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Original Research

Fire and Season of Postfire Defoliation Effects on Biomass, Composition, and Cover in Mixed-Grass Prairie[☆]

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ABSTRACT

North American prairies are acknowledged to have evolved with grazing following fire. Given this evolutionary fire-grazing interaction, our objective was to determine whether seasonal timing of defoliation following fire alters subsequent productivity and species composition. Following the April 2013 Pautre wildfire in the Grand River National Grasslands of South Dakota, we installed exclosures in three locations along the border of the fire. Grazing exclosures were paired across the fire line to create a burned and nonburned exclosure at each location. Four plots were demarcated in each exclosure. Three plots were defoliated via mowing to 6 cm either 2, 4, or 6 mo following fire, with the fourth maintained as a control. Productivity and species composition data were collected in November 2013, June 2014, August 2014, and July 2015. Fire increased productivity 56% during the 2013 growing season following fire. During the 2014 growing season, there was a tendency for burned sites to maintain greater production. June defoliation resulted in the greatest current-year productivity in 2014 regardless of fire treatment, whereas all other treatments resulted in similar productivity. Fire and defoliation effects on productivity were undetectable in 2015. Community composition was not affected by fire in 2013. *Melilotus officinalis* was increased by spring defoliation in 2014 and by fire in 2015. Litter was initially reduced by fire but was similar to nonburned levels by 2015. Results indicate that positive fire effects on productivity are limited to the first two growing seasons following fire, whereas defoliation effects manifest the second growing season following fire (first growing season after defoliation). With the exception of old dead material, fire and timing of defoliation affected biomass and community composition independently. Postfire rest from grazing appears unnecessary for the maintenance of plant productivity and species composition in northern mixed-grass prairie.

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Introduction

Current federal postfire land management recommendations decouple two natural disturbances that, in the prairies of North America, were historically linked. Federal recommendations state that grazing be deferred following fire, preferably for two growing seasons (Blaisdell et al., 1982; Bureau of Land Management, 2007). If grazing does occur the first growing season following fire, the recommended approach is to defer grazing until after seed set, when vegetation has completed active growth and dormancy is imminent. However, during

the evolution of the Great Plains ecoregion, evidence suggests that fire and grazing were intimately linked, with fire determining where grazing was likely to take place and vice versa (Fuhlendorf and Engle, 2001). These coupled disturbances have been described as one perturbation, pyric herbivory (Fuhlendorf et al., 2009). Evidence suggests that pyric herbivory may be an obligate ecological process, as more native conditions have been obtained when fire and grazing are applied in sequence rather than separately (Vinton et al., 1993). Given this close interaction, deferral of grazing following fire may undermine management goals.

Grazers are attracted to the relatively high-quality forage that grows following fire (Vinton et al., 1993; Knapp et al., 1999; Fuhlendorf and Engle, 2001; Vermeire et al., 2004). The degree to which forage quality is increased is largest soon after the resumption of growth (Hilmon and Hughes, 1965; McPherson et al., 1995). Thus, grazers are most attracted to regrowth shortly following fire, with no natural defoliation period. Foraging focuses on these areas until forage quality diminishes relative to adjacent nonburned areas in tallgrass prairie (Fuhlendorf et al., 2009), suggesting that northern mixed-grass prairie is also likely well adapted to withstand fire, as well as one or more defoliation events immediately following fire.

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Recommendations for 2 yr of rest are based on several assumptions. First, the vigor of plants will be lessened by fire, rendering the remaining tissues less able to withstand subsequent damage via defoliation, as indicated by data from the Great Basin examining *Pseudoroegneria spicata* (Pursh) Å. Löve, *Festuca idahoensis* Elmer and *Festuca campestris* Rydb. (Bailey and Anderson, 1978; Jirik and Bunting, 1994; Bunting et al., 1998). Secondly, the establishment of new plants via seed will constitute an important facet of recovery. If mature plants experience mortality directly from fire, they will need to be replaced by the recruitment of new individuals, possibly via the production and germination of seed. Thirdly, if defoliation must occur the first growing season following fire, it should be deferred until after seed set and the cessation of active growth. This assumption implies that the removal of actively growing tissue should be considered more detrimental post fire than the removal of senesced or dormant tissue. This recommendation again comes from observations of bunchgrasses *P. spicata* and *F. campestris* (McLean and Wikeem, 1985a, 1985b). Finally, deferment of postfire grazing is recommended to protect soil stability and health by providing a protracted interval in which litter can recover and lessen erosion because intense grazing has been implicated in reducing standing and fallen litter and increasing bare ground (Naeth et al., 1991). However, these assumptions are in disagreement with many of the ecological observations in North American prairies.

Few, if any, dominant native prairie grasses actually experience mortality following fire (Brockway et al., 2002; Haile, 2011). Additionally, surviving plants are often more productive (White and Currie, 1983) and of higher forage quality than nonburned counterparts (Hobbs and Spowart, 1984). As few plants experience mortality following fire, there is little need for replacement of lost plants in the recovery process. For example, 99% of shoots in tallgrass prairie have been attributed to tillering of surviving plants, rather than dependence on the establishment of new seedlings (Benson and Hartnett, 2006). Thus, rest designed to protect seedlings may not be necessary if seedlings contribute little to populations and recovery is not necessary in many situations. Lastly, litter is inarguably removed or reduced by fire, increasing erosion potential (Benkobi et al., 1993) and possibly degrading soil conditions (Hulbert, 1969). Alternatively, postfire grazing did not impede recovery of litter frequency and, thus, did not prolong the risk of erosion or degrade soil quality on burned, grazed sites compared with burned, rested sites in the Great Basin (Bates et al., 2009). Moreover, even though litter is temporarily reduced by fire, soil moisture retention was similar between burned and nonburned sites in eastern Montana, indicating that the benefits gained from litter may be regained even before litter recovers to preburn levels (Vermeire et al., 2011).

The northern mixed-grass prairie should be well adapted to withstand grazing the first growing season following a fire. However, postfire grazing effects may depend on not only whether or not defoliation occurs following a fire but also the time of the year during which grazing takes place. Grazing management systems are designed to control the season, intensity, and frequency of defoliation to minimize the effects of grazing on a plant community (Briske et al., 2011). The season of defoliation, in particular, will determine whether actively growing or senesced tissue is removed, in turn affecting resources and nutrients allocated to active plant tissues for growth and maintenance (Briske, 1991). The removal of actively growing tissue may weaken a plant's potential productivity by depleting reserves (McLean and Wikeem, 1985a, 1985b) or increase productivity via compensatory growth, in which losses are recovered through regrowth and subsequent sequestration and replacement of lost resources (McNaughton, 1983). In contrast, removal of senesced tissue during the dormant season will potentially have no effect, as these tissues are no longer physiologically active (McLean and Wikeem, 1985a, 1985b; Briske, 1991). Given the general lack of information on the effects of defoliation following fire, it is unclear if defoliation in one season should be considered more detrimental than another. However, deferment

until the end of the growing season is known to reduce diet quality and livestock growth (Waterman and Vermeire, 2011). This knowledge gap must be filled to facilitate development of postfire grazing management strategies.

We hypothesized that spring fire would increase current year productivity (White and Currie, 1983). Concurrently, we hypothesized that postfire defoliation would not negatively impact subsequent-year productivity, nor would it negatively impact subsequent-year community composition (Bates et al., 2009; Vermeire et al., 2014). Additionally, we hypothesized that season of defoliation during the first postfire growing season would not affect subsequent-year productivity or community composition. Finally, we hypothesized that while litter would initially be reduced by fire, season of defoliation would not impact the rate of recovery. We expected recovery of the litter layer to occur within 2 yr.

Methods

Wildfire and Study Sites

The Pautre fire occurred on 3 April 2013, approximately 12 km east of Lodgepole, South Dakota and 31 km southwest of Lemmon, South Dakota (45°52'54"N 102°32'52"W), with total containment declared on 7 April 2013, burning a total of 4322 ha of Grand River National Grassland, Grand River Cooperative Grazing Association, and private lands. Study sites were selected from the burned portion of the Grand River National Grassland. Three sites were selected along the perimeter of the wildfire in order to span the north-south gradient of the burn, with one site located in the 3B pasture and two sites at the northern and southern ends of the 4B pasture (N4B and S4B, respectively).

Dominant soil types in the area include Reeder-Lantry loams (fine-loamy, mixed, superactive, frigid Typic Argiustolls and fine-silty, mixed, superactive, calcareous, frigid Typic Ustorthents; 2–9% slopes); Amor-Cabba loams (fine-loamy, mixed, superactive, frigid Typic Haplustolls and loamy, mixed, superactive, calcareous, frigid, shallow Typic Ustorthents; 6–15% slopes); and the Vebar-Chogen complex (coarse-loamy, mixed, superactive, frigid Typic Haplustolls and loamy, mixed, superactive, calcareous, frigid, shallow Typic Ustorthents; 6–25% slopes) (Soil Survey Staff USDA-NRCS, 2008; Web Soil Survey, 2015).

The three sites captured a wide range of community compositions occurring in the area. The 3B pasture was dominated by the introduced, C3 grass *Agropyron cristatum* (L.) Gaertn. with lesser components of the native, C3 grass *Hesperostipa comata* (Trin. & Rupr.) Barkworth and C4 grass *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths. The N4B and S4B pastures contained dominant components of C3 native grasses *H. comata*, *Pascopyrum smithii* (Rydb.) Å. Löve, *Koeleria macrantha* (Ledeb.) Schult., and *Nassella viridula* (Trin.) Barkworth. The N4B pasture had a notable constituent of the introduced C3 grass *Poa compressa* L. Common forbs across all pastures included natives *Grindelia squarrosa* (Pursh) Dunal, *Ratibida columnifera* (Nutt.) Wooton & Standl., *Plantago patagonica* Jacq., and the invasive *M. officinalis* (L.) Lam. The only shrubs encountered, *Artemisia frigida* Willd. and *Symphoricarpos albus* (L.) S.F. Blake, were rare.

Average precipitation is 414 mm in Lodgepole, South Dakota and 460 mm in Lemmon, South Dakota with most occurring from April to September (National Climate Data Center, 2015). During the study period, annual precipitation was average to greater than average. In 2013 precipitation was 709 and 863 mm (171% and 188% of average), 474 and 457 mm (114% and 99% of average) in 2014, and 476 and 453 mm (115% and 98% of average) during 2015 in Lodgepole and Lemmon, respectively.

Defoliation Treatments

Following the wildfire, two 15 × 15 m enclosures were erected at each of the 3B, N4B, and S4B study sites, with one enclosure each located on the burned and nonburned sides of the fire perimeter. Enclosure

locations were identified by randomly selecting general areas on a map and then scouting to ensure soils were the same and that topography and plant community types were similar between burned and nonburned sides at each site. Within each enclosure, four plots (5 × 10 m) were delineated. Three of the four plots were defoliated via mowing to 6 cm during June, August, or November 2013 (hereafter referred to as spring, summer, or fall defoliation, respectively). The fourth plot in each enclosure was maintained as a nondefoliated control. Mowed clippings were bagged and disposed of away from the enclosures. Mowing was used as a proxy for defoliation by grazing and would most closely mimic a severe or heavy defoliation event common to historic grazers in which use was uniform and selectivity minimal.

Sampling

In November 2013, biomass, community composition, and basal cover were sampled in the burned and nonburned control plots only. Biomass was determined by clipping eight 0.1-m² quadrats from each plot and drying the samples at 60°C until no additional loss in weight was detected. Canopy and basal cover composition were measured via the point-intercept method (Caratti, 2006). Observations were made along a 10-m transect at 20-cm intervals for a total of 50 observations. Canopy and basal observations were delineated at each point. Canopy composition and basal coverage were measured in all plots in June 2014, August 2014, and July 2015. Biomass was measured in all plots in August 2014 and July 2015.

Statistical Analysis

Where outlier values were suspected, we tested all subsamples using the Generalized Extreme Studentized Deviate test and removed identified outliers from further analysis. Removal of outliers did not cause any missing values at the experimental unit level. The SAS mixed procedure was used to perform analysis of variance in order to test for effects of fire, defoliation, and their interactions (Littell et al., 2006). Plot was the experimental unit. Defoliation treatment and fire treatment were used as fixed effects. Pasture was included as a random-effect, stratifying the comparisons within each set of paired enclosures. Data were analyzed by year because of heterogeneous variances among years. Response variables for the mixed linear models included total standing biomass, old standing dead, current-year productivity, species richness, Shannon's diversity index (calculated using canopy frequency from the line-intercept transect), basal cover, and community composition by species and functional group (functional groups used were C3 grasses, C4 grasses, annual grasses, sedges, shrubs, and forbs). Raw frequency data were used to confirm that any observed shifts in composition were due to shifts in actual as opposed to relative abundance. Changes in composition due only to relative abundance will be mentioned but reported in terms of actual abundance. A significance level of $\alpha = 0.05$ was used to identify differences, and a $0.05 < P < 0.1$ was used to identify trends. The PDIF option of SAS was used to perform mean separations.

Results

Fire and defoliation did not have interacting effects on biomass, community composition, or basal cover, with the exception of old standing dead during 2015. Therefore, all other results are reported as main effects of fire or defoliation.

Biomass

Fire Effects

Total standing biomass was reduced on burned sites by 25% in 2013, the first growing season following the fire (Table 1). This reduction can be attributed to the total removal of old standing dead from the burned

Table 1

Fire effects on biomass (kg ha⁻¹) across defoliation treatments with standard errors of the difference and *P* values for biomass component within-year comparisons following the April 2013 Pautre wildfire.

Yr	Biomass component	Nonburned	Burned	SE _{diff}	<i>P</i> value
2013	Old dead	1359	0	71	< 0.0001
	Current year	1271	1984	223	0.0330
	Total standing	2630	1984	197	0.0377
2014	Old dead	1001	986	61	0.8074
	Current year	3061	3385	174	0.0832
	Total standing	4062	4371	230	0.2022
2015	Current year	2006	2171	193	0.4050
	Total standing	3279	3537	209	0.2384

sites. Current-year production, in contrast, increased by 56% on burned sites. By 2014, two growing seasons after fire, a trend remained for 10% greater current-year production on burned sites while no differences were detected between burned and nonburned sites for old standing dead and standing biomass. In 2015, three growing seasons post fire, current-year production and standing biomass were similar between burned and nonburned sites.

Defoliation Effects

In 2014, control plots and spring defoliated plots, while similar to one another, contained an average of 21% greater standing biomass than both summer and fall defoliated plots (Table 2). Control, summer defoliated and fall defoliated plots yielded similar current-year production, whereas spring defoliated plots contained an average of 22% greater current-year production than all other treatments. Control plots contained an average 65% more old standing dead than any defoliated plots. By 2015, no differences were detected for current-year production and standing biomass across all treatments. Fire and defoliation interacted in their effects on old standing dead in 2015 (Fig. 1; $P = 0.0415$). Nondefoliated plots contained the least standing dead regardless of whether the plots had burned. Nonburned, spring defoliated and burned, fall defoliated plots had the most old standing dead, with about 1.8 times the amount in nondefoliated plots. There was considerable overlap among all other treatment combinations and no clear trend for fire or defoliation effects.

Community Composition

Fire Effects

A total of 43 species were observed across the three study sites, 35 of which were native. Species richness and Shannon's diversity index were unaffected by fire in 2013, 2014, and 2015 (4.3 vs. 5.6 species, 11.7 vs. 11.8 species, and 8.3 vs. 8.0 species; $P = 0.4557, 0.8869, 0.7759$ and 1.1 vs. $0.7, 1.7$ vs. 1.7 , and 1.4 vs. 1.4 ; $P = 0.2801, 0.7516, 0.9803$, respectively). In 2013, no differences in composition were observed on the basis of functional groups (Table 3) or individual species. In 2014, no shifts in composition with respect to functional groups were observed. However, *Sphaeralcea coccinea* (Nutt.) Rydb. was more abundant on nonburned sites in 2014 (1.9 vs. $0.1 \pm 0.7\%$; $P = 0.0184$). In 2015 an apparent reduction in C3 grass cover and an increase in forb cover on burned sites were observed. Importantly, the apparent reduction in C3 grasses was attributable to a shift in relative rather than actual abundance, with actual abundance remaining similar. Forbs comprised a larger percentage of cover on burned than nonburned plots, and shrubs trended toward the opposite. Among individual species, *K. macrantha* was greater on nonburned sites (2.1 vs. $0.0 \pm 0.8\%$; $P = 0.0217$) and *A. frigida* (1.6 vs. $0.2 \pm 0.7\%$; $P = 0.0647$) and *Asclepias viridiflora* Raf. (2.8 vs. $0.1 \pm 1.5\%$; $P = 0.0849$) trended toward greater abundance on nonburned sites. *M. officinalis* was more abundant on burned than nonburned sites (21.3 vs. $9.6 \pm 4.3\%$; $P = 0.0162$), and *Descurainia pinnata* (Walter) Britton followed a similar trend (0.2 vs. $1.4 \pm 0.6\%$; $P = 0.0542$).

Table 2

Timing of defoliation effects on biomass (kg ha^{-1}) across fire treatments with standard errors of the difference and *P* values for biomass component within-year comparisons following the April 2013 Pautre wildfire.

Yr	Biomass component	Control	Spring	Summer	Fall	SE _{diff}	<i>P</i> value
2014	Old dead	1413 a	936 b	776 b	850 b	86	< 0.0001
	Current year	3165 b	3730 a	2982 b	3014 b	245	0.0299
	Total standing	4578 a	4666 a	3758 b	3864 b	326	0.0258
2015	Current year	2004	2186	2063	2101	272	0.9234
	Total standing	2997	3657	3410	3567	296	0.1688

Defoliation Effects

Species richness in 2014 had a tendency to be greater in fall defoliated plots than spring defoliated plots, but no differences were detected across all other comparisons of defoliation treatments (11 species in spring defoliated plots vs. 11, 11, and 13 species in control, summer, and fall defoliated plots, respectively; $P = 0.0878$). Richness was similar across all defoliation treatments in 2015 (8 species in all treatments; $P = 0.9429$). Shannon’s diversity index was greater in summer and fall defoliated plots when compared with the control in 2014 (1.5, 1.7, 1.8, and 1.9 in the control, spring, summer, and fall defoliated plots; $P = 0.0253$), but no differences were detected across all defoliation treatments in 2015 (1.3, 1.3, 1.5, and 1.6 in the control, spring, summer, and fall defoliated plots; $P = 0.4973$). In 2014, no differences were observed across defoliation treatments in C3 grasses, C4 grasses, annual grasses, sedges, or shrubs (Table 4). A trend toward increased forbs in spring defoliated plots was apparent. This trend is primarily attributable to the large, 14% average increase of *M. officinalis* in spring defoliated plots when compared with all other treatments (6.8, 22.5, 9.6, and $9.3 \pm 5.4\%$ in the control, spring, summer, and fall defoliated plots; $P = 0.0488$). *K. macrantha* tended to increase in summer defoliated plots when compared with control and spring defoliated plots (2.9, 3.9, 8.0, and $5.8 \pm 1.8\%$ in the control, spring, summer, and fall defoliated plots; $P = 0.0564$). In 2015, no effects of defoliation treatments were observed with respect to either functional group composition or individual species.

Basal Cover

Fire Effects

Litter was completely eliminated by fire, and bare ground increased 54% compared with nonburned sites in 2013 (Table 5). No differences in other basal cover components were observed. In 2014, litter on burned sites was 14.5% less and bare ground was 11.3% greater than on nonburned sites. By 2015, no differences were detected between burned and nonburned sites for litter and bare ground. *B. gracilis* trended toward greater basal cover on nonburned sites in 2014 (7.8 vs. $4.7 \pm 1.7\%$; $P = 0.0829$), but no effects were apparent during 2015. *M. officinalis* trended toward greater basal cover on burned sites in 2015 (4.5 vs. $0.3 \pm 2.3\%$; $P = 0.0953$).

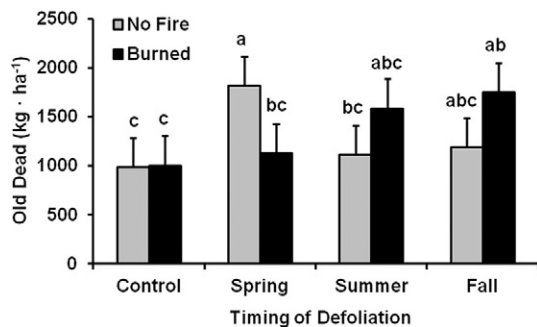


Figure 1. Old dead biomass ($\text{kg} \cdot \text{ha}^{-1}$) during the third growing season following the April 2013 Pautre wildfire (2015) with standard errors of the difference for interacting effects of fire and timing of defoliation.

Defoliation Effects

No defoliation treatment effects were detected for litter cover during 2014 ($44.3 \pm 6.0\%$; $P = 0.1080$) and 2015 ($54.9 \pm 7.4\%$; $P = 0.1256$). Similarly, no differences in bare ground were detected among defoliation treatments during 2014 ($17.3 \pm 6.0\%$; $P = 0.8664$) or 2015 ($5.2 \pm 3.4\%$; $P = 0.9031$). During 2014, *K. macrantha* trended toward greater basal cover in summer defoliated plots compared with the control and *N. viridula* trended toward greater abundance in control than summer defoliated plots (Table 6). *Carex duriuscula* C.A. Mey. was more abundant in summer defoliated than nondefoliated and fall defoliated plots. There were no defoliation treatment effects for basal cover of any individual species during 2015.

Discussion

The lack of compounding, interacting effects caused by both fire and defoliation should alleviate the concern that defoliation following fire, especially during active growth, will exacerbate any negative effects of fire. Most observed effects could be attributed to fire or defoliation independently. In the only case of fire and defoliation interaction, old standing dead in 2015, all combinations of burned and defoliated treatments either had greater biomass or were similar to the burned and nonburned nondefoliated controls. This suggests that postfire defoliation does not produce negative effects at the community level when compared with sites that have been rested. These results align with those of previous studies in mixed-grass prairie (Vermeire et al., 2014) and in sagebrush steppe (Bates et al., 2009) in which sites grazed after fire recovered similarly to rested sites, indicating that, at least in these systems, 2 yr of rest following fire may be unnecessary. The generally wet conditions throughout the study may have mitigated postfire defoliation effects. However, the study by Bates et al. (2009) occurred during drought and Vermeire et al. (2014) conducted repeated experiments with dry and wet postfire grazing conditions. This indicates that the response to postfire grazing is similar for not only these systems but also across a range of postfire precipitation levels.

Table 3

Fire effects on functional group composition (%) across defoliation treatments with standard errors of the difference and *P* values for functional group within-year comparisons following the April 2013 Pautre wildfire.

Yr	Functional group	Nonburned	Burned	SE _{diff}	<i>P</i> value
2013	C ₃ grasses	85.4	73.8	12.7	0.4540
	C ₄ grasses	5.5	10.9	3.3	0.2462
	Annual grasses	0.0	0.0	—	—
	Sedges	7.8	14.5	9.2	0.5452
	Shrubs	0.0	0.0	—	—
	Forbs	1.2	0.9	0.2	0.1839
2014	C ₃ grasses	69.0	68.3	4.7	0.8767
	C ₄ grasses	4.8	4.4	1.2	0.7220
	Annual grasses	0.3	0.1	0.2	0.3606
	Sedges	7.6	9.0	2.4	0.5677
	Shrubs	0.2	0.7	0.7	0.4708
	Forbs	18.0	17.5	3.2	0.8627
2015	C ₃ grasses	71.7	59.9	5.4	0.0474
	C ₄ grasses	5.2	5.0	2.5	0.9353
	Annual grasses	0.2	0.0	0.1	0.1493
	Sedges	2.2	4.9	2.4	0.2852
	Shrubs	1.7	0.2	0.7	0.0594
	Forbs	19.0	30.0	4.3	0.0232

Table 4

Timing of defoliation effects on functional group composition (%) across fire treatments with standard errors of the difference and *P* values for functional group within-year comparisons following the April 2013 Pautre wildfire.

Yr	Functional group	Control	Spring	Summer	Fall	SE _{diff}	<i>P</i> value
2014	C ₃ grasses	69.2	64.1	72.2	69.1	6.7	0.6798
	C ₄ grasses	5.9	4.2	4.7	3.6	1.7	0.5752
	Annual grasses	0.0	0.2	0.6	0.0	0.3	0.1814
	Sedges	10.1	8.6	9.2	5.4	3.4	0.5589
	Shrubs	0.4	0.0	1.5	0.0	1.0	0.4287
	Forbs	14.3 bc	22.9 a	11.8 c	21.9 ab	4.6	0.0733
2015	C ₃ grasses	70.3	75.2	58.1	59.7	7.7	0.1217
	C ₄ grasses	3.6	4.5	8.0	4.1	3.6	0.6040
	Annual grasses	0.0	0.2	0.0	0.2	0.2	0.5252
	Sedges	4.4	1.3	3.0	5.5	3.4	0.6472
	Shrubs	1.8	0.0	1.2	0.8	1.0	0.3704
	Forbs	19.9	18.8	29.8	29.6	6.1	0.1707

The hypothesis that burning increases current-year productivity and does not negatively impact subsequent-year productivity is supported by the data. While more modest increases in productivity might be expected, the 56% increase in current-year productivity the first growing season following fire is not unprecedented in the literature. In mixed-grass prairie, a 10–15% increase in the productivity of spring burned *Carex filifolia* Nutt. compared with nonburned controls and *B. gracilis* production increased by 40% (White and Currie, 1983). In pine savanna herbaceous understory, increases in herbage yield following fire ranged in magnitude from 10–55% (Harris and Covington, 1983). The increase following the Pautre fire likely stems from the removal of litter and standing dead material and the release of soil nutrients. If the nonburned sites are representative of the conditions before fire, this area contained approximately 1 400 kg ha⁻¹ of old standing dead material at the time of the fire, amounting to 48% of the standing biomass and 40% litter basal cover. While modest amounts of old standing dead material and litter have beneficial effects on soil retention, quality, and moisture (Hulbert, 1969; Benkobi et al., 1993), overaccumulation can lead to depressed production by immobilizing nutrients, decreasing light availability, and decreasing soil moisture via interception (Knapp and Seastedt, 1986; Facelli and Pickett, 1991). In tallgrass prairie, removal of litter had the potential to double productivity (Hulbert, 1969). The increased productivity on burned sites in the Pautre fire was short lived, with the degree of increased productivity diminishing the second growing season following fire and disappearing by the third. This is likely due to the relatively rapid increase in litter cover and old standing dead material on the burned sites resulting in inhibition of growth.

Defoliation had a more modest and shorter-lived but relatively positive effect on productivity. Spring defoliation, the only treatment to substantially influence productivity in comparison to the control, resulted in a 19% increase observable during the 2014 growing season. The increase in productivity is similar to the overcompensation via compensatory growth observed when plants were stressed before defoliation and had an adequate growth period in which to recover biomass (Oosterheld and McNaughton, 1991). The increase in *M. officinalis* in spring defoliated plots could have contributed to the increase in

Table 5

Spring wildfire effects on litter cover and bare ground (%) across defoliation treatments with standard errors of the difference and *P* values for within-year comparisons.

Component	Yr	Nonburned	Burned	SE _{diff}	<i>P</i> value
Litter	2013	42.7	0.0	8.4	0.0363
	2014	51.5	37.0	4.3	0.0043
	2015	57.2	52.7	5.3	0.4069
Bare ground	2013	11.3	65.3	10.1	0.0333
	2014	11.6	22.9	4.2	0.0183
	2015	3.5	6.8	2.4	0.1854

Table 6

Timing of defoliation effects on basal cover (%) across fire treatments and during the second growing season after fire (2014) with standard errors of the difference and *P* values for species within-year comparisons following the April 2013 Pautre wildfire.

Species	Control	Spring	Summer	Fall	SE _{diff}	<i>P</i> value
<i>Koeleria macrantha</i>	1.0 b	1.5 ab	3.7 a	2.5 ab	1.0	0.0928
<i>Nassella viridula</i>	4.2 a	2.2 ab	1.2 b	3.7 ab	1.2	0.0812
<i>Carex duriuscula</i>	0.2 b	1.3 ab	2.3 a	0.5 b	0.6	0.0083

productivity. Importantly, no defoliation treatment resulted in production less than the controls on either burned or nonburned sites in 2014 or 2015. This indicates that rest from defoliation is unnecessary to protect future vigor following fire when that defoliation is relatively uniform but also that deferral from grazing until after seed-set the first growing season following fire is not required. Grazing might be applied as early as 2 mo following a spring wildfire in the northern mixed-grass prairie with no deleterious effects on subsequent-year productivity.

Community composition with respect to functional groups remained relatively stable throughout the study period, lending support to the hypothesis that neither fire nor defoliation will negatively impact the plant community as a whole. However, a few minor or introduced components of the community did respond to either fire or defoliation, indicating that staticity should not be expected. The cover of C₃ grasses, which make up a majority of the community, C₄ grasses, annual grasses, and sedges, remained unaffected by fire or defoliation throughout the study period. A trend toward increased forbs in spring defoliated plots in 2014 and an increase in burned plots in 2015 can be attributed to the invasive forb, *M. officinalis*. In comparison, native species exhibited few responses. Of the 35 native species observed, only 8 (*K. macrantha*, *N. viridula*, *C. duriuscula*, and *B. gracilis* in 2014 and *A. frigida*, *A. viridiflora*, and *D. pinnata* in 2015) responded to either fire or defoliation. Neither richness nor Shannon's diversity index were affected by fire during the study period. Defoliation resulted in richness that was similar to or greater than nondefoliated plots. These results indicate that while non-native and minor components of the community can be temporarily affected by fire or defoliation, the community as a whole remains relatively stable with no negative effects on richness or diversity. As diversity is considered an indicator of ecosystem health (Chapin et al., 2000; Folke et al., 2004), the maintenance or increases in diversity observed here in response to fire and defoliation indicate that the northern mixed-grass prairie plant community is well adapted to these disturbances.

A. frigida, one of only two shrubs observed, was reduced by fire in 2015, causing the concurrent trend toward reduced shrubs. The removal of woody plants is an expected effect of fire, as is the lag in recovery of shrubs when compared with herbaceous community components (Beck et al., 2009). Reductions in *A. frigida* have been reported following heavy, season-long grazing as well, indicating that postfire grazing may further prolong recovery of this particular species (Jinhua et al., 2005).

K. macrantha, the only native C₃ grass responding to defoliation treatment in canopy measurements, was similar to or greater than the control in all defoliation treatments. Correspondingly, in an Alberta, Canada prairie, *K. macrantha* increased in response to light rotational grazing (Smoliak, 1965). The increase in *K. macrantha* was corroborated by basal cover estimates. Basal cover is a resistant measure, more indicative of long-term change than canopy measurements (Cosgrove et al., 2001). These basal cover dynamics suggest that *K. macrantha* increased in not only foliage but also diameter or number of bunches as well. *K. macrantha* is a palatable native forage, making this a desirable shift. The native sedge, *C. duriuscula*, was similarly equivalent to or greater than the control under all seasons of defoliation. *C. duriuscula* may be a palatable early-season forage like its relative, *C. filifolia* (White and Currie, 1983), and, as a rhizomatous species, provides soil stability (Morgan and Rickson, 2003).

N. viridula, another palatable, native C3 grass, trended toward decreased basal cover in response to defoliation during summer compared with nondefoliated plots in 2014. *N. viridula* has been documented to decrease under grazing pressure, particularly when defoliation is severe or applied during the growing season, as it was in this case (Reed and Peterson, 1961). Though decreases in *N. viridula* by defoliation may be expected when compared with rest, decreases in this desirable, climax species can be minimized by application of light to moderate defoliation (Reed and Peterson, 1961).

B. gracilis, the only native C4 species observed to respond to fire, trended toward depressed basal cover on burned sites in 2014. This is in contrast to expectations, as *B. gracilis* is generally reported as favored or unaffected by dormant season fire (Ford, 1999). However, some studies have observed temporary reductions, lasting 1 or 2 yr post fire, attributed to decreased tillering (Launchbaugh, 1964; Whisenant and Uresk, 1989). As this tendency toward reduced basal cover on burned sites was not observed in either 2013 or 2015, we suspect the status of *B. gracilis* following fire was not at risk.

Native forbs, generally expected to increase following a dormant season fire (Biondini et al., 1989), showed mixed responses, with reduction of *S. coccinea* in 2014 and *A. viridiflora* in 2015 and a trend for increased *D. pinnata* in 2015. The increase in forbs reported by Biondini et al. (1989) occurred after repeated dormant season fires. As these data represent the effects of only one spring wildfire, the disturbance may not have been severe or frequent enough to produce a clear trend in the dynamics of the forb community. The slight shifts observed may be due to the temporary shift from competition for light, to competition for belowground resources caused by the removal of vegetation by the fire. Defoliation, contrastingly, had no effect on native forbs.

As a biennial species, the increases in *M. officinalis* due to spring defoliation in 2014 and fire in 2015 can be attributed to factors that either enhanced germination or seedling establishment in the year before flowering. *M. officinalis* emergence peaks in March and April (Van Assche et al., 2003). Seedlings emerging during this period on nonburned sites or following the fire would be released from light competition via the removal of the overstory vegetation. The increased light availability may have allowed for more seedlings to establish, overwinter, and flower in 2014. Fire effects were possibly delayed to 2015 if germination was enhanced by a combination of factors rather than by fire alone. Germination may have been enhanced through heat treatment via fire (Kline, 1984; Van Assche et al., 2003) and subsequent cold stratification during the 2013–2014 winter (Martin, 1945). This combined effect may have succeeded in breaking the coats of hard seed, improving germination success in 2014 and flowering in 2015 (Van Assche et al., 2003). Due to its biennial nature, without another fire, severe defoliation, or alternative germination enhancing event, the surges in *M. officinalis* should be short-lived.

Litter, identified as a moderator of soil moisture, temperature, (Hulbert, 1969) and erosive potential (Benkobi et al., 1993) was eliminated by fire in 2013, reduced compared with nonburned plots in 2014, and comparable across burned and nonburned sites by 2015. Bare ground displayed the inverse dynamics. This indicates that, given adequate moisture, differences in litter cover between burned and nonburned sites may not be distinguishable within three growing seasons following fire, regardless of defoliation the first postfire growing season. This is similar to observations in sagebrush steppe, where litter cover accumulated similarly following fire under grazing or rest (Bates et al., 2009), but appears to differ with results from mixed prairie where 50% postfire utilization depressed litter biomass 2 yr following fire (Vermeire et al., 2014). These results may not be incompatible, as a thinner or less dense litter layer may cover a similar area of the soil surface. Benefits of litter cover may be recovered by the second growing season following fire even if litter cover or mass is reduced, as was observed in burned and summer defoliated plots. A reduced litter layer on summer-burned sites provided soil moisture retention comparable with nonburned sites (Vermeire et al., 2011). Postfire utilization of

17–34% also resulted in similar litter accumulation across burned sites that are grazed or rested (Vermeire et al., 2014). As such, litter recovery following fire may be hastened by lighter utilization than employed in this study.

Mowing is not synonymous with grazing, and results may have differed had plots been grazed rather than mowed. However, neither is any particular form of grazing representative of grazing in general. Grazing is a process that is complex in its many forms and effects on vegetation. Manipulation of factors including animal selectivity, grazing seasonality, defoliation frequency, and grazing intensity is the foundation of grazing management. A recent meta-analysis comparing grazing and mowing effects on a variety of grassland conservation measures concluded some differences and many similarities exist between the two, but effect sizes were small (Tälle et al., 2016). Mowing events, as applied in this study, were of short duration and high intensity with tightly defined seasonality to test hypotheses about postfire defoliation versus rest and to compare plant response to seasonal timing of defoliation. Selectivity was limited to the relative differences between plant and cutting heights and was not assessed. Therefore, our defoliation treatments are most representative of a short-duration, high-intensity grazing system.

Implications

In no case did close, uniform defoliation at any time during the first growing season following the Pautre fire depress productivity in comparison with the control. Additionally, in only one case, *N. viridula* basal cover, was a trend toward decreased cover due to defoliation observed. These observations indicate that exclusion of defoliation following fire is not necessary for the maintenance of northern mixed prairie productivity or community composition. Additionally, defoliation need not be deferred until after seed set the first growing season following the fire. While a small number of minor, native species increased or decreased in response to fire or defoliation, the magnitude of the effects was small. With the exception of dynamics driven by *M. officinalis*, the community composition with respect to functional group remained relatively similar across fire and defoliation treatments throughout the study period. While litter cover initially decreased and bare ground increased due to fire, both were comparable with nonburned sites within three growing seasons following the fire, regardless of defoliation treatment. These results indicate that northern mixed-grass prairie productivity increases following spring wildfire and is resistant to postfire defoliation between late spring and early fall during the first postfire growing season. As such, less emphasis on postfire rest may be appropriate in this system. However, the large-scale dynamics driven by *M. officinalis* are a reminder that while the native vegetation of this system may be well adapted to and respond neutrally or positively to fire and postfire defoliation, the presence of prolific, invasive species can add a confounding, potentially undesirable dynamic to a system's response.

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