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Early succession following prescribed fire in low sagebrush (*Artemisia arbuscula* var. *arbuscula*) steppe

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Abstract.—We evaluated plant community succession following prescribed fire on *Artemisia arbuscula* var. *arbuscula* (Nutt.) McMinn (low sagebrush) steppe in southeastern Oregon. Treatments were "prescribed burned" (burn; fall 2012) and "unburned" (control) *A. arbuscula* steppe, and the study design was a randomized complete block with 4 replicates per treatment. Herbaceous yield and vegetation canopy cover and density were compared between treatments (2012–2020). Fire practically eliminated *A. arbuscula* and there was no recruitment of new plants in the first 8 years after burning. Herbaceous yield in the burn treatment was about double the control for most of the postfire period. Native perennial grasses and forbs constituted 94% to 96% and *Bromus tectorum* L. (cheatgrass) 0.2% to 2% of total herbaceous yield in the control. In the burn treatment, perennial grasses and forbs constituted 83% to 87%, native annual forbs 2% to 5%, and *B. tectorum* 3% to 9% of total herbaceous yield. Despite an increase in *B. tectorum*, the burned *A. arbuscula* sites were dominated by herbaceous perennial grasses and forbs and exhibited high levels of resilience and resistance. After prescribed fire, for the study sites and comparable *A. arbuscula* associations, weed control or seeding are not necessary to recover the native herbaceous community. However, the results in our study are for low-severity prescribed fire in intact *A. arbuscula* plant communities. Higher-severity fire, as might occur with wildfire, and in *A. arbuscula* communities having greater prefire invasive weed composition should not be assumed to develop similarly high levels of community resilience and resistance.

Resumen.—Evaluamos la sucesión de comunidades de plantas después de un incendio prescrito de *Artemisia arbuscula* var. *arbuscula* (Nutt.) McMinn (artemisa baja) en el sureste de Oregón. Los tratamientos se llevaron a cabo en estepa *A. arbuscula* quemada (Quema; otoño de 2012) y sin quemar (Control), y el estudio se diseñó en un bloque completo al azar con cuatro repeticiones por tratamiento. Se comparó el rendimiento herbáceo y la cobertura y densidad del dosel vegetal entre los tratamientos (2012–2020). El fuego prácticamente eliminó *A. arbuscula* y no hubo reclutamiento de nuevas plantas los primeros ocho años después de la quema. El rendimiento herbáceo en el tratamiento con Quema fue aproximadamente el doble del Control durante la mayor parte del período posterior al incendio. Los pastos y herbáceos perennes nativos comprendieron el 94%–96% y *Bromus tectorum* L. (espiguilla) comprendió el 0.2% a 2% del rendimiento herbáceo total en el Control. En el tratamiento de Quema, las gramíneas y las hierbas perennes comprendieron entre el 83% y el 87%, las herbáceas nativas anuales entre el 2% y el 5% y *B. tectorum* entre el 3% y el 9% del rendimiento herbáceo total. A pesar de un aumento de *B. tectorum*, los sitios quemados de *A. arbuscula* se encontraban dominados por pastos y malezas herbáceas perennes y exhibían altos niveles de resiliencia y resistencia. Después del incendio prescrito, en los sitios de estudio y asociaciones comparables de *A. arbuscula*, se observó que no fue necesario controlar la maleza o la siembra para recuperar la comunidad herbácea nativa. Sin embargo, los resultados de nuestro estudio aplican a incendios prescritos de baja severidad en comunidades de plantas intactas de *A. arbuscula*. No se debe suponer que, en el caso de incendios más graves, tal como podría ocurrir durante incendios forestales, las comunidades de *A. arbuscula* que tienen una mayor composición de malezas invasoras antes de un incendio, desarrollen niveles similares altos de resiliencia y resistencia.

Fire is the major natural disturbance affecting sagebrush (*Artemisia* L.) steppe communities and is often deliberately applied to achieve various land management goals and objectives (Boyd et al. 2017). A multitude of studies from site to landscape levels and for various fire conditions have evaluated fire effects and postfire community recovery in *Artemisia tridentata* L. (big sagebrush) steppe, providing an extensive and growing knowledge base useful to both land management and ecological research (Innes 2017, 2019). However, knowledge gaps remain, and this is true for examining fire effects and postfire recovery of

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plant communities dominated by the various species of dwarf sagebrush such as *Artemisia arbuscula* var. *arbuscula* (Nutt.) McMinn (low sagebrush).

Artemisia arbuscula communities occupy roughly 11.2 million ha in the western United States (Beetle 1960). In common with big sagebrush and other dwarf sagebrush species, *A. arbuscula* is easily killed by fire and, because it is a nonsprouting species, its recovery from fire extends over a protracted time period (Britton and Ralphs 1979, Bunting et al. 1987). Fire rotations in *A. arbuscula* communities are estimated to range from 90 to 300 years, which is up to 4 times longer than in *A. tridentata* communities (Baker 2006, Bukowski and Baker 2013). Herbaceous species assemblages in *A. arbuscula* communities often overlap with *Artemisia tridentata* ssp. *wyomingensis* (Beetle and A.L. Young) S.L. Welsh (Wyoming big sagebrush) and *Artemisia tridentata* ssp. *vaseyana* (Rydb.) Beetle (mountain big sagebrush) communities (Hironaka et al. 1983, Shiflet 1994). Thus, herbaceous response to fire in *A. arbuscula* communities may be similar to understory recovery following fire in big sagebrush communities. Because fuel loading is significantly lower in *A. arbuscula* than *A. tridentata* communities (Reiner et al. 2010), it is possible that fire severities and damage to herbaceous understories are reduced.

Fire is a concern in sagebrush systems with low ecological resistance and resilience attributes, particularly low-elevation, warm-dry areas (e.g., *A. t.* ssp. *wyomingensis* alliance) because of their vulnerability to conversion to exotic annual grassland, mainly *Bromus tectorum* L. (cheatgrass) (Chambers et al. 2014a, 2014b). Sagebrush communities at higher elevations (e.g., *A. t.* ssp. *vaseyana* alliance) with increased precipitation and cooler temperatures have high ecological resistance and resilience and readily recover after fire (Chambers et al. 2007, 2014a, Freund et al. 2021). The response of *A. arbuscula* communities to fire is likely to vary and display a range of recovery potentials given the species' wide distribution from low to high elevation across the western United States.

We evaluated shrub cover and herbaceous cover, density, and yield responses to prescribed fire in intact *A. arbuscula* var. *arbuscula* (*A. arbuscula*) steppe in southeastern Oregon. Intact plant communities as defined by Davies et al. (2006) meet the following criteria: (1) the understory is dominated by native perennials, (2) exotic species are a minor to nonexistent component, and (3) sites are dominated by mature sagebrush (no recorded fire at sites for >50 years). Our study hypotheses were based on fire effects and recovery in intact big sagebrush communities (e.g., Miller et al. 2013, Bates et al. 2019); thus, (1) fire would largely eliminate *A. arbuscula* cover, with no measurable recovery within the first decade postfire; (2) herbaceous yield would be twofold greater in the burn than in the unburned control the second year after fire; (3) perennial grasses would remain the dominant herbaceous component; and (4) *B. tectorum* would increase and represent 10% of herbaceous yield within the first decade postfire.

METHODS

Site Description

The study was conducted in the High Desert Ecoregion (Anderson et al. 1998), on the Northern Great Basin Experimental Range, 56 km west of Burns, Oregon. Paired (burn, control) study sites were at elevations of 1430–1560 m on west-facing aspects with slopes from 1% to 10%. Distance between paired sites was 0.4–1.6 km. Soils series were mainly Ninemile (extremely cobbly loam) with inclusions of Carryback soils (silty clay loam) (Lentz and Simonson 1986). These soil series share several attributes; both are mollisols and are characterized by strong argillic B-horizons, and underlain by fracked bedrock at depths of 45 cm for Ninemile and 62 cm for Carryback. Carryback soils have thicker A-horizons and deeper soil profiles, making them more productive. Most precipitation arrives in winter through mid-May. Crop-year precipitation (1 October–15 June) has averaged about 280 mm since the 1930s. Drought (crop-year precipitation <75% of the 80-year average) occurred in the 2012, 2013, and 2018 growing seasons, and crop year precipitation was below average in 2014.

Artemisia arbuscula var. *arbuscula* (Nutt.) McMinn (low sagebrush) was the dominant shrub. Big sagebrush (*A. tridentata* ssp. *tridentata* Nutt. and *A. t. vaseyana*), *Chrysothamnus viscidiflorus* (Hook.) Nutt. (yellow rabbitbrush), *Eriogonum sphaerocephalum* Douglas ex Benth. (rock buckwheat) and *Linanthus pungens* (Torr.) J.M. Porter & L.A. Johnson (granite prickly phlox) were subdominant shrubs with covers <0.5%. *Juniperus occidentalis* Hook. (western juniper) has slowly expanded into these *A. arbuscula* communities though cover was low, between 0.5% and 1%. *Festuca idahoensis* Elmer (Idaho fescue) was the principal perennial bunchgrass. *Poa secunda* J. Presl (Sandberg's bluegrass), *Pseudoroegneria spicata* (Pursh) Á. Löve (bluebunch wheatgrass), *Koeleria macrantha* (Ledeb.) J.A. Schultes (prairie Junegrass), and *Achnatherum thurberianum* (Piper) Barkworth (Thurber's needlegrass) were subdominant perennial grasses. *Bromus tectorum* was present in trace amounts (<0.1% cover). Perennial forbs included *Crepis acuminata* Nutt. (taper-tip hawksbeard), *Erigeron* L. (fleabane species), *Lupinus* L. (lupine species), *Astragalus* L. (milkvetch species), and *Phlox hoodii* Richardson (Hood's phlox). Native annual forbs included *Collinsia parviflora* Lindl. (blue-eyed Mary), *Microsteris gracilis* (Hook.) Greene (slender phlox), and *Draba verna* L. (spring whitlow-grass). The sites had typical characteristics of intact, lower productivity *A. arbuscula*/*F. idahoensis* plant associations of southeastern Oregon, where sagebrush cover averages 13.6% ± 2.2%, perennial grass and forb cover averages 20.3% ± 1.5%, and invasive annual grass cover is absent or negligible (EOARC 2021).

Experimental Design and Treatment

A randomized block design was used to compare vegetation dynamics between burned (burn) and unburned (control) *A. arbuscula* sagebrush steppe. Blocking was done to remove any differences associated with soils and to increase accuracy of the results. Four 3- to 6-ha blocks, composed of two 1.5- to 3-ha plots, were randomly assigned to either the burn or control treatment in spring 2012 in an 800-ha field. Prescribed burning (strip-head fires) was done in early October (5–7 October) 2012. Fires were ignited using drip torches, and burns were largely complete across treatment plots, killing all but a few scattered low sagebrush individuals. During the burns, wind speeds varied between 12 and 24 km/h, with gusts up to 32 km/h; air temperatures were 12 to 21 °C; and relative humidity varied from 10% to 22%. Moisture content of fine fuels (herbaceous vegetation) was between 4% and 7%, and fine fuel loads ranged between 440 and 590 kg/ha. Fine fuel loads were lower than recommended levels of 700–800 kg/ha for successful prescribed burning of *A. arbuscula* communities (Wright et al. 1979, Bradley et al. 1992). The area has a long history of livestock grazing, first by domestic sheep in the early 1900s and then by cattle since the research range was organized in the late 1930s (Copeland et al. 2021). Plots were not grazed in the years 2010–2015 and 2020. Plots were grazed moderately (40% to 60% utilization) by cattle in the spring (2019), late summer (2016, 2018), and fall (2017).

Vegetation Measurements

Vegetation response to treatment was evaluated by quantifying shrub canopy and herbaceous foliar cover, perennial herbaceous density, and herbaceous yield. Three 50-m transects were randomly placed within each treatment plot. Plots were measured in late May (2012) and early June (2014, 2017, 2020). Shrub canopy cover and density were measured by species using line intercept (Canfield 1941) and belt transect (2×50 m) methods, respectively. Canopy gaps <10 cm were included in the shrub cover measurements (Boyd et al. 2007). Herbaceous foliar cover was estimated visually, by species, inside 0.2-m^2 frames located at 3-m intervals on each transect line (starting at 3 m). Perennial plant density (bunchgrasses and forbs) was determined by counting all individuals rooted inside the 0.2-m^2 frames. Herbaceous cover and density were not measured in 2020 because COVID-19 restrictions limited fieldwork.

Herbaceous yield was measured by clipping (Slatyer 1968) in early June 2012, 2013, 2014, 2017, and 2020 by functional group (i.e., perennial bunchgrasses, *Poa secunda*, tall perennial forbs, mat perennial forbs, annual forbs, and *B. tectorum*). *Poa secunda* was collected separately from other perennial bunchgrasses because it initiates growth and matures earlier in the spring (USDA 1937, Passey et al. 1982). Tall perennial forbs are highly resistant to fire damage because their growth points are belowground and they tend to be taller than the mat-forming perennial forbs. Mat perennial forbs are suffruticose forbs, often having exposed growth points, that make them vulnerable to fire damage, and tend to be <7 cm tall. Perennial grasses and forbs were harvested from 15 randomly located 1-m^2 frames per treatment plot, avoiding areas clipped in prior years. Annual forbs and *B. tectorum* were collected from 0.20-m^2 plots nested inside the 1-m^2 frames. Perennial bunchgrasses were clipped to a 2-cm stubble. *Poa secunda*, perennial forbs, *B. tectorum*, and annual forbs were clipped to near ground level. For mat perennial forbs, only half of each plant was harvested to avoid damaging the growth points. Weights for mat perennial forbs were then doubled after drying. Biomass was dried at 48 °C to a constant weight. Clippings from perennial grasses and *Poa secunda* were sorted into yield (current year's growth) and residual (previous year's growth) and weighed separately (Culley et al. 1933). Forbs and *B. tectorum* required no further sorting as all biomass consisted of current year's growth.

Statistical Analysis

Repeated measures analysis of variance using the PROC MIXED procedure (SAS Institute ver. 9.4, Cary, N.C.) was applied to a randomized complete block design to compare treatment, time (year), and time × treatment effects between burn and control treatments for plant species and functional group cover and yield, and perennial species density. An autoregressive order-one covariance structure was used because it provided the best model fit (Littell et al. 1996). Response variables included shrubs, perennial bunchgrass, *P. secunda*, tall and mat perennial forb, annual forb, and *B. tectorum*. Because of a strong year effect, we also analyzed measurement years individually using ANOVA for randomized complete block design to simplify presentation of the results and to assist in explaining interactions. Mean separation involved comparison of least squares using the LSMEANS procedure. Data were tested for normality using the SAS univariate procedure (SAS Institute ver. 9.4, Cary, NC). Data not normally distributed were log transformed to stabilize variance. Back-transformed means are reported in the results. Statistical significance of all tests was set at $P < 0.05$.

Results

Shrubs

Low sagebrush cover and density were lower in the burn treatment than in the control after fire ($P < 0.001$). In 2020, *A. arbuscula* cover in the burn treatment was 0.15% ± 0.07% versus cover in the control of 11.8% ± 0.4%. *A. arbuscula* density in the burn treatment (0.005 plants/m^2) was about 300 times less than in the control (1.42 ± 0.18 plants/m^2). Cover and density of *A. arbuscula* was only provided by plants surviving the fire, as there was no shrub recruitment during the 8 years postfire. Cover of *C. viscidiflorus* did not differ between treatments ($P = 0.365$) or across years ($P = 0.148$). Cover of *A. tridentata* and *L. pungens*, already quite low (<0.5%), did not differ between treatments ($P = 0.326$ and $P = 0.209$, respectively) or across years ($P = 0.063$ and $P = 0.251$, respectively). *Eriogonum sphaerocephalum* cover was greater in the control than the burn ($P = 0.001$) despite a cover decrease in the control ($P = 0.029$) between 2017 and 2020 from 0.42% ± 0.06% to 0.16% ± 0.08%. The decrease in *E. sphaerocephalum* cover appears to have been caused by ungulate browsing, with one or more of the culprits consisting of cattle, mule deer (*Odocoileus hemionus* [Rafinesque, 1817]), and pronghorn (*Antilocapra americana* [Ord, 1815]). All *J. occidentalis* individuals were killed on the burn treatment plots.

Ground Cover

Herbaceous cover was 1.4-fold greater in the burn treatment than the control after fire (Fig. 1A). The treatment × year interaction was significant for bare ground, litter, mosses and lichens, indicating that treatment differences occurred after fire (Fig. 1B–D). Bare ground was 1.2-fold greater in the burn treatment after fire (Fig 1B). Rock coverage, included in bare ground values, totaled about 11.5% in both treatments and was not different ($P = 0.516$). Litter cover decreased after fire and was 4- to 8-fold higher in the control in 2014 and 2017 (Fig. 1C). Moss cover was lost in the burn treatment after fire, and while mosses were beginning to recover in 2017, moss cover was 6 times less than in the control (Fig 1D). Lichen cover on the soil surface was lost with fire in the burn treatment and

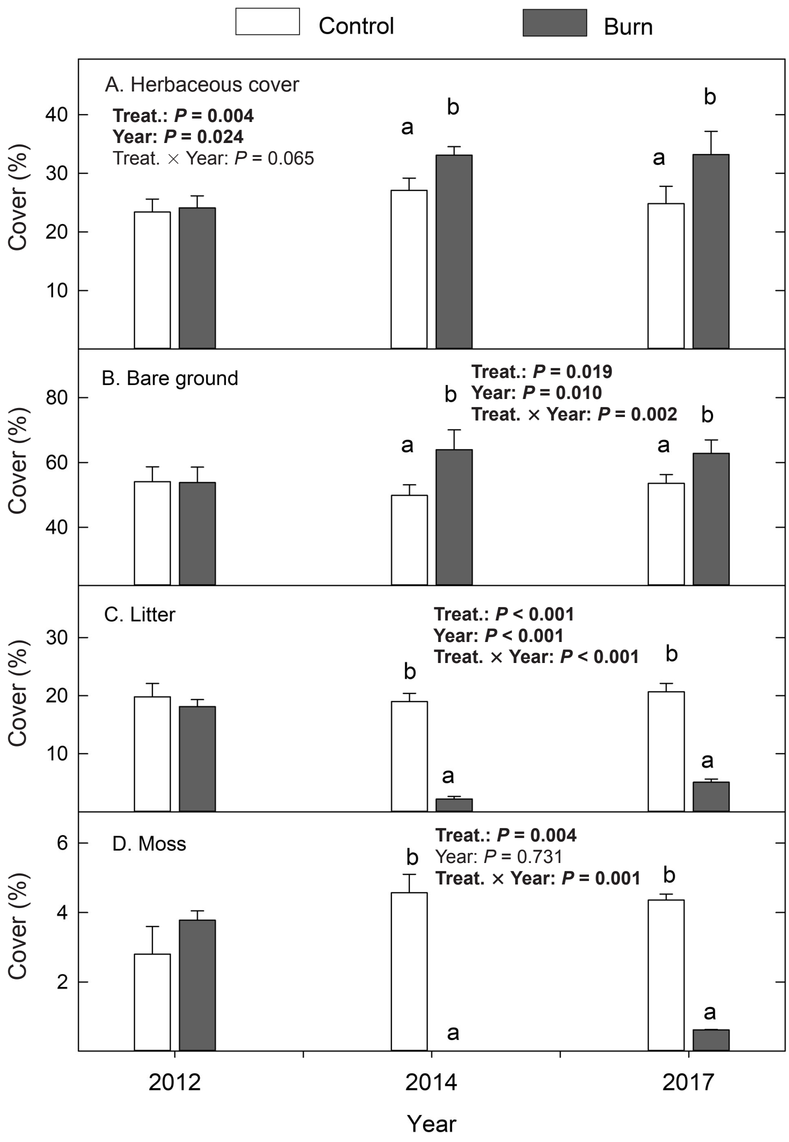

Fig 1. Cover of (*A*) herbaceous vegetation, (*B*) bare ground and rock, (*C*) litter, and (*D*) moss for the burn and control treatments in *Artemisia arbuscula* steppe, North Great Basin Experimental Range, Oregon, 2012–2017. Values represent means ± 1 standard error. Lowercase letters indicate significant differences ($P < 0.05$) between the treatments within year. Bolded *P* values indicate significant main effects and treatment (Treat.) × year interaction.

has remained far less than the control (P = 0.001). In 2017, 5 years after fire, lichen cover in the burn treatment was 0.08% ± 0.02% versus 1.5% ± 0.4% in the control.

Total Herbaceous Yield

The treatment × year interaction was significant for herbaceous yield ($P < 0.001$). Herbaceous yield was greater in the burn than the control treatment the second year after fire (2014) and has remained so into 2020. Herbaceous yield was 1.7- to 2.2-fold greater in the burn treatment ($\bar{x}$ = 1063 ± 48 kg/ha) compared to the control ($\bar{x}$ = 499 ± 8 kg/ha) between 2014 and 2020. Herbaceous yields fluctuated in both burn and control treatments in response to annual weather conditions.

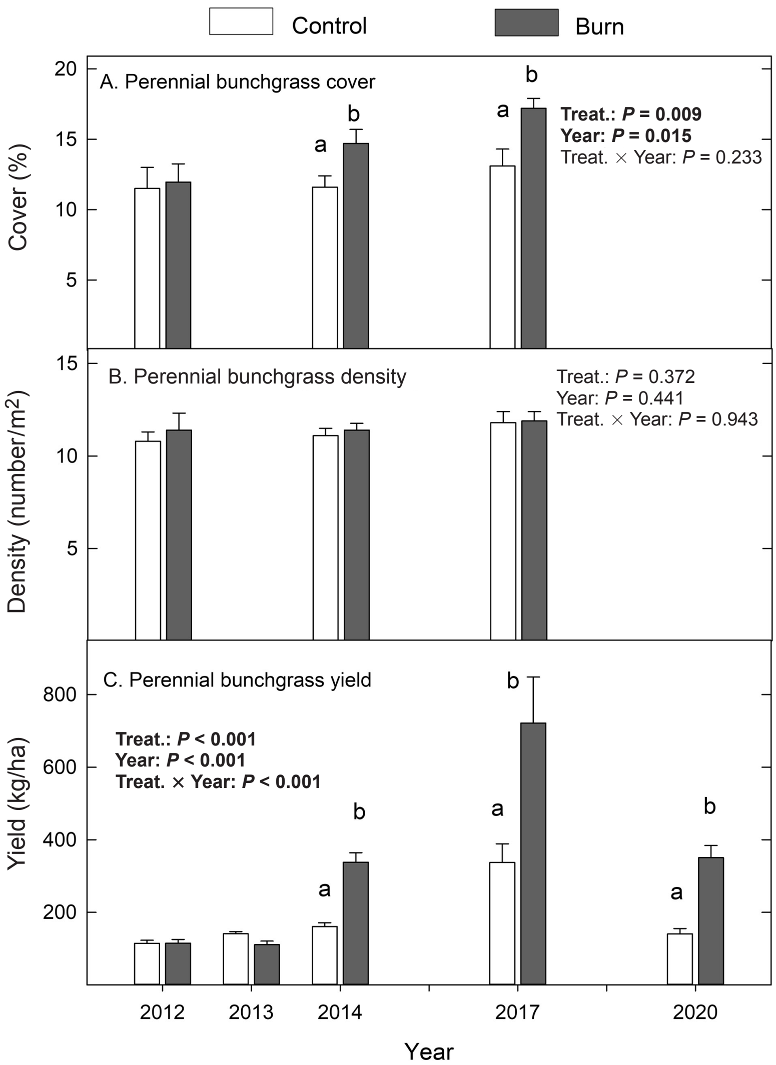

Fig. 2. Perennial bunchgrass (*A*) canopy cover, (*B*) density, and (*C*) yield for the burn and control treatments in *Artemisia arbuscula* steppe, North Great Basin Experimental Range, Oregon, (2012–2020). Values represent means ± 1 standard error. Lowercase letters indicate significant differences ($P < 0.05$) between the treatments within year. Bolded P values indicate significant main effects and treatment (Treat.) × year interaction.

Perennial Bunchgrasses and *Poa secunda*

The year ($P = 0.015$) and treatment ($P = 0.009$) main effects were significant for perennial bunchgrass cover (Fig. 2A). In 2014 and 2017, perennial bunchgrass cover was about 1.2-fold greater in the burn treatment compared to the control. In total, perennial bunchgrass density did not differ by treatment ($P = 0.372$; Fig 2B) or across years ($P = 0.441$). The treatment × year interaction was significant for perennial bunchgrass yield ($P < 0.001$). Perennial bunchgrass yield was 2- to 2.5-fold greater in the burn treatment compared to the control between 2014 and 2020 (Fig 2C).

Several bunchgrass species increased after fire (Supplementary Material 1). Cover of *P. spicata* increased 1.8-fold ($P = 0.031$) to 4.2% ± 0.7% by 2017, and density increased 1.3-fold ($P = 0.031$) in the burn treatment relative to the control. Cover of *K. macrantha* increased 1.5-fold ($P = 0.006$) to 2.7% ± 0.4% by 2017 in the burn treatment. After fire, density of *A. thurberianum* increased ($P = 0.007$)

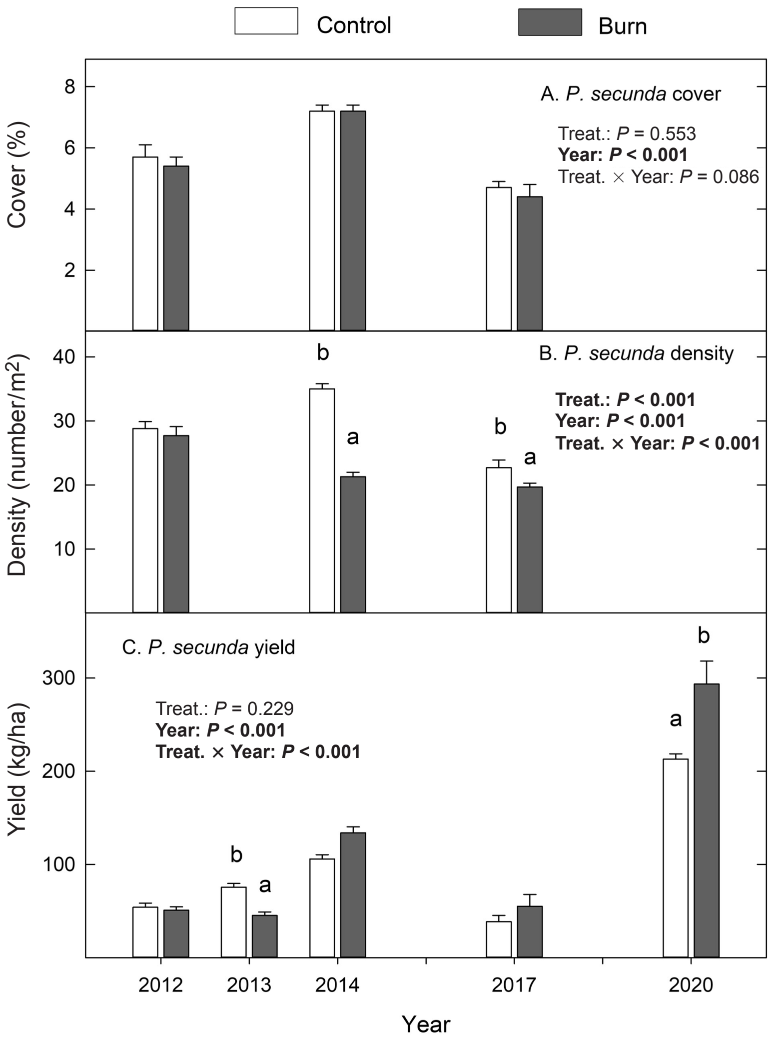

Fig. 3. *Poa secunda* (*A*) canopy cover, (*B*) density, and (*C*) yield for the burn and control treatments in *Artemisia arbuscula* steppe, North Great Basin Experimental Range, Oregon, 2012–2020. Values represent means ± 1 standard error. Lowercase letters indicate significant differences ($P < 0.05$) between the treatments within year. Bolded P values indicate significant main effects and treatment (Treat.) × year interaction.

and was 1.4-fold greater in the burn treatment (1.18 ± 0.18 plants/m^2) compared to the control (0.82 ± 0.21 plants/m^2).

Cover of *P. secunda* did not differ between treatments ($P = 0.533$) but did vary among years ($P < 0.001$; Fig. 3A). The treatment × year interaction was significant for density of *P. secunda* ($P < 0.001$; Fig. 3B), as *P. secunda* density was 1.6 times greater in the control than the burn treatment in 2014 and 2017. The treatment × year interaction was significant for *P. secunda* yield ($P < 0.001$; Fig 3C), with yield 1.7-fold greater in the control in 2013 ($P < 0.003$) and 1.4-fold greater in the burn treatment in 2020 ($P < 0.046$).

Tall Perennial Forbs

Overall, tall perennial forb cover and density only varied by year (Fig. 4A, B), increasing by about 1.6-fold in the control and 2-fold in the burn treatment between 2012 and 2017. Only in the second year after fire (2014) was tall forb cover and density greater (1.8- and 1.5-fold, respectively) in the burn treatment. Main effects and the interaction were not significant for tall perennial forb yield

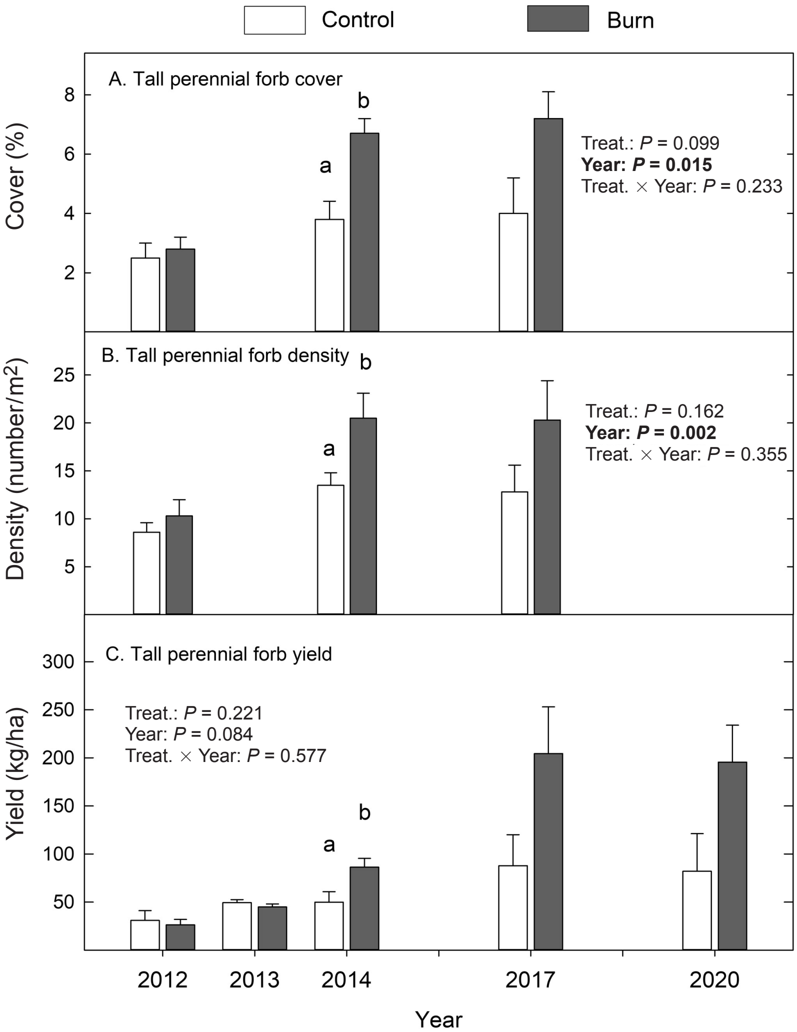

Fig. 4. Tall perennial forb (*A*) canopy cover, (*B*) density, and (*C*) yield for the burn and control treatments in *Artemisia arbuscula* steppe, North Great Basin Experimental Range, Oregon, 2012–2020. Values represent means ± 1 standard error. Lowercase letters indicate significant differences ($P < 0.05$) between the treatments within year. Bolded *P* values indicate significant main effects and treatment (Treat.) × year interaction.

(Fig. 4C). In only one year, 2014, was tall forb yield significantly greater in the burn treatment than in the control. Although tall perennial forb yields in the burn did not statistically differ from the controls, means were 116 and 154 kg/ha more in the burned sites in 2017 and 2020, respectively.

No species in the tall forb group declined in cover or density in response to fire (Supplementary Material 1). Cover ($P = 0.043$) and density ($P = 0.012$) increased for *Lupinus caudatus* Kellogg (tailcup lupine) after fire, representing about 15% of tall forb cover and 3% of tall forb density, while being rare or absent from the controls. Cover of *C. acuminata* was 1.8- to 2-fold greater in the burn treatment after fire ($P = 0.047$). Most tall forb response to fire was evident in density measurements. Densities increased and were 1.4- to 2.9-fold greater in the burn treatment compared to the control for *Astragalus purshii* Douglas ex Hook. (woollypod milkvetch; $P = 0.019$), *Calochortus macrocarpus* Douglas (sagebrush lily; $P = 0.018$), *C. acuminata* ($P < 0.001$), *Nothocalais troximoides* (A. Gray) Greene (sagebrush dandelion; $P < 0.001$), and

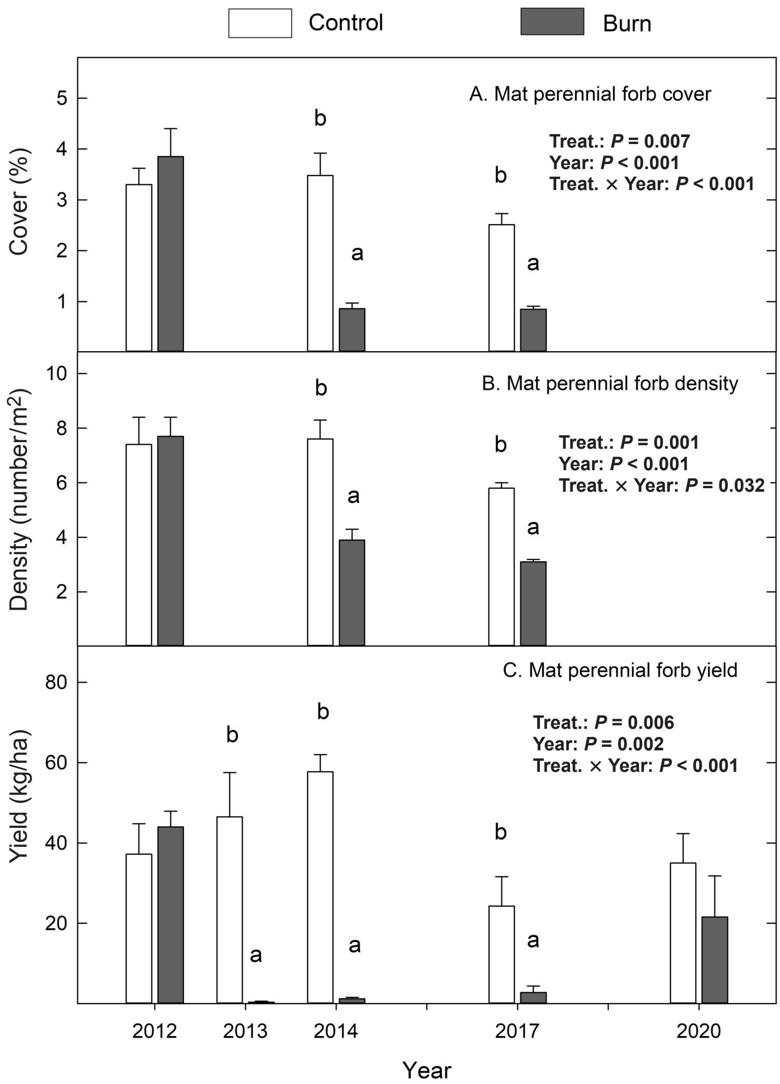

Fig. 5. Mat perennial forb (*A*) canopy cover, (*B*) density, and (*C*) yield for the burn and control treatments in *Artemisia arbuscula* steppe, North Great Basin Experimental Range, Oregon, 2012–2020. Values represent means ± 1 standard error. Lowercase letters indicate significant differences ($P < 0.05$) between the treatments within year. Bolded *P* values indicate significant main effects and treatment (Treat.) × year interaction.

Senecio integerrimus Nutt. (lambstongue ragwort; $P = 0.019$) (Supplementary Material 1).

Mat Perennial Forbs

In the burn treatment, there was a significant decline in mat perennial forb cover, density, and yield (Fig. 5A–C). Mat forb cover and density were 2.5- to 3.5-fold greater and 1.8-fold greater, respectively, in the control than the burn treatment following prescribed fire. Mat forb yield was 6- to 40-fold greater in the control than the burn treatment between 2013 and 2017 (Fig. 5C). In 2020, yield did not differ between treatments. In the control, mat forb cover and density declined by 25% and yield decreased 60% between 2014 and 2020.

In the burn treatment, *P. hoodii* cover ($P < 0.005$) and density ($P < 0.001$) decreased over 90% after fire (Supplementary Material 1). There was a small decline in density of about 30% for *Astragalus obscurus* S. Watson (arcane milkvetch; $P = 0.002$). *Erigeron linearis* (Hook.)

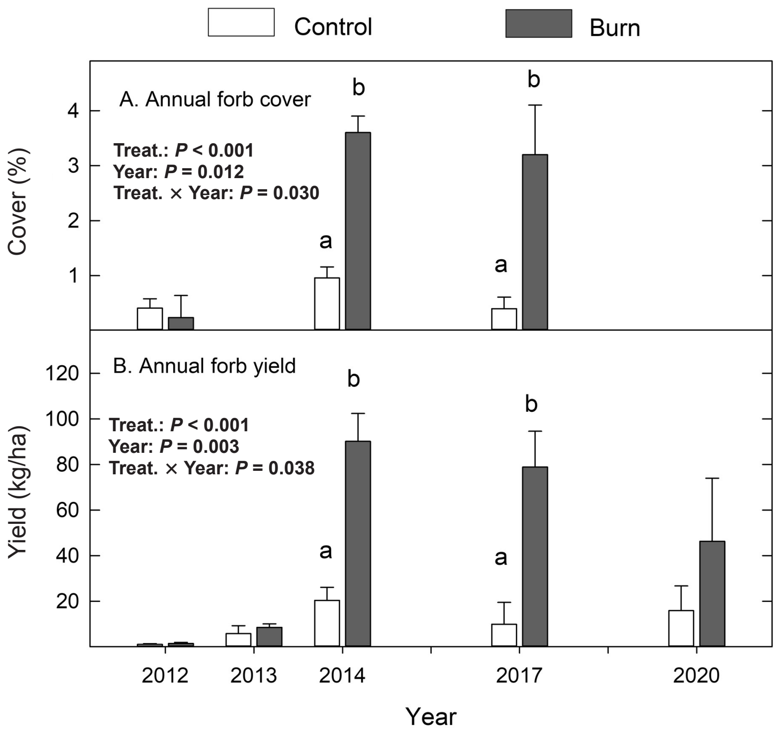

Fig. 6. Annual forb (*A*) canopy cover and (*B*) yield for the burn and control treatments in *Artemisia arbuscula* steppe, North Great Basin Experimental Range, Oregon, 2012–2020. Values represent means ± 1 standard error. Lowercase letters indicate significant differences ($P < 0.05$) between the treatments within year. Bolded P values indicate significant main effects and treatment (Treat.) × year interaction.

Piper (desert yellow fleabane) increased 1.8-fold in cover ($P = 0.009$) and density ($P = 0.034$) and was greater in the burn treatment than the control treatment the fifth year after fire (2017).

Annual Forbs and *Bromus tectorum*

Cover and yield of annual forbs were significant for the treatment × year interaction (Fig. 6A–B). Treatment differences were only evident the second year after fire (2014) when annual forb cover and yield were 3.6- and 4.5-fold greater, respectively, in the burn treatment.

Between 95% and 99% of annual forb cover in the control and burn treatments was provided by native annuals. Annual forbs that increased in cover (4- to 11-fold) following fire in the burn treatment were *C. parviflora* ($P = 0.014$), *Epilobium brachycarpum* C. Presl (tall willowherb; $P = 0.006$), *Gayophytum diffusum* Torr. & A. Gray (spreading groundsmoke; $P = 0.005$), *Leptosiphon septentrionalis* (H. Mason) J.M. Porter & L.A. Johnson (northern Linanthus; $P = 0.009$), *Phacelia linearis* (Pursh) Holz. (threadleaf phacelia; $P = 0.034$), and *M. gracilis* ($P = 0.006$) (Supplementary Material 1).

Bromus tectorum cover increased and was 3-fold greater in the burn treatment in 2017, 5 years after fire (Fig 7A). Yield of *B. tectorum* was significant for the treatment × year interaction (Fig. 7B). Treatment differences were evident the second year (2014) and eighth year (2020) after fire when yields were 20- and 50-fold greater in the burn treatment.

DISCUSSION

Artemisia arbuscula Response

The initial response to fire as well as postfire recovery of *A. arbuscula* developed as we hypothesized. Fire eliminated *A. arbuscula* cover, and there was no recruitment of new plants 8 years postfire. The absence of *A. arbuscula* recruitment on our sites was akin

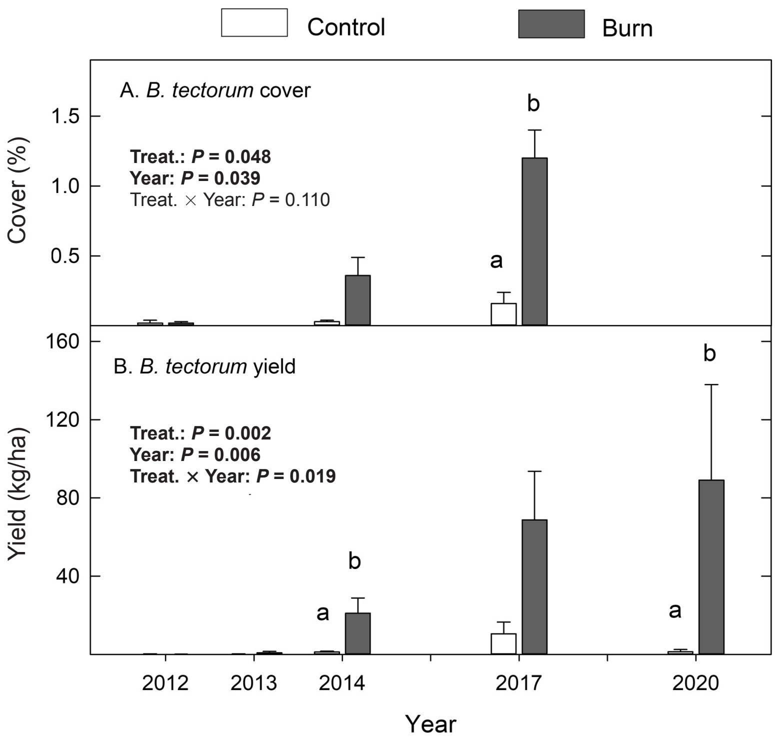

Fig. 7. *Bromus tectorum* (*A*) canopy cover and (*B*) yield for the burn and control treatments in *Artemisia arbuscula* steppe, North Great Basin Experimental Range, Oregon, (2012–2020). Values represent means ± 1 standard error. Lowercase letters indicate significant differences ($P < 0.05$) between the treatments within year. Bolded P values indicate significant main effects and treatment (Treat.) × year interaction.

to *A. t. wyomingensis* after fire. Recovery of *A. t. wyomingensis* after fire is slow and has been estimated to span periods between 50 and 250 years (Baker 2006, 2011, Shinneman and McIlroy 2016, Bates et al. 2019), while recovery of *A. t. vaseyana* occurs within 25 to 85 years (Zeigenhagen and Miller 2009, Nelson et al. 2014, Moffet et al. 2015).

The lack of *A. arbuscula* recruitment may have been influenced by pre- and postfire weather. Drought conditions (<75% average precipitation) prevailed in 2012 and 2013, which may have limited seed production in 2012 and seedling recruitment in 2013, the year after fire.

The recovery of *A. tridentata* species after fire is dependent on establishment from seed (Tisdale and Hironaka 1981), and recruitment is linked to wetter-than-average winters and higher snow cover (Cawker 1980, Maier et al. 2001). *Artemisia tridentata* recovery rate is also fastest when seedling establishment occurs within 1–4 years postfire (Blaisdell 1953, Walhof 1997, McDowell 2000, Ziegenhagen 2003). All these elements were lacking on the *A. arbuscula* sites in 2013 and 2014. In addition, rapid recovery and site occupancy by herbaceous plants limit sagebrush seedling establishment (Davies et al. 2017). On the *A. arbuscula* sites, the herbaceous component had increased substantially by the second year postfire, which may have interfered with shrub recruitment.

However, our results represent only a few sites, all located in close proximity. *Artemisia tridentata* recovery is highly variable, resulting from a number of factors, including geographic location, seed availability, seedling establishment, site and environmental characteristics, weather, fire severity and size, and species type (Innes 2017). *Artemisia arbuscula* communities are widespread in the Great Basin, and like big sagebrush species, postfire recovery doubtless exhibits a continuum of response as affected by site characteristics and the aforementioned factors.

Postfire Community

Herbaceous recovery at the *A. arbuscula* sites was similar to that of many intact *A. t. wyomingensis* and *A. t. vaseyana* plant communities after prescribed fire and wildfire (Bates et al. 2011, Ellsworth et al. 2016). Typically, 2 to 3 years are necessary for herbaceous yield and cover to surpass unburned areas (Davies et al. 2007, Miller et al. 2014, Bates et al. 2019). In the current study, herbaceous cover and yield increased the second year after fire, though yields failed to double as was hypothesized within that time frame. Doubling of herbaceous yield occurred between the third and fifth year postfire. The increases in herbaceous yield and cover result from greater availability of soil water and nutrients after fire in sagebrush systems (Davies et al. 2007, Roundy et al. 2014b).

Native species dominated the postfire community, representing about 94% of total yield, slightly below the control where native species composed 99% of total yield. This would indicate that the study sites had high resistance to exotic plant invasion and were resilient to fire. Postfire herbaceous yield composition in intact *A. t. wyomingensis* and *A. t. vaseyana* plant communities has been highly variable, with natives composing between 50% and 98% of total yield (Ellsworth et al. 2016, Bates et al. 2019, 2020, Davies and Bates 2020, EOARC 2021).

The loss of biocrust cover and diversity resulting from fire has been measured elsewhere in sagebrush steppe (Johansen et al. 1984, Hilty et al. 2004, Root et al. 2017). Star moss (*Tortula ruralis* [Hedw.] Gaertn., Mey. & Scherb.), the main biocrust on our sites, and other mosses and lichens were concentrated beneath shrubs and within bunchgrass canopies and were immediately lost with burning. The lack of postfire recovery of biocrust in early succession is consistent with other sagebrush steppe communities (Condon and Pyke 2018).

Perennial Bunchgrasses and *Poa secunda*

Perennial grasses remained the dominant herbaceous component, with perennial bunchgrasses and *Poa secunda* representing about 70% of total yield and total cover in both treatments. The 2- to 2.5-fold increase in yield, 30% increase in cover, and slight density increases of perennial bunchgrasses are similar to postfire recovery in *A. tridentata* plant communities. Studies in intact *A. tridentata* steppe in the Great Basin report 2- to 3-fold increases in yield and 10% to 50% increases in canopy cover of perennial bunchgrasses occurring by the second or third year following fire (Davies et al. 2007, Bates et al. 2009, 2019, Rhodes et al. 2010, Roundy et al. 2014a, Davies and Bates 2020). Annual weather variation also influenced perennial bunchgrass yield in burn and control treatments. Bunchgrass yields in 2020, in both treatments, were about half of their respective values measured in 2017. The winter (November–March) of 2019–2020 was drier than average (71% of normal), which likely limited perennial bunchgrass production in 2020. While spring precipitation (April–May) was 110% of normal, it arrived in small events (<15 mm) that likely did not penetrate much more than 6–7 inches into the soil profile, which would mostly benefit early-growing-season, shallow-rooted species, especially *P. secunda*.

The response of *P. secunda* after fire in sagebrush steppe varies from substantial decreases to large increases in cover and yield (Bates et al. 2011, 2019). In our study, *P. secunda* density decreased after fire but without a lasting effect on cover and yield. In both control and burn treatments, *P. secunda* yield was highly responsive to year, evidenced by high yields in 2020. Others have reported high annual variability in *P. secunda* yield as a result of timing and amount of precipitation (Passey et al. 1982, Sneva 1982). The timing of precipitation is probably a key determinant of *P. secunda* annual yield (Bates et al. 2006). Precipitation from October to June was greater in 2017 (251 mm) than in 2020 (218 mm), but precipitation between mid-April and mid-May was 3-fold greater in 2020 (52 mm) than in 2017 (18 mm). Mid-April to mid-May is the major period of growth for *P. secunda*; thus, higher spring precipitation may explain the large increase in its yield in 2020 compared to other measurement years.

Perennial Forbs

Overall, perennial forbs have generally not responded following fire with increased (or decreased) yield, cover, and abundance in intact *A. t. wyomingensis* (Cook et al. 1994, Hosten and West 1994, West and Yorks 2002, Wrobleski and Kauffman 2003, Beck et al. 2009, Rhodes et al. 2010, Bates et al. 2011, 2017, Ellsworth et al. 2016) and *A. t. vaseyana* (Fischer et al. 1996, Nelle et al. 2000, Davies et al. 2012) plant communities. In only a few studies have perennial forb cover and yield responded positively to fire (Martin 1990, McDowell 2000, Bates et al. 2011). The general lack of response should not be interpreted to mean that perennial forbs are not affected by fire. Studies that evaluate species or groups of species regularly show a variable response to fire, with some species increasing, some expressing no change, and others decreasing in cover, abundance, yield, flowering, and size (Wrobleski and Kauffman 2003, Miller et al. 2013, Bates et al. 2017, Love and Cane 2019). This was evident in our study where cover, density, and yields responded differently to fire based on the major forb grouping (tall forb, mat forb) and by species (Supplementary Material 1).

The lack of consistent, overall yield response of tall perennial forbs was likely influenced by site differences. For example, in 2017, tall perennial forb yields ranged between 34 and 465 kg/ha (burn treatment) and 22 and 259 kg/ha (control) among the 4 sites. These yield ranges result in high variation among individual sites resulting in nonsignificant treatment differences. Others have concluded that the frequent lack of perennial forb yield or cover response to fire in sagebrush steppe results from subtle differences in site characteristics, especially soil type and topographic location (Koniak 1985, Miller et al. 2014, Bates et al. 2017). Similar to other work, we measured species-specific responses to fire in the tall forb group. *Lupinus caudatus* increased in cover and density, and densities of *A. purshii*, *Calochortus macrocarpus*, Cichorieae tribe members (*C. acuminata*, *N. troximoides*), and *S. integerrimus* also increased. Others have measured increased abundance of *L. caudatus* and Cichorieae tribe members after fire in *A. t. wyomingensis* (Young and Evans 1978) and *A. t. vaseyana* (Blaisdell 1953, Mangan and Autenrieth 1984, Martin 1990, Pyle and Crawford 1996, McDowell 2000, Davis and Crawford 2015) plant communities. However, the lack of a fire effect, positive or negative, for many tall forb species suggests that they survived the fire but were unable to capitalize on available resources to increase in either cover or density postfire.

Mat-forming perennial forbs are vulnerable to fire damage because their growth points are unprotected by the soil surface (Paysen et al. 2000, Bates et al. 2011, Miller et al. 2013). Depending upon site characteristics and fire severity, mat perennial forbs are slightly to severely reduced by fire (Paysen et al. 2000, Bates et al. 2011, Miller et al. 2013). Overall, mat perennial forb cover, density, and yield declined dramatically following fire in the *A. arbuscula* sites, with much of the decline resulting from *P. hoodii* being largely eliminated. Others have measured severe reductions (Archibold et al. 2003, Bates et al. 2011) to large increases (Akinsoji 1988) in *P. hoodii* density or cover after fire. Recovery of mat perennial forbs in the burn treatment coupled with decreases in the control resulted in no treatment differences for the response variables 8 years (2020) after fire. The cause of increase in the burn treatment was from *Erigeron* species, especially *E. linearus*. Seeds of *Erigeron* species are wind dispersed, which likely contributed to *E. linearus* density increases in the burn treatment. The decrease in cover, density, and yield of mat perennial forbs in the control is unknown but probably a result of environmental conditions (e.g., drought in 2012–2013 and several dry years, 2014 and 2020) or a natural population cycle.

Annual Forbs and *Bromus tectorum*

The increases in cover and yields of annual forbs in our study is a predictable result following fire in most *Artemisia* communities of western North America (Miller et al. 2014). Postfire annual forb response in our study was dominated by native species. Nonnative forbs *Alyssum desertorum* Stapf (desert alyssum) and *Ceratocephala testiculata* (Crantz) Roth (burr buttercup) were present but did not increase, and cover was <0.1%. The cover and yield responses of annual forbs on the *A. arbuscula* sites are similar to results reported in intact *A. t. vaseyana* communities where native annual forbs commonly dominate this life form after fire (Bates et al. 2017, 2019). Annual forb composition following fire in intact *A. t. wyomingensis* communities varies with nonnatives (Bates et al 2011, 2017, 2019) or natives (Bates et al. 2011, Ellsworth et al. 2016) composing most of the annual forb component.

The native annual forb species (e.g., *C. parviflora*, *E. brachycarpum*, *G. diffusum*, *L. septentrionalis*, *P. linearus*, and *M. gracilis*) that increased in cover after burning in the *A. arbuscula* communities were similar to species and genera that regularly increase after fire in *A. tridentata* communities of eastern Oregon (Pyle and Crawford 1996, Bates et al. 2011, Davis and Crawford 2015, Ellsworth et al. 2016).

Bromus tectorum has become an established part of intact sagebrush steppe plant communities, though commonly present in only trace amounts, as herbaceous understories are dominated by native perennials (Davies et al. 2007, 2012, Miller et al. 2014, Bates et al. 2019, EOARC 2021). However, after fire, *B. tectorum* has consistently increased in cover and yield, though response levels vary considerably depending on residual herbaceous perennial composition and abundance as well as site characteristics (Chambers et al. 2007, Davies et al. 2009, Swanson et al. 2018, Rodhouse et al. 2020, Freund et al. 2021). In our study, *B. tectorum* cover and yield increased in the *A. arbuscula* sites as a result of the fire treatment, but this grass has remained a relatively minor herbaceous component. In 2017 and 2020, *B. tectorum* yield was 6% and 8.6% of total herbaceous yield, respectively. The increase in *B. tectorum* began the second year after fire. In *A. t. wyomingensis* and *A. t. vaseyana* communities, increases in *B. tectorum* typically occur 2 to 3 years postfire (Miller et al. 2014, Davies and Bates 2020), though several studies have reported longer response times, from 5 to 13 years (Bates et al. 2013, 2020). *Bromus tectorum* should remain a minor component of the herbaceous community in the *A. arbuscula* sites because herbaceous perennial composition and abundance remained intact and dominated postfire.

Conclusions

The study demonstrated that intact *A. arbuscula* plant communities have the potential to express high community resilience and resistance in response to prescribed fire disturbance in the presence of low levels of invasive, exotic annual grasses. For land management practitioners, this has relevant implications for evaluating fire effects as well as forecasting recovery in comparable, intact *A. arbuscula* plant communities following prescribed fire. Apart from sound grazing management, these sites do not need further weed control or seeding to recover from fire. Vegetation response to prescribed fire and recovery in the *A arbuscula* sites was similar in many respects to prescribed fire impacts and early succession in intact *A. t. wyomingensis* or *A. t. vaseyana* plant communities where native perennial grasses and forbs dominate postfire.

Nonetheless, the study sites represent only a fraction of representative, intact A. *arbuscula* associations found just within the High Desert Ecoregion (EOARC 2021), and thus, community response is likely to vary with different burning conditions, such as occur during wildfire. Therefore, the results from this study should be interpreted with caution until more extensive and comprehensive information becomes available regarding prescribed fire effects in intact *A. arbuscula* plant communities. In addition, communities experiencing high-severity fire, as may arise during wildfire, and *A. arbuscula* communities having greater prefire invasive weed presence should not be anticipated to develop similarly high levels of community resilience and resistance.

Supplementary Material

One online-only supplementary file accompanies this article (https://scholarsarchive.byu.edu/wnan/vol82/iss1/5).

Supplementary Material 1. Repeated measures analysis for treatment (Treat) and year effects and the interaction of herbaceous species cover and density in *Artemisia arbuscula* plant communities, Northern Great Basin Experimental Range, Oregon, 2012–2017.

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