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Quaking aspen woodland after conifer control: Tree and shrub dynamics[☆]

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ABSTRACT

Western juniper (*Juniperus occidentalis* spp. *occidentalis* Hook.) woodlands are replacing many lower elevation (< 2100 m) quaking aspen (*Populus tremuloides* Michx.) stands in the northern Great Basin. We evaluated two juniper removal treatments (Fall, Spring) to restore aspen woodlands in southeast Oregon, spanning a 15-year period. The Fall treatment involved cutting 1/3 of the juniper followed by a high severity broadcast burn one year later in October 2001. The Spring treatment involved cutting 2/3 of the juniper followed by a low severity broadcast burn 18 months later in April 2002. The cut trees increased the amount of dry fuels to carry fire through stands. We tested the effectiveness of treatments at removing juniper from seedlings to mature trees, assessed aspen ramet recruitment and development, and evaluated recovery of the shrub layer. In the Fall treatment, burning eliminated all remaining juniper trees and saplings, stimulated an 8-fold increase in aspen density (16,000 ha^{-1}) and increased aspen cover 6-fold compared to the untreated controls. After 15 years, aspen density in the Spring treatment was about 1/3 of the Fall treatment, however, aspen cover did not differ from the Fall treatment. Because spring burning was less effective at removing juniper, leaving about 20% of the mature trees and 50% of the saplings, retreatment of conifers will be necessary to maintain the aspen community. In the Fall treatment, juniper began establishing within 15 years after conifer control indicating re-treatment might be necessary earlier than expected. Total shrub cover and density in the Spring treatment was greater than the control and Fall treatments. Cover and density of sprouting shrub species, particularly western snowberry (*Symphoricarpus oreophilus* Gray), increased and were greater in the Spring treatments than the Fall treatment where they had declined. Shrubs that increased in the Fall treatment were species where seed germination is enhanced by fire, especially snowbrush (*Ceanothus velutinus* Douglas ex Hook) and wax currant (*Ribes cereum* Dougl.). If an objective is to maintain or increase native understories the Spring treatment was more effective than the Fall treatment for recovering the shrub layer.

1. Introduction

Quaking aspen (*Populus tremuloides* Michx.) woodlands are important plant communities in the interior mountains of the western United States. Aspen woodlands provide habitat for many wildlife species (Maser et al., 1984; Kuhn et al., 2011) and may contain a high diversity of understory shrub and herbaceous species (Bartos and Mueggler, 1981, 1982; McCullough et al., 2013). Aspen woodlands are of two main types, seral and stable stands. In seral aspen woodlands, disturbance, especially fire, is important for maintaining stands particularly to prevent replacement by conifers (Strand et al., 2009; Krasnow et al., 2012; Shinneman et al., 2013; Krasnow and Stephens, 2015). Stable aspen stands are maintained by continual tree recruitment by root sprouting, although stand maintenance may be enhanced by overstory mortality from drought, pathogens, and aging (Shinneman et al., 2013).

Seral aspen woodlands have declined due to lack of fire disturbance and encroachment by conifers (Bartos and Campbell, 1998; Wall et al., 2001; Kulakowski et al., 2013; Shinneman et al., 2013; Worrall et al., 2013), excessive browsing by native ungulates (Gruell, 1979; Bartos et al., 1994; Kay, 1995), and dieback of stands brought on by recent large-scale episodic droughts (Worrall et al., 2013). The decline of seral aspen stands has been well documented in the Rocky Mountain States (Bartos and Campbell, 1998) and the Great Basin (DiOrio et al., 2004, Miller and Rose, 1995, Wall et al., 2001). In the northern Great Basin there has been significant encroachment of western juniper (*Juniperus occidentalis* spp. *occidentalis* Hook.) into aspen woodlands below 2120 m (Wall et al., 2001). The recovery of aspen woodlands using prescribed fire can be challenging because of the limited periods when fuel moisture and weather conditions are favorable for burning (Jones and DeByle, 1985a). In addition, juniper dominance may reduce understory cover and biomass and limit abilities for fire to carry in plant

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communities (Miller et al., 2005; Roundy et al., 2014a).

We evaluated aspen, juniper and shrub responses over 15 years (2002–2016) after prescribed fire treatments (2001) were applied to control western juniper in upland aspen stands in southeast Oregon. Vegetation dynamics at these sites were initially evaluated for 3 years post-treatment (Bates et al., 2006). This evaluation indicated that partial juniper cutting followed by fall (FALL) and spring (SPRING) fire treatments were effective at increasing cover and density of aspen and cover of herbaceous understories compared to untreated woodlands. High severity fall burning was more effective at killing junipers of all age classes and increasing aspen than low severity spring burning.

The objectives of our study were to: (1) compare recovery of aspen and shrub density and cover in Fall and Spring treatments to untreated woodlands; and (2) evaluate cover and density response of western juniper to treatment. After 15 years, we hypothesized aspen and shrub cover and density would have continued to increase and be greater in Fall and Spring treatments compared to untreated woodlands as there remained large areas of open space for further expansion of aspen and shrubs three years after treatments. We hypothesized that juniper cover and density would be greater in Spring than Fall treatments, because many small trees survived the spring burn (Bates et al., 2006).

2. Materials and methods

2.1. Site description

The study sites were located along a 4 km stretch of Kiger Creek Canyon on Steens Mountain, Harney County, Oregon (Geo URI 42.829465-118.555172). Sites were on private and public (BLM –Bureau of Land management) property. Aspen stands were scattered along toe slopes above the riparian zone and on concave slopes in the uplands from 1645 to 1930 m elevation. Aspen plots averaged 0.6 ha, and ranged from 0.2 to 2-ha. Adjacent plant communities were mountain big sagebrush (*Artemisia tridentata* spp. *vaseyana* (Nutt.) Beetle & A. Young) grassland and curl-leaf mountain mahogany (*Cercocarpus ledifolius* (Nutt.) Torr. & Gray) thickets. Aspen stands were dominated by western juniper. Juniper began establishing in these stands in the 1860's and juniper that established prior to 1940 dominated the overstory (Miller and Bates, 2001). Juniper woodlands were rated as being in late to closed phases and all aspen stands were fragmented and in decline using descriptions by Bartos and Campbell (1998), Miller and Rose (1995), and Wall et al. (2001). These stands are characterized by tree cover dominated by conifers, aspen recruitment and cover are low and fragmented, and standing dead and fallen large aspen trees are prevalent.

The Ecological Site Description for the sites are ASPEN 16-35 PZ (NRCS, 2017). The aspen stands are of the seral montane aspen/conifer type (Shepperd et al., 2006; Shinneman et al., 2013). Soils were mainly the Hackwood series, with soil textures ranging from gravelly loams to loams, extending to depths of 100 cm or deeper and underlain by fractured basalt (NRCS, 2006). The closest weather station is the Fish Lake SNOTEL (Snow telemetry) site, 9–13 km southeast and 400–700 m higher in elevation than the study sites. Water year precipitation (October 1 - September. 30) at the SNOTEL site has averaged 1049 mm the past 17 years (Fig. 1). Most aspen areas in the western United States receive at least 380 mm of precipitation annually or are able to access addition water from snow drifts, subsurface flow, and elevated water tables (Jones and DeByle, 1985b).

Western snowberry (*Symphoricarpus oreophilus* Gray) and wax currant (*Ribes cereum* Dougl.) were the most common shrubs. Other shrubs that were minor components of the shrub layer, included black elderberry (*Sambucus racemosa* L.), rubber and green rabbitbrush (*Ericameria nauseosa* (Pall. ex Pursh) G.L. Nesom & Baird; *Chrysothamnus viscidiflorus* (Hook.) Nutt.), Wood's rose (*Rosa woodsii* Lindl.), and western serviceberry (*Amelanchier alnifolia* Nutt.). Occasional trees included curl-leaf mountain mahogany and common chokecherry (*Prunus virginiana* L.). Species identification used nomenclature from USDA Plants Database (2017).

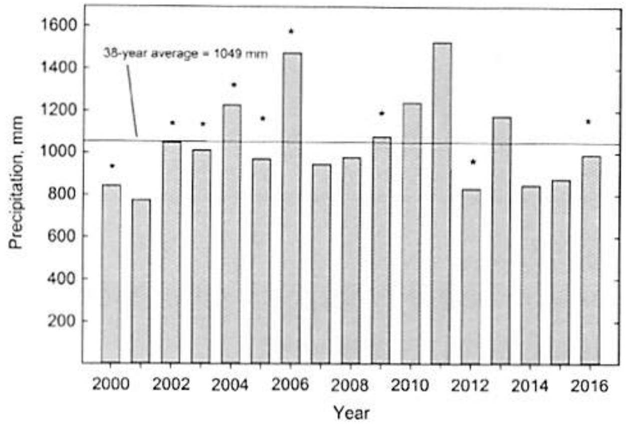

Fig. 1. Water year precipitation (Oct 1-Sept 30), 2000–2016, and 38 year average from the Fish Creek Snotel, Oregon, (42°43′N; 118°38′ min W; Elevation: 2335 m). Asterisks indicate years when aspen plots were measured.

2.2. Study design and burn applications

We used a randomized block design (Peterson, 1985). Ten, 0.60-ha blocks were established in aspen stands in May 2000. A block consisted of three plots: an untreated woodland (control), juniper cutting followed by fall prescribed fire (Fall), and juniper cutting followed by early spring prescribed fire (Spring). Buffer strips to separate treatments resulted in treatments plots of about 0.13 ha. Livestock were excluded from the area two years prior and the first three years after conifer treatment.

Cutting involved felling mature (dominant and subcanopy) juniper trees, evenly distributed through the stand. Junipers were cut in winter and spring 2001 and allowed to dry prior to burning. An average of 106 (range 55–175) juniper trees were cut in Fall plots, which represented approximately 1/3 of the dominant and subcanopy juniper. An average of 232 (range 140–372) juniper trees were cut in Spring plots, representing approximately 2/3 of the dominant and subcanopy juniper. The cut trees served to increase the level of dry fuels (0–4 m in height) to carry fire through stands. Fall burning was applied in October 2001 by personnel of the Bureau of Land Management (BLM), Burns District, Oregon. The prescribed fire technique used was a spot head fire using helicopter-dropped delayed action ignition devices (DIADS). DIADS were chemically injected ping-pongs. To prevent dropping of ignition devices in Control and Spring treatments these areas were marked with strips of butcher block paper, located 100–200 m from plots requiring protection. Spring burning were head fires, applied in late April 2002 using drip torches containing a 50:50 mixture of gasoline and diesel. Fuel continuity of the cut junipers was sufficient for fire to carry with minimal re-ignition.

Fire severity was estimated by adapting severity categories developed by Bartos et al. (1994) for evaluating plant community response to fire (Bates et al., 2006). Greater litter and fuel moisture content and higher relative humidity during spring burning resulted in a less severe fire. About 55% of remaining live juniper and almost 76% of the adult aspen stems were killed by the fire treatment. Fire severity in the Spring treatment was rated as having no impact to the understory and having moderate impact to remaining live juniper. In the Fall treatment, all downed juniper material but the trunks were fully consumed. Litter and understory consumption was > 95% and juniper and aspen kill were 99% and 100%, respectively. Fire severity in the Fall treatment was high (Bates et al., 2006).

2.3. Vegetation measurements

Pre-treatment measurements were made in July 2000. Post-treatment measurements were made in June 2002–2006, 2009, 2012, and 2016. In each plot, three permanent 40-m transects were established with transects spaced 10-m apart. Juniper was separated into three size classes: dominants (trees equal to or greater than 75% of stand height), sub-canopy (> 1-m height up to 75% of stand height), and saplings (≤1 m in height). Aspen was also separated into two classes: trees (> 5 cm DBH) and ramets (≤5 cm DBH). Tree and shrub canopy cover were estimated by line intercept along the 40-m transects. Tree densities were estimated by counting all rooted individuals within three, 6 × 40 m belt transects. Densities of aspen ramets, sapling junipers, and shrub species were estimated by counting all rooted individuals within three, 2 × 40 m belt transects. Herbivory was estimated by counting browsed aspen leaders in the 2 × 40 m belt transects.

2.4. Statistical analysis

The study sites were included in a prescribed fire project encompassing 2850 ha. Burn treatments were applied individually. Because of fuel characteristics in the burn area, weather, and method of ignition, there was the potential that some Spring and Control plots would be unintentionally burned during fall prescribed fire. Of the 10 blocks, Spring and Control plots in 5 of the blocks (10 plots total) were entirely or partially disturbed during the Fall treatment and were excluded from the analysis. A repeated measures mixed model analysis (PROC MIX, SAS Institute, Release 9.3 Edition, 2012, Cary, North Carolina) for a randomized block design (df = 4) was used to assess the influence of year (df = 6), treatment (df = 2), and the year by treatment interaction (df = 120 and error (df = 59) cover and density of juniper (dominant and subcanopy, saplings), aspen (ramets, trees) and other tree and shrub species. An auto-regressive order-one covariance structure was used because it provided the best model fit (Littell et al., 1996). Significance of all tests was set at $P < .05$. Because of the strong year effect, years were also analyzed separately using a generalized model (Proc GLM, SAS Institute) to simplify presentation of the results and to assist in explaining interactions. Treatment means were separated using Fisher's protected LSD.

3. Results

3.1. Aspen

Aspen cover and density did not differ among treatments prior to cutting and burning. The Fall and Spring treatments resulted in large, but variable, increases in aspen cover and ramet density compared to the controls (Fig. 2). Thus, treatment by year interaction was significant for aspen cover and density of aspen trees and ramets (Table 1).

The first growing season after burning, aspen cover (ramets and trees) in Spring and Fall treatments declined by 60–80% from pre-burn levels, respectively (Fig. 2A). Aspen cover recovered and by the second year post-treatment (2003) cover in Fall and Spring treatments was similar to the Control. Aspen cover in Fall and Spring treatments increased over time and exceeded the Control by the 5th year post-treatment (2006). Cover of aspen has not differed between Fall and Spring treatments since 2012, the 11th year after treatment. Aspen cover in the control decreased over time by 50%, with most of the decline occurring the past decade.

All aspen trees were top-killed by fire in the Fall treatment. In the Spring treatment about 50% of the aspen trees survived the fire treatment (Fig. 2B). Tree density increased in Fall and Spring treatments and were not different than the Control 5 years post-treatment (2006). Aspen tree density continued to increase in Fall and Spring treatments and by 2016, tree density in the Fall treatment was nearly double the Control. In the Control, aspen tree density declined from about 700 trees ha^{-1} in 2000 to about 430 trees ha^{-1} in 2016, a drop of 40%.

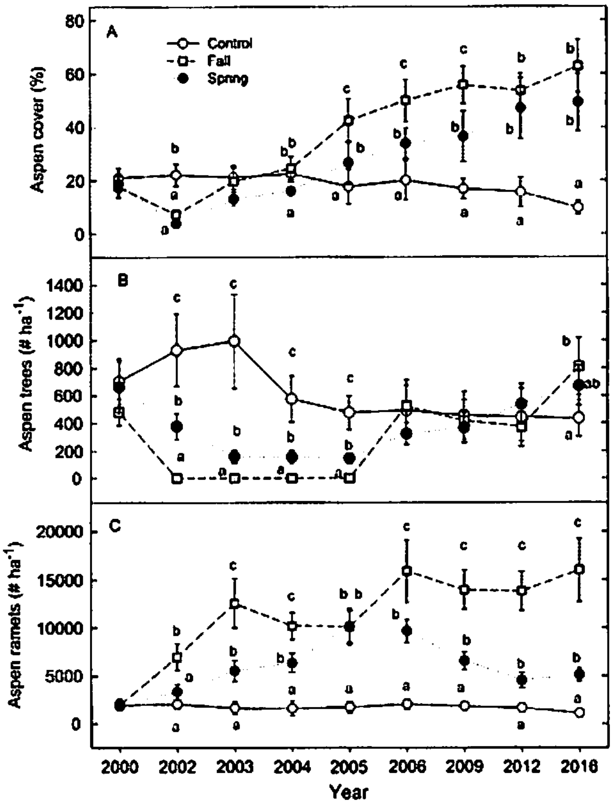

Fig. 2. Aspen (A) cover (%), (B) tree density (trees ha^{-1}), and (C) ramet density (ramets ha^{-1}), for Control, Fall, and Spring treatments, Kiger Canyon, Oregon, 2000–2016. Data are means ± one standard error. Means sharing a common lower case letter within year are not significantly different ($P > .05$).

Aspen ramet density was greater in the Fall treatment, in all post-treatment years (aside from 2005) than the Spring and Control treatments (Fig. 2C). Ramet density in the Fall treatment averaged about 16,000 stems ha^{-1} between 2006 and 2016. Ramet density in the Spring treatment peaked in 2005 at almost 10,000 stems ha^{-1} after which density has steadily declined to just over 5000 stems ha^{-1} in 2016. Aspen ramet density in the Control was less than both treatments by the 2nd year post treatment, averaging less than 1750 stems ha^{-1} and, in recent years, ramet density has trended downward. There was no noticeable ungulate browsing of aspen during the study.

3.2. Western juniper

Juniper cover and density did not differ among treatments prior to cutting and burning. The Fall and Spring treatments resulted in large reductions in juniper cover and density compared to the controls (Fig. 3). Thus, treatment by year interactions were significant for juniper cover and density of all juniper size classes (Table 1). In the Fall treatment, juniper cover was reduced to zero and did not increase until 15 years after treatment (2016), though cover was below 1% (Fig. 3A). All dominant and subcanopy juniper were killed (Fig. 3B) and the density of juniper saplings were reduced by nearly 100% in the Fall treatment (Fig. 3C). Juniper tree density remained less than the Control and Spring treatment during the study. By 2016 juniper tree density (> 1 m tall) was 50 trees ha^{-1} in the Fall treatment, about 15 times less than the Control. In the Fall treatment, juniper began reestablishing about 8 years after treatment (2009) and by 2016 juniper sapling density was not different than the Spring treatment.

In the Spring treatment, juniper cover was reduced by 90% the first year after treatment (Fig. 3A). The Spring treatment was effective at

Table 1

Tree and shrub response variable P-values from mixed model analysis for the aspen Recovery study, Steens Mountain, southeast Oregon (2000–2016). Values in bold indicate significant treatment (Control, Fall, Spring) differences for main (treatment, year) effects and the interaction (treatment x year).

Response variable	Treatment	Year	Treatment × year
Tree cover			
Western juniper	**< 0.001**	**0.040**	**0.008**
Quaking aspen	**0.006**	**< 0.001**	**< 0.001**
Curl-leaf mountain-mahogany	0.491	0.700	0.389
Common chokecherry	0.053	0.345	0.347
Tree density			
Western juniper sapling	**< 0.001**	**< 0.001**	**0.048**
Western juniper tree	**< 0.001**	**< 0.001**	**< 0.001**
Quaking aspen ramet	**0.002**	**< 0.001**	**0.002**
Quaking aspen tree	**0.013**	**0.036**	**< 0.001**
Curl-leaf mahogany	**0.012**	**0.016**	0.238
Common chokecherry	0.464	0.214	0.759
Shrub cover			
Big sagebrush	0.693	**0.032**	**0.014**
Snowbrush	**0.012**	0.096	0.137
Gray rabbitbrush	0.249	0.086	0.816
Green rabbitbrush	**0.026**	**0.021**	**0.005**
Black elderberry	0.061	0.670	0.654
Western snowberry	**< 0.001**	0.408	**0.019**
Wax currant	0.051	**0.046**	0.446
Wood's rose	0.053	**0.009**	0.594
Total shrub	**0.020**	**0.012**	**0.008**
Shrub density			
Big sagebrush	0.079	**0.011**	0.137
Snowbrush	0.067	0.474	**0.039**
Gray rabbitbrush	0.464	0.184	0.347
Green rabbitbrush	**< 0.001**	**< 0.001**	**0.042**
Black elderberry	**0.016**	0.535	0.675
Western snowberry	**< 0.001**	0.059	0.501
Wax currant	**0.045**	**< 0.001**	0.191
Wood's rose	**< 0.001**	**0.033**	0.782
Total shrub	**< 0.001**	0.076	**0.029**

killing juniper dominants (80% removed), but was less effective on subcanopy trees and saplings. In the Spring treatment, about 33% of the subcanopy juniper and 45% of the saplings survived the cut and burn treatment (Fig. 3C). Juniper cover and tree density increased over time in the Spring, most noticeably eight (2009) to 15 years (2016) after treatment. In the Spring treatment, tree cover was about 20% and tree density was about 50% of the Control, respectively, in 2016. Tree density in the Spring treatment recovered to pre-treatment levels by 2016, although most of these trees were small, not exceeding 2-m in height. Juniper cover in the Control increased during the study from about 48% to 55%. Juniper tree density nearly doubled because saplings were beginning to exceed 1-m in height.

3.3. Other trees

Cover and density of common chokecherry did not differ among treatments (Fig. 4; Table 1) and cover of curl-leaf mountain mahogany did not differ among treatments (Table 1). Density of mahogany was greatest in the Spring and lowest in the Fall treatment (Fig. 4).

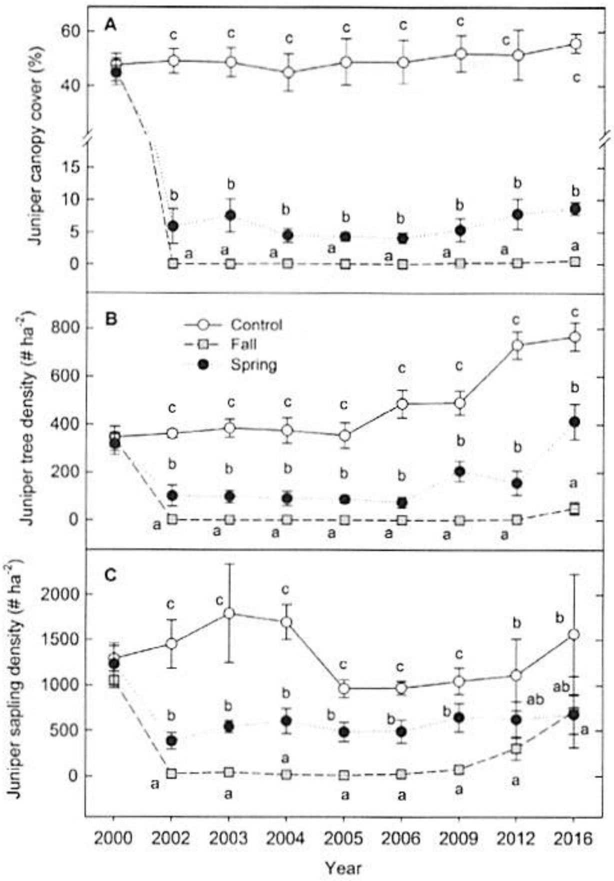

Fig. 3. Juniper (A) canopy cover (%), (B) tree density (dominants and subcanopy; trees ha^{-1}), and (C) sapling density (< 1 m tall; sapling ha^{-1}), for Control, Fall, and Spring treatments, Kiger Canyon, Oregon, 2000–2016. Data are means ± one standard error. Means sharing a common lower case letter within year are not significantly different ($P > .05$).

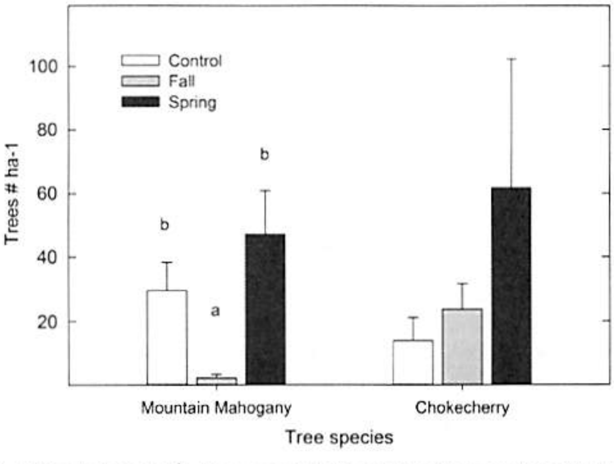

Fig. 4. Density (trees ha^{-1}) of common chokecherry and curl-leaf mountain mahogany for Control, Fall, and Spring treatments in 2016, Kiger Canyon, Oregon. Prior to treatment there were no differences among treatments in shrub species densities. Data are means + one standard error. Means sharing a common lower case letter within year are not significantly different ($P > .05$).

3.4. Shrubs

Total shrub and species cover and densities did not differ among treatments prior to cutting and burning (Fig. 5; Table 1). Shrub cover was largely eliminated in the Fall treatment and was less than the Spring treatment in most years following the fires (Fig. 5A). The Fall treatment was less than the Control until 2012, 11 years after juniper treatment. Shrub cover was similar between the Spring and the Control until 2016 when the Spring treatment surpassed the Control. Thus, treatment by year interaction was significant for total shrub cover (Table 1). Western snowberry comprised the bulk of shrub cover and post-treatment dynamics mirrored total shrub cover (Fig. 5B). Western snowberry comprised 50–75% of total shrub cover in the Spring treatment. After treatment, snowberry cover was 6–8 times greater in the Spring than the Fall treatment. In 2016, snowberry cover was 2.5-fold greater in the Spring than the Control. Cover of other shrubs were

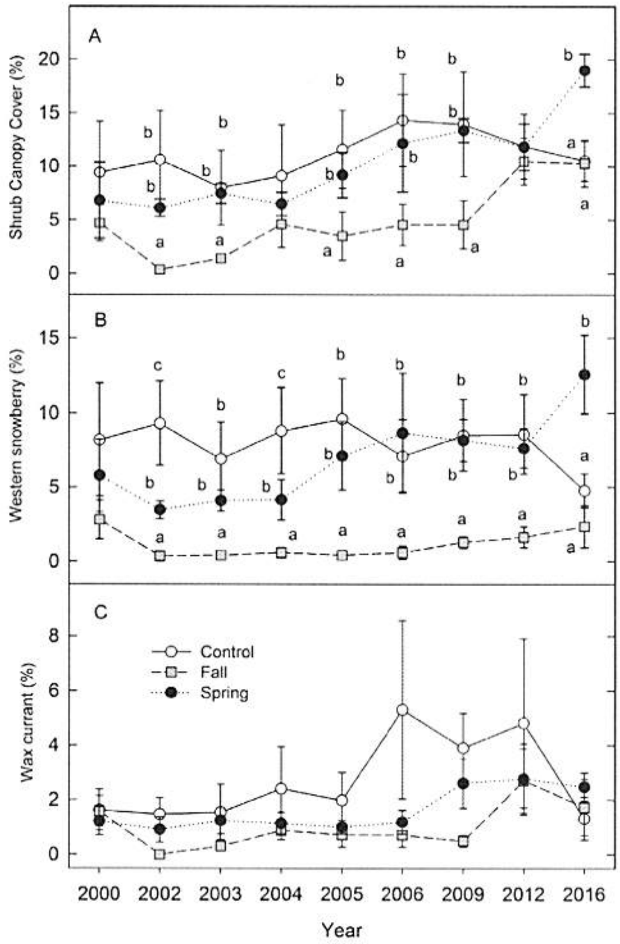

Fig. 5. Canopy cover (%) of (A) total shrub, (B) western snowberry, and (C) wax currant for Control, Fall, and Spring treatments, Kiger Canyon, Oregon, 2000–2016. Data are means ± one standard error. Means sharing a common lower case letter within year are not significantly different ($P > .05$).

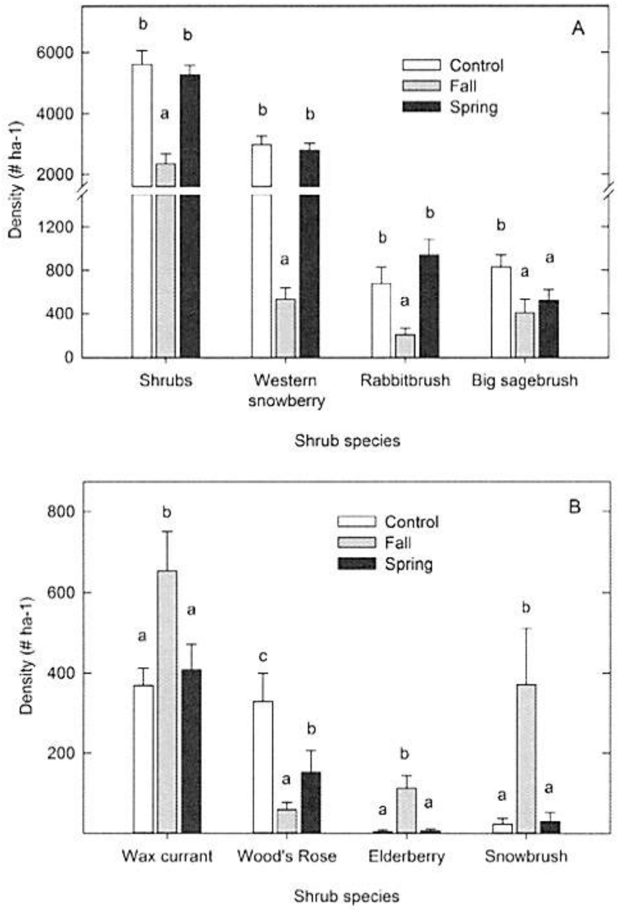

Fig. 6. Density (shrubs ha^{-1}) of (A) total shrub, western snowberry, rabbitbrush and big sagebrush; and (B) wax currant, Wood's rose, black elderberry and snow brush, for Control, Fall, and Spring treatments in 2016, Kiger Canyon, Oregon. Prior to treatment there were no differences among treatments in shrub species densities. Data are means + one standard error. Means sharing a common lower case letter within year are not significantly different ($P > .05$).

generally less than 1 or 2% or highly variable among treatment plots generating few significant treatment or year effects. Green rabbitbrush cover was highest in the Spring treatment (Table 1). Cover of rabbitbrush, Wood's rose, and wax current (Fig. 5C) varied significantly among years (Table 1). Cover of these species tended to be greater between 2006 and 2012 than other years. Snowbrush (*Ceanothus velutinus* Douglas ex Hook) cover was about 50% greater in the Fall (1.4 + 0.4%) than Control and Spring treatments (Table 1).

Total shrub and shrub species densities exhibited patterns similar to shrub cover results (Fig. 6A and B; Table 1). Western snowberry density was consistently 4 to 6-fold greater in Control and Spring treatments than the Fall treatment after juniper reduction (Fig. 6A). In the last several measurement years (2009–2016), densities of other shrub species appeared to be separating into distinct treatment responses. In 2016, densities of rabbitbrush and Wood's rose were 2- to 6-fold greater in the Control and Spring than the Fall treatment (Fig. 6A and B). Densities of elderberry, snowbrush, and wax currant were 1.5 to 20-fold greater in the Fall than Spring and Control treatments. These current differences in density may, in the future, manifest into cover differences for the various shrub species.

4. Discussion

4.1. Aspen response

The high fire severity Fall treatment was more effective at stimulating aspen recruitment than the low fire severity Spring treatment. It is acknowledged that a minimum of 80–90% of mature aspen be killed to disrupt apical dominance and stimulate greater root sprouting (Bartos and Mueggler, 1981; Brown, 1985; Schier, 1973). In the Fall treatment, aspen and juniper mortality was 100% which contributed to the greater ramet response compared to the Spring treatment. In the Spring treatment, survival of 24% of adult aspen stems as well as surviving aspen ramets and remaining juniper probably limited aspen sprouting response. Others have measured significantly greater aspen density in areas impacted by high severity fire compared to moderate and low severity burned areas (Keyser et al., 2005, Krasnow and Stephens, 2015).

Greater aspen ramet density in the Fall treatment may also be a result of higher resource availability and more favorable environmental conditions. Conifer cutting or burning increases soil water availability and nutrient availability is enhanced as fire severity increases (Roundy et al., 2014b, Bates and Davies, 2017). Full sunlight and higher soil temperatures are important for increasing cytokinin production in root meristems, which further stimulates aspen ramet response (Farmer, 1962; Schier et al., 1985). In the Fall treatment, the soil surface was exposed and blackened which typically results in higher soil temperatures the first growing after fire. The greater herbaceous cover and litter layers may have insulated soils and limited soil heating in the Spring treatment (Bates and Davies, In review).

The levels of aspen ramet response was lower than many values reported elsewhere after applying treatments to restore aspen. Burning or clear-cutting aspen stands has increased aspen ramet numbers from 17,000 to 150,000 stems per hectare (Bartos, 1979; Bartos and Mueggler, 1981, 1982; Crouch, 1983; Keyser et al., 2005). These values are 1.2–30 times greater than stem densities reported for the Fall treatment. Krasnow and Stephens (2015) also measured low aspen ramet density response following severe wildfire in the Sierra Nevada range of California. They attribute aspen sprout density to be determined by (1) resource availability and (2) available root mass and carbohydrate reserves. In our study, aspen stands occupy small, deeper-soil areas within a large area of mountain big sagebrush associations in a 12–18″ (30–46 cm) precipitation zone. The location of the aspen stands within this precipitation zone may limit soil water availability during the growing season. The aspen stands at our sites were also in decline, prior to treatment, which may have indicated lower root mass and energy reserves, therefore limiting ramet response.

However, the continued increase in aspen cover resulting from growth and expansion into previously unoccupied woodland gaps and edges indicates that treated stands have likely increased rooting mass and stored energy reserves. Further expansion of these aspen stands will, however, be limited by site characteristics. The aspen stands are only found in deeper soils on toe-slopes and concave slopes where surface (runoff) and subsurface water sources are likely able to collect.

A factor in the regeneration and growth of aspen in Fall and Spring treatments was the lack of ungulate browsing of aspen ramets. Aspen response to fire and conifer treatments can be limited when excessive browsing of regenerating ramets by ungulates occurs (Bartos et al., 1994; Kay and Bartos, 2000; Rhodes et al., 2017; Seager et al., 2013). The lack of aspen browsing may have been a result of the fire treatment, burning 2800-ha surrounding the aspen sites. Bartos and Mueggler (1981) suggested that prescribing larger burn areas may disperse animals across the landscape, permitting aspen to reestablish successfully post-fire.

4.2. *Western juniper response*

The Fall treatment was initially more effective at removing juniper and, in following years, maintained lower conifer cover and densities than the Spring treatment. After fifteen years juniper cover was still less than 1%, with most of the trees consisting of saplings. However, juniper sapling density exceeded 600 plants ha^{-1}, after 15 years, in both Fall and Spring treatments which provides a sufficient number of future trees to dominate the aspen stands. The rapid increase in juniper saplings in the Fall treatment within the past decade was likely the result of seed deposited by frugivorous birds, which are the main vectors of juniper seed dispersal (Chambers et al., 1999). Nearby trees and stands of mature juniper were likely supplying this seed source. In the Spring treatment, the steady increase in tree density and juniper cover indicate juniper will increase earlier than the Fall treatment. However, based on previous conifer expansion estimates (Miller and Rose, 1995; Wall et al., 2001; Bates et al., 2006), juniper is likely to represent a significant portion of the overstory of both treatments by the end of this century absent additional conifer control.

4.3. *Shrubs and other trees*

Shrub species present in the aspen stands, with the exception of big sagebrush, are tolerant of fire, sprouting from root crowns and rhizomes or establishing from seed. The emergence of snowbrush in the fall treatment was likely due to its presence in the soil seed bank. Snowbrush seed remains viable in soils for periods exceeding 200 years and may appear after fire where it was not previously present (Kramer and Johnson, 1987; Halpern, 1989; Bradley et al., 1991; Tonn et al., 2000). The greater cover and density of snowbrush in the fall treatment was likely enhanced by high fire severity, conditions which increase snowbrush seed germination and establishment (Anderson, 2001; Weiner et al., 2016; Halpern, 1989; Johnson, 1998). Severe fires can also stimulate seed germination of elderberry and wax currant (Bradley et al., 1991, 1992; Quick, 1962) which may explain their greater densities in the Fall treatment. Wax currant is a weak sprouter and plants may be killed by fire, thus recovery is often dependent on establishment from seed.

Shrubs that tend to be robust sprouters after fire (rubber and green rabbitbrush, western snowberry, Wood's rose) decreased following the high severity fall fire and recovered after low severity fire in the Spring treatment. Others have noted that root crowns and rhizomes of these species may be injured by severe fires, causing their decreased abundance (Anderson and Bailey, 1979; Bartos et al., 1994; Hauser, 2007; Fryer, 2008; Zschaechner, 1985). Kauffman and Martin (1990) measured higher shrub mortality after early fall burns with high fuel consumption than after spring burns with low fuel consumption. Fire in the Fall treatment consumed all round-wood up to the 100-h fuel class and partially consumed wood in the 1000-h fuel class.[1] At this level of consumption sub-surface (2 cm deep) soil temperatures typically exceed 200 °C during fire in encroaching juniper woodlands (Bates et al., 2011, 2014). Mortality of plant roots and meristematic growth points can occur between 48 and 94 °C (Neary et al., 1999). In the Spring treatment, round-wood consumption did not exceed the 10-h and 100-h fuel classes and fire impacts to the soil were confined to areas with downed juniper. Under these circumstances sub-surface soil temperatures have not exceeded 79 °C (Bates et al., 2011, 2014). Thus, low severity fire in the Spring treatment not only maintained the presence of adult shrubs, but in areas of fire impact, resulted in survival of belowground root crowns of shrubs, thus, resulting in recovery of the shrub layer. In addition, in the Fall treatment, the sprouting response of shrub species may have been suppressed by the greater densities of aspen.

Curl-leaf mountain-mahogany trees and seed banks are eliminated by severe fire (Gruell et al., 1985) which explains its lower density in the Fall treatment. The reestablishment of mountain mahogany after severe fires is often dependent on off-site seed sources (Crane and Fischer, 1986; Noste and Bushey, 1987). The presence of nearby mature mountain mahogany woodlands are likely providing this seed source. The higher mahogany density in the Spring treatment was a combination of survival of trees present prior to burning and establishment from seed. We attribute the increase in mahogany density in the Spring treatment to off-site seed dispersal and from the seed bank. Mahogany seeds in soil seed banks often survive low severity fires (Gruell et al., 1985; Johnson, 1998).

Chokecherry is adapted to fire by re-sprouting from root crowns and rhizomes (Volland and Dell, 1981; Brockway and Lewis, 1997). However chokecherry was only a minor component within the aspen stands before and after fire. Aspen, especially in the Fall treatment, was able to occupy and dominate following fire, limiting chokecherry response.

5. Conclusions

Aspen woodlands can be difficult to prescribe burn because favorable environmental conditions are often limiting (Jones and DeByle, 1985b; Miller et al., 2000; Wall et al., 2001). Our study indicates that partial cutting of overstory conifers may be effective at increasing surface fuels to eliminate remaining live conifers with fire in aspen woodlands. However, woodland characteristics will vary with site conditions, conifer encroachment stage, and year (Wall et al., 2001). Thus, the level of conifer cutting will probably require adjustment when applied in other areas. The time of year that fire treatments are applied also influences pre-burn conifer cutting levels. In this study, cutting a third and two-thirds of the juniper for fall and spring burning,

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[1] 1-h fuels are wood less than 0.64 cm in diameter; 10-h fuels are wood, 0.64–2.54 cm in diameter; 100-h fuels are wood, 2.54–7.62 cm in diameter; 1000-h fuels are wood, 7.62–20.32 cm in diameter.

respectively, were effective at eliminating or reducing conifer presence and increasing aspen cover and density. For fall burning treatments it may be possible to reduce conifer cutting levels. In stands with only half the juniper cover of our study, felling one-quarter of western juniper was effective at eliminating remaining juniper that were dominating sagebrush steppe plant communities (Bates et al., 2011). We are confident that combinations of partial cutting and prescribed fire treatments can be applied to aspen woodlands being invaded by other conifer species in the western United States.

Lower fire severity in the Spring treatment made it less effective at controlling juniper and as a result may require earlier conifer retreatment to maintain the aspen communities. However, if a management objective is to maintain or increase native understories the Spring treatment was more effective than the Fall treatment for restoring the shrub layer, as well as the herbaceous understory (Bates et al. 2006; Bates and Davies, In review). In addition, spring burning is easily managed and fire can be confined to the treatment area without risk of escape. This would be important to managers charged with maintaining sagebrush habitat. Many aspen stands in the Great Basin are intermixed with sagebrush plant communities which provide habitat for sagebrush obligate wildlife species, particularly sage-grouse (Davies et al., 2011). The high numbers of juniper saplings establishing in these aspen stands, within 15 years of treatment, indicate that retreatment of juniper will be necessary earlier than previously concluded (Bates et al., 2006). This indicates that conifer treatments might be expanded to control nearby stands of seed producing juniper to limit or slow reestablishment in aspen stands.

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