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NITROGEN CYCLING, PLANT COMPETITION, AND THE STABILITY OF TALLGRASS PRAIRIE

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Abstract. Five perennial grass species (*Schizachyrium scoparium* (Michx.) Nash, *Andropogon gerardi* Vitman., *Poa pratensis* L., *Agropyron repens* (L.) Beauv., and *Agrostis scabra* Willd.) were grown on an experimental soil nitrogen (N) gradient. In competition plots on low-N soils, the two prairie bunchgrasses, *Andropogon* and *Schizachyrium*, completely displaced the other three species within three years. However, displacement did not occur on high-N soils. In N-cycling studies using monocultures, the two prairie species reduced soil N supply rates compared to the other species by tying up N in their slowly decomposing litter. These species, therefore, create the low-N conditions for which they are superior competitors. This positive feedback between plant competition and N cycling may be a critical process in tallgrass prairie. Alteration of the N cycle can disrupt this feedback, however. High rates of atmospheric N deposition caused by air pollution may be sufficient in parts of the Midwest to seriously threaten the stability of tallgrass prairie remnants.

INTRODUCTION

Prior to settlement, the tallgrass prairie covered a vast section of North America. Considering the dramatic variation in soil type and climate within this region, the vegetation was surprisingly uniform. The dominant plant species were a set of warm-season grasses: big bluestem (*Andropogon gerardi* Vitman.), little bluestem (*Schizachyrium scoparium* (Michx.) Nash), Indian grass (*Sorghastrum nutans* (L.) Nash), and switchgrass (*Panicum virgatum* L.). How the tallgrass prairie was able to dominate such a large and diverse region and why, on the other hand, it was so vulnerable to numerous disturbances, including overgrazing and the invasion of exotic species, is only beginning to be understood. In the last few decades, ecologists have recognized the critical role of fire in maintaining tallgrass prairie (Knapp and Seastedt 1986, Axelrod 1985). The results presented in this paper suggest nitrogen (N) cycling may also play a critical role.

Experiments, both in the Kansas Flint Hills (Owensby et al. 1970, Seastedt et al. 1991) and in Minnesota sand prairies (Tilman 1987), have shown that N is the nutrient most frequently limiting the productivity of tallgrass prairie in non-drought years. Thus, the widely held assumption that moisture limitation is the primary constraint on productivity in tallgrass prairie (Weaver 1954) needs to be reconsidered. In contrast to increased productivity due to N addition, water addition did not result in significant increases in productivity (Owensby et al. 1970, Tilman 1990). Using several different precipitation parameters as predictors, only 14% of the variability in above-ground net primary production could be accounted for in a 50 year study of tallgrass prairie in the Kansas Flint Hills (Towne and Owensby 1984). This contrasts sharply with the strong correlation of precipitation and productivity found in the short- and mixed-grass prairies of the Great Plains (Sala et al. 1988). Nutrient dynamics, especially for N, must be addressed in understanding the structure and functioning of the tallgrass prairie ecosystem. In this paper, we review and summarize the previously published results of experimental studies comparing the N dynamics of prairie and non-prairie grasses, discuss the unique N cycle of the tallgrass prairie, and suggest that disruption of the N cycle may be important in the destabilization of tallgrass prairie.

METHODS

This research was part of the Long Term Ecological Research program at the University of Minnesota's Cedar Creek Natural History Area. Cedar Creek is located on a glacial outwash sandplain in east-central Minnesota. These studies focused on the five most abundant grasses in the abandoned old fields and native prairies at Cedar Creek. Little bluestem and big bluestem are native warm-season bunchgrasses dominant in late-successional fields and undisturbed prairies and oak savannahs. Ticklegrass (*Agrostis scabra* Willd.) is a native, cool-season bunchgrass found in early successional fields. Quackgrass (*Agropyron repens* (L.) Beauv.) and Kentucky bluegrass (*Poa pratensis* L.) are both non-native, cool-season rhizomatous grasses found in early- to mid-successional fields at Cedar Creek (Tilman 1988). These species were planted as monocultures and in mixed-species plots on soils ranging from sand (0.3% organic matter and 90 mg of N per kg of dry soil) to a sandy-loam black soil (3.0% organic matter and 1,100 mg/kg total N). By mixing different ratios of these two soils, an experimental gradient in soil fertility from low N to high N conditions was created. Black-soil plots that received an additional 5.6 g N m^{-2} yr^{-1} as NH_4NO_3 fertilizer were the most fertile plots of the gradient. To insure that N was the only soil resource limiting growth, all plots were watered and fertilized with all nutrients except N. The controlled garden situation allowed us to address 1) the N-use efficiency of these grasses (Wedin 1990), 2) their competitive interactions under high- and low-N conditions (Tilman and Wedin 1991a, Wedin 1990), and 3) their effects on N cycling (Wedin and Tilman 1990) and soil NH_4 and NO_3 concentrations (Tilman and Wedin 1991b). These various experiments are only summarized here; complete methods and results can be found in the above citations.

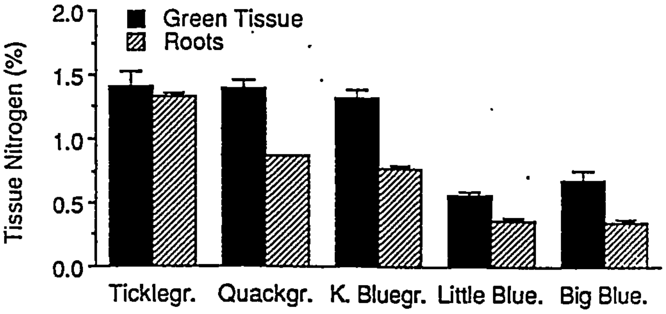

Figure 1. Tissue N concentrations (means and standard errors) in late July for five grass species (ticklegrass, quackgrass, Kentucky bluegrass, little bluestem and big bluestem) growing in monocultures on a sandy-loam black soil.

RESULTS AND DISCUSSION

Nitrogen-Use Efficiency

Little and big bluestem had low tissue N concentrations in both their leaves and roots compared to the cool-season grasses (Figure 1). The same pattern is seen in the N concentration of dead tissues. although values are somewhat lower following senescence for all species (Wedin and Tilman 1990). These low N concentrations are not simply due to differences among the species in photosynthetic pathway. that is. C_4 (warm season) versus C_3 (cool season). The warm-season grasses which dominate the moisture-limited Great Plains (blue grama and buffalo grass) have tissue N concentrations considerably higher than the 0.5%-0.7% found in mid-season green tissues of big and little bluestem in the N-limited tallgrass prairie. Thus. the two prairie grasses have high N-use efficiency. that is. they produce a unit of biomass with a very low investment of N (Chapin 1980, Vitousek 1982).

The two bluestems also allocated a large proportion of their biomass below ground. a pattern well documented by Weaver (1958) and others. In the three-year-old monocultures growing on black soil. 70% of the annual net productivity of big and little bluestem occurred below ground. while 52% occurred below ground for quackgrass and Kentucky bluegrass. and only 15% for ticklegrass (Wedin 1990). After three years. the below-ground biomass of the two bluestems (approximately 1200 g/m² for both species) was over twice that of either quackgrass or Kentucky bluegrass (approximately 500 g/m²) and over twenty times that of ticklegrass (45 g/m²)(Wedin 1990, Tilman and Wedin 1991b). Thus, these two prairie grasses have a high N-use efficiency and, because of their large root system, are efficient at acquiring below-ground resources. including N.

Interspecific Competition

Little bluestem and big bluestem completely displaced the other three grasses within three years in the mixed-species plots on the infertile, sandy soils (Tilman and Wedin 1991a. Wedin 1990). In pairwise competition experiments with little bluestem versus quackgrass or Kentucky bluegrass, little bluestem completely eliminated the two non-native species on the low-N soils even when little bluestem was added as seed to one-year-old monocultures of the competing species. However, at the high end of the fertility gradient, little bluestem did not have a competitive advantage over quackgrass or Kentucky bluegrass (Wedin 1990).

The competitive advantage of the two prairie species on the infertile soils corresponded to their ability to deplete the concentration of available soil N to lower levels than the three other species. The concentration of available soil N. estimated as 0.01M KCl-extractable soil NO_3 and NH_4, was significantly lower in the three-year-old little bluestem and big bluestem monocultures than in the monocultures of ticklegrass, quackgrass, and Kentucky bluegrass (Tilman and Wedin 1991b). These differences among monocultures in the concentration of available soil N were highly correlated with differences among the species in root biomass (Tilman and Wedin 1991b). However, at the high end of the fertility gradient, the two prairie species did not deplete available soil N to levels significantly lower than did Kentucky bluegrass and quackgrass. This corresponded to the lack of a competitive advantage for big and little bluestem over the two non-native, cool-season species under more productive conditions.

These competition results are consistent with other Cedar Creek experiments. When N was added (as NH_4NO_3 fertilizer) to a sand prairie at Cedar Creek dominated by little bluestem, high N addition rates (greater than 9 g N m^{-2} yr^{-1}) led to the complete displacement of little bluestem by Kentucky bluegrass and quackgrass after seven years (Tilman 1987, 1990). A shift in species composition and the loss of dominance by little bluestem occurred at N addition rates of only 1 to 2 g N m^{-2} yr^{-1} (Tilman 1990). Although originally present in smaller amounts than little bluestem, big bluestem showed the same decline following N addition (Tilman 1987).

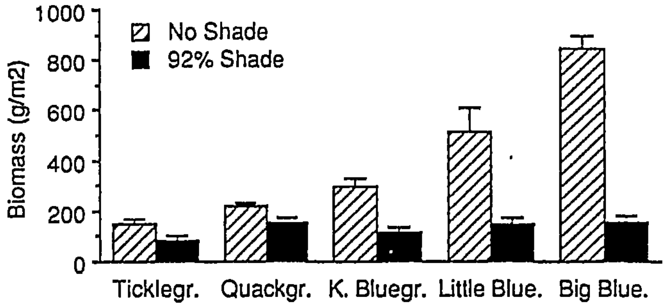

Figure 2. Effects of shade (92% of ambient light removed) on the total (above- and below-ground) biomass of three-year-old monocultures of five grass species growing on a mixed (sand and sandy-loam) soil (means and standard errors).

Why do the two prairie grasses lose their competitive advantage when N supply rates and productivity increase? A consequence of high N-use efficiency and high allocation of biomass to roots is vulnerability to light limitation, which becomes more important with increasing productivity (Chapin 1980, Knapp and Seastedt 1986. Tilman 1988). In a related study, monocultures of these five grasses were grown under different levels of shade. Under heavy shade, the two bluestems had a much larger drop in biomass than the other three grasses, most of which was caused by a dramatic drop in root biomass (Figure 2). The two bluestems also had large increases in their tissue N concentration under heavy shade. an increase of approximately 200% compared to an increase of approximately 50% for the three cool-season species (Wedin 1990). Thus, the traits which appear to confer a high competitive ability for N to the two prairie grasses are severely impacted by light limitation. We conclude. therefore. that the competitive superiority of the warm-season prairie grasses disappears with the shift from a N-limited to a light-limited environment.

Decomposition and Nitrogen Cycling

The supply rate of N in most terrestrial ecosystems is determined largely by the rate of N mineralization. the rate at which NH_4 and NO_3 are released from decomposing organic matter in the soil. Because the decomposition rate of litter (dead plant material) can vary depending on the quality of that litter, differences in litter quality among plant species can lead to differences in N cycling (Vitousek 1982). Litter types with low N concentrations and high lignin concentrations provide a low quality substrate for the decomposers. The litter of big and little bluestem has a very low N concentration and has been shown to decompose very slowly. tying up, or immobilizing, available N for more than two years. before it begins to release, or mineralize, N (Pastor et al. 1987a. Seastedt 1988).

We used an *in situ* incubation technique to measure the N mineralization rates in the five species' monocultures over three years (Wedin and Tilman 1990). By the third year of the study, there was a dramatic divergence in N mineralization rates under the different species, with low rates (1-2 g N m^{-2} yr^{-1}) in the big and little bluestem plots, intermediate rates (3-4 g N m^{-2} yr^{-1}) in the quackgrass and kentucky bluegrass plots, and high rates (12 g N m^{-2} yr^{-1}) in the ticklegrass plots at the black soil end of the experimental fertility gradient. These differences in N mineralization rate were highly correlated with the differences among the species in the quantity and quality of litter produced, especially below ground

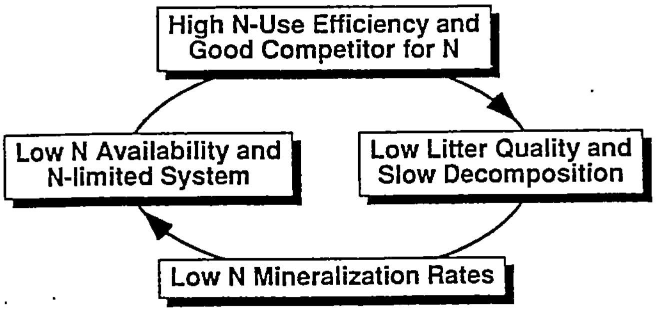

Figure 3. A proposed positive feedback between plant competition and N cycling for the tallgrass prairie.

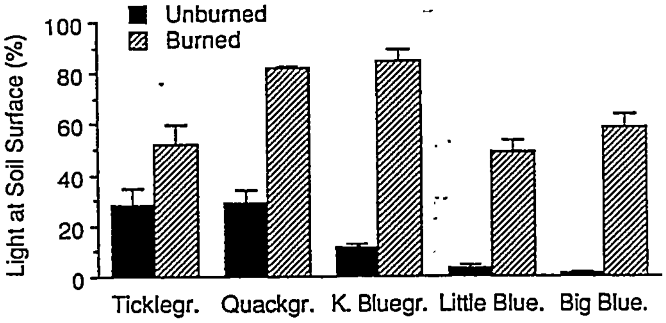

Figure 4. Light penetration (means and standard errors) in unburned monocultures with five years' litter accumulation and burned monocultures of five grass species on a sandy-loam black soil.

(Wedin and Tilman 1990). Sharp reductions in N mineralization rates in plots of big and little bluestem corresponded to their production of large amounts of low N organic matter below ground.

Nitrogen Cycling and the Stability of Tallgrass Prairie

Summarizing the results of these various experiments: the warm-season prairie grasses are able to produce biomass with low investments of N, that is, they have a high N-use efficiency, and they allocate most of their biomass below ground. Because of this, they are able to deplete the amount of available soil N to low levels, making them good competitors under N-limited conditions. Finally, their low litter quality leads to slower N cycling and a reduction in the soil's N supply rate. Together, these factors create a positive feedback: through their effects on N cycling, these warm-season grasses create a N-limited environment in which they have a competitive advantage (Figure 3). Part of the reason tallgrass prairie was able to dominate such a large and diverse area may be that the dominant prairie grasses created a favorable N cycle over a wide range of climates and soils.

A characteristic of positive feedback systems, however, is that they are vulnerable to disruption (DeAngelis et al. 1989). Given a large enough disturbance, they are inherently unstable. This may partly explain why the tallgrass prairie was vulnerable to so many types of disturbance. Disruption of the feedback at any point can lead to the system's collapse and its replacement by another system, such as a Kentucky bluegrass or quackgrass field. An important disruption of this positive feedback in the tallgrass prairie is litter accumulation caused by lack of fire. The low litter quality of little bluestem and big bluestem that results in reduced N supply rates also leads to slow decomposition and the accumulation of above-ground litter. After five years, the unburned monocultures of the two prairie grasses had accumulated more above-ground litter than the other three species, even though all species had comparable above-ground productivities on the sandy-loam black soil. Consequently, light penetration (the percent of available light at the soil surface) in the unburned monocultures of big and little bluestem was almost zero (Figure 4). In comparable burned monocultures, however, there was no litter accumulation and light penetration was relatively high for all five species. As discussed above, under light-limited conditions the competitive advantage of the warm-season prairie grasses declines. Fire is critical, therefore, because it prevents heavy litter accumulation under the prairie grasses and thus prevents a shift from N limitation to light limitation (Knapp and Seastedt 1986). The faster the rate of litter accumulation, that is, the more productive the prairie, the more critical fire becomes.

Other disturbances which can disrupt the positive feedback between the warm-season prairie grasses' competitive ability and their effects on N cycling include overgrazing, soil disturbance, and climate changes. Heavy grazing leads to decreased N-use efficiency and decreased below-ground biomass allocation, both of which affect the prairie grasses' ability to compete for N and their feedback effects on N cycling (Holland and Detling 1990). Grazers also return, via urine, a high proportion of the N they consume, increasing the N supply rate (McNaughton et al. 1988). Soil disturbance or shifts in climate will also affect decomposition and N mineralization rates. Fertilizing a tallgrass prairie with N is a direct disruption of the prairie N cycle and leads to an increase in non-native grasses and forbs (Owensby et al. 1970, Tilman 1987).

A more subtle, but potentially important, disturbance to the tallgrass prairie is the dramatic increase in rates of atmospheric N deposition in the last 30 years caused by increased levels of both NO_3 and NH_4 in air pollution. Emissions of NO_3 are primarily caused by the burning of fossil fuels and are highest in the industrial eastern Midwest. Emissions of NH_4 come from the use of NH_4 fertilizer and from intensive livestock operations and are higher in the western part of the Midwest. Both fossil fuel consumption and N fertilizer use have increased sharply since World War II. For example, N fertilizer use nationwide quadrupled between 1960 and 1980 (National Research Council 1989).

In 1989, N deposition in precipitation ranged from roughly 0.4 g N m^{-2} yr^{-1} on the western edge of the tallgrass prairie in eastern Kansas and Nebraska to over 0.8 g N m^{-2} yr^{-1} in southern Michigan (National Atmospheric Deposition Program / National Trends Network 1990). The actual N deposition rates experienced by prairie remnants in the Midwest may be considerably higher than this for two reasons. First, although measurements of N deposition in dryfall (gas exchange and fine particulates) are quite inaccurate, data from NADP/NTN and the NOAA/ATDD CORE/Satellite network (Meyers and Sisterson 1989) suggest that the wetfall data can be increased by a factor of 1.5 to approximate total N deposition in the Midwest. Total atmospheric N deposition estimates therefore range from roughly 0.6 g N m^{-2} yr^{-1} on the western edge of the tallgrass prairie to over 1.2 g N m^{-2} yr^{-1} in the eastern Midwest. Given a N mineralization rate in tallgrass prairie soils of 3-6 g N m^{-2} yr^{-1} (Risser and Parton 1982, Pastor et al. 1987b, Ojima et al. 1990), atmospheric deposition has increased N supply rates on the order of 10-25%. A second consideration is that NADP/NTN sites are chosen to be away from local sources of air pollution, such as urban centers, fertilized fields, or feedlots. Many prairie preserves are in just such areas. Some of these preserves probably have N deposition rates greater than 2 g N m^{-2} yr^{-1}. N addition rates which led to the displacement of little bluestem by Kentucky bluegrass and quackgrass in Cedar Creek experiments (Tilman 1987, 1990).

There has been a chronic loading of N to prairie remnants in the Midwest over the last 20-30 years. The resulting increases in productivity may lead to the loss of tallgrass prairie species and the invasion of exotic grasses and woody vegetation. The invasion of cool-season rhizomatous grasses, such as quackgrass, Kentucky bluegrass, and smooth brome, in prairie remnants in the eastern Midwest is a widespread management problem, particularly in sites surrounded by agricultural fields. Increased N deposition from both regional and local sources may be one cause of this problem. Clearly, further research is needed to understand the role of this disturbance. One implication, however, is that managers may need to rethink their fire regimes. The natural fire regimes that are thought to have occurred in pre-settlement times may be less relevant under modern conditions of higher productivity and faster litter accumulation. More frequent fires would not only prevent increased litter accumulation, but would also volatilize most of the N in litter (Ojima et al. 1990), helping to counteract N loading from atmospheric deposition. Of course, managers must also consider the impact of increased fire frequency on forbs, invertebrates, and other prairie components.

In conclusion, the N cycle is a critical component in our understanding of the tallgrass prairie ecosystem. We suggest that the disruption of the distinctive N cycle found in the tallgrass prairie is a significant threat to the prairie. In contrast to overt disturbances of the prairie, such as tilling, overgrazing, fertilization, or the exclusion of fire, recent increases in atmospheric N deposition rates are a subtle threat that merits further consideration, particularly in the eastern Midwest.

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