



# Contingency in Defoliation and Moisture Effects on Northern Mixedgrass Prairie Composition and Diversity<sup>☆</sup>



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## ABSTRACT

Little is known about how defoliation intensity and frequency alter plant community composition and diversity in northern Great Plains mixedgrass communities. We evaluated defoliation effects in combination with watering on vascular plant composition and diversity in two contrasting ecological sites, a drier upland and more mesic lowland, in the Dry Mixedgrass natural subregion of Alberta, Canada. Treatments were applied for three growing seasons (2010 through 2012, inclusive) and included defoliation regimes of high intensity at high frequency, high intensity at low frequency, low intensity at high frequency, and defoliation deferred until the end of the growing season. Moisture regimes were ambient and elevated. Defoliation rather than moisture was the primary determinant of plant composition after 3 yr, particularly in the lowland site. Watering effects on composition were more apparent in the drier upland. All growing season defoliation regimes markedly altered composition relative to the deferred control, with relatively minor differences in composition among growing season defoliation treatments, particularly in the mesic lowland site. We conclude that growing season defoliation alters mixedgrass composition by reducing canopy dominant grasses (*Pascopyrum smithii* and *Hesperostipa comata*) and releasing shorter-statured grasses and forbs, which can either increase or decrease diversity depending on site (edaphic) conditions and the relative dominance of midgrasses and shortgrasses (*Koeleria macrantha* and *Bouteloua gracilis*). Finally, increased moisture did not ameliorate defoliation effects during the growing season, suggesting compositional responses were predictable and independent of growing season defoliation regime.

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## Introduction

Grazing intensity and growing season precipitation are key determinants of plant species composition within grasslands. Early models of successional theory predicted that grassland composition responds similarly to these factors along a linear pathway (Clements, 1936). Grazing effects may also interact with precipitation, such that favorable growing conditions may ameliorate, and environmental or resource stress exacerbate, adverse effects of defoliation on plants (Milchunas et al., 1989). Within the mixedgrass prairie, dominant grasses include taller-statured decreaser species and more decumbent increasers (Coupland, 1961), suggesting that linear successional theory may adequately predict the relative effects of defoliation (grazing severity) and moisture (precipitation) on community composition.

As plant species composition influences aboveground phytomass in mixedgrass prairies (Smoliak, 1965; Willms and Jefferson, 1993), the maintenance of composition is an important objective of grazing management (Adams et al., 2005). Management recommendations are to stock conservatively to minimize defoliation intensity on desirable plants and, in turn, maximize range health and the abundance of tall-statured grasses under the premise that this will maximize ecosystem goods and services, including forage productivity (Adams et al., 2005).

Manipulation of defoliation regimes during the growing season represents another common management practice that may maintain desirable grassland composition. By regulating the distribution and timing of livestock presence, different grazing systems can improve control over defoliation timing and frequency (Derner et al., 1994). As a result, grazing systems involving intermittent defoliation such as rotational grazing are often perceived as superior for maintaining range health and forage productivity (Teague et al., 2013), despite recent evidence to the contrary (Briske et al., 2008; Briske et al., 2011). Nevertheless, because of growing interest in using these systems on semiarid grasslands, it is important to understand how various defoliation intensities and frequencies affect mixedgrass plant community composition, including under different moisture conditions.

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Overall plant diversity may also respond to changes in defoliation regime. Diversity can be defined on the basis of the number of species (i.e., richness), relative abundance of species (i.e., evenness), or an index that considers both these measures (e.g., Shannon's index; Shannon, 1948). Diversity is important because it promotes ecosystem productivity and stability (Tilman et al., 2001; Tilman et al., 2006) and has intrinsic and conservation value (Symstad and Jonas, 2011). Within grasslands of the Great Plains, defoliation can have varying influences on diversity, depending on whether tallgrasses or shortgrasses are dominant. Diversity peaks under moderate grazing in tallgrass prairie and at little or no grazing in shortgrass prairie (Milchunas et al., 1988). However, diversity responses within mixedgrass communities remain unclear given that both shorter and taller species codominate in these grasslands (Symstad and Jonas, 2011). Grazing intensity effects on mixedgrass diversity may also be indeterminate and site specific (Bai et al., 2001; Willms et al., 2002), but few studies have examined this directly using controlled defoliation.

Another key to understanding defoliation and moisture effects on plant community composition is to identify mechanisms driving those changes. These mechanisms can be classified as direct or indirect (McNaughton, 1979; White et al., 2014b). For example, moisture can promote plant growth but also indirectly alter growth of the same species due to changes in interspecific competition arising from differential growth responses of neighboring species. Likewise, defoliation can alter light, soil moisture, and soil temperature regimes, and, in turn, influence plant competition or even ameliorate defoliation effects. For instance, compensatory effects of defoliation may result from increased moisture availability and subsequent improvements to regrowth. This is because defoliation can reduce leaf area and associated evapotranspiration, thereby increasing water-use efficiency in plants (McNaughton, 1979), perhaps by promoting shoot growth over root growth (Caldwell et al., 1981).

This study evaluated defoliation and moisture effects on plant community composition and diversity in northern mixedgrass prairie. Specific questions addressed include: 1) What are the relative effects of defoliation and moisture on plant community composition? 2) Is composition more sensitive to defoliation intensity or frequency during the growing season? and 3) How does plant diversity within different ecosites respond to changes in defoliation regime? Additionally, this study examined changes in environmental conditions in response to treatments to better understand the mechanisms responsible for plant community divergence. Defoliation effects on soil moisture were of particular interest given that this may be one compensatory mechanism aiding plant recovery.

## Materials and Methods

### Site Description

Treatments were conducted at two sites, including a relatively mesic lowland and drier upland, both situated in the Brooks Plain of the Dry Mixedgrass Prairie Natural Subregion in Alberta, Canada (Adams et al., 2005). Mean annual precipitation and daily temperature are 354 mm and 4.2°C, respectively (Environment Canada, 2013), and the growing season (days above 5°C) is approximately 185 days (Alberta Agriculture and Rural Development, 2013). Sites were chosen on the basis of internal uniformity of topography (both were level) and an initial late-seral plant community composition. The lowland site (lat 50°53'40.2"N; long 111°52'26.3"W) was subirrigated from adjacent uplands and had a Gleyed Eluviated Brown Chernozemic soil (pH = 6.3, EC = 37  $\mu\text{s cm}^{-1}$ , organic matter content = 2.5%). Soil at this site was relatively finer (Sandy Loam) compared with the upland (Loamy Sand). The upland site (lat 50°52'23.8"N; long 111°52'26.2"W) had a Rego Brown Chernozemic soil (pH = 6.7, EC = 27  $\mu\text{s cm}^{-1}$ , organic matter content = 1.3%). Initial range health scores based on the Alberta Range Health Assessment Guide for both sites were 80%, or healthy (Adams et al., 2003),

and each had a long history of previous cattle grazing at moderate stocking rates (~0.6 animal unit month [AUM] ha<sup>-1</sup>).

### Experimental Design and Treatments

Treatments of defoliation and moisture were combined in a fully randomized factorial design (4 × 2), with six replicates per site. Treatments were applied to 1 × 1 m plots and separated by at least 0.5 m. Defoliation treatments were deferred (i.e., control), high intensity at low frequency (HILF), high intensity at high frequency (HIHF), and low intensity at high frequency (LIHF), conducted for three consecutive growing seasons from 2010 through 2012. In late May of 2010, all plots were initially hand raked to remove litter (standing dead tillers and thatch). Plots in the HIHF and HILF treatments were clipped at 2-cm height every 3 and 6 weeks, respectively, from late May through the end of August each year, and ensured extensive removal of leaf area. In contrast, LIHF plots were clipped at a more conservative 5-cm height every 3 weeks during the early and midportions of the growing season; this height was used to prevent shorter-statured species (e.g., *Bouteloua gracilis*) from escaping defoliation. All plots, including deferred plots, were clipped to a 2-cm stubble height in late August, typically after the growing season and coincident with the onset of dormancy brought on by moisture stress at the end of the summer. It is important to note that all plots received defoliation each year, including the deferred treatment. This was done to maintain consistency with ongoing land use (cattle grazing) in the region and also enable quantification of accumulated herbage yield responses, which are reported elsewhere. While end-of-year defoliation represented an intense defoliation event, our treatments facilitated testing of the additive impact of early-season and midseason growing season defoliation at different intensities and/or frequencies on plant community responses.

Moisture treatments included no watering (i.e., ambient moisture) and watering of plots to augment summer rainfall and maintain 150 mm of monthly precipitation throughout the growing season. Water was obtained from a freshwater wetland near the Mattheis Ranch headquarters and tested for salinity and nutrient content, both of which indicated negligible levels. This is roughly double the average precipitation in June, the month of highest rainfall, and was used to ensure soil moisture availability did not constrain plant growth. Watering occurred at approximately 10-d intervals from early June to late August. Ambient precipitation during the study period tended to be greater than the 30-yr average (Table 1), mostly due to wet conditions early in the growing season, especially in 2010 and 2012, followed by drier than average conditions in July and August.

### Vegetation and Environmental Assessment

We assessed plant species composition in 2010, 2011, and 2012, the final-year treatments were applied. During 2010 and 2011, composition was assessed in early June and late August with ocular estimates of vascular plant foliar cover, while in 2012 the same was done at three times during the growing season: May 27, July 10, and August 20. To encompass all species (e.g., short-lived ephemerals) and account for the variable abundance of cool- and warm-season species during the growing

**Table 1**

Growing season (April–August) and total growing season precipitation (mm) recorded at the Brooks weather station for 2010–2012 compared with the recent long-term (30-yr) average (Environment Canada, 2013).

Time period	2010	2011	2012	30-yr average (1981–2010)
April	42	20	30	17
May	89	25	59	39
June	88	81	153	65
July	35	32	13	45
August	33	25	40	35
Total	244	163	265	183

season, cover values from all assessments (June–August) were averaged to create a composite measure.

Soil moisture and soil temperature were measured every minute during the growing season (June to August) during 2012 with a 5TM sensor and EM50 data logger (Decagon Devices, Pullman, WA). The logger was programmed to store a single mean value every 24 h. This device uses signal filtering to minimize texture and salinity effects and has an accuracy of 3–4% in fine to medium textured soils (Czarnomski et al., 2005). Light was measured three times during the growing season in 2012 with an AccuPar LP-80 light meter (Decagon Devices, Pullman, WA) and recorded as the ratio of photosynthetically active radiation (PAR) ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) measured below and above the canopy. Phytomass harvested from each plot during individual defoliation events, including at year end in late August, was collected, dried at 60°C for 48 h, and weighed. Aggregate production for each plot was determined as the sum of all phytomass harvested throughout 2012.

#### Data Analysis

Shannon's diversity ( $H'$ ) was estimated for each plot as  $H' = -\sum (P_i \times \ln P_i)$ , where  $P_i$  is proportional foliar cover (relative to total cover) of each species. Simpson's dominance index was calculated as  $1/(\sum P_i^2)$ , where  $P_i$  is the same as defined earlier for all species. Evenness was calculated as  $H' \div \ln(s)$ , where  $s$  is species richness and  $\ln$  is the natural log. Shannon's diversity, evenness and richness, as well as soil moisture, soil temperature and PAR ratio measurements, were checked for normality and homogeneity of variance with Shapiro-Wilk and Levene's tests (SAS 9.2-SAS Institute, 1989), respectively, and subsequently analyzed with a two-way analysis of variance (ANOVA). Ecological sites were analyzed independently in 2012 due to diversity response interactions with defoliation ( $P < 0.001$ ). Mean separation tests of significant fixed effects (defoliation and moisture) and their interactions were Tukey's adjusted. Significance was assessed at an alpha of  $P \leq 0.05$ .

Multivariate techniques in PC-Ord v.6 (MJM Software Design, Gleneden Beach, OR) were used to summarize multidimensional plant community responses (using nonmetric multidimensional scaling [NMS]), assess whether plant composition responses were influenced by defoliation and moisture treatments (using a permutation-based MANOVA [PerMANOVA]), and identify the specific plant species driving community responses (using an indicator species analysis [ISA]). Sorensen's distance measure was used in all analyses. The perMANOVA assessed significance based on 4 999 randomizations and the proportion of randomized trials with an indicator cover greater or equal to the observed cover value. An indicator species analysis was run with 4 999 randomizations of the Monte Carlo test (Dufrene and Legendre, 1997). NMS procedures involved 100 runs with real data, a stability criterion of 0.000001, 10 iterations to evaluate stability, and a maximum of 500 iterations. The procedure was run five times to verify results. Using a vector scaling cut-off value of  $r^2 > 0.2$ , environmental factors (e.g., PAR ratio, soil moisture, and soil temperature), significant indicator species cover, and other metrics (e.g., accumulated aboveground phytomass, the proportion of total phytomass composed of forbs, and diversity metrics of Shannon's diversity and Simpson's dominance index, as well as species evenness and richness) were overlaid on the final ordination scatter plots from 2012 (Fig. 1).

## Results

#### Plant Community Composition

While plots were randomly assigned treatments within uniform ecological sites, to confirm whether any a priori differences occurred at the start of the study, perMANOVA tests were performed on initial composition (in late May 2010), which showed there were no initial defoliation ( $P \geq 0.43$ ) or moisture ( $P \geq 0.44$ ) effects at either site. By 2012, the perMANOVA tests indicated composition in the lowland ecological

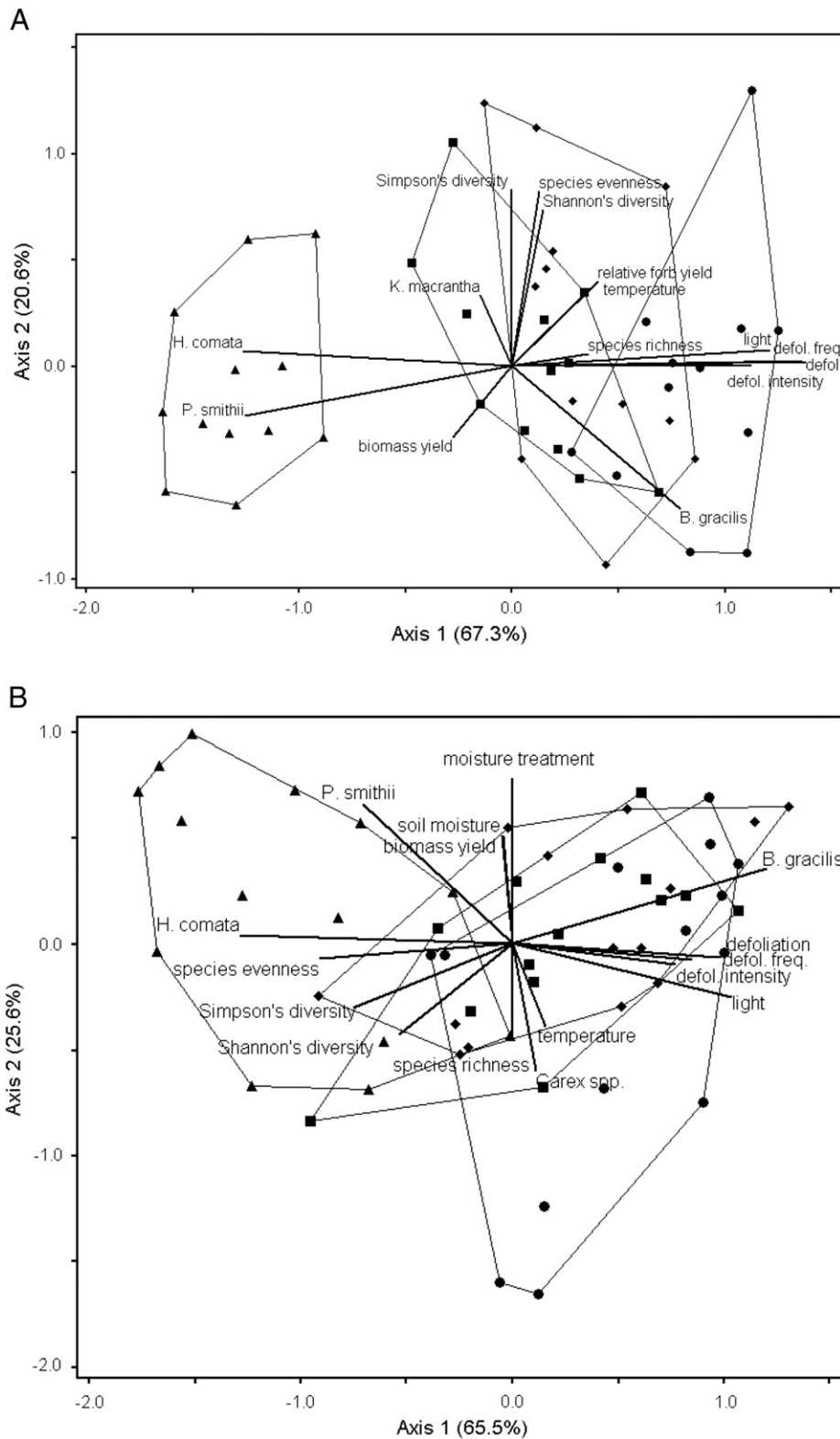
site was influenced by defoliation ( $F = 14.1, P < 0.001$ ) and moisture ( $F = 2.90, P = 0.032$ ), but not their interaction ( $F = 1.20, P = 0.30$ ). Moreover, all defoliation treatments differed from one another ( $P < 0.05$ ), indicating divergent effects of defoliation frequency and intensity during the growing season. Significant indicator plant species for the defoliation treatments included *Hesperostipa comata* ( $P < 0.001$ ) and *Pascopyrum smithii* ( $P < 0.001$ ) with deferred defoliation (Table 2), *Tragopogon dubius* ( $P = 0.006$ ) with HILF, *Koeleria macrantha* ( $P = 0.029$ ) and *Gaura coccinea* ( $P = 0.041$ ) with LIHF, and *Bouteloua gracilis* ( $P = 0.026$ ), *Cirsium arvense* ( $P = 0.048$ ) and *Crepis tectorum* ( $P < 0.001$ ) with HIHF. For the moisture treatments, only *B. gracilis* was associated with moisture addition ( $P = 0.017$ ).

Plant composition in the upland ecological site was influenced by both defoliation ( $F = 9.29, P < 0.001$ ) and moisture ( $F = 8.94, P < 0.001$ ) according to the perMANOVA. However, only the deferred treatment differed from all others ( $P < 0.001$ ), while the HILF, LIHF, and HIHF remained similar ( $P > 0.10$ ). The significant defoliation by moisture interaction in the PerMANOVA ( $F = 2.18, P = 0.022$ ) indicated communities under HILF were similar regardless of moisture treatment ( $P = 0.112$ ), whereas all other defoliation treatments differed under contrasting moisture treatments ( $P < 0.05$ ). Significant indicator species for defoliation again included *H. comata* and *P. smithii* with deferred defoliation ( $P < 0.001$ , and see Table 2), and *Carex* spp. was marginally significant for HIHF ( $P = 0.055$ ). Between moisture treatments, *P. smithii* ( $P < 0.001$ ) and *B. gracilis* ( $P = 0.046$ ) were associated with moisture addition, whereas *Carex* spp. ( $P = 0.010$ ) and *Erysimum inconspicuum* ( $P < 0.001$ ) were associated with ambient moisture, and *T. dubius* was marginally significant for the latter ( $P = 0.083$ ).

NMS ordination provided two-dimensional solutions for both study sites with final stress scores of 15.03 and 13.01 (min  $P = 0.0004$ ) for the lowland and upland sites, respectively. Axes 1 and 2 represented 67.3% and 20.6% of the species-axes variation, respectively, within the lowland site, and 65.5% and 25.6% of variation, respectively, in the upland site (see Fig. 1). In both sites, defoliation explained most species variance, as this treatment had a strong positive association with the primary (first) axis ( $r = 0.883$  and  $0.749$ , for the lowland and upland sites, respectively). In contrast, moisture treatment was associated with the second axis, though variably between sites. Moisture was negatively associated with the secondary axis in the lowland ( $r = -0.389$ ) and positively with the secondary axis in the upland ( $r = 0.668$ ). An overlay of environmental variables onto the ordinations suggested defoliation increased PAR ( $r > 0.76$ ) and soil temperature ( $r > 0.29$ ), as these were associated with the primary axis at both locations. Similarly, moisture addition was associated with the secondary axis in both sites ( $r > |0.30|$ ). Within the upland site specifically, PAR ( $r = 0.38$ ) and soil temperatures ( $r = 0.47$ ) were associated with the secondary axis, consistent with the moisture treatment, suggesting these parameters were reduced by moisture addition. These results were corroborated by the ANOVA results (Tables 3 and 4).

Ordination also showed that plant community diversity metrics corresponded differently with the primary axis at each site, suggesting defoliation had opposing effects on diversity at each location. For example, richness ( $r = 0.48$ ), Shannon's diversity ( $r = 0.41$ ), and evenness ( $r = 0.40$ ) were positively associated with the primary axis from the lowland site, although aboveground phytomass was negatively ( $r = -0.48$ ) associated with this same axis. Also in the lowland, the proportion of biomass composed of forbs was positively associated with the primary axis ( $r = 0.57$ ). Within the upland site, Simpson's dominance index ( $r = -0.65$ ), Shannon's diversity ( $r = -0.55$ ), and evenness ( $r = -0.72$ ) were all negatively associated with the primary axis. Indicator species responses were similar between sites, such that *H. comata* ( $r > |0.79|$ ) and *P. smithii* ( $r > |0.63|$ ) were negatively, and *B. gracilis* ( $r > 0.53$ ) positively, associated with the primary axis.

Combined, these results suggest select growing season defoliation regimes (HILF and LIHF) increased plant diversity in the lowland site relative to the deferred control by reducing canopy dominant, decrease



**Figure 1.** NMS ordination of (A) a lowland mixedgrass prairie site and (B) an upland mixedgrass prairie site, after 3 years of exposure to moisture and defoliation (frequency and intensity) treatments. Plots are overlaid ( $|r| > 0.2$ ) with treatments, environmental parameters (light [PAR], soil temperature, and soil moisture), diversity measures (Shannon's, Simpson's, evenness, and richness), significant ( $P < 0.05$ ) indicator species (*Pascopyrum smithii*, *Hesperostipa comata*, *Koeleria macrantha*, and *Bouteloua gracilis*), plot biomass yield, and relative forb yield (proportion of plot biomass consisting of forbs). Percent of variation associated with each axis is in parentheses, and shapes represent defoliation treatments: deferred control [▲], high intensity at low frequency [■], low intensity at high frequency [◆], and high intensity at high frequency [●].

grasses (*H. comata* and *P. smithii*) and promoting the shortgrass species *B. gracilis*, while at the same time reducing aboveground phytomass and favoring other forbs. In contrast, high-frequency defoliation regimes

(LIHF, HIHF) reduced diversity (but not richness) in the upland site relative to the deferred control, apparently by similarly reducing the abundance of dominant grasses. Canopy-dominant grasses may have been

**Table 2**

Comparison of the mean ( $\pm 95\%$  confidence interval) cover of dominant grasses among the defoliation treatments within each of the lowland and upland ecological sites during 2012. Data on initial composition of the deferred treatment in 2010 are shown for comparison. All data are averaged for ambient and moisture addition treatments.

Site Treatment	<i>Pascopyrum smithii</i>	<i>Hesperostipa comata</i>	<i>Koeleria macrantha</i>	<i>Bouteloua gracilis</i>
<b>Lowland site</b>				
Deferred (initial)	23.3 ( $\pm 4.5$ )	32.1 ( $\pm 6.0$ )	3.8 ( $\pm 5.6$ )	4.2 ( $\pm 1.6$ )
Deferred	58.2 ( $\pm 10.6$ )	17.4 ( $\pm 3.9$ )	13.0 ( $\pm 4.8$ )	8.9 ( $\pm 3.2$ )
HILF	18.8 ( $\pm 3.7$ )	8.1 ( $\pm 2.7$ )	7.4 ( $\pm 2.4$ )	30.6 ( $\pm 8.5$ )
LIHF	15.3 ( $\pm 4.7$ )	3.0 ( $\pm 2.0$ )	15.5 ( $\pm 6.1$ )	29.9 ( $\pm 9.7$ )
HIHF	12.8 ( $\pm 4.2$ )	1.9 ( $\pm 1.0$ )	1.9 ( $\pm 1.3$ )	38.1 ( $\pm 10.3$ )
<b>Upland site</b>				
Deferred (initial)	17.5 ( $\pm 4.7$ )	33.2 ( $\pm 9.6$ )	0	18.2 ( $\pm 7.6$ )
Deferred	29.6 ( $\pm 9.7$ )	27.8 ( $\pm 6.9$ )	1.6 ( $\pm 1.8$ )	19.5 ( $\pm 4.4$ )
HILF	10.3 ( $\pm 3.0$ )	11.3 ( $\pm 3.3$ )	0.2 ( $\pm 0.5$ )	44.0 ( $\pm 9.1$ )
LIHF	12.2 ( $\pm 5.2$ )	9.2 ( $\pm 3.7$ )	0.1 ( $\pm 0.2$ )	45.6 ( $\pm 11.3$ )
HIHF	8.2 ( $\pm 3.4$ )	4.8 ( $\pm 2.6$ )	0.4 ( $\pm 0.5$ )	41.2 ( $\pm 12.2$ )

HILF, high intensity at low frequency; LIHF, low intensity at high frequency.

less prevalent in the deferred treatment of the upland site, which was the case for *P. smithii*, and earlier defoliation failed to promote the abundance of forbs to the same degree at this location.

Despite some minor discrepancies, moisture addition generally had a similar influence on diversity and species responses within both sites. Both Simpson's dominance index ( $r > |0.41|$ ) and Shannon's diversity ( $r > |0.45|$ ) were consistently associated with the secondary axis. Evenness ( $r = 0.49$ ) and richness ( $r = -0.51$ ) were associated with the secondary axis in the lowland and upland sites, respectively. Within the upland site, phytomass ( $r = 0.54$ ) and the relative contribution of forbs to plant biomass ( $r = -0.39$ ) were positively and negatively, respectively, associated with the secondary axis. Across both sites, *B. gracilis* was consistently associated with the secondary axis ( $r > |0.45|$ ), a result confirmed by the indicator species analyses. Overall, moisture addition reduced diversity at both sites (this was confirmed by the ANOVA for the upland site only) by promoting *B. gracilis* and reducing forbs.

A total of 47 different plant species were documented, with 33 and 29 in the lowland and upland sites, respectively. In the lowland, only defoliation influenced diversity (Shannon's index), richness, and evenness

**Table 3**

Summary of analysis of variance *F* and *P* values for tests of the defoliation and moisture treatments on plant community attributes (Shannon's diversity, species richness and evenness) and environmental conditions (photosynthetically active radiation ratio, soil moisture, and soil temperature) within both a lowland and upland ecological site in the mixedgrass prairie. Subscripts with *F* values indicate numerator and denominator degrees of freedom, respectively.

Site Treatment	Shannon's diversity		Species richness		Species evenness	
	<i>F</i> value	<i>P</i> value	<i>F</i> value	<i>P</i> value	<i>F</i> value	<i>P</i> value
<b>Lowland site</b>						
Defoliation	6.67 <sub>3, 40</sub>	<0.001	4.55 <sub>3, 40</sub>	0.008	6.53 <sub>3, 40</sub>	0.001
Moisture	2.15 <sub>1, 40</sub>	0.15	0.30 <sub>1, 40</sub>	0.59	3.16 <sub>1, 40</sub>	0.083
Def. x moist.	0.72 <sub>3, 40</sub>	0.55	0.12 <sub>3, 40</sub>	0.95	1.12 <sub>3, 40</sub>	0.35
<b>Upland site</b>						
Defoliation	3.76 <sub>3, 48</sub>	0.017	0.64 <sub>3, 48</sub>	0.59	5.10 <sub>3, 48</sub>	0.004
Moisture	7.45 <sub>1, 48</sub>	0.009	8.40 <sub>1, 48</sub>	0.006	0.41 <sub>1, 48</sub>	0.52
Def. x moist.	1.33 <sub>3, 48</sub>	0.28	1.05 <sub>3, 48</sub>	0.38	0.48 <sub>3, 48</sub>	0.69
Site Treatment	PAR ratio		Soil moisture		Soil temperature	
	<i>F</i> value	<i>P</i> value	<i>F</i> value	<i>P</i> value	<i>F</i> value	<i>P</i> value
<b>Lowland site</b>						
Defoliation	96.3 <sub>3, 40</sub>	<0.001	0.01 <sub>3, 40</sub>	1.00	12.0 <sub>3, 40</sub>	<0.001
Moisture	28.8 <sub>1, 40</sub>	<0.001	44.4 <sub>1, 40</sub>	<0.001	24.3 <sub>1, 40</sub>	<0.001
Def. x moist.	2.58 <sub>3, 40</sub>	0.067	2.87 <sub>3, 40</sub>	0.048	1.75 <sub>3, 40</sub>	0.17
<b>Upland site</b>						
Defoliation	118.8 <sub>3, 48</sub>	<0.001	0.65 <sub>3, 48</sub>	0.59	5.77 <sub>3, 48</sub>	0.002
Moisture	42.0 <sub>1, 48</sub>	<0.001	112.7 <sub>1, 48</sub>	<0.001	37.2 <sub>1, 48</sub>	<0.001
Def. x moist.	10.6 <sub>3, 48</sub>	<0.001	0.54 <sub>3, 48</sub>	0.66	2.00 <sub>3, 48</sub>	0.13

(all  $P < 0.01$ ; Table 3), with no effect of moisture treatment on any diversity metric ( $P > 0.08$ ). Within the upland, moisture treatment influenced diversity and richness (both  $P < 0.01$ ), and defoliation influenced diversity and evenness (minimum  $P < 0.02$ ). At both sites, growing season defoliation treatments remained similar to one another in diversity, richness and evenness, but select differences existed between the growing season treatments and the deferred control. Within the lowland site, high-frequency defoliation (LIHF and HIHF) had greater richness relative to the deferred defoliation treatment, while both the HILF and LIHF had greater Shannon's diversity and evenness relative to the deferred control (Table 4). Species richness did not respond to defoliation within the upland ( $P = 0.59$ ), but both the LIHF and HIHF had lower diversity and evenness compared with the deferred treatment at this location (see Table 4). Finally, moisture addition reduced species richness and diversity in the upland ( $P < 0.01$ ) but did not alter evenness ( $P = 0.52$ ) (see Table 4).

### Environmental Responses

At both sites, the defoliation and moisture treatments influenced PAR and soil temperature (minimum  $P < 0.002$ ; see Table 3), whereas soil moisture was influenced by the moisture treatments only ( $P < 0.001$ ). Additionally, there was a defoliation by moisture interaction influencing PAR in the upland ( $P < 0.001$ ), but not the lowland ( $P = 0.067$ ). Defoliation increased PAR levels relative to deferred defoliation by at least 64% and 39% in the lowland and upland sites, respectively, with the greatest increases evident under HIHF defoliation (see Table 4). In contrast, moisture addition reduced PAR by 13% and 9% in the lowland and upland sites, respectively. However, a defoliation by moisture interaction within the upland site ( $P < 0.001$ ) revealed moisture addition reduced PAR only in the deferred defoliation treatment at this location. The nearly significant defoliation by moisture interaction ( $P = 0.067$ ) at the lowland site indicated moisture addition reduced PAR under both deferred and HILF defoliation (data not shown). All early-season defoliation treatments increased soil temperatures by at least 0.5°C, and plots were slightly warmer ( $\approx 0.6^\circ\text{C}$ ) under the ambient moisture treatment.

Predictably, water addition increased soil moisture by 24% and 40% in the lowland and upland sites, respectively. However, a defoliation by moisture interaction occurred in the lowland site ( $P = 0.048$ ) where in water addition increased soil moisture only within the deferred and HILF treatments.

### Discussion

#### Mixed-Prairie Comparative Responses to Defoliation and Moisture

Previous studies have drawn contrasting conclusions about whether grazing intensity or interannual variability of precipitation is the predominant driver of plant community compositional change in grasslands (precipitation: Biondini and Manske, 1996; Biondini et al., 1998; Buitenwerf et al., 2011; grazing: Fuhlendorf et al., 2001). Mixedgrass composition in this study after 3 yr of treatment was influenced predominantly by growing season defoliation at both sites, although moisture treatment effects remained apparent and were relatively more important in the drier upland. The latter finding is notable given that ambient moisture conditions were above average for part of the study period, which could have reduced the magnitude of moisture-induced treatment effects on plant composition.

Defoliation effects were particularly evident at the mesic lowland site, within which plant communities of divergent composition had formed in relation to all growing season defoliation regimes according to the PerMANOVA. Although edaphic conditions varied between study sites, other characteristics also differed between the lowland and upland sites, the most notable being initial plant species composition. Late-seral, grazing-sensitive grasses such as *P. smithii* and

**Table 4**

Means and standard errors (in parentheses) for plant species diversity (Shannon's index), richness, and evenness, as well as photosynthetically active radiation (PAR) ratio (comparing below to above the canopy), volumetric soil moisture, and soil temperature (°C) under defoliation (deferred [control], high intensity at low frequency [HILF], low intensity at high frequency [LIHF], and high intensity at high frequency [HIHF]) and moisture (ambient vs. addition) treatments. Post hoc mean comparisons are Tukey's adjusted. Data represent responses in the third consecutive year of treatment (2012). Within rows, means with different letters differ ( $P < 0.05$ ). NS indicates the main effect was nonsignificant.

	Defoliation				SE	Moisture		SE
	Control	HILF	LIHF	HIHF		Addition	Ambient	
<b>Lowland site</b>								
Shannon's diversity	1.45 <sup>B</sup>	1.81 <sup>A</sup>	1.78 <sup>A</sup>	1.63 <sup>AB</sup>	(0.06)	NS		—
Species richness	7.92 <sup>B</sup>	9.42 <sup>AB</sup>	10.50 <sup>A</sup>	10.08 <sup>A</sup>	(0.53)	NS		—
Species evenness	0.67 <sup>B</sup>	0.78 <sup>A</sup>	0.77 <sup>A</sup>	0.72 <sup>AB</sup>	(0.02)	NS		—
PAR ratio	0.48 <sup>C</sup>	0.79 <sup>B</sup>	0.78 <sup>B</sup>	0.87 <sup>A</sup>	(0.02)	0.68 <sup>b</sup>	0.78 <sup>a</sup>	(0.01)
Soil moisture	NS	—	0.31 <sup>a</sup>	0.25 <sup>b</sup>	(0.01)			
Temperature	18.94 <sup>B</sup>	19.82 <sup>A</sup>	19.52 <sup>A</sup>	19.75 <sup>A</sup>	(0.12)	19.22 <sup>b</sup>	19.79 <sup>a</sup>	(0.08)
<b>Upland site</b>								
Shannon's diversity	1.54 <sup>A</sup>	1.38 <sup>AB</sup>	1.26 <sup>B</sup>	1.26 <sup>B</sup>	(0.07)	1.27 <sup>b</sup>	1.45 <sup>a</sup>	(0.05)
Species richness	NS	—	6.14 <sup>b</sup>	7.43 <sup>a</sup>	(0.31)			
Species evenness	0.81 <sup>A</sup>	0.74 <sup>AB</sup>	0.69 <sup>B</sup>	0.65 <sup>B</sup>	(0.03)	NS	—	
PAR ratio	0.64 <sup>C</sup>	0.89 <sup>B</sup>	0.88 <sup>B</sup>	0.94 <sup>A</sup>	(0.01)	0.80 <sup>b</sup>	0.88 <sup>a</sup>	(0.01)
Soil moisture	NS	—	0.21 <sup>a</sup>	0.15 <sup>b</sup>	(0.004)			
Temperature	20.99 <sup>B</sup>	21.58 <sup>A</sup>	21.51 <sup>A</sup>	21.53 <sup>A</sup>	(0.12)	21.05 <sup>b</sup>	21.75 <sup>a</sup>	(0.08)

*H. comata* were more prevalent in the lowland, where they were closely associated with deferred defoliation after 3 yr. Other studies support the notion that defoliation effects are greater under higher moisture (Gillen and Sims, 2006; Cheng et al., 2011). This may occur because more productive areas tend to have greater species richness (Connell and Orias, 1964), and consequently, competitive interactions among plants may play a larger role in regulating composition (Grime, 2001). This is supported here as the lowland site had 40% greater richness compared with the upland, and with contrasting tolerances and responses to defoliation, a more species rich pool could account for the observed increase in diversity.

As the relative influence of water addition on community composition differed between sites, moisture effects are likely to differ across areas with contrasting soil conditions. This could account for why a generalized ecological theory regarding drivers of species composition in Great Plains grasslands remains so elusive (see Symstad and Jonas, 2011). Nevertheless, drought is commonly recognized as a significant driver of plant community change (Biondini and Manske, 1996; Biondini et al., 1998), and the relative effect of both defoliation and moisture is likely to depend on the magnitude of a given perturbation. By more than doubling growing season precipitation, soil moisture regimes were markedly altered in this experiment, though ambient rainfall remained modestly elevated during at least a portion of two growing seasons. As community composition of plots presumably equilibrated under the prevailing moisture regimes, the lack of a severe soil moisture limitation within our ambient plots may have constrained effects of moisture treatment in this study. Interestingly, weather data collected by Agriculture and AgriFood Canada at the Onefour Research Station, about 150 km southeast of the current study area, indicates average annual precipitation has risen from 280 mm over the period 1929–1948 to 353 mm between 1994 and 2013. Moreover, while effects of defoliation on plant communities may be relatively acute (Butler and Briske, 1988), the time frame for this experiment was quite short (3 yr) and the effects of interannual variation in precipitation may manifest under longer time periods (Smoliak, 1986). For example, White et al., (2014a) documented greater resistance in grassland biomass to extended drought in arid mixedgrass prairie of Saskatchewan compared with grasslands in wetter climatic zones of neighboring Alberta and Manitoba.

Favorable moisture may also influence the composition of perennial grasses by promoting tiller recruitment given that regeneration by seed can account for less than 1% of annual tiller increases (Benson and Hartnett, 2006). Meristem limitations can occur in grasses of semiarid regions (Dalglish and Hartnett, 2006), and with parent tillers relying on annual tillering for regeneration (Langer, 1956; Hendrickson and Briske, 1997), the ability of grasses to increase in abundance may

depend on its preexisting tiller population, coupled with the ability of those tillers to recruit more ramets each growing season. Indeed, tiller recruitment following growing seasons of high precipitation may not occur until subsequent growing seasons (Hendrickson et al., 2000) and could explain why semiarid grasslands fail to realize the same relative biomass increases during wet periods that occur in humid grasslands (Knapp and Smith, 2001; Reichmann et al., 2013). As our moisture addition treatments increased total herbage yield (by 89% in 2012; unpublished data) despite minimal changes in species composition, we postulate that these yield improvements reflect short-term increases in the size of existing mixedgrass plants rather than compositional changes. The northern mixedgrass prairie generally goes through decadal shifts in moisture regime (Sauchyn et al., 2003; Trouet et al., 2013) and, coupled with slow plant demographic responses, may require longer-term experiments to fully test compositional responses.

Two important grass species positively associated with moisture addition in this experiment were *B. gracilis* and *P. smithii*. The former is a decumbent, warm-season grass that increases with grazing, whereas the latter is a canopy-dominant, cool-season species known to decline under increased grazing (Coupland, 1961; Smoliak, 1974). This shared response to moisture addition is perplexing considering these grasses have contrasting morpho-physiological characteristics. However, one feature common to these grasses is that both are rhizomatous in the prairie of western Canada (Moss, 1994), with *B. gracilis* having short rhizomes in this region, unlike its relatives in the southern plains. Rhizomatous grasses are often associated with humid areas of the Great Plains (Sims et al., 1978; Mack and Thompson, 1982), suggesting rhizomes favor grasses in mesic environments. Rhizomes are underground shoots that are a source of meristems (basal buds), as well as stored carbohydrates and nutrients for growth (Reece et al., 2001). Rhizomes act as connective tissue for resource sharing between tillers (Cullen et al., 2005) and between tillers and roots of successive tiller generations (Jonsdottir and Callaghan, 1988). Consequently, rhizomes may assist tiller recruitment under high soil moisture by ameliorating meristem limitations, directly providing stored resources for growth, and promoting water and nutrient uptake, as well as resource sharing among genets.

#### Composition Responses to Defoliation Frequency and Intensity

Another objective of this study was to examine whether defoliation frequency or intensity during the growing season differentially influenced plant community composition in mixedgrass prairie. Grazing systems are often used to control defoliation timing, frequency, and/or intensity (Teague et al., 2013). Indeed, the impetus for grazing systems is based on the perception that regulating the timing and frequency of

defoliation can maintain a desirable plant community (Briske et al., 2008). Results here suggest that overall differences in grassland composition arose primarily due to the presence of growing season defoliation, with only minor variation therein due to changes in defoliation regime. Moreover, while useful for testing specific defoliation impacts, we caution that the controlled defoliation study used here is unlikely to fully represent the complex ecological impacts of cattle grazing likely to occur in grasslands due to the removal of animal trampling, nutrient redistribution, and selective defoliation.

The more productive, taller-statured grasses (*H. comata* and *P. smithii*) favored by deferred (i.e., dormant season) defoliation appeared to be largely responsible for the differentiation in composition among plant communities in response to defoliation, particularly in the drier upland site. Although unique communities formed under each defoliation treatment in the lowland, growing season defoliation treatments remained more similar to one another than to the deferred “control,” and the former did not lead to marked divergence in richness or diversity from one another. Of the three combinations of variable intensity and frequency of growing season defoliation tested, the HILF regime produced a community most similar to the deferred control, while HIHF defoliation was most dissimilar. This provides some evidence that defoliation frequency, rather than intensity, may play a greater role in regulating composition by helping maintain late-seral, canopy-dominant grasses in mixedgrass prairie, at least in more mesic areas where midgrasses (wheat grasses and needle grasses) dominate.

#### Plant Diversity

Defoliation and moisture had divergent effects on plant diversity at the two sites examined. Indeed, both Willms et al., (2002) and Bai et al., (2001) found that mixedgrass prairie diversity responses to grazing were site dependent. Within the Great Plains, diversity is hypothesized to peak under moderate grazing in tallgrass prairie and no grazing in shortgrass prairie (Milchunas et al., 1988). The more mesic lowland and xeric upland sites examined here had responses similar to those hypothesized for tallgrass and shortgrass prairies, respectively.

Our results from the lowland indicate growing season defoliation promotes diversity in mixedgrass prairie because it reduces the abundance of canopy dominant grasses, thereby providing a niche for forbs and allowing more decumbent, grazing-tolerant grasses to increase. This was corroborated here by the tallest grasses, *H. comata* and *P. smithii*, which were more abundant under deferred defoliation in the lowland site. Reducing these grasses with growing season defoliation promoted forbs, including *Tragopogon dubius*, *Gaura coccinea*, and *Crepis tectorum*, as well as the invasive weed *Cirsium arvense*. Although forbs make up a relatively small proportion of plant biomass compared with grasses within prairie systems, they contribute disproportionately more to diversity (Damhoureyeh and Hartnett, 1997). In contrast, growing season defoliation may reduce diversity in arid mixedgrass communities (similar to the upland site tested here) because of increases in the prevalence of already dominant grazing-tolerant shortgrasses (Milchunas et al., 1988). Defoliation impacts at this location specifically increased *B. gracilis* at the expense of *P. smithii* and *H. comata*, and this may have limited species richness responses to increasing intensity and frequency of defoliation.

Moisture conditions also changed diversity, but only in the upland site. Substantial moisture limitations under ambient rainfall may have allowed for a greater number of minor plant species to flourish at this location. Contrary to evidence that richness is greater in more mesic communities (Connell and Orlas, 1964), and in wetter years compared with drier years (Adler and Levine, 2007; Wilson, 2007), moisture addition unexpectedly reduced richness and diversity within the upland. This treatment also increased *P. smithii* and *B. gracilis*, suggesting these perennial grasses may have outcompeted other plant species under high moisture.

#### Role of Environment in Regulating Composition

Defoliation and moisture effects on plants, and thus community composition, can be both direct and indirect (McNaughton, 1983; White et al., 2014b). Although direct effects influence plant morphology via the loss of photosynthetic tissue, indirect effects result through altered environmental conditions and may compensate for direct effects. For example, defoliation may improve plant water status by reducing evapotranspiration and increasing soil moisture availability (McNaughton, 1979), which is important given that moisture and fertility limit production in semiarid grasslands (Willms and Jefferson, 1993; Burke et al., 1998). Studies from other grasslands in Alberta have found that defoliation and grazing can increase (Deutsch et al., 2010), decrease (Naeth et al., 1991; Zhao et al., 2011), or have no effect on soil moisture (Mapfumo et al., 2003), the latter of which was observed in this study. Soil temperature and PAR were both greater under growing season defoliation and could have increased evaporation, which would nullify beneficial effects of defoliation on moisture conservation through reduced transpiration. While water addition increased moisture, it also reduced soil temperature and PAR availability, suggesting enhanced vegetation growth may have led to greater competition for light.

#### Management Implications

A number of conclusions can be drawn regarding the role of defoliation and moisture in regulating mixedgrass prairie composition. First, these communities were sensitive to all growing season defoliation regimes after 3 yr, especially in wetter, more productive areas, than to changes in moisture, although the latter may play a greater role in drier areas of the landscape. Moisture availability also did not alter or ameliorate growing season defoliation effects on composition. Aside from deferring defoliation, controlling defoliation frequency, as opposed to intensity, may help mitigate defoliation impacts during the early to mid-summer growing season on the abundance of late-seral, grazing-susceptible perennial grasses. Second, the primary effect of growing season defoliation on community composition appeared to be a reduction in canopy-dominant, taller-statured grasses, which in turn, either increased or decreased plant diversity, depending on site conditions. Where taller grasses predominated, higher diversity occurred through the release of forbs, which may have benefited from increased resources, including light. Where taller grasses are less prevalent, diversity may decrease given that shortgrasses dominate and displace other species. Similarly, increasing moisture may reduce diversity in mixedgrass communities by favoring competitive perennial grasses well adapted to exploit moisture increases, particularly rhizomatous species such as *B. gracilis* and *P. smithii*. Overall, these results indicate growing season defoliation has the potential to influence grassland composition and diversity in as little as 3 yr. Where defoliation is to take place during early to mid-summer in areas where midgrasses dominate, an HILF defoliation regime may be better able to maintain late-seral, grazing-susceptible grasses and lead to conditions more similar to that observed under deferred defoliation.

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