EFFECTS OF GRAZING ON GROWTH AND MORPHOLOGY OF RHIZOMATOUS AND
CAESPITOSE GRASSES IN TALLGRASS PRAIRIE

by

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Abstract

Herbivory is one of the major biotic interactions shaping the structure and dynamics of grassland plant populations and community structure. The two major grass growth forms, rhizomatous and caespitose species, may show different grazing tolerance and short-term overcompensation may offset long-term reductions in plant performance and fitness. The objectives of this study were to assess 1) the effects of long-term ungulate grazing on plant architecture, population structure, and life history traits of the caespitose perennial grass, *Schizachyrium scoparium* (little bluestem), and the rhizomatous *Bouteloua curtipendula* (sideoats grama) in tallgrass prairie, and 2) the effects of grazing intensity (frequency of defoliation) on growth responses of little bluestem.

Long-term bison grazing decreased the cover, frequency, tiller height, and proportion of tillers producing seed in little bluestem, but caused no changes in tiller density and total genet size. Grazed little bluestem plants maintained a significantly larger belowground bud bank. Bison grazing had no long-term effect on the abundance, bud bank densities, or rhizome growth of the rhizomatous side-oats grama grass. Biomass, tiller density, relative growth rates, and proportion of tillers flowering in little bluestem all decreased with increasing frequency of defoliation. However, even an intense grazing regime (9 defoliations over a 12 month period) caused no plant mortality and no changes in new tiller emergence rates, or bud bank densities. Increasing defoliation frequency did result in shifts in plant architecture, as an increasing proportion of extravaginal tillers led to a more lateral, decumbent growth form.

These results show that the rhizomatous side-oats grama grass has a significantly higher grazing tolerance than does little bluestem, and/or that bison selectively graze little bluestem. Results from responses to the experimental defoliation regimes suggest that little bluestem shows lower tolerance to high frequency of defoliation, and its maintenance of a reserve belowground bud bank may be its primary tolerance mechanism, allowing tiller populations to recover following severe defoliation.

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Dedication

I dedicate this thesis to the two guys who made my stay here very memorable and worth it, my husband Yapo Genevier N'Guessan and my son Yapo Daniel N'Guessan. Yapo, thanks for always reminding me that I could make it, especially when I entertained thoughts of quitting. And Daniel, you have been a very good boy even when mummy did not spend as much time with you as she wanted to. You two are the best.

CHAPTER 1 - EFFECTS OF LONG-TERM GRAZING ON A DOMINANT CAESPITOSE (LITTLE BLUESTEM) AND RHIZOMATOUS (SIDEOATS GRAMA) GRASS IN TALLGRASS PRAIRIE

Abstract

The long-term effects of ungulate grazers on plant architecture, population structure, and demography of two C_4 perennial grasses in tallgrass prairie, little bluestem (*Schizachyrium scoparium*), which possesses a caespitose growth habit, and sideoats grama (*Bouteloua curtipendula*), which has a rhizomatous growth habit, were studied. I also tested the hypothesis that compensatory responses to grazing are size-dependent in caespitose grasses.

Long-term bison grazing decreased cover, frequency, average tiller height and proportion of flowering tillers of little bluestem. However, long-term grazing caused no significant changes in average tiller numbers per genet and tiller density, but caused a significant increase in number of belowground vegetative buds per tiller for this species. Generally, there seemed be an effect of genet size on little bluestem plant performance in both grazed and ungrazed treatments, and the large size class seemed to be the most adversely affected by long-term grazing.

Conversely, long-term grazing caused only a slight decrease in sideoats grama average tiller height, but had no effect on frequency, cover, number of belowground rhizome buds per tiller, and average rhizome length. However, mean rhizome length in sideoats grama differed significantly between years.

These results suggest that sideoats grama has a significantly higher grazing tolerance than does little bluestem. However, these results may also be due to bison selectively grazing little bluestem against sideoats grama (due to interspecific differences in forage quality).

Introduction

Herbivory is widely recognized as one of the major biotic interactions shaping the structure of plant communities in tallgrass prairie. Herbivores can have a pronounced effect on plant establishment, growth, plant form, reproductive success, and plant community diversity (Karki et al. 2000, Orodho et al. 1990). Hartnett et al. (1996) assert that in tallgrass prairie bison grazing at moderate intensity increases diversity by releasing the subdominant grasses and forbs from the competitive effects of the dominant prairie grasses which are preferentially consumed by large herbivores. In general, herbivory is assumed to cause a significant loss of plant growth, survival and fecundity (Tuomi et al. 1994, de Mazancourt et al. 1998), but some studies have shown that plants may exhibit a continuum of responses to herbivory (Maschinski and Whitman 1989, Tuomi et al. 1994, Vinton and Hartnett 1992, de Mazancourt et al. 1998). It has been suggested that herbivores may benefit the plants they eat by causing increases in fruit and seed production, biomass production, shoot production, rosette production, prop roots and tiller production, and nutrient supply (Maschinski and Whitman 1989, Paige 1992). However, according to Maschinski and Whitman (1989) and Trlica and Rittenhouse (1993), many studies of agricultural systems and fewer studies of natural systems support the widely held view that plants are negatively affected by herbivores which can limit plant distribution, reduce reproductive potential, and modify competitive ability. Between these extremes lie studies reporting that herbivores have no effect on the plants they eat (Lee and Bazzaz 1980, Maschinski and Whitman 1989).

Plant traits that reduce the probability of a plant being grazed (grazing avoidance) or those that increase its ability to recover following grazing (grazing tolerance) are two primary mechanisms by which plants cope with herbivory (Briske 1991, Lee and Bazzaz 1980, Pfeiffer

and Hartnett 1995, Tiffin and Inouye 2000). Putative avoidance strategies that reduce herbivory include structural compounds such as silica and lignin (Fahnestock and Detling 2000), morphological traits such as a short stature and a decumbent growth form (Fahnestock and Detling 2000, Karki et al. 2000, Smith 1998), anatomical features such as spines and awns, and biochemical mechanisms such as plant synthesis of toxic secondary metabolites (Briske and Anderson 1990). Grasses also possess morphological and physiological traits which can facilitate their recovery from herbivory resulting in compensation, and even overcompensation of tissue lost. Trlica and Rittenhouse (1993) suggested that an individual plant might exhibit overcompensation for herbivory under most favorable environmental conditions, but under less-than-favorable conditions this same individual might exhibit either equal compensation or undercompensation. Basal meristems, increased tillering and rapid growth rates following defoliation (Fahnestock and Detling 2000) and more horizontal display of leaf blades (Smith 1998) are important morphological characteristics contributing to plant capacity for compensation and consequently herbivory tolerance (Fahnestock and Detling 2000). Increased gas exchange rates in tissue remaining or produced after grazing, increased C allocation to shoots and increased nutrient absorption following grazing are important physiological functions that can increase capacity for compensation or tolerance, and thus resilience, of grasses to herbivory (Fahnestock and Detling 2000, Smith 1998).

Immediate grazing-induced changes in the physical structure of grasses can affect their physiological capacities as well, especially their ability to acquire critical resources such as radiant energy and water. According to Fahnestock and Detling (2000), reduction in leaf area through grazing has an immediate effect on whole plant carbon gain by reducing photosynthetic capacity; and following defoliation, photosynthetic rates of leaves and grazed grasses increase, decrease or remain similar to predefoliation rates, depending on the timing of herbivory and its

intensity and frequency. Grazing can also potentially affect physiological processes within plants by altering water availability: reducing transpiring leaf area can conserve soil moisture or, by contrast, can increase bare ground evaporative losses (Fahnestock and Detling 2000). In sum, grazing can result in short- and long-term plastic or genetic changes in the morphological structure and physiological function of grasses, and thereby alter community structure, energy flow and nutrient cycling in grasslands (Fahnestock and Detling 2000, Smith 1998).

Although herbivory resistance is most frequently viewed as an organismal attribute, populations of species may also display structural attributes which influence their ability to cope with herbivory; for example, the density, size class distribution and spatial arrangement of plants and tillers in a population may potentially influence herbivory avoidance by influencing plant appearance and biomass accessibility (Briske and Anderson 1990). Similarly, population structure may potentially affect herbivory tolerance by influencing tiller recruitment, resource acquisition, and inter- and intra-specific competitive interactions within the community (Briske and Anderson 1990).

The growth habit of grasses can have important implications for the way these species recover from disturbances such as grazing. Caespitose (i.e. tussock or bunch) and rhizomatous (and stoloniferous) perennial grasses represent distinct grass growth forms that variously dominate different grassland and savanna systems (Derner and Briske 2001). Caespitose (or bunchgrass) and stoloniferous or rhizomatous growth forms differ in number, disposition, and ramification of tillers and leaves (Klink 1994), belowground stem mass (rhizomes) and clone size (Derner and Briske 2001). Caespitose graminoids can be distinguished by the compact spatial arrangement of ramets within individual clones established by the emergence of juvenile ramets from buds within the subtending leaf blades and sheaths of parental ramets (Welker and Briske 1992). Caespitose grasses lack rhizomes or stolons. According to Williams and Briske

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(1991) an assemblage of connected ramet generations functioning as an autonomous unit (physiological individual) in the assimilation, allocation and utilization of resources within a clone usually exists within bunchgrasses; for example, resource allocation has been demonstrated within ramet hierarchies composed of three connected ramet generations in *Schizachyrium scoparium*. Rhizomatous grasses, on the other hand, spread through belowground stems (rhizomes). These rhizomes terminate in a shoot that emerges some distance from the mother plant. As these new shoots mature, they will also produce rhizomes that eventually produce new shoots. Resource translocation between parent and daughter tillers probably exists in rhizomatous grasses also and persistence of the connection may be influenced by the rhizome longevity. Caespitose and rhizomatous grasses not only differ in their architecture and demography, but are hypothesized to differ in other ecologically significant processes such as patterns of resource accumulation. According to Derner and Briske (2001), caespitose grasses tend to concentrate nutrients in shallow soils directly beneath clones in both mesic and semi-arid grasslands but rhizomatous grasses do not concentrate nutrients in soils even when grown in the same environments as caespitose grasses. However, the absence of substantial nutrient concentrations in soils beneath rhizomatous grasses may be offset by the presence of rhizomes that function as important below-ground storage organs for both carbon and nitrogen in this growth form (Derner and Briske 2001). This difference in patterns of resource accumulation may also potentially affect the way these two growth forms respond to both long-term and short-term grazing pressure. Klink (1994) and Mack and Thompson (1982) suggest that rhizomatous and caespitose habits are extremes to which perennial grasses have evolved at least in partial response to high versus low selection pressure by large mammals. According to Mack and Thompson (1982) as a morphologic group caespitose grasses are more susceptible to ungulate activity and may be altered to a prostate growth form with repeated grazing. Caespitose grasses

with intravaginal tillering place the emerging culm in a more exposed position to herbivory than the horizontally emerging extravaginal tillers of rhizomatous grasses (Mack and Thompson 1982). Mack and Thompson (1982) also argue that trampling damage in a rhizomatous grass mat creates at least the opportunity for recovery as the grass regenerates from severed rhizomes and each segment of the disarticulated turf may survive individually.

Bunchgrass populations exhibit two levels of structure: 1) the individual ramet or tiller and 2) the genet or plant (Butler and Briske 1988). According to Butler and Briske (1988), herbivory may influence bunchgrass demography at both levels of population structure. At the genet level, for example, longevities of perennial grasses have been observed to be lengthened, shortened or unaffected by herbivory (Butler and Briske 1988). Similarly, basal areas of individual perennial grasses have been observed to decrease in *Agropyron desertorum*, *Festuca idahoensis* and *Schizachyrium scoparium*, increase in *Andropogon greenwayi*, and remain constant in *Danthonia caespitosa* and *Muhlenbergia montana* in response to actual or simulated herbivory (Butler and Briske 1988). Perennial bunchgrasses with marked tolerance to defoliation have been described as rapid tillering, prostate forms with short leaves (Carman 1985). Upon herbivory-induced removal of apical meristems, this replacement potential (replacement of photosynthetically active surfaces) depends on the number of active axillary buds, or tillering rate, a condition which is under complex hormonal control and varies genetically both within and among species (Carman 1985).

The objective of this study was to assess the long-term effects of ungulate grazers on plant architecture, population structure, and demography of two C_4 perennial grasses in tallgrass prairie, *Schizachyrium scoparium* (Michx.) Nash (little bluestem) and *Bouteloua curtipendula* (Michx.) Torr. var. *curtipendula* (sideoats grama). Little bluestem has a caespitose growth form, while the variety of sideoats grama occurring at the study site has a rhizomatous growth form.

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Both species are abundant and co-occur throughout most of the study area, enabling me to compare the responses of the sympatric caespitose and rhizomatous growth forms in response to grazing under similar environmental conditions (i.e. water availability, soil moisture content and radiation energy). I also sought to test the hypothesis that compensatory responses to grazing are size-dependent in caespitose grasses.

Materials and Methods

This study was conducted on the Konza Prairie Biological Station (KPBS), a 3,487 ha native tallgrass prairie preserve located in the Flint Hills region of northeastern Kansas (39° 05´ N, 96° 35´ W). This preserve is owned by The Nature Conservancy and managed for ecological research and education by the Division of Biology, Kansas State University. The vegetation of KPBS is predominantly unplowed native tallgrass prairie, dominated by warm-season perennial C_4 grasses including big bluestem (*Andropogon gerardii* Vitman), little bluestem (*Schizachyrium scoparium* (Michx.) Nash), switchgrass (*Panicum virgatum* L.), Indian grass (*Sorghastrum nutans* L.) and sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.).

Konza Prairie is divided into 60 watersheds (mean size = 65 ha) subjected to prescribed fire at intervals from 1 to 20 years. Bison (*Bos bison*) were introduced onto Konza Prairie in 1987 and are free to move among ten watersheds that are burned annually or at 2-yr, 4-yr or 20-yr intervals. Each fire × grazing treatment is replicated two to four times at the watershed level. Replicated prescribed fire treatments were initiated in 1971 and grazing treatments in 1987. Average annual total precipitation is 835 mm with 75% falling during the growing season. The years 2004 and 2005 were above-average years for total rainfall for Konza Prairie (2004: 987.6 mm, 17% above average; 2005: 891 mm, 7% above average).

Sideoats grama and little bluestem plants were sampled at the end of the growing season (October 2005 and October 2006 respectively) in six watersheds, three ungrazed (K1B, 1B and 2C) and three watersheds that have been grazed (N1A, N1B and N2B) since 1987 and 1991. For each treatment two of the watersheds were spring burned annually while one watershed was spring burned biennially. According to Trager et. al (2004) bison in Konza Prairie wallow and graze throughout the designated grazing enclosure, but summer wallowing is concentrated on

relatively flat grazing "lawns" primarily located on mid-level terraces and uplands. Plants on grazed watersheds were therefore sampled in these grazing lawns.

Species abundance assessment

Ten year (1994 – 2004) vegetation species composition (data code PVC02) data for the watersheds used in this study (one watershed for the ungrazed treatment level and two watersheds for the grazed treatment level) were obtained from the Konza Prairie Long Term Ecological Research (LTER) dataset (Hartnett 2004). Canopy cover and frequency of each species are measured twice each season (May and August) in five replicate 10 m^2 circular plots along replicate transects in each watershed. The canopy cover of each species is usually estimated and assigned a cover class (modified Daubenmire scale: 1 = 0 – 1 %; 2 = 1 – 5 %; 3 = 5-25 %; 4 = 25 – 50 %; 5 = 50 – 75 %; 6 = 75 – 95 %; and 7 = 95 – 100 %). Frequency is the percent of the plots in which the species occurred. For each species, the maximum cover and frequency value (May or August) is retained for analysis. Further details on the methodology may be found at the Konza Prairie Long-Term Ecological Research (LTER) Program homepage <http://www.konza.ksu.edu/konza>. Ten year cover and percent frequency for each of the two grass species for the two treatment levels (grazed and ungrazed) were calculated. One-way analysis of variance was used to test the effects of long term bison grazing on cover and frequency of the two grass species. Significant differences among means were assessed using Fischer's protected LSD and were considered significant at the $\alpha = 0.05$ level.

Sideoats grama

Sideoats grama (B*outeloua curtipendula*) is a mid-size (up to 80 cm), perennial grass that reproduces sexually and vegetatively via rhizomes. Its short, pendent spikes – usually hanging down to one side of the flowering stalk – make it a very striking grass. There are three varieties

of *B. curtipendula*, but only *B. curtipendula* var. *curtipendula* (possessing a rhizomatous growth form as opposed to variety *tenuis* which has a stoloniferous growth habit (Engstrom 2004) and variety *caespitosa* with a caespitose growth form) occurs throughout the eastern United States, including most of the Great Plains. *B. curtipendula* is a C_4 grass, well adapted to the intense solar radiation, high temperatures, and droughts characteristic of the Great Plains. The species also is adapted to ungulate grazing and fire, two ecological processes closely associated with the prairies (Engstrom 2004).

For each watershed, ten individual tillers were randomly selected based on detection of the inflorescence (a total of 30 tillers in ungrazed prairie and 30 tillers in grazed prairie) and tiller heights were measured. The plants were then harvested by excavating an 8 cm radius soil core at the plant base. Excess soil was washed off and the plants' rhizomes and belowground buds were analyzed. Some of the tillers had a persistent rhizome connection to the previous season parent tiller, so the previous season's rhizome lengths were measured whenever available. Current season rhizome lengths were also measured. Total number of belowground rhizome buds per tiller was also measured. The effect of grazing on average tiller height, rhizome length and number of belowground rhizome buds per tiller was assessed with one-way analysis of variance. Significant differences among means were assessed using Fischer's protected LSD and considered significant at the α = 0.05 level.

Little bluestem

Little bluestem (*Schizachyrium scoparium*) is a perennial bunchgrass widely distributed throughout the eastern two-thirds of the U.S. However, it is most abundant in the True Prairie Association of the eastern Great Plains. The bunch or caespitose growth form originates from the intravaginal pattern of juvenile ramet development and complete absence of rhizomes and stolons. Genets are long lived, possess the C_4 photosynthetic pathway and reproductive ramets

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attain heights up to 1.5m (Williams and Briske 1991). In the Konza Prairie, juvenile ramets are recruited in the spring and autumn in undisturbed populations. Ramets in the spring cohort frequently complete their life in one growing season while ramets of the autumn cohort overwinter and complete their life during the subsequent season (Williams and Briske 1991).

For each watershed, ten genets were randomly selected (a total of 30 genets per treatment). Five tillers were then randomly selected within each genet and their heights were measured and used to estimate the average tiller height for each genet. Two basal diameter measurements were obtained from the wide and narrower sides of each genet, and basal areas were calculated using the formula for area of an ellipse

$$\text{Area} = \pi ab \quad (1)$$

where:

a is the major radius (semi-major axis) of the ellipse

b is the minor radius (semi-minor axis) of the ellipse

π is Pi, approximately 3.142

The genets were divided into three basal area size classes, $<50 \text{ cm}^2$, $50\text{-}100 \text{ cm}^2$ and $>100 \text{ cm}^2$ to evaluate the measured responses as a function of size class. Total number of tillers per genet was determined destructively (i.e. through clipping off the aboveground biomass). Proportion of flowering tillers and vegetative tillers within each genet was also determined. The entire remaining belowground biomass for each genet was excavated and excess soil was washed off from the cores and the plants' belowground buds were analyzed. To determine average number of belowground buds per tiller, ten tillers were randomly selected and their total number of buds was counted. One-way analysis of variance was used to test the effect of grazing on average tiller height, number of tillers per genet, flowering to vegetative tiller ratio and number of belowground vegetative buds per tiller. Significant differences among means were assessed

using Fischer's protected LSD and Student-Newman-Keuls test and were considered significant at the α = 0.05 level. Two-way analysis of variance procedure was used to test if the above responses were size class dependent in both ungrazed and long-term grazed treatments.

Results

Species abundance assessment

The two warm season C_4 grass species responded very differently to long-term grazing. Long-term bison grazing resulted in a large (50%) and statistically significant reduction in cover of little bluestem compared to its cover in ungrazed watersheds (Figure 1.1b). Similarly, the frequency of little bluestem was also significantly lower (20% decrease) in grazed watersheds compared to ungrazed watersheds (Figure 1.1a). By contrast, grazing caused no significant change ($P > 0.05$) in sideoats grama percent frequency (Figure 1.1a) or cover (Figure 1.1b).

Little bluestem traits

Long term grazing caused no significant change in little bluestem aboveground tiller density or total number of tillers per plant ($P > 0.05$) (not shown). However, grazing resulted in a significant ($P < 0.05$) 15% increase in number of belowground buds per tiller (Figure 1.2a). Conversely, average tiller height for grazed little bluestem plants was about 23% lower compared to ungrazed plants ($P < 0.05$) (Figure 1.2b) and grazed little bluestem plants exhibited a marked reduction (about 70%) in proportion of flowering tillers to vegetative tillers ($P < 0.05$) (Figure 1.2c).

Little bluestem size class effect

Parallel to trait responses to grazing, number of belowground buds per tiller in little bluestem increased significantly ($P = 0.0024$) under long-term grazing (Figure 1.3a), while average tiller height and proportion of tillers flowering were significantly decreased ($P = 0.0014$ and $P = 0.0099$ respectively) in response long-term grazing (Figure 1.3b and Figure 1.3c). For each response variable differences among size classes were not significant (i.e. $P = 0.5408$ for

number of belowground buds per tiller, P = 0.4686 for average tiller height, and P = 0.5263 for proportion of tillers flowering). There was also no significant grazing × size class interaction for all the response variables (i.e. P = 0.1785 for number of belowground buds per tiller, P = 0.7649 for average tiller height, and P = 0.9964 for proportion of tillers flowering).

Sideoats grama traits

Grazing had much smaller effects on performance and traits of sideoats grama grass. Grazing caused a relatively smaller (compared to the effect on little bluestem) but statistically significant (P < 0.05) reduction (approximately 15%) in tiller height (Figure 1.4a), but had no effect on number of belowground rhizome buds per tiller (Figure 1.4b) or on rhizome traits (i.e. length) (Figure 1.4c). This is consistent with species abundance patterns showing that sideoats grama grass was much less affected by grazing than was little bluestem (i.e. Figure 1.1). By contrast, mean rhizome length in sideoats grama (a measure of lateral clonal spread via vegetative reproduction) differed significantly between years (P<0.05) (Figure 1.4c) Comparison of rhizome growth rates between years and between treatments indicate that inter-annual resource availability (e.g. water) has a much larger effect on rhizome growth than does grazing.

Discussion

The two dominant tallgrass warm season C_4 perennial grass species studied responded very differently to long-term grazing. Long-term bison grazing markedly decreased both cover and frequency of little bluestem. By contrast, more than two decades of bison grazing caused no change in sideoats grama average frequency or cover.

Long-term grazing caused no changes in tiller density and total tiller population size per genet in little bluestem. Grazed little bluestem plants had significantly reduced average tiller heights and proportion of flowering tillers compared to ungrazed plants, but produced a larger number of belowground vegetative buds per tiller.

Generally, there seemed to be no effect of genet size on little bluestem plant performance in both grazed and ungrazed treatments. For each response variable, differences among size classes were not significant, and there was no significant grazing × genet size interaction.

Long-term grazing had much smaller effects on performance and traits of the rhizomatous species, sideoats grama. Long-term grazing caused slight (compared with little bluestem) decrease in average tiller height, but had no effect on number of belowground rhizome buds per tiller or average rhizome length. However, mean rhizome length in sideoats grama differed significantly between years.

Certain of the native grasses of the tallgrass prairie either have disappeared from or have been greatly weakened in grazed areas where they were abundant at the time of settlement by Europeans and their domestic animals (Miller Neiland and Curtis 1956). According to Fowler (2002), range scientists have identified plant species that increase and decrease under various levels of grazing, but the mechanisms causing these changes in plant community composition have generally not been investigated. For example, we do not know whether "decreasers"

decrease in abundance when grazed because they are preferred by grazing ungulates or because they are more sensitive to equivalent levels of defoliation than are "increasers", and whether plant competition reinforces or weakens the effects of grazing.

Engstrom (2004) reports that as a rhizomatous variety, sideoats grama is well adapted to grazing pressure. Engstrom (2004) further asserts that in the Cross Timbers of northern Texas, the species increased in abundance or stayed the same under grazing pressure in many pastures studied, while most of the larger tallgrass prairie species showed large declines. Sideoats grama's habit of carrying the bulk of its foliage within several centimeters of the ground, as well as its vigorous rhizomatous nature, were believed to be the factors responsible for its persistence (Engstrom 2004). Miller Neiland and Curtis (1956) also described sideoats grama as an "increaser", while Fowler (2002) described the species as a "decreaser". Little bluestem on the other hand has mostly been described as a "decreaser" species (Fowler 2002, Miller Neiland and Curtis 1956). Towne et al. (2005) report that little bluestem cover decreased over time in bison pastures. My results support the view of little bluestem as a "decreaser" and sideoats grama as an "increaser" in that long-term grazing significantly reduced cover and frequency of little bluestem but had no effect on sideoats grama abundance. This suggests that sideoats grama has a higher grazing tolerance (compensation) than little bluestem, or bison selectively graze little bluestem against sideoats grama (due to interspecific differences in forage quality), or a combination of both factors. Brown and Stuth (1993) have shown that *Schizachyrium scoparium* tillers were selected by herbivores in preference to *Paspalum plicatulum* in a Texas grassland regardless of season or stocking rate, and defoliation intensity was not proportional to availability. On the other hand, Miller Neiland and Curtis (1956) report that in studies of establishment and survival of sideoats grama and little bluestem in Wisconsin, sideoats grama increased in density under four clippings made at 28 day intervals during two consecutive years while little bluestem

showed a decrease (but slight) in density over the same time period. According to Miller Neiland and Curtis (1956) the "increaser" status of sideoats grama under grazing of mixed stands is believed to be related to the low amounts of photosynthetic tissue removed from this short, rhizomatous plant; at the same time the taller (e.g. little bluestem), more erect species suffer excessive losses and are rapidly weakened. It therefore seems that both herbivore selectivity and sideoats grama's high tolerance (due to less tissue removed per grazing event) contribute to the species abundance patterns that I observed. In addition, as sideoats grama typically occurs in a mixed sward with other preferred forage grasses, its increase may also be partially attributed to reduced competition from its heavily grazed neighbors.

One of the most common morphological responses to grazing pressure conferring increased grazing tolerance in grasses is a short stature and a decumbent growth form (Fahnestock and Detling 2000, Karki et al. 2000, Smith 1998). Reduced tiller height in response to long-term grazing has been observed in many grass species; for example, Fahnestock and Detling (2000) report that long term grazing by wild horses in the Montana Pryor mountains resulted in reduced tiller heights in *Pseudoroegneria spicata*, *Festuca idahoensis* and *Elymus lanceolatus*. Sims et al. (1970) also report that mowing decreased average tiller height for sideoats grama. Long-term grazing significantly reduced average tiller height for both little bluestem and sideoats grama in my study. The short stature renders a greater proportion of tissue as unavailable to grazers, effectively reducing future defoliation intensity by ungulates.

Grazed populations of several perennial grasses have been observed to consist of individuals with smaller basal areas in comparison with ungrazed populations, and this decrease in individual plant basal area is very likely a consequence of the fragmentation of individual large plants into smaller units (Briske 1991). Consequently, plant density may remain constant or even increase while basal area per plant decreases (Briske 1991). Further, an increase in tiller

number per unit of remaining basal area may initially offset the decrease in total basal area thereby maintaining a constant tiller density (Briske 1991). However, with continued severe grazing the decrease in individual plant basal area may become so great that tiller density declines within the population (Briske 1991). Wang (2004) reported that long-term grazing caused a decline in *Leymus chinensis* tiller density. Short-term severe grazing has been reported as not having an effect on tiller density in *Andropogon gerardii*, *Calamovilfa longifolia* (Mullahey et al. 1991) and *Schizachyrium scoparium* (Mullahey et al. 1990). However, Owensby et al. (1974) report that one year of intense clipping decreased *Andropogon gerardii* tiller density. Despite the fact that I sampled grazed plants from grazing lawns (which are mostly continuously grazed every year) tiller density and total tiller population size was similar between long-term grazed and ungrazed treatments. Thus, demographic compensatory responses within genets (stimulation of greater tiller initiation) may offset effects of fragmentation and reduced basal area, maintaining high tiller densities.

Populations of grasses exposed to grazing by vertebrates often exhibit reduced flowering. This is often interpreted as an adaptive response that reduces grazing damage (i.e. flowering tillers are usually taller and may attract or be more accessible to herbivores) (Kotanen and Bergelson 2000), or it may be due to increased sink strength of vegetative parts in response to defoliation, resulting in decreased carbon and nutrient allocation to flowering. Grazing has been shown to reduce flowering in *Schizachyrium scoparium* (Butler and Briske 1988), *Ammophila breviligulata* and *Spartina patens* (Seliskar 2003). I also observed a marked decrease in proportion of flowering tillers under long-term grazing. The reduction in flowering associated with grazing was much larger in magnitude (~ 75% reduction) than effects on plant growth. This is consistent with other studies indicating reproduction is more sensitive to grazing or other stresses than is growth or other plant responses. On the other hand, this may, concurrent with

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reduced tiller heights, be more of a mechanism for grazing avoidance other than just being evidence for reduced fitness.

In perennial-dominated savannas, grasslands and many other communities, plant densities and vegetation structure and dynamics may be regulated principally by patterns of vegetative reproduction and the demography of perennating organs, rather than by seed reproduction and seed banks (Hartnett et al. 2006). The belowground population of meristems associated with rhizomes or other perennating organs (the 'bud bank') can play a fundamental role in local plant population persistence and dynamics, vegetation structure and productivity, and the resilience of plant communities to factors such as drought, grazing pressure, or invasion of exotic plant species (Hartnett et al. 2006). Hartnett et al. (2006) further assert that recent studies of tallgrass prairies of the North American central grasslands indicate that regeneration and maintenance of perennial grass populations is regulated principally by vegetative reproduction and belowground bud bank dynamics. Long-term grazing has been shown to affect belowground vegetative buds and rhizome demography differently for different species. For example, Hendrickson et al. (1997) report that long-term grazing of *Bouteloua curtipendula* and *Hilaria belangeri* by domestic herbivores influenced axillary bud availability by modifying population structure of these two species; bud number per square meter was decreased in *B. curtipendula* but greatly increased in *H. belangeri* in the long-term grazed community. These patterns, however, were linked to the aboveground stem densities in that *B. curtipendula* had decreased while *H. belangeri* had increased tiller number per plant and plant number per meter squared in long-term grazed communities. My results show that long-term bison grazing had no effect on sideoats grama total number of rhizome buds per tiller or on rhizome length. However, rhizome lengths differed significantly between years. These results are consistent with most of the previously discussed traits, and, alongside other traits, reinforce this species' grazing

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tolerance capacity. The difference in rhizome lengths between years rather than between treatments indicates that inter-annual resource availability (e.g. water) has a much larger effect on rhizome growth and lateral clonal spread than does grazing for this species. On the other hand, long-term grazing significantly increased total number of vegetative buds per tiller in little bluestem. This increased number of buds, with no corresponding increase in aboveground tiller numbers indicates that little bluestem populations maintain high reserve bud bank densities, even under constant long-term grazing, a characteristic that may potentially increase their resilience and their ability to recover after long-term grazing.

Butler and Briske (1988) reported that steer herbivory influenced the size distribution of little bluestem plants by decreasing the number of large individuals while concomitantly increasing the number of small individuals and tiller density. This was due to fragmentation of large individual plants into smaller units with reduced basal area and greater number of tillers per cm^2 of the remaining basal area. Nevertheless, Butler and Briske (1988) did not report any fragmentation (and possibly complete mortality) of the small little bluestem individuals, which may suggest that smaller little bluestem individuals are more herbivory tolerant. However, Pfeiffer and Hartnett (1995) have shown that in burned tallgrass prairie, small plants were most abundant but were grazed least frequently. The perceived enhanced tolerance of smaller little bluestem plants could therefore be misleading and may actually reflect greater grazing avoidance of small genets as grazers (bison) select larger size classes over smaller ones. My results showed no effect of genet size on little bluestem plant performance in both grazed and ungrazed treatments for all the responses measured. These results therefore do not support the hypothesis that compensatory responses to grazing are size-dependent in caespitose grasses.

In conclusion, sideoats grama seems to be tolerant and well adapted to long-term grazing while little bluestem seems sensitive to some extent to long-term grazing. It is not clear whether

these differences in response are due to sideoats grama having a significantly higher grazing

tolerance (compensation) than does little bluestem, or due to bison selectively grazing little

bluestem over sideoats grama (due to interspecific differences in forage quality), or a

combination of both factors. However, little bluestem maintained a high population of

belowground vegetative buds, and this may be the main mechanism enabling the species to

persist under long-term constant grazing. Many studies of plant species responses to grazing

have shown that defoliation significantly affects plant performance. Authors then assume

(without demonstration) that these effects at the individual level cause population level change in

species relative abundance. In this study clear interspecific differences in individual plant traits

also were reflected in interspecific differences in long-term population responses.

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Figures and Tables
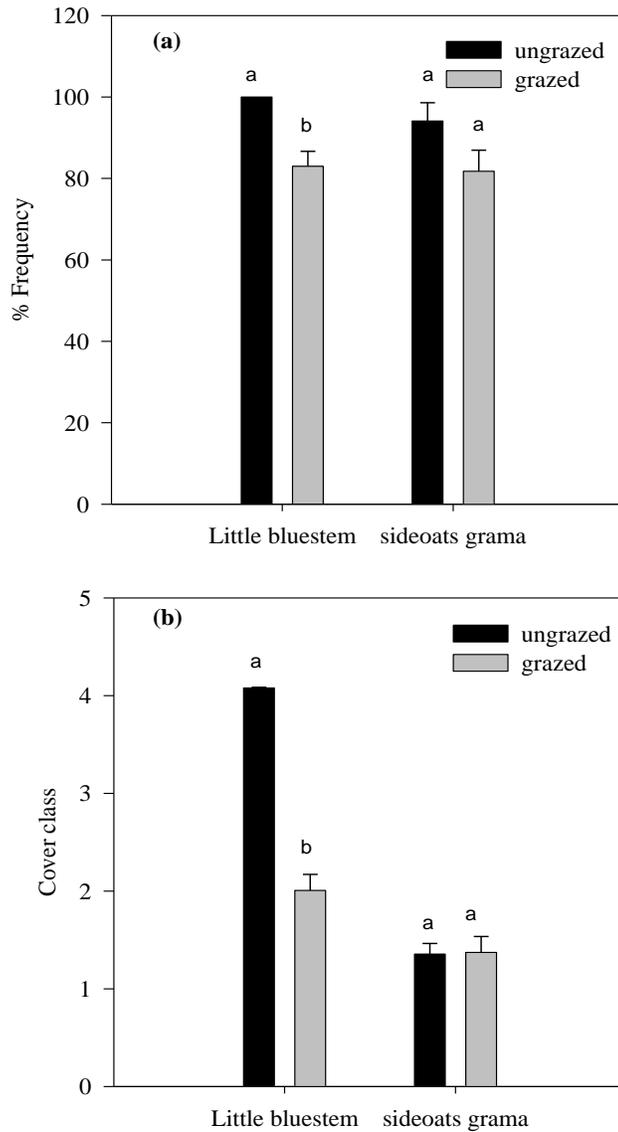
Figure 1.1 Ten year (1994-2004) a) percent frequency and b) average cover for little bluestem and sideoats grama in ungrazed and grazed prairie (cover classes 1 = 0 – 1 %; 2 = 1 – 5 %; 3 = 5-25 %; 4 = 25 – 50 %; 5 = 50 – 75 %; 6 = 75 – 95 %; and 7 = 95 – 100 %). Error bars are ± 1 SE of the mean. Bars with the same letter are not significantly different (P >0.05).
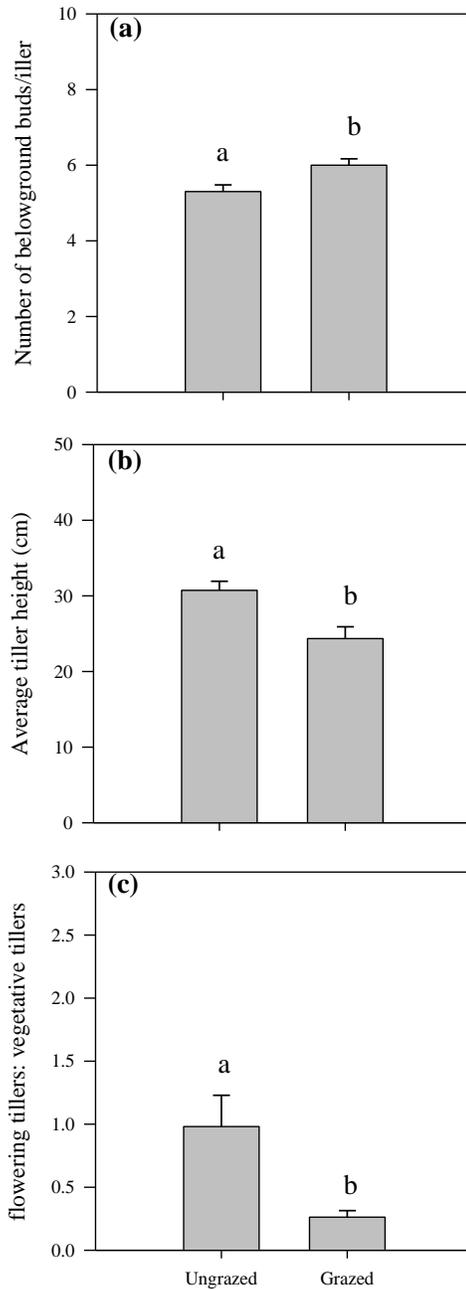
Figure 1.2 Little bluestem a) belowground buds per tiller, b) average tiller height and c) flowering to vegetative tiller ratio in ungrazed and grazed prairie. Error bars are ± 1 SE of the mean. Bars with the same letter are not significantly different (P >0.05).
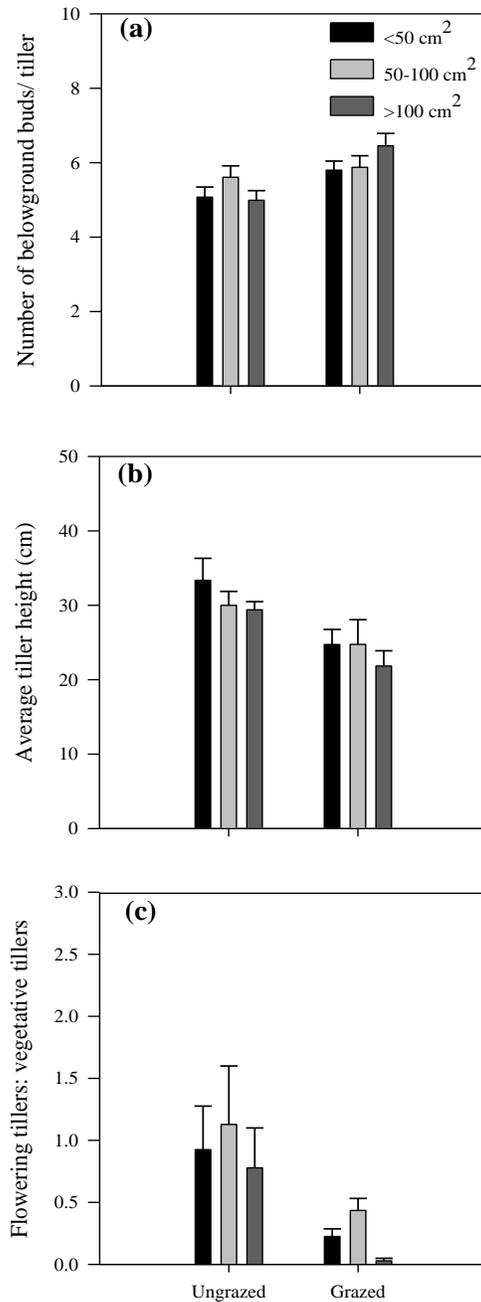
Figure 1.3 Little bluestem a) belowground buds per tiller, b) average tiller height and c) flowering to vegetative tiller ratio as a function of genet size in ungrazed and grazed prairie. Error bars are ± 1 SE of the mean. For each response variable differences between grazed and ungrazed treatments are significant (P < 0.01). Differences among size classes were not significant and there was no significant grazing × size class interaction (P > 0.05).
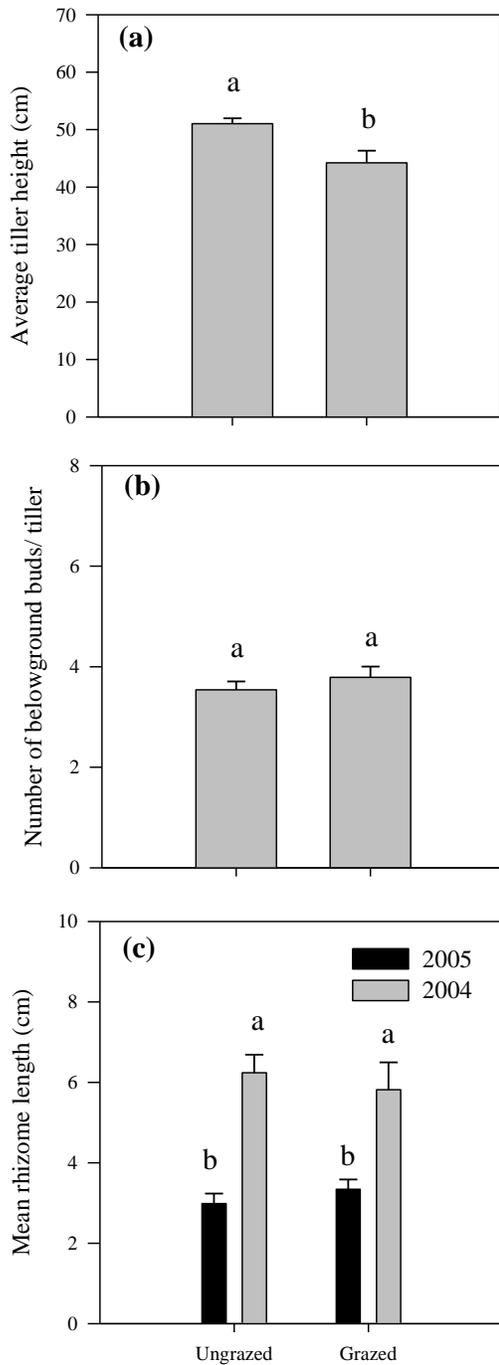
Figure 1.4 Sideoats grama a) average tiller height, b) belowground buds per tiller and c) mean rhizome length in ungrazed and grazed prairie. Error bars are ± 1 SE of the mean. Bars with the same letter are not significantly different (P >0.05).

CHAPTER 2 - EFFECTS OF CLIPPING FREQUENCY ON LITTLE BLUESTEM

Abstract

The objectives of this study were 1) to assess the relationship between clipping frequency and growth responses (compensatory regrowth and plant architecture) of little bluestem (*Schizachyrium scoparium*) in tallgrass prairie, and 2) to assess plant seed and vegetative reproduction and bud bank population threshold responses to simulated overgrazing (more frequent clipping) in tallgrass prairie.

Little bluestem generally responded to repeated defoliation by exhibiting significant reductions in above-ground biomass accumulation, total tillers per genet, tiller density and proportion of tillers flowering. These responses were generally non-linear, with a large decrease with $1 - 3$ defoliations, no further change with $4 - 7$ defoliations, and then additional reduction in growth with additional defoliations the following season. In contrast to these non-linear growth responses, proportion of tillers flowering generally decreased linearly with increasing frequency of defoliation. Plant relative growth rates decreased progressively with increasing clipping frequency during the first growing season, but additional clipping early in the second growing season caused no further effects. Repeated defoliation did not affect new tiller emergence and overall genet survivorship. While defoliation frequency did not change number of belowground vegetative buds per tiller, increasing defoliation frequency changed belowground vegetative bud architecture by increasing incidence of more extravaginal versus intravaginal buds per genet.

The traits I measured under full competition from neighbors mostly showed under-compensation and exact-compensation for all defoliation frequencies. Repeated defoliation

seems to exacerbate this species inability to tolerate herbivory. To ensure persistence of the

species in rangelands, I recommend avoiding close repeated defoliation especially if the species

is preferred by the grazers over other species.

Introduction

Herbivory has traditionally been considered as detrimental to plant growth, survival and fecundity, an assumption that has always been highly debated. According to Leriche et al. (2003) negative impacts of grazing on plant growth have often been reported especially in agricultural systems and some semi-arid and arid rangelands. However, Leriche et al. (2003) and de Mazancourt et al. (1998) note that many authors have suggested that herbivory can have a positive effect on plants and their productivity. Leriche et al. (2003) suggest that under moderate plant removal levels, net primary production (NPP) should be maintained (compensatory growth) or stimulated (overcompensatory growth).

Some plants can compensate, or even overcompensate (i.e. increased seed yield or vegetative productivity following natural or simulated grazing) for the loss of productivity caused by herbivory (Tuomi et al. 1994), which constitutes herbivory tolerance. This compensation may be achieved through mechanisms such as leaf replacement potential, compensatory photosynthesis, resource reallocation and activation of lateral meristems (Briske 1991, Tuomi et al. 1994). Trlica and Rittenhouse (1993) suggested that an individual plant might exhibit overcompensation for herbivory under most favorable environmental conditions, but under less-than-favorable conditions this same individual might exhibit either exact compensation or undercompensation. In a field study by Maschinski and Whitman (1989) using an herbaceous species, *Ipomopsis arizonica*, plants were subjected to varying levels of soil water and nutrient availability, interspecific competition and defoliation timing. Evidence for overcompensation (increased fruit set) occurred only when grazed plants were supplemented with nutrients and growing free of competition. However, defoliated plants grown in association with grasses or where nutrients were not supplemented exhibited undercompensation. Generally,

most of the studies reporting overcompensation have been carried out under controlled artificial environments and may not adequately represent field conditions such as interspecific competition and transient resource patterns (e.g. rainfall variability).

According to Trlica and Rittenhouse (1993) the three most important, manageable variables that influence plant response to grazing and degree of compensatory growth are (1) the timing of the grazing event in relation to the opportunity to grow or regrow, (2) the frequency of defoliation of an individual plant and its neighbors, and (3) the intensity of use (i.e., the level of defoliation). In addition to the above factors, Maschinski and Whitman (1989) add that the degree of compensatory regrowth is also influenced by water availability, nutrient availability, history of defoliation, and type and age of tissue eaten. Different plant species may respond differently to any combination of the above-mentioned factors, and a clear understanding of how these factors interact at species level is crucial for the proper management and sustainability of rangelands. For example, Mullahey et al. (1990) report a difference in response to defoliation timing between *Bouteloua gracilis* (blue grama) and *Pseudoroegneria spicata* subsp. *spicata* (bluebunch wheatgrass). Highest yield of blue grama resulted from clipping in June or July with earlier and later defoliations giving lower total yields, while defoliation at early growth stages of bluebunch wheatgrass was less damaging to forage production than clipping at mid-season. Differential response to a combination of clipping frequency and time interval between clippings has also been observed within species, for example Mullahey et al. (1990) report that clipping at 4-week intervals produced greater yields of 'Jose' tall wheatgrass (*Thinopyrum ponticum*) than clipping at 1- or 2-week intervals.

According to Owensby et al. (1974) heavy forage use (i.e. increased grazing intensity and frequency) may seem advisable in rangeland management programs in a given year. If temporary heavy use severely limits growth and vigor in following years, it may not be an advisable

management strategy (Owensby et al. 1974). Management must be based on the amount of

forage that can be removed without lessening plant vigor (Owensby et al. 1974). Generally,

reduced herbage yields have been reported with increased clipping frequency. According to

Mullahey et al. (1991) frequent defoliation of warm-season grasses severely reduced root

development, inhibited rhizome development, and reduced herbage yield compared to unclipped

plants.

Little bluestem is one of the dominant C4 warm-season grass species found in tallgrass

and mixed grass prairie, and although the species is usually considered less valuable for grazing

due to its tussock growth form and perceived lower forage quality, early regrowth especially in

annually burned prairie usually makes this grass palatable to the grazers. However, little is

known especially about the effects of clipping frequency on little bluestem. Plants do not always

respond linearly to environmental pressures (such as repeated defoliation) and therefore cannot

be predicted by studies considering only the lower end of possible intensities (Del-Val and

Crawley 2005). Understanding the effects of environmental pressures on plant fitness requires

the study of a broader range of intensities and consideration of possible response thresholds (Del-

Val and Crawley 2005). It is therefore essential to evaluate tolerance thresholds in response to

defoliation frequency for this species so as to establish an optimum management strategy for the

species in tallgrass prairie.

The objectives of this study therefore were to (1) assess the relationship between clipping

frequency and growth responses (compensatory regrowth and plant architecture) of little

bluestem in tallgrass prairie and (2) assess plant seed and vegetative reproduction and bud bank

population threshold responses to simulated overgrazing (more frequent clipping) in tallgrass

prairie. Plants allocate resources to various traits differentially depending on plant longevity

(annual or perennial), phenology and numerous abiotic (e.g. water stress, nutrient availability)

and biotic (e.g. interspecific competition) conditions. According to Gutman et al. (2001) the two dominant modes of partitioning are between root and shoot and between vegetative and reproductive structures. Grazing can influence both processes by affecting the demand for resources in either shoots or roots (sink strength) as well as the availability of meristems and their commitment to vegetative or reproductive growth (Gutman et al. 2001). I propose that differential allocation to different plant attributes in response to clipping frequency will result in a dissimilar pattern of response for all the measured growth responses. I therefore expect growth response patterns to conform to either one of the following three hypotheses:

> Hypothesis A – a linear decrease in plant performance with increasing defoliation frequency,
>
> Hypothesis B – a threshold response (non-linear decrease) with increasing defoliation frequency, and
>
> Hypothesis C – no effect on plant performance (e.g. high compensatory capacity) with increasing defoliation frequency.

Materials and Methods

This study was conducted on the Konza Prairie Biological Station (KPBS), a 3,487 ha native tallgrass prairie preserve located in the Flint Hills region of northeastern Kansas (39˚ 05´ N, 96˚ 35´ W). This preserve is owned by The Nature Conservancy and managed for ecological research and education by the Division of Biology, Kansas State University. The vegetation of KPBS is predominantly unplowed native tallgrass prairie, dominated by warm-season perennial C4 grasses including big bluestem (*Andropogon gerardii* Vitman), little bluestem (*Schizachyrium scoparium* (Michx.) Nash), switchgrass (*Panicum virgatum* L.), Indian grass (*Sorghastrum nutans* L.) and sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.).

Konza Prairie is divided into watersheds (mean size = 65 ha) subjected to prescribed fire at intervals from 1 to 20 years. Bison (*Bos bison*) were introduced onto Konza Prairie in 1987 and are free to move among ten watersheds that are burned annually or at 2-yr, 4-yr or 20-yr intervals. Each fire × grazing treatment is replicated two to four times at the watershed level. Replicated prescribed fire treatments were initiated in 1971 and grazing treatments in 1987. Average annual total precipitation is 835 mm with 75% falling during the growing season.

This study was carried out over two growing seasons (May 2005 – October 2006) in two ungrazed watersheds that are burned annually in spring (K1B and SpB), and it involved subjecting plants to varying frequencies of defoliation throughout the 2005 and early 2006 growing season and then measuring subsequent growth responses through the end of the 2006 growing season.

Species description

Little bluestem (*S. scoparium*) is a perennial bunchgrass widely distributed throughout the eastern two-thirds of the U.S. However, it is most abundant in the True Prairie Association of

the eastern Great Plains. The bunch or caespitose growth form originates from the intravaginal pattern of juvenile ramet development (new tillers arise from buds from inside the subtending leaf sheath) and complete absence of rhizomes and stolons. Genets are long lived, possess the C_4 photosynthetic pathway and reproductive ramets attain heights up to 1.5m (Williams and Briske 1991). In the Konza Prairie, juvenile ramets are recruited in the spring and autumn in undisturbed populations. Ramets in the spring cohort frequently complete their life in one growing season while ramets of the autumn cohort overwinter and complete their life during the subsequent season (Williams and Briske 1991).

Pre-clipping treatment (May 2005)

At each site, eighty genets (clumps) of little bluestem with different basal areas were randomly selected, flagged and tagged. Two basal diameter measurements were obtained from the wide and narrower sides of each genet, and basal areas were calculated using the formula for area of an ellipse

$$\text{Area} = \pi ab \quad (1)$$

where:

a is the major radius (semi-major axis) of the ellipse

b is the minor radius (semi-minor axis) of the ellipse

π is Pi, approximately 3.142

Clipping treatment (May 2005 – May 2006)

Eight genets were randomly assigned to each clipping treatment level of 0, 1, 2, 3, 4, 5, 6, 7, 8 and 9 clippings throughout the growing season. A total of seven clippings were carried out through the 2005 growing season (May -August) and the last one and two clippings for treatment levels 8 and 9 respectively were carried out in May 2006. Clipping treatments were carried out

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every two weeks (see Appendix A), and the plants were clipped to a residual height of 4 cm

(which according to Pfeifer and Hartnett (1995) is the level to which bison, the major ungulate

grazer grazes). The biomass offtake at each clipping interval was dried and weighed. Average

relative growth rate (RGR) of genets at the end of each clipping treatment was determined using

the formula

$$RGR(gg^{-1}d^{-1}) = \left[\ln \overline{(W_t + 1)} / (t_2 - t_1) \right] \qquad (2)$$

Where $\ln \overline{(W_t)}$ is the mean of the ln-transformed plant weights at time t.

The integer 1 was included in the calculations because some of the weight values were 0.

$t_2 - t_1$ represents the time since the last clip.

Post – clipping treatment (May 2006 – October 2006)

Basal areas for all the genets were re-measured at the beginning of the second growing

season (May 2006). Genet survivorship and new tiller emergence date were also assessed for all

genets. Total number of surviving tillers per genet at the end of the second growing season

(September 2006) was determined. Proportion of flowering tillers and vegetative tillers within

each genet was also determined. The entire aboveground biomass for each genet was harvested,

dried and weighed to determine total biomass production during the second growing season. The

entire remaining belowground biomass for each genet was excavated, excess soil was washed

from the roots and the plants' vegetative buds were analyzed. To determine average number of

belowground buds per tiller, ten tillers were randomly selected their total number of buds were

counted. Newly emerging tillers that were not counted during the tiller counts (usually < 2.5 cm

in length) were counted as buds. During the bud counts I noticed some differences in the position

and morphology of buds on the individual tillers (i.e. erect buds mostly occurring inside every

leaf sheath (intravaginal buds) or mostly stacked lower lying (curved) buds concentrated close to

the roots and covered by one or no leaf sheath (extravaginal buds)). Presence of extravaginal buds was therefore assessed for all the sampled tillers from each genet. A genet was regarded as having some extravaginal buds if more than one of the ten sampled tillers from each genet had some extravaginal buds.

Data analysis

One-way analysis of variance was used to test the effect of clipping treatment on average biomass per genet, average number of tillers per genet, tiller density (number of tillers per cm^2 of basal area), percent basal area change, end of treatment relative growth rate (RGR), flowering to vegetative tiller ratio and number of belowground buds per tiller. Significant differences among means were assessed using Fischer's protected LSD ($P<0.05$). Percent frequency of extravaginal buds for each treatment level was calculated using PROC FREQ (SAS program). Fisher's exact test was used to test if there is a difference between clipping treatment level and percent frequency of extravaginal buds.

Results

Pre-clipping treatment basal area (May 2005)

Average initial genet basal area for all the treatments was approximately 380 cm^2.

Genet survivorship and new tiller emergence date (April – May 2006)

The watersheds used in this study, K1B and SpB, received their prescribed annual spring burn on April 12 and April 27 2006 respectively. Genet survivorship and new tiller emergence date was assessed after the burn. Some new tiller emergence was observed in all genets in both watersheds about a week after the burn. None of the genets experienced complete mortality, but increasing defoliation frequency tended to result in lower tiller emergence rates. More frequently clipped genets tended to have most of their emerging tillers located towards the genet periphery and a large dead center (personal observation). On the other hand, tiller emergence was more uniformly distributed in less frequently clipped genets.

Post - clipping growth responses (May 2006 – October 2006)

Final biomass

There was a significant reduction (up to about 50% reduction between unclipped plants and genets clipped three times per season) in little bluestem genet growth (final end-of season standing crop aboveground biomass) with increasing frequency of defoliation ($P < 0.05$) (Figure 2.1). However, increasing frequency of defoliation beyond 3 clips (4 to 7 clips per season) caused no further decrease in biomass (Figure 2.1). The little effect of additional clipping is perhaps due to lower growth rates towards the latter half of the growing season which resulted in comparatively little additional tissue loss. Additional early season clips in the subsequent

growing season (8 to 9 clips) resulted in further significant ($P < 0.05$) reductions in genet

biomass (Figure 2.1). In sum, 3 clips in the first growing season resulted in an approximately

50% reduction in genet biomass, and additional clipping in the second growing season resulted

in another 50% reduction in genet biomass.

Number of tillers per genet

Tiller numbers per genet yielded a similar pattern to that observed for genet biomass

(about 50% reduction in tiller number due to repeated clipping during the first half of the first

season, and additional reductions in tiller number with additional clipping in the second season)

($P < 0.05$) (Figure 2.2). However, there was a slight increase in tiller number with 5, 6 or 7 clips

(Figure 2.2).

Tiller density

Parallel to the response shown in Figure 2.2, tiller density decreased with defoliation

frequency in a pattern similar to total tiller population size ($P < 0.05$) (Figure 2.3). However,

additional clippings in the second growing season did not result in a further decrease in tiller

density as observed in Figure 2.2 (Figure 2.3).

Basal area

Although plant biomass and total tiller numbers decreased markedly with increased

defoliation frequency, there was less change in genet basal area due to repeated defoliation in

this bunchgrass ($P = 0.08$) (Figure 2.4).

Relative growth rate

The final clips for the plants that were clipped 1 to 7 times occurred towards the end of

the first growing season (August 2005) while plants that were clipped 8 to 9 times received their

final clips early in the second growing season (May 2006). Relative growth rate following each clipping treatment decreased with increasing number of prior clips in a pattern similar to that observed for genet biomass and total tiller population size ($P < 0.05$) (Figure 2.5). Plants clipped early in the growing season through mid-growing season (3 to 4 previous clips) exhibited a significant reduction (about 50%) ($P < 0.05$) in relative growth rate following the clipping treatment compared with plants clipped only early in the growing season (1 to 2 previous clips) (Figure 2.5). Subsequent clipping through to the end of the growing season further decreased relative growth rate significantly by an additional 50% ($P < 0.05$) (Figure 2.5). Plant relative growth rate is usually quite high at the beginning of the growing season. However, genets that were clipped 8 to 9 times had the lowest relative growth rates (Figure 2.5), despite receiving their final clip early into the growth season, which shows that individual effects of repeated defoliation on growth rates are cumulative.

Proportion of flowering tillers

Unlike the pattern observed for genet biomass, total tiller numbers and relative growth rate (i.e. a marked reduction in response with clips incurred earlier in the growing season followed by little reduction in response with clips incurred later in the growing season) the proportion of tillers flowering decreased quite linearly with increasing defoliation frequency ($P < 0.05$) (Figure 2.6).

Belowground vegetative buds per tiller

Unlike the other measured growth responses that showed a decline with increasing defoliation frequency (Figure 2.1 to Figure 2.6), total number of belowground vegetative buds per tiller remained constant (albeit with smaller bud sizes) at an average of about six buds per tiller with increasing defoliation frequency ($P = 0.1407$) (Figure 2.7).

Belowground architecture

While defoliation frequency did not change number of belowground vegetative buds per tiller (Figure 2.7), increasing defoliation frequency changed belowground vegetative bud architecture. Repeated defoliation resulted in an increased incidence of more extravaginal versus intravaginal buds per genet ($P < 0.05$) (Figure 2.8).

Discussion

When growing under natural or full competitive conditions, little bluestem generally responded to repeated defoliation by exhibiting significant reductions in above-ground biomass accumulation, total tillers per genet, tiller density and proportion of tillers flowering. These responses were generally non-linear, with a large decrease with $1-3$ defoliations, no further change with $4-7$ defoliations, and then additional reduction in growth with additional defoliations the following season. In contrast to these non-linear growth responses, proportion of tillers flowering generally decreased linearly with increasing frequency of defoliation.

Plant relative growth rates decreased progressively with increasing clipping frequency during the first growing season, but additional clipping early in the second growing season caused no further effects.

Repeated defoliation did not affect new tiller emergence dates and overall genet survivorship per se, but increasing defoliation frequency tended to result in lower tiller emergence rates and increased tiller emergence towards the genet periphery and a large dead center. While defoliation frequency did not change number of belowground vegetative buds per tiller, increasing defoliation frequency changed belowground vegetative bud architecture by increasing incidence of more extravaginal versus intravaginal buds per genet.

In North American grasslands, overcompensation is a non-equilibrium plant response to grazing; photosynthate that would be stored as reserves and used for root growth and flower and seed production instead is used to replace lost leaf area (Turner et al. 1993). This, in addition to typically higher rates of photosynthesis in residual and regrowth tissue after defoliation, results in higher foliage productivity. Diverse effects of defoliation frequency on grass biomass production have been reported. Turner et al. (1993) investigated production of tallgrass prairie

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vegetation (grasses and forbs) under varying levels of defoliation intensity and frequency in a previously ungrazed prairie. Their results showed that mean (cumulative) grass above-ground biomass production on plots mowed 1, 3 and 6 times to ground level (for three consecutive years) was 19, 38 and 61% greater than on unmowed plots (at the end of the third year). Grasses therefore overcompensated for foliage removal, and aboveground production was maximized by the most frequent mowing treatment. Their study was carried out in large 10m × 5m plots and all plants within the plots were mowed, unlike my study in which only the experimental plants were clipped whereas neighboring plants were left intact. A three year field experiment by Mullahey et al. (1991) imposed up to three defoliations per season (i.e. June (vegetative stage), July (early elongation stage) and August (boot to early head stage)) on two Sandhill grasses, sand bluestem (*Andropogon gerardii* var. *paucipilus* (Nash) Fern.) and prairie sandreed (*Calamovilfa longifolia* (Hook.) Scribn.). Following the initial year of treatment, multiple defoliations increased dry matter (DM, biomass) yield of both grasses. After 3 years of repeated treatment, annual DM yield of sand bluestem for all defoliation treatments was lower than for the control. On the other hand, a June-August defoliation of prairie sandreed over a 3-year period increased annual DM yield compared to all treatments and the control. A similar study, still by Mullahey et al. (1990), this time on little bluestem (*Schizachyrium scoparium*), showed that multiple defoliations generally reduced biomass yield. My study also showed a decline (albeit non-linear) in little bluestem above-ground biomass accumulation in response to repeated defoliation. The small response to additional clipping during the latter half of the first growing season could be ensuing from lower growth rates towards the end of the growing season resulting in relatively little regrowth and hence little additional tissue loss, given that bison graze to a relatively constant residual height. Further decrease in biomass accumulation with subsequent clips early in the second growing season probably indicates that individual effects of repeated grazing on biomass

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accumulation in little bluestem are cumulative, and that grazing-induced reduction in storage of carbon and nutrient reserves in one season may reduce regrowth capacity in the next season.

Increased tillering has been described as one of the major responses aiding herbivory tolerance, especially in bunchgrasses. In the previously mentioned study by Mullahey et al. (1990), tiller numbers in defoliated little bluestem plants were similar to control plants in the first year of treatment, less than control plants in the second (comparatively drier) year, and higher (in single early defoliation) than control plants in the third year (which experienced above-normal precipitation). Another study by Brown and Stuth (1993) evaluating plant performance under three stocking rates (conservative, heavy and extreme) showed that when all the grazing treatments were pooled, little bluestem tiller recruitment declined approximately 50% over four years. The results of my study concurred with Brown and Stuth's (1993) observation, that is generally a decrease in tiller number per genet with repeated defoliation. However, I also observed an increase in tiller numbers per genet with subsequent clipping during the latter half of the first growing season. Perhaps early and late season clipping stimulated belowground bud activity and capacity for some compensatory increases in new tiller emergence in the following growing season. This mechanism is supported by the results of this study showing the maintenance of high bud bank densities under a range of clipping frequencies, and results of my previous study (Chapter 1) showing that regularly grazed populations of little bluestem maintain higher bud bank densities. Olson and Richards (1988) showed that grazing during culm elongation period (which is towards the end of the growing season) in *Agropyron desertorum* usually reduced tiller relative growth rates, but stimulated the growth of axillary tillers. The decline in tiller numbers per genet showed a similar non linear pattern to that observed for genet aboveground biomass. This may indicate that the primary cause for reduction in bunchgrasses

plant biomass (and NPP) due to grazing is demographic (reductions in tiller population density rather than reduction in individual tiller size).

Vinton and Hartnett (1992) reported that *Andropogon gerardii* tillers which had been grazed repeatedly the previous year had reduced relative growth rates, suggesting that (previous season) short-term increases in relative growth rates after defoliation had a cost on future plant growth and tiller survival. My study also shows that defoliation frequency history has a negative impact on plant growth, with relative growth rates following clipping treatments decreasing with increasing frequency of defoliation. Greatly reduced relative growth rates observed during subsequent clips early in the second season also corroborate Vinton and Hartnett's (1992) observation, and show cumulative effect of repeated defoliation on relative growth rate.

Butler and Briske (1988) reported that steer herbivory on little bluestem decreased individual plant basal area and increased total plant density by apparently fragmenting individual large plants into smaller units with reduced basal areas but greater tiller numbers per cm^2 of remaining basal area. Although herbivores have a great potential to influence bunchgrass basal area through their feeding habits and trampling, Butler and Briske (1988) purport that direct physical impact of livestock on individual bunchgrass genets was assumed to be minimal based on observation and the small number of marked tillers lost or removed by grazing. Severe drought has also been documented to induce fragmentation of bunchgrasses, and Butler and Briske (1988) report that the second year of their study received about 30% less rainfall compared to the long-term average, hence the observed decrease in little bluestem basal areas could have been exacerbated by the drought conditions. I noticed a little (a maximum of about -0.3%) mostly non-significant decrease in basal area with increasing defoliation frequency, and none of the clumps completely fragmented. This may be due to the short duration of my experiment (2 growing seasons) whereas the changes in genet structure are likely to occur over a

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longer time scale than individual growth responses. This may also be due to clipping not adequately representing grazing behavior of herbivores. Also most of my clippings were carried out during an above average (by about 7%) rainfall year, so environmental conditions were not conducive for bunch fragmentation. If these current climatic conditions persist it may probably take a long time to see significant shifts in population structure (i.e. size class distribution).

While Butler and Briske's (1988) study reported increase in tiller density even under severe defoliation (primarily due to the fragmentation of the clump), tiller density decreased with increasing defoliation frequency in my study. As bunchgrasses age and increase in size, initial tiller generations die and decompose within the clump resulting in formation of hollow crowns (i.e. dead center portion). According to Derner and Briske (2001), once this hollow crown is extended to the plant periphery, rapid fragmentation of plant occurs. A decrease in tiller density with increasing plant size in little bluestem has been observed by Derner and Briske (2001). Frequent defoliation seemed to increase the extent of hollow crowns and promoted peripheral new tiller emergence in my treatments (personal observation). The increase in the extent of hollow crowns (but never resulting in total plant fragmentation) was therefore the causal factor for the observed decrease in tiller density with increasing defoliation frequency. The similar pattern between defoliation frequency induced decreases in total tiller population size and tiller density is possibly an artifact of the occurrence and extent of hollow crowns. Butler and Briske (1988) also reported increased incidence of tiller recruitment on the plant periphery especially under sever defoliation, an observation that is supported by my study.

Butler and Briske's (1988) study reports that herbivory increased tiller mortality especially in the most severely grazed plants, but they do not report any entire plant mortality. Although increasing defoliation frequency seemed to result in lower new tiller emergence rates, complete plant mortality was also not observed in my study. Severe defoliation also did not

appear to delay new tiller emergence date in Butler and Briske's (1988) study, which was also corroborated by my study.

Total aboveground biomass, tiller population size per genet, tiller density and relative growth rate in little bluestem generally showed a similar pattern in response to defoliation frequency. These therefore appear to be inter-connected responses, collectively constituting the bulk of the vegetative aspect of the plants. These responses appear to be particularly sensitive to early season defoliation (which resulted in largest amounts of tissue removed) as shown by marked decreases in the response, but are much less affected by continued late season defoliations which resulted in less amount of tissue removed (e.g. no further decrease in biomass and tiller density, slight increase in tiller number per genet and a decrease in relative growth rate). All responses by and large showed a decrease with subsequent defoliations early in the second growing season, which shows a cumulative effect of defoliation (frequency) for all the responses.

Populations of grasses exposed to grazing by vertebrates often exhibit reduced flowering. This is often interpreted as an adaptive response that reduces grazing damage (i.e. flowering tillers are usually taller and may attract or be more accessible to herbivores) (Kotanen and Bergelson 2000), or it may be due to increased sink strength of vegetative parts in response to defoliation resulting in decreased allocation to flowering. A study by Seliskar (2003) showed that sexual reproduction responses in *Ammophila breviligulata* (American beachgrass) and *Spartina patens* (salt meadow hay) were especially sensitive to grazing by feral horses compared to stem growth and demography. Butler and Briske (1988) have also reported a decrease in the number of reproductive tillers in little bluestem in response to defoliation severity. I also observed a decrease in proportion of little bluestem tillers flowering with increasing frequency of defoliation. The linear pattern of decline may reflect the decreased allocation to flowering in

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favor of vegetative plant parts, and flowering in little bluestem seems to be cumulatively sensitive to any amount of tissue removal (i.e. late growing season defoliations which resulted in less tissue removed still caused reductions in proportion of tillers flowering).

In perennial-dominated savannas, grasslands and many other communities, plant densities and vegetation structure and dynamics may be regulated principally by patterns of vegetative reproduction and the demography of perennating organs, rather than by seed reproduction and seed banks (Hartnett et al. 2006). The belowground population of meristems associated with rhizomes or other perennating organs (the 'bud bank') can play a fundamental role in local plant population persistence and dynamics, vegetation structure and productivity, and the resilience of plant communities to factors such as drought, grazing pressure, or invasion of exotic plant species (Hartnett et al. 2006). Hartnett et al. (2006) further assert that recent studies of tallgrass prairies of the North American central grasslands indicate that regeneration and maintenance of perennial grass populations is regulated principally by vegetative reproduction and belowground bud bank dynamics. While proportion of flowering tillers (and consequently the seed bank) decreased under repeated defoliation as did plant growth and biomass, number of belowground vegetative buds per tiller in little bluestem was unaffected and remained constant even with repeated defoliation. In the first year of their three year study on defoliation effects on little bluestem production and morphological development, Mullahey et al. (1990) found that even though annual aboveground biomass yield from non-defoliated little bluestem plants was two times greater than that for all defoliated plants, bud numbers were similar between treatments. Mullahey et al. (1991) also observed similar bud numbers between controls and defoliated plants in *Andropogon gerardii* (sand bluestem) and *Calamovilfa longifolia* (prairie sandreed) following the initial year of treatment in a three year study. This maintenance of a large bud bank even under repeated defoliation may either show that this trait is

highly conservative or has a relatively low allocation cost. This maintenance of a large bud bank even under repeated defoliation may potentially confer high resilience and recovery rates following heavy grazing. This study only shows response to short term (mostly one growing season) frequent defoliation, and the response may not be the same under long-term frequent defoliation. Continued defoliation in ensuing years resulted in a decrease in bud numbers in both little bluestem (Mullahey et al. 1990) and sand bluestem and prairie sandreed (Mullahey et al. 1991). There is therefore need to assess the long-term effect of successive repeated defoliation on little bluestem in tallgrass prairie.

The bunchgrass growth form in little bluestem originates from intravaginal tiller development (emergence of juvenile ramets from buds within the subtending leaf blades and sheaths of parental ramets). While number of buds per tiller remained constant even under repeated defoliation, increasing frequency of defoliation seemed to change the belowground vegetative bud architecture of little bluestem. Repeated defoliation resulted in an increased incidence of more extravaginal (buds protruding laterally through the subtending leaf sheath) versus intravaginal buds per genet. Perennial bunchgrasses with marked tolerance to defoliation have been described as rapid tillering, prostate forms with short leaves (Carman 1985). The prostate form that has been observed in bunchgrasses with a history of defoliation could therefore be resulting from the shift in belowground bud architecture. Increased frequency of extravaginal buds in little bluestem will result in greater horizontal growth and less vertical growth, which will result in a greater proportion of tissue being inaccessible to herbivores. The shift from production of intravaginal buds to more extravaginal buds in little bluestem appears to be a plastic trait, as it was observed in such a short time of treatment.

In conclusion, repeated defoliation of little bluestem in tallgrass prairie resulted in decreases in aboveground biomass, total tiller population size, tiller density, relative growth rate

and proportion of flowering tillers. Aboveground biomass, total tiller population size, tiller density and relative growth rate seemed to be more sensitive to defoliations early in the growing season while all defoliations, irregardless of when they occurred in the growing season were detrimental to little bluestem flowering. Defoliation frequency caused only slight changes in genet basal area, and if prevalent climatic conditions persisted, it may take a longer time to see major shifts in population structure (i.e. size class distribution). Short-term frequent defoliation caused no change in new tiller emergence dates, number of belowground buds per tiller and did not cause genet mortality. However, increased defoliation frequency resulted in shifts in belowground bud architecture by increasing incidence of more extravaginal buds, a response leading to more decumbent growth. My results support my hypotheses that different little bluestem attributes are not affected similarly by repeated short-term defoliation. Data on proportion of flowering tillers (and to some extent percent basal area change) supports my first hypothesis of a linear decrease in plant performance with increasing frequency of defoliation. Findings with respect to average biomass, total tiller population size, tiller density and relative growth rate, on the other hand, support my second hypothesis of a threshold response (non-linear decrease) in plant performance with increasing frequency of defoliation. Finally, data on number of belowground buds per tiller supports my third hypothesis of no effect on plant performance (e.g. high compensatory capacity) with increasing defoliation frequency.

While little bluestem is unlikely to become locally extinct in this grassland (Konza Prairie), any herbivore selectivity on the species over other species in mixed stands would probably greatly reduce plant vigor, as all the traits I measured under full competition from neighbors mostly showed under-compensation and exact-compensation for all defoliation frequencies. Repeated defoliation seemed to exacerbate the species' inability to tolerate

herbivory. To insure persistence of the species in rangelands, I recommend avoiding close

repeated defoliation especially if the species is preferred by the grazers over other species.

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Figures and Tables
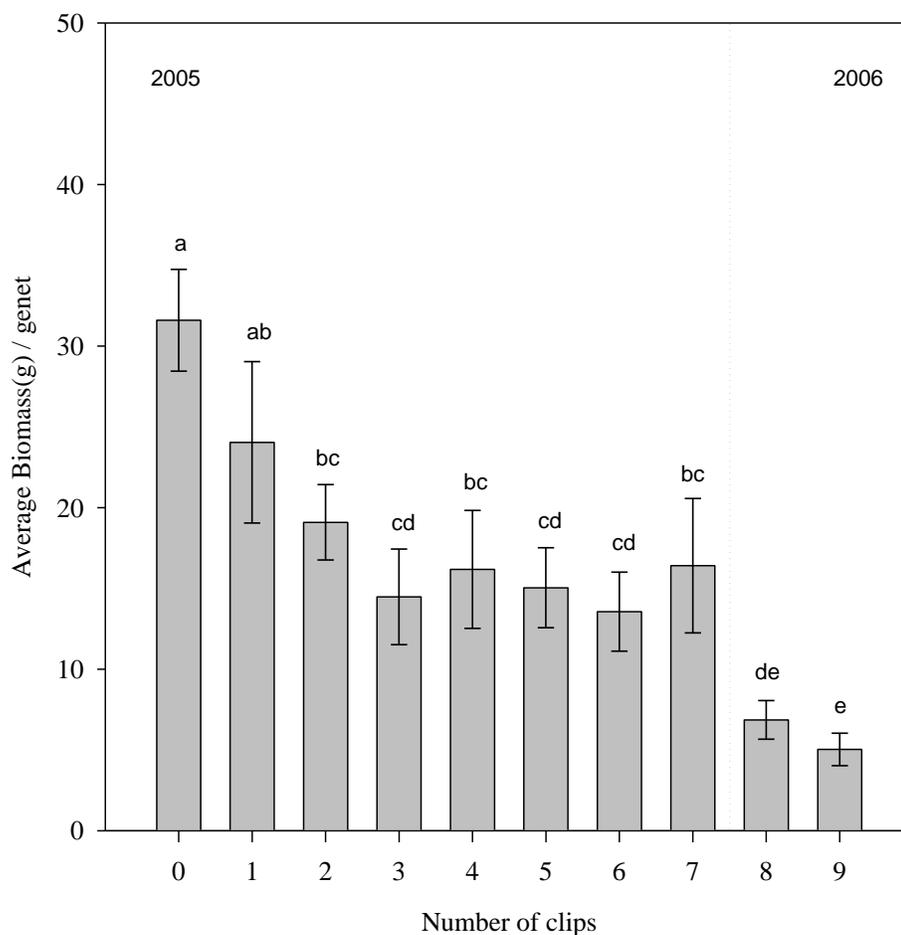
Figure 2.1 Effect of clipping frequency on average standing crop biomass per genet of little bluestem at the end of the second (2006) growing season after varying number of defoliations over the 2005 and early 2006 growing seasons. Error bars are ± 1 SE of the mean. Bars with the same letter are not significantly different ($P > 0.05$). Note: End of season biomass for the 8 and 9 clip treatments in 2006 is an underestimate of total production because it does not include 2006 offtake biomass.
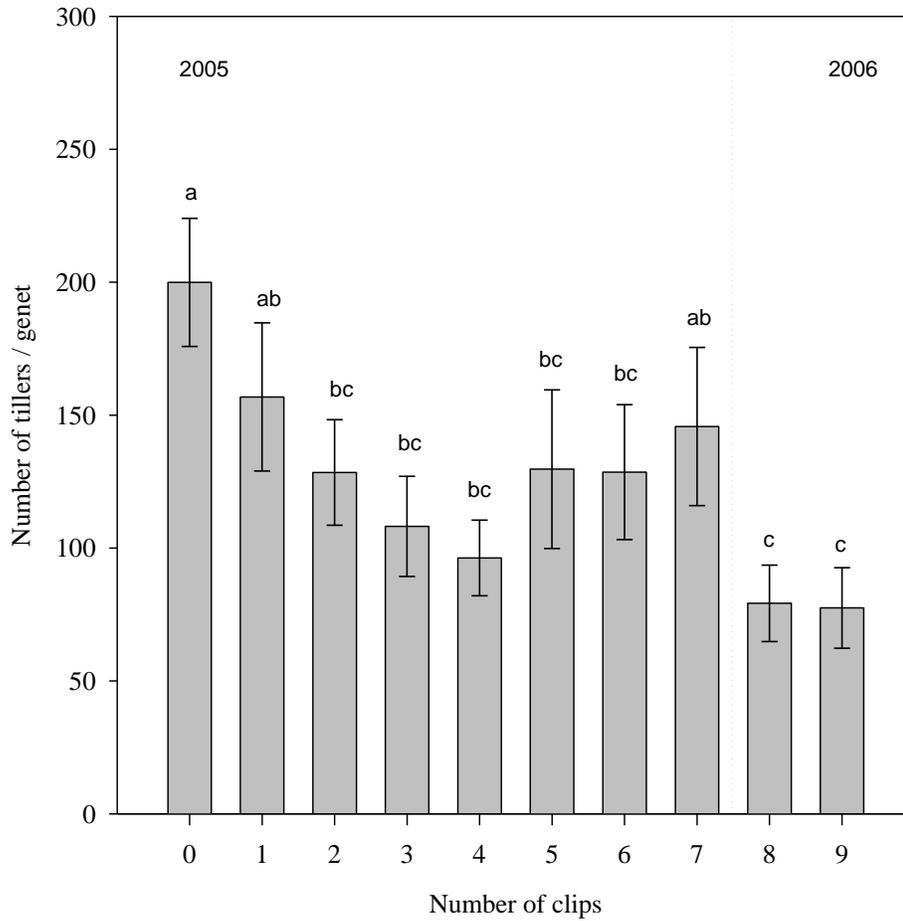
Figure 2.2 Effect of clipping frequency on total number of tillers per genet of little bluestem at the end of the second (2006) growing season. Error bars are ± 1 SE of the mean. Bars with the same letter are not significantly different (P > 0.05).
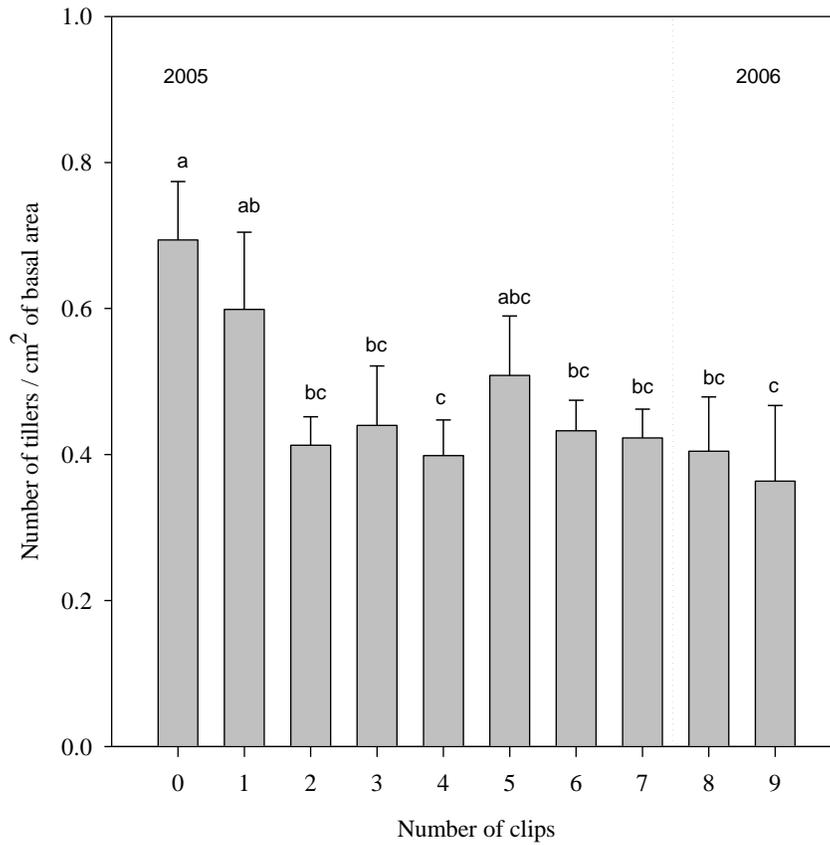
Figure 2.3 Effect of clipping frequency on tiller density of little bluestem at the end of the second (2006) growing season. Error bars are ± 1 SE of the mean. Bars with the same letter are not significantly different (P > 0.05).
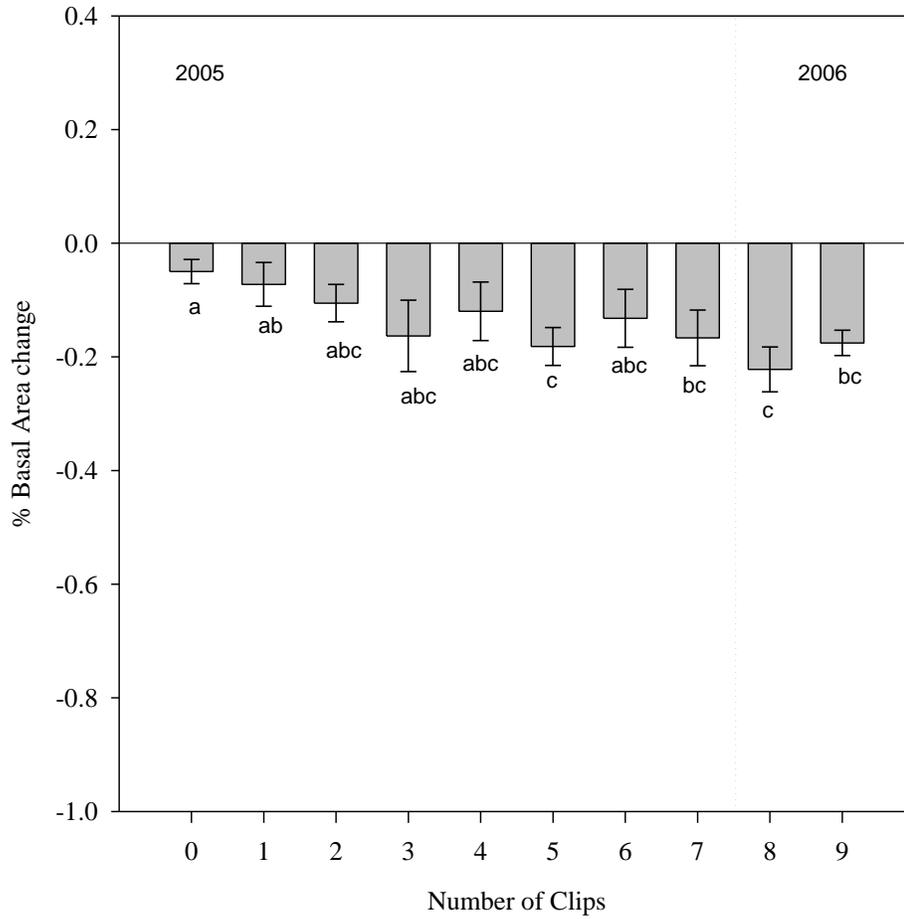
Figure 2.4 Effect of clipping frequency on percent basal area change per genet of little bluestem at the end of the second (2006) growing season. Error bars are ± 1 SE of the mean. Bars with the same letter are not significantly different (P > 0.05).
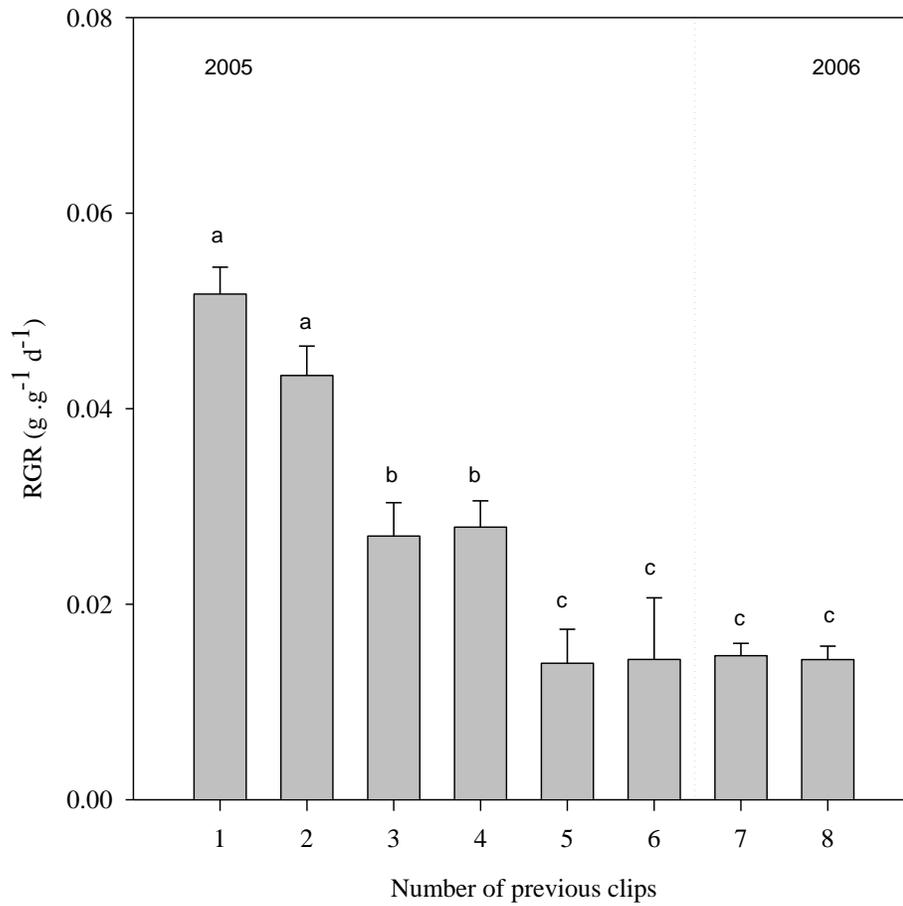
Figure 2.5 Effect of clipping frequency on relative growth rate of little bluestem. Error bars are ± 1 SE of the mean. Bars with the same letter are not significantly different (P > 0.05).
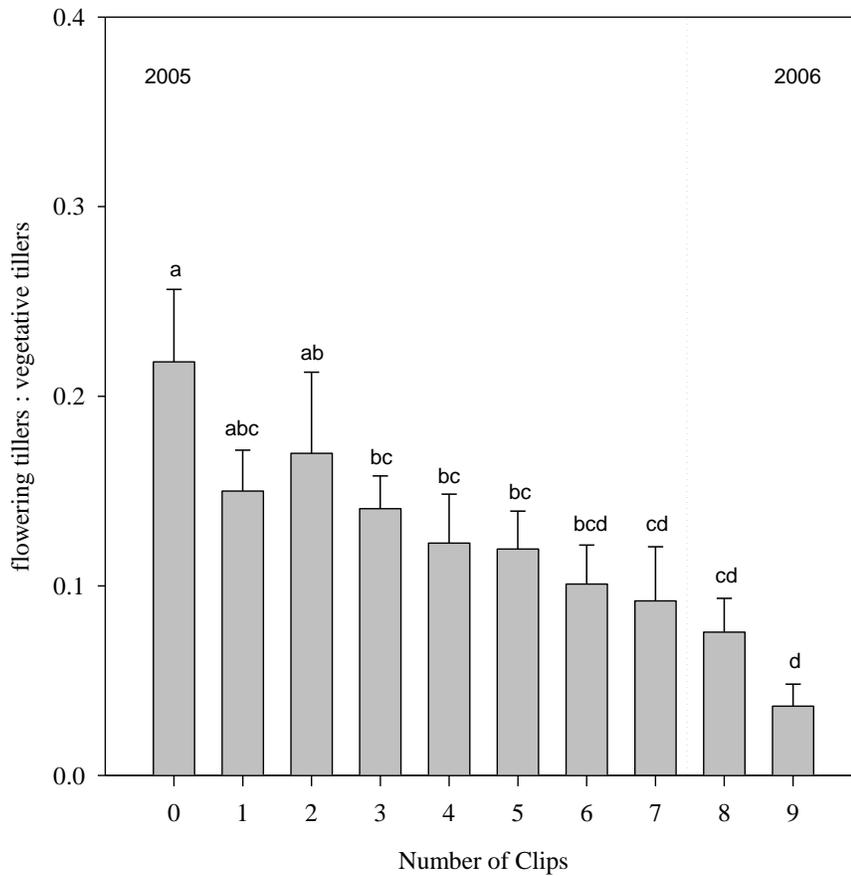
Figure 2.6 Effect of clipping frequency on flowering to vegetative tiller ratio of little bluestem at the end of the second (2006) growing season. Error bars are ± 1 SE of the mean. Bars with the same letter are not significantly different (P > 0.05).
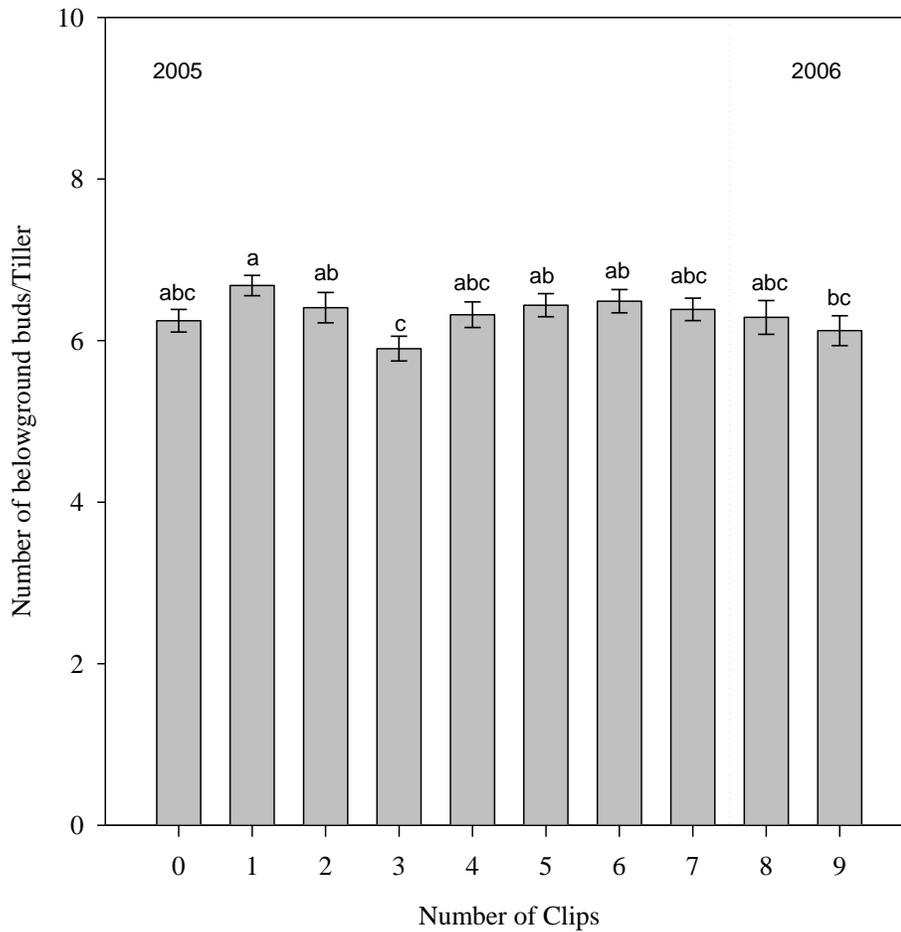
Figure 2.7 Effect of clipping frequency on number of belowground buds per tiller of little bluestem at the end of the second (2006) growing season. Error bars are ± 1 SE of the mean. Bars with the same letter are not significantly different (P > 0.05).

120

100

80

60

Percent frequency of extravaginal buds

40

20

0

2005

P-value = 1.637E-05

2006

0   1   2   3   4   5   6   7   8   9

Number of clips
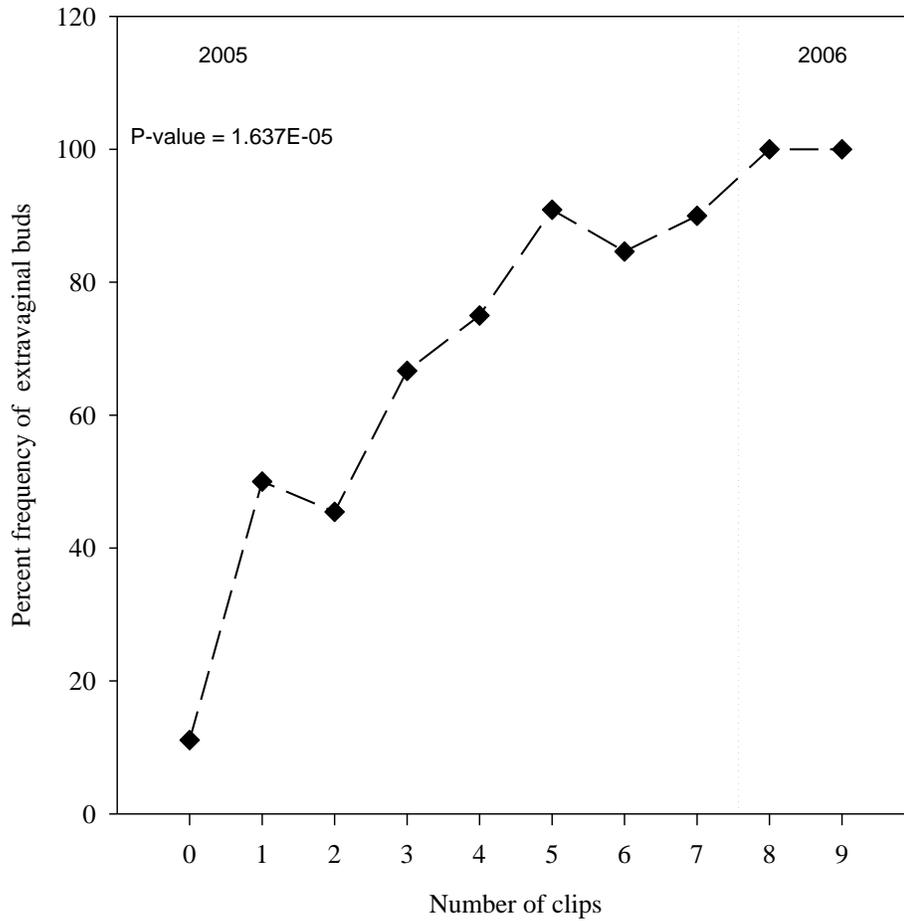
Figure 2.8 Effect of clipping frequency on presence of belowground extravaginal buds per genet of little bluestem at the end of the second (2006) growing season.

Appendix A - Dates for clipping treatments

Table A. 1 Clipping dates for Watershed K1B

# of clippings	5/19/05	6/1/05	6/15/05	6/29/05	7/13/05	7/27/05	8/10/05	5/24/06	6/7/06
0									
1			×						
2			×			×			
3		×		×			×		
4	×		×		×		×		
5		×	×	×	×	×			
6	×	×		×	×	×	×		
7	×	×	×	×	×	×	×		
8	×	×	×	×	×	×	×	×	
9	×	×	×	×	×	×	×	×	×

Table A. 2 Clipping Dates for Watershed SpB

# of clippings	5/19/05	6/1/05	6/15/05	6/29/05	7/13/05	7/27/05	8/10/05	5/31/06	6/14/06
0									
1			×						
2			×			×			
3		×		×			×		
4	×		×		×		×		
5		×	×	×	×	×			
6	×	×		×	×	×	×		
7	×	×	×	×	×	×	×		
8	×	×	×	×	×	×	×	×	
9	×	×	×	×	×	×	×	×	×