

## Short- and long-term changes in elk use and forage production in sagebrush communities following prescribed burning

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**Abstract.** Burning shrub and grassland communities often leads to increases in plant production and nutritional quality that benefit herbivores, resulting in increased herbivore use of burned areas. Increased use has been ascribed more specifically to changes in plant community structure, community composition and diversity, nutritional quality, and seasonal availability. These hypotheses can be evaluated more precisely if changes in plant communities following burning are monitored concurrently with changes in herbivore use, especially in longer-term studies. From 1988 to 1999, we examined responses of elk (*Cervus elaphus*) following prescribed burning of areas burned in 1984 and 1988 that had been formerly dominated by mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) in south-central Montana (USA), with concurrent monitoring of changes in plant production, nutritional quality, and community composition. Elk made increased use of burned sites up to 15 years after burning. Burning transformed big sagebrush-dominated communities into native herbaceous communities that persisted for 15 years without sagebrush reinvasion. Forage biomass and protein content remained higher on burned sites for 15 years, although differences were not significant in every year and declined as time elapsed after burning. Forage production, forage protein, and elk use were temporally correlated, suggesting the possibility that grazing by elk might have contributed to persistence of elevated plant production and protein levels on burned sites.

### Introduction

Fire is an ecological process that profoundly affects plant community composition, structure and function (Wright and Bailey 1982; Briggs and Knapp 2001). Burning removes litter (Antos et al. 1983; Redmann et al. 1993; Blair 1997; Tracy and McNaughton 1997), allowing more UV light to reach soil surfaces and boost rates of photosynthesis and primary productivity (Blair 1997; Turner et al. 1997; Tracy and McNaughton 1997; Johnson and Matchett 2001). Burning also leads to increased soil temperatures that may enhance earlier germination and growth in some species, particularly C4 grasses (Antos et al. 1983). Together, these effects may lead to increases in aboveground net primary productivity on burned sites, particularly in grasslands or in shrublands that succeed to grasslands following burning (Blair 1997; Turner et al. 1997; Tracy and McNaughton 1997; Johnson and Matchett 2001). Thus,

managers often manipulate natural fires or apply prescribed burning to sites where such increased production may benefit wild or domestic herbivores, particularly grazing ungulates. These considerations may be particularly important on western rangelands, where, in the absence of recurrent fire, established communities of large shrubs such as big sagebrush (*Artemisia tridentata*) produce conditions of water demand, litter accumulation, shading, and possibly allelopathic inhibition that restrict the invasion, spread, or productivity of grasses and forbs that may be of greater forage value for grazers.

Grazing ungulates have been observed to make increased use of burned sites (Hobbs et al. 1991; Vinton et al. 1992; Pearson et al. 1995; Singer and Harter 1996; Biondini et al. 1999). Once attracted to a burned site, grazers facilitate changes that alter community structure and function, including increased rates of nutrient cycling (Risser and Parton 1982), increased spatial heterogeneity (Steinhauer and Collins 1995), reduced litter and fuel accumulation (Hobbs et al. 1991; Frank and Groffman 1998), and increased species richness (Collins 1987; Collins and Glenn 1988; Puerto et al. 1990). Thus, an understanding of the synergistic effects of grazing and burning on plant community diversity can be an important component of long-term biodiversity conservation in plant communities managed by grazing, burning, or both.

Further, understanding foraging site selection by ungulates is of importance to managers because site quality influences ungulate health and survivorship, particularly on winter ranges which are often inadequate in amount and quality of forage for animal maintenance (Torbit et al. 1985). Ungulates store energy throughout the summer and catabolize it in winter when forage quantity and quality fall below maintenance requirements. Because prescribed burning on winter range usually improves the production and nutritional levels of plants, it may contribute to improved animal condition and increased survivorship.

Elk (*Cervus elaphus*) are grazing ungulates of high conservation value on western range lands in North America and, thus, have been the subject of numerous investigations of their responses to prescribed burning. Many studies have demonstrated that the physical and physiological condition of wintering elk has been enhanced on winter ranges subjected to prescribed burning (Rounds 1981; Rowland et al. 1983; Jourdonnaise and Bedunah 1990; Van Dyke et al. 1991). In particular, elk using burned areas in these studies ate more grass and less browse (Rowland et al. 1983), weighed more and were in better condition (Rowland et al. 1983), and maintained adequate dietary protein levels (Van Dyke et al. 1991). Such responses may be attributed, at least in part, to the fact that burned sites may have higher levels of protein, calcium, phosphorus, and other digestible nutrients than unburned sites, as well as greater production of grasses and forbs, categories of plants that form the bulk of elk diets in many areas (Van Dyke et al. 1991).

Many studies have examined the effects of fire and grazing separately, fewer have simultaneously monitored changes in plant community structure, quantitative and qualitative responses of plants, and changes in herbivore use

following burning. Additionally, most studies of such effects have been of short duration and could not evaluate longer-term responses. Simultaneous consideration of these dimensions of the effects of prescribed burning over longer time periods would be of value to managers who must consider longer-term and comprehensive effects of prescribed burning when making management decisions.

To address these concerns, we coupled an investigation of changes in plant community structure, production, and nutritional quality following burning of a Montana (USA) winter range with concurrent monitoring of changes in elk use from 1988 to 1999. Our purpose was to provide wildlife and range managers with more specific and accurate information regarding the response of plant communities and elk to prescribed burning in sagebrush-dominated communities, allowing them to better predict the outcomes of management plans that consider the use of prescribed burning as a means to benefit elk or to affect the structure, composition, or diversity of plant communities. The fundamental questions we wished to answer were (1) would prescribed burning lead to changes in site production and nutritional qualities of plants; (2) if such changes occurred, how long would they last; (3) to what extent would elk increase their use of burned sites if production and nutritionally enhanced forage increased in an otherwise homogeneous winter range dominated by plant communities of relatively low nutritional quality; and (4) would elk continue to make higher use of burned sites as long as structural characteristics of the plant community remained distinct from surrounding areas?

### Study area

North Line Creek, a prominent, south-facing drainage basin descending from the south face of the Line Creek Plateau in south-central Montana, USA (45°1' N, 109°16' W), is part of the annual range of the Line Creek and Bennett Creek elk populations that receives use by elk from November through May (Van Dyke and Klein 1996; Van Dyke et al. 1998). Personnel of the U.S. Forest Service (USFS), aware of the intensive use of this part of the basin, conducted an experimental 40 ha prescribed burn in the southern part of the drainage in October 1984. Informed by ongoing studies of seasonal range use and movements of these elk populations by the senior author (Van Dyke and Klein 1996; Van Dyke et al. 1998), they selected another site for a burn of similar size (30 ha) in April 1988 in the upper (northern) part of the drainage. Burned areas covered elevations from approximately 1850–1900 m (1984 burn) and from 1920 to 1975 m (1988 burn). Hereafter the 1984 burn will be referred to as the South burn and the 1988 burn as the North burn. Although the North burn rarely received use by Bennett Creek elk, it received extensive use by Line Creek elk throughout the winter (Van Dyke et al. 1998).

The North Line Creek basin consisted of sagebrush-covered ravine slopes and bottoms, with a scattered overstory of limber pine (*Pinus flexilis*) on

the upper portions of slopes and adjacent ridge crests. Burned areas were small relative to the size of the basin. Sagebrush-dominated communities were characteristic of the entire area at these elevations, and are typical for *Artemisia tridentata*-*Festuca idahoensis* habitat type (Mueggler and Stewart 1980) present on western rangelands. Most sagebrush was *Artemisia tridentata* ssp. *vaseyana*, but a few individuals of black sagebrush, (*Artemisia arbuscula* ssp. *nova*) also were present on drier microsites in and around the South burn. Other shrub species were rare. Idaho fescue (*Festuca idahoensis*) and bluebunch wheatgrass (*Agropyron spicatum*) were the most common grasses interspersed among or beneath sagebrush overstory. Other frequently encountered, but less abundant, grasses included various bluegrasses (*Poa* spp.), needle-and-thread grass (*Stipa comata*), and king fescue (*Hesperochloa kingii*). Common forbs included species of milkvetch and locoweed (*Astragalus* spp.) and phlox (*Phlox* spp.).

The climate was characterized by short, cool summers and long, cold winters. Average January temperature at a similar elevation (1757 m) approximately 20 km N at Red Lodge, Montana, USA, the closest weather station to the study area, was  $-6^{\circ}\text{C}$ , and average annual precipitation was 56 cm, mostly in the form of snow from November to May (Van Dyke et al. 1991).

Livestock were not permitted on USFS land in North Line Creek, nor were there any human residences or activities. Roads to North Line Creek were primitive, unmaintained, and covered with large rocks, which discouraged vehicular travel into the area. Aside from USFS personnel, the senior author, and various seasonal field assistants, human visitation to the area was low and primarily limited to recreational hikers during spring and summer and, in autumn, to big game hunters.

## Material and methods

### *Field measurements*

Five permanent 404 m<sup>2</sup> plots (20.1 m × 20.1 m) were established on each burned site in 1988. One permanent plot of the same size was established on an unburned site within the drainage in the same year prior to the burn, a concession to limits of time and manpower that constrained us at the beginning of this study. We established plots only on sites with <35% slope because fire history and topographic position of a site are often interactive in their effects on plant production (Turner et al. 1997) and observations of elk in the area indicated animals fed primarily on slopes of <35% (Van Dyke et al. 1991). Prior to burning, sagebrush communities on this range were extremely homogeneous. Such uniformity permitted us to select plots that were highly similar to one another in slope, aspect, pre-burn vegetation, and disturbance history as determined by slope measurement, visual examination in the field, and review of Forest Service management records.

Because ungulates may be expected to increase their duration and number of foraging bouts in habitat patches that are more profitable, we chose elk use days (EUD) as the best index to express the combined effect of the duration and intensity of elk foraging in a plot. In June of 1988–1993 and 1999, after elk had left the North Line Creek basin and moved to higher elevation summer ranges, we estimated elk use in each plot by counting the number of elk pellet groups within 1 m of 6 randomly selected 20.1 m transects laid perpendicular to the baseline of each plot, thus permitting a calculation of pellet group density. We spray-painted and scattered pellets after counting to avoid repeat counting in subsequent surveys. We converted the estimated density of pellets to an index of EUD by dividing the estimate of density by 13, an estimated average number of dropping groups/elk/day, based on observations in other studies (Hayden-Wing 1979).

We determined foliar vegetation coverage, by species, concurrently with determinations of elk use in June of each year. However, limited budgets, time, and manpower from 1989 to 1992 forced us to restrict the more labor-intensive sampling of vegetation coverage to one plot per site (South burn, North burn, unburned) during these years. In this effort, we estimated the percent foliar coverage by cover class (<1%, 1–5%, 6–15%, 16–25%, 26–35%, 36–45%, 46–55%, 56–65%, 66–75%, 76–85%, 86–95%, >95%) of each species within each of 5, 25.4 cm × 50.8 cm visually calibrated frames (microplots) placed at randomly selected locations along each transect, a total of 30 microplots per plot. Using the midpoint value of each cover class range, the average percent coverage of each species within the plot was estimated as the summed microplot coverage divided by 30. Coverage values of individual species were summed by categories of forbs, grasses, and shrubs as an index to overall community composition. Additional funding and manpower in 1993 and 1999 released aforementioned sampling constraints and permitted us to establish four additional plots in unburned vegetation for elk use and to evaluate vegetation coverage in all plots on all sites in these years.

In late August, at the end of the growing season on this range, from 1988 to 1992 and 1999, we clipped and sorted, by category, grasses and forbs from a random subset of the original six transects and 30 microplots sampled within the plot in June. Clipped material was combined by transect in order to have sufficient quantities for chemical analysis in each sample and because budgetary constraints limited the number of nutritional analyses that could be performed each year. We also chose not to evaluate the production and nutritional condition of shrubs because they contributed little to elk diets during most of the winter and spring in this population (Van Dyke et al. 1991). Thus, we considered grasses and forbs to reflect the quantity and quality of most of the forage consumed by elk during their time on these sites and concentrated nutritional analyses on these categories. Plant samples were used to estimate plant production (kg/ha, dry weight), moisture, and protein (% dry weight). Moisture levels were determined by air-drying and used to estimate dry weight of samples, which were then converted to dry weight estimates of plant production. Protein

levels were determined by standard procedures described by the Association of Official Analytical Chemists (A.O.A.C 1965) at the Analytical Chemistry Laboratory of the Agricultural Experiment Station of Montana State University (MSU), Bozeman, USA. Budgetary constraints forced us to forego nutritional analyses of plant material in 1993.

### *Quantitative and statistical analysis*

We evaluated EUD through time on each burned site via separate repeated measures AOV. Tukey's mean separation test was used to determine where significant differences occurred. To evaluate longer-term (1993–1999) effects of treatment, we compared burned and unburned sites through a single repeated measures AOV for these years.

To evaluate longer-term effects of prescribed burning on plant communities, we compared the percent coverage (arcsine transformed) of grasses, forbs, and sagebrush on burned and unburned sites between 1993 and 1999 using a repeated measures AOV. Confidence interval estimates (95% CI) of coverage in these categories in 1993 and 1999 were compared to single (one plot) estimates of coverage from 1989 to 1992 to assess differences between short- and longer-term plant responses. In cases where significant treatment-year interactions were detected in 1993 and 1999, we compared coverage in different treatments in a given year through unpaired *t*-tests with Bonferroni adjustments.

To evaluate plant community characteristics relative to treatment, we determined plant species richness from coverage data. We compared species richness between years using procedures previously described for evaluating changes in plant coverage. To assess quantity and quality of forage on burned and unburned sites in the short-term, we compared grass and forb production and protein content between burned and unburned sites from 1988 to 1992 using a two-way AOV, with year and treatment as factors. As with plant coverage, we compared production and protein among sites in a given year through unpaired *t*-tests with Bonferroni adjustments if significant year-treatment interaction was detected. To assess differences between burned and unburned plots in the longer term, we compared treatment differences in grass and forb production and protein content in 1999 (11 and 15 years after burning on the North and South units, respectively) via multiple comparison analysis (MCA). In all evaluations,  $p \leq 0.05$  was considered significant.

## **Results**

### *Changes in elk use*

Elk use on the North and South burns varied by year (Figure 1) (North burn,  $F = 2.89$ ,  $df = 6$ ,  $p = 0.03$ ; South burn,  $F = 5.08$ ,  $df = 6$ ,  $p < 0.01$ ; separate repeated measures AOV). On the North burn, EUD in 1992, the year

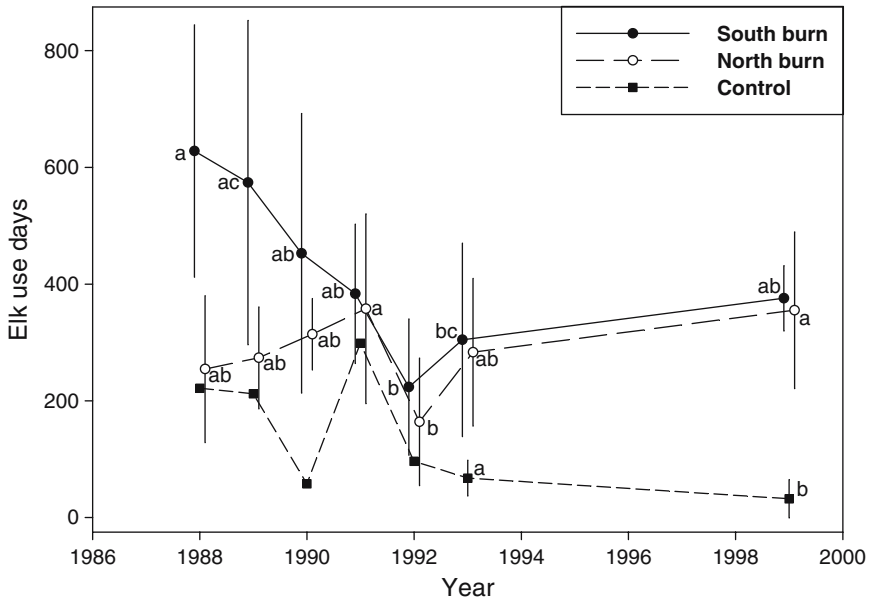


Figure 1. EUD on two burned sites and an unburned control site in North Line Creek, south-central Montana, USA, from 1988 to 1993 and 1999. Burns conducted in 1984 (South burn) and 1988 (North burn). Bars represent 95% CI. Means with different letters are different from means in other years on the same site (Tukey's mean separation test). Means without bars are single plot estimates from unburned sites in 1988–1992.

of lowest elk use, differed from the 2 years of highest use, 1991 and 1999. On the South burn, the year of highest use (1988) differed from the 2 years of lowest use (1992 and 1993), and the year of second highest use (1989) also differed from the year of lowest use (1992). Use levels on the South burn were more than twice that of the North burn when monitoring began in 1988, but EUD values on the two sites had converged to similar levels by 1999.

Elk used burned sites more than unburned sites. Single plot estimates of use on unburned sites in 1988, 1989, and 1991 fell above variation observed in 1993 and 1999 with longer-term use. The range of elk use on unburned sites in these years (212–299 annual EUD) was within normal variation observed in elk use on the North burn during the same years, but declined over time (Figure 1). In longer-term assessment (1993–1999), EUD varied among treatments ( $F = 85.38$ ,  $df = 1$ ,  $p < 0.01$ ), with higher elk use on burned sites, but did not vary among years ( $F = 0.32$ ,  $df = 1$ ,  $p = 0.58$ ), nor was there a year-treatment interaction ( $F = 2.53$ ,  $df = 1$ ,  $p = 0.14$ ).

#### *Changes in plant communities*

Prescribed burning transformed sagebrush-dominated communities into grass- and forb-dominated communities, and such differences persisted for  $\leq 15$  years

Table 1. Long-term responses in vegetation communities on burned and unburned plots in south-central Montana, USA, originally dominated by mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*), 1993 and 1999.

	Species richness	Graminoid coverage (%)	Forb coverage (%)	Sagebrush coverage (%)
<i>Unburned</i>				
1993	13.80(1.24)	11.07(1.40)	2.80(0.59)	41.35(3.42)
1999	20.80 (1.36)	11.20(0.54)	8.97(1.46)	32.63(7.29)
<i>South burn</i>				
1993	18.60(0.68)	19.19(0.77)	5.90(0.28)	0.10(0.07)
1999	20.80(1.28)	23.71(2.03)	6.88(2.04)	0.36(0.34)
<i>North burn</i>				
1993	25.80(2.22)	30.80(0.97)	28.80(1.59)	0.20(0.20)
1999	25.20(1.28)	21.95(2.74)	13.04(1.30)	1.32(0.67)
<i>F (south/north)</i>				
Treatment	3.24/20.13	50.93/63.37	1.06/101.80	142.01/116.09
Year	22.04/6.24	3.37/8.09	23.98/3.29	1.34/0.11
Year*treatment	6.00/8.80	2.39/9.66	14.06/94.19	2.11/4.74
<i>p (south/north)</i>				
Treatment	0.11/ <0.01	<0.01/ <0.01	0.33/ <0.01	<0.01/ <0.01
Year	<0.01/0.04	0.10/0.02	0.01/0.10	0.28/0.74
Year*treatment	0.04/0.02	0.16/0.01	0.01/ <0.01	0.18/0.06

Repeated measures AOV. SE in parentheses.

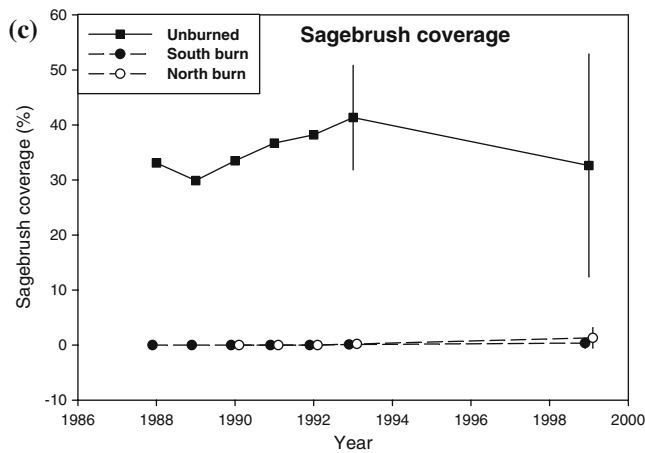
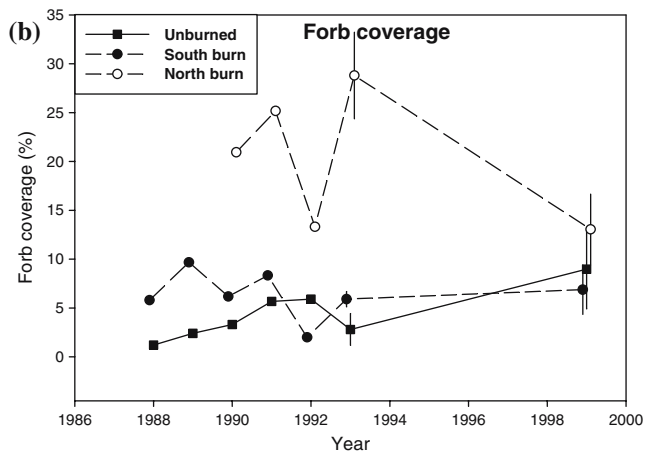
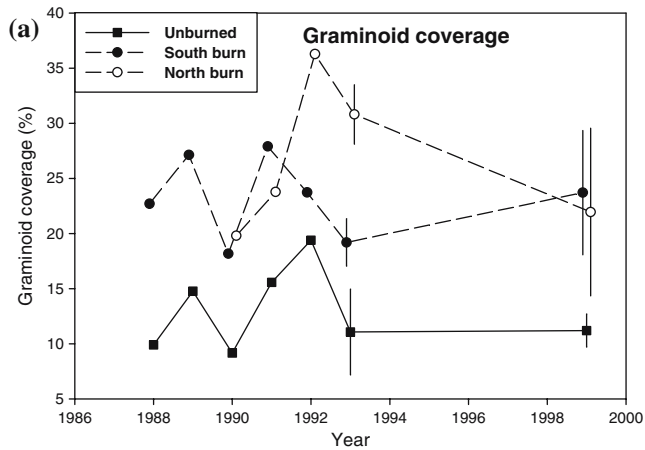
(Table 1, Figure 2). Sagebrush remained at approximately 30–40% coverage on unburned plots from 1988–1999, but failed to attain >1% coverage on burned plots up to 15 years after burning (Figure 2c, Table 1).

From 1988 to 1999, changes in graminoid and forb coverage followed similar patterns of increase and decrease on burned and unburned plots (Figure 2), suggesting an overriding importance of climate variation in plant response. Despite annual variation, graminoid cover was consistently lower on unburned plots. Forb cover was more variable. Burned sites retained higher graminoid coverage than unburned sites over the longer-term (1993–1999), although on the North burn, treatment differences were confounded by year and year-treatment effects (Table 1). Given the presence of interactive effects in graminoid coverage, we evaluated years (1993 and 1999) separately on the North burn to unburned sites, and did the same for forb coverage where interactive effects were detected for both burns. Graminoid coverage was greater on the North burn in 1993 ( $t = -11.58$ ,  $df = 8$ ,  $p < 0.01$ ) and 1999 ( $t = -3.85$ ,



Figure 2. Graminoid (a), forb (b), and mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) (c) coverage associated with plant communities on burned and unburned 404 m<sup>2</sup> plots originally dominated by sagebrush in North Line Creek, south-central Montana, USA, 1988–1999. Samples from 1988 to 1992 are single estimates (one plot sampled per treatment). Bars associated with means in 1993 and 1999 reflect 95% CI associated with multiple plot samples.





df = 8,  $p = 0.01$ ). Forb coverage was higher on both burned sites than on unburned sites in 1993 (North burn,  $t = -15.31$ , df = 8,  $p < 0.01$ ; South burn,  $t = -4.78$ , df = 8,  $p < 0.01$ ), but forb coverage was unaffected by treatment in 1999 (North burn,  $t = -2.08$ , df = 8,  $p = 0.14$ ; South burn,  $t = 1.22$ , df = 8,  $p = 0.52$ ).

From 1988 to 1999, a cumulative total of 71 species of forbs and 14 species of grasses were identified on burned and unburned plots. Eighty-five percent (60 species) of forbs and 93% (13 species) of grasses were perennials. Two forbs (*Taraxacum officinale* and *Tragopogon dubius*) and one grass (*Bromus tectorum*) were non-native species. Species richness was generally higher on burned sites, but differences between treatments had converged to similar levels by 1999 (Figure 3). As with plant coverage, longer-term (1993–1999) treatment differences were confounded with year and year-treatment effects, so years were evaluated separately by Bonferroni adjusted  $t$  tests. In 1993, species richness was greater on both burned sites than on unburned sites (North burn,  $t = -4.71$ , df = 8,  $p < 0.01$ ; South burn,  $t = -3.39$ , df = 8,  $p = 0.02$ ). By 1999, there were no differences between treatments ( $p \geq 0.07$ , all cases).

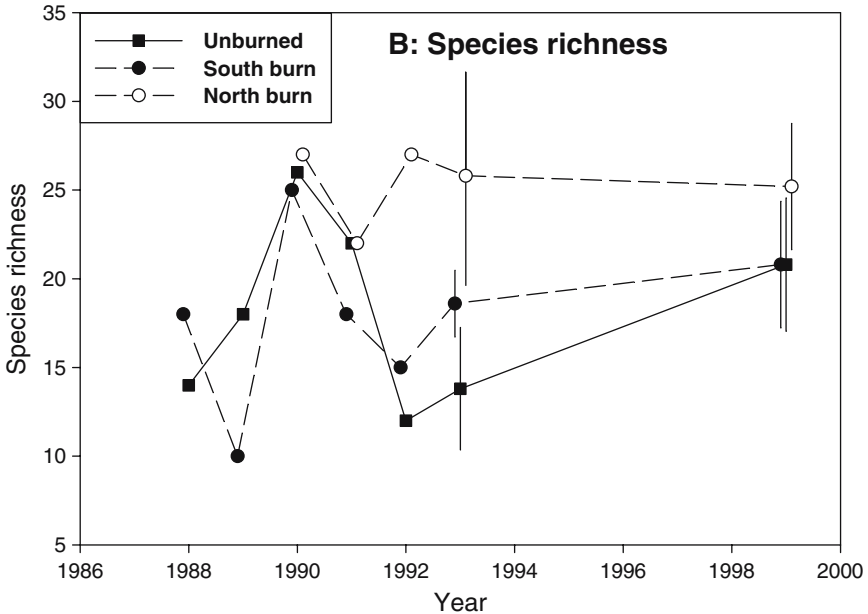


Figure 3. Species richness of plant communities on burned and unburned 404 m<sup>2</sup> plots originally dominated by mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) in south-central Montana, USA. Samples from 1988 to 1992 are single estimates (one plot sampled per treatment). Bars associated with means in 1993 and 1999 reflect 95% CI associated with multiple plot samples.

*Changes in forage quantity and quality*

In short-term response from 1988 to 1992 (1–8 years after burning), forage production was greater on burned sites. Graminoid production was higher on both burn sites than on unburned sites in every year (Figure 4a, Table 2). Forb production also was higher on burned sites, although differences associated with the South burn were marginally non-significant (Figure 4b, Table 2). Graminoid production was independent of year on the North burn, but not on the South burn, where production levels in 1992 differed from 1988 and 1989, the 2 years of lowest production (1988 and 1989,  $p < 0.05$ , Tukey's mean separation test). Forb production was independent of year in all cases, and in no comparisons were treatment-year interactions significant.

Compared to forage on unburned plots, protein levels were higher on the more recent North burn, but not the older South burn (Table 2). Changes in protein levels were not independent of year on either burn (Table 2, Figure 5). Significant treatment-year interactive effects were detected on the North burn and evaluated further through Bonferroni-adjusted  $t$  tests in individual years. Treatment differences in graminoid protein were significant in 1990 ( $t = -4.69$ ,  $df = 7$ ,  $p = 0.01$ ) and 1992 ( $t = -9.83$ ,  $df = 7$ ,  $p < 0.01$ ). Although absolute differences in forage protein levels were greatest in 1988, immediately following burning on the North burn, sample sizes of graminoid protein were insufficient to conduct a  $t$  test in that year. Sample sizes associated with forb protein were insufficient to conduct a  $t$  test in any individual year during this period. Significant year effects in both graminoid and forb protein, combined with similar patterns of change over time on all sites, suggested that forage protein levels may have been more sensitive to annual climatic variation than to prescribed burning (Figure 5).

In longer-term analysis of forage production and protein, treatment differences declined over time. Although forage production and protein were generally higher on burned sites in 1999, 11 (North burn) and 15 (South burn) years after burning, responses were variable and most differences were not significant (Table 3). Compared to unburned sites, graminoid protein levels on the North burn remained higher than on unburned sites even 11 years after burning ( $F = 5.82$ ,  $p = 0.04$ , MCA test). There were no significant treatment differences in forage production or in levels of forb protein.

Elk use, forage production, and forage protein appeared interactive. On the South burn, declines in elk use were concurrent with declines in graminoid production and protein from 1988 to 1992, but rose with increases in these variables from 1992 to 1999 (Figure 6). On the North burn, increases in elk use rose with increases in graminoid production from 1988 to 1991 despite declining levels in forage protein (Figure 7). 1992 witnessed a steep decline in elk use despite increases in forage production and protein in that year, but elk use increased from 1992 to 1999 concurrent with increases in forage protein levels and despite declines in forage production.

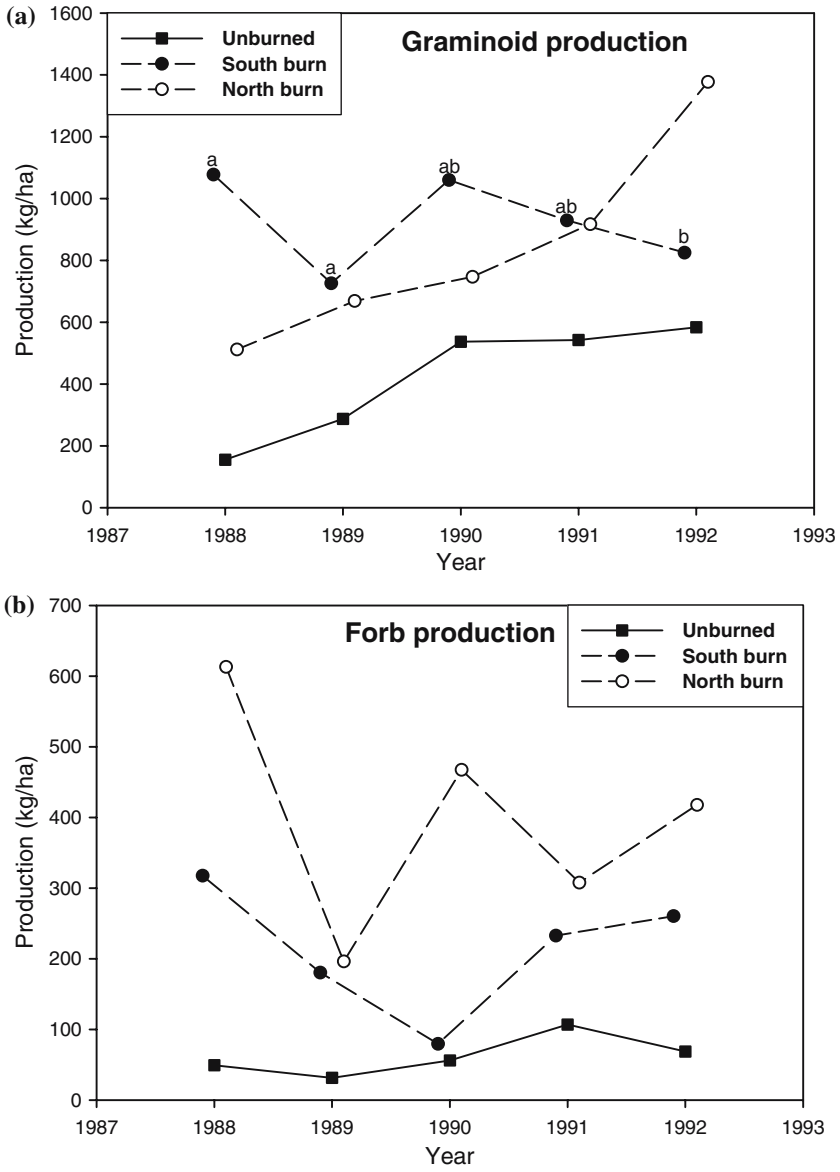


Figure 4. Graminoid (a) and forb (b) production on burned and unburned plots from 1988 to 1999 in North Line Creek, south-central Montana, USA. Means with different letters are different from means in other years on the same site (Tukey's mean separation test).

Table 2. Short-term responses in characteristics of production (kg/ha) and protein (% dry weight) in graminoids and forbs on burned and unburned plots in south-central Montana, USA, originally dominated by mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*), 1988 and 1989.

	1988				1989				1990				1991				1992				F		P		
	Treatment		Year		Treatment*		Year		Treatment*		Year		Treatment*		Year		Treatment		Year		Treatment		Year		
	Treatment	Year	Treatment	Year	Treatment	Year	Treatment	Year	Treatment	Year	Treatment	Year	Treatment	Year	Treatment	Year	Treatment	Year	Treatment	Year	Treatment	Year	Treatment	Year	
<i>Graminoid production</i>																									
Unburned	155.00(-)	287.53(70.21)	536.96(164.64)	542.52(96.70)	583.60(125.95)																				
South burn	511.70(3.70)	668.60(166.86)	746.74(66.32)	917.00(200.61)	1377.36(168.60)																				
North burn	1077.28(31.96)	725.93(132.04)	1059.70(141.24)	929.10(46.85)	824.92(165.66)																				
<i>Graminoid protein</i>																									
Unburned	5.70(-)	6.37(0.30)	5.88(0.27)	5.50(0.16)	4.83(0.18)																				
South burn	6.45(0.33)	5.60(0.15)	6.28(0.35)	5.26(0.22)	5.32(0.24)																				
North burn	8.55(0.15)	6.67(0.37)	7.90(0.34)	5.38(0.20)	6.60(0.08)																				
<i>Forb production</i>																									
Unburned	49.30(-)	31.50(-)	56.10(-)	107.00(-)	68.80(-)																				
South burn	317.53(36.08)	180.30(80.10)	79.60(-)	232.70(95.90)	260.40(73.91)																				
North burn	613.00(170.50)	196.10(50.22)	467.37(159.58)	307.70(20.93)	417.60(153.64)																				
<i>Forb protein</i>																									
Unburned	3.60(-)	7.50(-)	7.10(-)	7.50(-)	10.40(-)																				
South burn	7.17(0.43)	8.15(0.35)	8.30(-)	5.40(1.70)	8.34(0.56)																				
North burn	9.35(0.15)	10.83(0.15)	8.80(0.47)	6.88(0.28)	9.82(0.49)																				

Two-way AOV. SE in parentheses.

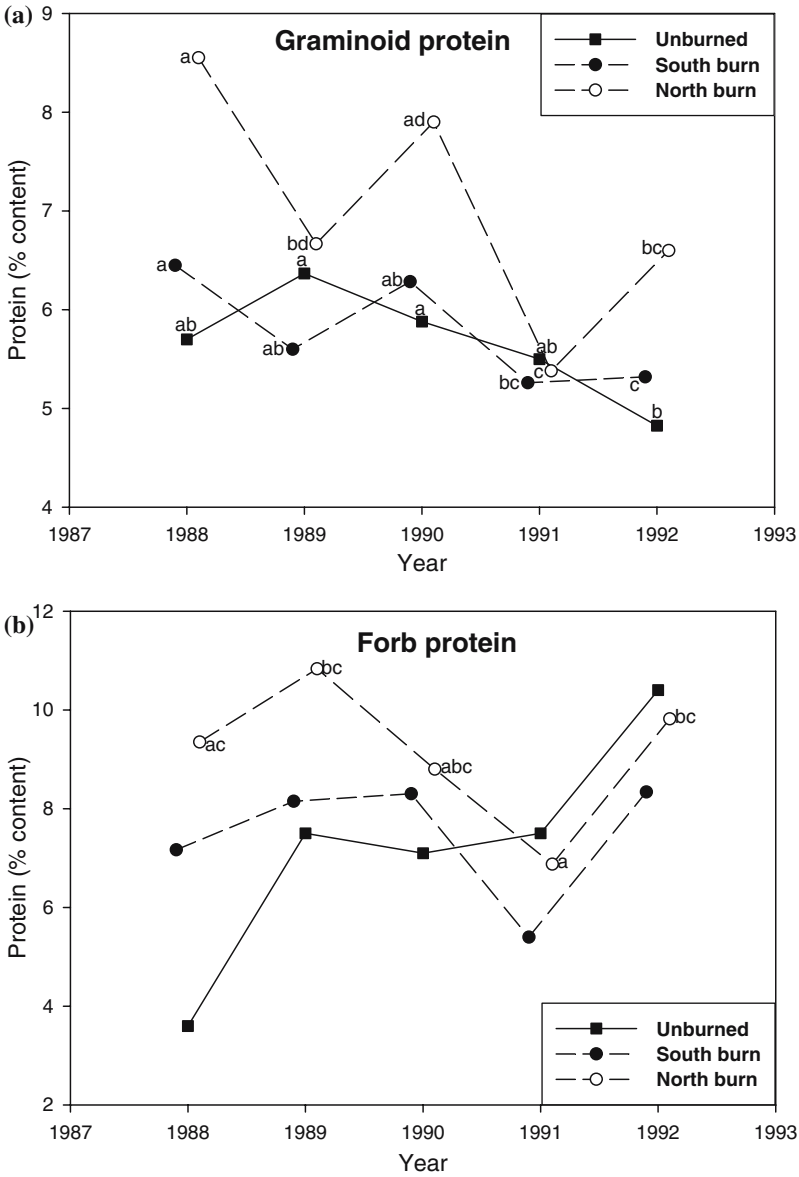


Figure 5. Graminoid (a) and forb (b) protein levels on burned and unburned plots from 1988 to 1999 in North Line Creek, south-central Montana, USA. Means with different letters are different from means in other years on the same site (Tukey's mean separation test).

Table 3. Differences in production (kg/ha) and protein (% dry weight) in graminoids and forbs on burned and unburned plots in south-central Montana, USA, originally dominated by sagebrush (*Artemisia* spp.), in 1999, 11 and 15 years after burning.

	Unburned		South burn		North burn		F	p
	X	SE	X	SE	X	SE		
<i>Graminoid</i>								
Production	477.63	177.40	737.67	88.60	1136.20	380.62	1.79	0.25
Protein	5.60 <sup>a</sup>	0.31	5.73 <sup>ab</sup>	0.18	8.00 <sup>b</sup>	0.90	5.82	0.04
<i>Forb</i>								
Production	220.03	154.12	601.37	270.29	495.97	103.81	1.08	0.40
Protein	8.57	1.22	6.70	0.97	9.80	0.60	2.62	0.15

MCA, standard F-statistic, df = 2 and 6. Means with different letters are different from means from other sites, Tukey's mean separation test,  $p \leq 0.05$ .

## Discussion

### *Effects of prescribed burning and elk grazing on plant communities*

Invasions facilitated by fire and associated sagebrush removal produced pronounced changes in plant community composition and structure. Plant succession on North Line Creek sites followed the typical pattern of grass invasion and domination of recently burned sites, a pattern attributable to the superior establishment capabilities of grasses on disturbed areas, to the removal of litter that may have inhibited germination by other species (McGinley and Tilman 1992), and to the capacity of grasses to rapidly increase plant density under favorable conditions (Briggs and Knapp 2001). Forb species also contributed a much larger component of total coverage, a pattern typical of recently burned sites (Harniss and Murray 1973; West and Hassan 1985; Briggs and Knapp 2001). Sagebrush remained rare ( $\leq 1\%$ ) on burned sites up to 15 years after the fire event. The post-burn grass-forb communities established in North Line Creek were relatively stable in life-form composition and not easily re-invaded by sagebrush, and we expect burned sites to remain as grass-forb dominated communities for at least the next 15 years.

### *Effects of fire on plant production and nutritional quality*

On traditional sagebrush sites, sagebrush removal has been justified because of the perception of its dramatic increases throughout western sagebrush steppe landscapes at the expense of grassland habitats (Arno and Gruell 1983; Miller et al. 1991), the belief that range degradation was associated with increasing abundance of sagebrush (Huber-Sannwald and Pyke 2005), and the expectation of subsequent higher production and nutritional quality of grasses and forbs following sagebrush removal (Wambolt et al. 2001). Ecologically, the expectation of increased grass production following sagebrush removal is

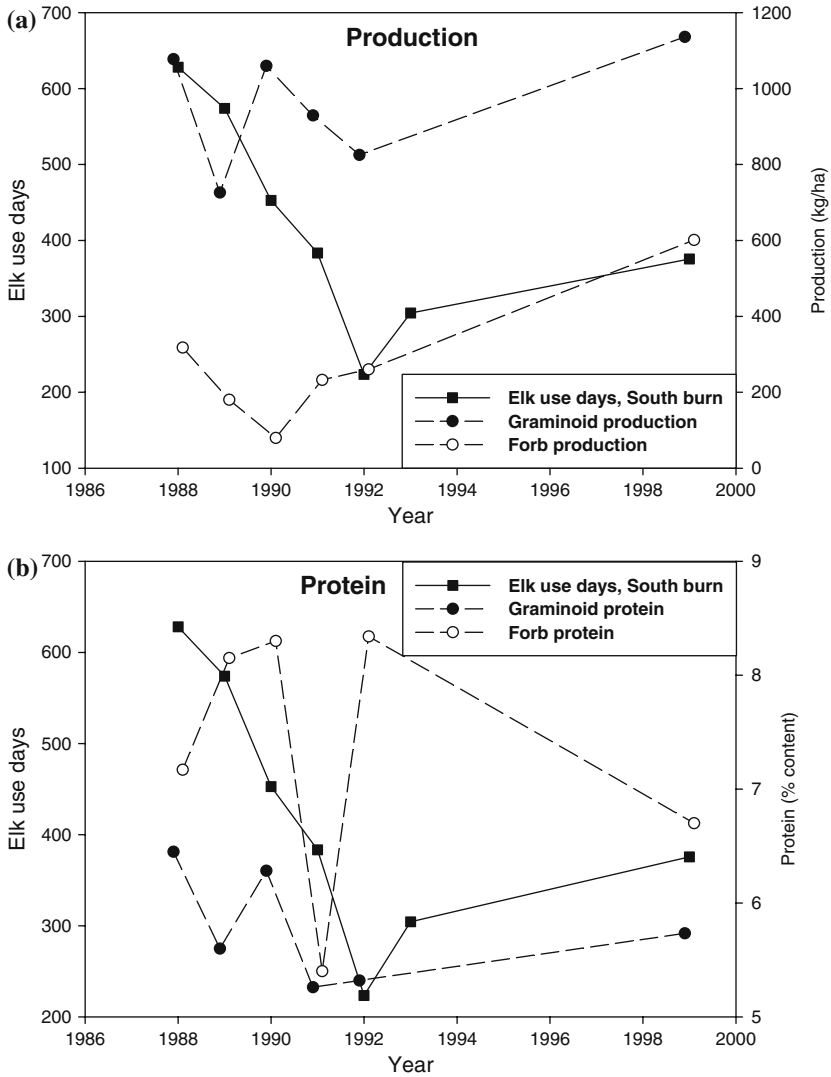


Figure 6. Concurrent changes in elk use, forage production (a), and forage protein levels (b) on plots in North Line Creek burned in 1984 (South burn) and originally dominated by mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) in south-central Montana, USA from 1989 to 1999.

supported by the fact that sagebrush is superior at nutrient uptake compared to its associated grass species (Caldwell et al. 1991a; Miller et al. 1991; Black et al. 1994; Cui and Caldwell 1998), shows increased root proliferation in the presence of grass species (Caldwell et al. 1991b), and is efficient at upper soil water removal (Donovan and Ehrlinger 1994), all traits suggesting that sagebrush



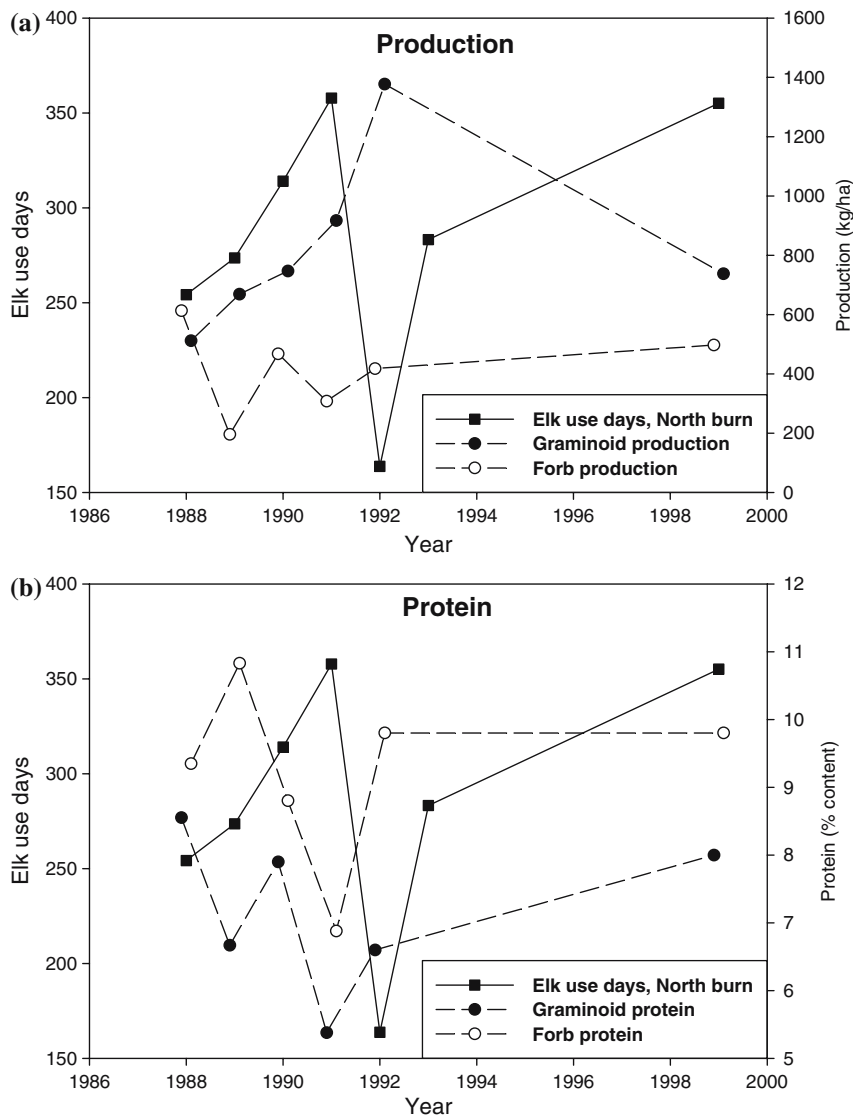


Figure 7. Concurrent changes in elk use, forage production (a), and forage protein levels (b) on plots in North Line Creek burned in 1988 (North burn) and originally dominated by mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) in south-central Montana, USA from 1989 to 1999.

removal would stimulate release of grasses. Consistent with this expectation, many studies have demonstrated short-term increases in production of herbaceous species following burning or poisoning of sagebrush (Johnson 1969; Thilenius and Brown 1974; Van Dyke et al. 1991; Van Dyke et al. 1996;

McDaniel et al. 2005) and higher levels of grazing capacity for livestock (Allen-Diaz and Bartolome 1998).

Fire, as an agent of sagebrush removal, also contributes directly to increased herbaceous production. In tallgrass prairies, increased plant production following fire (Kucera and Enrenreich 1962; Gibson and Hurlbert 1987; Towne and Owensby 1984; Knapp and Seastedt 1986; Turner et al. 1997) has been attributed to increased N mineralization rates due to removal of surface litter and elevated soil temperatures (enhanced mineralization hypothesis) or to a temporary release of plants from multiple resource constraints, especially light and N, during which a switch from energy to N limitation occurs (transient maxima hypothesis) (Blair 1997). Light and N are exploited by plants after a spring burn when plants experience a period of N availability (combined with high light availability) leading to a short-term pulse of increased productivity. Although our original community was sagebrush, not prairie, and our investigation was not designed to test these alternative explanations, available data leads us to infer that the higher levels of forage production we observed on burned sites immediately after burning probably resulted from a similar release from light limitation leading to increased rates of photosynthesis, release from N limitation leading to elevated plant production and protein, and release from the competitive effects of sagebrush leading to increased abundance of grasses and forbs.

In North Line Creek, burned sites had consistently higher forage production than unburned sites, but there was no long-term decline in production or protein with time as the transient maxima hypothesis would have predicted (Blair 1997; McCarron and Knapp 2003) or as has been the case in many long-term studies of sagebrush removal (Johnson 1969; Allen-Diaz and Bartolome 1998; Wambolt et al. 2001). Forb and graminoid production on the South burn were highest in 1999, 15 years after this site was burned, and 25% higher than in 1988, only 4 years after the fire. Similarly there was no consistent decline in forage protein on either burn, although protein levels were higher on the more recently burned North unit.

#### *Changes in elk use following fire*

Elk use on burned sites in our study is consistent with those of numerous other investigations that demonstrate that elk make increased use of burned sites (Hobbs et al. 1991; Vinton et al. 1992; Pearson et al. 1995; Singer and Harter 1996; Biondini et al. 1999), as the senior author also has documented for other burns in this area (Van Dyke et al. 1991; Van Dyke et al. 1996). Most studies, however, show that, compared to unburned sites, increased use of burn sites by elk is a temporary, unsustainable phenomena. Our results are unusual in documenting sustained levels of elevated use up to 15 years after burning and, in the case of the North (1988) burn, even increasing use near historic maximums up to 11 years after burning.

Grazing by elk can have a depressing effect on plant production (Hobbs et al. 1996), but studies in similar habitat in this region have shown no detrimental effect of elk grazing on plant production on recently burned sites (Tracy and McNaughton 1997). If elk had depressed forage production on these sites, increasing elk use should have been correlated with decreasing production, especially in graminoids. This was not the case. In most years these variables were positively correlated on both sites, especially on the older South unit. These patterns suggest that elk may perceive and exploit increased quantity and quality of forage by increasing their use of burned sites. On the South burn, when quantity and quality of forage declined, elk reduced their use of burned sites to pre-burn levels, and then reversed this trend by increasing use of the South burn when levels of production rose in subsequent years. Elk use of the North burn followed the same pattern from 1988 to 1991, then diverged from it in 1992 when all time highs in forage production were accompanied by all time lows in elk use. Elk use on the North burn returned to more typical levels in 1993 and 1999, although graminoid production declined over this period. It is possible that changes in use were influenced by factors external to the study sites. For example, periods of low use on these burns might have been coincident with increases in forage availability in nearby areas. However, our data provide no means to evaluate this hypothesis.

An important property of grazing ecosystems worldwide is a high spatio-temporal variation in forage. A second is the close association between grazing ungulates and the spatio-temporal arrangement of such forage, as ungulates apparently track changes in forage production and nutritional levels to increase their grazing efficiency and diet quality (Frank et al. 1998). Consistent with this general pattern, burned sites in North Line Creek show correlations between changes in elk use and changes in plant production and nutritional quality. Explanations invoked to explain these correlations differ. Some investigators (Hobbs et al. 1991; Vinton et al. 1992) have asserted that elk select burned sites primarily because of structural characteristics and plant species composition. Others have suggested that enhanced nutritional quality (Van Dyke et al. 1991; Turner et al. 1994; Tracy and McNaughton 1997) or earlier seasonal availability (Biondini et al. 1999) of vegetation on burned sites are the factors that most strongly influence elk selection. In North Line Creek, plant production, plant protein levels, and elk use often rose simultaneously, making it difficult to be dogmatic in our interpretation or to unequivocally endorse one of these hypotheses at the expense of others. Further, structural characteristics of the plant communities on burned sites remained relatively constant over the study period. We suspect that, by their initial visits to sites in late autumn-early winter periods of each year, elk made assessments of multiple variables of range condition (structural characteristics, production, and forage quality) that were all factors in their site tenure. Site-specific grazing, once entrenched by traditional annual behavior, might have established positive feedback pathways that contributed to enhanced levels of production and nutrition in plants

beyond the time span expected and documented in most studies of prescribed burning on similar ranges.

### **Management implications – long-term effects of prescribed burning and herbivory in sagebrush**

Managers must consider effects of management actions on the quantity and quality of available forage for managed species. Prescribed burning of sagebrush does not always result in increased production of forage, even in the short term (Wambolt et al. 2001). However, if burns are applied to change plant communities, their effects may persist for >15 years. If prescribed burns are justified with the expectation of rapid reinvasion and recovery of sagebrush and enhanced productivity of sagebrush following burning, as is increasingly the case on western range lands (Wambolt et al. 2001), our results suggest that such expectations will not be fulfilled.

Although elevated forage production and nutritional quality of vegetation associated with newly burned sites are not always as persistent as was the case in this study, managers should recognize that such benefits may nevertheless be of strategic importance to elk on nutritionally stressed winter ranges even if of short duration. Condition of wintering ungulates is often enhanced on burned grasslands, even when burning does not increase protein levels in forage (Rowland et al. 1983; Hobbs and Spowart 1984; Seip and Bunnell 1985). Thus, prescribed burning may be an appropriate strategy on winter ranges where ungulate health is a concern. Interactive models of ungulate populations, fire, and vegetation indicate that burned areas become particularly important to ungulate survivorship in average to severe winters, when enhanced forage production and quality on burned areas leads to increased survival (Turner et al. 1994).

Our results lead us to disagree with Wambolt et al. (2001) who claimed, after review of multiple studies of prescribed burning, that ‘no clear short or long-term benefits to grasses or forbs have become evident...’. In our study, prescribed burning led to long-term increases in coverage of grasses and forbs, changes which resulted in long-term increased use of burned sites by elk. It is important for managers to note, however, that our results occurred on sagebrush-dominated sites that, based on Forest Service records, had not been burned for 30 years or longer. Re-burning of such sites, once grass-forb communities are established, may not lead to further increases in productivity (Antos et al. 1983; Redmann et al. 1993) or to additional increases in use by elk.

Although we can not support the position that prescribed burning in sagebrush is of no benefit to grasses, forbs, or wildlife, we believe that managers should avoid the opposite view that prescribed burning in sagebrush is universally beneficial to conservation. Sagebrush communities are unique habitats used by many species, including many that can be considered sagebrush-dependent, such as Brewer’s sparrow (*Spizella breweri*) and sage grouse (*Centrocercus urophasianus*). In addition, removal of sagebrush through

burning may lower carrying capacities of some species on burned sites. For example, some large herbivores, such as mule deer (*Odocoileus hemionus*), which use proportionately greater quantities of browse in their diet, may find reduced supplies of dry matter, metabolizable energy, and N in forage on burned sites because of the reduction in shrub biomass (Hobbs and Swift 1985).

Sagebrush communities have suffered widespread alteration and destruction via chaining, tilling and rotocutting, herbicides, and prescribed burning. Such alterations have sometimes been justified in individual cases for the sake of increasing site-specific (alpha) diversity or increasing forage for game animals, such as elk, or for domestic livestock. However, large-scale removal or modification of sagebrush is likely to lower overall habitat and landscape (beta) diversity and may reduce populations of historically indigenous species. Further, large-scale removals cannot provide managers opportunity for precise evaluations of differences in plant and animal responses between sagebrush and non-sagebrush communities. In fact, models relating fire, grazing, and landscape characteristics predict that programs of prescribed burning that affect  $\geq 60\%$  of the winter range will produce no site-specific responses in ungulates and may actually reduce winter survival (Turner et al. 1994). It is often the precise spatial location, not the total extent, of burns that is a key determinant of ungulate survivorship (Turner et al. 1994).

For these reasons, we advocate using small, dispersed prescribed burns similar to those applied in this study. A limited number of such burns spread throughout a landscape over many years permits ungulates continued accessibility to newly burned sites that provide enhanced levels of plant production and nutritional quality compared to older burns and to unburned sites. Such a strategy also permits greater monitoring precision for managers who must assess the effects of prescribed burning. At the same time, this approach would increase landscape biodiversity by providing refugia for plant species of low abundance in the surrounding sagebrush-dominated ecosystem.

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