



SPECIAL FEATURE:
SAGEBRUSH STEPPE TREATMENT EVALUATION PROJECT

Long-term effects of tree expansion and reduction on soil climate in a semiarid ecosystem

BRUCE A. ROUNDY,^{1,†} R. F. MILLER,² R. J. TAUSCH,³ J. C. CHAMBERS,³ AND B. M. RAU⁴

¹Department of Plant and Wildlife Sciences, Brigham Young University, Provo, Utah 84602 USA

²Eastern Oregon Agricultural Research Center, Oregon State University, Corvallis, Oregon 97331 USA

³USDA Forest Service, Rocky Mountain Research Station, Reno, Nevada 89521 USA

⁴USGS New England Water Science Center, Northborough, Massachusetts 01532 USA

Citation: Roundy, B. A., R. F. Miller, R. J. Tausch, J. C. Chambers, and B. M. Rau. 2020. Long-term effects of tree expansion and reduction on soil climate in a semiarid ecosystem. *Ecosphere* 11(9):e03241. 10.1002/ecs2.3241

Abstract. In sagebrush ecosystems, pinyon and juniper tree expansion reduces water available to perennial shrubs and herbs. We measured soil water matric potential and temperatures at 13–30 and 50–65 cm soil depths in untreated and treated plots across a range of environmental conditions. We sought to determine the effects of tree expansion, tree reduction treatments, and expansion phase at time of treatment over 12–13 yr post-treatment. Because the effects of tree reduction on vegetation can vary with the soil temperature/moisture regime, we also analyzed differences in soil climate variables between the mesic/aridic-xeric and frigid/xeric regime classifications for our sites. Growing conditions during all seasons except spring were greatly limited by lack of available water, low temperatures, or both. Advanced tree expansion reduced wet days (total hours per 24 hr when hourly average soil water matric potential >-1.5 MPa), especially in early spring. Fire and mechanical tree reduction increased wet days and wet degree days (sum of hourly soil temperatures $>0^{\circ}\text{C}$ when soil is wet per 24 hr) compared with no treatment for most seasons. Burning resulted in higher soil temperatures than untreated or mechanically treated woodlands. Tree reduction at advanced expansion phases increased wet days in spring more than when implemented at earlier phases of expansion. Added wet days from tree reduction were negatively associated with October through June precipitation and vegetation cover, rather than time since treatment, with more wet days added on drier sites and years. The longer period of water availability in spring supports increased growth and cover of not only shrubs and perennial herbs, but also invasive weeds on warmer and drier sites, for many years after tree reduction. We found that sites classified as mesic/aridic-xeric had warmer soil temperatures all seasons and were drier in spring and winter than sites classified as frigid/xeric. Land managers should consider reducing trees at earlier phases of expansion or consider revegetation when treating at advanced phases on these warmer and drier sites that lack perennial herb potential.

Key words: cheatgrass; fire; fuel; juniper; pinyon; sagebrush; soil temperature; soil water; Special Feature: Sagebrush Steppe Treatment Evaluation Project.

Received 17 January 2020; revised 13 April 2020; accepted 20 April 2020; final version received 27 May 2020.
Corresponding Editor: James McIver.

Copyright: © 2020 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** bruce_roundy@byu.edu

INTRODUCTION

For more than a century, woody plants have been expanding into semiarid grasslands and shrublands worldwide (Archer et al. 2017). Because semiarid lands have short growing periods when soil water and nutrients are available and temperatures are favorable, the expansion of woody plants may reduce available resources, alter ecosystem functioning, and fundamentally change the ecological services provided by the pre-expansion plant community (Archer and Predick 2014, Archer et al. 2011, 2017, Williams et al. 2018). In the western United States, pinyon (*Pinus* spp.) and juniper (*Juniperus* spp.) trees are expanding into sagebrush (*Artemisia* spp.) ecosystems in the Great Basin and Colorado Plateau (Romme et al. 2009, Davies et al. 2011, Miller et al. 2019). Environmental consequences may include loss of important perennial shrubs and herbs, increase in woody fuels and potential severity of wildfire, and higher runoff and erosion associated with depleted ground cover (Pierson et al. 2010, Young et al. 2013, Miller et al. 2014a, b, 2019, Roundy et al. 2014a, Williams et al. 2017, 2018). Cascading effects can be loss of wildlife habitat (Miller et al. 2011, 2017, Wilson et al. 2011), exotic grass dominance after wildfire (D'Antonio and Vitousek 1992, Chambers et al. 2016), and loss of ecosystem productivity (Williams et al. 2018).

The climate of sagebrush ecosystems in the Great Basin of the western United States consists of cool wet winters and warm dry summers (Lefler and Ryel 2012, Williams et al. 2018, Miller et al. 2019). Shrubs, herbs, and trees all rely on available water in spring for growth. Ryel et al. (2008) and Lefler and Ryel (2012) have referred to the upper 30 cm of soil as the resource growth pool (RGP) and soil depths below 30 cm as the maintenance pool (MP). Soil nutrients, especially N, are most available in the upper 30 cm and can move to roots at soil water potentials >-1.5 MPa. Available water below 30 cm helps sustain plants through the dry summers but supports limited growth because of limited nutrient availability. Thus, reduction in trees as major water users should result in longer periods of water availability for nutrient transport in the RGP to support growth of shrubs and herbs, and more water for maintenance of shrubs in the MP during dry

summer periods (Bates et al. 2000, Lefler and Ryel 2012, Mollnau et al. 2014, Roundy et al. 2014b). Tree reduction could also increase soil water availability by reducing tree cover and interception of precipitation (Williams et al. 2018).

Understanding the effects of increasing tree dominance and the associated shrub and perennial herb loss may be helpful in determining the successional timing of tree reduction treatments to reduce fuels and risk of severe wildfire. Expansion has been classified into three phases of increasing tree dominance (Miller et al. 2005): Phase I, perennial shrubs and herbs dominate with scattered trees; Phase II, understory perennials and trees share dominance; and Phase III, trees dominate. Because the amount of understory cover remaining in relation to expanding tree cover may vary greatly among sites (Roundy et al. 2014a), it is useful to evaluate the effects of tree expansion and reduction on resources across a wide range of sites.

Trees and other woody fuels are usually reduced by prescribed fire or mechanical means such as cutting or shredding (Miller et al. 2019). The Sagebrush Treatment and Evaluation Project (SageSTEP) was initiated in 2005 to follow short- to long-term effects of woody fuel reduction treatments across a wide range of sites (McIver et al. 2010, McIver and Brunson 2014). SageSTEP and other studies have reported shorter-term (1–6 yr after treatment) effects of fire and mechanical tree reduction on soil moisture and temperature. Mechanical tree reduction increases the time of soil water availability in the RGP (Bates et al. 2000, Young et al. 2013, Roundy et al. 2014b, 2018) and MP (Mollnau et al. 2014), while fire increases soil water availability and soil temperatures (Roundy et al. 2014b, 2018, Cline et al. 2018). Fire generally reduces both trees and shrubs long term, and temporarily reduces cover of perennial grass for about 2–3 yr (Roundy et al. 2014a, Miller et al. 2014b, Williams et al. 2017). Mechanical treatments maintain shrub and grass cover, and shade patches of the soil surface with woody debris (Cline et al. 2010, Young et al. 2013). Previously, we found that soil water availability in spring was equally increased by both fire and mechanical tree reduction up to 4 yr after treatment (Roundy et al. 2014b). Tree reduction increased time of available water most when

implemented at Phase III expansion where less understory plant cover probably resulted in lower transpiration compared with treatments applied at Phases I and II. Williams et al. (2017) considered that this extra soil water availability in spring supported major increases in perennial grass cover 6 yr after tree reduction at high pretreatment tree dominance, although perennial grass cover still remained lower than when trees were reduced at less pretreatment tree dominance.

Resilience to disturbance and resistance to exotic annual grasses have been associated with soil temperature and moisture in sagebrush ecosystems (Chambers et al. 2007, 2014, Condon et al. 2011, Davies et al. 2012). More favorable environmental conditions for native plant establishment and growth and greater productivity of perennial herbaceous species due to higher precipitation and cooler temperatures typically equate to greater resilience at higher than lower elevations (Condon et al. 2011, Davies et al. 2012, Knutson et al. 2014, Chambers et al. 2014). Also, climate suitability to exotic annual grasses decreases as soil temperatures become colder resulting in greater resistance to these grasses at higher than lower elevations (Brooks et al. 2004, Chambers et al. 2007, 2014, Condon et al. 2011). Chambers et al. (2017, 2019), Miller et al. (2014a, 2019), and Pyke et al. (2017) have based management recommendations on soil temperature/moisture regimes as classified by the US Department of Agriculture Natural Resources Conservation Service (USDA NRCS 1999). These regimes are defined by estimated conditions at the 50 cm soil depth. Freund et al. (2020) found differences in vegetation response to fuel control treatments between mesic/aridic-xeric and frigid/xeric soil temperature/moisture regimes. However, soil temperature and moisture conditions in the RGP have not been quantified by on-site measurements of these NRCS regimes.

Understanding the longer-term effects of treatment, expansion phase at time of treatment, and longevity of these effects on resource availability after treatment can help land managers decide when, where, and how to conduct fuel treatments. Sites in Phases I to II are often more resilient to treatments (Chambers et al. 2014, Roundy et al. 2014a, Bybee et al. 2016, Williams et al. 2017). Similarly, sites in earlier phases are

typically more resistant to invasive annual grasses and forbs (Chambers et al. 2014, Roundy et al. 2014, Bybee et al. 2016, Williams et al. 2017). However, both resilience to treatments and resistance to invasive annual grasses are strongly influenced by residual vegetation and resource availability. Reducing trees when and where enough residual and desirable vegetation is available to use the resources that the trees previously used may increase the capacity for recovery and help maintain ecosystem resilience.

For the current study, we measured seasonal soil water availability and temperature continuously on 11–12 expansion sites within plots that were either untreated or received tree reduction treatments up to 13 yr earlier. Our purpose was to evaluate the responses of seasonal soil water availability and temperature to (1) tree expansion phase, (2) prescribed fire compared with mechanical tree reduction, (3) phase of expansion at the time of tree reduction, and (4) time since tree reduction. We also compared seasonal soil water availability and temperature between the mesic/aridic-xeric (expected warmer and drier) and frigid/xeric (expected cooler and wetter) NRCS soil temperature/moisture regimes into which our sites were classified. This study is unique in the years of measurement after treatment, geographical scope, range of environmental conditions, and the intensity of measurement at each site.

METHODS

Study sites

This study was implemented as part of the Sagebrush Steppe Treatment Evaluation Project (SageSTEP), a Great Basin regional research project described by McIver et al. (2010) and McIver and Brunson (2014). Study sites included four different cover types; four western juniper (*Juniperus occidentalis*) sites in California and Oregon (Blue Mountain, Walker Butte, Bridge Creek, and Devine Ridge); four single-leaf pinyon (*Pinus monophylla*)–Utah juniper (*Juniperus osteosperma*) sites in central Nevada (pinyon–juniper; Seven Mile, South Ruby, Marking Corral, Spruce Mountain); and two Utah juniper (Stansbury and Onaqui) and two Utah juniper–Colorado pinyon (*Pinus edulis*) sites (juniper–pinyon; Scipio, Greenville) in Utah (McIver et al. 2010, Miller

et al. 2014*b*, Freund et al. 2020). Sites were selected as wooded shrublands (Romme et al. 2009) or expansion woodlands (Miller et al. 2008, McIver et al. 2010) where trees have expanded into sagebrush (*Artemisia* spp.) communities on loam soils with native species still present in the understory across a range of tree cover (Roundy et al. 2014*a*). Sites represent a wide range in elevation, soil, and climatic conditions, but some regional characteristics are evident. Across the Great Basin from west to east, western juniper sites represent the lowest elevation, pinyon–juniper sites in central Nevada have the highest elevation, and Utah juniper sites in Utah are intermediate (Roundy et al. 2014*b*). On the northwestern Great Basin sites, soils are derived from basalt lava flows and the climate is Pacific maritime, with most precipitation falling between November and June (McIver et al. 2010, Rau et al. 2011, Miller et al. 2014*b*). The central and eastern sites include igneous, metamorphic, and sedimentary-based soils, which are carbonatic. The climate is more continental, with lower precipitation than Pacific maritime between November and June, and highly variable summer precipitation in July and August (McIver et al. 2010, Rau et al. 2011, Miller et al. 2014*b*).

Treatments

Treatments were applied across the network as a randomized complete block, with each site considered a block (Roundy et al. 2014*a*, Miller et al. 2014*b*). We attempted to place treatment plots at each site within the same ecological site (Miller et al. 2014*b*). Plots were fenced where necessary to exclude cattle grazing. Throughout the network at each site, three 8- to 20-ha treatment plots were left as an untreated control plot or received a broadcast burn, or cut-and-drop treatment. In addition, the four Utah sites received tree mastication (shredding) treatment. The Blue Mountain, Walker Butte, and Bridge Creek western juniper sites and the Seven Mile, South Ruby, and Marking Corral pinyon–juniper sites all had an untreated control, prescribed fire, and cut-and-drop treatment plots. The Utah juniper or juniper–pinyon sites of Stansbury, Onaqui, Scipio, and Greenville all had these same treatments plus an additional mastication treatment plot. Because plots could not all be burned in the same year (Miller et al. 2014*b*), treatments were applied

in 2006 and 2007 for all but the South Ruby site, where treatments were applied in 2009. This stagger-start design avoids the potential restricted inferences associated with implementing all treatments under the same set of climatic conditions (Loughlin 2006). Plots were burned between August and October, and trees were cut or shredded from September through November. The fire treatment was a broadcast burn ranging from low to moderate severity across all sites (Miller et al. 2014*b*). The reduction in tree canopies in the fire treatment and mechanical treatments averaged 86%, across the 11 study sites (Roundy et al. 2014*a*, Miller et al. 2014*b*), indicating that treatments were effective in accomplishing targeted tree removal goals. The burn treatment resulted in 90% reduction in shrub cover and <5% remaining tree canopy cover (Miller et al. 2014*b*). For the mechanical treatment, all trees >2 m tall were cut or shredded and debris left in-place on the ground. Tree cutting was done by chain saw and mastication by rotation of a large, toothed drum or Fecon Bullhog attachment (Fecon, Lebanon, Ohio, USA) mounted on a large rubber-tired vehicle as described by Cline et al. (2010). Tree canopies were reduced to <1% in the mechanically treated plots.

Measurements

Soil water and temperature measurement stations were located in three tree expansion phases within treatments at each site by observing relative tree, shrub, and perennial herb cover to determine dominance of life forms. Eight sites, Blue Mountain, California; Devine Ridge and Bridge Creek, Oregon; Marking Corral and South Ruby, Nevada; and Stansbury, Onaqui, and Greenville, Utah, were fully instrumented by the year after treatment (2007–2008). One of these sites, Stansbury, was measured through spring 2009 until a wildfire burned the treatment plots. Another site in Utah, Scipio, was fully instrumented starting in 2011, while two other sites, Walker Butte, Oregon, and Seven Mile, Nevada, were fully instrumented in summer 2014. The Spruce Mountain, Nevada, untreated plot was instrumented in 2006. Since tree reduction treatments were never applied on this site, data were only used to determine expansion effects. When fully instrumented, stations were installed on

untreated, burned, cut, and shred plots at expansion Phases I, II, and III. Each of these sites had 9 stations (3 phases \times 3 treatments; untreated, burned, cut) or 12 stations (Utah sites only; 3 phases \times 4 treatments; untreated, burned, cut, shred).

Each of the soil water and temperature stations installed across the 12 study sites was equipped with a Campbell Scientific CR10X or CR1000 micrologger and multiplexer that measured 16 soil temperature and soil water matric potential sensors. At each station, thermocouples to measure temperature and gypsum blocks (Delmhorst) to measure soil water matric potential were buried at 1–3, 13–15, 18–20, and 28–30 cm deep in tree and shrub microsites at the east-side dripline and on two interspaces between shrubs or trees (4 depths \times 4 microsites = 16 thermocouples and 16 gypsum blocks at each station). Starting in 2011, an additional thermocouple was installed at 50 cm deep to measure soil temperature and gypsum blocks were installed at 50 and 65 cm depths where possible to measure matric potential. These sensors were installed in one interspace for each station. Microloggers were programmed to read sensors every 60 s and to store hourly averages. We converted gypsum block resistance data to water potential using standard calibration curves (Campbell Scientific 1983). Although some error may be introduced by not individually calibrating each gypsum block, blocks calibrated with standard equations were relatively consistent and sensitive to soil drying in a growth chamber study (Taylor et al. 2007). We also measured air temperature and precipitation (1–1.5 m height) on one station at each site (untreated Phase III). Precipitation was measured with an electronic tipping bucket rain gage (Texas Electronics) and removable precipitation adapter for snowfall (Campbell Scientific). Air temperature was measured in a gill shield using a Campbell Scientific Model 107 temperature probe.

Derived variables were calculated for six seasons: early spring (March–April), late spring (May–June), all of spring (March–June), summer (July–August), fall (September–November), and winter (December–February). Derived variables included total number of wet days (total hours per 24 hr when hourly average soil water matric potential > -1.5 MPa), wet degree days (sum of

hourly average soil temperatures for each hour that average soil temperature was $> 0^\circ\text{C}$ per 24 hr and when soil water matric potential > -1.5 MPa), and hourly average soil temperatures (Rawlins et al. 2012, Roundy et al. 2014b, 2018, Cline et al. 2018).

Analysis

Mixed model analysis (Proc Glimmix, SAS v9.3; SAS Institute, Cary, North Carolina, USA) was used to test fixed effects of year of measurement and expansion phase on untreated plots for 10–12 sites, depending on the year (2008 through spring 2018). Site, site \times phase, and site \times phase \times year were considered random variables in these analyses. Similarly, mixed model analysis was also used to test fixed effects of year of measurement, treatment, and expansion phase (subplot within treatment) for 7–11 sites, depending on the year. Site, site \times treatment, site \times treatment \times phase, and site \times treatment \times phase \times year were considered random variables. Using the same fixed and random variables, we also conducted analyses on the difference between untreated and treated responses for each expansion phase on these sites during the same year to best adjust for differences in annual weather among sites. This allowed us to determine additional wet days, wet degree days, and soil temperature degrees associated with tree reduction. Tukey's tests were used to determine significant differences among years, treatments, or phases when significant. All analyses were conducted separately for each season (Roundy et al. 2014b, 2018). Significance was at $P < 0.05$ unless stated otherwise. Data were not transformed because examination of residual plots indicated that assumptions for analysis of variance were generally met as well without as with transformation. Data from tree shredding and cutting were pooled for Utah sites because preliminary analysis showed similar responses. To best represent the RGP, we analyzed across the depth intervals of 13–15, 18–20, and 28–30 cm and across the four microsites (Roundy et al. 2014b). To represent the MP, we analyzed wet degree days and average soil temperatures at 50 cm deep and wet days across the 50 and 65 cm depths. Regression analysis was used to determine correlations among spring wet days, added spring wet days, October through June precipitation, and total and herbaceous vegetation cover. Data from all available

years and sites from spring 2008 through 2018 were used with spring wet days and additional wet days averaged across burn and mechanical treatments, including averages across phases, microsites, and depths to produce one data point per site per year. Foliar vegetation cover was quantified as described in Freund et al. (2020). To quantify differences in soil temperature/moisture regimes in the RGP, we analyzed data from fall 2014 through spring 2018 when the maximum number of sites was fully instrumented. Six sites were classified as mesic/aridic-xeric (Bridge Creek, Greenville Bench, Marking Corral, Onaqui, Scipio, and South Ruby) and four sites were classified as frigid/xeric (Blue Mountain, Devine Ridge, Seven Mile, and Walker Butte) according to Freund et al. (2020). Mixed model analysis of seasonal wet days and soil temperature was used to test significance of the fixed factors of soil temperature/moisture regime, tree reduction treatment, phase at time of tree reduction, and their interactions. Site, site \times regime, site \times regime \times treatment, and site \times regime \times treatment \times phase were considered random variables.

RESULTS

Seasonal effects

As expected, wet days were highest in early spring, wet degree days were highest in early spring and late spring, and soil temperatures were highest in summer (Fig. 1). Although winter had a high number of wet days, it had limited wet degree days due to low soil temperatures. While fall had warm soil temperatures, wet degree days were limited due to few wet days. The RGP and MP reflected similar seasonal patterns with the RGP usually having more wet days, wet degree days, and higher soil temperatures than the MP (Fig. 1). An exception was that the MP had 1.9°C higher average soil temperature than the RGP in winter. In late spring, soil temperatures averaged 16.3°C higher in the RGP than MP (Fig. 1).

Effects of expansion

For the RGP on untreated plots, wet days, wet degree days, and soil temperatures had a trend toward decreasing with increasing woodland expansion phase, but the trend was only significant for all three variables in early spring (Fig. 1;

Appendix S1: Table S1). Soil temperatures in the RGP were also lower for Phase III than Phase I in fall, but the difference was small (0.9°C). Although year was significant for all three variables and for all seasons, the year-by-phase interaction was not. Wet days and wet degree days were greater in some years than others, while soil temperatures were cooler in the wetter years. Response to phase of expansion for these variables paralleled each other over the different years, with the numerical order of Phase I > Phase II > Phase III, but differences among phases on a given year were small.

For the MP, none of the response variables varied by phase, although there was a trend toward decreasing response with increasing phase for early spring, as occurred with the RGP (Fig. 1; Appendix S1: Table S1). Wet days differed significantly by year for early spring, late spring, and winter, with some years wetter than others. For example, wet days in spring ranged from a low of 29.4 ± 8.19 in 2018 to a high of 98.8 ± 8.35 in 2016. Wet degree days and average soil temperature varied among years for all seasons, but the year-by-phase interaction was not significant, indicating that whether years were wetter or drier, variables responded similarly to phase.

Effects of treatments

Mechanical tree reduction had more wet days than no treatment for the RGP in all seasons and for the MP in early spring and late spring (Fig. 2; Appendix S1: Table S2). The burn treatment had more wet degree days than no treatment for all seasons in the RGP, and for early spring in the MP. Wet days and wet degree days were generally similar for burn and mechanical treatments, except that for the RGP, wet days were greater for the mechanical than burn treatment in late spring. The burn treatment had the highest soil temperatures for all seasons in the RGP, and a trend toward highest temperatures in the MP (Fig. 2).

Effects of phase of expansion when treated

For the RGP, tree reduction added more wet days at Phase II and Phase III than were added at Phase I in early spring and late spring, and more wet days were added at Phase III than Phases I and II in summer, fall, and winter

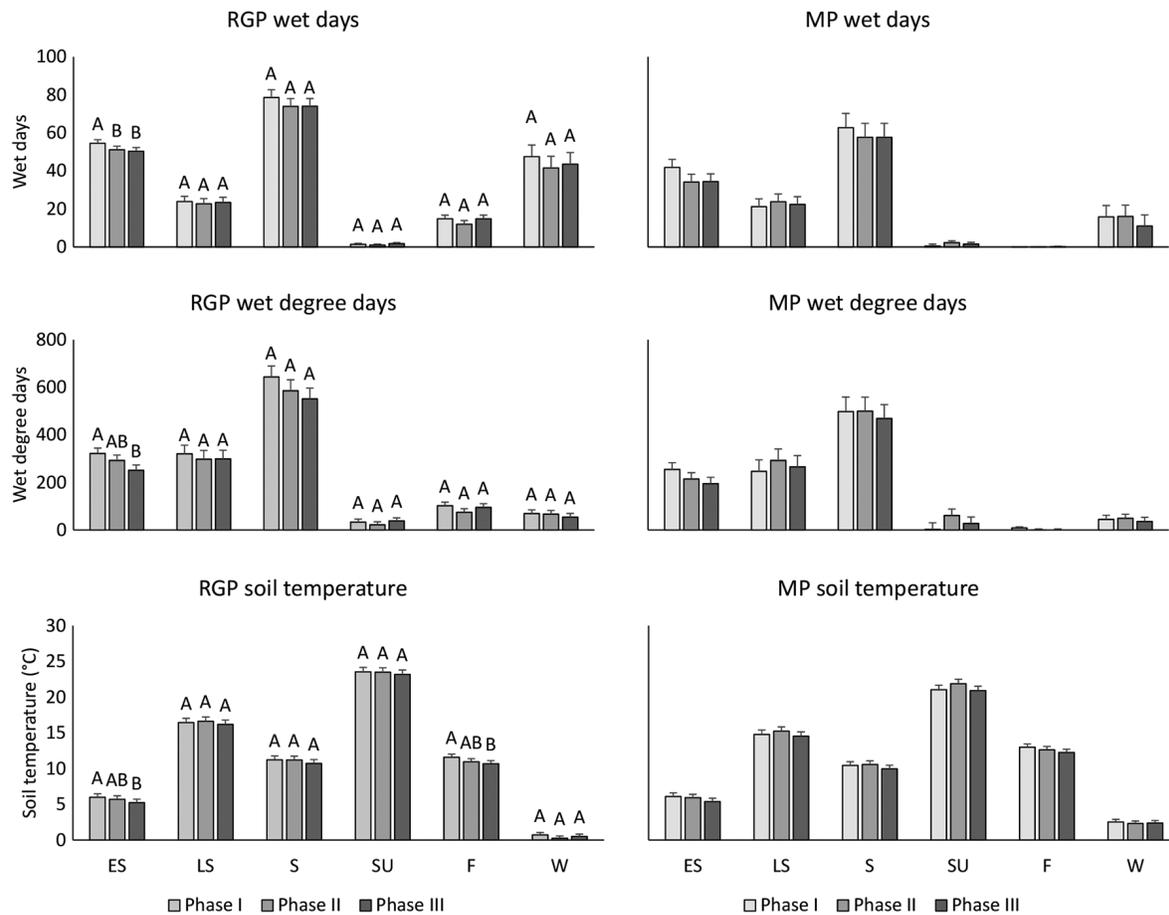


Fig. 1. Effects of tree expansion (phase) for untreated plots on wet days (top), wet degree days (middle), and soil temperature (bottom) for the resource growth pool (RGP, left, 13–30 cm soil depth) and maintenance pool (right, 50–65 cm soil depth for wet days and 50 cm soil depth for others) for different seasons (ES, early spring; LS, late spring; S, all of spring; SU, summer; F, fall; W, winter). Different letters above bars for a season indicate a significant difference ($P < 0.05$). Lines above bars indicate 1 standard error.

(Fig. 3; Appendix S1: Table S3). The MP had a similar trend, but phases were not significantly different. Additional wet degree days followed a similar response to phase as did additional wet days. Treating at Phase III warmed soils more than treating at Phase I for early spring in the RGP and for all seasons except summer for the MP (Fig. 3). Warming differences among phases were small ($<1.6^{\circ}\text{C}$).

Annual effects and time since treatment

For the RGP, wet days for all treatments and additional wet days after treatment varied significantly by year for all seasons (Appendix S1: Tables S2, S3). However, annual variation was

much more related to annual weather than years since treatment (Fig. 4). All sites except South Ruby were treated in either 2006 or 2007 so that 2008 was 2–3 yr after treatment and most recent data were 12–13 yr after treatment. Instead of following a pattern of decreasing wet days with time after tree reduction, treated and untreated wet days in spring tracked October through June precipitation. The additional wet days from tree reduction in the RGP were highest on drier years such as 2012, 2015, and 2018, and least on wetter years such as 2010, 2011, and 2016 (Fig. 4). Additional wet day differences after tree reduction between wet and dry years were greatest in early spring, but also occurred in late spring (Fig. 4).

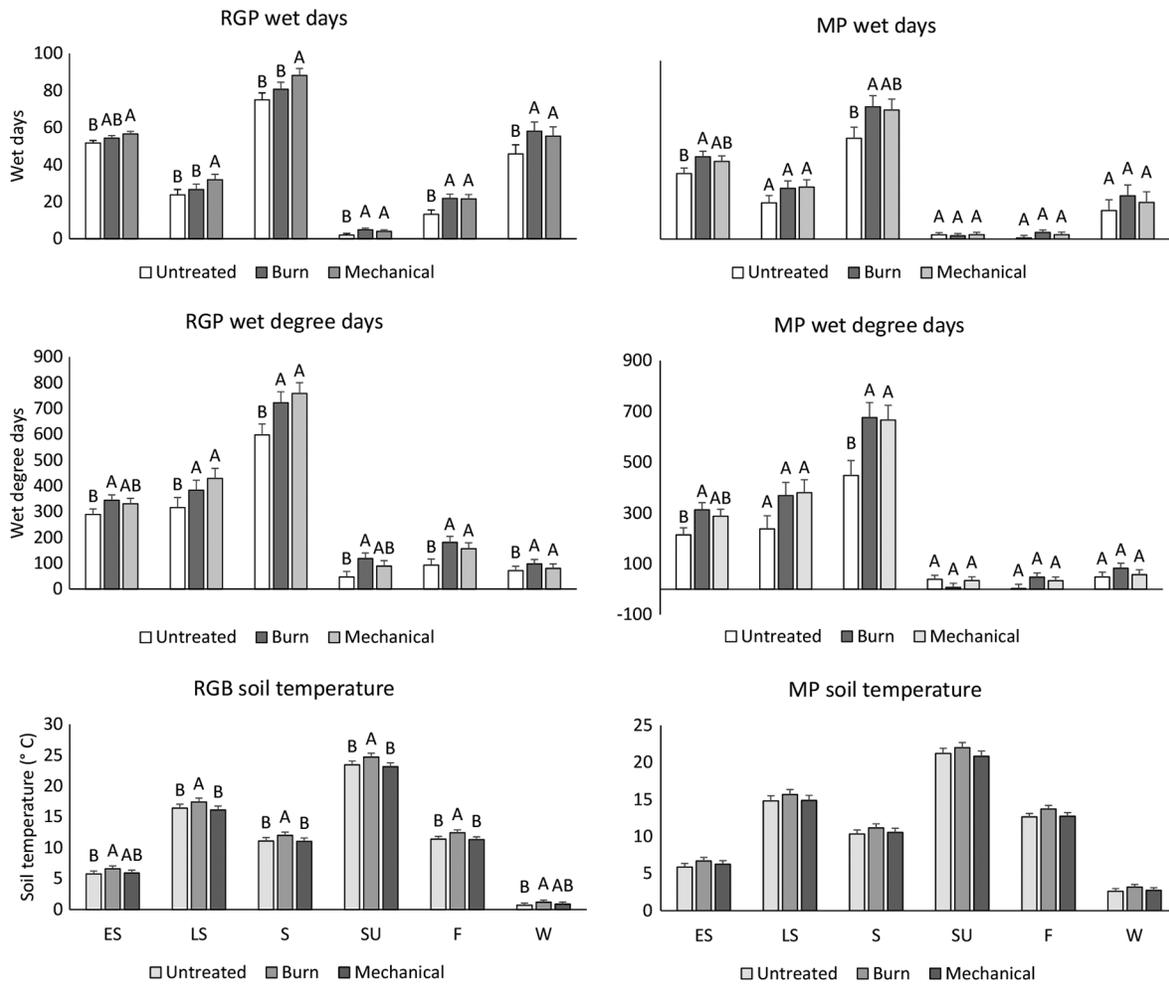


Fig. 2. Effects of tree reduction on wet days (top), wet degree days (middle), and soil temperature (bottom) for the resource growth pool (RGP, left, 13–30 cm soil depth), and maintenance pool (MP, right, 50–65 cm soil depth for wet days and 50 cm for others) for different seasons (ES, early spring; LS, late spring; S, all of spring; SU, summer; F, fall; W, winter). Different letters above bars for a season indicate a significant difference ($P < 0.05$). Lines above bars indicate 1 standard error.

Even 12–13 yr after treatment, tree reduction at Phase III still added 20.8 ± 3.63 wet days and 281 ± 46.67 wet degree days in the RGP in spring of 2018, a relatively dry year. Wet degree days generally followed the same response as wet days, being driven more by wet days than soil temperature.

For the MP, wet days varied significantly among years for all seasons except summer, and additional wet days varied significantly among years for all but summer and winter (Appendix S1: Tables S2, S3). Wet days in the MP

followed the same pattern as the RGP, with more wet days added by tree reduction on drier years, rather than responding to time since treatment. However, data for the MP were not available until 2012, which was already 5–6 yr after treatment for all sites except South Ruby.

For both the RGP and MP, soil temperatures varied by year for every season (Appendix S1: Table S2). Treatments paralleled each other over the years with the burn treatment always highest (Fig. 5). As with wet days, soil temperatures were associated with October through June

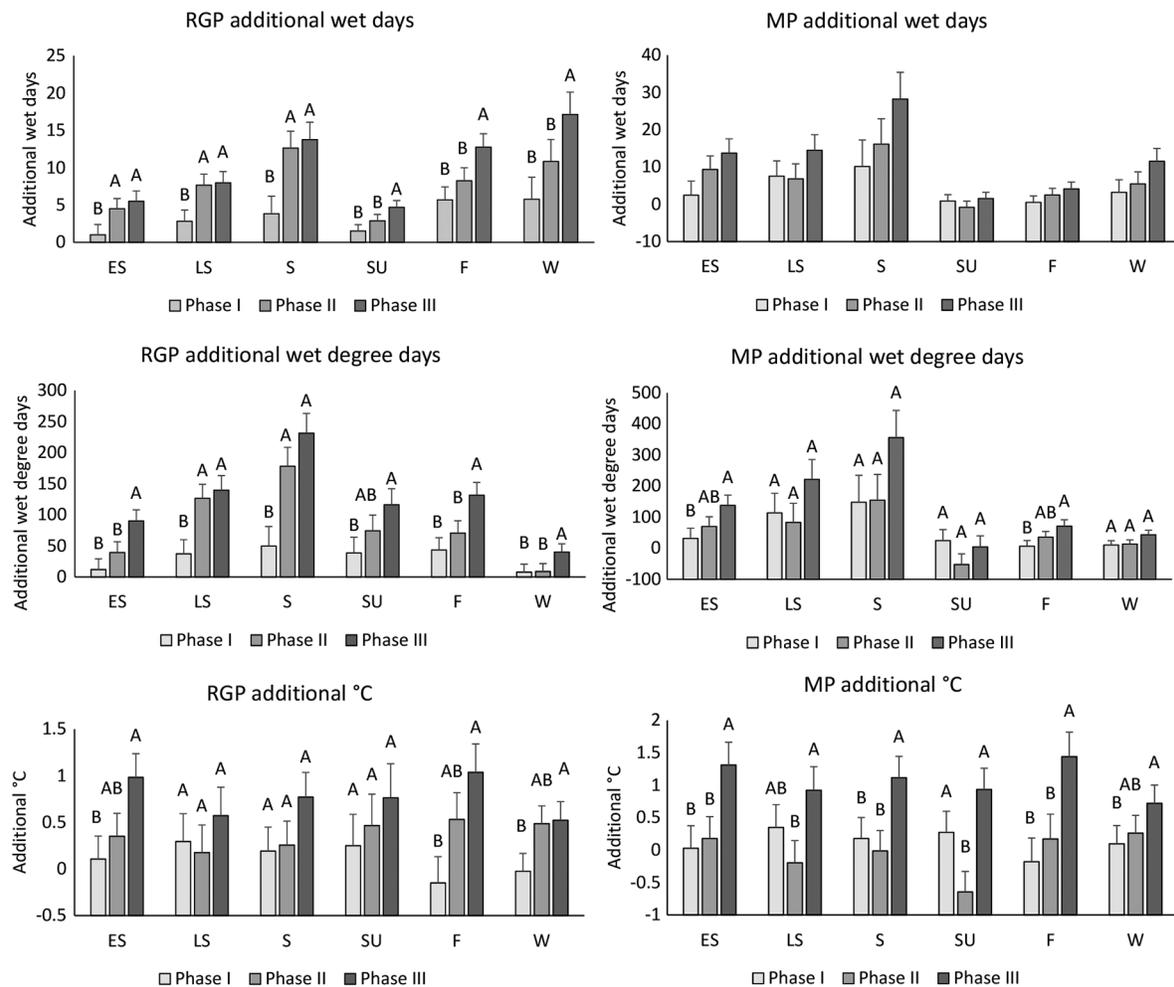


Fig. 3. Additional wet days (top), wet degree days (middle), and soil temperature (bottom) for the resource growth pool (RGP, left, 13–30 cm soil depth), and maintenance pool (MP, right, 50–65 cm soil depth for wet days and 50 cm for others) for different seasons (ES, early spring; LS, late spring; S, all of spring; SU, summer; F, fall; W, winter), after tree reduction by fire and mechanical methods. Different letters above bars for a season indicate a significant difference ($P < 0.05$). Lines above bars indicate 1 standard error.

precipitation. However, soil temperatures were cooler on years when October through June precipitation was higher (e.g., in 2010 and 2011). There was no strong warming trend seen over the 9–10 yr shown for the RGP, or for the 6–7 yr shown for the MP in Figure 5. The RGP generally had warmer temperatures than the MP, except in fall and winter (Fig. 5).

Interactions of year, treatment, and phase

The year-by-treatment interaction was significant for additional wet days for the RGP in early spring (Appendix S1: Table S3). Added wet days

were greater for the mechanical than burn treatment on most years, but there was little difference between treatments on wetter years. The interaction of year and phase was significant for additional wet days in the MP in late spring. Additional wet days were greater for Phase III compared with Phase I in drier than wetter years. The interactions of treatment by phase and treatment by year were both significant for the RGP for late spring for additional soil temperature degrees. Burning added more soil temperature degrees than the mechanical treatment at Phase III than at Phase I or Phase II. Burning also

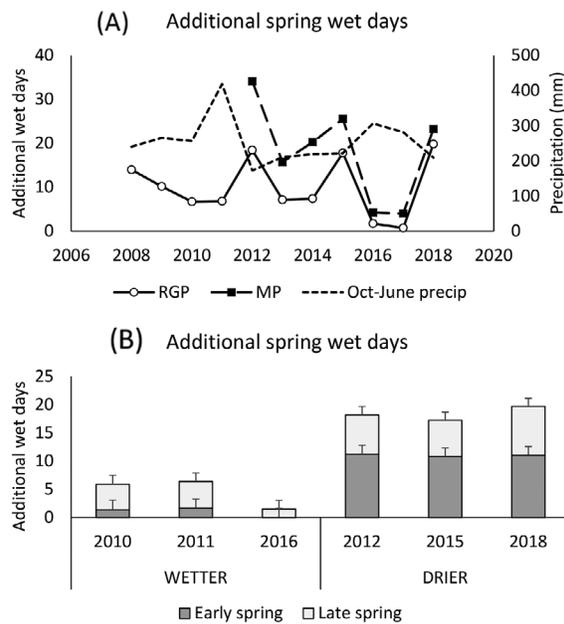


Fig. 4. Additional wet days in spring after tree reduction for the RGP (resource growth pool) and MP (maintenance pool) in relation to October through June precipitation (A). Additional wet days for early spring and late spring on wetter and drier years for the RGP (B). Lines above bars are 1 standard error.

added many more soil temperature degrees than the mechanical treatment on some years than others. Burning had a small, but long-term effect on increasing soil temperatures in both the RGP and MP, especially when implemented at Phase III. Both the RGP and MP dried to <-1.5 MPa by late spring every year of measurement.

Spring wet day and added wet day associations with precipitation and vegetation cover

For the RGP, spring wet days and added spring wet days from tree reduction had a quadratic response to October through June precipitation (Fig. 6, $P < 0.0001$, $R^2 = 0.46$, for spring wet days, $P < 0.0001$, $R^2 = 0.37$, for added spring wet days). However, spring wet days were positively correlated, while added spring wet days were negatively correlated with October through June precipitation (Fig. 6). Correlations of total and herbaceous vegetation cover with October through June precipitation were positive and significant ($P < 0.0003$), but had low r^2 values (0.14 for total and 0.15 for herbaceous cover).

Correlations of total and herbaceous cover with added spring wet days were negative and significant ($P < 0.0002$), also with low r^2 values (0.19 for total and 0.17 for herbaceous cover).

Comparison of soil temperature/moisture regimes

The frigid/xeric regime had 19 ± 7.9 more wet days in spring than the mesic/aridic-xeric regime across the time interval of fall 2014 through spring of 2018 (Table 1; Appendix S1: Table S4). In contrast, soil temperatures were higher for the mesic/aridic-xeric than frigid/xeric regime for all seasons except winter. Some regime \times treatment interactions were significant for some seasons (Appendix S1: Table S4). Wet days in spring were greater for the frigid/xeric than mesic/aridic-xeric regime for all treatments, but less so for the burn than mechanical treatment (Table 1). On the other hand, soil temperatures for all seasons were more similar among treatments in the mesic/aridic-xeric regime, while in the frigid/xeric regimes, warmest temperatures were in the burn treatment and coolest temperatures were in the mechanical treatment (Table 1).

DISCUSSION

Resource growth pool

Effects of expansion.—Advanced tree expansion decreased wet days (time of available water), especially in early spring. Wet days on untreated plots had a decreasing trend with increasing tree dominance. Reasons for this are likely greater interception and lower net precipitation as tree cover increased, as well as greater transpiration by trees than from shrubs and herbs. Interception by individual trees ranges from 30% to 70% (Williams et al. 2018). Individual tree and stand-level interception vary depending on tree cover and amount of precipitation falling as snow compared with rainfall, as well as variations in intensity, and duration. Interception is substantial enough that it affects soil water inputs and is implicated in understory decline with expanding woodlands (Mollnau et al. 2014, Williams et al. 2018). Pretreatment tree cover for untreated plots ranged from about 9% at Phase I to about 42% at Phase III (Williams et al. 2017). This expanding tree leaf surface area increases both tree interception of precipitation and transpiration. Ivans et al. (2006) considered that the greater stand-

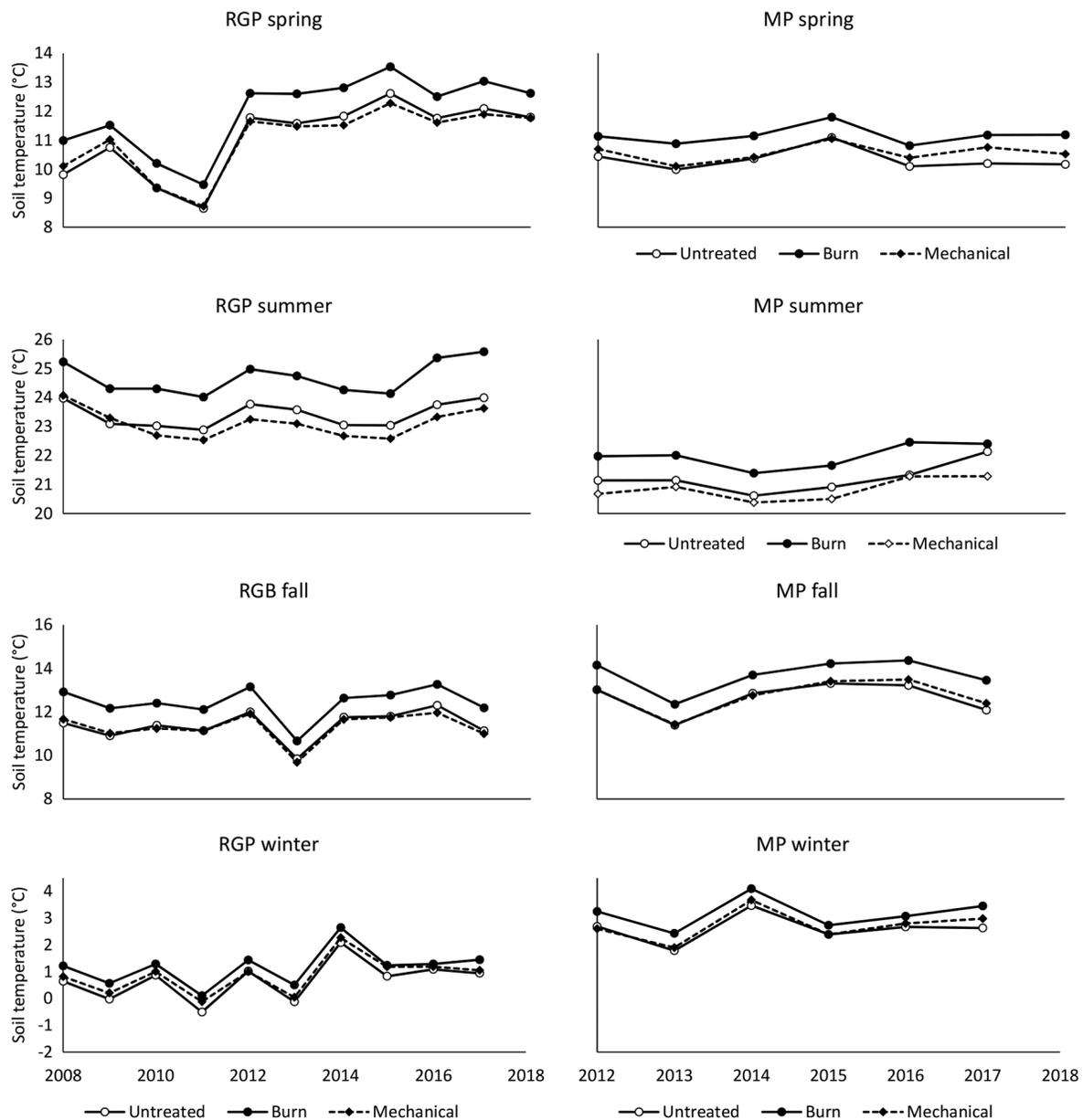


Fig. 5. Seasonal soil temperatures for untreated, burned, and mechanically treated plots for the resource growth pool (RGP, 13–30 cm soil depth) and maintenance pool (MP, 50 cm soil depth). Note that RGP data range from 2008 to 2018 and MP data from 2012 to 2018. Average standard errors (°C) are spring, 0.57; summer, 0.64; fall, 0.48; and winter, 0.36.

level leaf area index for juniper compared with sagebrush and bunchgrass-dominated communities was largely responsible for its greater seasonal CO_2 uptake and water flux. Another way that tree expansion may decrease water availability is through increased bare ground and

associated runoff, which varies with many different site conditions such as soil texture, slope, and incidence of high-intensity rainfall (Williams et al. 2018).

Effects of treatments.—For most seasons, burned and mechanical plots had similar wet days

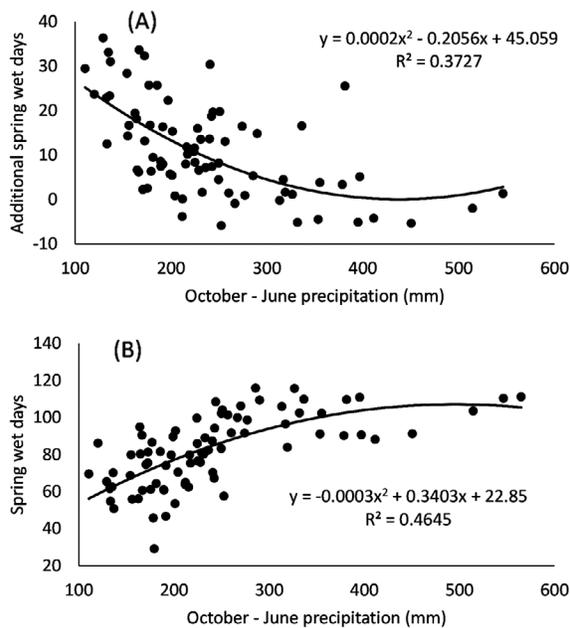


Fig. 6. Additional spring wet days (A) and spring wet days after tree reduction (B) at 13–30 cm in spring in relation to October through June precipitation. Each data point represents one site and year between 2008 and 2018, $N = 78$. Additional wet day and wet day data were averaged across prescribed fire and mechanical tree reduction treatments. All data were averaged across three tree expansion phases, four microsites, and three soil depths.

(Fig. 2). Even though they had less shrub cover than mechanically treated plots, burned plots had fewer wet days than mechanical plots in late spring (Fig. 2). Burned plots had consistently but only slightly warmer soil temperatures than mechanical and untreated plots (Fig. 2). Slightly warmer soils could make a difference in growth and transpiration over a long period, especially from annual grasses. Much warmer temperatures on burned plots in surface soils (1–3 cm, Cline et al. 2018) and slightly warmer temperatures in burned plots at 13–30 cm may have resulted in greater evaporation from soil and greater transpiration from perennial and annual herbs than occurred on mechanically treated plots. Decreased canopy shading and increased absorption of solar radiation would be expected to increase soil temperatures after fire. Young et al. (2013) found that woody debris from shredding trees in Phase III

woodlands decreased soil temperatures in spring, but that shredded woodlands still had warmer soils and more wet days than intact woodlands when averaged or summed across all seasons. Our burned plots also had greater cover of cheatgrass and annual forbs (Williams et al. 2017, Freund et al. 2020). Fewer wet days in spring on burned compared with mechanically treated plots may have been associated with higher transpirational water loss from cheatgrass and annual herbs. In addition, soil water repellency, indicated by unvegetated patches on some burned tree mounds, may have reduced soil water availability on some burned plots (Zvirzdin et al. 2017).

Effects of phase when treated.—Tree reduction by fire or mechanical means added more wet days and wet degree days in most seasons when treated at Phase III than at Phase I and sometimes Phase II (Fig. 3). One reason for this is that on untreated plots, wet days and wet degree days were less in early spring at Phase III than at Phases I and II (Fig. 1). This difference only accounts for part of the added wet days and wet degree days from tree reduction at Phase III. For example, on untreated plots in spring, Phase III had 4.6 fewer wet days than Phase I woodlands over the years of measurement. Yet reducing trees at Phase III added 13.8 wet days compared with 3.8 wet days added when reducing trees at Phase I (Figs. 1, 3). After tree reduction at Phase III, plant cover was dominated by perennial and annual herbs, whereas trees provided the dominant plant cover for untreated Phase III. Shrub cover is limited at Phase III expansion both before and after treatment (Williams et al. 2017, Freund et al. 2020). Transpiration would be expected to be reduced most when trees are controlled at Phase III because understory herb and shrub residuals are fewer and cover of these components takes more time to recover from effects of expansion at Phase III than at the other phases (Williams et al. 2017, Freund et al. 2020).

Treatment effects over time.—In this longer-term study, we found that October through June precipitation had a greater effect on added wet days from tree reduction than time since treatment (Figs. 4, 5). Measurement of water potential in the RGP up to 4 yr after tree reduction showed a declining trend in added spring wet days with time since treatment (Roundy et al. 2014b). This was considered a result of increasing herb and

Table 1. Wet days and soil temperature \pm standard error for tree reduction treatments in two soil temperature/moisture regimes for different seasons from fall 2014 through spring 2018.

Season	Regime	Wet days			Soil temperature ($^{\circ}$ C)		
		Untreated	Burn	Mechanical	Untreated	Burn	Mechanical
Early spring	Mesic/aridic	42.5 \pm 1.89	50.6 \pm 1.89	51 \pm 1.87	7.5 \pm 0.43	7.9 \pm 0.43	8 \pm 0.43
	Frigid/xeric	55.7 \pm 2.3	52.8 \pm 2.36	58.4 \pm 2.36	5.4 \pm 0.52	6.8 \pm 0.53	4.7 \pm 0.53
Late spring	Mesic/aridic	16.9 \pm 4.21	18.4 \pm 4.21	22.2 \pm 4.2	18.6 \pm 0.69	18.8 \pm 0.69	18.2 \pm 0.69
	Frigid/xeric	27.4 \pm 5.15	25.7 \pm 5.18	39.3 \pm 5.18	15.4 \pm 0.84	17.3 \pm 0.85	14.5 \pm 0.85
Spring	Mesic/aridic	59.4 \pm 5.43	68.8 \pm 5.44	73.4 \pm 5.42	13.2 \pm 0.58	13.5 \pm 0.58	13.2 \pm 0.58
	Frigid/xeric	82.6 \pm 6.65	78.5 \pm 6.71	97.7 \pm 6.7	10.4 \pm 0.71	12 \pm 0.72	9.6 \pm 0.72
Summer	Mesic/aridic	1.3 \pm 0.84	2.7 \pm 0.84	1.7 \pm 0.83	24.7 \pm 0.68	25.3 \pm 0.69	24.5 \pm 0.68
	Frigid/xeric	1.5 \pm 1.02	3.3 \pm 1.05	3.5 \pm 1.04	21.5 \pm 0.84	24.2 \pm 0.85	20.5 \pm 0.85
Fall	Mesic/aridic	8.8 \pm 2.52	14.8 \pm 2.52	13.4 \pm 2.5	12.4 \pm 0.44	13 \pm 0.44	12.8 \pm 0.44
	Frigid/xeric	14.2 \pm 3.08	21.2 \pm 3.14	21.1 \pm 3.13	10.5 \pm 0.53	11.8 \pm 0.54	9.3 \pm 0.54
Winter	Mesic/aridic	38.9 \pm 6.97	53.1 \pm 6.97	50.7 \pm 6.95	1.5 \pm 0.46	2 \pm 0.46	2.1 \pm 0.46
	Frigid/xeric	65.9 \pm 8.52	70.4 \pm 8.58	64.4 \pm 8.57	0.9 \pm 0.56	1.2 \pm 0.56	0.3 \pm 0.56

shrub cover with time since treatment (Roundy et al. 2014, Miller et al. 2014b, Williams et al. 2017). With a longer measurement period, we found that on drier years, such as 2012, 2015, and 2018, tree reduction added many more wet days in spring than on wetter years such as 2010, 2011, and 2016 (Fig. 4). For example, increased spring wet days from tree reduction averaged 13.8 ± 2.34 for Phase III over a 10-yr period of measurement (2008 through spring of 2018), but were 20.8 ± 3.63 in spring of 2018, when the October 2017–June 2018 precipitation was relatively low (Fig. 4). This could be due to several interacting factors. Wet days are limited in summer and fall while wet days are high in winter, but wet degree days are limited by cool temperatures. Therefore, spring is the season when water availability and warm temperatures best coincide to support plant growth. This is further evidenced by the much higher wet degree days in spring than any other season (Figs. 1, 2). Regression analysis indicated the positive correlations between spring wet days and vegetation cover with October through June precipitation, but negative correlation between spring wet days added by tree reduction and October through June precipitation (Fig. 6). There was also a negative, but weaker correlation of added spring wet days and total or herbaceous vegetation cover. This negative correlation may indicate that transpiration by vegetation extant after tree reduction is affecting spring soil water availability. In

drier years or on drier sites for a given year, plant transpiration is reduced due to low growth and productivity of shrubs and perennial herbs. Also, the establishment and growth of both native annuals and nonnative invasive annuals are significantly less, further reducing plant community productivity and water use. In contrast, a longer period of available water in the RGP on wetter years and on wetter sites supports more establishment, growth, and production of plants.

Water availability in sagebrush ecosystems is a zero-sum game because available water for growth is transient, even in wet years. Predominately, winter precipitation generally creates a block of time when water is stored and then available in the RGP as spring begins in March. On wet years, this time of continuously available water ended the first week of May for both untreated and treated plots, while on drier years it ended by the third week of April on untreated plots and by the first or second week of May on treated plots. This suggests another factor that may be especially affecting water availability in Phase III woodlands during dry years. Because the time of water availability is truncated on drier years, removal of trees as the major interceptor of precipitation and major water user in the RGP, especially at Phase III, may be contributing to a longer period of available water compared with wetter years. This is especially probable during years when establishment and

productivity of the residual native and nonnative invasive species are low on areas where trees have been reduced. During wetter years and on untreated areas, net precipitation might increase for some storms if the canopy storage is saturated, interception capacity is exceeded, and more through-fall occurs. Thus on wetter years, spring wet days on untreated and treated areas could be more similar due to reduced effects of interception. On drier years, interception may reduce the net precipitation more than on wetter years because canopy saturation may be less likely. Normally, interception and evapotranspiration water losses would be expected to increase with increased tree cover (Williams et al. 2018), but specific quantitative effects on cooler and wetter vs. warmer and drier years have not been determined. More complete measurement of hydrologic inputs and outputs is needed to better understand differential effects of tree reduction on wetter compared with drier years.

Tree reduction, especially when implemented at Phase III, can add weeks to the limited spring growth period in sagebrush ecosystems and favor plants that are available to use the additional resource. Perennial grasses recover much more quickly than shrubs when trees are reduced at Phase III (Williams et al. 2017, Freund et al. 2020). By both 6 and 10 yr after mechanical tree reduction, cover of both sagebrush and perennial grasses had increased relative to pretreatment, but perennial grass cover was much higher than sagebrush cover (Williams et al. 2017, Freund et al. 2020). Additionally, cover of both was higher on the mechanical than on the burn treatment. Because invasive weeds may also use the added resource, increased wet days in the RGP for drier and warmer sites and drier years after tree reduction also present a risk.

Soil temperature/moisture regimes.—Field measurements of the RGP confirmed that the mesic/aridic-xeric regime was warmer most seasons and drier in spring than the frigid/xeric regime. Sites with warmer and drier springs are associated with more cheatgrass and less perennial grass cover, and especially on burn compared with mechanical treatments (Roundy et al. 2018, Freund et al. 2020). Where climate supports perennial grass recovery (cooler, wetter, especially with wetter winters and wetter early springs) and residual populations are sufficient

to respond to increased resources with tree reduction, a perennial grass-dominated community on burned treatments and on Phase III-treated mechanical treatments should resist invasive grass and forb dominance as shrubs slowly recover (Roundy et al. 2018). However, on drier and warmer sites, especially with warm, wet falls and warmer late springs where cheatgrass is more favored than perennial grasses (Roundy et al. 2018), invasive weed dominance is a continued risk. Reducing trees at earlier phases of tree dominance or revegetating sagebrush and perennial herbs in association with tree reduction at high pretreatment tree dominance may best support ecosystem resilience and resistance to nonnative invasive plants on warmer and drier sites. Deciding not to reduce woody fuels could result in severe wildfire, and the subsequent increased soil water availability in spring and higher seedbed and RGP temperatures could support dominance of cheatgrass and recurrent high-frequency fire. High fire severity can result in over 85% mortality of perennial grasses occupying the site, reducing both resilience and resistance to invasive annual grasses (Bates et al. 2011).

The cooler temperatures of the mechanical treatment compared with the warmer temperatures of the burn for the frigid-xeric regime suggest that mechanical treatment is better suited to resist cheatgrass for this regime. Burning increases seedbed temperatures and cheatgrass germination potential (Cline et al. 2018). Increased soil temperatures in the RGP after fire could also support increased growth and seed production of cheatgrass (Chambers et al. 2007). However, for this regime, cheatgrass cover responded differently to burn compared with mechanical treatments in relation to pretreatment tree dominance (Freund et al. 2020). By 10 yr after treatment, cheatgrass cover on the burn treatment was highest at low pretreatment tree dominance and then decreased with increasing pretreatment tree dominance. On the mechanical treatment, cheatgrass cover was slightly lower than that on the burn at low pretreatment tree dominance and then increased slightly with increasing pretreatment tree dominance. At the same time, the dominant perennial grass, *Festuca idahoensis*, cover was higher on the mechanical than burn treatment at low-to-

moderate pretreatment tree dominance, but decreased greatly and was replaced by the lower successional *Elymus elymoides* on both the mechanical and burn treatments at high pretreatment tree dominance (Freund et al. 2020). Even though the lower cover of cheatgrass on the mechanical than burn treatment for this regime at low pretreatment tree dominance was associated with lower soil temperatures, it was also associated with greater perennial grass cover. The cooler soil temperatures for the mechanical treatment may have disfavored cheatgrass, while the greater number of wet days in spring may have favored perennial grass for this regime (Table 1). Thus, the soil climate response to mechanical tree reduction compared with burning for this regime may have increased resistance to cheatgrass.

Maintenance pool

The consequences of tree expansion and reduction on the MP relative to plant succession are less clear than for the RGP. On untreated plots in spring, the maximum dry period or maximum period when soil water potential < -1.5 MPa began as late as the third week in May. As with the RGP, wet days were limited in summer and fall (Fig. 1). Cavitation resistance of trees (for juniper shoots = -8.2 MPa, for pinyon shoots = -2.7 MPa, Koepke and Kolb 2013), shrubs (-5 MPa, Leffler and Ryel 2012), and perennial grass (-2.5 MPa, Leffler and Ryel 2012) occurs at water potentials lower than -1.5 MPa, the lower limit that we were able to measure with gypsum blocks. Leffler and Ryel (2012) considered that available water (soil water potential $>$ cavitation water potential) at lower soil depths was necessary to maintain shrub survival through the dry summers of the Great Basin. Bates et al. (2000) found much higher summer water potentials in a few small western juniper trees left uncut in tree-cut plots than in uncut plots, indicating a definite effect of summer water use by trees. Decreased water availability for maintenance as trees infill from Phase I to Phase III may contribute to shrub mortality and declining shrub cover. On drier years on some sites, soils at 50–65 cm did not wet up from winter and spring precipitation. This could result in lack of maintenance water in summer and contribute to shrub mortality. For the MP, we found a trend of decreasing wet days in spring with tree expansion on

untreated plots from Phase I to Phase II and Phase III (Fig. 1), and also a significant increase in spring wet days with tree reduction (Fig. 2). Our data suggest that expansion limits and tree reduction increases MP soil water availability needed to support shrub survival.

CONCLUSIONS

Managers remove trees to reduce fuel loads and increase cover and density of desirable understory species. Tree expansion decreased, while tree removal by prescribed fire or mechanical means increased the time of available water in springtime, which is associated with a longer period of nutrient diffusion to roots and growth of whichever plants are present (Leffler and Ryel 2012). We found that the time of soil water availability for understory plant growth was increased even 12–13 yr after tree reduction. This increase was greatest when trees were reduced at an advanced phase of expansion and when measured on drier years. Tree expansion had the most severe negative effects on soil water availability for understory vegetation on drier years. On the other hand, increased water availability from tree reduction may support not only establishment and growth of perennial shrubs and herbs, but also invasive annual grasses and forbs for many years. Reducing trees at earlier phases of expansion to maintain the community, or revegetation with shrubs and perennial herbs in association with tree reduction at advanced phases of expansion are recommended to increase resistance to invasive plants. This is especially important after prescribed fire and on warmer and drier sites that have limited perennial grass cover and where resistance to invasive annual grasses is low. On cooler and wetter sites with limited perennial grass cover, tree reduction by mechanical methods rather than by fire may best resist cheatgrass by avoiding associated increased soil temperatures.

ACKNOWLEDGMENTS

This is contribution number 140 of the Sagebrush Steppe Evaluation Project (SageSTEP) funded by the U.S. Joint Fire Science Program, Bureau of Land Management, National Interagency Fire Center, Great Basin Landscape Conservation Cooperative, and

Brigham Young University. The authors thank the many students and others who helped install equipment and collect and process field data.

LITERATURE CITED

- Archer, S. R., E. M. Andersen, K. I. Predick, S. Schwinning, R. J. Steidl, and S. R. Woods. 2017. Woody plant encroachment: causes and consequences. Pages 25–83 in D. D. Briske, editor. *Rangeland systems*. Springer Series on Environmental Management. Springer, New York, New York, USA.
- Archer, S. R., K. W. Davies, T. E. Fulbright, K. C. McDaniel, B. P. Wilcox, and K. I. Predick. 2011. Brush management as a rangeland conservation strategy: a critical evaluation. Pages 105–170 in D. D. Briske, editor. *Conservation benefits of rangeland practices*. US Department of Agriculture Natural Resources Conservation Service, Washington, D.C., USA.
- Archer, S. R., and K. L. Predick. 2014. An ecosystem services perspective on brush management: research priorities for competing land-use objectives. *Journal of Ecology* 102:1394–1407.
- Bates, J. D., K. W. Davies, and R. N. Sharp. 2011. Shrub-steppe early succession following juniper cutting and prescribed fire. *Environmental Management* 47:468–481.
- Bates, J. D., R. F. Miller, and T. J. Svejcar. 2000. Understorey dynamics in cut and uncut western juniper woodlands. *Journal of Range Management* 53:119–126.
- Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. *BioScience* 54:677–688.
- Bybee, J. B. A., K. R. Roundy, A. Young, D. B. Hulet, L. Roundy, Z. Crook, D. L. Aanderud, D. L. Eggett, and N. L. Cline. 2016. Vegetation response to piñon and juniper tree shredding. *Rangeland Ecology & Management* 60:224–234.
- Campbell Scientific. 1983. Model 227 Delmhorst cylindrical soil moisture block manual. Campbell Scientific, Logan, Utah, USA.
- Chambers, J. C. M. L., M. J. Brooks, J. D. Germino, D. I. Maestas, M. O. Board, M. O. Jones, and B. W. Allred. 2019. Operationalizing resilience and resistance concepts to address invasive grass-fire cycles. *Frontiers in Ecology and Evolution* 7: Article 185.
- Chambers, J. C., M. J. Germino, J. Belnap, C. S. Brown, E. W. Schupp, and S. B. St. Clair. 2016. Plant community resistance to invasion by *Bromus* species: the roles of community attributes, *Bromus* interactions with plant communities and *Bromus* traits. Pages 275–304 in M. J. Germino, J. C. Chambers, and C. S. Brown, editors. *Exotic brome grasses in arid and semiarid ecosystems of the western US. Causes, consequences, and management implications*. Springer Series on Environmental Management. Springer International Publishing, Switzerland.
- Chambers, J. C., J. D. Maestas, D. A. Pyke, C. S. Boyd, M. Pellant, and A. Wuenschel. 2017. Using resilience and resistance concepts to manage persistent threats to sagebrush ecosystems and greater sagegrouse. *Rangeland Ecology & Management* 70:149–164.
- Chambers, J. C., R. F. Miller, D. I. Board, J. B. Grace, D. A. Pyke, B. A. Roundy, E. W. Schupp, and R. J. Tausch. 2014. Resilience and resistance of sagebrush ecosystems: implications for state and transition models and management treatments. *Rangeland Ecology & Management* 67:440–454.
- 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*? *Ecological Monographs* 77:117–145.
- Cline, N. L., B. A. Roundy, S. P. Hardegrave, and W. Christensen. 2018. Using germination prediction to inform seeding potential: II. comparison of germination predictions for cheatgrass and potential revegetation species in the Great Basin, USA. *Journal of Arid Environments*. 150:82–91.
- Cline, N. L., B. A. Roundy, F. B. Pierson, P. Kormos, and C. J. Williams. 2010. Hydrologic response to mechanical shredding in a juniper woodland. *Rangeland Ecology & Management* 63:467–477.
- Condon, L., P. L. Weisberg, and J. C. Chambers. 2011. Abiotic and biotic influences on *Bromus tectorum* invasion and *Artemisia tridentata* recovery after fire. *International Journal of Wildland Fire* 20:1–8.
- D'Antonio, C. M., and P. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63–87.
- Davies, G. M., J. D. Bakker, E. Dettweiler-Robinson, P. W. Dunwiddie, S. A. Hall, J. Downs, and J. Evans. 2012. Trajectories of change in sagebrush steppe vegetation communities in relation to multiple wildfires. *Ecological Applications* 22:1562–1577.
- Davies, K. M., C. S. Boyd, J. L. Beck, J. D. Bates, T. J. Svejcar, and M. Gregg. 2011. Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush plant communities. *Biological Conservation* 144:2573–2584.
- Freund, S. M., B. A. Newingham, J. C. Chambers, B. A. Roundy, A. K. Urza, and J. H. Cushman. In Revision. 2020. Decade-long responses of sagebrush plant communities to conifer removal across a regional-scale experiment. *Ecosphere*.

- Evans, S., L. Hipps, A. J. Leffler, and C. Y. Ivans. 2006. Response of water vapor and CO₂ fluxes in semi-arid lands to seasonal and intermittent precipitation pulses. *Journal of Hydrometeorology* 7:995–1010.
- Knutson, K. C., D. A. Pyke, T. A. Wirth, R. S. Arkle, D. S. Pilliod, M. L. Brooks, J. C. Chambers, and J. B. Grace. 2014. Long-term effects of seeding after wildfire on vegetation in Great Basin shrubland ecosystems. *Journal of Applied Ecology* 51:1414–1424.
- Koepke, D. F., and T. E. Kolb. 2013. Species variation in water relations and xylem vulnerability to cavitation at a forest-woodland ecotone. *Forest Science* 59:524–535.
- 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.* CAB International, Cambridge, Massachusetts, USA.
- Loughlin, T. 2006. Improved experimental design and analysis for long-term experiments. *Crop Science* 46:2492–2506.
- McIver, J. D., et al. 2010. The sagebrush steppe treatment evaluation project (SageSTEP): a test of state-and-transition theory. RMRS-GTR-237. US Department of Agriculture, Forest Service, Fort Collins, Colorado, USA.
- McIver, J., and M. Brunson. 2014. Multidisciplinary, multisite evaluation of alternative sagebrush steppe restoration treatments: the SageSTEP project. *Rangeland Ecology and Management* 67:435–439.
- Miller, R. F., J. D. Bates, T. J. Svejcar, F. B. Pierson, and L. E. Eddleman. 2005. Biology, ecology, and management of western juniper (*Juniperus occidentalis*). Technical Bulletin 152. Oregon State University Agricultural Experiment Station, Corvallis, Oregon, USA.
- Miller, R. F., J. C. Chambers, L. Evers, C. J. Williams, K. A. Snyder, B. A. Roundy, and F. B. Pierson. 2019. The ecology, history, ecohydrology, and management of pinyon and juniper woodlands in the Great Basin and Northern Colorado Plateau of the western United States. General Technical Reports RMRS-GTR-403. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Miller, R. F., J. C. Chambers, and M. Pellant. 2014a. A field guide for selecting the most appropriate treatment in sagebrush and piñon-juniper ecosystems in the Great Basin: evaluating resilience to disturbance and resistance to invasive annual grasses, and predicting vegetation response. RMRS-GTR-322-rev. US Department of Agriculture, Forest Service, Fort Collins, Colorado, USA.
- Miller, R. F., J. Ratchford, B. A. Roundy, R. J. Tausch, A. Hulet, and J. Chambers. 2014b. Response of conifer-encroached shrublands in the Great Basin to prescribed fire and mechanical treatments. *Rangeland Ecology & Management* 67:468–481.
- Miller, R. F., S. T. Knick, Pyke, D. A., C. W. Meinke, S. E. Hanser, M. J. Wisdom, and A. L. Hild. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. Pages 145–184 in S. T. Knick and J. W. Connelly, editors. *Greater sage-grouse, ecology and conservation of a landscape species and its habitats (Studies in Avian Biology, Book 38).* University of California Press, Berkeley, California, USA.
- Miller, R. F., D. E. Naugle, J. D. Maestas, C. A. Hagen, and G. Hall. 2017. Special Issue: targeted woodland removal to recover at-risk grouse and their sagebrush-steppe and prairie ecosystems. *Rangeland Ecology and Management* 70:1–8.
- Miller, R. F., R. J. Tausch, E. D. McArthur, D. D. Johnson, and S. C. Sanderson. 2008. Age structure and expansion of piñon-juniper woodlands: a regional perspective in the Intermountain West. RMRS-RP-69. US Department of Agriculture, Forest Service, Fort Collins, Colorado, USA.
- Mollnau, C., M. Newton, and T. Stringham. 2014. Soil water dynamics and water use in a western juniper (*Juniperus occidentalis*) woodland. *Journal of Arid Environments* 102:117–126.
- Pierson, F. B., C. J. Williams, P. R. Kormos, S. P. Hardegre, P. E. Clark, and B. M. Rau. 2010. Hydrologic vulnerability of sagebrush steppe following pinyon and juniper encroachment. *Rangeland Ecology & Management* 63:614–629.
- Pyke, D. A., et al. 2017. Restoration handbook for sagebrush steppe ecosystems with emphasis on greater sage-grouse habitat- Part 3. Site level restoration decisions. U.S. Geological Survey Circular 1426. <https://doi.org/10.3133/cir1426>
- Rau, B. M., D. W. Johnson, R. R. Blank, R. J. Tausch, B. A. Roundy, R. F. Miller, T. G. Caldwell, and A. Lucchesi. 2011. Woodland expansion's influence on belowground carbon and nitrogen in the Great Basin U.S. *Journal of Arid Environments* 75:827–835.
- Rawlins, J. K., B. A. Roundy, D. Egget, and N. Cline. 2012. Predicting germination in semi-arid wildland seedbeds II. Field evaluation of wet thermal-time models. *Environmental and Experimental Botany* 76:68–73.
- Romme, W. H., et al. 2009. Historical and modern disturbance regimes stand structures, and landscape

- dynamics in piñon-juniper vegetation of the Western United States. *Rangeland Ecology and Management* 62:203–222.
- Roundy, B. A., J. C. Chambers, D. A. Pyke, R. F. Miller, R. J. Tausch, E. W. Schupp, B. Rau, and T. Gruell. 2018. Resilience and resistance in sagebrush ecosystems are associated with seasonal soil temperature and water availability. *Ecosphere* 9: Article e02417.
- 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 treatments across tree dominance gradients in the Great Basin. *Rangeland Ecology & Management* 67:482–494.
- 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 increases soil water availability of the resource growth pool. *Rangeland Ecology & Management* 67:495–505.
- Ryel, R. J., C. Y. Ivans, M. S. Peek, and A. J. Leffler. 2008. Functional differences in soil water pools: a new perspective on plant water use in water-limited ecosystems. *Progress in Botany* 69:397–422.
- Taylor, J. R., B. A. Roundy, and P. S. Allen. 2007. Soil water sensor accuracy for predicting seedling emergence using a hydrothermal time model. *Arid Land Research and Management* 21:229–243.
- US Department of Agriculture Natural Resources Conservation Service [USDA-NRCS]. 1999. Soil taxonomy: a basic system of soil classification for making and interpreting soil surveys. *Agricultural Handbook No. 436*. ftp://ftp-fc.sc.egov.usda.gov/NSSC/Soil_Taxonomy/tax.pdf
- Williams, C. J., K. A. Snyder, and F. B. Pierson. 2018. Spatial and temporal variability of the impacts of pinyon and juniper reduction on hydrologic and erosion processes across climatic gradients in the western US: a regional synthesis. *Water* 10:1607.
- Williams, R. E., B. A. Roundy, A. Hulet, R. F. Miller, R. J. Tausch, J. C. Chambers, J. Matthews, R. Schooley, and D. Eggett. 2017. Pretreatment tree dominance and conifer removal treatments affect plant succession in sagebrush communities. *Rangeland Ecology and Management* 70:759–773.
- Wilson, T. L., F. P. Howe, and T. C. Jr Edwards. 2011. Effects of sagebrush treatments on multi-scale resource selection by pygmy rabbits. *Journal Wildlife Management* 75:393–398.
- Young, K. R., B. A. Roundy, and D. Eggett. 2013. Tree reduction and debris from mastication of Utah juniper alter the soil climate in sagebrush steppe. *Forest Ecology and Management* 310:777–785.
- Zvirzdin, D. L., B. A. Roundy, N. S. Barney, S. L. Petersen, V. J. Anderson, and M. D. Madsen. 2017. Post-fire soil water repellency in piñon-juniper woodlands: extent, severity, and thickness relative to ecological site characteristics and climate. *Ecology and Evolution* 7:4630–4639.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3241/full>