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Original Research

Intermittent Growing Season Defoliation Variably Impacts Accumulated Herbage Productivity in Mixed Grass Prairie☆

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ABSTRACT

To evaluate mechanisms by which defoliation alters grassland productivity, we examined mixed grass prairie herbage yields under recurring treatments that included hand-clipping of plots over five growing seasons at high intensity and low frequency (HILF), low intensity and high frequency (LIHF), high intensity and high frequency (HIHF), or the end of the growing season (deferred control), combined with water treatments of ambient rainfall or water addition. The study was repeated in a drier upland and mesic lowland range site. Yield was assessed as annual accumulated herbage production and, for HILF and control treatments in 2012 (year 3), evaluated separately for forbs and major graminoids. Temporal changes in the proportional yield during the growing season were also examined for the HILF and HIHF treatments. Moisture addition increased accumulated herbage, especially in the upland, and exacerbated differences among defoliation effects in select years. Productivity was greatest in the deferred controls, suggesting no treatment led to overcompensation, even with moisture addition. Among growing season treatments, yields under HILF exceeded that of the HIHF in 6 of 10 different combinations of site and year, particularly early in the study and under high moisture. Observed herbage yields suggest deferred patches of grassland may boost productivity and limit the ability of HILF defoliation to increase production, a pattern magnified by a reduction in *Pascopyrum smithii* in lowlands before mid-July. Accumulated herbage yield did respond favorably to HILF defoliation in uplands due to increased yields of *Bouteloua gracilis* (Willd. *ex* Kunth) Lag. *ex* Griffiths. Overall, these results suggest that any growing season defoliation reduces yields, although where defoliation is necessary at that time, production may be more likely to be maintained under HILF defoliation. More studies examining long-term growth responses to defoliation that include variation in vegetation types, environmental conditions, and defoliation regime are warranted.

Introduction

Compelling arguments have been made regarding the superiority of rotational grazing (RG) over season-long continuous grazing (CG) (Savory, 1999; Teague et al., 2013; Voisin, 1961). There are many variations of RG, but the general process involves subdivision of a land area into smaller paddocks where livestock grazing is concentrated for shorter periods. RG can differ from CG if animal density is used to reduce selectivity and promote uniformity of grazing (e.g., De Bruijn and Bork 2006). Managerial control over defoliation timing and frequency under RG allows for extended rest periods between grazing events (Derner et al., 1994; Volesky, 1994). Provided sward productivity is maximized at some optimal defoliation intensity, frequency, and timing (McNaughton, 1983), RG in theory could maximize accumulated herbage yield. However, recent meta-analyses suggest RG does not increase productivity relative to CG on rangelands (Briske et al., 2008; Holechek et al., 2000), though no definitive explanations exist as to why. To reconcile this, it may be necessary to first understand the fundamental trade-offs associated with variation in growing season defoliation intensity and frequency on plant productivity, which, in turn, requires controlled manipulative studies.

Rangelands often consist of arid to semiarid native grasslands, but RG may be better suited to pastures composed of grazing tolerant forages and relatively mesic soils. Indeed, northern temperate pastures dominated by introduced forages have been found to tolerate intense and infrequent defoliation and yield similarly to, or in some cases more than, both defoliation deferred until the end of the growing season and low-intensity defoliation regimes conducted at high frequencies (De Bruijn and Bork, 2006; De Bruijn et al., 2010; Donkor et al., 2002; Donkor et al., 2003). Similar responses have been documented for native grasslands in the tall grass prairie (Turner et al., 1993) and

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saltmarshes (Hik et al., 1991), as well as introduced swards of *Bromus inermis* (Dyer et al., 1991). Unifying characteristics among these studies appear to be that the dominant plant species tested had high grazing tolerance and/or environments favorable for regrowth (e.g., high moisture and fertility) for much of the growing season. Under these conditions, primary constraints on productivity tend to be available light and space for growth (Burke et al., 1998), which, in turn, may increase productivity from recurrent growing season defoliation through reduced litter accumulation (Knapp and Seastedt, 1986) or increased nutrient cycling (Hik et al., 1991).

In contrast, productivity may be constrained by low soil moisture and nutrients in arid grasslands (Burke et al., 1998; Willms and Jefferson, 1993). Additionally, vegetation under these conditions may be less tolerant of defoliation and therefore fail to respond favorably to intermittent defoliation within the growing season, in part because the time required for recovery exceeds growing season length (Bailey and Brown, 2011). Even in the Great Plains of North America, where vegetation evolved under abundant herbivory (Mack and Thompson, 1982), historical grazing likely involved long "rest" periods between defoliation events. Herbivores may have tracked wildfire and rainfall, preferentially grazing previously defoliated and burned areas to capitalize on regrowth (Fuhlendorf and Engle, 2001; Vinton et al., 1993). Thus although intense mob grazing may have occurred, it was seldom recurrent in a given location within a single growing season (McNaughton, 1993). The resulting regime of intense defoliation followed by long recovery could have maximized productivity (Douglas and McNaughton, 1993), with a lack of adequate rest following grazing limiting productivity (Milchunas and Lauenroth, 1993; Pantel et al., 2010). This notion brings into question the ability of semiarid grasslands to maintain production under multiple bouts of defoliation within a growing season.

For mixed grass prairies of the Great Plains, productivity may also decline under recurrent grazing because of changes in plant composition. The mixed grass is so named because mid and short grasses coexist (Coupland, 1961), and these groups are differentially adapted to either canopy dominance or defoliation tolerance, respectively (Milchunas et al., 1988). Under increased grazing pressure, late-seral mid grasses are replaced by defoliation tolerant short grasses (Weaver, 1954), a response also evident with frequent, intense summer defoliation (Broadbent et al., 2016). This change is accompanied by a decrease in productivity given that short grass species such as *Bouteloua gracilis* (Willd. *ex* Kunth) Lag. *ex* Griffiths are less productive than canopy-dominant mid grasses, including *Hesperostipa comata* (Trin. & Rupr.) Barkworth and *Pascopyrum smithii* (Rydb.) Á. Löve (Coupland, 1961; Smoliak, 1965; Willms and Jefferson, 1993).

This study examined forage yield within the mixed grass prairie under extended treatments of different intensities and frequencies of growing season defoliation, combined with different moisture and edaphic conditions. We use this manipulative experiment to theorize that if plant communities can tolerate some intermittent level of defoliation during the growing season, and potentially result in favorable regrowth, then RG may have merit in increasing accumulated season-long forage yields relative to CG. Specific research objectives were to 1) quantify aggregate production responses under various combinations of growing season defoliation intensity and frequency, 2) investigate whether moisture conditions exacerbate or dampen these yield differences, and 3) use these variable production responses to model potential aggregate yield differences between RG and CG systems.

Methods

Site Description

Two study sites were investigated, both located in the mixed grass prairie natural subregion of SE Alberta, Canada (Adams et al., 2005), approximately 35 km north of Brooks, Alberta. Mean annual precipitation and daily temperature in this area are 354 mm and 4.2°C, respectively (Adams et al., 2005). Sites had contrasting edaphic conditions but were internally uniform in topography and vegetation composition. Site 1 (50°53′40.2″N; 111°52′26.3″W) was a mesic lowland with a Gleyed Eluviated Brown Chernozemic soil (Soil Classification Working Group [SCWG], 1998) of sandy loam texture (pH = 6.3, EC = 37 μs cm^{-1}, organic matter = 2.5%). Vegetation consisted mostly of *P. smithii,* with *Koeleria macrantha* (Ledeb.) J. A. Schultes and *H. comata* subdominant. Site 2 (50°52′23.8″N; 111°52′26.2″W) was a relatively xeric upland with a Rego Brown Chernozemic soil (SCWG, 1998) of loamy sand texture (pH = 6.7, EC = 27 μs cm^{-1}, organic matter = 1.3%). Dominant vegetation at this site included *P. smithii, H. comata,* and *B. gracilis.* Both sites were grazed by cattle before the start of this investigation at light to moderate stocking rates in a rotational system and had range health scores of 80%, or healthy, at the start of the study using the protocol of Adams et al. (2003).

Experimental Design and Treatments

Defoliation and moisture treatments were combined in a fully randomized factorial (4 × 2) design, with 6 − 7 replicates per site, and applied to 1 × 1 m plots, separated by at least 0.5 m. Areas were fenced to exclude livestock in April 2010. Defoliation treatments included clipping throughout the growing season at either high intensity and low frequency (HILF), high intensity and high frequency (HIHF), low intensity and high frequency (LIHF), or a control where defoliation was deferred to a single event at the end of each growing season. Plots within the HILF and HIHF defoliation treatments were clipped annually at 2-cm stubble height every 6 wk ($n = 3$ times in total) and 3 wk ($n = 5$ times), respectively, while LIHF plots were clipped at 5-cm height every 3 wk ($n = 5$ times). High-intensity clipping was used to attain extensive removal of leaf material while low-intensity clipping was set at a height ensuring shorter-statured species (e.g., *B. gracilis*) did not escape defoliation. All plots, including deferred controls, were clipped to a 2-cm stubble height in late August of each year to quantify total accumulated herbage mass throughout the growing season.

Moisture treatments included not watering (i.e., ambient moisture) and watering to augment rainfall and maintain an equivalent of 150 mm of monthly precipitation during June through August; this is double the average precipitation of June, the month of greatest rainfall. Watering was intended to eliminate moisture limitations for plant growth (and regrowth). Watering treatments were limited in magnitude during the fourth year of the study (2013) to the monthly addition of 24 mm of supplemental moisture due to a shortage of labor but resumed to normal levels in 2014. Watering occurred at 2-wk intervals (mid and end of month) and, together with defoliation, commenced and terminated in late May and the end of August, respectively, from 2010 through 2014. Before initiating treatments, plots were hand-raked to remove litter and prevent confounding effects of litter presence (Willms et al., 1986).

Response Parameters and Data Analyses

Within the central 0.5 × 0.5 m portion of plots, all harvested plant material was sorted to growth form, dried at 60°C for 48 hr, and weighed. For the HILF and deferred treatments in 2012, forbs (together as one component) and each species within the graminoid component were harvested separately. This was done to better understand how defoliation influenced yield composition and assist in interpreting production responses relative to the HILF treatment.

Annual plot yield represented accumulated aboveground herbage from all sequential clipping events. Data were checked for normality and homogeneity of variance with Shapiro-Wilk and Levene's tests, respectively, and analyzed with a repeated measures two-way mixed-model analysis of variance (ANOVA), using defoliation, moisture, and year of sampling as fixed factors and replicate plots as random (SAS

Table 1

Ambient growing season precipitation (mm) and long-term historical norms for the Brooks[1] area of Alberta, Canada. Bolded values indicate those months with > 40% variance from normal (underlined indicate below normal)

	Study yr						Long-term normal[2]
	2009[2]	2010	2011	2012	2013	2014	
April	2	34.5	20	32.6	23.7	32	25
May	14.3	**81.8**	$\underline{\textbf{23.2}}$	**65.2**	**67.5**	29.6	42
June	54	**123**	77	**135**	92.6	93.1	70
July	**137**	52	36	48	54.0	33.8	39
August	39	$\underline{\textbf{20}}$	23	29	$\underline{\textbf{17.1}}$	29.6	36
Total (April-August)	246	311	181	310	254	218	212
Deviation from norm	+16%	+47%	−15%	+46%	+20%	+3%	

[1] All data are from the Environment Canada (2013), Brooks Crop Development Center location.

[2] 2009 represents the year preceding the study period.

9.2, SAS Institute, 1989); year of sampling was treated as a repeated measure. Sites were analyzed independently due to known differences in environmental conditions. Mean separation tests for significant main effects and any interactions were based on least-significant differences (LSDs) and an alpha of 5%; emphasis in comparisons was placed on testing differences among defoliation regimes within moisture treatments and years.

The contribution of species to forage yield in the HILF and deferred treatments during 2012 was determined as the proportion of yield accruing over successive intervals during the growing season, both for individual species and all vegetation. This "yield phenology" of each species was determined for the HILF treatment by calculating the percentage of total biomass accruing for three consecutive periods: prior to early June, early June to mid-July, and mid-July to late August. The same was done for total yield in the HILF and HIHF treatments. Data were summarized using Proc Means (SAS 9.2) to obtain means and confidence intervals, and significance was based on the 95% confidence intervals. For the final year of harvest in 2014, we calculated the proportion of accumulated biomass composed of grasses and evaluated this relative to the treatments using mixed-model ANOVA.

Results

Growing Conditions

Summer precipitation was above average in 2010 and 2012, with ambient rainfall exceeding the long-term norms by 47% and 46%, respectively (Table 1). This was due to increased rainfall in May and June, while July and August precipitation remained near average. Rainfall in the last 2 yr was typical of long-term norms.

Total Herbage Yield

Distinct patterns in total accumulated forage yield in response to defoliation were evident at both locations, although these patterns were further modified by moisture addition and sampling year. Defoliation and moisture treatments both affected herbage yield within each range site ($P < 0.0001$) but also interacted with year of sampling ($P < 0.0001$). Defoliation effects further varied by moisture and year as evident by three-way interactions at each site ($P < 0.01$; Table 2).

Total yield (averaged across years and treatments) was 51% greater in the lowland (Table 3) than the upland (Table 4) site at 2207 and 1464 kg ha^{-1}, respectively. Productivity declined within the lowland and upland sites over time, particularly during the final 2 yr (2013 and 2014), a pattern that occurred even for the deferred defoliation and added moisture treatment combination. Increases in yield under added moisture fell to only 11% in 2014 and did not differ from the ambient treatment at either site, and they coincided with reduced water addition the year prior. In general, yields under the defoliation treatments exhibited the following trend: deferred > HILF > LIHF > HIHF. Marked separation among defoliation treatments occurred early on in the study. These were more apparent in the moisture addition than the ambient treatment and also more evident in the lowland site than the upland. However, significant differences among defoliation treatments weakened over time, with heavily muted responses by 2014, particularly in the upland site, where no differences remained.

Within the lowland site, mean separation occurred among defoliation treatments as early as the first treatment year. Of the growing season defoliation treatments, LIHF and HIHF defoliation yielded less accumulated herbage than the HILF treatment under ambient rainfall, all of which were lower than the deferred treatment (see Table 3). A similar pattern was found under moisture addition, but only during the 2011 and 2013 sampling years. Added moisture in the first year (2010) resulted in similar forage yield between the HIHF and LIHF treatments, and these remained lower than the deferred and HILF treatments. The deferred treatment was consistently greater in herbage yield compared with all the growing season defoliation treatments, with the exception of the ambient moisture condition in 2014. Finally, there were several periods during which no differences were observed between the treatments representing growing season defoliation (HIHF, LIHF, and HILF) within the lowland, including ambient moisture conditions in 2011 and 2013 and added moisture in 2012 and 2014 (see Table 3).

Defoliation-induced differences in herbage yield within the upland site were less apparent, particularly under ambient moisture (Table 4). Within the latter, no differences were evident among defoliation treatments except in 2013, at which time the HILF and deferred treatments were greater than the HIHF and LIHF. With added moisture in the upland, the deferred and HILF treatments again exceeded the HIHF and LIHF during 2011, and a similar trend existed in 2013; however, the HILF and LIHF remained similar at all other times. No differences in herbage yield were apparent among defoliation treatments under moisture addition in 2014 (see Table 4).

Yield Composition and Phenology

In comparison with deferred controls, HILF defoliation increased the contribution of *B. gracilis* to accumulated yields during the third

Table 2

Herbage yield analysis of variance *F* and *P* values testing the fixed factors of defoliation, moisture, and year of sampling on season-long accumulated plot yield within each of a lowland and upland site sampled in the mixed grass prairie of southeastern Alberta, Canada from 2010 through 2014

Effect	Lowland site		Upland site	
	F stat	*P* value	*F* stat	*P* value
Defoliation	20.9 $_{(3, 40)}$[1]	< **0.0001**	2.10 $_{(3, 48)}$	0.11
Moisture	31.7 $_{(1, 40)}$	< **0.0001**	72.8 $_{(1, 48)}$	< **0.001**
Defoliation × Moisture	1.58 $_{(3, 40)}$	0.21	0.45 $_{(3, 38)}$	0.72
Year	175.4 $_{(4, 160)}$	< **0.0001**	105.9 $_{(4, 192)}$	< **0.0001**
Year × Defoliation	4.46 $_{(12, 160)}$	< **0.0001**	5.85 $_{(12, 19)}$	< **0.0001**
Year × Moisture	27.5 $_{(4, 160)}$	< **0.0001**	39.2 $_{(4, 192)}$	< **0.0001**
Year × Defol. × Moist.	2.53 $_{(12, 160)}$	**0.005**	2.79 $_{(12, 192)}$	**0.002**

[1] *F*-ratio numerator and denominator degrees of freedom, respectively.

Table 3
Season-long accumulated herbage yield (g m^{-2}) means (standard errors in parentheses) for the **lowland site** in relation to all significant ($P < 0.05$) fixed effects and interactions of defoliation, moisture, and year of sampling. Defoliation treatments included deferred (control), high intensity at low frequency (HILF), low intensity at high frequency (LIHF), and high intensity at high frequency (HIHF)

Treatment level	Sampling yr					Average
	2010	2011	2012	2013	2014	
Defoliation						
Deferred	349 a[1]	338 a	295 a	261 a	195 a	288 a
HILF	312 b	252 b	212 b	154 b	161 ab	218 b
LIHF	254 c	226 bc	212 b	135 c	139 b	193 bc
HIHF	251 c	212 c	209 b	110 c	137 b	184 c
	(13.0)[3]	(13.0)	(13.0)	(13.0)	(13.0)	(10.4)
Moisture						
Ambient	275 b	213 b	170 b	151 b	150 a	192 b
Addition	309 a	301 a	294 a	179 a	166 a	250 a
	(9.2)	(9.2)	(9.2)	(9.2)	(9.2)	(7.4)
Defoliation × Moisture						
Deferred, ambient moist.	343 a	269 a	202 a	232 a	172 a	
HILF, ambient moist.	290 b	190 b	146 b	126 b	164 a	
LIHF, ambient moist.	230 c	195 b	165 ab	131 b	127 a	
HIHF, ambient moist.	235 c	198 b	167 ab	114 b	137 a	
Deferred, added moist.	356 a	406 a**	387 a**	290 a**	218 a*	
HILF, added moist.	334 a*[2]	315 b**	278 b**	181 b**	159 b	
LIHF, added moist.	278 b*	259 c**	258 b**	139 bc	152 b	
HIHF, added moist.	267 b	227 c	251 b**	106 c	138 b	
	(18.4)	(18.4)	(18.4)	(18.4)	(18.4)	
Overall	292 a	257 b	232 c	165 d	158 d	
	(6.5)	(6.5)	(6.5)	(6.5)	(6.5)	

[1] Letters denote mean separation within columns and treatments ($P \le 0.05$).
[2] *,** Denote added moisture means that differ from the ambient moisture mean within the same defoliation treatment and yr at $P \le 0.10$ and $P \le 0.05$, respectively.

year of treatment (2012) by 2.9 and 1.7 fold within the lowland and upland sites, respectively (Table 5). Other notable alterations in the contribution of major plant species to yield included a 43% decrease in *P. smithii* and a twofold increase in upland *Carex* species under HILF defoliation within the lowland and upland sites, respectively (see Table 5). Moisture influences were limited to *H. comata* in the lowland, where the contribution of this species to plot yield declined 65% under moisture addition (see Table 5).

Most forage yield in 2012 originated from the three dominant graminoid species, particularly in the lowland site, and defoliation influenced the contribution of these to yield. Under deferred defoliation in the lowland site, the top three species accounted for 84% of production and included, from greatest to least, *P. smithii, K. macrantha,* and *H. comata*. In contrast, under HILF defoliation, 65% of plot yield originated from *P. smithii, B. gracilis,* and *K. macrantha*, in that order. Although *P. smithii* contributed the most to yield in both these

Table 4
Season-long accumulated herbage yield (g m^{-2}) means (standard errors in parentheses) for the **upland site** in relation to all significant ($P < 0.05$) fixed effects and interactions of defoliation, moisture, and yr of sampling. Defoliation treatments included deferred (control), high intensity at low frequency (HILF), low intensity at high frequency (LIHF), and high intensity at high frequency (HIHF)

Treatment level	Sampling yr					Average
	2010	2011	2012	2013	2014	
Defoliation						
Deferred	167 b[1]	186 a	181 a	146 a	104 a	157 a
HILF	201 a	186 a	162 a	122 a	97 a	154 ab
LIHF	178 ab	149 b	169 a	82 b	100 a	136 b
HIHF	186 ab	147 b	169 a	82 b	113 a	140 ab
	(9.8)	(9.8)	(9.8)	(9.8)	(9.8)	(7.2)
Moisture						
Ambient	152 b	112 b	118 b	98 b	98 a	116 b
Addition	214 a	221 a	223 a	118 a	109 a	177 a
	(6.9)	(6.9)	(6.9)	(6.9)	(6.9)	(5.1)
Defoliation × Moisture						
Deferred, ambient moist.	139 a	119 a	139 a	135 a	93 a	
HILF, ambient moist.	142 a	122 a	110 a	115 a	101 a	
LIHF, ambient moist.	160 a	99 a	105 a	65 b	90 a	
HIHF, ambient moist.	165 a	110 a	117 a	78 b	108 a	
Deferred, added moist.	194 b**	254 a**	223 a**	157 a	116 a	
HILF, added moist.	260 a**	250 a**	214 a**	128 ab	93 a	
LIHF, added moist.	195 b*	199 b**	233 a**	99 bc*	110 a	
HIHF, added moist.	207 b**	183 b**	222 a**	87 c	118 a	
	(13.8)	(13.8)	(13.8)	(13.8)	(13.8)	
Overall	183 a	167 b	170 b	108 c	104 c	
	(4.9)	(4.9)	(4.9)	(4.9)	(4.9)	

[1] Letters denote mean separation within columns and treatment ($P \le 0.05$).
[2] *,** Denote added moisture means that differ from the ambient moisture mean within the same defoliation treatment and yr at $P \le 0.10$ and $P \le 0.05$, respectively.

Table 5
Mean contribution (%) of various herbage components to total season-long accumulated yield (with 95% confidence intervals in parentheses) in relation to 2 defoliation (deferred [control] and high intensity low frequency [HILF]) and 2 moisture (addition and ambient) treatments during 2012

Site & species/group	Defoliation		Moisture	
	Control	HILF[1]	Addition	Ambient
Lowland site				
Hesperostipa comata	13.5 $^{(21.3-5.7)}$	8.5 $^{(13.2-3.9)}$	5.7 $^{(8.4-3.1)}$	16.3 $^{(23.4-9.2)}$
Pascopyrum smithii	54.0 $^{(67.1-40.9)}$	30.6 $^{(39.2-22.0)}$	50.2 $^{(65.6-34.8)}$	34.4 $^{(44.1-24.8)}$
Bouteloua gracilis	6.9 $^{(9.5-4.2)}$	20.0 $^{(26.6-13.4)}$	14.9 $^{(23.0-6.9)}$	12.0 $^{(17.6-6.3)}$
Koeleria macrantha	16.3 $^{(24.7-7.9)}$	14.4 $^{(21.3-7.5)}$	13.9 $^{(19.9-8.0)}$	16.7 $^{(25.8-7.7)}$
Carex spp.	6.3 $^{(9.6-3.1)}$	14.1 $^{(19.4-8.8)}$	8.1 $^{(13.2-2.9)}$	12.4 $^{(17.3-7.4)}$
Other graminoids	0.0	1.1 $^{(2.3-0.0)}$	0.7 $^{(1.5-0.0)}$	0.4 $^{(1.4-0.0)}$
Forb spp.	2.9 $^{(5.6-0.3)}$	11.3 $^{(15.9-6.7)}$	6.5 $^{(11.7-1.3)}$	7.7 $^{(12.2-3.2)}$
Upland site				
Hesperostipa comata	23.8 $^{(31.3-16.3)}$	18.3 $^{(25.0-11.6)}$	22.0 $^{(29.9-14.1)}$	20.1 $^{(26.8-13.4)}$
Pascopyrum smithii	26.4 $^{(35.9-16.8)}$	18.4 $^{(23.6-13.3)}$	27.7 $^{(36.6-18.7)}$	17.2 $^{(22.5-11.8)}$
Bouteloua gracilis	22.5 $^{(29.3-15.6)}$	37.8 $^{(41.8-33.9)}$	32.6 $^{(40.3-25.0)}$	27.7 $^{(34.8-20.6)}$
Koeleria macrantha	1.7 $^{(4.3-0.0)}$	0.6 $^{(1.7-0.0)}$	0.6 $^{(1.7-0.0)}$	1.7 $^{(4.3-0.9)}$
Carex spp.	9.5 $^{(11.6-7.4)}$	19.1 $^{(21.8-16.4)}$	14.4 $^{(17.7-11.0)}$	14.3 $^{(18.8-9.7)}$
Other graminoids	0.0	0.5 $^{(1.0-0.0)}$	0.3 $^{(0.7-0.0)}$	0.2 $^{(0.6-0.0)}$
Forb spp.	16.1 $^{(31.9-0.3)}$	5.3 $^{(8.5-2.0)}$	2.5 $^{(4.5-0.5)}$	18.8 $^{(33.8-3.9)}$

[1] HILF indicates high intensity - low frequency defoliation.

treatments, the relative contribution of *P. smithii* to total production nevertheless remained lower under HILF defoliation (see Table 5). In general, *P. smithii* was not as dominant in the upland site, especially under HILF defoliation, where *B. gracilis, Carex* spp., and *P. smithii* comprised 75% of the yield. In contrast, 73% of the yield from deferred controls within the upland was composed of *P. smithii, H. comata,* and *B. gracilis,* in that rank order.

Among dominant forage species, 90% of yield was produced by mid-July during 2012 (Table 6). This was particularly evident for *P. smithii* (96%) and *K. macrantha* (93%). In contrast, *B. gracilis* accumulated only 67% of its total biomass by mid-July. Production phenology also varied between defoliation treatments, with the HILF accruing more herbage earlier in the growing season compared with that under HIHF defoliation (e.g., 82% vs. 66%). Moisture conditions did not appreciably alter production phenology (see Table 6).

Discussion

Aggregate Forage Yield

Rotational grazing systems strive to balance defoliation and vegetation recovery to simultaneously maintain livestock and forage productivity (Briske et al., 2011). While several previous studies have concluded that grassland production is not altered by RG (see Briske et al., 2008 for a review), many of these studies are not designed to specifically evaluate how defoliation frequency and intensity during the growing season regulate plant productivity. This information is needed to gain insight into how specific defoliation practices alter plant growth and thereby evaluate the potential utility of RG. In theory, if RG allows for greater managerial control over defoliation (Derner et al., 1994), any improvement to plant growth by maintaining, increasing, or prolonging growth under a given defoliation regime could benefit forage supply throughout the growing season.

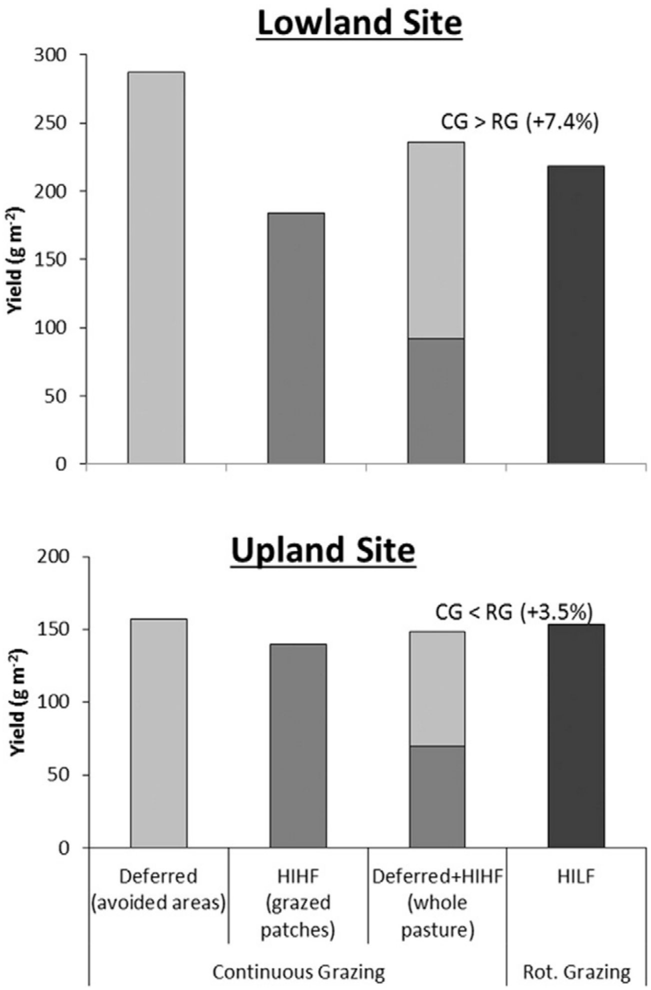
In the current study, nearly all growing season defoliation regimes either reduced forage yield or failed to increase production relative to the deferred controls: the lone exception being HILF defoliation initially under moisture addition within the upland site, though this was not sustained beyond the first year. These findings indicate there is little potential for overcompensation of herbage growth in this semiarid environment, regardless of defoliation regime, and contrast with other studies that have found compensatory growth in grasslands of higher productivity, such as the tallgrass prairie (Turner et al., 1993) and aspen parkland (Donkor et al., 2003). Belsky (1986) indicated that most cases of overcompensation are limited to situations of high productivity and low competition for resources, such as in cropland and greenhouse experiments, conditions unlike those on typical semiarid grasslands. Moreover, given that the majority of plant biomass accumulation was complete at our study sites by mid-July, regardless of moisture treatment, this suggests factors other than available moisture may limit the potential for growth of mixed grassland after that date. Achieving maximum herbage production in these grasslands therefore appeared to depend on attaining maximum growth during the early to mid-growing season and could coincide with little to no defoliation in that period if producers are able to defer grazing until mid-July.

Table 6
Mean contribution (%) of various herbage components to total yield (95% confidence intervals in parentheses) accruing at sequential times during the growing season for various defoliation and moisture treatments. Species-level yield data were collected during 2012

	Before June	Early June to mid-July	Mid-July to late August
Species			
Hesperostipa comata	38.6 $^{(43.2-34.0)}$	43.9 $^{(48.1-39.6)}$	17.6 $^{(19.8-15.3)}$
Pascopyrum smithii	40.1 $^{(43.0-37.3)}$	55.4 $^{(58.9-51.9)}$	4.5 $^{(5.6-3.3)}$
Bouteloua gracilis	13.6 $^{(15.7-11.6)}$	53.0 $^{(55.2-50.8)}$	33.4 $^{(36.7-30.0)}$
Koeleria macrantha	57.3 $^{(61.9-52.6)}$	36.0 $^{(39.0-33.1)}$	6.7 $^{(10.0-3.4)}$
Carex spp.	53.0 $^{(58.6-47.5)}$	36.0 $^{(39.7-32.3)}$	11.0 $^{(13.6-8.4)}$
Forb spp.	27.1 $^{(36.1-18.2)}$	57.8 $^{(66.9-48.6)}$	15.1 $^{(20.2-9.9)}$
Treatments			
HIHF[1] defoliation	27.5 $^{(28.9-26.2)}$	38.6 $^{(39.8-37.5)}$	33.8 $^{(35.5-32.2)}$
HILF[2] defoliation	33.1 $^{(34.9-31.4)}$	48.5 $^{(50.0-47.0)}$	18.3 $^{(20.6-16.1)}$
Moisture addition	29.3 $^{(31.1-27.5)}$	43.3 $^{(45.5-41.1)}$	27.4 $^{(30.8-24.0)}$
Ambient moisture	31.4 $^{(33.3-29.4)}$	43.8 $^{(46.3-41.3)}$	24.8 $^{(28.6-21.0)}$

[1] High intensity, high frequency.

[2] High intensity, low frequency.



Model 1. Conceptual model depicting accumulated season-long herbage productivity under continuous and rotational grazing in lowland and upland sites of the mixed grass prairie, assuming that yield under continuous grazing consists of identical proportions (50:50 mix) of both avoided areas (yielding similar to deferred defoliation) and recurrently grazed patches (yielding similar to high-intensity, high-frequency defoliation), while rotationally grazed pastures are uniformly defoliated at high intensity and low frequency.

While we did not consistently find overcompensation, our results do provide evidence that variation in defoliation regimes within the growing season can impact total forage yields. More specifically, total production within the HILF treatment remained greater than that observed under the high-frequency defoliation treatments (HIHF and/or LIHF) during 3 of 5 sample yr for each study site, though these differences were limited largely to the added moisture treatment. Hilbert et al. (1981) demonstrated that compensatory growth is more likely for slow-developing plants growing below their maximum potential under low-resource environments, as they require less of an increase in growth to achieve compensation. Our observed dependence of defoliation impacts and associated forage yield on moisture availability is consistent with the notion that superior regrowth following growing season defoliation is most likely to occur under greater resource availability (Belsky, 1986; Hawkes and Sullivan, 2001) and is in support of our hypothesis that improved regrowth can occur under elevated moisture. Moreover, these results were evident in both the mesic lowland and upland sites. Our results also parallel those observed elsewhere in the northern mixed grass prairie, where Zhang and Romo (1994) found greater production under less frequent defoliation. In the latter study, any growing season defoliation decreased yield relative to deferred defoliation.

Although water addition increased total herbage yields, a finding consistent with the notion that water limits growth in mixed grass ecosystems of western Canada (Willms and Jefferson, 1993), water addition failed to consistently facilitate benefits from HILF defoliation on production during all years. While the lack of segregation between the HILF and high-frequency defoliation treatments is not surprising in the last year of the study (2014) given the reduction in water application that occurred during 2013 and the fact that previous year's precipitation influences current production (Smoliak, 1986), the inconsistent benefit of HILF defoliation in maintaining yields warrants closer scrutiny. Indeed, loss of HILF production benefits in 2012 resulted from modest reductions in the yield of this treatment at both sites and coincided with increases in production under the LIHF and HIHF treatments within the upland, potentially due to the high ambient rainfall that year (see Table 1). Notably, benefits of HILF defoliation under water addition reappeared during 2013 despite widespread reductions in yield associated with the return of more normal summer precipitation. Taken collectively, our results suggest that during most years, particularly those early on in the study and with high moisture, HILF defoliation was capable of increasing herbage yields over other growing season defoliation regimes, although whether this increase can be sustained long term remains unclear.

Potential Implications for Grazing Systems and Future Research

Exactly how the growing season defoliation treatments imposed here under controlled conditions reflect different grazing systems is uncertain, particularly with the lack of direct effects of large herbivores. However, the more favorable productivity of HILF defoliation relative to the high-frequency regimes is noteworthy given that this treatment best approximates the defoliation regime of short-duration RG. In contrast, CG can result in "patch grazing," where previously defoliated patches are used repeatedly and other areas avoided (Ring et al., 1985; Willms et al., 1988). In the fore-mentioned situation, the deferred and HIHF defoliation treatments tested here could be considered to represent forage yield in recurrently avoided and grazed patches during the growing season, respectively. If one assumes that CG areas consist of similar contributions of both patch types and HILF defoliation achieves relatively uniform use throughout, overall productivity can be modeled relatively simply for areas exposed to either CG or RG (Model 1). Using this theoretical framework, when low-yielding HIHF patches are combined with areas left nondefoliated by cattle (i.e., deferred areas), as often occurs under CG, their combined herbage yields were greater than in uniformly defoliated RG areas within the lowland site (see Model 1). Conversely, the opposite was evident in the upland, with combined yields under uniform RG greater than that of the combined HIHF and deferred treatments.

Greater modeled yields under CG (by 7.4%; see Model 1) for the lowland site arise due to the high yield of deferred controls, which compensate for lower yields under HIHF defoliation (i.e., frequently defoliated patches at high intensity). This would be especially evident if avoided areas were to make up more than 50% of the pasture, as a shift to 75% in the area avoided would increase overall production benefits of CG to 16.6%. This simple modeling exercise highlights that although grassland patches receiving heavy and frequent recurrent defoliation may have lower productivity, neighboring avoided patches can compensate for any overall reduction in productivity associated with HIHF defoliation. This could account, at least in part, for the similar productivity observed from CG and RG systems in previous studies on rangelands (Briske et al., 2008; Holechek et al., 2000), although this also assumes that patch grazing occurs at relatively small spatial and temporal scales (Norton, 1998). In contrast to the lowland, more similar yields under all growing season defoliation regimes in the upland account for the similar modeled yields in both avoided and recurrently grazed patches (see Model 1). In fact, modeled herbage yields at this site tended to be greater under HILF defoliation compared with simulated CG (i.e., HIHF and deferred defoliation combined). This suggests that RG systems making use of high livestock densities to promote uniform utilization but accompanied by lengthy rest periods may have some potential to maintain productivity in arid mixed grass prairie.

While useful in highlighting the potential contributions of areas defoliated at variable frequencies within grasslands to total accumulated herbage production, the exercise described earlier is not without limitations. Small plot work with controlled defoliation poorly represents the activities of grazing animals and the emergent effects associated with complex rangeland landscapes (Teague et al., 2013). Most importantly, our approach used fixed clipping heights and set time intervals, thereby eliminating the flexibility associated with adapting grazing periods to changing animal needs, environmental conditions, and producer objectives (Teague et al., 2013). Consequently, we consider this study a first step in trying to separate the impacts of variable defoliation regimes on plant growth and suggest more long-term studies are needed to test different intensities and frequencies of defoliation. Indeed, our fixed defoliation intensities and intervals, combined with the year-end defoliation to quantify accumulated herbage yield, may have exceeded the fundamental tolerance of these mixed grass communities to defoliation and, in the process, account for the decline in herbage yields over time within all treatments. This is particularly important as aside from the deferred treatment, the HILF demonstrated the greatest benefit over HIHF defoliation during the first 3 yr.

Yield Composition and Phenology

Differences in vegetation composition, along with how dominant grasses respond to defoliation, may account for the divergent effects of defoliation on productivity observed between sites. *P. smithii* was initially dominant in the lowland but declined under HILF defoliation as the less productive species (*B. gracilis* and upland *Carex* species) increased. Given that *P. smithii* is a highly productive grass in the mixed grass prairie (Coupland, 1961; Smoliak, 1986; Willms et al., 2002), this accounts for the decreased yield observed under HILF defoliation relative to the deferred treatment within the lowland. In contrast, vegetation changes under HILF defoliation were not as pronounced in the upland (Broadbent et al., 2016), suggesting greater inherent resistance to HILF defoliation. Within the upland, *P. smithii* was not as dominant and *B. gracilis* was more abundant from the start of the study. High tolerance of *B. gracilis* to defoliation could account for why HILF defoliation was better able to maintain its production in the upland relative to other treatments, including deferred defoliation, and in turn, could help account for the modeled ability of RG to maintain similar (or marginally greater) production relative to CG at this location (see Model 1). *B. gracilis* was common in the upland and has previously demonstrated compensatory growth due to its high growth rate and tolerance to defoliation under ample moisture (Alward and Joern, 1993). Moreover, given the prevalence of *B. gracilis,* increases in this species may have compensated for the minor reduction in yield associated with canopy-dominant cool-season grasses.

Intermittent defoliation may also promote herbage growth by maintaining more consistent production throughout the growing season. The sigmoidal growth pattern of vegetation entails that biomass increases are rapid for only a short period during spring green up (Lauenroth and Whitman, 1977). Voisin (1961) postulated that intermittent defoliation combined with appropriate rest periods can counter this by promoting regrowth. This was tested here using total and species-specific biomass by examining production phenology as the proportion of yield accruing during consecutive periods of the third growing season, but only for the HILF and HIHF defoliation regimes. Under HILF defoliation, > 80% of yield accrued by mid-July, regardless of moisture conditions. This was true for the forb component and all major graminoids except *B. gracilis,* which accumulated 66% of its biomass by that time, likely because *B. gracilis* is the only warm-season graminoid common to all plots. This corroborates findings that spring precipitation largely determines productivity in the mixed grass prairie (Derner and Hart, 2007; Derner et al., 2008; Milchunas et al., 1994; Schellenberg et al., 1999) because midgrasses such as *P. smithii* and *H. comata,* which contribute the most to herbage yields (Willms and Jefferson, 1993), are cool-season species that grow early in the year (Manley et al., 1997; Pantel et al., 2010). Our observations suggest that increasing the frequency of intense defoliation does not alter the fundamental growth pattern of these grasslands (see Table 6). Given this, limited potential for regrowth exists for cool-season midgrasses in this environment, further restricting their ability to increase production under select defoliation regimes during the growing season.

In general, plant phenology in this study reflects the region's precipitation pattern, which is not surprising given that plant growth is heavily influenced in the northern mixed grass prairie by growing season rainfall together with accumulated fall and winter precipitation (Heitschmidt et al., 2005; Smoliak, 1986). Cool-season midgrasses exploit dormant season moisture by growing in the spring. As even large increases in summer moisture under water addition failed to alter overall growth phenology, it appears mixed grass vegetation lacks the phenotypic plasticity to respond to increased summer rainfall. This finding probably arises because higher temperatures limit stomatal conductance and photosynthesis in cool-season grasses, especially *P. smithii* (Kemp and Williams, 1980). Surprisingly, even the warm-season grass *B. gracilis* failed to accumulate more biomass in the latter part of the growing season under moisture addition, potentially due to the cool nights typically occurring in this northern mixed grass environment. More productive cool-season grasses may be better suited to mesic areas of the northern mixed grass prairie (such as in the lowland site) because despite being a semiarid environment (Ode et al., 1980), these plants can preemptively exploit available soil water early in the growing season before temperatures have reached the optimum for warm-season plants (Epstein et al., 1997).

In comparing production phenology between the HILF and HIHF treatments, the latter accumulated more yield later in the growing season. Two mechanisms may explain this. First, HIHF defoliation may have stressed and subsequently slowed plant development, thereby prolonging regrowth later in the year. Alternatively, HIHF defoliation favored *B. gracilis* (Broadbent et al., 2016) and this warm-season species would inherently shift production later in the growing season (Derner and Hart, 2007). This suggests that recurrently grazed (i.e., HIHF) patches that occur under CG may be important for maintaining forage quality later in the growing season (Mack and Thompson, 1982). By extension, our results suggest that if the same intensity of defoliation was applied across a large pasture using tightly controlled RG and followed by a 6-wk or longer rest period (similar to the HILF pattern tested here), overall plant productivity could be maintained by retaining more cool-season midgrasses. In any case, future work should explore more conservative frequencies of defoliation on accumulated herbage yields.

Management Implications

Recent literature reviews suggest that RG does not enhance community productivity relative to CG (Briske et al., 2008; Briske et al., 2011; Holechek et al., 2000). For RG to enhance productivity during the growing season, defoliation at certain intensities and/or frequencies must promote growth over other defoliation regimes. We hypothesized that growing season compensatory responses would be more likely under defoliation regimes that included a lengthy rest period, as well as conditions with greater moisture (mesic range site or moisture addition). While all growing season defoliation regimes reduced season-long accumulated production relative to defoliation deferred to the end of the summer, HILF defoliation had greater aggregate yields than HIHF defoliation in 6 of 10 different combinations of site and year and typically coincided with moisture addition and/or more favorable growing conditions. Our observed production responses suggest the inability of tightly controlled frequent defoliation under RG to increase production may arise because of the high yield contribution of unused (i.e., deferred) patches. Additionally, the decline of key productive cool-season species such as *P. smithii* and their tendency to complete growth early in the year appeared to limit mixed grass prairie yield responses to HILF defoliation. In contrast, presence of *B. gracilis* and high moisture may increase the ability of HILF defoliation to recover a portion of herbage yields. Additional studies are necessary to understand the fundamental trade-offs associated with altering defoliation regimes during the growing season on plant growth, including how aggregate yield responses change with the adaptation of plant species (i.e., inherent growth phenology and defoliation tolerance), environmental conditions, and further changes in defoliation regime.

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