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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