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Original Research

Contingency in Defoliation and Moisture Effects on Northern Mixedgrass Prairie Composition and Diversity☆

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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.

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 µs 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 µs 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^{-1}).

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

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