3-2015

# Tallgrass Prairie Vegetation Response to Spring Fires and Bison Grazing

Stephen L. Winter
wintersl8944@gmail.com

Brady W. Allred
*University of Montana*, brady.allred@umontana.edu

Karen R. Hickman
*Oklahoma State University*, karen.hickman@okstate.edu

Samuel D. Fuhlendorf
*Oklahoma State University*, sam.fuhlendorf@okstate.edu

# TALLGRASS PRAIRIE VEGETATION RESPONSE TO SPRING FIRES AND BISON GRAZING

STEPHEN L. WINTER,* BRADY W. ALLRED, KAREN R. HICKMAN, AND SAMUEL D. FUHLENDORF

*572 East 5th Street, Winona, MN 55987 (SLW)*
*College of Forestry and Conservation, University of Montana, Missoula, MT 59812 (BWA)*
*Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, OK 74078 (KRH, SDF)*
**Correspondent: stephen.winter@okstate.edu*

ABSTRACT—Spring fires in tallgrass prairie can create environmental conditions conducive to plant growth in the subsequent growing season. Following fires, burned areas can also be attractive to grazing animals such as bison (*Bison bison*). Sustained grazing activity within recently burned areas can alter vegetation structure relative to nearby landscape patches that haven't burned recently. In 2007, we collected data on bison grazing activity, vegetation structure, and the growth and reproduction of a perennial forb, *Arnoglossum plantagineum*, in Oklahoma tallgrass prairie. We compared these variables in landscape patches that had burned in the spring of 2007 to measurements of these variables in adjacent landscape patches that had burned in the spring of 2004 or 2005. Our results demonstrate that bison grazing activity and many vegetation structure variables can differ markedly in landscape patches that differ in their time since fire but are directly adjacent to each other.

RESUMEN—Las quemas de primavera en la pradera de pastos altos pueden crear condiciones ambientales propicias al crecimiento vegetal en la subsecuente temporada de crecimiento . A raíz de los incendios, las áreas quemadas también pueden ser atractivas para pastoreo de animales como el bisonte (*Bison bison*). Actividad de pastoreo sostenida dentro de las áreas recientemente quemadas puede alterar la estructura de la vegetación en relación con parches de paisaje cercano que no se han quemado recientemente. En 2007, recogimos datos de actividad de pastoreo del bisonte , estructura de la vegetación y el crecimiento y la reproducción de una hierba perenne, *Arnoglossum plantagineum*, en la pradera de pastos altos de Oklahoma. Comparamos estas variables en parches de paisaje que habían quemado en la primavera de 2007, a las medidas de estas variables en parches de paisaje adyacentes que habían quemado en la primavera de 2004 o 2005. Nuestros resultados demuestran que la actividad de pastoreo del bisonte y muchas variables de estructura de la vegetación pueden diferenciar marcadamente en parches de paisaje que difieren en su tiempo desde la quema, estando a la par uno del otro.

Around the world, fire has a profound influence on the distribution and behavior of a multitude of herbivores, both wild and domestic (Moe and Wegge, 1997; Archibald and Bond, 2004; Murphy and Bowman, 2007; Van Dyke and Darragh, 2007; Sensenig et al., 2010; Allred et al., 2011; Cazau et al., 2011). Herbivores tend to preferentially forage in recently burned areas (patches) within a landscape, and the preference for a patch is correlated with the length of time since that patch was burned relative to other patches in the same landscape (Fuhlendorf and Engle, 2004; Allred et al., 2011). This effect of fire on herbivore distribution and foraging activity can generate concurrent effects on vegetation structure and composition. Patches that have recently burned, and are being heavily grazed, tend to be characterized by low herbaceous biomass or cover, particularly that of graminoids (Coppedge et al., 1998*a*; Fuhlendorf and Engle, 2004; Vermeire et al., 2004). Conversely, patches within the same landscape that have not burned recently, and are being grazed minimally, tend to be characterized by high levels of herbaceous biomass or cover, particularly that of graminoids (Coppedge et al., 1998*a*; Fuhlendorf and Engle, 2004; Vermeire et al., 2004). As patches transition from being recently burned and heavily grazed to not having burned for an extended period of time and being minimally grazed, the biomass of forbs can increase for a period of time before decreasing (Fuhlendorf and Engle, 2004; Winter et al., 2012); this unimodal response of forbs is presumably a function of their interaction with graminoids whereby the competitive ability of graminoids is altered by the level of grazing they are experiencing (Fahnestock and Knapp, 1993, 1994; Damhoureyeh and Hartnett, 1997; Fuhlendorf and Engle, 2001; Winter et al., 2013).

To better understand how fire interacts with bison (*Bison bison*) grazing to influence tallgrass prairie vegetation, including the effects on an individual tallgrass

prairie forb, we conducted research at The Nature Conservancy's Tallgrass Prairie Preserve (TPP) in northeast Oklahoma. The TPP is managed to promote the fire-grazing interaction, termed pyric herbivory, where fire and grazing are allowed to interact over a large, complex landscape (Hamilton, 2007; Fuhlendorf et al., 2009). We sampled individual plants of *Arnoglossum plantagineum*, a perennial forb common in tallgrass prairies of the southern Great Plains (Smeins and Diamond, 1983; Hickman and Derner, 2007; Polley et al., 2007; Winter et al., 2013). Additionally, we measured levels of bison grazing activity and vegetation structure variables in the immediate area surrounding each sampled *A. plantagineum* individual. Our sampling occurred in patches that had recently burned and were being heavily grazed as well as in patches that had not recently burned and were being minimally grazed. The objectives of our study were to compare recently burned patches with patches that had not recently burned in terms of the following variables: 1) measurements of bison grazing activity, 2) measurements of tallgrass prairie vegetation structure, and 3) measurements of *A. plantagineum* growth and reproduction.

METHODS—*Study Area*—Our study site was the 15,700-ha (TPP) in Osage County, Oklahoma, owned and managed by The Nature Conservancy (36°50′N, 96°25′W). Long-term (1945–2007) average precipitation was 89 cm at the nearby Foraker weather station in Osage County (www.ncdc.noaa.gov; www.mesonet.org). In 2006 and 2007, the annual total precipitation was 61 cm (68% of the long-term average) and 133 cm (149% of the long-term average), respectively. Soils where sampling occurred were derived from sandstone, shale, limestone, and chert of Permian and Pennsylvanian age (USDA–NRCS, 2009) with slopes of 0–15%. Tallgrass prairie is the predominant vegetation of the TPP, and the dominant grass species include *Andropogon gerardii*, *Sorghastrum nutans*, *Sporobolus compositus*, *Panicum virgatum*, and *Schizachyrium scoparium* (Palmer, 2007).

Management of the TPP includes restoration of the evolutionary interaction between fire and bison grazing. Within the TPP's bison pasture (9,532 ha in 2007), fire is applied in a spatially random manner so that burns are approximately distributed among the seasons as follows: 40% of the area burned during March–April; 20% of the area burned during July–September; and 40% of the area burned during November–December (Hamilton, 2007). The resulting fire-return interval for most areas of the bison pasture is approximately 3 y (Hamilton, 2007). Bison are free to move throughout the pasture during the year, they receive no supplemental feed but are provisioned with salt and trace minerals provided on a free-choice basis at multiple locations, and water is provisioned by streams and stock ponds throughout the pasture (Hamilton, 2007). Distribution of bison throughout the pasture has repeatedly been demonstrated to correlate strongly with the location of burned patches, and areas characterized by the highest levels of bison activity have consistently been patches that had been burned most recently (Coppedge and Shaw, 1998; Schuler et al., 2006; Allred et al., 2011).

*Data Collection*—During 17–24 June 2007, we located three sites of paired patches where recently burned patches (March–April of 2007) were directly adjacent to patches burned in the same season but during 2005 or 2004. Patches burned in the spring of 2007 were 88–366 ha (mean = 194 ha) while patches burned in the spring of 2005 or 2004 were 113–293 ha (mean = 184 ha). At each site of paired patches, we located a population of *A. plantagineum* where the population was subdivided by the boundary between the burned patches. Within each subpopulation, we located 40 flowering individuals of *A. plantagineum.* Flowering individuals of *A. plantagineum* were characterized by a stem, 45–115 cm tall, terminating in a broad inflorescence consisting of multiple capitula (cluster of florets). Nonflowering *A. plantagineum* consisted of vegetative basal rosettes which were readily obscured by the surrounding grass canopy and thus difficult to locate. Our sampling was restricted to single-stemmed individuals, which is the typical condition of this species at our study site.

During field activities, a 1-$m^2$ frame was centered on each focal individual of single-stemmed, flowering *A. plantagineum* and the following variables were measured: percent bare ground; percent cover of litter, live vegetation, dead vegetation, live grass, live forbs, live shrubs, and bison fecal pats; the height of the tallest grass and tallest forb; and the frequency of grass defoliation. Frequency of grass defoliation was determined by the presence or absence of at least one blade of grass that had been clipped at a right angle to the long axis of the blade. This method of quantifying grass defoliation was similar to the approach of Dwyer (1961) for determining grazing preferences of cows in tallgrass prairie of this region of Oklahoma. The height of the tallest grass and tallest forb and the frequency of grass defoliation were recorded in each quarter (0.25 $m^2$) of the 1-$m^2$ frame. For the tallest grass and tallest forb measurements, the average of the four measurements in each plot was used in subsequent analyses. Grass defoliation measurements were subsequently analyzed as frequency at the 0.25-$m^2$ scale and at the 1.0-$m^2$ scale.

Within each plot, we harvested the focal individual of single-stemmed, flowering *A. plantagineum* by cutting at the ground surface. We transported harvested individuals to a laboratory for subsequent measurements of plant height and number of capitula. Vegetative tissue and reproductive tissue were separated by cutting the stem at the base of the lowest stem leaf that was paired with a pedicel supporting at least one capitula originating from its axis. Vegetative and reproductive biomasses were oven dried at 60°C for 48 h and then weighed to obtain measurements of vegetative biomass, reproductive biomass, and total biomass.

*Data Analyses*—For bison fecal pat and plant height (height of the tallest grasses and tallest forbs within plots) variables, we used *t*-tests to assess differences in response to burn age. To compare frequency of occurrence of grazed grasses in recent burns to older burns, we used a $\chi^2$ test. For plant community and *A. plantagineum* variables (percent bare ground, percent cover of litter, live vegetation, dead vegetation, live grass, live forbs, live shrubs; *A. plantagineum* height, number of capitula, reproductive biomass, and total biomass), we used a permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) to assess plant community and *A. plantagineum* differences between recent burns and older burns. For all analyses, statistical significance was set at $\alpha = 0.05$. PERMANOVA was performed in R (R Development Core Team, 2014) and

TABLE 1—Percent cover values (mean ± SE) of bare ground and vegetation structure variables in recent (2007) and older (2004 or 2005) spring burns in tallgrass prairie grazed by bison in Oklahoma. Percent cover variables differed (permutational multivariate analysis of variance; $\alpha = 0.05$; $P < 0.001$) between recent and older burns.

| Vegetation structure response variables | Recent spring burns (2007) | Older spring burns (2004 or 2005) |
|---|---|---|
| Bare ground (%) | 24.04 ± 1.30 | 6.21 ± 0.72 |
| Litter (% cover) | 8.33 ± 0.53 | 42.75 ± 2.31 |
| Live vegetation (% cover) | 75.04 ± 1.00 | 80.04 ± 0.88 |
| Dead vegetation (% cover) | 7.25 ± 0.41 | 39.67 ± 2.08 |
| Live grass (% cover) | 67.13 ± 1.15 | 70.00 ± 1.13 |
| Live forbs (% cover) | 56.00 ± 1.20 | 56.21 ± 1.16 |
| Live shrubs (% cover) | 2.79 ± 0.63 | 0.92 ± 0.31 |

all other analyses were performed in SigmaPlot Version 12.0 (Systat Software, San Jose, CA; www.sigmaplot.com).

RESULTS—The indices of bison activity differed when recent spring burns (burned in 2007) were compared to older spring burns (burned in 2004 or 2005). Percent cover (mean ± SE) of bison fecal pats was lower ($t_4 = -7.236$; $P = 0.001$) in recent burns (1.04 ± 0.08) compared to older burns (2.04 ± 1.10). At the 0.25-m$^2$ scale, frequency of grazed grasses was higher ($\chi^2 = 109.106$; $df = 4$; $P < 0.001$) in recent burns (0.55) compared to older burns (0.04). At the 1.0-m$^2$ scale, frequency of grazed grasses was higher ($\chi^2 = 101.640$; $df = 1$; $P < 0.001$) in recent burns (0.74) compared to older burns (0.09).A comparison of the height (cm) of the tallest grass tissue within plots approached significance ($t_4 = -2.312$; $P = 0.082$) when recent spring burns (45.65 ± 5.72) were compared to older spring burns (59.14 ± 1.17), while the height (cm) of the tallest forbs within plots was lower ($t_4 = -3.253$; $P = 0.031$) in recent burns (39.35 ± 1.15) compared to older burns (47.68 ± 2.29). Percent cover values of bare ground and vegetation structure variables differed when recent burns were compared to older burns (PERMANOVA; $P < 0.001$). Percent bare ground was higher while percent cover litter was lower in recent burns (sample means ± SE provided in Table 1). Percent cover of live vegetation, dead vegetation, and live grass was lower in recent burns when compared to older burns. There was little difference, however, in the percent cover of live forbs between recent and older burns. Percent cover of live shrubs was higher in recent burns than in older burns. *Arnoglossum plantagineum* growth and reproductive variables did not differ as a whole between recent and older burns (PERMANOVA; $P > 0.050$; sample means ± SE provided in Table 2).

DISCUSSION—One of our measures of bison grazing activity, frequency of grazed grasses at the 1.0-m$^2$ and the 0.25-m$^2$ scales, supported previous studies that fire and grazing are largely interactive. Our results revealed a substantial difference in the frequency of bison grazing that occurred in patches that had burned the spring we collected data relative to patches that had not burned for at least 2 y. These findings are especially remarkable considering the sampled patches were directly adjacent to each other. Grazing herbivores are attracted to recently burned patches because forage in those patches is characterized by increased leaf nutrient concentrations, leaf:stem ratios, live:dead tissue ratios, and dry matter digestibility (Van De Vijver et al., 1999; Anderson et al., 2007; Mbatha and Ward, 2010; Sensenig et al., 2010; Allred et al., 2011).

Results for our other measure of bison grazing activity, percent cover of bison fecal pats, were contradictory to what might have been expected. Instead of a high level of bison activity in recently burned patches resulting in a high percent cover of fecal pats, percent cover of fecal pats was higher in patches that had not recently burned. Previous research at this study site documented complete combustion of bison fecal pats during prescribed burns conducted in September, December, and April (Crockett and Engle, 1999). The burns that were conducted in the spring of 2007, 2–3 mo prior to our sampling in those patches, may have consumed much or all of the fecal pat material that was present. Thus, the percent cover of fecal

TABLE 2—Values of *Arnoglossum plantagineum* variables (mean ± SE) in recent (2007) and older (2004 or 2005) spring burns in tallgrass prairie grazed by bison in Oklahoma. *Arnoglossum plantagineum* variables did not differ (permutational multivariate analysis of variance; $\alpha = 0.05$; $P < 0.001$) between recent and older burns.

| *Arnoglossum plantagineum* response variables | Recent spring burns (2007) | Older spring burns (2004 or 2005) |
|---|---|---|
| *A. plantagineum* height (cm) | 76.46 ± 0.95 | 79.88 ± 1.10 |
| Number of *A. plantagineum* capitula | 116.10 ± 5.67 | 121.62 ± 7.02 |
| *A. plantagineum* reproductive biomass (g) | 2.96 ± 0.19 | 3.06 ± 0.24 |
| *A. plantagineum* total biomass (g) | 11.72 ± 0.51 | 12.03 ± 0.63 |

pats we measured in the recently burned patches may have reflected what accumulated in only 2–3 mo compared to what accumulated over 2–3 y in patches that had not burned since at least 2005.

Patches that had recently burned had markedly higher amounts of bare ground and markedly lower amounts of litter and dead vegetation when compared to patches that had not recently burned. Recently burned patches would have thus been characterized by greater levels of solar radiation reaching the soil surface, resulting in higher levels of light resources for growing plants and warmer soil temperatures in the spring (Knapp and Seastedt, 1986). Bison are predominately graminivores (Krueger, 1986; Plumb and Dodd, 1993; Coppedge et al., 1998*b*), and a greater level of bison grazing activity within recently burned patches was reflected in lower percent cover values of live grass in those patches. However, when we analyzed data for height of the tallest grass tissue within plots, the difference between lower values in the recently burned patches and higher values in patches that had not recently burned only approached significance. This may have been a function of measuring the tallest grass tissue within the plots whereas bison and other large grazers preferentially graze leaf tissue over other tissues such as stems (Pfeiffer and Hartnett, 1995; Laca et al., 2001). If we had restricted our measurements to grass leaf tissue, our results likely would have indicated a significant difference. Nonetheless, within recently burned patches the high level of grass herbivory interacted with recent consumption of vegetation biomass by fire, creating optimal environmental conditions for nongraminoids.

Selective grazing of grasses around prairie forbs, as can occur within a recently burned patch, can create a favorable growing environment as a result of greater levels of light and higher soil temperatures (Fahnestock and Knapp, 1993, 1994). Prairie forbs growing in grazed areas can be shorter than conspecifics growing in areas where grazing is minimal or absent (Fahnestock and Knapp, 1993, 1994; Damhoureyeh and Hartnett, 1997), implying that forbs growing among ungrazed grasses need to be taller to obtain sufficient light resources. Our results for height of tallest forbs may corroborate this, as this measurement was lower in recently burned patches of our study where bison grazing activity was relatively high. However, an alternative explanation for our results is that forbs located in patches burned in the spring of 2007 were shorter than forbs located in patches that were burned in the spring of earlier years because they had to reinitiate growth later in the 2007 growing season following fires that occurred in March–April of that year. This alternative explanation may also clarify why there was minimal difference in percent cover of forbs within plots and heights of *A. plantagineum* when recent burns were compared to older burns. Finally, tallgrass prairie shrubs can exhibit a positive response to the postfire environment of high light levels and soil temperatures (McCarron and Knapp, 2003; Heisler et al., 2004); our results for percent cover of live shrubs, which was higher in recently burned patches, may exemplify this.

Our measures of *A. plantagineum* growth and reproduction (height, number of capitula, reproductive biomass, total biomass) did not differ when comparisons were made between individuals located in patches with different burn histories. However, previous analyses of a larger dataset generated from this research demonstrated that response of *A. plantagineum* growth and reproductive variables to the interaction of fire and bison grazing depended on topographical position (Winter et al., 2013), a level of analysis we did not consider in the current study. Additionally, density of flowering *A. plantagineum* individuals, as opposed to individuals that did not flower and were present only as a rosette of basal leaves, was higher in recently burned patches relative to patches that had not burned recently (Winter et al., 2013). If greater resource availability allows greater reproductive effort in *A. plantagineum*, reproductive effort may be expressed primarily in whether or not an individual of this species produces a flowering stem and not in other measures of reproductive effort such as number of capitula or mass of reproductive structures (Winter et al., 2013).

Tallgrass prairie vegetation can respond to spring fires in a manner that differs from the response to fires in other seasons (Towne and Kemp, 2008; Howe, 2011). However, the preference for recently burned areas among large grazers is consistent regardless of fire season (Fuhlendorf and Engle, 2004; Vermeire et al., 2004; Allred et al., 2011). Our previous analyses indicated that *A. plantagineum* growth and reproductive measures responded to the interaction of fire, bison grazing, and topography in areas that were burned in the spring as well as in areas that were burned in the summer (Winter et al., 2013). The presence of grazers following a fire may have a relatively greater influence on vegetation response than the season at which a fire occurs.

In summary, we documented the profound influence of spring fires on grazing activity of bison in Oklahoma tallgrass prairie and concurrent effects on vegetation structure variables. Recent spring fires created patches where environmental conditions were conducive for plant growth but they also created conditions that were attractive to foraging bison. The interaction of fire and bison grazing at our study site resulted in a landscape mosaic where adjacent landscape patches were markedly different in both grazing animal activity and vegetation structure.

Funding was provided by a State Wildlife Grant under Project T-30-P of the Oklahoma Department of Wildlife Conservation and Oklahoma State University and administered through the Oklahoma Cooperative Fish and Wildlife Research Unit; and by the National Research Initiative of the United States Department of Agriculture Cooperative State Research, Education and

Extension Service, grant number 2003-35101-12928. The Oklahoma Chapter of The Nature Conservancy provided logistical assistance and lodging during the field season. Assistance with field sampling and laboratory procedures was provided by A. Ainsworth, M. Howe, K. Spears, L. Wilkerson, and J. Worthington. Spanish translation of the abstract was provided by A. Hawkins and T. Hawkins.

## Literature Cited

Allred, B. W., S. D. Fuhlendorf, D. M. Engle, and R. D. Elmore. 2011. Ungulate preference for burned patches reveals strength of fire-grazing interaction. Ecology and Evolution 1:132–144.

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26:32–46.

Anderson, T. M., M. E. Ritchie, E. Mayamba, S. Eby, J. B. Grace, and S. J. McNaughton. 2007. Forage nutritive quality in the Serengeti ecosystem: the roles of fire and herbivory. American Naturalist 170:343–357.

Archibald, S., and W. J. Bond. 2004. Grazer movements: spatial and temporal responses to burning in a tall-grass African savanna. International Journal of Wildland Fire 13:377–385.

Cazau, M., M. Garel, and D. Maillard. 2011. Responses of heather moorland and Mediterranean mouflon foraging to prescribed-burning and cutting. Journal of Wildlife Management 75:967–972.

Coppedge, B. R., D. M. Engle, C. S. Toepfer, and J. H. Shaw. 1998*a*. Effects of seasonal fire, bison grazing and climatic variation on tallgrass prairie vegetation. Plant Ecology 139:235–246.

Coppedge, B. R., D. M. Leslie Jr., and J. H. Shaw. 1998*b*. Botanical composition of bison diets on tallgrass prairie in Oklahoma. Journal of Range Management 51:379–382.

Coppedge, B. R., and J. H. Shaw. 1998. Bison grazing patterns on seasonally burned tallgrass prairie. Journal of Range Management 51:258–264.

Crockett, J. S., and D. M. Engle. 1999. Combustion characteristics of bison (*Bison bison*) fecal pats ignited by grassland fires. American Midland Naturalist 141:12–18.

Damhoureyeh, S. A., and D. C. Hartnett. 1997. Effects of bison and cattle on growth, reproduction, and abundances of five tallgrass prairie forbs. American Journal of Botany 84:1719–1728.

Dwyer, D. D. 1961. Activities and grazing preferences of cows with calves in northern Osage County, Oklahoma. Oklahoma Agricultural Experiment Station, Stillwater, Bulletin B-588.

Fahnestock, J. T., and A. K. Knapp. 1993. Water relations and growth of tallgrass prairie forbs in response to selective grass herbivory by bison. International Journal of Plant Sciences 154:432–440.

Fahnestock, J. T., and A. K. Knapp. 1994. Plant responses to selective grazing by bison—interactions between light, herbivory and water-stress. Vegetatio 115:123–131.

Fuhlendorf, S. D., and D. M. Engle. 2001. Restoring heterogeneity on rangelands: Ecosystem management based on evolutionary grazing patterns. BioScience 51:625–632.

Fuhlendorf, S. D., and D. M. Engle. 2004. Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. Journal of Applied Ecology 41:604–614.

Fuhlendorf, S. D., D. M. Engle, J. Kerby, R. Hamilton. 2009. Pyric herbivory: rewilding landscapes through the recoupling of fire and grazing. Conservation Biology 23:588–598.

Hamilton, R. G. 2007. Restoring heterogeneity on the Tallgrass Prairie Preserve: applying the fire-grazing interaction model. Pages 163–169 in Proceedings of the 23rd Tall Timbers Fire Ecology Conference: Fire in Grassland and Shrubland Ecosystems. Tall Timbers Research Station, Tallahassee, Florida.

Heisler, J. L., J. M. Briggs, A. K. Knapp, J. M. Blair, and A. Seery. 2004. Direct and indirect effects of fire on shrub density and aboveground productivity in a mesic grassland. Ecology 85:2245–2257.

Hickman, K. R., and J. D. Derner. 2007. Blackland tallgrass prairie vegetation dynamics following cessation of herbicide application. Rangeland Ecology and Management 60:186–190.

Howe, H. F. 2011. Fire season and prairie forb richness in a 21-year experiment. Ecoscience 18:317–328.

Knapp, A. K., and T. R. Seastedt. 1986. Detritus accumulation limits productivity of tallgrass prairie. BioScience 36:662–668.

Krueger, K. 1986. Feeding relationships among bison, pronghorn, and prairie dogs: an experimental analysis. Ecology 67:760–770.

Laca, E. A., L. A. Shipley, and E. D. Reid. 2001. Structural anti-quality characteristics of range and pasture plants. Journal of Range Management 54:413–419.

Mbatha, K. R., and D. Ward. 2010. The effects of grazing, fire, nitrogen and water availability on nutritional quality of grass in semi-arid savanna, South Africa. Journal of Arid Environments 74:1294–1301.

McCarron, J. K., and A. K. Knapp. 2003. $C_3$ shrub expansion in a $C_4$ grassland: positive post-fire responses in resources and shoot growth. American Journal of Botany 90:1496–1501.

Moe, S. R., and P. Wegge. 1997. The effects of cutting and burning on grass quality and axis deer (*Axis axis*) use of grassland in lowland Nepal. Journal of Tropical Ecology 13:279–292.

Murphy, B. P., and D. M. J. S. Bowman. 2007. The interdependence of fire, grass, kangaroos and Australian Aborigines: a case study from central Arnhem Land, northern Australia. Journal of Biogeography 34:237–250.

Palmer, M. W. 2007. The vascular flora of the Tallgrass Prairie Preserve, Osage County, Oklahoma. Castanea 72:235–246.

Pfeiffer, K. E., and D. C. Hartnett. 1995. Bison selectivity and grazing response of little bluestem in tallgrass prairie. Journal of Range Management 48:26–31.

Plumb, G. E., and J. L. Dodd. 1993. Foraging ecology of bison and cattle on a mixed prairie: implications for natural area management. Ecological Applications 3:631–643.

Polley, H. W., B. J. Wilsey, and J. D. Derner. 2007. Dominant species constrain effects of species diversity on temporal variability in biomass production of tallgrass prairie. Oikos 116:2044–2052.

R Development Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Schuler, K. L., D. M. Leslie Jr., J. H. Shaw, and E. J. Maichak. 2006. Temporal-spatial distribution of American bison (*Bison bison*) in a tallgrass prairie fire mosaic. Journal of Mammalogy 87:539–544.

Sensenig, R. L., M. W. Demnent, and E. A. Laca. 2010. Allometric

scaling predicts preferences for burned patches in a guild of East African grazers. Ecology 91:2898–2907.

Smeins, F. E., and D. D. Diamond. 1983. Remnant grasslands of the Fayette Prairie, Texas. American Midland Naturalist 110:1–13.

Towne, E. G., and K. E. Kemp. 2008. Long-term response patterns of tallgrass prairie to frequent summer burning. Rangeland Ecology and Management 61:509–520.

USDA-NRCS. 2009. Web Soil Survey. United States Department of Agriculture Natural Resources Conservation Service.

Van De Vijver, C. A. D. M., P. Poot, and H. H. T. Prins. 1999. Causes of increased nutrient concentrations in post-fire regrowth in an East African savanna. Plant and Soil 214:173–185.

Van Dyke, F., and J. A. Darragh. 2007. Response of elk to changes in plant production and nutrition following prescribed burning. Journal of Wildlife Management 71:23–29.

Vermeire, L. T., R. B. Mitchell, S. D. Fuhlendorf, and R. L. Gillen. 2004. Patch burning effects on grazing distribution. Journal of Range Management 57:248–252.

Winter, S. L., S. D. Fuhlendorf, C. L. Goad, C. A. Davis, K. R. Hickman, and D. M. Leslie. 2012. Restoration of the fire-grazing interaction in *Artemisia filifolia* shrubland. Journal of Applied Ecology 49:242–250.

Winter, S. L., K. R. Hickman, C. L. Goad, S. D. Fuhlendorf, and M. S. Gregory. 2013. Seasonal fires, bison grazing and the tallgrass prairie forb *Arnoglossum plantagineum* Raf. Natural Areas Journal 33:327–338.

*Submitted 5 November 2013.*

*Acceptance recommended by Associate Editor, Florence M. Oxeley, 22 November 2014.*