Competition, nutrient reduction and the competitive neighbourhood of a bunchgrass

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Abstract. The bunchgrass, *Schizachyrium scoparium* (Michx.) Nash-Gould, is often the dominant species on unproductive, nitrogen-poor, sandy soils in Minnesota. Removal of all neighbouring plant biomass within a 2 m radius of individual *Schizachyrium scoparium* bunches resulted in a 3·8-fold increase in the biomass of *S. scoparium* bunches and demonstrated that the neighbouring plants had been reducing the level of extractable ammonium plus nitrate by 3·9-fold. Contrary to Grime's (1979) assertion, this suggests that there may be strong competition in this unproductive habitat. The mechanism of competition may be nutrient consumption. *Schizachyrium scoparium* significantly reduced nitrate and ammonium levels within a 60–75 cm radius around individual plants, with the magnitude of reduction decreasing with distance from an individual. The neighbourhood from which a *S. scoparium* bunch obtains nitrogen thus had an area of 1–1·5 m² and may include hundreds of other individual plants.

Key-words: *Schizachyrium scoparium*, nutrient reduction, neighbourhood competition, nitrate, ammonium, competition for nitrogen

Introduction

All plants require light, water and a variety of soil nutrients for growth. If any of these resources are in short supply, plants may, in theory, compete for them. The simplest, and probably most common, mechanism of plant competition may be through resource consumption and the resulting reduction in resource availability (Tilman, 1982, 1988). Resource reduction, though, is a localized phenomenon. Because terrestrial plants are sessile and finite in size, each individual plant should create a region of resource reduction in its immediate vicinity. In the case of competition for light, the size of the neighbourhood in which resource reduction (shading) occurs can be easily observed. However, because it is difficult to determine the spatial distribution of the roots of an individual plant and the effects of these roots on soil resources, there is no comparably simple way to observe either the size of the neighbourhood of nutrient reduction by a plant or the magnitude of nutrient reduction or the effects of such reduction on the growth of potential competitors. Indeed, Grime (1979) offered the often quoted, though controversial (e.g. Newman, 1973; Grubb, 1985; Tilman, 1987a, 1988), suggestion that plant competition is weak in nutrient-poor habitats, but is intense in nutrient-rich habitats in which light is more limiting.

In this paper, I report an experiment in which neighbouring biomass was removed from around individual plants. It was performed in a nitrogen-poor, unproductive habitat and was designed to determine (1) the extent to which the biomass of the dominant species, a bunchgrass, was inhibited by its neighbours, (2) the magnitude of soil nutrient reduction by these neighbours and (3) the spatial pattern (i.e. neighbourhood) of soil nutrient reduction by the bunchgrass.

Materials and methods

This work was performed in 1987 in a 30-year-old field at Cedar Creek Natural History Area. This field, called Field B (Tilman, 1987b), is dominated by *Schizachyrium scoparium* (Michx.) Nash-Gould (little bluestem; formerly *Andropogon scoparius*), *Poa pratensis* L., *Panicum oligosanthes* Schult., *Lespedeza capitata* Michx., *Cyperus filiculmis* Vahl. and several goldenrod (*Solidago*) species. Its excessively well-drained sandy soils (Grigal *et al.*, 1974) are nitrogen poor, with total soil N averaging about 450 mg of N per kg of dry soil (Tilman, 1987b; Inouye *et al.*, 1987). Above-ground living plant biomass (dry) has a growing season maximum of about 130 g m⁻². which is one third of the average Risser (1985) reported for the North American tallgrass prairie biome. Nutrient addition experiments in operation since 1982, have shown that only nitrogen is a significant limiting soil resource in this field (Tilman, 1987b, 1988).

The most abundant plant is the bunchgrass *S. scoparium* which is N limited in this field (Tilman, 1987b). This experiment was designed to determine if the growth of *S. scoparium* bunches was inhibited by its neighbours, the size of the neighbourhood in which *S. scoparium* bunches reduce mineral N, and the magnitude of nutrient reduction caused by its neighbours. The experiment was located in a 10 m × 40 m area adjacent to existing nutrient addition experiments in the field (Tilman, 1987b).

At the start of the growing season in early May 1987, 10 approximately equally-sized *S. scoparium* bunches, with basal diameters of 10–15 cm, were selected so as to be separated by at least 4 m from each other. Each was designated as the centre of a circular plot with a radius of 2 m. Five plots were randomly assigned to a neighbourhood biomass removal treatment and five served as unmanipulated controls.

The neighbourhood biomass removal treatment consisted of killing all living biomass within a plot except the central *S. scoparium* bunch by spray application of a short-lived, biodegradable herbicide, N-(phosphonomethyl)glycine (trade name: Roundup), at a rate of 0.82 g m^{-2}. The central *S. scoparium* bunch was protected from spray by enclosing it within a plastic bag. Herbicide was reapplied (a total of five more times in 1987) to localized areas as needed throughout the growing season to keep the areas free of any living plants. Herbicide was similarly applied throughout the 1988 growing season.

On 6 August, 25 August and 4 September (1987) and on 21 July 1988, a series of 10 cm deep by 2.5 cm diameter soil cores were collected at various distances (see Fig. 1) from the central *S. scoparium* bunch in each plot. On 6 August, soil cores were collected from two additional depths, 10–20 cm, and 20–40 cm, but only in two plots per treatment. For each soil sampling, a coordinate system was randomly established with four perpendicular lines extending out from the central plant in each plot. A soil sample was collected on each of the four transects at each distance from each central plant. The four samples from a given distance in a given plot were composited and mixed. Immediately, a sub-sample was placed in a pre-weighed covered tin for determination of soil moisture, and a separate sub-sample (*c* 15 cm^3) was added to a 75 ml pre-weighed vial containing 50 ml of 2 M KCl for determination of extractable ammonium and nitrate. After all soil samples were collected, KCl vials and tins were weighed. KCl vials were shaken for 30 min and allowed to settle

at 4 °C overnight. Ammonium and nitrate concentrations in the clear supernatant were then measured using a Technicon Autoanalyser. Tins were opened, and soils dried for 24 h at 103 °C. For each composited soil sample, the observed mass of soil added to the KCl vials and the water content of this soil were used in calculating the mg of extractable N (ammonium or nitrate) per kg of dry soil.

On 4 September 1987, the maximum height of each central plant was measured. Its above-ground biomass was harvested, sorted into living biomass (this year's production) and litter (produced during preceding years), dried and weighed.

Results

The removal of all neighbouring biomass resulted in significantly higher nitrate concentrations within a 1 m radius of central *S. scoparium* bunches than in controls (Table 1). Ammonium was significantly higher for two of the three sampling dates in 1987 and for the 1988 sample, but the ammonium response was not as large as the nitrate response (Table 1). Linear regression showed that extractable ammonium and nitrate did not change significantly with distance from central *S. scoparium* bunches in the control plots, and that extractable ammonium did not change with distance in the biomass removal plots (Fig. 1). Nitrate concentration had a definite spatial pattern in the biomass removal plots. It increased significantly with distance from the central *S. scoparium* bunches for the first 60 or 70 cm, and then reached an asymptote (Fig. 1). This effect occurred for the 0–10 cm depth soil samples on all dates, as well as for the 10–20 cm depth and the 20–40 cm depth soil samples on the one date they were collected. Regressions of nitrate on distance for the biomass removal plots had lower slopes for 10–20 cm depth samples than for the 0–10 cm samples and the 20–40 cm samples had lower slopes than the 10–20 cm soil samples.

The highest concentrations of extractable nitrogen occurred at about 1 m from the centre of the biomass removal plots, which is also about 1 m from the outer edge of these plots. This location represents the furthest possible distance from living plants within the biomass removal plots. In 1987, the concentration of nitrate-N in the upper 10 cm of soil averaged 5.7 mg kg^{-1} at the 1 m distance in the biomass removal plots and averaged 0.13 mg kg^{-1} at this distance in the controls. Thus, removal of plants led to a 44-fold increase in extractable nitrate in the region
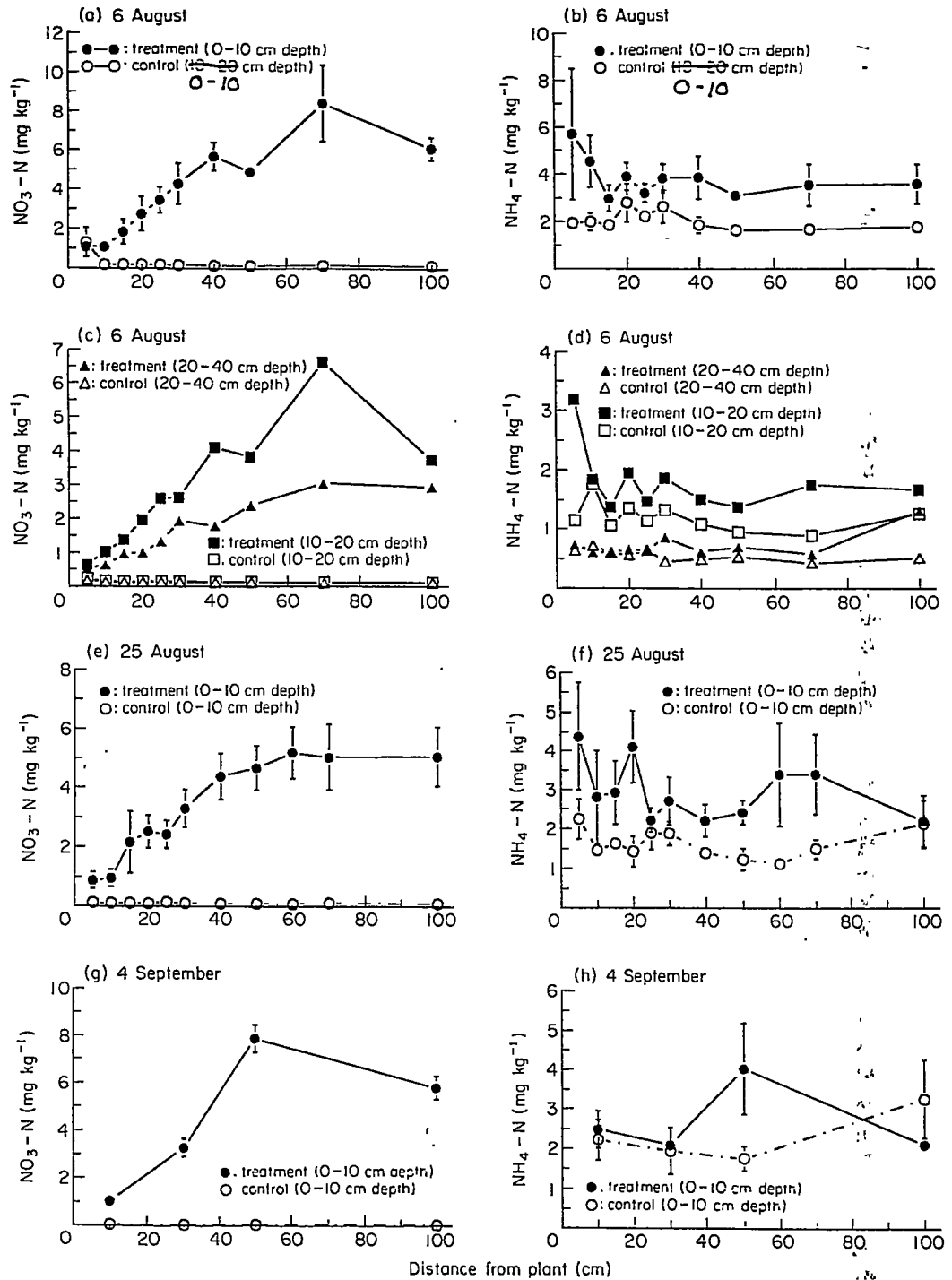
Fig. 1. Each point shows the mean and standard error ($n = 5$) for 2M KCl extractable nitrate or ammonium. Solid symbols are for neighbourhood biomass removal plots. Open symbols are for unmanipulated control plots. for which standard errors are often less than the size of the symbol. The abscissa is the distance from the *S. scoparium* bunch that is at the centre of each plot. Parts a, b, e, f, g and h are based on soil samples for 0–10 cm depth. Parts c and d show data for 10–20 and for 20–40 cm depth soil samples, for which standard errors are not shown because only two replicates per treatment were sampled.

Table 1. Ammonium and nitrate concentrations in 0–10 cm soil cores from control plots versus neighbourhood biomass removal plots (treatment) are compared using one-tailed Student t to test the *a priori* hypothesis that biomass removal causes a significant increase in ammonium and nitrate. In all cases, treatment-average nutrient concentrations were higher in biomass removal plots than in controls (Fig. 1). To avoid pseudoreplication, t-tests use the average ammonium or nitrate concentration for an entire plot, with the average based on all samples collected for all distances from 0–100 cm from the plot centre. There are eight degrees of freedom for error; ***means $P \leq 0.001$; NS means $P > 0.05$.

Date	Nitrate-N (mg kg^{-1})			Ammonium-N (mg kg^{-1})		
	Control	Treatment	t-value	Control	Treatment	t-value
6 August 1987	0·26	3·96	6·66***	2·02	3·83	3·46***
25 August 1987	0·10	2·78	5·63***	1·78	2·65	2·12***
4 September 1987	0·03	4·48	31·62***	2·30	2·69	0·74 NS
21 July 1988	0·28	8·66	8·71***	2·10	6·94	5·65***

furthest from the potential effects of plant uptake. The concentration of ammonium-N in 1987 for this location was 2·6 mg kg^{-1} for the removal plots and 2·0 mg kg^{-1} for the controls, indicating a 1·3-fold increase. The sum of nitrate-N and ammonium-N was 3·9-fold higher at the 1 m distance in the biomass removal plots than in the controls.

Removal of neighbourhood biomass had a significant effect on *S. scoparium* biomass. Living biomass (i.e. that produced in 1987) averaged 39·2 g per plant for control plots, but 147·4 g per plant for neighbourhood biomass removal plots. A t-test revealed a significant difference between these means ($t = 2·98$, d.f. $= 8$, $P < 0·02$), as did the Wilcoxon two sample test ($T = 15$, $n = 5,5, 0·01 < P < 0·05$). In contrast, litter per plant, an estimate of plant biomass prior to treatment, did not differ significantly ($t = 1·51$, d.f. $= 8$, $P > 0·10$). Little bluestem height was greater in the neighbourhood biomass removal plots (83·8 cm *vs* 59·4 cm), but not significantly so ($t = 1·73$, d.f. $= 8$, $P > 0·10$).

Discussion

These experiments demonstrate four significant effects of removal of neighbourhood biomass: (1) the biomass of *S. scoparium* increased 3·8-fold following neighbourhood biomass removal; (2) the concentration of ammonium-N plus nitrate-N increased · 3·9-fold after biomass removal; (3) nitrate concentration increased with distance from the central *S. scoparium* bunches in the neighbourhood biomass removal plots; but (4) ammonium concentration, though higher, was not distance-dependent. The lack of distance-dependence for ammonium may result from the effects of nitrifying bacteria, which convert ammonium to nitrate and thus tend to keep ammonium levels

constant, or may result from differences in usage of ammonium and nitrate by *S. scoparium*.

The 3·9-fold increase in extractable ammonium plus nitrate that occurred at 1 m from the centre of the biomass removal plots suggests that plants were responsible for a major reduction of mineral nitrogen concentrations in these nitrogen-poor soils. The 3·8-fold increase in *S. scoparium* biomass in the neighbourhood biomass removal plots suggests that this dominant species is greatly and significantly inhibited by its neighbours. The apparent similarity of the magnitudes of these two effects (3·8 and 3·9), though, is probably coincidental. Because low to moderate rates of N addition caused a significant increase in *S. scoparium* biomass in this field (Tilman, 1987b), and because biomass removal resulted in increased mineral N, the mechanism whereby other plants inhibit *S. scoparium* is likely to be through their consumption of mineral N. Because plant biomass is low in these plots and because *S. scoparium* was taller than its neighbours, light competition seems unlikely to be important.

When the neighbouring plants were killed by the herbicide, their organic matter, which was mainly below-ground, would have begun to decompose. After an initial period of N immobilization, this should have increased the rate of N mineralization in the soils. Such mineralization could have been partially responsible for the higher concentration of extractable N in the neighbour removal plots and for the increased biomass of neighbourless *S. scoparium* bunches. However, this would not negate the existence of competition between *S. scoparium* and its neighbours. The N mineralized by the decomposition of neighbours had been consumed, and thus had been made unavailable to *S. scoparium*, by those neighbours. The significant increase in the biomass of *S.*

scoparium in the herbicide treated plots, whether caused mainly by the cessation of uptake by the neighbours or by their decomposition, demonstrates that *S. scoparium* was inhibited by its neighbours. Although there can always be alternative interpretations for any field manipulation experiment (Bender, Case & Gilpin, 1984), these results, when combined with the changes in species composition that resulted from N addition (Tilman, 1987b), support the hypothesis that plants are competing for mineral N in these N-poor soils. Such inhibition of *S. scoparium* by its neighbours is inconsistent with Grime's (1979) suggestion that plants do not compete on nutrient poor soils.

The discrete nature of all individual plants means that each individual is likely to cast a nutrient reduction shadow. The cumulative effect of such localized resource depletion by the neighbours of *S. scoparium* bunches may explain their ability to inhibit the growth of this dominant bunchgrass on the N-poor soils. Similarly, *S. scoparium* could potentially influence the growth of any plants with roots in its zone of nutrient reduction. Because there are from 400–1400 stems m^2 in these old fields (S. Gleeson and D. Tilman, personal observations) each *S. scoparium* could potentially inhibit the growth of, and be inhibited by, hundreds of other plants through their effects on the pool of mineral N in the soil. The large number of individual plants included within the neighbourhood of any given individual may mean that plant nutrient competition can be modelled as if plants were competing for a common nutrient pool, which has been a common assumption in models of resource competition (e.g. Tilman, 1980, 1982, 1988; but see Pacala & Silander, 1985; Pacala. 1986).

Acknowledgments

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