

Fire and Nitrogen Addition Increase Forage Quality of *Aristida purpurea*

N. A. Dufek,¹ L. T. Vermeire,² R. C. Waterman,³ and A. C. Ganguli⁴

Authors are ¹Agricultural Science Research Technician, US Department of Agriculture–Agricultural Research Service, Rangeland Resources Research Unit, Cheyenne, WY 82001, USA; ²Ecologist and ³Nutritionist, US Department of Agriculture–Agricultural Research Service, Fort Keogh Livestock and Range Research Laboratory, Miles City, MT 59301, USA; and ⁴Assistant Professor, New Mexico State University, Las Cruces, NM 88003, USA.

Abstract

Purple threeawn (*Aristida purpurea* Nutt.) is a native perennial bunchgrass with limited forage value that dominates sites with disturbed soils and persists with repeated severe grazing. Fire and nitrogen addition have been used to reduce threeawn and can increase grazing utilization of threeawn by livestock. We evaluated effects of fire, spring urea addition, and phenological stage on purple threeawn forage quality 1 yr postfire on two similar sites in southeastern Montana during the 2011 (site 1) and 2012 (site 2) growing seasons. Fire (no fire, summer fire, fall fire) and rate of nitrogen addition (0, 46, 80 kg N·ha⁻¹) were arranged in a completely randomized, fully factorial design. Samples were collected at five phenological stages throughout each growing season. Forage quality was assessed using nutrient analyses of crude protein (CP), net energy (NE_m), and total digestible nutrients; antiquality analyses of neutral detergent fiber (NDF), acid detergent fiber, and silica; in vitro fermentation for organic matter disappearance (IVOMD) and NDF disappearance; and gas production (asymptotic [maximum] gas production, fractional rate of gas production, lag time, and average fermentation rate). In vegetative stages, summer and fall fire increased CP from 6.2% to 12.1% and 13.0%, respectively, and NDF decreased from 72.1% to 69.4% and 68.2%, respectively. Summer and fall fire reduce silica content from 7.0% to 4.1% and 4.3%, respectively. Purple threeawn IVOMD increased by 14.0% and 13.0% following summer and fall fire, respectively, compared to nonburned plots. Nitrogen addition increased CP from 7.5% to 8.0% and 8.4%, respectively, with 46% and 80 kg N·ha⁻¹, respectively. In vitro fermentation and gas production variables did not change due to nitrogen addition. Fire generally improved purple threeawn forage quality to a greater extent than did nitrogen addition. Results indicate fire can potentially improve the suitability of purple threeawn as a forage species.

Key Words: digestibility, gas production, in vitro fermentation, prescribed burning, purple threeawn, silica

INTRODUCTION

Purple threeawn (*Aristida purpurea* Nutt.) is a warm-season (C₄) perennial bunchgrass native to North America. Purple threeawn varieties are mostly found on hillsides and dry upland areas of rangelands (Evans and Tisdale 1972), but can also be found in pastures where it is often considered to be undesirable for forage and wildlife habitat (Hyder et al. 1975). In the western United States, purple threeawn has been shown to dominate overgrazed rangelands and disturbed areas such as old fields and roadsides (Klippel and Costello 1960; Evans and Tisdale 1972). Purple threeawn is generally unpalatable to grazing animals due to sharp awns and calluses that can irritate or injure the mouth, nostrils, and eyes (Vallentine 1961). Purple threeawn also has high fiber and low protein concentrations, which reduce forage value relative to other rangeland grasses (Rauzi et al. 1969; Cogswell and Kamstra 1976; Meyer and

Brown 1985; Ramirez et al. 2004). Purple threeawn reproduces vegetatively and is also capable of producing abundant seeds, which enter the ground quickly and have a high probability of germination (Evans and Tisdale 1972; Fowler 1984). Seedlings rapidly develop a deep, robust root system, making purple threeawn very competitive and increasing purple threeawn's ability to withstand drought and herbivory (Evans and Tisdale 1972; Fowler 1984; Busso et al. 2001).

Purple threeawn is of poor to fair forage nutritive quality in most regions (Dittberner and Olsen 1983; Ramirez et al. 2004). It is generally accepted that fire improves forage quality of grasses by removing mature, less palatable plant material, thus increasing both crude protein and digestibility of grasses (Norton 1982; Mbatha and Ward 2010). Fire can also indirectly improve forage quality by creating more optimal conditions for nitrogen mineralization through combustion of litter, thereby increasing plant-available nitrogen (Seastedt and Knapp 1993). Large herbivores favor burned areas with new succulent vegetation over nonburned areas where biomass has accumulated from previous years (Tomor and Owen-Smith 2002; Vermeire et al. 2004). Although fire effects on purple threeawn density and competitive ability are well-documented (Evans 1967; Trlica and Schuster 1969; Wright et al. 1978; Russell et al. 2013), there are few data describing how fire affects its forage quality. Improving forage quality of purple threeawn relative to other forage species in the plant community is paramount for improved herbivory in a targeted grazing strategy.

Soil nitrogen availability can limit forage quality and quantity, especially in semiarid rangelands (Wilman 1975;

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Correspondence: Lance Vermeire, USDA–ARS Fort Keogh Livestock and Range Research Laboratory, 243 Fort Keogh Rd, Miles City, MT 59301, USA. Email: lance.vermeire@ars.usda.gov

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Seastedt et al. 1991). As an invasive species management tool, nitrogen addition is predominantly prescribed for improving the competitive abilities of desirable species (Sheley and Jacobs 1997). Alternatively, others indicated that differences between native and invasive species performances are important across levels of nutrient availability rather than being specific to nutrient abundance (Ordonez and Olff 2013). Application of ammonium nitrate has been shown to decrease threeawn cover when it was a dominant component of rangeland (Hyder and Bement 1972). However, mechanisms by which high levels of soil nitrogen adversely affect threeawn are not fully elucidated. Evaluating the effects of fire and nitrogen addition and their interaction on purple threeawn forage quality could facilitate development of each tool as potential prerequisite treatments for targeted grazing and improved utilization.

When considering grazing as a tool to manage undesirable species, the potential impacts the target plant species will have on herbivore diet quality should be evaluated (Launchbaugh and Walker 2006). The objectives of this research were to evaluate fire and nitrogen and their potentially interacting effects on purple threeawn forage quality characteristics during the first growing season following treatment. We evaluated three properties of purple threeawn forage quality to determine fire and nitrogen-addition effects on animal productivity and health. First, we evaluated crude protein (CP) and calculated total digestible nutrients (TDN) and net energy for maintenance (NE_m). Secondly, we measured neutral detergent fiber (NDF), acid detergent fiber (ADF), and silica content as antiquality factors that can inhibit forage selection and reduce digestibility. Finally, we conducted in vitro fermentation and gas production tests to predict rumen degradation of purple threeawn. We hypothesized that purple threeawn available as forage would have: 1) greater CP, TDN, and NE_m ; 2) less NDF, ADF, and silica; and 3) greater in vitro fermentation and gas production following fire and nitrogen additions. If realized, each of the hypothesized changes would increase forage quality.

METHODS

Data were collected on US Department of Interior, Bureau of Land Management property near Terry, Montana (lat 46°69'N, long 105°3'W). The area is comprised of level, upland plains with an average elevation of 687 m above sea level. Research sites are sandy ecological sites with the Degrand soil series (a fine-loamy over sandy or sandy-skeletal, mixed, superactive, frigid Aridic Argiustolls; USDA, NRCS, 2010). The climate is semiarid with an average annual precipitation of 297 mm, and with less than 250 mm of rainfall occurring in 1 out of every 7 yr. Spring and fall are cool, with average daily maxima of 20°C and 8°C. Summers are typically hot and dry, with daily maximum temperatures averaging 29°C (WRCC 2012). Average precipitation is 140 mm from April through June, and 100 mm from July through September (WRCC 2012).

Purple Threeawn Collection and Preparation

This experiment was repeated over 2 consecutive yr on two separate study sites located within 3 km of each other. Three species comprised 89% of the species composition: 58% purple threeawn, 23% crested wheatgrass (*Agropyron cristatum* [L.]

Gaertn.), and 8% needle and thread (*Hesperostipa comata* [Trin. & Rupr.] Barkworth) (Strong et al. 2013). Within each study site, fire and nitrogen amendment treatments were randomly assigned to 27 plots (20 × 20 m) separated by 10-m alleys in a factorial design with three fire and three nitrogen treatments and three replications for each treatment combination. Fire treatments were: 1) summer fire, 2) fall fire, and 3) no fire. Summer is the primary wildfire season in the region and fall is often selected for prescribed fire. Nitrogen addition treatments were: 1) 0 kg N · ha⁻¹, 2) 46 kg N · ha⁻¹, and 3) 80 kg N · ha⁻¹.

Summer fire treatments were applied on 12 August 2010 (28–32°C, 8–11 km · h⁻¹ winds, and 36–42% relative humidity) and 7 September 2011 (29–31°C, 5–13 km · h⁻¹ winds, and 15–20% relative humidity) following purple threeawn summer senescence. Fall fire treatments were applied 18 October 2010 (17–18°C, 8–13 km · h⁻¹ winds, and 35–37% relative humidity) and 31 October 2011 (16–20°C, 13–30 km · h⁻¹ winds, and 28–34% relative humidity) following the season's first killing frost (< -2°C). Fuel load at each site was approximately 2000 kg · ha⁻¹ (Strong et al. 2013). Nitrogen was broadcast onto plots as urea granules on 26 April 2011 and 5 April 2012 to coincide with cool spring temperatures and predicted precipitation to minimize volatilization and maximize incorporation into soil. Plants were sampled approximately every 2 wk, based on developmental stage, from June through August 2011 at site 1 and May through July 2012 at site 2 by randomly hand-clipping approximately 70 g of purple threeawn from each plot.

Plants were clipped above the crown (approximately 3 cm from soil surface) to minimize soil and litter contamination of the samples, but included live and dead material. Average plant phenology was described for each experimental plot to allow a qualitative description of plant condition and its relation to forage quality throughout the growing season. Phenological sampling stages were: 1) vegetative, 2) boot, 3) flowering, 4) maturity, and 5) senescence. Samples were promptly transported in a cooler with ice to the Fort Keogh Livestock and Range Research Laboratory (LARRL) and frozen at -4°C. Frozen samples were lyophilized for 72 h and ground (Thomas-Wiley Laboratory Mill, Model 4, Arthur H Thomas Company, Philadelphia, PA) to pass a 2-mm sieve.

Ground samples for each experimental plot along with grass hay and alfalfa standards were analyzed for dry matter (DM), organic matter (OM), in vitro organic matter disappearance (IVOMD), NDF (Goering and Van Soest 1970), in vitro neutral detergent fiber disappearance (IVNDFD), gas production (Menke et al. 1979), and silica content (Galyean, 1997). Approximately 10 g of ground sample from each treatment plot were packaged and sent to an independent commercial laboratory for analyses of CP (combustion method), ADF (Ankom filter bag technique), TDN, and NE_m .

Animals and Management

The Fort Keogh Livestock and Range Research Laboratory (LARRL) Institutional Animal Care and Use Committee approved all animal handling and experimental procedures used in this study (IACUC No. 021308-1).

Rumen liquor for IVOMD, IVNDFD, and gas production was collected from two ruminally-cannulated beef cows (8 and

5 yr of age). Cows were fed a standard hay diet and allowed ad libitum access to water for 14 d prior to the first in vitro experiment and between all subsequent experiments. Rumen liquor was collected from the interface between the mat and liquid layer. Extrusa samples were placed into a collection Dewar (Nalgene 4150-200- StevenJo & Steph, Rochester, NY) that had been previously warmed to 39°C for 12 h. Rumen liquor samples were transported to the lab immediately after collection and strained through four layers of cheese cloth into a 4-L beaker which was continuously under CO₂ bubbling. Each donor animal provided approximately 350 mL of rumen liquor at each collection. A 250 mL sample of rumen liquor from each cow was measured and then samples were combined to make a 500-mL sample. Rumen liquor was then combined with 1 000 mL of McDougal's buffer (Tilley and Terry 1963), and placed in a prewarmed 39°C water bath under continuous CO₂ bubbling. This mix will subsequently be referred to as inoculum.

In Vitro Substrate Fermentation and Gas Production

IVOMD was measured using the Tilly and Terry laboratory technique (Tilly and Terry 1963). Previously weighed in vitro tubes containing 0.5 g substrate (six tubes per treatment plot) were placed in a 39°C water bath, then filled with 30 mL inoculum using a Brinkman dispenser (5–25-mL bottle-top dispenser; Brinkman Instruments, Westbury, NY), flushed with CO₂, and tightly sealed with plastic screw caps. Tubes were randomly placed in metal racks, inserted into an incubator (39°C), and manually agitated. In vitro racks were agitated every 2 h for the first 12 h, then every 4 h for the second 12 h, and every 6 h throughout the last 24 h until being removed at 48 h. The plastic screw caps were loosened to release gases and tubes were frozen at –4°C for 24 h. The frozen samples were lyophilized for 72 h before removal from the tubes for OM and NDF disappearance assessment procedures.

Gas production was measured using the technique described by Menke et al. (1979). In vitro gas production syringes (100 mL) containing 0.25 g of substrate (3 syringes per treatment plot) were filled with 20 mL of inoculum that was under continuous CO₂ bubbling using a Brinkman dispenser (5–25 mL bottle top dispenser; Brinkman Instruments). Excess air was released before sealing and placing syringes into two 60-syringe water baths maintained at 39°C. Gas measurements were recorded at 0, 2, 4, 6, 8, 10, 12, 14, 16, 24, 30, 36, 48, 54, 60, 72, and 96 h by measuring gas displacement. If gas displacement exceeded 90 mL, gas was released until syringes indicated 80 mL of displacement (to ensure plungers were not blown out of the syringes), then measurement of subsequent gas displacement resumed for the remainder of the data collection period.

Calculations and Statistical Analyses

In vitro gas production variables were derived using GraphPad Prism¹ (GraphPad Software, Inc. 2003), from the exponential equation $G = A[1 - \exp[-K(t - \text{Lag})]]$ where G (mL · g⁻¹ OM) represents total gas production, A (mL · g⁻¹ OM) represents the asymptotic (maximum) gas production (AGP), K (h⁻¹) is the fractional fermentation rate, Lag (time in h) is the initial delay

in the onset of gas production after introduction of the inoculum, and t (h) is the gas reading time (France et al. 2000). The average fermentation rate (AFR; mL gas · h⁻¹), defined as the average gas production rate between the start of incubation and the time at which the cumulative gas production was half of its asymptotic value, was calculated as $\text{AFR} = A \times K / [2(\ln 2 + K \times \text{Lag})]$.

Data were tested with analysis of variance using the MIXED procedure of SAS (Littell et al. 1996) with phenological stage within a year as a repeated measure and plot as the experimental unit. The models for each response variable included the effects of phenological stage, fire treatment, nitrogen addition rate, and their interactions. Year of study was the random effect. Significant interactions ($P \leq 0.05$) were followed by pair-wise tests of simple effects at $\alpha = 0.05$.

RESULTS

Climatic Conditions

Early growing-season temperatures (April through July) were 1.4°C cooler during 2011 and 1.7°C warmer during 2012 than the recorded 63-yr average. Growing-season precipitation (April through June) following nitrogen additions was 227% (317 mm) and 79% (110 mm) of the 63-yr average (140 mm), with 2011 being the wettest spring on record and 2012 very dry. Fall through spring precipitation (October through June) following fires was 190% (374 mm) and 76% (150 mm) of the 63-yr average during the first and second study years, respectively.

Phenological Stage

Changes in nutritional and antiquality variables with phenological progression of purple threeawn were apparent in this study (Table 1). Net energy for maintenance and TDN decreased with advancing phenological stage. Acid detergent fiber increased with advancing phenology. The pattern of change in silica content with advancing phenology was not as clear. The boot and senescence stages yielded increased silica content compared to the flowering and maturity stages and the vegetative stage was similar to all but the boot stage.

Gas production and in vitro fermentation measurements generally decreased with advancing phenology of purple threeawn plants (Table 1). Asymptotic gas production was greater in the vegetative and boot stages compared to all other stages and was greater during the maturity stage than the senescence stage, with no difference for either compared to the flowering stage. Lag time decreased with advancing phenology with the exception of the senescence stage, which was less than the vegetative stage and greater than the boot, flowering, and maturity stages. In vitro OM disappearance decreased from the boot stage through senescence, with the vegetative stage producing intermediate values to those of the boot and senescence stages.

Fire

Fire and nitrogen did not interact ($P > 0.10$) in their effects on any of the measured variables. Net energy for maintenance and TDN each varied by fire treatment (Table 2) and CP varied by the interacting effects of fire treatment and phenological stage

¹Available at <http://www.graphpad.com/scientific-software/prism/>

Table 1. Least squares means \pm standard error definition (SEc) for purple threeawn samples collected at different phenological stages 1 yr posttreatment in 2011 and 2012. ($n=54$).

Measurement ¹	Phenological stage					SEc	P value
	Vegetative	Boot	Flowering	Maturity	Senescence		
NE _m (Mcal · kg ⁻¹)	1.14 a ²	1.08 b	1.06 b	1.03 c	1.00 c	0.01	< 0.01
TDN (% DM)	53.89 a	51.65 b	51.01 b	49.67 c	48.52 c	0.61	< 0.01
ADF (% DM)	42.67 c	44.64 b	45.20 b	46.38 a	47.37 a	0.54	< 0.01
Silica (% DM)	5.2 bc	5.8 a	4.9 c	5.1 c	5.6 ab	0.2	< 0.01
AGP (mL · g ⁻¹ OM)	67.0 a	65.7 a	61.9 bc	62.8 b	60.3 c	0.8	< 0.01
Lag (h)	2.13 a	1.50 c	1.33 c	0.68 d	1.90 b	0.10	< 0.01
IVOMD (% OM)	59.5 bc	68.8 a	61.1 b	58.8 c	47.4 d	0.9	< 0.01

¹NE_m indicates net energy for maintenance; SEc, standard error of the comparison; TDN, total digestible nutrients; DM, dry matter; ADF, acid detergent fiber; AGP, asymptotic gas production; OM, organic matter; Lag, lag time; and IVOMD, in vitro organic matter disappearance.

²Means within rows with a common letter do not differ ($P > 0.05$).

($P < 0.01$; Fig. 1A). Fire increased NE_m and TDN, with fall fire showing the greatest improvement. Crude protein concentrations were greater with fire compared to controls in all phenological stages. Fall fire increased CP more than summer fire in the vegetative stage. However, summer fire increased CP more than fall fire within the flowering stage. No differences in CP were detected between summer and fall fire for the boot, maturity, or senescence stages.

Silica and ADF were reduced by summer fire and further reduced by fall fire (Table 2). Silica content was about 1.5 and 1.6 times greater for nonburned than summer- and fall-burned plants. NDF varied with interacting effects of fire treatment and phenological stage ($P < 0.05$; Fig. 1B). Fall and summer fire similarly reduced NDF in the vegetative stage compared to the control. Fire did not affect NDF during the boot, flowering, or maturity stages. Fall fire increased NDF during the senescence stage compared to summer fire. However, neither fall nor summer fire differed from the control.

Fire increased AGP about 15%, with no difference between summer and fall fire (Table 2). Similarly, summer and fall fire reduced lag time by about 0.5 h. Fire effects on K ($P < 0.01$) and AFR ($P < 0.01$) varied by fire treatment and phenological stage, with increases due to fire during all phenological stages (Fig. 2A, B). Values of K did not differ between summer and fall fire treatments during the vegetative, boot, or senescence stages. However, summer fire increased K in the flowering and maturity stages compared to fall fire. Fall fire increased AFR within the vegetative stage compared to summer fire and the opposite was observed in the maturity stage. Average fermentation rate did not differ between fall and summer fire in the boot, flowering, or senescence stages. Fire increased IVOMD at least 7.8% relative to controls, with no difference between summer and fall fire (Table 2). Fire effects on IVNDFD varied by fire treatment and phenological stage ($P < 0.01$; Fig. 2C). Fall and summer fire increased IVNDFD in the vegetative, boot, and flowering stages compared to controls. Only summer fire increased IVNDFD in the maturity stage compared to controls and all treatments were similar at senescence. Summer and fall fire effects on IVNDFD were similar to each other at each phenological stage.

Nitrogen Addition

Nitrogen addition affected all nutrient and antiquality variables of purple threeawn (Table 3). Crude protein increased with

increasing nitrogen rate. Both 46 and 80 kg N · ha⁻¹ rates similarly reduced NDF and silica relative to controls. Addition of 80 kg N · ha⁻¹ increased NE_m and TDN and reduced ADF. Nitrogen addition effects were not detected for any gas production measurement (AGP; $P > 0.53$, lag time; $P > 0.26$, K; $P > 0.14$, and AFR; $P > 0.46$). Nitrogen addition effects were also not detected for IVOMD ($P > 0.96$) or IVNDFD ($P > 0.75$).

DISCUSSION

Effects of fire on forage quality varied across phenological stages and seasons of fire, whereas the effects of nitrogen addition varied by rate of application. As expected, forage quality of purple threeawn tended to be greater during the early part of the growing season, with or without fire. Fire generally improved forage quality to a greater extent than did nitrogen addition. Of particular importance in fire's effect on forage quality is the improvement relative to standard measurements of forage quality in common forage grasses (Rauzi et al. 1969; Cogswell and Kamstra 1976; NRC 2000; Waterman and Vermeire 2011). For example, fire increased CP and TDN from deficient to meeting NRC requirements for beef cattle (NRC 2000). Additionally, these results are the first indication we are aware of that fire can reduce silica content in a plant.

Table 2. Least squares means \pm standard error definition (SEc) for purple threeawn samples collected throughout the growing season from two sites 1 yr following fire treatments ($n=54$).

Measurement ¹	Burn treatment			SEc	P value
	No fire	Summer fire	Fall fire		
NE _m (Mcal · kg ⁻¹)	0.97 c ²	1.09 b	1.12 a	0.01	< 0.01
TDN (% DM)	47.50 c	52.02 b	53.34 a	0.47	< 0.01
ADF (% DM)	48.28 a	44.32 b	43.16 c	0.41	< 0.01
Silica (% DM)	7.0 a	4.7 b	4.3 c	0.2	< 0.01
AGP (mL · g ⁻¹ OM)	57.7 b	66.4 a	66.5 a	0.6	< 0.01
Lag (h)	1.84 a	1.36 b	1.33 b	0.08	< 0.01
IVOMD (% OM)	53.6 b	62.3 a	61.4 a	0.9	< 0.01

¹NE_m indicates net energy for maintenance; TDN, total digestible nutrients; SEc, standard error of the comparison; DM, dry matter; ADF, acid detergent fiber; AGP, asymptotic gas production; OM, organic matter; Lag, lag time; and IVOMD, in vitro organic matter disappearance.

²Means within rows with a common letter do not differ ($P > 0.05$).

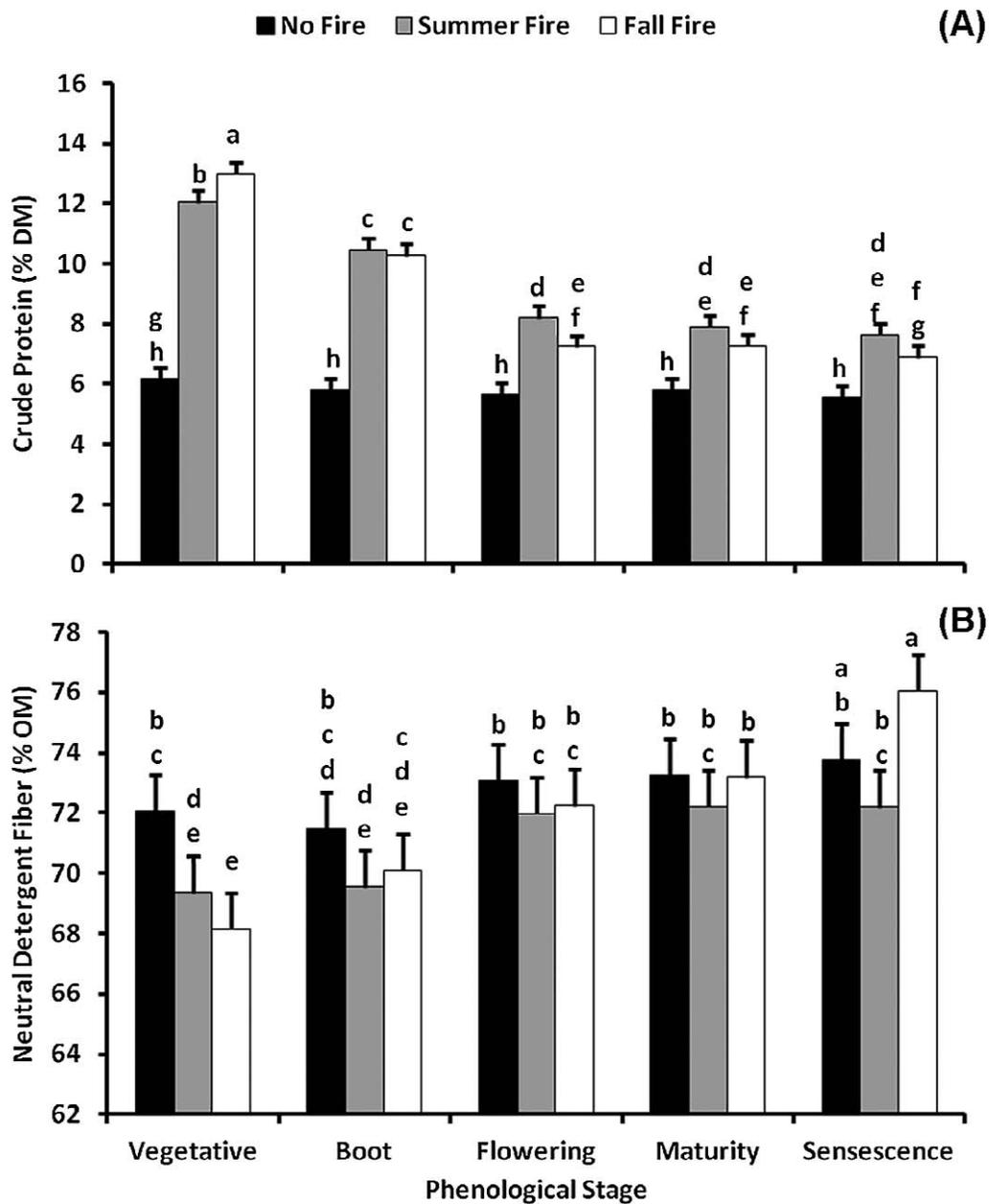


Figure 1. Least squares means \pm standard error of the mean for fire treatment \times phenological stage for (A) crude protein (CP, % dry matter [DM]); and (B) neutral detergent fiber (NDF, % organic matter [OM]) for purple threeawn samples collected in the growing season of the year following the fire treatments. Means with a common letter do not differ ($P > 0.05$).

In semiarid grasslands, precipitation is the most limiting factor to plant productivity (Gutierrez and Whitford 1987; Huxman et al. 2004). In rangeland management planning, it is difficult to predict the posttreatment precipitation. However, the fire and nitrogen addition effects observed on purple threeawn forage quality between very wet and dry growing seasons indicate results are applicable within a broad range of years with less extreme levels of precipitation.

Plant Phenology

As the growing season progresses in semiarid grasslands, forage quality tends to decline with increasing temperatures, less

precipitation, and an increasing proportion of senesced plant tissue (Grings et al. 2004; Waterman et al. 2007; Mbatha and Ward 2010). Greater NE_m and TDN values in the early phenological stages are evidence that purple threeawn adheres to this trend. The seasonal trend in ADF concentration indicates that the proportion of more digestible plant tissue is reduced with advancing phenology in purple threeawn. Acid detergent fiber concentration remained greater than most common forage species throughout the growing season (Hart et al. 1983; Shewmaker et al. 1989; Jefferson et al. 2004). The fluctuation in silica concentration with phenology might be due to the large proportion of standing dead litter in nonburned

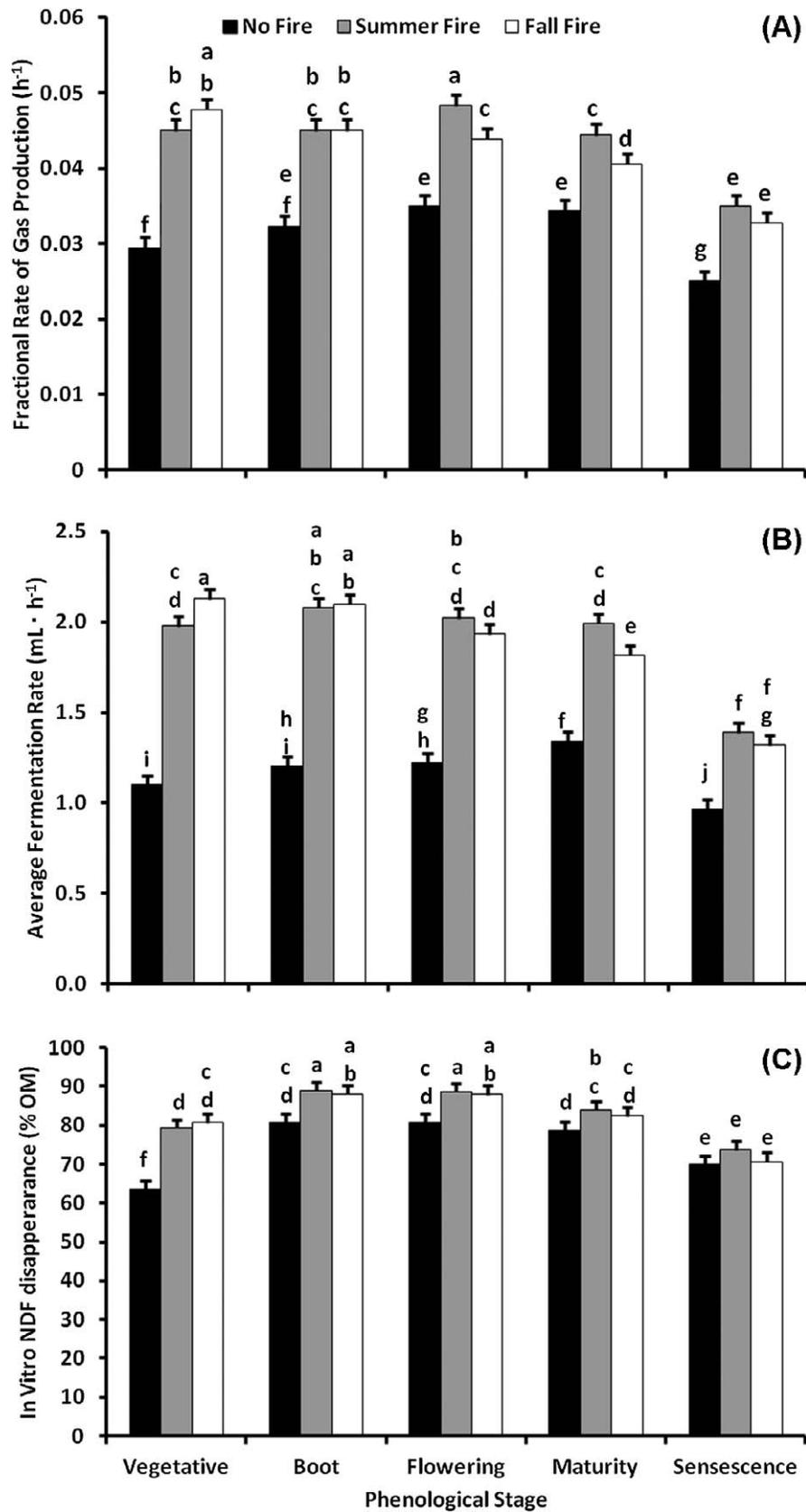


Figure 2. Least squares means \pm standard error of the mean for fire treatment \times phenological stage for (A) fractional rate of gas production ($K; h^{-1}$); (B) average fermentation rate (AFR; $mL \cdot h^{-1}$); and (C) in vitro neutral detergent fiber disappearance (NDFD; % organic matter [OM]) for purple threeawn samples collected in the growing season of the year following the fire treatments. Means with a common letter do not differ ($P > 0.05$).

Table 3. Least squares means \pm standard error of the comparison (SEc) for purple threeawn samples collected in the growing season following nitrogen addition treatments ($n=54$).

Measurement ¹	Nitrogen addition (kg N · ha ⁻¹)			SEc	P value
	0	46	80		
CP (% DM)	7.5 c ²	8.0 b	8.4 a	0.2	< 0.01
NE _m (Mcal · kg ⁻¹)	1.04 b	1.05 b	1.09 a	0.01	< 0.01
TDN (% DM)	50.24 b	50.65 b	51.95 a	0.47	< 0.01
NDF (% OM)	72.9 a	71.72 b	71.13 b	0.54	< 0.01
ADF (% DM)	45.8 a	45.5 a	44.4 b	0.4	< 0.01
Silica (% DM)	5.9 a	5.2 b	5.0 b	0.2	< 0.01

¹CP indicates crude protein; DM, dry matter; NE_m, net energy for maintenance; TDN, total digestible nutrients; NDF, neutral detergent fiber; OM, organic matter; and ADF, acid detergent fiber.

²Means within a row with a common letter do not differ ($P > 0.05$).

plants throughout the growing season. As a chemically inert mineral, silica can be less prone to reductions by weathering than other structural components such as hemicellulose, cellulose, and lignin (Shewmaker et al. 1989). Similar to most rangeland forage species (Kirby and Parman 1986; Olson et al. 1994), purple threeawn digestibility tends to decline with advancing phenology as indicated by our results for AGP, IVOMD, and lag time.

Fire

Improvements in CP, NE_m, and TDN following fire were clear. Postfire levels of CP throughout the growing season are comparable to common rangeland grass of high forage quality (Rauzi et al. 1969; Cogswell and Kamstra 1976; NRC 2000; Waterman and Vermeire 2011), indicating that fire could increase threeawn consumption by grazers. Both CP and TDN following fire exceed diet nutrient density requirements for beef cows, whereas both were deficient in nonburned plots (NRC 2000). Increased nutrient concentrations in postfire grass might be attributed to a number of factors. For example, ash leaching into the soil following fire might be one direct cause for increases in certain nutrients (Frost and Robertson 1987). However, in a grassland setting, these increases have been considered negligible (Boerner 1982; Van de Vijver et al. 1999), are predominantly minerals, and would not account for our increase in CP and NE_m. In tallgrass prairie, fire-enhanced nutrient content has been attributed to increased mineralization near the soil surface due to increased soil surface temperature (Knapp and Seastedt 1986). Mineralization also depends on adequate soil moisture (Hayes and Seastedt 1989). However, summer fire effects on soil moisture and temperature have been shown to be minor and vary among years in northern mixed prairie (Vermeire et al. 2011). It would be challenging to draw any conclusion regarding mineralization from this study, given the extreme temperature and moisture differences between study years. Enhanced CP, NE_m, and TDN were most likely due to the increased proportion of young plant tissue in burned plots (Van de Vijver et al. 1999; Mbatha and Ward 2010). Nonburned plots contained nearly 50% of previous year's biomass, whereas burned plots contained very little (Dufek 2013). Differences between fall and summer fire treatments for

NE_m and TDN were small, but consistently greater with the fall fire. Given the longer chance for regrowth during the growing season of the fire, summer fire treatments might have contained a slightly higher proportion of less nutritious, standing dead tissue than fall plots.

Fire consistently reduced NDF, ADF, and silica concentration in purple threeawn. A direct effect of fire is the removal of older plant material, leaving mostly young tissue during the following growing season. Consequently, young growth contains less cell wall constituents such as NDF, ADF, and silica (Griffin and Jung 1983; Shewmaker et al. 1989). This is also evident in the fire-phenological stage interaction for NDF, with postfire regrowth in the early stages showing the lowest NDF concentrations relative to later stages. The NDF concentrations in the vegetative and boot stages and mean ADF values following fire are comparable to many common forage species of fair to high forage quality (Hart et al. 1983; Jefferson et al. 2004). It is also interesting to note the reduction, due to fire, from what is considered near dangerous levels of silica for cattle health (over 6%) to levels of acceptable tolerance (Parker 1957; Smith et al. 1971). Examining long-term fire and grazing data, Melzer et al. (2010) observed no fire effects on concentration of silica taken up by plants, but indicated that fire might promote silica storage in plants by indirect effects that increase productivity. Our results clearly contrast with those of Melzer et al. (2010), with fire reducing silica concentration by about one-third of the nonburned values.

Fire effects on in vitro fermentation are consistent with previous work on postfire digestibility. Fire reduced the proportion of previous years' growth relative to nonburned plants, leaving more young leaves. Digestibility tends to be greater in young, green leaves compared to older, more mature leaves (Norton 1982; Mbatha and Ward 2010). Studies examining postfire gas production for single grass species are lacking. However, Brown et al. (2002) found a strong relationship between gas production and fermentation patterns in grass silage. Our findings confirm this with increased gas production as well as increased in vitro OM and NDF disappearance in postfire purple threeawn.

Nitrogen Addition

Consistent improvements in CP, NE_m, TDN and reductions in NDF, ADF, and silica due to nitrogen addition were evident in this study. Similar studies involving forage quality response to nitrogen addition support our results of increasing CP, NE_m, and TDN (Allen et al. 1976; Mitchell et al. 1994; Cohen et al. 2004; Mbatha and Ward 2010). Decreases in NDF, ADF, and silica content with nitrogen addition might be an indication of nitrogen limiting productivity in purple threeawn-dominated sites. As plant productivity increases, so does the proportion of young leaves, thus decreasing the proportion of less digestible plant tissue components (Norton 1982) such as NDF, ADF, and silica. On the contrary, this is not reflected in our gas production or in vitro fermentation results. Although differences in nutrient concentrations and antiquality factors are statistically significant, the biological differences might not be great enough to translate into increased animal productivity with nitrogen addition.

IMPLICATIONS

Forage quality of purple threeawn one growing season following fire treatment showed marked improvement compared to nonburned plots, whereas nitrogen addition effects were not as substantial. In terms of potential effects on animal production and health, postfire purple threeawn forage quality is comparable to that of many commonly utilized rangeland forages. Of particular interest was the fact that fire reduced silica content. High silica content is a recognized problem in purple threeawn, and our evidence is the first we are aware of that indicates that fire can reduce silica content. Justifying nitrogen addition as a prerequisite treatment to grazing would be difficult based in limited response in our results and the costs of nitrogen. Results indicate fire and nitrogen addition each improve multiple purple threeawn forage quality factors throughout the growing season. However, because of animal avoidance of purple threeawn following seed head emergence, encouraging grazing utilization of purple threeawn would likely require early-season grazing to avoid the flowering stage or delay flowering. Prescribed fire shows strong potential as a prerequisite treatment for increasing the suitability of purple threeawn as a forage species.

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