ELSEVIER

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Effects of conifer treatments on soil nutrient availability and plant composition in sagebrush steppe



Jonathan D. Bates *, Kirk W. Davies

Rangeland Scientists, USDA-Agricultural Research Service, Eastern Oregon Agricultural Research Center, 67826-A Hwy 205, Burns, OR 97720, USA

ARTICLE INFO

Article history: Received 19 May 2017 Received in revised form 12 June 2017 Accepted 13 June 2017

Keywords: Cheatgrass Fuel reduction Nitrogen Phosphorus Prescribed fire Resin probes Western juniper

ABSTRACT

Piñon-juniper woodlands of the western United States have expanded 2 to 10-fold since the late 1800's. Tree control measures using chainsaws, heavy equipment and prescribed fire have been used to reduce woodlands and restore big sagebrush steppe and decrease woody fuel loading. We evaluated nutrient availability and herbaceous recovery following various cutting and prescribed fire treatments in late succession western juniper woodlands on two sites in southeast Oregon from 2007 to 2012. Sites were a cool, wet big sagebrush-Idaho fescue association (FESCUE), highly resistant to exotic annual grasses and a warm dry big sagebrush-bluebunch wheatgrass association (BLUEBUNCH), moderately resistant to annual grass invasion. Treatments were untreated controls, partial cutting followed by fall broadcast burning (SEP), cut and leave (CUT), and cut and burn in winter (IAN) and spring (APR). Soil inorganic N (NO₃, NH₄), phosphorus (H₂PO₄), potassium (K⁺), and cover of herbaceous species were measured in three zones; interspace, litter mats around the tree canopy (canopy), and beneath felled trees (debris). Following woodland cutting, the results of the various slash treatments measured significant differences through time in the availability of inorganic N, P, and K and vegetation composition. Peak nutrient availability tended to occur within the first two years after treatment. The increases in N, P, and K were greatest in severely burned debris and canopy zones of the SEP and APR treatments. Invasive annual grass cover was positively correlated to soil inorganic N concentrations. Herbaceous composition at the FESCUE site was generally resistant to annual grasses after juniper treatments and native plants dominating post-treatment even in highly impacted debris and canopy zones of the SEP treatment. The BLUEBUNCH site was less resistance and resilient, thus, exotic annual grasses were a major component of the understory especially when tree and slash burning was of high fire severity. To lessen these impacts requires slash burning be applied from late fall to early spring, when fuel moisture and relative humidity are higher, to maintain an adequate perennial herbaceous composition for recovery.

Published by Elsevier B.V.

1. Introduction

In the past 150 years, juniper (Juniperus spp.) and piñon (Pinus spp.) coniferous woodlands have increased 2 to 10-fold across 9 ecoregions of the Intermountain area of the western United States (Omernik, 1987; Romme et al., 2009). Woodland expansion is well documented in semi-arid regions of the inland northwest where western juniper (Juniperus occidentalis spp. occidentalis Hook.) is estimated to occupy about 4 million hectares. About 95% of woodland expansion has occurred in sagebrush (Artemisia spp.) steppe communities (Miller et al., 2011). Woodland dominance results in lower diversity and production of herbaceous and shrub layers, loss of habitat for shrub obligate wildlife, altered soil and litter nutrient distribution, and may cause negative impacts to

watershed processes (Doescher et al., 1987; Klemmedson and Tiedemann, 2000; Miller et al., 2005; Pierson et al., 2010).

To reverse these impacts, control of conifer woodlands by mechanical treatments and prescribed fire has been applied since the 1950's. The recovery of plant communities after treatment of conifers is well documented and is influenced by a number of factors including phase of woodland treated, type of treatment, disturbance severity, residual plant composition following treatment, and site resilience and resistance to invasion by exotic annual grasses (Miller et al., 2014; Roundy et al., 2014). Low and moderate severity fires often cause only nominal damage to herbaceous understories and recovery is dominated by native plant communities (Bates et al., 2006, 2014; Miller et al., 2014; Roundy et al., 2014). Severe fires that cause high levels of native plant mortality often result in post-fire weed dominance (Bates et al., 2006, 2013, 2014; Condon et al., 2011). A key determinant for recovery immediately after woodland treatment is initial plant composition. Sites

^{*} Corresponding author.

E-mail address: jon.bates@oregonstate.edu (J.D. Bates).

with relatively intact residual understories recover within 5 years' post-treatment while sites with less intact understories require longer recovery periods, achieve only partial recovery with a mix of native and exotic species, or become dominated by invasive weeds. The lower a plant community's resistance and resilience the higher risk of conversion to invasive annual grass dominance after disturbance (Chambers et al., 2007, 2014).

Management treatments and natural disturbances in conifer woodlands and other semi-arid systems effect soil physical, chemical, and biological properties and processes which feedback to influence spatial, temporal, and compositional recovery of plant communities (DeBano et al., 1998; Neary et al., 1999). Fire and mechanical treatments increase short-term available soil water, N, P, and other nutrients in semiarid woodlands and shrublands (DeBano and Klopatek, 1988; Blank et al., 1994; Bates et al., 2000, 2002; Davies et al., 2007; Rau et al., 2007; Roundy et al., 2014). Available soil nutrients may remain elevated from 1 to 5 years depending on type of woodland treatment, although peak increases typically occur within the first two years after treatment (Covington et al., 1991; DeBano et al., 1998). However, greater resource availability caused by woodland treatment can increase invasibility and may promote dominance by exotic weeds (Blank, 2008; Rau et al., 2014; Chambers et al., 2014). How completely weeds occupy areas after conifer control is primarily determined by site characteristics, disturbance severity, and residual composition of native herbaceous species (Davies and Bates, 2017; Bates et al., 2014). Concurrent evaluation of soil resource pools and vegetation dynamics are lacking in sagebrush steppe, particularly after woodland treatments. It is important to improve our understanding of the effects of pinon-juniper control to ecological processes and assess linkage between soil resource availability and plant community recovery because large scale woodland reduction treatments are likely to continue into the future.

We evaluated the impact of cutting and prescribed fire on soil nutrient availability (N, P, K) and herbaceous composition for 6 years after western juniper control. Our objectives were to: (1) assess the effects of juniper removal on growing season (April-Iuly) soil nutrient availability in juniper canopy areas, under cut juniper trees, and interspaces; (2) determine the duration and temporal variability of treatment effects on growing season soil nutrient availability; and (3) evaluate treatment impacts on composition of native and exotic species. We hypothesized that available nutrient pools would increase after conifer reduction because nutrient availability often increases following mechanical and fire treatments in pinon-juniper woodlands. We further hypothesized that elevated nutrient pools among the treatments would be greatest within the first 2-3 years following conifer control, which has typically been reported following woodland control. We hypothesized that treatments of lesser disturbance severity would be dominated by native herbaceous species and treatments with greater disturbance severity would result in dominance by invasive weeds; these conditions that have been frequently reported following woodland and forest treatments. Greater disturbance may result in higher soil nutrient availabilities, thus, we hypothesized that greater soil inorganic N levels would be positively correlated to greater invasive weed cover.

2. Methods and materials

2.1. Study sites

Two different plant associations were located on Steens Mountain, southeast Oregon, 80–90 km south of Burns. The two sites were basin big sagebrush/bluebunch wheatgrass-Thurber's needlegrass (*Artemisia tridentata* Nutt. spp. *tridentata* (Rydb.)

Beetle/Pseudoroegneria spicata (Pursh) A. Löve - Achnatherum thurberianum (Piper) Barkworth) [BLUEBUNCH] and mountain big sagebrush/Idaho fescue (Artemisia tridentata Nutt. spp. vaseyana (Rydb.) Beetle/Festuca idahoensis Elmer) [FESCUE] plant associations. The BLUEBUNCH and FESCUE sites were classified as Phase 3 woodlands as juniper presence had eliminated the shrub layer and depleted the understory (Miller et al., 2005; Bates et al., 2014).

The BLUEBUNCH site (42° 56′ 10″ N, 118° 36′ 30″ W) was located on a west aspect (slope 15-22%) at 1550 to 1600 m elevation. The ecological site is a Droughty Loam (280-330 mm) PZ (precipitation zone) (NRCS, 2017). Soils are a clayey-skeletal, frigid, Lithic Argixerolls (NRCS, 2006). Soil pH (0-10 cm) was 7.5 in interspace soils and 7.6 under tree canopies. Soil textures (0-10 cm) were a silt-loam in the interspaces and a loam under tree canopies. Bulk density of the soils was 1.2 g cm⁻³ in the interspace and canopy zones. Prior to treatment, juniper canopy cover averaged 26%, the interspace was 95% bare ground and Sandberg's bluegrass (Poa secunda J Pres.), a shallow rooted perennial grass, was the main understory species. Invasiveness of annual grasses in the Great Basin may be enhanced on sites with warmer temperatures, higher soil water variability, and lower ecological condition (Koniak, 1985; Chambers et al., 2007; Davies, 2008; Condon et al., 2011). These characteristics apply to the BLUEBUNCH site and previous low disturbance conifer removal on this site indicate it is only moderately resistant to annual grass invasion (Bates et al., 2005; Bates and Svejcar, 2009).

The FESCUE site $(42^{\circ} 53' 25'' N, 118^{\circ} 34' 18'' W)$ was on an east facing slope (20-45%) at 1650-1730 m elevation. The ecological site was a North Slope (304-406 mm) PZ (NRCS, 2017). Prior to treatment, juniper canopy cover averaged 35%, the interspace was 60% bare ground and Idaho fescue and perennial forbs dominated the understory. Soils are a loamy-skeletal, mixed, frigid Pachic Haploxerolls (NRCS, 2006). Soil pH (0-10 cm) was 6.9 ± 0.1 in interspaces and 7.2 ± 0.2 in tree canopy zones. Soil textures (0-10 cm) were loams and soil bulk density was $1.1 \pm 0.1 \text{ g cm}^{-3}$ in interspace and canopy zones.

Precipitation in the northern Great Basin occurs mostly from late fall into late spring. Water year precipitation (October 1 – September. 30) at the Steens Mountain BLUEBUNCH site averaged 352 ± 20 mm the past 12 years and ranged from 275 to 543 mm during the study (Bates and Davies, 2016). Precipitation is likely to be greater at the FESCUE site as it is 8 km further up the mountain and 100 m higher than the BLUEBUNCH site.

2.2. Experimental design and treatment application

The experimental design at each site was a randomized complete block (Peterson, 1985) with three cut-and-burn treatments, a cut-and-leave (CUT) treatment, and untreated woodlands (control). There were five treatment replicates at each site. Cut-andburn treatments included fires applied in September (SEP), January (JAN), and April (APR). All juniper in the JAN, APR, and CUT treatments were felled in July 2006. JAN fires were applied on 17 and 19 Jan 2007, on the BLUEBUNCH, and FESCUE sites, respectively. These fires were of low severity (Bates et al., 2014). APR fires were applied on 6 Apr 2007 at both sites and fires were of low (interspace) to high (beneath cut trees) severity. JAN and APR burns required igniting individual or clusters of trees as snow or green herbaceous vegetation prevented fire from carrying in the interspaces. On SEP treatments, one-third of the juniper were cut in June 2006 and these were used to carry strip-head fires to kill remaining live trees. The SEP fires were of moderate to high severity and were applied on 25 and 26 Sep 2006, at the BLUEBUNCH and FESCUE sites, respectively. Burn conditions were typical for applications used to broadcast burn (SEP) and reduce western juniper fuel loads in winter and spring (Bates et al., 2014).

Fine fuel and soil water content (0–4 cm deep) were drier for SEP and APR treatments than the JAN treatment (Bates et al., 2014). Flame lengths, burn duration, area burned, soil temperatures and fuel consumption were lowest in JAN treatments and greatest in SEP treatments (Table 1; Bates et al., 2014). In canopy and felled tree zones of SEP and APR treatments, fires consumed all 1-h, 10-h and 100-h fuels and partly consumed the 1000-h fuels. In interspaces of SEP treatments herbaceous fine fuels were consumed as were scattered shrubs. Interspace zones in APR treatments did not burn though heat damage was noted for plants in close proximity to burning trees. In JAN treatments, fuel consumption only consumed 1-h fuels in the felled tree zones while canopy and interspace zones did not burn.

2.3. Soil Nutrients

Concentrations of soil nitrate (NO_3^-), ammonium (NH_4^+), phosphate ($H_2PO_4^-$, HPO_4^{2-}), and potassium (K^+), were collected using Plant Root Simulator probes ($PRS^{\mathbb{IM}}$ -probes; Western Ag Innovations, Saskatoon, Saskatchewan, Canada) for each treatment in three blocks at each site. Ion-exchange resin membranes on the $PRS^{\mathbb{IM}}$ -probes collect anions and cations in the soil solution using electrostatic attraction (Jowkin and Schoenau, 1998). The $PRS^{\mathbb{IM}}$ -probes were planted vertically in the soil with the membrane section of the probe collecting ions from 1.3 to 6.8 cm deep. Probes were left *in situ* from early to mid-April until late July, each year, from 2007–2012. Probes were not isolated and plant roots could compete with the ion resins for soil nutrients. Thus, estimates of

Table 1Surface and 2-cm deep soil temperatures (°C) in the canopy, debris and interspace zones, plot area burned, and maximum fuel consumption for the prescribed burning treatments at the BLUEBUNCH and FESCUE sites, Steens Mountain, Oregon. All juniper trees (>1.5 m) were cut in July 2006 in the JAN and APR treatments. The SEP treatment was a partial cut (1/3 of trees >2.0 m tall were cut) with fire killing the remaining live trees.

Site Measurement (units)	SEP (2006)	Treatments JAN (2007)	APR (2007)
Bluebunch site Canopy Zone Soils Surface soil temp. (°C) 2 cm deep soil temp. (°C)	649–871 191–316	No effect ^a	427-704 156-302
Debris Zone Soils Surface soil temp. (°C) 2 cm deep soil temp. (°C)	760–1038 171–288	No effect	649 - 927 177 - 316
Interspace Soils Surface soil temp. (°C) 2 cm deep soil temp. (°C)	135–538 <121	No effect	No effect No effect
Plot area burned (%) Maximum juniper fuel consumed	100 100–1000-h ^b	12-18 1-h	30-38 10-1000-h
Fescue site			
Canopy Zone Soils			
Surface soil temp. (°C) 2 cm deep soil temp. (°C)	760–816 191–316	No effect	No effect No effect
Debris Zone Soils Surface soil temp. (°C) 2 cm deep soil temp. (°C)	649-982 93-177	No effect	538-927 121-204
Interspace Soils Surface soil temp. (°C) 2 cm deep soil temp. (°C)	79–316 <107	No effect	No effect No effect
Plot area burned (%) Maximum juniper fuel consumed	95–100 100-h	18-22 1-h	20-27 100-h

^a No temperature changed detected on the soil surface (paint strips under snow) and frozen soils prevented placement at 2 cm.

ion concentrations are likely lower than potential. At the end of the sampling, probes were collected, washed with deionized water, locked in polyethylene bags, and returned to Western Ag Innovations where they were extracted with 0.5 N HCl and analyzed either colourimetrically with an auto-analyzer or by plasma emission spectroscopy to determine nutrient concentrations. Nutrients were measured in three zones; interspace, litter mats beneath formerly standing trees (canopy), and beneath felled trees (debris). The debris zone was former interspace overlain by felled trees. Four probe sets (one set is one cation and one anion probe) were randomly placed in in each zone within a treatment. In the controls probes were placed in canopy (beneath live trees) and interspace zones.

2.4. Vegetation

Density and canopy cover of herbaceous species were measured inside $0.2-m^2$ (0.4 × 0.5 m) frames in May 2006 and June 2007– 2012. Herbaceous canopy cover and density were estimated spatially by zone: interspace, canopy, and debris. Canopy zones were measured in the four cardinal directions around eight randomly selected stumps (treated) or trees (control) in each plot and frames were placed on the inside edge of the litter area or drip line (1-2.5 m from the stump or bole). For the debris zone, frames were arbitrarily placed under eight randomly selected cut juniper trees (4 frames per tree). Canopy and debris zone trees were marked with metal tags for re-measurement. Interspace zones were randomly sampled in areas between cut trees and canopy zones within each plot (32 frames). Further zonal descriptions and as a percentage of plot area are detailed in Bates et al. (2014) and Bates and Davies (2016). Shrubs were not present on the BLUE-BUNCH site and shrub cover on the FESCUE site was <2% six years after treatment

2.5. Analysis

We used the mixed models procedure (Proc Mix) in SAS ver. 9.3 (SAS Institute Inc., Cary, NC) to determine the effect of juniper treatments on soil nutrient and herbaceous vegetation response variables. Soil nutrients in canopy and debris-interspace zones were analyzed for year, treatment, and the interaction. Blocks and block by treatment interactions were treated as random variables. An auto regressive order one covariance structure was used in the models as it provided the best fit for data analysis. Treatment effects were also analyzed in each year of the study using mixed model GLMs, because the response of sagebrush communities often varies significantly over time since disturbance (Davies et al., 2007). Herbaceous foliar cover was grouped into native (perennials and annuals) and non-native classes (annual grasses and annual forbs) and analyzed for the last year of the study (2012). Data were evaluated for normality using the univariate procedure in SAS ver. 9.3 (Littell et al., 1996) and were transformed when necessary. All graphic presentations display original data (i.e. non-transformed), unless noted. Regressions were performed for peak annual grass cover and average annual inorganic N values (2007-2012) to evaluate relationships between N availability and annual grass to treatments using the SigmaPlot regression function (Systat Software Inc., San Jose, CA). Differences between treatment means were significant at P < 0.05.

3. Results

3.1. Inorganic nitrogen

At the BLUEBUNCH site inorganic N (NO_3^-, NH_4^+) varied by the interaction between treatment and year in canopy and

^b 1-h fuels are juniper wood less than 0.64 cm in diameter; 10-h fuels are juniper wood, 0.65–2.54 cm in diameter; 100-h fuels are juniper wood, 2.55–7.62 cm in diameter; 1000-h fuels are juniper wood, 7.63–20.32 cm in diameter.

debris-interspace zones (Fig. 1A and B; Table 2). In canopy soils, inorganic N in all treatments exceeded the control in 3 of 6 years with the largest differences occurring the first three years after tree reduction (Fig. 1A). The largest increase was in the SEP treatment where greater levels of juniper fuels were consumed and caused higher perennial bunchgrass mortality. Treatments and control did not differ the fourth and fifth year after tree reduction, however, six years after treatment inorganic N was twice as great in treatments versus the control. In debris and interspace soils there were large increases in inorganic N in year one for the treatments compared to the control interspace (Fig. 1B; Table 2). The greatest increase in inorganic N in year one were in the debris zone of the SEP and APR treatments which were 2.5-18 times greater than the other treatments and control. After year one, differences in inorganic N among treatments tended to disappear with the exception of the CUT debris zone. The CUT debris zone had largest inorganic N levels the 3rd through the 6th year after treatment and was 2-10 times greater than the other treatments and control.

At the FESCUE site, inorganic N varied by the treatment and year interaction in canopy and debris-interspace zones (Fig. 2A and B; Table 2). In canopy zones, inorganic N in the treatments exceeded the control in 3 of 6 years after tree reduction (Fig. 2A). The largest increase was in the SEP treatment where inorganic N was 4 to 45-fold greater than the other treatments and control the first three years after juniper reduction. One pattern that emerged was that inorganic N was greater in the CUT

treatment than other treatments (except Jan) and control from 4 to 6 years after treatment. In debris-interspace soils of the FESCUE site, inorganic N in year one was 3 to 27-fold greater in the treatments than the control (Fig. 2B; Table 2). Inorganic N in the SEP debris zone was greater than the other debris and interspace zones (treated and control) the first two years after tree reduction. Between 2009 and 2012 there were two trends; (1) inorganic N in the CUT debris zone peaked the fourth year after treatment and was 6–18 times greater than the other treatments and control; and (2) inorganic N was not different among SEP, JAN, APR debris zones and treated and control interspaces.

3.2. Phosphorus

Available P (H₂PO₄, HPO₄²) at the BLUEBUNCH site varied by the interaction between treatment and year in canopy, debris, and interspace zones (Fig. 3A and B; Table 2). In canopy soils, available P in the treatments exceeded the control 1.5 to 5-fold in 5 of the 6 years following tree reduction (Fig. 3A). Among the treatments the largest levels of P were in the SEP (2007, 2011) and the Cut treatment (2010). In debris and interspace zones, P was 1.5 to 6-fold greater in all the treatments than the control interspace the first and last year of measurement following tree reduction (Fig. 3B; Table 2). The greatest levels of P in year one were in the SEP, JAN, and APR debris zones exceeding the CUT debris and treated and control interspaces. The main pattern that developed

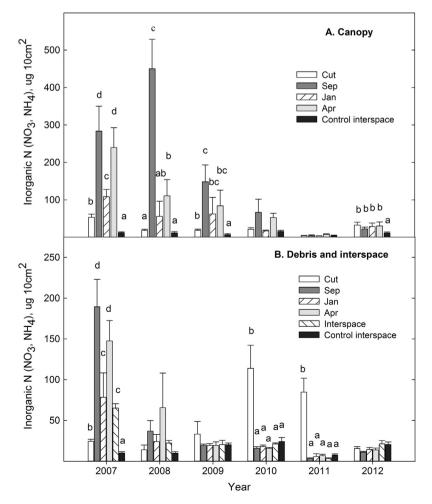


Fig. 1. Inorganic N (NH $_4^4$, NO $_3^-$) dynamics (April – July) for the various western juniper control treatments at the BLUEBUNCH site, Steen's Mountain, Oregon, 2007–2012. Data are means + one standard error. Means sharing a common lower case letter are not significantly different (P > 0.05). The first year after treatment begins in 2007. Except for CUT and control the other treatment designations correspond to the month burning was applied.

Table 2Soil nutrient P-values from mixed model analysis for the western juniper removal study sites on Steen's Mountain, southeast Oregon (1991–2016). Values in bold indicate significant treatment (Cut, control) differences for main (treatment, year) effects and the interaction (treatment × year).

Study site and response variable	Canopy mound ^a			Debris and interspace ^a			
	Treatment	Year	$Treatment \times Year$	Treatment	Year	$Treatment \times Year$	
Bluebunch site							
Inorganic N	0.001	<0.001	<0.001	0.001	<0.001	<0.001	
NO_3^-	0.005	<0.001	<0.001	0.004	<0.001	<0.001	
NH ₄ ⁺	0.108	<0.001	<0.001	0.091	<0.001	0.040	
Phosphorus	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	
Potassium	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	
Fescue site							
Inorganic N	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	
NO_3^-	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	
NH ₄ ⁺	0.006	<0.001	0.040	0.236	<0.001	0.040	
Phosphorus	<0.001	<0.001	0.094	<0.001	<0.001	0.011	
Potassium	0.007	<0.001	<0.001	<0.001	<0.001	<0.001	

^a Not shown are the statistical comparisons between canopy and debris/interspace zones. Main effects and interactions were highly significant indicating higher peaks in the canopy influenced soils for inorganic N and K. Overall these zones tended not to differ for phosphorus.

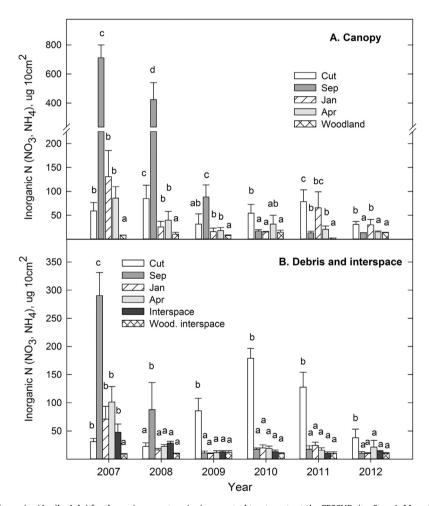


Fig. 2. Inorganic N (NH_4^* , NO_3^*) dynamics (April – July) for the various western juniper control treatments at the FESCUE site, Steen's Mountain, Oregon, 2007–2012. Data are means + one standard error. Means sharing a common lower case letter are not significantly different (P > 0.05). The first year after treatment begins in 2007. Except for CUT and control the other treatment designations correspond to the month burning was applied.

from the 3rd year after tree reduction were that P in SEP and CUT debris zones were greater than the control interspace. In addition, P in the CUT debris zones, was greater than all the treatments and control the 5th and 6th year after treatment.

Available P at the FESCUE site varied by the interaction between treatment and year in canopy, debris, and interspace zones

(Fig. 4A and B; Table 2). There were two main patterns in canopy zones. Available P in all treatments were 1.5 to 2.5-fold greater than the control the first two years after conifer reduction (Fig. 4A). In subsequent years' differences among treatments and the control were generally not consistent, with one exception; available P in the SEP treatment was, overall, greater than all treatments and

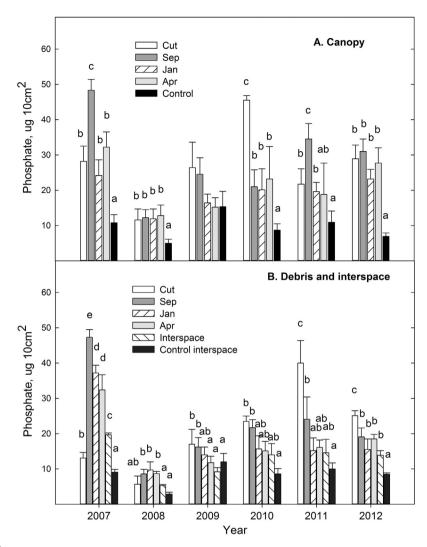


Fig. 3. Inorganic P ($H_2PO_4^-$) dynamics (April – July) for the various western juniper control treatments at the BLUEBUNCH site, Steen's Mountain, Oregon, 2007–2012. Data are means + one standard error. Means sharing a common lower case letter are not significantly different (P > 0.05). The first year after treatment begins in 2007. Except for CUT and control the other treatment designations correspond to the month burning was applied.

the control the last four years. There were large increases in P in year one for the SEP, JAN, and APR debris zones and all were greater than the CUT debris zone and interspaces (treated, control) (Fig. 4B). Aside from the SEP debris zone, the other treatments did not differ from the control after the first year (2007). Available P in the SEP treatment was regularly greater than the other debris treatments and the interspaces (treated, control) between 2009 and 2012.

3.3. Potassium

Available K^+ at the BLUEBUNCH site varied by the interaction between treatment and year in canopy and debris-interspace zones (Fig. 5A and B; Table 2). In canopy zones, available K^+ in treatments exceeded the control by 2 to 3-fold the first year after woodlands were reduced. Treatment differences in following years did not develop any distinct patterns in the canopy zones. In debris and interspace zones, available K^+ was 3 to 7-fold greater in the treatments than the control the first year after treatment. In later years (2010–2012) the CUT debris zone had highest levels of K^+ than the other treatments and control. Available K^+ in the other treatments also exceeded the control the second (2008) and sixth year (2012) after treatment.

Available K⁺ at the FESCUE site varied by the treatment and year interaction in canopy, debris, and interspace zones (Fig. 6A and B; Table 2). In canopy zones, K⁺ in the treatments exceeded the control 5 to 6-fold the first year after woodland reduction, after which they were frequently (2009, 2011, 2012) about half the value of the control (Fig. 6A). Available K⁺ was 4 to 7-fold greater in debris and interspace zones of the treatments than the control interspace the first year following treatment (Fig. 6B). In subsequent years, available K⁺ was frequently (2009, 2010, 2012) greater in CUT debris zones than one or more of the treated debris zones and interspaces (treated, control). Available K⁺ in the treatments (debris, interspace) exceeded, by 1.25 to 2-fold, the control interspace the sixth year (2012) after treatment.

3.4. BLUEBUNCH site vegetation

In 2012, bunchgrass density was 2 to 8-fold greater in interspaces than canopy and debris zones at the end of the study (Fig. 7A; Table 3). In canopy zones, bunchgrass density about doubled in the JAN and CUT treatment and decreased by 60% in the SEP and APR treatments from pretreatment values of 1.9 ± 0.2 plants m⁻². In the interspace, bunchgrass density increased 2 to 3-fold, across all treatments, from pretreatment values of 2.9 ± 0.4 plants

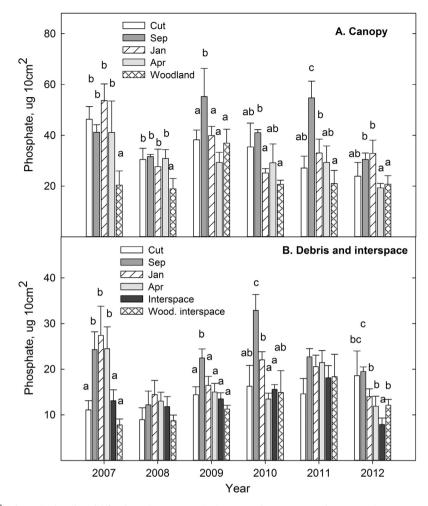


Fig. 4. Inorganic $P(H_2PO_4^-)$ dynamics (April – July) for the various western juniper control treatments at the FESCUE site, Steen's Mountain, Oregon, 2007–2012. Data are means + one standard error. Means sharing a common lower case letter are not significantly different (P > 0.05). The first year after treatment begins in 2007. Except for CUT and control the other treatment designations correspond to the month burning was applied.

 ${\rm m}^{-2}$. In debris zones, bunchgrass density about doubled in the JAN treatment and decreased by half in CUT, SEP, and APR treatments from pretreatment values of 2.8 \pm 0.4 plants ${\rm m}^{-2}$.

Foliar cover of native perennials was 2 to 4-fold greater in the treated interspace than other treated and control zones (Fig. 7B). In canopy zones, cover of native perennials did not differ from controls in CUT, JAN, and APR treatments and the SEP treatment cover declined by almost 50%. Cover of native perennials in the interspace increased about 4-fold from pre-treatment (2006) values of 4.7 ± 0.8 %. In debris zones, perennial cover doubled in the Jan treatment, remained unchanged in CUT and APR treatments, and was 50% lower than pretreatment values (4.5 ± 0.7 %) in the SEP treatment. Cover of non-native annual weeds increased 4 to 9fold in the canopy zone and 3 to 5-fold in interspace and debris zones compared to the control and pre-treatment values (Fig. 7C). In the treatments, the largest increases in annual weed cover tended to be in the canopy (CUT, SEP and APR) and debris zones (SEP, APR). The lowest increase in weed cover were in the debris zone of CUT and JAN treatments.

3.5. FESCUE site vegetation

In 2012, bunchgrass densities had doubled in all treatment interspaces compared to the control interspace and the values were equal to densities in the canopy zone of CUT, JAN, APR, and control treatments (Fig. 8A; Table 3). Bunchgrass densities in the canopy zone of the SEP treatment were reduced to half of pretreatment

values. In debris zones, bunchgrass densities increased by about 50% (CUT, JAN, APR), or were not different (SEP) from pretreatment values.

Foliar cover of native perennials was 1.3 to 1.5-fold greater in treatment interspaces (CUT, SEP, JAN, APR), canopy zones of the CUT, JAN, and APR treatments, and debris zone of the JAN and APR treatments than the SEP (canopy, debris), CUT (debris), and control (interspace, canopy) treatments (Fig. 8B). Cover of nonnative annual weeds in the SEP canopy zone was 2 to 8-fold greater than other treated zones and controls. Cheatgrass made up between 92 and 97% of the weeds (Fig. 8C). In the other treatment and control zones weed cover was generally zero or less than 2% and comprised between zero and 5% of total herbaceous cover.

3.6. Inorganic N and invasive plant species

At the BLUEBUNCH site there was a positive correlation between post treatment inorganic N and annual grass cover ($R^2 = 0.86$, P < 0.001; Fig. 9A). At the FESCUE site a positive correlation between inorganic N and annual grass cover was measured after log transforming the data ($R^2 = 0.57$, P = 0.004; Fig. 9B).

4. Discussion

The two study sites are representative of big sagebrushbunchgrass plant communities that have the potential to be

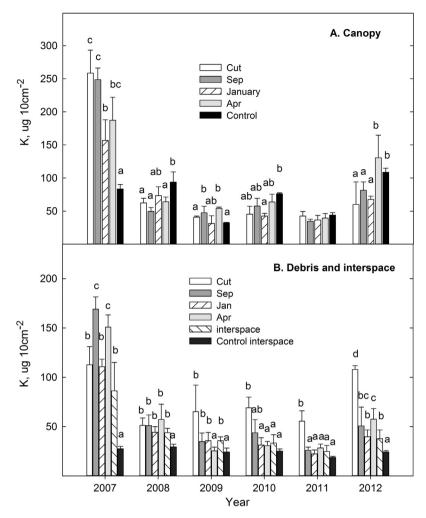


Fig. 5. Mineralized potassium (K^+) dynamics (April – July) for the various western juniper control treatments at the BLUEBUNCH site, Steen's Mountain, Oregon, 2007–2012. Data are means + one standard error. Means sharing a common lower case letter are not significantly different (P > 0.05). The first year after treatment begins in 2007. Except for CUT and control the other treatment designations correspond to the month burning was applied.

dominated by western juniper. Following woodland cutting, the various slash treatments differed through time in vegetation composition and in the availability of inorganic N, P, and K. The results further indicate that management of conifer slash in semi-arid environments has both short and longer-term impacts on ecosystem processes and secondary succession.

4.1. Nitrogen

At both sites the increase in inorganic N following juniper woodland treatments were a response typically measured following fire and mechanical removal or thinning of woody vegetation (Neary et al., 1999; Bates et al., 2002; Davies et al., 2007; Rau et al., 2008; Stephens et al., 2012). Aside from the CUT debris zone, the highest inorganic N levels in the canopy zone occurred within the first two years after treatment and in debris and interspace zones the first year after treatment.

Inorganic N levels in canopy zones of both sites, while decreasing overtime, remained dynamic with small differences among treatments and controls lasting into the sixth year post-treatment. Multi-year periods of elevated inorganic N levels following disturbance in areas of high litter deposition appears to be characteristic of semi-arid ecosystems. Covington et al. (1991) and Rau et al. (2007) measured greater levels of inorganic N in

burned canopy litter layers beneath sagebrush and pinyonjuniper trees 4 years following fire compared to untreated areas.

At both sites, soil inorganic N levels tended not to differ among debris and interspace treatment zones (except the CUT debris zone) and the control interspace following the first year after treatment. This outcome was unexpected because in the debris zones, much like the canopy zones, there were clear differences among the slash treatments in disturbance severity that effected herbaceous plant composition, litter and woody fuel consumption, soil heating, and levels of bare ground (Bates et al., 2014; Bates and Davies, 2016). In contrast, inorganic N in CUT-debris zones peaked 4 years after treatment and was generally greater than the other debris areas and interspaces from the 3rd to 6th year after conifer reduction. Evans and Young (1985) reported that it took 3-5 years after felling juniper for soil inorganic N to increase in litter deposition areas. The delay in peak inorganic N in the CUT debris zones may be in response to a continual source of leaf litter deposited from felled trees which lasts for about 3-4 years after cutting. Microbial N immobilization tends to occur with inputs of litter with high C/N ratios (Davidson et al., 1992), which is characteristic of juniper leaf litter (Bates et al., 2007). In treated woodlands and forests it may require 2 to 3 years before litter N is released into soils (Bates et al., 2007; Hart et al., 1992; Klemmedson et al., 1985; Yavitt and Fahey, 1986). The later increase in inorganic N

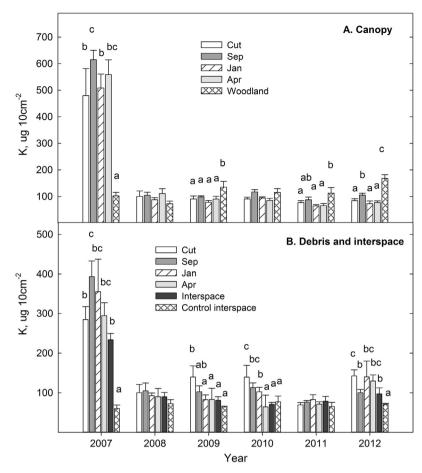


Fig. 6. Mineralized potassium (K^*) dynamics (April – July) for the various western juniper control treatments at the FESCUE site, Steen's Mountain, Oregon, 2007–2012. Data are means + one standard error. Means sharing a common lower case letter are not significantly different (P > 0.05). The first year after treatment begins in 2007. Except for CUT and control the other treatment designations correspond to the month burning was applied.

levels in CUT debris soils may result from lower plant N uptake because herbaceous cover was lower in this treatment zone (both sites) than debris zones of the other treatments and the interspace (Bates and Davies, 2016).

The patterns and treatment differences in inorganic N were likely the result of post-fire spatial and temporal variations in plant uptake, microbial immobilization, N mineralization, N-fixation, soil organic matter and quantity and quality of litter substrates. In SEP (canopy and debris zones, both sites) and APR treatment (debris zone both sites; canopy zone, Bluebunch site) fire consumed litter and eliminated or reduced the herbaceous understory resulting in high levels of bare ground. Soil temperatures during fires in these zones were high enough to reduce microbial populations and kill plants and propagules, and were likely responsible for greater inorganic N levels than the other treatment from 50 to 121 °C and mortality of plant roots and seeds occur between 48 and 94 °C (Neary et al., 1999). In the SEP and APR treatments, soil temperatures were on the order of several hundred degrees higher. Inorganic N levels in these treatment zones decreased as herbaceous vegetation recovered and by probable recolonization by soil microbes. Recovery of the microbial biomass is concurrent with recolonization and recovery of plants (Certini, 2005). Leaching of nitrate might also have contributed to the reduced inorganic N after year 1 in these zones as there was little plant recolonization the first two years after fire (Bates and Davies, 2016).

In the other treatment zones, particularly interspaces and all zones of the JAN treatment, where soil heating was lower or nonexistent, there was minimal perennial herbaceous mortality. Plant cover in these areas recovered more quickly and initial

increases in inorganic N were consequently lower and tended to not differ from the control by the second year after treatment. A rapid increase in perennial grass production the second year after burning sagebrush steppe also results in similar levels of inorganic N between burned and control treatments (Davies et al., 2012).

4.2. Phosphorus and potassium

Inorganic P and K increased in all treatment zones at both sites as a result of tree cutting and burning. These increases are characteristic of treatments that remove woody plants in shrublands and forests (Gifford, 1981; Debano et al., 1998; Neary et al., 1999; Rau et al., 2007). Heating of soils from burning mineralizes organic forms of P and K and ash deposition can contribute large amounts of these nutrients following fire (Giovannini et al., 1990; Debano et al., 1998; Neary et al., 1999). This was likely the main pathway for increased P and K in the SEP (all zones at both sites), APR (debris zones, both sites, canopy mound, BLUEBUNCH site), and Jan (debris zone) treatments. Increases in these nutrients in interspaces (Apr, Cut and Jan), canopy (Apr [FESCUE site], Cut, Jan) and cut debris zones were likely from increased mineralization and leaching from juniper leaves (cut trees) and litter (debris and canopy mounds). Typically soil concentrations of these nutrients return to pretreatment levels within a year of two after disturbance (DeBano and Klopatek, 1988; Debano et al., 1998; Rau et al., 2007). In our study, soil inorganic P and K remained elevated above controls in debris and interspace zones in one or more of the treatments through the sixth year after disturbance.

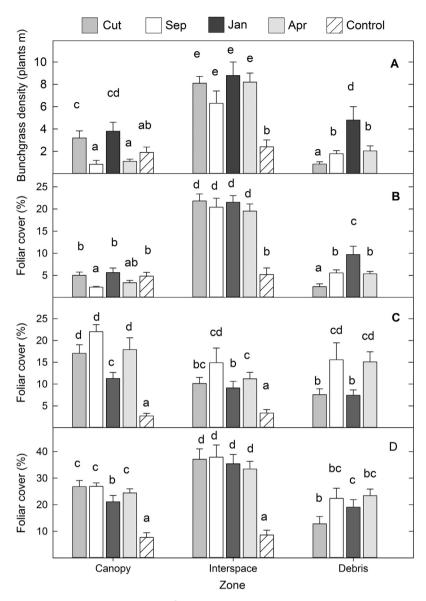


Fig. 7. Post-treatment (2012) (A) perennial bunchgrass density (plants m⁻²) (B) perennial herbaceous cover (%), and (C) annual grasses cover (%) for the various western juniper treatments and control woodland at the BLUEBUNCH site, Steen's Mountain, Oregon. Data are means + one standard error. Means sharing a common lower case letter are not significantly different (*P* > 0.05). Except for Cut and control the other treatment designations correspond to the month burning was applied.

Table 3Herbaceous response variable P-values from mixed model analysis for the western juniper cutting study on Steen's Mountain, southeast Oregon (1991–2016). Values in bold indicate significant treatment (Cut, Control) differences for main (treatment, year) effects and the interaction (treatment × year).

Study site and response variable	Treatment (T)	Year (Y)	Zone (Z)	$T\timesY$	$T\timesZ$	$Y\timesZ$	$T\times Y\times Z$
Bluebunch site							
Bunchgrass density	<0.001	<0.001	0.266	0.004	0.867	<0.001	0.701
Perennial herb. cover	<0.001	<0.001	<0.001	<0.001	0.103	<0.001	0.049
Annual grass cover	<0.001	<0.001	<0.001	0.139	<0.001	0.073	0.114
Fescue site							
Bunchgrass density	<0.001	0.021	<0.001	0.012	<0.001	0.370	0.458
Perennial herb. cover	<0.001	<0.001	0.027	< 0.001	<0.001	0.029	0.819
Annual grass cover	<0.001	0.022	0.113	0.139	0.010	0.997	0.824

4.3. Vegetation recovery and nutrients

Eliminating juniper cover by prescribed fire and cutting often results in increased cover and density of herbaceous and shrub species (Roundy et al., 2014; Bates et al., 2014). In our study, understory plants increased after treating conifers, with recovery

dependent on disturbance severity, residual vegetation, and site characteristics (Bates et al., 2014).

Overall the BLUEBUNCH site was moderately resilient after the various juniper treatments and resistant to annual grass increases. However, these characteristics were modified by zone and disturbance severity. Interspaces recovered best of the three zones as

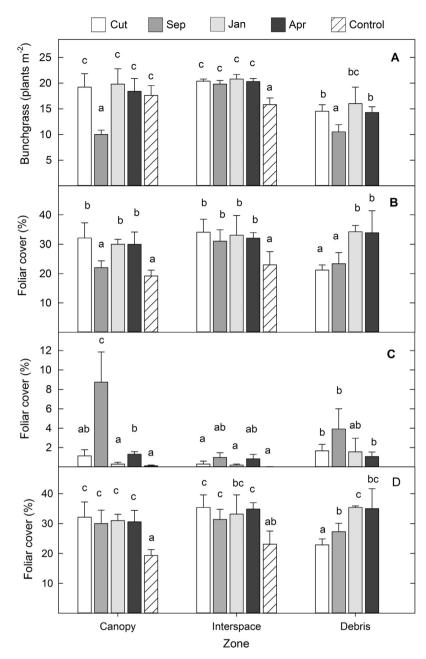


Fig. 8. Post-treatment (2012) (A) perennial bunchgrass density (plants m⁻²) (B) perennial herbaceous cover (%), and (*C*) annual grasses cover (%) for the various western juniper treatments and control woodland at the Fescue site, Steen's Mountain, Oregon. Data are means + one standard error. Means sharing a common lower case letter are not significantly different (*P* > 0.05). Except for Cut and control the other treatment designations correspond to the month burning was applied.

they were dominated by perennial bunchgrasses despite an increase in annual grasses which represented 30-43% of total herb cover. Annual grasses became the dominant component of the understory in canopy and debris zones for all treatments except the debris zone of the JAN treatment. There was a benefit to the JAN treatment as annual grass cover was lower and perennial bunchgrass cover and density were higher than the other debris treatments. In other treatment canopy and debris zones, perennials were reduced and/or unable to establish new plants which permitted annual grasses to dominate, representing between 60% and 96% of total herb cover. These treatment zones exhibited low resistance and resilience in response to conifer treatment. This was especially apparent in the most highly impacted zones (APR and SEP debris and canopy zones). It was in these zones where greater inorganic N levels were measured and there was positive correlation with annual grass cover. Exotic annual grass cover has also been positively correlated to soil inorganic N and P (Blank, 2008; Johnson et al., 2011; Rau et al., 2014). In other woodlands and dry forested systems, decreased herbaceous perennial cover and increased cover of invasive species were associated with greater fuel consumption and fire severity (Armour et al., 1984; Griffis et al., 2001; Brockway et al., 2002; Sabo et al., 2009; Kane et al., 2010). Lower densities or greater gaps between bunchgrasses have also been associated with greater levels of exotic grasses in sagebrush steppe (Davies, 2008; Rau et al., 2014).

Herbaceous composition at the FESCUE site was resilient to juniper treatments with native plants dominating post-treatment even in highly impacted debris and canopy zones of the SEP treatment. Inorganic N content was not as highly correlated to cheatgrass cover at the FESCUE sites as was the BLUEBUNCH site because there was more of a residual native perennial component and perennials continued to recolonize debris and canopy zones

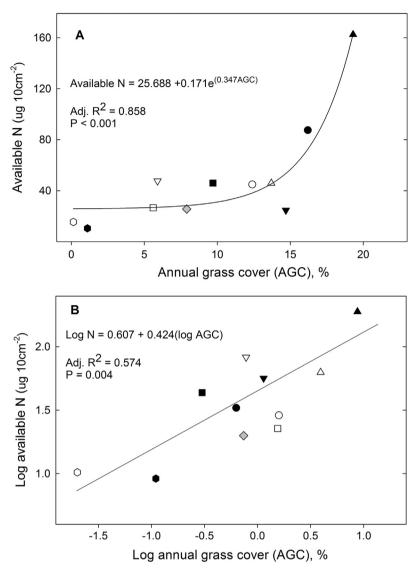


Fig. 9. Relationship between peak invasive annual grass cover and mean inorganic N values (2007–2012) for the various juniper treatments at the (A) BLUEBUNCH site and (B) the FESCUE site, Steen's Mountain, Oregon. Treatments are designated; Cut (∇ , ∇), Sep (\triangle , \triangle), Jan (\blacksquare , \square), Apr (\bigcirc , \bigcirc); treated interspace (\bigcirc); control (\bigcirc , \bigcirc). Symbols in black are for the canopy and symbols in white are for the debris zone.

(Bates and Davies, 2016). Fires in the SEP treatment at the FESCUE site only consumed up to 100-h fuels which contributed to the higher residual perennial composition. When 1000-h fuels are consumed, mortality of perennials increases substantially in this association which may results in spatial to community level dominance by cheatgrass (Bates et al., 2013; Bates and Davies, 2016).

Cutting and leaving trees (CUT) resulted in reduced cover in debris zones at both sites compared to most of the other treatment zones and interspace. The lower herbaceous cover appears to be a result of shading and smothering of plants by cut trees which slows recovery in the debris zones (Bates et al., 2005; Bates and Davies, 2016; Bates and Svejcar, 2009).

5. Conclusions

The management recommendation for treating conifer wood-lands are to remove trees in early to mid-succession stages when shrub-understory composition remains largely intact and desired vegetation recovery is probable, thus, maintaining resistance to invasion by exotic annuals (Maestas et al., 2015; Roundy et al., 2014). As woodlands develop shrub-understory composition is

often depleted and fuel loading increases making woodland treatments somewhat riskier by increasing the potential for weedy annuals to increase or dominate (Bates et al., 2013; Bates and Davies, 2016; Roundy et al., 2014; Stebleton and Bunting, 2009). However, treating late successional woodlands remains necessary because when wildfire does occur in these areas fire severity is often high which may lower site resistance to a point where large scale conversion to weedy annual dominance occurs (Tausch, 1999).

There are many options available for controlling late successional woodlands including cut and pile burning, mastication, and the various cut and burning treatments described in our study. All these treatment options will increase soil nutrient availability and water, thus, keys to successful recovery of sagebrush steppe in late successional woodlands are site selection, timing, and method of slash reduction. On sites with high resistance and resilience characteristics our results indicate that treatment of late successional western juniper woodlands, by cutting and burning slash, were generally effective at promoting recovery of perennial herbaceous composition as long as fire disturbance severity is low to moderate. On sites with lower resistance and resilience characteristics exotic annual grasses are likely to form a major

component of the understory, particularly, when tree and slash burning occurs at higher fire severities. To reduce these impacts on these areas requires slash burning be applied from late fall to early spring to maintain an adequate residual perennial herbaceous component for recovery. If these areas are burned with high fire severity then seeding of perennial grasses and shrubs has proven effective at recovery of sagebrush steppe vegetation (Davies et al., 2014; Sheley and Bates, 2008).

Acknowledgements

Many thanks to the Fred Otley (Otley Brothers Ranch, Diamond, Oregon) for providing land for the study. The fire crew was C. Poulsen, R. Sharp and J. Bates. We recognize the many summer range technicians who assisted in the field and laboratory for the study: C. Archuleta, I. Davies, I. Ellis, K. Haile, A. Herdrich, I. Jackson, I. Louder, K. Mumm, R. O'Connor, E. O'Connor, J. Jackson, J. Price, K. Price, J. Pyrse, K. Ralston, D. Randall, E. Rhodes, B. Smith, J. Svejcar, M. Zabala, T. Zaugg and D. Zvirdin. We thank Dr. T. Svejcar and Dr. R. Blank, and anonymous reviewers for their comments on previous drafts of this manuscript. The research was supported by the Agricultural Research Service and Oregon State Agricultural Experiment Station in Burns, Oregon. The Eastern Oregon Agricultural Research Center is jointly funded by the USDA-Agricultural Research Service and Oregon State Agricultural Experiment Station. USDA-ARS and Oregon State University are equal opportunity providers and employers.

References

- Armour, C.D., Bunting, S.C., Neuenschwander, L.F., 1984. Fire intensity effects on the understory in ponderosa pine forests. J. Range Manage. 3, 44–49.
- Bates, J., Miller, R.F., Svejcar, T.S., 2000. Understory dynamics in cut and uncut western juniper woodlands. J. Range Manage. 53, 119–126.
- Bates, J.D., Svejcar, T., Miller, R.F., 2007. Litter decomposition in cut and uncut western juniper woodlands. J. Arid Environ. 70, 222–236.
- Bates, J., Svejcar, T.S., Miller, R.F., 2002. Effects of juniper cutting on nitrogen mineralization. J. Arid Environ. 51, 221–234.
- Bates, J.D., Miller, R.F., Svejcar, T., 2005. Long-term successional trends following western juniper cutting. Rangel. Ecol. Manage. 58, 533–541.
- Bates, J.D., Miller, R.F., Davies, K.W., 2006. Restoration of quaking aspen woodlands invaded by western juniper. Rangel. Ecol. Manage. 59, 88–97.
- Bates, J.D., Svejcar, T.J., 2009. Herbaceous succession after burning cut western juniper trees. West. North Am. Natural. 69, 9–25.
- Bates, J.D., Davies, K.W., Sharp, R.N., 2013. Sagebrush steppe recovery after fire varies by development phase of *Juniperus occidentalis* woodland. Int. J. Wildland Fire 23, 117–130.
- Bates, J.D., O'Conner, R., Davies, K.W., 2014. Vegetation response to seasonal burning of western juniper slash. Fire Ecol. 10, 27–48.
- Bates, J.D., Davies, K.W., 2016. Seasonal burning of western juniper woodlands and spatial recovery of herbaceous vegetation. For. Ecol. Manage. 361, 117–130.
- Blank, R.R., 2008. Biogeochemistry of plant invasion: a case study with downy brome (*Bromus tectorum*). Invasive Plant Sci. Manage. 1, 226–238.
- Blank, R.R., Allen, F., Young, J.A., 1994. Extractable anions in soils following wildfire in a sagebrush-grass community. Soil Sci. Soc. Am. J. 58, 564–570.
- Brockway, D.G., Gatewood, R.G., Paris, R.B., 2002. Restoring grassland savannas from degraded pinyon-juniper woodlands: effects of mechanical overstory reduction and slash treatment alternatives. J. Environ. Manage. 64, 179–197.
- Chambers, J.C., Roundy, B.A., Blank, R.R., Meyer, S.E., Whittaker, A., 2007. What makes great basin sagebrush ecosystems invasible by *Bromus tectorum*? Ecol. Monographs 77, 117–145.
- Chambers, J.C., Bradley, B.A., D'Antonio, C., Germino, M.J., Grace, J.B., Hardegree, S.P., Miller, R.F., Board, D.I., Pyke, D.A., Roundy, B.A., Grace, J.B., Schupp, E.W., Tausch, R.J., 2014. Resilience and resistance of sagebrush ecosystems: implications for state and transition models and management treatments. Rangel. Ecol. Manage. 67, 440–454
- Certini, G., 2005. Effects of fire on properties of forest soils: a review. Oecologia 143, 1–10
- Condon, L., Weisberg, P.J., Chambers, J.C., 2011. Abiotic and biotic influences on Bromus tectorum invasion and Artemisia tridentata recovery after fire. Int. J. Wildland Fire 20, 597–604.
- Covington, W.W., Debano, L.F., Huntsberger, T.G., 1991. Soil nitrogen changes associated with slash pile burning in pinyon-juniper woodlands. For. Sci. 37, 347–355
- Davidson, E.A., Hart, S.C., Firestone, M.K., 1992. Internal cycling of nitrate in soils of a mature coniferous forest. Ecology 73, 1148–1156.

- Davies, K.W., 2008. Medusahead dispersal and establishment in sagebrush steppe plant communities. Rangel. Ecol. Manage. 61, 110–115.
- Davies, K.W., Bates, J.D., 2017. Restoring big sagebrush after controlling encroaching western juniper with fire: aspect and subspecies effects. Restoration Ecol. 25, 33–41.
- Davies, K.W., Bates, J.D., Miller, R.F., 2007. Short-term effects of burning Wyoming big sagebrush steppe in southeast Oregon. Range. Ecol. Manage. 60, 515–522.
- Davies, K.W., Bates, J.D., Nafus, A.M., 2012. Comparing burning and mowing treatments in mountain sagebrush steppe. Environ. Manage. 50, 451–461.
- Davies, K.W., Bates, J.D., Madsen, M.D., Nafus, A.M., 2014. Restoration of mountain big sagebrush steppe following prescribed burning to control western juniper. Environ. Manage. 53, 1015–1022.
- DeBano, L.F., Klopatek, J., 1988. Phosphorus dynamics of pinyon-Juniper soils following simulated burning. Soil Sci. Soc. Am. J. 52, 27–277.
- DeBano, L.F., Neary, D.G., Ffolliott, P.F., 1998. Fire Effects on Ecosystems. John Wiley & Sons, New York.
- Doescher, P.S., Eddleman, L.E., Vaitkus, M.R., 1987. Evaluation of soil nutrients, pH, and organic matter in rangelands dominated by western juniper. Northwest Sci. 61, 97–102.
- Evans, R.A., Young, J.A., 1985. Plant succession following control of western juniper (*Juniperus occidentalis*) with picloram. Weed Sci. 33, 63–68.
- Gifford, G.F., 1981. Impact of buirning pinyon-juniper debris on select soil properties. J. Range Manage. 34, 357–359.
- Giovannini, G., Lucchesi, S., Giachetti, M., 1990. Beneficial and detrimental effects of heating on soil quality. In: Goldammer, J.G., Jenkins, M.J. (Eds.), Fire and Ecosystem Dynamics: Mediterranean and Northern Perspective. SPB Academic Publishing, Hague, The Netherlands, pp. 95–102.
- Griffis, K.L., Crawford, J.A., Wagner, M.R., Moir, W.H., 2001. Understory response to management treatments in northern Arizona ponderosa pine forest. For. Ecol. Manage. 146, 239–245.
- Hart, S.C., Firestone, M.K., Paul, E.A., 1992. Decomposition and nutrient dynamics of ponderosa pine needles in a Mediterranean-type climate. Can. J. For. Res. 22, 306–314.
- Johnson, B.G., Johnson, D.W., Chambers, J.C., Blank, R.R., 2011. Fire effects on the mobilization and uptake of nitrogen by cheatgrass (*Bromus tectorum L.*). Plant Soil 341, 437–445.
- Jowkin, V., Schoenau, J.J., 1998. Impact of tillage and landscape position on nitrogen availability and yield of spring wheat in the Brown soil zone in southwestern Saskatchewan. Can. J. Soil Sci. 78, 563–572.
- Kane, J.M., Varner, J.M., Knapp, E.E., Powers, R.F., 2010. Understory vegetation response to mechanical mastication and other fuels treatments in a ponderosa pine forest. Appl. Veg. Sci. 13, 207–220.
- Klemmedson, J.O., Meier, C.E., Campbell, R.E., 1985. Needle decomposition and nutrient release in ponderosa pine ecosystems. For. Sci. 31, 647–660.
- Klemmedson, J.O., Tiedemann, A.R., 2000. Influence of western juniper development on distribution of soil and organic layer nutrients. Northwest Sci. 74, 1–11.
- Koniak, S., 1985. Succession in pinyon-juniper woodlands following wildfire in the Great Basin. Great Basin Natural. 45, 556–566.
- Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., 1996. SAS System for Mixed Models. SAS Institute, Cary, NC.
- Maestas, J.D., Roundy, B.A., Bates, J.D., 2015. Conifer Removal in the Sagebrush Steppe: The why, when, where, and how. Great Basin Fact Sheet Series, no. 4, Sage-Grouse Initiative. https://www.sagegrouseinitiative.com/conifer-removal-in-the-sagebrush-steppe/.
- Miller, R.F., Bates, J.D., Svejcar, T.J., Pierson, F.B., Eddleman, L.E., 2005. Biology, ecology, and management of western juniper. Oregon State University Agricultural Experiment Station Technical Bulletin 152. Corvallis, Oregon, IISA
- Miller, R.F., Knick, S.T., Pyke, D.A., Meinke, C.W., Hanser, S.E., Wisdom, M.J., Hild, A.L. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. In: S.T. Knick and J.W. Connelly (EDS.). Greater Sage-Grouse: Ecology and Conservation of Landscape Species and Its Habitats. University of California Press, Berkeley, CA, USA, pp. 146–184.
- Miller, R.F., Ratchford, J., Roundy, B.A., Tausch, R.J., Hulet, A., Chambers, J., 2014. Response of conifer-encroached shrublands in the Great Basin to prescribed fire and mechanical treatments. Rangel. Ecol. Manage. 67, 468–481.
- Neary, D.G., Klopatek, C.C., DeBano, L.F., Ffolliot, P.F., 1999. Fire effects on below ground sustainability: a review and synthesis. Forest Ecol. Manage. 122, 51–71.
- NRCS, 2006. Soil Survey of Harney County Area. Oregon. USDA Natural Resource Conservation Service, Washington, District of Columbia, USA.
- NRCS. 2017. Ecological site description. USDA Natural Resource Conservation Service. Washington, District of Columbia, USA. Last accessed March, 2017. https://esis.sc.egov.usda.gov/Welcome/pgReportLocation.aspx?type=ESD.
- Omernik, J.M., 1987. Ecoregions of the conterminous United States. Ann. Assoc. Am. Geograph. 77, 118–125.
- Peterson, R.G., 1985. Design and Analysis of Experiments. Marcel Dekker Inc., New York, p. 429.
- Pierson, F.B., Williams, C.J., Kormos, P.R., Hardegree, S., Clark, P.E., Rau, B.M., 2010. Hydrologic vulnerability of sagebrush steppe following pinyon and juniper encroachment. Rangel. Ecol. Manage 63, 614–629.
- Rau, B.M., Blank, R.R., Chambers, J.C., Johnson, D.W., 2007. Prescribed fire and time: Soil extractable nitrogen and phosphorus dynamics in a Great Basin sagebrush ecosystem. J. Arid Environ. 71, 362–375.
- Rau, B.M., Chambers, J.C., Blank, R.R., Johnson, D.W., 2008. Prescribed fire, soil, and plants: burn effects and interactions in the central Great Basin. Rangel. Ecol. Manage. 61, 169–181.

- Rau, B.M., Chambers, J.C., Pyke, D.A., Roundy, B.A., Schupp, E.W., Doescher, P., Caldwell, T.G., 2014. Soil resources influence vegetation and response to fire and fire-surrogate treatments in sagebrush-steppe ecosystems. Rangel. Ecol. Manage. 67, 506–521.
- Romme, W.H., Allen, C.D., Bailey, J.D., Baker, W.L., Bestelmeyer, B.T., Brown, P.M., Eisenhart, K.S., Floyd, M.L., Huffman, D.W., Jacobs, B.F., Miller, R.F., Muldavin, E. H., Swetnam, T.W., Tausch, R.J., Weisberg, P.J., 2009. Historical and Modern Disturbance Regimes, Stand Structures, and Landscape Dynamics in Piñon: Juniper Vegetation of the Western United States. Rangel. Ecol. Manage. 62, 203– 222.
- Roundy, B.A., Young, K., Cline, N., Hulet, A., Miller, R.F., Tausch, R., Chambers, J.C., Rau, B., 2014. Pinon-juniper reduction increases soil water availability of the resource growth pool. Rangel. Ecol. Manage. 67, 495–505.
- Sabo, K.E., Hull-Sieg, C., Hart, S.C., Bailey, J.D., 2009. The role of disturbance severity and canopy closure on standing crop of understory plant species in ponderosa pine stands in northern Arizona, USA. For. Ecol. Manage. 257, 1656–1662.

- Sheley, R., Bates, J.D., 2008. Restoring western juniper infested rangeland after prescribed fire. Weed Sci. 56, 469–476.
- Stebleton, A., Bunting, S., 2009. Guide for quantifying fuels in sagebrush steppe and juniper woodlands of the Great Basin. Technical Note 430. Bureau of Land Manage., Denver, CO. 81 p.
- Stephens, S.L., McIver, J.D., Ralph, E.J., Boerner, R.E.J., Fettig, C.J., Fontaine, J.B., Hartsough, B.R., Kennedy, P.I., Schwilk, D.W., 2012. The effects of forest fuel-reduction treatments in the United States. Bioscience 60, 549–560.
- Tausch, R.J., 1999. Transitions and thresholds: influences and implications for management in pinyon and Utah juniper woodlands. In: Monsen, S.B., Stevens, R., Tausch, R.J., Miller, R., Goodrich, S. [Eds.], Proceedings: Ecology and Management of Pinyon-Juniper Communities Within the Interior West. USDA For. Ser. Proceed. RMRS-P-9. Rocky Mountain Res. Sta., Ogden, Utah, USA. p. 61– 65.
- Yavitt, J.B., Fahey, T.J., 1986. Litter decay and leaching from the forest floor in *Pinus contorta* (Lodgepole pine) ecosystems. J. Ecol. 74, 525–545.