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Quaking aspen woodland after conifer control: Herbaceous dynamics☆

Jonathan D. Bates*, Kirk W. Davies

United States Department of Agriculture, Agricultural Research Service, USA.

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ABSTRACT

Western juniper (*Juniperus occidentalis* Hook.) woodlands are replacing low elevation (< 2100 m) quaking aspen (*Populus tremuloides* Michx.) stands in the northern Great Basin. Restoring aspen woodlands is important because they provide wildlife habitat for many species and contain a high diversity of understory shrubs and herbaceous species. We measured herbaceous cover, density, and diversity for 15 years following two juniper control treatments in aspen woodlands. Treatments included cutting one-third of mature juniper trees followed by early fall burning (Fall), cutting two-thirds of the juniper followed by early spring burning (Spring), and untreated woodlands (Control). Junipers were selectivly cut to increase dry surface fuels to carry fire and kill the remaining conifers. The Fall treatment resulted in significant initial reductions in herbaceous cover and a long-term reduction in perennial forb cover and diversity. Herbaceous recovery in the Fall treatment was dominated by non-native species which represented about 68% of total herbaceous cover. By the end of the study the main non-natives in the Fall treatment were Kentucky bluegrass (*Poa pratensis* L.) and cheatgrass (*Bromus tectorum* L.). In contrast, native perennials in Spring and Control treatments represented, on average, above 60% of total herbaceous cover. Herbaceous cover in the Spring treatment increased and was greater than the Fall treatment and the Control. Perennial forb cover in the Spring treatment was 2- and 6-times greater than Control and Fall treatments, respectively. Perennial forb density was about 7 times greater in the Spring than Fall treatment. Because of lower fire severity, spring burning resulted in greater recovery of the herbaceous layer while maintaining a more diverse native understory than fall burning. The severe fire effects from fall burning aspen woodlands probably requires reseeding of native perennials to maintain understory composition and diversity and limit weed encroachment.

1. Introduction

Quaking aspen (*Populus tremuloides* Michx.) woodlands are important plant communities in the interior mountains of the western United States. Aspen woodlands typically deliver diverse understory communities supporting a wide variety of wildlife species (Houston, 1954; Maser et al., 1984; DeByle, 1985; Mueggler, 1985, 1988; Kuhn et al., 2011). Aspen woodlands are of two main types, seral and stable stands. In seral aspen woodlands, disturbance, especially fire, is important for maintaining stands, mainly, to prevent replacement by conifers (Harniss and Harper, 1982; Strand et al., 2009; Krasnow et al., 2012; Rogers et al., 2014; Krasnow and Stephens, 2015). Stable aspen stands are maintained by continual tree recruitment by root sprouting, although stand maintenance may be augmented by overstory mortality from drought, pathogens, and aging (Shinneman et al., 2013; Rogers et al., 2014).

The decline of seral aspen stands has been documented across much of the Mountain West (Bartos and Campbell, 1998) and Great Basin, USA (DiOrio et al., 2004; Miller and Rose, 1995; Wall et al., 2001). 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), excessive browsing by native ungulates (Gruell, 1979; Bartos et al., 1994; Kay, 1995; Seager et al., 2013), past management (Rogers et al., 2014), and potentially episodic events, such as drought, resulting from climate warming (Rehfeldt et al., 2009; Worrall et al., 2013). An extensive survey of aspen in the northern Great Basin reported 75% of aspen woodlands below 2150 m in elevation have either been replaced or are in the process of being supplanted by western juniper (*Juniperus occidentalis* Hook.) (Wall et al., 2001). These aspen woodlands are seral communities that depend on disturbance, primarily fire, to regenerate stands and prevent replacement by juniper. Similar to other regions of the Mountain West, reintroduction of fire, prescribed or natural, is considered necessary for restoring and maintaining seral aspen

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* Corresponding author at: USDA-ARS, EOARC, 67826-A Hwy. 205, Burns, OR 97720, USA.
E-mail address: jon.bates@ars.usda.gov (J.D. Bates).

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woodlands in the Great Basin (Wall et al., 2001; Strand et al., 2009; Krasnow et al., 2012).

Conifer replacement of aspen typically reduces understory biomass and diversity (Bartos and Campbell, 1998; Stam et al., 2008; McCullough et al., 2013). In the northern Great Basin, as juniper cover increased herbaceous plant cover decreased and bare ground increased (Wall et al., 2001). The response of herbaceous understories to conifer control in aspen woodlands varies, and is contingent upon method of conifer treatment, disturbance severity, site characteristics, and residual herbaceous composition. Prescribed burning produces variable fire severities and intensities which influence plant composition and successional response in aspen and encroaching conifer woodlands (Bartos and Mueggler, 1981; Bartos et al., 1994; Bates et al., 2006, 2014; Krasnow and Stephens, 2015; Williams et al., 2017).

Recovery of herbaceous understories following fire and other conifer treatments in aspen stands have focused on short-term succession. One long-term study indicated herbaceous biomass remained greater in light, moderate, and heavily burned aspen stands than unburned controls for 12 years after prescribed fire (Bartos et al., 1994). However, Bartos et al. (1994) suggested the suppression of aspen suckers by elk and cattle may have contributed to persistently elevated herb production. Thus, longer-term treatment evaluations are necessary to ascertain the effectiveness of conifer treatments on recovery of herbaceous understories and adjust and improve management practices.

The objective of the study was to assess herbaceous community responses 15 years (2002–2016) after prescribed fire treatments removed western juniper from seral-montane aspen sites in southeast Oregon. Vegetation responses at these sites were previously evaluated for three years after fall (Fall) and spring (Spring) burning (Bates et al., 2006). This assessment indicated juniper treatments were effective at increasing cover and density of aspen and cover of herbaceous understories compared to untreated woodlands. Fall burning was of high severity and was more effective at increasing aspen than low severity Spring burning. Fall burning caused high mortality of native perennials and recovery was dominated by fire-stimulated native forbs, non-native weeds, and Kentucky bluegrass (*Poa pratensis* L.), a rhizomatous grass not originally native to the western U.S. The herbaceous understory in the Spring treatment remained intact resulting in higher cover and diversity of native perennials.

We hypothesized that herbaceous cover would be greater in Fall and Spring treatments compared to untreated areas as there remained sizeable areas of bare ground (30–60%) for further colonization three years after fire treatments. Additionally, we hypothesized herbaceous composition differences, measured in early succession (Bates et al., 2006), between Spring and Fall treatments would persist with the Spring treatment having greater cover and composition of native perennials and the Fall treatment having higher composition of annual and non-native species.

2. Materials and methods

2.1. Site description

The study site was located along a four km stretch of Kiger Creek Canyon on Steens Mountain, southeastern Oregon (Geo URI 42.829465-118.555172). Aspen stands were scattered along toe slopes above the riparian zone and in concave slopes in adjacent uplands from 1645 to 1930-m elevation. Individual aspen stands were small, averaging 0.4-ha in area, and ranging from 0.20 to 2-ha in size. Surrounding plant communities consisted of mountain big sagebrush (*Artemisia tridentata* spp. *vaseyana* (Nutt.) Beetle & A. Young) grassland and mountain mahogany (*Cercocarpus ledifolius* (Nutt.) Torr. & Gray) thickets. Aspen was reduced in cover and density and stands were dominated by western juniper (Bates et al., 2006). Juniper woodlands in the study were considered to be in late- to closed-successional phases and all aspen stands were in decline using descriptions from Miller and Rose (1995), Bartos and Campbell (1998), and Wall et al. (2001). There was a high diversity of forbs and grasses with 89 species identified. Western snowberry (*Symphoricarpus oreophilus* Gray) and wax currant (*Ribes cereum* Dougl.) were the common shrubs with another eight shrubs contributing minor levels of cover (Bates et al., 2006).

The Ecological Site Description for the sites is 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; Rogers et al., 2014). 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 site, about 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. Most aspen areas in the western United States receive at least 380 mm of precipitation annually or are able to access elevated water tables (Jones and DeByle, 1985).

2.2. Study design and burn applications

The study was a randomized complete block design (Peterson, 1985). Ten, 0.60-ha blocks were established in aspen stands in May 2000. A block consisted of three treatment plots: an untreated control (Control), juniper cutting followed by fall prescribed fire (Fall), and juniper cutting followed by early spring prescribed fire (Spring). Plots were about 0.20-ha, including buffer strips between treatments.

Cutting involved felling mature (dominant and subcanopy) juniper trees, evenly distributed through the stand. Junipers were cut in winter and early spring, 2000–2001, and allowed to dry during the summer. An average of 106 (range 55–175) juniper trees were cut per hectare in Fall plots, representing about 1/3 of the dominant and subcanopy juniper. An average of 232 (range 140–372) juniper trees were cut per hectare in Spring plots, representing around 2/3 of the dominant and subcanopy juniper. Trees were cut to increase the level of dry surface (0–4 m) fuels to carry fire through stands. Fall burning was applied in October 2001 by the Bureau of Land Management (BLM), Burns District, Oregon. The prescribed fires were spot head fire using helicopter-dropped delayed action ignition devices (DIADS). DIADS were chemically injected ping-pong balls. Spring burns were head fires, applied in late April 2002 using drip torches with a 50:50 mixture of gas and diesel. Fuel continuity of the cut junipers was sufficient for fire to carry with minimal re-ignition during spring burning.

Fire severity was estimated by adapting severity categories developed by Bartos et al. (1994) for evaluating plant community response to fire. Severity categories were light (1–20% of litter and understory consumed, needles and small branches of downed juniper consumed, and only a few mature aspen/juniper killed), moderate (21–80% of litter and understory consumed, large branches and trunks remained on downed juniper, and < 90% of adult aspen/juniper killed), and high (81–100% of litter and understory consumed, only trunks of downed juniper remaining, and > 90% of adult aspen/juniper killed) (Bates et al., 2006). Soil and fuel moisture, and humidity were lower and wind speed was greater for the Fall versus Spring treatment. In the Fall treatment, all downed wood but trunks were consumed, litter and understory consumption was > 95%, and mature juniper and aspen kill were 99% and 100%, respectively. Fire severity in the Fall treatment was high. In the Spring treatment, consumption of surface litter and the understory was less than 1% and only suspended needles and small branches of felled juniper were consumed. About 55% of remaining live juniper and 76% of the adult aspen stems were killed by the fire. Fire severity in the Spring treatment was rated as having no impact to the understory and having moderately high impacts on live trees. Further details on fire conditions and fuel moisture are in Bates et al. (2006).

Livestock were excluded from the area two years pre-treatment and for three years post-treatment. Livestock used the area in a deferred rotational system during summers (2005–2016) and all grazing took place after seed development of the major grasses. Understory measurements were completed prior to livestock entry. Grazing was evaluated yearly using methods developed by Anderson and Currier (1973) and from height-weight relationships (Eastern Oregon Agricultural Research Center, Burns, unpublished guide) Grazing was rated light on all aspen plots aside from one Control plot which generally received moderate use.

2.3. Herbaceous measurements

Pre-treatment herbaceous measurements were made in July 2000. Post-treatment measurements were made in July 2002–2006, 2009, 2012, and 2016. In each plot, three permanent 40-m transects were marked with 50-cm re-bar stakes. Transects were spaced 10-m apart. Understory canopy cover and perennial herbaceous density were sampled inside 0.2-m^2 frames (0.4 × 0.5-m). Frames were placed every 2-m along transect lines (39 frames per plot). Foliar cover (perennials, biennials, annuals) and density (perennials, biennials) were estimated by species. Percentage bare ground, rock, juniper litter, deciduous litter, moss, and lichen were also estimated inside the frames. A species list (number) was compiled for each treatment plot using nomenclature from the USDA Plants Database (2017).

2.4. Statistical analysis

The study sites were included in a prescribed fire project encompassing 2850-ha in Kiger Canyon and adjacent uplands. Because aspen plots were separated by several hundred meters up to 3.2-km, plot 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 inadvertently burned during the October prescribed fire. Of the 10 blocks, Spring and Control plots in 5 of the blocks were entirely or partially disturbed in the Fall treatment, thus, these blocks were removed from the analyses. A repeated measures mixed model analysis (PROC MIX, SAS Institute, 2012. Release 9.3 Edition, SAS Institute, 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 = 12, error df = 59) on herbaceous cover (functional group and species), perennial density (functional group and species), species richness, and ground cover (bare ground and rock, juniper litter, deciduous litter, moss and lichen). Functional groups were perennial bunchgrass and tufted sedges, perennial forb, rhizomatous graminoids (grasses and sedges), native annual forbs, cheatgrass (*Bromus tectorum* L.), and non-native forbs. An auto regressive order one covariance structure was used because it provided the best model fit (Littell et al., 1996). Data were tested for normality using the SAS univariate procedure (SAS Institute, 2002). Data not normally distributed were arcsine-square root transformed to stabilize variance. 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. Back transformed means are reported in the results. Statistical significance of all tests was set at $P < .05$.

3. Results

3.1. Ground cover

Bare ground and rock was 3 times greater in the Fall than Control and Spring treatments the first three years after burning and remained greater than one or more of these treatments into the 10th year (2012) after burning (Table 1; Fig. 1A). Juniper litter declined over time in all treatments with the greatest decreases in Fall and Spring treatments (Fig. 2B). Juniper litter cover in Spring and Fall treatments has been less than 5% since 2006 and on average declined 83% from pre-treatment levels. Juniper litter decreased about 50% in the Control between 2000 and 2016. Deciduous litter decreased 85% and 43%, respectively, in Fall and Spring treatments in response to burning and were less than the Control the first three years after fire (Fig. 1C). Deciduous litter in Fall and Spring treatments recovered to pre-treatment levels about eight years post fire. Since 2006, deciduous litter was generally greater (8–81%) in the Fall than Spring and Control treatments. Herbaceous cover increased in all treatments the first five years (2002–2006) after fire, with the largest increases in the Spring treatment (Fig. 1D). During this period, herbaceous cover in the Spring was 1.3–3-fold greater than Control and Fall treatments. Between 2006 and 2016 herbaceous cover trended downward in Fall and Spring treatments decreasing by about 30%, although cover remained greater in the Spring treatment. Herbaceous cover in the Control about doubled from pretreatment (2000) levels in 2016. Moss and lichen were eliminated by the Fall treatment and by 2016 cover was only 0.1 ± 0.4%. The Control treatment had the highest cover of moss and lichen, averaging 2.0 ± 0.2%. Cover of moss and lichen was greater in the Spring compared to the Fall treatment, but declined continuously and by the end of the study was 0.3 ± 0.1%.

Table 1
Herbaceous response variable P-values from the mixed model analysis for the aspen recovery study, Steen's Mountain, southeast Oregon (2000–2016). Values in bold indicate significant treatment (Control, Fall, Spring) differences for main (treatment, year) effects and the interaction (treatment × year).

Response variables	Treatment	Year	Treatment × Year
Perennial grass cover			
Perennial bunchgrass	**< 0.001**	**< 0.001**	**0.002**
Achnatherum nelsonii	**< 0.001**	**0.040**	**0.008**
Achnatherum occidentale	**0.006**	**< 0.001**	**< 0.001**
Bromus marginatus	0.688	0.700	0.389
Elymus caninus	0.053	0.345	0.347
Elymus elymoides	**0.003**	**< 0.001**	0.073
Festuca idahoensis	**< 0.001**	0.615	0.340
Carex multicostata	**0.017**	0.552	0.655
Poa ampla	**< 0.001**	**0.016**	**0.021**
Poa pratensis	0.266	**< 0.001**	0.760
Other bunchgrasses	**0.011**	0.072	0.284
Perennial forb cover	**< 0.001**	**0.006**	0.135
Achillea millefolium	**< 0.001**	**< 0.001**	**< 0.001**
Arnica cordifolia	**< 0.001**	**0.008**	0.086
Antennaria spp.	**< 0.001**	0.382	0.370
Lupinus argenteus	0.088	**< 0.001**	**< 0.001**
Viola spp.	**< 0.001**	**0.005**	0.051
Other perennial forbs	**0.028**	**0.020**	**0.037**
Native annual forb cover	0.389	**< 0.001**	0.063
Bromus tectorum	**< 0.001**	**0.018**	**0.024**
Non-native forb cover	**< 0.001**	0.183	**0.033**
Ceratocephala testiculata	**0.022**	0.643	0.639
Verbascum thapsus	**< 0.001**	**< 0.001**	**< 0.001**
Herbaceous Total	**< 0.001**	**< 0.001**	**0.015**
Bareground and rock	**< 0.001**	**< 0.001**	**< 0.001**
Juniper litter	**0.001**	**< 0.001**	**< 0.001**
Deciduous litter	0.355	**< 0.001**	**< 0.001**
Moss	**< 0.001**	0.354	0.675
Lichen	**0.045**	0.563	0.788

Species nomenclature are derived from the USDA Plants Database (https://plants.usda.gov/java/), consulted in spring 2017.

3.2. Perennial bunchgrasses

In the Spring treatment, perennial bunchgrasses and tufted *Carex* species cover increased and was 20–30% of total herb cover (Table 1; Fig. 2A). Cover of bunchgrasses was 2–8-fold greater in the Spring than Control and Fall treatments until the last year of measurement. Cover of bunchgrasses increased in Fall and Control treatments and were double pre-treatment values by 2016. As a percentage of total cover,

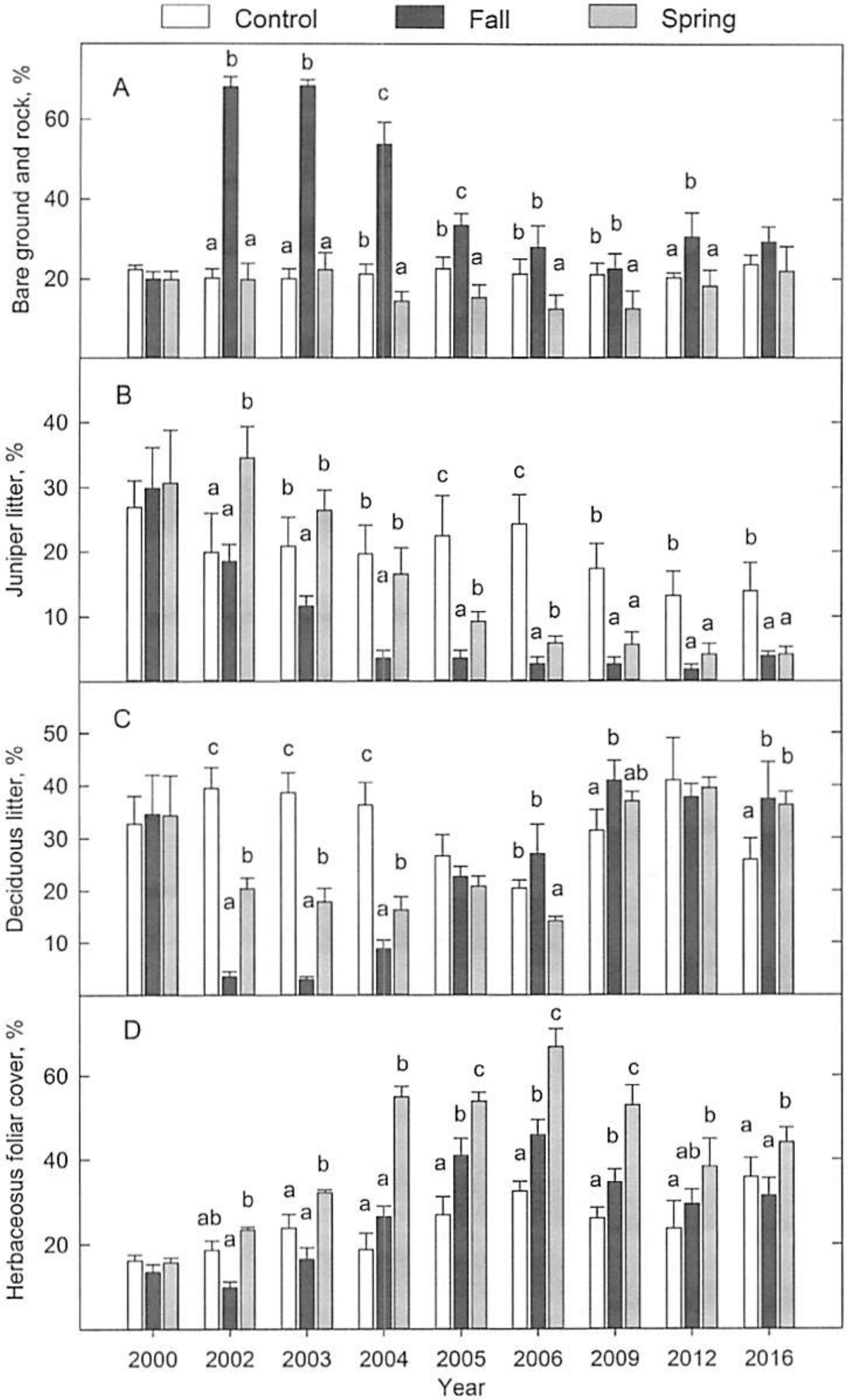

Fig. 1. Percent cover (%) of (A) bare ground and rock, (B) juniper litter, (C) deciduous litter, and (D) herbaceous foliar cover for Control, Fall, and Spring treatments, Kiger Canyon, Oregon, 2000–2016. Data are means ± one standard error. Means sharing a common lower case letter within year are not significantly different (P > .05).

bunchgrass cover in the Fall treatment increased from a low of 6% in 2003 to 26% in 2016. Bunchgrass density increased by 2–2.5-fold in the Spring treatment after 2002 and was greater than Fall and Control treatments between 2003 and 2016 (Table 2; Fig. 2B). Bunchgrass density (plants m^{-2}) averaged 5.2 ± 0.3, 4.4 ± 0.8, and 11.3 ± 1.1 in Control, Fall, and Spring treatments, respectively. Bunchgrass and tufted *Carex* species that comprised the most cover and density of this lifeform in Spring and Control treatments were Columbia needlegrass (*Achnatherum nelsonii* (Scribn.) Barkworth), mountain brome, (*Bromus marginatus* Nees ex Steud), squirreltail (*Elymus elymoides* (Raf.) *Swezey*), Idaho fescue (*Festuca idahoensis* Elmer), Sherman big bluegrass (*Poa ampla* J. Presl), and many-rib sedge (*Carex multicostata* Mack.) (Table 2). In the Fall treatment, bunchgrass cover and density were mainly represented by Columbia needlegrass and squirreltail.

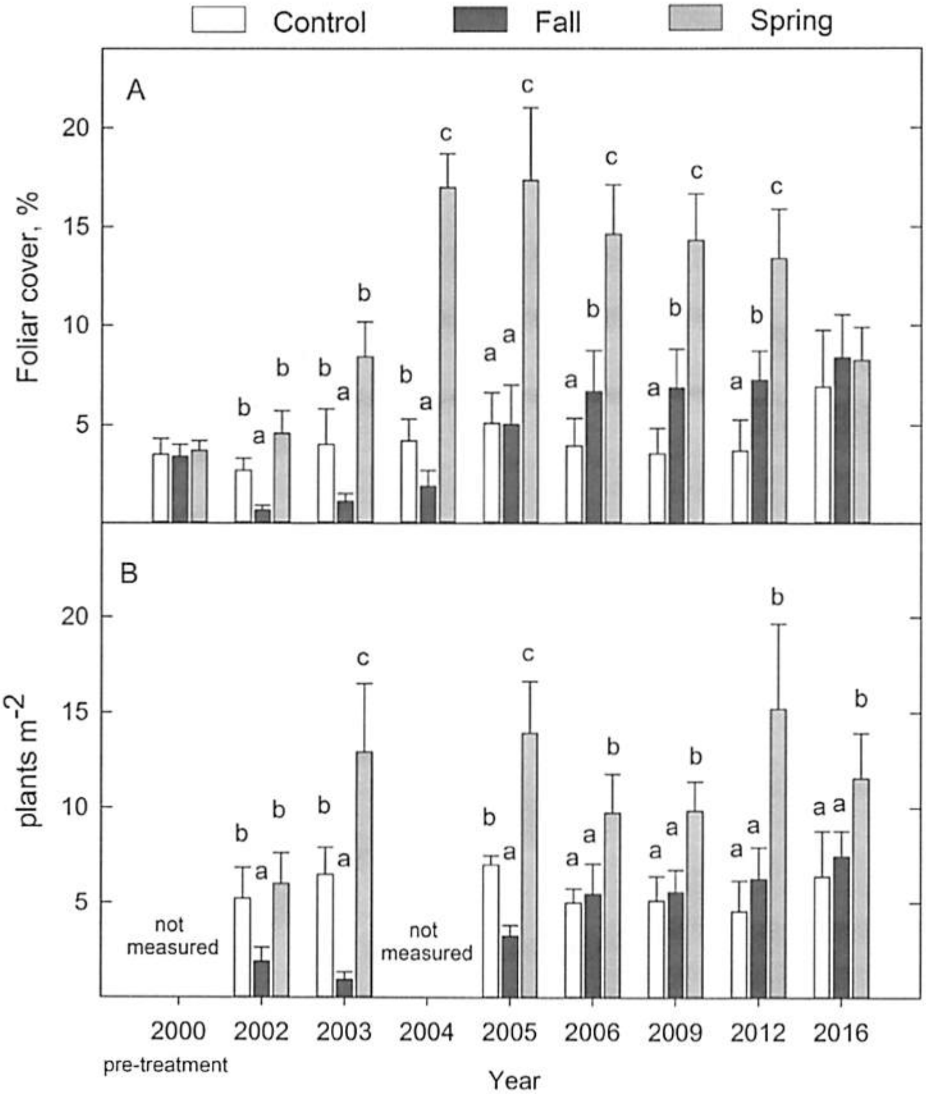

Fig. 2. Perennial bunchgrass (A) foliar cover (%) and (B) density (plants m^{-2}) for Spring, Fall, and Control treatments, Kiger Canyon, Oregon, 2000–2016. Data are means ± one standard error. Means sharing a common lower case letter within year are not significantly different ($P > .05$).

3.3. Perennial forbs

After treating juniper, cover of perennial forbs was 1.4–10-fold greater in the Spring than the Fall treatment and the Spring was greater than the Control (1.4–2.3-fold) in all years but 2012 (Table 1; Fig. 3B). Perennial forb cover in the Spring treatment ranged between 21 and 39% of total herbaceous cover from 2005 and 2016. In the Fall treatment, forb cover increased from pre-treatment levels until 2004 after which cover declined, averaging 3.5 ± 0.3% between 2005 and 2016 (< 10% of total herb cover). Perennial forb density (plants m^{-2}) was 5–14-fold greater in Control and Spring treatments than the Fall treatment after burning (Table 2; Fig. 3B). Perennial forb density averaged 35.2 ± 2.5, 4.3 ± 0.4, and 32.8 ± 2.8 in Control, Fall, and Spring treatments, respectively. Perennial forbs that comprised the most cover and density in Spring and Control treatments were yarrow (*Achillea millefolium* L.), heart-leaf arnica (*Arnica cordifolia* Hook), silvery lupine (*Lupinus argenteus* Pursh.), pussytoes (*Antennaria* Gaertn.) and violets (*Viola* spp. L.) (Table 2).

3.4. Rhizomatous graminoids

Rhizomatous grasses and sedges increased from pre-treatment levels in all treatments and the greatest increases were in the Spring treatment (Table 1; Fig. 4A). Cover was 2–3-fold greater in the Spring than the Control from 2004 to 2009. In 2012 and 2016 cover did not differ among the treatments. Non-native Kentucky bluegrass comprised > 95% of foliar cover in this functional group. In Spring and Fall treatments, Kentucky bluegrass averaged about 34% of total herbaceous cover and in the Control about 39%.

3.5. Native annual forbs

Native annual forbs did not differ among treatments and averaged less than 2% cover during the period of study (Table 1; Fig. 4B). In 2005 and 2006 annual forb cover was greater than other years measured.

3.6. Cheatgrass and non-native forbs

Cover of cheatgrass and non-native forbs increased in the Fall treatment and was greater than the Control and Spring treatments across much of the study period (Table 1; Fig. 4C & D). Cover of cheatgrass began increasing in 2004 and was 3–20-fold greater than Spring and Control treatments through 2016. Cheatgrass cover in the Fall treatment represented from 7 to 23% of total herbaceous cover during this period. Cover of non-native forbs was greater in the Fall than the other treatments in 2003–2006 and 2012. Non-native forb

Table 2
Perennial herbaceous density and species number response variable P-values from mixed model analyses for the aspen recovery study, Steen's Mountain, southeast Oregon (2000–2016). Values in bold indicate significant differences.

Response variables	Treatment	Year	Treatment × Year
Perennial bunchgrass	**< 0.001**	**0.023**	0.280
Achnatherum nelsonii	**0.025**	**0.029**	0.124
Achnatherum occidentale	0.929	**0.007**	0.317
Bromus marginatus	**0.002**	0.259	0.467
Elymus caninus	0.115	**< 0.001**	0.401
Elymus elymoides	**0.004**	**0.050**	0.662
Festuca idahoensis	0.108	0.913	0.714
Carex multicostata	**< 0.001**	**0.010**	0.452
Poa ampla	**< 0.001**	**< 0.001**	**< 0.001**
Other bunchgrasses	0.331	0.260	0.311
Perennial forbs	**< 0.001**	0.178	0.409
Achillea milliforium	**< 0.001**	0.345	0.218
Arnica cordifolia	**< 0.001**	0.209	**0.009**
Lupinus argenteus	0.876	**0.019**	0.358
Microseris nutans	**0.002**	**< 0.001**	**< 0.001**
Other perennial forbs	**0.037**	0.462	0.591
Nonnative biennial forbs	**0.040**	**0.047**	0.328
Verbascum thapsus	**0.005**	**< 0.001**	0.119
Species Number			
Perennial graminoid	**< 0.001**	0.191	0.698
Perennial forb	**< 0.001**	**< 0.001**	**0.001**
Native annual forb	0.553	**< 0.001**	**0.043**
Exotic annual forb	**< 0.001**	0.065	0.074
Noxious weeds	**< 0.001**	**< 0.001**	**0.008**
All exotics	**< 0.001**	**0.001**	**0.001**
Native species total	**< 0.001**	**< 0.001**	**0.016**
Herbaceous total	**< 0.001**	**< 0.001**	**0.036**

cover in the Fall treatment averaged 5.8 ± 0.7% during these years and primarily consisted of curve-seed butterwort (*Ceratocephala testiculata* (Crantz) Roth), thistle species (*Cirsium* Mill.), and mullein (*Verbascum thapsus* L.) (Table 1).

3.7. Species numbers

The number of species (perennial graminoids and forbs, native species, and total species) were greater in the Spring than Control and Fall treatments following burning (Table 2; Fig. 5). The number of perennial graminoid and forb species were 1.5 and 3-fold greater, respectively, in the Spring than Fall treatment. In the Control, numbers of perennial graminoid and forb species were 1.2 and 2.2-fold greater, respectively, than the Fall treatment. The Fall treatment had nearly twice as many exotic annual forb and noxious weed species than the Spring and Control treatments.

4. Discussion

The results establish that herbaceous succession in the aspen communities were influenced by season of fire which caused dissimilar fire severity effects, therefore yielding different post-fire understory recovery dynamics, levels, and composition. In the Fall treatment, high severity fire caused major disruptions to understory composition resulting in herbaceous cover being dominated by non-native species. The low severity fire in the Spring treatment resulted in post-fire dominance by native herbaceous perennials.

4.1. Ground cover dynamics

In the Fall treatment, high fuel consumption increased levels of bare ground which were greater than Control and Spring treatments, especially the first three years after fire. It required more than eleven years for bare ground to decrease in the Fall and approach the other treatments. In the Fall treatment, fire caused high mortality of perennial grasses and forbs effecting recovery composition in subsequent years. The loss of perennial herbaceous species combined with increased bare ground opened these aspen stands to establishment and spread of non-native species principally Kentucky bluegrass, cheatgrass, and exotic forbs. In the Fall treatment, these species comprised between 60 and 76% of total herbaceous cover from 2004 to 2016. The loss of perennial bunchgrass and forb cover from high severity fire followed by increased cover of non-native species has been frequently reported in forests and woodlands of the western U.S. (Armour et al., 1984; Griffis et al., 2001; Sabo et al., 2009; Bates et al., 2014; O'Connor et al., 2013). However, others have measured no significant differences in native understory cover or species richness following early season (June) and late-season (September/October) prescribed burns (Kerns et al., 2006; Knapp et al., 2007).

Native perennials in Spring and Control treatments represented between 50 and 65% of total cover across the same time period. Burning the aspen stands in the spring when fuel and soil moisture and relative humidity were higher and temperatures cooler reduced fire severity which maintained the native perennial herbaceous understory. Low severity fires in winter and spring in other juniper woodland treatments has been effective at limiting native plant mortality, after which, rapid increases in perennial herbaceous vegetation has restricted or nullified establishment and expansion of non-native plants (Bates and Svejcar, 2009; O'Connor et al., 2013; Bates et al., 2014).

Herbaceous cover in Fall and Spring treatments peaked in 2006. Greater herbaceous cover, production and frequency has been a widespread trend following various conifer treatments in pine forests (Strahan et al., 2015; Uresk et al., 2000), aspen woodland (Bartos and Mueggler, 1981, 1982), and sagebrush steppe (Bates et al., 2011, 2014; Davies et al., 2012; Roundy et al., 2014). However, by 2009 (eight years post-treatment) herbaceous cover was declining and by 2016 differences among the treatments and the Control had narrowed. The decreases in understory cover in Fall and Spring treatments appear to have begun once cover of woody species (aspen, shrubs, juniper) began exceeding about 50% (Bates and Davies, 2017). Understory biomass has been negatively correlated with increasing aspen basal area or stand density (LaRade and Bork, 2011; Woods et al., 1982), although relationships appear to vary depending on site characteristics (Severson and Kranz, 1976). The near doubling of herbaceous cover in the Control from pretreatment levels we attribute to changes in livestock management, primarily by means of deferment and lower stocking.

The decrease in moss and lichen in the Fall and Spring treatments appears to be a common occurrence following juniper control. Large reductions in moss and lichen have been measured after cutting or burning of juniper woodlands in sagebrush steppe (Bates et al., 2013, 2014; O'Connor et al., 2013). Star moss (*Tortula ruralis* [Hedw.] G. Gaertn., B. Mey. & Scherb) was the dominant species prior to juniper treatment in the aspen woodlands. Star moss, other moss and lichen were immediately lost in the Fall treatment as they tended to concentrate beneath juniper trees. In the Spring treatment decreases in moss and lichen were steady and possibly resulted from changes in environmental conditions such as increased solar radiation with the loss of juniper canopies.

There were major changes in litter composition which may influence soil chemistry and nutrient cycling. Litter in the Spring and Fall treatments was primarily deciduous litter generated by herbaceous plants and increasingly from aspen leaf litter fall as aspen cover increased. Intact aspen stands have been noted to support lower soil pH and lower amounts of salts, lime, and sulfate, and greater amounts of magnesium, iron, manganese, and copper than aspen woodlands dominated by juniper (Wall et al., 2001). Aspen produces higher amounts of litter annually than conifers, and aspen litter decomposes at a faster rate than conifer litter, especially western juniper (Bartos and DeByle, 1981; Bates et al., 2007).

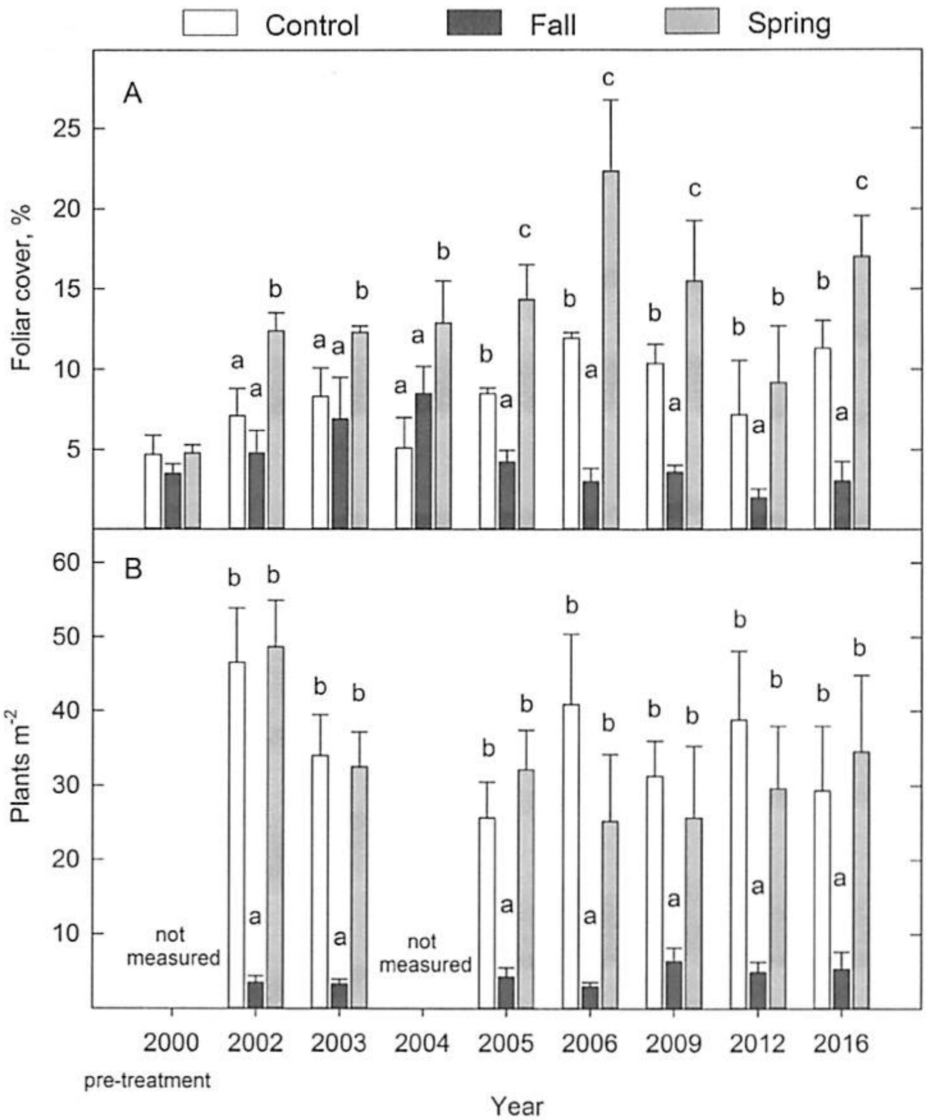

Fig. 3. Perennial forb (A) foliar cover (%) and (B) density (plants m^{-2}) for Spring, Fall, and Control treatments, Kiger Canyon, Oregon, 2000–2016. Data are means ± one standard error. Means sharing a common lower case letter within year are not significantly different ($P > .05$).

4.2. Native species

Native species dynamics varied among the treatments. In the Spring treatment, native species cover increased and peaked by the 4th year after juniper reduction (2006). After 2006, cover of perennial bunchgrasses and forbs (perennials and annuals) decreased, mimicking the trends discussed for total herbaceous cover. Densities of perennial bunchgrasses and forbs were largely stable after 2003, not changing appreciably over the course of the study. The Spring treatment did not lose understory species and gained additional perennials beginning the second year after treatment. Compared to the Fall treatment, species composition of the understory remained largely intact in the Spring treatment.

Perennial bunchgrasses slowly increased in cover and density in the Fall treatment indicating their ability to recolonize severely burned aspen stands. In the Fall treatment, perennial forb cover peaked in 2004 at about 8% and was mainly composed of two early successional species, silvery lupine and long-sepaled globe mallow (*Iliamna longisepala* {Torr.} Wiggins). Cover of these species declined after 2004 after which perennial forb cover never exceeded 4%. The lack of forb cover response was mainly a result of the loss of yarrow, heart-leaf arnica, pussy-toes, and violets in the Fall treatment. These species made up 60–70% of the perennial forb cover in Control and Spring treatments.

Native perennial bunchgrasses in the Control increased during the course of the study and equaled the other treatments. This increase we again attributed to changes in livestock management.

4.3. Non-native species

Non-native species represented about 50% of total cover prior to treating juniper. So even prior to juniper treatment non-natives, especially Kentucky bluegrass, had become an established and naturalized component of the aspen understories. Even with high native plant diversity, aspen woodlands have not proven to be resistant to invasive plants (Chong et al., 2001; Stohlgren et al., 2003). In Rocky Mountain National Park, Colorado, of 42 invasive species found, 90% were documented in what were considered pristine aspen woodlands (Chong et al., 2001). Although cover of invasive species was low, Chong et al. (2001) warned that with suitable disturbances, exotic plants might displace native species. In both Fall and Spring treatments non-natives increased, however, increases were greater in the Fall treatment and comprised of several species while in the Spring treatment the increase was only from Kentucky bluegrass. Non-native forbs in the Fall did decline overtime after cover peaked in 2006. Species such as mullein, butterwort and thistle were early colonizers but were replaced by grasses (native and non-native). Cheatgrass has mainly been considered

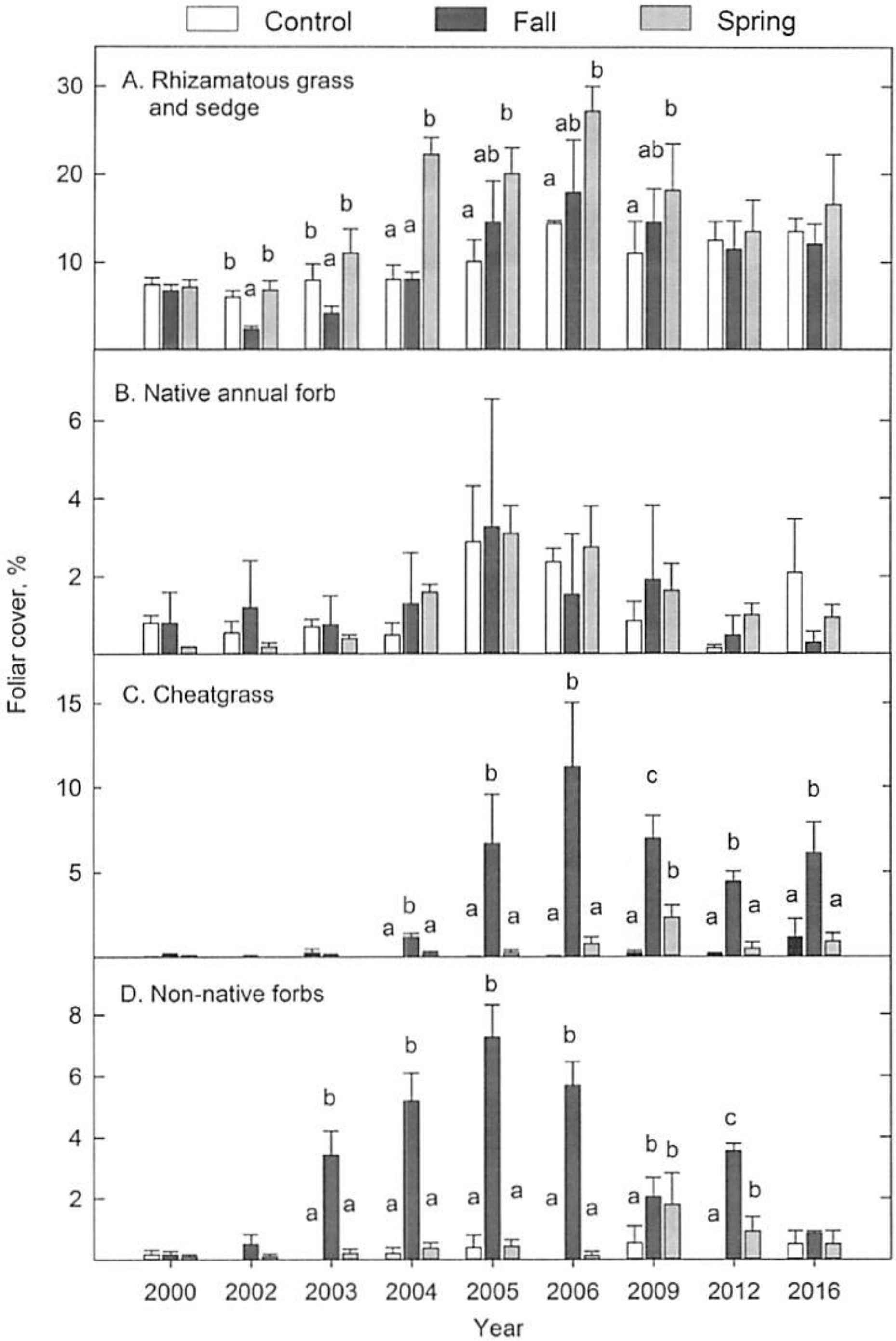

Fig. 4. Foliar cover (%) of (A) rhizomatous grasses and sedges, (B) native annual forb, (C) cheatgrass, and (D) non-native forbs for Spring, Fall, and Control treatments, Kiger Canyon, Oregon, 2000–2016. Data are means ± one standard error. Means sharing a common lower case letter within year are not significantly different ($P > .05$).

a problem in drier low-elevation sagebrush steppe communities where it may dominate after fire (Chambers et al., 2007). However, cheatgrass has increasingly become a concern following fire and fuel reduction treatment in Ponderosa pine forest and juniper woodlands invading high elevation sagebrush steppe (Bates et al., 2013, 2014; Bates and Davies, 2016; Davies and Bates, 2017; McGlone et al., 2009; Youngblood et al., 2006). In our study, cheatgrass was able to invade following severe fire in the aspen woodlands and maintain a significant presence 15 years following fire.

5. Conclusions

Treatment of conifers for maintenance or recovery of aspen communities is important, particularly for wildlife habitat, biodiversity, and watershed values. In our study, the Spring treatment resulted in greater recovery of understory cover and perennial density while maintaining a more diverse native understory than the Fall treatment. Spring burning is easily managed and fire can be confined to the treatment area without risk of escape, which may be important to managers charged with maintaining sagebrush habitat for species of concern. Many aspen stands in the Great Basin are intermixed with sagebrush plant communities which provide habitat for sagebrush obligate wildlife species,

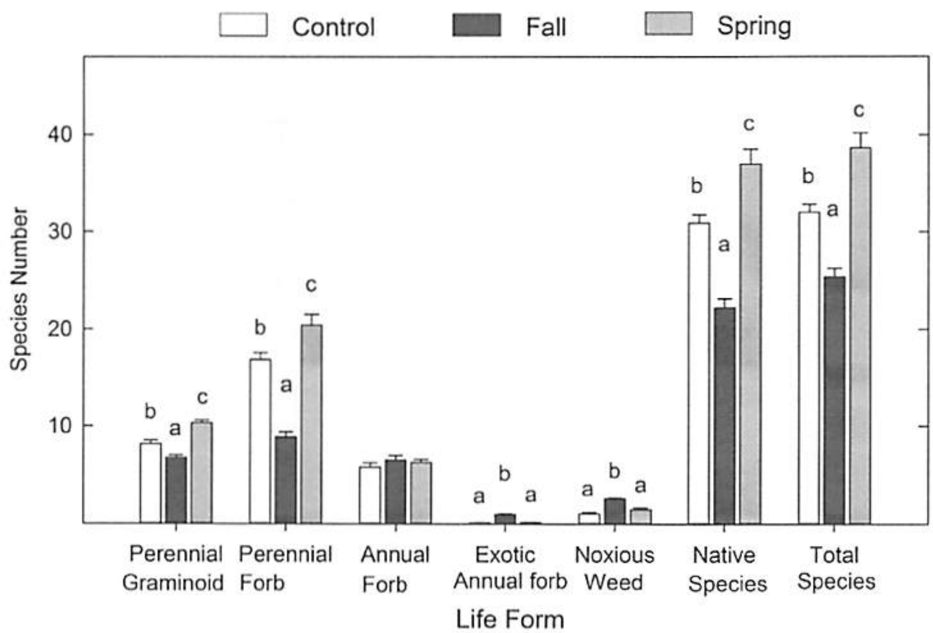

Fig. 5. Average numbers of species by life form after treatment for Spring, Fall, and Control treatments, Kiger Canyon, Oregon, 2002–2016. Data are means ± one standard error. Life form group means sharing a common lower case letter are not significantly different ($P > .05$).

particularly sage-grouse (Davies et al., 2011). Fall burning was detrimental to understory recovery by promoting non-native species and reducing and causing loses of native species, especially perennial forbs. In the future, aspen stands with understory characteristics similar to our sites will require seeding to recover native bunchgrasses and forbs, and limit exotics, when fire is of high severity as in the Fall treatment.

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