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Longer-term post-fire succession on Wyoming big sagebrush steppe

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Abstract. We assessed plant community succession following prescribed fire on ungrazed Wyoming big sagebrush steppe, eastern Oregon. Treatments were burned (Burn; September and October, 2002) and unburned (Control) sagebrush steppe. Herbaceous yield, vegetation canopy cover and density were compared between treatments after fire (2003–18). Herbaceous yield in the Burn treatment was about double the Control for most of the study period. Prior to fire, native perennials comprised 90–95% of herbaceous yield. After fire, native perennials represented 78% (range 67–93%) and exotic annuals 22% (range 7–33%) of total yield. Exotic annuals increased after fire and responded in two stages. In the first 8 years after fire, desert alyssum dominated the annual plant composition. In the last half of the study, cheatgrass co-dominated the annual component with alyssum. Sagebrush recovery was slow and we estimated sagebrush cover would return to pre-burn levels, at the earliest, in 115 years. Burning Wyoming big sagebrush steppe would be detrimental to sagebrush-obligate wildlife for an extended time period, because of lost cover and structure provided by sagebrush. The additional forage provided on burned areas may give livestock manager's greater flexibility to rest or defer unburned habitat for wildlife species of critical concern.

Additional keywords: *Alyssum* spp., bio-crust, cheatgrass, Great Basin, perennial bunchgrass, prescribed fire.

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Introduction

Many terrestrial ecosystems have experienced widespread environmental and ecological alterations because of expanding human development and resource demands. This often affects ecosystem integrity and may alter responses to historical disturbances that shaped these ecosystems in the past. In the interior western USA, the big sagebrush (*Artemisia tridentata* Nutt.) steppe is considered threatened because ~50% of the ecosystem has been converted to other land uses or degraded by invasive annual grasses and native conifer woodland expansion (West and Young 2000; Knick *et al.* 2003; Rowland and Wisdom 2005). Wildland fire is the major natural and often deliberately applied disturbance affecting big sagebrush steppe dynamics. Fire has become of great concern in areas with low resistance and resilience attributes, such as the Wyoming big sagebrush (*A. tridentata* Nutt. ssp.wyomingensis [Beetle & Young] S.L. Welsh) alliance because it is vulnerable to conversion to invasive annual grassland after fire (Chambers *et al.* 2007). Exotic annual grass invasion, particularly cheatgrass (*Bromus tectorum* L.), has in many areas altered the historical fire regimes by increasing the frequency and size of fires (D'Antonio and Vitousek 1992; Brooks *et al.* 2004; Balch *et al.* 2013; Pilliod *et al.* 2017; Bradley *et al.* 2018). Maintenance and recovery of this complex is important because of its significant value for wildlife, particularly sage-grouse, and for livestock grazing (Davies *et al.* 2011). In remaining Wyoming big sagebrush steppe, fire disturbance will remain a major factor shaping the development of this alliance's various plant associations. Understanding the longer-term post-fire dynamics in these communities is needed to improve management and to prioritise restoration efforts and fire suppression.

In the past several decades, our knowledge of the response and recovery of intact Wyoming big sagebrush communities to fire has increased from studies at the local site level and across multiple locations and fire conditions. Intact communities as defined by (Davies *et al.* 2007) meet the following criteria: (1) the understorey is dominated by native perennial bunchgrasses and forbs, (2) exotic species are a minor to non-existent component, (3) evidence of limited historic and present livestock use based on criteria developed by Passey *et al.* (1982), (4) sites are dominated by mature stands of Wyoming big sagebrush (no recorded fire at sites for >50 years) and (5) no

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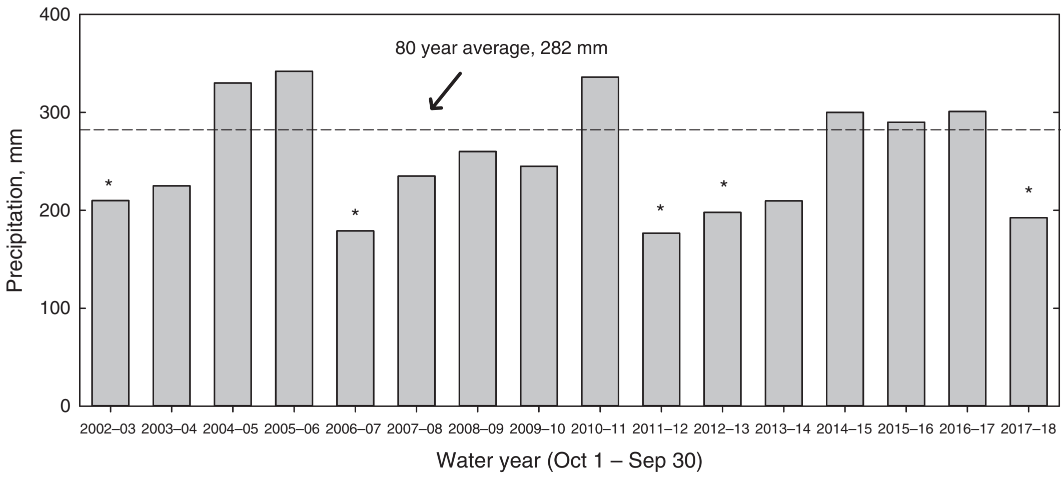

Fig. 1. Crop year (1 Oct–30 June) precipitation for 2002–8 at the Northern Great Basin Experimental Range, Oregon. *Drought year (precipitation <75% of average).

other disturbances evident. The major insights of these efforts are that recovery of intact Wyoming big sagebrush is slow, requiring 50 years to over a century (Baker 2006, 2011; Shinneman and McIlroy 2016), which is comparable to earlier recovery estimates postulated by Wright and Bailey (1982), and that herbaceous recovery is variable, ranging from weed- to native-dominated plant communities (Bates *et al.* 2011; Davies *et al.* 2012; Ellsworth *et al.* 2016; Urza *et al.* 2017; Swanson *et al.* 2018). Post-fire herbaceous response is a product of pre-fire plant composition, as well as the resilience of the plant community to fire. After fire, sites maintaining their native composition tend to be dominated by native perennials (Bunting 1985; West and Yorks 2002; Davies *et al.* 2007; Rhodes *et al.* 2010; Swanson *et al.* 2018). At the other extreme, areas that lose the native herbaceous community as a result of fire or that lacked an intact native component before fire are dominated by exotic annuals (Young and Evans 1978; Chambers *et al.* 2007; Davies *et al.* 2016; Swanson *et al.* 2018).

Our objectives were to (1) evaluate recovery of intact Wyoming big sagebrush–bunchgrass steppe, 16 years after prescribed fire, comparing plant canopy cover, density and herbaceous yield between burned and unburned sites and (2) estimate a time period for sagebrush to recover. Vegetation dynamics at these sites were previously evaluated in two short-term studies (Davies *et al.* 2007; Rhodes *et al.* 2010). Early succession at the sites indicated the herbaceous response in the burn treatment mainly comprised perennial grasses and desert alyssum (*Alyssum desertorum* L.); sagebrush cover, 5 years after fire, was ~10% of the unburned areas and native forbs and cheatgrass were unresponsive to the fire disturbance, not differing from unburned areas.

Here we provide a longer-term, detailed assessment of herbaceous and shrub recovery following fire in a Wyoming big sagebrush community. Hypotheses were developed from the sites early successional responses (Davies *et al.* 2007; Rhodes *et al.* 2010) and included: (1) sagebrush cover and density would increase in burn treatments, though remain lower than unburned areas, (2) herbaceous yield would be greater in the burn versus the unburned treatment, but would show signs of decline as a result of increasing shrub cover and (3) perennial grasses would remain the dominant herbaceous component.

Materials and 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. The sites are at an elevation of 1400 m and slopes are 1–4%. Soils are a complex of three soil series sharing several attributes: all are Durixerolls, soil surface texture is sandy loam to loamy sand and they are well drained with a duripan beginning at a depth of 40–55 cm (Lentz and Simonson 1986; Davies *et al.* 2007). Most precipitation arrives from mid-November to May. Annual precipitation has averaged ~280 mm since measurements began in the 1930s. Drought occurred in the 2003, 2007, 2012, 2013 and 2018 growing seasons and crop year precipitation (Oct 1–June 15) was also below average in 2004, 2008–10 and 2014 (Fig. 1).

Wyoming big sagebrush was the dominant shrub and basin big sagebrush (*Artemisia t.* subsp. *tridentata*) and yellow rabbitbrush (*Chrysothamnus viscidiflorus* Hook. (Nutt.)) were subdominant shrubs. Idaho fescue (*Festuca idahoensis* Elmer), Thurber's needlegrass (*Achnatherum thurberianum* (Piper) Barkworth) and bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve) were the principle perennial bunchgrasses. Sandberg's bluegrass (*Poa secunda* Vasey), prairie Junegrass (*Koeleria macrantha* (Ledeb.) J.A. Schultes) and bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey) were subdominant perennial grasses. Cheatgrass was present in trace amounts. Perennial forbs included taper-tip hawksbeard (*Crepis acuminata* Nutt.), milkvetch species (*Astragalus* L.), common yarrow (*Achillea millefolium* L.) and long-leafed phlox (*Phlox longifolia* Nutt.). Native annual forbs included blue-eyed Mary (*Collinsia parviflora* Lindl.) and slender phlox (*Microsteris gracilis* (Hook.) Greene). Non-native desert alyssum was the prevalent annual forb.

The sites were representative of intact Wyoming big sagebrush plant associations in south-east Oregon. Sagebrush cover averaged 10% (range 6–17%) and grass-forb cover exceeded

15% (Davies *et al.* 2007). Sagebrush and total herbaceous cover values were about average for Wyoming big sagebrush communities for the region and cover of invasive annuals was minor at <1% (Davies *et al.* 2007). Sites were a mix of two plant associations and included Wyoming big sagebrush–bluebunch wheatgrass and Wyoming big sagebrush–Idaho fescue–bluebunch wheatgrass–Thurber's needlegrass (Bates and Davies 2019).

Experimental design and treatment

A randomised block design was used to compare vegetation dynamics between burned (Burn) and unburned (Control) Wyoming big sagebrush steppe. Blocking was done to remove differences associated with soils and dominant herbaceous vegetation and to increase precision of the results. Five, 4.2-ha blocks, comprising two 2.1-ha plots, randomly assigned to either the Burn or Control treatment, were established in 2001. Prescribed burning (strip head fires) was done in late September and early October 2002. Fires were ignited using a gel-fuel terra torch (Firecon, Inc., Ontario, OR, USA). Burns were largely complete across treatment plots, killing ~90–95% of the Wyoming big sagebrush. Wind speeds varied between 5 and 20 km hr^{-1}, air temperatures were 20–25°C and relative humidity varied from 10% to 35% during the burns. Moisture content of fine fuels (herbaceous vegetation) was between 8% and 12% and fine-fuel loads ranged between 350 and 420 kg ha^{-1}. Plots have not been grazed since 1999. Between 1937 and 1999, grazing by cattle was moderate (50% utilisation), in a deferred-rotation management system.

Vegetation measurements

Vegetation response to treatment was evaluated by quantifying shrub and herbaceous canopy cover, perennial herbaceous density and herbaceous yield. Five, 50-m transects were randomly placed within each treatment plot in 2001. Transects were permanently marked using rebar stakes for re-measurement in subsequent years. Canopy cover was measured in June 2001 to 2006, 2008, 2012 and 2018. Pretreatment vegetation measurements (2001, 2002) were conducted before fire application (Davies *et al.* 2007). Shrub canopy cover was measured by species using line intercept (Canfield 1941) and shrub density by belt transect (2 × 50 m). Canopy gaps less than 15 cm were included in the shrub cover measurements (Boyd *et al.* 2007). Herbaceous canopy 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, forbs and Sandberg's bluegrass) was determined by counting all individuals rooted inside the 0.2-m^2 frames.

Herbaceous yield was measured in mid-June 2002–07, 2009–13, 2015, 2017 and 2018 by functional group (perennial bunchgrasses, Sandberg's bluegrass, perennial forbs, annual forbs and cheatgrass). Bunchgrasses were clipped to a 2-cm stubble. Sandberg's bluegrass, perennial forbs, cheatgrass and annual forbs were clipped to near ground level. Perennial grasses and forbs were harvested from 15, 1-m^2 randomly located frames per treatment plot, avoiding areas clipped in prior years. Cheatgrass and annual forbs were collected from a 0.20-m^2 nested plot inside the 1-m^2 frames. Samples were oven-dried at 48°C for 48 h to a constant weight before weighing.

Statistical analysis

Repeated-measures analysis of variance with the PROC MIXED procedure (SAS Institute ver. 9.4, Cary, NC, USA) was used for a randomised complete block design to compare time, treatment and year by treatment effects between Burn and Control treatments for plant species and functional group cover and yield, and perennial species density. An auto regressive order one covariance structure was used because it provided the best model fit (Littell *et al.* 2006). Linear regression models (SigmaPlot 12.5) were developed to estimate recovery times for sagebrush canopy cover and density. Yield response variables were perennial bunchgrass, Sandberg bluegrass, perennial forb, annual forb, cheatgrass and total herbaceous yield. Because of a strong year effect, we also analysed measurement years using ANOVA for randomised complete block design to simplify the presentation of 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 2003). Data not normally distributed were log-transformed to stabilise variance. Back-transformed means are reported in the results. Statistical significance of all tests was set at $P < 0.05$.

Results

Shrub cover and density

Wyoming big sagebrush cover was lower in the Burn treatment than the Control after fire ($P < 0.001$; Fig. 2*a*). In 2018, Wyoming big sagebrush cover in the Burn treatment was 1.8%, which was ~18% of pre-burn (or Control) cover (10.2 ± 1.1%). The rate of recovery of sagebrush cover has been linear, increasing at ~0.09% per year (adjusted $R^2 = 0.965$; $P < 0.001$). At this rate, sagebrush cover would return to pre-burn levels in 115 years. Wyoming big sagebrush density was lower in the Burn treatment after fire ($P < 0.001$; Fig. 2*b*). Sagebrush density in 2003, the year after fire, was ~11% of pre-burn levels. In 2018, sagebrush density in the Burn treatment was ~18% of pre-burn (or control) density. The rate of increase of sagebrush has been linear at 0.0013 plants m^{-2} per year (adjusted $R^2 = 0.795$; $P < 0.027$). Should this rate be maintained, sagebrush density would recover to pre-burn levels in ~250 years.

Year by treatment effect were significant for yellow rabbitbrush cover ($P = 0.016$; Fig. 2*c*). Rabbit brush cover was reduced 10-fold the first year after fire, recovering to equal and exceed the Control in subsequent years. In 2006 and 2018, rabbitbrush cover in the Burn treatment was 2- and 2.5-fold greater than the Control, respectively. Density of rabbitbrush did not differ between treatments ($P = 0.651$) or across years ($P = 0.725$; Fig. 2*d*).

Total herbaceous yield and cover

The year and treatment interaction were significant for herbaceous yield (Fig. 3*a*; $P < 0.001$). Herbaceous yield was greater in the Burn than the Control treatment by the second year after fire and remained so until 2018. Herbaceous yield was

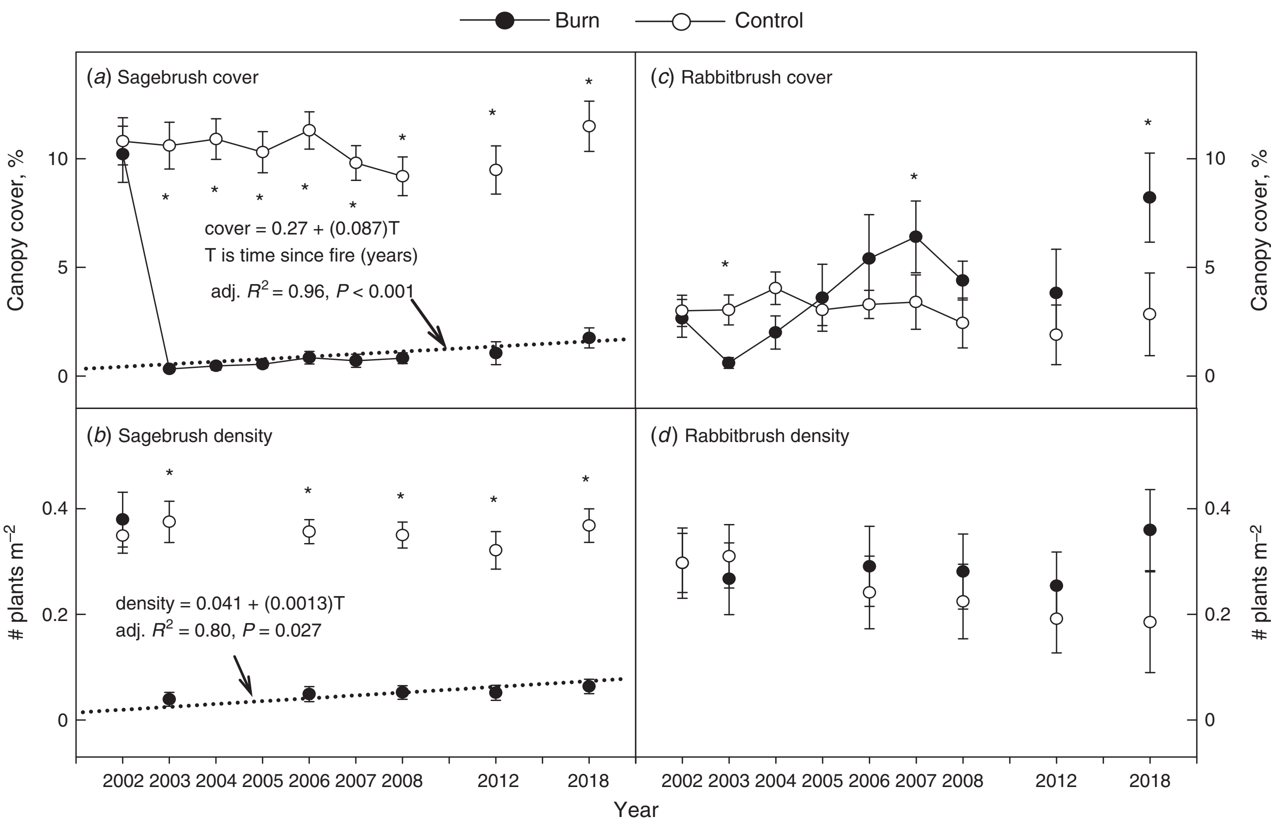

Fig. 2. Wyoming big sagebrush (*a*) cover and (*b*) density and yellow rabbitbrush (*c*) cover and (*d*) density for the Burn and Control treatments in Wyoming big sagebrush steppe, Northern Great Basin Experimental Range, Oregon (2002–18). Values represent mean ± 1 standard error. *Significant difference ($P < 0.05$) between treatments within year.

1.4–1.9-fold greater in the Burn treatment compared with the Control between 2004 and 2017. Herbaceous yields fluctuated in both Burn and Control treatments in response to yearly environmental conditions.

The year by treatment interaction was significant for total herbaceous cover ($P = 0.018$; Fig. 3*b*). Differences between treatments occurred in the first 5 years after fire (2003–07). Since 2008, herbaceous cover has not differed between the Burn and Control treatments.

Perennial bunchgrasses

The year by treatment interaction was significant for perennial bunchgrass yield ($P < 0.001$; Fig. 4*a*) and cover ($P = 0.025$; Fig. 4*b*). Between 2003 and 2018, perennial bunchgrass yield was 1.3–2.3-fold greater in the Burn treatment compared with the Control after fire. Cover was 15–70% greater in the Burn treatment from 2004 to 2008. Since 2012, bunchgrass cover has not differed between the Burn and Control treatments. Perennial bunchgrass density varied by treatment ($P = 0.044$; Fig. 4*c*). The treatment effect was apparent the first 4 years after fire when density was ~20% greater in the Burn treatment than the Control. The year effect reflected (1) increased density in the Burn treatment the first 3 years following fire and (2) ~12% decline in density from pre-burn levels in both treatments from 2007 to 2018.

Sandberg's bluegrass

Sandberg's bluegrass yield varied by year ($P < 0.001$; Fig. 5*a*) and treatment ($P = 0.031$). Among years, bluegrass yield differed between 2- and 7-fold. Following fire, bluegrass yield averaged 30% greater in the Control (61.0 ± 4.4 kg ha^{-1}) than the Burn treatment (45.3 ± 4.0 kg ha^{-1}). Cover of Sandberg's bluegrass only varied by year ($P < 0.001$; Fig. 5*b*). When evaluating within individual years, cover was 50% greater in the Control in 2012 and 2018. Density of Sandberg's bluegrass only varied by year ($P < 0.002$; Fig. 5*c*). The year effect reflects substantial increases and decreases in density over time.

Perennial forbs

Perennial forb yield varied by treatment ($P = 0.017$) and year ($P < 0.001$) effect (Fig. 6*a*). Perennial forb yield ranged by up to 5-fold across years and yield in the Control exceeded that of the Burn treatment in 8 of the 13 post-fire years. Treatment differences since fire indicated that forb yield was significantly greater in the Control (53.7 ± 3.2 kg ha^{-1}) than the Burn treatment (43.1 ± 2.8 kg ha^{-1}; $P = 0.016$). Cover ($P < 0.001$) and density ($P < 0.001$) of perennial forbs only varied by year, with cover varying up to 3-fold across years (Fig. 6*b*), and density in both treatments decreasing by ~55% between 2002 and 2018 (Fig. 6*c*). The decline in perennial forb density mainly involved three species: sickle-pod milkvetch (*Astragalus*

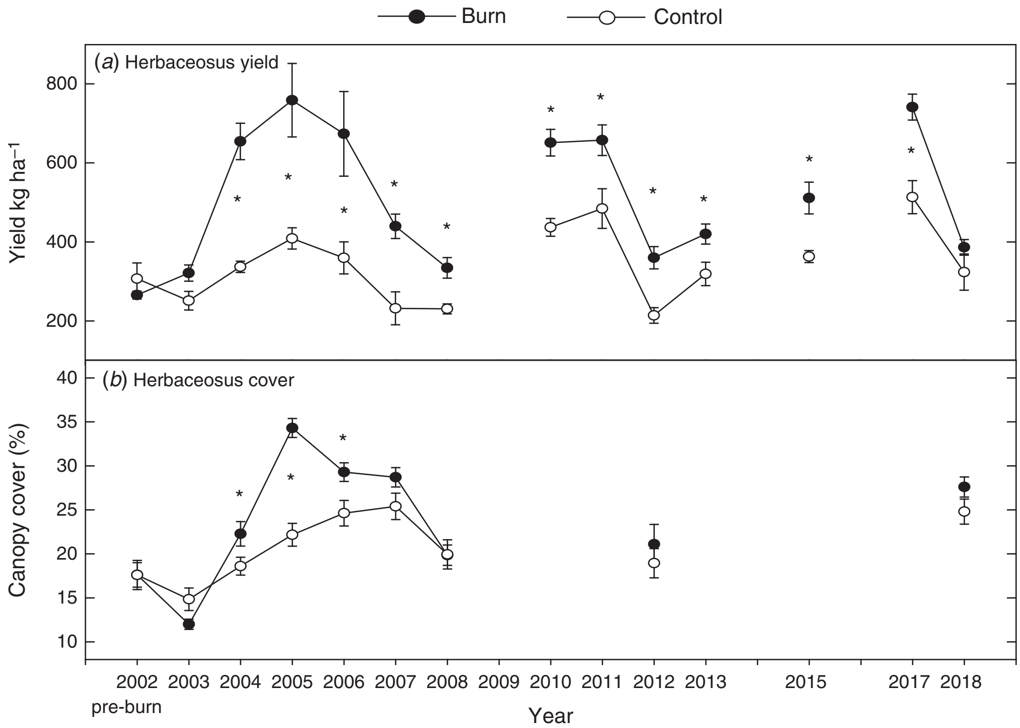

Fig. 3. Herbaceous (*a*) yield and (*b*) canopy cover for the Burn and Control treatments in Wyoming big sagebrush steppe, Northern Great Basin Experimental Range, Oregon, (2002–18). Values represent mean ± 1 standard error. *Significant difference ($P < 0.05$) between treatments within year.

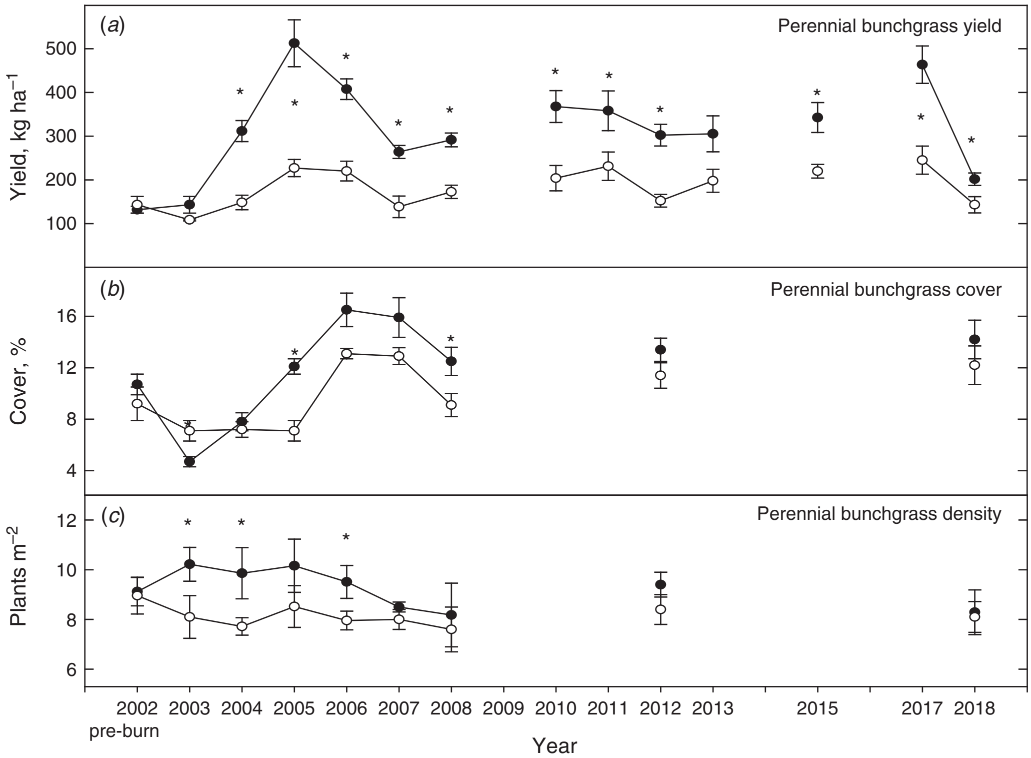

Fig. 4. Perennial bunchgrass (*a*) yield, (*b*) canopy cover and (*c*) density for the Burn and Control treatments in Wyoming big sagebrush steppe, Northern Great Basin Experimental Range, Oregon (2002–18). Values represent mean ± 1 standard error. *Significant difference ($P < 0.05$) between treatments within year.

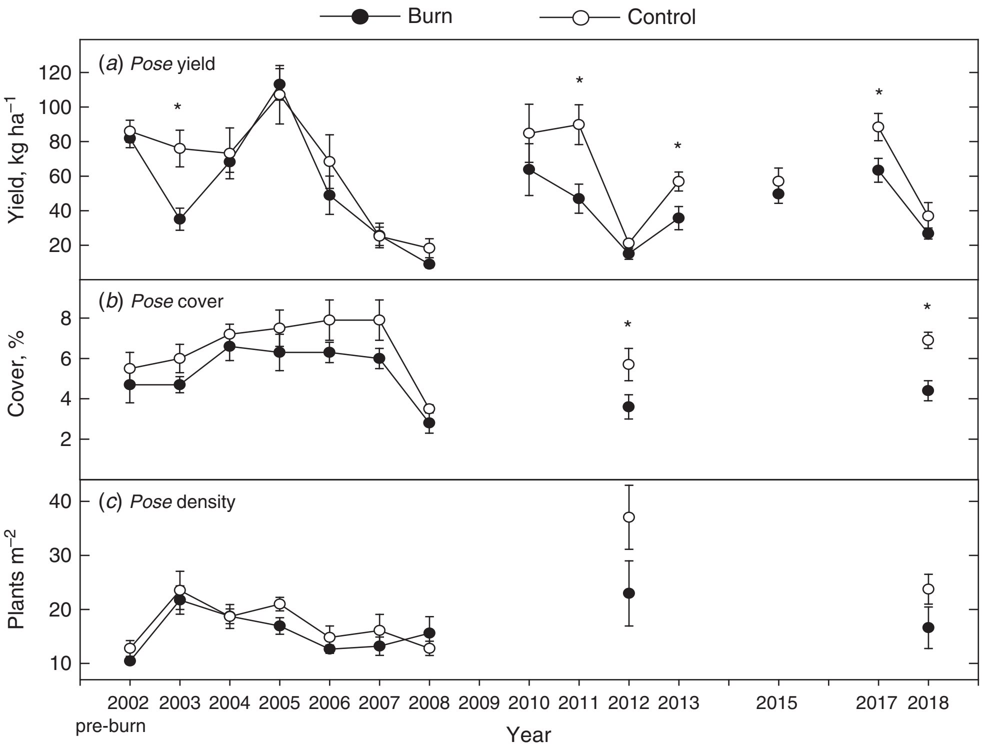

Fig. 5. Sandberg's bluegrass [Pose] (*a*) yield, (*b*) canopy cover, and (*c*) density for the Burn and Control treatments in Wyoming big sagebrush steppe, Northern Great Basin Experimental Range, Oregon (2002–18). Values represent mean ± 1 standard error. *Significant difference ($P < 0.05$) between treatments within year.

curvicarpus [Sheld.] MacBr.) ($P = 0.035$), long-leafed phlox ($P < 0.001$) and Hood's phlox (*Phlox hoodii* Rich.) ($P = 0.006$).

Annual forbs

Yields of annual forbs were significant for year ($P < 0.001$) and treatment ($P = 0.032$) effects (Fig. 7*a*). Treatment differences were most pronounced the first 7 years after fire, with an annual forb yield was 2–5-fold greater in the Burn treatment compared with the Control. Annual forb cover only varied by year, mainly caused by large changes in cover in the Burn treatment ($P < 0.001$). Greater annual forb cover in the Burn treatment was evident the first 4 years after fire; however, cover values have converged since 2008. Between 90% and 95% of annual forb cover in the Burn treatment was provided by desert alyssum, an introduced Old World weed.

Cheatgrass

The year by treatment interaction was significant for cheatgrass yields (P 0.021; Fig. 8*a*). Cheatgrass yield increased overtime in the Burn treatment, with increases beginning in 2009, 7 years following fire. Prior to 2008, cheatgrass yield averaged 0.9 ± 0.3 kg ha^{-1} yr^{-1} in the Burn and did not differ from the Control. Since 2010 the cheatgrass yield has averaged 47.5 ± 10.2 kg ha^{-1} yr^{-1}and has been as much as 5–10-fold greater in the Burn treatment than in the Control.

Cheatgrass cover increased over time for both treatments ($P = 0.003$; Fig. 8*b*), but did not differ between the Burn and Control ($P = 0.264$).

Bare ground and other cover

The year by treatment interaction was significant for bare ground ($P = 0.006$), surface litter ($P < 0.001$) and biological crust ($P = 0.008$). Prior to burning, cover of these three response variables did not differ between the Burn and Control treatments. In the first 3 years (2003–05) after fire, bare ground was lower and litter cover was greater in the Control treatment. Since 2006, bare ground (60.3 ± 1.5%) and litter (17.3 ± 1.1%) cover have been similar for the two treatments. Biological crust in the Burn treatment continued to recover, increasing from zero in 2003 to 3.0 ± 0.9% in 2018. Biological crust cover in the Burn treatment was less than half that measured in the Control (6.5 ± 0.8%) in 2018. Approximately 85% of the biological crust in both treatments consisted of star moss (*Tortula ruralis* [Hedw.] Gaertn., Meyer, & Scherb).

Discussion

Shrub dynamics

Sixteen years after burning, sagebrush cover and density had slowly increased but remained well below site potential. Lesica *et al.* (2007) measured only a 5% recovery of Wyoming big sagebrush canopy cover after wildfires (time since fire was 7–23 years) in south-western Montana. In Idaho, sagebrush cover was ~20% of pre-burn levels 14 years after prescribed fire (Beck *et al.* 2009). In our study, Wyoming big sagebrush cover and density were both ~18% of the unburned Control. The linear increase of sagebrush cover and density was comparable to early successional changes after wildfire reported by Shinneman and

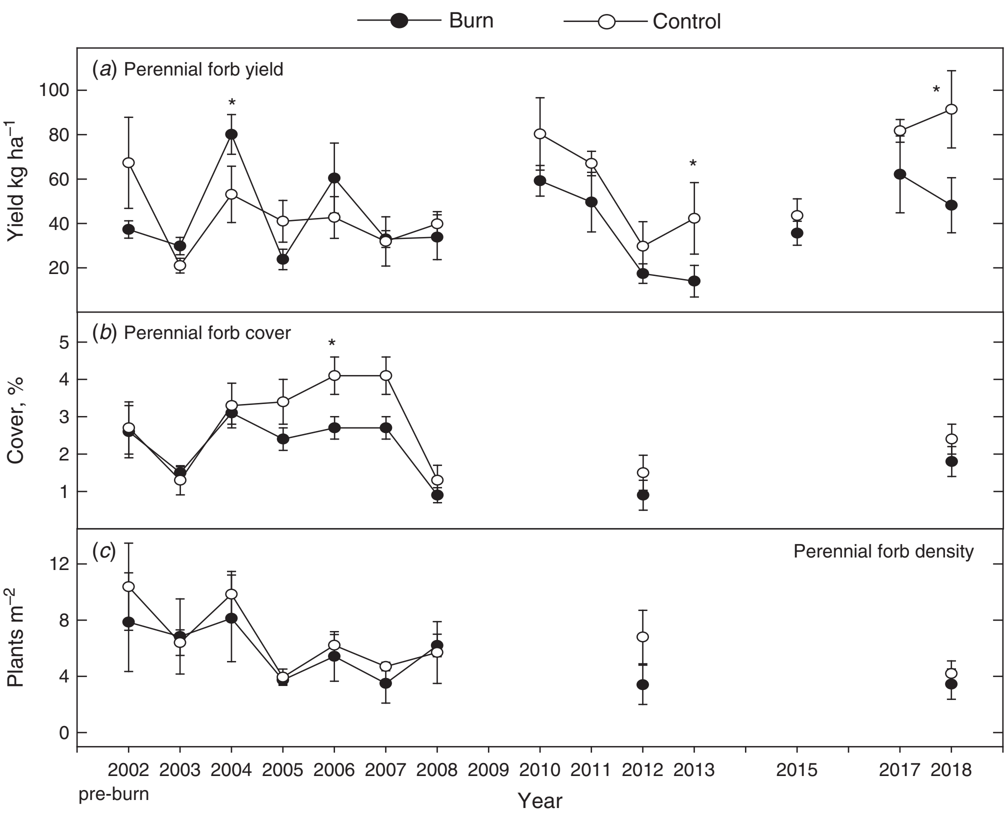

Fig. 6. Perennial forb (*a*) yield, (*b*) canopy cover and (*c*) density for the Burn and Control treatments in Wyoming big sagebrush steppe, Northern Great Basin Experimental Range, Oregon (2002–18). Values represent mean ± 1 standard error. *Significant difference ($P < 0.05$) between treatments within year.

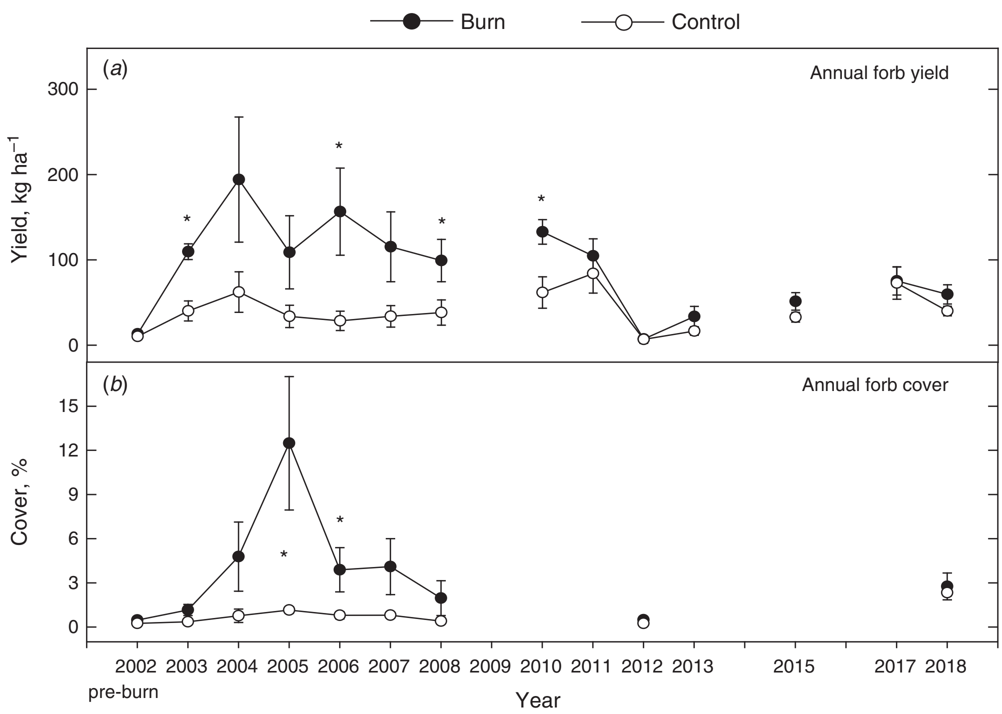

Fig. 7. Annual forb (*a*) yield and (*b*) canopy cover for the Burn and Control treatments in Wyoming big sagebrush steppe, Northern Great Basin Experimental Range, Oregon (2002–18). Values represent mean ± 1 standard error. *Significant difference ($P < 0.05$) between treatments within year.

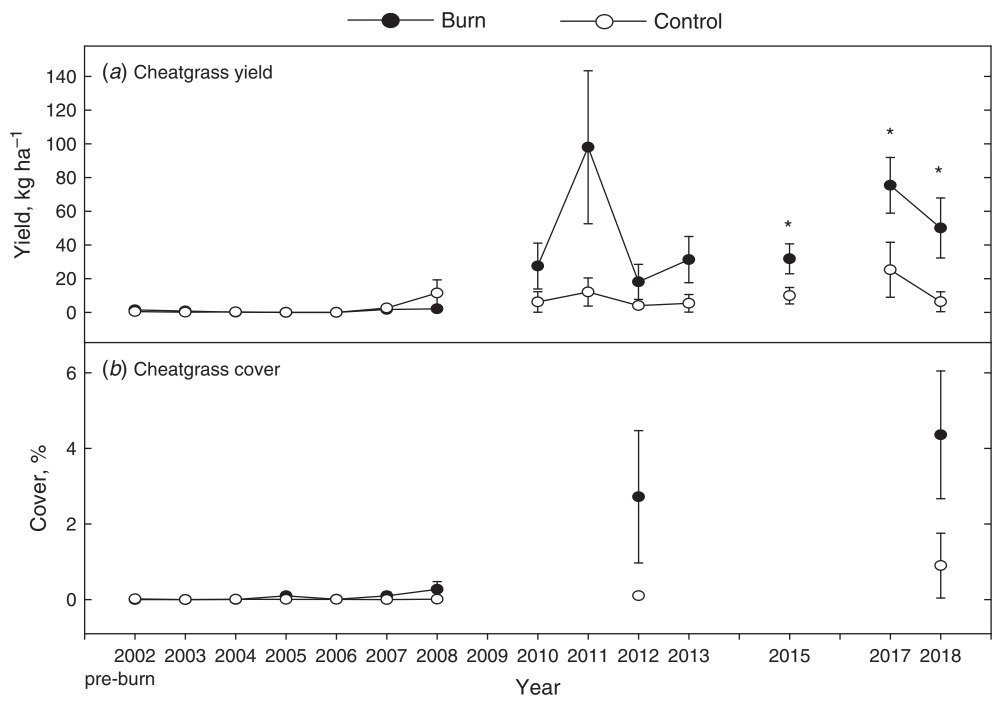

Fig. 8. Cheatgrass (*a*) yield and (*b*) canopy cover for the Burn and Control treatments in Wyoming big sagebrush steppe, Northern Great Basin Experimental Range, Oregon (2002–18). Values represent mean ± 1 standard error. *Significant difference ($P < 0.05$) between treatments within year.

McIlroy (2016). They estimated increases in sagebrush cover and density were linear for the first two decades after fire, after which recovery rates increased, probably because of increased recruitment during favourable establishment years. Thus, Shinneman and McIlroy (2016) and Baker (2006, 2011) estimated ~50–120 years for Wyoming big sagebrush to recover after fire. Our estimates for recovery of sagebrush fall within these estimates for canopy cover (115 years), but not density (250 years), which indicates that sagebrush recruitment must increase above its present rate, otherwise canopy cover could take longer than 115 years to recover. The long-term recovery of big sagebrush species after fire is largely dependent on establishment from seed (Tisdale and Hironaka 1981), which is often problematic, because (1) Wyoming big sagebrush seed production in most years is lacking or minimal (Bates *et al.* 2006), (2) recruitment appears linked to wetter than average winters and higher snow cover (Cawker 1980; Maier *et al.* 2001) and (3) site occupancy by herbaceous plants also limits sagebrush re-establishment. We did not track sagebrush reproductive effort, but there were only 3 years when winter precipitation was substantially greater than average, which may, in part, explain the limited level of sagebrush recruitment. Once herbaceous layers recover, essentially fully occupying a site, sagebrush re-establishment becomes limited (Davies *et al.* 2017). In our study, herbaceous cover and yield could be considered recovered by the third year after fire.

Yellow rabbitbrush is a vigorous re-sprouter and seed producer, often increasing within a few years after fire (Blaisdell 1953; Tisdale and Hironaka 1981). Rabbitbrush cover in the Burn exceeded the Control in only the last year of the study. There was a decline in rabbitbrush cover between 2007 and 2012, resulting from a reduction in foliage and shrub die-back. The likely explanation for this is that rabbitbrush was sensitive to the multiple years of drought that occurred between 2007 and 2012.

Herbaceous lifeform response

Herbaceous yield, cover and perennial densities in the Burn treatment recovered or exceeded the Control by the second year after fire. After fire, a 2–3-year initial recovery period is typical for the herbaceous layer in intact big sagebrush communities, as herbaceous species take advantage of the increased availability of soil water and nutrients (Blaisdell 1953; Harniss and Murray 1973; West and Yorks 2002; Davies *et al.* 2007; Bates *et al.* 2011). Perennial bunchgrasses comprised over 50% of understorey cover and yield after fire. Consequently, the Burn treatment had the appearance of a perennial grassland before the 10th (2013) year after treatment. In the last several years, the Burn treatment appearance was either perennial grassland or shrub–grassland, with yellow rabbitbrush as the main shrub.

The response of Sandberg bluegrass to fire is often variable, ranging from severe reductions to slight increases (Wright and Klemmedson 1965; Bates *et al.* 2011). Aside from the first year after fire, bluegrass was unaffected by the fire treatment until about midway through the study, when yields were lower than in the Control. The lower yields of bluegrass after the Burn treatment during the latter years of the study may result from competitive interference from other native perennials and exotic annuals.

The lack of perennial forb response following fire is typical, as evidence indicates there is limited potential for enhancing perennial forb yield or abundance after fire in Wyoming big sagebrush steppe. Other studies have failed to detect any increase in perennial forb diversity or abundance after burning in Wyoming big sagebrush communities or similar warm-dry sagebrush sites (Fischer *et al.* 1996; Nelle *et al.* 2000; Wrobleski and Kauffman 2003; Beck *et al.* 2009; Rhodes *et al.* 2010; Miller *et al.* 2013; Bates *et al.* 2017). Several factors may account for the limited native forb response to fire, including site potential and interference by perennial grasses and exotics. Perennial forb cover in most Wyoming big sagebrush associations of the northern Great Basin comprises 15–22% of total herbaceous cover (Davies *et al.* 2007) and yields of perennial forbs and native annual forbs in Wyoming big sagebrush associations average ~20% (5–30%) and 3% (0–8.5%) of total yield, respectively (Bates and Davies 2019). Prior to fire, perennial forb cover and yield represented 14% and 13% of total herbaceous cover and yield, respectively. After fire the ratio of perennial forbs to total herbaceous yield declined to below 10% because of increases in perennial bunchgrasses and exotics. The greater response of perennial grasses and exotics, therefore, may have interfered with the ability of native forbs to increase after fire. Rather than disturbance, the amount and timing of precipitation and temperature appear to have a major influence on forb yields and cover in Wyoming big sagebrush steppe (Sneva 1982; Bates *et al.* 2006). Perennial forbs increased in cover or yield in years with higher precipitation, but these increases have been similar on burned and adjacent unburned sites.

The response of exotic annuals was characterised by two phases. In the first 8 years after fire, desert alyssum dominated annual plant composition. In the latter half of the study cheatgrass increased and co-dominated the annual plant component with desert alyssum. Cheatgrass typically increases the second or third year after fire in many sagebrush communities (West and Yorks 2002; Miller *et al.* 2013). However, the delay in cheatgrass response is fairly common in the High Desert Province of eastern Oregon following fire in sagebrush steppe and juniper woodlands, often taking in excess of 5 years for substantial increases to occur (Bates *et al.* 2011, 2014). The potential for desert alyssum to interfere with establishment and growth of native species is unknown. In our study, areas where alyssum was concentrated were not colonised by natives and it was in these areas that cheatgrass began increasing.

Post-fire community dynamics

Herbaceous yield and cover were largely composed of native perennial plants before and after fire. Natives comprised 90–95% of herbaceous yield before fire in the Burn treatment site and throughout the study in the Control site. After fire the native species yield represented 78% (range 67–93%) of total yield and exotic annuals comprised 22% (range 7–33%) of total yield in the Burn treatment. Increases in exotic annuals after fire in intact Wyoming big sagebrush steppe of the Great Basin is commonly reported and persists for more than a decade in longer-term studies (West and Yorks 2002; Ellsworth *et al.* 2016; Swanson *et al.* 2018). The level of exotic weed increases also varies after fire. In only a few examples have native understories dominated post-fire recovery in intact Wyoming big sagebrush, with little measurable exotic annual presence (Bates *et al.* 2011; Swanson *et al.* 2018). In extreme cases the pre-fire native community can be largely replaced by exotic annuals post-fire (Davies *et al.* 2009; Bates *et al.* 2011; Swanson *et al.* 2018). Thus, Swanson *et al.* (2018) conclude that pre-fire native species dominance does not ensure native herbaceous species will dominate post-fire and that community transition to dominance by exotic annuals is likely a product of fire severity and site characteristics.

Intact communities that are vulnerable to exotic annual dominance appear to be those with high sagebrush cover or greater fine-fuel accumulation, which increase fire severity and mortality of native perennial bunchgrasses (Davies *et al.* 2009, 2016; Boyd *et al.* 2015; Hulet *et al.* 2015). High fine-fuel build-up in long-term, ungrazed big sagebrush associations contributed to perennial bunchgrass mortalities of 50–95% after fire, resulting in post-fire dominance by cheatgrass and other weedy species (Davies *et al.* 2009; Bates *et al.* 2011). On similar associations that had a history of moderate grazing use, fine-fuel levels and perennial bunchgrass mortalities were lower, which resulted in post-fire dominance by native perennials (Davies *et al.* 2018). The burned sites in our study were moderately grazed for over 60 years, which may have limited fine-fuel litter accumulation. This may be a contributing factor for the lack of detectable mortality among native perennial bunchgrasses stemming from the fire, which allowed them to persist as the dominant herbaceous lifeform post-fire.

The decline in bio-crust was a result of fire applications. Star moss, the principle bio-crust on site, and other bio-crust was mainly concentrated beneath sagebrush and within bunchgrass canopies. When these areas burned the bio-crust was immediately lost. High losses of bio-crust cover and diversity have been measured after fire elsewhere in sagebrush steppe (Johansen 2001; Hilty *et al.* 2004; Bates *et al.* 2011; Root *et al.* 2017). The subsequent recovery of bio-crust is probably limited by the lack of micro-habitat provided by sagebrush canopies. The limited post-fire recovery of bio-crust in our study was consistent with other work in sagebrush steppe, suggesting a long time period for recovery of the bio-crust community component (Condon and Pyke 2018).

Conclusions

Evaluating fire or other disturbances in ecosystems is challenging because the effects can be construed negatively, positively or neutral depending upon the objectives, scale and duration of the analyses. There is no indication that prescribed burning in Wyoming big sagebrush steppe provides immediate benefits to sagebrush-obligate wildlife. Burning big sagebrush steppe reduces shrub cover used for nesting and roosting, as well as diminishes or eliminates forage provided by sagebrush for sage-grouse, which would be especially damaging in year-round and wintering habitat (Beck *et al.* 2009; Rhodes *et al.* 2010). Population studies indicate sage-grouse numbers decline following fire in Wyoming big sagebrush communities (Connelly and Braun 1997; Connelly *et al.* 2000). Our study indicated it may take at least 115 years to fully recover Wyoming big sagebrush habitat.

The immediate benefit after burning Wyoming big sagebrush steppe was the increase in herbage yields. In the Burn treatment, available herbaceous forage almost doubled, which was sustained across much of the study period. The additional forage provided on burned areas may afford livestock managers greater flexibility to rest or defer unburned seasonal habitat for wildlife (Bates and Davies 2014). Burning may benefit granivorous wildlife species, because grass seed yields tripled post-fire on these sites (Bates *et al.* 2009). If prescribed burning is applied to the Wyoming big sagebrush habitat it should only be practiced when mortality of native perennial grasses and forb species can be minimised and should avoid areas where cheatgrass and other exotic species are of concern.

Conflicts of interest

The authors declare no conflicts of interest.

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