Ecology, 78(3), 1997, pp. 732–739

LITTER DECOMPOSITION AND NITROGEN DYNAMICS IN ASPEN FOREST AND MIXED-GRASS PRAIRIE

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Abstract. Temperature and moisture have larger effects on litter decomposition than litter quality on regional scales. We tested whether this also holds for microclimatic differences between adjacent habitats. We placed litter of aspen (*Populus tremuloides*) and prairie grasses in both forest and prairie. Microclimate was varied by shading half the litter in both habitats. Litter was set out in May and retrieved after 4, 9, 16, and 21 wk. Decomposition rates averaged across sites and treatments were significantly lower for aspen (k = 0.44 yr^{-1}) than grass litter (1.36 yr^{-1}), reflecting differences in nitrogen (N) content between litter types (aspen, 0.62%; grass, 1.07%). Decomposition rates were highest in unshaded prairie, suggesting that shade may limit decomposition in forests. N mineralized from the litter was collected by ion-exchange resins placed under the litter, while uncovered resins collected mineral N deposited from the atmosphere. Less mineral N was collected by resins under litter than by uncovered resins, suggesting that litter accumulated mineral N deposited from the atmosphere. The N accumulation rates were significantly higher in aspen than grass litter, in accordance with a lower N concentration in aspen litter. Thus, on a local scale, decomposition rates and N dynamics were more strongly affected by litter quality than by shading or habitat.

Key words: decomposition; deposition; forest; habitat; immobilization; ion-exchange resin; litter quality; microclimate; mineralization; nitrogen; Populus tremuloides; *temperate grassland.*

INTRODUCTION

Litter decomposition is a major component of the nitrogen cycle and varies among species (Melillo et al. 1982, Taylor et al. 1989). Species may affect decomposition either directly through litter quality or mass (Berendse et al. 1994), or indirectly through microclimate or decomposer communities (McClaugherty et al. 1985, Vitousek and Walker 1989). Direct and indirect effects are difficult to separate because both litter and microclimate usually change simultaneously as species vary along environmental gradients. Our objective was to examine these effects separately in prairie and adjacent aspen forest.

Within the same habitat, litter quality indices based on the nitrogen content of the litter are the best predictors of decomposition rates (Taylor et al. 1989, Stump and Binkley 1993). In general, litter with a high N concentration decays faster than litter with a low N concentration and equal lignin content (Fog 1988).

Comparisons on regional scales, however, suggest that precipitation and temperature can affect decomposition rates more strongly than litter quality (Berg et al. 1993, Vitousek et al. 1994). The importance of microclimate relative to litter quality in comparisons on local scales has received little attention.

Adjacent habitats like forest and prairie differ considerably in their microclimate. Soil moisture is usually higher and maximum temperatures lower in forest than in prairie due to shading and reduced evapotranspiration (Wesser and Armbruster 1991, Wilson 1993). Decomposition rates of aspen litter (*Populus*; Lousier and Parkinson 1976, Zlotin and Khodashova 1980, Bartos and DeByle 1981) and prairie grass litter (Abouguendia and Whitman 1979, Vossbrinck et al. 1979, Zlotin and Khodashova 1980, Pastor et al. 1987, Seastedt et al. 1992) show high variability and considerable overlap among studies. We therefore predicted that decomposition across the forest-prairie ecotone was more strongly affected by shading than by litter type.

We examined the effect of litter quality, shading, and habitat type on decomposition and N dynamics in a factorial field experiment. Descriptions of N dynamics of decomposing litter usually consider N originally contained in the litter (e.g., Pastor et al. 1987, Seastedt et al. 1992, Rustad 1994) but not mineral N deposited from the atmosphere (Aber et al. 1989). We measured atmospheric N deposition and included it in our calculations.

METHODS

Study area

The experiment was conducted at White Butte Recreation Site (50°28′ N, 104°22′ W; 617 m above sea level), 18 km east of Regina, Saskatchewan, Canada. The vegetation consists of aspen forests (*P. tremuloides*; Bird 1930, Looman 1987) and mixed-grass prairie dominated by *Stipa comata, Bouteloua gracilis, Koe-*

Manuscript received 11 December 1995; revised 30 April 1996; accepted 15 May 1996; final version received 17 June 1996.

leria gracilis, Carex sp., and *Selaginella densa* (Coupland 1950, Looman 1980). Forests at the site have higher aboveground, belowground, and litter mass (7467 g/m^2, 2413 g/m^2, and 1854 g/m^2, respectively) than prairie (112 g/m^2, 808 g/m^2, and 159 g/m^2, respectively) (Wilson 1993). The root : shoot ratio, however, is lower in forest than prairie.

The soils in both habitats are regosols on silty sand with a mull to mull-like moder humus horizon. Forest soils have more available N and more moisture than prairie during June–September (Wilson 1993).

The regional climate is arid cold-temperate (Walter and Lieth 1967). Mean annual temperature in Regina is 2.6°C, with a daily mean of −17°C in January and 19°C in July (Atmospheric Environment Service 1993*b*). Mean daily minimum temperatures are above zero from May to September, but frost can occur in all months. Seventy percent of the mean annual precipitation (364 mm) fall from May till September, but potential evaporation exceeds precipitation from May till October (Müller 1982).

Experimental design

We used a factorial design with two levels of each of three factors: habitat (forest and prairie), litter type (aspen and grass), and shading (shaded and open), for a total of eight treatment combinations. Each treatment combination had four replicates for each of four measuring dates. The entire experiment was performed at three sites within a 2 km^2 area. Forest at these sites had sparse understory vegetation so that the influence of species other than aspen was small. At each site one forest plot was paired with one prairie plot 30–200 m away. Each plot contained 128 subplots (1.5 × 1.5 m). Forest plots were established in the oldest part of the forest that had a closed tree canopy and was at least 3 m from the forest edge. The average age of all forest plots was 29 yr (determined from stem cores of the center and corner trees of each plot, SD = 7 yr). Litter type, shade level, and harvest date were randomly assigned to subplots within each plot.

Half the subplots were shaded to create microclimatic conditions comparable to those under forest canopy. Shade cloth was set up on the southeast and southwest sides of subplots so that the center of each subplot was shaded most of the day. Light penetration in shaded prairie subplots was reduced to 53% until 18 June and then by additional layers of shade cloth to 16%. Light penetration in forest subplots without shade cloth in late June was 19%, not significantly different from shaded prairie subplots ($P > 0.05$).

We assumed that soil moisture under shades would be higher than in the open. To prevent soil moisture directly under the litter bags from moving sideways we inserted plastic tubes (10 cm diameter, 15 cm long) vertically into the soil under each shade so that the top rim was level with the soil surface.

In order to quantify the microclimatic differences between forest and prairie, we measured temperature, evapotranspiration, and accumulated precipitation in all plots in intervals of 2–3 wk. Temperature was measured 1 cm above the soil surface within 2 h of solar noon. We determined soil moisture with three shaded lysimeters per plot in each habitat. Lysimeters consisted of a plastic tube (10 cm diameter, 15 cm long) with a 1-mm plastic screen at the bottom and containing a prairie soil core with intact vegetation. Lysimeters were weighed every 2–3 wk. At the end of the experiment, lysimeter soil was dried at 90°C to constant mass and the relative soil moisture content was calculated for each measuring date.

Aspen litter shed in 1992 (mainly the O_L humus layer) and litter of prairie graminoids (henceforth called grass litter) were collected in late April 1993 at the three experimental sites and at one additional site within the study area. We did not collect litter in fall because winter decomposition in prairie and forest is small compared to summer decomposition in mixed-grass prairie (Abouguendia and Whitman 1979, see also Wiegert and Evans 1964), presumably because snow cover is too thin for insulation (Bleak 1970). We measured the size of the area from which we collected the litter to calculate mean litter mass per square meter. Leaves of other species, twigs, and bark were removed by hand from the aspen litter. Grass litter of the preceding year was obtained by raking to remove old litter, clipping the remaining plants 1 cm above the ground, and sorting by hand. Litter of all plots was pooled by litter type to make two composite mixes, one of grass and the other of aspen. Moisture content of litter used in the experiment was determined from fresh 3-g subsamples of each litter type (aspen: 5.3%, SD = 2.6%, n = 14; grass: 5.1%, SD = 2.3%, n = 18).

Litter bags (10 × 10 cm) made of 3-mm mesh plastic netting were filled with 2 g (dry mass equivalent) of aspen or grass litter. This mass was similar to litter mass on the forest floor. We used the same mass of grass litter as of aspen litter so that resin bags under grass litter were well covered. Litter bags were fixed to the ground by four stainless steel pins during 29 April–4 May 1993.

Litter bags were retrieved on 29 May, 1 July, 23 August, and 24 September 1993. Bags were cleaned to remove plants, arthropods, and sand. Bags severely damaged by rodents or containing parts of ant hills were excluded from the analysis. Litter was dried at 105°C to constant mass and weighed. Mass data were fit to the model $\ln Y = -kt + b$, where Y is the ratio of remaining to initial litter mass, k is the decomposition rate, t is decomposition time in years, and b a fitted intercept (Olson 1963, Taylor and Parkinson 1988*a*). One k value was determined for each treatment combination at each site.

We placed ion-exchange resin bags under the litter bags to collect mineralized N. Resin bags (3 × 3 cm) made from nylon stockings were separated from the

soil below by a plastic net (4 × 4 cm, 2-mm mesh) to reduce uptake of ions from soil. Resin bags contained 2 g wet mixed-bed ion-exchange resin beads (AG 501-X8 [BioRad, Hercules, California, USA] and Amberlite MB 1 [Rohm & Haas, Philadelphia, Pennsylvania, USA], blended 1:1) with 1.0 mmol/g of both anion and cation exchange capacity. We calculated that this amount of resin contained 7 times more ion-exchange sites than the amount of ion equivalents in precipitation and litter leachate (Lousier and Parkinson 1978, Pastor and Bockheim 1984) so that the resin would not become saturated during the experiment and all ions would be retained. Resin and bags were washed in 2 mol/L NaCl and rinsed with distilled water to wash out N from fabrication (Sibbesen 1977, Binkley and Vitousek 1991).

We deployed resin bags that were not covered by litter bags in order to measure N deposition from the atmosphere. There were three uncovered bags for each of the four harvest dates in each plot. Uncovered resins potentially collect both dry and wet deposited atmospheric ammonia and nitrous oxide compounds while commonly only wet deposition or bulk deposition (i.e., wet deposition plus gravity-driven dry deposition) is measured by meteorological stations. In addition, the exchange capacity of resins will cause more N to accumulate on resins than on standard inert surfaces used to determine deposition rates. Measurements by resins agree well with traditional measurements of wet atmospheric N deposition and estimates of total N deposition (M. Köchy, *unpublished data*).

Most uncovered resin bags assigned to the third and fourth harvest in prairie plots were badly damaged by rodents. Seven remaining bags were retrieved on 27 July. Fresh bags for the fourth harvest were put out on 18 August, protected by a 4-mm mesh stainless steel wire screen. In order to calculate N deposition over the whole summer, we estimated the amount of N that would have been in resins in the prairie on 18 August from a regression equation based on deposition until 27 July. We then added this estimate to the amount of N collected from 18 August until the end of the experiment. We calculated one estimate for all sites, because prairie deposition for the first two harvest dates, as well as forest deposition for all harvest dates, showed no significant differences among sites. Some resin bags under litter had also been damaged by rodents and were removed from the analysis.

Resin bags were set out and retrieved at the same time as litter bags. Retrieved resin bags were not obviously penetrated by roots or hyphae at the end of the experiment. Bags were stored dry in closed plastic vials at room temperature until after the last harvest when they were extracted in 25 mL of 2 mol/L KCl (Binkley and Vitousek 1991). Extract nitrate was converted to ammonium and total ammonium was measured with an ion-selective electrode (Orion, Boston, Massachusetts, USA).

In order to determine the amount of N actually collected by resins in the field, we measured the N content of six resin bags that were washed and stored dry for 4 mo. They contained 35.2 ± 3.2 μg N (mean ± 1 SD). We also determined the rate at which extraction recovered N from washed and stored resin bags by loading 16 bags with NH_4Cl and KNO_3 solutions of known concentration. Extraction recovered 75.6 ± 11.3% of loaded N. We corrected the N content of extractions from deployed bags by subtracting the N content of unused bags and dividing the result by 75.6%. We expressed the results as grams of nitrogen per square meter.

N collected by resins under litter could originate either from N mineralized from litter or from atmospheric deposition, or both. The amount of N collected by uncovered resins greatly exceeded the amount of N collected by resins under litter, indicating that litter retained a major portion of both mineralized and deposited N, resulting in a net accumulation of N in litter. We therefore calculated the net amount of N that was retained in the litter (N_{ret}) as $N_{ret} = N_{unc} - N_{ul}$, where N_{unc} is the amount of N collected by uncovered resins and N_{ul} is the amount of N collected by resins under litter.

We calculated the rate of N accumulation for each treatment combination at each site. In analogy to mass loss, we used a linearized exponential model, $\log(Y+1) = ft + b$, where Y is the amount of accumulated N, f is the accumulation rate, t is time of exposure in years, and b is a fitted intercept.

We determined the N concentration of four litter samples of each type at the start of the experiment with a CHN analyzer (Carlo-Erba Strumentazione, Milan, Italy). We also determined the N concentration at the end of the experiment in each litter type and shading treatment combination in each prairie plot. We pooled the replicates of each treatment combination. We measured only litter from prairie plots because we were more interested in comparing litter type than habitats, and because preliminary results indicated that mass loss rates were similar in forest and prairie.

Statistical analyses

Rates of mass loss and N accumulation were examined by analyses of variance (ANOVA) for a blocked factorial design with site as a block treatment and random effect, and habitat type, litter type, and shading as fixed effects (Zar 1974). Visual inspection suggested that rates were approximately normally distributed. Mass loss rates had homogeneous variances, but N accumulation rates were heteroscedastic. ANOVA, however, is relatively robust against heterogeneous variances, especially for equal-sized samples (Kirk 1968:60).

We tested if site × treatment interactions could be pooled with the residual error term to increase its degree of freedom for the ANOVAs (Kirk 1968:214–215, Glaser 1978:182). For this, we first calculated ANOVAs that comprised all possible interactions of all fac-

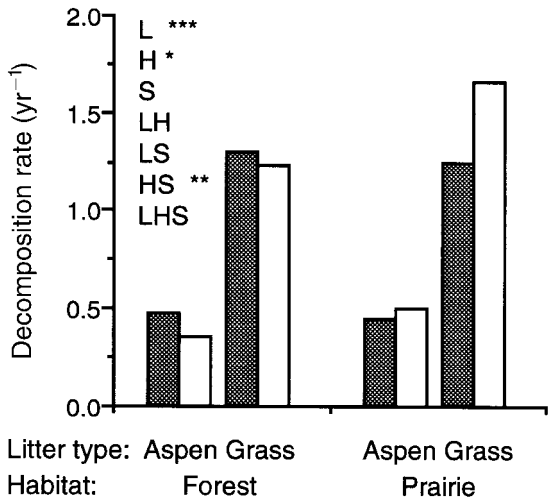

FIG. 1. Mean decomposition rates of two litter types (aspen and grass) in two habitats (forest and prairie) under shade (shaded bars) and in the open (open bars). Decomposition rates were measured as $\ln(m_t/m_0)/t$, where m denotes mass in grams and t denotes time. L, H, and S denote treatment effects examined with ANOVA. L = litter effect; H = habitat effect; S = shading effect. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

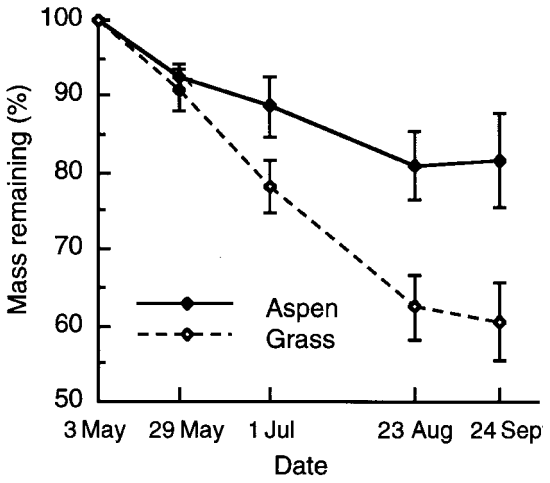

FIG. 2. Relative litter mass (mean ± 1 SD, n = 90–94) over time for aspen and grass litter, averaged over habitat and shading treatments.

tors. There were no significant site × treatment interactions for decomposition and accumulation rates ($P > 0.20$). Therefore, all site × treatment interactions were pooled with the residual error term.

All statistics were calculated with the program JMP (SAS 1992), except for F values for mixed-effect ANOVAs. These were calculated according to the formulas given by Zar (1974:374) because SAS Institute applies nonstandard calculation of F values in mixed-effect ANOVAs (Ayres and Thomas 1990).

RESULTS

Habitat conditions

Litter mass at the start of the experiment was significantly higher in forest (192.7 g/m^2) than in prairie (69.5 g/m^2, $t = 4.29$, $P < 0.01$).

Mean air temperature was significantly lower in shaded forest (21.4°C) than shaded prairie (22.8°C; $t = 4.1$, $P < 0.001$). Precipitation in forest (229 mm, May–September) was significantly lower than in prairie (372 mm; $t = 29$, $P < 0.001$), but gravimetric soil moisture in shaded forest lysimeters (16%) was significantly higher than in shaded prairie lysimeters (12%; $t = 14$, $P < 0.001$).

Accumulated precipitation from May to September was 443 mm in Regina, 176% of the 1960–1990 average for the same period and the highest amount since 1958 (Atmospheric Environment Service 1958–1994, 1993*b*). For each month except May, however, precipitation was within the range of 1 SD around the long-term monthly mean. Precipitation in May was below that range. Mean monthly temperatures from May to September were 1.5°C lower than the 1960–1990 averages ($t = 2.34$, $P < 0.05$).

Decomposition

Decomposition rates (Fig. 1) were significantly lower for aspen than for grass litter ($F_{1,14} = 324$, $P < 0.001$). After 146 d in the field, 81% of the original aspen and 59% of the original grass litter mass remained, averaged over all treatments (Fig. 2). Litter mass loss was nearly linear until 23 August after which loss slowed or mass was gained (Fig. 2). The gain was not significant.

Decomposition rates were lower in forest than in prairie (Fig. 1, $F_{1,14} = 6.05$, $P < 0.05$). Artificial shade had no significant direct effect on decomposition, but there was a significant shading × habitat type interaction ($F_{1,14} = 10.4$, $P < 0.01$) because decomposition rates in unshaded prairie were higher than in all other treatment combinations (Fig. 1). Experimental shades in the forest did not have a significant effect on decomposition rate, and decomposition rates in artificially shaded prairie subplots did not differ significantly from those under natural canopy in forests. There were no other significant interactions among habitat type, litter type, and shading (Fig. 1).

In summary, decomposition rates were influenced most strongly by litter type. Habitat had a smaller though significant effect, and the shade treatment suggested that sunlight was responsible for higher decomposition rates in prairie.

Nitrogen dynamics

Resins under litter collected less N than uncovered resins (overall means 0.30 vs. 0.66 g/m^2) in all treatment combinations except shaded grass litter in one prairie and one forest site, suggesting that litter accumulated N deposited from the atmosphere. N accu-

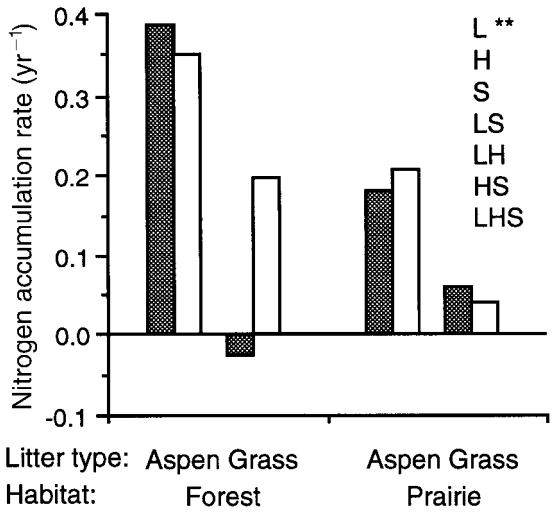

FIG. 3. Mean nitrogen accumulation rates (log[g·m^{-2} + 1]·yr^{-1}) of aspen and grass litter in two habitats (forest and prairie) under shade (■) and in the open (□). L, H, and S denote treatment effects examined with ANOVA. L = litter effect; H = habitat effect; S = shading effect. ** $P < 0.01$.

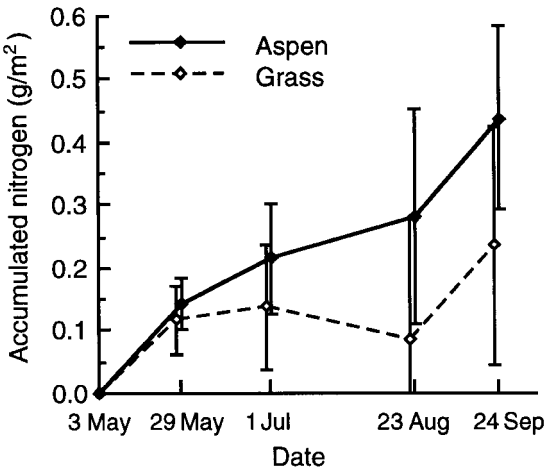

FIG. 4. Accumulated nitrogen over time (mean ± 1 SD, n = 90–94) in aspen and grass litter (initial litter mass = 0.2 kg/m^2), averaged over habitat and shading treatments and measured with ion-exchange resins.

mulation rates were significantly higher in aspen litter than in grass litter (Fig. 3, $F_{1,14} = 12.44$, $P < 0.01$). In spite of large differences among other means (Fig. 3, pooled SE = 0.085 log[g·m^{-2} + 1]·yr^{-1}), rates did not differ significantly between habitats or shading levels, or with any other interaction. N in aspen litter accumulated steadily over the growing season, but tended to level off in grass litter after 1 July (Fig. 4).

Resins under aspen litter collected significantly less N than those under grass litter (0.20 vs. 0.41 g/m^2, $F_{1,2} = 43.25$, $P < 0.05$). A significant litter × habitat type interaction ($F_{1,2} = 28.92$, $P < 0.05$) occurred because resins under aspen litter collected less N in forest than in any other litter × habitat combination. N in resins under litter did not vary significantly with habitat type or shading, or with any other interaction.

The amount of N in uncovered resins did not differ significantly between forest and prairie for the first and second harvests (Fig. 5). We did not compare third and fourth harvests because most assigned resin bags in prairie were destroyed and we calculated total amount of N from replacement bags. Over the course of the experiment, total accumulation of N in uncovered resins did not vary greatly between forest (0.63 g/m^2) and prairie (0.70 g/m^2, Fig. 5).

Over the course of the experiment, the concentration of N in aspen litter increased from 0.62 to 0.81% and in grass litter from 1.07 to 1.15%. The effects of both litter type and time were significant ($F_{1,16} = 60.79$, $P < 0.001$; $F_{1,16} = 7.22$, $P < 0.05$, respectively), but there was no significant interaction between them. Shading had no main effect or interaction with litter type on final N concentration.

In summary, resin bags suggested that litter accumulated N from the atmosphere. As with decomposition rates, N accumulation rates were influenced most strongly by litter type.

DISCUSSION

Direct and indirect effects on decomposition

Decomposition rates differed greatly between litter types (Figs. 1 and 2) but varied less between habitat types or shading (Fig. 1). This suggests that any differences in decomposition rate between prairie and forest are more likely to be related to the direct effects of litter quality than the indirect effects of shading. Aspen litter decomposed more slowly than grass litter (Fig. 1), probably due to a lower N concentration (0.62%) than grass

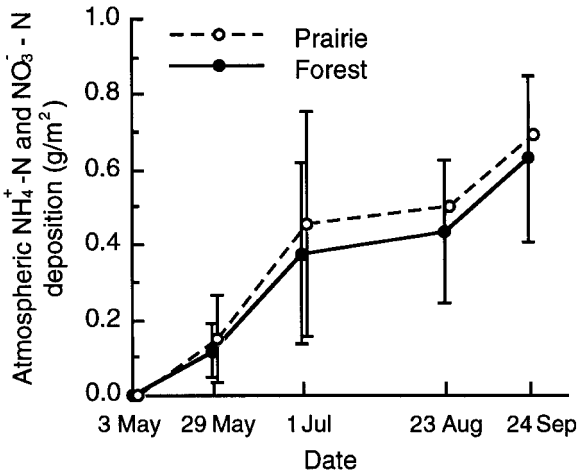

FIG. 5. Cumulative ammonium-N and nitrate-N deposition from atmosphere (mean ± 1 SD, n = 11–17) in mixed-grass prairie and aspen forest from May to September. Error bars are not shown for the last two prairie means because these values are based partly on estimates.

(1.07%; Berg and Staaf 1981, Taylor et al. 1989). Other authors have related decomposition rates to lignin:N ratios (Melillo et al. 1982, Taylor et al. 1989, Gallardo and Merino 1993), but these are comparable for aspen and grass (22 vs. 19, Taylor et al. 1989).

Decomposition rates were higher in open prairie than in the three other types of subplots (artificially shaded forest, naturally shaded forest, artificially shaded prairie; Fig. 1), suggesting that high temperature or insolation in prairie accelerated decomposition (Moorhead and Reynolds 1989). Moisture may not have been limiting because more than twice the average precipitation fell during July and August (Atmospheric Environment Service 1993*a*) and soil moisture did not differ much between forest and prairie.

The relatively weak effect of environment on mass loss (i.e., habitat and habitat × shading interactions, Fig. 1) was surprising since decomposition varies with moisture and temperature both at large scales (Upadhyay et al. 1989, Berg et al. 1993, Vitousek et al. 1994) and in microcosms (Taylor and Parkinson 1988*b*). In our study, higher temperature may have canceled out lower moisture in prairie and lower temperature may have canceled out higher moisture in forest. Other litter exchange studies also found small environmental effects (Hunt et al. 1988, Elliott et al. 1993, Mudrick et al. 1994). In the absence of large microclimatic differences, soil fauna and humus quality may have had significant effects on decomposition rates (Bocock and Gilbert 1957, Elliott et al. 1993) and may have contributed to the small environmental effect.

Decomposition rates

Decomposition rates in our study (aspen: $k = 0.44$ yr^{-1}, grass: $k = 1.36$ yr^{-1}, Fig. 1) may have been higher than those in most other field studies (e.g., Vossbrinck et al. 1979, Bartos and DeByle 1981, Blair et al. 1990) possibly because precipitation and temperature were particularly favorable. Rates may also have been higher because our results are based on summer decomposition, whereas most others are based on a full year of decomposition. We calculated summer decomposition rates from figures and tables of comparable studies where decomposition of grass and aspen was measured starting in the previous fall. Summer decomposition rates of aspen litter were lower in the Rocky Mountains (0.18 yr^{-1}, Lousier and Parkinson 1976) but higher in a Russian forest-steppe (1.23 yr^{-1}, Zlotin and Khodashova 1980). The lowest summer decomposition rates of grass litter are reported for the N-poor *Schizachyrium scoparium* (0.13 yr^{-1}, Pastor et al. 1987) and *Andropogon gerardii* (0.50 yr^{-1}, Seastedt et al. 1992) which have less than half the N concentration of our litter. Our grass litter also decomposed faster than litter of similar composition and in similar climate (0.80 yr^{-1}, Abouguendia and Whitman 1979), possibly because that litter was placed on soil from which vegetation had been removed, which may have hampered access by decomposers.

Grass decomposition rates observed in our experiment may have been higher than in truly natural situations because grass litter remains attached to the living plant above the ground for ≈9 mo (Sims and Coupland 1979), but our litter lay on the soil surface and may have been quickly colonized by decomposers or exposed to a more favorable microclimate. The effect of soil contact can be large (Lousier and Parkinson 1978, Seastedt et al. 1992) or small (Old 1969).

As decomposition of both aspen and grass can be described by an exponential equation (see also Pastor et al. 1987, Taylor and Parkinson 1988*a*, Seastedt et al. 1992) treatment effects on summer decomposition rates are representative for their influence during the whole ''accumulation phase'' (sensu Berg and Staaf 1981).

Nitrogen content in abscised aspen leaves in fall ranges from 0.44 to 1.05% (Lousier and Parkinson 1976, 1978, Bartos and DeByle 1981) and in prairie grass litter from 0.34 to 1.4% (Pigden 1953, Heinrichs and Carson 1956, Smoliak and Bezeau 1967). Large variation in litter quality within and among species likely causes similarly large variation in decomposition rates. This, along with variation among methods, presents a challenge for using comparisons of litter quality among species to understand differences in species effects on nutrient cycling (e.g., Hobbie 1992, Berendse 1994).

Nitrogen dynamics

N deposited from the atmosphere was retained by both aspen and grass litter and significantly increased the nitrogen concentration of the litter. This was observed, to an even greater extent, in European forests (Tietema 1993, Laskowski et al. 1995) and Chilean piedmont shrubland (Cisternas and Yates 1982). It also agrees with results of experiments with ^{15}N-labeled artificial deposition (van Vuuren and van der Eerden 1992). Atmospheric N originating from industrial processes is a potential source of N input even in remote regions, as has been shown in North America (Linsey et al. 1987, Lovett 1992) and Europe (Draaijers et al. 1989, Eiden et al. 1989). Although N deposited from the atmosphere does not seem to accelerate decomposition (Fog 1988, van Vuuren and van der Eerden 1992), it does accumulate in litter, suggesting that mineralization studies based on chemical analyses of litter N concentration should incorporate atmospheric sources of N accumulation.

Accumulated N in both litter types was probably immobilized by decomposers because initial litter N concentration was below the requirements of decomposers (Berg and Staaf 1981, Fog 1988). Aspen litter may have accumulated and immobilized more deposited N than grass litter (Fig. 3) because it had a lower initial N concentration (Tietema 1993). Litter N was increased by deposition, but this may not have been sufficient to allow net mineralization (Fog 1988, van

Vuuren and van der Eerden 1992). The high concentration of recalcitrant lignins in aspen and grass litter (about the same as in white spruce, *Picea glauca*, Taylor et al. 1989) may also be responsible for the lack of net mineralization (Berg and Staaf 1981).

Habitat had no significant effect on N accumulation in our study (Fig. 3). In contrast, a strong habitat type effect and a significant litter type × habitat interaction effect on N accumulation was found in comparisons of prairie, mountain meadow, and pine forest (Hunt et al. 1988). That result was attributable to the inclusion of *Pinus contorta* litter that has a very high lignin:N ratio (85, Dyer et al. 1990) and may have specialized decomposer communities.

The accumulation of N in litter measured by resins was confirmed by an increase in litter N concentration over the course of the experiment. If, however, the accumulated amount of N retained by the litter is subtracted from the final amount of N in the litter, the intrinsic concentration of N in litter at the end of the study (aspen: 0.58%, grass: 0.95%) was not significantly different from the initial concentration in either litter type. This suggests that the increase of the concentration of N can be accounted for by the addition of deposited N, indicating that no net mineralization occurred, as was found in the results from resins.

Lower rates of decomposition of aspen than grass litter disagree with higher concentrations of extractable N in forest soils than prairie soils at the study site (Wilson 1993). The higher litter mass in forest probably makes up for lower N concentration of aspen litter to account for the difference.

In summary, decomposition rates and nitrogen dynamics were affected most strongly by litter type, with N-rich grass litter decomposing faster than N-poor aspen litter. Mass loss was highest in plots exposed to sun, but N dynamics did not vary significantly between the environments of forest and prairie.

Acknowledgments

We thank the Saskatchewan Department of Parks and Recreation for permission to work at White Butte Recreation Site, D. Binkley for help with the ion-exchange method, E. Brunner for statistical advice, and D. Binkley, C. Prescott, D. Wedin, and one anonymous reviewer for helpful comments on the manuscript. This research was supported by a German Academic Exchange Service (DAAD) scholarship to M. Köchy and a Natural Sciences and Engineering Research Council of Canada grant to S. Wilson.

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