

## How herbivory affects grazing tolerant and sensitive grasses in a central Texas grassland: integrating plant response across hierarchical levels

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The hypothesis that herbivore selectivity, rather than plant response to defoliation, is the overriding factor in determining community level responses to grazing was tested in a Texas grassland. We monitored defoliation intensity and subsequent regrowth and reproduction of herbaceous dominants *Schizachyrium scoparium* and *Paspalum plicatulum* at the individual tiller, population, and community levels of organization. While long-term observations indicate that *Schizachyrium* declines and *Paspalum* increases in response to herbivory, individual *Schizachyrium* tillers exhibited little response to any level of defoliation and were able to fully compensate for lost tissue on a seasonal basis. Conversely, individual *Paspalum* tillers responded negatively to defoliation throughout much of the growing season, failing to compensate for leaf tissue lost to herbivory.

Defoliation intensity was not proportional to availability. *Schizachyrium* tillers were selected by herbivores in preference to *Paspalum* tillers regardless of season or stocking rate. Herbivore pressure required to achieve uniform defoliation exceeded levels required to allow grazers to maintain adequate forage intake.

New tiller recruitment per unit area declined over a four-year period as herbivore pressure increased for *Schizachyrium*. In contrast, *Paspalum* tiller recruitment remained constant over four years. The inability of heavily defoliated *Schizachyrium* plants to recruit new tillers and the ability of *Paspalum* to avoid defoliation and recruit new tillers into the population was manifest in measurements of standing crop over the same period. The ratio of *Schizachyrium* to *Paspalum* standing crop increased from 1.3 to 1.5 in protected areas. In treatments with extreme herbivore pressure the ratio declined from 1.3 to 0.6. Our hypothesis that herbivore selectivity, rather than defoliation tolerance, is the overriding factor mitigating species change was supported by these experiments and we suggest that predictions of competitive interactions within a lifeform based on individual and species responses to disturbances such as defoliation may not provide a valid assessment of community level responses.

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How plant populations within a community respond to herbivory may not reflect individual or species responses (Brown and Allen 1989). The response of an individual or species to defoliation is dictated by physiological ability to mobilize nutrient reserves, produce

new tissue, and increase photosynthetic efficiency in remaining undamaged tissue (Davidson and Milthorpe 1966, Caldwell et al. 1981, Cable 1982). In turn, these factors govern the ability of an individual to compete with surrounding plants for available resources (Jame-

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son 1963, Westoby 1989). However, differential selectivity among species by grazers may alter those competitive relationships and result in a different outcome than would be predicted based on species responses (Archer and Detling 1984).

Herbivory has been hypothesized to benefit plants by a variety of mechanisms that result in compensation for lost tissue by a damaged plant (Owen and Wiegert 1976, Stenseth 1978, Petelle 1981, McNaughton 1986, Dyer et al. 1991). Most data used to test this hypothesis have been collected at the individual plant level and expressed in terms of photosynthetic tissue production (McNaughton et al. 1983) or fecundity (Paige and Whitam 1987). These studies adequately identify mechanisms of plant response to defoliation but lack integration of different hierarchical levels (see Archer and Tieszen 1986). As a result, the controversy over the effect of herbivory on plant fitness has been the source of ongoing debate, but remains poorly tested (Belsky 1986, 1987, McNaughton 1986, Crawley 1987, Aarssen and Irwin 1991).

Experiments dealing with graminoid response to defoliation have commonly focused on responses of individual tillers or plants in controlled environments with simulated herbivory (e.g. Mueggler 1972, McNaughton et al. 1983, Wallace et al. 1984, Dyer et al. 1991). This approach has provided key insights into plant response to defoliation and has fueled much discussion. However, regardless of the effects of defoliation on individual tillers, grazing resistance (or long-term survival) in perennial graminoids is dependent upon ability to recruit new tillers into the population (Briske 1986, Olson and Richards 1989). Therefore, it is important to determine if individual, population, and community level responses are similar and how they are linked (Brown and Allen 1989).

A recent emphasis has emerged on integration across multiple hierarchical levels as a means to improve interpretation of data in herbivory experiments (Carney 1989). However, current information integrating the effects of herbivory across hierarchical levels is lacking, especially in environments with multiple plant species. This study examines responses at individual tiller, population, and community levels in an attempt to integrate those levels as a means of predicting vegetation response to herbivory. We examined defoliation intensity and regrowth of individual tillers, tiller recruitment, and standing crop dynamics of two dominant warm-season bunchgrasses in a grazing experiment to test the hypothesis that although species may exhibit different levels of defoliation tolerance, herbivore selectivity mediates population level responses and subsequently alters community composition.

## Study area and methods

Research was conducted at the Texas A&M Univ. Native Plant and Animal Conservancy near College Station (30°37'N, 96°21'W; elevation 150 m). This area is representative of the Post Oak Savanna Region with deciduous trees, primarily *Quercus stellata* interspersed in a grassland matrix (Gould 1975). Mean precipitation in the region is 1000 mm per year and is distinctly bimodal. Greatest amounts of rainfall occur in the spring and early summer. A second precipitation peak, although lower in total amount and shorter in duration, occurs in late summer and autumn.

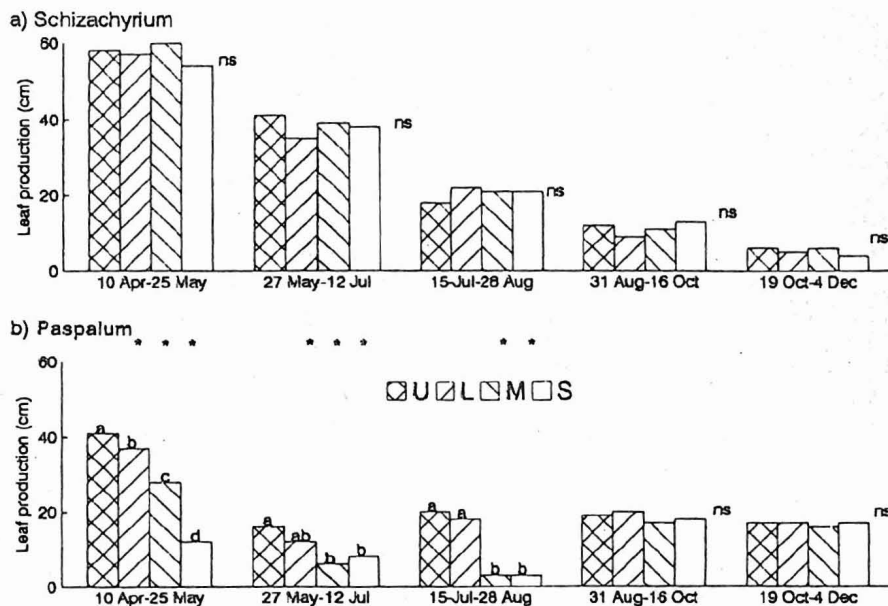
Soils are Tabor and Axtell fine sandy loam, both Udic Paleustalfs (USDA 1958). Both soils are characterized by a 25 cm or less A horizon underlain by a tight clay B horizon capable of restricting root growth.

*Schizachyrium scoparium* var. *frequens* Hubb. and *Paspalum plicatulum* Michx., both native species, are herbaceous dominants on the site, comprising about 65% of the total annual above-ground biomass production. *Schizachyrium* generally decreases when grazing pressure is heavy while *Paspalum* increases in the community. Both species are C<sub>4</sub> bunchgrasses. Axillary bud elongation and tiller recruitment is the primary means of reproduction for both species in this study, as in most perennial grasslands (Briske 1986). Seedling establishment was not encountered for either species during the course of this experiment.

*Schizachyrium* elongates axillary buds in the spring. These tillers remain vegetative throughout the summer and elongate culms in the fall (Smith 1975). *Paspalum* elongates axillary buds in the summer or early autumn. Tillers overwinter in a quiescent state, grow rapidly in spring and elongate flowering culms in late spring (De Costa 1969). One-hundred eighty tillers of each species were selected for study in March, 1982. Four transect lines, each with five marked tillers per species, were randomly located in each of eight rotationally grazed paddocks and an adjacent control (ungrazed) area. Yearling steers (*Bos taurus*) grazed paddocks at the dates indicated in Fig. 1 at stocking rates representing conservative (0.217 AU/ha), heavy (0.435 AU/ha), and extreme (0.571 AU/ha) levels of herbivory. An AU (animal unit year) is equivalent to 4300 kg dry matter per year or 2.6% of body weight for a 455 kg ruminant per day.

Measurements immediately before and after grazing provided an estimate of defoliation intensity (foliage removal) for individual tillers. Tillers were then separated into four categories according to percentage leaf tissue removed during each grazing period: <5% removed - undefoliated, 6-30% removed - lightly defoliated, 31-65% removed - moderately defoliated, >66% removed - severely defoliated. In succeeding nongrazed periods, measurements of leaf tissue production per tiller using the marked-leaf method (Jones et al. 1982) were made during each nongrazed period.

Fig. 1. Leaf production (cm of new leaf growth) of (a) *Schizachyrium* and (b) *Paspalum* tillers in response to defoliation intensity (U = undefoliated, L = lightly defoliated, M = moderately defoliated, S = severely defoliated). Bars are mean value per tiller. Bars within the same sampling period without the same letter are significantly different at the  $p < 0.05$  level. No significance = ns. Asterisks indicate significant differences between species within treatments.



Mean values of leaf production per tiller are reported with standard errors. When analysis of variance indicated significant differences ( $P > 0.05$ ), Duncan's Mean Separation Test was used to infer differences in leaf tissue production among defoliation categories within each sampling period (Snedecor and Cochran 1980). Differences in leaf production were also tested between species within a defoliation category at the same level of significance. There were no significant differences in leaf production for tillers in the control when compared to undefoliated tillers in grazed treatments, so data were pooled. Chi-square analysis was used to determine if significant differences existed in percentage of tillers in defoliation categories among herbivory treatments (Snedecor and Cochran 1980).

*Schizachyrium* tillers originally marked in March were monitored throughout the growing season. The phenology of *Paspalum* necessitated marking a new group of tillers prior to the 31 August nongrazed period. All marked *Paspalum* tillers flowered before that time and new tillers were produced. Therefore, these data represent a complete turnover in *Paspalum* tillers in late summer. All tillers sampled at any time in the study had a minimum of three fully exerted leaves.

Estimates of tiller populations per unit area were made monthly throughout the growing season from 1981 through 1985 using line transects (Kothmann et al. 1986). Tiller numbers were averaged for each year and all grazing treatments were pooled and compared to the control treatment for each species.

Estimates of standing crop were made before and after grazing during the growing season from 1981-1984 and mean values are reported (J. Casco, unpubl.). Standing crop estimates were also made on a nearby site

that had been protected from grazing for at least 40 yr and a site that had been heavily grazed for the same length of time. Soils were similar on these sites to the grazing trials.

## Results

Defoliation intensity did not significantly alter leaf production per tiller for *Schizachyrium* during any of the sampling periods (Fig. 1). Using criteria suggested by Brown and Allen (1989), tillers of *Schizachyrium* fully compensated for tissue lost to herbivory. We also found that the amount of green leaf tissue per tiller in each treatment was similar after the nongrazing periods regardless of the amount of green leaf remaining after the preceding grazing period (Stuth et al. 1986).

*Paspalum* leaf production was significantly reduced in response to increasing defoliation intensity during the spring and summer (Fig. 1). However, there were no statistical differences among defoliation categories during the final two periods. Therefore, on a season-long basis, *Paspalum* failed to fully compensate for the removal of leaf by the production of new leaf tissue.

Our observations indicated that during periods 1-3, *Paspalum* responded to increasing levels of herbivory by elongating flowering culms, a strategy that may be classified as defoliation avoidance (Briske 1986). *Paspalum* leaf production was significantly less than *Schizachyrium* for lightly, moderately and severely defoliated tillers during the first three sampling periods. However, there were no significant differences for the undefoliated category throughout the experiment.

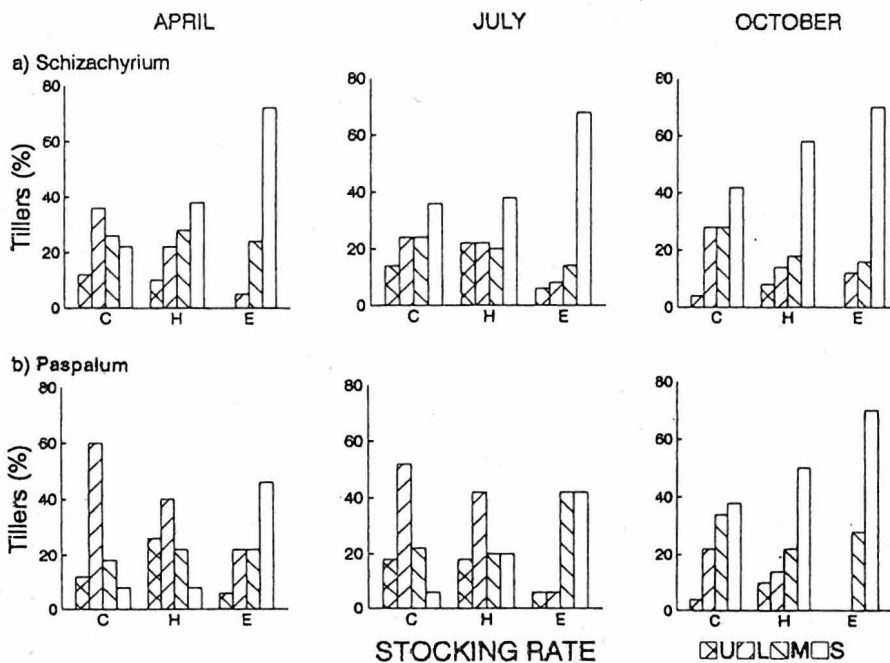


Fig. 2. Defoliation intensity (percent leaf removed) of a) *Schizachyrium* and b) *Paspalum* tillers in treatments with conservative (C), heavy (H), and extreme (E) levels of herbivore stocking rate. Defoliation categories are: undefoliated (U), lightly defoliated (L), moderately defoliated (M) and severely defoliated (H). Percent tillers in defoliation categories within a date was always significantly different ( $\chi^2$  test for homogeneity,  $p < 0.05$ ).

With the exception of the conservative treatment in the April trial, the greatest number of *Schizachyrium* tillers were in the severely defoliated category (Fig. 2). This was the initial trial in the study and standing crop was greatest at this time. In every grazing trial and every treatment, more than 50% of *Schizachyrium* tillers were either heavily or severely defoliated. In contrast, extreme herbivore pressure was required to defoliate more than 50% of *Paspalum* tillers moderately or severely during the April and July trials. Only during the October grazing trial was defoliation of *Paspalum* tillers similar to *Schizachyrium* tillers. Another aspect of this study indicated that adequate animal intake could not be maintained at the extreme level (Stuth et al. 1986).

Herbivore selectivity did have an impact on long-term population attributes. Longer term estimates of changes at the population level indicate that *Schizachyrium* responded negatively to increasing levels of herbivory and *Paspalum* was affected little (Fig. 3). When all grazing treatments were pooled *Schizachyrium* tiller recruitment declined approximately 50% over four years. In the ungrazed treatments, *Schizachyrium* tiller recruitment increased 40% over the same period. *Paspalum* tiller populations in both the ungrazed and grazed treatments remained near pretreatment levels. *Paspalum* tiller recruitment actually remained more constant in grazed treatments compared to ungrazed populations. The ability of populations of these competing species to recruit new tillers was further manifest at the community level of organization. Standing crop of *Schizachyrium* and *Paspalum* was approximately equal at the initiation of the study (Fig. 4), but the ratio shifted

toward *Paspalum* as herbivore pressure increased. The ratio remained near unity in the ungrazed treatments.

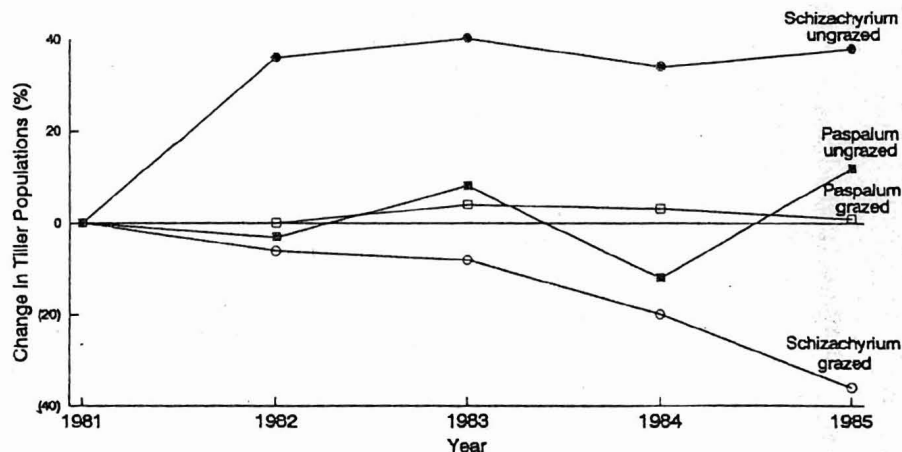
Estimates of standing crop on long-term grazed and protected areas also indicated that the species composition continued to shift toward dominance by *Paspalum*. In long-term heavily grazed areas, *Schizachyrium* standing crop was approximately half as great as *Paspalum*. In protected areas, the ratio was near unity (Brown and Archer 1989).

## Discussion

Examining individual plant response to defoliation illustrates greater tolerance of defoliation of *Schizachyrium* and an avoidance-oriented response to herbivory by *Paspalum*. Branson (1953) and Briske (1986) have contrasted these avoidance and tolerance mechanisms, and discussed their importance in determining population response to grazing. Species that produce reproductive culms and elevate meristems within vegetative tillers are thought to be more susceptible to defoliation, while species that delay culm elongation less so.

In our experiment, *Schizachyrium* maintained vegetative tillers throughout the growing season and individual tillers exhibited little response to defoliation. In contrast, *Paspalum* new tissue production decreased as level of utilization increased, especially in the spring and early summer when tillers responded to defoliation by elongating culms. As new tillers were produced in

Fig. 3. Percentage change in grazed and ungrazed *Schizachyrium* and *Paspalum* tiller populations per unit area (from Kothmann et al. 1986).



late summer, *Paspalum* showed little response to defoliation. The response of individual tillers on a season long basis to defoliation would predict that the more tolerant *Schizachyrium* should dominate the community at the expense of the less tolerant *Paspalum*. However, long-term observations indicate that when stocking rates increase beyond what we have defined as conservative, *Paspalum* becomes dominant.

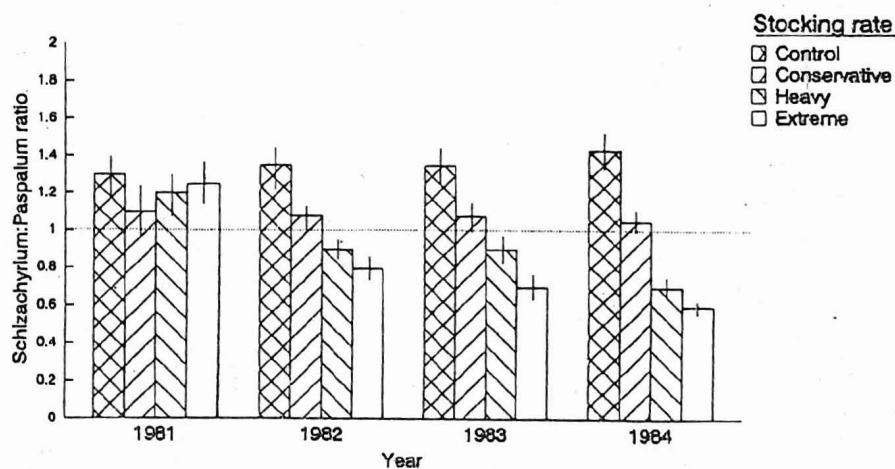
Caldwell et al. (1981) explained the dominance of one *Agropyron* bunchgrass over another by greater flexibility in resource allocation patterns following defoliation by clipping. Although total resource levels were similar, *A. spicatum* curtailed leaf growth and maintained root growth when defoliated, while *A. desertorum* reestablished canopy and curtailed root growth. The increased aboveground growth of *A. desertorum* resulted in enhanced photosynthetic capacity of remaining leaves and elongation of axillary buds (Richards and Caldwell 1985). They identified canopy reestablishment after grazing as indicative of grazing tolerance. However, in herbivore trials the tolerance of *A. spicatum* was re-

duced when defoliation was severe or occurred after culm elongation (Olson and Richards 1988a, b).

Detling et al. (1979) and Painter and Detling (1981) also used differences in photosynthetic capacity and regrowth patterns following defoliation to explain community level responses of two species, *Agropyron smithii* and *Bouteloua gracilis* in shortgrass steppe of North America. In addition, temporal separation of growing seasons of *A. smithii*, a C<sub>3</sub> species, and *B. gracilis*, a C<sub>4</sub> species, may at least partially explain observed differential responses to herbivory. Exploiting different periods of favorable growing conditions may allow different species to garner resources necessary for growth and reproduction and to maintain co-dominance when stocking rate is light or moderate even though individuals of the two species respond differently to defoliation.

In these examples, individual tiller or plant responses reflected observed community level dynamics. In our study, however, the mechanism for increasing dominance by *Paspalum* does not occur at the individual

Fig. 4. Ratio of *Paspalum* to *Schizachyrium* standing crop (from Casco 1984). Bars represent mean for each grazing treatment. Vertical lines represent  $\pm$  one standard error (J. Casco unpubl.).



plant level and individual tiller responses do not appear to be linked to community dynamics. *Schizachyrium* tillers were able to compensate fully for tissue lost to herbivory throughout the growing season. Conversely, *Paspalum* tillers did not compensate throughout the majority of the growing season. Our observations suggest that the mechanism for species change occurs at a different level of organization.

At the population level, herbivory has been shown to alter *Schizachyrium* population structure by reducing plant basal area and fragmenting tussocks into smaller units (Butler and Briske 1988). This alteration of tiller dispersion patterns failed to affect resource acquisition at the plant level in a transplant garden (Briske and Anderson 1990). However, severe levels of herbivory reduced tiller recruitment even in monospecific stands (Butler and Briske 1988).

Greater herbivore pressure on *Schizachyrium*, compared to *Paspalum*, throughout the growing season ultimately reduces the ability of tillers to elongate axillary buds and form new tillers in subsequent years. The reduction in tiller populations for *Schizachyrium* in response to heavy grazing and the ability of *Paspalum* to escape defoliation in spring and maintain tiller recruitment during autumn provide the mechanism accounting for long-term shifts in dominance at the community level.

In this grassland, herbivore selectivity and the resulting differences in defoliation intensity appear to be the overriding factor determining response to grazing at the community level. *Schizachyrium*, more tolerant of all levels of defoliation is more intensively defoliated over a wide range of stocking rates and throughout most of the year. Only when stocking rate was increased beyond levels where grazers could maintain adequate daily intake did defoliation intensity of *Paspalum* approach that of *Schizachyrium*. This level of herbivore pressure was not sustainable even on a short-term basis (Stuth et al. 1986).

Based on our data, manipulation of species composition by grazing alone would be extremely difficult in this grassland. However, Scifres and Duncan (1982) suggested burning as an alternative to grazing as a means of manipulating *Schizachyrium* and *Paspalum* composition in Post Oak Savanna grasslands. Nonselective tissue removal by dormant season burning significantly reduced the amount of *Paspalum* in the community by increasing tiller mortality and direct damage to dormant tillers. If herbivore pressure remains light following burning, the balance may be shifted toward *Schizachyrium*.

O'Connor (1991) has described how temporal and spatial patterns of herbivory may result in the decline and local extinction of perennial grass species. Sustained heavy grazing during periods of reproduction is compounded by the presence of unpalatable species that escape defoliation and compete for resources with more palatable species. While *Schizachyrium* is unlikely

to become locally extinct in this grassland, its ability to reproduce is severely impacted by herbivory.

We conclude that species composition, and associated community attributes are controlled primarily by the impacts of herbivore selectivity in this grassland. In any grassland, while individual tiller responses to defoliation may provide an explanation of the observed community level responses, individual or groups of parameters describing individual tiller response to defoliation may be poor tools for prediction at higher levels of organization. Care should be exercised when extrapolating across hierarchical levels of organization to evaluate the potential effects of herbivory on plants.

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