Seasonal Availability of Cool- and Warm-Season Herbage in the Northern Mixed Prairie

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On the Ground

- Variability in spatial and temporal patterns of herbage production is common in grasslands and can affect land uses, such as grazing.
- Total herbage biomass in northern mixed grass prairie was similar on loamy and sand dune ecologic sites but varied in composition.
- Cool-season grasses were uniformly produced throughout the grazing season, whereas warm-season grasses grew rapidly during August.
- Litter conservation was important for increasing cool-season grass biomass, whereas warm-season grasses remained independent of litter.
- Biomass and composition of herbage in the northern mixed grass varies spatially and intra-annually, affecting seasonal grazing opportunities for livestock.

Keywords: ecologic site, forage production, inverse texture effect, litter, seasonal grazing opportunities.

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A key challenge in cattle production on rangelands is matching natural changes in the seasonal availability of forage production, with ongoing grazing activities throughout the growing season. Ideally, changes in seasonal plant growth and associated forage supply will provide a steady supply of nutrients that coincides with all phases of the beef production cycle, including spring green-up, early to mid-summer peak lactation, and when cattle begin putting on energy reserves in late summer in preparation for winter. In the northern regions of the Great Plains, much attention has been dedicated to minimizing the cost of livestock grazing due to the relatively short growing season.[1]

Within the mixed grass prairie, forage supply is known to be variable in both space[2,3] and time.[4,5] Variability in space is regulated by changes in ecologic site conditions, including factors that alter resource availability (water and nutrients) combined with associated changes in plant species composition. Among the critical soil characteristics altering grassland productivity is texture,[6] which has a marked impact on a number of soil properties regulating plant growth, including water infiltration rates, moisture holding capacity, nutrient exchange, and plant rooting opportunities. Although sandy soils tend to have lower water and nutrient availability compared with finer-textured soils, sandy soils enable deeper root penetration,[7] which can facilitate water use from the subsoil, including moisture that may have accumulated over the dormant season. In addition, sandy soils have the benefit of facilitating rapid water entry into the ground, allowing moisture to escape evaporation from the ground surface, a process that is particularly important when rainfall events are small. This can lead to greater production in sandy soils compared with adjacent loam soils,[8,9] a phenomenon known as the "inverse texture effect."[10] Variations in ecologic site conditions ultimately lead to many different plant community types in the northern mixed grass prairie,[8,11] each of which has its own expected level of productivity and corresponding grazing opportunities.[12]

Temporal variability in herbage production is caused by changes in growing conditions, which, in the case of the northern mixed grass, is mostly precipitation.[4,5] Moisture deficits in particular constrain plant production and grazing opportunities in the mixed grass region of western Canada.[13] Although the majority of precipitation occurs during the summer and therefore coincides with peak water demand from plant growth,[13] dormant season precipitation also contributes positively to production.[5] Moisture falling during the dormant season enters the soil and contributes to water recharge, which is then available to support plant growth the following summer.

Across the United States, grasslands dominated by either cool or warm-season species lead to a unimodal production pattern, whereas mixed communities can produce a bimodal pattern of seasonal plant production.[14] Limited information exists quantifying seasonal changes in herbage availability during the growing season in the northern mixed grass prairie of western Canada, including how changes in ecologic site conditions (soil texture) and associated changes in plant composition may alter this availability. Production in the northern mixed prairie is typically dominated by select cool-season grasses, such as needle-and-thread grass, together with western wheatgrass.[15] However, as vegetation in this region includes a mix of cool and warm-season plant species,[11] herbage availability is likely to reflect a combination of both components. Up to 90% of plant growth was complete in Montana grasslands by July 1,[16] largely due to dominance by cool-season grasses, and areas with mean annual temperatures below 10°C are typically dominated by cool-season grasses, such as in Montana, North Dakota, South Dakota, and northeast Colorado.[17] However, parallel investigations from western Canada are lacking, where mean temperatures seldom exceed 6°C. Grasslands with abundant cool-season species experience a marked pulse of early-season growth in spring[8,18] and then declines over the growing season.[19] Cool-season grasses are highly opportunistic of surface soil moisture, which they rapidly exploit with the initiation of growth in early spring.[20] Consequently, cool-season grass abundance tends to increase with winter precipitation.[21]

In contrast, prairie communities dominated by warm-season grasses produce little growth early in the growing season, only to produce disproportionately more biomass in mid- to late summer[8,22] and therefore rely directly on increases in summer precipitation.[21] In the case of some warm-season grasses found on dune areas, such as prairie sandreed (*Calamovilfa longifolia*), these species are deeper rooted[7] and are therefore better able to mitigate summer moisture stress,[20] presumably by accessing deep soil moisture reserves. Following the summer biomass peak, relative production of warm-season species declines and is progressively replaced by cool-season grasses into the fall.[22] Collectively, these changes in biomass production may alter season-long opportunities for cattle grazing across the landscape.

We quantified changes in herbage availability throughout the growing season across several locations of a northern temperate mixed grass prairie, representing contrasting ecologic sites varying primarily in soil texture. Specific objectives included (1) comparison of total herbage production and seasonal forage availability throughout the growing season, (2) quantification of the contribution of cool-season and warm-season grasses to forage availability, and (3) identification of implications for cattle grazing across the region.

Mattheis Research Ranch

We evaluated seasonal herbage dynamics at the Mattheis Research Ranch. The Mattheis ranch is a recently established research facility operated by the University of Alberta in southeastern Alberta (Fig. 1) situated in the Dry Mixed Grass Prairie (50°53'N; 111°52'W) Natural Subregion,[23] which extends east into Saskatchewan and south into eastern Montana and North Dakota. This area of northern temperate native grasslands comprises a wide diversity of plant communities and vascular species, including both cool-season and warm-season grasses.[12] Moreover, the ranch has a combination of landforms across the property, including level prairie (Fig. 2, left) and rolling sand dunes (Fig. 2, right) that have stabilized. Consequently, a variety of ecologic sites are found within the Mattheis Ranch borders, including loamy and sand dune soils, enabling further quantification of seasonal herbage dynamics under different soil textures and growing conditions.

Loam areas (largely sandy loams comprising the Orthic Brown Chernozem Pemukan soil series) are dominated by needle-and-thread grass (*Hesperstipa comata*), western wheatgrass (*Pascopyrum smithii*), and blue grama grass (*Bouteloua gracilis*) and are representative of the Stipa-Bouteloua-Agropyron faciation,[11] with up to 40%, 28%, and 22% of biomass comprising these three groups, respectively. Adjacent sand dunes (loamy sand textured areas comprising Rego Brown Chernozems of the soil series Ventisant) include similar species but with less wheatgrass and the additional presence of prairie sandreed (*Calamovilfa longifolia*), an early successional rhizomatous species found across significant areas of southern Alberta and Saskatchewan.[11,24] Although most grasses are cool-season species, both blue grama and sandreed represent important warm-season components of this ecosystem.

Long-term growing conditions at Duchess, Alberta, 20 km south of the Mattheis Ranch, averages 354 mm, with 60% falling during the growing season from April 1 through August 31. However, dormant season precipitation from September through March is known to be important for increasing production in the mixed grass prairie.[5] During 2009, the year of data collection in this investigation, antecedent (September through March) and growing-season (April through August) moisture were 116 mm and 246 mm, respectively, the latter being 116% of the long-term mean. The growing season moisture was above average overall, whereas the early-season (April through June) rainfall was below normal (70 versus 137 mm), and late summer precipitation was elevated, in large part due to high rainfall during July (137 mm).

Herbage Sampling

In early May of 2009, plots were set up in a randomized complete block design to assess seasonal patterns of herbage growth. At each of four locations (blocks), we sampled standing biomass (i.e., above-ground net primary production) monthly from early June through early September, inclusive. Two blocks were situated in the loamier prairie, and two others were within the stabilized sand dune complex; all sites were established in relatively level terrain to eliminate confounding effects of topography. Within each block, five

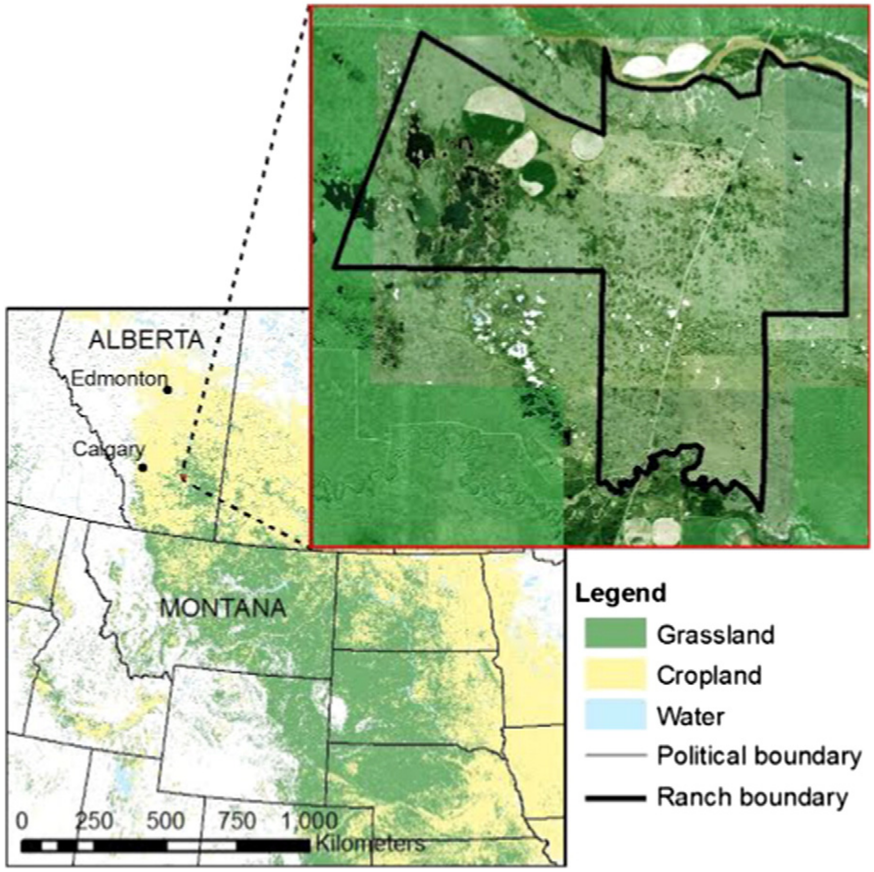

Figure 1. Location of the Mattheis Research Ranch in southeast Alberta, Canada.

plots were sampled on each date. Plots were sampled prior to livestock grazing to ensure maximum biomass and were not protected from wildlife grazing, although use from elk, deer, and antelope was relatively low across the area.

Plots were 50 × 50 cm in size and harvested to ground level. Above-ground biomass was sorted to litter (carryover growth from previous years), broadleaf forbs, cool-season grasses, and warm-season grasses. Samples were promptly dried, weighed, and converted to kilograms per hectare (kg/ha) for reporting of changes in seasonal forage availability. Total biomass and the biomass of each component were each analyzed by using an analysis of variance (ANOVA), with ecologic site (loam vs sand) and sampling month as fixed factors to characterize spatial and temporal variations in productivity. Replicate blocks within ecologic site and replicate plots within each site and sampling time were random in the analysis. To isolate the additive effect of litter levels on herbage production, litter biomass sampled within plots at each sampling time was included as a covariate during analysis.

Seasonal Herbage Dynamics

Seasonal assessment of biomass revealed that total herbaceous biomass did not differ between the ecologic sites, both overall and across sampling times throughout the growing season (Table 1). Peak herbaceous production of both the loam (1707 kg/ha) and sand dune (1461 kg/ha)

Figure 2. Comparison of loam (*left*) and sand dune (*right*) ecologic sites found across the Mattheis Research Ranch and sampled during 2009. Photo credits: A. Tastad and C. Carlyle.

Table 1. Summary of significance tests (*P* values) associated with the evaluation of standing biomass of cool and warm-season graminoids (grasses and sedges), forbs, and total herbage, in relation to different ecological sites (loam versus sand dune) and monthly sampling times. Litter mass was run as a covariate. Bold values indicate significance ($P < 0.10$).

	Graminoids			Total
Factor	**Cool-season**	**Warm-season**	**Forbs**	**herbage**
Litter (covariate)	**0.002**	0.27	0.75	**0.05**
Ecologic site type	0.30	**0.09**	0.69	0.68

Sampling month	**0.009**	**0.01**	0.38	<**0.0001**
Ecologic site x S. month	0.60	0.44	0.85	0.27

ecologic sites occurred in August (Fig. 3). Despite this, patterns of current annual growth over the growing season were dissimilar between the ecologic sites. In early June, the loam and sand dune sites had achieved 39% and 48% of peak recorded biomass, and by early July, this proportion had increased to only 52% of peak biomass on loam soils but had risen sharply to 87% of peak on sand dune soils (see Fig. 3). By early fall (September), available biomass declined to 62% and 74% of peak biomass on the loam and sand dune sites, respectively.

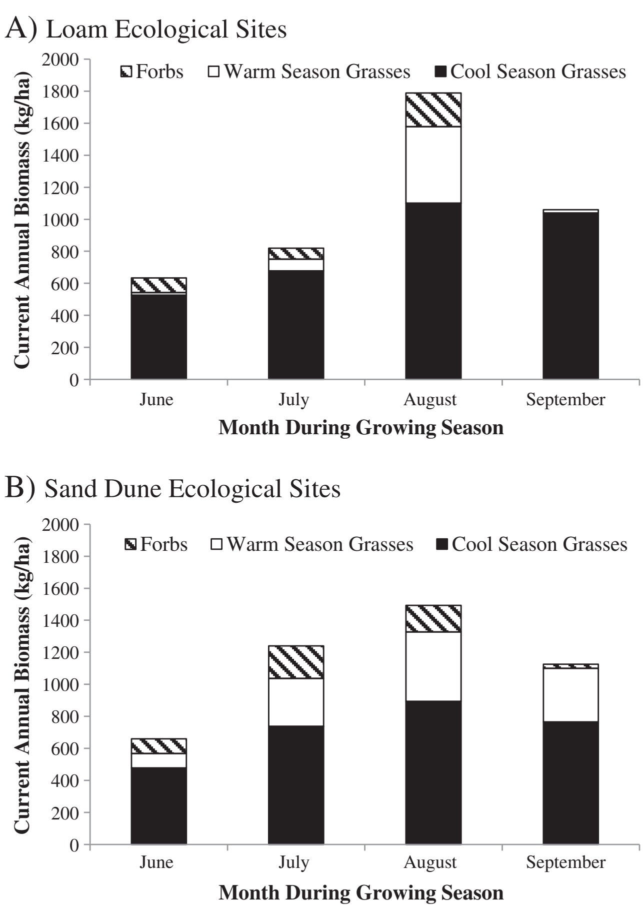

Figure 3. Relative contribution of forbs, cool-season and warm-season grasses to total standing biomass within each of the (**A**) loam and (**B**) sand dune ecologic sites, at the Mattheis Research Ranch.

Forb biomass did not differ between the ecologic sites or months of sampling (see Table 1) and comprised less than 16% of biomass at all sampling times, regardless of site type (see Fig. 3). Cool-season grass biomass also did not differ between the ecologic sites (see Table 1) but varied distinctly across sampling times (Fig. 4). Mean cool-season grass biomass was 502 kg/ha in June, increasing to a peak of 953 kg/ha in August, and remained relatively stable into September (902 kg/ha). In contrast, warm-season grasses differed in biomass between the ecologic sites (see Table 1). The overall mean monthly production of warm-season grasses within the sand dune ecologic sites (290 kg/ha) was greater than that observed on loam sites (146 kg/ha), a pattern that did not vary with sampling time throughout the growing season. Patterns of seasonal growth indicated little warm-season grass biomass was present in June or July and then increased sharply in August, only to decline by September to levels similar to those observed in early-summer (see Fig. 4). Relative contributions of warm-season grasses to total herbage biomass remained low in June (7.6%) and July (17.1%), peaked in August at just over a quarter of total biomass (28.7%), and then declined in September (16.7%).

The inclusion of litter as a covariate in the analysis of seasonal standing biomass was significant for several vegetation components (see Table 1). Although litter was significantly related to total herbage, closer examination revealed that litter was not associated with forb biomass. Moreover, litter effects on biomass were related specifically to the biomass of cool-season grasses rather than warm-season grasses (see Table 1). Further inclusion of litter by sampling time effects in our analytical models indicated a litter-by-month interaction on cool-season grass biomass.[i] Litter impacts on cool-season grasses were positive and particularly apparent during the months of August and September—the second half of the growing season (Fig. 5). Finally, litter levels differed between the ecologic sites,[ii] being 25% greater in

[i] $P = 0.004$.

[ii] $P = 0.006$.

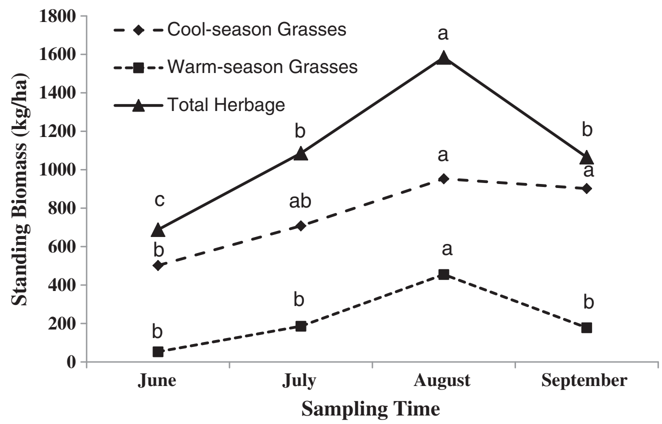

Figure 4. Temporal changes in standing biomass of cool-season and warm-season grasses, as well as total herbage, throughout the growing season in mixed prairies of the Mattheis Ranch. Data are averaged over four locations and two ecologic sites. Within a vegetation component, means with different letters differ ($P < 0.05$).

loam sites (2,109 kg/ha) than sand dune sites (1,684 kg/ha). However, no significant litter by ecologic site type effects were detected for any of the vegetation components assessed.

Contribution of Cool-Season and Warm-Season Grasses

Most of the biomass produced in these grasslands was associated with perennial grasses, which is consistent with previous studies on the prairie regions of Canada.[11] Although the values found here (approximately 1,500–1,700 kg/ha) are within the range of those reported across the mixed grass prairie environments of the United States (1,010–2,700 kg/ha),[14] relative to other mixed grass ecosystems in Canada, standing biomass levels in the grasslands in our study tended to exceed those found elsewhere. Most other studies in the region have suggested that annual production values seldom exceed 1,000 kg/ha and are often well below these values.[11,13] More favorable production may also be occurring due to elevated rainfall across the region over the last decade, which overall may have led to enhanced plant vigor and associated forage yields.

Relatively little standing biomass comprised forbs within these grasslands despite the fact that they contribute substantially to species diversity.[25] Among grasses, cool-season species provided the majority of biomass throughout the growing season. Both needle-and-thread grass and western wheatgrass are known to provide a large proportion of total biomass within these grasslands.[25] As cool-season species, they benefit from spring soil moisture[20] and are thought to produce much of their biomass prior to June 15.[18] Although it has been suggested that western wheatgrass produces little new growth after mid-July,[26] the sustained

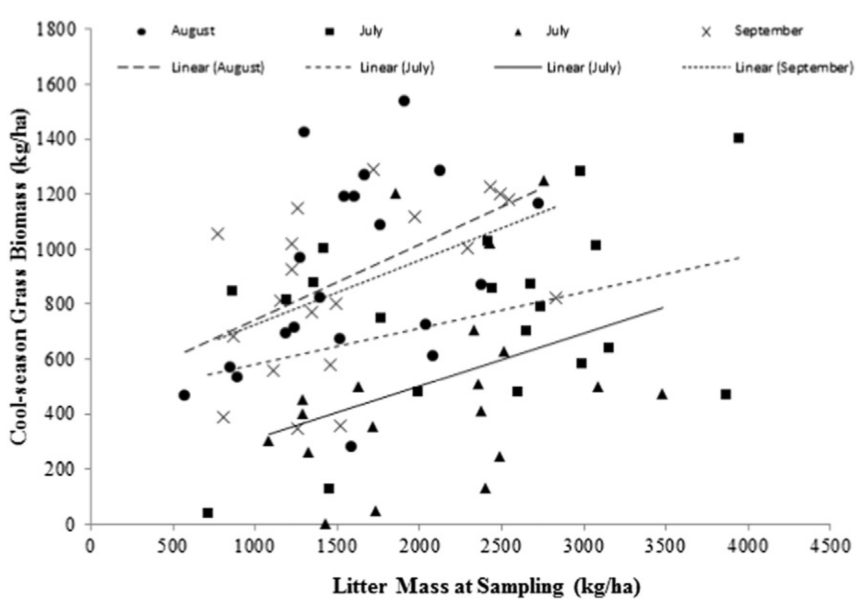

Figure 5. Cool-season grass production was positively related to litter mass at all four sampling times throughout the growing season ($P < 0.05$).

increase in cool-season grass biomass we observed through August suggests that the most common cool-season grasses at our study area continued to exhibit growth increases through late summer. The above-normal rainfall in July would have aided this growth, but it is notable that this occurred despite a relatively dry spring, which can be expected to shut down growth of cool-season species.

In contrast, warm-season grasses produced little biomass prior to July in the current study, and this finding is consistent with the notion that these species grow primarily from mid-June through mid-July in the mixed grass region of western Canada.[18] Favorable growth of warm-season grasses during July of 2009 was also likely facilitated by high mid-summer rainfall. Despite the ideal growing conditions for warm-season grasses, the limited biomass of this component (i.e., under ideal conditions) highlights the fact that cool-season species provide the majority of biomass and associated forage production in the grasslands of the region. It also supports the notion that cool-season grasses consistently outperform warm-season grasses and that the latter are not recommended as agronomic plantings north of 51° latitude (the Mattheis Ranch is near this latitude at 50° 53").[27]

Ecologic Site Differences

We found similar total herbaceous biomass within the loam and sand dune ecologic sites at the Mattheis Research Ranch. These results are similar to regional level studies indicating that soil texture contributes little to spatial models accounting for variation in production,[28] and similar findings have been reported by others in comparative field studies.[29] Nevertheless, these results are surprising, given that many other investigations suggest soil texture is an important local determinant of production.[30] Although we expected sand dune sites to demonstrate greater total herbage production under low rainfall based on the inverse texture effect[10] and previous field studies,[8,31] this did not occur in the present study. Moreover, below-normal rainfall early in the 2009 growing season should have increased the importance of rapid water infiltration for conserving soil moisture, further increasing the opportunities for comparative growth increases within our sand dune sites. Similar observed patterns of total plant growth within these contrasting ecologic sites suggest that they lead to comparable overall opportunities for livestock grazing.

Despite similarities in total production, sand dune sites did contain a greater proportion of warm-season grass biomass, a finding consistent with previous studies in the Great Plains.[6] As warm-season species are highly responsive to pulses of summer precipitation,[19] our favorable yields of warm-season grasses, as well as total herbage, within sand dune sites may partly reflect the above-normal precipitation received during July. Warm-season grasses demonstrated a particularly large growth surge between early July and August, over which warm-season grasses increased to nearly a third of total biomass. This increase would be further heightened by increased water use efficiency within warm-season plants,[32] findings similar to observations from other regions. For example, little growth of warm-season grasses has been found on deep sand sites in Nebraska before May 22.[33] As our study area is within the northern extent of the mixed grass prairie, it is likely that the main period of warm-season grass growth does not occur in this region until into July.

Finally, although not tested directly here, we note that topography itself may be an important factor regulating the abundance of warm-season and cool-season species. In comparison with uplands, lowlands often comprise a greater proportion of cool-season species compared with warm-season species.[22] The loam sites in our study followed this pattern, since they were typically on level to gently rolling plains and dominated by western wheatgrass, which has a moderately deep root system capable of capitalizing on spring moisture reserves.[7] Western wheatgrass, in particular, has been positively associated with more fine-textured soils.[34] In contrast, the primary warm-season grass on these sites was blue grama, a shallow-rooted shortgrass species that contributes limited amounts to overall grassland biomass.[11] Within the sand dune ecologic sites in our study, one of the primary warm-season grasses was prairie sandreed, a species known to prefer these sites and possessing a deep root system (down to 3 m),[34] which enables it to access deep soil moisture reserves.[7] This adaptation would help maintain production during the middle of the growing season.

Contingency in Litter Effects

Litter effects on standing biomass were only evident on cool-season grasses rather than warm-season grasses, and this response was consistent across sampling times throughout the growing season. Cool-season grasses rely heavily on spring soil moisture, at which time they rapidly exploit stored moisture, including soil water accumulated during the previous fall and winter.[5] As litter is important for lowering soil temperatures and increasing soil moisture availability,[35] this can promote the growth of cool-season grasses, a response that, in part, may reflect their reduced water use efficiency relative to warm-season grasses.[32] Previous studies have shown that biomass production can be reduced in the mixed grass prairie of western Canada by as much as 60% simply due to litter removal.[36] It is also notable that the benefits of litter to cool-season grass growth documented here occurred despite a trend for elevated precipitation over the last 10 or more years in the region, which might have been expected to reduce the importance of litter.

Decoupling of warm-season grass production from litter presence may reflect several key factors. First, as noted previously, sandy soils are less likely to experience evaporation following rapid infiltration of rainfall, consistent with the inverse texture effect,[10] and this, in turn, would reduce the need for high litter levels to minimize surface evaporation. Second, both warm-season grasses commonly found in our study region have morphologic adaptions likely to minimize their reliance on litter and associated moisture conservation. Within loam sites, blue grama grass is the main warm-season species, and with its dense but shallow root system, this species may be more efficient at capturing and utilizing rainfall in mid-summer. Within sand dune sites, the primary warm-season grass was prairie sandreed, whose deep roots may better capture soil water, thereby reducing the need for litter to conserve surface moisture. Finally, warm-season grasses may also be negatively impacted directly by litter accumulation due to their lower tolerance for reduced light, which could impact patterns of initial plant green-up. Regardless of the mechanism, our results suggest warm-season grass production is less dependent on litter for maximizing biomass production.

Implications for Livestock Grazing

Our results indicate that peak levels of herbaceous standing crop occur in early August within this northern mixed grass ecosystem. Although similar biomass levels were evident between the loam and sand dune ecologic sites, a greater proportion of total biomass within the sand dune sites was comprised of warm-season grasses, which demonstrated the greatest plant growth between early July and August. Loam areas, dominated primarily by cool-season mid-grasses, also reached maximum yields in August but, unlike warm-season grasses, maintained a greater proportion of biomass into September. These findings indicate that although both ecologic sites are important for supporting livestock production, early season-grazing opportunities will be substantially greater in loam areas dominated by more cool-season species, whereas sandy areas may be particularly important for late summer grazing. As grazing can replace productive cool-season grasses with short-statured warm-season grasses, such as blue grama,[26] this species shift has been known to reduce overall production,[37] highlighting the need to modify grazing to conserve cool-season species.

Conclusions

Our results indicate that litter conservation should remain an important objective in the management of native grasslands across this region,[36] although they also add further clarification on the specific benefits of litter. Retention of litter was particularly important for promoting the production of cool-season rather than warm-season grasses, regardless of the seasonality of production. As cool-season grasses dominated biomass on both ecologic sites examined in this northern mixed ecosystem, we recommend that litter conservation continue to be a priority in the management of these grasslands.

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References

1. McCartney, D.H. 1993. History of grazing research in the Aspen Parkland. *Canadian Journal of Animal Science* 73:749-763.
2. Ayad, M.A.G., and R.L. Dix. 1964. An analysis of a vegetation-microenvironmental complex on prairie slopes in Saskatchewan. *Ecological Monographs* 34:421-442.
3. Epstein, H.E., W.K. Lauenroth, I.C. Burke, and D.P. Coffin. 1997. Productivity patterns of C3 and C4 functional types in the U.S. Great Plains. *Ecology* 78:722-731.
4. Coupland, R.T. 1958. The effects of fluctuations in weather upon the grasslands of the Great Plains. *Botanical Review* 24:273-317.
5. Smoliak, S. 1986. Influence of climatic conditions on production of Stipa-Bouteloua prairie over a 50-year period. *Journal of Range Management* 39:100-103.
6. Epstein, H.E., W.K. Lauenroth, and I.C. Burke. 1997. Effects of temperature and soil texture on ANPP in the U.S. Great Plains. *Ecology* 78:2628-2631.
7. Coupland, R.T., and R.E. Johnson. 1965. Rooting characteristics of native grassland species in Saskatchewan. *Journal of Ecology* 53:475-507.
8. Coupland, R.T. 1950. Ecology of mixed prairie in Canada. *Ecological Monographs* 20:271-315.
9. Sala, O.E., W.J. Parton, L.A. Joyce, and W.K. Lauenroth. 1988. Primary production of the Central Grassland Region of the United States. *Ecology* 69:40-45.
10. Noy-Meir, I. 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4:23-51.
11. Coupland, R.T. 1961. A reconsideration of grassland classification in the Northern Great Plains of North America. *Journal of Ecology* 49:135-167.
12. Adams, B.H., J. Richman, L. Poulin-Klein, K. France, D. Moisey, and R.L. McNeil. 2013. Rangeland plant communities for the Dry Mixed grass Natural Subregion of Alberta. 2nd Approximation. Lethbridge, Alberta: Rangeland Management Branch, Policy Division, Alberta Environment and Sustainable Resource Development. Pub. No. T/040. 135 pp.
13. Willms, W.D., and P.G. Jefferson. 1993. Production characteristics of the mixed prairie: constraints and potential. *Canadian Journal of Animal Science* 73:765-778.
14. Sims, P.L., and J.S. Singh. 1978. The structure and function of ten western North American grasslands. II. Intra-seasonal dynamics in primary producer compartments. *Journal of Ecology* 66:547-572.
15. Coupland, R.T. 1992. Mixed prairie. In: & Coupland RT, editor. Ecosystems of the world 8A: Natural grasslands. New York, NY: Elsevier Science Publishing Co. Inc. p. 151-179.
16. Vermeire, L.T., R.K. Heitschmidt, and M.J. Rinella. 2009. Primary productivity and precipitation-use efficiency in mixed grass prairie: a comparison of northern and southern US sites. *Rangeland Ecology and Management* 62:230-239.
17. Sims, P.L., J.S. Singh, and W.K. Lauenroth. 1978. The structure and function of ten western North American grasslands: I. Abiotic and vegetational characteristics. *Journal of Ecology* 66:251-285.
18. Redmann, R.E. 1975. Production ecology of grassland plant communities in western North Dakota. *Ecological Monographs* 45:83-106.
19. Skinner, R.H., J.D. Hanson, G.L. Hutchinson, and G.E. Schuman. 2002. Response of C3 and C4 grasses to supplemental summer precipitation. *Journal of Range Management* 55:517-522.

20. Barnes, P.W., and A.T. Harrison. 1982. Species distribution and community organization in a Nebraska sandhills Mixed Prairie as influenced by plant/soil-water relationships. *Oecologia* 52:192-201.
21. Paruelo, J.M., and W.K. Lauenroth. 1996. Relative abundance of plant functional types in grasslands and shrubland of North America. *Ecological Applications* 6:1212-1224.
22. Ode, D.J., L.L. Tieszen, and J.C. Lerman. 1980. The seasonal contribution of C3 and C4 plant species to primary production in a mixed prairie. *Ecology* 61:1304-1311.
23. Natural Regions Committee, 2006. Natural Regions and Subregions of Alberta. Compiled by D. J. Downing and W. W. Pettapiece. Government of Alberta, Pub. No. T/852.
24. Hulett, G.K., R.T. Coupland, and R.L. Dix. 1966. The vegetation of dune sand areas within the grassland region of Saskatchewan. *Canadian Journal of Botany* 44:1307-1331.
25. Broadbent, T. 2014. Clipping and watering effects on caespitose and rhizomatous grasses: implications for grazing management. PhD Thesis in Wildlife and Rangeland Resources. Edmonton, Alberta, Canada: Dept. of Agricultural, Food and Nutritional Science, University of Alberta. p. 274.
26. Hart, R.H., S. Clapp, and P.S. Test. 1993. Grazing strategies, stocking rates, and frequency and intensity of grazing on western wheatgrass and blue grama. *Journal of Range Management* 46:122-126.
27. Jefferson, P.G., W.P. McCaughey, K. May, J. Woosaree, L. MacFarlane, and S.M.B. Wright. 2002. Performance of American native grass cultivars in the Canadian prairie provinces. *Natural Areas Journal* :24-33.
28. Bradford, J.B., W.K. Lauenroth, I.C. Burke, and J.M. Paruelo. 2006. The influence of climate, soils, weather, and land use on primary production and biomass seasonality in the US Great Plains. *Ecosystems* 9:934-950.
29. Potvin, M.A., and A.T. Harrison. 1984. Vegetation and litter changes of a Nebraska sandhills prairie protected from grazing. *Journal of Range Management* 37:55-58.
30. Veron, S.R., J.M. Paruelo, O.B. Sala, and W.K. Lauenroth. 2002. Environmental controls of primary production in agricultural systems of the Argentine Pampas. *Ecosystems* 5:625-635.
31. Sims, P.L., G.R. Lovell, and D.F. Hervey. 1971. Seasonal trends in herbage and nutrient production of important sandhill grasses. *Journal of Range Management* 24:55-59.
32. Caldwell, M.M., R.S. White, R.T. Moore, and L.B. Camp. 1977. Carbon balance, productivity, and water use of cold-winter desert shrub communities dominated by C3 and C4 species. *Oecologia* 29:275-300.
33. Volesky, J.D., W.H. Schacht, P.E. Reece, and T.J. Vaughn. 2005. Spring growth and use of cool-season graminoids in the Nebraska sandhills. *Rangeland Ecology and Management* 58:385-392.
34. Epstein, H.E., W.K. Lauenroth, I.C. Burke, and D.P. Coffin. 1998. Regional productivities of plant species in the Great Plains of the United States. *Plant Ecology* 134:173-195.
35. Deutsch, E.S., E.W. Bork, and W.D. Willms. 2010. Soil moisture and plant growth responses to litter and defoliation impacts in Parkland grasslands. *Agriculture, Ecosystems and Environment* 135:1-9.
36. Willms, W.D., S. Smoliak, and A.W. Bailey. 1986. Herbage production following litter removal on Alberta native grasslands. *Journal of Range Management* 38:536-539.
37. Smart, A.J., B.H. Dunn, P.S. Johnson, L. Xu, and R.N. Gates. 2007. Using weather data to explain herbage yield on three Great Plains plant communities. *Rangeland Ecology and Management* 60:146-153.

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