Effects of fire, mowing and nitrogen addition on root characteristics in tall-grass prairie

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Abstract. Root harvests and root windows were used to study the influence of fire, mowing and nitrogen additions on root lengths, biomass, and nitrogen content in tall-grass prairie. Four years of nitrogen additions ($10 \, g \, m^2 \, yr^{-1}$) increased below-ground mass by 15 % and nitrogen concentration in that mass by 77 %. In general, live roots and rhizomes exhibited greater increases in nitrogen concentrations than detrital roots and rhizomes. After four years of treatment, live roots and rhizomes immobilized an additional 1.5 to 5 g/m^2 of nitrogen, depending upon specific treatment, while dead roots and rhizomes immobilized an additional 3 to 3.5 g/m^2. Average root growth parameters, as measured with root windows, were positively correlated with above-ground peak foliage biomass; however, the only significant correlation was between average new root growth and above-ground peak foliage biomass ($r = 0.73$, $p \leq 0.04$). Root growth and decay, as measured by annual mean values for eight root windows over a four year interval, were insensitive to climatic and treatment effects.

Keywords: Below-ground Biomass; Rhizome; Root growth; Root window.

Nomenclature: Gould (1975).

Introduction

Our knowledge of roots and root turnover in tall-grass prairie is derived largely from studies conducted by Weaver and his colleagues (e.g. Weaver 1950, 1958; see Sun et al. 1997), which often consisted of descriptive inventories of root standing crops. Subsequent studies have provided time-series estimates of root production using root harvesting procedures (Dahlman & Kucera 1965) or harvesting and root window procedures (Hayes & Seastedt 1987; Seastedt 1988). Neither study however, described how these patterns might be related to resource availability or above-ground primary productivity.

Nitrogen limitation to primary production occurs in many terrestrial ecosystems (Vitousek & Howarth 1991) and is particularly common in frequently burned tall-grass prairie (Seastedt et al. 1991). A key factor to nitrogen limitation of primary production in the tall-grass prairie is the immobilization potential of microbes associated with root detritus. Micro-organisms rapidly assimilate and use easily degradable organic substances during the initial stages of root decomposition (Waid 1977). Nutrients such as N, P and S which micro-organisms require for biosynthesis are immobilized until the micro-organisms die and decompose. Thus, patterns of root death and subsequent nitrogen immobilization may have a direct influence on future primary productivity. For example, a year of high root production may be followed by a year of severe nitrogen limitation due to high immobilization of nitrogen by microbes. As a consequence of this reduced nitrogen availability, a reduction in above-ground plant growth may be observed.

Studies have noted the effects of previous above-ground plant growth or previous year's rainfall on subsequent productivity (Towne & Owensby 1984; Abrams et al. 1986), but the mechanisms behind these relationships have not been identified. Tilman & Wedin (1991) demonstrated that year-to-year patterns in plant productivity can be chaotic, with high production followed by low production. We suggest that a knowledge of below-ground production is crucial to understanding plant contributions to soil nitrogen immobilization and mineralization patterns, and that foliage production data cannot be used with sufficient accuracy to estimate root response (e.g. Chapin 1991). Here, we present observations of root growth and decay patterns, and compare these data to standing crop estimates obtained after four years of treatment with various combinations of fire, mowing and nitrogen additions. The objectives of our study were to: (1) test the null hypothesis that no relationship exists between root growth dynamics and peak foliage production in tall-grass prairie, and (2) compare root growth dynamics to root standing crops and peak foliage production obtained from a long-term fire, mowing and nitrogen enrichment experiment. Data from this experiment also were used to test the hypothesis that nitrogen additions would affect root production and therefore alter the soil sink strength for carbon.

Material and Methods

The study was conducted at Konza Prairie Research Natural Area (KPRNA), a site owned by the Nature Conservancy and located 10 km south of Manhattan, Kansas (39° 3' N, 96° 3' W). Vegetation in this area is dominated by *Andropogon gerardii*, *A. scoparius* and *Sorghastrum nutans* (for details, see Hulbert 1988). Rainfall averages 830 mm/yr, of which ca. 75 % occurs in the growing season from April through September (Brown & Bark 1971). During the data collection period (1986 - 1989), annual rainfall was normal or above normal for every year except 1988. In 1988, annual rainfall was only 513 mm, 39 % below normal. Although annual precipitation was normal in 1989, the rainfall generally occurred after plant growth had ended.

Root windows

Root windows were installed by excavating a trench at a 15° angle ca. 40 cm deep into a south-facing slope at Konza Prairie. The soil at the site is a silty clay loam, a fine mixed mesic Udic Haplustoll, with ca. 1 m to bedrock (Hayes & Seastedt 1987). Two plexiglass windows were installed in the early spring in 1984; small gaps between the window and soil were carefully backfilled with soil removed from the excavation. Windows were covered with 15 cm of styrofoam insulation and covered with canvas when not in use. The windows were of a uniform size (40 cm × 50 cm) and were installed to the specifications stated in Hayes & Seastedt (1987). Methodologies and results on lengths, growth and disappearance of roots in these windows for the 1984 and 1985 growing seasons are summarized in Hayes & Seastedt (1987). Six more windows were installed at the same location in the spring of 1985. Four of the eight windows were located beneath plots burned annually in late April, and four beneath unburned plots. In 1987, two burned and two unburned windows were randomly selected to be mowed to a foliage height of 5 cm to simulate grazing. Mowing frequency was constrained by rainfall amounts; in 1987 these windows were mowed twice in May and once in early June, while in 1988 and 1989, plots were mowed only once, in early June of each year.

Total root length and new root growth were determined directly from tracings of roots visible in each window made on clear acetate sheets. Tracings were made about every other week, 10 - 11 × over the growing season, with starting dates in each year (1986 - 1989) determined by indications of root activity. Each window was divided into nine, 10 cm × 10 cm quadrats to measure lengths; results from the nine quadrats were summed prior to analysis. Disappearance between sampling periods was determined by roots visible in the previous week's tracing (time $t-1$) but not visible in the present week's tracing (time t). Total root length was the absolute length of roots at time t, and new root growth was equivalent to roots present at time t that were not present at time $t-1$. There are a number of assumptions and potential errors associated with the root window technique (Hayes & Seastedt 1987; Seastedt & Ramundo 1990), but we have no reason to believe that biases, if present, would affect either treatment or year-to-year comparisons. Each window was used to produce a single annual estimate of average total root length, average new root length, and average disappearance of roots. Without biomass or volume information, these values only represent indices of root growth dynamics.

We used a one-way ANOVA to measure fire effects on the 1986 root-window data. A two-factor factorial design was used to evaluate yearly treatment comparisons for the 1987-1989 fire and mowing treatments. Among-year effects for the entire 1986-1989 interval was conducted on seasonally averaged data using a repeated measures ANOVA. Means comparison analyses were performed using the Student-Newman-Keuls test.

Below-ground biomass plots

The below-ground plots were established in 1986 as a replicated, factorial experiment designed to study plant and soil biological processes in tall-grass prairie. 32 10 m × 10 m plots with a 5-m buffer between plots were installed ca. 150 m from the root windows on a site burned in 1985. The soil of these plots was similar to that found at the root windows site, a silty clay loam, a fine mixed mesic Udic Argiustoll. The experimental design used here involved fire, mowing and nitrogen addition treatments, with eight replicates of each treatment. Plots were mowed annually in June to a height of 5 cm and raked. Fertilizer additions consisted of annual applications of 10 g m^{-2} yr^{-1} of nitrogen as ammonium nitrate pellets applied in late April or early May of each year. This amount was in excess of plant needs and appeared sufficient to minimize nitrogen immobilization (Seastedt et al. 1991).

Table 1. Summary of experimental designs and sample sizes for the root windows and below-ground plots.

Root windows	1986	1987 - 1989	
		Mowed	Unmowed
Burned	$n = 4$	$n = 2$	$n = 2$
Unburned	$n = 4$	$n = 2$	$n = 2$
Below-ground plots		No nitrogen	Nitrogen added
Unburned	Unmowed	$n = 4$	$n = 4$
Unburned	Mowed	$n = 4$	$n = 4$
Burned	Unmowed	$n = 4$	$n = 4$
Burned	Mowed	$n = 4$	$n = 4$

Two soil cores (5 cm diameter × 20 cm depth) were taken from each plot in early autumn of 1989 after four years of treatment. Samples were composited, washed in a root elutriator (Smucker et al. 1982), and rinsed through a 0.5 mm mesh sieve. The root segments were then refloated in a shallow pan and separated into live and dead roots and rhizomes based on color, friability, and the condition of the stele. Samples were then dried at 70 °C and weighed. Subsamples were ground in a Wiley mill and nitrogen analyses were conducted using a sulfuric acid digest followed by colorimetric measurements with an Alpkem autoanalyzer.

Rhizomes and large forb roots were estimated by hand sorting a $0.1 \, m^2 \times 0.3$ m deep soil monolith for each plot. Rhizomes and the large tuberous or fibrous forb roots were washed, sorted into live and dead categories, trimmed of fine roots, dried, weighed and subsampled for nitrogen content as described above. Statistical evaluation of the root and rhizome data used a blocked design with fire, mowing and nitrogen as main effects. A summary of experimental designs with sample sizes for both experiments is shown in Table 1. Peak foliage production was measured in August of each year by clipping four $0.1\text{-}m^2$ quadrats on each of the plots used to measure root and rhizome mass. These results have already been reported in Seastedt et al. (1991). In addition, we estimated peak foliage biomass from data collected as part of the Long-Term Ecological Research (LTER) program (e.g. Briggs et al. 1989). For each year, 10 replicate $0.1\text{-}m^2$ samples were collected in August from an annually burned and unburned watershed.

Fig. 1. Average root lengths, root disappearance and new root growth for each year by treatment. Values for each date are means and standard errors of four windows in 1986 and means of two windows thereafter.

Results

Annual patterns in root window measurements

Results for peak foliage production at the root window sites were somewhat different from those observed at other sites on Konza Prairie. Peak foliage biomass showed a significant positive fire response in 1987 ($p \le 0.05$, Fig. 1). In both 1988 and 1989, above-ground biomass was significantly higher in unburned prairie and not statistically different in 1986 ($p \le 0.05$, Fig. 1). Below-ground, there were no significant differences due to the fire or mowing treatments for any of the parameters measured with the root windows during the 1987, 1988 or 1989 growing seasons (Fig. 1). However, in 1986, for all parameters measured, average root lengths in burned prairie were significantly higher than in unburned prairie ($p \le 0.05$, Fig. 1).

Peak foliage biomass was significantly lower in 1989 than in the previous three years ($p \le 0.05$, Fig. 1). The below-ground measurements obtained for this s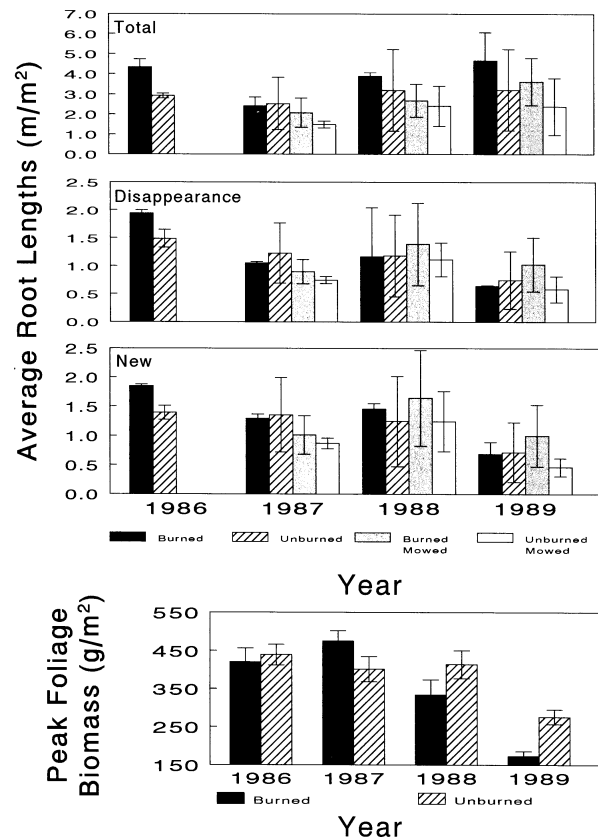ame interval did not show this effect for total root lengths (Table 2), but did show statistically different results for average new root length in 1989 relative to all other years (Table 2, $p \le 0.05$). Disappearance rates were statistically higher in 1986, but showed no differences among the other three years (Table 2, $p \le 0.01$). We correlated growth parameters for each window with peak foliage estimates. While all parameters suggested positive correlations, only the correlation between peak foliage and average new root growth was statistically significant ($r = 0.73$, $p \le 0.04$).

Below-ground biomass, fire, mowing and nitrogen

Roots and rhizomes each responded differently to the various treatments. After four years of treatment, live root mass exhibited no fire or nitrogen main effects, but did exhibit significant fire and mowing, and mowing and nitrogen interactions (Table 3). Total (live plus dead) root biomass from the burned, unmowed plots averaged $921 \, g/m^2$, while the unburned, unmowed treatment produced significantly less at $699 \, g/m^2$ ($p \le 0.05$, Fig. 2). Mowing stimulated dead root mass under

Table 2. Root Window Characteristics: ANOVA F-Values[1].

Source of variation	df	Length	New	Disappearance
Year	3	1.66	4.31 *	5.43 **
Fire (B)	1	3.29	2.38	1.40
Mowing (C)	1	2.88	0.17	0.04
B*C	1	0.09	0.15	0.16
Error	25			

[1]F-value obtained by entering variable last into model;* $p \leq 0.05$; ** $p \leq 0.01$.

Table 3. Effects of fire, mowing and nitrogen additions on live and dead root mass harvested in 1989 after 4 yr of treatment.

Variable	df	Live roots F-value[1]	p	Dead roots F-value[1]	p
Fire[2] (A)	1	3.29	0.167	1.39	0.324
Mowing[3] (B)	1	9.87	0.051	13.46	0.035
Nitrogen (C)	1	1.09	0.301	3.65	0.062
A*B[3]	1	20.10	0.021	9.37	0.054
A*C	1	2.80	0.101	0.23	0.636
B*C	1	4.37	0.043	0.15	0.705
A*B*C	1	0.33	0.571	0.23	0.631
Error	24				

[1]F-value obtained by adding variable last into model;
[2]Values obtained by using block*burn as an error term;
[3]Values obtained by using block*burn*mow as error term; all other analyses used complete error term in calculation of F-value.

unburned conditions; consequently, when live and dead roots were summed, mowing had a strong effect on total root mass (Fig. 2). In contrast to results for grass roots, live rhizomes and forb roots exhibited a positive response to fire, but also exhibited a fire and mowing interaction (Table 4).

Surprisingly, nitrogen additions had little effect on either live or dead root and rhizome standing crops (Tables 3 and 4). However, there was a significant interaction between nitrogen and mowing for live root mass (Table 3). When results for total roots and rhizomes were pooled and compared, total mass in the

fertilized plots was increased by 15%. However, this increase was small in comparison to the 77 % increase in average nitrogen amounts in this root and rhizome material (13.8 g/m² on fertilized plots, 7.8 g/m² unfertilized).

Nitrogen concentration of both live roots and rhizomes was increased significantly by nitrogen additions ($p \leq 0.05$, Fig. 3). Dead roots and rhizomes exhibited smaller, but still significant, increases in nitrogen concentration due to fertilization ($p \leq 0.05$, Fig. 3). Nitrogen concentration of live roots under the unburned, unmowed, unfertilized treatment was significantly higher than under the other three treatments ($p \leq 0.05$). Nitrogen amounts in roots and rhizomes of fertilized plots increased the most in the burned, unmowed treatment, while unburned, unmowed plots exhibited the smallest increase (Fig. 4). Dead roots and rhizomes were capable of immobilizing 3 to 3.5 g/m² of the added nitrogen without a corresponding significant increase in mass
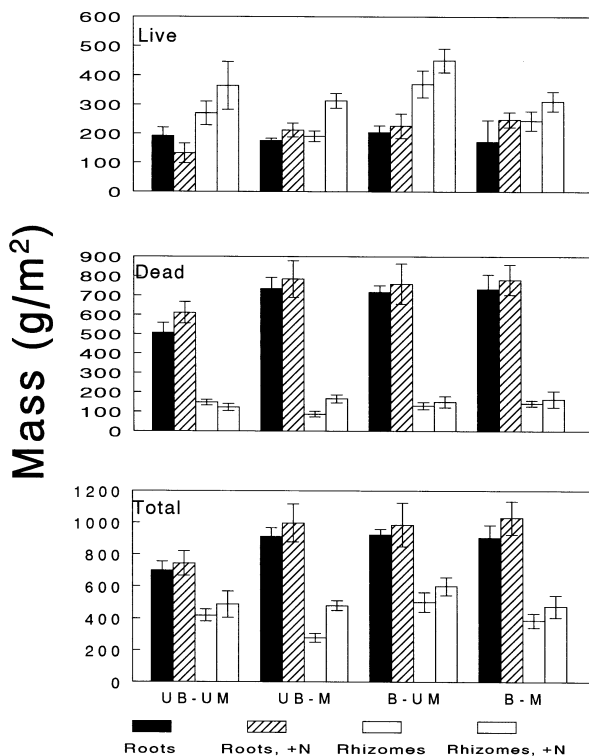

Fig. 2. Live, dead and total (live plus dead) root and rhizome mass collected from below-ground plots after 4 yr of treatment. Values are means and standard errors of four replicates per treatment. Symbols indicate burned (B) or unburned (UB), mowed (M) or unmowed (UM).

Table 4. Effects of fire, mowing and nitrogen additions on live and dead rhizome and forb root mass harvested in 1989 after 4 yr of treatment.

Variable	df	Live rhizomes + forbs F-value[1]	p	Dead rhizomes F-value[1]	p
Fire[2] (A)	1	43.74	0.007	2.65	0.202
Mowing[3] (B)	1	6.45	0.084	0.02	0.886
Nitrogen (C)	1	3.38	0.073	1.92	0.172
A*B[3]	1	35.67	0.009	0.75	0.450
A*C	1	0.23	0.637	0.04	0.844
B*C	1	2.76	0.103	2.53	0.193
A*B*C	1	2.46	0.124	2.24	0.142
Error	24				

[1]F-value obtained by adding variable last into model;
[2]Values obtained by using block*burn as an error term;
[3]Values obtained by using block*burn*mow as error term; all other analyses used complete error term in calculation of F-value.
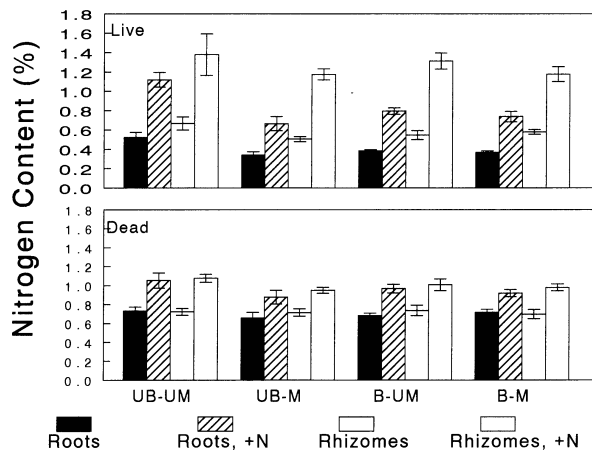
Fig. 3. Nitrogen concentration of live and dead root and rhizome mass collected from below-ground plots after 4 yr of treatment. Values are means and standard errors of four replicates per treatment. Symbols indicate burned (B) or unburned (UB), mowed (M) or unmowed (UM).

with the exception of the unburned, mowed treatment (Figs. 3 and 4). Live roots and rhizomes exhibited increases from 1.5 to 5 g/m² of nitrogen, again without significantly increasing mass except in the unburned, mowed treatment (Figs. 2 and 4).
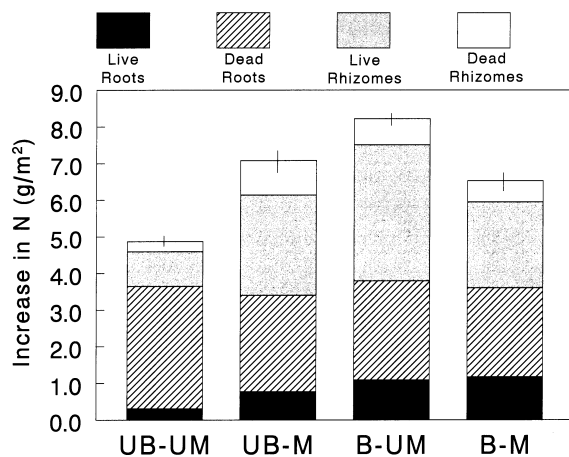
Fig. 4. Increase in nitrogen amounts of roots and rhizomes in below-ground plots after 4 yr of treatment. These results were obtained by multiplying biomass estimates by concentration data for the respective samples. These values were then converted to an areal estimate. Fertilized averages were then subtracted from unfertilized averages to obtain the increase for the treatments shown. Symbols indicate burned (B) or unburned (UB), mowed (M) or unmowed (UM).

Discussion

Average annual estimates of length, new growth and disappearance were similar over the period of our study. Wet years may not result in large root increases since water and nutrient needs may be met by a modest root network. In dry years, more roots are needed, but the amount of carbohydrate reserves or dryness itself may limit new root growth. The net effect of these plant carbon allocation responses to resource needs may ameliorate year-to-year differences in root productivity.

Fire and mowing had little within-season effect on total root length, new growth and disappearance of roots when compared to the between year differences in these same parameters. Our conclusions about both climate and treatment effects are limited by having only two windows for each treatment. Consequently, only very large differences are detectable by analysis of variance, and such differences were not observed here.

Average root growth parameters were not strongly positively correlated with above-ground peak foliage production and our root window data suggest that the timing of new root growth and disappearance is only partially related to precipitation. Data from this study suggest that root growth may be largely constrained by growing season phenology and soil moisture as mediated by treatment. Growth appears to occur in late spring with opportunistic pulses thereafter in response to precipitation. Thus, 'good' years of production may not necessarily produce high amounts of root detritus. Constraints on peak foliage production by plant growth strategies and time lags in responding to favorable conditions may provide some explanation for the weakness of the correlation between above-ground and below-ground productivity. Lauenroth & Sala (1992) reported that above-ground forage production showed time lags of several years in responding to increases in precipitation. They concluded that change in vegetation structure of short grass prairie has a characteristic response time, which constrained production responses in wet years. The absence of a strong relationship between plant foliage production and precipitation in the tall-grass prairie is equally evident (Towne & Owensby 1984; Abrams et al. 1986). The lack of consistent patterns in root growth observed in this study would also contribute to this lack of coupling between plant foliage production and precipitation.

Results from our fertilization experiments indicate that both living and dead plant roots and rhizomes can accumulate nitrogen. Root and rhizome biomass was only moderately increased by a large addition of nitrogen (Tables 2 and 3), but the concentration of nitrogen in roots and rhizomes increased substantially. The greatest overall increase occurred in the burned, unmowed treatment where an additional 8.5 g/m² of nitrogen was

contained in both live and dead roots and rhizomes. Vegetation on frequently burned prairie has been shown to be more nitrogen limited than unburned prairie (Seastedt et al. 1991); consequently, roots in burned prairie should have a higher immobilization potential.

Finally, chronic nitrogen additions increased living and dead below-ground plant mass by ca. 15 %. However, we believe that this response represents a transient maximum (Seastedt & Knapp 1993) and that continued nitrogen additions will result in species shifts that will subsequently decrease soil carbon inputs (e.g. Lorenz & Rogler 1972; Tilman et al. 1996). Continued studies of the plots described here will test this hypothesis.

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