Little bluestem litter dynamics in Minnesota old fields

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Summary. We studied the decay and nitrogen dynamics of little bluestem *(Schizachyrium scoparium)* litter in fertilized and unfertilized Minnesota old fields, using the litterbag technique. Annual decay rates and nitrogen leaching losses during the first month of decay were highly correlated with N content of litter and not with fertilizer additions. After the first month of decay, nitrogen was immobilized for at least 18 months. In contrast to decay rates and early N leaching losses, these immobilization rates were correlated with the amount of ammonium nitrate added in fertilizer rather than with initial %N. Therefore, litter quality and exogenous nitrogen supply appear to have different and independent effects on decay rates and N dynamics of little bluestem litter.

Key words: *Schizachyrium scoparium-* Decomposition-Nitrogen - Fertilization

The decay of litter to humus, with concommitant release of nutrients, is a major process in all terrestrial ecosystems because it controls the availability of nitrogen, the nutrient most frequently limiting to plant growth. There have been hundreds of studies on nitrogen dynamics of decaying forest litter. Litter decomposition studies in grasslands are less common (Koelling and Kucera 1965; Kucera et al. 1967; Landerholm and Hadley 1975; Wiegert and Evans 1964; Vossbrink et al. 1979; Abouguendia and Whitman 1979; Deshmukh 1985; Holland and Coleman 1987) despite the importance of humus formation in grasslands (Dokuchaev 1883), and organic matter dynamics in old fields (Odum 1960). Furthermore, we know of only three papers which examine both decay and nitrogen dynamics of grass litter (Koelling and Kucera 1965; Vossbrink et al. 1979; Holland and Coleman 1987).

Nitrogen dynamics of decaying litter are not as straightforward as mass loss, which often follows an exponential decay curve (Olson 1963). Berg and Staaf (1981) suggest a three stage process for nitrogen dynamics: 1. a brief period of initial leaching 2. a period of absolute increase in N content associated with rapid microbial growth, known as N immobilization, and 3. a period in which nitrogen is release in mineral form (mineralization) upon the decline of the microbial population. During this entire process, the C: N ratio of the material is declining as C is released while N is gained, as demonstrated for grasses by Koelling and Kucera (1965) and Vossbrinck et al. (1979).

Grasslands often receive exogenous inputs of nitrogen, either in precipitation or as fertilizer in managed rangelands and pastures, or locally in urine spots. Additions of nitrogen may affect the rate of decay as well as both the rate and trend of changing C:N ratios (Melillo et al. 1984).

We studied decay and nitrogen dynamics of little bluestem *(Schizachyrium scoparium)* litter in two old fields in Minnesota dominated by prairie grasses under three fertilizer treatments.

Study area

The Cedar Creek Natural History Area is located on a 20-40 m deep sandy outwash plain deposited by streams draining the receding Wisconsinan ice sheet around 14000 years BP. Native, pre-European settlement vegetation on the sand plain was a mosaic of prairie, wetland, oak savanna, and hardwood forest (Pierce 1954). The area was farmed starting in the late 1800s. From about 50 years ago through the present, various fields have been abandoned.

The decay of little bluestem litter was studied in two fields where *Schizachyrium scoparium* has become a dominant species. Field B was last farmed to soybeans before abandonment in 1957. Field C was last farmed to corn before abandonment in 1934. Further details of vegetation dynamics are given in Tilman (1983, 1984, 1986) and in Inouye et al. (1987). The soils in all fields are Sartell or Zimmerman sands (Typic Udipsamments and Alfic Udipsamments, respectively; Grigal et al. 1974). Humus nitrogen mineralization was 3.4 g/m^2 per year in field B and 4.8 g/m^2 per year in field C (Pastor et al. 1987).

Experimental design and methods

In each field, we established an experimental nitrogen gradient by fertilizing each of six replicate $4 \text{ m} \times 4 \text{ m}$ plots with either 0.0 (control), 3.54, 9.92, or 28.4 g/m^2 of N. The 24 plots in each field formed an experimental nitrogen gradient. The fertilizer was applied as $NH₄NO₃$ in a top dressing in two installations per year each spring beginning in 1982. All plots except the controls also received simultaneous additions of P $(4.6 \text{ g/m}^2/\text{yr})$, K $(6.1 \text{ g/m}^2/\text{yr})$, Ca $(8.0 \text{ g/m}^2/\text{yr})$, Mg $(3.0 \text{ g/m}^2/\text{yr})$, S $(4.0 \text{ g/m}^2/\text{yr})$, and a mixture of trace elements (Cu, Zn, Co, Mn, Mo, and B).

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Table 1. Decay rates and nitrogen dynamics of little bluestem litter

Field	Nitrogen additions (g/m^2) (per yr)	k	Initial $\%N$	A^a	B ^a	r^2	$\%$ N at onset of N factor immobilization	(mg/g) original mass)	N equivalent $(mg/g \text{ mass loss})$
B		-0.220	0.54	134.4	79.6	$0.922**$	0.44	1.27	0.0189
	3.54	-0.215	0.45	125.9	86.4	$0.933**$	0.34	1.19	0.189
	9.92	-0.216	0.44	117.6	52.3	$0.819**$	0.42	2.41	0.0410
	28.4	-0.259	0.72	109.9	27.4	$0.874**$	0.55	5.51	0.1003
\mathcal{C}		-0.225	0.48	139.6	101.5	$0.729*$	0.36	1.20	0.0172
	3.54	-0.301	0.82	134.2	76.0	$0.924**$	0.41	1.82	0.0272
	9.92	-0.293	0.77	127.8	59.3	$0.916**$	0.42	2.67	0.0419
	28.4	-0.322	0.84	117.7	39.0	$0.978**$	0.50	3.88	0.0659

^a % mass remaining $= A - B$ (%N in remaining material)

Regressions fit to data from imobilization phase (see Aber and Melillo 1982)

 $*P<0.05$; $*P<0.01$

Litter from standing dead little bluestem was collected in October, 1982, from each plot within each treatment and field and composited by treatment and field to yield homogenous samples. It was necessary to homogenize litter samples to control for possible plot-to-plot variation in litter chemistry. Later in October, six litterbags, each with approximately 5-10 g of litter in 1 mm mesh nylon bags, were then placed back in each plot in the treatment from which the litter had been collected. One bag from each of six replicate plots in each treatment in each field was collected after 1, 6, 9, 12, and 18 months of decay, yielding a total of six bags collected from each treatment during each sampling period. An additional collection at 2 months was made in field C.

Litter was returned to the laboratory, dried at 60 C, and weighed. The material was then ground in a Wiley mill and analyzed for %N by persulfate digestion.

Mass loss data were fit to an exponential decay model (Olson 1962):

 $v = 1.0e^{-kt}$,

where y is % of original mass remaining at time t (in years) and k is the decay constant. Nitrogen concentrations were also regressed against the corresponding % mass remaining and various descriptors of nitrogen dynamics were calculated from the slopes and intercepts of these regressions (cf. Aber and Melillo 1982; Melillo et al. 1984).

Results

Initial nitrogen concentrations of the litter, which ranged from 0.44 to 0.84%, did not correlate with fertilizer levels (Table 1). The factors affecting initial %N are not known, but it does not appear that fertilizer additions are one of them.

Decay constants ranged from 0.215 to 0.322 (Table 1, Fig. 1). These are comparable to those found by Deshmukh (1985), Koelling and Kucera (1965), and Abouguendia and Whitman (1979) for other prairie grasses, but much slower than that reported by Risser et al. (1981) for pure cellulose strips in various western North American prairies.

Initial N concentrations were stronger determinants of decay rates than were fertilizer additions. Decay constants were highly correlated with initial %N in field B ($r = 0.967$, $P<0.01$), in field C ($r=0.987$, $P<0.01$), and in both fields combined $(r=0.957, P<0.01)$. Decay constants were not

Fig. 1 A-H. Changes in mass *(solid line* and *closed symbols)* and nitrogen content *(dashed line* and *open symbols)* during decomposition of little bluestem litter. Fertilizer N additions in g/m^2 are shown above each graph. *Vertical bars* indicate one standard deviation above and below means

Fig. 2. Time course in months of changes in $\%$ N with decreases in mass. Leaching phase shown as dashed line and immobilization phase shown as *solid line. Vertical* and *horizontal bars* indicate one standard deviation around means. Data are for the control plots (0.0 N added) in Field B

correlated with fertilizer additions in field C or across both fields and only weakly correlated with fertilizer additions in field B $(r=0.920, P<0.05)$.

Between 4% and 56.9% of original nitrogen content was lost during the first month (Fig. 1). This loss was highly correlated with the initial %N ($r = 0.837$, $P < 0.01$). Presumably, this rapid initial loss of N was due to leaching of soluble N compounds, the level of which appears to increase with increasing N content of litter.

The initial leaching phase was followed by a period of absolute increases in amounts of nitrogen (Fig. 1). Increases in the absolute amount of nitrogen during the second phase are known as nitrogen immobilization.

Rates of N immobilization could be calculated directly from the data in Fig. 1, but there is a more elegant method. Aber and Melillo (1982) have shown that nitrogen concentrations increase linearly with declines in mass during the nitrogen immobilization phase. Furthermore, rates of N immobilization can be calculated from regressions of mass remaining vs. N concentration in remaining tissue (Aber and Melillo 1982; Melillo et al. 1984). In the present experiment (Fig. 2), the initial leaching phase produced a decline in N concentration accompanying the initial mass loss, followed by the linear increases observed by Aber and Melillo (1982) for forest litters. In order to characterize this second, immobilization phase more fully we regressed %N against % mass remaining (Aber and Melillo 1982), using the % mass remaining at 1 month as the initial value (i.e., setting it equal to 100 and calculating subsequent mass loss from this value). All regressions (Table 1) were significant at $P \lt \mathbb{R}$ 0.05 and most were significant at $P < 0.01$. From the regression parameters, the following nitrogen dynamics were calculated (Table 1): 1. the nitrogen factor, the amount of N immobilized per unit mass remaining at the beginning of the immobilization phase, and 2. the nitrogen equivalent, the amount of nitrogen immobilized per unit mass loss during this phase (cf. Aber and Melillo 1982; Melillo etal. 1984).

Fertilization levels explained more of the variation in these dynamics than initial %N or the %N at the beginning of the immobilization phase. The nitrogen factor and the nitrogen equivalent were both highly correlated with the level of added nitrogen in field B $(r=0.991$ and $r=0.993$, respectively, $P < 0.001$ in both cases), in field C ($r = 0.976$ and $r=0.985$, respectively, $P<0.001$ in both cases), and for both fields combined ($r = 0.949$ and $r = 0.944$, respectively, $P < 0.001$ in both cases). The field X added nitrogen interactions were negligable.

In contrast to decay rates and the magnitude of early N leaching loss, the N factor and N equivalent were not correlated with the initial %N of the litter. Nor were these measures of nitrogen dynamics correlated with the %N at the beginning of the immobilization phase in field B; and they were only weakly correlated with $\%$ N at the beginning of the immobilization phase in field C $(P<0.05$ in both cases). However, they were more strongly correlated with the $\%$ N at the beginning of the immobilization phase when data from both fields were combined $(r=0.907$ and $r=$ 0.902, respectively, $P < 0.01$ in both cases).

By the end of the experiment, N mineralization had not begun. However, the increases in N contents appeared to level off between the t2 month and 18 month sampling in most cases. What is important is that, except for an initial leaching phase during the autumn after plant senescence, nitrogen is not released from decaying little bluestem litter until at least the second growing season after litterfall.

Discussion

The quality of little bluestem litter and the rates of exogenous N inputs appeared to have different and somewhat independent effects on decay rates and N dynamics. The initial N concentration, an estimate of quality of material to decomposers, appeared to strongly control decay rates whereas additions of fertilizer N had no effect. Fertilizer inputs did not appear to affect initial %N of litter. Much of the variation in initial $\%$ N and its effect on decay rates may be due to variation in amounts of easily leachable and labile nitrogen compounds (amino acids, protein, etc.) because the proportion of original N leached was highly correlated with the initial %N.

The fertilizer additions were more important than tissue nitrogen concentration in controlling the patterns of nitrogen dynamics during the immobilization phase. Microbial N immobilization (both per unit original mass and per unit mass loss) increased with increasing nitrogen supply but was not related to initial %N. Berg and Ekbohm (1983) found similar results in an experiment on N immobilization by Scots pine *(Pinus sylvestris)* needle litter. Thus, the microbial immobilization of nitrogen during the conversion of litter to humus may be as important a mechanism of nitrogen retention in grasslands as has been demonstrated in forests (Vitousek et al. 1982; Vitousek and Matson 1985).

The present study also demonstrates the importance of litter quality for decomposition rates and dynamics. Even within this single species, variation in initial nitrogen was high, and contributed substantially to variation in decay rates and early nitrogen leaching losses from the material. Other estimates of litter quality (lignin, soluble sugars, etc.) were not measured, but undoubtely also have an effect. This lends some support to the model of Parton et al. (1983) which explicitly considers litter quality with regard to the conversion of litter to humus in croplands and grasslands.

In contrast to forest ecosystems, interspecies variation in litter quality in grasslands has not been extensively char-

acterized. Several forest ecosystem models (Abet et al. 1982; Pastor and Post 1986) and several field studies in forests (Flanagan and Van Cleve 1983; Nadelhoffer et al. 1983; Pastor et al. 1984; McClaugherty et al. 1985) have shown that population and species dynamics during succession or across environmental gradients can affect nitrogen cycling through shifts in litter quality. If grassland species show comparable variation in litter quality, then their population dynamics may also have similar effects on carbon and nitrogen cycling through their interactions with the decomposer community.

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References

- Abet JD, Melillo JM (1982) Nitrogen immobilization in decaying hardwood leaf litter as a function of initial nitrogen and lignin content. Can J Bot 60:2263-2269
- Abouguendia ZM, Whitman WC (1979) Disappearance of dead plant material in a mixed grass prairie. Oecologia (Berlin) $42:23 - 29$
- Berg B, Staaf H (1981) Leaching, accumulation and release of nitrogen in decomposing forest litter. In: Clark FE, Rosswall T (ed) Terrestrial nitrogen cycles. Eco Bull 32:373-390
- Berg B, Ekbohm G (1983) Nitrogen immobilization in decomposing litter at variable carbon: nitrogen ratios. Ecology 64: 63-67
- Deshmukh I (1985) Decomposition of grasses in Nairobi National Park, Kenya. Oecologia (Berlin) 67:147-149
- Dokuchaev VV (1883) Russian Chernozem. Israeli Program for Scientific Translations, Jerusalem
- Flanagan PW, Van Cleve K (1983) Nutrient cycling in relation to decomposition and organic-matter quality in taiga ecosystems. Can J For Res 13:795-817
- Grigal DF, Chamberlain LM, Finney HR, Wroblewski DV, Gross ER (1974) Soils of the cedar creek natural history area. Miscellaneous report 123, University of Minnesota Agricultural Experiment Station, Saint Paul, Minnesota, USA
- Holland EA, Coleman DC (1987) Litter placement effects on microbial communities and organic matter dynamics in a Colorado agroecosystem. Ecology (in press)
- Inouye RS, Huntly NJ, Tilman D, Tester JR, Stillwell MA, Zinnel KC (1987) Old field succession on a Minnesota sand plain. Ecology (in press)
- Koelling MR, Kucera CL (1965) Dry matter losses and mineral leaching in bluestem standing crop and litter. Ecology 46:529-532
- Kucera CL, Dahlman RC, Koelling MR (1967) Total net productivity on an energy basis for tallgrass prairie. Ecology 48 : 536-541
- Landerholm WA, Hadley EB (1975) Decomposition of natural and simulated litter in Oakville Prairie. In: Wali MK (ed) Prairie: A multiple view. University of North Dakota, Grand Forks, North Dakota, USA
- Melillo JM, Naiman RJ, Aber JD, Linkens AE (1984) Factors controlling mass loss and nitrogen dynamics of plant litter decaying in northern streams. Bull Mar Sci 35:341-356
- McClaugherty CA, Pastor J, Aber JD, Melillo JM (1985) Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. Ecology $66:259-265$
- Nadelhoffer KJ, Aber JD, Melillo JM (1983) Leaf-litter production and soil organic matter dynamics along a nitrogen-availability gradient in southern Wisconsin (USA). Can J For Res 13 : 12-21
- Odum EP (1960) Organic production and turnover in old field succession. Ecology 41:34-49
- Olson JS (1963) Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44:322-331
- Parton WJ, Perrson J, Anderson DW (1983) Simulation of organic matter in Swedish soils. In: Lauenroth LW, Skogerboe GV, Flug M (eds) Analysis of ecological systems: State of the art in ecological modelling. Elsevier, Amsterdam, Netherlands
- Pastor J, Aber JD, McClaugherty CA, Melillo JM (1984) Aboveground production and N and P dynamics along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. Ecology 65:256-268
- Pastor J, Post WM (1986) Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. Biogeochemistry 2:3-27
- Pastor J, Stillwell MA, Tilman D (1987) Nitrogen mineralization and nitrification in four Minnesota old fields Oecologia (Berlin) 71:481-485
- Pierce RL (1954) Vegetation cover types and the land use history of Cedar Creek Natural History Reservation, Anoka and Isanti Counties, Minnesota. MS Thesis, University of Minnesota, Minneapolis, Minn, USA
- Risser PG, Birney EC, Blocker HD, May SW, Parton WJ, Wiens JA (1981) The true prairie ecosystem. US/IBP Synthesis Series 16, Hutchinson Ross, Stroudsburg, Penn, USA
- Tilman D (1983) Plant succession and gopher disturbance along an experimental gradient. Oecologia (Berlin) 60:285~292
- Tilman D (1984) Plant dominance along an experimental gradient. Ecology 65 : 1445-1453
- Tilman D (1986) Nitrogen-limited growth in plants from different successional stages. Ecology 67:555-563
- Vitousek PM, Gosz JR, Grier CC, Melillo JM, Reiners WA (1982) A comparative analysis of potential nitrification and nitrate mobility in forest ecosystems. Ecol Mono 52:155-177
- Vitousek PM, Matson PA (1985) Disturbance, nitrogen availability, and nitrogen losses in an intensively managed loblolly pine plantation. Ecology 66: 1360-1376
- Vossbrinck CR, Coleman DC, Woolley TA (1979) Abiotic and biotic factors in litter decomposition in a semiarid grassland. Ecology 60:265-271
- Wiegert RG, Evans FC (1964) Primary production and disappearance of dead material on an old field in southeastern Michigan. Ecology 45 : 49-63

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