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T. R. Seastedt

Kansas State University, Manhattan, Kansas

R. A. Ramundo

Kansas State University, Manhattan, Kansas

D. C. Hayes

Kansas State University, Manhattan, Kansas

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SILICA, NITROGEN, AND PHOSPHORUS DYNAMICS OF TALLGRASS PRAIRIE

T. R. Seastedt, R. A. Ramundo, and D. C. Hayes
Division of Biology, Kansas State University, Manhattan, Kansas 66506

Abstract. Experiments were conducted on big bluestem (*Andropogon gerardii* Vitman) in the greenhouse and on a tallgrass site on Konza Prairie to evaluate the effects of simulated grazing on the cycling of silica (SiO₂), nitrogen, and phosphorus. Concentrations of all elements increased in vegetation that had been clipped or pruned. The absolute amount of nitrogen obtained by plants in the greenhouse experiment was increased by clipping foliage. Phosphorus exhibited only neutral or negative responses, while the absolute amount of silica declined in all but one experiment involving root pruning. In that experiment, the absolute amount of silica in roots was increased 25% by cutting a portion of the root system. These results suggest that the direct effects of clipping or pruning on the absolute amounts of elements cycled through vegetation are usually neutral or negative. Increased silicification or grazed foliage is suggested to be a consequence of delayed senescence and reduced leaf area. This interpretation provides a proximate reason why silicification is an "inducible defense" against herbivores.

Key Words. big bluestem, *Andropogon gerardii*, simulated grazing, nutrients, productivity, roots, Kansas

INTRODUCTION

McNaughton and Tarrants (1983) and McNaughton *et al.* (1985) presented findings indicating that silica concentrations in African grasslands increase in response to herbivory. Subsequent work by Brizuela *et al.* (1986) indicated that the North American grasses western wheatgrass (*Agropyron smithii* Rydb.) and little bluestem (*Andropogon scoparius* Michx.) also had higher silica concentrations in more heavily grazed areas. These studies have also explored the possibility that silica deposition in leaf tissues was an inducible response to foliage removal. Certain grasses appeared to increase in silica content following foliage removal, but this response did not appear to be a characteristic of all grasses.

The present study used field and laboratory manipulations to test whether the dominant tallgrass species, big bluestem (*Andropogon gerardii* Vitman), and other grasses exhibited enhanced concentrations of silica in response to simulated grazing of foliage and/or roots. Increased concentrations of silica following grazing may not, however, represent an "inducible response" to herbivory. If plants maintained a constant rate of silica uptake with reduced leaf area (i.e., if root uptake of dissolved silica is not affected by foliage removal), then silica concentrations in foliage would increase as a consequence of reduced leaf area. In other words, the same amount of silica is deposited in a reduced area of foliage, thereby increasing the concentrations of this material. A better test of the hypothesis that plants use silica as an inducible defense would be to measure total silica uptake of grazed and ungrazed plants. If the absolute amount of silica found in plants increased in response to herbivory, then this finding would provide strong support for the hypothesis. Therefore, quantitative estimates of silica uptake were obtained by harvesting foliage, roots, and rhizomes on an area basis in the field, and similar measurements were obtained on greenhouse plants. In addition to silica measurements, nitrogen and phosphorus measurements were concurrently made to evaluate the overall nutrient status of clipped or pruned plants and control plants.

STUDY SITE AND METHODS

Research was conducted on Konza Prairie Research Natural

Area in the Flint Hills of northeastern Kansas, a site owned by the Nature Conservancy and managed by Kansas State University. The area is on the western edge of the tallgrass prairie biome, and has a typical big bluestem, little bluestem, and indiagrass [*Sorghastrum nutans* (L.) Nash] dominated vegetation characteristic of this region (Hulbert 1973).

The prairie site was on a relatively deep soil, annually burned upland area. A randomized design was used to divide the area into eight mowed and eight unmowed plots (10 x 5 m). The mowed plots were clipped to a height of 5 cm five times during the growing season (twice in May and once per month thereafter to August). A final aboveground clipping to ground level in all plots was conducted in October. Samples of foliage were obtained by clipping a quadrat (0.1 m²) from each plot at the time of mowing. Roots were obtained with soil cores (5 cm diameter x 30 cm deep), washed with a root elutriator (Smucker *et al.* 1982), then sorted into live and dead categories, dried and weighed using procedures discussed in Hayes and Seastedt (1987). Rhizomes were obtained by hand sorting soil monoliths (0.1 m²), washed and sorted into live and dead categories as described in Seastedt (1988). All samples were dried at 70 C, weighed, and stored for subsequent nutrient analysis.

In early June, a subset of the unmowed plots were subjected to a treatment that cut approximately one-half of the roots at a depth of about 10 cm. In the autumn root cores were taken from these root-pruned plots, and results compared to root biomass from unmowed controls.

The effects of clipping and root pruning were also investigated using these variables in a two-factor factorial design in an indoor study. This greenhouse experiment was initiated by harvesting 48 individual rhizomes of big bluestem and planting in plastic pots (1.5 l). These pots were placed on a single table, numbered sequentially from 1 to 48, and a specific treatment was assigned to each pot using a random number generator. Treatments consisted of 1) foliage clipping, defoliating the plants to a height of 5 cm twice during the growing season; 2) root pruning, cutting roots by sawing half-way through the pots at 5 cm depth twice during the growing season; 3) by imposing both treatments; or 4) by allowing plants to grow undisturbed. Foliage, roots and rhizomes were harvested at the end of the growing season and processed as described above.

Silica (SiO₂), as reported here, is equivalent to acid insoluble residue (Kucera and Ehrenreich 1962). Values represent the filterable solids left after dry ashing samples at 500 C and treating the ash with 20% sulfuric acid. The filtrate from this procedure was collected in ash-free filter paper, re-ashed, and weighed. A second, largely equivalent method involved collecting filterable solids following sample digestion in hot concentrated sulfuric acid (i.e., following a micro Kjeldahl digestion). These solids were subsequently ashed and weighed. Comparisons of values obtained here with those obtained with more sophisticated procedures (Lanning and Eleuterius 1987) indicated comparable results for foliage, and values for roots fall within those reported by McNaughton *et al.* (1985). However data from this procedure likely includes some non-silica residue and some insoluble aluminum and iron compounds. Nonetheless, treatment comparisons should not be affected by this potential contamination, because there is no reason

to believe that potential contaminants would differ in their relationship with silica across treatments. Nitrogen and phosphorus concentrations were measured using a micro Kjeldahl digestion followed by colorimetric determination using a Technicon Autoanalyzer.

RESULTS

Greenhouse Experiment

Both clipping and root pruning had a negative effect on the productivity of plants grown in the greenhouse. Total plant biomass (roots, rhizomes, and foliage) of clipped, root pruned, or plants subjected to both treatments averaged 53%, 88%, and 49%, respectively, of the biomass of controls. The relatively larger effect of clipping may reflect the fact that the plants were given adequate water and were grown on relatively nutrient rich soil. Hence, productivity was apparently limited more by the availability of leaf area than by water and nutrients. Clipping of foliage resulted in significantly higher nitrogen and phosphorus concentrations in

plant foliage and rhizomes compared to unclipped controls (Table 1). Silica concentrations were also higher in foliage of clipped plants than in controls. Root pruning had less visible influence on elemental concentrations. An increase in the silica concentrations of rhizomes in response to root pruning was the only significant effect measured (Table 1). When the average concentrations of elements for the total plant biomass are analyzed relative to the treatments, only clipping was important, and then only for nitrogen and phosphorus concentrations (Figure 1). The absolute amounts of the various elements obtained by the plants, however, exhibited a variable response to the treatments. Based on the results of a two-factor factorial ANOVA, the absolute amount of silica was unaffected by root pruning, but significantly declined in response to foliage removal (Figure 2). Phosphorus amounts were unaffected by either treatment, while the absolute amount of nitrogen increased in response to foliage removal (Figure 2). The amount of nitrogen accumulated by foliage clipped plants was, on average, 14% higher than for unclipped plants ($p < 0.05$).

Table 1. Silica, nitrogen, and phosphorus concentrations (% of mass) of big bluestem (*Andropogon gerardii* Vitman) subjected to foliage and/or root cutting (n = 12/treatment).

Plant part	Element	Concentration (standard error)			Controls
		Foliage clipped	Root pruned	Both treatments	
Autumn foliage	Si	8.59a ¹ (0.27)	6.15b (0.39)	9.04a (0.44)	7.87b (1.53)
	N	0.49a (0.05)	0.25b (0.01)	0.54a (0.04)	0.23b (0.02)
	P	0.35a (0.02)	0.14b (0.01)	0.36a (0.01)	0.12b (0.01)
Autumn rhizomes	Si	4.93b (0.38)	5.70a (0.67)	5.59a (0.45)	4.41b (0.35)
	N	0.91a (0.07)	0.70b (0.04)	0.83a (0.04)	0.77b (0.05)
	P	0.11a (0.01)	0.07b (0.01)	0.10a (0.01)	0.09b (0.01)
Autumn live roots	Si	14.44 (3.94)	9.12 (0.75)	12.56 (1.47)	10.06 (0.90)
	N	0.72a (0.05)	0.52b (0.02)	0.85a (0.05)	0.47b (0.02)
	P	0.20 (0.09)	0.08 (0.01)	0.13 (0.01)	0.08 (0.01)
Clipped foliage	Si	4.52 (0.28)	---	4.64 (0.17)	---
	N	1.44 (0.07)	---	1.44 (0.06)	---
	P	0.22 (0.01)	---	0.21 (0.01)	---
Clipped roots	Si	---	13.05 (1.27)	14.94	---
	N	---	0.52b (0.02)	0.78a (0.08)	---
	P	---	0.17 (0.09)	0.08 (0.01)	---

¹Means within rows followed by different letters are significantly different (Duncans New Multiple Range test following two-way ANOVA, $p < 0.05$).

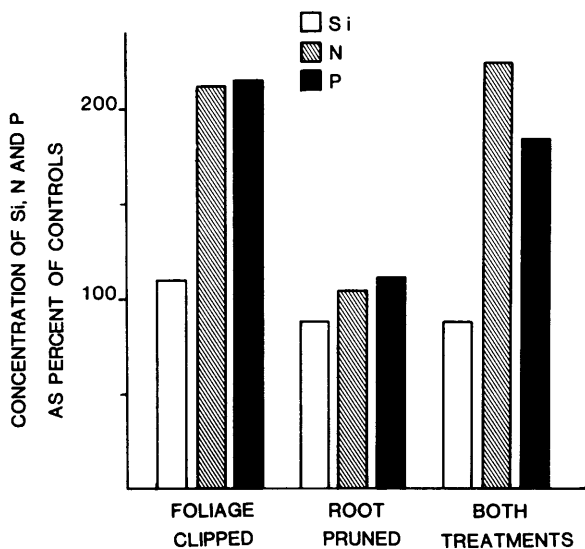


FIG. 1. Silica, nitrogen, and phosphorus concentrations for total plant biomass of foliage clipped and/or root pruned big bluestem as percentages of non-manipulated plants (Note: values for silica shown here and in subsequent figures are for SiO₂, not just Si).

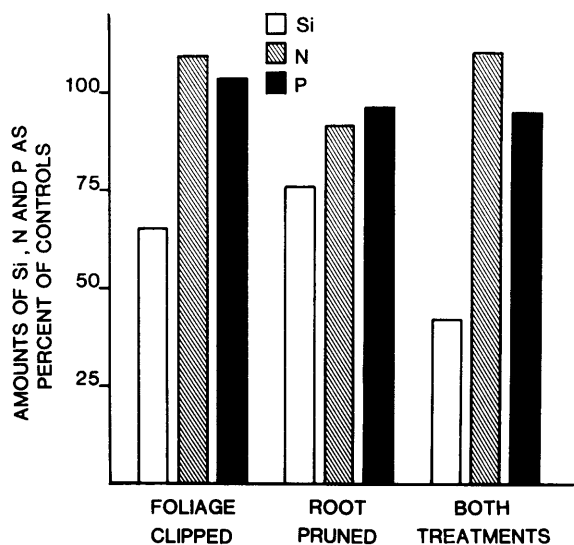


FIG. 2. Total amounts of silica, nitrogen, and phosphorus accumulated by plants subjected to foliage clipping and/or root pruning as percentages of non-manipulated plants.

Field Experiments

Plots mowed (to 5 cm) five times over the growing season averaged about 79% of the production of unmowed plots. Concentrations of silica in foliage increased through time (Figure 3). By autumn, silica content of the mowed plots was significantly greater than that of the controls. However, the differential abundance of flowering stems likely affected these results. Flowering stems of big bluestem were much lower in silica content than foliage (Lanning and Eleuterius 1987), and therefore "diluted" the

total aboveground estimate. Flowering was not common on the mowed areas. Nitrogen and phosphorus concentrations tended to be higher in the clipped vegetation throughout the growing season. As in the greenhouse experiment, silica concentrations and amounts were highest in the roots (Figures 4 and 5). Less silica was found in foliage, and the least amount of silica was found in rhizomes. Dead roots and dead rhizomes had higher silica concentrations as a consequence of the loss of carbon compounds to microbial respiration. The absolute amounts of silica, nitrogen, and phosphorus in the plant tissues of mowed plants was 261, 16.9, and 1.3 g/m², respectively, as compared to 322, 22.3, and 1.8 g/m² of Si, N, and P, respectively, in unmowed plants (t-test, p < 0.05 for all tests). Thus, clipping the vegetation in this experiment resulted in a decline in the amount of all elements or compounds cycled by the plants.

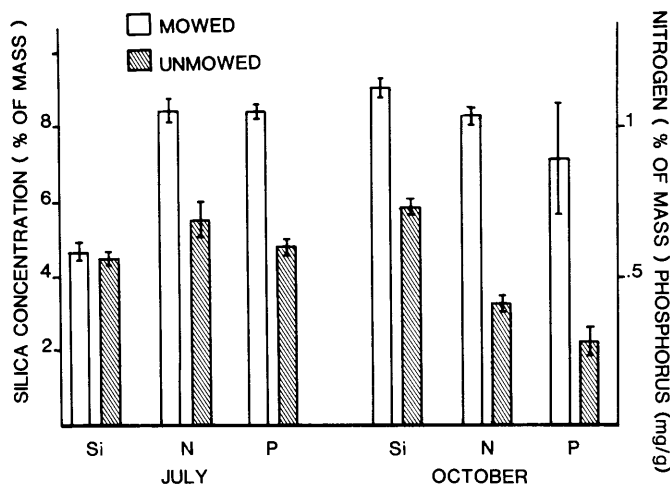


FIG. 3. Silica, nitrogen, and phosphorus concentrations of mowed and unmowed prairie foliage measured in July and October. The error bar represents one standard error of 8 replicates.

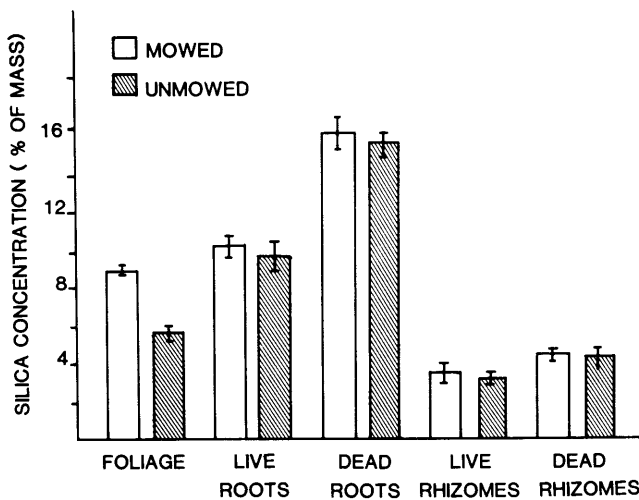


FIG. 4. Silica concentrations of plant parts harvested in October from mowed and unmowed plots.

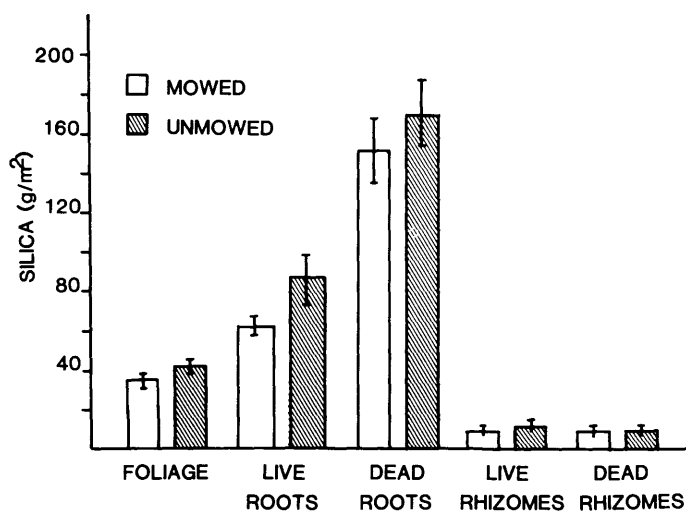


FIG. 5. Silica amounts in vegetation from mowed and unmowed prairie. Foliage amounts from mowed plots includes offtake.

Root biomass and phosphorus concentrations and amounts in vegetation subjected to pruning were not significantly different from controls (Table 2). Nitrogen concentrations increased as in the greenhouse experiment, while the absolute amount of nitrogen between treatments was not significantly different. Silica concentrations and the absolute amounts of silica from treated plots were significantly higher than controls, suggesting that plants responded to the pruning by depositing more silica in the roots. The total amount of silica in living and dead roots was 367 g/m² in the pruned plots versus 257 g/m² of silica in the control plots. Unfortunately, foliage from these plots was not concurrently harvested. Therefore, it is not known if the absolute amount of silica uptake increased in response to root pruning. The results do suggest, however, that silicification of roots occurs in response to damage occurring early in the growing season.

Table 2. Silica, nitrogen, and phosphorus concentrations and amounts of damaged (pruned) and undamaged roots.

Variable	Mean (standard error)			
	Damaged roots		Undamaged roots	
Live Roots				
Mass (g/m ²)	794	(48.5)	878	(98.6)
N (%)	0.65a ¹	(0.02)	0.56b	(0.02)
N (g/m ²)	5.2	(0.4)	4.9	(0.5)
P (%)	0.05	(0.01)	0.05	(0.01)
P (g/m ²)	0.4	(0.03)	0.5	(0.07)
Si (%)	13.4a	(1.3)	9.0b	(0.7)
Si (g/m ²)	108.8a	(14.0)	86.9b	(13.0)
Dead Roots				
Mass (g/m ²)	1,231	(95.1)	1,083	(92.1)
N (%)	0.98a	(0.02)	0.89b	(0.02)
N (g/m ²)	12.0a	(0.8)	9.5b	(0.9)
P (%)	0.06	(0.01)	0.06	(0.01)
P (g/m ²)	0.7	(0.06)	0.6	(0.06)
Si (%)	20.6a	(0.72)	15.6b	(0.60)
Si (g/m ²)	258.3a	(26.3)	170.3b	(18.5)

¹Means within rows followed by different letters are significantly different ($P > 0.05$).

DISCUSSION

Clipping of foliage appears to consistently increase silica, nitrogen and phosphorus concentrations of regrowth foliage (Table 1, Figures 3 and 4). This response may be attributed to the fact that surviving and/or regrowth foliage tends to be more physiologically active per unit of mass or leaf area than is ungrazed foliage (Detling *et al.* 1979, Dyer *et al.* 1982). Clipping or grazing also resulted in plants remaining more physiologically active much longer into the growing season. While flowering of cut grasses was reduced in this study, the retranslocation of nitrogen into rhizomes was delayed (Figure 3). This physiologically more active plant tissue may therefore remove more nitrogen from the soil over the growing season than unclipped controls (Figure 2). However, this ability of grazed vegetation to pump more nitrogen was undoubtedly under climatic control as well as governed by nitrogen availability in soils. In contrast to the greenhouse study, the clipped vegetation in the field extracted less nitrogen than controls. Both field and greenhouse studies indicated that the amounts of silica and phosphorus cycled by foliage-clipped vegetation was equal to or less than controls. Such results suggest that silica is not an inducible defense to herbivory in the tallgrass prairie.

In contrast to other experiments, the root-pruning experiment conducted in June resulted in absolute increases in the amounts of silica in roots harvested in autumn. Unlike the other work, these results suggest that enhanced uptake of silica resulted from the manipulation and provides support that silicification can be induced by certain types of herbivory. These results should be viewed with some caution. Consistent with McNaughton *et al.* (1985), the roots contained the highest concentrations of silica of all plant tissues. If concentrations reflect the intensity of defenses (indeed, this is a basic premise for silicification of grasses), then roots are the most heavily defended of the plant tissues, while foliage is less defended, and rhizomes are least defended. However, adequate data are not available on the seasonal changes in roots and rhizomes, nor are data available on other chemicals in these plant parts that could also be discouraging herbivory. Increased silicification to plants sustaining root damage would be a logical response. However, plants also increased the nitrogen concentrations of remaining roots in response to cutting (Table 2), which made these roots more attractive to herbivores (Seastedt *et al.* 1988). Increased silica concentrations may adversely affect herbivores, but increased silicification could also be a consequence of the physiological changes induced by cutting. Increased silicification will occur if plants become more physiologically active or remain physiologically active longer as a result of damage to foliage or root tissues. If plant senescence can be delayed by clipping, then even absolute increases in silica uptake and enhanced rates of silica cycling by grazed plants could be a consequence of this response. The seasonality of dissolved silica in soil water might also explain these results. If silica concentrations of soil water increase during the growing season, then plants more physiologically active later in the growing season could passively accumulate more silica. Thus, while there exists little controversy that silicification has negative impacts on herbivores, and that the coevolution of grasses and grazers has likely resulted in the high levels of silica found in grasses (McNaughton and Tarrants 1983), the question as to whether silicification is an inducible defense remains unresolved, at least for tallgrass species. Until the "cost" of silica uptake to the plants is established, alternative hypotheses cannot be rejected.

ACKNOWLEDGEMENTS

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