation,

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, BM = Blue Mountain, BC = Bridge Creek, DR = Devine Ridge, MC = Marking Corral, SR = South Ruby, GV = Greenville Bench, SC = Scipio, OJ = Onaqui Woodland, ST = Stansbury.

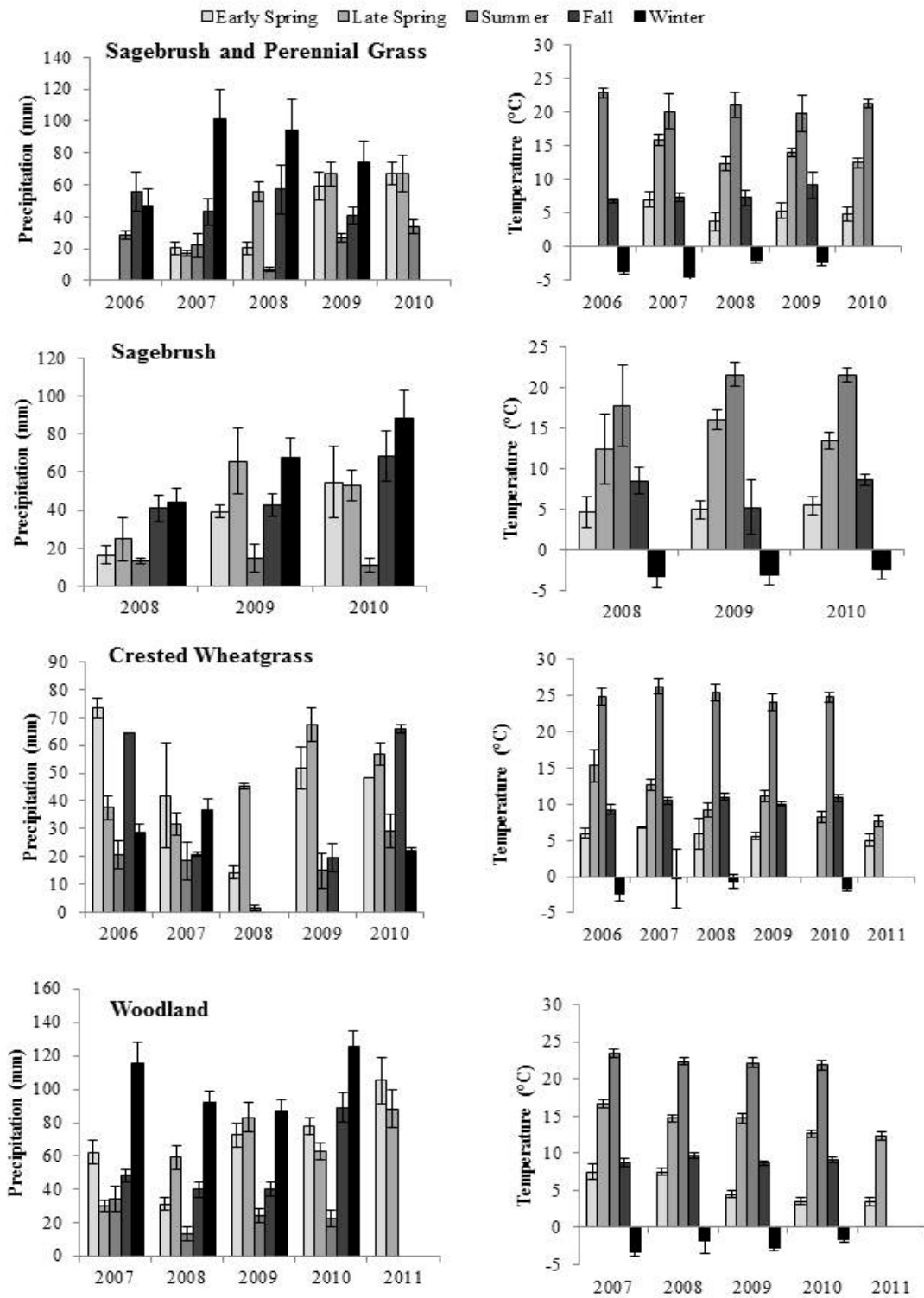


Figure 1-3. Average precipitation and air temperature by season for each experiment. Error bars represent ± 1 standard error.

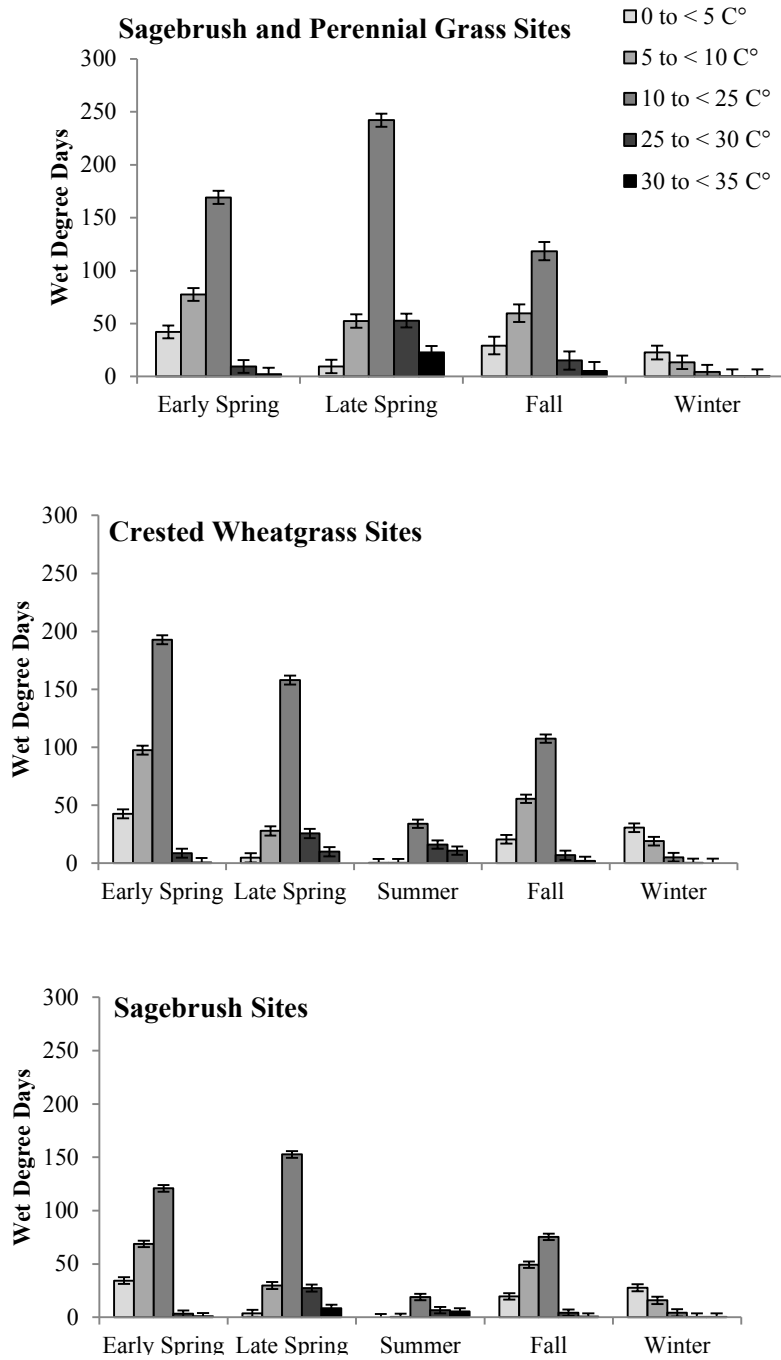


Figure 1-4. Wet degree days by five temperature ranges and seasons for sagebrush and perennial grass, crested wheatgrass, and sagebrush sites. Error bars represent ± 1 standard error.

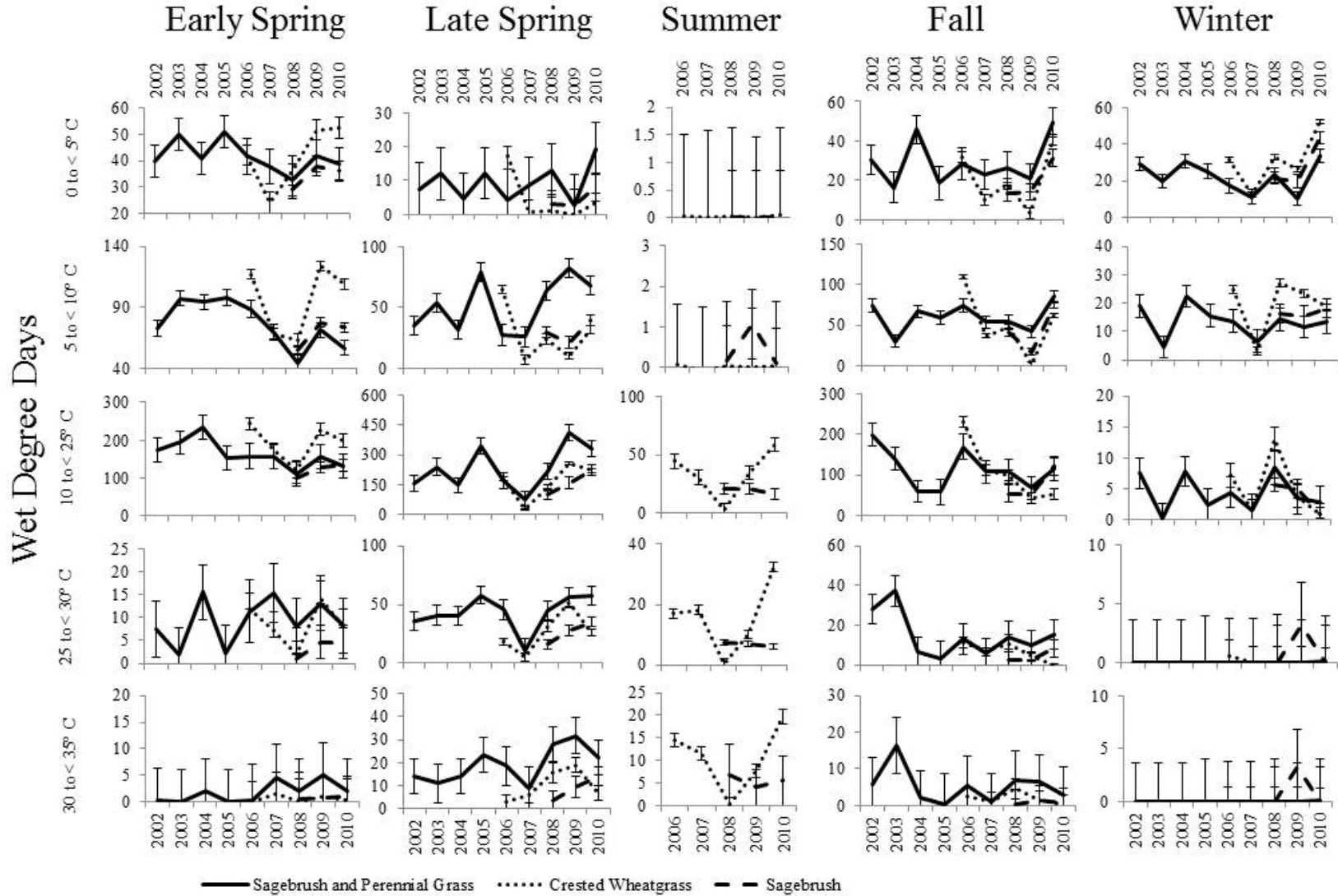


Figure 1-5. Average annual wet degree days by season and temperature range. Error bars represent ± 1 standard error.

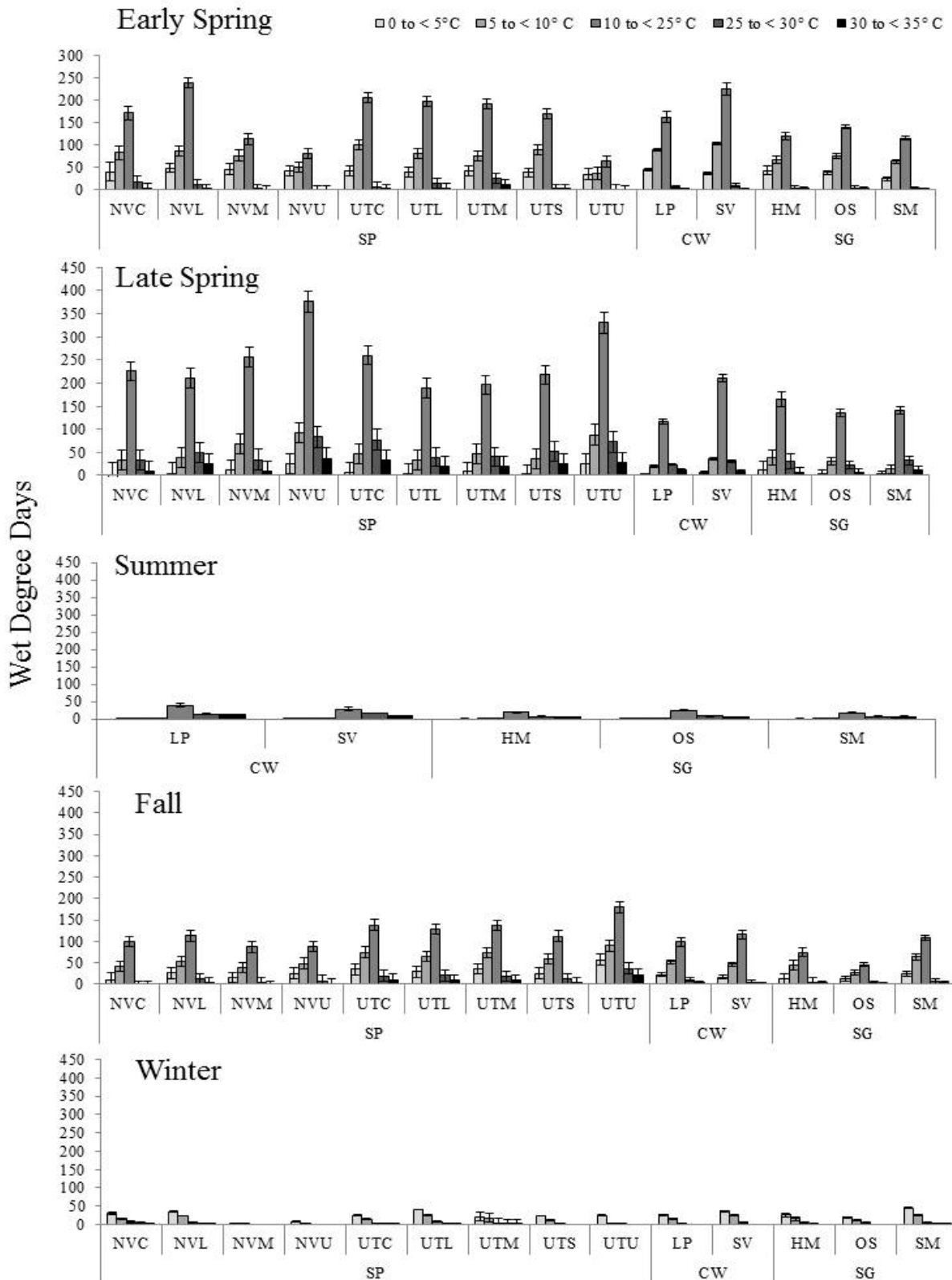


Figure 1-6. Wet degree day estimates by site, season and temperature range. Experimental

designs are SP = Sagebrush & Perennial Grass sites, CW = Crested Wheatgrass sites, and SG = Sagebrush sites. 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, BM = Blue Mountain, BC = Bridge Creek, DR = Devine Ridge, MC = Marking Corral, SR = South Ruby, GV = Greenville Bench, SC = Scipio, OJ = Onaqui Woodland, ST = Stansbury. Error bars represent ± 1 standard error.

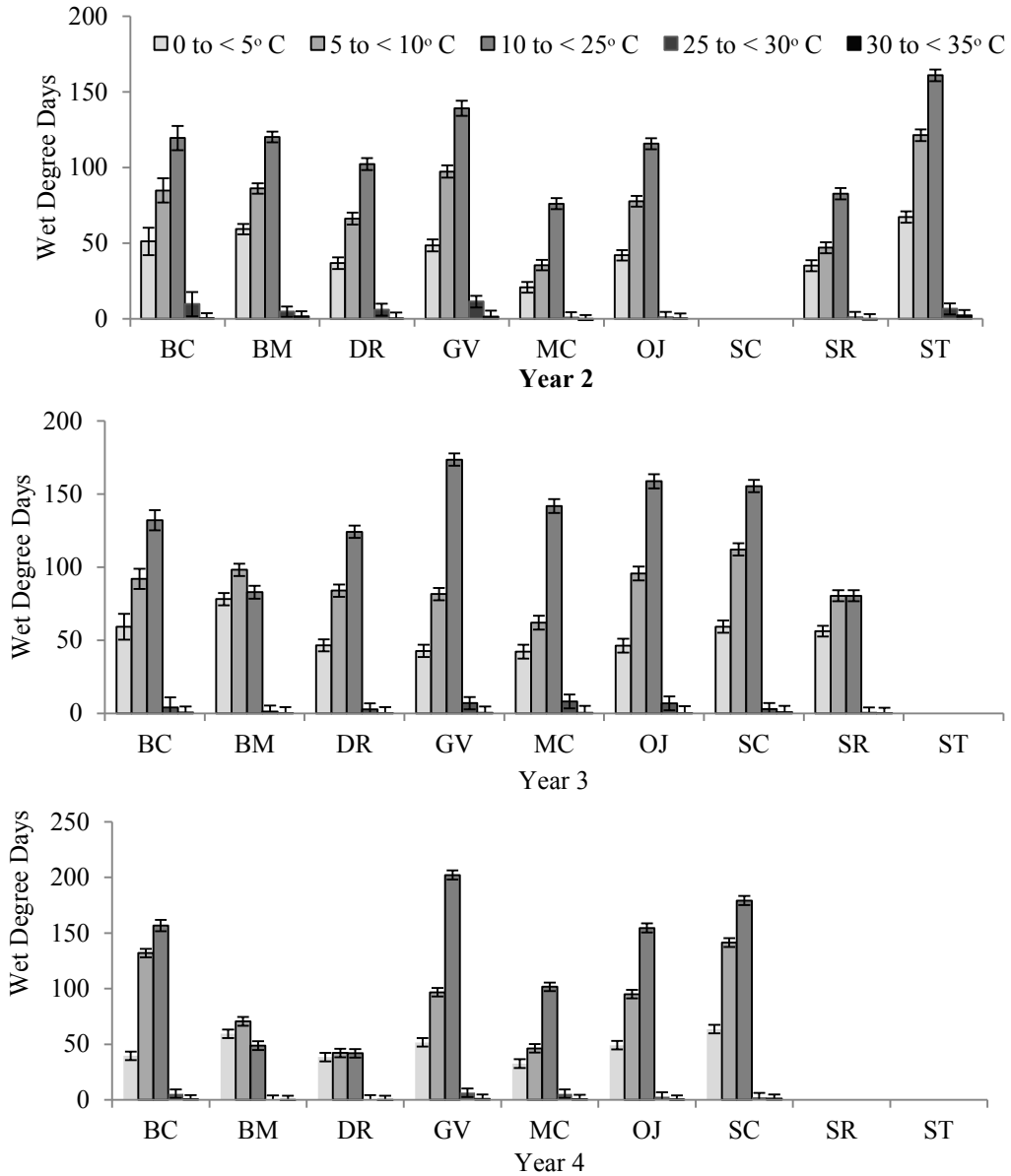


Figure 1-7. Site averages of wet degree days for second, third, and fourth years since tree reduction treatments for seedbed temperature ranges in early spring. Data are averages of untreated and treated plots. Sites are BC = Bridge Creek, BM = Blue Mountain, DR = Devine

Ridge, MC = Marking Corral, OJ = Onaqui Juniper, SC = Scipio, SR = South Ruby, and ST = Stansbury. Error bars are ± 1 standard error.

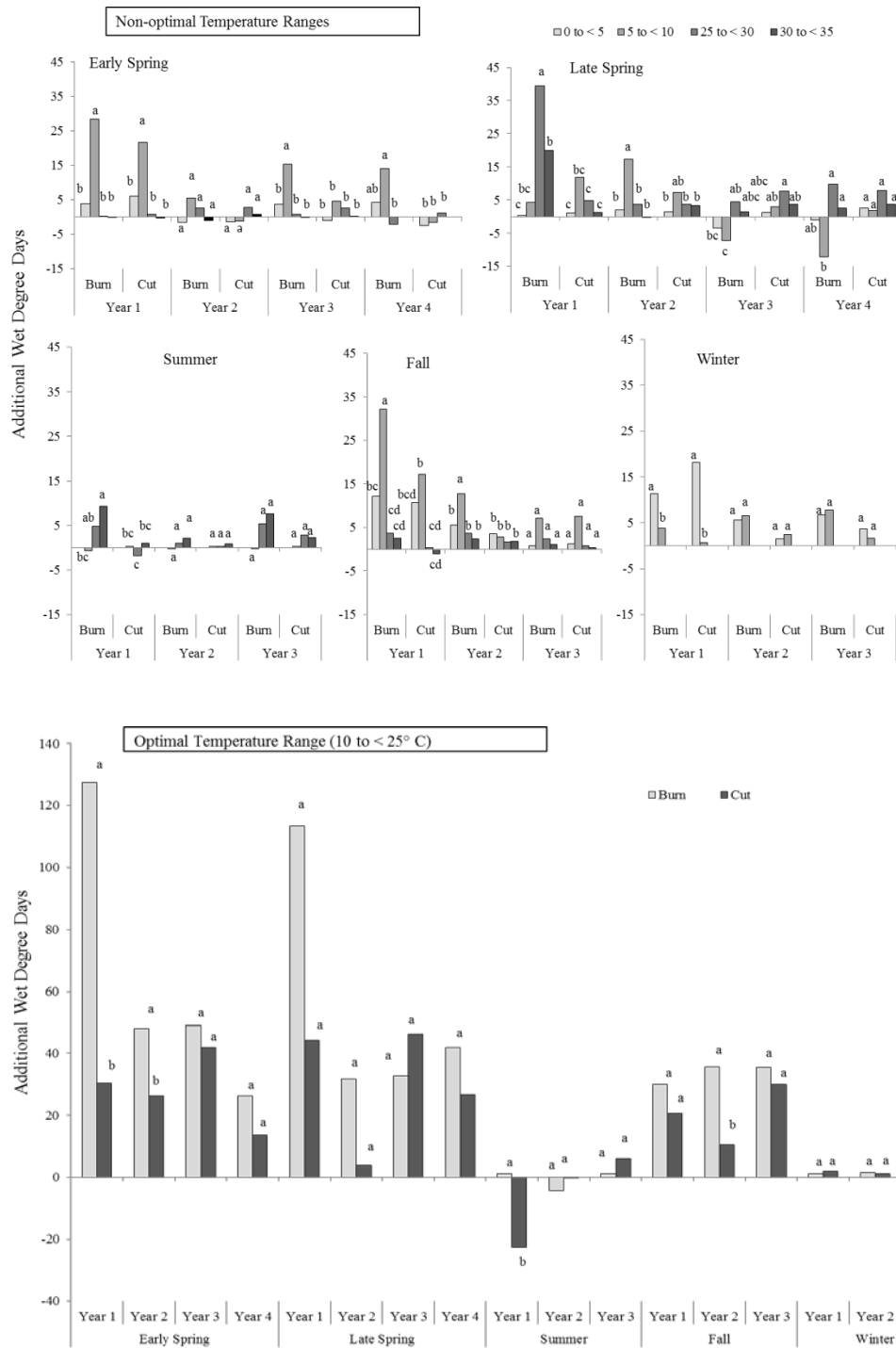


Figure 1-8. Seasonal additional wet degree days by treatment for non-optimal (top) and optimal (bottom) temperature ranges. Comparisons are within year.

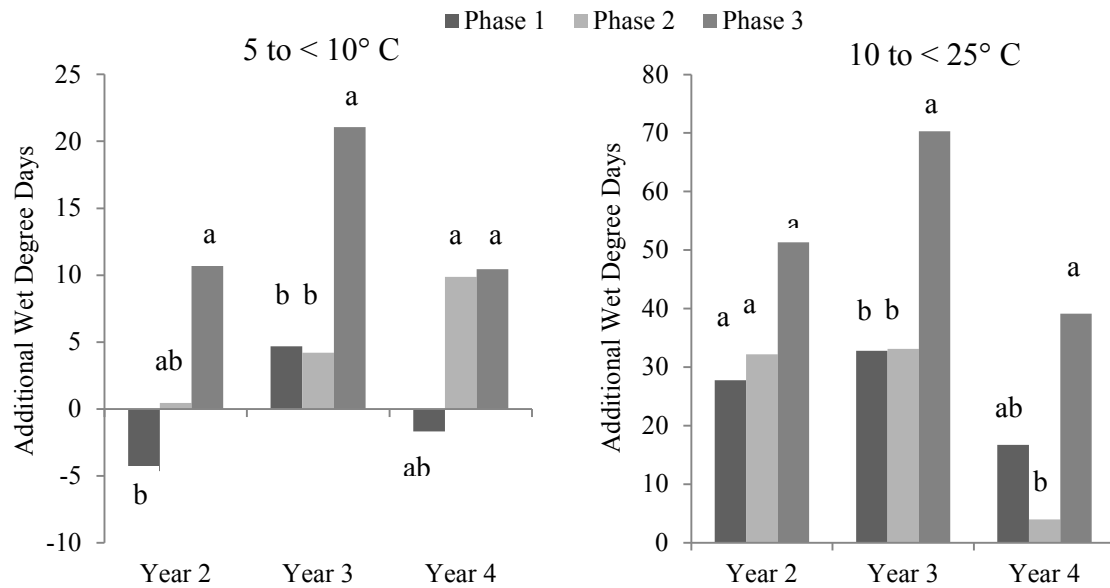


Figure 1-9. Additional wet degree days (tree treatment wet degree days-untreated wet degree days) for three woodland infilling phases at temperature ranges of 5 to < 10° C and 10 to < 25° C. Shown are the second through fourth year since treatment during the early spring. Different letters indicate significant differences between phases with each year.

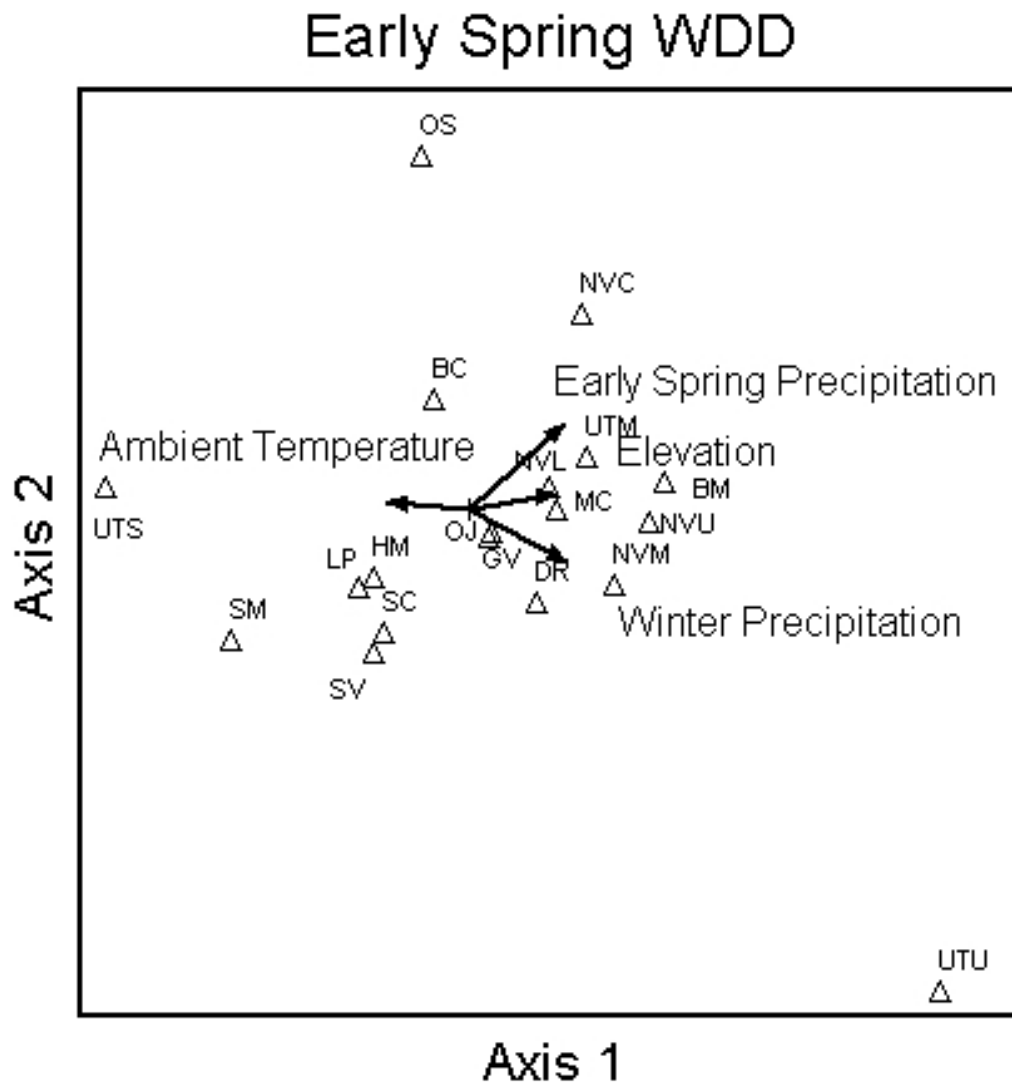


Figure 1-10. The distribution of wet degree days for 19 sagebrush steppe sites in the Great Basin as explained by six site physical characteristics. Site physical characteristics were winter precipitation, early spring precipitation, ambient air temperature, elevation, solar radiation, and slope. Only site physical characteristics with $r^2 > 0.2$ are illustrated with black arrows. 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, BM = Blue Mountain, BC = Bridge Creek, DR = Devine Ridge, MC = Marking Corral, GV = Greenville Bench, SC = Scipio, OJ = Onaqui Woodland.

CHAPTER 2: GERMINATION PREDICTION OF 30 PLANT MATERIALS USING SOIL
WATER POTENTIAL AND TEMPERATURE AT 24 GREAT BASIN SITES

Nathan L. Cline¹, Bruce A. Roundy², Stuart Hardegree³, and Jennifer Rawlins⁴

Authors are ¹Research Associate, Brigham Young University, Provo, UT, USA 84602, ²Professor Range Science, Brigham Young University, Provo, UT, USA 84602, ³ Plant Physiologist, Northwest Watershed Research Center USDA-ARS, Boise, ID, USA, ⁴ previously Research Assistant, Brigham Young University, Provo, UT, USA 84602.

This is Contribution Number 54 of the Sagebrush Steppe Treatment Evaluation Project (SageSTEP), funded by the U.S. Joint Fire Science Program, the Bureau of Land Management, the National Interagency Fire Center, and The Great Basin Native Plant Project.

Correspondence: Bruce A. Roundy, Department of Plant and Wildlife Sciences, 275 WIDB, Brigham Young University, Provo, UT 84602, Email: bruce_roundy@byu.edu.

Proposed Journal: Environmental and Experimental Botany

ABSTRACT

Preventing cheatgrass (*Bromus tectorum* L.) dominance associated with frequent wildfires requires successful establishment of desirable species in rehabilitation and fuel-control projects. Germination prediction models may provide useful criteria for selecting among alternative plant materials by predicting relative performance under seedbed water potential and temperature conditions of specific sites. Using a wet thermal time model for germination prediction, progress toward germination (PTG) was estimated as a function of seedbed temperature ($> 0^{\circ}\text{C}$) when soils were above a threshold water potential of -1.5 MPa. Progress toward germination is summed over time and a value > 1 indicates positive germination potential at a given site. We estimated and compared PTG for 31 seedlots (10 species) using near surface (1-3 cm) soil water potential and temperature at 24 sites in the Great Basin. We determined the effects of site, season, year, tree removal method, tree infilling phase, and microsite on estimated PTG. Sites included grassland (*Elymus* spp. and *Agropyron* spp.) and sagebrush stands (*Artemisia* spp.) with and without woodland species (*Juniperus* spp. and *Pinus* spp.). Soils were wet and warm enough in early spring, late spring, and fall for $\text{PTG} > 1$ indicating potential germination for most plant materials and species. In general, estimated PTG was highest for cheatgrass collections followed by perennial grasses and then forbs. Progress toward germination varied significantly for seasons, years, and sites. Prescribed burning increased PTG three times more than either tree cutting or mechanical shredding. Progress toward germination was highest for tree reduction treatments implemented at an advanced phase of infilling and for tree drip line compared to other microsities. Winter precipitation, elevation, and solar radiation were most strongly positively associated with early spring PTG, while air temperature was negatively associated with PTG. Because seedbed temperatures and water potentials do not appear to be

limiting to germination for the plant materials tested, selection based on germination potential alone may not improve rangeland seeding success for these materials. Selection based on higher or lower PTG results in selecting for earlier or later germination, which could have implications for seedling survival. Prediction of germination in conjunction with root growth predictions may allow for potential seedling survival predictions and plant material screening.

INTRODUCTION

Land managers plant seeds on rangelands to establish desirable plant species, stabilize soils and prevent weed dominance (Call and Roundy, 1991; Whisenant, 1999). Plant materials are selected based on regional adaptation, but germination in particular is constrained by site and year-specific soil water and temperature conditions (Rawlins et al., 201b). Germination prediction models may aid in plant material selection by predicting germination timing using site-specific soil temperature and seedbed water potential (Roundy et al., 2007; Rawlins et al., 2012b). Thermal time models that estimate potential germination are developed by measuring percent germination over time for a range of constant incubation temperatures of a seedlot. The inverse of time to germination (germination rate) for each seed subpopulation at various constant temperatures are fitted to linear and non-linear regression equations for each seedlot (Garcia-Huidobro et al., 1982a; 1982b; Roundy and Biedenbender, 1996; Hardegree et al., 1999; McDonald, 2002a; 2002b; Hardegree, 2006; Rawlins et al., 2012a). Germination rate is summed as progress toward germination (PTG) and a value > 1 indicates positive germination potential at a given site. Some germination models incorporate soil water potential and use hydrothermal-time to predict PTG under dynamic field soil water conditions (Alvarado and Bradford, 2002; Bradford, 2002; Meyer and Allen, 2009). Continuous measurements of soil water potential at seeding depths, however, have proven problematic due to technology limitations (Taylor et al., 2007).

Thermal time models that characterize soil conditions as either wet or dry using a threshold water potential (wet thermal time) rather than incorporating continuous water potential measurements provide a more simplistic approach to utilizing soil water data in the development of thermal time germination models (Finch-Savage and Phelps, 1993; Finch-Savage et al., 2001;

Roundy et al., 2007; Rawlins et al., 2012b). Roundy et al. (2007) utilized wet thermal time models to compare potential PTG in cheatgrass (*Bromus tectorum* L.) seedlots. Wet thermal time models produced relatively accurate predictions for germination of six species at two locations in Utah (Rawlins et al., 2012b). Utilizing wet thermal time models to predict PTG for multiple seedlots and species under a range of field conditions may aid in successful plant material selection by identifying seed populations with a greater or lesser potential for germination.

To help identify suitable plant material for revegetation projects where soil moisture and temperature have not been monitored, PTG may be estimated using associated site characteristics. Precipitation and temperature would be expected to influence wet thermal time (Roundy et al., 2007). Likewise, site characteristics, such as slope, elevation, and solar radiation also influence soil moisture and temperature and, consequently, may influence PTG (Reid, 1973; Cantón et al., 2004; Weisberg et al., 2007; Bochet et al., 2007). Yet, their association to PTG has not been quantified.

Seedbed water potential and temperature conditions were sufficient for cheatgrass subpopulations to germinate in the fall and spring most years on nine big sagebrush (*Artemisia tridentata* Nutt.) sites in the Great Basin (Roundy et al., 2007). Sagebrush and perennial grass removal had much less effect on cheatgrass germination than season, site, or year (Roundy et al., 2007). Also, cheatgrass germinates at faster rates than perennial grasses under simulated seedbed temperature and soil water conditions (Hardegree et al., 2003; 2013). Cheatgrass has not been found to significantly deplete soil moisture when compared to perennial grasses across the soil profile (Cline et al., 1977; Ryel et al., 2010). With sufficient wet thermal time, successful germination of revegetation plant materials may occur regardless of the presence of cheatgrass.

Although site, season, year, various tree removal methods, tree infilling phase, and various

microsites affect the time of soil water availability (Roundy et al., 2014b), effects of these factors on potential germination of weeds and revegetation species have yet to be determined.

Here we investigated differences in PTG in revegetation seed populations and cheatgrass by site, season, year, various tree (*Juniperus* spp. and *Piñus* spp.) removal methods, tree infilling phase, and various microsites. We also quantified the influence of site characteristics of seasonal precipitation, air temperature, solar radiation, slope, and elevation on PTG.

METHODS

Study Sites

We used soil water potential and temperature data collected for four experiments (located on 24 total sites) described in Cline et al. (2014). The four experiments were designated (1) sagebrush (*Artemisia* spp.) and perennial grass, (2) crested wheatgrass (*Agropyron cristatum* L.), (3) sagebrush, and (4) woodland (Cline et al., 2014). The sagebrush and perennial grass 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 (Blank et al., 2007; Chambers et al., 2007; Roundy et al., 2007; Cline et al., 2014). The crested wheatgrass experiment was located in two crested wheatgrass monocultures with data from 2006 to the spring of 2011 (Hulet et al., 2010; Rawlins et al., 2012b; Cline et al., 2014). The sagebrush experiment was located on three sagebrush and perennial bunchgrass sites (separate from the sagebrush and perennial grass experiment) and was measured from 2008 to the spring of 2011 (McIver et al., 2010; Cline et al., 2014). The woodland experiment was located on four Utah

juniper (*Juniperus osteosperma* (Torr.) Little) sites, two piñon (*Pinus edulis* Engelm.)-juniper, and three western juniper (*Juniperus occidentalis* Hook.) sites for varying years of data since tree reduction treatment (Table 1; Cline et al., 2014; Roundy et al., 2014b). Plots used in the sagebrush and perennial grass, crested wheatgrass, and sagebrush 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.

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). Collection of soil water matric potential, soil temperature, air temperature, precipitation, slope, solar radiation, and elevation data are described in Cline et al. (2014). Cline et al. (2014) also described the experimental design as well as the collection of soil water potential and temperature data. Cline et al. (2014) also characterized the climate, as well as seedbed soil moisture and temperature conditions for each experiment over the same time periods as in the present study.

We compiled 19 germination prediction equations for median germination rate of 19 seedlots (eight cheatgrass, two crested wheatgrass, two bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) A. Löve], and one squirreltail) from previous studies (Table 2; Roundy et al., 2007; Rawlins et al., 2012a). Another 11 seedlot equations (five species) were derived from constant incubation temperature data compiled from Hardegree et al. (2008, 2010).

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 2, 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 ($< 5^{\circ}\text{C}$, 10°C , or sometimes 15°C) as described in Hardegree 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 soil temperature 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. Increasing PTG sums of > 1 indicate increasing potential for seeds to germinate. Roundy et al. (2007) and Rawlins et al. (2011b) described two methods to sum hourly PTG: cumulative - summing across intermittent wet periods in a season and singular - requiring thermal summation to occur within a single wet period. Our study reports 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 (SAS® Institute, Inc., 2001) to analyze each experiment separately. Site was considered a random block across the region for the sagebrush and perennial grass, sagebrush, 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 crested wheatgrass experiments, while woodland experiments had additional fixed factors of tree removal methods, tree infilling phase, and microsites of the tree drip line, shrub mound, and interspace. The tree drip line is defined as the perimeter of where canopy covers the surface. 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). Significant differences among fixed factors were determined by the Tukey-Kramer multiple comparison test ($P < 0.05$).

We summarized the effects of site characteristics on the PTG of seedlots for early spring, late spring, and from 1 September to 30 June using Canonical Correspondence Analysis (CCA) in PC-ORD®. Site characteristics for each time period were precipitation seasonal average air temperature, slope, solar radiation, and elevation. For early spring, winter and early spring precipitation were included in the analysis. Sites with missing data were excluded. Default CCA settings were used and significance was determined using a randomization test ($P < 0.05$).

RESULTS

Percentages of PTG estimations for seasons, sites, treatments, infilling phases, and microsites where seedbeds accumulated enough PTG to sum to 1 or greater averaged from $62.8 \pm 14.8\%$ (sagebrush) to $78.7 \pm 4.94\%$ (sagebrush and perennial grass) for fall, from $18.2 \pm 4.54\%$ (sagebrush and perennial grass) to $23.6 \pm 8.25\%$ (crested wheatgrass) for winter, from $86.6 \pm 3.55\%$ (sagebrush and perennial grass) to $94.3 \pm 0.86\%$ (crested wheatgrass) for early spring, and from $79.3 \pm 3.42\%$ (crested wheatgrass) to $90.1 \pm 1.85\%$ (sagebrush) for late spring among all four experiments. Percent of potential germination estimated for each site by season is noted in Table 3. Generally, seedbeds summed enough PTG to predict at least 50% germination during

fall, early spring, and late spring for a majority of plant materials tested. With some exceptions, germination was predicted for < 30% of tested instances during the winter. At Bridge Creek, 76.1% of potential predictions summed sufficient PTG for germination during the winter.

Sagebrush and Grasslands

Seedbeds in early and late spring generally averaged nearly three times the PTG needed to predict 50% germination while in fall, seedbeds summed nearly two times the PTG required for germination (Fig. 1). In winter, seedbeds always averaged < 1 PTG for the nonwoodland experiments. Because the number of days was uneven for each season, we compared annual PTG for each season separately for all experiments (Roundy et al., 2014b; Cline et al., 2014).

Progress toward germination varied by sites, years, and seedlots for each season ($P < 0.05$). Progress toward germination averaged as high as 5.15 ± 0.27 in early spring, 8.93 ± 0.22 in late spring, 5.52 ± 0.14 in fall, and 1.11 ± 0.04 in winter (Fig. 2). The effects of year and seedlot were significant for all seasons and for sagebrush and perennial grass, crested wheatgrass, and sagebrush experiments (Table 4, $P < 0.05$). Nearly all the interactions between seedlots and year were also significant for every season for the sagebrush and perennial grass, crested wheatgrass, and sagebrush experiments ($P < 0.05$). For sites, the majority of PTG was summed during early and late spring (Fig. 3). Summation of PTG generally was highest in cheatgrass seedlots, followed by perennial grasses and then forbs (Fig. 4). As expected, years with the highest precipitation had the highest PTG (Cline et al. 2014).

Tree Removal Response

Seedbeds in woodlands were similar to those on the sagebrush and grassland sites with early and late spring having the most seasonal PTG, followed by fall and winter (Table 5).

Progress toward germination rankings among seedlots for woodland seedbeds were also similar to those for the other experiments (cheatgrass > perennial grasses > forbs) (Fig. 5). The effects of seedlot, tree removal methods, and tree infilling phase were generally significant (Table 6, $P < 0.05$). Because of significant site differences (Fig. 7), 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.

Main effects and interactions on additional PTG were generally significant for tree removal methods, tree infilling phase, and microsites through the third year after treatment (Table 6, $P < 0.05$). While treatment was significant during the early spring ($F_{1,3812} = 66.03$, $P < 0.0001$) of the fourth year, treatment was not significant for late spring ($F_{1,3284} = 0.73$, $P = 0.3944$). Burning added as much as 1.05 ± 0.15 additional PTG for a season, while tree cutting added as much as 0.88 ± 0.14 additional PTG (Fig. 8). Burning generally resulted in more additional PTG than tree cutting for all four seasons of the first 2 yr and early spring of the third and fourth years after tree reduction ($P > 0.05$). Mechanical shredding added as much as 1.99 ± 0.93 additional PTG (yr 1) at Utah sites. In comparison with burning and tree cutting at Utah sites, shredding exhibited as much as 0.4 PTG less than burning and as much as 1.3 PTG more than tree cutting during the early spring, late spring, and fall of the first year following treatment ($P < 0.05$). However, during the second year shredding and burning were not different ($P > 0.05$). During the third and fourth years, shredding added as much as 0.3 PTG more than both burning and tree cutting during the late spring ($P < 0.05$). Implementation of tree reduction at Phase 3 of woodland infilling generally added more PTG than tree reduction at Phases 1 and 2 for most treatments and microsites during early spring, late spring, and fall (Fig. 9, $P < 0.05$). Tree microsites added more PTG than shrub and interspace microsites during the first year following

treatment at Utah sites and during early spring for the second, third, and fourth year following treatment at all woodland sites (Fig. 10, $P < 0.05$).

According to the CCA, PTG for September through June was associated with precipitation, elevation, and solar radiation, while early spring PTG was associated with temperature, elevation, winter precipitation, and solar radiation (Fig. 11, $P = 0.006$). The CCA for late spring was not significant ($P > 0.05$). For September through June, total variation explained by the CCA was 59.4 % (axis 1 = 49.2 %, axis 2 = 7.8 %, and axis 3 = 2.4 %). For early spring, total variation explained by the CCA was 64.3% (axis 1 = 58.2 %, axis 2 = 5.7 %, and axis 3 = 0.5 %). As the majority of the variation explained was in the first two axes for both ordinations, we focused our analysis axis 1 and 2. For September through June, axis 1 had a positive correlation with elevation ($R^2 = 0.130$), but a negative correlation with solar radiation ($R^2 = -0.572$) and precipitation ($R^2 = -0.681$). Axis 2 had a positive correlation with solar radiation (0.176) but a negative correlation with elevation ($R^2 = -0.647$) and precipitation ($R^2 = -0.265$). For early spring, axis 1 had a positive correlation with solar radiation ($R^2 = 0.222$), winter precipitation ($R^2 = 0.751$), and elevation ($R^2 = 0.243$), but had a negative correlations with air temperature ($R^2 = -0.507$). Axis 2 had a positive correlation with air temperature ($R^2 = 0.694$) and winter precipitation ($R^2 = 0.014$), but had a negative correlation with solar radiation ($R^2 = -0.549$) and elevation ($R^2 = -0.885$). For September through June, woodland sites were associated with more precipitation, while sagebrush sites tend to be associated with less precipitation. For early spring, higher elevation sites were associated with increased elevation, solar radiation, and winter precipitation. Warmer, drier sites were more associated with temperature.

DISCUSSION

Use of soil microclimate conditions to evaluate potential germination response in field seedbeds has been limited, but has potential for improved revegetation decision-making (Hardegree et al. 2010). Roundy et al. (2007) assessed PTG using the wet thermal time model for 18 seedlots of *B. tectorum* across 4 yr and nine sites in NV and UT. Hardegree et al. (2008, 2010, 2003, 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 based on soil microclimate conditions at two sites in UT for 3 yr. Their study assessed potential germination for five species. Our study evaluated 31 species and seedlots from previous studies (Roundy et al., 2007; Hardegree 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; Hardegree et al., 2010; Rawlins et al., 2012b), added three sagebrush sites with the sagebrush experiment, and added nine sites with the woodland experiment.

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; Leffler and Ryel, 2012; Roundy et al., 2014b). For our sites, seedbeds summed sufficient thermal time when seedbeds were wet in fall, early, and late spring to predict germination of 50% of the seed population for most of the plant materials we studied. These findings are consistent with Roundy et al., (2007) where cheatgrass seedlots were found to potentially germinate at the sagebrush and perennial grass sites for most years during the fall and spring. Though, potential germination was predicted for most plant materials and sites, we found the PTG varied with season, site, and year.

Roundy et al., (2007) also found that season had the greatest effect on PTG, followed by sites and years.

Results of Roundy et al. (2007) and our study suggest that germination does not generally limit plant establishment on these sagebrush zone sites in the Great Basin on most years during the growing season. These findings coincide with James et al. (2011) who found that when comparing successful transitions between perennial grass life stages, germination was among those with the highest probability for success. This finding limits the utility of using germination thermal time models as a tool to improve plant material selection for revegetation projects. Germination estimates do provide comparisons between plant materials that may lend understanding to niche competition and also indicate which plant materials have the most time to extend their roots. For example, while seedbeds generally summed more than enough PTG for potential germination during either early spring or late spring for most plant materials, the entire spring was required to sum sufficient PTG for basin wildrye (*Leymus cinereus* (Scribn. & Merr.) Á. Löve) and lupine (*Lupinus arbustus* Douglas ex Lindl.) to germinate if planting date was on 1 March. Delayed germination could limit seedling survival for these species if seminal root extension does not remain in wet soils ahead of the soil drying front (Cline et al., 2014b). Germination timing, especially when grouped with root growth timing, may be useful in determining the potential for seedling survival and may be a useful plant material selection tool.

The competitive ability of sown perennial grasses and forbs compared to cheatgrass has been identified a possible reason for the invasion and dominance of cheatgrass after fire rehabilitation seedings conducted by land management agencies in the Intermountain West (Call and Roundy, 1991; Whisenant, 1999). Hardegree et al. (2010) and Rawlins et al. (2012a) found that cheatgrass has a faster germination rate than perennial grasses. In support of their findings,

PTG in our study generally ranked highest in cheatgrass, followed by perennial grasses, and then forbs for every experiment. Previous research found evidence that faster germination and establishment in cheatgrass may reduce plant available water for slower germinating perennial grasses and forbs (Chambers et al., 2007; Roundy et al., 2007). Yet Ryel et al. (2010) found that cheatgrass has very little effect on plant available water in the top 3 m of the soil profile during the spring. However, their most shallow soil moisture measurement was at 30 cm soil depth and not at the seedbed. Fast germination in cheatgrass may also facilitate early soil nitrogen utilization during the fall and early spring compared to perennial grasses (Leffler et al., 2011; 2013). Cheatgrass seedlings have a higher nitrogen absorption rate compared to some common revegetation plant materials, such as *A. cristatum*, *E. Elymoidies*, and *P. spicatum* (Leffler et al., 2011), at temperature ranges where wet degree days are highest in the seedbed (Cline et al., 2014). The invasibility of cheatgrass increases with increased nitrate and soil water availability as a result of vegetation disturbance (Chambers et al., 2007).

Percent cheatgrass cover increased with increasing pretreatment tree cover by the third year post treatment for the woodland experiment (Roundy et al., 2014a). Bates et al. (2013) discovered that cheatgrass replaced native plants at Phase 3 infilling of a western juniper woodland. At temperature ranges between 5° C and 25° C where the majority PTG is summed, Cline et al. (2014) found an increase in wet degree days with treatment and increasing infilling phase. We found that tree removal added PTG for all 31 plant materials, including cheatgrass. We also found that implementing tree reduction at woodland infilling Phase 3 added more PTG than implementation at lower infilling phases. While effects of tree reduction on increasing time of available water may be expected to diminish over time as residual understory plants grow and

transpire, Roundy et al. (2014b) and Cline et al. (2014), reported that these effects extend at least to the fourth spring since treatment.

Miller et al. (2014) indicated that postburn vegetation recovered and surpassed preburn cover percentages by the second or third year following treatment. They also noted that perennial grass cover increased during second and third year following mechanical treatments at the woodland sites. However, the increase in cover came primarily from residual plant growth and not from new seedlings. Low seedling density initially following treatment may result from tree exclusion of understory plants and reduction of propagules. Yet our findings for this study indicate that for most tested seedlots, including cheatgrass, seedbeds sum additional PTG as a result of tree removal. As a result, tree removal improves the likelihood of germination and subsequent establishment. Seeding desirable plant materials following tree removal may be needed to accomplish restoration goals where desirable residual propagules are limited (Bybee, 2013).

Prescribed burning added more wet degree days in the seedbed than tree cutting during the spring only (Cline et al., 2014). Yet we found that burning resulted in twice the additional PTG as tree cutting during every season at least up to the second year after treatment. By the fourth year after treatment, prescribed burned seedbeds had more additional PTG than those in cut treatments only in early spring. Tree shredding produced similar additional PTG as prescribed burning in early spring, but less than half of the additional PTG as produced by prescribed fire during late spring. One intriguing exception was during the fourth year, when shredding added more additional PTG than both burning and tree cutting during early and late spring (Fig. 8). Shredding reduces runoff from hill slopes and adds wet degree days to seedbeds (Cline et al. 2010, 2014). 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). The additional PTG in shredded plots may be an indication of a prolonged resource pulse as a result of shredded material limiting the use of resources by colonizers.

We found more additional PTG at the tree drip line compared to interspace microsites during early spring. Also, Roundy et al. (2014b) reported that tree reduction increased wet days more at the tree drip line than at other microsites at 18 to 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; 2014; Young et al., 2013). Also, piñon and juniper tree structure filters water away from its trunk to the tree drip line. Interspace microsites have been found to dry more rapidly than tree mounds (Breshears et al., 1998). Presumably by reducing transpiration soil water loss, tree reduction increases time of available soil water more than does ground cover by tree litter or shredded debris (Young et al., 2013). However, tree reduction and soil cover by litter or debris may additively increase time of available soil water (Young et al., 2013).

Influence of Site Characteristics

Cline et al. (2014) found that winter and early spring precipitation as well as air temperature and elevation positively influenced wet degree days across the majority of our sites during the early spring. However, we did not find a significant association with PTG and early spring precipitation. We also found that early spring PTG associated positively with winter precipitation, elevation, and solar radiation, while PTG associated negatively with air temperature, probably because increased air temperature was associated with fewer wet days in the seedbed. This provides further evidence that winter precipitation has an important role in

successful seedling establishment. Reasons for the difference between PTG and wet degree days are unclear; however Cline et al. (2014) included only one measure of wet degree days per site per year, while our CCA had increased site resolution because we included 3 yr averages of PTG of 31 plant materials.

Precipitation, elevation, and solar radiation were positively associated with PTG for September through June ($P < 0.05$). Increased elevation resulted in a decreased in temperature and subsequent decreased total PTG during this time period. Also, increasing precipitation and solar radiation in woodlands and sagebrush communities might be expected to increase PTG by increasing plant available water and the thermal environment of the soil. Yet our CCA analysis indicates that they associated with decreasing precipitation and solar radiation. As water is limiting in these communities, increased plant available water may be transpired by existing vegetation for increased growth, as was the case when trees were removed at our woodland sites (Miller et al., 2013; Roundy et al., 2013). When shrub and herbaceous cover were probably reduced because of drought (decreased precipitation) at sagebrush and perennial grass sites, PTG was decreased. Conversely, increased tree infilling in woodlands may result in competitive exclusion of understory species also increasing bare ground (Miller et al., 2008). Thus, increasing precipitation at sites where understory vegetation is not present to transpire newly available plant available water results in increased PTG.

Conclusions

Development and use of wet thermal time regressions for a large number of species and seedlots provided an opportunity to predict 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 were found, these factors rarely influence 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. Though thermal time models for germination do not appear to be discriminate enough for plant material selection based solely on the potential for germination, estimation of germination timing in conjunction with root growth timing may be used as a tool for plant material selection and generally evaluate sites and plant materials for potential revegetation.

LITERATURE CITED

- Alvarado, V., and K. J. Bradford. 2002. A hydrothermal time model explains the cardinal temperatures for seed germination. *Plant, Cell, Environ.* 25:1061–1069.
- Bates, J. D., R. N. Sharp, and K. W. Davies. 2013. Sagebrush steppe recovery after fire varies by development phase of *Juniperus occidentalis* woodland. *Int. J. Wildland Fire* <http://dx.doi.org/10.1071/WF12206>
- Blank, R. R., J. C. Chambers, B. A. Roundy, and A. Whittaker. 2007. Nutrient availability in rangeland soils: Influence of prescribed burning, herbaceous vegetation removal, overseeding with *Bromus tectorum*, season, and elevation. *Rangeland Ecol. Manage.* 60:644–655.
- Bochet, E., P. García-Fayos, B. Alborch, and J. Tormo. 2007. Soil water availability effects on seed germination account for species segregation in semiarid roadslopes. *Plant Soil* 295:179–191.
- Bradford, K. J. 2002. Applications of hydrothermal time to quantifying and modeling seed germination and dormancy. *Weed Sci.* 50:248–260.
- Breshears, D. D., J. W. Nyhan, C. E. Heil, and B. P. Wilcox. 1998. Effects of woody plants on microclimate in a semiarid woodland: Soil temperature and evaporation in canopy and intercanopy patches. *Int. J. Plant Sci.* 159:1010.
- Bybee, J. 2013. Understory vegetation response to mechanical mastication of piñon and juniper woodlands [thesis]. Provo, UT, USA: Brigham Young Univeristy.

- Call, C. A., and B. A. Roundy. 1991. Perspectives and processes in revegetation of arid and semiarid rangelands. *J. Range Manage.* 44:543–549.
- Cantón, Y., A. Solé-Benet, and F. Domingo. 2004. Temporal and spatial patterns of soil moisture in semiarid badlands of SE Spain. *J. Hydrol.* 285:199–214.
- 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*? *Ecol. Monogr.* 77:117-145.
- Cline, J. F., D. W. Uresk, and W. H. Rickard. 1977. Comparison of soil water used by a sagebrush-bunchgrass and a cheatgrass community. *J. Range Manage.* 30:199.
- Cline, N. L., B. A. Roundy, and W. F. Christensen. 2014. Wet-thermal time at five temperature ranges in seedbeds of the sagebrush steppe ecosystem. *Rangeland Ecol. Manage.* xx:xx-xx.
- Cline, N., B. Roundy, F. Pierson, P. Kormos, and C. J. Williams. 2010. Hydrologic response to mechanical shredding in a juniper woodland. *Rangeland Ecol. Manage.* 63:467-477.
- Finch-Savage, W. E., and K. Phelps. 1993. Onion (*Allium cepa* L.) seedling emergence patterns can be explained by the influence of soil temperature and water potential on seed germination. *J. Exp. Bot.* 44:407-414.
- Finch-Savage, W. E., K. Phelps, J.R.A. Steckel, W.R. Whalley, and H.R. Rowse. 2001. Seed reserve-dependent growth responses to temperature and water potential in carrot (*Daucus carota* L.). *J. Exp. Bot.* 52:2187-2197.

- Garcia-Huidobro, J., J. L. Monteith, and G. R. Squire. 1982a. Time, temperature and germination of pearl millet (*Pennisetum typhoides* S. & H.): I. Constant temperature. *J. Exp. Bot.* 33:288–296.
- Garcia-Huidobro, J., J. L. Monteith, and G. R. Squire. 1982b. Time, temperature and germination of pearl millet (*Pennisetum typhoides* S. & H.) II. Alternating temperature. *J. Exp. Bot.* 33:297–302.
- Hardegree, S. P. 2006. Predicting germination response to temperature. I. Cardinal-temperature models and subpopulation-specific regression. *Ann. Bot.* 97:1115–1125.
- Hardegree, S. P., T. A. Jones, F. B. Pierson, P. E. Clark, and G. N. Flerchinger. 2008. Dynamic variability in thermal-germination response of squirreltail (*Elymus elymoides* and *Elymus multisetus*). *Environ. Exp. Bot.* 62:120–128.
- Hardegree, S. P., T. A. Jones, and S. S. Van Vactor. 2002. Variability in thermal response of primed and non-primed seeds of squirreltail [*Elymus elymoides* (Raf.) Swezey and *Elymus multisetus* (J. G. Smith) M. E. Jones]. *Ann. Bot.* 89:311–319.
- 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. *Environ. Exp. Bot.* 69:320–327.

- Hardegree, S. P., S. S. Van Vactor, F. B. Pierson, and D. E. Palmquist. 1999. Predicting variable-temperature response of non-dormant seeds from constant-temperature germination data. *J. Range Manage.* 52:83–91.
- Hillel, D. 2004. Introduction to environmental soil physics. Page 112. *Elsevier Science (USA), Oxford, UK.*
- Hulet, A., B. a. Roundy, and B. Jessop. 2010. Crested wheatgrass control and native plant establishment in Utah. *Rangeland Ecol. Manage.* 63:450–460.
- James, J. J., T. J. Svejcar, and M. J. Rinella. 2011. Demographic processes limiting seedling recruitment in arid grassland restoration. *J. Appl. Ecol.* 48:961–969.
- Jordan, G. L., and M. R. Haferkamp. 1989. Temperature responses and calculated heat units for germination of several range grasses and shrubs. *J. Range Manage.* 42:41–45.
- Leffler, A. J., J. J. James, and T. A. Monaco. 2013. Temperature and functional traits influence differences in nitrogen uptake capacity between native and invasive grasses. *Oecologia* 171:51–60.
- Leffler, A. J., T. A. Monaco, and J. J. James. 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.
- Leffler, A. J., and R. J. Ryel. 2012. Resource pool dynamics: Conditions that regulate species interactions and dominance. Pages 57–78 in T. A. Monaco and R. L. Sheley, editors.

Invasive plant ecology and management: Linking processes to practice. *CABI Publishing, Wallingford, GB.*

McDonald, C. K. 2002a. Germination response to temperature in tropical and subtropical pasture legumes. 1. Constant temperature. *Australian Journal of Experimental Agriculture* 42:407–419.

McDonald, C. K. 2002b. Germination response to temperature in tropical and subtropical pasture legumes. 2. Alternating temperature. *Aust. J. Exp. Ag.* 42:421–429.

McIver, J., M. Brunson, S. Bunting, J. Chambers, N. Devoe, P. Doescher, J. Grace, D. Johnson, S. Knick, R. Miller, M. Pellant, F. Pierson, D. Pyke, K. Rollins, B. Roundy, E. Schupp, R. Tausch, and D. Turner. 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.*

Meyer, S. E., and P. S. Allen. 2009. Predicting seed dormancy loss and germination timing for *Bromus tectorum* in a semi-arid environment using hydrothermal time model. *Seed Sci. Res.* 19:225-239.

Miller, R. F., J. Seufert, B. A. Roundy, R. J. Tausch, C. Pereira, A. Hulet, and J. C. Chambers. 2013. Short-term response of woodlands in the Intermountain West to prescribed fire and mechanical treatments. *Rangeland Ecol. Manage.* x:xx-xx.

Rawlins, J. K., B. A. Roundy, S. M. Davis, and D. Egget. 2012a. Predicting germination in semi-arid wildland seedbeds. I. Thermal germination models. *Environ. Exp. Bot.* 76:60–67.

- Rawlins, J. K., B. A. Roundy, D. Egget, and N. L. Cline. 2012b. Predicting germination in semi-arid wildland seedbeds II. Field validation of wet thermal-time models. *Environ. Exp. Bot.* 76:68–73.
- Reid, I. 1973. The influence of slope orientation upon the soil moisture regime, and its hydrogeomorphological significance. *J. Hydrol.* 19:309–321.
- Roundy, B. A., and S. H. Biedenbender. 1996. Germination of warm-season grasses under constant and dynamic temperatures. *J. Range Manage.* 49:425–431.
- Roundy, B. A., S. P. Hardegree, J. C. Chambers, and A. Whittaker. 2007. Prediction of cheatgrass field germination potential using wet thermal accumulation. *Rangeland Ecol. Manage.* 60:613–623.
- Roundy, B. A., R. F. Miller, R. J. Tausch, K. Young, A. Hulet, B. Rau, B. Jessop, J. C. Chambers, and D. Eggett. 2014a. Understory cover responses to piñon-juniper control across tree cover gradients in the Great Basin. *Rangeland Ecol. Manage.* xx:xx–xx.
- Roundy, B. A., K. Young, N. Cline, A. Hulet, R. F. Miller, R. J. Tausch, J. C. Chambers, and B. Rau. 2014b. Piñon-juniper reduction effects on soil temperature and water availability of the resource growth pool. *Rangeland Ecol. Manage.* xx:xx–xx.
- Ryel, R. J., A. J. Leffler, C. Ivans, M. S. Peek, and M. M. Caldwell. 2010. Functional differences in water-use patterns of contrasting life forms in Great Basin steppelands. *Vadose Zone J.* 9:548–560.

- Taylor, J. R., B. a. Roundy, P. S. Allen, S. E. Meyer, and D. L. Eggett. 2007. Soil water sensor accuracy for predicting seedling emergence using a hydrothermal time model. *Arid Land Res. Manage.* 21:229–243.
- Weisberg, P. J., E. Lingua, and R. B. Pillai. 2007. Spatial patterns of pinyon-juniper expansion in Central Nevada. *Rangeland Ecol. Manage.* 60:115–124.
- Whisenant, S. G. 1999. Repairing damaged wildlands: a process orientated, landscape-scale approach. Pages 130–132. Cambridge University Press, New York, New York, USA.
- Young, K. R., B. A. Roundy, and D. L. Eggett. 2013. Tree reduction and debris from mastication of Utah juniper alter the soil climate in sagebrush steppe. *Forest Ecol. Manage.* 310:777–785.

TABLES

Table 2-1. List of woodland sites, year of treatment, and years of soil moisture and temperature year data used for post treatment and woodland infilling phase analysis. * Years where only early spring and late spring data was used. Reproduced from Cline et al. (2014).

Site	Treatment and phase comparison				
	Year treated	Year data used for year since treatment			
		Year 1	Year 2	Year 3	Year 4*
Blue Mountain	2007		2009	2010	2011
Bridge Creek	2006		2008	2009	2010
Devine Ridge	2007		2009	2010	2011
Marking Corral	2006		2008	2009	2010
South Ruby	2008		2010	2011*	
Stansbury	2007	2008	2009*		
Onaqui	2006	2007	2008	2009	2010
Scipio	2007			2010	2011
Greenville	2007		2009	2010	2011
Total number of sites		2	7	7	7

Table 2-2. 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
<i>Cheatgrass (Bromus tectorum L.)</i>			
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
<i>Perennial Grass</i>			
<i>Crested wheatgrass (Agropyron ssp.)</i>			
AGCR	Hycrest	Rawlins et al., 2012a	Rawlins et al., 2012a
AGDE	Nordan	Rawlins et al., 2012a	Rawlins et al., 2012a
<i>Bluebunch wheatgrass (Pseudoroegneria spicata (Pursh) Á. Löve)</i>			
APSSP	Anatone	Rawlins et al., 2012a	Rawlins et al., 2012b
GPSSP	Goldar	Hardegree et al., 2010	Present Study
WPSSP	Whitmar	Hardegree et al., 2010	Present Study
<i>Snake River wheatgrass (Elymus wawawaiensis J. Carlson & Barkworth)</i>			
ELWA2	Secar	Rawlins et al., 2012a	Rawlins et al. 2012b
<i>Bottlebrush Squirreltail (Elymus elymoides (Raf.) Swezey)</i>			
ELEL	Sanpete	Hardegree et al., 2008	Present Study
T-1202	Hwy 75 X 20, ID	Hardegree et al., 2008	Present Study
T-1205-98	W. Hill City, ID 1998	Hardegree et al., 2008	Present Study
T-1205-99	W. Hill City, ID 1999	Hardegree et al., 2008	Present Study
T-1175-98	Ditto Creek, ID 1998	Hardegree et al., 2008	Present Study

T-1175-99	Ditto Creek, ID 1999	Hardegree et al., 2008	Present Study
Big Squirreltail (<i>Elymus multisetus</i> M. E. Jones)			
ELMU-1	Sand Hollow	Hardegree et al., 2010	Present Study
ELMU-2	Sand Hollow	Hardegree et al., 2010	Present Study
Basin wildrye (<i>Leymus cinereus</i> (Scribn & Merr.) Á. Löve)			
LECI-1	Magnar	Hardegree et al., 2010	Present Study
LECI-2	Trailhead	Hardegree et al., 2010	Present Study
Sandberg bluegrass (<i>Poa secunda</i> J. Presl.)			
POSE-1	Commercial Seed Co.	Hardegree et al., 2010	Present Study
POSE-2	Commercial Seed Co.	Hardegree 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

Table 2-3. Percentages of PTG estimations for seasons, sites, treatments, infilling phases, and microsites where seedbeds accumulated enough PTG to sum to 1 or greater for different experimental sites in the Great Basin.

Experiment	Sites	Fall	Winter	Spring	Early Spring	Late Spring
Sagebrush & Perennial Grass	NVC	56.5	36.5	98.6	93.1	86.0
	NVU	72.9	3.0	99.7	77.8	98.6
	NVM	53.3	0.7	95.9	87.2	91.2
	NVL	81.4	26.6	96.6	90.6	84.1
	UTC	85.6	12.6	97.8	93.2	75.9
	UTU	93.5	16.1	97.6	61.3	96.6
	UTM	92.4	20.1	98.9	91.8	89.9
	UTL	88.8	38.7	97.0	92.8	83.6
	UTS	83.7	9.1	97.2	91.2	81.8
Crested Wheatgrass	LP	75.7	16.3	94.7	93.5	82.3
	SV	79.4	32.8	98.4	95.2	75.5
Sagebrush	HM	58.2	12.8	96.9	83.5	93.5
	OS	39.9	2.8	96.6	92.5	89.7
	SM	90.4	48.4	96.9	92.0	87.1
Woodlands	BC	89.1	76.1	99.5	93.9	97.6
	BM	87.2	15.7	99.1	86.9	97.3
	DR	92.0	8.1	99.3	85.3	98.5
	GV	52.6	10.0	84.2	81.8	67.1
	MC	72.6	2.2	92.4	86.3	64.5
	OJ	61.0	12.3	94.4	88.3	73.4
	SC	87.7	20.1	98.1	92.0	93.1
	SR	50.3	9.6	96.4	89.4	92.1
	ST	92.3	38.9	98.9	92.6	95.7

Table 2-4. Fixed effects on progress toward germination from mixed model analysis for sagebrush and perennial grass, crested wheatgrass, and sagebrush experiments. SL = seedlot; NDF and DDF= numerator and denominator degrees of freedom.

	Season	Effect	ND	DD	F-	Pvalu
Sagebrush/ Perennial	Early	YEAR	8	211	84.69	<.000
		SL	28	211	86.75	<.000
		YEAR*S	224	211	0.67	0.999
	Late	YEAR	8	200	230.15	<.000
		SL	30	200	55.24	<.000
		YEAR*S	240	200	1.4	0.000
	Fall	YEAR	8	185	86.76	<.000
		SL	30	185	35.53	<.000
		YEAR*S	240	185	0.51	1
Winter	YEAR	8	197	69.34	<.000	
	SL	30	197	46.81	<.000	
	YEAR*S	240	197	0.99	0.547	
Crested	Early	SL	30	893	100.5	<.000
		YEAR	4	893	206.46	<.000
		YEAR*S	120	893	1.09	0.245
	Late	SL	30	873	19.38	<.000
		YEAR	4	875	242.04	<.000
		YEAR*S	120	873	1.11	0.206
	Fall	YEAR	4	101	1261.8	<.000
		SL	30	101	75.82	<.000
		YEAR*S	120	101	6.73	<.000
Winter	SL	30	956	149.49	<.000	
	YEAR	4	957	285.22	<.000	
	YEAR*S	120	956	4.45	<.000	
Sagebrush	Early	YEAR	2	160	82.98	<.000
		SL	30	160	57.32	<.000
		YEAR*S	60	160	0.37	1
	Late	YEAR	2	147	748.29	<.000
		SL	30	147	64.54	<.000
		YEAR*S	60	147	3.76	<.000
	Fall	YEAR	2	163	1318.5	<.000
		SL	30	163	61.33	<.000
		YEAR*S	60	163	9.56	<.000
Winter	YEAR	2	164	15.55	<.000	
	SL	30	164	117.55	<.000	
	YEAR*S	60	164	7.47	<.000	

Table 2-5. Progress toward germination (\pm SE) for 31 seedlots at woodland sites for each year since tree reduction treatment.

	Early Spring	Late Spring	Fall	Winter
Year 1	3.40 \pm 0.85	3.64 \pm 2.92	3.07 \pm 1.39	0.56 \pm 0.29
Year 2	3.38 \pm 0.37	4.63 \pm 1.03	1.98 \pm 0.29	0.47 \pm 0.19
Year 3	3.60 \pm 0.22	5.40 \pm 0.69	2.67 \pm 0.55	0.01 \pm 0.00
Year 4	3.62 \pm 0.57	6.10 \pm 0.95		

Table 2-6. Fixed effects on PTG from mixed model analysis for different years since tree reduction for woodland sites. SL= seedlot, TRT = tree removal method.

Year	Season	Effect	NDF	DDF	F-value	P-value
Year 1	Early Spring	SL	30	1580	102.91	<.0001
		TRT	2	1580	620.81	<.0001
		SL*TRT	60	1580	3.17	<.0001
	Late Spring	SL	30	1580	25.89	<.0001
		TRT	2	1580	127.75	<.0001
		SL*TRT	60	1580	0.71	0.9542
	Fall	SL	30	1301	34.6	<.0001
		TRT	2	1301	223.95	<.0001
		SL*TRT	60	1301	1.05	0.3746
	Winter	SL	30	1580	152.46	<.0001
		TRT	2	1580	34.08	<.0001
		SL*TRT	60	1580	1.35	0.0392
Year 2	Early Spring	SL	30	5294	244.44	<.0001
		TRT	2	5294	372.21	<.0001
		SL*TRT	60	5294	1.95	<.0001
	Late Spring	SL	30	4923	125.46	<.0001
		TRT	2	4923	72	<.0001
		SL*TRT	60	4923	1.06	0.351
	Fall	SL	30	5466	156.89	<.0001
		TRT	2	5466	457.25	<.0001
		SL*TRT	60	5466	2.23	<.0001
	Winter	SL	30	5357	135.67	<.0001
		TRT	2	5357	94.21	<.0001
		SL*TRT	60	5357	1.1	0.2744
Year 3	Early Spring	SL	30	5295	434.49	<.0001
		TRT	2	5296	681.58	<.0001
		SL*TRT	60	5295	3.61	<.0001
	Late Spring	SPP	30	5666	157.37	<.0001
		TRT	2	5666	99.75	<.0001
		SPP*TRT	60	5666	1.4	0.0236
	Fall	SL	30	5605	152.19	<.0001
		TRT	2	5605	158.6	<.0001
		SL*TRT	60	5605	0.8	0.8658
	Winter	SL	30	5574	142.15	<.0001
		TRT	2	5574	20.81	<.0001
		SL*TRT	60	5574	0.32	1
Year 4	Early Spring	SL	30	5730	236.69	<.0001
		TRT	2	5730	79.04	<.0001
		SL*TRT	60	5730	0.48	0.9998
	Late Spring	SL	30	5730	237.19	<.0001
		TRT	2	5730	37.83	<.0001
		SL*TRT	60	5730	0.24	1

Table 2-7. Fixed effects on additional progress toward germination for tree reduction treatments compared to no tree reduction 3 yr after treatment. SL= seedlot, TRT = tree removal method, PHASE = tree infilling phase.

Season	Effect	NDF	DDF	F-	P-
Early	TRT	1	3321	36.83	<.0001
	PHASE	2	3320	138.83	<.0001
	TRT*PHASE	2	3319	23.35	<.0001
	MS	2	3316	9.13	0.0001
	TRT*MS	2	3316	16.01	<.0001
	MS*PHASE	4	3316	2.95	0.019
	TRT*MS*PHASE	4	3316	4.3	0.0018
Late	TRT	1	3200	47.48	<.0001
	PHASE	2	3229	113.67	<.0001
	TRT*PHASE	2	3230	18.66	<.0001
	MS	2	3227	13.65	<.0001
	TRT*MS	2	3227	1.99	0.1365
	MS*PHASE	4	3227	5.39	0.0003
	TRT*MS*PHASE	4	3227	5.33	0.0003
Fall	TRT	1	3598	2.02	0.1548
	PHASE	2	3596	107.27	<.0001
	TRT*PHASE	2	3598	11.13	<.0001
	MS	2	3599	0.66	0.5185
	TRT*MS	2	3599	8.57	0.0002
	MS*PHASE	4	3599	2.65	0.0317
	TRT*MS*PHASE	4	3599	34.41	<.0001
Winter	TRT	1	3662	2.05	0.152
	PHASE	2	3661	60.83	<.0001
	TRT*PHASE	2	3662	28.42	<.0001
	MS	2	3660	11.07	<.0001
	TRT*MS	2	3662	3.67	0.0256
	MS*PHASE	4	3661	4.31	0.0018
	TRT*MS*PHASE	4	3660	2.37	0.0504

FIGURES

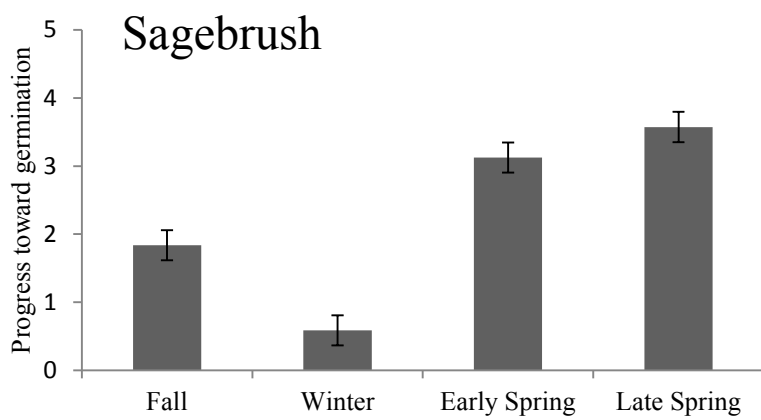
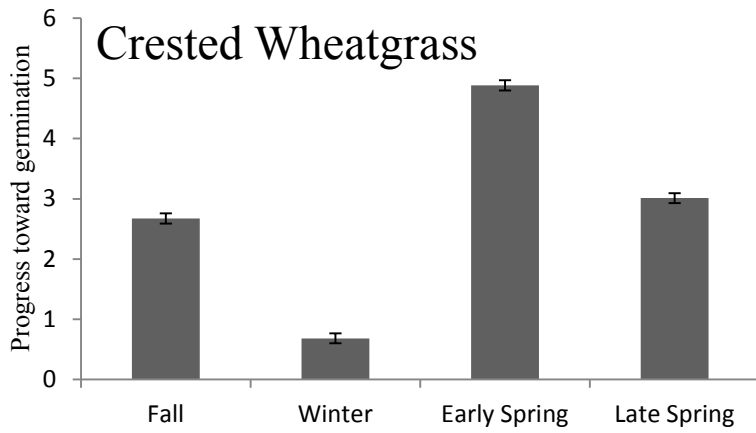
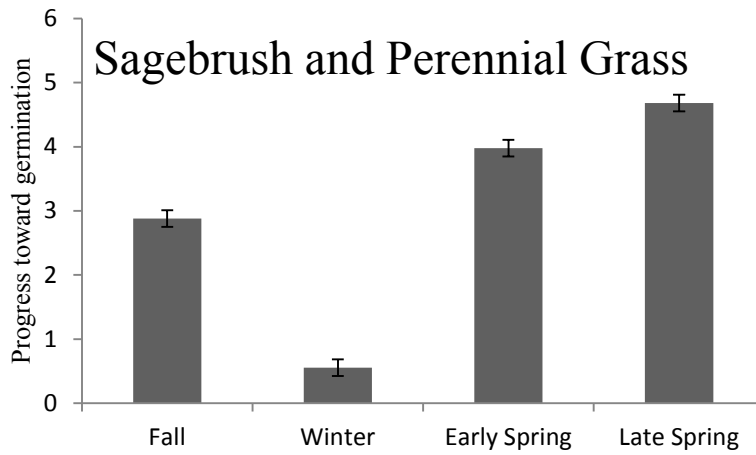


Figure 2-1. Seasonal progress towards germination. Error bars are ± 1 standard error of the mean.

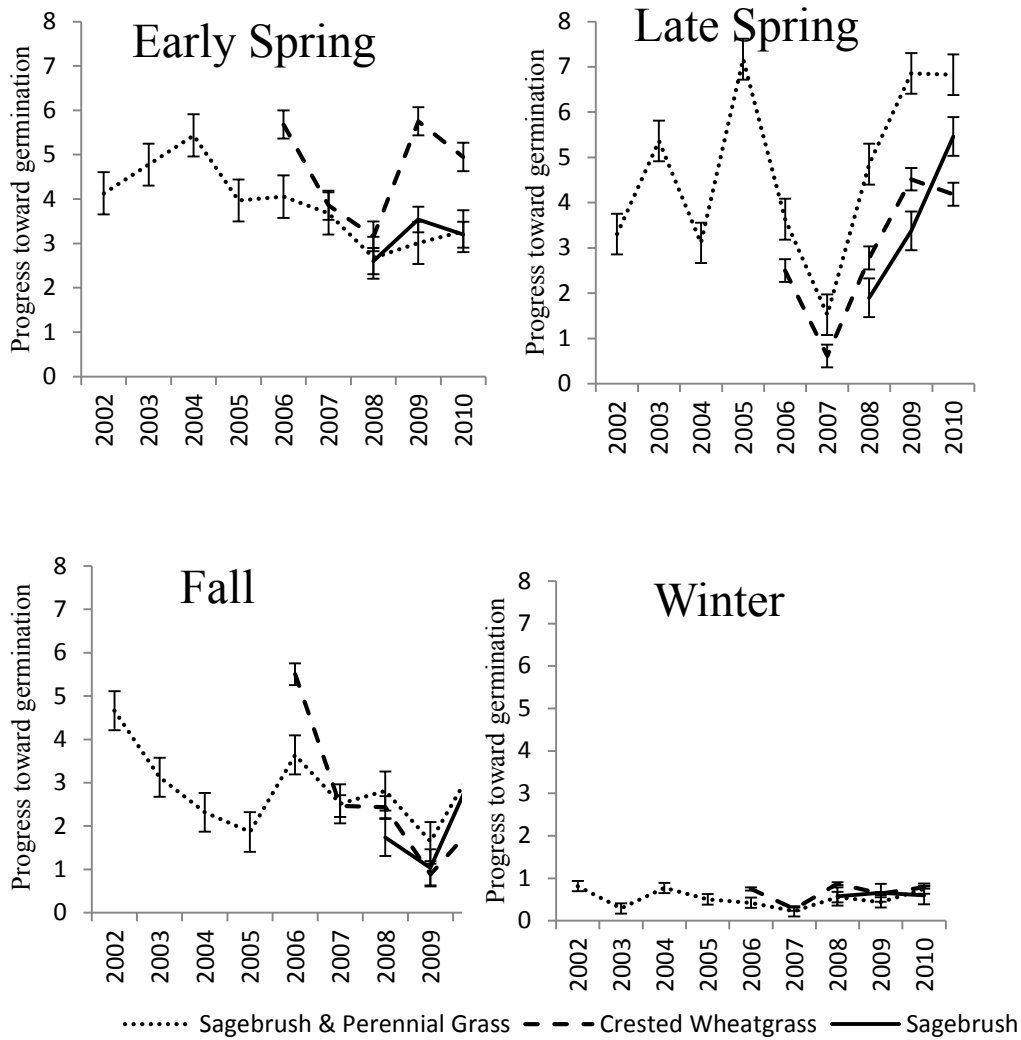


Figure 2-2. Annual progress toward germination by season across all seedlots for sagebrush and perennial grass, crested wheatgrass, and sagebrush sites. Error bars are ± 1 standard error of the mean. Seasons were early spring – 1 March to 30 April, late spring – 1 May to 30 June, fall – 1 September to 31 November, and winter – 1 December to 28 February.

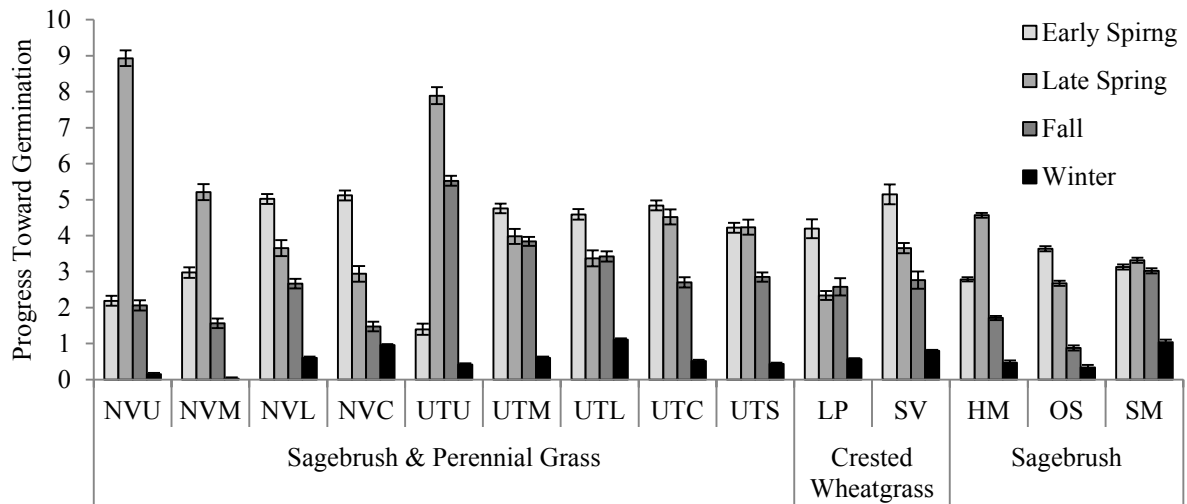


Figure 2-3. Seasonal progress toward germination averaged across all seedlots by site and experiment. Error bars are ± 1 standard error of the mean. Seasons were early spring – 1 March to 30 April, late spring – 1 May to 30 June, fall – 1 September to 31 November, and winter – 1 December to 28 February. 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 ELEV, HM = Hart Mountain, OS = Onaqui Sagebrush, SM = Saddle Mountain, SV = Skull Valley, LP = Lookout Pass.

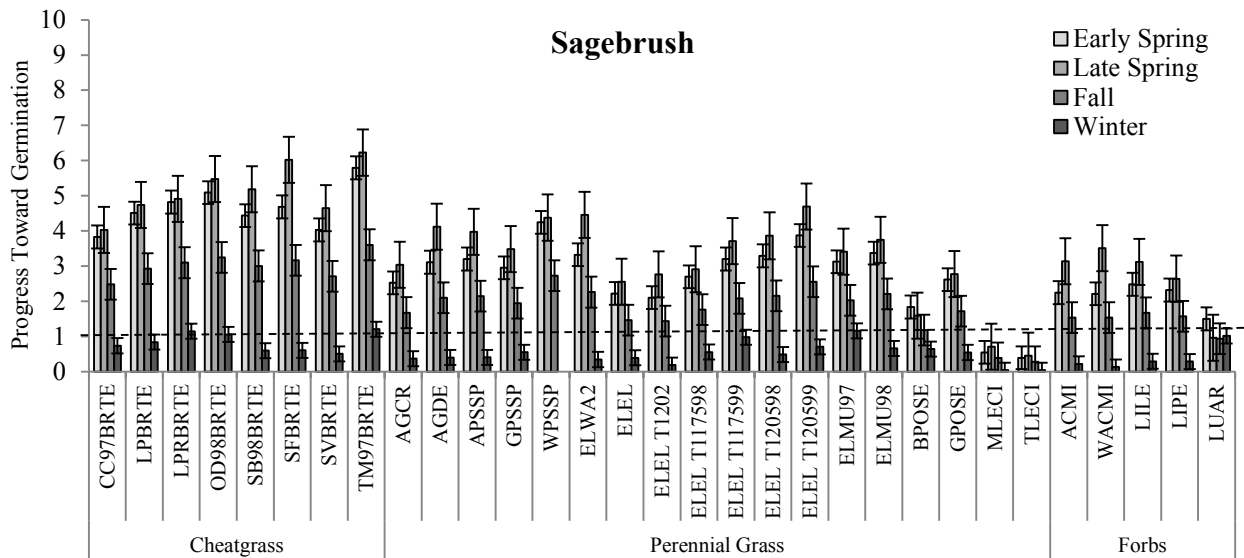
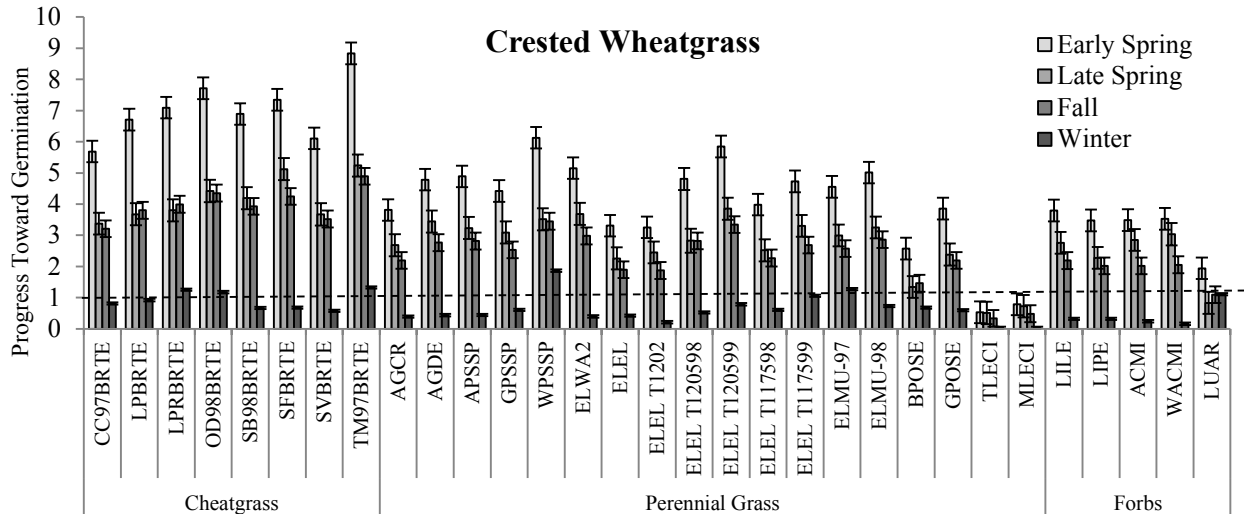
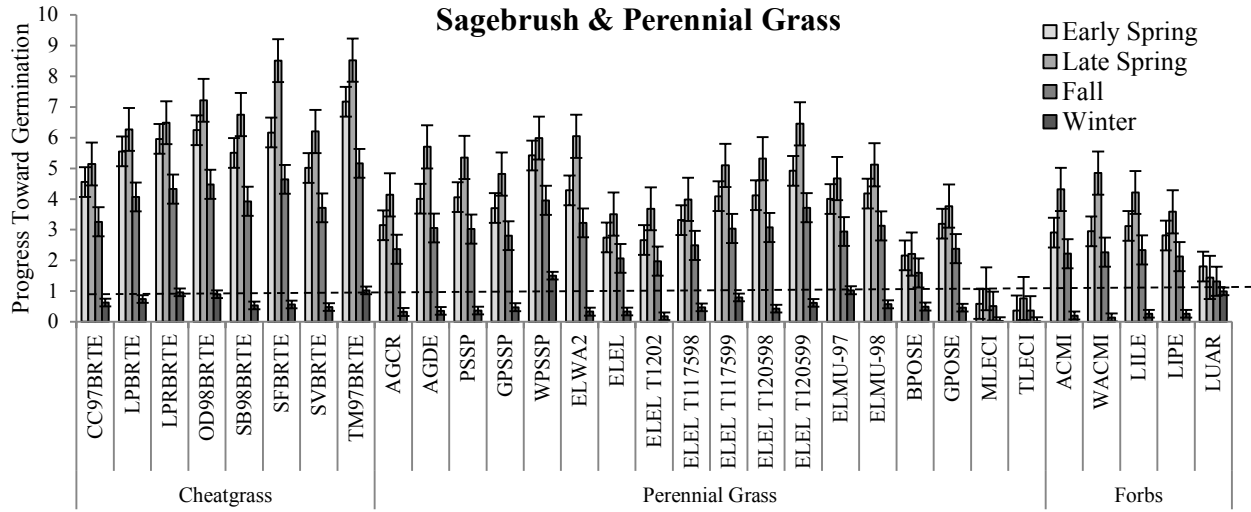


Figure 2-4. Seasonal progress toward germination by seedlot and plant functional group for

sagebrush and perennial grass (top), crested wheatgrass (middle), and sagebrush (bottom) experimental 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.

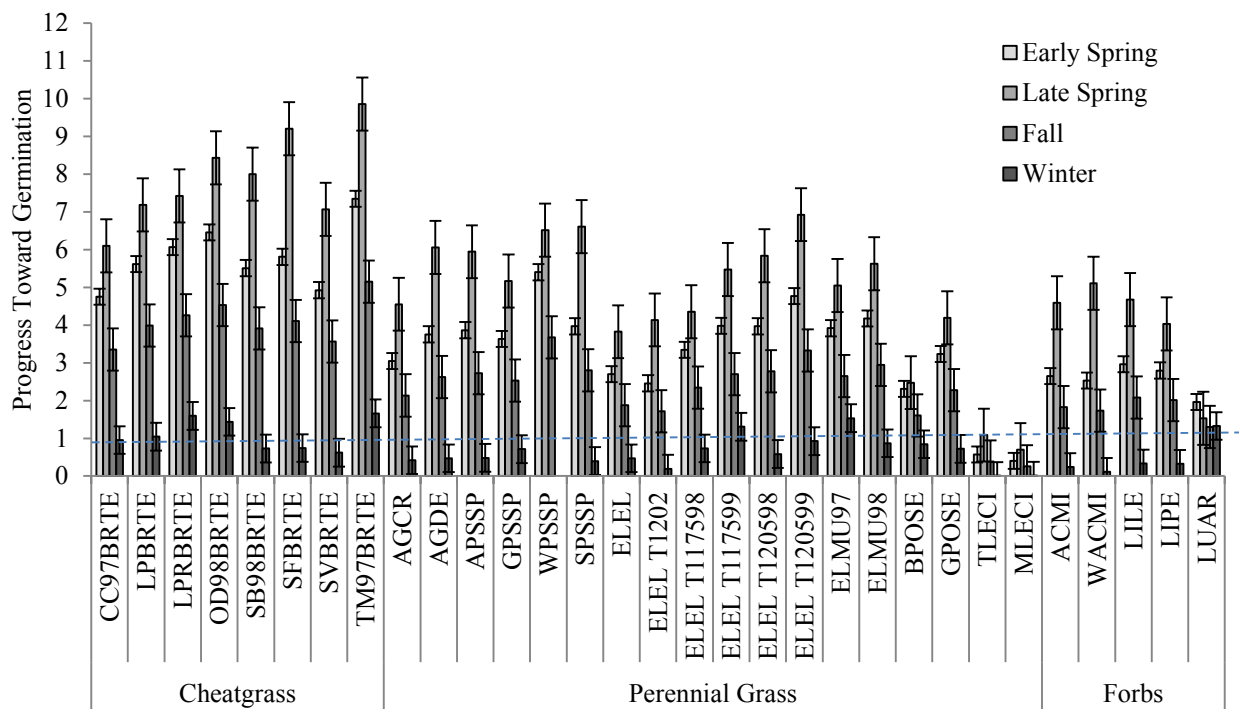


Figure 2-5. Seasonal progress toward germination by seedlot and functional group for the woodland experiment. Error bars are $1 \pm$ standard error of the mean. Seasons were early spring – 1 March to 30 April, late spring – 1 May to 30 June, fall – 1 September to 31 November, and winter – 1 December 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.

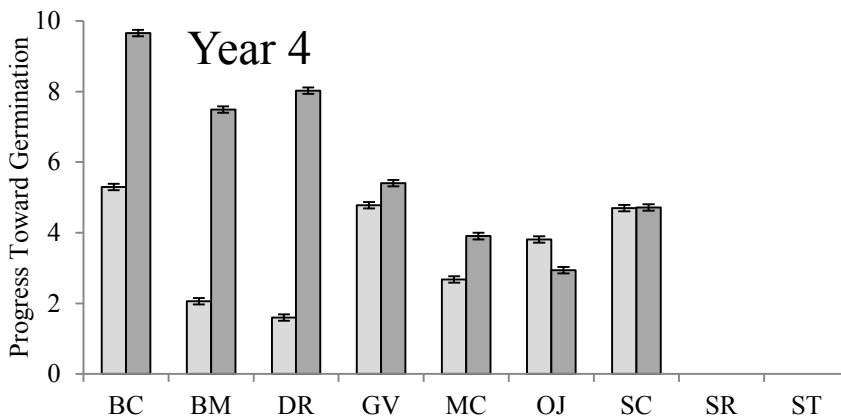
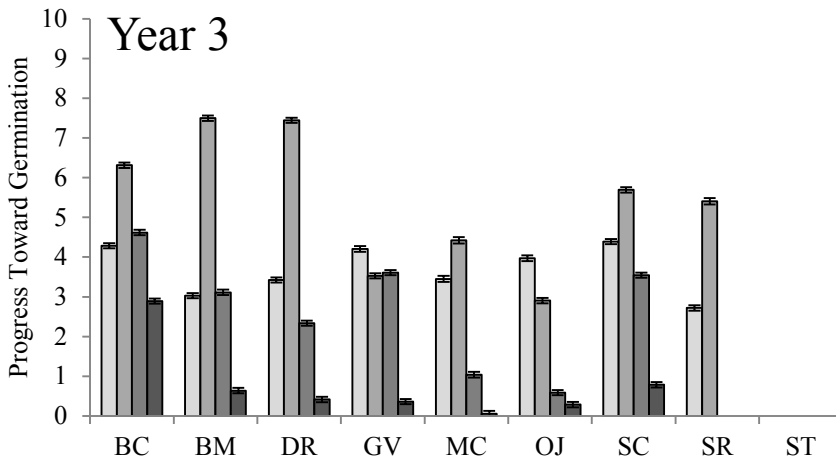
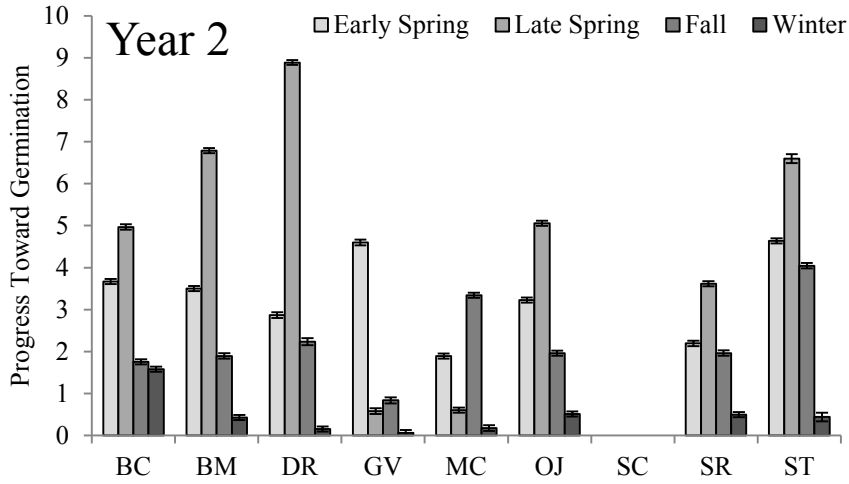


Figure 2-6. Seasonal progress toward germination averaged across all seedlots by woodland site for year 2 (top), year 3 (middle), and year 4 (bottom) since implementation of tree reduction

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.

All woodland sites

Utah woodland sites

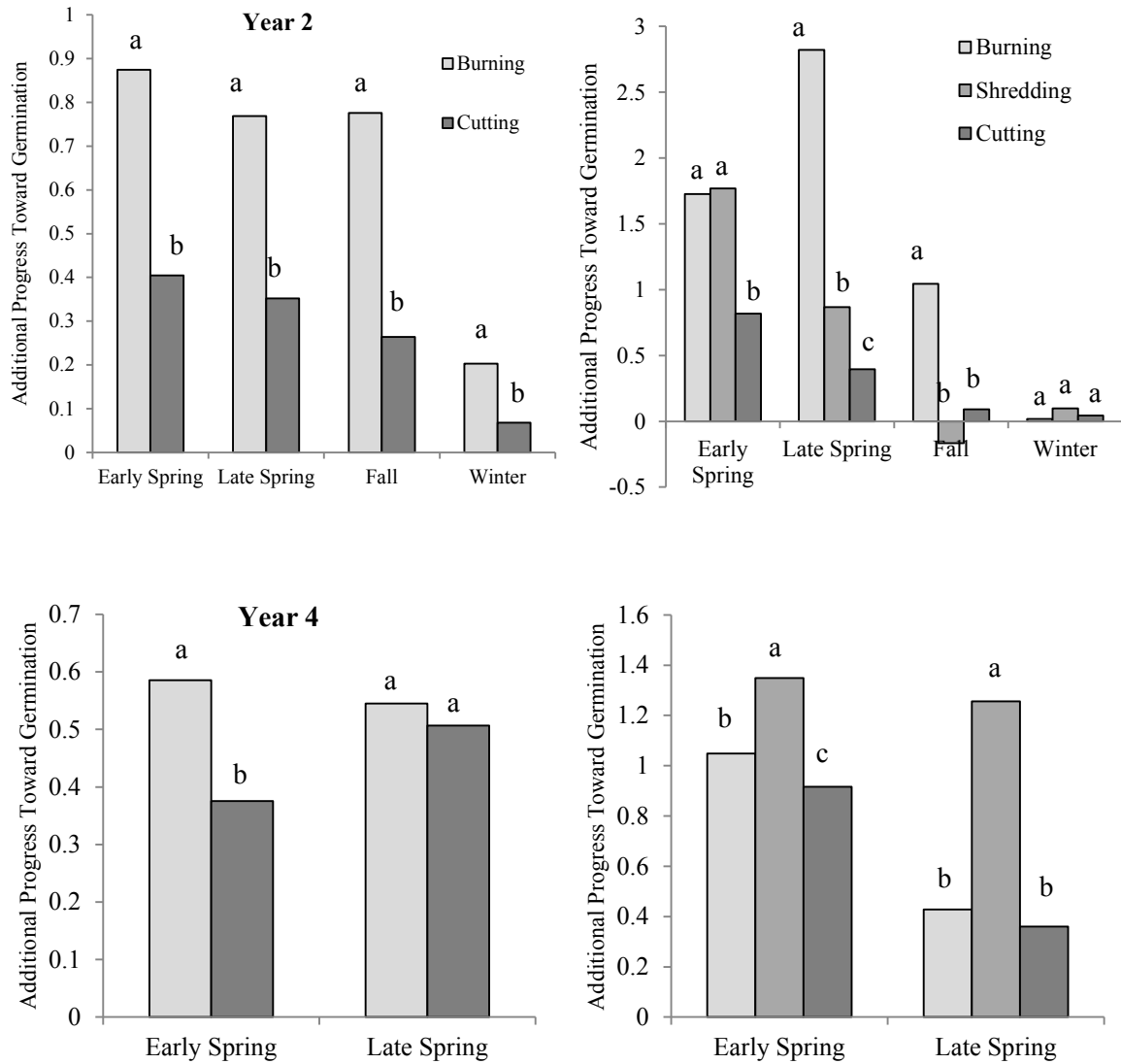


Figure 2-7. Additional progress toward germination averaged across all seedlots for tree removal methods by season for all woodland sites (left) and Utah sites (right) for the second (top) and fourth (bottom) years since treatment. Different letters indicate significant differences within a season.

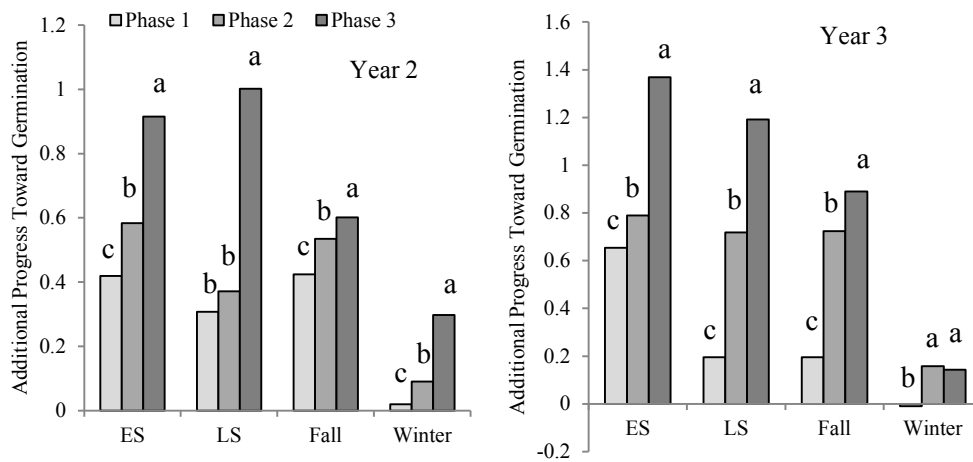


Figure 2-8. Additional progress toward germination averaged across all seedlots for tree reduction treatments implemented at different phases of tree infilling for the second (left) and third (right) year since treatment by season. Different letters indicate significant differences within a season. ES and LS= early and late spring.

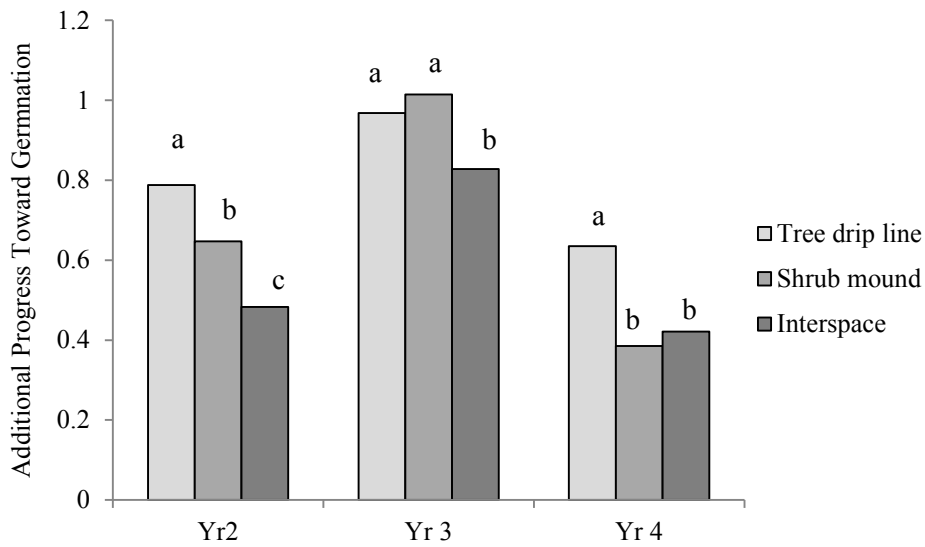


Figure 2-9. Additional progress toward germination averaged across all seedlots for each microsite by year since tree reduction treatment for late spring (1 May to 30 June). Different letters indicate significant differences within a season.

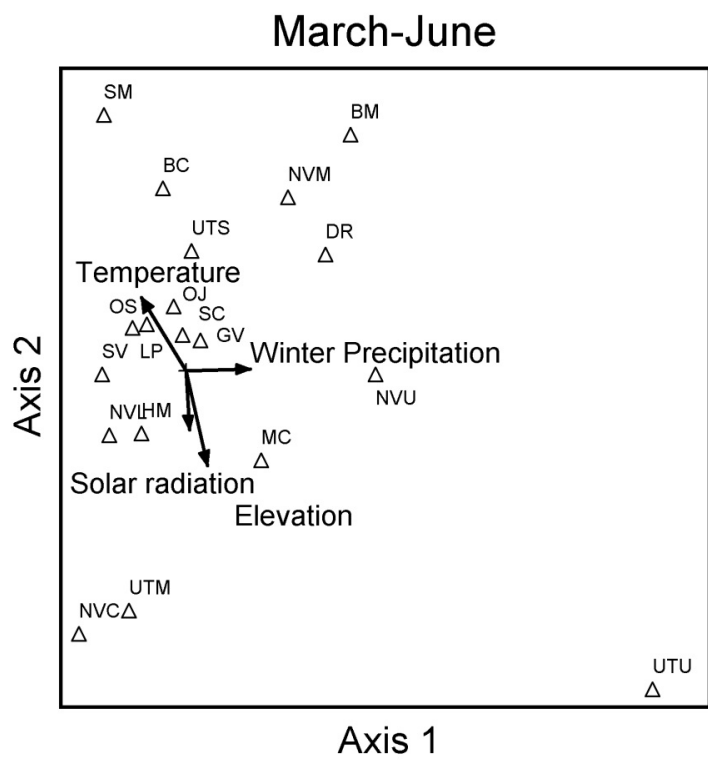
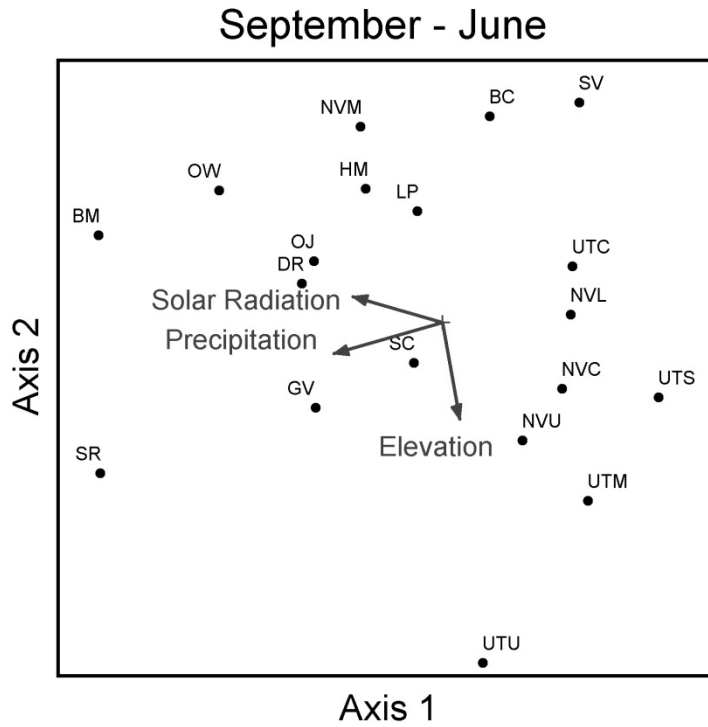


Figure 2-10. Canonical correspondence analysis (CCA) associating site progress toward

germination with early spring (1 March to 30 June) (top) and 1 September to 30 June (bottom) precipitation. Arrow length indicates comparative strength of association between winter and spring precipitation. 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.

CHAPTER 3: SPRING DRYING AND WETTING FOR SEEDLING ROOT ZONES IN THE
GREAT BASIN

Nathan L. Cline¹, Bruce A. Roundy², Kert Young³, and William F. Christensen⁴

Authors are ¹Research Associate, Brigham Young University, Provo, UT, USA 84602,

²Professor Range Science, Brigham Young University, Provo, UT, USA 84602, ³Assistant

Professor (Post-Doc), New Mexico State University, Las Cruces, NM, 88003, USA, ⁴Professor

Statistics, Brigham Young University, Provo, UT, USA 84602.

This is Contribution Number 103 of the Sagebrush Steppe Treatment Evaluation Project

(SageSTEP), funded by the U.S. Joint Fire Science Program, the Bureau of Land Management,

the National Interagency Fire Center, and The Great Basin Native Plant Project.

Correspondence: Bruce A. Roundy, Department of Plant and Wildlife Sciences, 275 WIDB,

Brigham Young University, Provo, UT 84602.

Proposed Journal: Vadose Zone Journal

ABSTRACT

To determine the potential success of post wildfire revegetation, we have developed seedling root-growth prediction models. These models estimate seedling root depth as a function of temperature and time. To determine how well these models could work under actual soil temperature and water potential dynamics, we measured soil water matric potential and temperature at nine sites in the Great Basin, USA to quantify spring drying patterns and rates, time of plant available water (wet days or days when soil water matric potential was > -1.5 MPa), and wet thermal time (wet degree days or degree days when the soil was > -1.5 MPa) over five temperature ranges. Each site had plots where trees (*Pinus* spp. and *Juniperus* spp.) were either left untreated or removed by prescribed fire, cutting, or shredding. Soils generally dried from the top down. Wet days before the initial spring drying period ranged from 37.3 at 3 cm soil depth to 87.3 at 30 cm and were increased by as much as 34.7 ± 6.56 with tree removal. Initial spring drying front rates averaged 2.6 ± 0.3 cm day⁻¹ and ranged from 1.61 cm day⁻¹ for 3-15 cm of soil depth to 3.98 cm day⁻¹ for 20-30 cm. Root zones when wet were generally within the temperature ranges used to develop seminal root growth models. Thermal root growth models hold promise for predicting seedling establishment with and without vegetation removal treatments after appropriate field tests.

INTRODUCTION

Revegetation plant materials often fail to establish as a result of drought in the soils of the Great Basin (Call and Roundy, 1999). In water limited ecosystems, seedling growth and establishment may depend on rapid seminal root growth into moist soil layers ahead of soil drying and subsequent development of adventitious roots (Briske and Wilson, 1978). Longer seedling growth periods may result in increased seedling survival. The climate of the Great Basin consists of a short period in the spring when soil water is available and temperatures are conducive to plant growth (Caldwell 1985, Smith et al., 2011). This general pattern can vary greatly with annual weather, elevation, and topography (Smith et al., 2011; Roundy et al., 2014b; Cline et al., 2014). Winter precipitation is considered key to plant growth and establishment in the Great Basin because it extends plant available water before the first spring drying period (Gifford and Shaw, 1973; Cline et al., 1977; Anderson et al., 1987; Eissenstat and Caldwell, 1988; Schwinning et al., 2003; Schwinning and Sala, 2004; Bates et al., 2006; Ryel et al., 2010). Late spring and summer precipitation that occurs after the first spring drying period contributes to plant maintenance, but may not provide sufficient plant available water to promote plant growth (Ivans et al., 2003; Snyder et al., 2004; Ryel et al., 2010; Leffler and Ryel, 2012). Also, Great Basin soils are heterogeneous in their physical characteristics which influence plant available water and the thermal environment (Jensen et al., 1989). We have developed models that predict seminal root depth as a function of soil temperature under unlimited water (Young and Roundy, 2012; Roundy et al., 2014). Characterization of soil drying front patterns and rates, time of plant available water (total days when soil water matric potential > -1.5 MPa), and wet thermal time (degree days when the soil is > -1.5 MPa) may allow us to apply seminal root depth models to Great Basin plant materials and predict potential seedling survival.

Root growth prediction models work on the premise of drying occurring from the soil surface-downward and that root growth is a function of temperature when the soils are wet (> -1.5 MPa) (Aguirre and Johnson, 1991; Kremer and Running, 1996; Breshears et al., 1997). Predicting seedling survival is based on determining whether root growth as a function of soil temperature is adequate for seminal roots to stay ahead of the soil drying front so that the seedling continues to grow and does not die from drought (Briske and Wilson, 1977; Roundy et al., 1993). Therefore, rates and patterns of root zone drying for the first and last spring drying periods provide the environmental context for determining what plant materials, sites, and annual weather conditions will result in seedling survival or desiccation using thermal-driven seminal root growth models. Drying patterns have been found to vary in semiarid and arid soils (Ryel et al., 2010; Hardie et al., 2011) and may affect the accuracy of predicted seedling root growth for Great Basin sites. This lack of uniformity in drying patterns may result from soil physical conditions influencing water infiltration into soils, seasonal weather characteristics, and transpirational soil water loss resulting from differences in plant community structure (Jensen, 1989, Leffler et al., 2002; Ryel et al. 2002, 2010; Schenk and Jackson, 2002).

Changes in evapotranspiration as a result of wildfire or the removal of *Juniperus* spp. and *Piñus* spp. trees that have encroached on *Artemisia* spp. communities alter the time of plant available water, as well as the soil thermal environment by changing canopy structure and soil cover. Root zone water is temporarily increased for a few years after vegetation disturbance until other plants or colonizers grow sufficiently to use the available resource (Gifford and Shaw, 1973; Davis and Pelsor, 2001; Chambers et al., 2007; Davies et al., 2007).

Site and annual weather variations in the Great Basin had a more significant effect on predicted potential germination of cheatgrass (*Bromus tectorum*) than disturbance (Roundy et al.,

2007). Disturbance effects on soil drying conditions may attenuate as soil depth increases due to insulation from solar radiation and ambient air temperature (Campbell and Norman, 1998). Effects of vegetation disturbance on soil water availability may increase with depth, however, as root zone transpirational water use decreases. Understanding soil drying conditions in relation to tree removal may allow for application of wet thermal time models to estimate root growth or time to a maximum root depth for species sown on treated woodlands of the Great Basin. Desirable grasses, shrubs and forbs are often sown on these woodlands in conjunction with tree reduction to lower woody fuel loads and decrease probability of high intensity wildfires (Bybee, 2013).

One concern for use of thermal time models to predict seed germination and plant growth is that very little is known about seed germination and root growth responses at extreme temperatures ($< 5^{\circ}\text{C}$ and $> 25^{\circ}\text{C}$) (Hardegree et al., 2002, Rawlins et al., 2012a, 2012b). Hardegree et al. (2002) found a more variable germination response at 3°C and above 25°C . Germination rates fit temperatures between 5° and 25°C rather well ($r^2 > 0.7$) (Roundy et al., 2007; Rawlins et al. 2011a.). Thermal time models for estimating growth in seminal roots for rangeland species have only been developed at temperatures ranging from $7\text{-}30^{\circ}\text{C}$ (Young and Roundy, 2012). The models were relatively accurate at predicting root growth response to 15 cm soil depth under growth chamber programmed to simulate diurnal soil temperatures in spring for sagebrush steppe communities. Response to more extreme temperature ranges have not been tested due to the difficulty in maintaining low growth chamber temperatures and also because it has been assumed that insufficient wet-thermal time is summed under these temperatures to influence model accuracy (Rawlins et al., 2012b).

Roundy et al. (2014b) determined the effect of tree removal on plant available water and the overall wet thermal conditions in the top 30 cm of the root zone, but did not determine soil drying patterns and conditions. Our study fills this knowledge gap by quantifying patterns and rates of drying for the first and last spring drying periods in treated and untreated woodlands. We also quantified wet days and wet degree days both before and after the first spring drying period as measures of plant available water and the wet thermal environment. Also, we determined the effects of tree removal, tree infilling phase, and microsite differences on soil drying and plant available water variables. We quantified wet degree days at five temperature ranges and we associated spring drying rates for the different sites with spring and winter precipitation.

METHODS

Study Sites

We measured soil water matric potential and soil temperature data at nine sites where trees (*Juniperus occidentalis* Hook., *Pinus edulis* Engelm. – *Juniperus osteosperma* (Torr.) Little, and *Juniperus osteosperma* (Torr.) Little) have encroached into sagebrush (*Artemisia* L. spp.)-bunch grass communities. Experiments at the sites were originally designed to determine the effects of tree removal treatments on understory vegetation recovery. For detailed site descriptions see McIver et al. (2010) and Cline et al. (2014).

Study Design and Tree Removal

Tree removal treatments were applied in a randomized block design using the nine sites as blocks. Tree removal treatments included untreated woodlands, prescribed burning, tree cutting (or cut and drop), and mechanically shredding trees (or mastication). Mechanical shredding was only applied at the four Utah sites. Each tree removal method was applied in 8-20

ha plots at each site. Within each tree removal plot, soil monitoring stations were installed for each pretreatment tree infilling phase. Phase 1 signifies a community where understory vegetation is dominant with trees present. Phase 2 signifies a codominate community of both understory vegetation and trees. Phase 3 signifies a tree dominant community (Miller et al., 2007). At each soil monitoring station, soil water matric potential and temperature were measured at three nearby (< 3 m) microsites: at a tree drip line, at a shrub mound, and in an interspace between shrubs and trees. Treatment procedures are described in detail in McIver et al. (2010). The year that treatments were implemented varied by site (Table 1), therefore, we analyzed response variables by the year since treatment.

Meteorological stations are described in detail in related studies by Roundy et al. (2014b) and Cline et al. (2014). We estimated soil water matric potential using gypsum blocks, and soil temperature with thermocouples at 1-3 cm, 13-15 cm, 18-20 cm, and 28-30 cm soil depths. These depths will be referred to by their deepest point of 3 cm, 15 cm, 20 cm, and 30 cm. Measurements were made every minute and hourly averages were recorded on Campbell Scientific®, Inc. CR10X and CR1000 microloggers. Water potential measurements of > -1.5 MPa were considered "wet", while soil water potentials measurements of \leq -1.5 MPa were considered "dry". We measured precipitation and ambient air temperature with a Texas Electronics®, Inc. tipping-bucket rain gauge and a thermistor from Campbell Scientific®, Inc. (107 temperature probe with gill shield).

Root Zone Conditions and Analysis

Soil water matric potential and temperature data were used to derive wet days and wet degree days both before and after the first spring (1 March to 30 June) drying period, wet period

frequency after the first spring drying period, the first and last spring drying rates, and wet degree days at five temperature ranges. Wet days are the total hours when the soil water matric potential was > -1.5 MPa for a season divided by 24 hr in a day. Wet degree days is the summation of hourly temperatures $> 0^{\circ}$ C for all hours when the matric potential is > -1.5 MPa for a season divided by 24 hr in a day (Roundy et al., 2014b). Drying rates are the difference in soil depths divided by. The pattern of drying was determined by comparing soil water potential transitions from wet to dry at each depth and then calculating the percentage of downward (soil water matric potential at shallower soil depths decrease to ≤ -1.5 MPa at least 1 day before deeper soil depths), upward (soil matric potential at deeper soil depths decreased to ≤ -1.5 MPa at least 1 day before shallower soil depths), and even (soil matric potential for shallow and deep soil depths dry out on the same day) soil drying between the soil depths. The drying rate was determined by dividing the distance between probes at the four soil depths and the time between the more shallow soil depth and the deeper soil depth needed to decrease to at least -1.5 MPa. Drying rates were determined for the first and last drying period of the spring. We determined the first spring drying period by ascertaining the day and hour when soil matric potential first descended to ≤ -1.5 MPa at each soil depth during the spring. While, the final spring drying period was determined by ascertaining the last incident when soil matric potential descended to ≤ -1.5 MPa when there was at least one additional wetting of the 3-15 cm soil layers following the first spring drying period. For wet period frequency, we summed the number of wet periods following the first spring drying period. Wet days and wet degree days were summed before and after the first spring drying period. Also, we summed wet degree days at five temperature ranges (0 to $< 5^{\circ}$ C, 5 to $< 25^{\circ}$ C, 10 to $< 25^{\circ}$ C, 25 to $< 30^{\circ}$ C, 30 to $< 35^{\circ}$ C) to determine the amount of wet thermal time spent at each temperature range. As little research was found characterizing

root zone soil temperatures for the Great Basin, we defined temperature ranges based on the thermal time model reports of seedbed wet period duration reported in Rawlins et al. (2012b). Because 10 to < 25° C is a 15° C interval compared to 5° C intervals of the other temperature ranges, 10 to 25° C was separately analyzed from the other temperature ranges.

We used mixed model analysis of variance (SAS® Institute, Inc.) to determine the fixed effects of soil depth, tree removal treatments, tree infilling phases, and microsites on response variables. Significant differences among fixed factors were determined by the Tukey-Kramer multiple comparison test ($P > 0.05$). Sites were considered random blocks over the region. We used Best Unbiased Linear Predictors (BLUPs) to estimate site differences (Littell et al., 1996). We summarized the association of winter and spring precipitation on the first spring drying rate for each site using Canonical Correspondence Analysis (CCA) in PC-ORD®. We used default CCA settings and significance was determined by a randomization test ($P < 0.05$).

RESULTS

Precipitation was generally equal to or below the 20 yr PRISM (2013) average at four of nine sites during the winter and at six of nine sites during the spring (Fig. 1). Winter precipitation ranged as high as 157 mm at Scipio for the fourth year since treatment and as low as 35.0 mm at Stansbury for second year since treatment. Spring precipitation ranged as high as 271 mm at Blue Mountain for the fourth year since treatment and as low as 20.1 mm at Marking Corral for the second year. Spring temperatures averaged as high as 14.8° C at Blue Mountain and as low as 6.47° C at Marking Corral both during the second year since treatment.

The average date of drying by soil depth ranged from 27 March to 14 April at 3 cm, from 23 April to 17 May at 15 cm, from 28 April to 24 May at 20 cm, and from 2 May to 26 May at

30 cm (Fig. 2). For the greatest percentage of time, the initial and final drying direction was from the soil surface downward (Table 2). Spring drying frequency decreased with soil depth averaging 2.96, 0.71, 0.44, and 0.34 wet periods at soil depths of 3, 15, 20, and 30-cm deep following the initial drying period (Fig. 3). Sixty seven-80% of hourly soil water matric potential measurements dry downward for the initial spring drying period. Because sensors generally indicated that soils at 15-30 cm dried at a frequency of less than 0.5, final drying rate was only determined between 3-15 cm. For the final spring drying period, the drying direction was from the soil surface downward for 50-60% of soil matric potential measurements taken across all 4 yr since treatment. The final drying rate was more variable among sites than was the drying rate for the first drying period. For the final drying period, percentage of hourly soil matric potential measurements ranged from 7- 65.5% where drying was upward and ranged from 9-24% where drying was even across soil depths.

Effect of Soil Depth

Wet days and wet degree days before the first spring drying period tended to increase with increasing soil depth for all 4 yr since treatment (Figs. 4 and 5). Increases in wet days from 3 to 30 cm soil depths ranged from 34.3 to 44.3. While, increases in wet degree days ranged from 445 to 489. Conversely, wet days and wet degree days following the first spring drying period tended to decrease with increasing soil depth. Decreases in wet days from 3 to 30 cm ranged from 38.3 to 10.5, and decreases in wet degree days ranged from 397 to 146. The first spring drying period rates tended to increase with depth with rates between 20-30 cm of 1.82 cm day⁻¹ and 2.45 cm day⁻¹ faster than between 3-15 cm and 15-20 cm ($P < 0.05$) (Fig. 6). Average final drying rate between 3-15 cm and across all sites, treatments, phases, and microsites was 3.38 ± 0.42 cm day⁻¹.

Also increasing with soil depth were summed wet degree days at the 10 to < 25° C temperature range (Fig. 7). There were 72.1 to 181.5 more wet degree days at 30 than at 3 cm deep. Wet degree days for other temperature ranges ranked from highest to lowest at all four soil depths as follows: 5 to < 10° C, 0 to < 5° C, 25 to < 30° C, and 30 to < 35° C (Fig. 8). In general, wet degree days at 5 to < 10° C increased with soil depth from 3 to 30 cm by as much as 88.2 wet degree days during the first year to 104.0 wet degree days for the fourth year since tree reduction. Wet degree days for all other temperature ranges generally did not vary among soil depths.

Tree Removal Response

Before the first spring drying period, wet days varied significantly for tree removal treatments for all 4 yr since treatment and across all four soil depths (4 yr, $F_{2,574} = 22.36$, $P < 0.0001$). Wet degree days similarly varied with tree removal both before (4 yr, $F_{2,640} = 3.46$, $P = 0.0319$) and after (4 yr, $F_{2,640} = 7.45$, $P = 0.0006$) the first spring drying period. Usually, tree removal did not change wet days (4 yr, $F_{2,625} = 0.26$, $P = 0.7731$) and wet period frequency (3 yr, $F_{2,529} = 2.07$, $P = 0.0111$) after the first spring drying period. First (4 yr, $F_{2,363} = 0.49$, $P = 0.6113$) and final (4 yr, $F_{2,37.9} = 1.62$, $P = 0.2115$) spring drying period rates were not significantly affected by tree removal treatments. The interactions of tree removal treatments with soil depth were not usually significant for most variables ($P > 0.05$). Treated plots had more wet days and wet degree days than untreated plots. In order to account for variability among sites (Table 3), we determined the magnitude of change in wet days and wet degree days as a result of each tree removal treatment by subtracting untreated plot from treated plot responses for each site, year, treatment, phase, and microsite.

Additional Wet days and Wet Degree Days Before and After the First Spring Drying Period

Soil Depth. The effect of soil depth on additional wet days (2 yr, $F_{3,341} = 3.02$, $P = 0.0301$) and wet degree days (2 yr, $F_{3,412} = 6.48$, $P = 0.0003$) before and after the first spring drying period due to tree removal treatments was usually significant for the first 2 yr following treatment. Where significant, increasing soil depth from 3 to 30 cm may result in as much as 37.9 additional wet days and 500.0 additional wet degree days before the first spring drying period (Figs. 9 and 10). After the first spring drying period, increased depth resulted in no change or a loss by as much as 26 wet days and 284 wet degree days between 3-30 cm.

Tree Removal Treatment. Interactions with treatment and soil depth were not significant for wet days or wet degree days before or after the first spring drying period ($P > 0.05$). Across all soil depths, the effect of tree removal treatments on wet days (4 yr, $F_{1,423} = 5.16$, $P = 0.0236$) and wet degree days (3 yr, $F_{1,403} = 12.44$, $P = 0.0005$) before the first spring drying period were significant for 3 of 4 and 2 of 4 years since treatment. In general, the highest additions were observed during the first year since treatment at the two Utah sites (Fig. 9). After the first year, reduced additions or no changes were estimated across all sites for prescribed burn and cutting before the first drying period (Fig. 10). Changes in wet days after the first drying period were not typically different from zero. Prescribed burn plots had 22 more wet days and 388 more wet degree days than untreated plots before the first spring drying during the first year since treatment (Figs. 10 and 11). However, by the third and fourth year since treatment, tree cutting added more wet days and wet degree days before the first spring drying than prescribed fire ($P > 0.05$).

Where measured at sites in Utah, across all four soil depths and during the first year and before initial spring drying, mechanical shredding plots had approximately 12 wet days less than prescribed burn plots. Shredded plots had approximately 280 wet degree days more than untreated plots before the first drying period during the first 2 years since treatment. There were no other differences found between mechanical shredding, prescribed burning and tree cutting for other comparisons ($P > 0.05$).

Tree Infilling Phase. The effect of tree infilling phase was significant for wet days (yr 4, $F_{2,423} = 4.09$, $P = 0.0174$) and wet degree days (yr 4, $F_{2,423} = 9.58$, $P < 0.0001$) before the first spring drying period 3 of 4 and 4 of 4 years since treatment, respectively. After the first spring drying period, phase was significant for wet days (yr 3, $F_{2,404} = 4.77$, $P = 0.0089$) and wet degree days (yr 4, $F_{2,342} = 6.5$, $P = 0.0017$) 2 of 4 and 3 of 4 years since treatment, respectively. Generally, additions of each response increased with increasing tree infilling phase, with phase 3 significantly higher than phase 1 (Fig. 12) ($P < 0.05$).

Microsite Differences. The effect of microsite differences across all four soil depths was significant for wet days (yr 3, $F_{2,397} = 4.08$, $P = 0.0175$) and wet degree days (yr 4, $F_{2,423} = 3.18$, $P = 0.0425$) before the first spring drying period for 3 of 4 and 4 of 4 years since treatment, respectively. After the first spring drying period, the effect of microsite was not significant for wet days (yr 4, $F_{2,424} = 0.16$, $P = 0.8484$) and wet degree days (yr 4, $F_{2,341} = 1.23$, $P = 0.2942$). The interaction between microsite and soil depth was not significant for any comparison ($P > 0.05$). Typically, more wet days and wet degree days were added at the tree drip line microsite compared to interspace before the first spring drying compared and during the first year since treatment (Fig. 9, $P < 0.05$). More wet days and wet degree days tended to be added for shrub than tree drip line and interspace microsites, but values were not significantly different from

either ($P > 0.05$). After the first year since treatment, shrub mounds usually had less wet days and wet degree days than tree drip lines ($P < 0.05$), but neither was generally different from interspaces ($P > 0.05$).

Winter versus Spring Precipitation

The first spring drying rate across treated and untreated plots was associated with both winter (axis 1 $R^2 = 0.931$, axis 2 $R^2 = 0.364$, axis 3 $R^2 = 0.000$) and spring (axis 1 $R^2 = 0.594$, axis 2 $R^2 = -0.804$, axis 3 $R^2 = 0.000$) precipitation and the resulting ordination of sites was significant (Fig. 14, $P = 0.025$). Winter precipitation was positively correlated with axes 1 and 2, while spring precipitation was positively correlated with axis 1 and negatively correlated with axis 2. Axis 1 explained 51.7 % of the variation in first spring drying rates, while axis 2 explained only 0.3%. Because axis 2 explained little variation and axis 3 had $R^2 = 0.000$ for both winter and spring precipitation, we focused our analysis on axis 1. The first spring drying rates for the Blue Mountain, Stansbury, and Scipio sites were associated with increasing winter and spring precipitation, while the first spring drying rates for Bridge Creek, Devine Ridge, Greenville Bench, Marking Corral, Onaqui, and South Ruby sites were associated with decreasing winter and spring precipitation.

DISCUSSION

Soils predominantly dried from the soil surface downward for the first spring drying period with drying rates increasing with soil depth (Table 2, Fig. 3). Starting at the end of March or the first of April (Fig. 2), soils dried an average of $1.62 \pm 0.15 \text{ cm day}^{-1}$, $2.25 \pm 0.06 \text{ cm day}^{-1}$, and $4.07 \pm 0.24 \text{ cm day}^{-1}$ for the 3-15 cm, 15-20 cm, and 20-30 cm soil intervals for an average of $2.64 \pm 0.28 \text{ cm day}^{-1}$. Conversely, the final drying rate between 3-15 cm was $3.38 \pm 0.42 \text{ cm day}^{-1}$.

day⁻¹. The final drying rate was similar to that reported by Roundy et al. (1997), who found that soils dried at a Sonoran desert grassland site after summer rainfall in Arizona at about 3.6 cm day⁻¹ for the top 8 cm of the soil surface. The percentage of soil water matric potential measurements that dried evenly or upward increased with year since treatment and during the final spring drying period. Increased upward drying is probably associated with increased transpiration from recovering plants. Bybee (2013), Miller et al. (2014) and Roundy et al. (2014a) reported increased perennial herbaceous cover after tree removal treatments.

Winter and spring precipitation has been shown to strongly influence seedbed wet degree days at several of our sites in a companion study (Cline et al., 2014). The current study also indicates that the first spring drying rates were associated with winter and spring precipitation (Fig. 13). The duration of the first spring wet period leading to the first drying period primarily resulted from winter storage deposited by rain or snowfall. This period is prolonged by frequent early spring rain or snowfall and cooler early spring temperatures which are associated with lower evaporative demand (Noy-Meir, 1973; Bates et al., 2006; Smith et al., 2011). Conversely, late spring precipitation events are usually limited by amount, by the rate of water infiltration, and by the duration of force of the hydraulic head of the wetting front (Hillel, 2004). Also, late spring temperatures often are associated with higher evaporative and transpirational demand. The influence of late spring precipitation events on plant available water equates to a relatively small resource pulse in comparison to winter and early spring (Noy-Meir, 1973). These short term resource pulses likely have little effect on plant growth, but have been found to improve plant water status in herbaceous vegetation and shrubs (Donovan and Ehleringer, 1994; Bates et al., 1998; Snyder et al., 2004). Therefore, successfully modeling root growth to predict seedling survival should focus more on wet periods before and during the first spring drying period.

Roundy et al. (2014b) reported increased time of wet days, as well as degree days, with increasing soil depth, as would be expected with soil drying from the soil surface downward. We similarly found increased wet days and wet degree days before the first spring drying period with increasing soil depth (Fig. 3 and 4). Conversely, wet days and wet degree days after the first spring drying period decreased with soil depth. This decrease in plant available water with increasing soil depth is likely a result of the short time and sufficient water to percolate to the deeper soil depths before the precipitation event ends and the surface soils dry out. The drying of the surface soils reduces the hydraulic pressure on soil water moving down (Hillel 2006).

Similar to the findings of Cline et al. (2014) for Great Basin seedbeds, we found that the vast majority of wet degree days at every measured soil depth were summed between 5 and 25° C. Soils when at 0 to < 5° C temperature range summed as high as 80 wet degree days at 30 cm and soils when at temperatures above 25° C summed as much as 84 wet degree days. *B. tectorum*, *Pseudoroegneria spicata* (Pursh) Á. Löve, 'Nordon' *Agropyron desertorum* (Fisch. Ex Link) Schult, and *Elymus elymoides* (Raf.) Swezey may require approximately 200 to 300 degree days in wet conditions for seminal roots to extend 15 cm (Young and Roundy, 2012; Roundy et al., 2013). Also, the additional 40 to 120 wet degree days needed for germination in the seedbed before roots begin to extend further limit time of exposure to cooler temperatures in the spring (Cline et al., 2014), Therefore, we conclude that the majority of wet degree days needed to extend roots to 15 cm are summed between 5-25 C°. Because root zone temperatures when soils are wet are generally summed within the range of model development, seminal root growth predicted by thermal time models for field root zones should be fairly accurate. However, because of variability in soil temperature, nutrient status variability, and soil texture, further root growth trials at these temperatures may be needed to be able to predict root growth at locations

where summations of wet degree days are significantly higher at $< 5^{\circ} \text{C}$ and $> 25^{\circ} \text{C}$ (Cline et al., 2014; Leffler and Ryel, 2012; Chambers et al., 2007; Jensen, 1989).

Tree Removal Response

Roundy et al. (2014b) and Cline et al. (2014) have found that tree removal added time of plant available water (wet days) with increasing tree infilling phase in both the seedbed and root zone. Throughout the upper 30 cm of root zone and before the first spring drying period, we similarly found additional wet days and wet degree days with tree removal, often increasing with tree infilling phase. The extensive root systems of piñon and juniper trees utilize a large percentage of plant available water and nutrients needed for growth and maintenance (Ryel et al., 2010; Leffler and Ryel, 2012; Roundy et al., 2014b). As trees infill, understory vegetation may be competitively excluded due to a lack of soil water. Tree removal at an increased phase of tree infilling leaves available water unutilized. Thus after tree removal, root zones exhibit increased wet days and wet degree days before the first spring drying period.

Resource pulses may allow for increases in vegetation cover (Davis et al., 2000; Chambers et al., 2007; Bybee, 2013; Roundy et al. 2013b). The additional wet days and wet degree days before the first spring drying period may provide species seeded in revegetation projects more time to extend their seminal roots and develop adventitious roots, thereby increasing probability of survival. Wilson and Briske (1979) found that if adventitious roots have not been initiated, blue grama (*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths) seedlings did not survive. The lack of additional wet days and wet degree days from tree reduction after the first spring drying period is not well understood, but it could be that the differences are too small to measure at the scale of this study or that spring vegetation growth and evaporation with

increased temperatures have allowed for more equal use of plant available water across tree removal treatments.

Differences in time of plant available water between prescribed burning and mechanical treatments were expected but not found across the top 1-30 cm of soil depth (Roundy et al., 2014b). Understory vegetation initially decreases following a prescribed burn but recovers by the second or third year since treatment (Miller et al., 2014). Therefore, effects of removing trees by fire or mechanical treatments throughout the seedbed and root zone are most likely to be observed during the first year since treatment before understory vegetation increases. Also, burning reduces shrub cover while tree cutting or shredding does not (Bybee, 2013; Roundy et al., 2014a; 2014b). Cline et al. (2014) reported that prescribed burning added nearly twice as many wet degree days between 5 and 25° C in the seedbed during the first spring since treatment. In our study at the two Utah sites measured during the first year since treatment (Table 1), prescribed burning added at least 12 wet days and 296 wet degree days before the first spring drying period over both mechanical treatments ($P < 0.05$). After the first drying period of the first year, there was little or no difference between tree removal methods ($P > 0.05$). Before the first drying period of the first spring following a prescribed burn, the lack understory vegetation undoubtedly reduced soil water loss from transpiration which added wet days and wet degree days. As a result of these additional wet days and wet degree days, seedlings may gain needed time to extend roots sufficient for seedling survival.

Our analysis comparing microsites indicated that before the first spring drying period, more wet days and wet degree days were added by tree reduction treatments at the tree drip line than at the other microsites. More wet days and wet degree days were added at shrub mounds than interspaces during the first year since treatment at the two Utah sites. This might be

expected where prescribed burning removes shrubs (Roundy et al., 2014b) and tree cutting may increase the potential for hydraulic redistribution around remnant shrubs (Ryel et al., 2002; 2009). However, by the second year following treatment, more wet degree days were added in interspaces than shrub mounds. Shrub mounds are known as “fertile islands” in arid and semiarid environments because of increased soil nutrients (from organic matter decomposition), soil aggregate stability, infiltration, and canopy protection from solar radiation and raindrop impact (Whitford et al., 1997; Parsons et al., 2003). As a result, it should be expected that these microsites may increase in herbaceous cover faster than areas that were interspaces. The resulting increase in vegetation may be reducing the additional plant available water that was initially present following tree removal.

In summary, thermal time models that estimate root growth timing will best estimate seedling growth periods before and during the first spring drying period. Subsequent spring precipitation may increase the time of available soil water and thus seedling growth period and plant survival. Field experiments should be designed to test the importance of initial and subsequent spring drying patterns on seedling root growth and survival. Plant available water before the first drying period is of longer duration and is lost much slower than during subsequent drying periods. Removing trees at increasing tree infilling phase adds time of plant available water mainly before and during the initial drying period, and adds wet degree days both before and after this period. This additional time of available water may make the difference in germination and seedling survival for both invasive and revegetation plant materials on some years. Additional plant available water, as well as differences in tree removal methods and microsites, appears to decrease with time since treatment as understory plant cover increases.

LITERATURE CITED

- Aguirre, L., and D. A. Johnson. 1991. Root morphological development in relation to shoot growth in seedlings of four range grasses. *J. Range Manage.* 81:341–346.
- Anderson, M. L., N. L. Toft, and J. E. Shumar. 1987. Control of the soil water balance by sagebrush and three perennial grasses in a cold-desert environment. *Arid Soil Res. Rehab.* 1:224–229.
- Bates, J. D., R. F. Miller, and T. J. Svejcar. 1998. Understory patterns in cut western juniper woodlands. *Great Basin Nat.* 58:363–374.
- Bates, J. D., T. J. Svejcar, R. F. Miller, and R. A. Angell. 2006. The effects of precipitation timing on sagebrush steppe vegetation. *J. Arid Environ.* 64:670–697.
- Breshears, D. D., P. M. Rich, F. J. Barnes, and K. Campbell. 1997. Overstory-imposed heterogeneity in solar radiation and soil moisture in a semiarid woodland. *Ecol. Appl.* 7:1201–1215.
- Briske, D. D., and A. M. Wilson. 1977. Temperature effects on adventitious root development in blue grama seedlings. *J. Range Manage.* 30: 276-290.
- Briske, D. D., and A. M. Wilson. 1978. Moisture and temperature requirements for adventitious root development in blue grama seedlings. *J. of Range Manage.* 31:174–178.
- Bybee, J. A. 2013. Understory vegetation response to mechanical mastication of piñon and juniper woodlands. MS thesis. Brigham Young Univ., Provo, UT.

- Caldwell, M. 1985. Cold desert. In: Chabot, B. F., H. A. Mooney (eds.) *Physiological ecology of North American plant communities*. Chapman and Hall, New York. pp. 198-212.
- Campbell, G. S., and J. M. Norman. 1998. *An introduction to environmental biophysics*. Springer Science, New York, New York, USA. P. 15-16.
- Cantón, Y., A. Solé-Benet, and F. Domingo. 2004. Temporal and spatial patterns of soil moisture in semiarid badlands of SE Spain. *J. Hydrol.* 285:199–214.
- Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Whittaker. 2007. What makes Great Basin sagebrush ecosystems invulnerable by *Bromus tectorum*? *Ecol. Monogr.* 77:117.
- Cline, J. F., D. W. Uresk, and W. H. Rickard. 1977. Comparison of soil water used by a sagebrush-bunchgrass and a cheatgrass community. *J. Range Manage.* 30:199-201.
- Cline, N. L., B. A. Roundy, and W. F. Christensen. 2014. Wet-thermal time at five temperature ranges in seedbeds of the sagebrush steppe ecosystem. *Rangeland Ecol. Manage.* xx:xx-xx.
- Davies, K. W., J. D. Bates, and R. F. Miller. 2007. Short-term effects of burning Wyoming big sagebrush steppe in southeast Oregon. *Rangeland Ecol. Manage.* 60:515–522.
- Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: A general theory of invasibility. *J. Ecol.* 88:528–534.
- Davis, M. A., and M. Pelsor. 2001. Experimental support for a resource-based mechanistic model of invasibility. *Ecol. Lett.* 4:421-428.

- Donovan, L. A., and J. R. Ehleringer. 1994. Water stress and use of summer precipitation in a Great Basin shrub community. *Functional Ecology* 8:289–297.
- Eissenstat, D. M., and M. M. Caldwell. 1988. Competitive ability is linked to rates of water extraction a field study of two aridland tussock grasses. *Oecologia* 75:1–7.
- Gifford, G. F., and C. B. Shaw. 1973. Soil moisture patterns on two chained pinyon-juniper sites in Utah. *J. Range Manage.* 26:436–440.
- Hardegree, S. P., T. A. Jones, and S. S. Van Vactor. 2002. Variability in thermal response of primed and non-primed seeds of squirreltail [*Elymus elymoides* (raf.) Swezey and *Elymus multisetus* (J. G. Smith) M. E. Jones]. *Ann. Bot.* 89:311–319.
- Hardie, M. a., W. E. Cotching, R. B. Doyle, G. Holz, S. Lisson, and K. Mattern. 2011. Effect of antecedent soil moisture on preferential flow in a texture-contrast soil. *J. Hydrol.* 398:191–201.
- Hillel, D. 2004. Introduction to environmental soil physics. Elsevier Science (USA), Oxford, UK. P. 112, 337-361.
- Ivans, C. Y., A. J. Leffler, U. Spaulding, J. M. Stark, R. J. Ryel, and M. M. Caldwell. 2003. Root responses and nitrogen acquisition by *Artemisia tridentata* and *Agropyron desertorum* following small summer rainfall events. *Oecologia* 134:317–24.
- Jensen, M. E. 1989. Soil characteristics of mountainous Northeastern Nevada sagebrush community types. *Great Basin Nat.* 49:469–481.

- Jensen, M. E., G. H. Simonson, and R. E. Keane. 1989. Soil temperature and moisture regime relationships within some rangelands of the Great Basin. *Soil Sci.* 147:134–139.
- Kremer, R. G., and S. W. Running. 1996. Simulating seasonal soil water balance in contrasting semi-arid vegetation communities. *Ecol. Model.* 84:151–162.
- Leffler, A. J., and R. J. Ryel. 2012. Resource pool dynamics: conditions that regulate species interactions and dominance. In T. A. Monaco and R. L. Sheley, editors. *Invasive plant ecology and management: Linking processes to practice*. CABI Publishing, Wallingford, GB. P. 57–78
- Leffler, A. J., R. J. Ryel, L. Hipps, S. Ivans, and M. M. Caldwell. 2002. Carbon acquisition and water use in a northern Utah *Juniperus osteosperma* (Utah juniper) population. *Tree Phys.* 22:1221–1230.
- Littell, R. C., G. A. Milliken, W. W. Siroup, and R. D. Wolfinger. 1996. SAS system for mixed models. *Cary NC*. P. 633.
- McIver, J., M. Brunson, S. Bunting, J. Chambers, N. Devoe, P. Doescher, J. Grace, D. Johnson, S. Knick, R. Miller, M. Pellant, F. Pierson, D. Pyke, K. Rollins, B. Roundy, E. Schupp, R. Tausch, and D. Turner. 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.

- Miller, R. F., J. D. Bates, T. J. Svejcar, F. B. Pierson, and L. E. Eddleman. 2007. Western juniper field guide : Asking the right questions to select appropriate management actions. U.S. Geological Survey Circular 1321, 26 p.
- Miller, R. F., J. Seufert, B. A. Roundy, R. J. Tausch, C. Pereira, A. Hulet, and J. C. Chambers. 2013. Short-term response of woodlands in the intermountain west to prescribed fire and mechanical treatments. *Rangeland Ecol. Manage.* xx:xx-xx.
- Noy-Meir, I. 1973. Desert ecosystems: Environment and producers. *Annu. Rev. Ecol. Syst.* 4:25–51.
- Parsons, A. J., J. Wainwright, W. H. Schlesinger, and A. D. Abrahams. 2003. The role of overland flow in sediment and nitrogen budgets of mesquite dunefields, Southern New Mexico. *J. Arid Environ.* 53:61–71.
- PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>, created 11 November 2013.
- Rawlins, J. K., B. A. Roundy, S. M. Davis, and D. Egget. 2012a. Predicting germination in semi-arid wildland seedbeds. I. Thermal germination models. *Environ.l Experi. Bot.* 76:60–67.
- Rawlins, J. K., B. A. Roundy, D. Egget, and N. L. Cline. 2012b. Predicting germination in semi-arid wildland seedbeds II. Field validation of wet thermal-time models. *Environ. Experi Bot.* 76:68–73.
- Roundy, B. a., L. B. Abbott, and M. Livingston. 1997. Surface soil water loss after summer rainfall in a semidesert grassland. *Arid Soil Res. Rehab.* 11:49–62.

- Roundy, B. A., S. P. Hardegree, J. C. Chambers, and A. Whittaker. 2007. Prediction of cheatgrass field germination potential using wet thermal accumulation. *Rangeland Ecol. Manage.* 60:613–623.
- Roundy, B. A., R. F. Miller, R. J. Tausch, K. Young, A. Hulet, B. Rau, B. Jessop, J. C. Chambers, and D. Eggett. 2014a. Understory cover responses to piñon-juniper control across tree cover gradients in the Great Basin. *Rangeland Ecol. Manage. Management* x:xx–xx.
- Roundy, B. A., K. Young, N. Cline, A. Hulet, R. F. Miller, R. J. Tausch, J. C. Chambers, and B. Rau. 2014b. Piñon-juniper reduction effects on soil temperature and water availability of the resource growth pool. *Rangeland Ecol. Manage.* xx:xx-xx.
- Ryel, A. R. J., M. M. Caldwell, A. J. Leffler, and C. K. Yoder. 2009. Rapid soil moisture recharge to depth by roots in a stand of *Artemisia tridentata*. *Ecology* 84:757–764.
- Ryel, R. J., M. M. Caldwell, C. K. Yoder, and A. J. Leffler. 2002. Hydraulic redistribution in a stand of *artemisia tridentata*: Evaluation of benefits to transpiration assessed with a simulation model. *Oecologia* 130:173–184.
- Ryel, R. J., A. J. Leffler, C. Ivans, M. S. Peek, and M. M. Caldwell. 2010. Functional differences in water-use patterns of contrasting life forms in Great Basin steppelands. *Vadose Zone J.* 9:548–560.
- Schenk, H. J., and R. B. Jackson. 2002. Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *J. Ecol.* 90:480.

- Schwinning, S., and O. E. Sala. 2004. Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. *Oecologia* 141:211–20.
- Schwinning, S., B. I. Starr, and J. R. Ehleringer. 2003. Dominant cold desert plants do not partition warm season precipitation by event size. *Oecologia* 136:252–60.
- Shaw, N.; Pellant, M. 2013. Great Basin native plant selection and increase Project: 2012 Progress Report. Boise, ID: U.S. Department of Agriculture, Rocky Mountain Research Station and U.S. Department of the Interior, Bureau of Land Management. 278 p. Available at www.treesearch.fs.fed.us/pubs/43735.
- Smith, T. J., J. P. McNamara, A. N. Flores, M. M. Gribb, P. S. Aishlin, and S. G. Benner. 2011. Small soil storage capacity limits benefit of winter snowpack to upland vegetation. *Hydrol. Process* 25:3858–3865.
- Snyder, K. A., L. A. Donovan, J. J. James, R. L. Tiller, and J. H. Richards. 2004. Extensive summer water pulses do not necessarily lead to canopy growth of Great Basin and Northern Mojave Desert shrubs. *Oecologia* 141:325–334.
- Svejcar, T. 2003. Applying ecological principles to wildland weed management. *Weed Sci.* 51:266–270.
- Whitford, W. G., J. Anderson, and P. M. Rice. 1997. Stemflow contribution to the “fertile island” effect in creosotebush, *Larrea tridentata*. *J. Arid Environ.* 35:451–457.
- Wilson, A., D. Briske. 1979. Seminal and adventitious root growth of blue grama seedlings on the Central Plains. *J. of Range Manage.* 32: 209-213.

Young, K., and B. Roundy. 2012. Modeling seedling root growth of Great Basin species. Native Plant Meeting, Salt Lake City, Utah, USA. February 21-22, 2012.

TABLES

Table 3-1. List of woodland sites, year of treatment, and years of soil moisture and temperature year data used for post treatment and woodland infilling phase analysis. Table reprinted from Cline et al. (2014).

Site	Treatment and phase comparison				
	Year treated	Year data used for year since treatment			
		Year 1	Year 2	Year 3	Year 4
Blue Mountain	2007		2009	2010	2011
Bridge Creek	2006		2008	2009	2010
Devine Ridge	2007		2009	2010	2011
Marking Corral	2006		2008	2009	2010
South Ruby	2009		2010	2011	
Stansbury	2007	2008	2009		
Onaqui	2006	2007	2008	2009	2010
Scipio	2007			2010	2011
Greenville	2007		2009	2010	2011
Total number of sites	9	2	8	8	7

Table 3-2. Percentage of time that soils dried at shallower soils before deeper soils (down), soils dried occurred at deeper soils before shallower soils (up), or both shallow and deep soils dried at the same time (even) during spring (1 March to 30 June) for the first and last drying periods of the season across treated and untreated plots. 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.

		First Spring Drying			Last Spring Drying		
		Down	Even	Up	Down	Even	Up
Years since treatment for soil depths	Year 2	80.1	13.0	6.9	63.9	11.1	25.0
	Year 3	78.8	13.4	7.8	59.3	21.2	19.5
	Year 4	77.0	11.4	11.6	48.9	14.2	37.0
Between soil depths	3 and 15 cm	93.7	4.0	2.4	60.9	14.1	25.0
	15 and 20 cm	72.1	17.1	10.8	-	-	-
	20 and 30 cm	70.0	17.0	13.0	-	-	-
Sites	BC	67.3	20.0	12.7	76.2	9.5	14.3
	BM	83.4	13.9	2.7	60.0	8.9	31.1
	DR	74.1	14.6	11.3	79.1	13.4	7.5
	GV	90.3	5.3	4.3	37.5	12.5	50.0
	MC	76.2	9.9	13.9	56.1	2.4	41.5
	OJ	80.4	13.9	5.7	64.4	24.0	11.5
	SC	77.7	10.8	11.5	38.9	22.2	38.9
	SR	79.7	13.7	6.5	62.5	12.5	25.0
ST	76.4	9.7	13.9	20.7	13.8	65.5	

Table 3-3. Site drying and wetting conditions (\pm standard error and \pm , - confidence intervals) across treated and untreated sites. 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. Parentheses next to sites indicate number of years included in estimates.

		Sites								
Soil		BC (3 yr)	BM (3 yr)	DR (3 yr)	GV (3 yr)	MC (3 yr)	OJ (4 yr)	SC (2 yr)	SR (2 yr)	ST (2 yr)
Before 1st Drying Period										
Wet Days										
3	83.3 \pm 2.96	132 \pm 3.02	120 \pm 3.08	97.0 \pm 3.08	67.1 \pm 2.96	83.7 \pm 2.74	101 \pm 3.21	72.1 \pm 3.56	103 \pm 3.57	
15	114 \pm 3.13	157 \pm 2.99	148 \pm 3.17	135 \pm 3.15	93.1 \pm 3.04	121 \pm 2.74	128 \pm 3.13	84.8 \pm 3.62	133 \pm 3.74	
20	123 \pm 3.08	161 \pm 2.99	154 \pm 3.31	142 \pm 3.23	93.1 \pm 3.04	128 \pm 2.79	133 \pm 3.15	93.9 \pm 3.65	33 \pm 3.81	
30	127 \pm 3.11	166 \pm 3.01	155 \pm 3.45	148 \pm 3.31	93.2 \pm 3.09	133 \pm 3.21	140 \pm 3.11	100 \pm 3.80	138 \pm 3.77	
Wet degree days										
3	164 \pm 29.3	401 \pm 28.8	281 \pm 29.8	202 \pm 29.8	64.6 \pm 29.3	120 \pm 26.9	219 \pm 30.9	217 \pm 35.2	207 \pm 28.4	
15	551 \pm 29.3	624 \pm 28.8	546 \pm 29.8	590 \pm 29.8	481 \pm 29.3	503 \pm 27.0	486 \pm 30.8	537 \pm 35.2	612 \pm 28.4	
20	620 \pm 29.3	658 \pm 28.8	617 \pm 30.2	694 \pm 29.8	576 \pm 29.3	611 \pm 26.9	545 \pm 30.8	639 \pm 35.2	664 \pm 28.4	
30	672 \pm 29.3	723 \pm 28.8	645 \pm 29.8	776 \pm 29.8	640 \pm 29.3	673 \pm 26.9	632 \pm 30.8	669 \pm 35.2	730 \pm 28.4	
Initial drying rate(cm/day)										
3 to 15	0.90 \pm 0.29	2.72 \pm 0.29	1.93 \pm 0.30	1.46 \pm 0.27	0.87 \pm 0.29	0.90 \pm 0.25	1.59 \pm 0.29	1.40 \pm 0.34	2.25 \pm 0.33	
15 to 20	2.00 \pm 0.30	2.78 \pm 0.27	2.45 \pm 0.30	1.92 \pm 0.28	2.16 \pm 0.30	1.60 \pm 0.25	2.51 \pm 0.30	2.16 \pm 0.34	4.84 \pm 0.44	
20 to 30	4.66 \pm 0.31	3.79 \pm 0.27	4.98 \pm 0.33	3.12 \pm 0.28	2.76 \pm 0.30	4.52 \pm 0.25	3.45 \pm 0.29	4.14 \pm 0.34	5.05 \pm 0.35	
After 1st Drying Period										
Frequency										

123

3	4.73 (+0.67, - 0.60)	1.22 (+0.26, - 0.23)	2.01 (+0.37, - 0.33)	2.12 (+0.37, -0.33)	5.04 (+0.72, -0.64)	4.50 (+0.58, -0.52)	4.02 (+0.62, -0.55)	2.72 (+0.27, -0.24)	3.7 (+0.28, - 0.24)
15	1.47 (+0.31, - 0.28)	0.38 (+0.16, - 0.15)	0.68 (+0.22, - 0.19)	0.34 (+0.16, -0.14)	0.49 (+0.18, -0.16)	1.09 (+0.22, -0.20)	1.21 (+0.27, -0.24)	0.32 (+0.54, -0.47)	1.07 (+0.32, -0.28)
20	1.07 (+0.25, - 0.23)	0.33 (+0.16,- 0.14)	0.48 (+0.20, - 0.18)	0.17 (+0.14, -0.11)	0.38 (+0.17, -0.15)	0.49 (+0.16, -0.15)	0.74 (+0.21, -0.19)	0.13 (+0.16, -0.14)	0.79 (+0.78, -0.24)
30	0.84 (+0.23, - 0.20)	0.11 (+0.13, - 0.11)	0.46 (+0.21, - 0.18)	0.06 (+0.13, -0.11)	0.53 (+0.19, -0.18)	0.23 (+0.14, -0.12)	0.34 (+0.16, -0.15)	0.18 (+0.17, -0.14)	0.60 (+0.25, -0.22)
Wet Days									
3	52.5 ±1.83	28.0 ±1.84	41.5 ±1.88	33.8 ± 1.85	42.2 ± 1.84	35.1 ± 1.70	37.1 ± 1.90	39.5 ± 2.08	44.5 ± 2.10
15	28.1 ±1.90	7.31 ±1.84	18.9 ±1.91	9.25 ± 1.85	15.8 ± 1.90	11.5 ± 1.72	13.9 ± 1.88	15.1 ± 2.09	19.7 ± 2.16
20	24.2 ±1.88	4.25 ±1.84	14.7 ±1.97	5.23 ± 1.84	12.2 ± 1.91	6.26 ± 1.74	9.56 ± 1.88	10.4 ± 2.09	16.9 ± 2.18
30	21.1 ±1.88	0.81 ±1.85	11.8 ±2.03	2.27 ± 1.85	10.1 ± 1.88	3.79 ± 1.77	6.24 ± 1.88	10.1 ± 2.09	13.9 ± 2.17
Wet Degree Days									
3	655 ± 18.6	279 ± 18.3	408 ± 18.9	343 ± 16.8	373 ± 18.6	369 ± 15.1	444 ± 17.8	312 ± 22.3	497 ± 16.1
15	397 ± 18.6	113 ± 18.3	223 ± 18.9	105 ± 16.8	192 ± 18.6	182 ± 15.1	225 ± 17.8	123 ± 22.3	216 ± 16.1
20	358 ± 18.6	85.9 ±18.3	175 ± 19.1	52.2 ± 16.8	156 ± 18.6	102 ± 15.1	152 ± 17.8	72.9 ± 22.3	160 ± 16.1
30	293 ± 18.6	26.6 ±18.3	134 ± 18.9	22 ± 16.8	123 ± 18.6	57.5 ± 15.1	81.0 ± 17.8	66.9 ± 22.3	112 ± 16.1
Final Drying Rate									
3 to 15	3.43 ±0.35	4.64 ±0.37	4.59 ±0.39	4.01 ± 0.49	2.91 ± 0.52	4.81 ± 0.35	3.48 ± 0.57	3.49 ± 0.62	4.27 ± 0.63

FIGURES

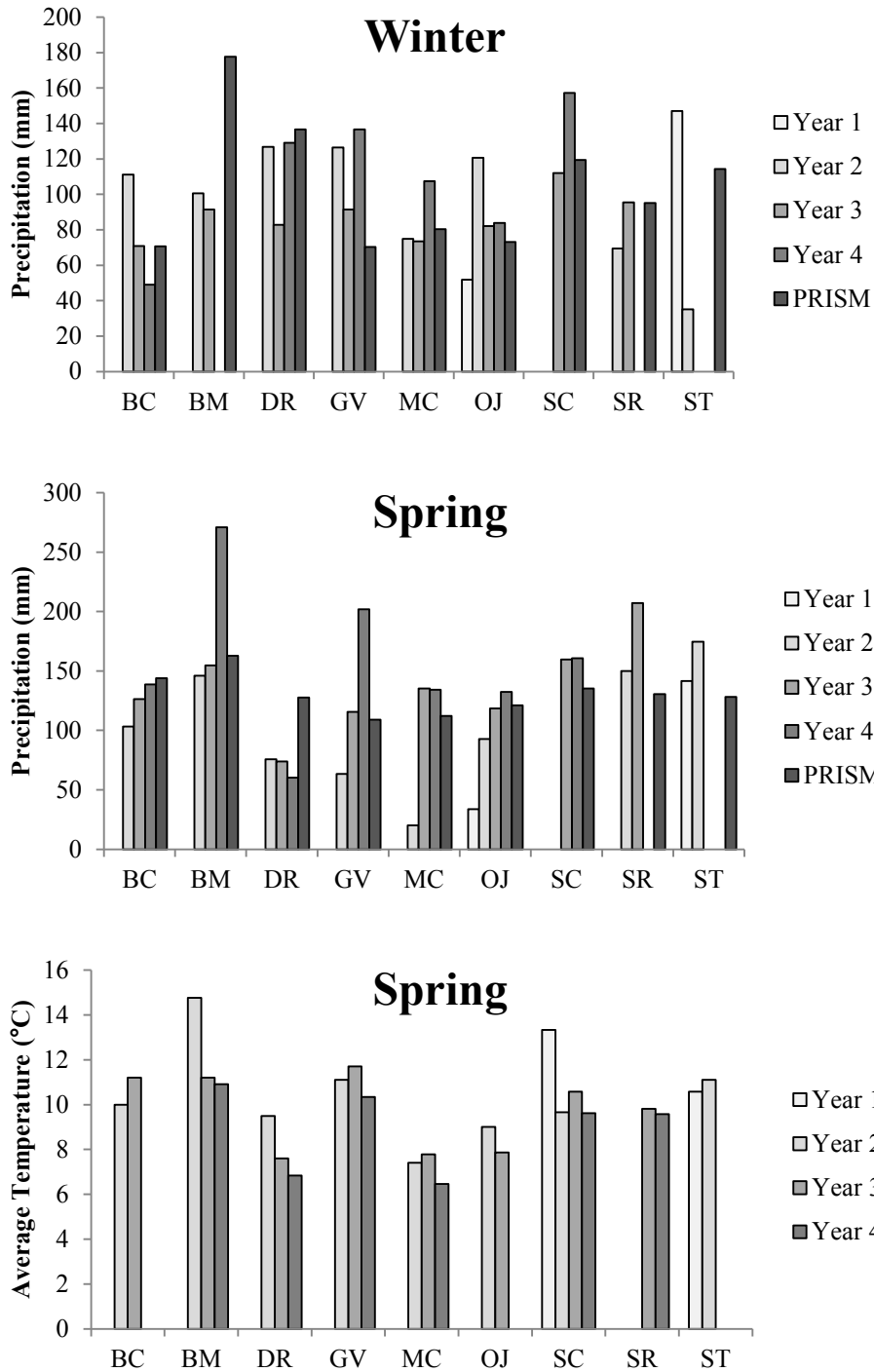


Figure 3-1. Winter precipitation (top), spring precipitation (middle), and average spring temperature (bottom) for four years since tree reduction treatments. Sites are BC – Bridge Creek,

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. PRISM (2013).

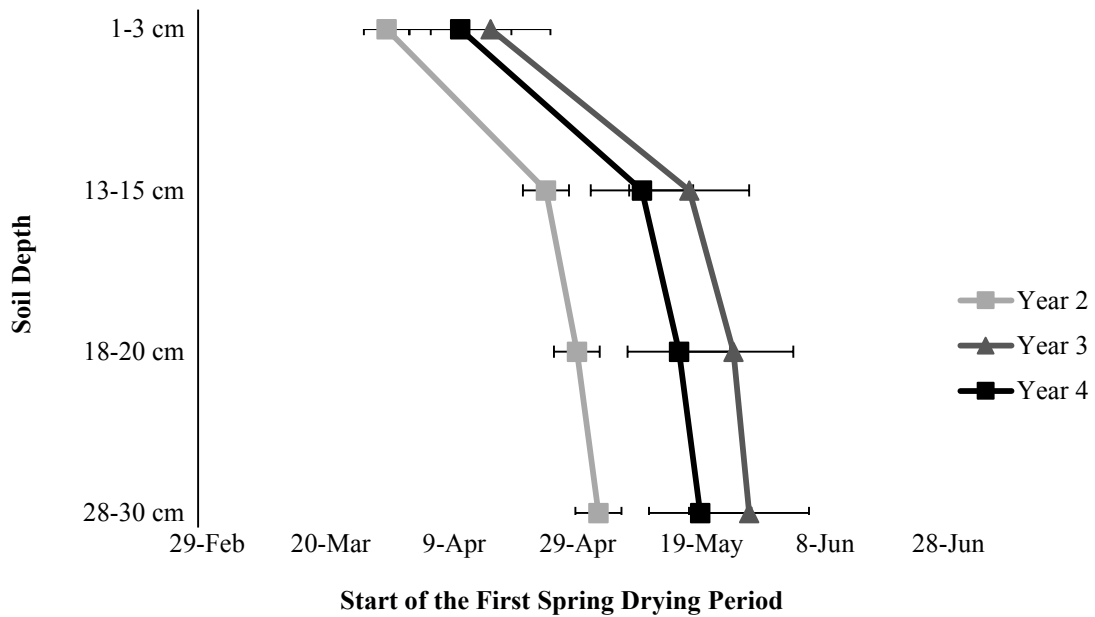
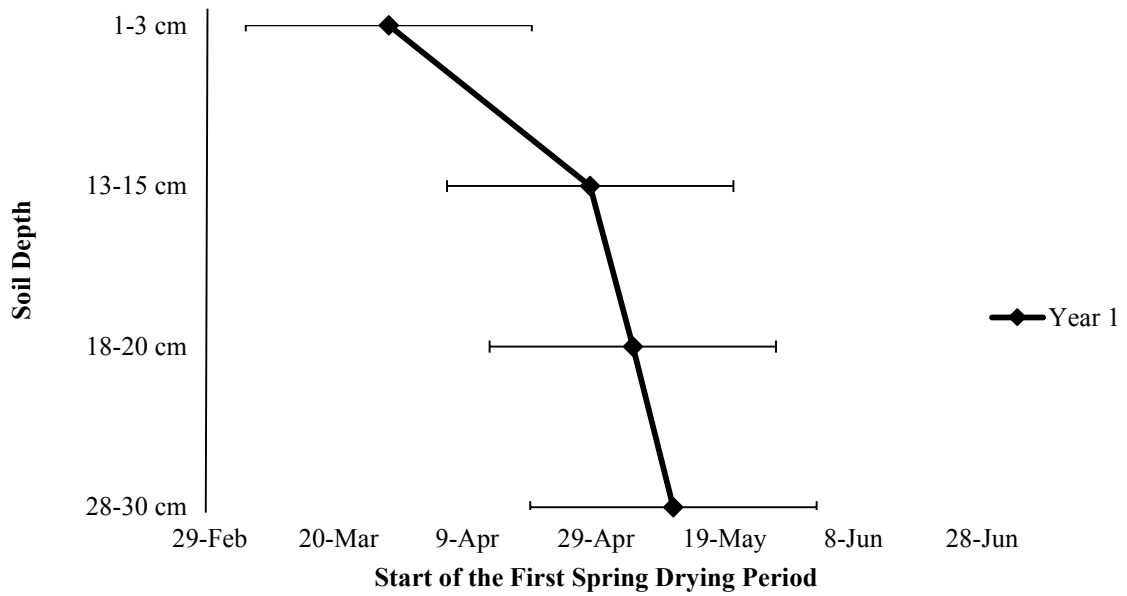


Figure 3-2. Date of the first spring drying period by soil depth across treated and untreated plots. Year 1 (Top) is represented by two Utah sites, Years 2-4 (bottom) are represented by six to eight sites each. Error bars = 1 standard error.

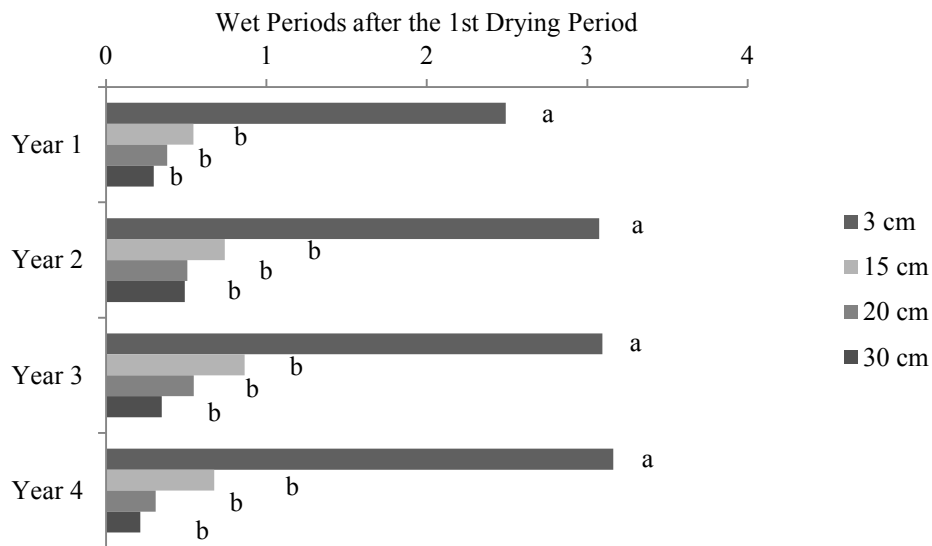


Figure 3-3. Spring wet period frequency (number of wet periods from 1 March to 30 June) after the first drying period at four soil depths for 4 yr since tree reduction treatments across treated and untreated plots. Each year was separately analyzed and different letters indicate significant differences among soil depths for that year ($P < 0.05$).

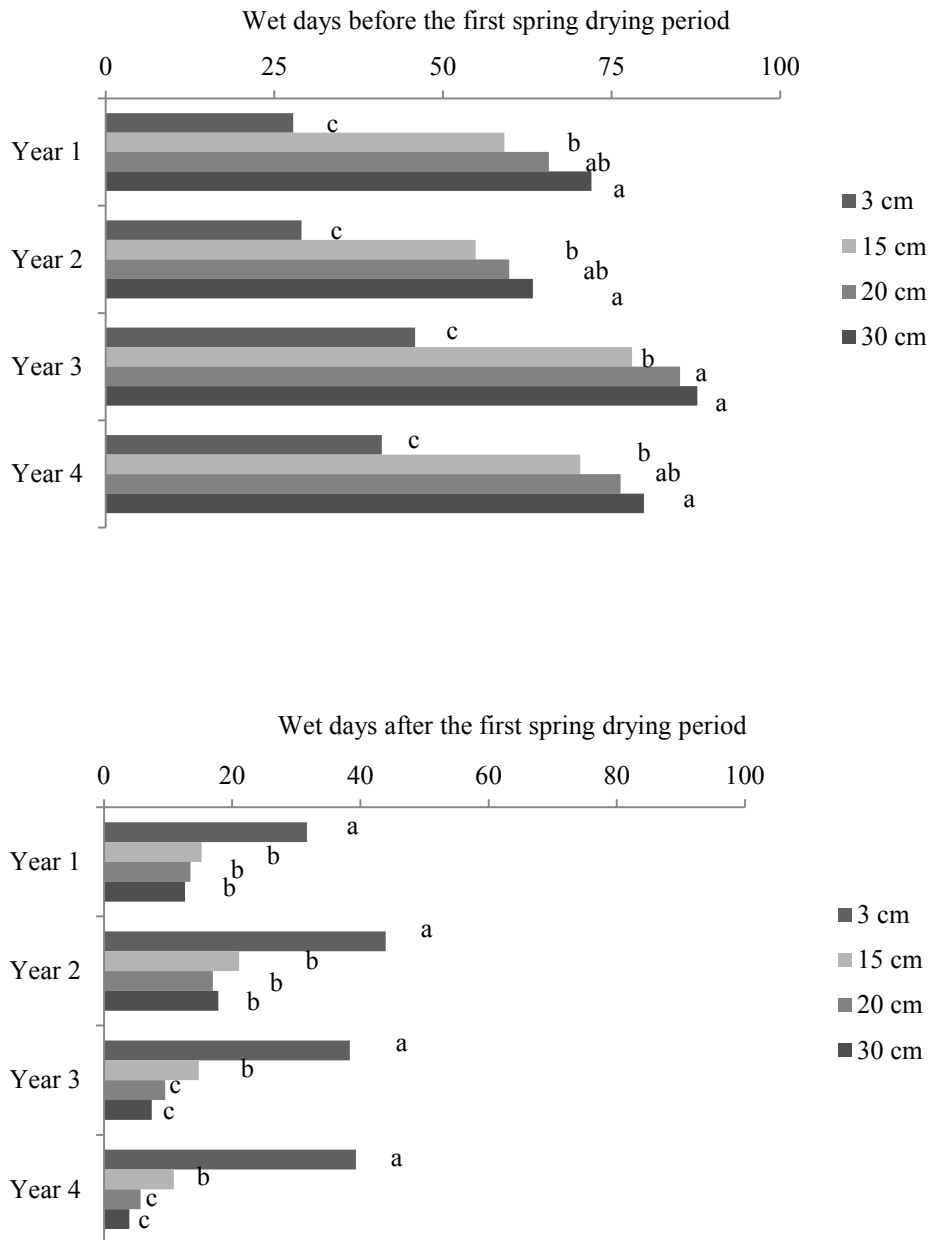


Figure 3-4. Spring wet days (1 March to 30 June) before (top) and after (bottom) the first spring drying period at four soil depths for 4 yr since tree reduction treatments across treated and untreated plots. Each year was separately analyzed and different letters indicate significant differences between soil depths for that year ($P < 0.05$).

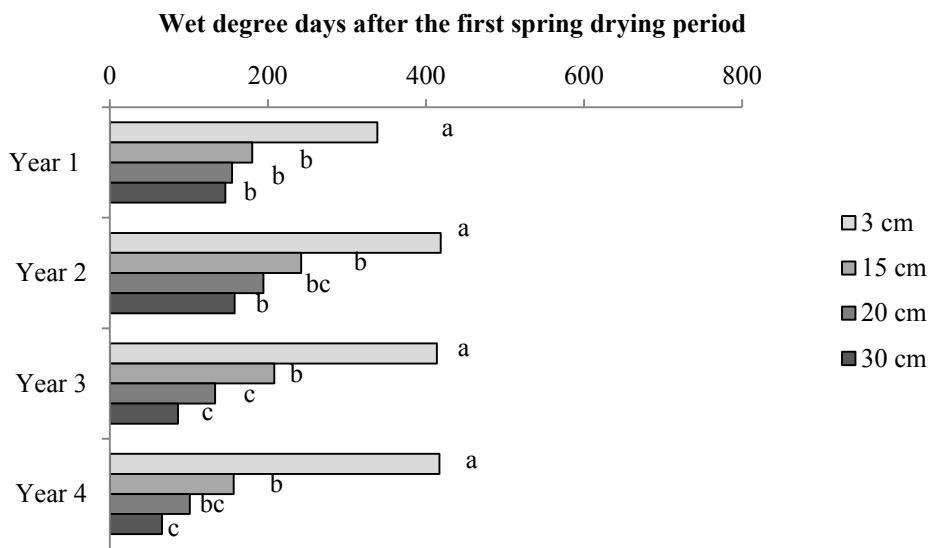
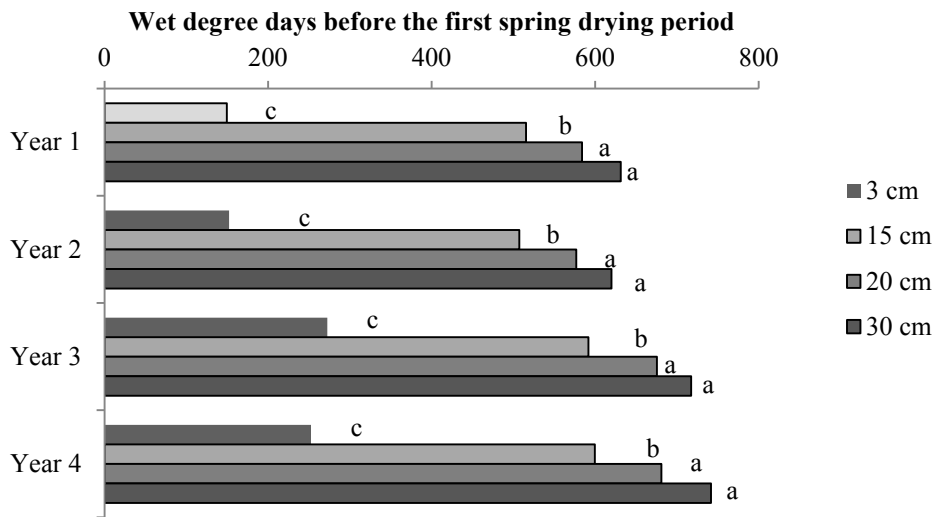


Figure 3-5. Spring (1 March to 30 June) wet degree days before and after first spring drying period at four soil depths for 4 yr since tree reduction treatments across treated and untreated plots. Each year was separately analyzed and different letters indicate significant differences between soil depths for that year ($P < 0.05$).

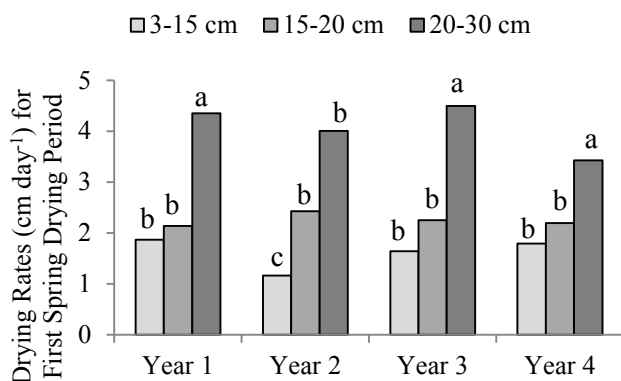


Figure 3-6. Drying rates for the first spring (1 March to 30 June) drying period between soil depths for 4 yr since tree reduction treatments across treated and untreated plots. Each year was analyzed separately and different letters indicate significant differences between soil depths for that year ($P < 0.05$).

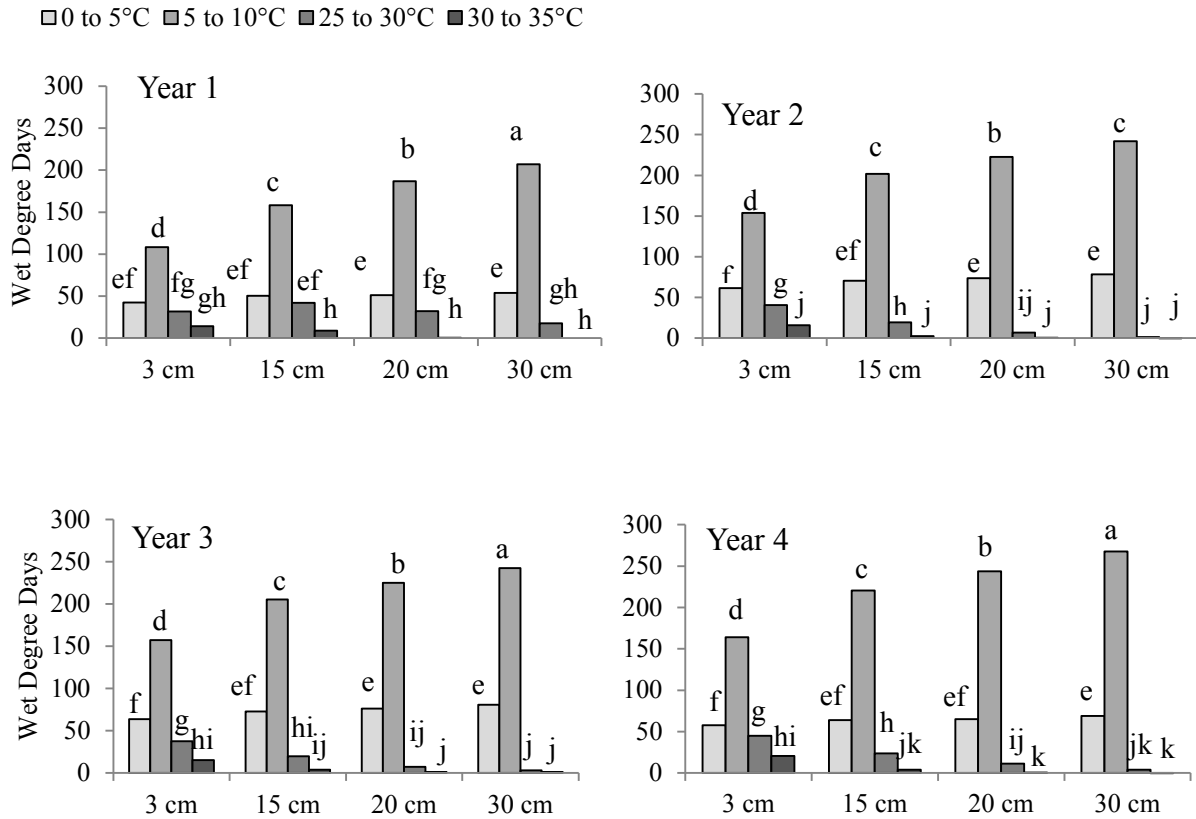


Figure 3-7. Wet degree days in spring (1 March to 30 June) at four temperature ranges for four soil depths and 4 yr since tree reduction treatments across treated and untreated plots. Each year and was separately analyzed and different letters indicate significant differences between soil depths and temperature ranges for that year ($P < 0.05$).

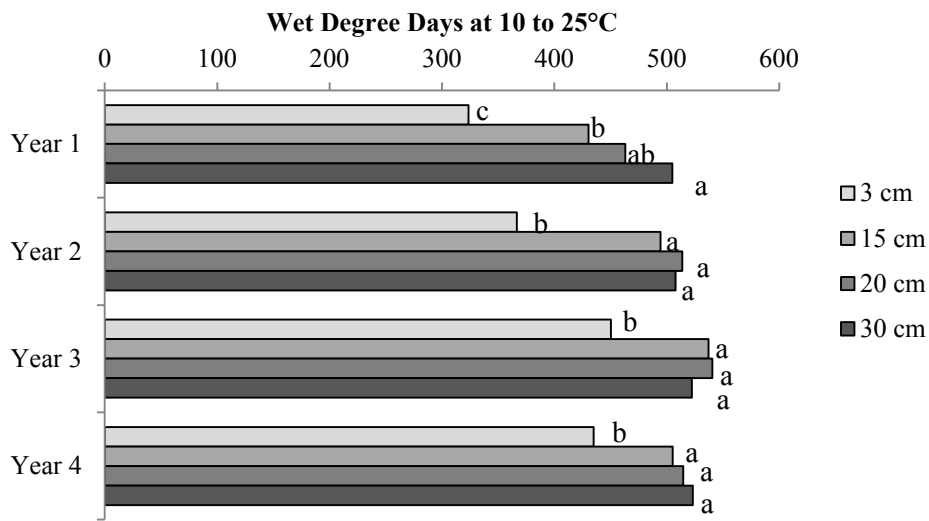


Figure 3-8. Spring wet degree days for 4 yr since tree reduction treatments at the 10 to 25° C temperature range at four soil depths across treated and untreated plots. Each year was separately analyzed and different letters indicate significant differences between soil depths for that year ($P < 0.05$).

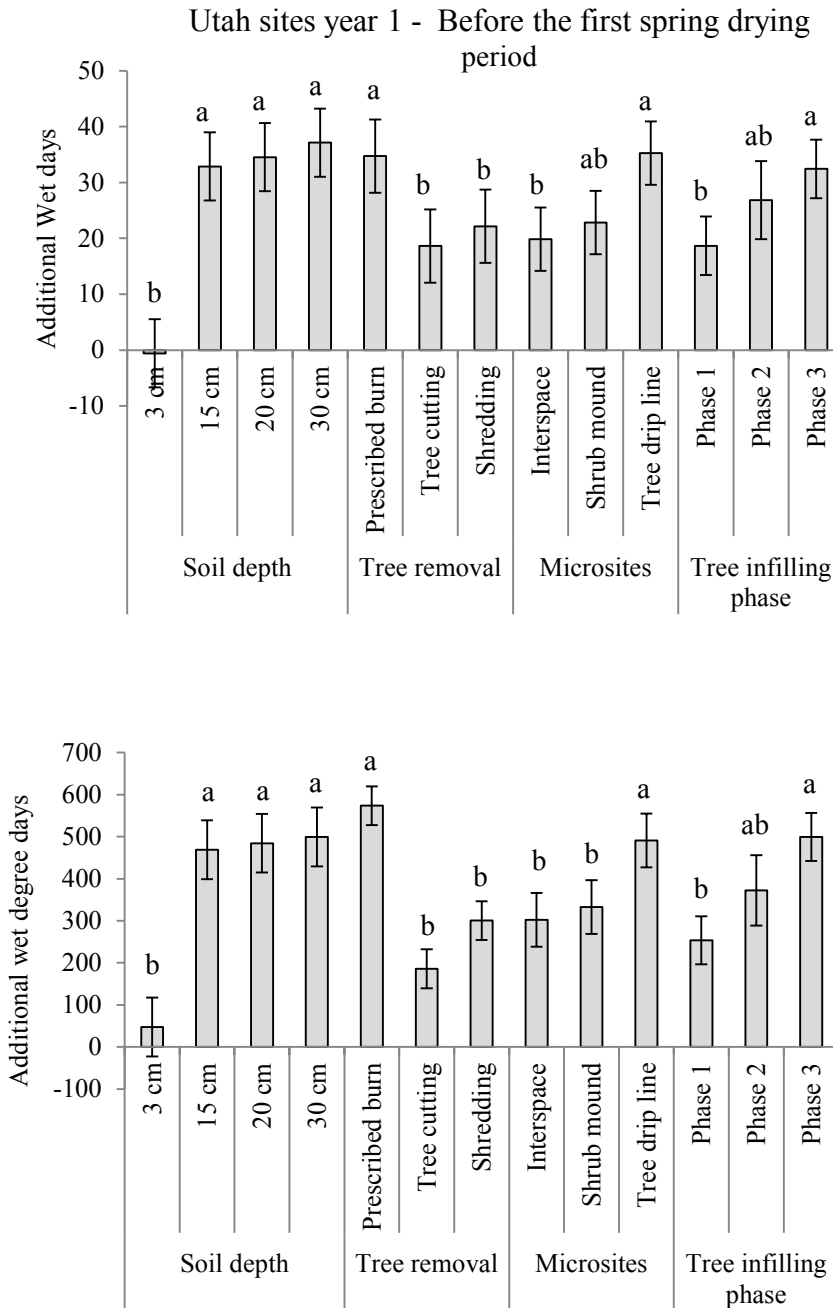


Figure 3-9. Additional wet days (top) and wet degree days (bottom) for soil depth, tree removal methods, microsities, and tree infilling phases the first year after tree reduction. Factors were separately analyzed and different letters indicate significant differences between soil depths for that year ($P < 0.05$).

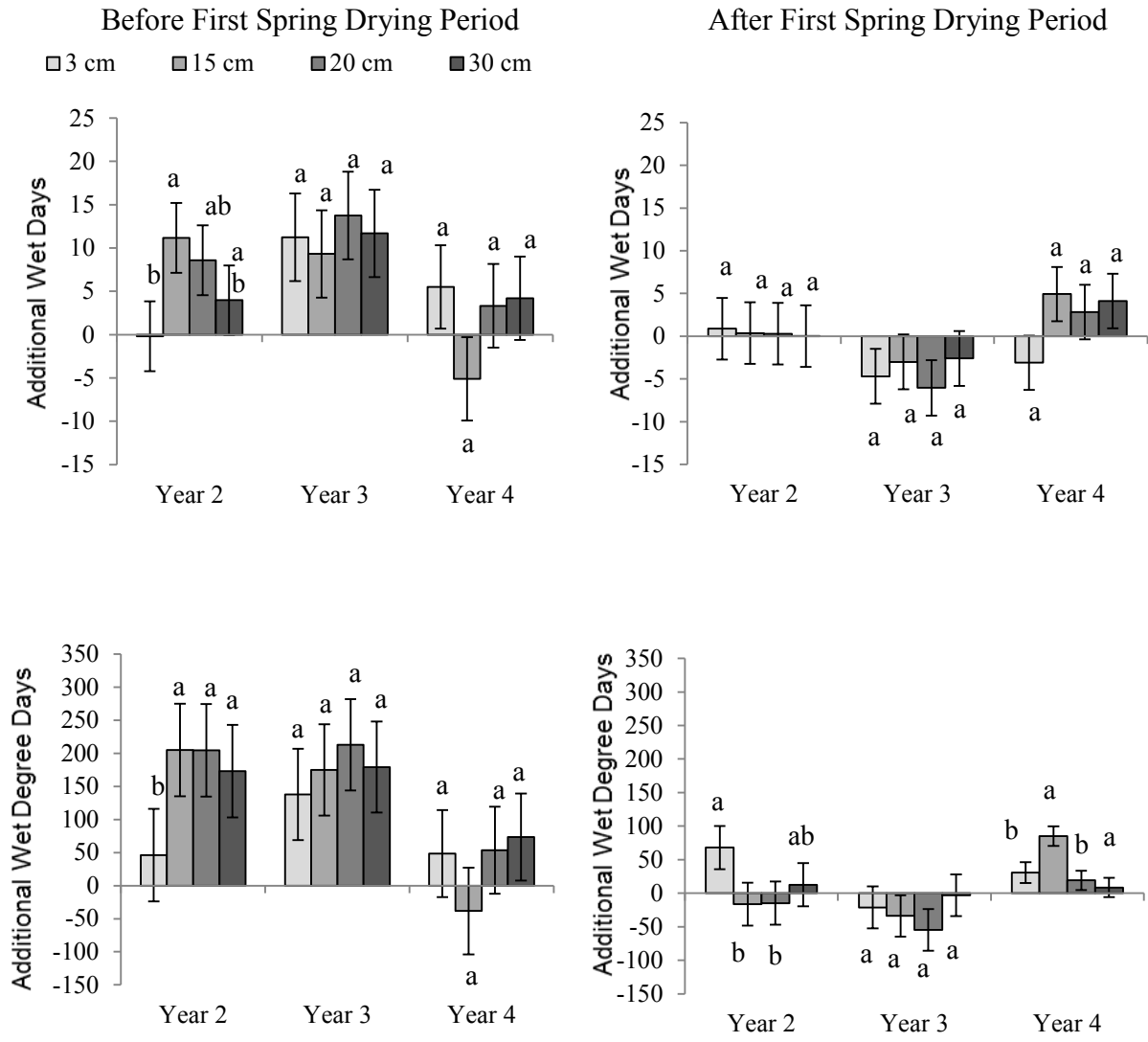


Figure 3-10. Additional wet days (top) and wet degree days (bottom) before (left) and after (right) the first spring (1 March to 30 June) drying period by soil depth. Bars are standard error of the mean. Each year was separately analyzed and different letters indicate significant differences between soil depths for that year ($P < 0.05$).

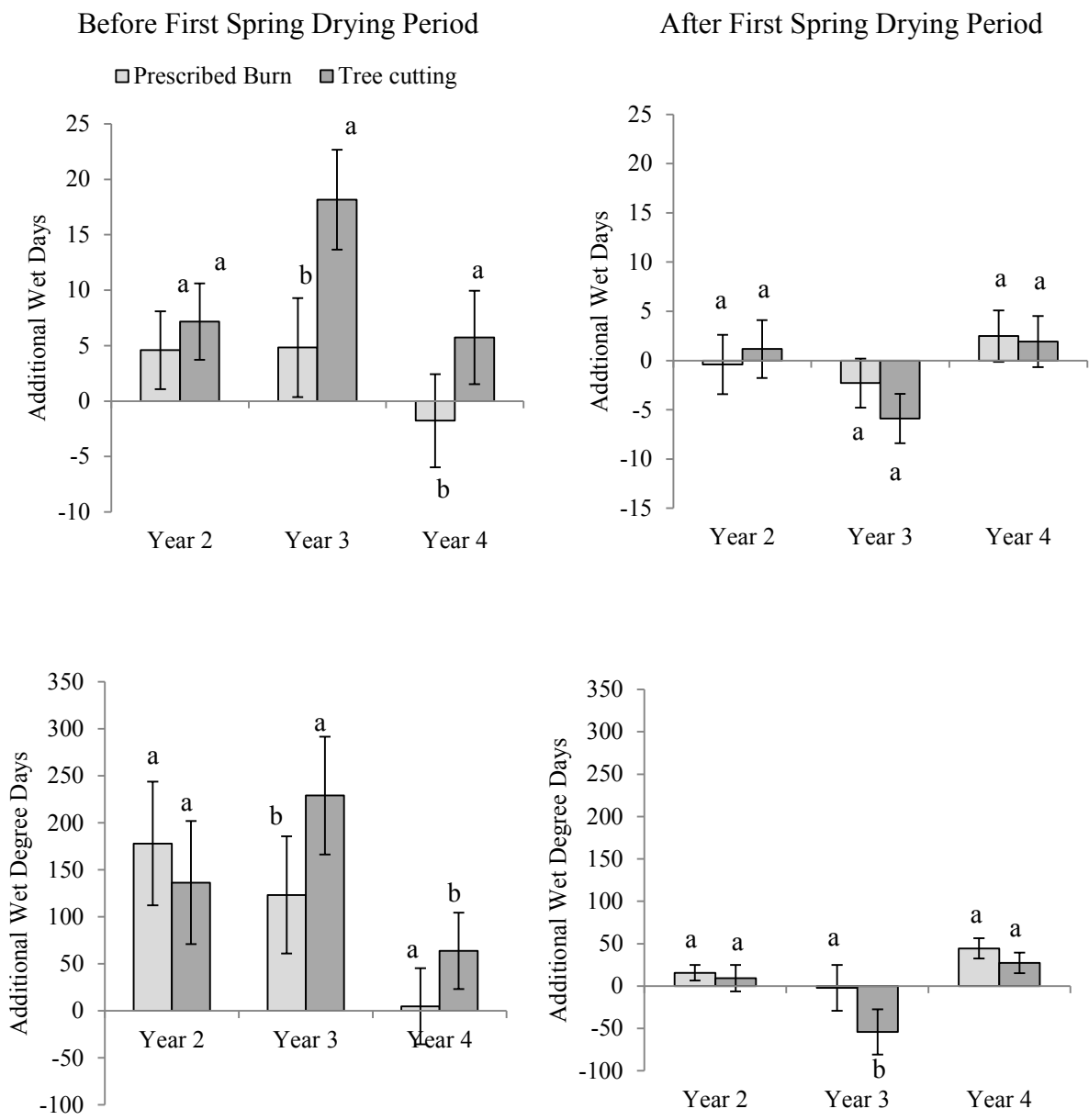


Figure 3-11. Additional wet days (top) and wet degree days (bottom) after prescribed burning and tree cutting before (right) and after (left) the first spring (1 March to 30 June) drying period. Bars are standard error of the mean. Each year after treatment was analyzed separately and different letters indicate significant differences among treatments for that year ($P < 0.05$).

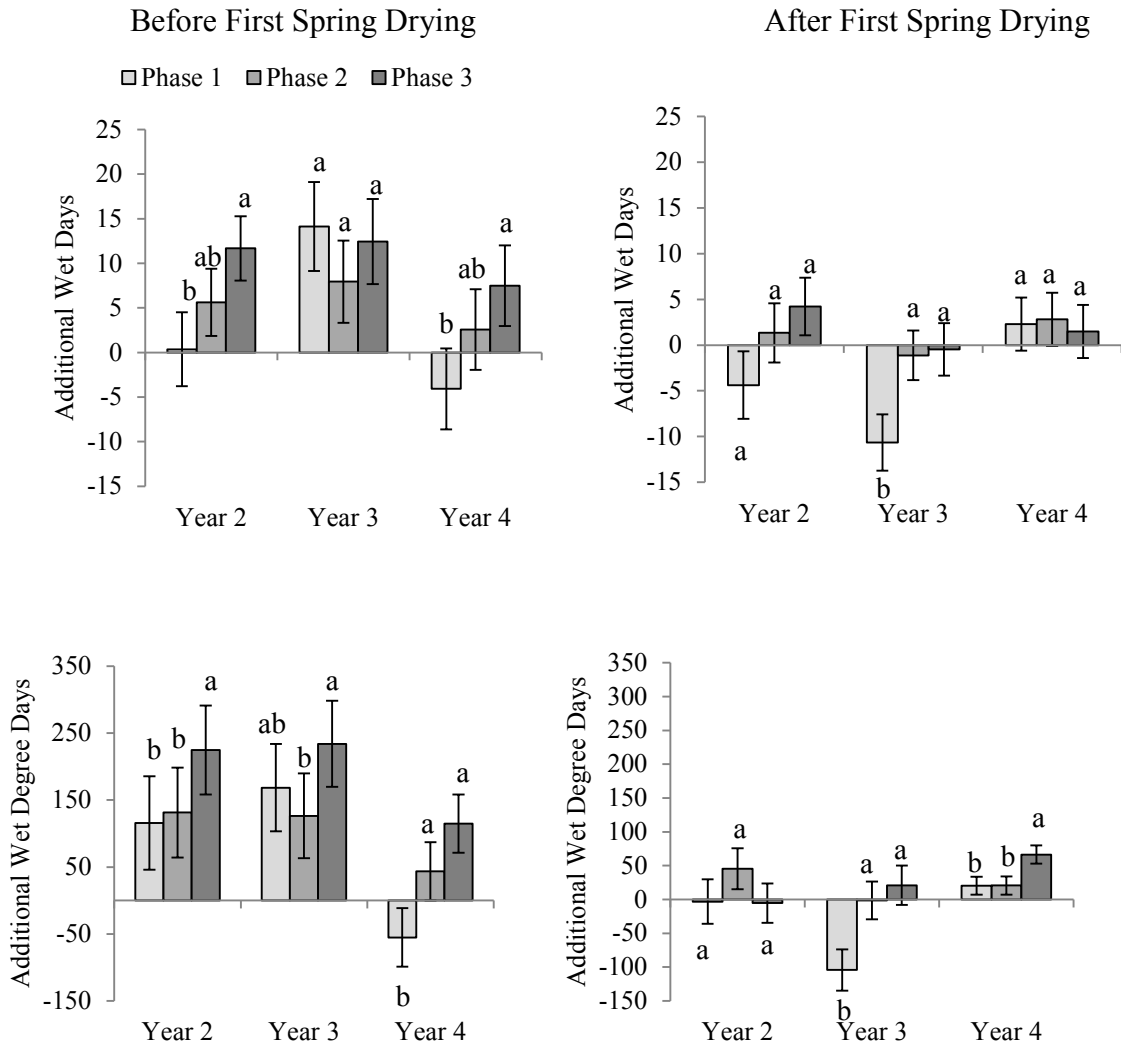


Figure 3-12. Additional wet days (top) and wet degree days (bottom) for the before (right) and after (left) the first spring (1 March to 30 June) drying period when trees were reduced by prescribed burning or cutting at different phases of tree infilling. Error bars are standard error of the mean. Each year was separately analyzed and different letters indicate significant differences between soil depths for that year ($P < 0.05$).

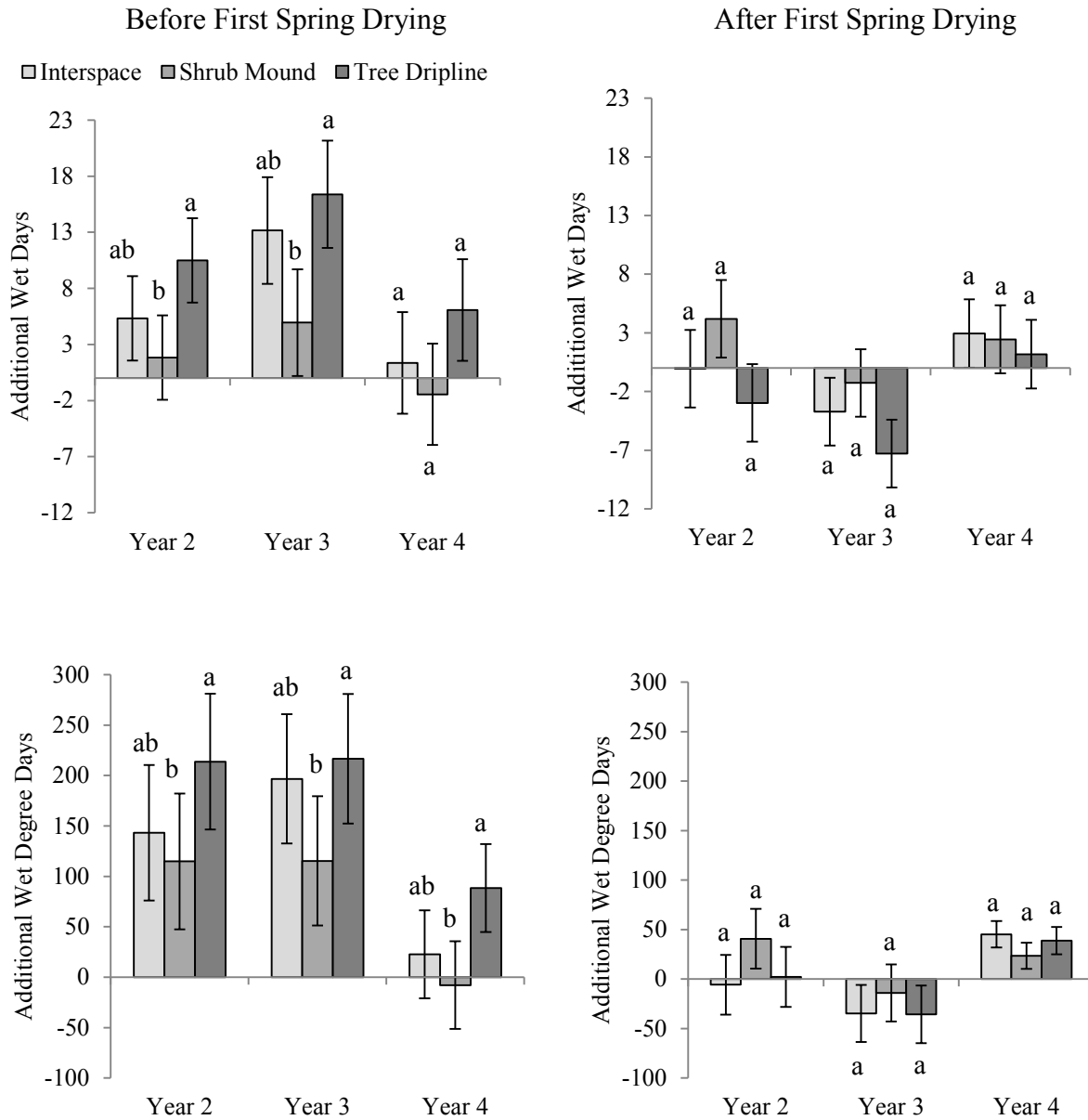


Figure 3-13. Additional wet days (top) and wet degree days (bottom) for before (right) and after (left) the first spring (1 March to 30 June) drying period for different microsites and after tree reduction treatments. Error bars are standard error of the mean. Each year was separately analyzed and different letters indicate significant differences between soil depths for that year ($P < 0.05$).

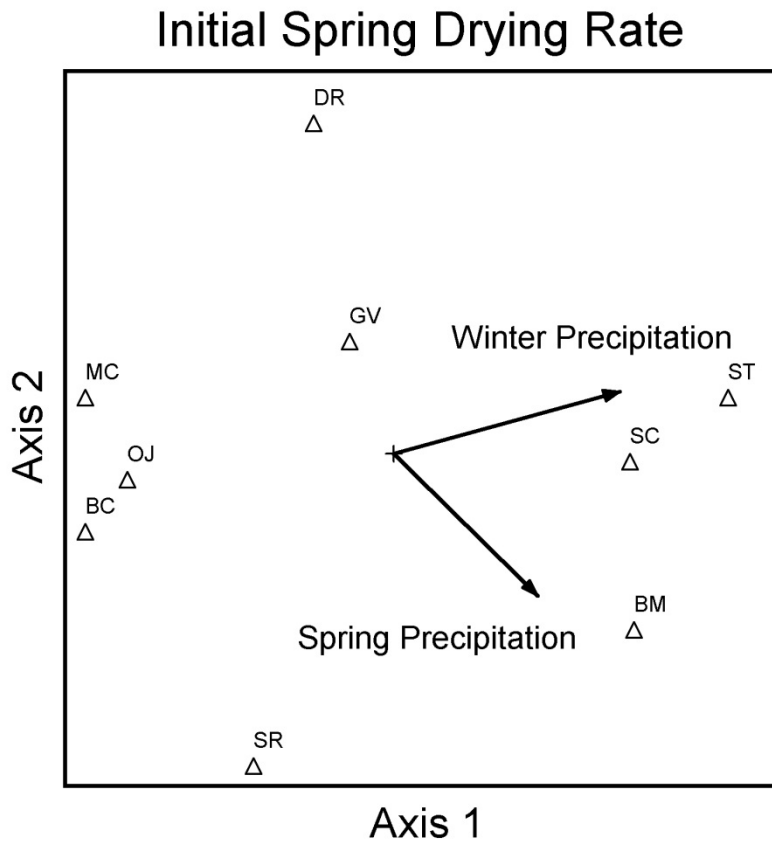


Figure 3-14. Canonical correspondence analysis (CCA) associating initial spring soil drying rate for nine Great Basin woodland sites with winter (1 December to 28 February) and spring (1 March to 30 June) precipitation. Arrow length indicates comparative strength of association between winter and spring precipitation. 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.