Differential responses to defoliation frequency in little bluestem (*Schizachyrium scoparium*) in tallgrass prairie: implications for herbivory tolerance and avoidance

Maipelo N'Guessan · David C. Hartnett

Abstract Plant responses to herbivory are complex. In grasses, relative growth rate (RGR), seed, and vegetative reproduction, resource allocation, and architecture vary differentially and often nonlinearly with grazing intensity. High grazing tolerance may be achieved through compensatory photosynthesis and leaf growth, or through demographic mechanisms such as activation of a belowground dormant bud bank. This study assessed the relationship between grazing frequency and responses of *Schizachyrium scoparium* (little bluestem) in a tallgrass prairie, and examined the roles of tiller growth, reproduction, and bud (meristem) populations in its persistence under grazing. Genets were subjected to varying simulated grazing frequencies for a period of 2 years. Strong differential responses were observed among plant traits. RGR, biomass, and flowering showed strong nonlinear reductions in response to increasing clipping frequency, with no evidence of threshold effects. However, meristem density was unaffected, and plants maintained a large bud bank across all clipping treatments. Tiller natality decreased initially, but increased with >4 clippings, suggesting that declines in tiller RGR are partially offset by increasing tiller natality, and that variation in genet size is driven more by demography than by variation in individual

tiller growth. Increased grazing frequency also resulted in differential activation of buds at different positions (emerging within vs. outside the subtending leaf sheath), explaining the shift to a more prostrate growth form observed in many caespitose grasses under persistent grazing. Thus, although this grass species lacks the capacity for compensatory foliage re-growth, the maintenance of a large dormant bud bank and the differential activation of buds in different positions contribute to its grazing tolerance and avoidance, respectively, and its long-term persistence in grazed grasslands.

Keywords Bud banks · Grasses · Grazing · Demography · Herbivory · Compensation

Introduction

The effects of herbivory on plant growth and reproduction are complex and not always directly proportional to the amount of plant tissue lost (de Mazancourt et al. 1998; Leriche et al. 2003). Plants may cope with tissue loss to defoliation, fire, or drought through physiological mechanisms such as compensatory photosynthesis, resource reallocation, activation of lateral meristems, or increases in whole plant light or water availability with partial canopy removal (Briske 1991; Tuomi et al. 1994). Although not as well studied, defoliation may also elicit

M. N'Guessan · D. C. Hartnett (✉)
Division of Biology, Kansas State University,
Manhattan, KS 66506, USA
e-mail: dchart@ksu.edu

changes in the demography of plant parts and plant architecture in ways that subsequently influence plant grazing tolerance and/or avoidance (Mullahey et al. 1991; N'Guessan 2007; Dalgleish and Hartnett 2009). Much recent research on plant–herbivore interactions has focused on the patterns, mechanisms, and trade-offs between herbivory tolerance and avoidance; and the effects of environmental factors, genetics, and phenotypic plasticity on the ability of plants to cope with herbivores (e.g., Maurico et al. 1997; Cingolini et al. 2005; Dannell et al. 2006; Rusch et al. 2009).

Variation in plant responses to herbivory is a result of the interacting influences of the type of plant parts removed (e.g., leaves, buds, and flowers), the timing, intensity, and frequency of defoliation, and the influences of plant density, neighborhood effects, and resource availability on the defoliated plant (Maschinski and Whitman 1989; Mullahey et al. 1990, 1991; Trlica and Rittenhouse 1993). Different species may respond differentially to these factors, and a clear understanding of how these factors interact at the species level is necessary for understanding effects of herbivory on plant populations and communities and for the conservation and sustainability of grazed or browsed ecosystems.

Despite the importance of variation in the intensity and frequency of defoliation, much of the ecological literature on grazing effects attempts to draw general conclusions based on simple binary comparisons of "grazed" and "ungrazed" treatments (e.g., Vinton and Hartnett 1992; Veen (Ciska) et al. 2008; Spasojevic et al. 2010), whereas range scientists have more closely examined effects of variation in the intensity and frequency of defoliation under varying grazing regimes (e.g., Dwyer et al. 1963; Gillen et al. 1990; Mullahey et al. 1990; Derner et al. 1994). In grazed ecosystems, variation in defoliation frequency experienced by a given forage species is associated with temporal variation in resource availability, local community composition, and/or variation in management such as animal stocking densities, grazing period, or grazing systems.

Grasslands globally are experiencing changing grazing regimes and pressure, along with altered precipitation patterns, increased drought frequency and intensity, and altered species composition (Fuhlendorf and Engle 2001; Sala 2001). A predictive understanding of effects of herbivory under these changing environmental conditions requires a sound mechanistic understanding of responses of grass plants and populations to variation in herbivory regimes.

Plants do not always respond linearly to environmental pressures such as defoliation frequency or intensity. Compensatory growth is often observed only under low to moderate grazing intensities, with large reductions in plant growth observed under intense defoliation regimes. A mechanistic understanding the effects of herbivory on different aspects of plant performance and these nonlinear threshold responses requires the study of a broader range of intensities (Del-Val and Crawley 2005).

Harper (1977) noted that "the effects of herbivory do not fall equally on all parts of the plant." Within a species, plant growth, root:shoot ratio, resource allocation, plant architecture, seed production, and vegetative reproduction may all respond differently to a given defoliation intensity. Differential effects of herbivores on seed reproduction and vegetative reproduction (tillering) via basal or below meristems (the bud bank) in grasses is particularly important because these two types of propagules vary in importance to grass population dynamics across grasslands. For example, in undisturbed tallgrass prairie, >99% of aboveground stems arise from buds rather than seeds (Benson et al. 2004; Benson and Hartnett 2006), and although establishment from seed is higher in disturbed micro sites, recruitment from the belowground bud bank still accounts for the majority of shoots re-colonizing disturbed patches (Rogers and Hartnett 2001). By contrast, recruitment from seed is much more important in semi-arid to arid grasslands, and in ecosystems dominated by annual grasses (Fair et al. 1999; Peters 2002). Thus, a reserve of propagules, in the form of a seed bank or bud bank may play an important role in the resilience of plant populations to variation in herbivory, and meristem limitation may be an important constraint on the capacity of grass populations to tolerate frequent defoliation or recover from over-grazing.

Plasticity in resource allocation and plant architecture also influence plant tolerance to herbivory. Grazing can alter allocation of resources between root and shoot and between vegetative and reproductive structures by affecting the demand for resources in each (sink strength) as well as the availability of meristems and their commitment to vegetative or

reproductive growth (Gutman et al. 2001). Persistent grazing influences grass canopy architecture by altering the demography of the bud bank or the spatial positions and fates of buds. Changes in the proportion of dormant buds in grasses making different developmental transitions (e.g., intravaginal tiller development, extravaginal tiller development, lateral elongation as a rhizome, sustained dormancy, or death) may be an important mechanism by which grazers alter canopy architecture and subsequent accessibility to grazers. Our recent studies (N'Guessan 2007; Dalgleish and Hartnett 2009) suggest that bud bank dynamics and plasticity in the activation and spatial distribution of dormant buds may be an important component of grazing tolerance and avoidance in perennial grasses.

The objective of this study was to assess the influence of defoliation frequency on different components of growth, reproduction, and architecture in *Schizachyrium scoparium* (Michx.) Nash (little bluestem) in tallgrass prairie. Our general hypothesis was that defoliation would result in differential responses of different plant traits. Little bluestem is a perennial caespitose species (bunchgrass) and one of the dominant C_4 grass species found in several grassland communities (tallgrass, mixed grass, sand, and hill prairies) throughout the Great Plains. It is grazed by large herbivores and is defoliated at varying frequencies (up to >6 defoliations per growing season) under varying livestock management regimes (Derner et al. 1994; Pfeiffer and Hartnett 1995).

We tested four specific hypotheses regarding relationships among defoliation frequency and genet (bunch) growth, flowering, and bud banks: (1) Genet relative growth rate (RGR) and biomass show a threshold response to increasing defoliation frequency. We predicted that compensatory tiller growth and/or increased tiller natality through release of apical dominance would result in no significant decreases in genet growth under infrequent defoliation but large declines in growth after a threshold number of cumulative defoliation events. (2) Flowering will decrease more rapidly than vegetative growth with increasing defoliation frequency. (3) Belowground bud density (buds/tiller) will be the least sensitive to increasing defoliation frequency. (4) Increasing defoliation frequency will result in a shift in relative activation of dormant buds in different positions.

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, switchgrass (*Panicum virgatum* L.), Indian grass (*Sorghastrum nutans* L.) and sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.). Average annual total precipitation is 835 mm with 75% falling during the growing season.

KPBS is divided into 60 watershed units (mean size = 65 ha), each subjected to prescribed fire at intervals from 1 to 20 years, and one of three grazing treatments (grazed by bison, cattle, or ungrazed) (Knapp et al. 1998). 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 (by clipping to a constant residual height) throughout the 2005 and early 2006 growing season, simulating the range of defoliation frequencies experienced by plants under natural or managed conditions, and then measuring subsequent growth and reproductive responses through the end of the 2006 growing season.

Species description

Little bluestem is widely distributed throughout the eastern two thirds of the USA. 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 the absence of rhizomes or stolons, resulting in a genet composed of a densely packed clump of tillers. Genets are long lived, possess the C_4 photosynthetic pathway, and reproductive ramets attain heights up to 1.5 m (Williams and Briske 1991). At the Konza Prairie, juvenile ramets are recruited in the spring and autumn in undisturbed populations. A cohort of

ramets arising from vegetative buds in the spring frequently complete their life in one growing season while ramets of the autumn cohort during winter and complete their life during the subsequent season (Williams and Briske 1991).

Pre-clipping measurements

At each site, 80 genets of little bluestem varying in basal area were randomly selected, flagged and tagged in May 2005 and their basal areas were measured. Two perpendicular 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.

Clipping treatments

Eight genets were randomly assigned to each defoliation treatment level of 0, 1, 2, 3, 4, 5, 6, 7, 8, or 9 repeated clippings. A total of seven clippings were carried out through the 2005 growing season (May–August). Clipping treatments were carried out every 2 weeks. The single defoliation plants were clipped on June 15, the plants receiving two defoliations were clipped on June 15 and July 27, and the plants receiving three defoliations were clipped on June 1, June 29, and 10 August. Each of the other treatments (4–7 defoliations) was similarly clipped at regular intervals through August 10, and plants defoliated eight or nine times received additional clippings on May 24 and June 7, 2006. At each defoliation, the plants were clipped to a constant residual height of 4 cm, to closely simulate the residual height to which bisons defoliate plants as they graze (Pfeiffer and Hartnett 1995). Previous studies on Konza Prairie have shown that these grazing simulations (clipping) that match the residual height of plants grazed naturally by bisons result in the same plant growth responses as naturally grazed plants (Vinton and Hartnett 1992). In addition, the growth and tillering responses to 2–3 clippings measured in this study are within very similar ranges to the responses of little bluestem to similar frequencies of natural bison grazing recorded in previous Konza Prairie studies (Pfeiffer and Hartnett 1995). Thus, our clipping treatments represent a very good simulation of natural grazing patterns.

The biomass off-take at each clipping event was dried and weighed. Average RGR of genets at the end of each clipping treatment was determined using the formula.

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

where $\ln\left(\overline{W_t}\right)$ 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 clipping event.

Post-clipping response measurements

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 dates were also recorded 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, soil was washed from the roots, and basal vegetative buds were counted. To determine the average number of belowground buds per tiller, 10 tillers were randomly selected, and their total number of buds was counted. Newly emerging tillers that were not counted during the tiller counts (usually <2.5 cm in length) were counted as buds. Differences in the positions and morphologies of buds on the individual tillers were noted (i.e., erect buds mostly occurring intravaginally inside every leaf sheath or mostly stacked lower lying extravaginal buds concentrated close to the roots and covered by one or no leaf sheath). Frequency of extravaginal buds was 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 change in genet basal area, RGR, flowering to vegetative tiller ratio, and number of belowground buds per tiller. Data on percent change in genet basal area, although not bounded, did not meet normality criteria and were arcsine transformed before analysis. Significant differences among means were assessed using Fischer's protected LSD ($P < 0.05$). Activation of buds in different position was measured as the percent frequency of extravaginal buds, and was examined using PROC FREQ (SAS program), and Fisher's exact test was used to test for differences between clipping treatment levels.

Results

Pre-clipping treatment basal area

The average initial genet basal area for all the treatments was approximately 380 cm^2, and there were no differences in the mean initial (pre-treatment) genet basal areas among treatments.

Genet survivorship and new tiller emergence date

The watersheds used in this study, K1B and SpB, were subjected to their prescribed annual spring fires on April 12 and April 27, 2006, respectively. Genet survivorship and new tiller emergence date were recorded after the burn. A few new tiller emergences were 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 toward the genet periphery and had a large dead center (personal observation). By contrast, tiller emergence was more uniformly distributed in less frequently clipped genets.

Post-clipping growth responses

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 genet biomass) with increasing frequency of defoliation up to three clips (Fig. 1;
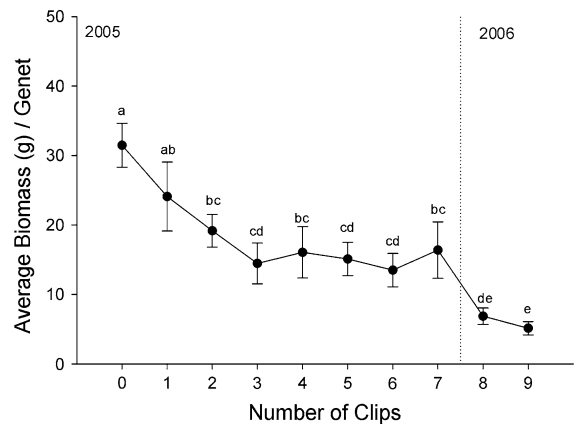

Fig. 1 Effect of clipping frequency on average genet biomass in little bluestem at the end of the second (2006) growing season after varying number of defoliations over the 2005 and early 2006 growing seasons. *Error bars* are ± 1 SE of the mean. Means with the same letter are not significantly different at the $P = 0.05$ level. Note: End of season biomass for the eight and nine clip treatments in 2006 is an underestimate of total production because it does not include 2006 off-take biomass. *Years* indicate when clippings occurred, not the time of biomass measurement

Table 1). However, increasing frequency of defoliation beyond three clips (4–7 clips per season) caused no further decrease in biomass (Fig. 1). The minimal effect of additional clipping is perhaps due to inherently lower growth rates toward the latter half of the growing season which resulted in comparatively little additional tissue loss. Additional clips in the beginning of the subsequent growing season (8–9 clips) resulted in further significant ($P < 0.05$) reductions in genet biomass (Fig. 1). In sum, three clips early in the first growing season resulted in an approximately 50% reduction in genet biomass, and additional clipping early in the second growing season resulted in an additional 50% reduction in genet biomass.

Tiller numbers per genet yielded a similar pattern to that observed for genet biomass. There was a 48% reduction in tiller number due to initial clippings during the first half of the first season (Fig. 2), a response very similar to the 45% reduction in little bluestem numbers recorded on Konza Prairie in response to natural bison grazing (Pfeiffer and Hartnett 1995). Although the trends in tiller numbers (Fig. 2) suggest a slight increase in tiller number with 5–7 clips, these were not significantly different from the treatments with 1–4 clips. Parallel to the response

Table 1 Results of analysis of variance in plant growth, tillering, reproduction, and bud banks in response to defoliation frequency in little bluestem

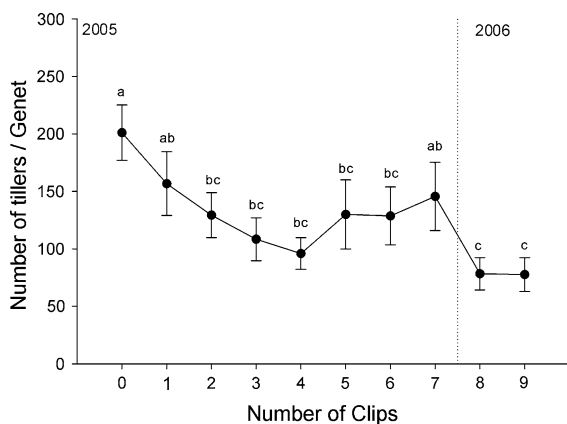| Variable	Model df	Error df	F	P
Genet biomass	9	129	7.01	<0.0001
Tillers genet^{-1}	9	129	2.77	0.0054
% change in basal area	9	141	1.85	0.06
RGR	7	116	17.22	<0.0001
Flow. tillers: Veg. tillers	9	128	3.76	0.0003
Buds tiller^{-1}	9	131	1.54	0.1407
	df		X^2	P
Frequency of extravaginal tillers	9		35.35	<0.0001

Fig. 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. Means with the same letter are not significantly different at the $P = 0.05$ level

Fig. 3 Effect of clipping frequency on percent basal area change in little bluestem genets at the end of the second (2006) growing season. *Error bars* are ±1 SE of the mean. Means with the same letter are not significantly different at the $P = 0.05$ level

shown in Fig. 2, tiller density within genets (tillers per cm^2 basal area) decreased with defoliation frequency in a pattern similar to total tiller number per genet ($P < 0.05$), data not shown. However, additional clippings in the second growing season resulted in a further reduction in number of tillers per genet ($P < 0.05$, Fig. 2), but did not result in a further significant decrease in tiller density.

Although plant biomass and total tiller numbers decreased markedly with increased defoliation frequency, there was only a marginally significant trend of decreasing genet basal area due to repeated defoliation in this bunchgrass ($P = 0.06$) (Fig. 3; Table 1). All treatments, including unclipped controls, showed less than a 1% change in basal area between years.

The final clips in 2005 occurred toward the end of the first growing season (August), while plants that
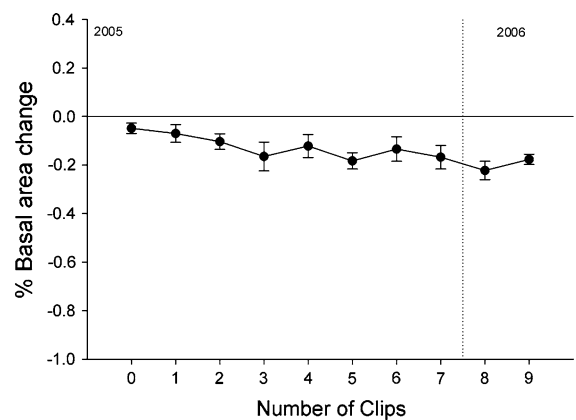
were clipped 8–9 times received their final clips early in the second growing season (May 2006). Relative growth rate measured over the 2-week interval following each clipping treatment decreased with increasing number of prior clips in a strongly nonlinear pattern similar to that observed for genet biomass and total tiller population size ($P < 0.05$) (Fig. 4). Each increase in number of clips from one up to six times during the growing resulted in significant steep reductions in RGR, but additional clipping in the range of 7–9 times (6–8 prior clips) caused no further change in RGR (Fig. 4). Plant relative growth rate is usually quite high at the beginning of the growing season. However, genets that were clipped 8–9 times had the lowest RGR (Fig. 4), despite receiving their final clips early in the 2006 growing season, indicating that individual effects of repeated defoliation on growth rates are cumulative.
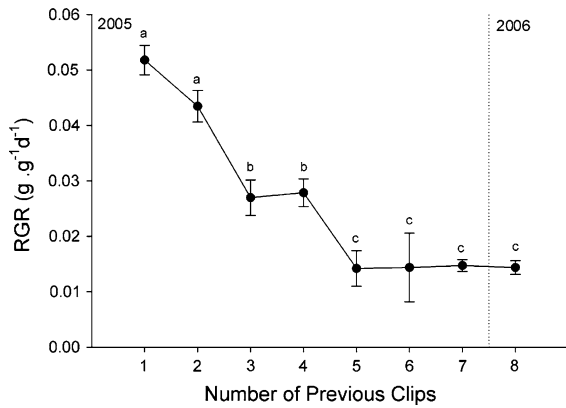
Fig. 4 Effect of clipping frequency on relative growth rate (RGR) of little bluestem. RGR measured over the 2-week interval after clipping. Number of clips refers to the number of prior clips experienced before the measurement interval. *Error bars* are ±1 SE of the mean. Means with the same letter are not significantly different at the $P = 0.05$ level

Fig. 6 Effect of clipping frequency on number of belowground buds per tiller in little bluestem at the end of the second (2006) growing season. *Error bars* are ±1 SE of the mean. Means with the same letter are not significantly different at the $P = 0.05$ level

In unclipped control genets, about 20% of the mature tillers flowered and 80% were vegetative (Fig. 5). Clipping significantly reduced the proportion of tillers flowering (Table 1). However, unlike the nonlinear pattern observed for genet biomass, total tiller numbers, and relative growth rate, the proportion of tillers flowering decreased quite linearly with increasing defoliation frequency ($P < 0.05$) (Fig. 5), and showed no leveling off as observed for the growth responses.
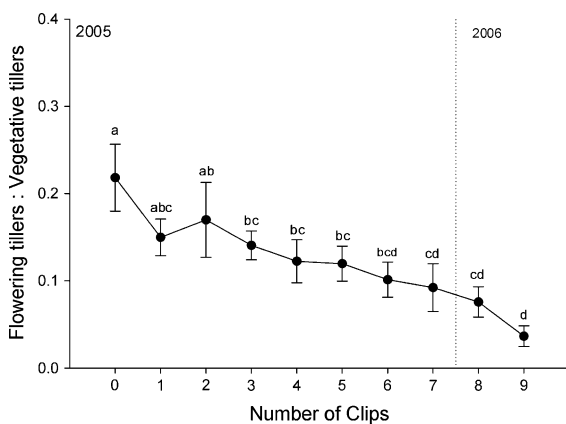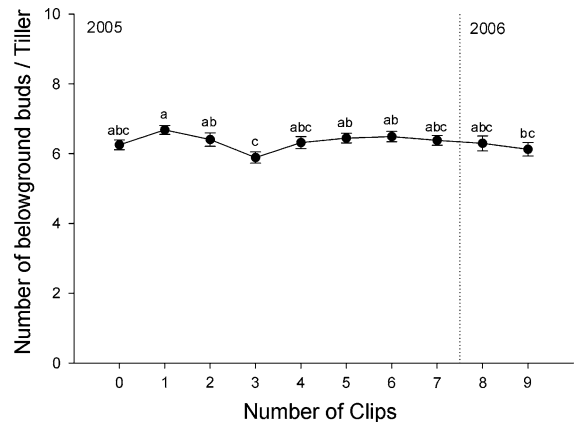

Fig. 5 Effect of clipping frequency on the ratio of flowering tillers to vegetative tillers in little bluestem at the end of the second (2006) growing season. *Error bars* are ±1 SE of the mean. Means with the same letter are not significantly different at the $P = 0.05$ level

Unlike the various measured growth responses or flowering, which showed significant declines with increasing defoliation frequency (biomass, tillering, RGR, etc,), total number of belowground buds per tiller remained remarkably constant across all defoliation frequency treatments ($P = 0.14$, Fig. 6; Table 1). Plants defoliated up to nine times maintained the same number of buds (approximately 6 buds per tiller) as undefoliated controls. However, while defoliation frequency did not affect the number of belowground vegetative buds per tiller, it did significantly alter canopy architecture by greatly increasing the proportion of extravaginal buds relative to intravaginal buds. Undefoliated plants had only 10% of their buds in the extravaginal position whereas tillers clipped eight or nine times produced 100% of their buds in the extravaginal position, resulting in a more laterally branching rather than erect growth form among frequently grazed genets (Fig. 7).

Discussion

Little bluestem relative growth rates and total plant biomass showed similar nonlinear reductions in response to increasing clipping frequency. Plant relative growth rate was progressively and significantly reduced with 1–3 clippings, but then leveled off with no further growth reductions with 4–9

Fig. 7 Effect of clipping frequency on the relative proportion of extravaginal buds in little bluestem at the end of the second (2006) growing season

clippings. With three or more clippings during the 2005 growing season, plant RGR and total biomass was reduced to about one half that of unclipped plants. This was opposite our hypothesized prediction of little to no reductions in growth under infrequent clipping but large reductions in growth after a threshold defoliation intensity is reached, the typical response of plants that exhibit high grazing tolerance through compensatory growth. When defoliation frequency was increased from seven clippings during 2005 to include two additional clippings in early 2006, RGR continued to remain unchanged at about 50% of ungrazed controls, but total plant biomass showed a further reduction. This further reduction in total plant biomass was due to a further reduction in number of tillers per plant with the additional defoliation in 2006. The number of tiller per genet showed a very similar pattern across clipping frequencies to that observed for genet aboveground biomass. This suggests that the primary mechanism responsible for the reduction in total genet biomass (and NPP) due to grazing is demographic (reductions in tiller population density rather than reduction in individual tiller size).

In North American grasslands, grazing compensation is a nonequilibrium plant response involving mechanisms such as re-allocation of stored reserves to replace lost leaf area (Turner et al. 1993), increased tillering through release of apical dominance, and/or higher rates of photosynthesis in residual and/or re-growth tissue after defoliation. Diverse effects of defoliation frequency on grass

biomass production have been reported. Turner et al. (1993) reported overcompensation in tallgrass prairie vegetation subjected to repeated mowing. Mullahey et al. (1991) similarly reported increased biomass in sand bluestem (*Andropogon hallii* Hack.) and prairie sandreed (*Calamovilfa longifolia* (Hook.) Scribn.) in response to multiple defoliations, but reduced biomass after 3 years of repeated treatment. By contrast, Mullahey et al. (1990) showed reduced biomass yield in little bluestem with multiple defoliations, consistent with the plant (genet) responses found in our study.

The leveling off of RGR and final plant biomass with additional clippings during the latter half of the first growing season (4–7 clippings) is likely due to generally lower inherent growth rates toward the end of the growing season resulting in relatively little re-growth and hence relatively little additional tissue removal with these additional clipping, given that large grazers (e.g., bison or cattle) graze to a relatively constant residual height. This response could also be partially due to some compensatory growth response toward the end of the summer, when clipped plants with less transpiring leaf area may experience less drought stress.

Given the large reductions in relative growth rate and plant biomass with just a few clippings, how does little bluestem persist under repeated grazing? Our results suggest that other mechanisms contribute the persistence of little bluestem under a range of grazing intensities. First, plants maintain a large bud bank (>6 buds per tiller) across a wide range of clipping frequencies. Remarkably, the number of buds per tiller in plants clipped up to nine times was the same as that of unclipped controls. In a parallel field study at KPBS, N'Guessan (2007) showed that little bluestem populations in watersheds grazed by bison maintain consistently higher overall bud bank densities than populations in ungrazed watersheds. The maintenance of a dormant bud bank is important in many perennial-dominated grasslands where plant densities and vegetation structure and dynamics are 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 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 or grazing pressure (Hartnett et al. 2006). This maintenance of a large bud bank even under repeated defoliation shows that this trait is highly conservative. This suggest that the fitness benefits of the maintenance of a large dormant bud bank are large relative to its costs, which likely include significant opportunity costs (reduction in potential genet growth and fecundity by maintaining bud dormancy) as well as small carbon allocation costs (Vesk and Westoby 2004). Tuomi et al. (1994) suggested that repeated long-term defoliation may select for restrained bud activation (maintenance of a large number of buds in a dormant condition), enabling grasses to recover from higher levels of damage than would be possible with high activation sensitivity and small bud bank size.

Mullahey et al. (1991) also observed similar bud numbers between un-defoliated controls and defoliated plants in sand bluestem and prairie sandreed. However in these two rhizomatous grasses, continued defoliation in ensuing years resulted in a decrease in bud numbers (Mullahey et al. 1991). Persistent grazing for many years and compensatory new tiller production may gradually deplete the bud bank, particularly in rhizomatous grasses, reducing a species' future capacity for recovery.

Second, little bluestem-tillering responses to defoliation showed that the number of tillers per genet decreased by more than 50% with 1–4 clippings during 2005, but showed no further decrease with additional clippings (up to 7). This relationship between number of tillers per genet and clipping frequency suggests that, with a relatively intense defoliation regime during 2005 (5–7 clippings), declines in RGR of extant tillers may be partially offset by maintaining high tiller natality. Olson and Richards (1988) similarly showed that late grazing (during the culm elongation period) in crested wheatgrass *Agropyron desertorum* (Fisch. ex Link) Schult usually reduced tiller relative growth rates, but stimulated the production of axillary tillers. This and other studies (e.g., Mullahey et al. 1990) suggest that increased tillering is one of the major responses conferring resilience to herbivory, especially in bunchgrasses or other species that lack compensatory photosynthesis and compensatory increases in growth rates of residual or re-growth foliage. Brown and Stuth (1993), however, reported that, after 4 years of grazing, little bluestem tiller recruitment declined

approximately 50%, suggesting that tillering, like the maintenance of bud banks, may be limited in its capacity to sustain populations under persistent grazing for many years.

Third, while number of buds per tiller remained constant even under repeated defoliation, bud position changed significantly. Specifically, the proportion of extravaginal buds/tillers increased significantly and the proportion of intravaginal buds/tillers decreased with increasing defoliation frequency. This resulted in a strong shift in growth form from fewer tall and erect tillers (emergence of intravaginal tillers from buds within the subtending leaf blades and sheaths of parental ramets) to many horizontal extravaginal tillers (arising from buds protruding laterally through the subtending leaf sheath) and a more spreading, prostrate growth form. The increased natality of tillers arising from extravaginal buds in little bluestem results in greater horizontal growth and less vertical growth, which results in a greater proportion of tissue being inaccessible to herbivores, contributing to grazing "avoidance." Although this relative shift in canopy architecture from a more erect to a more prostrate growth form has been observed in other grass species, the underlying mechanism (differential activation of intravaginal versus extravaginal buds) has not previously been demonstrated. This differential activation of buds in little bluestem appears to be a plastic trait, as it was observed over the short time scale of treatment.

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 simply be a consequence of decreased carbon or other resources available and increased sink strength of vegetative parts in response to defoliation resulting in decreased allocation to flowering. Seliskar (2003) showed that sexual reproduction responses in *Ammophila breviligulata* Fern. (American beachgrass) and *Spartina patens* (Aiton) Muhl. (salt meadow hay) were especially sensitive to grazing 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. We also observed a decrease in proportion of little bluestem tillers flowering with

increasing frequency of defoliation. The linear pattern of this decline suggests decreased allocation to flowering in favor of vegetative plant parts, and flowering in little bluestem seems to be cumulatively sensitive to any amount of tissue removal. Late growing season defoliations that resulted in less tissue removed still caused similar reductions in the proportion of tillers flowering. Thus, the nonlinear growth rate and plant biomass responses may be a function of the timing as well as the frequency of defoliation. Early season defoliation during the period of rapid tiller growth results in large reductions in plant growth, but later season defoliations are at the expense of flowering rather than growth. In grass species of arid, semi-arid, or disturbed habitats that depend strongly on seeds rather than buds for population maintenance, a grazing regime that significantly enhances vegetative tillering and reduces seed reproduction consistently over many years may ultimately result in seed limitation and long term consequences for the maintenance of genetic diversity and their ability to adapt to longer-term environmental changes.

In conclusion, little bluestem shows nonlinear responses to increasing defoliation frequency and differential responses among traits, such as tiller growth, demography, seed reproduction, and bud bank size, as defoliation frequency increases. The persistence of little bluestem under frequent defoliation is explained principally by the demographic response of plant parts rather than by the physiological and growth responses of individual tillers. Although little bluestem shows no evidence of compensatory tiller growth in response to defoliation, alternative mechanisms for coping with herbivory allow populations to persist in regularly grazed communities. These responses include the maintenance of a large reserve population of buds or meristems for recovery, maintenance of high tiller natality rates, and a shift in bud position resulting in a shift in canopy architecture from tall, erect, and reproductive tillers to many lateral extravaginal tillers that both compensate for tissue loss at the genet level and reduce the accessibility of re-growth tissue to grazing animals. Thus, management or environmental changes that alter the timing or frequency of defoliation in this grass species may have long-term consequences for its population structure, dynamics and genetic diversity.

Reference

Benson E, Hartnett DC (2006) The role of seed and vegetative reproduction in plant recruitment and demography in tallgrass prairie. Plant Ecol 187:163–177

Benson E, Hartnett DC, Mann K (2004) Belowground bud banks and meristem limitation in tallgrass prairie plant populations. Am J Bot 91:416–421

Briske DD (1991) Developmental morphology and physiology of grasses. In: Heitschmidt RK, Stuth JW (eds) Grazing management: an ecological perspective. Timber Press, Portland, pp 85–108

Brown JR, Stuth JW (1993) How herbivory affects grazing tolerant and sensitive grasses in a central Texas grassland: integrating plant response across hierarchical levels. Oikos 67:291–298

Butler JL, Briske DD (1988) Population structure and tiller demography of the bunchgrass *Schizachyrium scoparium* in response to herbivory. Oikos 51:306–312

Cingolini AM, Posse G, Collantes MB (2005) Plant functional traits, herbivore selectivity and response to sheep grazing in Patagonian steppe grasslands. J Appl Ecol 42:50–59

Dalgleish HJ, Hartnett DC (2009) The effects of fire frequency and grazing on tallgrass prairie plant composition and productivity are mediated through bud bank demography. Plant Ecol 201:411–420

Dannell K, Bergstrom R, Duncan P, Pastor J (2006) Large herbivore ecology, ecosystem dynamics and conservation. Cambridge University Press, Cambridge, p 522

de Mazancourt C, Loreau M, Abbadie L (1998) Grazing optimization and nutrient cycling: when do herbivores enhance plant production? Ecology 79:2242–2252

Del-Val E, Crawley MJ (2005) Are grazing increaser species better tolerators than decreasers? an experimental assessment of defoliation tolerance in eight British grassland species. J Ecol 93:1005–1016

Derner JD, Gillen RL, McCollum FT, Tate KW (1994) Little bluestem tiller defoliation patterns under continuous and rotational grazing. J Range Manag 47:220–225

Dwyer DD, Elder WC, Single G (1963) Effects of height and frequency of clipping on pure stands of range grasses in north central Oklahoma, Oklahoma Agric Exp Bull 614

Fair J, Lauenroth WK, Coffin D (1999) Demography of *Bouteloua gracilis* in a mixed prairie: analysis of genets and individuals. J Ecol 87:233–243

Fuhlendorf SD, Engle DM (2001) Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. Bioscience 51:625–632

Gillen RL, McCollum FT, Brummer JE (1990) Tiller defoliation patterns under short duration grazing in tallgrass prairie. J Range Manag 43:95–99

Gutman M, Noy-Meir I, Pluda D, Seligman NA, Rothman S, Sternberg M (2001) Biomass partitioning following

defoliation of annual and perennial Mediterranean grasses. Conserv Ecol 5:1: http://www.consecol.org/Journal/vol5/iss2/art1

Harper JL (1977) Population biology of plants. Academic Press, London, p 892

Hartnett DC, Setshogo MP, Dalgleish HJ (2006) Bud banks of perennial savanna grasses in Botswana. Afr J Ecol 44:256–263

Knapp AK, Briggs J, Hartnett DC, Collins SL (eds) (1998) Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, New York, p 336

Kotanen PM, Bergelson J (2000) Effects of simulated grazing on different genotypes of *Bouteloua gracilis*: how important is morphology? Oecologia 123:66–74

Leriche H, Le Roux X, Desnoyers F, Simioni G, Abbadie L (2003) Grass response to clipping in an African savanna: testing the grazing optimization hypothesis. Ecol Appl 13:1346–1354

Maschinski J, Whitman TG (1989) The continuum of plant responses to herbivory: the influence of plant association, nutrient availability and timing. Am Nat 134:1–19

Maurico R, Rausher MD, Burdick DS (1997) Variation in the defense strategies of plants: are resistance and tolerance mutually exclusive? Ecology 78:1301–1311

Mullahey JJ, Waller SS, Moser LE (1990) Defoliation effects on production and morphological development of little bluestem. J Range Manag 43:497–500

Mullahey JJ, Waller SS, Moser LE (1991) Defoliation effects on yield and bud and tiller numbers of two sand hills grasses. J Range Manag 44:241–245

N'Guessan M (2007) Effects of grazing on growth and morphology of rhizomatous and caespitose grasses. Thesis, Kansas State University

Olson BE, Richards JH (1988) Tussock regrowth after grazing: intercalary meristem and bud activity of tillers of *Agropyron desertorum*. Oikos 51:374–382

Peters DPC (2002) Recruitment potential of two perennial grasses with different growth forms at a semiarid-arid transition zone. Am J Bot 89:1616–1623

Pfeiffer KE, Hartnett DC (1995) Bison selectivity and grazing responses of little bluestem in tallgrass prairie. J Range Manag 48:26–31

Rogers W, Hartnett DC (2001) Temporal vegetation dynamics and recolonization mechanisms on different-sized soil disturbances in tallgrass prairie. Am J Bot 88:1634–1642

Rusch GM, Skarpe C, Halley DJ (2009) Plant traits link hypothesis about resource-use and response to herbivory. Basic Appl Ecol 10:466–474

Sala OE (2001) Temperate grasslands. In: Chapin FS III, Sala OE, Huber-Sannwald E (eds) Global biodiversity in a changing environment. Scenarios for the 21st century, ecological studies 152. Springer, New York

Seliskar DM (2003) The response of *Ammophila breviligulata* and *Spartina patens* (Poaceae) to grazing by feral horses on a dynamic mid-Atlantic barrier island. Am J Bot 90:1038–1044

Spasojevic MJ, Aicher RJ, Koch GR, Marquardt ES, Mirotchnick N, Troxler TG, Collins SL (2010) Fire and grazing in a mesic tallgrass prairie: impacts on plant species and functional traits. Ecology 91:1651–1659

Trlica MJ, Rittenhouse LR (1993) Grazing and plant performance. Ecol Appl 3:21–23

Tuomi J, Nilsson P, Astrom M (1994) Plant compensatory responses: bud dormancy as an adaptation to herbivory. Ecology 75:1429–1436

Turner CL, Seastedt TR, Dyer MI (1993) Maximization of aboveground grassland production: the role of defoliation frequency, intensity, and history. Ecol Appl 3:175–186

Veen (Ciska) GF, Blair JM, Smith MD, Collins SL (2008) Influence of grazing and fire frequency on small-scale plant community structure and resource variability in native tallgrass prairie. Oikos 117:859–866

Vesk PA, Westoby M (2004) Funding the bud bank: a review of the cost of buds. Oikos 106:200–208

Vinton MA, Hartnett DC (1992) Effects of bison grazing on *Andropogon gerardii* and *Panicum virgatum* in burned and unburned tallgrass prairie. Oecologia 90:374–382

Williams DG, Briske DD (1991) Size and ecological significance of the physiological individual in the bunchgrass *Schizachyrium scoparium*. Oikos 62:41–47