The Effects of Defoliation and Competition on Regrowth of Tillers of Two North American Mixed-Grass Prairie Graminoids
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Source: *Oikos*, Vol. 43, No. 3 (Dec., 1984), pp. 351-357
Published by: Blackwell Publishing on behalf of Nordic Society Oikos
Stable URL: http://www.jstor.org/stable/3544152

OIKOS 43: 351–357. Copenhagen 1984

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Archer, S. and Detling, J. K. 1984. The effects of defoliation and competition on regrowth of tillers of two North American mixed-grass prairie graminoids. – Oikos 43: 351–357.

Field defoliation experiments were employed on a mixed-grass prairie site to ascertain the tradeoff between competition and intraplant resource sharing. Tillers (ramets) of *Andropogon gerardi* (big bluestem) and *Carex filifolia* (threadleaf sedge) were subjected to various defoliation regimes under full and reduced competition. Subsequent trends in leaf biomass production, leaf exsertion kinetics, tiller mortality, and biomass of storage organs were measured over 70 days. Tillers defoliated under conditions of full competition produced significantly less leaf biomass than tillers defoliated under reduced competition. Apparent mortality of tillers defoliated biweekly was 95% under full competition and 20% under reduced competition. *Andropogon* tillers subjected to multiple defoliation under reduced competition produced approximately three more leaves per tiller than nondefoliated tillers or tillers similarly defoliated under full competition. All defoliated tillers had substantial reductions in biomass of storage organs relative to nondefoliated tillers. Tillers defoliated under full competition had stembase biomass reductions comparable to those of tillers defoliated under reduced competition but produced significantly less leaf biomass.

The results suggest that the positive aspects of resource sharing among interconnected tillers were outweighed by the negative aspects of intra- and interspecific competition. Because of the potential importance of competitive interactions on individual plant response to defoliation, care must be taken when designing field and laboratory defoliation experiments and interpreting and extrapolating their results. At the community level, herbivores may mediate competitive interactions among primary producers through the differential defoliation of plants.

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Проведены полевые опыты по дефолиации в стации разнотравной прерии для установления отношения между конкуренцией и распределением ресурсов внутри растений. Побеги (отдельные представители клонов) бородача *Andropogon gerardi* и осоки *Carex filifolia* подвергались разным способом дефолиации при полной и сниженной конкуренции. Последовательные тенденции в создании биомассы, кинетике появления листьев, отмирания побегов и биомассы запасающих органов наблюдались в течение 70 дней. Побеги, дефолиированные в условиях полной конкуренции, давали значительно меньшую биомассу листвы, чем побеги, дефолиированные при снижении конкуренции. Очевидная смертность побегов, дефолиированных раз в две недели, составляла 95% при полной конкуренции и 20% при сниженной конкуренции. Проростки бородача, подвергнутые многократной дефолиации, при сниженной конкуренции давали примерно втрое больше листьев на побег, чем недефолиированные побеги или побеги, дефолиированные таким же способом при полной конкуренции. У всех дефолиированных побегов существенно снижалась биомасса запасающих органов по сравнению с недефолиированными побегами. У побегов, дефолиированных при полной конкуренции, сокращалась биомасса основания стебля, в сравнении с побегами, дефолиированными при сокращенной конкуренции, но биомасса листьев была значително ниже. Результаты показали, что позитивные аспекты распределения ресурсов между взаимосвязанными побегами подавляются негативными аспектами внутри- и межвидовой конкуренции. Потенциальная значимость конкурентных взаимоотношений для реакции отдельных растений на дефолиацию учитивать при постановке полевых и лабораторных опытов по дефолиации, интерпретации и экстраполяции этих результатов. На уровне сообщества фитофаги могут опосредовать конкуретные взаимоотношения между первичными продуцентами путем дифференцированной дефолиации растений.

Accepted 7 February 1984

Introduction

Defoliation techniques are often used to examine how individual plants respond to frequency, intensity, and season of grazing. However, the potential effects of inter- or intraspecific competition on the outcome of such defoliation experiments are often ignored, although such effects have been qualitatively acknowledged for some time (Daubenmire 1940).

When herbivores graze at relatively light intensities, it is common for them to defoliate some graminoid tillers while leaving other nearby tillers of the same or other species ungrazed. Regrowth of the defoliated tillers may be affected in two different ways by nearby tillers. If nearby undamaged tillers are part of the same plant and still connected to the defoliated tillers, they may support the regrowth of those tillers through translocation of stored reserves or recently produced photosynthate (Marshall and Sagar 1965, Forde 1966, 1968, Gifford and Marshall 1973, Ong et al. 1978). On the other hand, nearby ungrazed or lightly grazed plants may out-compete more heavily grazed plants for resources such as water, light, and nutrients (White 1973). In one of the few studies done on the interaction between defoliation and competition in North American range plants, Mueggler (1970, 1972, 1975) observed that herbage production and flower stalk numbers of *Festuca idahoensis* and *Agropyron spicatum* decreased with increasing levels of competition and intensity of clipping. Regardless of the severity of defoliation, plants under competition had greater reductions in biomass and flower production, and were slower to recover from defoliation, than were plants under reduced competition.

In this study, we tested the hypothesis that reductions in competition lessen the negative effects of defoliation under field conditions. Growth and survival of individual tillers clipped under conditions of full and reduced competition was monitored and the trade-off between competition and intra-plant resource sharing among differentially defoliated graminoids was examined. *Carex filifolia,* a short-statured, caespitose sedge with a tussock-like growth form and *Andropogon gerardi,* a tall, erect, weakly rhizomatous grass were selected as target plants. Both species were common throughout the research area where they are utilized by resident herbivores. *C. filifolia,* a C_3 plant, is common on dry prairies while the C_4 *A. gerardi* tends to occupy more mesic sites in the area.

Methods

Study area

Experiments were conducted on a mixed-grass prairie hillside in Wind Cave National Park, located on the SE edge of the Black Hills in SW South Dakota. Mean annual precipitation there is 450 mm, 70% of which occurs between May and September. Mean air temperature is 21°C in July and −5°C in January. Park elevation ranges from 1111 to 1528 m a.s.l. Summaries of the vegetative characteristics of dominant range sites can be found in Lovaas and Bromley (1972). Plant nomenclature follows Van Bruggen (1976).

All experiments were conducted within a 168-ha exclosure which has prohibited grazing by resident herds of bison *Bison bison,* elk *Cervus canadensis,* and pronghorn *Antilocapra americana* since 1938. Mule deer *Odocoileus hemionius* have been observed in the exclosure but do not typically consume graminoids. Species selected for study were the tall, warm-season (C_4) grass *Andropogon gerardi* (big bluestem) and the short, cool-season (C_3) sedge *Carex filifolia* (threadleaf sedge). Both are weakly rhizomatous, common throughout the park, and utilized by resident herbivores (Coppock et al. 1980). All experiments were conducted in relatively homogeneous stands of each species.

Experimental design

Individual tillers of *A. gerardi* and *C. filifolia* were selected and marked at the four- and five-leaf stage, respectively, on 11 June, 1981. Twenty tillers were selected for each of four treatments, and leaves on each tiller were consecutively numbered prior to treatment. Four treatments were conducted simultaneously on each species. In the first treatment, target tillers were defoliated by clipping below the ligule of the lowest (oldest) leaf blade on 11 June. Subsequent regrowth was removed at approximately two-week intervals until 20 August. All surrounding plants were left intact, thus potentially allowing for transfer of resources (e.g., carbohydrates, nutrients, etc.) from intact ramets to defoliated ramets as well as for intra- and interspecific competition. The second treatment was identical except that all surrounding plants within a 60-cm radius of the target tillers were defoliated. Since defoliated tillers were selected from homogeneous stands of their respective populations, this treatment served to greatly reduce primarily intraspecific competition that might occur between defoliated and undefoliated tillers. Further, since both species were weakly rhizomatous, we assumed that this treatment would stress most, if not all, tillers (ramets) in the plant (genet), thus minimizing the ability of the selected tiller to receive resources from others in the rhizome system. The third treatment involved a similar defoliation of target tillers on 11 June, but tillers in this treatment were not redefoliated, and all surrounding vegetation was left intact. The final treatment involved monitoring the growth of a similar group of marked, nondefoliated tillers also growing under full competition. These treatments will be referred to hereafter as multiple defoliation with full competition (MD-FC), multiple defoliation with reduced competition (MD-RC), single defoliation with full competition (SD-FC), and non-defoliated with full competition (ND-

FC), respectively. Time and man-power limitations prohibited further elaboration of the experimental design.

Number of leaf blades exserted on each target tiller was recorded at two-week intervals in each treatment. In the two multiple defoliation treatments, dry weight of removed foliage was also determined at two-week intervals. In the ND-FC treatment, plant height and leaf numbers of target tillers also were recorded at two-week intervals. Tillers having similar heights and leaf numbers were then selected from the immediate population, clipped, dried, and weighed for biomass determination. Because stem base and sheath components are important reservoirs of carbohydrates and nutrients in graminoids (White 1973, Caldwell et al. 1981), and because a biomass decline of these organs likely reflects a mobilization of carbohydrate reserves used for shoot growth and tiller maintenance (Hickman and Pitelka 1975), stem bases were collected from tillers of all treatments (n = 20), dried, and weighed at the termination of the experiment.

Analysis of variance (AOV) (Ryan et al. 1981) was used to test for the significance of treatment effects on leaf number and biomass and crown biomass. Tukey's Q procedure (Kirk 1968) was used to test for significant differences among means. A chi-square test (Cochran and Cox 1957) was used to determine the significance of differences between observed and expected patterns in tiller mortality among treatments. All differences were accepted as significant at $P \leqq 0.05$ unless otherwise stated.

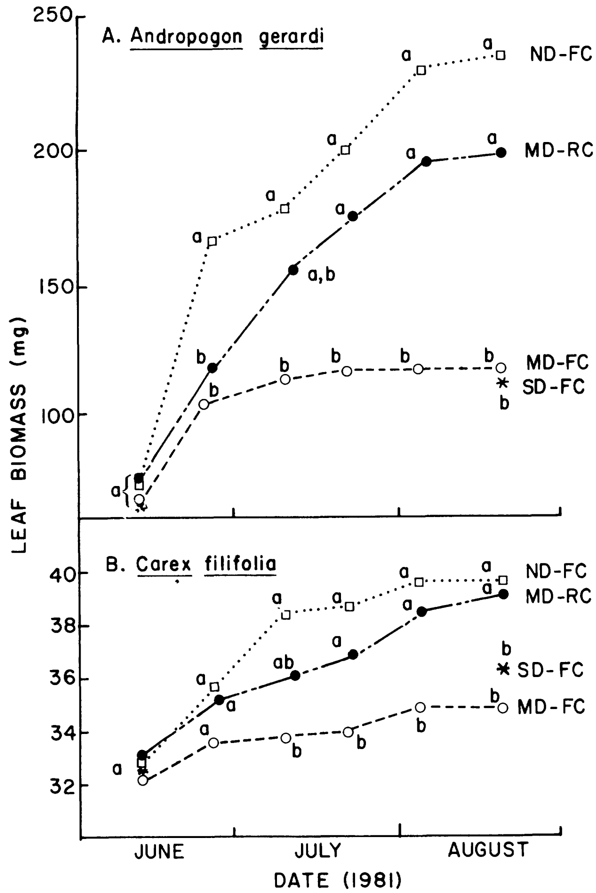

Fig. 1. Mean cumulative biomass in *Andropogon gerardi* (A) and *Carex filifolia* (B) tillers subjected to various defoliation treatments (ND-FC = not defoliated-full competition; MD-RC = multiple defoliation-reduced competition; MD-FC = multiple defoliation-full competition). AOV results for treatment (ND-FC, MD-RC and MD-FC) and date effects were significant ($P \leqq 0.01$) for both species. Treatment by date interaction was significant for *A. gerardi* only. Tillers in the SD-FC treatment (single defoliation – full competition) were harvested only at the termination of the experiment; thus, there were no intermediate points for its plot. Means among treatments at each date with the same letter were not significantly different. Standard errors, omitted for clarity, averaged 10.6, 3.6, 7.4 and 15.7% of the means for *A. gerardi* in the ND-FC, MD-RC and MD-FC and SD-FC treatments, respectively. Standard errors for *C. filifolia* averaged 2.9, 2.0, 2.1 and 2.7% of the means of the ND-FC, MD-RC, SD-FC and MD-FC treatments, respectively.

Results

Overall patterns of cumulative leaf biomass production were similar for both species. The tall C_4 species, *A. gerardi,* produced considerably more leaf biomass than the short C_3 species, *C. filifolia* (Fig. 1). For *A. gerardi,* treatment, date, and treatment by date interactions were significant ($P \leqq 0.01$) (Fig. 1A). The significant interaction resulted from tillers in the ND-FC and MD-RC treatments maintaining higher growth rates throughout the summer than the MD-FC tillers, whose growth slowed markedly after the second defoliation. MD-RC tillers produced less leaf biomass than ND-FC tillers throughout the experiment. However, the differences were significantly different at only one sample date. MD-FC tillers produced significantly less leaf biomass than tillers in the ND-FC and MD-RC treatments throughout most of the experiment. By mid-August, tillers receiving a single defoliation under full competition (SD-FC) had produced approximately the same amount of leaf biomass as did the MD-RC tillers. Thus, the number of clipping events had no significant effect on leaf biomass produced with full competition.

Treatment and date main effects were significant for *C. filifolia* ($P \leqq 0.01$), but the treatment by date interaction was not (Fig. 1B). As with *A. gerardi,* leaf production of MD-RC *C. filifolia* tillers did not differ significantly from that of ND-FC tillers. Leaf production in both of these treatments was significantly greater than leaf production of MD-FC tillers after the third defoliation. Although SD-FC tillers produced slightly more biomass than MD-FC tillers, this difference was not significant.

Multiply defoliated tillers with reduced competition maintained a higher proportion of actively growing tillers than those defoliated under full competition (Fig.

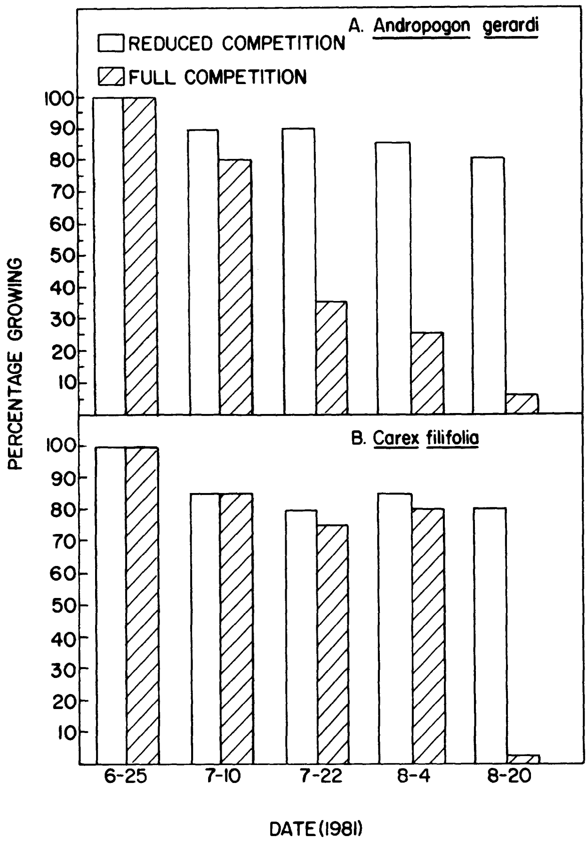

Fig. 2. Percentage of *Andropogon* and *Carex* tillers subjected to multiple defoliation showing leaf growth during measurement period. Shaded bars represent treatment when surrounding tillers were not clipped (full competition). Clear bars represent tillers for which surrounding vegetation was clipped to ground level (reduced competition) (n = 20). A chi-square test showed differences for both species to be significant at $P \leqq 0.01$. Methodology employed did not enable an accurate assessment of growth activity in control tillers and tillers defoliated once.

2). *Andropogon* tillers clipped with full competition suffered a 95% reduction in the number of actively growing tillers by the end of the treatment period, while tillers clipped under reduced competition had only a 20% reduction (Fig. 2A). Although the pattern of mortality and reduced activity in *C. filifolia* tillers was different (Fig. 2B), the end result was the same as for *Andropogon*. *Carex* tiller activity through the first four clipping events was not differentially affected. However, by 20 August, only 5% of the tillers defoliated under full competition were active, while 80% of the tillers defoliated under reduced competition remained active. The overall differences in observed versus expected declines in activity for both species, as determined by a chi-square test, were significant at $P \leqq 0.01$.

Throughout most of the study, *A. gerardi* tillers that received the MD-RC and SD-FC treatments produced significantly more leaves than did tillers in the MD-FC and ND-FC treatments (Fig. 3A). Date and treatment effects were each significant ($P \leqq 0.01$). The date by treatment interaction was also significant, with MD-RC and SD-FC tillers producing new leaves at a faster rate than MD-FC and ND-FC tillers throughout most of the monitoring period. At the termination of the experiment, MD-RC and SD-FC tillers averaged 9.2 and 8.2 leaves, respectively, while tillers in the MD-FC and ND-FC treatments averaged 6.6 and 7.0 leaves, respectively. On any given date, no significant differences existed among tillers in the MD-RC and SD-FC groups, nor between tillers in the MD-FC and ND-FC groups. For *C. filifolia,* the main effect of treatment and the treatment-by-date interaction were not significant.

Biomass of stem bases of both species collected at the termination of the experiment (20 August) was significantly reduced, compared with that of nondefoliated plants (Fig. 4). Plants of *A. gerardi* that were clipped once under full competition and allowed to recover had a 30% reduction in stem base biomass relative to nondefoliated plants. Plants defoliated repeatedly under reduced and full competition had 56 and 63% reductions, respectively. For defoliated *Carex* tillers, neither the number of clipping events nor the level of competition had any effect on stem base weights. That stem base biomass was not significantly higher in *Carex* tillers defoliated only once than in those receiving multiple defoliations suggested that regenerated leaf tissue of this C_3 graminoid was unable to put the plant in a positive carbon balance during this period in the growing season.

Discussion

It has long been known that competitive interactions influence the expression of even the most dominant plants in natural communities (Daubenmire 1940), and studies on western North American rangelands offer many specific examples (Blaisdell 1949, Blaser et al. 1956, Frischknecht 1963, Cook 1965, Harris 1967, Rittenhouse and Sneva 1976, Davis and Bonham 1979, Clary and Jameson 1981). However, plant competition has much less frequently been evaluated in relation to plant herbivore interactions. Results obtained in these experiments on *C. filifolia* and *A. gerardi* agree with similar experiments conducted on *Agropyron spicatum* and *Festuca idahoensis* (Mueggler 1970, 1972, 1975), and support the hypothesis that the deleterious effects of defoliation can be significantly reduced by concurrent reductions in competition. Since competition was largely intraspecific in our experiments, it appears that the potentially positive aspects of resource sharing among interconnected tillers was substantially overshadowed by the negative aspects of the competitive interaction. In contrast, Bentley and Whittaker (1979) found that moderate defoliation had no significant effect on plants of two *Rumex* species when competing

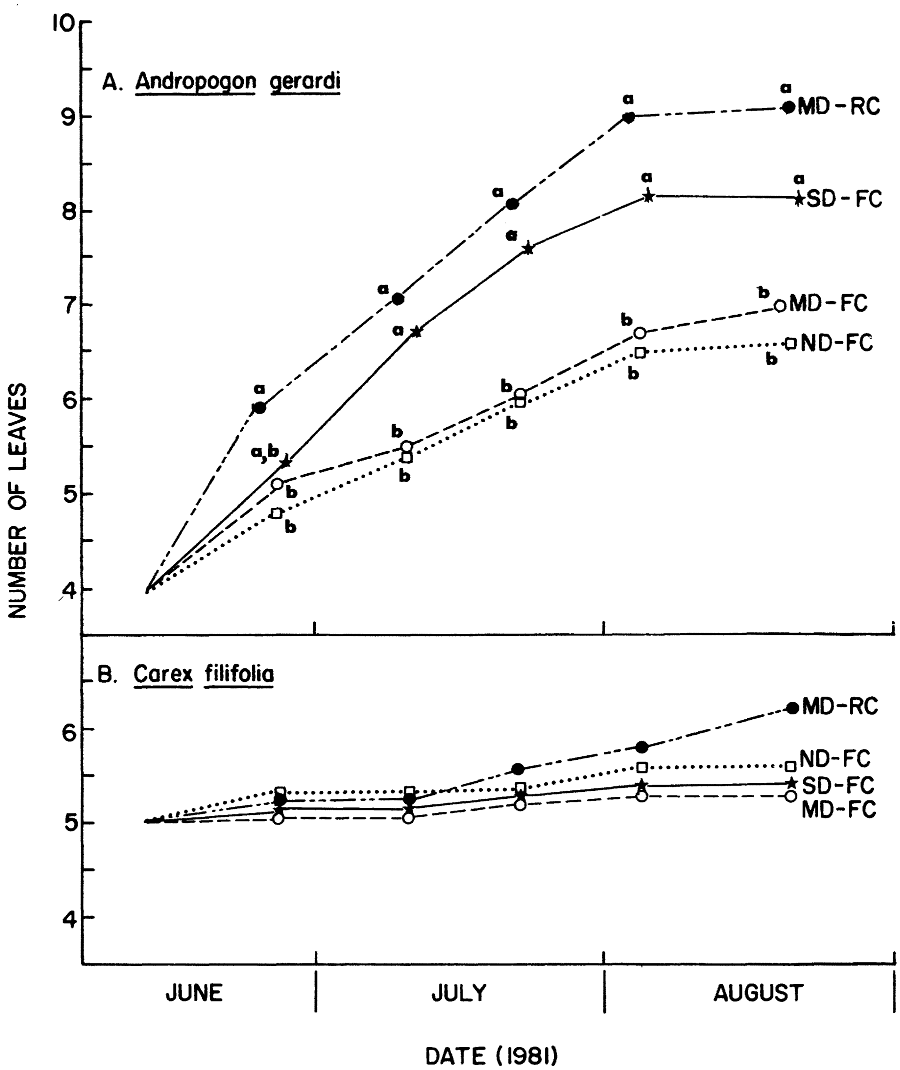

Fig. 3. Mean number of leaves exserted by *Andropogon* and *Carex* tillers between 12 June and 20 August, 1981. Treatments and symbols are as described in Fig. 1. Means reflect only tillers initiating growth in clipping treatments. For *A. gerardi*, date, treatment, and date by treatment interactions were significant as determined by AOV. No significant differences were noted for *Carex*. For each date, means with the same superscript were not significantly different. *Andropogon* standard errors, omitted for clarity, averaged 2.9, 4.3, 6.1 and 3.7% of the means for the MD-RC, SD-FC, MD-FC and ND-FC treatments, respectively. For *Carex*, standard errors averaged 3.8, 3.5, 2.3 and 3.7% of the means for the MD-RC, ND-FC, SD-FC and MD-FC treatments, respectively.

intraspecifically, but that defoliation did alter competitive relationships between the species when competing interspecifically.

Yield of individual grassland plants decreases with increasing plant density (Risser 1969). Westoby (1980) reported that *Phalaris* tillers grown at low densities had a size class distribution biased toward larger tillers, but that these larger tillers were less likely to survive close clipping than were the smaller tillers which dominated the size class distributions at higher tiller densities. Although not measured in this study, plant and tiller densities were relatively high for both species. Whether the pronounced effects of reduced competition observed in this experiment would hold at lower tiller densities remains to be investigated.

Competition for resources between defoliated and non-defoliated tillers apparently intensified the observed responses. For example, shading by undefoliated neighbors may have put the clipped tillers at a disadvantage and reduced their chances for recovery. Opening of the canopy by clipping all tillers in a 60-cm radius likely aided defoliated tillers in several ways. Alberda (1957) noted that defoliation had a marked influence on tillering rates only when light intensities were low. As light intensity was increased, recovery of defoliated tillers was enhanced. Additionally, Woledge (1977) found that opening of the canopy by clipping resulted in an increased photosynthetic capacity in newly formed leaves. Also, it should be noted that growing season precipitation during this experiment was about 30% greater than normal and was fairly uniformly distributed throughout the growing season (Archer 1983). In a more typical year of lower and more irregular precipitation, the observed differences among the treatments might be even greater, as water would become more of a limiting resource.

Belowground competition for water and nutrients may also influence the ultimate fate of a defoliated

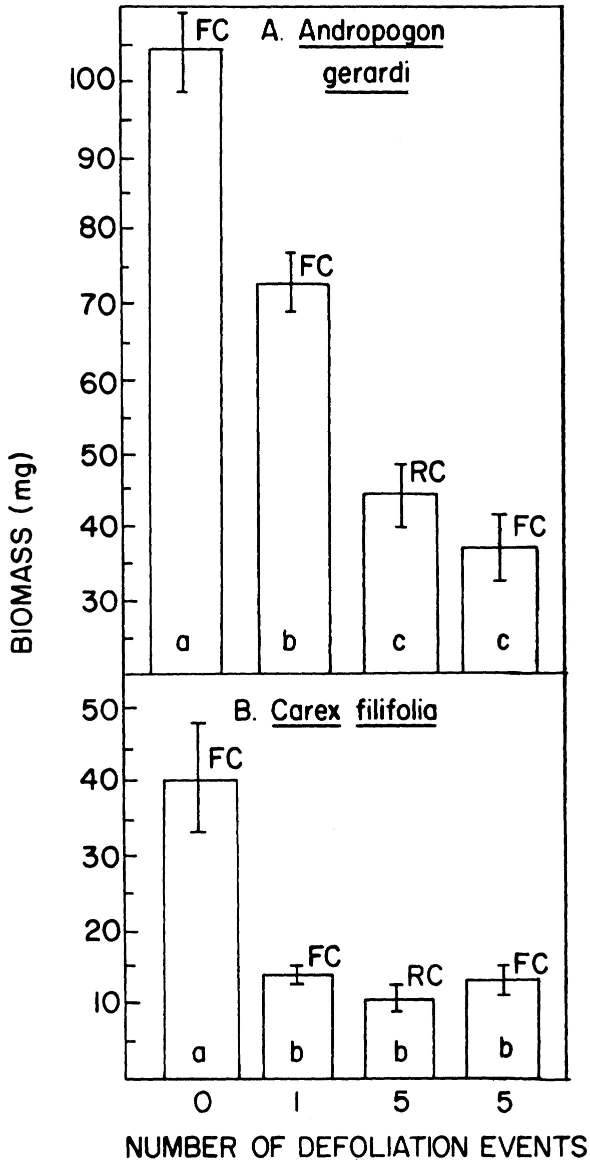

Fig. 4. Mean stem base biomass (±1 SE) of *Andropogon* and *Carex* tillers on 20 August at termination of defoliation trials (FC = full competition; RC = reduced competition). AOV results for both species were significant at $P \leqq 0.01$. Different letters within bars represent significantly different means.

tiller. Reductions in root growth following defoliation (Davidson and Milthorpe 1966, Evans 1972, Hodgkinson and Baas Becking 1977) may put repeatedly defoliated plants at a disadvantage relative to nondefoliated plants with regard to nutrient and water uptake, although some studies suggest that nutrient uptake is enhanced by defoliation (Chapin and Slack 1979). One must also consider the impacts of defoliation together with different rooting morphologies and phenologies of associated species (Hironaka 1961, Hull 1963, Frischknecht 1963, Harris 1977, Cline et al. 1977) and ascertain how defoliations at various times during the growing season might alter root growth patterns among competitors.

When evaluating plant responses to grazing, it is important to keep in mind effects of plant growth habit and morphology (Branson 1953), tradeoffs between resistance and avoidance (Archer and Tieszen 1980), and tradeoffs between competitive ability and grazing resistance. With regard to this latter aspect, Windle and Franz (1979) found that cultivars susceptible to insect attack were better competitors in the absence of the insect pests, but when insect interactions occurred, resistant cultivars replaced the susceptible one when insect feeding occurred. This and work of Archer and Tieszen (1980) suggests that plant attributes conferring a greater competitive ability are likely to preclude physiological and biochemical mechanisms of grazing avoidance.

Finally, because of the potential importance of competitive interactions in determining the outcome of defoliation experiments on individual plants, care must be taken when designing field and laboratory clipping experiments and interpreting their results. At the community level of organization, competitive interactions may constrain, control, or override individual plant responses to grazing. In grazing systems, herbivores likely play a key role in mediating competitive interactions among primary producers through the differential defoliation of plants that may be variously tolerant to defoliation.

Acknowledgements – We thank G. Archer for assistance with field work and data reduction. The cooperation of R. Klukas at Wind Cave National Park is appreciated. This research was supported by National Science Foundation Grant DEB 80-22380.

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