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Root and shoot responses of sand bluestem to defoliation

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Abstract

Knowledge of root response, as well as shoot response, to defoliation is needed to manage grasslands in environments where water and/or nutrients are limiting. The objective of this study was to document the response of sand bluestem (*Andropogon hallii* Hack.) roots and shoots to different times and frequencies of defoliation. Individual sand bluestem plants were grown in 15 × 100-cm polyvinyl chloride (PVC) containers which were placed in the plants' natural setting. Twelve plants (replications) were clipped to a 7-cm stubble height during mid-month for each of the following defoliation schedules: 1) June, July, and August; 2) June and August; 3) June; 4) July; 5) August; and 6) October. The October defoliation, after shoot senescence, served as the control. Multiple defoliations reduced ($P < 0.05$) root weight, root area, root length, and weight of total nonstructural carbohydrates (TNC) in roots by an average of 33, 42, 43, and 34%, respectively, compared to control plants. A single defoliation in June only reduced root weight, root area, root length, and weight of TNC in roots by 14, 19, 16, and 13%, respectively, compared to control plants. Defoliating plants during the growing season did not affect ($P > 0.05$) number of tillers, weight per tiller, above-ground weight, number of buds, weight of rhizomes, or weight of TNC in rhizomes. Grazing sand bluestem more than once during the growing season may reduce root growth and diminish its ability to compete for water and nutrients. Grazing during the dormant season or once during the early part of the growing season should be least detrimental to sand bluestem.

Key Words: *Andropogon hallii*, clipping, root area, root length, total nonstructural carbohydrates

Plant response to defoliation has been the objective of numerous research projects (Ellison 1960, Jameson 1963, Belsky 1986). Most studies have focussed on shoot response to defoliation. However, Stanton (1983) and Richards (1984) reported that defoliation reduced root production more than shoot production. Since moisture and/or nutrients are limiting factors for plant growth in many environments, it is also important to quantify root response to defoliation.

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Sand bluestem (*Andropogon hallii* Hack.) is a warm-season, rhizomatous, tall-grass species which is preferred by all classes of livestock (Stubbendieck et al. 1985). It contributes about 20% to dry matter production on good to excellent condition range sites in the Nebraska Sandhills. It is classified as a decreaser and is one of the first species to decline in the vegetation composition under excessive grazing pressure. The objective of this study was to determine the effect of time and frequency of defoliation on roots and shoots of individual sand bluestem plants.

Materials and Methods

Study Area

This study was conducted from 1989 through 1992 at the Gudmundsen Sandhills Laboratory located about 11 km northeast of Whitman, Nebraska. The location was on a typical sands range site as described by Burzlaff (1962) and Nichols et al. (1984). The soil was Valentine fine sand (mixed, mesic Typic Ustipsamment). Vegetation was dominated by sand bluestem, prairie sandreed [*Calamovilfa longifolia* (Hook.) Scribn.], and little bluestem [*Schizachyrium scoparium* (Michx.) Nash]. Thirty-year (1961–1990) average annual precipitation for the area was 535 mm of which about 70% fell from May through September (Owenby and Ezell 1992).

Plant Establishment

A containerized technique (Engel et al. 1993) which facilitated recovery and study of complete individual plants was used. Sand bluestem rhizomes with associated buds and roots were collected by excavating a 15 × 15 × 25-cm block of soil around vegetative tillers produced the previous year. Rhizomes were gathered in mid-April of 1989 from a 1,000-m^2 area within the study site. Excavated soil was sifted to remove other plant material and used for planting rhizomes and associated buds and roots in 15-cm diameter pots. Plants were grown in a greenhouse for 3 weeks and outside (covered at night to prevent freezing) for 1 week. Most plants developed only 1 tiller while in the greenhouse. Secondary tillers were removed to standardize plant material prior to transplanting to containers in the field. Additional pruning was not done after plants were established in the containers.

Containers were constructed from 15 × 100-cm polyvinyl chloride (PVC) pipe. Holes were drilled with a tractor-mounted auger in a 1.5-m grid. Containers were placed into the holes with their

top edges even with the soil surface. Soil collected on a tarp placed around the auger was sifted to remove plant material and placed inside containers with near natural stratification.

Plants were transplanted to PVC containers during mid-May while at the 2- to 3-leaf growth stage. Soil in each tube was saturated with water at transplanting. Grasshoppers were controlled by applying Fenvalerate [cyano(3-phenoxyphenyl) methyl-4-chloro-alpha-(1-methylethly) benzeneacetate] around the perimeter of the study area. Plants were allowed to grow for 1 year before defoliation treatments were imposed. Dead tillers were removed at ground level before growth began the second year.

Experimental Design and Defoliation Treatments

Experiment 1, initiated in 1989, consisted of the first growing season when plants established, a second growing season when defoliation treatments were imposed and above-ground plant variables measured, and the third spring when plants were extracted and below-ground variables measured. This complete experiment was repeated (experiment 2) beginning 1 year after the first experiment was initiated. The only procedural difference between the 2 experiments was that plants established in experiment 1 required a small amount of supplemental water in June of 1989 due to the dry spring (Table 1). Water was added when plants appeared wilted to insure plant survival.

Table 1. Deviations of precipitation recorded at the study site from 30-year monthly averages for May through September, 1989-1991.

Month	Average[1]	1989	1990	1991
			(mm)	
May	89	-38	+26	+21
Jun	92	-65	-38	+51
Jul	81	-57	+48	-11
Aug	60	-25	-11	+31
Sep	45	-04	-25	+02

[1]Owenby and Ezell (1992), Mullen 21 NW Station.

The experimental design was completely randomized with 12 replications of 6 defoliation treatments. An experimental unit consisted of all plant parts collected from a container. Defoliation treatments were imposed during the second growing season and consisted of clipping all tillers within a container to a 7-cm stubble height at mid-month for the following schedules: 1) June, July, and August; 2) June and August; 3) June; 4) July; 5) August; and 6) October. Previous measurements taken on sand bluestem tillers grazed by cattle indicated that the average bite point was 7 cm above the ground regardless of time, intensity, or frequency of grazing during the growing season (Unpublished data, Engel et al.). Plants defoliated in October, following shoot senescence, served as the control.

Data Collection

Number of tillers per plant was recorded every 2 weeks starting in May during the second growing season. Leaves and tillers that died during the growing season and plant material removed by clipping were collected from each plant. This material was combined with an end-of-season (mid-October), ground-level harvest to determine total, above-ground, seasonal dry matter production and average production per tiller for each plant. All plant material was oven-dried at 50° C for at least 96 hours prior to weighing. Water status of containerized plants was compared with native plants grown under natural conditions by measuring xylem tension of the youngest collared leaf with a PMS pressure chamber. Twelve containerized plants and 12 plants from the native plant community were measured about 1 hour before sunrise at mid-month during June, July, and August of the treatment year.

Containers were left in the ground over winter and removed prior to shoot growth the following spring. This was done to evaluate the amount of roots and total nonstructural carbohydrates (TNC) available for growth in the spring following the year of defoliation. Intact soil columns were removed from containers and soil was washed from roots with a gentle spray of water. Cleaning was further facilitated by submerging roots in a shallow pan of water. Rhizomes and dead stem bases were removed from roots and number of buds was counted on each rhizome. Length and area (2-dimensional) of roots were measured with a Decagon AgVision Computer Imaging System. Rhizomes and roots were oven-dried at 50° C and weighed.

Plant material from the 12 replications within a treatment were randomly combined (3:1) into 4 replications in order to obtain sufficient material for TNC analysis of rhizomes and roots. Roots and rhizomes were ground through a 2-mm screen using a Wiley mill and then through a 1-mm screen using a U/D cyclone mill. Nonstructural carbohydrates were extracted with 0.2 N sulfuric acid as described by Smith et al. (1964) and quantified on a glucose equivalent basis by using iodometric titration developed by Heinze and Murneck (1940) with modifications of reagents as suggested by the Association of Official Agriculture Chemists (1965). Weight of TNC was calculated by multiplying the decimal equivalent of percent concentration and weight of corresponding plant material.

Data Analysis

Analysis of variance for a series of experiments was performed as described by Cochran and Cox (1957) using the Statistical Analysis System (SAS) for micro-computers. Two plants (replications) were lost due to rodent damage during each experiment. To account for this loss, the general linear model procedure within SAS was used to test for experiment × treatment interactions, experiment main effects, and treatment main effects at the 0.05 level of probability. Experiment × treatment interactions were tested with residual mean squares and main effects were tested with experiment × treatment mean squares. When significant effects were detected, the least-squares means procedure within SAS was used to separate means.

Results

Containerized and adjacent, naturally-growing plants appeared similar in size throughout the study. Leaf xylem tension did not differ between containerized and native plants, except in July 1990 (Table 2). This indicated that containerized and native plants were under similar water regimes. The reason for the July discrepancy was not apparent. There were no significant experiment × treatment interactions, therefore only main effects are discussed. All stated reductions of measurements due to defoliation are related to the control (October defoliated plants).

Table 2. Average leaf xylem tension of native and containerized sand bluestem plants. Measurements were taken 1 hour before sunrise prior to defoliation treatments in June, July, and August of 1990 and 1991.

	June		July		August	
Plants	1990	1991	1990	1991	1990	1991
	(-kPa)					
Native	80.4 a[1]	103.4 a	101.1 a	74.7 a	295.9 a	77.6 a
Container	79.3 a	103.4 a	195.4 b	77.6 a	287.3 a	77.6 a

[1]Means within a column followed by the same letter are not significantly different (P > 0.05).

Root and Shoot Responses to Defoliation

Tiller and bud production were not affected by clipping treatments or experiments. Average number of tillers produced by an individual plant was 7.9 (SE=0.3), average weight per tiller was 0.51 g (SE=0.02), average weight per plant was 3.59 g (SE=0.11), and average number of buds produced per plant was 45.7 (SE=1.2). Defoliation did not affect average rhizome weight per plant. However, average rhizome weight was greater for plants in experiment 1 (1.50 g) than in experiment 2 (1.14 g).

Root production was greater for plants in experiment 1 (7.22 g) than in experiment 2 (5.52 g). Root weight was lower for all plants defoliated during the growing season compared to control plants (Table 3). Multiple defoliations reduced root weight by 33%, while a single defoliation in June only reduced root weight by 14%.

Average root area was larger for plants in experiment 1 (619 cm^2) than in experiment 2 (417 cm^2). Average root length was also larger for plants in experiment 1 (95.8 m) than in experiment 2 (56.8 m). Root area and length were reduced by defoliation during the growing season compared to control plants (Table 3). Multiple defoliations reduced both root area and length by about 43%. A single defoliation in June reduced root area by 19% and root length by 16%.

Table 3. Average total root weight, root area, root length, and weight of TNC in roots of sand bluestem plants defoliated at different times and frequencies.

Time of Defoliation	Root Weight	Root Area	Root Length	Weight of TNC in Roots
	(g)	(cm^2)	(m)	(g)
Jun-Jul-Aug	5.36 a[1]	415 a	60.0 a	0.63 a
Jun-Aug	5.41 a	408 a	60.2 a	0.62 a
Jun	6.92 c	582 c	87.9 c	0.83 c
Jul	6.06 b	477 b	71.2 b	0.71 b
Aug	6.41 bc	513 b	73.8 b	0.71 b
Oct	8.04 d	715 d	104.9 d	0.95 d

[1]Means within a column followed by the same letter are not significantly different (P > 0.05).

Nonstructural Carbohydrate Response to Defoliation

Concentration of TNC in sand bluestem roots was not affected by clipping treatments or experiments. Average concentration of TNC in roots was 11.6% (SE=0.1). Average weight of TNC in roots was larger for plants in experiment 1 (0.851 g) than in experiment 2 (0.634 g). Defoliation during the growing season also reduced weight of TNC in roots (Table 3). Multiple defoliations reduced the weight of TNC in roots by 34%, while a single defoliation in June only reduced the weight of TNC by 12% compared to control plants.

Table 4. Average concentration of TNC in rhizomes of sand bluestem plants defoliated at different times and frequencies.

Time of Defoliation	TNC
	(%)
Jun-Jul-Aug	9.9 a[1]
Jun-Aug	9.2 b
Jun	9.2 b
Jul	10.1 a
Aug	9.0 b
Oct	10.1 a

[1]Means within column followed by the same letter are not significantly different (P > 0.05).

Defoliation did not consistently reduce concentration of TNC in rhizomes, and the total range in concentration was only 1.1 percentage points (Table 4). Experiments did not affect concentration of TNC in rhizomes. Defoliation did not affect weight of TNC in rhizomes. However, average weight of TNC in rhizomes was greater for plants in experiment 1 (0.147 g) than in experiment 2 (0.108 g).

Discussion

Root and Shoot Response to Defoliation

Reports of plant response to defoliation have been mixed. Jameson (1963) cited results from defoliation studies that ranged from increases to decreases in above-ground productivity. Severity, frequency, time of year, plant species, and environmental conditions all influence plant response to defoliation. Jameson also indicated that more than 1 year of defoliation may be required to evaluate the response of above-ground production. Above-ground production of sand bluestem was not affected by defoliation during this study. However, it should be stressed that this was a short-term study, and detrimental effects may appear if defoliation treatments are continued over a longer period.

Belsky (1986) indicated that both shoot and root responses should be considered when evaluating the effect of defoliation on grasses. Biswell and Weaver (1933), Crider (1955), Baker (1957), Santos and Trlica (1978), and Harradine and Whalley (1981) reported reductions in root growth following defoliation. These studies utilized several cool- and warm-season grasses, including big bluestem (*Andropogon gerardii* Vitman). Results from this study support their findings because root weight, area, and length of sand bluestem were reduced by defoliation during the growing season, with multiple defoliations having the largest impact on root growth.

While washing soil from roots, we observed that roots from some plants grew to the bottom of the container and then accumulated by branching and growing around the inside of the container. This was especially evident for plants receiving a single defoliation in October or June.

Weinmann (1948), May (1960), Jameson (1963), Stanton (1983), and Richards (1984) indicated that defoliation may affect roots to a larger extent than shoots. Their conclusions were drawn from studies on a variety of cool- and warm-season grass species.

Stanton (1983) and Richards (1984) stated that allocation priority of nonstructural carbohydrates shifted toward shoot growth and away from root growth following defoliation of grazing sensitive species. Results from this study support their conclusions because a single year of defoliation during the growing season did not reduce shoot production, but it did reduce root production.

Weaver (1930) and Ellison (1960) indicated that root growth was important to the competitive ability of plants. When root growth is reduced, ability of plants to compete for water and nutrients is also reduced. This is especially important in semi-arid and arid environments where water and nutrients are limiting. Defoliating sand bluestem during the growing season reduced root growth, with multiple defoliations resulting in the greatest reductions. This indicates that preferred species such as sand bluestem could be put at a competitive disadvantage in grazing situations.

Nonstructural Carbohydrate Response to Defoliation

Ogden and Loomis (1972), Caldwell et al. (1981), Archer and Detling (1984), and Christiansen and Svejcar (1987) stressed the importance of reporting TNC content on the basis of pools or total amounts rather than concentrations. Concentration values alone can be misleading because the weight or amount of plant material involved is ignored, and it is required to determine the actual amount of TNC. Results from this study illustrate their point because concentration of TNC in roots was not affected by defoliation. However, when expressed on a weight basis, defoliation reduced TNC in roots.

Total nonstructural carbohydrate content of sand bluestem roots was reduced by defoliation during the growing season. Reductions in TNC content can have significant effects on plant survival and productivity. Cook (1966) and White (1973) stated that stored TNC are needed for respiration, winter growth, spring growth, regrowth, and any rapid growth that requires more carbohydrates than are being assimilated. Weinmann (1948) reported that lowered TNC levels could cause reductions in plant production for several years.

The effect of defoliation on stored TNC appears to be related more to a shift in priority or allocation of TNC than the actual use of stored TNC for regrowth. This has been suggested by several researchers including Ryle and Powell (1975), Caldwell et al. (1981), Stanton (1983), and Richards (1984). This reallocation priority can result in the reduction of root mass as pointed out earlier in describing root response to defoliation.

Conclusions

A single year of defoliation did not affect above-ground production of sand bluestem but did reduce root production. Multiple defoliations were most detrimental to root growth. A single defoliation in June was the least detrimental of all growing season defoliations to root growth. This could be especially important when managing grasslands in semi-arid and arid environments because reduced root growth also reduces a plants ability to compete for water and nutrients. Although this was a clipping study involving only one species, results should be applicable to situations where grazing selectivity occurs. Plant species, such as sand bluestem, that are preferred and/or sensitive to grazing pressure could be put at a competitive disadvantage when utilized to a greater degree than associated vegetation.

Grazing strategies which increase the probability of individual tillers being defoliated multiple times during the growing season may be harmful to preferred species such as sand bluestem. Grazing during the dormant season or once during the early part of the growing season should be least detrimental to species such as sand bluestem.

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