Analysis of litter decomposition in an alpine tundra

David M. Bryant, Elisabeth A. Holland, Timothy R. Seastedt, and Marilyn D. Walker

Abstract: Decomposition of plant litter regulates nutrient cycling and transfers of fixed carbon to soil organic matter pools in terrestrial ecosystems. Climate, as well as factors of intrinsic litter chemistry, often govern the rate of decomposition and thus the dynamics of these processes. Initial concentrations of nitrogen and recalcitrant carbon compounds in plant litter are good predictors of litter decomposition rates in many systems. The effect of exogenous nitrogen availability on decay rates, however, is not well defined. Microclimate factors vary widely within alpine tundra sites, potentially affecting litter decay rates at the local scale. A controlled factorial experiment was performed to assess the influence of landscape position and exogenous nitrogen additions on decomposition of surface foliage and buried root litter in an alpine tundra in the Front Range of the Rocky Mountains in Colorado, U.S.A. Litter bags were placed in three communities representing a gradient of soil moisture and temperature. Ammonium nitrate was applied once every 30 days at a rate of 20 g $N \cdot m^{-2}$ during the 3-month growing season. Data, as part of the Long-Term Inter-site Decomposition Experiment Team project, were analyzed to ascertain the effects of intrinsic nitrogen and carbon fraction chemistry on litter decay in alpine systems. Soil moisture was found to be the primary controlling factor in surface litter mass loss. Root litter did not show significant mass loss following first growing season. Nitrogen additions had no effect on nitrogen retention, or decomposition, of surface or buried root litter compared with controls. The acid-insoluble carbon fraction was a good predictor of mass loss in surface litters, showing a strong negative correlation. Curiously, N concentration appeared to retard root decomposition, although degrees of freedom limit the confidence of this observation. Given the slow rate of decay and N loss from root litter, root biomass appears to be a long-term reservoir for C and N in the alpine tundra.

Key words: litter decomposition, alpine tundra, nitrogen deposition, LIDET, Niwot Ridge.

Résumé : Dans les écosystèmes terrestres, la décomposition des litières végétales règle le cyclage des nutriments et les tranferts du carbone fixé aux réserves de matière organique du sol. Le climat, ainsi que des facteurs intrinsèques à la chimie de la litière, déterminent le taux de décomposition et ainsi la dynamique de ces processus. Dans plusieurs systèmes, la teneur initiale en azote et les composés carbonés récalcitrants sont de bons éléments de prédiction des taux de décomposition. L'effet d'une disponibilité d'azote exogène sur les taux de décomposition est cependant mal défini. Les facteurs microclimatiques varient beaucoup sur les sites de tundra alpine, ce qui est susceptible d'affecter les taux de décomposition de la litière à l'échelle locale. Les auteurs ont conduit une expérience factorielle contrôlée pour évaluer l'influence de la position dans le paysage et d'additions d'azote sur la décomposition en surface de feuillage et en profondeur de litière racinaire, dans une tundra alpine située dans le Front Range des montagnes Rocheuses au Colorado, U.S.A. Les sacs de litières ont été placés dans trois communautés représentant un gradient d'humidité et de température du sol. Du nitrate d'ammonium a été appliqué à tous les 30 jours à raison de 20 g $N \cdot m^{-2}$ au cours de la saison de croissance de 3 mois. Dans le cadre du projet en équipe « Long-Term Inter-site Decomposition », les auteurs ont analysé les données pour préciser les effets de l'azote intrinsèque et de la chimie de la fraction carbonée sur la décomposition des litières en milieu alpin. Il apparait que l'humidité du sol est le premier facteur contrôlant la perte de masse de la litière en surface du sol. La litière racinaire ne montre pas de perte de masse significative après la première saison. Les additions d'azote n'ont pas d'effet sur la rétention de l'azote, ou la décomposition, de la litière de surface ou racinaire enfouie, comparativement aux témoins. La fraction carbonée soluble à l'acide est un bon critère de prédiction de la perte de masse pour la litière de surface, montrant une forte corrélation négative. Curieusement, la concentration en N semble retarder la décomposition des racines, bien que les degrés de liberté limitent la confiance en cette observation. Étant donné le faible taux de décomposition et de la perte en N des litières racinaires, la biomasse racinaire semble constituer une réserve à long terme de C et de N en milieu alpin.

Received October 1, 1997.

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Mots clés : décomposition des litières, tundra alpine, addition d'azote, LIDET, Niwot Ridge.

[Traduit par la Rédaction]

Introduction

Decomposition of plant litter is an important regulator of nutrient cycling and carbon (C) flux in terrestrial ecosystems (Swift et al. 1979; Aber and Melillo 1991; Schlesinger 1991). The rate of decomposition often correlates with the initial relative concentrations of C compounds and the nitrogen (N) content of plant litter (Fogel and Cromack 1977; Aber and Melillo 1982; Melillo et al. 1982, 1989; Melillo and Aber 1984; Berendse et al. 1987; Aber et al. 1990; Taylor et al. 1989). Thus, indices of carbon to nitrogen ratio (C/N) (Fogel and Cromack 1977; Berendse et al. 1987; Taylor et al. 1989), lignin to nitrogen ratio (L/N) (Aber and Melillo 1982; Aber et al. 1990) and lignocellulose index (lignin/lignin + cellulose) (Melillo et al. 1989) have been used to predict decay rates in temperate forest and grassland systems.

The C/N ratio has also been shown to influence N dynamics of decaying litter. When litter C/N is high, decomposer microbes immobilize N and thus may delay N release (Aber and Melillo 1982; Melillo and Aber 1984). Low C/N ratios relieve microbial N limitation, potentially accelerating decay, N release, and increasing N availability (Aber et al. 1990).

While the relationship between the N content of litter and decay rate has been observed in numerous studies, no clear connection has been found between decomposition rate and exogenous N availability (Fog 1988). Comparisons at the plot level have occasionally produced positive correlations of N availability with litter decomposition rate (Kelly and Henderson 1978; Hunt et al. 1988). When data were compared across sites, however, the strengths of the relationships were reduced (McClaugherty et al. 1985; Hunt et al. 1988).

Meentmeyer (1978) observed that the negative effect of lignin content on decay rate increases with actual evapotranspiration (AET) across a latitudinal gradient. Thus, variations in environment appear to interact with litter chemistry to regulate decomposition rates.

The Niwot Ridge tundra ecosystem in the Colorado Front Range consists of a mosaic of plant communities, the distribution of which is influenced primarily by snow depth (Walker et al. 1993). Variation in topography, snow depth, soil moisture, and plant biomass combine to create a range of microclimates across the alpine landscape. In addition, atmospheric N deposition has been increasing at this site and may exceed 30 times preindustrial levels (Lewis et al. 1984; Bowman 1992; Sievering et al. 1992). Consequently, the potential exists for significant variation in decomposition and N cycling rates among communities.

The influence of intrinsic chemistry and environmental variables on litter decomposition have been extensively investigated in temperate forests (e.g., McClaugherty and Berg 1987), boreal forests (e.g., van Cleve 1974), grasslands (e.g., Seastedt et al. 1992), agroecosystems (e.g., Holland and Coleman 1987), and arctic tundra ecosystems (e.g., Hobbie 1996). The current literature on decomposition in alpine tundra, however, is sparse (e.g., O'Lear and Seastedt 1994).

The objectives of the current research were to (*i*) determine the variation in decomposition rates over the range of temperature and moisture found at the Niwot Ridge site; (*ii*) test the effect of exogenous N additions on decomposition of native litter; and (*iii*) determine the influence of litter chemistry on decay rate and N dynamics. These questions are addressed separately for surface foliage and buried fine root litter.

Methods

Site description

Niwot Ridge is a UNESCO Biosphere Reserve and a Long-Term Ecological Research Site (LTER). The site is located at 3510 m elevation, 5 km east of the Continental Divide, and 8 km west of Ward, Colo. (E 499.700, N 4,433,900 UTM). This study was performed in a 25-ha saddle area between two knolls, thus providing a toposequence of varying slope and aspect. Average annual precipitation is 930 mm, of which 82% falls as snow between late September and early June. Snow depth is variable across the saddle resulting from redistribution by high winds. Mean annual air temperature measured at a climate station 300 m above the saddle site is –3.8°C. The frost-free growing season averages 47 days beginning in late June and extending to mid-August (Walker et al. 1994).

Of the six major vegetation types described by May and Webber (1975) at the Saddle site, the dry, mesic, and wet communities occupy the largest area. Dry meadows are located on the wind-swept west facing knoll and are dominated by the sedge, *Kobresia myosuroides*, and the forb, *Acomostylis rossii*. The mesic meadow communities occupy the center portions of the saddle where *Acomostylis rossii* and a grass, *Deschampsia caespitosa*, are the most abundant species. The wet meadows are found adjacent to the snow fields at the base of the west knoll and are dominated by the forb, *Caltha leptasepala*, and a sedge, *Carex scopulorum*. These communities constitute a complex environmental gradient of moisture, plant biomass, snow depth, and topography among other variables.

Experimental design

Nitrogen × landscape treatment

A factorial design was implemented to measure the effects of landscape position and N additions on decomposition of native surface foliage and buried fine root litter. Six 1-m^2 plots were located randomly in each of the three community types (dry, mesic, and wet) resulting in a total of 18 plots. Nitrogen treatment bags were placed 75 cm downslope from the control bags in a split-plot arrangement to prevent runoff contamination of controls. Five of the 10 surface litterbags at each plot received N treatments, and five were exposed to ambient N levels. Four plots in each community type received eight root litter bags, four for each level of N addition.

Chemistry treatment

The influence of intrinsic chemistry on litter decay was determined using data obtained from the Long-Term Intersite Decomposition Experiment Team (LIDET) project. The study was initiated in 1990 as a large-scale, cross-site investigation, focusing on the influence of climate and litter chemistry on decay rates. Twenty-nine species of litter were incubated at 28 sites represent-

ing a latitudinal gradient from Central America to the North Slope of Alaska and elevational gradient from sea level to 3510 m.

Litter at the Niwot site was incubated within the mesic meadow community at four replicate plots. Baseline chemistry data were analyzed from pooled subsamples of each species and litter type for proximate C fraction (PCF) and N. The LIDET team chose six species of foliar litter (*Acer saccharum* Marsh., *Drypetes glauca*, *Pinus resinosa* Ait., *Quercus prinus* L., *Thuja plicata* Donn., and *Triticum aestivum* L.) and three species of root litter (*Drypetes glauca*, *Pinus elliotii* Engelm., and *Andropogon gerardi*) for the repeated annual collections.

Field methods

Native litter

Foliar litter consisted of a composite of graminoid litters from three sources. The major constituent was obtained from a pool of dried, archived material from live peak biomass collections occurring from 1984 through 1992. Methods of collection are described in Walker et al. (1994). Senesced litter was collected from the field in spring 1993 and combined with senesced *Deschampsia* litter from greenhouse grown plants. Senesced and green litters were placed in separate 40-L polyethylene bags. All litter was brought to 10% gravimetric water content by lightly spraying with deionized water to minimize fragmentation during weighing and handling. The litter was stored at 4°C for 24 h to allow for equilibration. Green and senesced foliage was combined at 1.5:1 ratio into 2-g samples and placed in 10 × 20 cm fiberglass screen litter bags of 1 mm mesh size. Litter bags were stapled closed and dried at 60°C to constant weight. Initial litter weight was obtained by subtracting the bag weight (including staples) from total weight following oven drying. An additional 30 foliage litter bags were prepared using knit polyester cloth with a mesh of <0.3 mm. These bags were placed at six of the paired plots as a control on litter bag mesh size. Surface foliage bags were secured to the tundra surface with nails.

Roots were collected by coring at Niwot Ridge and were not identified to species. Fine roots (<2 mm diameter) were separated from coarse roots (>2 mm diameter), but no attempt was made to separate live and dead roots. The remaining fine roots were hydrated as above and homogenized by hand mixing. A 2-g sample was placed in each 15 × 20 cm knit polyester litter bag (mesh < 0.3 mm) and oven-dried to constant weight at 60°C. A wedge (3 × 15 × 15 cm) was cut and removed from the soil, and the litter bag was inserted vertically. The wedge was replaced adjacent to the litter bag and pressed into place. The aluminum identification tag was left exposed at the surface to locate the bag for retrieval.

The treated bags of each plot received applications of N fertilizer in the form of aqueous NH_4NO_3. Treatments of 20 g $N \cdot m^{-2}$ were applied in June, July, and August of each year for a total of 60 g $N \cdot m^{-2} \cdot year^{-1}$. Surface litter bags were collected five times, at time of placement, fall 1993, spring 1994, fall 1994, and fall 1995. Time-zero (t_0) samples allowed correction of losses incurred during transport and weighing, as well as measurement of baseline chemical concentrations. Buried root litter bags were handled identically to surface bags with the exception of a time-zero harvest. Initial chemistry for fine roots was measured from subsamples of fine root litter taken while constructing root litter bags.

Soil temperature measurements were taken at a subset of five plots that encompass the range of slope and aspect for the Saddle research area. Thermisters were placed at 2- and 10-cm depths. Automated measurements were made starting June 16, 1994, through September 8, 1994, and stored in a Datapod 212 data logger (Omnidata International, Inc. Logan, Utah). Daily averages are reported here.

Soil moisture measurements were taken weekly at all litter bag sites during the 1994 growing season using the time-domain reflectometry (TDR) method described in Taylor and Seastedt (1994).

LIDET litter

Foliage was collected as senesced or abscised leaves and air-dried with the exception of *Drypetes glauca*, which was oven-dried. All material was shipped to the Forest Research Laboratory at Oregon State University (OSU), headquarters of the LIDET project. Roots were collected by excavation except in the case of *Andropogon gerardii*, which were collected from material exposed along stream banks. Surface litter bags were 20 × 20 cm^2 with 1-mm mesh on the top and 55-µm mm mesh on the bottom. Each surface bag received 10 g of litter and was labeled with aluminum number tags. Bags were threaded onto cords in random order. Strings of litter bags were staked to the ground at four sites in the mesic alpine meadow. Root litter bags were constructed of 55-µm mesh and filled with 5–7 g of fine root litter. A vertical cut in the soil was made with a shovel and a litter bag inserted vertically. A second parallel cut was made, adjacent to the first, to press the soil firmly against the litter bag.

One litter bag of each species was collected annually from each replicate site. Buried root bags were washed with deionized (DI) water to remove adherent soil from the surface of the bag. Litter was removed from bags, placed in paper bags, and oven-dried at 55°C to constant weight. Samples were sent to OSU for weighing and chemical analyses. Ash content of litter was determined by loss on ignition after collection.

Laboratory methods

Samples from each harvest were returned to the lab on the same day of collection. Any new roots were removed, samples were oven-dried at 60°C to constant weight, and ground in a Wiley mill to pass a 40-mesh screen. Native and LIDET litter samples were treated similarly with the exception that LIDET samples were shipped to OSU following oven drying and weighing. Subsamples of t_0 samples were composited and analyzed via the PCF method (Newman et al. 1995) to determine relative concentrations of extractive, acid-soluble (ACS) and acid-insoluble (AIS) fractions. These last two fractions have previously been termed holocellulose and lignin. While the acid-soluble fraction has been quantitatively identified as holocellulose (Effland 1977), lignin is a less well defined substance and thus is referred to here as an AIS fraction. Ash contents were determined by the loss on ignition method. Nitrogen and C concentrations of the native litter were measured by a Carlo Erba CHN elemental analyzer (Fison Instruments, Danvers, Mass.) as were the initial values for the LIDET litter. Litter chemistry data on the time course of decayed LIDET samples were not available from the LIDET team as of this writing; therefore, data presented here on those substrates were acquired through micro-Kjeldahl digestion, followed by colorimetric analysis, performed by at the University of New Hampshire, Durham, N.H.

Subsamples of native litter from surface and buried control plots and dry and wet surface N treatment plots were sent to the plant pathology laboratory at OSU for analysis of fungal and bacterial biomass. The techniques for microbial biomass determination are described in Ingham and Klein (1984).

Statistical methods

Data were analyzed using the JMP version 3.0 statistical software (SAS Institute Inc., Cary, N.C.). Mean values of each variable presented were calculated by lumping replicates within each community type and treatment separately. Absolute differences in decay and N release were compared using the ash-free percent original mass (POM) remaining at the time of harvest. The arcsine transformation was applied to percentage data to achieve independence of the mean and variance in each data set prior to statistical

Table 1. Initial nitrogen and proximate carbon fraction chemistry of native alpine and LIDET leaf and fine root litters used in litter decay experiment Niwot Ridge, Colorado, U.S.A.

Species	% N	% Extractive	% ACS	% AIS
Foliage				
Native	1.2	22	60	18
LIDET				
Chestnut oak (*Quercus prinus*)	1.0	41.0	42.0	17.0
Drypetes (*Drypetes glauca*)	1.7	46.1	42.6	9.3
Red pine (*Pinus resinosa*)	0.7	41.0	38.3	20.1
Sugar maple (*Acer saccharum*)	1.1	58.7	33.5	7.8
Western red cedar (*Thuja plicata*)	0.9	42.0	41.0	17.8
Wheat (*Triticum aestivum*)	0.3	30.5	52.1	17.4
Fine roots				
Native	1.1	15.0	50.0	35.0
LIDET				
Big blue-stem (*Andropogon gerardi*)	0.6	39.2	49.0	11.8
Drypetes (*Drypetes glauca*)	0.9	30.1	45.3	23.9
Slash pine (*Pinus elliotii*)	1.0	48.7	37.4	13.9

Note: See text for composition of native foliage. Extractives, polar + non-polar soluble fraction; ACS, acid soluble fraction; AIS, acid insoluble fraction.

Table 2. Exponential decay rates (*k* factor) of surface foliage and buried fine root litter (N treated and controls) during incubation in three alpine communities, Niwot Ridge, Colorado, U.S.A.

	k factor	R^2	Error	*p*
Foliage litter				
Controls				
Dry	0.021	0.8991	0.071	<0.0001
Mesic	0.025	0.7779	0.131	<0.0001
Wet	0.027	0.8655	0.103	<0.0001
N treatment				
Dry	0.013	0.9446	0.044	<0.0001
Mesic	0.022	0.8240	0.104	<0.0001
Wet	0.025	0.8293	0.114	<0.0001
Fine root litter				
Controls				
Dry	0.0062	0.3315	0.0863	<0.01
Mesic	0.0106	0.7404	0.0637	<0.0001
Wet	0.0067	0.2317	0.105	<0.02
N treatment				
Dry	0.010	0.5663	0.083	<0.01
Mesic	0.006	0.4271	0.0066	<0.0001
Wet	0.004	0.003	0.148	<0.32

Note: Error terms are root mean square error of the regression.

analysis. Differences in the mean absolute mass loss and mean percent of original N remaining (dependent variables) among community and N treatment effects were determined via model II, two-way analysis of variance (ANOVA) after Sokal and Rohlf (1995). Specific differences among community types were tested pairwise using Tukey's honestly significant difference (HSD). Differences among LIDET species effects were tested by repeated measures MANOVA and the pairwise comparison with Tukey's HSD.

Mass loss was compared with environmental variables of soil moisture, soil surface temperature (surface litter samples), soil temperature at 10 cm (buried fine root litter), and snow cover by least squares multiple regression.

Results

Litter chemistry

Results of initial PCF and N content analysis of all litters are shown in Table 1.

Surface litter mass loss

The pattern of decay in each community produced good fits with the exponential model for all treatments (Table 2). Percent original surface litter mass remaining in coarse-mesh litter bags varied significantly among communities for all harvests (Fig. 1A). Mass loss clearly decreases across the landscape from wet to dry sites. Soil moisture measurements were significantly correlated with POM remaining at 12 months ($p < 0.01$) (Fig. 2), while mean daily surface temperature was not.

Litter mass remaining in fine-mesh litter bags showed similar patterns of landscape and decomposition rates with the coarse mesh bags early in the study. However, in the fall 1994 harvest (15 months) the larger (1-mm) mesh bags showed a significant decrease in mass over fine-mesh bags ($p < 0.05$; data not shown). Landscape position is also significant in both treatments ($p < 0.01$) although landscape × mesh size interaction is not.

Additions of N produced no significant differences in surface mass loss among communities during the course of these measurements ($p = 0.06$) (Table 2).

Foliage litter showed significant differences in mass remaining among the LIDET species at each of the annual harvests for the first 3 years of the study (Fig. 1C). Differences in relative decay among all species are also significant (Table 3) with the exception *Drypetes glauca* and *Acer saccharum*. The pattern of decay shown in Fig. 1C appears to follow AIS concentrations; indeed, initial AIS correlates well with *k* for surface foliage (Fig. 3A). The species

Fig. 1. Litter mass loss for surface and buried fine-root litter in an alpine landscape. Native foliage (A) and buried fine-root (B) litters were incubated in three community types. LIDET litter (C, foliage; D, buried fine roots) were incubated in the mesic meadow community. Error bars are SE.

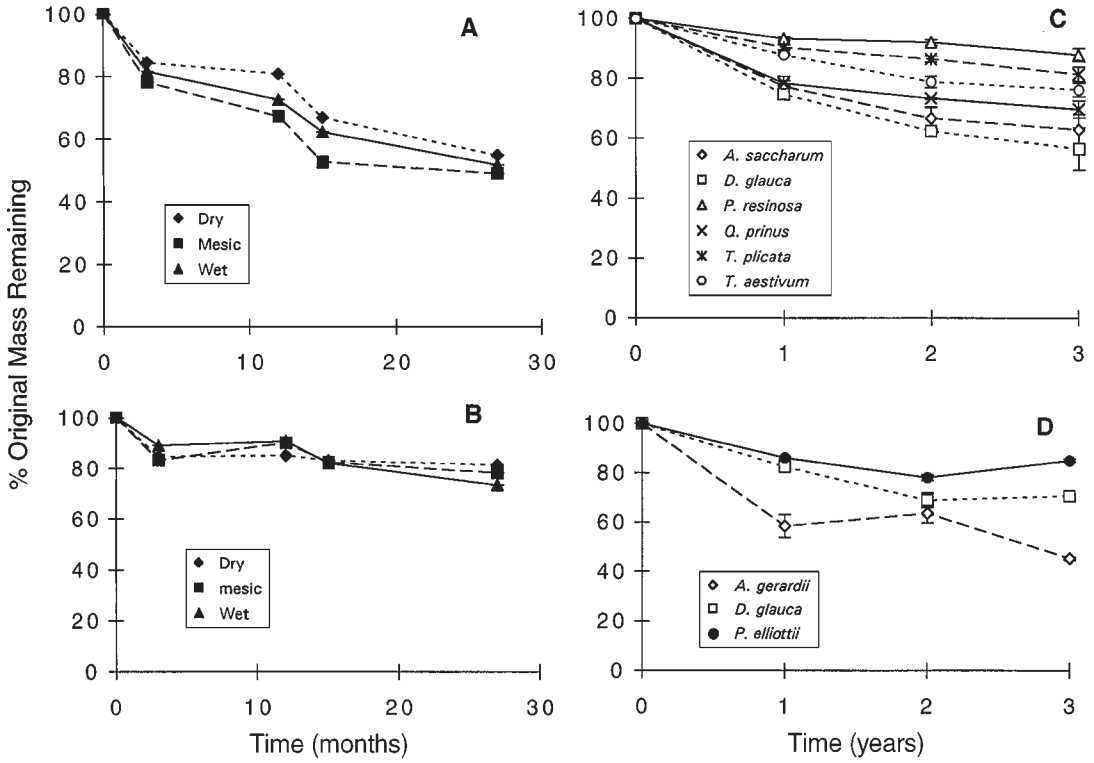


Fig. 2. Mass loss of native alpine surface foliage litter versus gravimetric soil moisture incubated in three alpine communities.

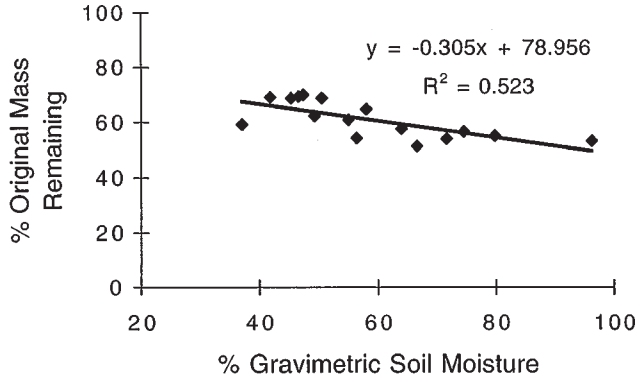


Table 3. Exponential decay rates of LIDET litter following 3-year incubation in a mesic alpine meadow, Niwot Ridge, Colorado, U.S.A.

Species	*k* factor	R^2	Error	*p*
Foliage				
P. resinosa	0.039	0.6851	0.031	<0.0001
T. plicata	0.067	0.8689	0.030	<0.0001
T. aestivum	0.093	0.8663	0.044	<0.0001
Q. prinus	0.116	0.8096	0.067	<0.0001
A. saccharum	0.157	0.7336	0.114	<0.0001
D. glauca	0.214	0.7358	0.153	<0.0001
Fine roots				
P. elliotii	0.059	0.4807	0.073	<0.01
D. glauca	0.124	0.6420	0.110	<0.01
A. gerardii	0.193	0.5781	0.197	<0.001

Note: Error terms are root mean square error of the regression, *p* value refers to significance fit to regression model.

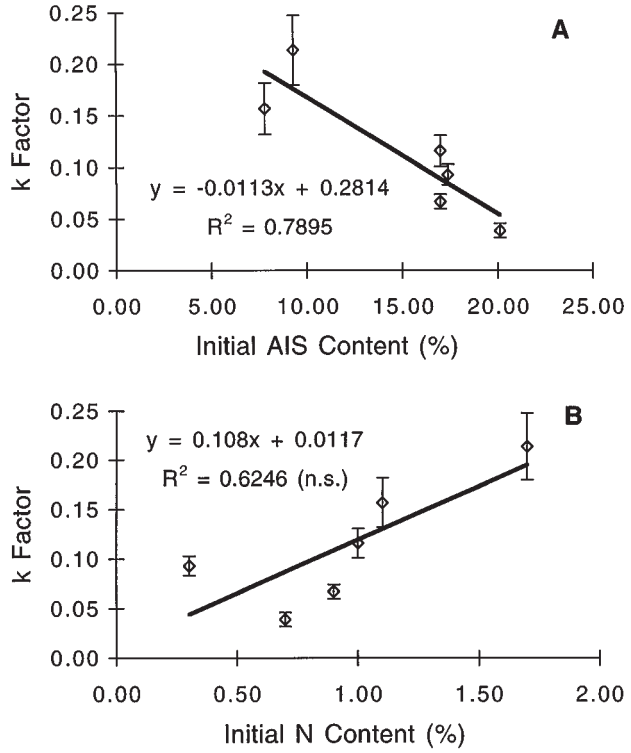
Quercus prinus, *Thuja plicata*, and *Triticum aestivum* have almost identical AIS fractions and thus group closely in this regression. Considerable variation along the *y* axis is apparent suggesting other sources, but no significant correlation with any other PCF was found. Initial N content produced a positive relationship with *k* but was only marginally significant ($p = 0.06$).

Fine root litter mass loss

Following an initial decline during the 1993 growing season, no significant changes in mass loss of native fine root litter were observed over the next four harvests. No significant differences in fine root POM remaining with landscape position (Fig. 1B) or N treatment (Table 2) was found within any harvest. Surface litter decay differed significantly from fine root litter in all treatments ($p < 0.0001$).

Decay of fine root litter in the LIDET experiment (Fig. 1D) also produced a good fit to the exponential decay function (Table 2). Regression of initial chemistry against *k* factor produced no significant relationship with any PCF value. Initial analysis of N concentration versus root *k* factor produced a surprisingly strong negative correlation ($R^2 = 0.9778$). This relationship suffered from degrees of freedom having only three species in the data set. The regression was rerun using the estimated annual *k* factor of each replicate at

Fig. 3. Relationships of exponential slope constant (*k* factor) and initial acid insoluble (AIS) fraction (A) and initial [N] (B) of LIDET surface litters. Error bars are SE.



year 3 (k = ln(POM)/t). The R^2 of the regression suffered slightly (see Fig. 5) but was still highly significant (p < 0.001).

Nitrogen dynamics

Surface litter

Release of N from decaying litter occurred in surface control plots during the first growing season. Figure 4A shows the percent of original N (PON) at each harvest. The pattern of N release was similar to that of mass loss across the landscape. Therefore, differences in N content were highly significant among communities (p < 0.001). No significant difference in PON remaining was observed during either the 12- or 15-month harvests, as surface litter in all communities converged to a mean of 61.5 ± 8.36% (mean ± SD) original N. Over the next 12 months, N contents diverged as litters accumulated N at different rates. However, differences among landscape positions or treatments were not significant. This observation compares well with results of microbial biomass measurements on control litter bags at 12 months (Table 4). Microbial biomass (fungal + bacterial) did not correlate with landscape position, litter mass remaining, N treatments, or N dynamics at 15 months.

The six species of LIDET surface litter also showed loss of N during the first 12 months (Fig. 4C). Four of the six surface litters began accumulating N by the following year with the exception of *Drypetes glauca* and *P. resinosa*, which did not show N accumulation until year 3. While PON is a good illustrator of N dynamics relative to initial content, the absolute quantity of N lost or gained is a better indicator of the N immobilization potential among species. Furthermore, recent studies with ^{15}N tracers show that changes in N content are the net result of simultaneous gains and losses of N by decaying litter (Berg 1987; van Vuuren and van Der Veerden 1992). Therefore, regressions of absolute net N immobilization were performed against species PCF chemistry and initial N content. Initial N content showed a negative correlation with N immobilization following the first year of incubation, but was not significant. Content of extractives however showed a highly significant negative (p < 0.0001) correlation to net N immobilization during this period (Fig. 6). The regression against the ACS fraction was likewise significant, but the slope was positive, suggesting merely a reflection of the correlation of ACS with extractives. This relationship declined in significance in the following two harvests.

Table 4. Microbial biomass (mg·g^{-1} dry wt.) for surface foliage and buried fine root litter in three alpine communities, Niwot Ridge, Colorado, U.S.A.

		Fungus		Bacteria		Ratio	
	N	Mean	SE	Mean	SE	Mean	SE
Foliage							
Dry	5	11	0.7	162	23.0	0.08	0.01
Mesic	5	13	1.5	244	46.6	0.06	0.01
Wet	5	20	7.4	290	63.6	0.08	0.04
Fine roots							
Dry	3	418	60.7	44	2.4	9.47	1.10
Mesic	2	390	31.3	67	9.3	5.96	0.36
Wet	4	268	24.5	65	9.9	4.95	1.46

Fine root litter

Native buried fine root litter released N in the first two growing seasons (Fig. 6B). Regardless of landscape position or N treatment, root litter retained an average of 79.3 ± 22.53% original N mass. Native root litter began accumulating N in all communities following 15 months incubation. No significant difference in N content was found among landscape positions. As in surface litter, mean values of C/N for root litter did not vary significantly from the original mean value of 41.

Fungal and bacterial biomass were significantly higher in buried roots than in surface litter. In addition, fungal to bacterial biomass ratios were two orders of magnitude higher in fine roots than in surface litter (Table 4). As with surface litter though, no correlations were found with landscape position or N treatment.

Following the same pattern as surface litter, LIDET root species lost N during the first year (Fig. 4D); nitrogen content was stable during the second year; and all species showed N accumulation by year 3. Nitrogen accumulation in *Drypetes glauca* roots was significantly greater than *P. elliotii* roots although neither species differed from *Andropogon gerardii*. Net N immobilization in fine root litter was not significantly correlated with any PCF fraction.

Fig. 4. Nitrogen dynamics of surface and buried fine-root litter in an alpine landscape. Native foliage (A) and buried fine-root (B) litters were incubated in three community types. LIDET litter (C, foliage; D, buried fine roots) were incubated in the mesic meadow community. Error bars are SE.

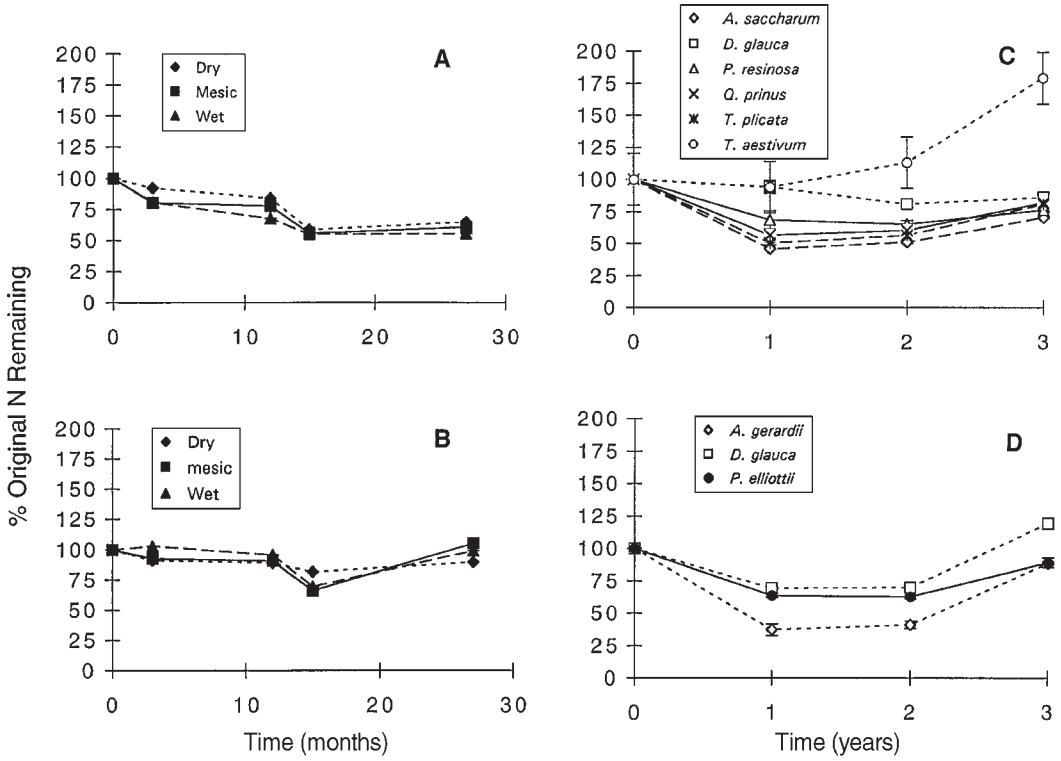


Fig. 5. Relationship of initial nitrogen concentration on *k* factors of individual replicates at 3 years for LIDET fine-root litter.

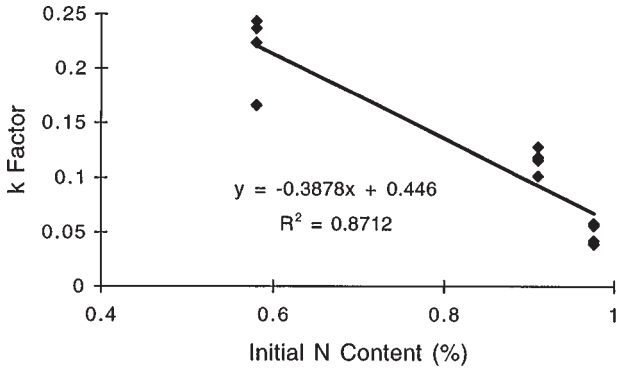
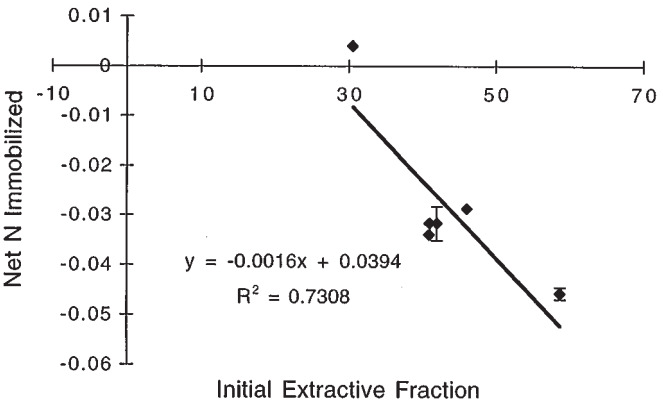


Fig. 6. Relationship of initial extractive fraction on net nitrogen immobilization of LIDET foliage litter following 12 months incubation. Negative values denote N loss. Error bars are SE.



Discussion

The differences in litter decay rates observed across community types are apparently driven by variation in soil moisture (Figs. 1A, 1B, and 2). In other systems, Vitousek et al. (1994) found temperature to have a greater influence than moisture on litter decomposition across an elevational gradient on Mauna Loa, Hawaii. Witkamp (1966) found similar results in temperate forests. Both observations agree with the relationship of decomposition and AET found by Meentmeyer (1978). The effects of these variables are difficult to separate, as they are not entirely independent. As temperature decreases however, the contribution to the AET function will certainly decline. Tundra sites are known to have large variations in soil moisture and low mean daily temperatures (Flanagan and Veum 1974). Given that the variation in soil moisture exceeds the magnitude of temperature variation at Niwot Ridge, the finding that moisture effect exceeds that of temperature is not surprising. Moreover, a synthesis of data from circumpolar sites shows moisture to be a primary factor controlling of litter decay rates in arctic systems (Heal and French 1974). Furthermore, if moisture limits microbial activity, temperature variation would have little effect other than to exacerbate the limitation through increased evaporation. This is supported by Flanagan and

Veum (1974) who found that the sensitivity of decomposition to temperature increased with soil moisture in wet coastal tundra.

Given the high concentration of extractive fractions in native surface litter we cannot rule out leaching as a large portion of mass loss during this relatively short-term study. While microbial biomass does not imply microbial activity, the lack of a significant correlation of litter mass loss with microbial biomass and the late onset of N immobilization supports leaching as a major contributor to mass loss. The strong negative relationship of extractives with N immobilization (or rather N losses) is particularly indicative (Fig. 6).

This leaching loss of N may explain the observation that N losses parallel mass loss as moisture availability increases. Fisk and Schimdt (1995) found a similar pattern of N mineralization, suggesting that N cycling rates are linked to moisture availability at this site.

Other nonmicrobial factors such as fragmentation may also be important, as evidenced by the differences in mass loss among fine- and coarse-mesh litter bags. While the source of this fragmentation is not known, communition from microarthopods is a good possibility as the 0.3-mm mesh litter bags would exclude most prostigmatid, and probably all orbatid, mites. Both are known to accelerate litter fragmentation (Seastedt and Crossley 1980) and have been collected at this site (O'Lear and Seastedt 1994). Given the harsh environment of the alpine, other causes of fragmentation such as wind, rain, hail, snow, or even trampling are equally likely. Fragmentation may perform a critical function in alpine tundra by ameliorating conditions for decomposition. Aside from increased surface area, smaller particles are more likely to be incorporated in the surface soil, where moisture availability for decomposer microbes would be higher than at the litter layer. Unfortunately, the litter bag technique does not measure decomposition dynamics at this scale.

The observation that N additions do not increase mass loss (Table 2) is consistent with earlier findings regarding exogenous N availability and litter decay rates (McClaugherty et al. 1985; Holland and Coleman 1987). The LIDET surface litters showed a weak (but not significant) correlation with litter N content and decomposition (Fig. 5). This evidence does not support the alternate hypothesis that N limits microbial decay of native litter. Therefore, the null hypothesis cannot be rejected. However, the delay in nitrogen accumulation (Fig. 4) suggests that microbial growth on these litters may be retarded during the first 2 years; thus, any effect of N availability may not yet be apparent. Future observations of the LIDET litters should provide additional data to address the question of intrinsic N content on decay and determine if additional long-term N addition experiments are required.

While the AIS content of LIDET surface litters was found to be the best predictor of decay (for the chemical components measured) (Fig. 4), the assumption that the recalcitrant fraction is hindering decay is premature at this stage. The AIS fraction is inherently correlated with extractive and ACS fractions, as any change in one fraction would necessitate an inverse change in one or both of the others. In addition, the degree of mass lost after 3 years is still well within the labile carbon fraction of these litters. This relationship could easily be expressed as a positive correlation of k factors with the sum of the labile pools (extractives + ACS or 1 – AIS). The increase in the percent of original N since the second-year harvest (Fig. 4C) also suggests that the microbial community has not reached the point of relative C limitation often associated with N mineralization in recalcitrant residues (Melillo and Aber 1984; McClaugherty and Berg 1987; Aber et al. 1982, 1990).

Fine root decay followed a pattern similar to surface litter with the exception of extremely slow rates (Figs. 1B and 1D). Losses during the first year do not exceed the percent mass of the extractive fraction for any species (including native fine roots). Curiously, no correlation was found for this fraction and mass loss during any time period. However, N losses in the first year, the lack of correlation of mass loss with microbial counts, and the exclusion of microarthopods by the fine-mesh root litter bags, suggest leaching as the primary factor for mass loss in fine roots as well as surface litters.

The apparent negative effect of intrinsic N on root decay (Fig. 5) could be explained by inhibition of lignocellulolytic enzymes. Kirk (1987) found secretion of lignin–peroxidase by certain species of white-rot fungi to be stimulated by N starvation and inhibited by the presence of N. While fungal biomass counts on buried root litter were high at 15 months (Table 4), species composition was not determined, and the presence of white rot fungi at this site is unknown. Furthermore, it is not known how widespread this enzyme system is among other species of fungi, nor the extent to which N availability controls enzyme functions among fungal species (see Leatham and Kirk 1983). Given the previous evidence for leaching losses, this observation could be explained by the high extractive fraction in *Andropogon gerardii*. However, no relationship of mass loss and extractive fraction was found for fine roots. Clearly, future investigations using more numerous and chemically varied species of root litter are required to test these hypotheses.

Decomposition of buried fine roots was markedly slower than any surface litter. Seastedt et al. (1992) observed that roots decomposed at an equal or greater rate than surface foliage in grasslands regardless of the lower quality of root substrate. As in grasslands, belowground biomass and production exceeds that for aboveground in arctic (Flanagan and Veum 1974) and alpine tundra (Webber and May 1977; Fisk 1995, Walker et al. 1994). The combination of higher belowground production and lower decay rates suggest that root biomass may be a significant long-term reservoir of C and N as well as the major contributor of these elements to tundra soil reservoirs.

Conclusions

(1) Moisture availability is the primary controlling variable in the early stages of surface litter decomposition in alpine tundra. This may be related to the large contribution of leaching to mass losses in early stages of decay.

(2) Nitrogen additions do not have a measurable effect on native litter decay at the Niwot Ridge site.

(3) Nitrogen release parallels mass loss across the alpine landscape and compares well with landscape patterns of N cycling found by other researchers (Fisk and Schmidt 1995).

N immobilization is delayed and thus does not stabilize N losses from litter as seen in other systems.

(4) Following an initial mass loss in the first growing season, buried fine-root litter decay does not vary significantly among communities. Mass remaining appears to stabilize at approximately 80% of original. While intrinsic N may influence root decay, more research is required to discern possible mechanisms involved.

(5) Surface foliage carbon turnover rates are greater than those of buried root litter. Taking into account greater proportional belowground production, and decreased decay of root litter, standing dead root biomass appears to be a long-term reservoir for C and may be a major contributor to soil organic matter.

(6) The level of original N retained in decaying root litter (~50%) suggests that standing dead root biomass is also a long-term reservoir for N in this system.

Acknowledgments

The authors thank Ed Rastetter and Bill Currie of the Ecosystem Center, Woods Hole, Mass. and two anonymous reviewers for comments that greatly improved earlier versions of the manuscript. John Aber and Steve Newman of the Complex Systems Research Center, University of New Hampshire, and Carol Wessman of The University of Colorado provided assistance and laboratory space for chemical analysis. Research was supported by the Niwot Ridge Long Term Ecological Research program and the Long Term Intersite Decomposition Experiment Team (NSF grant No. BSR-9108329), both funded by the National Science Foundation.

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