

Pattern of interspecific tiller defoliation in a mixed-grass prairie grazed by cattle

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Abstract

Permanently marked tillers of five perennial grasses, native to the mixed-grass prairie of North America, were monitored to determine patterns of defoliation, architectural attributes influencing probabilities of defoliation, and post-defoliation responses. Frequency of tiller defoliation was greatest for one of the dominant midgrasses, intermediate for the remaining midgrass and two dominant shortgrasses, and least for the subdominant midgrass. Midgrass species, including the infrequently grazed subordinate species, were consistently grazed more intensively than the shortgrass species. However, the relative intensity of defoliation did not vary among species or grazing periods indicating that intensity of defoliation was primarily a function of pre-defoliation tiller height. Tiller architecture, including height, lamina number and the presence of reproductive culms, did not significantly influence frequency or intensity of defoliation within a species. The lack of evidence supporting tiller architecture as a selection criterion within a species suggests that animals were selecting on vegetation parameters at higher levels of vegetation organization than individual tillers. Grazed tillers of the three midgrasses exhibited greater relative rates of tiller elongation between grazing periods than non-grazed tillers, particularly early in the season when environmental

conditions for growth were most favourable. The patterns of interspecific tiller defoliation observed in this study parallel the long-term patterns of grazing-induced species replacement observed in this grassland.

Introduction

The main aim of most grazing management strategies is to provide agriculturalists and resource managers with the ability to regulate the severity (frequency + intensity) of plant defoliation. Severe grazing ensures the efficient harvest of available forage, but may eventually decrease primary production by minimizing the subsequent capture of photosynthetically active radiation (Parsons *et al.*, 1983; Akiyama *et al.*, 1984). Alternatively, lenient grazing maximizes primary production, but a large percentage of the available forage is incorporated into detritus without being ingested by herbivores. Investigations of patterns of tiller defoliation can provide additional information for devising and evaluating grazing management strategies. Several important concepts have been verified with this research approach including: (i) identification of the relationship between defoliation severity and forage availability (Hodgson, 1966; Morris, 1969; Hart and Balla, 1982; Curll and Wilkins, 1982; Briske and Stuth, 1982), (ii) the relative relationship between defoliation frequency and intensity (Gammon and Roberts, 1978b; Clark *et al.*, 1984), and (iii) the importance of tiller architecture i.e., height, total lamina length and location in the canopy, in determining defoliation probabilities (Greenwood and Arnold, 1968; Hodgson and Ollerenshaw, 1969; Barthram and Grant, 1984). There have been suggestions that various attributes of sward architecture may be better indicators of forage availability to grazing herbivores pressure or

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herbage allowance (Allden and Whittaker, 1970; Chacon and Stobbs, 1976).

These concepts appear to be as equally applicable to multispecies communities as they are to single species swards in which they were initially derived (Gammon and Roberts, 1978a, b, c). However, additional complexity is associated with multispecies systems because of interspecific variation in abundance, patterns of distribution, periods of growth and maturation, and plant architecture. Gammon and Roberts (1978a) indicated that no single architectural attribute was sufficient to explain the patterns of tiller defoliation within *Hyperthelia*, *Sporobolus*, and *Themeda* dominated velds. Although percentage or frequency of tiller defoliation provided a good indication of animal preference, it was inconsistent among species and seasons.

The objectives of this investigation were: (i) to quantify the frequency and intensity of tiller defoliation, (ii) to identify pre-defoliation architectural attributes influencing defoliation patterns, and (iii) to assess post-defoliation growth responses of five perennial grasses native to the southern mixed-grass prairie of North America. Species were selected for investigation based on their relative preference, as demonstrated by cattle, and their abundance within the community.

Materials and methods

The study site was located on the Texas Experimental Ranch located in Throckmorton County, Texas, USA (99°14'W, 33°20'N). Climate is semi-arid continental with an average annual precipitation of 682 mm, which is bimodally distributed in the spring (May 95 mm) and autumn (September 118 mm). Mean daily temperatures range from -2 °C in January to 36 °C in July. Precipitation and temperatures throughout the study approximated to the long-term norms. Soils are predominantly deep well-drained clays and clay loams.

Vegetation is a diverse mixed-grass prairie dominated by perennial grasses. Dominant species include: sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.: BOCU), a warm-season, rhizomatous midgrass; Texas wintergrass (*Stipa leucotricha* Trin. & Rupr.: STLE), a cool-season caespitose midgrass; buffalograss (*Buchloe dactyloides* (Nutt.) Engelm.: BUDA);

and common curlymesquite (*Hilaria berlandieri* (Steud.) Nash: HIBE), warm-season, stoloniferous shortgrasses. Red threeawn (*Aristida longiseta* Steud.: ARLO) is a subdominant caespitose warm-season midgrass. BOCU, STLE, BUDA and HIBE are seasonally preferred forages, whereas ARLO is a non-preferred species. For a more detailed description of the climate, soils and vegetation of the study site, see Heitschmidt *et al.* (1985).

Grazing treatment

Research was conducted in one 4 ha pasture of a ten-pasture, one-herd rotational grazing system set-stocked with Hereford/Angus yearling heifers (mean initial weight 259 kg) at a rate of 0.24 ha AUM⁻¹. Length of the grazing period in the study pasture ranged from 2 to 4 days. Grazing periods (G) occurred on: 19–21 April (G1), 28–30 May (G2), 2–4 July (G3) and 7–10 August (G4). The study area had been grazed in the past by cattle at a moderate intensity. For a detailed analysis of the effects of the treatment on herbage dynamics, forage quality, and livestock performance, see Heitschmidt *et al.* (1982a, b, c).

Sampling procedures

Individual tillers of the five perennial grasses were permanently marked at the beginning of the study with small coloured-wire rings placed on the soil surface around the base of each tiller. Tillers were located within twenty 0.1 × 10 m belt transects within a 1 ha area of the pasture. Transects were subjectively located by dominance within a patch (four transects per patch), because the five species typically occur as a mosaic of small patches. However, tillers of all species were marked in all transects with the number of marked tillers per species varying in relation to species composition. Total numbers of tillers initially marked were 122, 169, 113, 106 and 46 BOCU, STLE, BUDA, HIBE and ARLO, respectively. At the end of the investigation 49, 36, 34 and 36% of the initially marked tillers, respectively, remained.

Phenological stage of development (vegetative or reproductive), tiller length (length of longest extended phytomer) and number of live and dead laminae were recorded for each tiller before and after each grazing period.

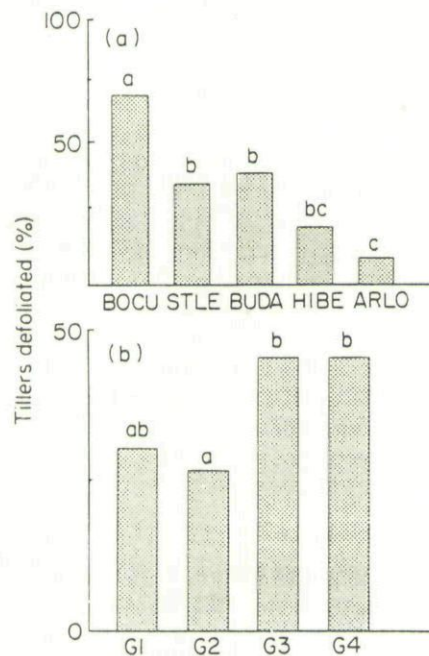


Figure 1. Mean percentage of tillers defoliated by (a) species averaged for all four grazing periods (G) and by (b) grazing period averaged for all five species. Histograms superscripted by same letter were not significantly different at $P < 0.05$. The species \times grazing period interaction was not significant.

(see Figure 5 for sampling dates). Grazed laminae were marked at the tip with non-toxic nail polish, prior to each grazing period, to facilitate the identification of subsequent grazing events. Marking in this manner does not appreciably influence animal selectivity (Gammon and Roberts, 1978a; Briske and Stuth, 1982).

Data handling and statistical analyses

A forward accounting procedure was used to summarize all tiller data to ensure that tillers lost between two sample dates, by ring displacement, livestock trampling, or tiller mortality, did not bias mean values. For example, mean values for sample date t were based only on tillers present on sampling date $t+1$. Frequency of defoliation was determined by identifying whether or not a tiller had been grazed in each of the four grazing periods. Intensity of defoliation and tiller extension were determined by subtraction of mean values before and after each grazing period. Relative values for defoliation intensity and tiller

extension were calculated by dividing the absolute differences by the respective initial values on an individual tiller basis.

Data were summarized by species in two ways: within all twenty transects (total sample population) and within only those transects dominated by a particular species. Variables subjected to analyses were: (i) percentage of tillers defoliated, (ii) frequency and intensity of tiller defoliation, and (iii) absolute and relative changes in tiller length, number of dead and live laminae, total number of laminae (live and dead) and live:dead lamina ratio within and among grazing periods (G1, G2, G3, G4). Absolute and relative changes in grazed tillers over time (i.e., during or between grazing periods) were adjusted relative to ungrazed tillers during the comparable time period.

Within-species data summaries (i.e., total sample population) were statistically analysed using paired t -tests. Within-transect summaries were statistically analysed using repeated measures least-squares analysis of variance. Main effects were defoliation (grazed or ungrazed), species and date. The error term for testing defoliation, species and the defoliation \times species interaction was species within transect. The residual mean square was used to test for date, defoliation \times date, species \times date, and defoliation \times species \times date interactions. Tukey's Q -mean separation test was used to separate means when analysis of variance revealed significant ($P < 0.05$) treatment effects. Chi-square procedures were used to determine the effect of phenological status on tiller defoliation.

Interpretive conclusions derived from the two analyses were then examined to ensure that within-transect sample size did not restrict or alter conclusions. Only minor statistical differences were detected between the two analyses; consequently only results from the within-transects analyses are presented unless otherwise noted (see Figure 5).

Results

Frequency of defoliation

Mean percentage of tillers grazed during the four grazing periods varied among species and grazing events (Figure 1). The largest percentage of grazed tillers occurred in BOCU (70%), the

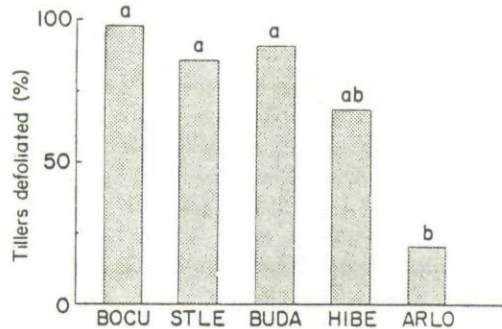


Figure 2. Percentage of tillers grazed at least once during the four grazing periods within the study. Histograms superscripted by same letter were not significantly different at $P < 0.05$.

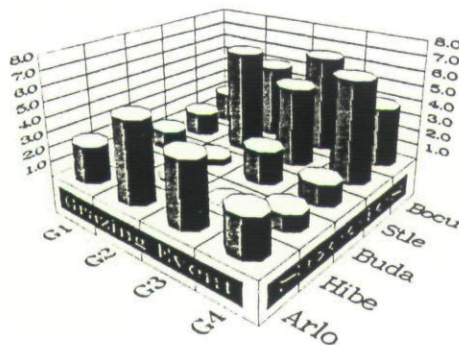


Figure 3. Percentage of tillers grazed 0, 1, 2, 3 or 4 times at the conclusion of four grazing periods within the study. Tukey Q_5 value for significant ($P = 0.05$) species \times grazing frequency interaction was 30.6%.

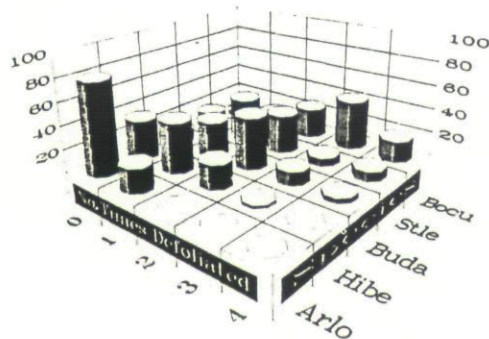


Figure 4. Absolute intensity of tiller defoliation (cm) for five species and four grazing periods. Tukey Q_4 value for significant ($P = 0.05$) species \times grazing periods interaction was 3.07 cm. Tukey Q_5 value for interaction effect was 3.27 cm.

lowest percentage in ARLO (20%), with the three remaining species showing intermediate values. The percentage of tillers defoliated, averaged for all five species, increased from approximately 30% during the first two grazing

periods to 45% in the two final grazing periods. The species \times grazing period interaction was not significant ($P < 0.05$).

Percentage of tillers grazed at least once during the investigation exceeded 85% for BOCU, STLE and BUDA, approached 70% for HIBE, but did not exceed 25% for ARLO (Figure 2). Frequency of tiller defoliation displayed a similar pattern among species with an appreciable percentage (5 to 40%) of BOCU, STLE and BUDA tillers grazed three or four times (Figure 3). No ARLO tillers were grazed more than once during the investigation. Tillers of BOCU, STLE, BUDA, HIBE and ARLO were grazed a mean of 2.6, 1.6, 1.7, 0.9 and 0.2 times, respectively, during the study.

Intensity of defoliation

Intensity of tiller defoliation varied among species and grazing period (Figures 4 and 5). A significant species \times grazing period interaction showed intensity of defoliation was greater for midgrasses than shortgrasses within successive grazing periods. A mean increment of 4.3, 5.0, 1.3, 0.2 and 3.6 cm was removed from BOCU, STLE, BUDA, HIBE and ARLO tillers, respectively, when averaged across all four grazing periods. Defoliation intensity was least during the first grazing period (1.8 cm), but increased to comparable values for the remaining three grazing periods (3.5, 3.2 and 3.1 cm for G2, G3 and G4, respectively). There were no differences among either species or grazing periods when defoliation intensities were expressed on a relative rather than an absolute basis. Mean relative grazing intensity averaged for species and grazing periods was 29%.

Number of live, dead and total (live + dead) laminae defoliated varied significantly among both species and grazing period ($P < 0.05$). Differences among species and dates in number of laminae per tiller prior to grazing appeared to be the primary source of variation. For example, total laminae number per tiller prior to defoliation (t) averaged 4.7, 3.4, 5.2, 4.6 and 3.8 for BOCU, STLE, BUDA, HIBE and ARLO, respectively (Figure 5). Total number of laminae defoliated (t + l) was 2.6, 1.7, 2.2, 1.8 and 1.2, which represented 56, 50, 41, 40 and 31% of the total number of laminae per tiller. The percentage of total laminae defoliated per

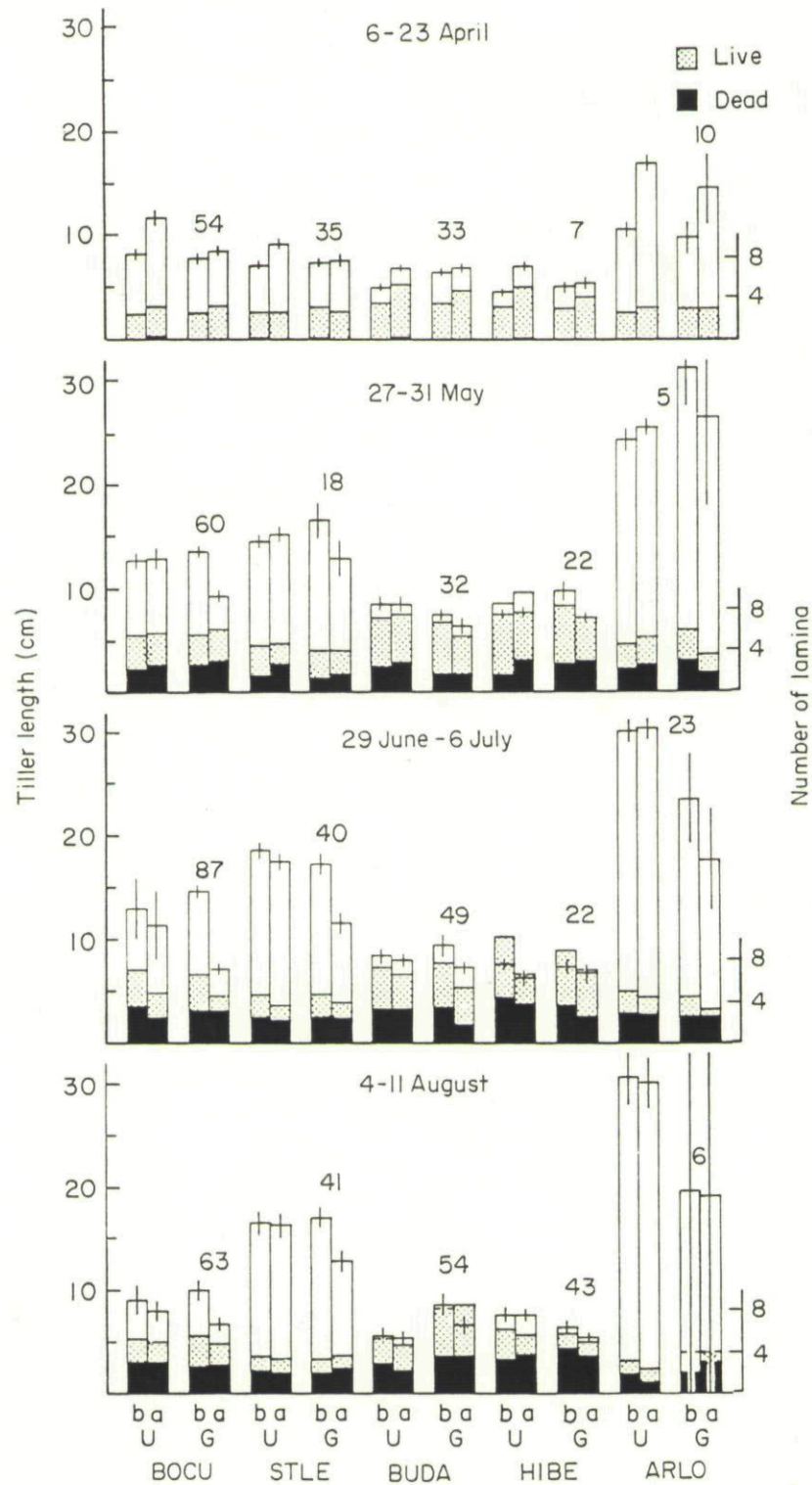


Figure 5. Tiller length (cm) and number of live, dead and total lamina per tiller for both grazed (G) and ungrazed (U) tillers of five species before (b) and after (a) each of four grazing periods. Vertical lines depict 1 SE of means. Numbers above grazed tiller histograms represent the percentage of total population defoliated.

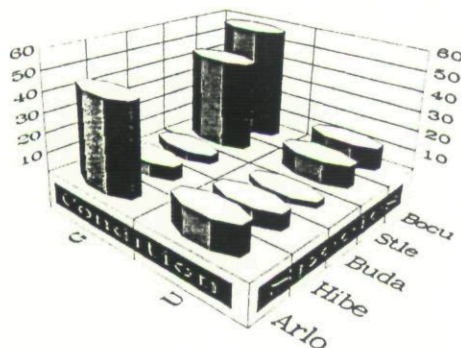


Figure 6. Relative change (%) in tiller length for grazed and ungrazed tillers of five species averaged for all three rest periods. Tukey Q_2 value for significant ($P=0.05$) species \times defoliation interaction was 22.6%. Tukey Q_3 value for interaction was 37.3%.

tiller paralleled trends established by the percentage of tillers defoliated by species (Figure 1a). Defoliation intensity was not evaluated on an individual lamina basis.

Tiller architecture \times defoliation interaction

The mid-grass species, STLE, ARLO and to a lesser extent BOCU, displayed the greatest tiller lengths both prior to and following grazing, as anticipated (Figure 5). Averaged across species, the mean number of laminae per tiller ranged from a minimum of 2.9 in April to a maximum of 6.7 in August. The greatest number of live laminae were present in the May and July grazing periods, with the number of dead laminae increasing as the season progressed. Live:dead lamina ratios did not vary among species within a grazing period, although they did vary seasonally. Averaged across species, live:dead lamina ratios ranged from 0.99 in April to 0.41 in August. Post-defoliation live:dead lamina ratios did not vary from pre-defoliation ratios.

Even though significant differences in tiller architecture were evident among species, no significant architectural differences were observed between grazed and ungrazed tillers within a species prior to any of the four grazing periods (Figure 5). Phenological stage of tiller development did not significantly ($P \geq 0.10$) alter tiller selection, with the exception of HIBE, in which an unexpectedly greater percentage of reproductive (38%) than vegetative tillers (17%) were grazed during the study. A relatively small percentage of the sample

population flowered during the study (2, 12, 23, 12 and 39% of BOCU, STLE, BUDA, HIBE and ARLO tillers, respectively).

Post-defoliation responses

Defoliation did not alter absolute changes in tiller length, number of live, dead and total laminae, or live:dead lamina ratios between grazing periods (rest) regardless of species or season (Figure 5). Similarly, defoliation did not alter relative changes in any of the variables measured with the exception of tiller extension (Figure 6). Averaged across species and rest periods, relative increases in tiller lengths between grazing periods averaged 32% for grazed and 10% for ungrazed tillers. However, these relative increases were significant only for the three midgrasses (BOCU, STLE and ARLO). Moreover, increased tiller elongation was limited primarily to the early portion of the growing season (Figure 5). However, the final seasonal effect was not statistically significant as indicated by the absence of a significant defoliation \times species \times grazing period interaction ($P=0.32$).

Discussion

Tiller defoliation patterns were not clearly distinguishable on the basis of mid- and short-grass categories. Frequency of tiller defoliation was greatest for one of the dominant midgrasses (BOCU), intermediate for the remaining midgrass (STLE) and dominant shortgrasses (BUDA and HIBE), and least for the subdominant midgrass (ARLO, Figures 1–3). Variation in defoliation frequency between BOCU and the shortgrasses probably originated from architectural differences displayed by these two plant groups (height and lamina number per tiller, Figure 5). Tillers displaying the greatest height or green leaf length have frequently been the most severely grazed (Greenwood and Arnold, 1968; Hodgson and Ollerenshaw, 1969; Gammon and Roberts, 1978a; Curll and Wilkins, 1982; Barthram and Grant, 1984). Despite its large stature, ARLO was grazed infrequently, suggesting the occurrence of morphological attributes that minimized the frequency of tiller selection by cattle.

The intensity of tiller defoliation was

influenced to a large extent by the architectural attributes of the various species (Figure 4). Midgrass species were consistently grazed more intensively than shortgrass species. Even the least frequently grazed midgrass, ARLO, was defoliated with an intensity comparable to the more frequently grazed midgrasses. Intensity of defoliation increased as the growing season progressed because forage consumption exceeded production as growing conditions became less favourable, i.e., soil water depletion and increased soil and air temperatures (see Heitschmidt *et al.*, 1982a for herbage dynamics information). However, relative intensity of defoliation did not vary among species or grazing periods, indicating that tillers were grazed in direct proportion to their pre-defoliation tiller heights (Figure 5). This also corroborates previous findings on frequency and intensity of tiller defoliation (Morris, 1969; Hart and Balla, 1982; Briske and Stuth, 1982; Clark *et al.*, 1984). Although highly variable, a defoliation intensity of approximately 20–30% of the pre-defoliation tiller height or total lamina length is frequently observed to be removed per defoliation event by sheep or cattle.

Tiller architecture, including height, lamina number, and the presence of reproductive culms, affected interspecific tiller selection but not intraspecific tiller selection within this multispecies grassland. These results suggest that there was insufficient intraspecific variation in tiller architecture to significantly influence animal selection compared to the greater amount of interspecific variation. The insignificant effect of reproductive culms on the severity of tiller defoliation is inconsistent with the findings of previous investigations (Stobbs, 1975; Gammon and Roberts, 1978a; Norton and Johnson, 1983). Asynchronous periods of phenological development among species and statistical limitations imposed by the relatively small number of reproductive tillers may have minimized this response.

The lack of evidence supporting tiller architecture as a selection criterion within a species suggests that cattle were selecting on vegetation parameters at higher levels of vegetation organization than individual tillers. Architectural characteristics associated with an assemblage of tillers in close proximity (i.e., live:dead lamina ratio or number of re-

productive culms per unit area or volume), rather than characteristics of individual tillers, may exert the greatest influence on animal selection. The presence of reproductive culms and litter in large caespitose grasses (e.g. ARLO) previously has been shown to minimize grazing severity by cattle (Willms *et al.*, 1980; Norton and Johnson, 1983).

Grazed tillers of the three midgrasses exhibited greater relative increases in tiller extension between grazing periods than non-grazed tillers (Figure 6), but absolute increases were similar (Figure 5). Severe grazing previously has been observed to retard tiller extension rates (Davies, 1974; Grant *et al.*, 1981), while relatively few investigations have documented increased extension rates following defoliation (Hart and Balla, 1982). Accelerated relative extension rates may have originated from increased rates of photosynthesis frequently observed to occur in partially grazed laminae or tillers, or from increased levels of irradiation on the remaining photosynthetic tissues (Gifford and Marshall, 1973; Nowak and Caldwell, 1984). Apparently, an insufficient amount of lamina area was removed from the shortgrass species to induce a similar response or the greater height and competitive ability of the midgrass species suppressed this response.

The patterns of interspecific tiller defoliation observed in this study parallel the long-term patterns of grazing-induced species replacement observed in this grassland. Generally, BOCU decreases in absolute abundance, STLE and ARLO remain relatively constant and BUDA and HIBE increase dramatically with increasing grazing severity (Heitschmidt *et al.*, 1985; 1989). Shortgrass species were more leniently grazed than dominant midgrasses because a greater portion of their total lamina area was in close proximity to the soil surface (Fig. 4, Detling and Painter, 1983; Briske, 1986). An alternative grazing avoidance strategy was displayed by ARLO, which was grazed intensively but infrequently. Grazing avoidance in this large caespitose grass apparently originates from the accumulation of reproductive culms and litter within the plant (e.g. Willms *et al.*, 1980; Norton and Johnson, 1983). STLE persists over a wide range of grazing regimes in this grassland even though it is grazed both frequently and intensively. This midgrass species appears to rely on a high degree of grazing tolerance (e.g.,

cleistogamous spikelets; Dyksterhuis 1945), in addition to an intermediate level of grazing avoidance, as its strategy of grazing resistance.

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