Ecology of grazing lawns on tallgrass prairie

by

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Abstract

A key feature of many grass-dominated ecosystems is the formation of grazing lawns, distinct patches characterized by intense grazing by mammalian herbivores and a dense short-statured grass canopy. A central concept of grazing lawns is the positive feedbacks between grazing animals and the grass resource. Intraspecific morphological plant trait changes and differences in plant species composition could both or individually play a role in the differences in characteristics of grazing lawns and neighboring tallgrass swards. I studied grazing lawns in North American tallgrass prairie to: a) test the 'architectural shift hypothesis' where continued grazing leads to changes in plant architecture resulting in more efficient foraging for grazers, creating a positive feedback that increases grazing and b) examine soil resource (nutrient and water) availability and grass nutritive quality on and off lawns to test the nutrient- and water-based pathways for grazing lawn maintenance. In a separate study (not reported here), we a) examined plant community structure on and off lawns to determine whether species composition differences account for the distinct grazing lawn characteristics and b) assessed effects of grazing lawn formation on tallgrass prairie plant species diversity.

Several differences in morphological traits between dominant grasses on grazing lawns and tallgrass swards support the architectural shift hypothesis. For *Sorghastrum nutans, Dichanthelium oligosanthes, and Pascopyrum smithii,* leaf-to-stem ratio was twice as high on grazing lawns compared to surrounding matrix tallgrass vegetation and tiller branching was higher and culm internode lengths were shorter on grazing lawns for these species. However, *Andropogon gerardii* traits did not differ between grazing lawns and tallgrass vegetation. For all four species, above-ground tiller biomass and number of below-ground buds were both higher

on grazing lawns. Overall, these morphological responses resulted in a higher grass canopy density (forage biomass per unit canopy volume) on grazing lawns and this increased grass canopy density in turn results in higher grazer foraging efficiency by increasing the amount of forage intake per bite and per unit time.

D. oligosanthes, P. smithii, and S. nutans plants on grazing lawns had a significantly lower carbon-to-nitrogen ratio and higher nitrogen content than plants in the matrix tallgrass vegetation, while *A. gerardii* showed no significant difference in nitrogen content or in carbon-to-nitrogen ratio between grazing lawns and surrounding matrix tallgrass vegetation. With regards to the total grass canopy (all grass species combined), nitrogen content was significantly higher on grazing lawns compared to tallgrass vegetation for all three field seasons, 2016, 2017, and 2018. All measured soil nutrients, ammonium, nitrate, phosphorus, and sodium, were significantly higher on grazing lawns compared to soils of surrounding tallgrass swards, while water content showed no significant difference between grazing lawns and surrounding tallgrass vegetation.

The results of this study strongly indicate that developmental and morphological shifts result in increased forage density and increased grazing efficiency on grazing lawns and that the frequent and intense activities of large grazers result in increased plant nitrogen content and lower C:N ratios in grasses on tallgrass prairie grazing lawns. Thus, at least two different mechanisms, plant architectural shifts and the nutrient-based pathway could both contribute to the positive feedbacks that encourage further grazing on lawns and grazing lawn maintenance on tallgrass prairie.

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There are numerous people that have helped me on this long and winding road towards my master's degree. I want to take this opportunity to express my utmost gratitude to them, for the ways they have helped me reach this milestone in my education.

First and foremost, to my major professor, Dr. David Hartnett, thank you! I feel that fate led you to be my mentor. I could have never accomplished this without your patience, trust, and guidance. Your understanding for my being a non-traditional student, beginning with offering me a very flexible undergraduate research opportunity, is what allowed me to follow this challenging road. Thank you for encouraging me to take adventures that I will never forget and for introducing me to goat seswaa, pap, and Amarula.

Also, thank you to Dr. Carolyn Ferguson and Dr. Jesse Nippert for your investment in being on my masters committee.

There are many colleagues who helped make my data collection during field season possible. I would especially like to mention Sammi Grieger. I could not have imagined a better lab partner. In less than a month, we had an abbreviated language all our own and flowed so well together. Also, Jeffrey Taylor, your immense knowledge of plant species and your time made a daunting task achievable. Emily Wedel and Sarah Shaffer, for braving the heat to help collect plants, and Sid Shaffer for helping with the tedious task of data checking, thank you. Lastly, Rory O'Connor, your help with statistical analyses was much needed and appreciated.

I would also like to thank Dr. Anthony Joern and Dr. David Haukos for initiating my interest and for their guidance in pursuing a graduate degree.

Finally, thank you to Kansas State University, the Division of Biology, the LTER, and the National Science Foundation for the learning opportunities, teaching experiences, financial assistance, and the ability to conduct research at Konza Prairie Biological Station that allowed me to pursue my educational and future career goals.

Dedication

I dedicate this thesis to my family. Lauren, Sarah, and Sid, thank you for your understanding when I decided to return to college. I know it was a big change for you all. And Phil, without your love and support, none of this would have been possible. You have always been my rock. I love you all more than words can say.

Chapter 1 - Introduction

Grasslands and savannas cover approximately 40% of the global terrestrial surface (Koerner *et al.* 2014) and are widely distributed, covering all continents except Antarctica. Major types of grasslands include montane, mesic, savanna, semi-arid, sedge meadow, salt marsh, and tallgrass prairie. Grassland ecosystems act as carbon sinks, potentially alleviating greenhouse gas emissions, act as water catchments, contribute to biodiversity, and are a large feeding base for livestock, making them an invaluable resource globally (Boval & Dixon 2012).

North American grasslands evolved under grazing pressure from large ungulates such as bison, elk, deer, and pronghorn, and other vertebrate and invertebrate herbivores (Axelrod 1985). However, with the spread of agriculture across the North American continent, cattle have replaced native grazers on contemporary grasslands, and a large fraction of native grasslands have been plowed and converted to crop agriculture.

Herbivores play a key role in determining vegetation structure, species composition, and biomass production in grasslands. While large ungulates have interacted with prairies for millennia, it has only been in the past few decades that ecologists have studied the role of bison, a keystone native grazer on North American grasslands. Bison (*Bison bison*) have now been reintroduced onto tall grass prairie sites large enough to observe their influence on biota and grassland ecosystem dynamics at the landscape scale. (Knapp *et al.* 1999).

Large grazing animals contribute directly to patchiness in grasslands through non-uniform defoliation, dung and urine deposition. In addition, large ungulate non-grazing activities, such as bison (*Bison bison*) trampling and wallowing, also affect plant community structure and vegetation heterogeneity (McNaughton 1979; Knapp *et al.* 1999; Howison *et al.*

2017). A key feature of many grass-dominated ecosystems is the formation of grazing lawns, distinct patches characterized by intense grazing by mammalian herbivores, a dense short-statured grass canopy, and maintained by positive grazer-vegetation feedbacks. Many grazing lawn grasses, particularly in Africa, are dominated by stoloniferous and rhizomatous grasses, storing much of their carbohydrates in the horizontal stolons or rhizomes, which helps to cope with trampling from ungulates (Hempson *et al.* 2015). Compared to tall grass swards, grazing lawns are often comprised of plants with a higher leaf to stem ratio (Stobbs 1973) and higher growth rate and productivity. In the Serengeti, biomass concentration of aboveground plant canopies on grazing lawns has been found to be twice as high, since grazing reduces height more than it reduces plant biomass (Mcnaughton 1984). Veldhuis *et al.* (2014) showed that in South African grasslands, grazed plants show lower evaporative water loss and also reduced photosynthetic carbon fixation, resulting in changes in plant carbon to nutrient ratios, which also contributes to higher nutrient content (Veldhuis *et al.* 2014). Various studies on grasslands globally have shown some grazing lawns to have a distinctly different plant community than ungrazed or lightly grazed areas as grazers alter plant competitive relationships (Karki, Jhala & Khanna 2000), indicating that lawn formation may be a driver for increased biodiversity on grasslands. In North American Tallgrass Prairie, grazing lawns represent a distinct patch in the landscape, and thus constitute “hotspots” of floristic diversity (Greiger *et al.* unpublished).

Grazing lawns are found across the globe and are created and maintained by numerous types of animals, including bison and geese in North America to wallabies and wombats in Australia and Tasmania. Grazing lawns have been widely studied in Africa, Australia and in subtropical grasslands in other regions. African grazing lawns have a long co-evolutionary history between the grazers and grasses (Mcnaughton 1984) and short grass specialists with relatively broad muzzles, such as the wildebeest (*Connochaetes taurinus*), hippopotamus (*Hippopotamus amphibius*), and white rhino (*Ceratotherium simum*), are able to transform grass swards into a lawn-like state by grazing them regularly (Hempson *et al.* 2015). In the Indian savanna, grazing stimulated 4-45% greater net primary production (Pandey & Singh 1992).

Relative to tropical and subtropical regions, little is known about the ecology of grazing lawns in temperate grasslands, and whether common characteristics of grazing lawns in other regions hold true for grazing ecosystems in North America. Our lack of knowledge about grazing lawns in temperate grasslands, such as tallgrass prairie, exists because previous studies in these grasslands have compared large sites or landscapes with and without the presence of grazers, but have not compared these patch types (grazing lawns versus adjacent matrix tall grass swards) within the larger grazed ecosystem.

Factors that may cause the initiation of grazing lawns include animal congregation for predator avoidance or in response to nutrient hotspots. In Africa, higher soil fertility often leads to enhanced plant productivity or forage nutritive quality (Anderson *et al.* 2010; Coetsee, Stock & Craine 2011; Donaldson *et al.* 2018), leading in turn to herbivore aggregations, which, depending on plant growing conditions may or may not contribute to grazing lawn maintenance by enhancing nutrient turnover and litter quality (McNaughton, Banyikwa & McNaughton 1997; Augustine & McNaughton 2006). In addition, large groups of herbivores requiring predator defense will converge in an area, thus creating an area of highly grazed plants, initiating the positive-feedbacks that promote grazing lawns.

Once initiated, the persistence of lawns happens through repeated grazing stimulating continual re-growth, maintaining grasses in an immature state with higher nutrient content, leaf-to-stem ratio, productivity and forage concentration than the surrounding tall grass vegetation, which in turn promotes further consumption (Stobbs 1973; McNaughton 1979; Mcnaughton 1984; Cromsigt & Olff 2008; Hempson *et al.* 2015). Plants on grazing lawns also may have higher nutritional quality (McNaughton 1979; Veldhuis *et al.* 2014), that occurs through deposition of dung and urine by mammalian herbivores, allowing the plants to receive nutrients and minerals in more readily available forms (Mcnaughton 1984; Howison *et al.* 2017). Grazers get more nutrients and phytomass per bite on grazing lawns compared to off lawns. Also, grazing lawn species persist by keeping much of their important structural components, such as buds and stems, largely below the reach of grazers (Hempson *et al.* 2015). Grasses are adapted to deal with the physical and abiotic conditions of frequent grazing. Traits exhibited by intensely grazed grasses include compact basal meristems, small stature, prostrate growth forms, high shoot density, deciduous shoots, rapid growth, and below-ground nutrient reserves. These traits are associated with both drought and grazing tolerance (Howison *et al.* 2017).

Recent studies indicate that the maintenance of grazing lawns happens through positive plant-grazer feedbacks that result in morphological and structural plant traits that increase phytomass concentration and elicit changes in soil, which both contribute to stimulate repeated grazing (Veldhuis *et al.* 2014; Donaldson *et al.* 2018). The classic nutrient-based pathway suggests that defoliation increases light and leads to compensatory growth, and fecal and urine deposition leads to nutrient mineralization, both leading to higher plant nutritional quality and promoting continued grazing (Figure 1) (Veldhuis *et al.* 2014) (Koerner *et al.* 2014; Veldhuis *et al.* 2014; Archibald & Hempson 2016; Howison *et al.* 2017).

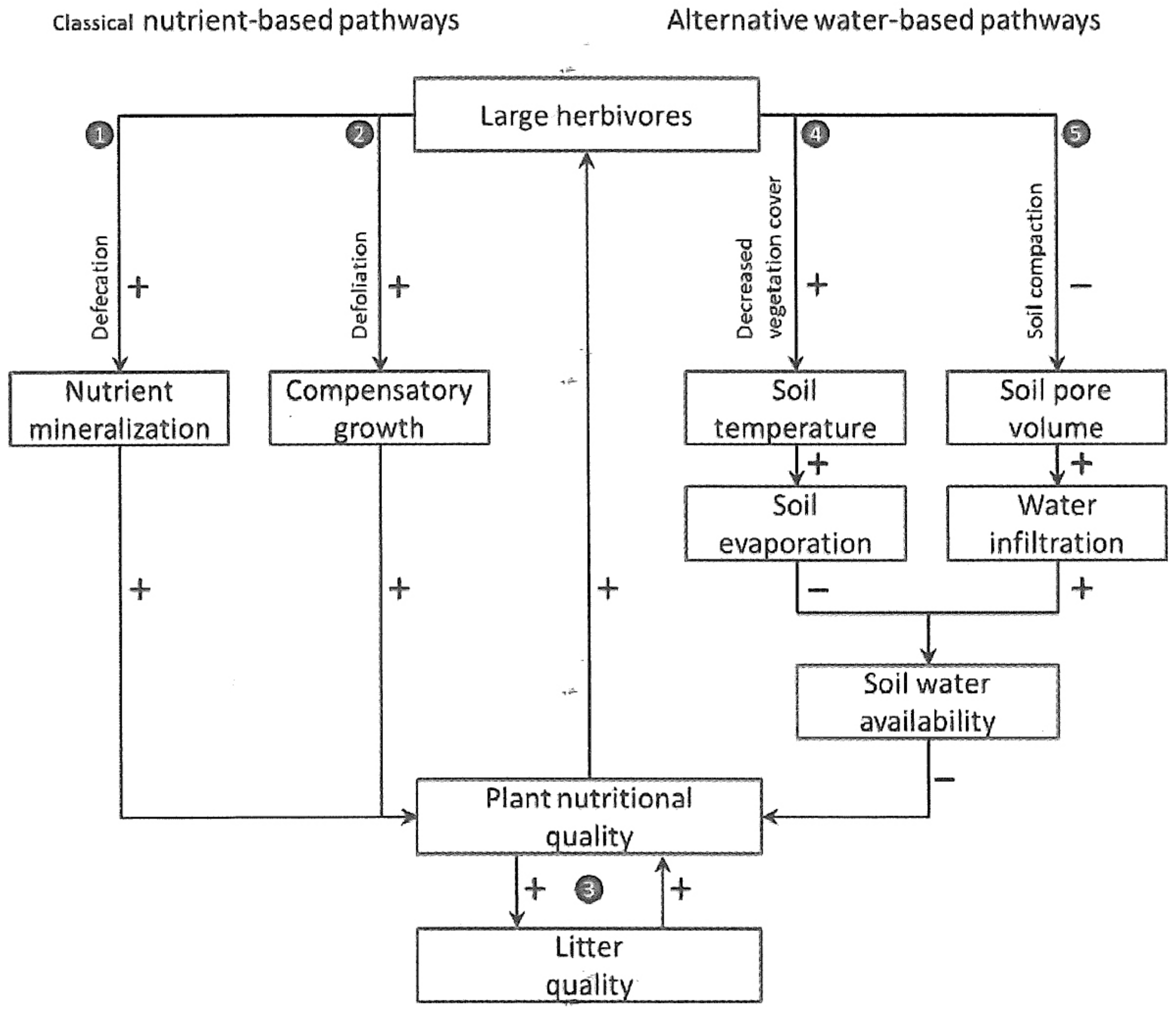

Figure 1.1: Overview of the influence of large herbivores on grass nutritional quality. The diagram shows five main pathways by which herbivores affect grass nutritional quality. (Veldhuis *et al*. 2014)

Excretory plant biomass produced by grazed grasses that have been broken down in the gut of large herbivores and their associated microflora allow nutrients to return through urine and feces to the grazing area in the most plant-available forms (Howison *et al.* 2017). In addition to the nutrient-based pathways, a water-based pathway also may generate positive feedbacks and promote continued large herbivore grazing. According to this hypothesis, soil compaction and decreased vegetation cover lead to changes in soil water availability, requiring plants to retain nutrients, thereby also increasing plant nutritional quality (Figure 1.1) (Veldhuis *et al.* 2014) (Veldhuis *et al.* 2014; Howison *et al.* 2017).

Hartnett (unpublished) has proposed another positive feedback mechanism, in addition to the nutrient and water-based pathways maintaining grazing lawns. He hypothesizes that defoliation and trampling leads to bud activation and altered outgrowth patterns of buds (Figure 1.2).

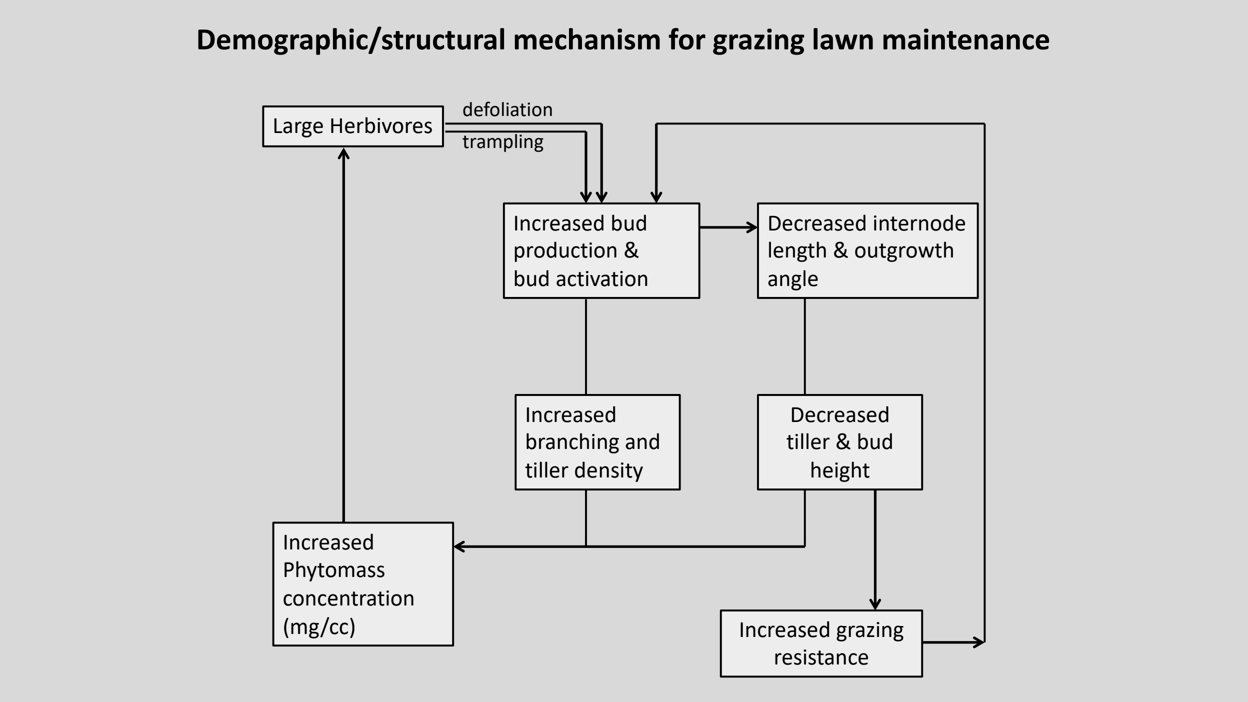

Figure 1.2: -Demographic and structural positive feedback mechanisms for grazing lawn maintenance. (Hartnett unpublished).

Bud activation results in increased tiller density, shorter internode lengths, and more horizontal bud outgrowth angles (N'Guessan and Hartnett 2011). In addition, the shorter tiller and bud height place meristems out of reach of grazers, leading to increased grazing resistance. These morphological changes in turn result in higher aboveground phytomass concentration, promoting increased grazing. This mechanism could explain the higher forage density that McNaughton found for Serengeti grasslands (McNaughton 1979).

In addition to morphological changes to plants on grazing lawns, floristic composition can also be different on grazing lawns when compared to tall grass swards. One unanswered question regarding grazing lawn floristic composition is: Do grazers cause the unique species composition of grazing lawns, or do patches with certain plant species composition cause grazers to aggregate? McNaughton (1984) noted that Serengeti grazing lawns differed from matrix vegetation in their floristic composition, with higher abundance of nutrient- and mineral-rich species that form key resources for grazing herbivores (Mcnaughton 1984). The 'species fidelity model' suggests that grazing lawns constitute very specific assemblages of plant species, whereas the 'plant species plasticity model' hypothesizes that the distinct traits of grazing lawns arise from intra-specific variation or ecotypic variation in nutritive quality, plant architecture or other plant traits (Arnold, Anderson & Holdo 2014). Understanding the source of variation in traits between lawns and tall grass swards is important for understanding the origin, maintenance and dynamics of heterogeneity within grazing ecosystems (Arnold *et al.* 2014).

A central concept of grazing lawns is the positive feedbacks between grazing animals and the grass resource. Intraspecific morphological plant trait changes and differences in plant species composition could both or individually play a role in the differences in characteristics of grazing lawns and neighboring tall grass swards. I studied grazing lawns in North America Tallgrass Prairie to, a) test the ‘architectural shift hypothesis’ where continued grazing leads to changes in plant architecture resulting in more efficient foraging for grazers, creating a positive feedback that increases grazing, b) examine soil resource (nutrient and water) availability and grass nutritive quality on and off lawns to test these alternative pathways for grazing lawn maintenance, c) examine plant community structure on and off lawns to test the ‘species fidelity model,’ and d) assess effects of grazing lawn formation on tall grass prairie plant species diversity. This thesis research addressed objectives a and b. Objectives c and d were addressed in a separate study (Grieger, Shaffer, and Hartnett (in review)). Ultimately, I hope to understand how grazing lawns contribute to forage for native grazers, plant species richness, and overall biodiversity of the grassland landscape, indicating their importance in terms of conserving the North American Tallgrass Prairie.

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Chapter 2 - Plant Architectural Shifts Contribute to Increased Forage Density on Grazing Lawns

Introduction

Large grazing animals contribute directly to patchiness in grasslands through non-uniform defoliation, dung and urine deposition. In addition, large ungulate non-grazing activities, such as bison trampling and wallowing, also affect plant community structure and vegetation heterogeneity (McNaughton 1979; Knapp *et al.* 1999; Howison *et al.* 2017). A key feature of many grass-dominated ecosystems is the formation of grazing lawns, distinct patches characterized by intense grazing by mammalian herbivores, a dense short-statured grass canopy, and maintained by positive grazer-vegetation feedbacks. Many grazing lawn grasses, particularly in Africa, are rhizomatous or stoloniferous, storing much of their carbohydrates belowground, which helps to cope with trampling from ungulates (Hempson *et al.* 2015). Compared to tall grass swards, grazing lawns are often comprised of plants with a higher leaf to stem ratio (Stobbs 1973) and higher growth rate and productivity. In the Serengeti, biomass concentration of aboveground plant canopies on grazing lawns has been found to be twice as high, since grazing reduces height more than it reduces plant biomass (Mcnaughton 1984). Veldhuis *et al.* (2014) showed that in South African grasslands, grazed plants show lower evaporative water loss and also reduced photosynthetic carbon fixation, resulting in changes in plant carbon to nutrient ratios, which also contributes to higher nutrient content (Veldhuis *et al.* 2014). Various studies on grasslands globally have shown some grazing lawns to have a distinctly different plant community than ungrazed or lightly grazed areas as grazers alter plant competitive relationships (Karki, Jhala & Khanna 2000), indicating that lawn formation may be a driver for increased biodiversity on grasslands. In North American Tallgrass Prairie, grazing lawns represent a distinct patch in the landscape, and thus constitute “hotspots” of floristic diversity (Greiger, Shaffer and Hartnett in review).

Once initiated, the persistence of lawns happens through repeated grazing stimulating continual re-growth, maintaining grasses in an immature state with higher nutrient content, leaf-to-stem ratio, productivity and forage concentration than the surrounding tall grass vegetation, which in turn promotes further consumption (Stobbs 1973; McNaughton 1979; Mcnaughton 1984; Cromsigt & Olff 2008; Hempson *et al.* 2015). Plants on grazing lawns also may have higher nutritional quality (McNaughton 1979; Veldhuis *et al.* 2014), that occurs through deposition of dung and urine by mammalian herbivores, allowing the plants to receive nutrients and minerals in more readily available forms (Mcnaughton 1984; Howison *et al.* 2017). Grazers get more nutrients and phytomass per bite on grazing lawns compared to off lawns. Also, grazing lawn species persist by keeping much of their important structural components, such as buds and stems, largely below the reach of grazers (Hempson *et al.* 2015). Grasses are adapted to deal with the physical and abiotic conditions of frequent grazing. Traits exhibited by grazed grasses include compact basal meristems, short stature, prostrate growth forms, high shoot density, deciduous shoots, rapid growth, and below-ground nutrient reserves. These traits are associated with both drought and grazing tolerance (Howison *et al.* 2017).

Recent studies indicate that the maintenance of grazing lawns happens through positive plant-grazer feedbacks that result in morphological and structural plant traits that increase phytomass concentration and elicit changes in soil, which both contribute to stimulate repeated grazing (Veldhuis *et al.* 2014; Donaldson *et al.* 2018). The classic nutrient-based pathway suggests that defoliation increases light and leads to compensatory growth, and fecal and urine deposition leads to nutrient mineralization, both leading to higher plant nutritional quality and promoting continued grazing (Figure 2.1) (Veldhuis *et al.* 2014) (Koerner *et al.* 2014; Veldhuis *et al.* 2014; Archibald & Hempson 2016; Howison *et al.* 2017).

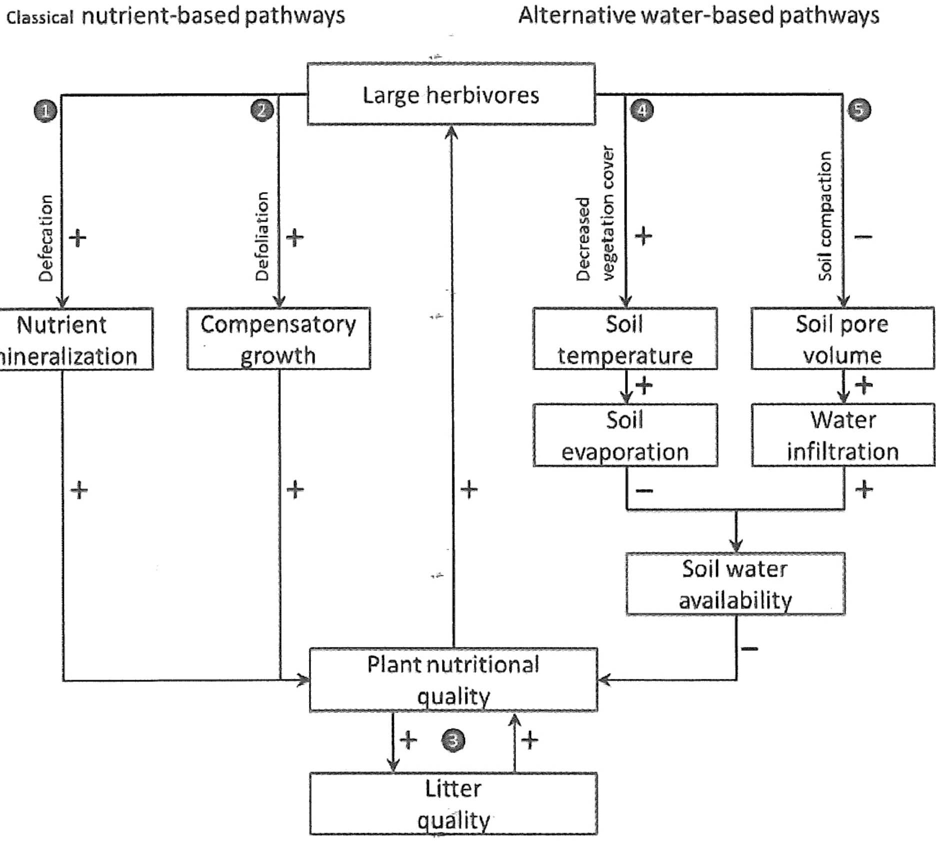


Figure 2.1: Overview of the influence of large herbivores on grass nutritional quality. The diagram shows five main pathways by which herbivores affect grass nutritional quality. (Veldhuis *et al*. 2014)

Excretory plant biomass produced by grazed grasses that have been broken down in the gut of large herbivores and their associated microflora allows nutrients returning in urine and feces to the grazing area in the most plant-available forms (Howison *et al.* 2017). In addition to the nutrient-based pathway, a water based pathway also may generate positive feedbacks and promote continued large herbivore grazing. According to this hypothesis, soil compaction and decreased vegetation cover lead to changes in soil water availability, requiring plants to retain nutrients thereby, also increasing plant nutritional quality (Figure 2.1) (Veldhuis *et al.* 2014) (Veldhuis *et al.* 2014; Howison *et al.* 2017).

Hartnett (unpublished) has proposed another positive feedback mechanism, in addition to the nutrient and water-based pathways maintaining grazing lawns. He hypothesizes that defoliation and trampling leads to bud activation and altered outgrowth patterns of buds (Figure 2.2).

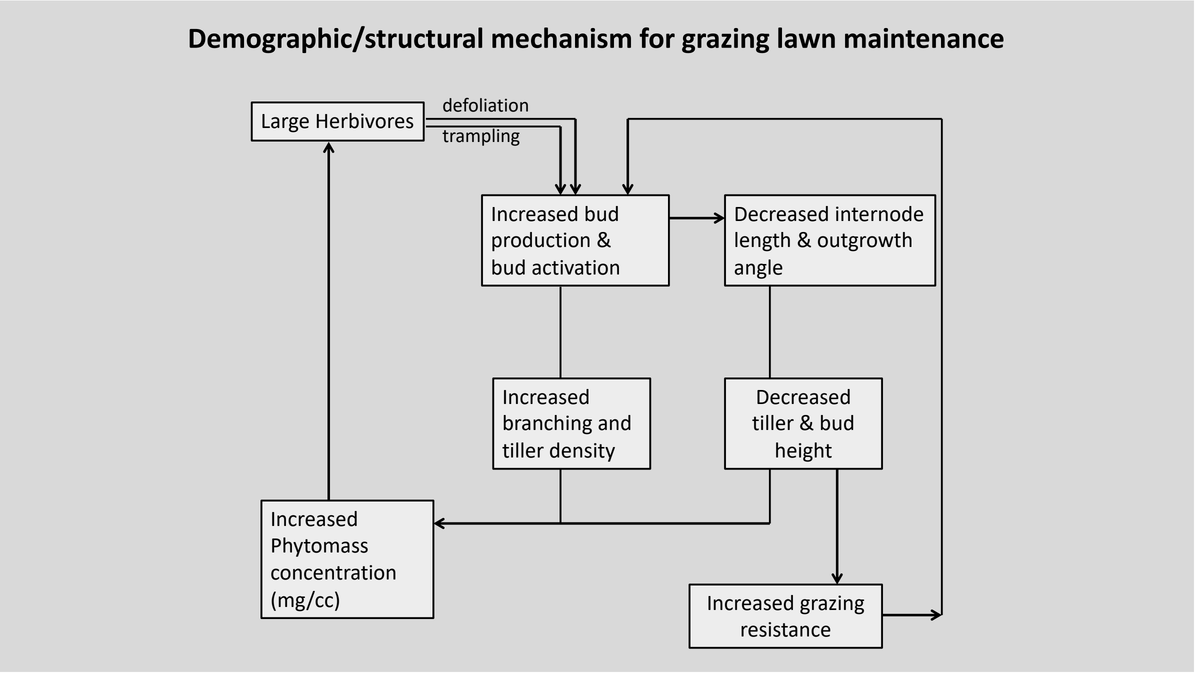


Figure 2.2:-Demographic and structural positive feedback mechanisms for grazing lawn maintenance. (Hartnett unpublished).

Grazing releases buds from dormancy and this activation results in increased tiller density and shorter internode lengths. In addition, grazing results in more horizontal bud outgrowth angles (N'Guessen and Hartnett 2011). The shorter tiller and bud height and horizontal outgrowth angles place meristems out of reach of grazers, leading to increased grazing resistance. These morphological changes in turn result in higher aboveground phytomass concentration, promoting increased grazing. This morphological mechanism could explain the higher forage density that McNaughton found for Serengeti grasslands (McNaughton 1979).

A central concept of grazing lawns is the positive feedbacks between grazing animals and the grass resource. Intraspecific morphological plant trait changes and differences in plant species composition could both or individually play a role in the differences in characteristics of grazing lawns and neighboring tall grass swards. In this chapter, I report on a study of grazing lawns in North America Tallgrass Prairie to test the 'architectural shift hypothesis' where continued grazing leads to changes in plant architecture resulting in more efficient foraging for grazers, creating a positive-feedback that increases grazing. I measured multiple plant traits for morphological changes, such as height, internode length, leaf-to-stem ratio, belowground buds, branching, flowering, and leaf and stem weight, as these can lead to higher density forage for grazers. Ultimately, I hope to understand how grazing lawns contribute to forage for native grazers, plant species richness, and overall biodiversity of the grassland landscape, indicating their importance in terms of conserving the North American Tallgrass Prairie.

Materials and methods

Study Site Description

I conducted this study in the spring and summer field seasons of 2016, 2017 and 2018 at the Konza Prairie Biological Station (KPBS), a 3,487 ha tallgrass prairie preserve in the Flint Hills region of Kansas (39°05’ N, 96°35’W). KPBS is owned by The Nature Conservancy and Kansas State University (KSU). The KSU Division of Biology manages the site for ecological research, education and grassland conservation. Grassland vegetation of KPBS is predominantly native tallgrass or bluestem prairie, principally perennial, warm-season C_4 grasses, *Andropogon gerardii, Sorghastrum nutans,* and *Panicum virgatum* (Freeman & Hulbert 1985). A highly diverse mixture of less abundant species includes warm-season (C_4) and cool-season (C_3) grasses, composites, legumes, other forbs, and patchily distributed shrubs. Average monthly temperatures range from a low in January of -2.7°C to a high in July of 26.6°C. Mean annual total precipitation (MAP) is 835mm with 75% falling during the growing season. For the 2016 growing season (Apr-Sept), precipitation was very close to MAP. However, precipitation during the growing seasons of 2017 and 2018 was significantly less than normal with 57% less than MAP in 2017 and a 45% less than MAP in 2018. Konza Prairie is divided into 60 experimental units, each constituting a separate watershed (average size = 0.55 km^2). Each watershed is subjected to prescribed burning at 1, 2, 4, or 20-year intervals. The majority of my study sites were in watersheds with a 4 year burn interval, with one in an annually burned watershed and one in a watershed burned at 20-year intervals. My project needed to be completed over multiple years due to the time constraints of when plants were flowering, but not senescing, and also the labor and time intensive processes of measuring multiple traits on a large number of samples (a sample being an individual tiller/ramet).

Grazing treatments at Konza Prairie are also applied at the watershed level, and include either bison (*Bison bison*), cattle (*Bos taurus*), or ungrazed treatments. After a nearly 100-year absence, bison were reintroduced to KPBS in 1987. Currently, a population of approximately 325 bison occupies a large area encompassing 2400 ha that spans over 10 watersheds with spring fire regimes at 1-, 2-, 4-, and 20-year burn intervals. Bison are free to roam over all 10 watersheds contained within the 2400 ha area. Each experimental watershed is given a 3-character label indicating the grazing treatment, fire interval, and replicate (A-D). For example, watershed N4D is grazed by native herbivores, burned at 4-year intervals, and is replicate D. The grassland vegetation structure within the bison watersheds is clearly bi-modal, with areas of shorter statured grazing lawns where bison grazing is concentrated and frequent, occurring within a matrix of tall perennial rhizomatous, intermediate, and caespitose grasses that is minimally utilized by the bison.

Methods

Four grass species (2 C_3 and 2 C_4) were collected over the course of 3 growing seasons. *Dichanthelium oligosanthes,* a C_3 grass, was collected in late June-early July and *Andropogon gerardii,* a C_4 grass, was collected end of August-early September of the 2016 field season. *Sorghastrum nutans,* a C_4 grass, was collected end of August-early September of the 2017 field season. *Pascopyrum smithii,* a C_3 grass, was collected early to mid-June of the 2018 field season. These species were chosen due to their abundance on both grazing lawns and tall grass swards, and also being native to the tallgrass prairie.

In watersheds N4A and N4D, 120 samples (eg. tillers or ramets) of *D. oligosanthes* were collected on grazing lawns and 112 samples were collected from the surrounding tall grass swards. Thirty-six samples of *A. gerardii* were collected from grazing lawns and from tall grass swards over watersheds N4A and N4D. Thirty-six grazing lawn and thirty-six tall grass sward samples of *S. nutans* were collected from watersheds N4D, N4A, and N1B. Sixty grazing lawn and sixty tall grass samples of *P. smithii* were collected from watersheds N4A, N20A, and N4B.

For each sampled individual of each species, measurements were taken of leaf dry weight, stem dry weight, total dry weight, leaf-to-stem ratio, canopy height, number of belowground buds, number of branches, internode length, and proportion of tillers flowering. Before plants were dried, canopy height, number of belowground buds, number of branches, internode length, and proportion of tillers flowering were measured. Four internode length measurements were taken starting from the base of the tiller. Dormant below-ground buds were counted using a dissecting scope. Buds were distinguished from juvenile tillers based on lack of greening or leaf expansion beyond the protective prophyll. For the dry weights and leaf-to-stem ratio, each sampled individual was separated into its component stem and leaf tissue, oven-dried at 60° C for a minimum of 48 hours and weighed to the nearest 0.01 g. Due to differences among species (eg. lack of branching, lack of flowering, fungal damage to buds) it was not possible to measure all traits for all species in both treatments.

Total aboveground vegetation biomass samples were also taken from the same sampling sites as the individual species collections. A 0.9 m^2 quadrat was used for sampling, and six samples were taken over five replicates for each treatment. Samples were then dried and grasses were separated from forbs and weighed separately. Mean overall canopy density (grasses and forbs) and grass canopy density was calculated for lawn and tall grass swards. Within each 0.9 m^2 quadrat, mean canopy height was determined by measuring the height of 10 randomly selected tillers. For total vegetation biomass samples, canopy density (grams of biomass per cm^3 canopy volume) was determined by dividing total aboveground vegetative biomass by canopy volume (0.9 m^2 x mean canopy height).

Data Analysis

Two-way analysis of variance (ANOVA) was used on all individual species traits to test for significance between treatments, sites, and interactions between treatments and sites. For some of the traits, patterns of variation in the data did not meet requirements for ANOVA, so the non-parametric Kruskal-Wallis test was used. These traits were: branches for *D. oligosanthes;* branches, buds, and flowers for *S. nutans;* branches, leaf-to-stem ratio, and flowers for *A. gerardii;* and branches, buds, and flowers for *P. smithii.*

For vegetation biomass samples, one-way analysis of variance was used to test if there was a significant difference in canopy forage density in lawn and tall grass treatments.

Results

Tables

	AG Lawns	AG Tallgrass	SN Lawns	SN Tallgrass
Leaf wt. (g)	1.20 ± 0.14	2.33 ± 0.23	1.08 ± 0.11	1.73 ± 0.10
Stem wt.(g)	0.85 ± 0.13	1.04 ± 0.13	0.49 ± 0.06	0.91 ± 0.06
Total wt. (g)	2.06 ± 0.25	3.36 ± 0.32	1.58 ± 0.15	2.64 ± 0.14
Leaf:Stem ratio	3.67 ± 1.28	6.82 ± 2.43	3.91 ± 0.69	2.00 ± 0.09
Canopy ht. (cm)	58.9 ± 3.76	72.5 ± 3.91	45.6 ± 2.62	61.8 ± 4.12
No. of buds/tiller	-	-	2.37 ± 0.29	2 ± 0.19
No. of branches/tiller	2 ± 0.22	2.5 ± 0.23	2 ± 0.21	1.94 ± 0.24
Internode length (cm)	6.14 ± 0.46	6.07 ± 0.41	3.97 ± 0.32	5.57 ± 0.43
Percent of tillers flowering	42%	39%	38%	48%

Table 2.1-Traits of the dominant C_4 grasses (*Andropogon gerardii* (AG) and *Sorghastrum nutans* (SN)) on grazing lawns and tall grass swards in tallgrass prairie. Values shown are means ± 1SE.

	DO Lawns	DO Tallgrass	PS Lawns	PS Tallgrass
Leaf wt. (g)	0.24 ± 0.01	0.26 ± 0.02	0.14 ± 0.01	0.18 ± 0.01
Stem wt. (g)	0.07 ± 0.01	0.16 ± 0.01	0.156 ± 0.01	0.19 ± 0.01
Total wt. (g)	0.31 ± 0.01	0.41 ± 0.03	0.30 ± 0.01	0.37 ± 0.02
Leaf:Stem ratio	3.60 ± 0.10	1.84 ± 0.06	3.29 ± 1.60	0.96 ± 0.05
Canopy ht. (cm)	17.0 ± 0.44	33.4 ± 1.04	39.3 ± 1.29	46.9 ± 0.98
No. of buds/tiller	3.56 ± 0.14	2.16 ± 0.10	1.88 ± 0.21	1.63 ± 0.14
No. of branches/tiller	2.72 ± 0.11	2.59 ± 0.12	1.78 ± 0.13	1.57 ± 0.10
Internode length	2.21 ± 0.06	4.80 ± 0.14	6.42 ± 0.32	8.36 ± 0.33
Percent of tillers flowering	-	-	90%	100%

Table 2.2-Traits of the dominant C_3 grasses (*Dichanthelium oligosanthes* (DO) and (*Pascopyrum smithii* (PS)) on grazing lawns and tall grass swards in tallgrass prairie. Values shown are means ± 1SE.

	Test*	d.f.	F-statistic	Probability
Height	ANOVA	1	284.0	<0.001
Internode	ANOVA	1	284.7	<0.001
Branching	ANOVA	1	1.9	0.168
Buds	ANOVA	1	69.6	<0.001
Total wt.	ANOVA	1	11.6	<0.001
Leaf wt.	ANOVA	1	1.1	0.296
Stem wt.	ANOVA	1	71.4	<0.001
Leaf to Stem ratio	ANOVA	1	257.0	<0.001

Table 2.3-Statistical tests for *Dichanthelium oligosanthes*. * ANOVA = two-way analysis of variance.

	Test*	d.f.	F or χ^2 - statistic	Probability
Height	ANOVA	1	11.7	<0.001
Internode	ANOVA	1	8.5	0.004
Branching	KW	1	0.01	0.905
Buds	KW	1	2.2	0.135
Flowers	KW	1	1.4	0.237
Total wt.	ANOVA	1	26.0	<0.001
Leaf wt.	ANOVA	1	21.8	<0.001
Stem wt.	ANOVA	1	25.0	<0.001
Leaf to Stem ratio	ANOVA	1	7.9	0.006

Table 2.4-Statistical tests for *Sorghastrum nutans.* *ANOVA = two-way analysis of variance. KW = Kruskal-Wallis test.

	Test*	d.f.	F or χ^2 - statistic	Probability
Height	ANOVA	1	14.5	<0.001
Internode	ANOVA	1	0.007	0.932
Branching	KW	1	2.5	0.111
Flowers	KW	1	0.1	0.721
Total wt.	ANOVA	1	15.9	<0.001
Leaf wt.	ANOVA	1	22.9	<0.001
Stem wt.	ANOVA	1	1.0	0.332
Leaf to Stem ratio	KW	1	6.2	0.012

Table 2.5-Statistical tests for *Andropogon gerardii.* *ANOVA = two-way analysis of variance. KW = Kruskal-Wallis test**.**

	Test*	d.f.	F or χ^2 - statistic	Probability
Height	ANOVA	1	22.0	<0.001
Internode	ANOVA	1	18.0	<0.001
Branching	KW	1	0.6	0.457
Buds	KW	1	0.4	0.504
Flowers	KW	1	6.3	0.012
Total wt.	ANOVA	1	13.2	<0.001
Leaf wt.	ANOVA	1	7.5	0.007
Stem wt.	ANOVA	1	10.4	0.002
Leaf to Stem ratio	ANOVA	1	0.7	0.42

Table 2.6-Statistical tests for *Pascopyrum smithii.* *ANOVA = two-way analysis of variance. KW = Kruskal-Wallis test.

	Test	d.f.	F-statistic	Probability
Grass 2016	ANOVA	1	25.2	<0.001
Grass 2017	ANOVA	1	1.6	0.211
Grass 2018	ANOVA	1	0.1	0.719

Table 2.7-Statistical tests for Canopy Grass Density (mg/cm^3). ANOVA = two-way analysis of variance.

	Test	d.f.	F-statistic	Probability
Total 2016	ANOVA	1	32.0	<0.001
Total 2017	ANOVA	1	6.6	0.013
Total 2018	ANOVA	1	14.1	<0.001

Table 2.8-Statistical tests for Canopy Total (Grass and Forb) Density (mg/cm^3). ANOVA = two-way analysis of variance.

Graphs

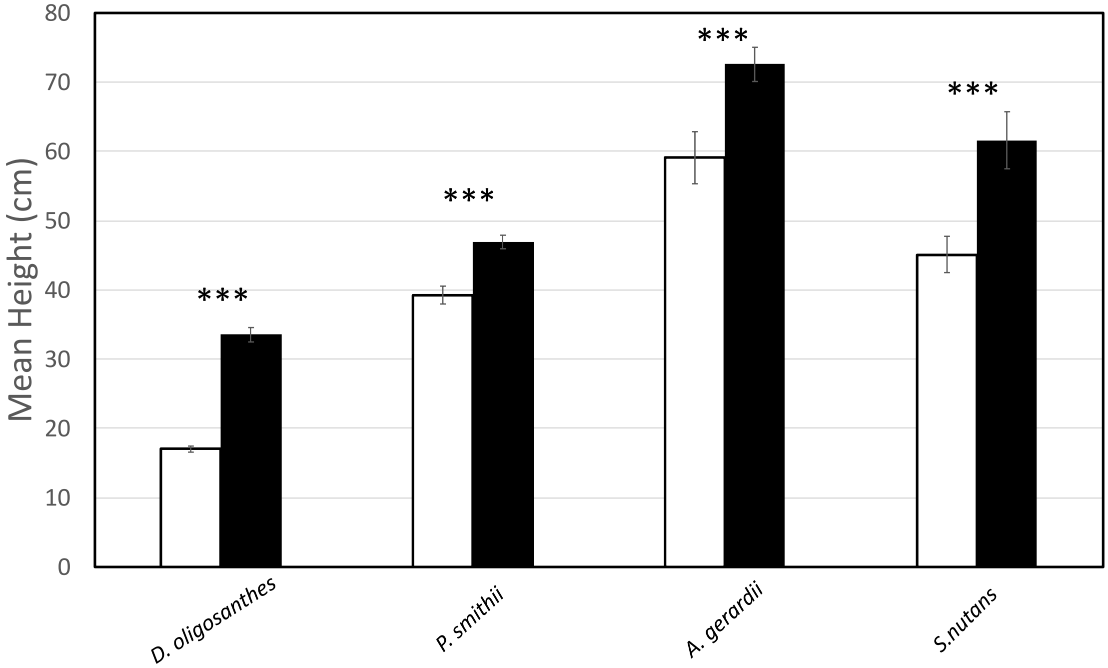


Figure 2.3-Relative difference in plant height between grazing lawns and surrounding tall grass swards in tallgrass prairie for four dominant prairie grasses. Bars indicate means ± 1SE. Open bars = grazing lawns. Shaded bars = tall grass swards. Significance- ***p≤ 0.001, **p≤ 0.01, *p≤ 0.05.

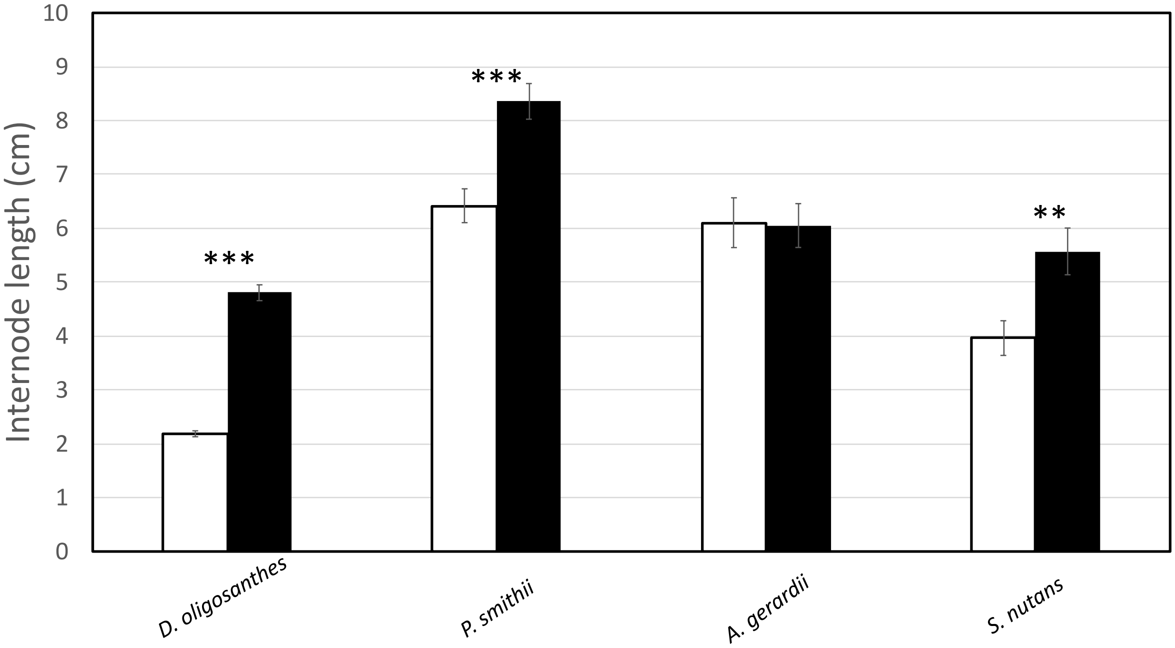


Figure 2.4- Relative difference in culm internode length between grazing lawns and surrounding tall grass swards for four dominant prairie grasses. Bars indicate means ± 1SE. Open bars = grazing lawns. Shaded bars = tall grass swards. Significance- ***p≤0.001, **p≤0.01, *p≤0.05.

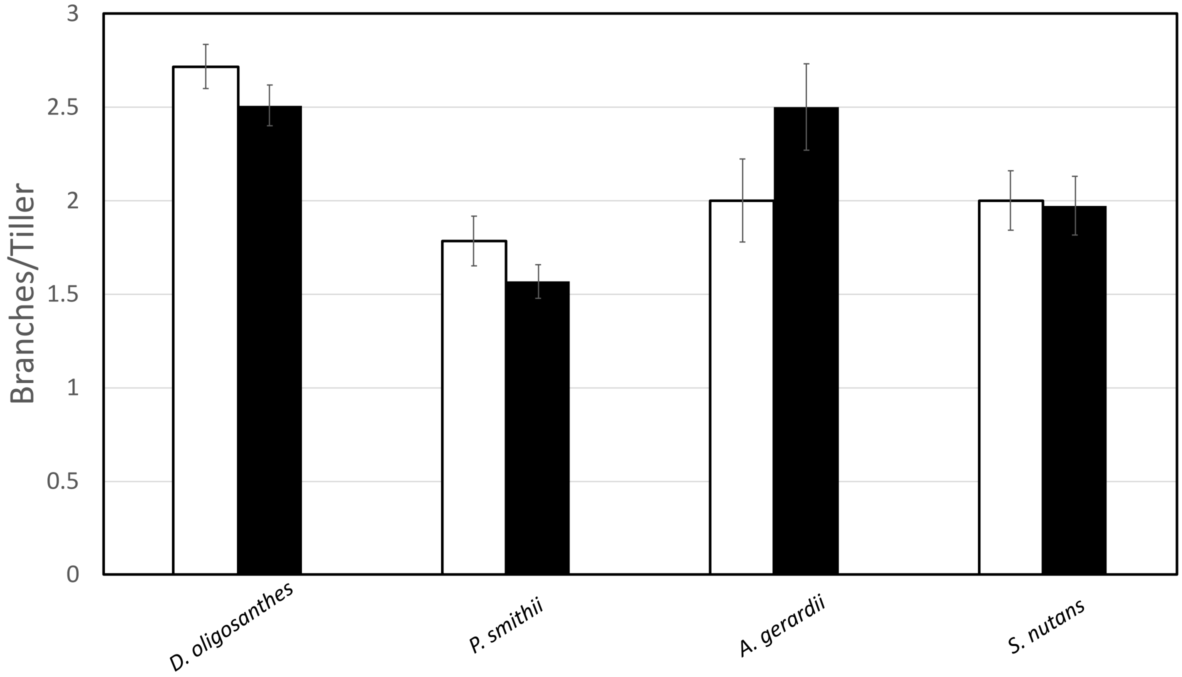


Figure 2.5- Relative difference in branching frequency between grazing lawns and surrounding tall grass swards for four dominant prairie grasses. Bars indicate means ± 1SE. Open bars = grazing lawns. Shaded bars = tall grass swards. Significance- ***p≤0.001, **p≤0.01, *p≤0.05.

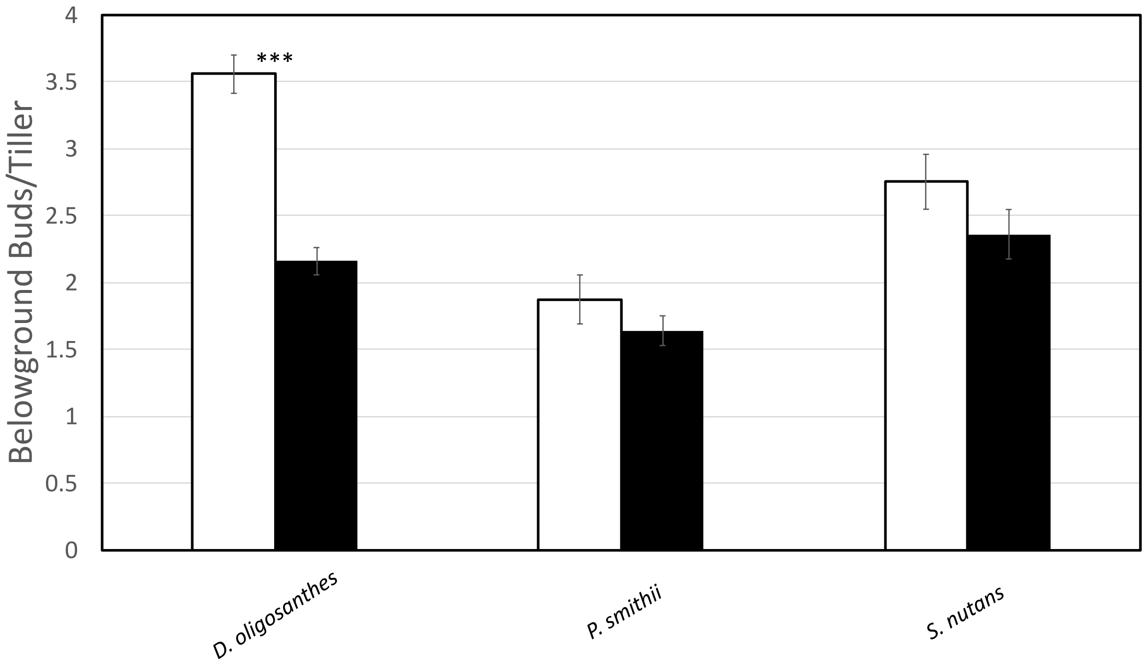


Figure 2.6- Relative difference in belowground bud number between grazing lawns and surrounding tall grass swards for four dominant prairie grasses. Bars indicate means ± 1SE. Open bars = grazing lawns. Shaded bars = tall grass swards. Significance- ***$p \leq 0.001$, **$p \leq 0.01$, *$p \leq 0.05$.

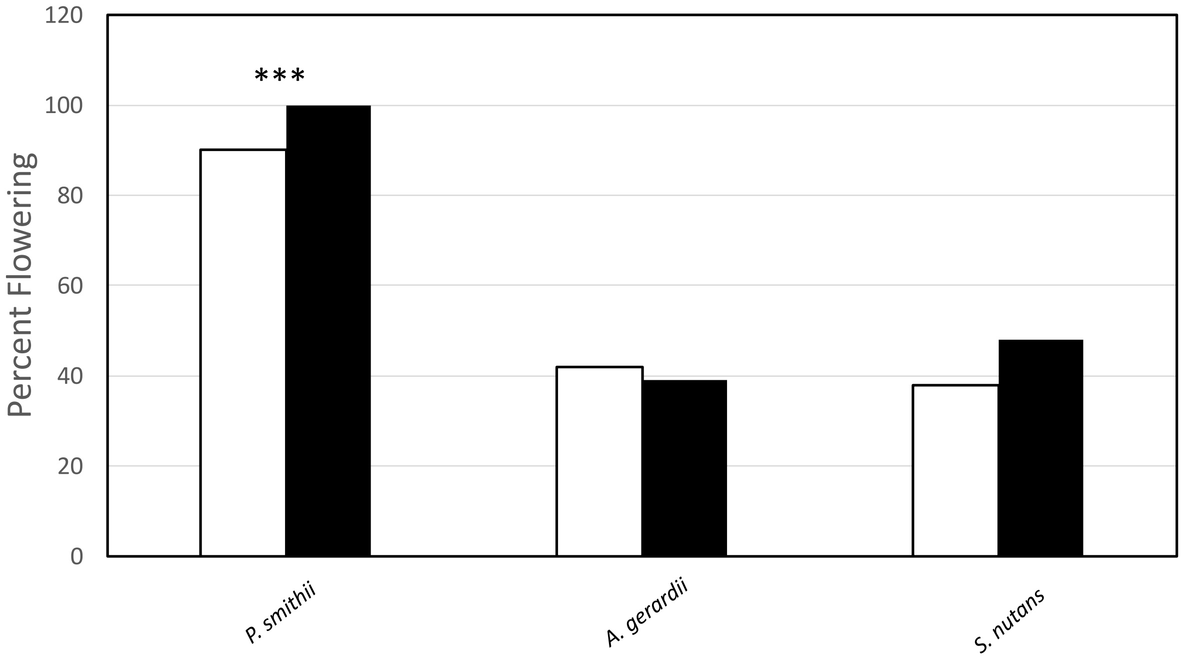


Figure 2.7- Relative difference in percent of tillers flowering between grazing lawns and surrounding tall grass swards for four dominant prairie grasses. Bars indicate means ± 1SE. Open bars = grazing lawns. Shaded bars = tall grass swards. Significance- ***p≤0.001, **p≤0.01, *p≤0.05.

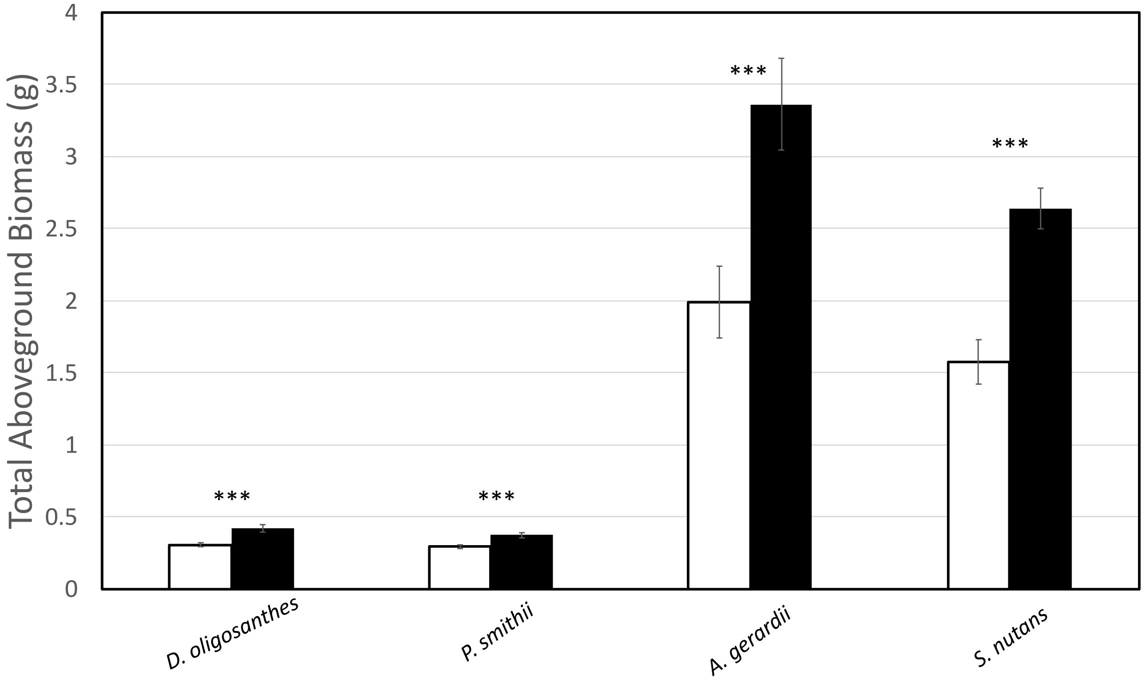


Figure 2.8- Relative difference in total aboveground biomass between tillers on grazing lawns and surrounding tall grass swards for four dominant prairie grasses. Bars indicate means ± 1SE. Open bars = grazing lawns. Shaded bars = tall grass swards. Significance- ***p≤0.001, **p≤0.01, *p≤0.05.

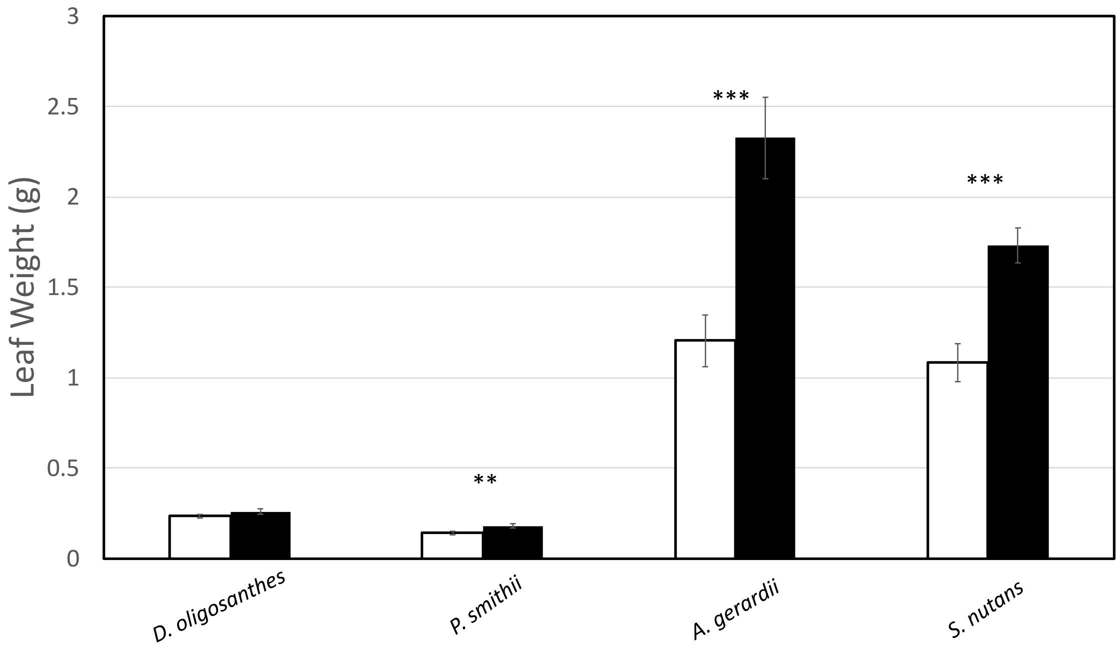


Figure 2.9- Relative difference in total leaf biomass between tillers on grazing lawns and in surrounding tall grass swards for four dominant prairie grasses. Bars indicate means ± 1SE. Open bars = grazing lawns. Shaded bars = tall grass swards. Significance- ***p≤0.001, **p≤0.01, *p≤0.05.

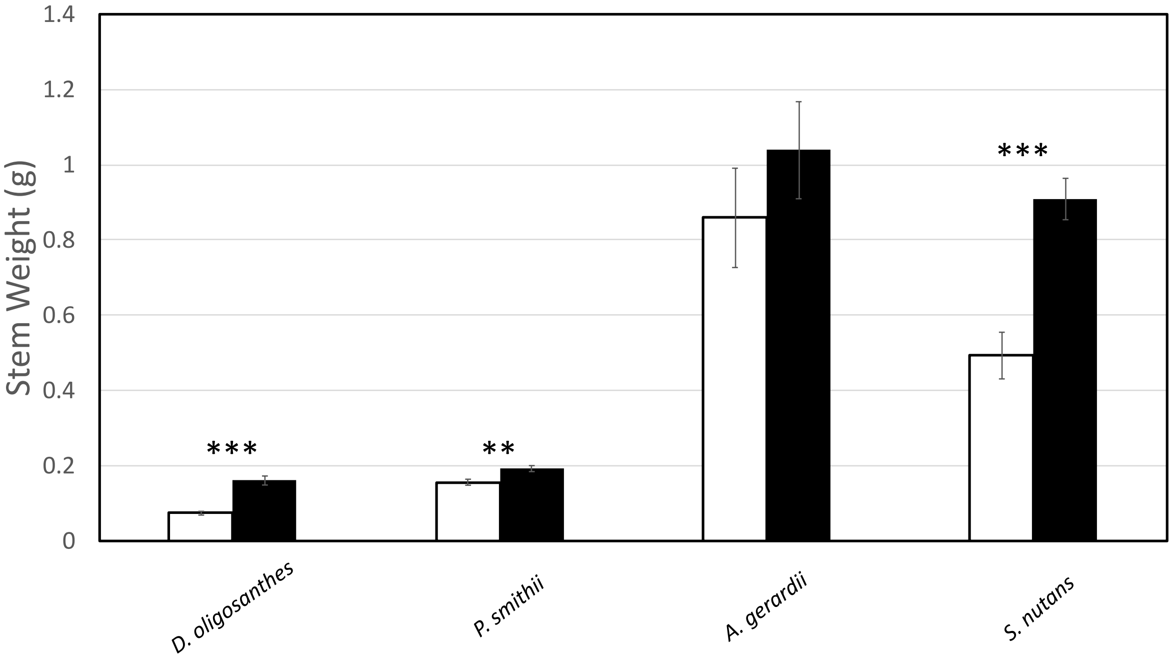


Figure 2.10- Relative difference in tiller stem weight between grazing lawns and surrounding tall grass swards for four dominant prairie grasses. Bars indicate means ± 1SE. Open bars = grazing lawns. Shaded bars = tall grass swards. Significance- ***p≤0.001, **p≤0.01, *p≤0.05.

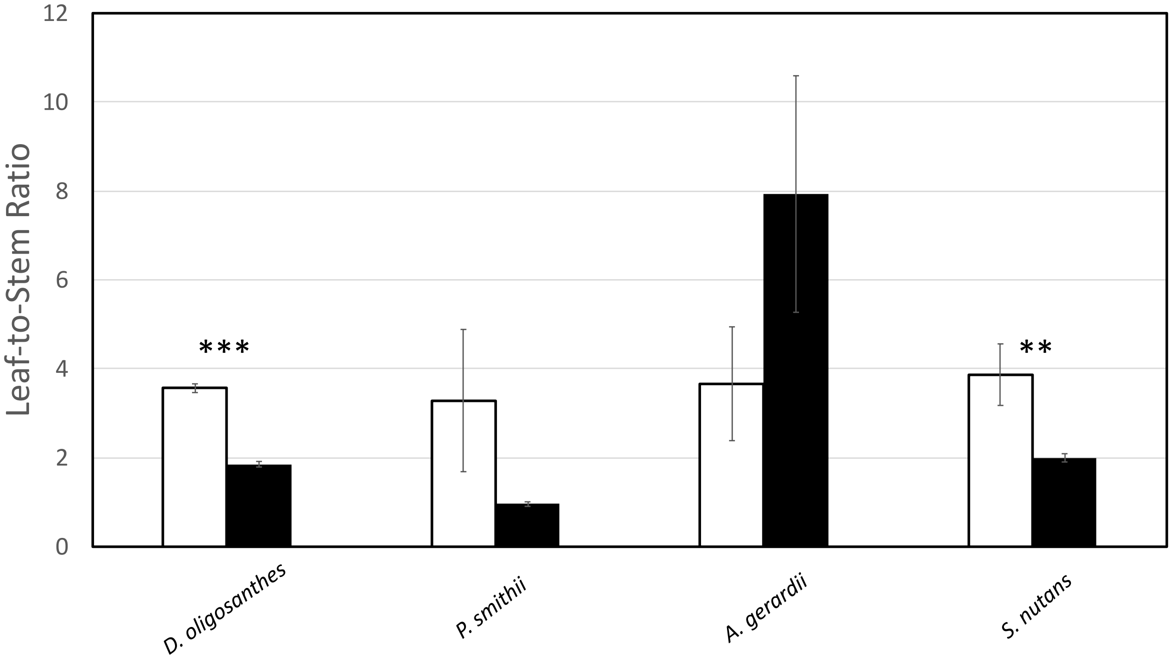


Figure 2.11- Relative difference in leaf-to-stem ratio between grazing lawns and surrounding tall grass swards for four dominant prairie grasses. Bars indicate means ± 1SE. Open bars = grazing lawns. Shaded bars = tall grass swards. Significance- ***p≤0.001, **p≤0.01, *p≤0.05.

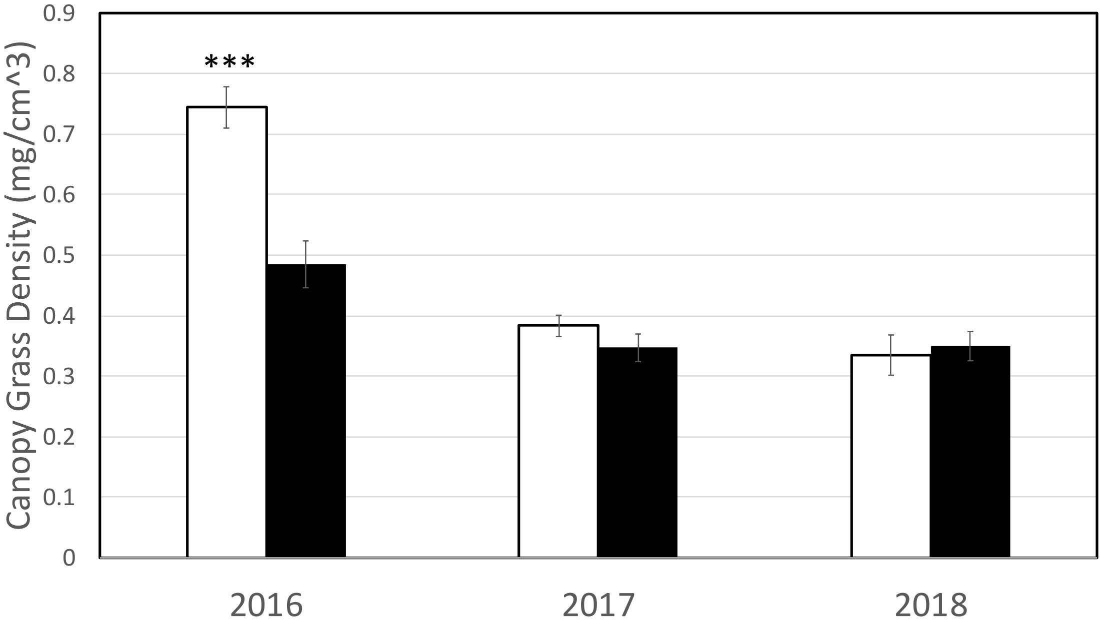


Figure 2.12- Grass (forage for bison) canopy density (mg grass/cm^3 canopy volume) on bison grazing lawns and adjacent tall grass swards on tallgrass prairie. Bars indicate means ± 1SE. Open bars = grazing lawns. Shaded bars = tall grass swards. Significance- ***$p \leq 0.001$, **$p \leq 0.01$, *$p \leq 0.05$.

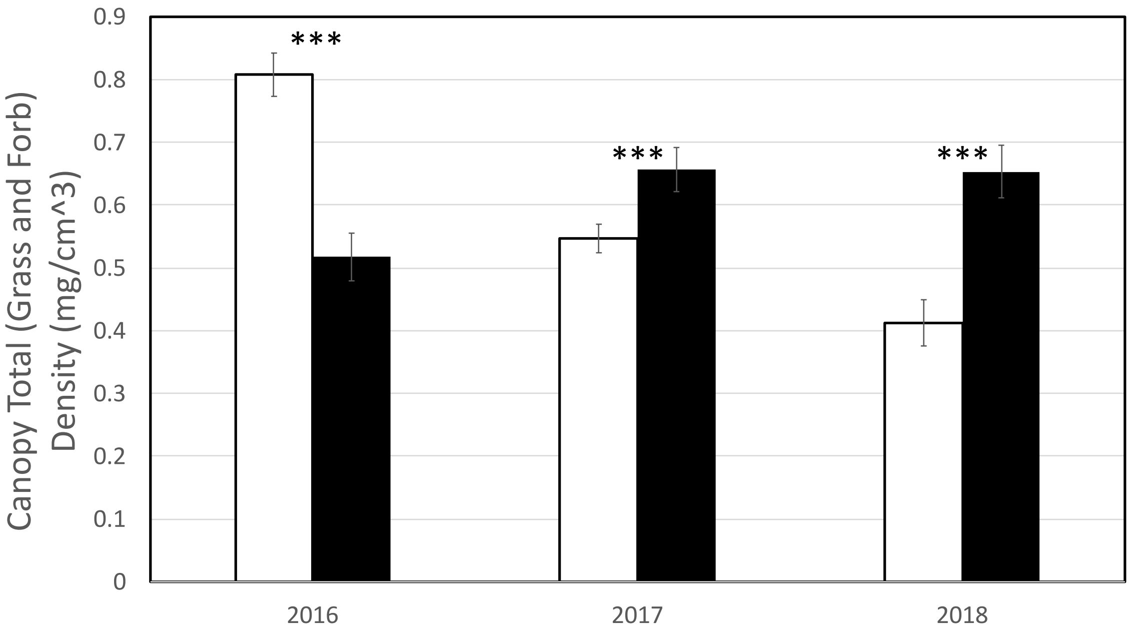


Figure 2.13- Total (grass and forb) canopy density (mg grass and forb/cm^3 canopy volume) on bison grazing lawns and adjacent tall grass swards on tallgrass prairie. Bars indicate means ± 1SE. Open bars = grazing lawns. Shaded bars = tall grass swards. Significance- ***$p \leq 0.001$, **$p \leq 0.01$, *$p \leq 0.05$.

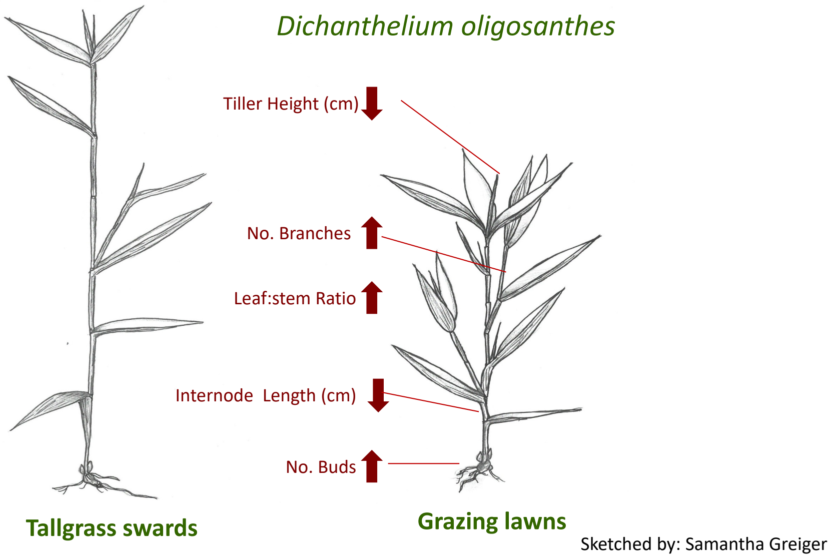
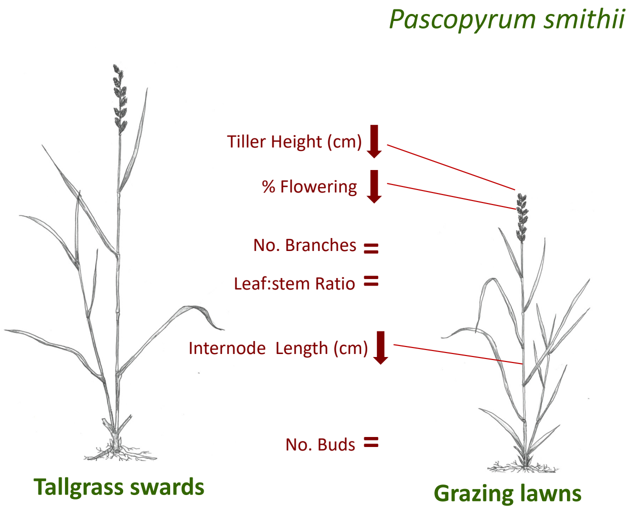


Figure 2.14 - Average plant characteristics taken from means of all plant samples for *Dichanthelium oligosanthes.*



Sketched by: Samantha Greiger

Figure 2.15 - Average plant characteristics taken from means of all plant samples for *Pascopyrum smithii.*

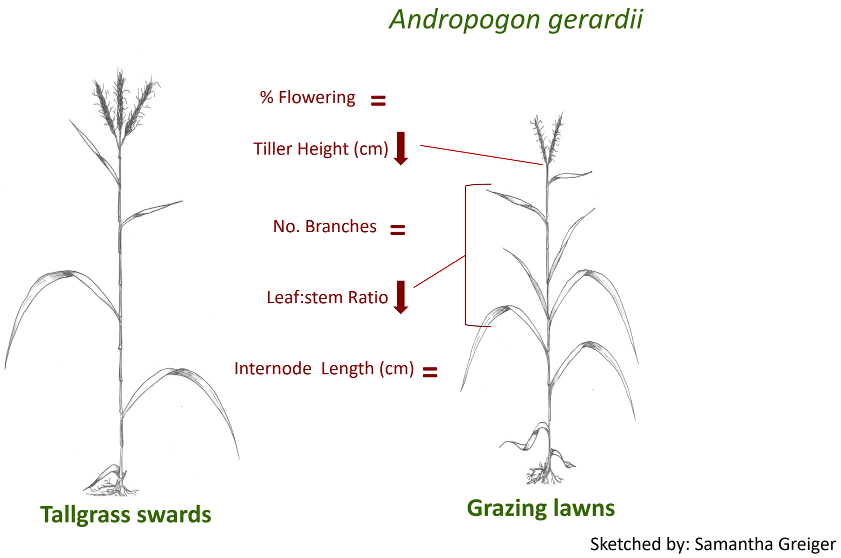


Figure 2.16 - Average plant characteristics taken from means of all plant samples for *Andropogon gerardii.*

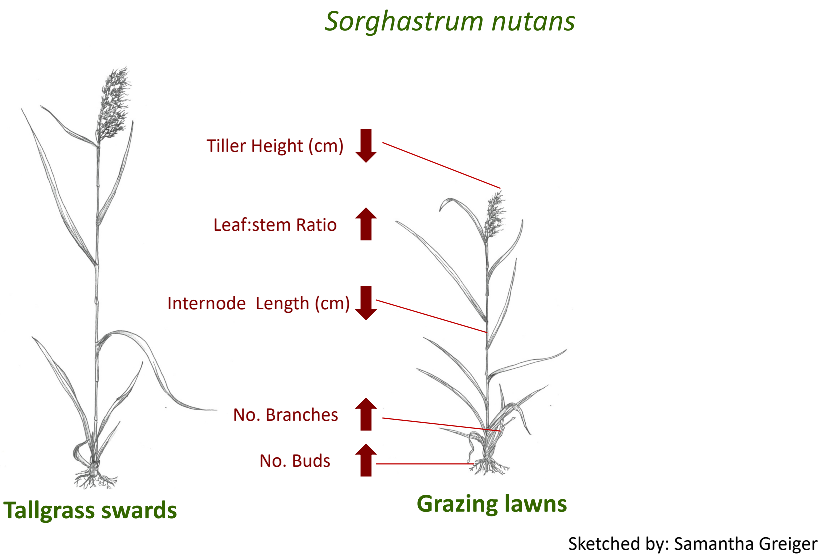


Figure 2.17 - Average plant characteristics taken from means of all plant samples for *Sorghastrum nutans.*

Dichanthemlium oligosanthes

The dominant C_3 grass *Dichanthelium oligosanthes* differed in several morphological traits between grazing lawns and the surrounding matrix tall grass swards. Total tiller biomass and tiller height were significantly lower on grazing lawns compared to tall grass vegetation (Figure 2.8, Figure 2.3, Figure 2.14, Table 2.3). Culm internode lengths were significantly shorter for tillers on grazing lawns compared to tillers in adjacent tall grass swards (Figure 2.4, Figure 2.14, Table 2.3), indicating that the reduction in tiller height on grazing lawns was a morphological shift in response to grazing and not simply a direct result defoliation. While mean tiller stem biomass was significantly lower on grazing lawns than in the matrix vegetation (Figure 2.10), mean tiller leaf biomass was not significantly different (Figure 2.9, Table 2.3).

Since stem biomass was reduced at a greater extent than leaf biomass on grazing lawns, leaf-to-stem ratio was significantly greater on grazing lawns compared to tall grass swards (Figure 2.11, Figure 2.14, Table 2.3). In addition, below-ground bud numbers were significantly higher on grazing lawns compared to adjacent tall grass swards (Figure 2.6, Figure 2.14). Each of these differences in morphological traits between tillers on grazing lawns and tall grass swards were consistent with predictions of the 'architectural shift hypothesis.' There was no significant difference in branching between tillers on grazing lawns and those on adjacent tall grass swards (Figure 2.5, Figure 2.14, Table 2.3). Due to time constraints, percent of tillers flowering was not measured for *D. oligosanthes.*

Pascopyrum smithii

The dominant C_3 grass *Pascopyrum smithii* also differed in several morphological traits between grazing lawns and the surround matrix tall grass swards. Total tiller biomass and tiller height were significantly lower on grazing lawns compared to tall grass vegetation (Figure 2.8, Figure 2.3, Figure 2.15). Culm internode lengths were significantly shorter for tillers on grazing lawns compared to tillers in adjacent tall grass swards (Figure 2.4, Figure 2.15, Table 2.6), indicating that the reduction in tiller height on grazing lawns was a morphological shift response to grazing and not simply a direct result of defoliation. In addition, both mean tiller biomass and leaf biomass were significantly lower on grazing lawns than in the matrix tall grass vegetation (Figure 2.10, Figure 2.9, Table 2.6). However, stem biomass was not reduced compared to leaf biomass on grazing lawns, and there was no significant difference in the leaf-to-stem ratio on grazing lawns compared to tall grass swards (Figure 2.11, Figure 2.15, Table 2.6). Lastly, the proportion of tillers flowering was significantly greater in the matrix tall grass vegetation than on grazing lawns (Figure 2.7, Figure 2.15, Table 2.6). Each of these differences in morphological traits between tillers on grazing lawns and tall grass swards were consistent with predictions of the architectural shift hypothesis. There were no significant differences in tiller branching or below-ground bud numbers between tillers on grazing lawns and those on adjacent tall grass swards (Figure 2.5, Figure 2.6, Figure 2.17, Table 2.6).

Andropogon gerardii

Unlike the other 3 species studied, the dominant C_4 grass *Andropogon gerardii* differed in only a few morphological traits between grazing lawns and the surrounding matrix tall grass swards. Total tiller biomass and tiller height were significantly lower on grazing lawns compared to tall grass vegetation (Figure 2.8, Figure 2.3, Figure 2.16, Table 2.5). Mean leaf biomass was significantly lower on grazing lawns than in matrix tall grass vegetation, however there was not a significant difference in mean stem biomass (Figure 2.9, Figure 2.10, Table 2.5) or in leaf-to-stem ratio between grazing lawns and tall grass vegetation (Figure 2.11, Figure 2.16, Table 2.5). For *A. gerardii,* the differences in the morphological traits total biomass, leaf biomass, and tiller height were consistent with predictions of the architectural shift hypothesis. However, unlike the other three species, there were no significant differences in culm internode lengths, tiller branching, or proportion or plants flowering between tillers on grazing lawns and those on adjacent tall grass swards (Figure 2.4, Figure 2.5, Figure 2.7, Figure 2.16, Table 2.5). Due to fungal growth that occurred on the basal/below-ground tissues of *A. gerardii*, I was unable to acquire measurements of bud number.

Sorghastrum nutans

The dominant C_4 grass *Sorghastrum nutans* differed in several morphological traits between grazing lawns and the surrounding matrix tall grass swards. Total tiller biomass and tiller height were significantly lower on grazing lawns compared to tall grass vegetation (Figure 2.8, Figure 2.3, Figure 2.17, Table 2.4). Culm internode lengths were significantly shorter for tillers on grazing lawns compared to tillers in adjacent tall grass swards (Figure 2.4, Figure 2.17, Table 2.4), indication that the reduction in tiller height on grazing lawns was a morphological shift in response to grazing and not simply a direct result of defoliation. In addition, both mean tiller stem biomass and leaf biomass were significantly lower on grazing lawns than in the matrix tall grass vegetation (Figure 2.10, Figure 2.9, Table 2.4). However, stem biomass was reduced to a greater extent than leaf biomass on grazing lawns, resulting in a significantly greater leaf-to-stem ratio on grazing lawns compared to tall grass swards (Figure 2.11, Figure 2.17, Table 2.4). Each of these differences in morphological traits between tillers on grazing lawns and tall grass swards were consistent with predictions of the architectural shift hypothesis. There was no significant difference in tiller branching, below-ground bud numbers, or proportion of tillers flowering between tillers on grazing lawns and those on adjacent tall grass swards (Figure 2.5, Figure 2.6, Figure 2.7, Figure 2.17, Table 2.4).

Canopy Density

During the 2016 field season, canopy grass density (mg grasses/cm^3 canopy volume) was significantly higher on grazing lawns compared to adjacent tall grass swards (Table 2.7). There was no significant difference in grass canopy density between grazing lawns or tall grass vegetation in the 2017 or 2018 field season (Table 2.7). Even though there was no significant difference, grazing lawns showed a trend of slightly higher canopy density in 2017, but by 2018 the grass canopy density on grazing lawns was slightly lower than on tall grass swards.

Total canopy density (mg grass and forbs/cm^3 canopy volume) was significantly higher on grazing lawns compared to adjacent tall grass swards during the 2016 field season (Table 2.8). The opposite pattern occurred in 2017 and 2018, when total canopy density was significantly higher in matrix tall grass swards compared to on grazing lawns (Table 8).

Discussion

My overall research objective was to understand the mechanisms maintaining grazing lawns and how the demographic/morphological mechanism contributes to forage for native grazers, plant species richness, and overall biodiversity of the grassland landscape, indicating their importance in terms of conserving the North American Tallgrass Prairie. In this study, I tested the architectural shift hypothesis, where continued grazing leads to changes in plant architecture resulting in more efficient foraging for grazers, thus creating a positive feedback that increases grazing. I found that several differences in morphological traits between dominant grasses on grazing lawns and tall grass swards support the architectural shift hypothesis. For *Sorghastrum nutans, Dichanthelium oligosanthes, and Pascopyrum smithii,* leaf-to-stem ratio was twice as high on grazing lawns compared to surrounding matrix tall grass vegetation. Also, tiller branching was higher and culm internode lengths were shorter on grazing lawns for these species. These morphological traits were opposite for *Andropogon gerardii* with a higher leaf-to-stem ratio and higher tiller branching in tall grass vegetation, and culm internode lengths that were longer on grazing lawns. For all four species, above-ground tiller biomass and number of below-ground buds were both higher on grazing lawns. And as to be expected, tiller height was lower on grazing lawns for all species.

Although tiller biomass and height were lower on lawns, this was not solely due to the direct removal of biomass by grazers, as evidenced by culm internode lengths that were significantly shorter on grazing lawns. Shorter culm internode lengths on grazing lawns indicates that the shorter tiller and canopy height on lawns was at least partially due to a developmental/morphological shift in growing tillers. As in *S.nutans, D. oligosanthes,* and *P. smithii,* the increases in branching frequency coupled with a reduction in height, is a pronounced morphological shift that results in increased grass canopy density. The increase in the leaf-to-stem ratios on lawns is also a developmental/morphological response to grazing, as grazers do not consume more stem than leaf tissue. The opposite, grazers consuming more leaf than stem tissue, is much more likely.

An unexpected finding was the higher number of below-ground buds on grazing lawns. Grazing typically increases dormant bud outgrowth and bud-to-tiller transition rates in grasses (Hartnett, unpubl.), which would actually decrease bud bank population size. The finding of a higher bud bank size on grazing lawns compared to those in tall grass vegetation suggests that chronic defoliation must also be accompanied by a compensatory increase in bud natality on grazing lawns. Another unexpected finding was the lack of response of these architectural shifts in *A. gerardii.* An increase in leaf-to-stem ratio, branching frequency, and shorter internode lengths that characterized all the other species was not observed in *A. gerardii.* These findings suggest that *A. gerardii* has much less phenotypic plasticity in its tiller development and may not respond to grazing morphologically the way the other grasses do. One speculation as to why this occurs is that *A. gerardii* is a drought tolerant species. Swemmer *et al.* (2006) found that during periods of reduced soil moisture, *A. gerardii* had a greater turnover of leaves, a greater allocation of biomass to roots, and a reduction in allocation to flowering (Swemmer *et al. 2006*). As 2017 and 2018 were drought years, *A. gerardii* could have potentially been allocating resources differently, and thus not demonstrating the same morphological shifts as *S. nutans, D. oligosanthes,* and *P. smithii.* And the reduced tiller height and biomass of *A. gerardii* could simply be a direct result of tissue removal by grazers. A study by Seastedt *et al.* (1989) found silica concentrations to be higher in clipped *A. gerardii* plants, than in controls (Seastedt *et al.* 1989). Higher silica concentration in grasses can be a deterrent for grazers, thus not initiating the positive feedback mechanisms that lead to morphological shifts.

A major contrast in grazing lawn responses between C_3 and C_4 species was their differences in flowering patterns. First, the overall percentage of tillers flowering was much higher in the C_3 species *P. smithii* (90-100%) compared to the two C_4 species, *A. gerardii* and *S. nutans* (both approximately 40%). Second, flowering rates were not affected by chronic grazing in the two C_4 species, but were significantly lower on grazing lawns for the C_3 species *P. smithii.*

This was an unexpected finding for the two C_4 species, because logically there should have been little to no flowering for any species on grazing lawns.

There are multiple consequences to grazers from these morphological shifts in the dominant grasses. Overall, these morphological responses result in a higher grass canopy density (forage biomass per unit canopy volume) on grazing lawns and this increased grass canopy density in turn results in grazer foraging efficiency by increasing the amount of forage intake per bite and per unit time. McNaughton's (1984) study found that in the Serengeti, tillering and subsequent high canopy density associated with defoliation led to higher biomass concentrations on grazing lawns (Mcnaughton 1984). These findings coincide with ours and demonstrate that these morphological shifts of grasses may be a general feature of grazing lawns across different grassland systems.

During our study period, the increase in canopy density on lawns compared to tall grass swards varied among years. It was highly significant during an average precipitation year, but was non-significant during two consecutive dry years. This pattern suggests that water limitation may constrain the positive feedback mechanisms that lead to morphological shifts that maintain grazing lawns and the increase in forage density could be constrained under drier conditions. Our study showed that during a drought, there was not a major change in grass cover between grazing lawns and tall grass vegetation. However, when forbs were included in canopy density measurements, patterns differed. Forb canopy and total canopy density were significantly higher in tall grass swards during the two dry years. This suggests that one consequence of higher drought frequency in the tall grass prairie region associated with climate change may be a reduction in forage quality (lower proportional grass cover and canopy density, but higher proportional forb canopy density) under persistent grazing. With increased interannual precipitation variability and increases in the intensity and frequency of droughts due to a changing climate, forage quality in the Great Plains could significantly decrease for native grazers.

While grazing impacts plant morphological traits, forage quality, and forage quantity, fire does not seem to play a role regarding the positive feedback mechanisms impacting grasses. My statistical analyses showed no significant interaction between 1-year, 4-year, or 20-year burn sites. A significant interaction only showed between treatments (i.e. grazing lawns and tall grass swards).

Multiple positive feedback mechanisms are integral to the maintenance of grazing lawns. The classic nutrient-based pathway includes nutrient mineralization and compensatory growth due to defoliation, both of which increase plant nutritional quality. The alternative water-based pathway predicts that a decrease in vegetation cover and increased soil compaction with intensive grazing leads to lower soil water availability. When water is limited for plants, they tend to retain nutrients, thus increasing plant nutritional quality. This also leads to a positive feedback for grazers, similar to the classic nutrient-based pathway.

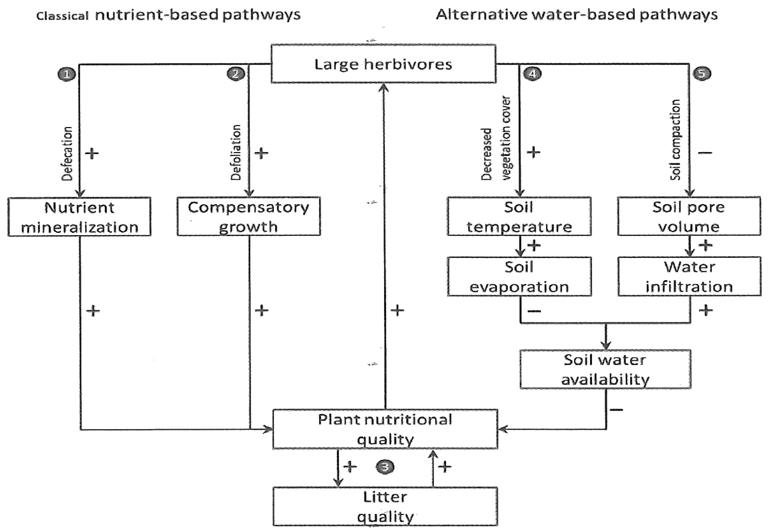


Figure 2.1: Overview of the influence of large herbivores on grass nutritional quality. The diagram shows five main pathways by which herbivores affect grass nutritional quality. (Veldhuis *et al*. 2014)

In addition to the nutrient and water-based positive feedback, Hartnett (unpublished) hypothesizes that the demographic/structural mechanism also contributes to the maintenance of grazing lawns. Defoliation and trampling lead to bud activation, shorter internode lengths, more horizontal bud outgrowth angles, shorter tiller and bud height, and a higher branching and tiller density. These morphological changes in turn lead to a higher phytomass concentration and forage density.

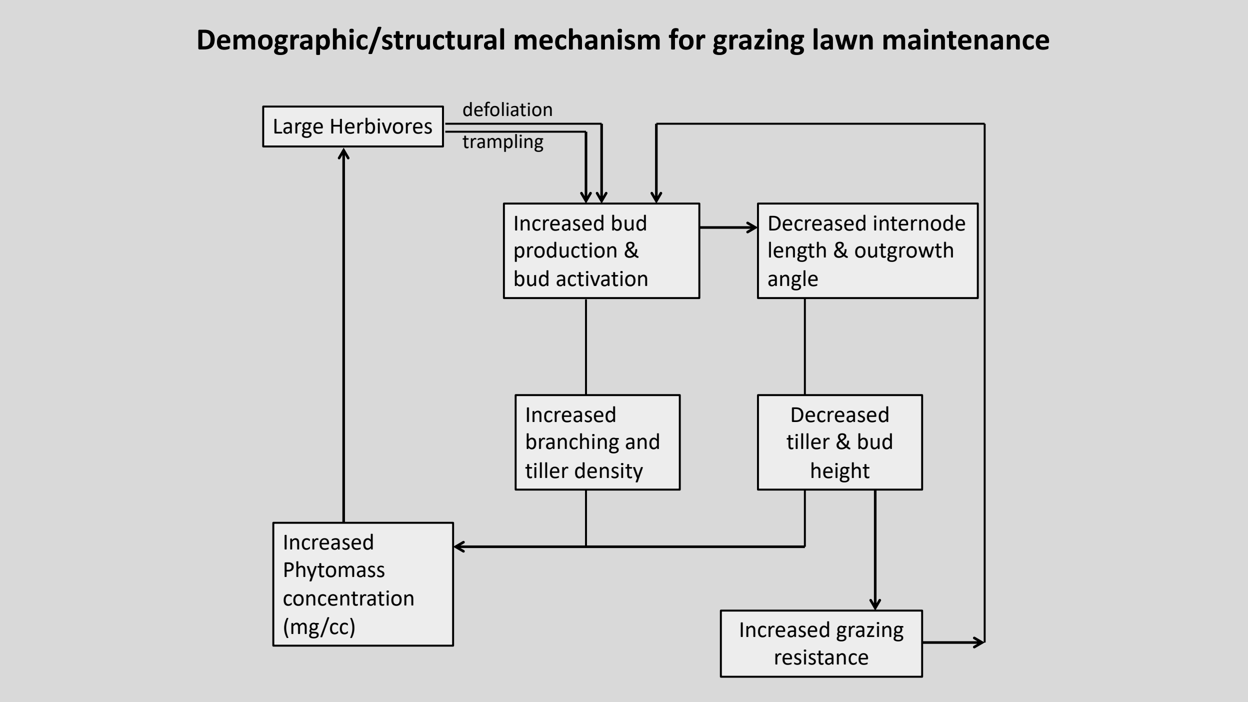


Figure 2.2:-Demographic and structural positive feedback mechanisms for grazing lawn maintenance. (Hartnett unpublished).

The results of this study strongly indicate that developmental and morphological shifts result in increased forage density and increased grazing efficiency on grazing lawns. Thus, the architectural shift hypothesis could contribute to the positive feedbacks that encourage further grazing on lawns and grazing lawn maintenance.

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Chapter 3 - Soil Resource Availability and Grass Nutritive Quality Effects on Grazing Lawn Maintenance

Introduction

Grasslands and savannas cover approximately 40% of the global terrestrial surface (Koerner *et al.* 2014) and are widely distributed, occurring on all continents except Antarctica. Major types of grasslands include montane, mesic, savanna, semi-arid, sedge meadow, salt marsh, and tallgrass prairie. Grassland ecosystems act as carbon sinks, potentially alleviating greenhouse gas emissions, act as water catchments, contribute to biodiversity, and are a large feeding base for livestock, making them an invaluable resource globally (Boval & Dixon 2012).

Large grazing animals contribute directly to patchiness in grasslands through non-uniform defoliation, dung and urine deposition. In addition, large ungulate non-grazing activities, such as bison trampling and wallowing, also affect plant community structure and vegetation heterogeneity (McNaughton 1979; Knapp *et al.* 1999; Howison *et al.* 2017). A key feature of many grass-dominated ecosystems is the formation of grazing lawns, distinct patches characterized by intense grazing by mammalian herbivores, a dense short-statured grass canopy, and maintained by positive grazer-vegetation feedbacks. Veldhuis *et al.* (2014) showed that in South African grasslands, grazed plants show lower evaporative water loss and also reduced photosynthetic carbon fixation, resulting in changes in plant carbon to nutrient ratios, which also contributes to higher nutrient content, initiating a positive feedback that promotes continued grazing (Veldhuis *et al.* 2014).

Factors that may cause the initiation of grazing lawns include animal congregation for predator avoidance or in response to nutrient hotspots. In African grasslands and savannas, higher soil fertility often leads to enhanced plant productivity and/or forage nutritive quality (Anderson *et al.* 2010; Coetsee *et al.* 2011; Donaldson *et al.* 2018), leading in turn to herbivore aggregations, which, depending on plant growing conditions, may or may not contribute to grazing lawn maintenance by enhancing nutrient turnover and litter quality (McNaughton 1979, Banyikwa & McNaughton 1997; Augustine & McNaughton 2006). In addition, large groups of herbivores requiring predator defense will converge in an area, thus creating an area of highly grazed plants, initiating the positive-feedbacks that promote grazing lawns.

Once initiated, the persistence of lawns happens through repeated grazing stimulating continual re-growth, maintaining grasses in an immature state with higher nutrient content, productivity and forage concentration than the surrounding tall grass vegetation, which in turn promotes further consumption (Stobbs 1973; McNaughton 1979; Mcnaughton 1984; Cromsigt & Olff 2008; Hempson *et al.* 2015; Veldhuis *et al.* 2016). Higher nutritional quality on grazing lawns (McNaughton 1979; Veldhuis *et al.* 2014) may also be promoted through deposition of dung and urine by mammalian herbivores, allowing the plants to receive mineral nutrients in more readily available forms (Mcnaughton 1984; Howison *et al.* 2017). Despite frequent defoliation, grazing lawn species persist by keeping much of their important structural components, such as buds and stems, largely below the reach of grazers (Hempson *et al.* 2015). Grasses acquire adaptations to deal with the physical and abiotic conditions of frequent grazing. Traits exhibited by grazed grasses include compact basal meristems, small stature, prostrate growth forms, high shoot density, deciduous shoots, rapid growth, and below-ground nutrient reserves. This suite of traits is associated with both drought and grazing tolerance (Howison *et al.* 2017).

Recent studies indicate that the maintenance of grazing lawns may be promoted through positive plant-grazer feedbacks that result in morphological and structural plant traits that increase phytomass concentration within the plant canopy or through changes in soil, which both contribute to stimulate repeated grazing (Veldhuis *et al.* 2014, 2016; Donaldson *et al.* 2018). The classic nutrient-based pathway suggests that defoliation increases light and leads to compensatory growth, and fecal and urine deposition leads to nutrient mineralization, both leading to higher plant nutritional quality and promoting continued grazing (Figure 3.7) (Frank & Evans 1997; Koerner *et al.* 2014; Veldhuis *et al.* 2014, 2016; Archibald & Hempson 2016; Howison *et al.* 2017).

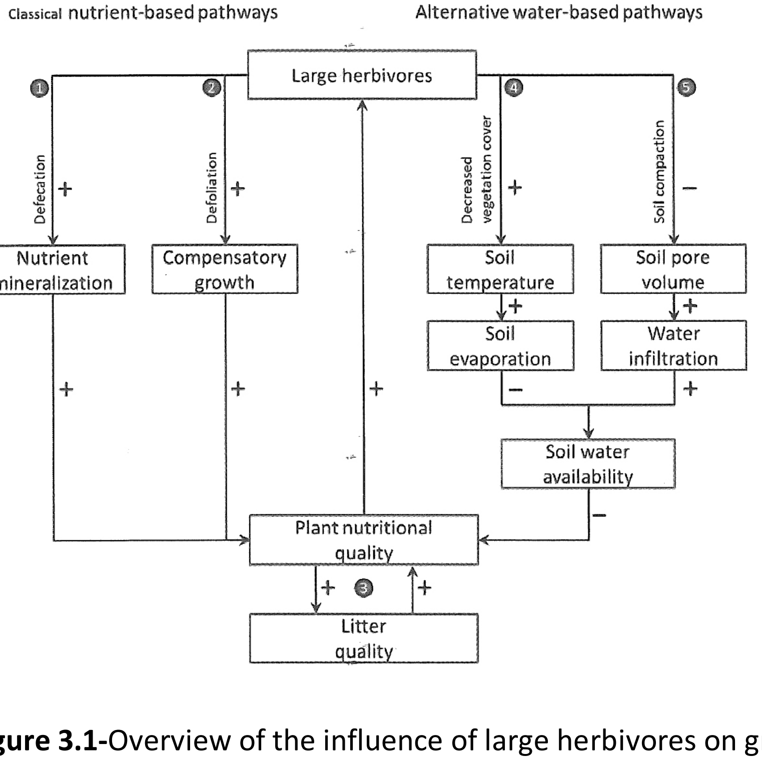

Figure 3.1-Overview of the influence of large herbivores on grass nutritional quality. The diagram shows five main pathways by which herbivores affect grass nutritional quality. (Veldhuis et al. 2014)

Excretory plant biomass that has been broken down in the gut of large herbivores and their associated microflora allows nutrients returning in urine and feces to the grazing area in the most plant-available forms (Howison *et al.* 2017). In addition to the nutrient-based pathways, a water-based pathway also may generate positive feedbacks and promote continued large herbivore grazing. According to this hypothesis, soil compaction and decreased vegetation cover lead to changes in soil water availability, requiring plants to retain nutrients thereby, also increasing plant nutritional quality (Figure 3.1) (Veldhuis *et al.* 2014; Howison *et al.* 2017).

A central concept of grazing lawns is the positive feedbacks between grazing animals and the grass resource. Intraspecific morphological plant trait changes and differences in plant species composition could both or individually play a role in the differences in characteristics of grazing lawns and neighboring tall grass swards. I studied grazing lawns in North America Tallgrass Prairie to: a) test the 'architectural shift hypothesis' where continued grazing leads to changes in plant architecture resulting in more efficient foraging for grazers, creating a positive feedback that increases grazing (see chapter 2) and b) examine soil resource (nutrient and water) availability and grass nutritive quality on and off lawns to test these alternative nutrient and water-based pathways for grazing lawn maintenance (this chapter). I measured plant tissue nitrogen content and C:N ratios, as these are two key indicators of forage nutrient quality in grasses. In addition, I conducted preliminary measurements of soil and water nutrient availability both on grazing lawns and in adjacent tall grass matrix vegetation. Ultimately, I hope to understand how grazing lawns contribute to forage for native grazers, plant species richness, and overall biodiversity of the grassland landscape, indicating their importance in terms of conserving the North American Tallgrass Prairie.

Materials and methods

Study Site Description

I conducted this study in the spring and summer field seasons of 2016, 2017 and 2018 at the Konza Prairie Biological Station (KPBS), a 3,487 ha tallgrass prairie preserve in the Flint Hills region of Kansas (39°05' N, 96°35'W). KPBS is owned by The Nature Conservancy and Kansas State University (KSU). The KSU Division of Biology manages the site for ecological research, education and grassland conservation. Grassland vegetation of KPBS is predominantly native tallgrass or bluestem prairie, principally perennial, warm-season grasses, *Andropogon gerardii, Sorghastrum nutans,* and *Panicum virgatum* (Freeman & Hulbert 1985). A highly diverse mixture of less abundant species includes warm-season (C_4) and cool-season (C_3) grasses, composites, legumes, other forbs, and patchily distributed shrubs. Average monthly temperatures range from a low in January of -2.7°C to a high in July of 26.6°C. Mean annual total precipitation (MAP) is 835mm with 75% falling during the growing season. For the 2016 growing season (Apr-Sept), precipitation was very close to the long term mean. However, precipitation during the growing seasons of 2017 and 2018 was significantly less than normal with 57% less than Apr-Sept precipitation in 2017 and a 45% less than Apr-Sept precipitation in 2018.

Konza Prairie is divided into 60 experimental units, each constituting a separate watershed (average size = 0.55 km^2). Each watershed is subjected to prescribed burning at 1, 2, 4, or 20-year intervals. The majority of my study sites were in watersheds with a 4 year burn interval, with one in an annually burned watershed and one in a watershed burned at 20-year intervals. My project needed to be completed over multiple years due to the time constraints of when plants were flowering but not senescing, and also the labor-and time-intensive processes of measuring multiple traits on a large number of samples (a sample being an individual tiller/ramet).

Grazing treatments at Konza Prairie are also applied at the watershed level, and include either bison (*Bison bison*), cattle (*Bos taurus*), or ungrazed treatments. After a nearly 100-year absence, bison were reintroduced to KPBS in 1987. Currently, a population of approximately 325 bison occupies a large area encompassing 2400 ha that spans over 10 watersheds with spring fire regimes at 1-, 2-, 4-, and 20-year burn intervals. Bison are free to roam over all 10 watersheds contained within the 2400 ha area. Each experimental watershed is given a 3-character label indicating the grazing treatment, fire interval, and replicate (A-D). For example, watershed N4D is grazed by native herbivores, burned at 4-year intervals, and is replicate D. The grassland vegetation structure within the bison watersheds is clearly bi-modal, with areas of shorter statured grazing lawns where bison grazing is concentrated and frequent, occurring within a matrix of tall perennial rhizomatous, intermediate, and caespitose grasses that is minimally utilized by the bison.

Methods

Four grass species (2 C_3 and 2 C_4) were collected over the course of 3 growing seasons. *Dichanthelium oligosanthes,* a C_3 grass, was collected in late June-early July and *Andropogon gerardii,* a C_4 grass, was collected end of August-early September of the 2016 field season. *Sorghastrum nutans,* a C_4 grass, was collected end of August-early September of the 2017 field season. *Pascopyrum smithii,* a C_3 grass, was collected early to mid-June of the 2018 field season. These species were chosen due to their abundance on both grazing lawns and tall grass swards, and also being native to the tallgrass prairie.

In watersheds N4A and N4D, 120 tillers (ramets) of *Dichanthelium oligosanthes* were collected on grazing lawns and 112 tillers were collected from the surrounding tall grass swards. Thirty-six tillers of *Andropogon gerardii* were collected from grazing lawns and thirty-six from tall grass swards over watersheds N4A and N4D. Thirty-six grazing lawn and thirty-six tall grass sward tillers of *Sorghastrum nutans* were collected from watersheds N4D, N4A, and N1B. Sixty grazing lawn and sixty tall grass tillers of *Pascopyrum smithii* were collected from watersheds N4A, N20A, and N4B. Grass samples were oven-dried at 60°C for a minimum of 48 hours and then combined to equal 1 gram, ground. Total non-structural Carbon and Total Nitrogen (dry combustion) sampling tests were run at the Kansas State University Soil and Plant testing laboratory.

Total aboveground vegetation biomass samples were also taken from the same sampling sites as the individual grass samples. A 0.9 m^2 quadrat was used for sampling, and six samples were taken over five replicates for each treatment. All aboveground grass and forb biomass was clipped and harvested from each 0.9m^2 quadrat. Samples were then dried and grasses were separated from forbs. One gram of grass biomass was ground and Carbon and Nitrogen sampling tests were run at the Kansas State University Soil and Plant testing laboratory.

Soil samples were collected in the 2017 field season. Wet weights of the fresh samples were taken. Samples were then dried at 60°C for a minimum of 48 hours, and weighed again to determine percent water content gravimetrically. Soil samples were then sent to the Kansas State University Soil and Plant testing laboratory to analyze percent mass of ammonium, nitrate, sodium, and phosphorus.

Data analysis

One-way analysis of variance (ANOVA) was used for plant tissue Carbon and Nitrogen content of the four grass species, *D. oligosanthes, P. smithii, A. gerardii,* and *S. nutans* to test for significance between treatments.

For 2016, 2017, and 2018 total vegetation biomass samples, one-way analysis of variance was used to test if there was a significant difference in canopy forage density between lawn and tall grass treatments.

One-way analysis of variance (ANOVA) was used for ammonium, nitrate, sodium, phosphorus, and water percent mass of soil samples to test for significance between treatments.

Results

	Test	d.f.	F-statistic	Probability
D. oligosanthes	ANOVA	22	27.4	<0.001
P. smithii	ANOVA	28	6.75	0.015
A. gerardii	ANOVA	40	0.001	0.974
S. nutans	ANOVA	72	20.9	<0.001

Table 3.1- Statistical tests for Carbon-to-Nitrogen ratio.

	Test	d.f.	F-statistic	Probability
D. oligosanthes	ANOVA	22	27.2	<0.001
P. smithii	ANOVA	31	11.3	0.002
A. gerardii	ANOVA	40	0.0006	0.981
S. nutans	ANOVA	70	17.2	<0.001

Table 3.2-Statistical tests for Nitrogen.

	Test	d.f.	F-statistic	Probability
2016 Nitrogen	ANOVA	34	32.4	<0.001
2016 C:N ratio	ANOVA	34	4.13	<0.001
2017 Nitrogen	ANOVA	58	17.7	<0.001
2017 C:N ratio	ANOVA	58	4.01	<0.001
2018 Nitrogen	ANOVA	58	54.4	<0.001
2018 C:N ratio	ANOVA	58	4.01	<0.001

Table 3.3-Statistical tests for 2016, 2017, and 2018 Total Grass Biomass.

	Test	d.f.	F-statistic	Probability
Ammonium	ANOVA	78	9.45	0.003
Nitrate	ANOVA	78	16.6	<0.001
Sodium	ANOVA	78	21.7	<0.001
Phosphorus	ANOVA	78	26.8	<0.001
Water	ANOVA	78	3.18	0.078

Table 3.4-Statistical tests for Soil Resources

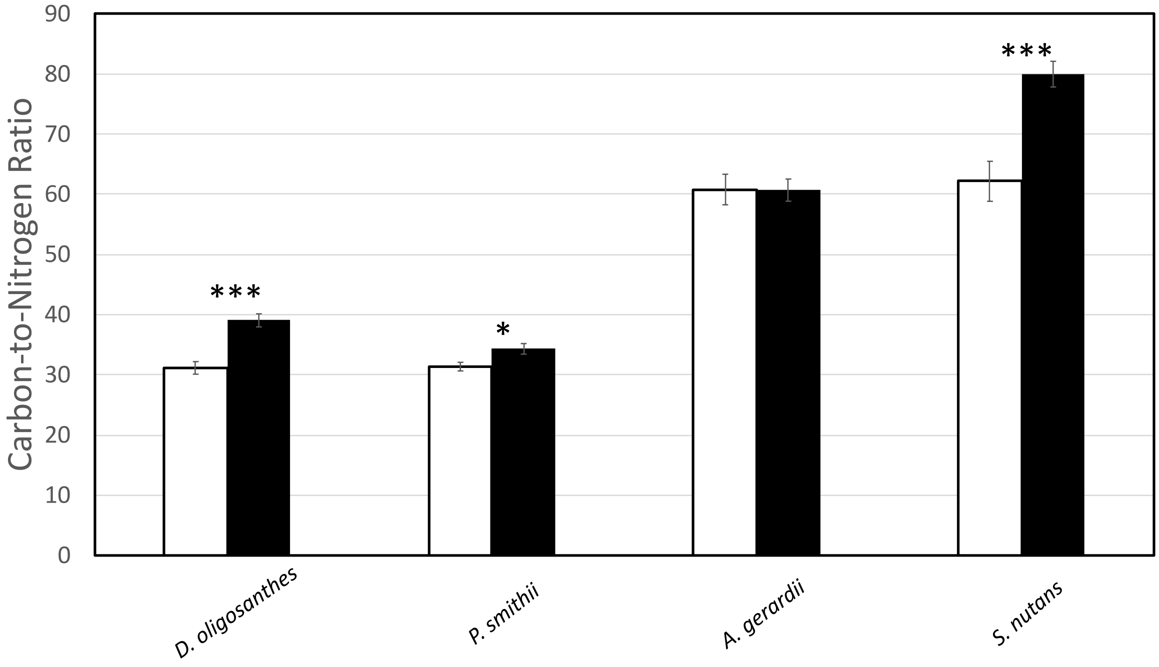

Figure 3.2-Relative difference in carbon-to-nitrogen Ratios between grazing lawns and surrounding tall grass swards for four dominant prairie grasses. Bars indicate means ± 1SE. Open bars = grazing lawns. Shaded bars = tall grass swards. Significance- ***$p \leq 0.001$, **$p \leq 0.01$, *$p \leq 0.05$.

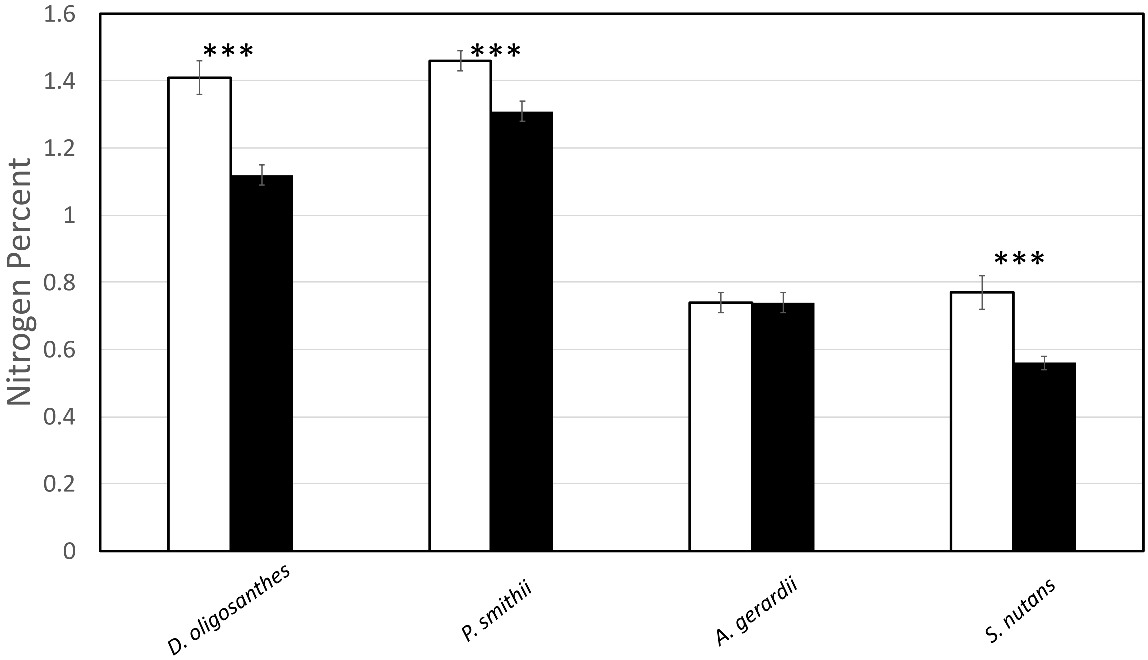

Figure 3.3- Relative difference in percentage of nitrogen between grazing lawns and surrounding tall grass swards for four dominant prairie grasses. Bars indicate means ± 1SE. Open bars = grazing lawns. Shaded bars = tall grass swards. Significance- ***p≤0.001, **p≤0.01, *p≤0.05.

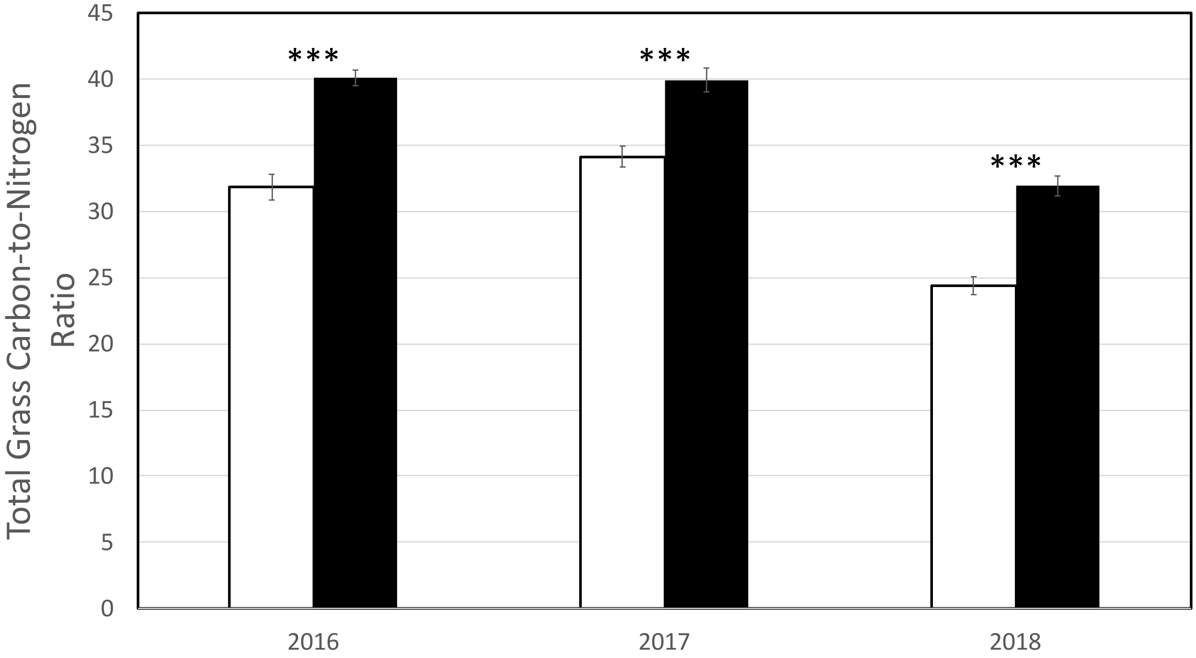

Figure 3.4- Relative difference in percentage of total grass carbon-to-nitrogen ratio between grazing lawns and surrounding tall grass swards for total grass sample. Bars indicate means ± 1SE. Open bars = grazing lawns. Shaded bars = tall grass swards. Significance- ***p≤0.001, **p≤0.01, *p≤0.05.

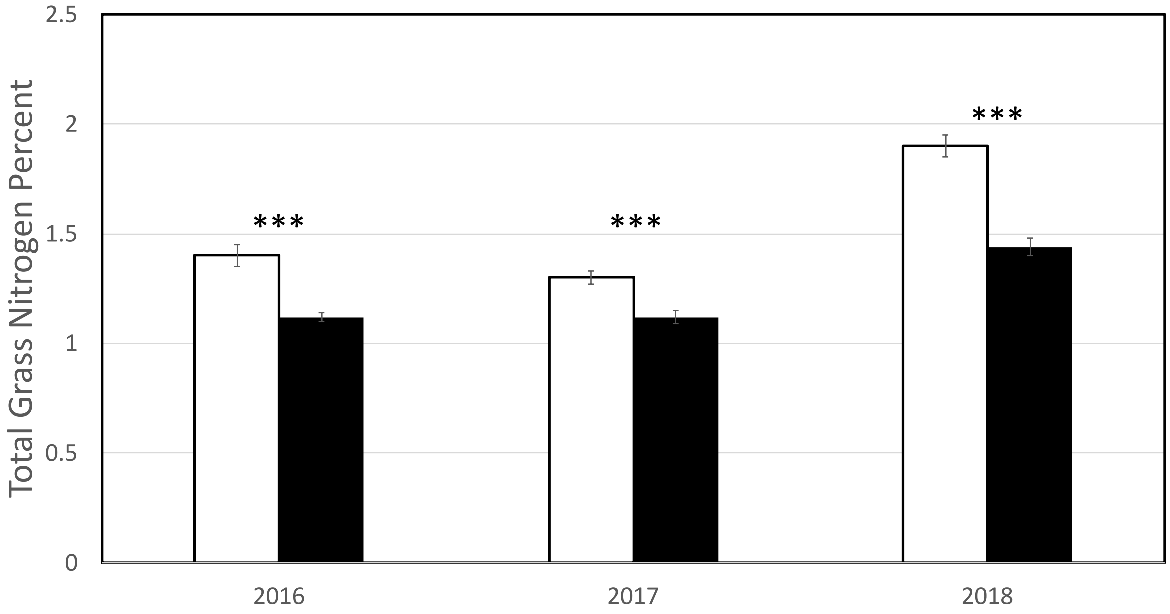

Figure 3.5- Relative difference in percentage of total grass nitrogen between grazing lawns and surrounding tall grass swards for total grass sample. Bars indicate means ± 1SE. Open bars = grazing lawns. Shaded bars = tall grass swards. Significance- ***p≤0.001, **p≤0.01, *p≤0.05.

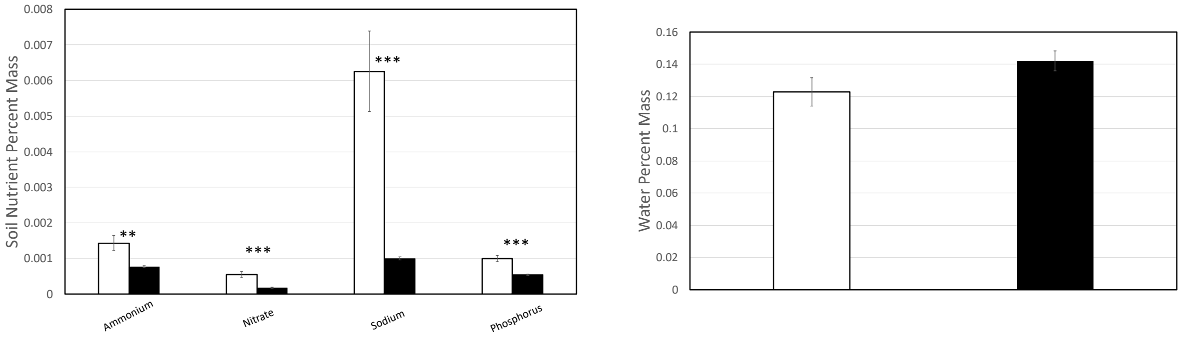

Figure 3.6- Relative difference in percentage of soil resources (nutrient and water) between grazing lawns and surrounding tall grass swards. Bars indicate means ± 1SE. Open bars = grazing lawns. Shaded bars = tall grass swards. Significance- ***p≤0.001, **p≤0.01, *p≤0.05.

Dichanthelium oligosanthes

For the dominant C_3 grass *Dichanthelium oligosanthes*, the carbon-to-nitrogen ratio was significantly lower on grazing lawns compared to tall grass swards (Figure 3.2, Table 3.1). Percent of nitrogen was significantly higher in plants on grazing lawns compared to those in surrounding tall grass vegetation (Figure 3.3, Table 3.2).

Pascopyrum smithii

For the dominant C_3 grass *Pascopyrum smithii*, the carbon-to-nitrogen ratio was significantly lower on grazing lawns compared to tall grass swards (Figure 3.2, Table 3.1). Percent nitrogen was significantly higher in plants on grazing lawns compared to those in surrounding tall grass vegetation (Figure 3.3, Table 3.2).

Andropogon gerardii

For the dominant C_4 grass *Andropogon gerardii,* there was no significant difference for the carbon-to-nitrogen ratio between plants on grazing lawns and those in tall grass vegetation (Figure 3.2, Table 3.1). There was also no significant difference in percent nitrogen between plants on grazing lawns and those in tall grass vegetation, unlike the other 3 grass species that showed significantly higher nitrogen content on grazing lawns (Figure 3.3, Table 3.2).

Sorghastrum nutans

For the dominant C_4 grass *Sorghastrum nutans,* the carbon-to-nitrogen ratio was significantly lower on grazing lawns compared to tall grass swards (Figure 3.2, Table 3.1). There was also a significantly higher percent nitrogen in plants on grazing lawns compared to those in tall grass vegetation (Figure 3.3, Table 3.2).

Total grass

For 2016 total grass samples there was a significantly higher carbon-to-nitrogen ratio in the tall grass vegetation and a significantly higher nitrogen content on grazing lawns (Figure 3.4, Figure 3.5, Table 3.3). 2017 total grass samples had a significantly higher carbon-to-nitrogen ratio in the tall grass vegetation and a significantly higher nitrogen content on grazing lawns (Figure 3.4, Figure 3.5, Table 3.3). In 2018, total grass samples had a significantly higher carbon-to-nitrogen ratio in the tall grass vegetation and a significantly higher nitrogen content on grazing lawns, similar to 2016 and 2017 (Figure 3.4, Figure 3.5, Table 3.3). In summary, carbon-to-nitrogen ratio was significantly higher in tall grass vegetation and nitrogen content was significantly higher on grazing lawns for all three sampling years.

Soil samples

All measured soil nutrients, ammonium, nitrate, phosphorus, and sodium, were significantly higher on grazing lawns compared to soils of surrounding tall grass swards. Water content showed no significant difference between grazing lawns and surrounding tall grass vegetation (Figure 3.6,Table 3.4).

Discussion

In this study, I examined both plant and soil nutrient concentrations both on and off lawns to test the hypotheses that grass nutritive quality is higher on grazing lawns, indicating the functioning of the classical nutrient-based pathway for grazing lawn maintenance on tallgrass prairie. I also conducted a preliminary comparison of soil water content on and off lawns as an initial test of the water-based pathway for grazing lawn maintenance (Veldhuis *et al.* 2014)

Multiple positive feedback mechanisms have been hypothesized to explain the maintenance of grazing lawns. The architectural shift pathway (see chapter 2) involves herbivore-induced shifts in plant architecture that result in greater canopy forage density, which are predicted to then increase foraging efficiency and promote continued grazing. The classic nutrient-based pathway includes nutrient mineralization and compensatory growth due to defoliation, both of which increase plant nutritional quality. The alternative water-based pathway suggests that a decrease in vegetation cover and increased soil compaction leads to lower soil water availability. When water is limited for plants, they tend to hold on to nutrients, thus increasing plant nutritional quality. This also leads to a positive feedback for grazers, just like the classic nutrient-based pathway.

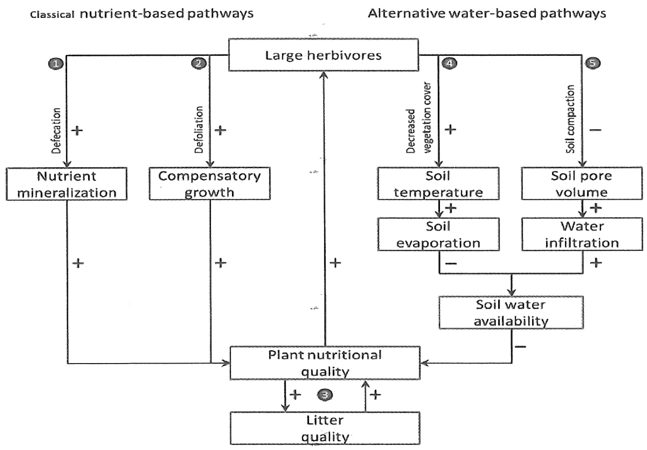

Figure 3.7-Overview of the influence of large herbivores on grass nutritional quality. The diagram shows five main pathways by which herbivores affect grass nutritional quality. (Veldhuis et al. 2014)

For three of the four grass species studied, *D. oligosanthes, P. smithii, and S. nutans,* the carbon-to-nitrogen ratio was significantly higher in plants in the matrix tall grass vegetation compared to those on grazing lawns. However, for *A. gerardii,* there was no significant difference in the carbon-to-nitrogen ratio between grazing lawns and surrounding matrix tall grass vegetation. The total grass (all grass species combined) carbon-to-nitrogen ratio was also significantly higher in surrounding tall grass matrix vegetation than on grazing lawns in all three field seasons, 2016, 2017, and 2018.

Consistent with the patterns in carbon:nitrogen ratios, grass nitrogen concentration was generally higher in plants on grazing lawns compared to those in surrounding tall grass swards.

For three of the four species studied, *D. oligosanthes, P. smithii, and S. nutans,* plant tissue nitrogen content was significantly higher in grasses on grazing lawns compared to those in tall grass vegetation. Again, *A. gerardii* was the only species not to show a significant difference between grazing lawns and surrounding matrix vegetation. With regards to the total grass canopy (all grass species combined), nitrogen content was significantly higher on grazing lawns compared to tallgrass vegetation for all three field seasons, 2016, 2017, and 2018.

In times of water stress, plant tissue tends to retain nutrients, thus increasing plant nutritional quality. 2017 and 2018 were drought years and there were some positive nutrient changes in relation to these significantly drier years. While nitrogen was significantly higher on grazing lawns compared to tall grass vegetation in all 3 years, 2018 showed the largest difference between means.

Conclusion

My overall objective was to understand the nutrient and water-based mechanisms maintaining grazing lawns on tallgrass prairie, and how grazing lawns contribute to forage for native grazers, plant species richness, and overall biodiversity of the grassland landscape, indicating their importance in terms of conserving the North American Tallgrass Prairie. The results of this study strongly indicate that the frequent and intense activities of large grazers result in increased plant nitrogen content and lower C:N ratios in grasses on tallgrass prairie grazing lawns, suggesting that the nutrient-based pathway generates positive feedbacks resulting in the maintenance of grazing lawns. The results of this study also show that soil mineral nutrients including ammonium, nitrate, sodium, and phosphorus, are significantly higher in concentration on grazing lawns compared to tall grass vegetation, providing further strong support for the nutrient-based pathway for grazing lawn maintenance. The soil water data showed a trend of lower soil water content on grazing lawns, as predicted by the water-based pathway, but the differences between grazing lawns and matrix sites was not significant. While the water percent mass was not significantly different on grazing lawns compared to tall grass swards, compaction and bioturbation must be taken into account. Nonetheless, this preliminary comparison provided little support for the water-based pathway. The results from chapter two provided strong support for the plant architectural-based pathway for grazing lawn maintenance. Thus, the results overall indicate that changes in grass nutrient content and shifts in plant architecture are at least two different mechanisms or pathways that operate on tallgrass prairie leading to positive plant-grazer feedbacks and grazing lawn maintenance.

Relative to tropical and subtropical regions, little is known about the ecology of grazing lawns in temperate grasslands. Our lack of knowledge about grazing lawns in temperate grasslands, such as tallgrass prairie, exists because previous studies in these grasslands have compared large sites or landscapes with and without the presence of grazers, but have not compared these patch types (grazing lawns versus adjacent matrix tallgrass swards) within the larger grazed ecosystem. Future research recommendations for grazing lawns in the tallgrass prairie include further evaluation of the water-based pathway with a more detailed study of plant and soil water relations over multiple field seasons. Also, further study of grass architectural changes could be performed, including bud banks and shifts in relative abundance of rhizomatous, intermediate and caespitose growth forms.

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Appendix A - Carbon in Soils and Grass on Grazing Lawns

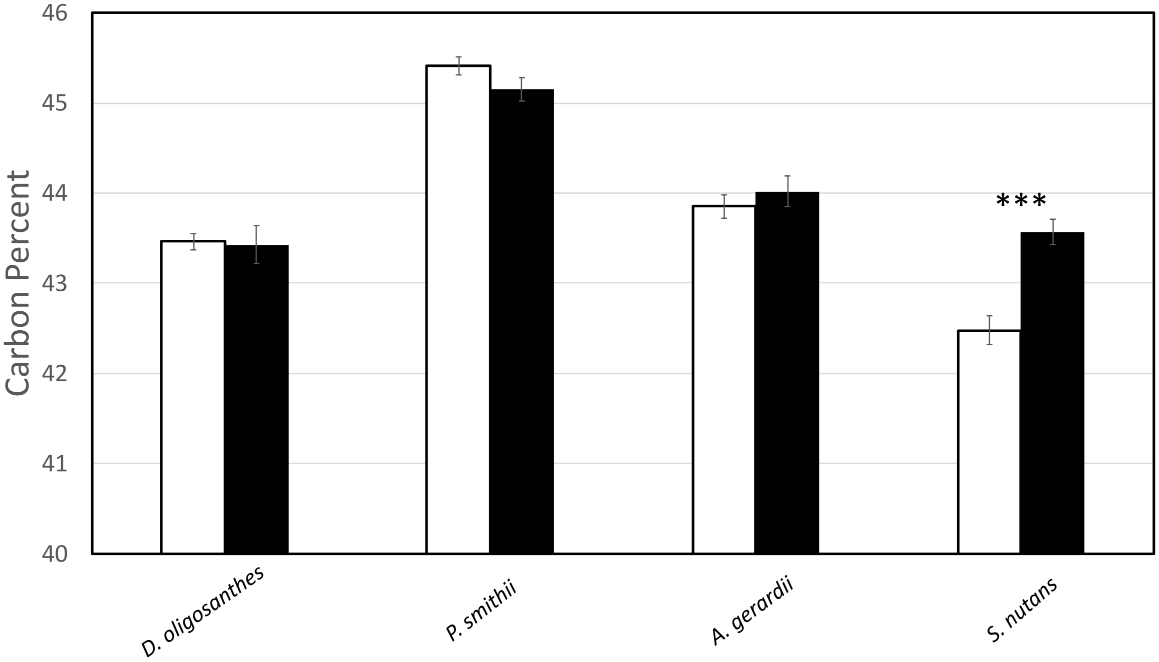

Figure A.1- Relative difference in percentage of carbon between grazing lawns and surrounding tall grass swards for four dominant prairie grasses. Bars indicate means ± 1SE. Open bars = grazing lawns. Shaded bars = tall grass swards. Significance- ***p≤0.001, **p≤0.01, *p≤0.05.

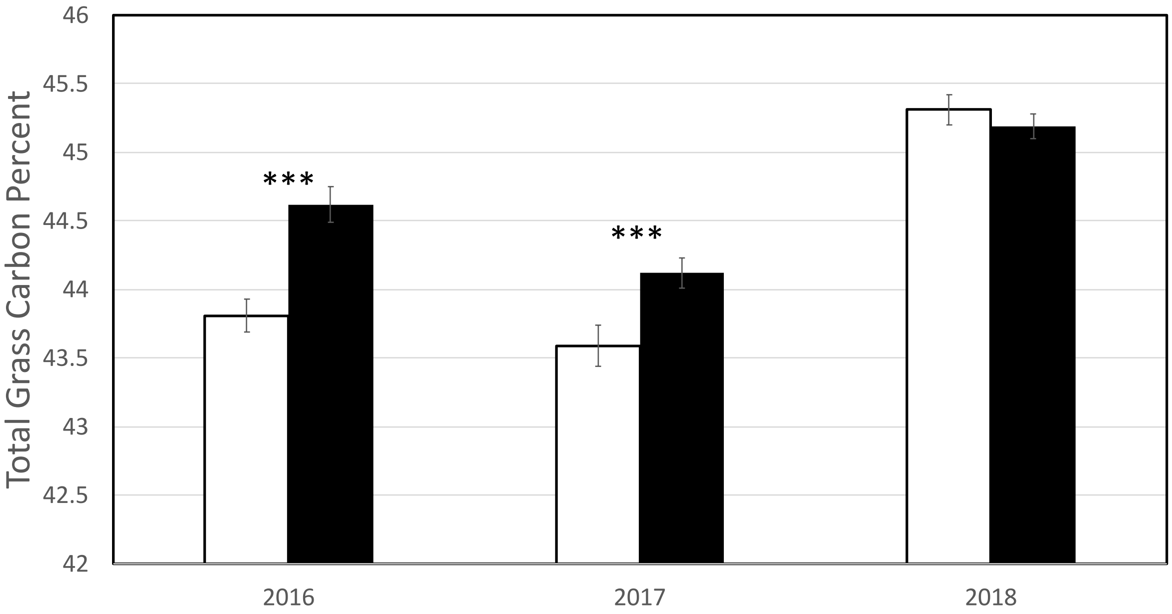

Figure A.2- Relative difference in percentage of total grass carbon between grazing lawns and surrounding tall grass swards for four dominant prairie grasses. Bars indicate means ± 1SE. Open bars = grazing lawns. Shaded bars = tall grass swards. Significance- ***p≤0.001, **p≤0.01, *p≤0.05.

	Test	d.f.	F-statistic	Probability
D. oligosanthes	ANOVA	22	0.02	0.881
P. smithii	ANOVA	31	2.3	0.140
A. gerardii	ANOVA	40	0.5	0.465
S. nutans	ANOVA	70	26.9	<0.001

Table A.1- Statistical tests for Carbon from 4 prairie species.

	Test	d.f.	F-statistic	Probability
2016	ANOVA	34	20.7	<0.001
2017	ANOVA	58	8	0.006
2018	ANOVA	58	0.7	0.415

Table A.2-Statistical tests for Carbon for Total Grass samples.