Sagebrush steppe recovery after fire varies by development phase of *Juniperus occidentalis* woodland

Jonathan D. Bates[A,C], *Robert N. Sharp*[B] *and Kirk W. Davies*[A]

[A]United States Department of Agriculture, Agricultural Research Service,
   Eastern Oregon Agricultural Research Center, Burns, OR 97720, USA.
[B]United States Department of Interior, Bureau of Land Management,
   Burns District Office, Burns, OR 97720, USA.
[C]Corresponding author. Email: jon.bates@oregonstate.edu

Abstract. Woodland ecosystems of the world have been changed by land use demands, altered fire regimes, invasive species and climate change. Reduced fire frequency is recognised as a main causative agent for *Pinus–Juniperus* L. (piñon–juniper) expansion in North American woodlands. Piñon–juniper control measures, including prescribed fire, are increasingly employed to restore sagebrush steppe communities. We compared vegetation recovery following prescribed fire on Phase 2 (mid-succession) and Phase 3 (late-succession) *Juniperus occidentalis* Hook. (western juniper) woodlands in Oregon. The herbaceous layer on Phase 2 sites was comprised of native perennial and annual vegetation before and after fire. On Phase 3 sites the herbaceous layer shifted from native species to dominance by invasive *Bromus tectorum* L. (cheatgrass). After fire, shrubs on Phase 2 sites were comprised of sprouting species and *Ceanothus velutinus* Dougl. (snowbrush). On Phase 3 woodland sites the shrub layer was dominated by *C. velutinus.* The results suggest that Phase 2 sites have a greater likelihood of recovery to native vegetation after fire and indicate that sites transitioning from Phase 2 to Phase 3 woodlands cross a recovery threshold where there is a greater potential for invasive weeds, rather than native vegetation, to dominate after fire.

Additional keywords: *Artemisia tridentata*, *Bromus tectorum*, Great Basin, mountain big sagebrush, state-and-transition, threshold.

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Introduction

Woodland ecosystems have undergone substantial change in most regions of the world as a result of land use demands, herbivore effects, altered fire regimes, invasive species and climate change. Woodlands are categorised as those being reduced or degraded (Zerihun and Backleus 1991; Yates and Hobbs 1997; Bucher and Huszar 1999; Angassa and Baars 2000; Breshears *et al.* 2005) and those that have expanded in range and in-filled (Brown and Archer 1989; Macdonald and Wissel 1992; Miller and Rose 1995; Holmes and Cowling 1997; Van Auken 2000; Ansley *et al.* 2001). Reduced fire frequency is recognised as a main causative agent for woodland expansion in North American woodlands (Brown and Archer 1989; Archer 1994; Miller and Wigand 1994). Where woodlands have expanded and in-filled, active management using fire or mechanical treatments has been employed to kill trees to maintain or restore grassland and shrubland ecosystems (Burrows *et al.* 1990; Angassa 2002; Owens *et al.* 2002; Smit 2004; Miller *et al.* 2005; Peterson *et al.* 2007; Teague *et al.* 2010).

In the western United States expansion and in-filling of *Pinus–Juniperus* L. (piñon–juniper) has caused widespread conversion of big sagebrush steppe (*Artemisia tridentata* Nutt.)

to coniferous woodland. A main cause of piñon–juniper expansion has been a lack of fire, a likely consequence of the grazing of fine fuels by livestock and, since the 1940s, more effective fire suppression (Burkhardt and Tisdale 1976; Miller and Rose 1999; Soulé *et al.* 2004; Miller *et al.* 2008). Pre-settlement mean fire return intervals (MFRI) in mountain big sagebrush steppe (*A. t.* Nutt. ssp. *vaseyana* (Rydb.) Beetle), a main area of piñon–juniper expansion, are estimated to have been <20 to <100 years (Miller *et al.* 2005, 2008; Miller and Heyerdahl 2008). Woodland development has a range of adverse effects on structural and functional properties of *A. t.* ssp. *vaseyana* steppe communities, including increased soil erosion and reduced water infiltration (Buckhouse and Mattison 1980; Reid *et al.* 1999; Pierson *et al.* 2007; Petersen *et al.* 2009), loss of steppe wildlife habitat (Schaefer *et al.* 2003; Noson *et al.* 2006; Reinkensmeyer *et al.* 2007), elimination of the shrub layer (Miller *et al.* 2000) and reduced herbaceous diversity and productivity (Clary and Jameson 1981; Bates *et al.* 2005, 2006, 2011). Thus, woodland control using fire or mechanical treatments to maintain or restore *A. t.* ssp. *vaseyana* steppe has been a major restoration focus in the western United States.

However, forecasting vegetation recovery following pre-scribed fire appears to become less predictable as piñon–juniper woodlands develop (Miller *et al.* 2008). Woodland development varies across landscapes (Johnson and Miller 2006) and has been categorised into three phases (Miller *et al.* 2005, 2008): in Phase 1 woodlands, shrubs and herbaceous species are the dominant vegetation with few trees present; in Phase 2 woodlands, trees co-dominate with shrubs and herbaceous plants; and in Phase 3 woodlands, trees are dominant and shrubs and herbaceous layers are reduced. The transition from Phase 2 to Phase 3 woodlands causes a shift from shrub and herbaceous fuels to a predomi-nance of tree canopy fuels, which influences fire behaviour and severity (Tausch 1999; Miller *et al.* 2008; Dicus *et al.* 2009; Romme *et al.* 2009). The increase in canopy fuels generates fires of greater severity than under the historic regime, and results in post-fire weed dominance because of high mortality of herba-ceous perennials (Tausch 1999; Bates *et al.* 2006, 2011; Condon *et al.* 2011). This indicates that many Phase 3 woodlands may have crossed a threshold, where natural recovery is uncertain and additional inputs, seeding and weed control may be required to restore *A. t.* ssp. *vaseyana* steppe communities.

The ability to forecast vegetation succession and dynamics as a result of management actions or natural disturbance events is central to natural resource professionals. To assist in predicting potential vegetation changes and identifying the driving factors, state-and-transition models (STMs), proposed by Westoby *et al.* (1989), have been increasingly refined and employed in eco-logical research. In the United States federal land agencies have accepted STMs for vegetation and habitat management where they serve as integral parts in the development of ecological site descriptions (ESDs) (Papanastasis and Chouvardas 2005; Chartier and Rostagno 2006; Briske *et al.* 2008; Petersen *et al.* 2009; Holmes and Miller 2010). STMs describe alternative plant community states and community transitions resulting from disturbance or management, for related vegetation associations or ESDs that can occur over time. Thus, ecological sites support multiple states or phases, comparable to successional or seral stages. Changes in disturbance regimes and introduction of exotic species can cause plant communities to decline in resil-ience and become unstable, with the potential for crossing a threshold to a new state(s) that differs in plant composition, structure and function. Once a threshold is crossed, a return to the former state is often difficult because of changes in species composition and site attributes (Westoby *et al.* 1989; Laycock 1991; Briske *et al.* 2008).

The development of threshold and resilience concepts and STMs for categorising woodland expansion and evaluating natural disturbances or management applications has been a building process since the late 1980s (Archer 1994; Milton *et al.* 1994; Briske *et al.* 2008; Petersen *et al.* 2009). Several detailed STMs have been proposed for describing the expansion of *J. occidentalis* Hook. (western juniper) woodlands (Miller *et al.* 2005; Briske *et al.* 2008; Petersen *et al.* 2009). Miller *et al.* (2005) developed STMs for *A. t.* ssp. *vaseyana* steppe with increasing western juniper dominance including multiple transitions and thresholds. However, the point at which thresh-olds are crossed during woodland development is yet to be specifically identified or tested (Briske *et al.* 2008). Identifying thresholds is important for applying appropriate methods of piñon–juniper control to recover *A. t.* ssp. *vaseyana* steppe vegetation. Information on vegetation recovery following pre-scribed fire treatments remains limited and there have been few integrated studies comparing *A. t.* ssp. *vaseyana* steppe recovery after fire among different phases in expanding *J. occidentalis* and piñon–juniper woodlands.

Our objective was to compare recovery of mountain big *A. t.* ssp. *vaseyana* steppe after prescribed fire in Phase 2 and Phase 3 *J. occidentalis* woodlands. We hypothesised that recovery of herbaceous and shrub species would occur earlier after fire in Phase 2 than in Phase 3 sites because initial shrub and herbaceous cover and densities are often greater in Phase 2 than Phase 3 woodlands (Miller *et al.* 2000), and because fire may result in high mortality of these life forms in Phase 3 woodlands (Bates *et al.* 2006, 2011). Because of lower levels of herbaceous cover and density, we expected there would be a greater potential for invasive weeds to increase after treating Phase 3 woodlands. One of our goals was to propose a revised STM for *J. occidentalis* woodlands based on woodland phases if war-ranted by our results.

Methods

Study area and treatment

The study was located in Kiger Canyon, Steens Mountain, south-eastern Oregon (45°54′N, 118°40′W). Elevation of the study sites ranged from 1700 to 1990 m, and aspects were from east to north. The ecological sites (ESD) were Loamy (12–16 Precipitation Zone, PZ (304–406 mm)) and Deep Loamy (12–16 PZ) (NRCS 2010*a*) and all study sites were *A. t.* ssp. *vaseyana–Festuca idahoensis* Elmer (Idaho fescue) plant associations. Soils at the sites are a complex of Westbutte–Lambring (Loamy-skeletal, mixed, frigid Pachic Haploxerolls) series formed in residuum and colluvium derived from basalt, andesite, rhyolite and welded tuff and are mod-erately deep and well drained (NRCS 2006). Twelve Phase 2 and nine Phase 3, 0.63-ha plots were established in May 2003. Criteria for determining woodland phase (cover of herbaceous, shrub and tree life forms) were taken from Miller *et al.* (2000, 2005). Phase 2 and Phase 3 woodlands were intermixed within an area of 15 km^2 and were independent of each other (Fig. 1). Nine of the Phase 2 plots were located adjacent to Phase 3 woodland plots, with others located randomly within the study area. Phase 2 woodland sites had greater initial cover and density of herbaceous and shrub species than did Phase 3 woodland sites. Herbaceous cover was 2.5 times, and shrub cover 3.5 times, greater in the Phase 2 woodlands (19.0 ± 1.0%; 19.7 ± 1.9%) than in Phase 3 woodlands (7.4 ± 1.2%; 5.5 ± 1.6%). *Bromus tectorum* L. (cheatgrass) was present in trace amounts on half of the sites for each woodland phase. Cover and density of *J. occidentalis* were 1.8 times and 1.5 times greater in the Phase 3 (47.0 ± 1.3%; 240 ± 25 trees ha^{-1}) than in the Phase 2 woodlands (25.2 ± 1.8%; 168 ± 21 trees ha^{-1}). The closest weather station, located at the Otley Brothers Ranch (1550-m elevation), is 7.2–11.3 km north-west of the sites. Annual precipitation (1 October–30 September) averaged 386 mm in the 10 years (Fig. 2).

Cutting involved felling ~1/3 of the dominant and sub-canopy *J. occidentalis* trees (>3 m tall) and cutting was evenly
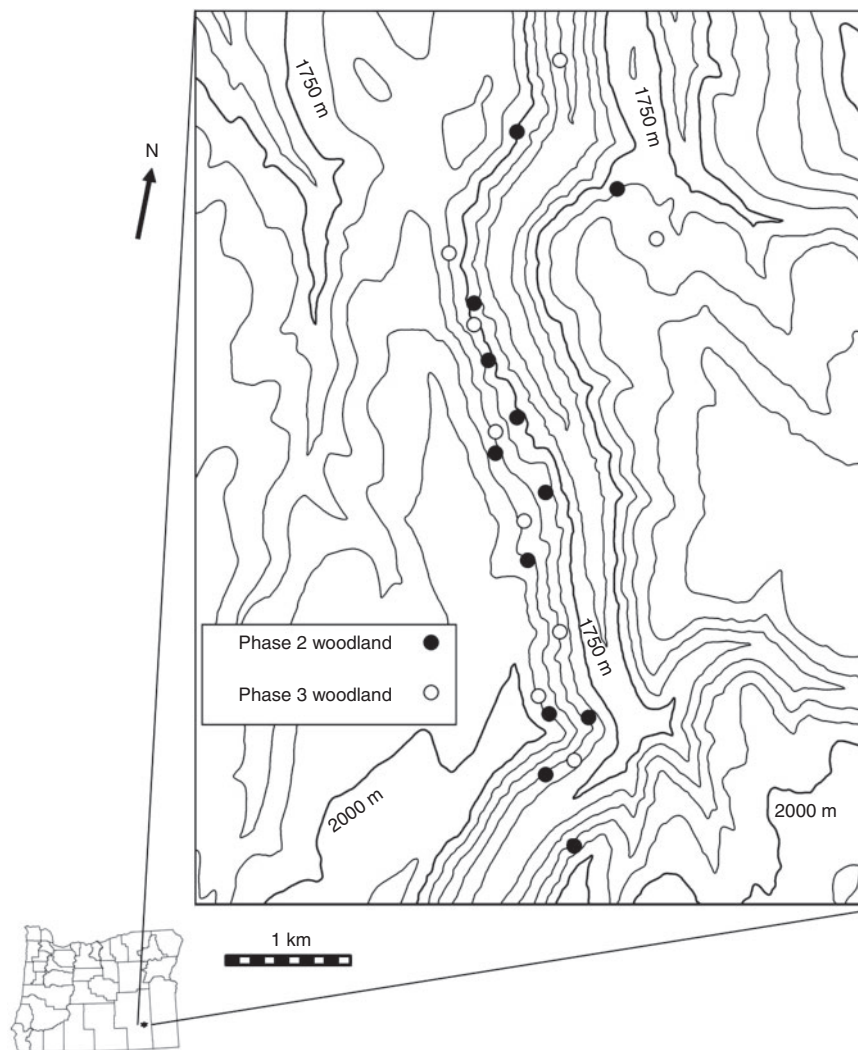
Fig. 1. Phase 2 and Phase 3 woodland sites for the Kiger Canyon study area, Steens Mountain, Harney County, Oregon, USA. Phase 2 woodlands represent a co-dominance of trees, shrubs and herbaceous plants and in Phase 3 woodlands, trees are dominant and shrubs and herbaceous layers are reduced.

distributed in stands. Trees were cut May–June 2003 and dried over the summer. On Phase 2 woodlands, an average of 47 ± 8 trees (range 8–23) were cut per hectare. On Phase 3 woodlands, an average of 71 ± 9 trees (range 43–110) were cut per hectare. Fall (autumn) burning was applied on 6 October 2003 by personnel of the Bureau of Land Management, Burns District. The prescribed fire technique used was a spot head fire using a heli-torch. Weather conditions were typical for fall burning in the northern Great Basin. Air temperatures were 18–26°C, relative humidity was 20–28% and winds were from the north-west at $6–15\,\mathrm{km\,h^{-1}}$. Soil water content (0–10 cm) and fuel moisture for 1-, 10-, 100- and 1000-h fuels were measured the day before fire application and were determined by drying samples at 100°C to a constant weight (Table 1). Recovery depended on natural succession and no post-fire seeding was undertaken. Livestock were excluded for 2 years before burning to increase fine fuel loads. Cattle grazed (<10% estimated utilisation) the area in late summer (August) following the herbaceous growing season in

2004, 2007 and 2008. The area was grazed moderately June–July (35–50% estimated utilisation) in 2010 and 2011.

Measurements

Vegetation characteristics were measured in June (2003–2007, 2009) and July (2012). On each plot, five 50-m transects were permanently established with transects spaced 25 m apart. Canopy cover of *J. occidentalis* and shrubs were estimated by line intercept along transects (Canfield 1941). Density of mature *J. occidentalis* (>2-m height) was estimated by counting individuals inside five 6×50-m belt transects. Density of shrubs and juvenile *J. occidentalis* (<2-m height) were estimated by counting all plants inside five, 2×50-m belt transects. Herbaceous canopy cover (perennials, annuals) and herbaceous perennial density were measured by species inside 0.2-m^2 frames (0.4×0.5 m). Frames were placed every 2 m along transects. Scientific nomenclature follows the Natural Resource Conservation Service Plant Database (NRCS 2010*b*).
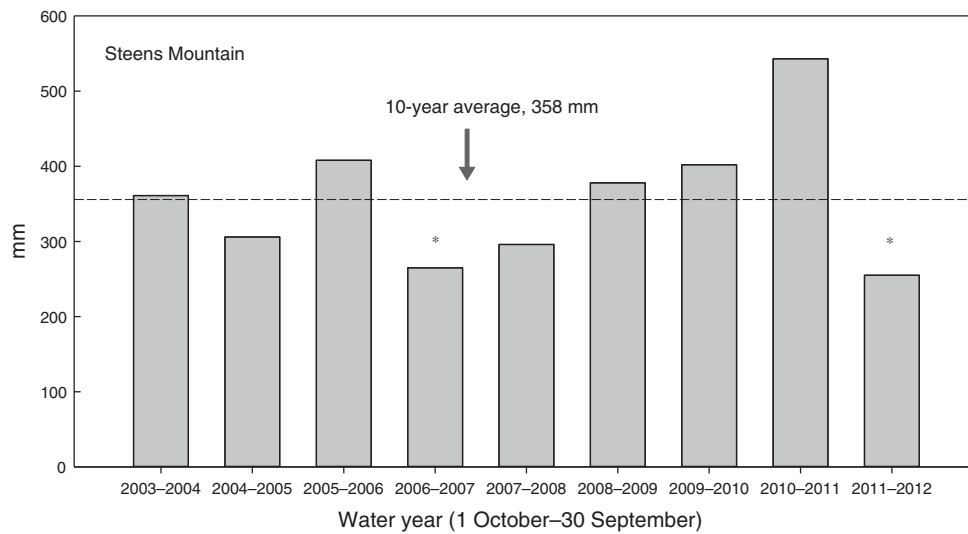
Fig. 2. Precipitation (2003–2012) totals by water year (1 October–30 September) for Kiger Canyon study area, Steens Mountain, Harney County, Oregon, USA. Drought (<75% of average precipitation of 358 mm year^{-1}) is indicated by an asterisk (*) located above the respective precipitation totals.

Table 1. Soil water content and fuel moisture for western juniper cutting–prescribed fire treatments in mountain big sagebrush communities, Steens Mountain, Oregon, October 2003

In the United States, wildland fuels are classified into four categories based on how they respond to changes in moisture. The four categories are: (i) 1-h fuels, up to 1/4 inch (0.64 cm) in diameter; (ii) 10-h fuels, 1/4 inch to 1 inch (0.64–2.54 cm) in diameter; (iii) 100-h fuels, 1–3 inches (2.54–7.62 cm) in diameter and (iv) 1000-h fuels, 3–8 inches (7.62–20.32 cm) in diameter. Examples of 1-h fuels are grass, leaves and litter. Fuel moisture in 1-h fuels can change within one hour as influenced by temperature, rain, humidity and shade. Larger diameter fuels (>10-h) are woody fuels (e.g. deadfalls, dead branches), which may take up to 1000 h to respond to changes in environmental factors

Parameter	Moisture (%)
Soil water content (0–10 cm)	8.6 ± 0.7
Fuel moisture	
1-h	
Herbaceous	5.1 ± 0.2
Surface litters	5.5 ± 0.4
10-h	5.2 ± 0.2
100-h	9.0 ± 0.3
1000-h	12.6 ± 0.5

Statistical analysis

Repeated-measures analysis of variance for a completely randomised design using a mixed model (PROC MIX; SAS Institute Inc., Cary, NC) was used to test for year, woodland phase and year-by-phase interaction for herbaceous, shrub and *J. occidentalis* response variables. Because the study lacks woodland controls the design does not permit separation of interannual variation, thus comparisons made between pre- and post-treatment response variables should be interpreted with caution. However, the response to the treatments in this study followed patterns similar to those measured in other studies comparing vegetation dynamics between treated and untreated woodlands (controls). These studies indicate that total herbaceous and life form cover typically increases within the first 2–3 years following cutting or burning of western juniper woodlands (Vaitkus and Eddleman 1987; Rose and Eddleman 1994; Bates *et al.* 2000, 2005, 2006, 2011).

Response variables were *J. occidentalis* cover and density, shrub cover and density (species), herbaceous cover (species and life form, bare ground and surface litter) and herbaceous density (species and life form). Herbaceous life forms were grouped as *Poa secunda* Vasey (Sandberg's bluegrass), perennial bunchgrasses (e.g. *F. idahoensis*, *B. marginatus* Nees ex Steud. (mountain brome), *Achnatherum lemmon2* (Vasey) Barkworth (Lemmon's needlegrass), *Elymus elymoides* (Raf.) Swezey (bottlebrush squirreltail)), *B. tectorum*, perennial forbs and annual forbs. *Poa secunda* was treated as a separate functional group from other perennial grasses because its phenological development occurs earlier (Link *et al.* 1990; Davies 2008). 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 (d.f. = 6), phase (d.f. = 1) and year-by-phase interaction (d.f. = 6; with the error term d.f. = 92). Mean separation involved comparison of least-squares using the LSMEANS statement (SAS Institute Inc., Cary, NC). All data were tested for normality using the Shapiro–Wilk test (Shapiro and Wilk 1965) and were log-transformed before analysis when necessary. Significant interactions were followed by tests of simple effects at α = 0.05.

Results

Juniper control and ground cover

The prescribed fires killed remaining uncut *J. occidentalis* trees in both Phase 2 and 3 woodland sites. Surface litters (herbaceous and juniper needles) were fully consumed by the fire, and shrubs were burned to the soil surface. Felled *J. occidentalis* were
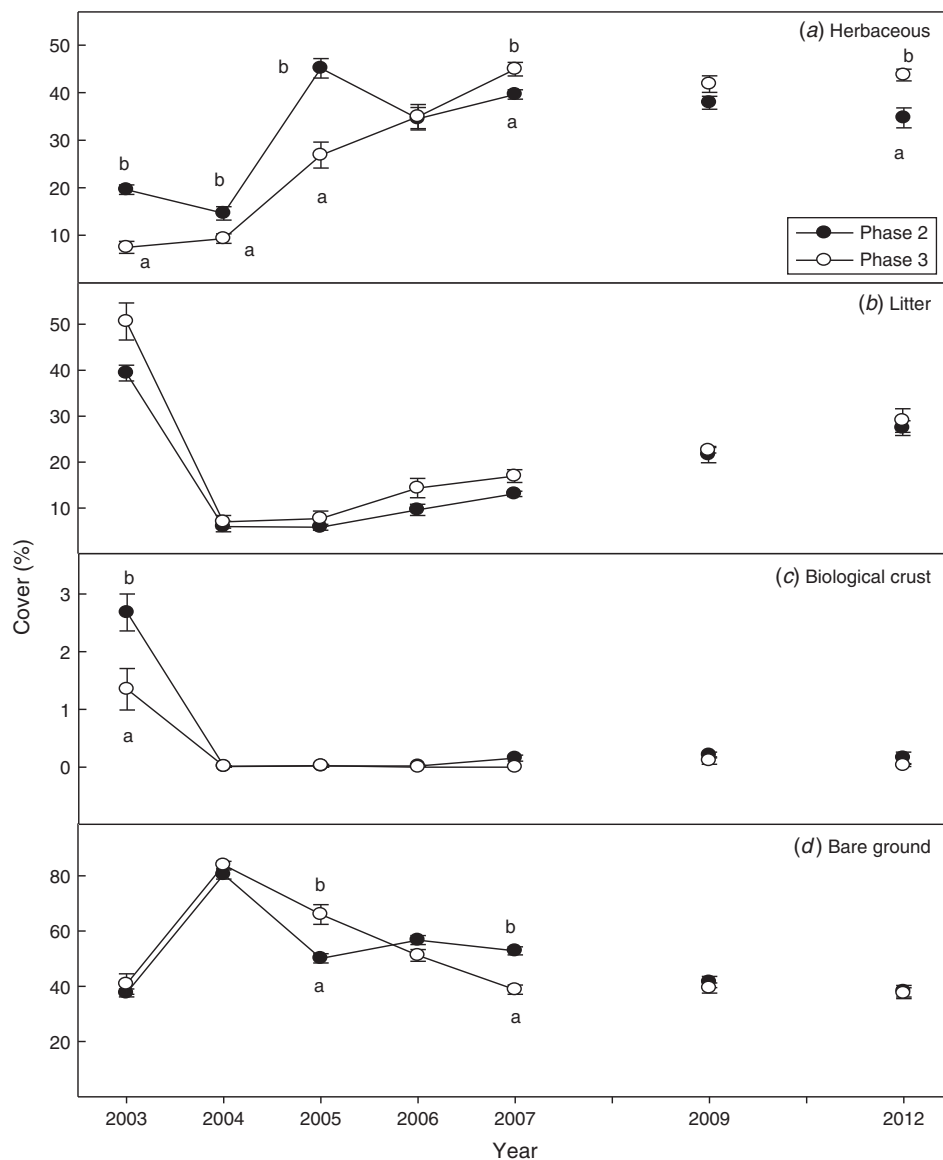
Fig. 3. Ground cover (%) values in burned Phase 2 and Phase 3 western juniper woodlands, Steens Mountain, Oregon (2003–2012; 2003 is the pre-fire year): (*a*) herbaceous; (*b*) litter; (*c*) biological crust and (*d*) bare ground. Data are means ± 1 standard error. Means sharing a common lowercase letter are not significantly different (*P* > 0.05). Phase 2 woodlands represent a co-dominance of trees, shrubs and herbaceous plants and in Phase 3 woodlands, trees are dominant and shrubs and herbaceous layers are reduced.

completely consumed or only trunks remained, indicating that all fuels up to and including 1000-h fuels were removed.

Pre-burn herbaceous cover was ~2.5 times greater in the Phase 2 than the Phase 3 sites (Fig. 3*a*; *P* < 0.0001). For the first 2 years after fire (2004–2005) herbaceous cover was 50% higher in Phase 2 than Phase 3 sites (*P* < 0.0001) but by 2007 (and also in 2009 and 2012) these differences had largely disappeared. Litter cover declined by 80% in the first year after fire in Phase 2 and 3 woodlands (Fig. 3*b*; *P* < 0.0001). Nine years after fire, litter was respectively 25 and 30% below pre-burn levels in Phase 2 and Phase 3 woodlands. Biological crust (moss, lichen) cover was 2 times greater in Phase 2 than Phase 3 sites before fire (Fig. 3*c*; *P* < 0.0001). The fires eliminated biological crust and

there was no recovery 9 years after fire. Bare ground doubled in Phase 3 and in Phase 2 sites the year after fire (Fig. 3*d*; *P* < 0.0001). Bare ground returned to pre-burn levels respectively on Phase 2 and Phase 3 sites the sixth year (2009) and fourth year (2007) after fire.

Life form cover and density

Prior to fire, perennial grass cover was 4 times (*P* < 0.0001) greater in Phase 2 sites than in Phase 3 sites (Fig. 4*a*). The first year after fire perennial grass cover decreased by 85% in Phase 2 sites and by 75% in the Phase 3 sites. Perennial grass cover returned to pre-burn levels the third year after fire and exceeded pre-burn levels the sixth year after fire in both Phase 2 and
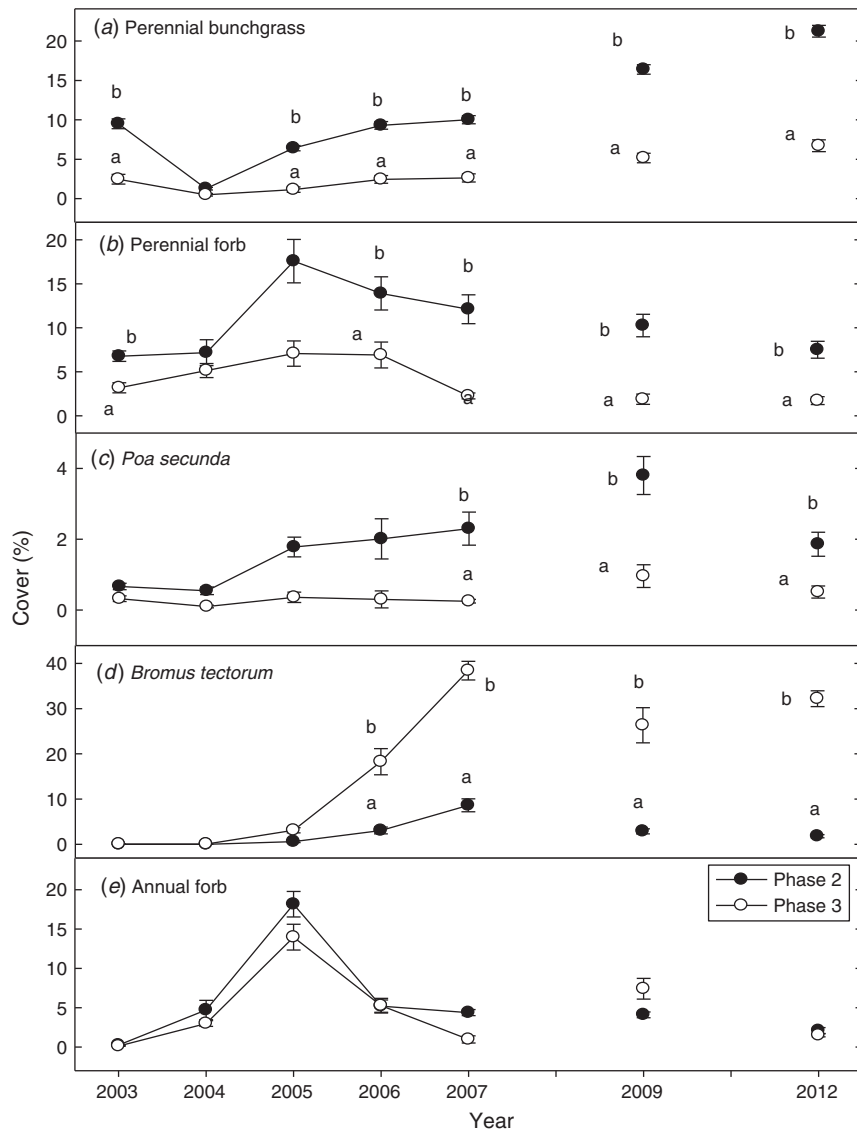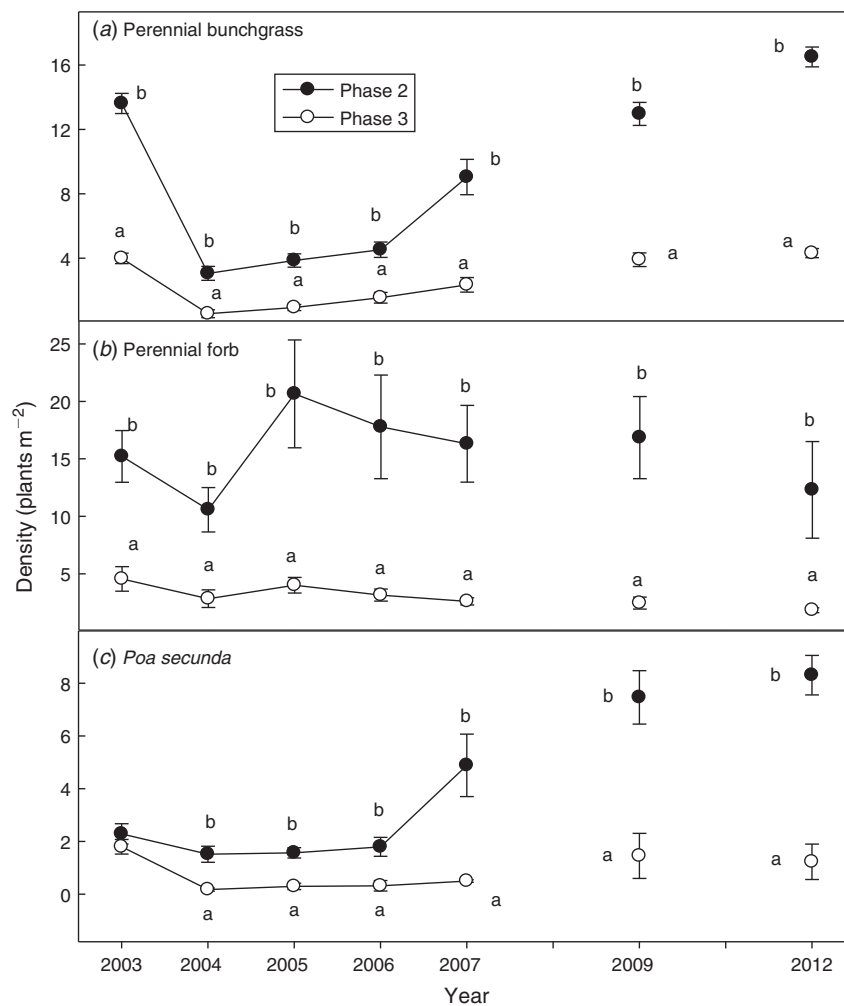
Fig. 4. Functional group cover (%) in burned Phase 2 and Phase 3 western juniper woodlands, Steens Mountain, Oregon (2003–2012; 2003 is the pre-fire year): (*a*) perennial grasses; (*b*) perennial forbs; (*c*) *Poa secunda*; (*d*) *Bromus tectorum* and (*e*) annual forbs. Data are means ± 1 standard error. Means sharing a common lowercase letter are not significantly different (*P* > 0.05). Phase 2 woodlands represent a co-dominance of trees, shrubs and herbaceous plants and in Phase 3 woodlands, trees are dominant and shrubs and herbaceous layers are reduced.

Phase 3 sites. From 2004 to 2012 perennial grass cover was 3–6 times greater (*P* < 0.0001) in Phase 2 than in Phase 3 sites. Perennial forb cover was 2 times (*P* < 0.0001) greater in Phase 2 than in Phase 3 sites before treatment (Fig. 4*b*). After fire, perennial forb cover was 2–10 times greater (*P* < 0.001) in Phase 2 than in Phase 3 sites. Cover of *P. secunda* was 3–7 times greater in Phase 2 sites after fire (Fig. 4*c*; *P* = 0.003). *Bromus tectorum*, present in trace amounts before treatment in both woodland phases, increased significantly after fire (Fig. 4*d*; *P* < 0.0001). *Bromus tectorum* cover was 4–16 times greater in the Phase 3 than the Phase 2 sites, in 2006–2012 (*P* < 0.0001). In Phase 2 and Phase 3 sites, annual forb cover increased from <1 to 16% and <1 to 20% by the second year post-fire (Fig. 4*e*;

P < 0.0001). In subsequent years (2005–2012), annual forb cover decreased to less than 4% cover on average in Phase 2 and Phase 3 sites.

Before fire, perennial grass density was 3 times greater in Phase 2 than in Phase 3 sites (Fig. 5*a*; *P* < 0.0001). Burning decreased perennial grass density by 78% in the Phase 2 sites, from ~14 to 2–3 plants m^{-2}. Phase 3 sites showed a decline of 95% in perennial grass density, from ~4 to <1 plants m^{-2} (*P* = 0.004). Perennial grass densities have increased in both phases since fire, but from 2005 to 2012 densities were 4–5 times greater in the Phase 2 sites (*P* < 0.0001). Densities of perennial forbs were 4–5 times greater in the Phase 2 than Phase 3 sites after fire (Fig. 5*b*; *P* = 0.002). Density of *P. secunda* did
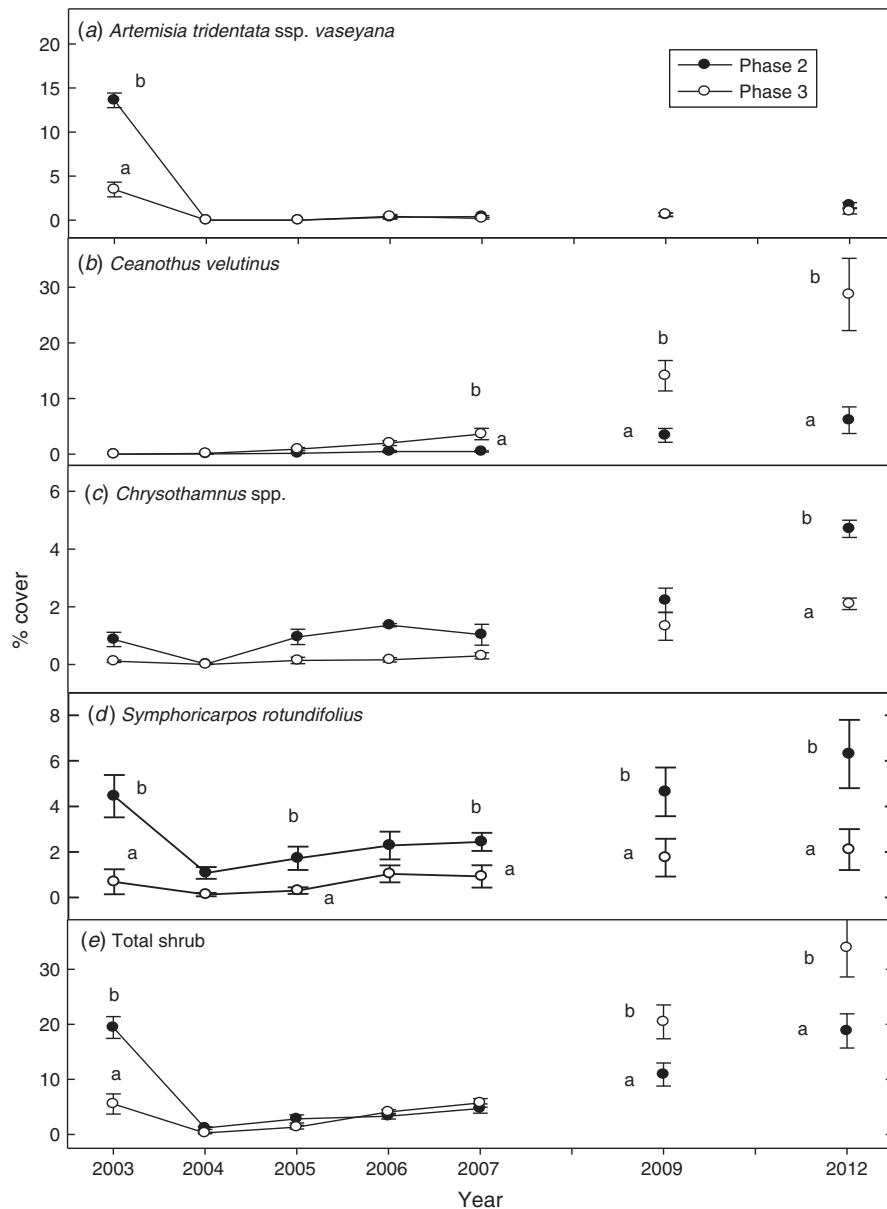
Fig. 5. Herbaceous perennial densities (plants m^{-2}) in burned Phase 2 and Phase 3 western juniper woodlands, Steens Mountain, Oregon (2003–2012; 2003 is the pre-fire year): (*a*) perennial grasses; (*b*) perennial forbs; (*c*) *Poa secunda*. Data are means ± one standard error. Means sharing a common lowercase letter are not significantly different (*P* > 0.05). Phase 2 woodlands represent a co-dominance of trees, shrubs and herbaceous plants and in Phase 3 woodlands, trees are dominant and shrubs and herbaceous layers are reduced.

not differ between phases before burning (Fig. 5*c*; *P* = 0.068) but after fire densities were 4–7 times greater in Phase 2 sites (*P* < 0.0001).

Shrub cover and density

Cover of *A. t.* ssp. *vaseyana* was approximately 3 times greater on Phase 2 than Phase 3 sites before fire (*P* < 0.0001). *A. t.* ssp. *vaseyana* was eliminated by the fires and cover was reduced to zero in both phases (Fig. 6*a*). Cover of *A. t.* ssp. *vaseyana* on sites of both phases was ∼1.5% in 2012 and was 75–85% below pre-burn levels. *Ceanothus velutinus* Dougl. (snowbrush), not present on either woodland phase before the fire, established after fire, particularly on the Phase 3 sites where it comprised 75% of total shrub cover by 2012 (*P* < 0.0001; Fig. 6*b*). Cover of *C. velutinus* was ∼5 times greater on the Phase 3 than Phase 2 sites in 2012 (*P* < 0.0001). Cover of *Chrysothamnus* Nutt. (rabbitbrush) spp. was not affected by fire as plants rapidly

re-sprouted the year after burning (Fig. 6*c*). Cover of *Chrysothamnus* spp. increased in both phase sites after fire and exceeded pre-burn levels by 2009, the sixth year after fire (*P* = 0.002). *Chrysothamnus* spp. comprised ∼30 and 15% of total shrub cover in Phase 2 and Phase 3 in 2012. Cover of *Symphoricarpos rotundifolius* var. *rotundifolius* Gary (western snowberry) returned to pre-burn levels the fourth year after fire (2006) in Phase 2 sites and the third year after fire in Phase 3 sites (*P* = 0.0005; Fig. 6*d*). Cover of *S. rotundifolius* averaged approximately 3 times greater in Phase 2 sites than Phase 3 sites, from 2004 to 2012 (*P* < 0.0001). *Ribes cereum* Dougl. (wax currant) increased in both sites after fire, but was greater in Phase 3 than Phase 2 sites in 2012 (*P* = 0.006). Cover of other shrub species, *Rosa woodsii* Lindl. (Wood's rose), *Berberis repens* Lindl. (Oregon grape), *Prunus emarginata* var. *emarginata* Dougl. (bitter cherry), *Sambucus mexicana* JPresl. (blue elderberry) and *Amelanchier utahensis* Koehne (serviceberry)
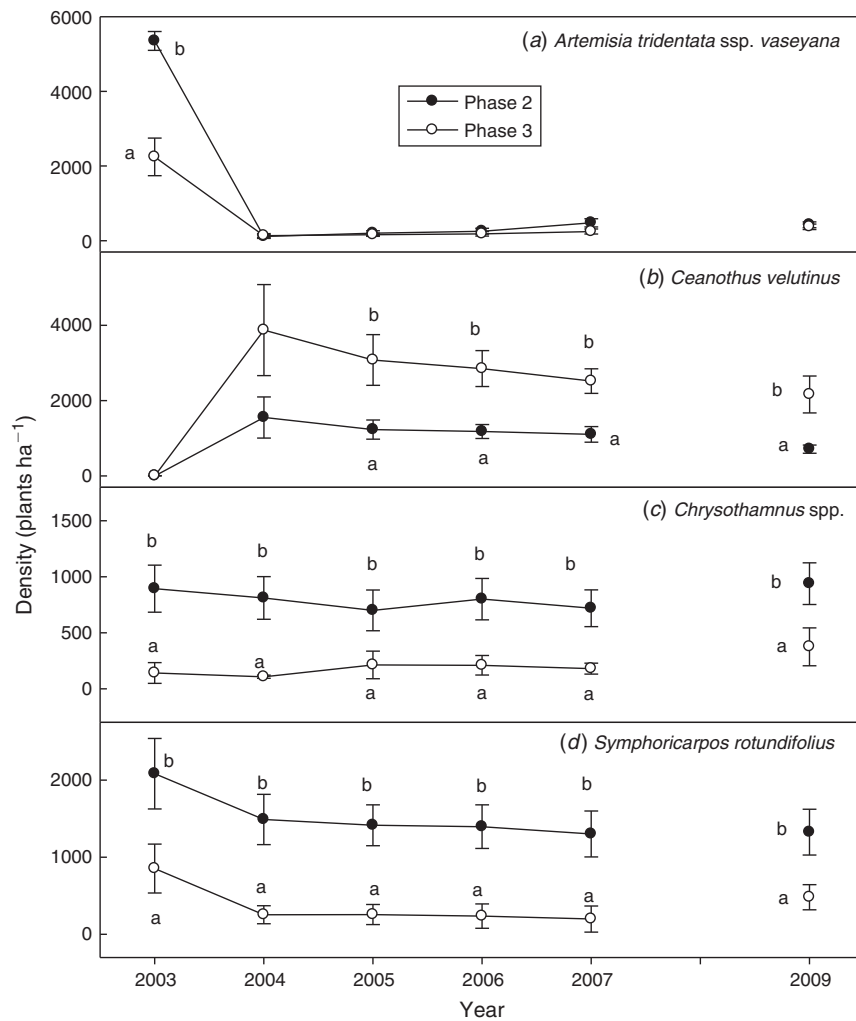
Fig. 6. Shrub cover (%) values in burned Phase 2 and Phase 3 western juniper woodlands, Steens Mountain, Oregon (2003–2012; 2003 is the pre-fire year): (*a*) *Artemisia tridentata* ssp. *vaseyana*; (*b*) *Ceanothus velutinus*; (*c*) *Chrysothamnus* spp.; (*d*) *Symphoricarpos rotundifolius* and (*e*) total shrub cover. Data are means ± 1 standard error. Means sharing a common lowercase letter are not significantly different ($P > 0.05$). Phase 2 woodlands represent a co-dominance of trees, shrubs and herbaceous plants and in Phase 3, woodlands trees are dominant and shrubs and herbaceous layers are reduced.

(which accounted for <0 0.1% of total shrub cover), did not differ between phases or across years. Total shrub cover was 4 times greater in Phase 2 than Phase 3 sites before fire (Fig. 6*e*; $P < 0.0001$). After fire total shrub cover did not differ between phases until 2009 and 2012, when cover was ~2 times greater in the Phase 3 sites ($P < 0.0001$).

Density of *A. t.* ssp. *vaseyana* was 2.5 times greater on Phase 2 sites before burning (Fig. 7*a*; $P < 0.0001$). Because fire eliminated *A. t.* ssp. *vaseyana* there were no differences in densities

between phases ($P = 0.369$). *Ceanothus velutinus* was the only species to increase in density after fire ($P < 0.0001$). The increase was 2–3 times greater in Phase 3 compared with Phase 2 sites between 2004 and 2012 (Fig. 7*b*; $P = 0.001$). Density of *Chrysothamnus* spp. increased after fire and was 4–10 times greater on Phase 2 than Phase 3 sites (Fig. 7*c*; $P < 0.0001$). *S. rotundifolius* density decreased by 32% in Phase 2 and 76% in Phase 3 sites after fire (Fig. 7*d*; $P = 0.019$). However, density of *S. rotundifolius* was 2–6 times greater in Phase 2 than Phase 3

Fig. 7. Shrub densities (plants ha^{-1}) in burned Phase 2 and Phase 3 western juniper woodlands, Steens Mountain, Oregon (2003–2012; 2003 is the pre-fire year): (*a*) *Artemisia tridentata* ssp. *vaseyana*; (*b*) *Ceanothus velutinus*; (*c*) *Chrysothamnus* spp. and (*d*) *Symphoricarpos rotundifolius*. Data are means ± 1 standard error. Means sharing a common lowercase letter are not significantly different ($P > 0.05$). Phase 2 woodlands represent a co-dominance of trees, shrubs and herbaceous plants and in Phase 3 woodlands, trees are dominant and shrubs and herbaceous layers are reduced.

sites ($P < 0.0001$). *Ribes cereum* density increased after fire, and was greater in Phase 3 (282 ± 56 plants ha^{-1}) than Phase 2 (52 ± 12 plants ha^{-1}) sites in 2012 ($P < 0.0001$).

Discussion

The combination of cutting and prescribed fire in two different phases of woodland development provided a distinct contrast in herbaceous and shrub recovery in *J. occidentalis*-invaded sagebrush steppe. The herbaceous layer on Phase 2 sites was dominated by native perennial and annual vegetation after fire. On Phase 3 sites the herbaceous layer shifted from native species to dominance by *B. tectorum* after fire. The shrub layer shifted from primarily *A. t.* spp. *vaseyana* to *C. velutinus* on Phase 3 sites and to an approximately equal mix of *Chrysothamnus* spp., *S. rotundifolius* and *C. velutinus* on Phase 2 sites. *Artemisia t.* ssp. *vaseyana* steppe recovery following fire in piñon–juniper

woodlands often varies in composition and rate, as a consequence of differing fire extent and severities, seed source, abundances and competitive abilities of native and exotic species, ecological site characteristics, herbivory and environmental variation (Barney and Frischknecht 1974; Koniak 1985; Chambers *et al.* 2007; Rau *et al.* 2008; Ziegenhagen and Miller 2009; Bates *et al.* 2011). Our results suggest that piñon–juniper woodland phase influences post-fire recovery in the *A. t.* ssp. *vaseyana* steppe ecosystem and indicates that Phase 2 woodland sites have a greater likelihood than do Phase 3 woodlands, of recovery to *A. t.* ssp. *vaseyana*-steppe vegetation following fall prescribed fire.

Herbaceous and ground cover response

The first two years after fire herbaceous recovery was mainly comprised of perennial and annual forbs on both burned

woodland phases. This successional stage is typical following fire in piñon–juniper woodlands (Barney and Frischknecht 1974; Koniak 1985; Bates *et al.* 2011). However, by the third year after fire, vegetation succession had diverged between phases, with *B. tectorum* dominating Phase 3 sites and herbaceous perennials dominating Phase 2 sites. Although perennial grasses on Phase 3 sites had returned to pre-burn levels of cover and density respectively by the fourth and sixth year after fire, this recovery was not sufficient to prevent *B. tectorum* dominance. Increasingly, experimental evidence indicates that the resilience of *A. t.* ssp. *vaseyana* steppe communities following fire recovery is dependent on the persistence of sufficient density of herbaceous perennial vegetation (Bates *et al.* 2006, 2011; Condon *et al.* 2011). The Phase 2 sites, after a 75% reduction in perennial grass density, retained 2–3 plants m^{-2} the year following fire. This level of perennial grasses was adequate for density to recover 4 years after fire and, in combination with higher densities of perennial forbs than that on Phase 3 sites, likely limited *B. tectorum* increases on Phase 2 sites. Others have indicated that greater presence and recovery of perennial herbaceous vegetation prevents annual grasses from dominating after fire in sagebrush steppe (Chambers *et al.* 2007; Davies *et al.* 2008; Bates and Svejcar 2009; Bates *et al.* 2011; Condon *et al.* 2011). Another element that may have supported native plant recovery on the Phase 2 sites was, potentially, a more complete soil seed bank. Koniak and Everett (1982) recorded greater seed numbers and diversity of soil seed banks in younger (Phase 1 and 2) than older (Phase 3) piñon–juniper woodlands.

The effects of fires on the understorey and early succession on Phase 3 sites were similar to those seen after high intensity and severity fires in forest and woodland ecosystems of the western United States and Canada (Tausch 1999; Brown and Smith 2000; Bauer and Weisberg 2009). High intensity wildfires in piñon–juniper woodlands of Nevada and Utah have resulted in post-fire dominance of *B. tectorum* and exotic weeds because of a lack of native herbaceous perennial species (Tausch 1999). Dhaemers (2006) and Condon *et al.* (2011) established that *B. tectorum* cover after fire was positively associated with pre-fire piñon–juniper cover and negatively associated with recovery of herbaceous perennials. In *P. tremuloides* communities invaded by *J. occidentalis* (Phase 3 woodlands), early-fall prescribed fire killed almost all perennial grasses, reduced perennial forbs by 60% and was followed by invasive weed dominance (Bates *et al.* 2006). In *P. ponderosa* Dougl. (ponderosa pine) forest perennial grass cover decreased and invasive species increased as fire intensity and litter consumption increased (Armour *et al.* 1984; Griffis *et al.* 2001; Bataineh *et al.* 2006; Sabo *et al.* 2009).

However, not all Phase 3 *J. occidentalis* woodlands that burn have responded with loss of desired perennial vegetation. In Phase 3 *J. occidentalis* woodlands in south-west Idaho, post-burn early succession was dominated by native forbs followed by recovery of perennial grasses 3 years after fire, despite presence of *B. tectorum* (Bates *et al.* 2011). In the study of Bates *et al.* (2011), where natives dominated post-fire recovery, densities of perennial grasses (0.7–2 plants m^{-2}) and forbs (5–25 plants m^{-2}) were greater the first year post-fire than in our study. Phase 3 sites where *B. tectorum* dominated after fire (Bates *et al.* 2006), including those in our study, had low

post-fire densities of perennial grasses (<0.3–0.6 plants m^{-2}) and forbs (<5 plants m^{-2}).

One question, which can only be answered following extended monitoring, is whether dominance by *B. tectorum* is a temporary or permanent feature on the burned Phase 3 woodlands. In our region, *B. tectorum* is typically of concern in drier *A. t.* ssp. *wyomingensis* Beetle & Young (Wyoming big sagebrush) plant communities and sites with mesic soil temperature regimes (Miller *et al.* 2008; NRCS 2010*a*). The ecological sites in this study have frigid soil temperature regimes and are *A. t.* ssp. *vaseyana* plant communities where native perennials typically should have a competitive advantage over *B. tectorum* (Chambers *et al.* 2007). Despite dominance by *B. tectorum*, perennial grass density and cover continued to increase after fire. Should this trend continue, native species may, over a longer period, replace *B. tectorum*. A concern with the current dominance by *B tectorum* is the potential for this species to alter the fire regime. Mean fire return intervals can shorten to as little as every 5 years as a result of *B. tectorum* dominance in *Artemisia* communities, which can limit recovery of native species (Whisenant 1990; Wisdom *et al.* 2005). However, recent calculations by Balch *et al.* (2013) indicate that fire return intervals for many cheatgrass areas may range between 49 and 78 years.

Shrub recovery

Recovery of shrubs on both woodland phase sites was characterised by species-specific adaptations to fire. Non-sprouting *A. t.* ssp. *vaseyana*, will take longer to recover or exceed pre-fire cover and density levels because re-establishment will depend on immigration of propagules from outside the burnt areas, and plants that emerged from seed after fire (Ziegenhagen and Miller 2009). *Artemisia t.* ssp. *vaseyana* that returned the first year after fire appear to have originated from the emergence from the seed bank. These new plants produced viable seed at 2 years of age as evidenced by seedlings establishing in close proximity to parent plants between 2009 and 2012. Recovery of *A. t.* ssp. *vaseyana* canopy cover has been reported to be between 20 and 40 years (Harniss and Murray 1973; Lesica *et al.* 2007; Ziegenhagen and Miller 2009). Cover and density of *A. t.* ssp. *vaseyana* in 2009 was approximately the same on Phase 2 and 3 sites, so we might expect that future recovery will be similar. However, Condon *et al.* (2011) indicated that re-establishment of *A. tridentata* following fire is positively related to cover of perennial herbaceous species. This relationship may influence the rate and magnitude of *A. t.* ssp. *vaseyana* recovery on the Phase 2 sites. To speed shrub recovery managers may consider seeding *A. t.* ssp. *vaseyana* following fire (Cox and Anderson 2004).

Sprouting shrub species, *S. rotundifolius* and *Chrysothamnus* spp., had either returned to or exceeded pre-fire cover by 2009. Typically, there is little fire-caused mortality and these species increase 3–5 years after fire (Anderson and Bailey 1979; Wright *et al.* 1979; Sieg and Wright 1996) and are important in recovery of shrub structure on *A. t.* ssp. *vaseyana* sites (Davies *et al.* 2012). However, response of *S. rotundifolius* can be variable and recovery may require up to 15 years or longer if ungulate browsing damages regrowth (Blaisdell 1953; Bartos *et al.* 1994). Severe fire can reduce sprouting (Young 1983), which may explain the slight decrease in *S. rotundifolius* densities in

our study. The emergence of *C. velutinus* was likely due to its presence in the soil seed bank. *Ceanothus velutinus* seed remains viable in soils for periods exceeding 200 years and can appear after fire where it was previously not present (Steen 1966; Kramer and Johnson 1987; Halpern 1989; Bradley *et al.* 1991; Tonn *et al.* 2000). In our study, large *C. velutinus* patches developed with the highest densities and cover in the Phase 3 sites. As *C. velutinus* is a nitrogen (N) fixer (Mozingo 1987), it is possible that increased soil available N facilitated the increase in *B. tectorum* on Phase 3 sites. Nitrogen fixing plants, such as *Lupinus argenteus*, Pursh (silvery lupine), have the potential to influence plant succession in *A. t.* ssp. *vaseyana* steppe by modifying post-fire N availability (Goergen and Chambers 2009). However, *B. tectorum* cover did not appear to be greater in the presence of *C. velutinus*, hence we concluded that the lack of perennial herbaceous vegetation on the Phase 3 sites allowed post-fire *B. tectorum* dominance.

State and transition models

State-and-transition models for interpreting expanding piñon–juniper woodlands using fire are essential for woodland management and sagebrush steppe restoration. Our interpretation applies to the two ecological sites used in our study (Loamy (12–16 PZ, 304–406 mm) and Deep Loamy (12–16 PZ); NRCS 2010*a*) and potentially other *A. t.* ssp. *vaseyana* ESDs with similar site characteristics, xeric soil moisture and frigid soil temperature regimes. The model assumes that all states except the Annual Grass state retain an intact native understorey with few or no weeds present. Our results suggest that sites in Phase 1 and Phase 2 woodland states will recover native herbaceous species composition following fire disturbances. Fire in Phase 3 woodlands has the potential for creating several transitional events, with surviving perennial plant density and invasive species presence becoming the prime determinants of early successional composition. We suggest that native species composition will recover when perennial grass and forb densities respectively exceed 1 and 5 plants m^{-2}, based on results from Bates *et al.* (2006, 2011). Sites with herbaceous values below these levels, as in our study, may have a greater chance of becoming dominated by invasive annual grasses following fire, indicating that a threshold may have been crossed. Our interpretation is marginal and suffers from a major drawback that is common to state-transition models in that they remain mainly observational and lack adequate predictive power. To acquire greater management utility for piñon–juniper woodlands, developing probabilities for transitional events, thresholds and outcomes is needed to refine STMs.

Management implications and conclusions

Piñon–juniper species continue to expand and in-fill woodlands as a result of reduced fire frequency and anthropogenic factors, and without active management the expansion will result in continued declines and loss of *A. t.* ssp. *vaseyana* steppe communities. It is currently estimated that 40% of piñon–juniper woodlands are Phase 1 and another 40% are Phase 2 (Miller *et al.* 2008). In 30–50 years, Phase 3 woodlands have the potential to increase from a current 20% to 75% of total woodland area (Johnson and Miller 2006). Because of increasing canopy fuel

loading, the potential for more intense fires is likely to increase in Phase 3 woodlands (Tausch 1999; Miller *et al.* 2008). Thus, burning in Phase 3 woodlands is less predictable because of depleted understorey components and the potential for greater fire severity effects on herbaceous vegetation, which may encourage subsequent weed dominance (Bates *et al.* 2006; Bates *et al.* 2011; Condon *et al.* 2011). Phase 3 woodlands that are burned by wildfire or prescribed fire in fall are more likely to require additional inputs, primarily seeding and weed control, for vegetation recovery goals to be accomplished (Cox and Anderson 2004; Miller *et al.* 2005; Sheley and Bates 2008). Applying alternative treatments that have less severe effects than fall fire may potentially improve community recovery in Phase 3 woodlands. Cutting all trees on Phase 3 woodland sites has recovered herbaceous and shrub vegetation without weed dominance (Vaitkus and Eddleman 1987; Bates *et al.* 2005). Clear cutting followed by winter or early spring burning of juniper fuels has resulted in low understorey plant mortality and earlier recovery of sagebrush and native herbaceous species (Bates *et al.* 2006; Bates and Svejcar 2009).

Because control efforts in Phase 3 piñon–juniper woodlands are expensive (Miller *et al.* 2005) and fall burning offers less predictable results, managers involved with shrub–steppe restoration should give priority to treatment of Phase 1 and Phase 2 woodlands. Phase 1 and Phase 2 woodlands, which have an intact understorey of shrubs and herbaceous species, will most likely be dominated by native vegetation after fire as our study has demonstrated. Managers should expect that it will take several decades for *A. t.* ssp. *vaseyana* to recover following burning of Phase 1 and 2 woodlands; however, there is greater potential for achieving recovery goals and preventing woodland dominance by reintroducing fire in Phase 2 and earlier stages of piñon–juniper woodland development.

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