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Original Research

Dormant-Season Prescribed Fires Can Enhance Forage Quality for Two Growing Seasons in the Northwestern Great Plains

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ABSTRACT

Fire is an ecological disturbance that can accelerate nutrient cycling and alter herbivore distribution in grasslands and shrublands. Historically and today, humans have used prescribed fire to enhance forage quality for wild and domestic herbivores, and to achieve other management objectives. Contextual factors such as ecosystem type, seasonality, and fuel characteristics can determine how prescribed fire affects forage quality. For example, forage quality enhancements are relatively short lived in shortgrass steppe and subhumid grasslands but may persist for multiple years in northern mixed-grass prairie and sagebrush steppe. Outcomes near ecosystem boundaries are uncertain. Using 152 independent, small-plot, prescribed burns completed over multiple years at 36 sites in Wyoming and South Dakota, USA, we tested the effects of ecosystem type (northern mixed-grass prairie vs. sagebrush grassland ecotone), burn seasonality (fall vs. spring), and fuel characteristics (ambient vs. added fuel) on forage quality. Across ecosystems, fall fires had strong positive effects on forage quality parameters during the first growing season after fire, and energy benefits that persisted into the second growing season after fire. In northern mixed-grass prairie, spring and fall prescribed fires implemented before the same growing season yielded similar forage quality enhancements for one season. Finally, artificially increased fuel loads had few effects on forage quality. Although forage quality rarely dropped below critical nutrition thresholds for ruminants regardless of burning, our findings suggest relatively consistent, positive forage quality responses to prescribed fire across ecosystem types, seasonality of dormant-season burns, and fuel characteristics. Many improvements lasted through one growing season, and some persisted into a second growing season. Managers could take advantage of short-term nutritional benefits via adaptive management strategies that allow animals access to burned and unburned areas.

Introduction

Access to high-quality forage is critical for ruminant livestock and wildlife (Buxton et al. 1995; Middleton et al. 2018). Forage quality influences animal intake and has nutritional implications for animal maintenance, growth, reproduction, and lactation (Van Soest 1994). Fire can increase forage quality directly by removing low-quality, senescent tissue, and by increasing soil nutrient availability and, as a result, the nutritional quality of newly growing tissue (Van de Vijver et al. 1999; Augustine and Milchunas 2009). Fire can also enhance forage quality indirectly by facilitating compositional shifts toward more nutritious plant species (e.g., Vermeire et al. 2004; Van Dyke and Darragh 2006a; Furquim et al. 2024). Finally, fire can shift plant phenology, altering the temporal availability of young, high-quality plant tissue (e.g., Wrobleski and Kauffman 2003). Because of these changes in forage quality, cattle and wild herbivores preferentially use recently burned areas (Fuhlendorf and Engle 2004; Vermeire et al. 2004; Van Dyke and Darragh 2006a; Sensenig et al. 2010; Allred et al. 2011; Wanchuk et al. 2024a) and often benefit through en-

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hanced or stabilized weight and body condition (Woolfolk et al. 1975; Rowland et al. 1983; Svejcar 1989; Allred et al. 2014; Spiess et al. 2020; Wanchuk et al. 2024a).

Historically and today, human cultures across the globe have regularly applied fire to a variety of landscapes for a plethora of reasons, including to enhance forage quality for large herbivores (Murphy and Bowman 2007; Butz 2009; Huffman 2013; Scasta et al. 2016a). Fire alone, and spatiotemporal interactions between fire and herbivores, can also affect other management objectives, such as grassland bird habitat and pollinator resources (Wrobleski and Kauffman 2003; Fuhlendorf and Engle 2004; Augustine and Derner 2015; Scasta et al. 2016b; Porensky et al. 2018). Successfully achieving multiple objectives requires clear understanding of the effects of management actions applied in different ways. For prescribed fire in grazing systems, identifying how season and intensity of fire affect herbivore nutrition in specific ecological contexts would help managers design fire strategies that balance multiple management objectives.

Although fire tends to enhance forage quality, the magnitude and duration of these effects can vary widely across ecosystems, fire conditions (e.g., intensity), burn seasonality, and postfire growing conditions. Forage quality encompasses a range of metabolic requirements of the herbivore of interest, including energy, protein, vitamins, and minerals. Fire studies from subtropical and tropical systems worldwide have focused on protein (i.e., nitrogen) and mineral (i.e., phosphorous) aspects of forage quality and have generally found positive effects that disappear within a few months (Grelen and Epps 1967; Batmanian and Haridasan 1985; e.g., Mes 1958; Singh 1993; Van de Vijver et al. 1999; Murphy and Bowman 2007). Fiber and digestibility, which are key metrics of how much energy herbivores can extract from forage, also responded favorably to fire in these systems; studies reported reduced fiber content (which enables enhanced forage intake) for up to 500 days (Sensenig et al. 2010) and enhanced in vitro organic matter digestibility during the first growing season after fire (Boughton et al. 2022). Similarly, studies from mesic temperate grasslands (e.g., Allen et al. 1976; Hobbs et al. 1991; Allred et al. 2011) and semiarid shortgrass steppes (Augustine and Milchunas 2009; Augustine et al. 2010; Gullap et al. 2018) have shown that multiple aspects of forage quality, including protein, digestibility, and mineral content, can improve for a short time following fire, but effects typically dissipate within a few months.

North America's northern mixed-grass prairie is one of the largest intact grasslands in the world, extending across the north-central United States and southern Canada (Scholtz and Twidwell 2022). Compared to other grassland and savanna ecosystems, forage quality responses to fire in northern mixed-grass prairies have been more variable and sometimes more persistent. For example, prescribed fire can enhance protein or nitrogen content by 20–350% for one growing season after fire (Dufek et al. 2014; Powell et al. 2018; Spiess et al. 2020; Vermeire et al. 2020; Wang et al. 2021; Vera-Velez et al. 2023; Wanchuk et al. 2024a), and effects can occasionally persist into a second growing season (Vera-Velez et al. 2023). Fiber and lignin content reductions of 2–12% can last for at least 1 yr (Dufek et al. 2014; Vermeire et al. 2020) and sometimes several years after fire (Vera-Velez et al. 2023; Wanchuk et al. 2024a). Macronutrients and digestibility can also be enhanced for one to several years since fire in northern mixed-grass systems (Dufek et al., 2014, 2023; Vermeire et al. 2020; Wanchuk et al. 2024a; Wanchuk et al. 2024b).

In western North American shrublands, which generally had a lower historical fire frequency than adjacent temperate grasslands (Guyette et al. 2012), effects of fire on forage quality can last much longer. In sagebrush steppe ecosystems, shifts in protein and fiber regularly persist for two to three growing seasons after fire (Cook et al. 1994; Van Dyke and Darragh 2006a; Greene et al. 2012) and protein remained elevated for up to 11 yr since fire in one study (Van Dyke and Darragh 2006b). In these studies, longer term effects were attributed to enhanced resource availability for herbaceous species due to the removal of shrubs, shifts in plant community composition toward a more diverse and nutritious assemblage, and/or the development of feedbacks between patches of high forage quality and enhanced herbivore use. Given the variability in forage quality responses to fire both within and among ecosystems, it is especially hard to predict the magnitude and persistence of forage quality shifts in ecotones (boundary zones) between ecosystems, such as the biodiverse ecotone found between sagebrush steppe and northern mixed-grass prairie in North America, hereafter called "sagebrush grassland" (Porensky et al. 2018).

The magnitude and duration of forage quality response to fire could also be sensitive to the timing or season of fire due to systematic differences in fire weather or fuel characteristics between seasons, shifts in the timing of regrowth, or differential effects on community composition (Wang et al. 2021). However, results related to season of burn (hereafter, called burn timing to distinguish from season of sampling) are inconsistent. Some studies suggest better forage quality outcomes when burns occur during seasons that typically have more extreme fire weather (Nichols et al. 2021; Wang et al. 2021), while other studies suggest better forage quality outcomes during less extreme seasons (Van Dyke and Darragh 2006a; Dufek et al. 2014) or similar outcomes regardless of burn timing (Grelen and Epps 1967; Allred et al. 2011; Spiess et al. 2020). Finally, in semiarid systems, different weather patterns can produce very different fuel loads, which can in turn affect fire intensity. Fire intensity may affect forage quality responses through its effects on the amount of dead material consumed by fire, species-specific mortality of perennating or reproductive materials, or nutrient dynamics (Van Wagtendonk 2018). These uncertainties make it difficult to manage for multiple objectives.

To reduce knowledge gaps in how prescribed fire affects forage quality, we examined the magnitude and duration of fall and spring prescribed fire effects on forage quality at 36 experimental sites across sagebrush grasslands in eastern Wyoming, USA and mixed-grass prairies in western South Dakota, USA, which represents an area in the Great Plains where research on prescribed fire effects is lacking (see Fig. 2 in Scasta et al. 2016a). We addressed three research questions.

1) *What is the magnitude and duration of prescribed fire effects on forage quality, and do these effects vary based on ecosystem type?* We expected that both fall and spring prescribed fires would enhance forage quality by removing low-quality, senescent biomass and increasing the quality of new growth during the first growing season (both spring and summer) after the fire, and we expected these effects to be absent in subsequent sampling periods. We expected forage quality improvements to be greater in sagebrush grassland than northern mixed-grass prairie sites due to the removal of sagebrush, which would increase both soil nutrient and light availability for new herbaceous plant growth.
2) *Do the effects of prescribed fire on forage quality vary based on burn timing?* We expected fall and spring prescribed fires to have similar effects on forage quality, since both burn timings occurred during the dormant season and would not greatly differ in their regrowth timing, which is strongly controlled by ambient temperature.
3) *Do the effects of prescribed fire on forage quality vary based on fuel load?* We used artificial fuel additions to explore the effects of higher fuel loads (e.g., after a very productive year) on fire outcomes. When compared to ambient fuel loads, we expected

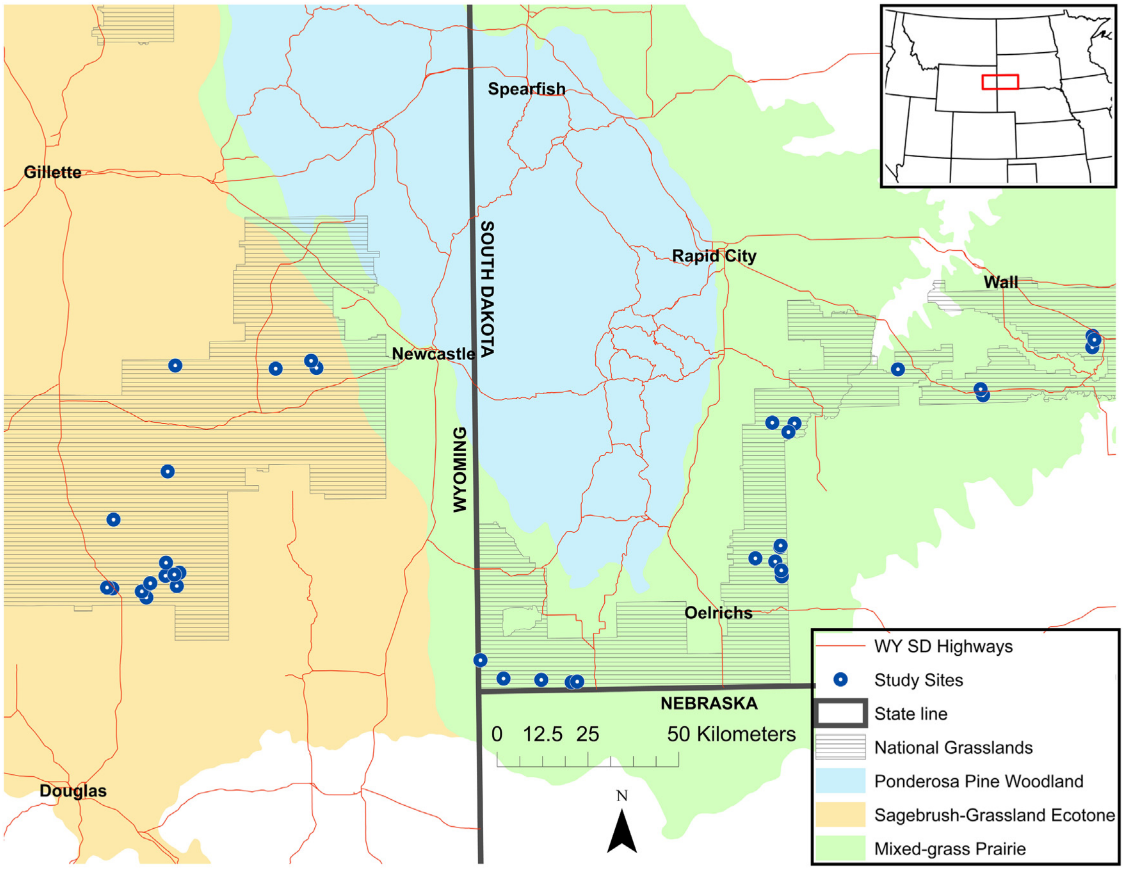

Figure 1. Map of 36 study sites in a sagebrush grassland ecotone (Wyoming) and northern mixed-grass prairie (South Dakota) in the northern United States.

that higher fuel loads would further enhance forage quality by causing more complete removal of low-quality, senescent biomass.

Methods

Study sites

Our study was conducted in 36 sites in the Northwestern Great Plains of North America (Fig. 1, EPA Level III Ecoregion 9.3.3, Omernik 1987). Twenty northern mixed-grass prairie sites were on Buffalo Gap National Grassland in southwestern South Dakota, USA (hereafter Northern Mixed-grass Prairie, or NMP) and the remaining sixteen sites were in sagebrush grasslands of the Thunder Basin region of northeastern Wyoming, USA (hereafter Sagebrush Grassland Ecotone, or SGE).

Plant communities of the NMP sites include a diverse assemblage of perennial C_3 (cool-season) grasses, including western wheatgrass (*Pascopyrum smithii* (Rydb.) Á. Löve), needle and thread (*Hesperostipa comata* (Trin. & Rupr.) Barkworth ssp. *comata*), green needlegrass (*Nassella viridula* (Trin.) Barkworth), and prairie Junegrass (*Koeleria macrantha* (Ledeb.) Schult.), and low-growing C_4 (warm-season) perennial grasses such as blue grama (*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths) and buffalograss (*Bouteloua dactyloides* (Nutt.) J.T. Columbus). Mean annual precipitation for the South Dakota Southwest Climate Division is 475 mm, with the majority falling in spring and summer, and mean temperature ranges from −4.5°C in January to 23.2°C in July (1991–2020 climate normal; NCEI NOAA 2025). Water Year Precipitation (total precipitation from October through September) for the South Dakota Southwest Climate Division during the years of the study was 521 mm in 2018 (October 2017–September 2018), 673 mm in 2019, 379 mm in 2020, 346 mm in 2021, and 394 mm in 2022 (NCEI NOAA 2025). Soil texture was evaluated using the hydrometer method (Bouyoucos 1962) at each site. Most sites were on clay soils ($n = 10$), with other sites being classified as sandy loam ($n = 4$), clay loam ($n = 3$), and loam ($n = 3$).

Twelve of the sixteen SGE sites were on the Thunder Basin National Grassland and four were on interspersed private lands. Floristically, Wyoming sites are in a broad ecotone between shrublands of the North American Deserts (EPA Level I ecoregion 10), and grasslands of the Great Plains (EPA Level I ecoregion 9) (Porensky et al. 2018). Plant communities commonly include a sparse overstory of Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young) and an understory characteristic of northern mixed-grass prairie. Common herbaceous plant species include the perennial graminoids blue grama, western wheatgrass, needle and thread, threadleaf sedge (*Carex filifolia* Nutt.), and Sandberg bluegrass (*Poa secunda* J. Presl), and the annual grasses cheatgrass (*Bromus tectorum* L.), field brome (*Bromus arvensis* L.), and 6 wk fescue (*Vulpia octoflora* (Walter) Rydb). Mean annual precipitation for the Wyoming Cheyenne Niobrara Drainage Climate Division is 378 mm with the majority occurring in spring and summer, and mean temperature ranges from −4.6°C in January to 21.8°C in July (1991–2020 climate normals; NCEI NOAA 2025). Water Year Precipitation for the Wyoming Cheyenne Niobrara Drainage Climate Division during the years of the study was 527 mm in 2018 (October 2017–September 2018), 463 mm in 2019, 251 mm in 2020, 321 mm in 2021, and 323 mm in 2022 (NCEI NOAA 2025). Sites were mostly on sandy loam soils ($n = 12$), with a few sites being classified as loam ($n = 3$) and sandy clay loam ($n = 1$).

Table 1
Number of plots in which forage quality was sampled by ecosystem, treatment, and year.

Burn characteristics				Number of plots sampled for postburn forage quality							
Burn year	Burn timing	Eco-system	Burn fuel	2019 Spring	2019 Summer	2020 Spring	2020 Summer	2021 Spring	2021 Summer	2022 Spring	2022 Summer
NA	Unburned	NMP	NA	20	20	7	5	7	7		
2018	Fall	NMP	Ambient	20	20						
2019	Spring	NMP	Ambient	13	13						
2019	Fall	NMP	Ambient			6	6	7	7		
NA	Unburned	SGE	NA	16	16	16	16	22	28	16	16
2018	Fall	SGE	Ambient	16	16	16	16				
2019	Fall	SGE	+50%			11	11	11	11		
2019	Fall	SGE	Ambient			21	21	21	21		
2021	Spring	SGE	+50%					9	9	9	9
2021	Spring	SGE	Ambient					11	11	11	11

Experimental design

The experiment had a randomized block design across 36 sites (20 in NMP and 16 in SGE) which had not experienced recent major disturbances, such as prairie dogs, tillage, or recent fire (>15+ yr since last known fire). At each site, six 2 m × 4 m plots separated by at least 5 m were randomly established. In SGE, each plot was centered on the nearest adult sagebrush individual. Plots were oriented with the 4-m edge running in the predominant wind direction (E-W or NW-SE in NMP and NE-SW in SGE). All plots were unfenced and open to grazing herbivores, including both livestock and wildlife. The timing, intensity, and duration of use by livestock varied widely across sites, consistent with regional livestock management regimes.

Treatments were randomly assigned to the six plots at each site. One plot was an unburned control and the remaining plots received various fire and fuel addition treatments that varied among sites because of logistical constraints (next paragraph). Treatments examined here include combinations of burn timing (fall, spring), year of fire (2018, 2019, 2021), and, for SGE sites only, fuel load (ambient, 50% addition; Table 1). Average herbaceous fuel loads were estimated to be 129 g m^{-2} in SGE (L.M. Porensky, unpublished data). These fuel loads are well above the level where grassland burns tend to become patchy with incomplete combustion (Augustine et al. 2014). For our 50%-fuel addition, we manually broadcast 64.5 g m^{-2} (516 g plot^{-1}) of weed-free hay (stored at ambient humidity) across the plot immediately prior to burning. All burns receiving different fuel treatments occurred on the same day at an individual site and were conducted within 1 h of each other.

Due to weather and COVID-19 limitations, the timing of fire application differed across sites and years (Table 1). Fall fires occurred 17–24 October 2018 and 8–17 October 2019 in NMP and 19–25 October 2018 and 14–17 October 2019 in SGE. Spring burns occurred 2–24 April 2019 in NMP and 9 March–2 April 2021 in SGE. Prescribed fire was applied using a 2 m × 4 m burn box with 1-m tall aluminum sides (Kral et al. 2015) with one side opened to allow a wind-driven headfire to develop. A ring of fire was laid down with a drip torch on the inside edges of the burn box and then drawn across the opening of the box to create the headfire. Fire weather (relative humidity, air temperature, and wind speed), soil moisture, fuel moisture and burn severity metrics were assessed at the time of fire and are summarized in Appendix A.

Data collection

Forage quality was sampled in the first and second growing seasons postfire, except in cases where sampling was limited due to COVID-19 (e.g., NMP in 2020, Table 1). We clipped all aboveground herbaceous biomass rooted in one 20 × 50 cm quadrat; we excluded cactus and shrubs because they are rarely consumed by cattle in these systems. We sampled twice annually (spring and summer, using separate quadrats for each sampling) to more accurately determine the duration of fire effects on forage quality. Spring sampling occurred in late May or early June, and summer sampling occurred in August. In NMP, the biennial legume sweetclover (*Melilotus officinalis* (L.) Lam.) was abundant at seven sites in summer 2019 and one site in spring and summer 2020. For these sites and sampling times, sweetclover was clipped separately and is not included in the current analysis because the species is generally avoided by cattle after it matures in summer, and its inclusion in analysis would strongly skew forage quality results. Samples were dried in a forced-air oven for 48 h at 60°C. Laboratory analyses were conducted by Ward Laboratories using NIRS (near infrared reflectance spectroscopy), and values are reported on a dry matter basis. Metrics analyzed were: neutral detergent fiber (NDF) and lignin, both of which are negatively correlated with intake and digestibility; fat, an indicator of high energy sources in feed; total digestible nutrients (TDN), an indicator of total energy; crude protein, which is related to nitrogen content and important for protein requirements of ruminant gut microbes as well as direct use by the animal; and ash, an indicator of mineral content.

Statistical analysis

Due to the logistical constraints described above (e.g., spring and fall burns occurred in separate years in SGE, and sampling was limited in 2020 in NMP), some outcomes could not be directly evaluated across both ecosystems and burn timings. Our analyses thus addressed the following revised questions. In all analyses, to account for spatially structured sampling and repeated measures, we included random intercepts for site, plot nested within site, and (except for the third question) sampling year, and we utilized a compound symmetry covariance structure to account for repeated measures where appropriate.

What is the magnitude and duration of FALL prescribed fire effects on forage quality, and do these effects vary based on ecosystem type? To answer this question, we analyzed 2019–2021 data from fall burns, with ambient fuel loads, that occurred in the same years in both ecosystems, and corresponding unburned plots. We ran a linear mixed model with growing seasons since fire (1, 2, >15), season of sampling (Spring vs. Summer), ecosystem (SGE vs. NMP), and all possible interactions as fixed effects.

What is the magnitude and duration of SPRING prescribed fire effects on forage quality within sagebrush grassland? To answer this question, we analyzed 2021–2022 SGE data from spring burns with ambient fuel loads and corresponding unburned plots. We ran a linear mixed model with growing seasons since fire, season of sampling, and their interaction as fixed effects.

Do the effects of prescribed fire on forage quality vary based on burn timing during the first growing season since fire within northern mixed-grass prairie? To answer this question, we used NMP data for the 2019 sampling season only. We ran a linear mixed model with burn timing (fall, spring, or unburned), season of sampling, and their interaction as fixed effects.

Do the effects of prescribed fire on forage quality vary based on fuel load within sagebrush grassland? For this question, we analyzed SGE data from burned plots only. For sites in which we burned plots with added fuel and ambient fuel during the same burn window ($n = 11$ for 2019 fall burns and $n = 9$ for 2021 spring burns; Table 1), we ran linear mixed models with fuel loading, burn timing, growing seasons since fire, season of sampling, and all interactions as fixed predictors.

All analyses were conducted in JMP (JMP®, Version 17.2.0. 2022-2023 JMP Statistical Discovery LLC). Data were transformed or variance-weighted when necessary to meet model assumptions. Results are reported as means ± SE and are discussed as significant at $\alpha < 0.05$. Effect sizes are reported as relative percent changes, not absolute percent changes; for example, a shift from 60% to 66% is described as a 10% increase. Post hoc comparisons were conducted using Tukey's honestly significant difference (HSD) test.

Results

Despite the small size of our burn boxes, fire affected the majority of the plot area (85% area burned, on average), and we generally achieved light to moderate fire severities (Tables A.5 and A.6).

Across ecosystems, does fall prescribed fire affect forage quality in the first or second years since fire?

Fall prescribed fires had strong positive effects on the energy components of forage quality (TDN and Fat, Figs. 2a and 2b), and these effects lasted into the second growing season since fire (GSSF). When compared to unburned plots, plots burned in the fall had 10% higher TDN during the spring of the first growing season after fire, and values remained 3–4% higher through the summer of the first growing season and the spring of the second growing season after fire, regardless of ecosystem type (Fig. 2a; GSSF*Sampling Season $F_{2,280} = 10.0$, $P < 0.0001$; Table B.1). Across ecosystems and sampling seasons, fall prescribed fire was associated with 12–26% higher fat values for both the first and second years since fire (Fig. 2b; GSSF $F_{2,222} = 22.7$, $P < 0.0001$; Table B.2). Fat values were also 17% higher in SGE than NMP (Ecosystem $F_{1,60} = 6.44$, $P = 0.01$), and 15% higher in summer than spring (Sampling Season $F_{1,284} = 12.1$, $P = 0.0006$).

Although NDF levels differed between ecosystems overall in spring samples (Fig. 2c; Ecosystem*Sampling Season $F_{1,267} = 9.45$, $P = 0.002$), fire's effect on NDF was consistent between SGE and NMP. Fall-burned plots had 11% and 3.5% lower NDF than unburned plots during the spring and summer of the first growing season after fire, respectively (Fig. 2c; GSSF*Sampling Season $F_{2,267} = 8.95$, $P = 0.0002$; Table B.3). Lignin concentrations in SGE spring samples were 12% lower in the first growing season since fire than the second growing season since fire, but neither of these differed from unburned conditions. Also, this effect was not present for NMP spring samples or for any summer samples (Fig. 2d; GSSF*Ecosystem*Season $F_{2,292} = 4.49$, $P = 0.01$; Table B.4).

Fall-burned plots had 27% higher crude protein during the spring of the first growing season after fire (Fig. 2e; GSSF*Sampling Season $F_{2,282} = 11.9$, $P < 0.0001$), and summer samples had higher crude protein in SGE than in NMP regardless of burning (Ecosystem*Sampling Season $F_{1,282} = 25.3$, $P < 0.0001$; Table B.5). Across sampling seasons, SGE samples from the first growing season since fire had >30% higher ash content than those from the second growing season since fire or from unburned plots; this effect was not present for NMP samples (Fig. 2f; GSSF*Ecosystem $F_{2,136} = 4.61$, $P = 0.01$). Spring samples had lower ash in SGE than in NMP (Ecosystem*Sampling Season $F_{1,258} = 8.94$, $P = 0.003$; Table B.6).

Within sagebrush grassland, does spring prescribed fire affect forage quality in the first or second years since fire?

Spring prescribed fire had positive effects on some aspects of forage quality in SGE sites during the first growing season after fire. Samples collected during the first growing season after spring prescribed fires had 2–3% higher TDN (GSSF $F_{2,35} = 5.50$, $P = 0.008$) and 2–5% lower NDF (GSSF $F_{2,33} = 8.48$, $P = 0.001$) than samples from unburned plots (Figs. 3a and 3b; Tables B.7 and B.8). Crude protein and fat content were 49% and 56% higher in summer samples from the first growing season since fire than those from the second growing season since fire, respectively, while samples from unburned plots were intermediate (Figs. 3c and 3d; GSSF*Sampling Season for crude protein: $F_{2,82} = 4.79$, $P = 0.01$; Fat: $F_{2,91} = 3.57$, $P = 0.03$; Tables B.9 and B.10). Spring-collected samples showed similar but nonsignificant trends for crude protein and fat content (Figs. 3c and 3d). Spring prescribed fire did not significantly affect lignin or ash content in either season (Figs. 3e and f; Tables B.11 and B.12). Overall, spring-collected samples had higher TDN ($F_{1,83} = 91$, $P < 0.0001$), lower NDF ($F_{1,81} = 77$, $P < 0.0001$), and lower lignin ($F_{1,88} = 56$, $P < 0.0001$) than summer-collected samples.

Within northern mixed-grass prairie, does burn timing affect forage quality outcomes in the first growing season since fire?

Although many forage quality parameters were enhanced during the first growing season after prescribed fires in NMP, spring and fall prescribed fires had similar forage quality outcomes. Across sampling seasons, TDN values were 9–10% higher and fat values were 19–25% higher in burned plots than unburned plots (TDN: $F_{2,33} = 21.4$, $P < 0.0001$; Fat: $F_{2,67} = 18.0$, $P < 0.0001$), but there was no significant difference between plots burned in spring and fall (Figs. 4a and 4b; Tables B.13 and B.14). Similarly, spring-collected samples from burned plots had ~40% higher crude protein and ~14% lower NDF than samples from unburned plots, regardless of the timing of fire, and prescribed fire did not affect crude protein and NDF in summer-collected samples (Figs. 4c and 4d; Burn Timing*Sampling Season for crude protein: $F_{2,50} = 6.35$, $P = 0.004$; NDF: $F_{2,33} = 5.86$, $P = 0.005$; Tables B.15 and B.16).

For both spring- and summer-collected samples, plots burned in spring had 10% lower lignin content than unburned plots, while plots burned in fall had intermediate lignin content (Fig. 4e; Burn Timing $F_{2,33} = 5.80$, $P = 0.007$; Table B.17). Summer-collected samples from fall-burned plots had lower ash content than those from unburned plots, while those from spring-burned plots had intermediate ash content (Fig. 4f; Burn Timing*Sampling Season $F_{2,50} = 3.48$, $P = 0.04$; Table B.18). Spring-collected samples from all plots had similar ash content. Spring-collected samples had higher TDN ($F_{1,50} = 257$, $P < 0.0001$), lower lignin ($F_{1,50} = 132$, $P < 0.0001$) and lower fat ($F_{1,50} = 13.6$, $P = 0.0005$) than summer-collected samples.

Within sagebrush grassland, does fuel load affect forage quality outcomes?

We observed minimal evidence that experimentally augmented fuel loads could alter forage quality outcomes from prescribed fire in SGE. For samples collected during the first growing season after prescribed burns, fat content was 8.7% higher in high fuel load plots than ambient fuel load plots, on average, but this difference disappeared during the second growing season since fire (Burn Fuel*GSSF $F_{1,108} = 3.79$, $P = 0.054$; Table B.19). All other forage quality parameters did not vary based on burn fuel or its interactions with other predictors (Tables B.20–B.24).

Discussion

Our study encompassed 152 different prescribed fires across 36 sites in northern mixed-grass prairies and a sagebrush grassland ecotone. Across ecosystems, we found strong positive effects

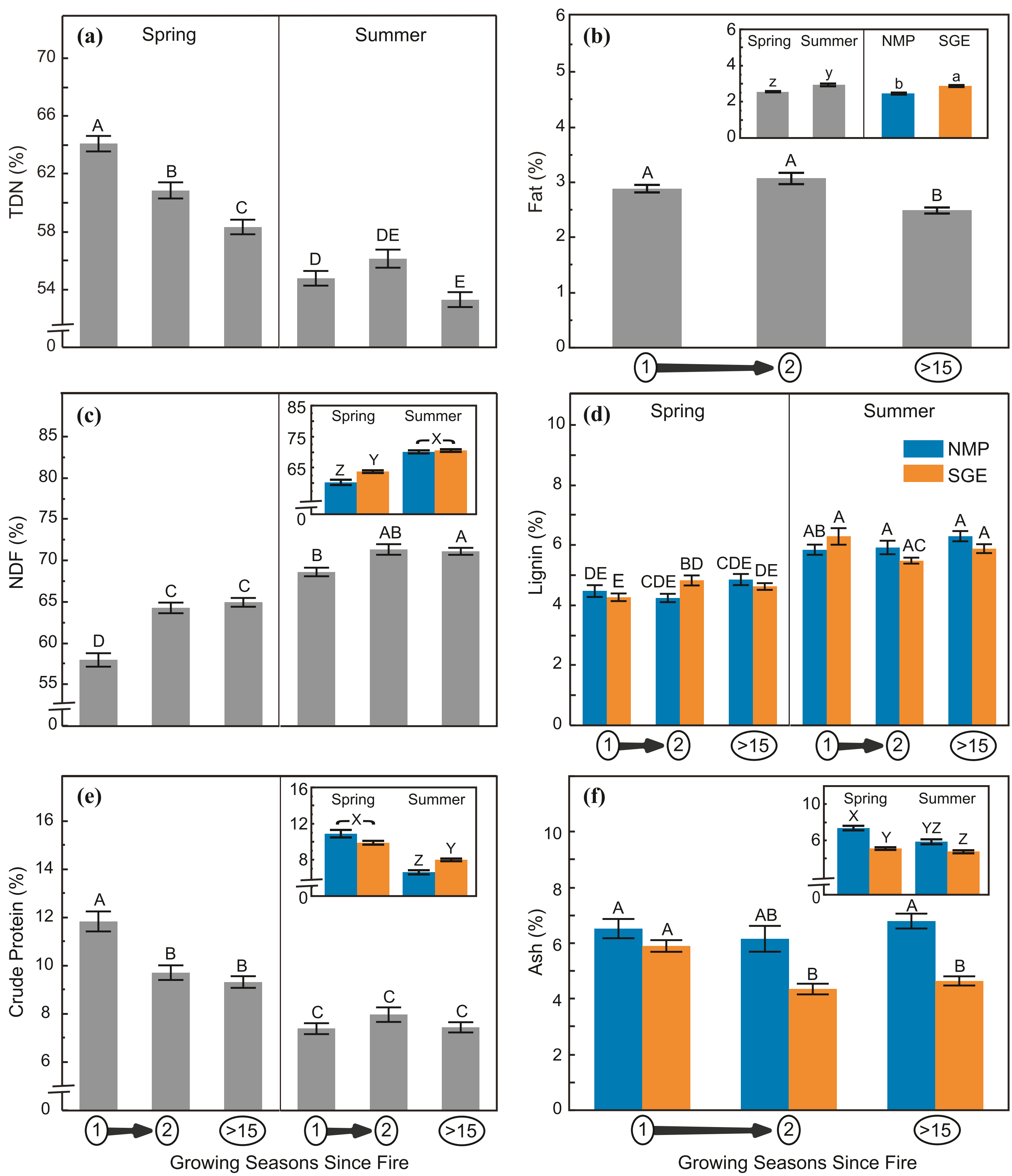

Figure 2. Fall burn effects on (**a**) total digestible nutrients (TDN), (**b**) fat, (**c**) neutral detergent fiber (NDF), (**d**) lignin, (**e**) crude protein, and (**f**) ash content in spring and summer forage samples across ecosystems during the first and second growing seasons since fire. NMP indicates northern mixed-grass prairie; SGE, sagebrush grassland ecotone. Within each panel or inset, bars sharing letters did not differ significantly based on post hoc Tukey HSD means comparison tests. All data are reported as percent dry basis. Figures display raw data (mean ± SE), but models included random effects and additional fixed effects.

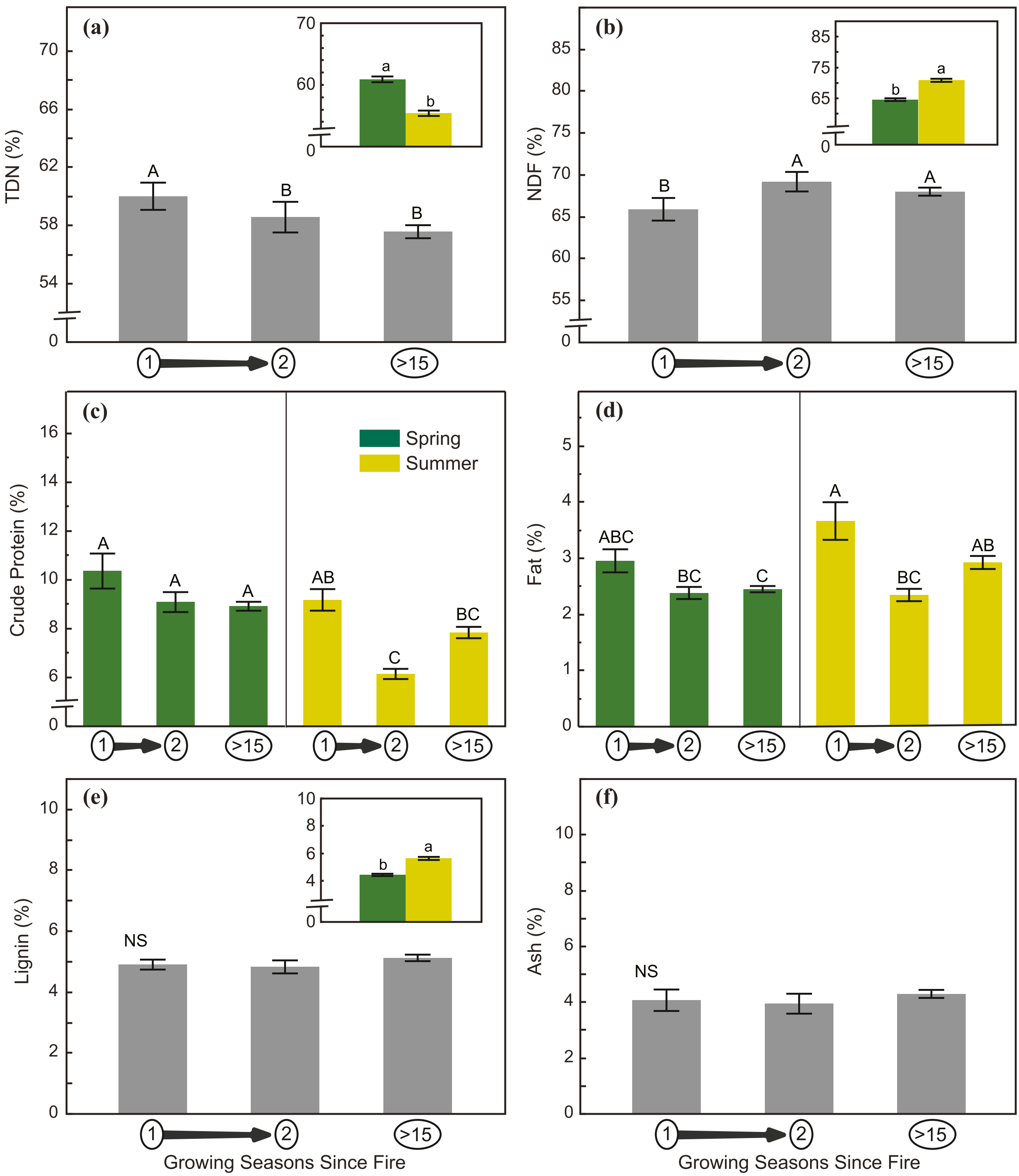

Figure 3. Spring burn effects on (**a**) total digestible nutrients (TDN), (**b**) neutral detergent fiber (NDF), (**c**) crude protein, (**d**) fat, (**e**) lignin, and (**f**) ash content in spring and summer forage samples in sagebrush grassland ecotone sites during the first and second growing seasons since fire. Within each panel or inset, bars sharing letters did not differ significantly based on post hoc Tukey HSD means comparison tests. All data are reported as percent dry basis. Figures display raw data (mean ± SE), but models included random effects and additional fixed effects.

of fall fires on many forage quality parameters during the first growing season after fire, as well as energy benefits that persisted into the second growing season after fire (Table 2). In the sagebrush grassland ecotone sites, effects of spring fires conducted prior to a different growing season than the fall fires were weaker and less durable (Table 2). In northern mixed-grass prairie sites where we were able to directly test the effects of burn seasonality on forage quality outcomes during the first growing season after fire, we found that outcomes of fall and spring fires were similar (Table 2).

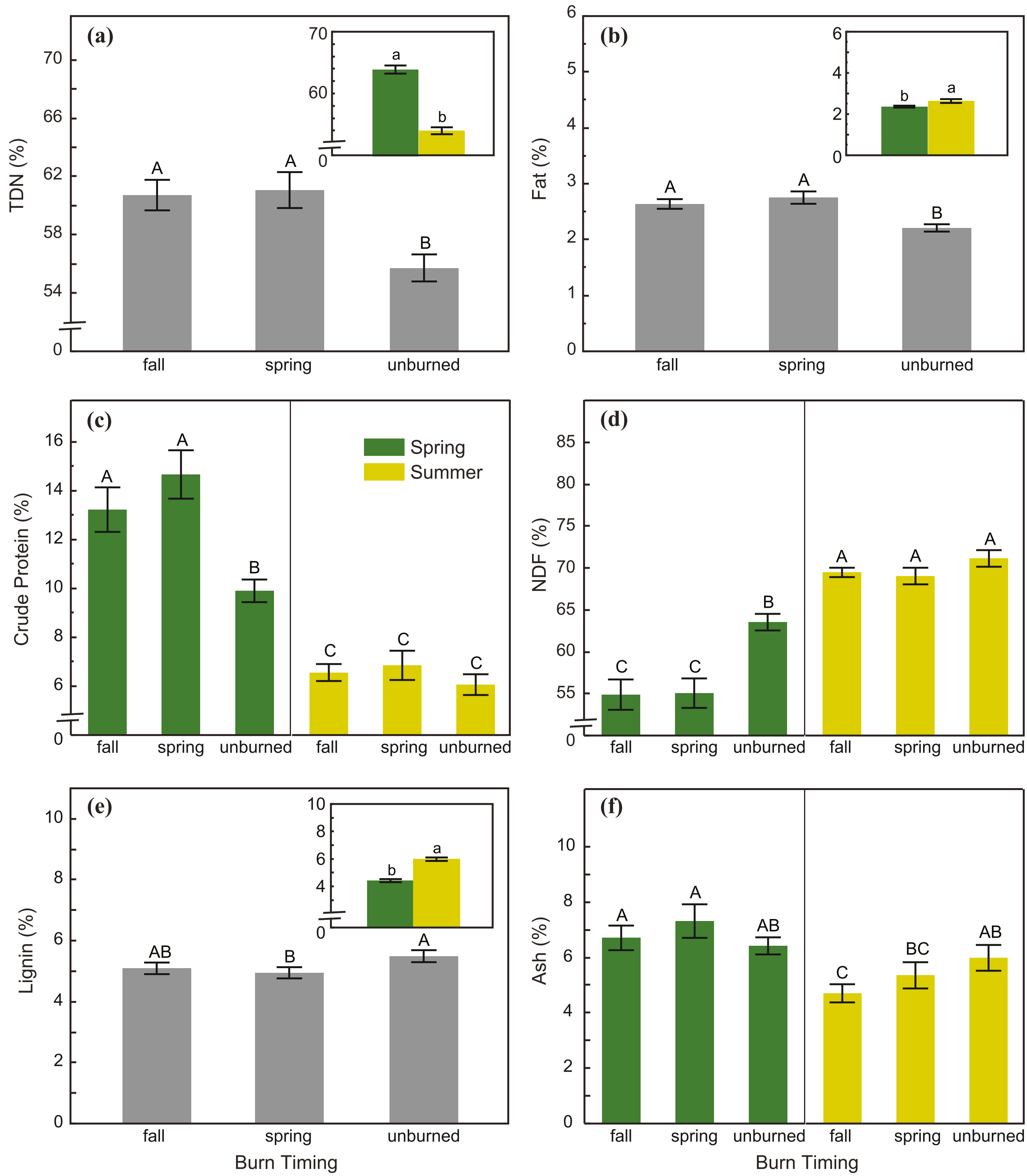

Figure 4. Burn timing effects on (**a**) total digestible nutrients (TDN), (**b**) fat, (**c**) crude protein, (**d**) neutral detergent fiber (NDF), (**e**) lignin, and (**f**) ash content in spring and summer forage samples in northern mixed-grass prairie sites during the first growing season since fire. Within each panel or inset, bars sharing letters did not differ significantly based on post hoc Tukey HSD means comparison tests. All data are reported as percent dry basis. Figures display raw data (mean ± SE), but models included random effects and additional fixed effects.

Consistent with our expectations, fall-burned plots had markedly less fiber (NDF), more energy (TDN), more fat, and more crude protein than unburned plots in the spring of the first growing season following fire, across both ecosystem types. In sagebrush grassland sites, forage from fall-burned plots also had more ash than unburned plots, which may reflect a short-term release of minerals from burning shrubs in this system and greater mineral availability to the regrowing herbaceous plants (Bodí et al. 2014). Fire-induced reductions in fiber content persisted through summer of the first growing season, increases in energy

Table 2
Summary of forage quality responses to dormant-season fire over 2 yr in two different ecosystems. Positive arrows indicate improved forage quality, relative to unburned sites. Long arrows indicate that at least one parameter changed by at least 10%, short arrows indicate changes less than 10%, and ns indicates no significant change.

Ecosystem	Burn timing	Energy (indicated by higher TDN, fat)				Digestibility (indicated by lower NDF, lignin)				Nutrients (indicated by higher CP, Ash)			
		1st year		2nd year		1st year		2nd year		1st year		2nd year	
		Spr	Su	Spr	Su	Spr	Su	Spr	Su	Spr	Su	Spr	Su
NMP	Fall	⬆	⬆	⬆	⬆	⬆	↑	ns	ns	⬆	ns	ns	ns
	Spring	⬆	⬆			⬆	⬆			⬆	ns		
SGE	Fall	⬆	⬆	⬆	⬆	⬆	↑	ns	ns	⬆	⬆	ns	ns
	Spring	↑	↑	ns	ns	↑	↑	ns	ns	ns	ns	ns	ns

NMP indicates northern mixed-grass prairie; SGE, sagebrush grassland ecotone; TDN, total digestible nutrients; NDF, neutral detergent fiber; CP, crude protein; Spr, spring sampling; Su, summer sampling.

content persisted through spring of the second growing season, and increases in fat content persisted through summer of the second growing season. Reduced fiber and enhanced fat both contribute to enhanced energy (TDN) and improved digestibility (Short et al. 1974; Weiss 1998). Herbaceous plant tissue is unlikely to persist as upright forage for two growing seasons, regardless of whether a fire occurred or not. Thus, these more durable effects suggest that fall fires not only remove pre-existing, low-quality, senescent tissue, but also enhance the energy available in new growth after the fire. Future research could determine whether these improvements are due to shifts in soil nutrient availability, shifts in plant composition, or some other factor.

We expected that forage quality improvements after fire would be stronger and more durable in a sagebrush grassland ecotone than in northern mixed-grass prairie. Although forage quality differed between ecosystems (even in unburned sites), we observed weak and inconsistent ecosystem-level differences in the magnitude and persistence of forage quality improvements after fall fire. Across ecosystems, the magnitude of fire-induced forage quality responses was similar to that observed in previous studies from northern mixed-grass prairie (e.g., Vermeire et al. 2020; Wanchuk et al. 2024a) and slightly less than that observed in some studies from sagebrush steppe (e.g., Cook et al. 1994; Van Dyke and Darragh 2006a). Similarly, the persistence of forage quality improvements in both ecosystem types was within the range of outcomes from northern mixed-grass prairie (e.g., Powell et al. 2018; Wang et al. 2021; Wanchuk et al. 2024a) and suggested more durable forage quality effects than in tropical systems, tallgrass prairie and shortgrass steppe (e.g., Hobbs et al. 1991; Augustine and Milchunas 2009; Boughton et al. 2022), but less durable effects than in sagebrush steppe (Cook et al. 1994; Van Dyke and Darragh 2006a). Our results support prior work suggesting that the herbaceous component of the sagebrush grassland ecotone plant community responds to disturbance similarly to northern mixed-grass prairie, while the shrub overstory responds more similarly to sagebrush steppe (Porensky et al. 2018). However, it is possible that if we were able to monitor these sites for more years, we might observe additional differences between the two ecosystem types.

We were able to evaluate forage quality responses to spring prescribed fires for two growing seasons at sagebrush grassland sites. Although results were qualitatively similar to those from fall fires, effects were generally weaker and no forage quality benefits from spring prescribed fires lasted into the second growing season since fire. There are several possible reasons for these weaker results. First, air temperatures and burn severities were generally lower in spring 2021 than in fall 2019 or fall 2018 (Tables A.2 and A.5), which could be related to less complete removal of senescent tissue and less nutrient and ash release. Second, we had only a quarter of the replication for spring burns compared to fall burns (Table 1), so it is possible that effects were present but the lower power analyses for spring burns were unable to detect them. Third, because spring burns took place in a different year than fall burns in sagebrush grassland sites, different weather conditions during the growing seasons following fire could have caused different responses. However, this third hypothesis seems unlikely because 2018 fall burns experienced wet conditions during their first growing season (2019), 2019 fall burns experienced dry conditions during their first growing season (2020), and 2021 spring burns experienced near average conditions during their first growing season (2021).

In northern mixed-grass prairie sites, we were able to directly compare fall and spring burns affecting the same subsequent growing season (2019). In this situation, consistent with our expectations, we observed minimal effects of burn timing on forage quality outcomes. Forage from spring-burned plots had slightly less lignin and more ash than forage from fall-burned plots, which may be due to early spring growth being removed by spring, but not fall, fire. However, these differences were not significant. Spring and fall fires in NMP were conducted under similar weather conditions (Table A.2) and achieved similar severities (Table A.5), although spring fires had higher soil moisture (Table A.3), lower fuel moisture (Table A.4), and slightly higher % area burned (Table A.6) than fall fires. Across both burn seasons, prescribed fires increased protein, energy, and fat content and reduced fiber content of forage. These results match prior work suggesting that within the dormant-season, burn timing is likely less important than other factors (e.g., fire history, fire weather, soils) in determining forage quality responses to fire (Engle and Bidwell 2001). This is especially likely when similar weather conditions exist and similar burn severities are achieved across seasons, as was the case in our study (Tables A.2 and A.5). For example, unlike burn timing, seasonality of sampling had strong and predictable effects on forage quality in our study (see also Scasta 2017). Prior work from our region suggests that cattle preferentially use burned areas regardless of burn seasonality (Vermeire et al. 2004), and our results suggest that that such a response would also be expected at our study sites.

We expected that higher fuel loads would further enhance forage quality by causing more complete removal of low-quality, senescent biomass, but we found that artificially enhanced fuel loads had minimal effects at our sagebrush grassland sites. Added fuel did enhance fat content during the first growing season after fire, consistent with our expectations. We hypothesize that once biomass exceeds a critical minimum level of fuel needed to carry a flame front, additional herbaceous fuel has relatively small effects on forage quality parameters. In contrast, the addition of woody fuels might cause bigger shifts via greater soil heating and shifts in plant community composition.

Implications

The forage quality improvements we observed after both fall and spring prescribed fires would likely support enhanced herbivore performance during the first growing season after fire (Svejcar 1989; Spiess et al. 2020; Wanchuk et al. 2024a). Managers would need to take advantage of the less durable crude protein benefits immediately and could potentially do so via adaptive management, patch-burn grazing management, or targeted grazing strategies that allow livestock access to recent burns, while still allowing them to move between burned and unburned areas to meet intake requirements (Fuhlendorf and Engle 2004; Scasta et al. 2016a; Bailey et al. 2019). In addition, our results indicate that managers could see longer-term benefits, into at least the second growing season, of prescribed fires in terms of energy availability. In general, even in unburned plots in our study, forage quality was sufficiently high for maintaining ruminant nutrition (e.g., crude protein values were rarely below 7%), but higher TDN and fat values in the second year postfire could provide moderate performance benefits as long as forage quantity was not limiting. It is also possible that grazing on recent burns could prolong the duration of various forage quality benefits by delaying plant maturation and stimulating the growth of young, high-quality tissue (e.g., Hempson et al. 2015), although the strength of these feedbacks may vary based on the reproductive traits and grazing tolerance of dominant plant species. Many of the dominant grasses in our plots (e.g., *B. gracilis* and *P. smithii*) are highly tolerant of grazing, even when grazed after fire (Augustine et al. 2010; Vermeire et al. 2014). All our plots were open to grazing herbivores, but the very small plot sizes may have limited their apparency to, and use by, grazing herbivores.

Given that fall and spring prescribed fires provided similar forage quality benefits, at least during the first growing season since fire, other factors that affect the relative utility of fall vs. spring prescribed burns are worth considering. In our system, fall fires were much easier to implement than spring fires. Fall fires were not in conflict with wildlife breeding seasons and were less likely to be affected by snowstorms, excessively high humidity, high wind speeds, highly variable burn windows, and high soil moisture (i.e., mud). In the sagebrush grassland ecotone sites, results provide some limited evidence that fall fires also resulted in stronger and more durable forage quality benefits.

Prescribed fire may be detrimental for certain management objectives, such as maintaining sagebrush shrub cover for wildlife habitat (Porensky et al. 2018). However, our findings indicate that in this region, as in other ecosystems worldwide, fire generally improves multiple aspects of forage quality. Prescribed fire may also be useful for achieving other objectives, such as short-term control of invasive species including annual grasses, improving wildlife habitat, and reducing wildfire extent and intensity (Pyke et al. 2010; Block et al. 2016; Hunter and Robles 2020; Vermeire et al. 2021). Careful consideration of the location, scale, frequency, and timing of prescribed fires may help managers trying to balance multiple objectives in complex rangeland landscapes.

Data Availability

Data is archived with the USDA FS Data Archive. DOI: https://doi.org/10.2737/RDS-2026-0007

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Lauren M. Porensky: Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **J. Derek Scasta:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Troy W. Ocheltree:** Writing – review & editing, Visualization, Project administration, Funding acquisition, Conceptualization. **Amy J. Symstad:** Writing – review & editing, Visualization, Validation, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Catherine E. Estep:** Writing – review & editing, Methodology, Investigation, Data curation. **Jacqueline P. Ott:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.rama.2026.05.003.

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