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Original Research

Initial Divergent Postfire Recovery Converges Over the Long-term: A Case Study in Juniper-Encroached Sagebrush Steppe☆

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ABSTRACT

Reduced fire frequency is recognized as a main cause of piñon–juniper (*Pinus–Juniperus* L.) expansion in western North American sagebrush steppe and grasslands. Piñon–juniper woodland control using prescribed fire and mechanical treatments have increased the past three decades with the goal of restoring sagebrush steppe plant communities. Factors shaping the response of sagebrush steppe communities following woodland treatment include shrub and herbaceous composition, level of tree dominance, and site characteristics. We compared vegetation recovery spanning 20 yr following prescribed fire on mid-succession and late-succession western juniper (*Juniperus occidentalis* Hook.) woodlands on Steens Mountain, Oregon. Our objective was to evaluate vegetation dynamics between early (first decade) and later successional (second decade) time periods after fire. The first decade after fire vegetation on burned mid-succession sites were codominated by native herbaceous perennials and sprouting shrub species and on late-succession sites vegetation was codominated by nonnative cheatgrass (*Bromus tectorum* L.) and snowbrush (*Ceanothus velutinus* Dougl.). During the second decade after fire, vegetation composition converged and both mid-succession and late-succession sites were codominated by herbaceous perennials, mountain big sagebrush (*Artemisia tridentata* spp. *vaseyana* [Rydb.] Beetle), round-leaf snowberry (*Symphoricarpos rotundifolius* A. Gray) and snowbrush. Herbaceous and shrub vegetation composition of both burned woodland phases proved to be highly resilient to fire, the difference was that native shrub-herbaceous recovery on late-succession sites required about twice as much time as mid-succession sites. The resilience of both mid-succession and late-succession woodland sites was likely a product of ecological site characteristics (e.g., elevation and precipitation zone) that affords a competitive advantage for native perennial species over invasive annuals.

Key Points

- The first decade after fire vegetation on burned mid-succession woodland sites were codominated by native herbaceous perennials and sprouting shrub species and on late-succession woodland sites vegetation was codominated by snowbrush and nonnative cheatgrass.
- The second decade after fire, vegetation composition converged and both burned mid-succession and late-succession sites were codominated by herbaceous perennials, mountain big sagebrush, round-leaf snowberry, and snowbrush.
- Vegetation composition of both burned woodland phases were highly resilient to fire; the difference was that recovery on late-succession sites required about twice as much time as mid-succession sites.

Introduction

The expansion and infilling of piñon–juniper (*Pinus* L.-*Juniperus* L.) woodlands in sagebrush (*Artemisia* L.) steppe and other plant communities of the western United States is a direct consequence of reduced fire disturbance the past 150 yr (Wall et al. 2001;

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Johnson and Miller 2006; Miller et al. 2008). Historically, mean fire return intervals of between 20 and 100 yr in sagebrush steppe were effective at preventing woodland expansion and development (Miller et al. 2005, 2008; Miller and Heyerdahl 2008). Woodland development and infilling lead to a reduction of shrub and herbaceous cover and production (Miller et al. 2005; Roundy et al. 2014; Bates et al. 2019), loss of shrub-steppe wildlife habitat (Schaefer et al. 2003; Noson et al. 2006; Reinkensmeyer et al. 2007), and an increased potential for soil erosion (Pierson et al. 2007, 2013; Williams et al. 2014). In addition, fires in fully developed woodlands are of higher severity than nonwoodland and open woodland sagebrush steppe, which increases the risk of postfire invasion and dominance by exotic annual grasses, particularly cheatgrass (*Bromus tectorum* L.; Miller and Tausch 2001; Williams et al. 2023).

Since the 1950s, public and private land managers have used controlled and prescribed fire and mechanical treatments to kill trees to prevent or reverse the impacts of piñon–juniper woodland development (Valentine 1989). Factors influencing the response of sagebrush steppe communities following woodland treatment include the method of tree control, residual shrub and herbaceous composition, level of tree dominance, site characteristics (elevation, aspect, and precipitation zone [PZ]), and ecological province, resulting in variable recovery rates of shrub-herbaceous communities (Miller et al. 2014; Roundy et al. 2014; Davies et al. 2019). In general, recovery of native shrub and herbaceous components occurs earlier and more predictably after treatment on, 1) sites with lower pretreatment tree dominance levels (early succession) compared with sites with high tree dominance levels (late-succession), 2) in woodlands treated mechanically compared with prescribed fire, and 3) on cooler-wetter sites with high prefire perennial grass cover (Chambers et al. 2014, 2021; Roundy et al. 2014; Davies et al. 2019).

Lacking in piñon–juniper woodland studies are longer-term (>10 yr) assessments of vegetation succession following prescribed fire, particularly fires in mid-successional and late-successional woodland phases. Long-term evaluations are needed to provide land managers with information when developing prescribed fire treatments in woodlands and to potentially forecast postfire vegetation recovery. Short-term studies indicate that prescribed fire in early and mid-successional woodlands generally result in postfire recovery of native shrubs and understory species and fire in late-successional woodlands result in large postfire increases and potential dominance by invasive annual grasses even in higher elevation cooler-wetter plant communities (Bates et al. 2011; Roundy et al. 2014; Chambers et al. 2021). The threat of invasive annual grass increases following woodland fire treatments is of concern as annual grasses have spread into higher elevations on sites once considered highly resistant to their invasion (Compagnoni and Adler 2014; Smith et al. 2022).

We compared shrub and herbaceous recovery of mountain big sagebrush (*Artemisia tridentata* spp. *vaseyana* [Rydb.] Beetle) steppe 20 yr following prescribed fire in mid-successional and late-succession western juniper (*Juniperus occidentalis* Hook.) woodlands. This is a continuation of a study reporting results of early succession vegetation recovery (2004–2012) in the two woodland phases (Bates et al. 2014a). There were two main results reported by Bates et al. (2014a): 1) mid-successional sites comprised native perennial herbaceous vegetation before and after fire and the postfire shrub layer was codominated by sprouting species and snowbrush (*Ceanothus velutinus* Dougl.); and 2) late-successional sites shifted from native species to postfire dominance by cheatgrass in the herb layer and the shrub layer was dominated by *C. velutinus.*

The objective of our longer-term assessment was to determine if our earlier conclusions persisted over a longer time scale. We hypothesized that mid-successional sites would maintain their resilience and native herbaceous and shrub vegetation would continue to dominate postfire and late-successional woodlands having lost site resilience after fire, would remain dominated in the understory by cheatgrass.

Methods

Study area and treatment

Study sites were situated in Kiger Canyon, Steens Mountain, southeast Oregon (45°54′N, 118°40′W). Elevation of the study site ranged from 1 700 m to 1 990 m and aspects were from east to north. The ecological sites were a Loamy (12–16 [304–406 mm] PZ) and Deep Loamy (12–16 PZ; Natural Resource Conservation Service [NRCS] 2010) and were classed as mountain big sagebrush/Idaho fescue (*Festuca idahoensis* Elmer)-bluebunch wheatgrass (*Pseudoroegneria spicata*) plant associations. Soils are a complex of Westbutte-Lambring (Loamy-skeletal, mixed, frigid Pachic Haploxerolls) series formed in residuum and colluvium including basalt, andesite, rhyolite, and welded tuff and are moderately deep (60–150 cm deep) and well-drained (NRCS 2006). Twelve mid-succession and nine late-succession woodlands, each 0.63 ha in area, were established in May 2003. Mid-succession and late-succession woodlands will be referred to as phase 2 and phase 3 woodlands, respectively, as developed by Miller et al. (2005) for classifying woodland phase. In phase 2 woodlands, juniper, shrubs, and the herbaceous layers codominate, tree recruitment and cone production are moderate to high, and the shrub layer is intact to thinning (Maestas et al. 2015). In phase 3 woodlands, juniper is dominant, tree recruitment and cone production are low to none, and the shrub layer reduced by 75% to being largely absent.

The phase 2 and phase 3 woodlands were scattered within an area of 15 km^2 and were independent of each other. Nine of the phase 2 plots were located adjacent to phase 3 woodland plots, with others located randomly within the study area. The phase 2 woodland sites had greater initial cover and density of herbaceous and shrub species than phase 3 woodland sites (Bates et al. 2014a). Preburn cover and density of western juniper were 1.8 times and 1.5 times greater in the phase 3 woodlands than the phase 2 woodlands, respectively (Bates et al. 2014a). Preburn herbaceous cover was 2.5 times greater in the phase 2 than the phase 3 sites. Perennial grass cover was four times ($P < 0.001$) greater and perennial forb cover was two times greater ($P < 0.001$) in phase 2 than the phase 3 woodlands. Cheatgrass was not present or present in only trace amounts (<0.1%) prior to woodland treatment.

Prior to prescribed fire, about one-third of the juniper (>3 m tall) were cut to increase dry fuel loads. Trees were cut in May–June 2002 and dried for 16 to 17 mo. On phase 2 woodlands, an average of 47 $\pm$ 8 (range, 16–91) trees were cut per hectare. On phase 3 woodlands, an average of 71 $\pm$ 9 (range, 43–110) trees were cut per hectare. Prescribed fires were applied on 6 October 2003 by Burns District-Bureau of Land Management personnel. Prescribed fires were spot head fires ignited by heli-torch. Weather conditions were typical for fall burning in the northern Great Basin and fires were rated high severity because of high bunchgrass mortality, complete consumption of aboveground shrub and herbaceous vegetation, and partial to complete burning of 1 000 fuels (7.6–20.3 cm wood diameter for the cut juniper trees; Bates et al. 2014a, 2014b). Livestock were excluded for 2 yr prior to burning to increase fine fuel loads. The area was largely rested from grazing in 2003 to 2006, and 2012. In 2004, about 50 cow-calf pairs briefly accessed the burn area in late summer (August) following the herbaceous growing; grazing utilization was estimated at 10% on about 20% of the area. The area was moderately grazed (0.12–0.20 ha $\cdot$ AUM^{-1}; animal unit month) in late June–August (35–50% estimated utilization) in 2007–2011, and 2013–2023.

Measurements

Vegetation was measured in June (2003–2007, and 2009) and July (2012, 2018, and 2023). At each plot, four 50-m transects were permanently established with transects spaced 25 m apart. Canopy cover of western juniper and shrubs were estimated by line intercept along transects (Canfield 1941). Density of mature juniper (>2 m height) was estimated by counting individuals inside five, 6×50 m belt transects. Density of shrubs and juvenile juniper (<2-m height) were estimated by counting all plants inside five, 2×50 m belt transects. Herbaceous percent canopy cover (perennials and annuals) and herbaceous perennial density was measured by species inside 0.2 m^2 frames (0.4×0.5 m; Daubenmire 1968). Herbaceous percent canopy cover was ocularly estimated and herbaceous perennial density was measured by counting rooted individuals inside each frame. Frames were placed every 3-m along transects.

Statistical analysis

Repeated measures analysis of variance for a completely randomized design using a mixed model (PROC MIX; SAS 2013) was used to test for year, woodland phase, and year by phase interaction for herbaceous, shrub, and western juniper response variables. The study lacks woodland controls therefore comparisons made between pre and post treatment response variables and woodland phases in other piñon–juniper woodlands should be interpreted with caution. Response variables were western juniper cover and density, shrub cover and density (species), herbaceous cover (species and life form) and density (perennial species and lifeform), and soil surface cover (bare ground, litter, and biological crust [moss and lichen]). Herbaceous life forms were grouped as Sandberg's bluegrass (*Poa secunda* Vasey), perennial bunchgrasses (e.g., Idaho fescue, mountain brome [*Bromus marginatus* Nees ex Steud.], and bottlebrush squirreltail [*Elymus elymoides* Raf. Swezey]), rhizomatous grasses (exclusively Kentucky bluegrass [*Poa pratensis* L.]), cheatgrass, perennial forbs, and annual forbs. Sandberg bluegrass was treated as a separate life form from other perennial bunchgrasses because it initiates growth and matures earlier in the spring (United States Department of Agriculture [USDA] Forest Service 1937; Passey et al. 1982). An auto regressive order one covariance structure was used as it provided the best fit for data analysis (Littell et al. 1996). The models included year (df = 8), phase (df = 1), and the year by phase interaction (df = 8). Mean separation involved comparison of least squares (LS) using the LSMEANS statement (SAS Institute 2013). All data were tested for normality using the Shapiro–Wilk test (Shapiro and Wilk 1965) and were log-transformed before analyses when necessary. Back transformed means are reported. Significant interactions were followed by tests of simple effects at $\alpha = 0.05$. Because of strong year and year by phase effects, years were also analyzed separately using general linearized models with means separated using Tukey's range test.

Results

Ground and vegetation cover

Litter (herbaceous and juniper needles) was largely consumed by the fires resulting in high levels of exposed soil the year after fire (Figs. 1A and 1B). Litter cover was influenced by year ($P <$ 0.001) but not by phase ($P = 0.640$) or the interaction ($P = 0.514$). Litter decreased 80% from prefire levels in both phases the year after fire. The past 12 yr surface litter has collectively averaged about 28%. Bare ground declined steadily since the year after fire ($P <$ 0.001) and 20 yr after fire averaged about 30% in both phase 2 and phase 3 sites. Biological crust (moss and lichen) cover was eliminated by the fires in phase 2 and phase 3 sites ($P < 0.0001$) and has failed to recover to preburn levels, collectively averaging <1% cover 20 yr after fire.

Prescribed fires killed all remaining uncut western juniper in the phase 2 and 3 woodlands. Juniper has not reestablished on either burned phase 2 or phase 3 sites. Total shrub cover was significantly affected by the year X phase interaction ($P < 0.001$; Fig. 1C). Shrub cover was four times greater in phase 2 than phase 3 sites prior to fire ($P < 0.001$). After fire total shrub cover did not differ between phases until between 2009 and 2023 when cover was 1.3 to 2 times greater in the phase 3 sites ($P < 0.0001$). Shrub cover increased in both phase 2 and 3 sites after fire ($P < 0.001$).

Total herbaceous cover was significantly affected by the year X phase interaction ($P < 0.001$; Fig. 1D) as cover increased after fire and phases traded leads in herbaceous cover values the first 9 yr since fire. Herbaceous cover was 1.5 to 2.5 times greater in phase 2 than phase 3 sites prior to fire (2003) and the first 2 yr after fire (Fig. 1D; $P < 0.001$). In 2007, 2009, and 2012 herbaceous cover was 1.1 to 1.3 times greater in burned phase 3 sites ($P = 0.026$). Herbaceous cover did not differ between phases in 2018 and 2023 ($P = 0.237$).

Herbaceous cover on phase 2 sites was dominated by native species and native species cover was significantly greater (Fig. 2; $P < 0.001$) than on phase 3 sites preburn and after fire, although that difference has become less apparent the past 5 yr (2018 and 2023). In contrast, herbaceous cover in phase 3 sites was largely composed of nonnative species (mainly cheatgrass) between the third (2006) and ninth (2012) year after fire. The nonnative component in phase 3 sites has declined significantly since 2012 and by 2023 ($P < 0.001$) there was no difference between the two phases ($P = 0.878$).

Shrubs

Mountain big sagebrush cover and density were significantly affected by the year X phase interaction ($P < 0.001$). Prior to burning sagebrush cover (Fig. 3A) and density was three and 2.5 times greater, respectively, on phase 2 than phase 3 sites before fire. The fires reduced sagebrush cover to zero in both phases, and sagebrush cover and density has not differed between the two phases since fire. Over the past decade sagebrush cover and density has increased ($P < 0.001$) on sites of both phases. Twenty years after fire, sagebrush cover on phase 2 sites (range of 1.5–24%) is about half of its preburn cover and on phase 3 sites sagebrush cover (range of 4–22%), doubling from preburn levels. On average sagebrush cover in both phases makes up about 25% of total shrub cover. Density of sagebrush in 2023 averaged 0.29 ± 0.05 plants $\cdot$ m^{-2} on phase 2 sites and 0.28 ± 0.04 plants $\cdot$ m^{-2} on phase 3 sites.

Snowbrush was not present on either woodland phase before fire. Fires stimulated a strong year response of snowbrush from the seedbank, particularly on the phase 3 sites where it comprised 75% of total shrub cover within the first decade after fire. Cover of snowbrush was significantly affected by the year X phase interaction ($P < 0.001$; Fig. 3B). Snowbrush cover was six times greater on phase 3 than phase 2 sites in 2012 ($P < 0.001$). Since 2012 snowbrush cover declined by about 66% on phase 3 sites. Snowbrush cover was not different between phase 2 and 3 sites in 2018 and 2023 ($P = 0.587$; $P = 0.282$, respectively) and comprised about one-third of total shrub cover. In 2023, snowbrush cover on phase 2 sites ranged from 0% to 24% and on phase 3 sites cover ranged from 1.4% to 33%. Snowbrush density increased after fire with an increase that was 2 to 3 times greater in phase 3 compared with phase 2 sites between 2004 and 2012 (year X phase interaction, $P < 0.001$). Snowbrush density declined significantly on sites in both

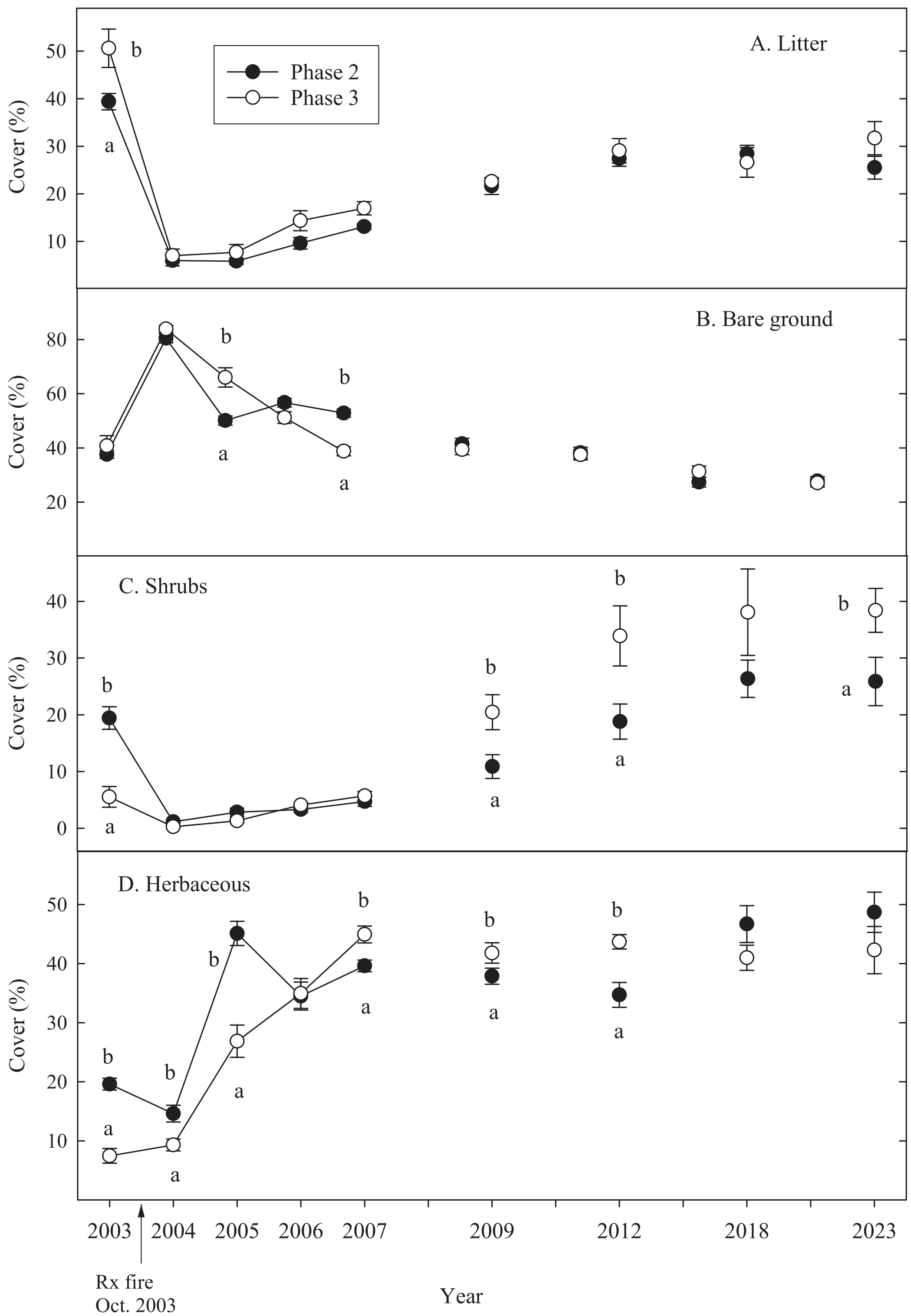

Figure 1. Ground cover (%) values in burned phase 2 and phase 3 western juniper woodlands, Steens Mountain, Oregon (2003–2023; 2003 is the prefire year): (**A**) litter; (**B**) bare ground; (**C**) shrubs; and (**D**) herbaceous. Data are means ± 1 standard error. Means sharing a common lower case letter are not significantly different ($P > 0.05$). Data for 2003–2012 years were previously published in Bates et al. (2014a).

phases ($P < 0.001$) and by 2023 there were no phase differences. Density of snowbrush in 2023 averaged 0.08 ± 0.02 plants · m^{-2} on phase 2 sites and 0.12 ± 0.04 plants · m^{-2} on phase 3 sites.

Cover and density of round-leaf snowberry was significantly affected by the year X phase interaction ($P < 0.001$; Fig. 3C). Snowberry cover regained preburn levels the fourth year after fire (2006) on phase 2 sites and the third year after fire on phase 3 sites. Cover of snowberry was about three times greater in phase 2 sites than phase 3 sites, from 2004 to 2012 ($P < 0.001$). Since 2012, snowberry cover and density have increased in phase 3 sites although not changing in phase 2 sites. There were no differences in snowberry cover ($P = 0.588$; 2018) and density ($P = 0.642$; 2023)

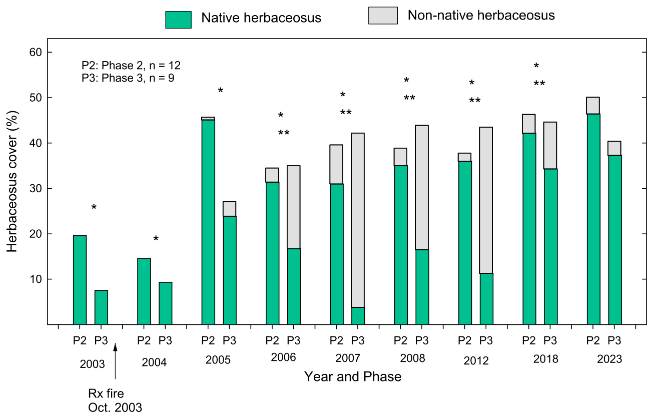

Figure 2. Native and nonnative herbaceous cover (%, means) composition in burned phase 2 and phase 3 western juniper woodlands, Steens Mountain, Oregon (2003–2023; 2003 is the prefire year). Single asterisks (*) indicate significantly different native herbaceous cover means between phase 2 and phase 3 sites ($P > 0.05$). Double asterisks (**) indicate significantly different nonnative herbaceous cover means between burned phase 2 and phase 3 sites ($P < 0.05$). Data for 2003–2012 years were previously published in Bates et al. (2014a).

between phases. In 2023, snowberry cover on phase 2 sites ranged from 1.0% to 17.5% and on phase 3 sites cover ranged from 1.2% to 36.2%. Density of snowberry in 2023 averaged 0.13 ± 0.03 plants · m^{-2} on phase 2 sites and 0.14 ± 0.05 plants · m^{-2} on phase 3 sites.

Cover and density of rabbitbrush species increased on sites of both phases after fire and exceeded preburn levels the sixth year (2009) after fire ($P = 0.001$; Fig. 3D). Cover ($P = 0.413$) and density ($P = 0.336$) of rabbitbrush did not differ between phases after 20 yr. Wax currant (*Ribes cereum* Dougl.) cover and density increased after fire in both phases but has been about four times greater in phase 3 sites ($P < 0.001$). Cover of wax currant in 2023 averaged 0.24% ± 0.18% on phase 2 sites and 0.92% ± 0.28 % on phase 3 sites. Cover of other shrub species including Wood's rose (*Rosa woodsii* Lindl.), Oregon grape (*Berberis repens* Lindl.), bitter cherry (*Prunus emarginata* var. *emarginata* Dougl.), blue elderberry (*Sambucus mexicana* J. Presl.), and serviceberry (*Amelanchier utahensis* Koehne) accounted for less than 1% of total shrub cover and did not differ between phases.

Perennial grass

Perennial bunchgrass cover and density was significantly affected by the year X phase interaction ($P < 0.001$; Figs. 4A and 4B). Perennial bunchgrass cover and density declined significantly the year after fire in both phases followed by rapid recovery in the phase 2 sites and slower recovery in phase 3 sites through 2012 (9 yr postfire). Perennial bunchgrass cover recovered to prefire levels 3 yr after fire (2006) and exceeded preburn levels 6 yr (2009) after fire in both phase 2 and phase 3 sites (Fig. 4A). Perennial grass cover was 3 to 6 times greater ($P < 0.001$) in phase 2 than phase 3 sites 1 to 9 yr (2004–2012) after fire. Similarly, perennial bunchgrass density was 4 to 5 times greater in phase 2 sites than phase 3 sites between 2004 and 2012 (Fig. 4B; $P < 0.001$). However, perennial bunchgrass cover ($P = 0.361$) and density ($P = 0.788$) has not differed between phases 15 (2018) and 20 (2023) yr after fire (Figs. 4A and 4B).

Sandberg bluegrass cover and density was significantly affected by the year ($P < 0.001$) and phase ($P = 0.002$). Phase differences were apparent the first decade postfire with Sandberg bluegrass cover and density 2 to 8 times greater on phase 2 sites. Fifteen (2018) and 20 (2023) yr after fire Sandberg bluegrass cover ($P = 0.947$) and density ($P = 0.805$) did not differ between phases. Collectively, Sandberg bluegrass cover and density averaged 5.4% + 0.5% and 10.4% ± 1.4% plants · m^{-2}, respectively, in 2023. Rhizomatous grass cover increased slightly across years ($P = 0.038$) but did not differ between phases ($P = 0.157$). Cover of rhizomatous grass was less than 1% in all years.

Perennial forbs

After fire, perennial forb cover was significantly affected by phase ($P < 0.001$) and year ($P < 0.001$) but not the interaction ($P = 0.190$). Perennial forb cover was 2 to 10 times greater in the phase 2 than phase 3 sites after fire (Fig. 5A). Phase differences, especially in the first decade after fire, were mainly driven by six forb species which were all greater in cover in the phase 2 sites than phase 3 sites, including: heart-leaved arnica (*Arnica cordifolia* Hook., $P = 0.001$), bunch arnica (*Arnica sororia* Greene, $P = 0.013$), taper-tip hawksbeard (*Crepis acuminata* Nutt., $P < 0.001$), foothill daisy (*Erigeron corymbosus* Nutt., $P = 0.007$), parsnip-flower buckwheat (*Eriogonum heracleoides* Nutt., $P < 0.001$), and silvery lupine (*Lupinus argenteus* Pursh., $P < 0.001$). Other perennial forbs that exhibited significant year effects increased in cover since fire (Table S1; available online at doi:10.1016/j.rama.2025.09.009).

Densities of perennial forbs were significantly affected by phase (Fig. 5B; $P < 0.001$) but not year ($P = 0.053$) or the interaction ($P = 0.703$). Perennial forb density was 2 to 6 times greater in phase 2 than phase 3 sites after fire (Fig. 5B). Density differences between phases were mainly a result of higher densities in phase 2 sites of the above-mentioned species (Table S1).

Cheatgrass and native annual forbs

Cheatgrass cover was significantly affected by the year X phase interaction ($P < 0.001$). Cheatgrass was present in trace amounts prior to treatment in both woodland phases but increased significantly during the first decade postfire (Fig. 6A). During this period cheatgrass cover was 4 to 16 times greater in phase 3 than phase 2 sites. Cheatgrass cover began decreasing in phase 2 sites following the 4th-year postfire and in phase 3 sites between the 9th- and 15th-year postfire. Twenty years after fire, cheatgrass cover did not differ between phases ($P = 0.145$), together averaging 2.9% ± 0.9%.

Native annual forb cover was significantly affected by the year X phase interaction (Fig. 6B; $P < 0.011$), where cover was greater in phase 2 sites in 2005 and 2007. Annual forb cover peaked the second year (2005) postfire in both phases. In the succeeding year, cover decreased significantly and has, on average, generally been below 3% in both phases. Twenty years after fire annual forb cover did not differ between phases ($P = 0.309$), collectively averaging 2.6% ± 0.4%.

Discussion

Our expectations that vegetation composition differences and trajectories in the burned phase 2 and phase 3 woodlands would persist into the second decade after fire were rejected. During the second decade, postfire herbaceous and shrub composition in burned phase 3 woodlands shifted from cheatgrass to perennial bunchgrass dominance in the understory and from snowbrush to sagebrush-snowberry-snowbrush codominance in the shrub layer, respectively. Thus, 20 yr after the prescribed fire, there were few differences separating vegetation composition in the two burned woodland phases. Herbaceous and shrub composition of both woodland phases proved to be highly resilient to fire, the difference was that recovery of the herbaceous layer, in particular, for the phase 3 sites required about twice as long as the phase 2 sites.

The delayed herbaceous recovery in the phase 3 woodlands was likely the result of low perennial cover and density, espe-

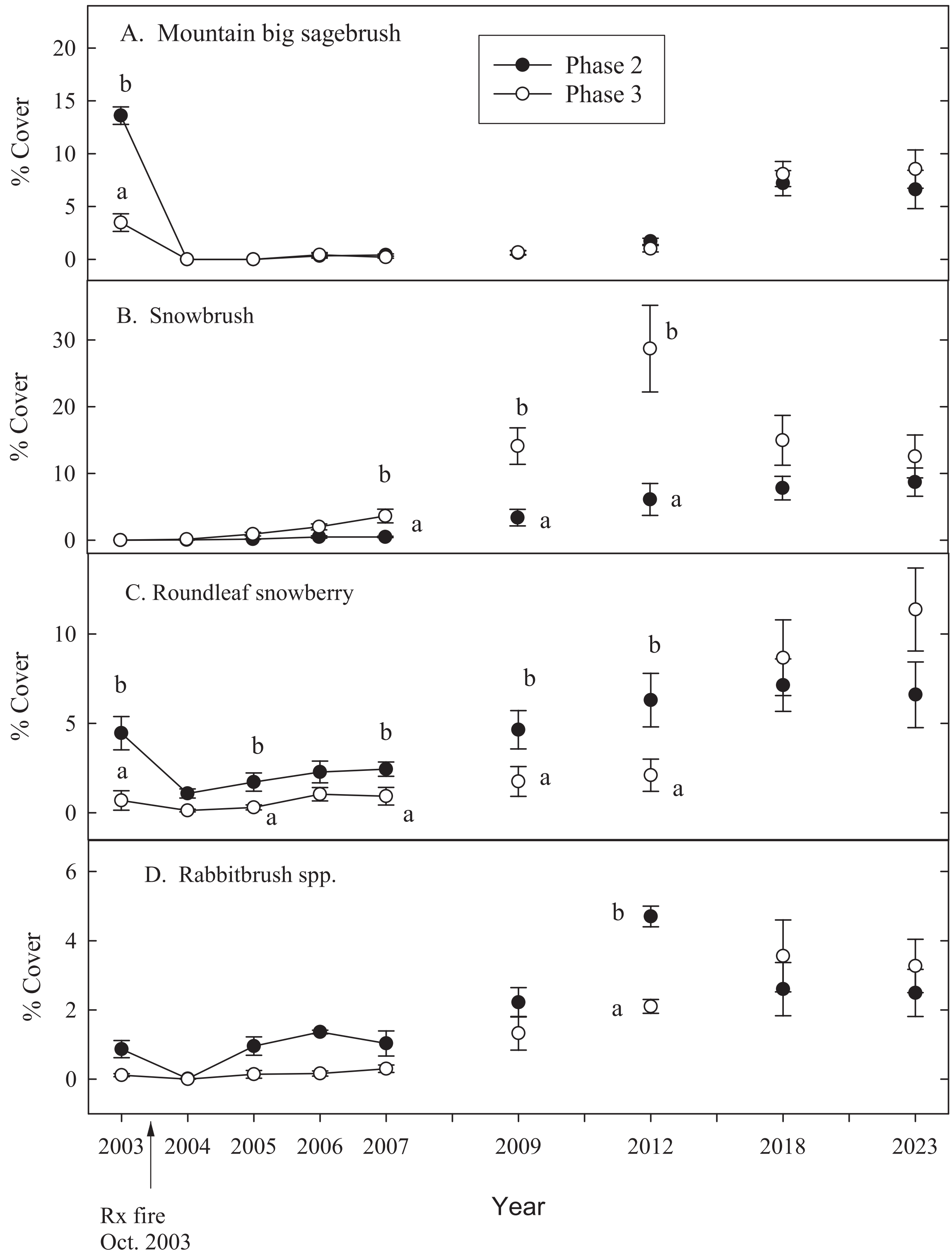

Figure 3. Shrub species cover (%) in burned phase 2 and phase 3 western juniper woodlands, Steens Mountain, Oregon (2003–2023; 2003 is the prefire year): (**A**) mountain big sagebrush; (**B**) snowbrush; (**C**) roundleaf snowberry; and (**D**) rabbitbrush spp. Data are means $\pm$ 1 standard error. Means sharing a common lower-case letter are not significantly different ($P > 0.05$). Data for 2003–2012 years were previously published in Bates et al. (2014a).

cially grasses, after fire. Perennial grass cover and density was four times lower in phase 3 compared with phase 2 woodland sites the first year after fire. Consequently, on phase 3 sites the level of perennial vegetation was inadequate for more rapid site recovery which allowed cheatgrass to dominate the herbaceous community by the third-year postfire. Greater abundance of perennial herbaceous vegetation, as in the phase 2 woodland sites, is essential to prevent cheatgrass from establishing and dominating in postfire sagebrush steppe (Chambers et al. 2007, 2014; Condon et al. 2011; Freund et al. 2021). Other phase 3 woodlands that had greater postfire densities of residual perennial bunchgrasses (<2 plants $\cdot$ m^{-2}) recovered more rapidly and were dominated by herbaceous

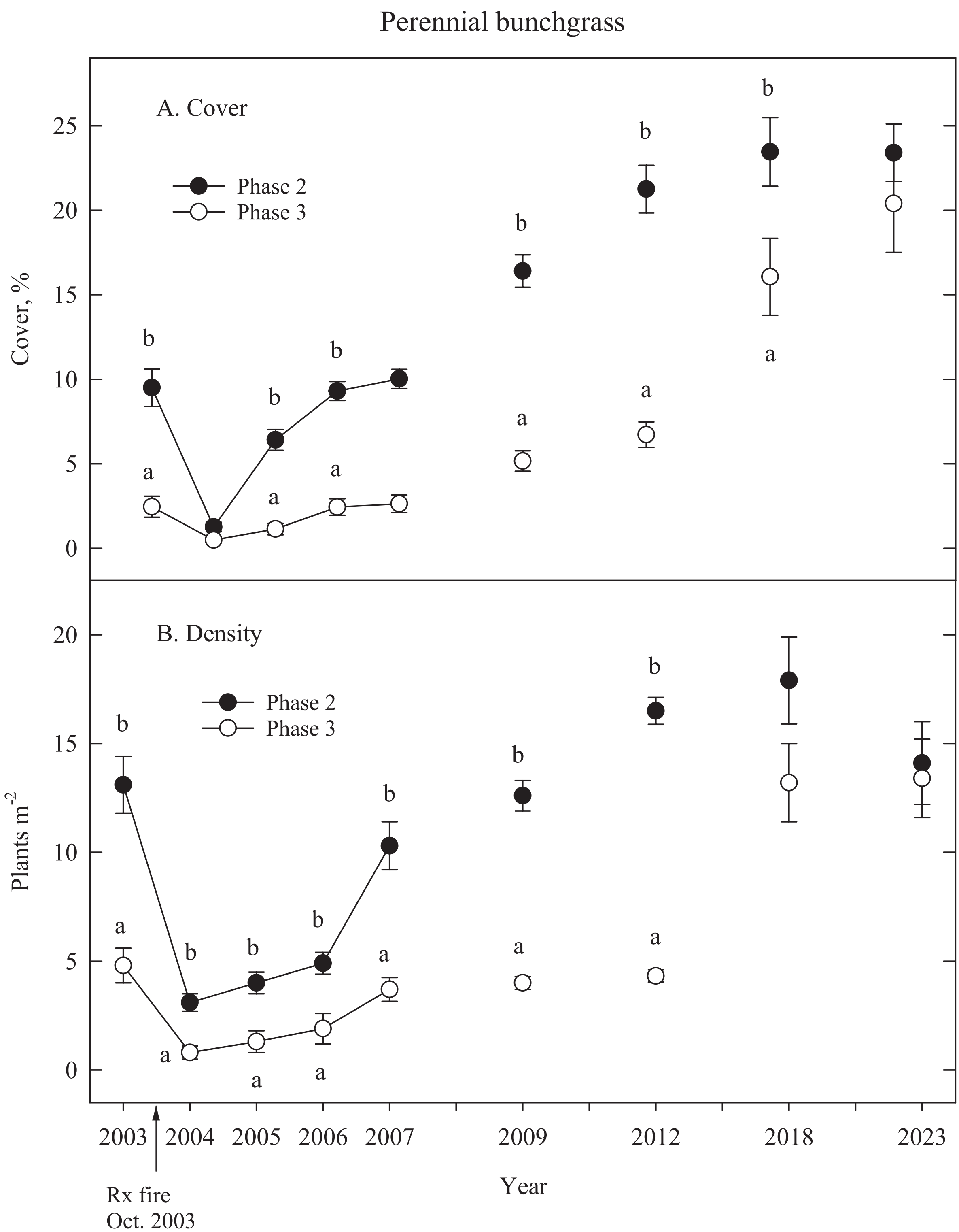

Figure 4. Perennial bunchgrass (**A**) cover (%) and (**B**) density in burned phase 2 and phase 3 western juniper woodlands, Steens Mountain, Oregon (2003–2023; 2003 is the prefire year). Data are means ± 1 standard error. Means sharing a common lower-case letter are not significantly different ($P > 0.05$). Data for 2003–2012 years were previously published in Bates et al. (2014a).

perennials within the first 4 yr following prescribed fire treatments (Bates et al. 2011, 2014b, 2019).

Despite the dominance of cheatgrass in phase 3 woodland sites perennial grass cover and density slowly increased to prefire levels the first decade postfire. We had ventured in Bates et al. (2014a) that "should this trend continue, native grass species may, over a longer time period, replace *B. tectorum*" in the phase 3 sites. This trend accelerated the second decade postfire and 20 yr after fire, perennial bunchgrass dominated the herbaceous understory. The resilience of the phase 3 sites is likely a product of ecological site characteristics. The ecological sites have a frigid soil temperature regime, are in a PZ above 300 mm annually (300–400 mm)

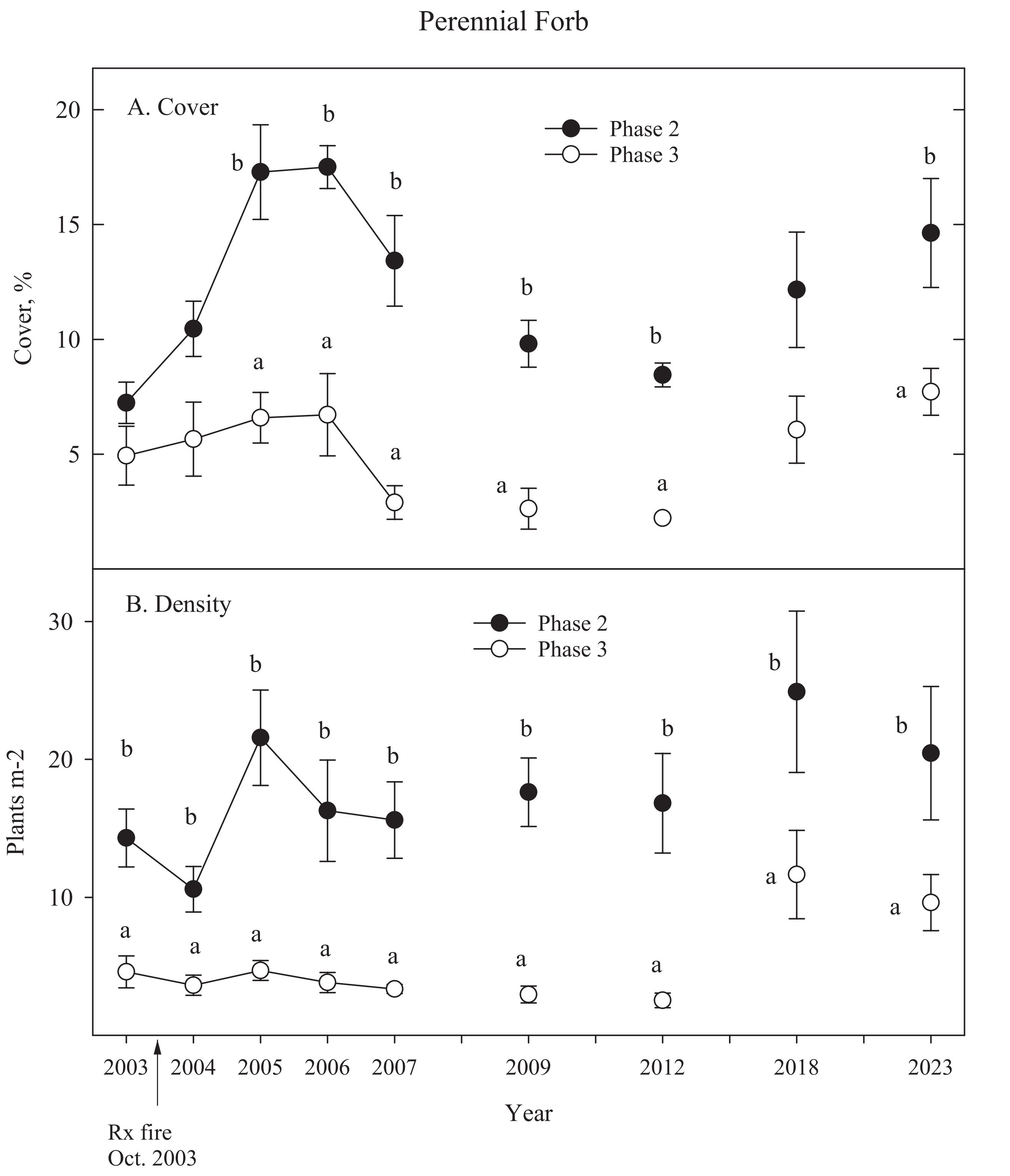

Figure 5. Perennial forb (**A**) cover (%) and (**B**) density in burned phase 2 and phase 3 western juniper woodlands, Steens Mountain, Oregon (2003–2023; 2003 is the prefire year). Data are means ± 1 standard error. Means sharing a common lower-case letter are not significantly different ($P > 0.05$). Data for 2003–2012 years were previously published in Bates et al. (2014a).

and the dominant vegetation is typically described as mountain big sagebrush/Idaho fescue-bluebunch wheatgrass associations (NRCS 2010). On other comparable ecological sites perennial bunchgrasses typically have a competitive advantage over invasive annual grasses (Chambers et al. 2007) and have tended to dominate after burning of all phases of western juniper occupancy (Bates et al. 2011, 2014b, 2019; O'Connor et al. 2013).

The results also suggest that perennial bunchgrasses are superior to perennial forbs in preventing and suppressing cheatgrass. In phase 2 woodland sites, cheatgrass increased during early succession despite high perennial forb cover. Cheatgrass on the phase 2 sites did not begin declining (6 yr postfire) until perennial bunchgrasses cover exceeded 10%. Similarly, cheatgrass on phase 3 woodland sites did not relinquish understory dominance until peren-

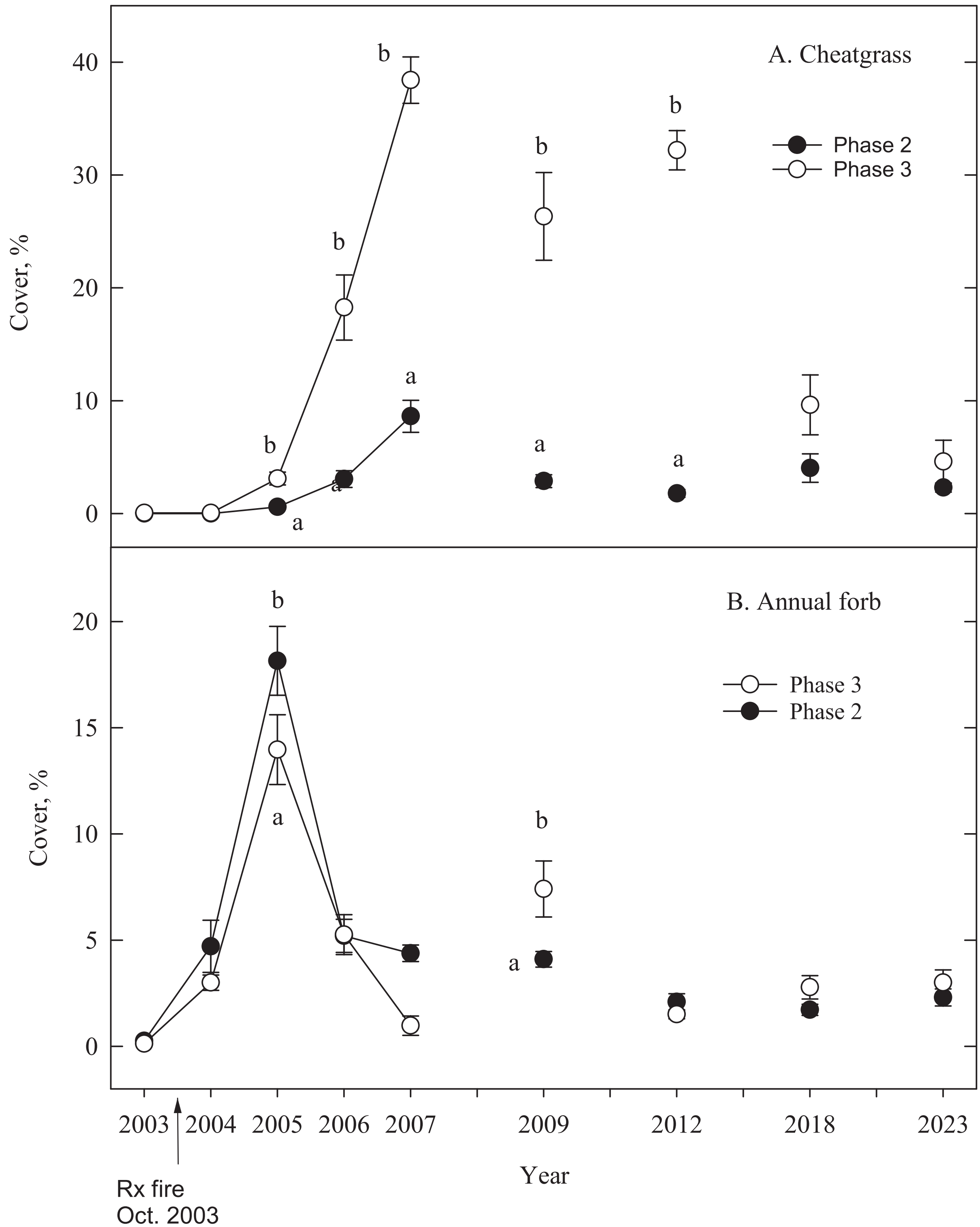

Figure 6. Cover (%) of (**A**) cheatgrass and (**B**) annual forbs in burned phase 2 and phase 3 western juniper woodlands, Steens Mountain, Oregon (2003–2023; 2003 is the prefire year). Data are means ± 1 standard error. Means sharing a common lower-case letter are not significantly different ($P > 0.05$). Data for 2003–2012 years were previously published in Bates et al. (2014a).

nial bunchgrasses cover exceeded 10%, around 15 yr postfire. The increase in shrub cover may also have assisted perennial bunchgrasses in suppressing of cheatgrass.

The lack of an increase in perennial forbs in phase 3 woodland sites after fire is not unusual in mountain big sagebrush communities. It was reported that perennial forbs did not increase about 50% of the time following fire in mountain big sagebrush communities (Bates et al. 2017). The lack of perennial forb response following fire is attributed to site characteristics and potential (Bates et al. 2017). Because phase 2 and 3 woodland sites share the same ecological sites, other factors are likely responsible for the different postfire recovery of the perennial forb functional group. These factors include different residual starting points following fire as well as interspecific competition. Perennial forb cover and density in phase 3 sites were well below phase 2 sites which likely resulted in lower seed production and recruitment as well as propagule development. The rapid increase in cheatgrass dominance during early succession followed by supremacy of perennial bunchgrasses the second decade postfire may have further limited perennial forb recruitment and growth.

Shrub composition in phase 2 and phase 3 woodland sites differed the first decade after fire and converged the second decade postfire with fairly equal levels of mountain big sagebrush, snowbrush and round-leaf snowberry. This development was mainly because of a decline of snowbrush and an increase of round-leaf snowberry in phase 3 woodland sites. There is little information on factors involved in the decline of snowbrush in the sagebrush steppe though in forested systems it is effectively suppressed with increasing conifer cover (Zavitkovski and Newton 1968). The increase in snowberry was observed to occur frequently within snowbrush canopies in the phase 3 woodland sites. Snowbrush occurrence on the study area is likely temporary because prior to fire it was not present, emerging after fire from the seedbank. Viability of snowberry seed in soil seed banks exceeds 200 yr and often emerges after fire where it was previously not recorded (Steen 1966; Kramer and Johnson 1987; Halpern 1989; Bradley et al. 1991; Tonn et al. 2000). Mountain big sagebrush has continued to increase but remains about 50% below site potential (about 20% cover) after 20 yr. Recovery of mountain big sagebrush canopy cover generally requires between 20 and 40 yr (Harniss and Murray 1973; Lesica et al. 2007; Ziegenhagen and Miller 2009). Overall shrub cover was greater in phase 3 compared with phase 2 woodland sites which may be a legacy of early successional herbaceous recovery. Phase 2 woodland sites were dominated by herbaceous perennials after fire which may have limited shrub establishment and growth. Perennial bunchgrasses are reported to interfere with mountain big sagebrush shrub establishment (Davies et al. 2017) which may explain the lower shrub cover value in the phase 2 woodland sites.

Implications

Both burned phase 2 and 3 western juniper woodlands, after 20 yr, demonstrated high resilience in response to severe fire effects because of the recovery and dominance of native herbaceous and shrub species. In this regard, patience and appropriate grazing management was all that was required to allow these sites to recover. However, additional management inputs, mainly seeding perennial bunchgrasses, should be considered for several reasons. First, seeding would speed recovery and potentially avoid a cheatgrass phase during succession as measured on phase 3 sites. Second, cheatgrass is increasingly spreading into sites considered resistant to invasion at higher elevations which may be exacerbated by predicted climate warming in this century (Compagnoni and Adler 2014; Snyder et al. 2019; Smith et al. 2022). Avoiding a cheatgrass phase is important as cheatgrass is associated with increased fire activity across the Great Basin (Balch et al. 2013) which can limit recovery of native plant communities. Seeding of native perennial bunchgrass species following fire on similar ecological sites has proven highly successful in the establishment of bunchgrasses and limits cheatgrass invasion and occupancy (Sheley and Bates 2008; Davies and Bates 2019). Although mountain big sagebrush on the burned woodland sites is recovering within an acceptable time frame, managers may consider seeding mountain big sagebrush following fire if earlier recovery is necessary (Davies et al. 2014; Davies and Bates 2017).

Piñon–juniper species continue to spread and infill and without efforts to control woodland expansion a progressive decrease and loss of sagebrush steppe plant communities can be expected. Woodland control options include prescribed fire and a variety of mechanical options, including use of chainsaws and heavy equipment. Fire, as used in this study, can be highly effective at recovering sagebrush steppe; and is also more effective than mechanical treatments at conserving sagebrush steppe communities across longer time frames (Davies et al. 2019). Recovery after fire is, however, riskier and less predictable because of the potential for greater fire severity effects to vegetation, which may encourage subsequent weed dominance (Bates et al. 2014a). Managers should exercise caution when using fire to control western juniper expansion because of the presence of invasive annual grasses. Mechanical treatments offer less disturbance and typically are more effective than fire at earlier recovery of both sagebrush and herbaceous perennials (Bates et al. 2014b; Freund et al. 2021; Williams et al. 2023). However, mechanical treatments are typically only effective at maintaining sagebrush steppe communities over short-term time frames compared with fire disturbance because of earlier reoccupancy by juniper (Davies et al. 2019). Thus, when developing woodland control programs managers must acquire knowledge of benefits and drawbacks of all treatment options available.

Author Contributions

Jonathan D. Bates: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing – original draft. Kirk W. Davies: Conceptualization, Writing – original draft, Writing – review & editing. Rory C. O'Connor: Data curation, Investigation, Writing – review & editing. Stella M. Copeland: Resources, Writing – review & editing.

Data Availability Statement

The datasets used in this study are available on request but will be uploaded to USDA's National Agricultural Library-Ag Commons (https://agdatacommons.nal.usda.gov/) after manuscript acceptance.

CRediT authorship contribution statement

Jonathan D. Bates: Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Kirk W. Davies:** Writing – review & editing, Writing – original draft, Conceptualization. **Rory C. O'Connor:** Writing – review & editing, Investigation. **Stella M. Copeland:** Writing – review & editing, Resources.

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Supplementary materials

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