Biogeochemistry **35:** 327–338, 1996.

Winter regulation of tundra litter carbon and nitrogen dynamics

SARAH E. HOBBIE* & F. STUART CHAPIN, III
Department of Integrative Biology, University of California, Berkeley CA 94720-3140
(current address: Department of Biological Sciences, Stanford University, Stanford CA 94305; Phone and Fax: 415-725-1856; shobbie@leland.stanford.edu)*

Received 18 October 1994; accepted 4 April 1996

Key words: *Eriophorum*, freeze-thaw, *Hylocomium*, litter nitrogen, *Sphagnum*, tundra decomposition

Abstract. Mass and nitrogen (N) dynamics of leaf litter measured in Alaskan tussock tundra differed greatly from measurements of these processes made in temperate ecosystems. Nearly all litter mass and N loss occurred during the winter when soils were mostly frozen. Litter lost mass during the first summer, but during the subsequent two summers when biological activity was presumably higher than it is during winter, litter mass remained constant and litter immobilized N. By contrast, litter lost significant mass and N over both winters of measurement. Mass loss and N dynamics were unaffected by microsite variation in soil temperature and moisture. Whether wintertime mass and N loss resulted from biological activity during winter or from physical processes (e.g., fragmentation or leaching) associated with freeze-thaw is unknown, but has implications for how future climate warming will alter carbon (C) and N cycling in tundra. We hypothesize that spring runoff over permafrost as soils melt results in significant losses of C and N from litter, consistent with the observed influx of terrestrial organic matter to tundra lakes and streams after snow melt and the strong N limitation of terrestrial primary production.

Introduction

Tundra ecosystems could feed back significantly to rising concentrations of atmospheric CO_2. However, whether this feedback will be positive or negative is unclear. Increased decomposition of the large stocks of tundra soil organic matter under a warmer climate could increase CO_2 inputs to the atmosphere, causing a positive feedback to rising CO_2 (Post 1990). Indeed, recent warming in the Arctic may already be causing substantial losses of carbon from these regions (Oechel et al. 1993). Alternatively, greater nutrient availability associated with faster decomposition could stimulate plant production, taking CO_2 out of the atmosphere and causing a negative feedback if production is stimulated more than respiration (Shaver et al. 1992). Underlying both of these feedback scenarios is the assumption that warming will significantly increase soil decomposition and nitrogen (N) mineralization. This assumption is often incorporated into models used to estimate the

feedback magnitude as a positively exponential temperature-response curve for decomposition (e.g., Townsend et al. 1992; McKane et al. In preparation).

Predicting warming effects on decomposition is potentially complicated by the demonstration in both temperate and alpine ecosystems that decomposing litter can lose significant mass during winter (Bleak 1970; Gosz et al. 1973; Lousier & Parkinson 1975; McBrayer & Cromack 1980; Hågvar & Kjøndal 1981). This mass loss likely results primarily from biological activity beneath the snowpack during periods of constant temperatures, including those below 0 °C (McBrayer & Cromack 1980; Coxson & Parkinson 1987). Freeze-thaw cycles probably also promote mass loss by fragmenting litter and causing release of soluble compounds that are either respired (Ivarson & Sowden 1970; Skogland et al. 1988) or leached during spring run-off (Gosz et al. 1973). Demonstration of significant respiration and decomposition during winter suggests that using simple Q_{10} relationships and growing season air temperatures to predict warming effects on litter or soil decomposition may be inaccurate. For example, because of the insulating effects of snow cover, air warming may have different effects on soil temperature in winter than in summer (Kane et al. 1992). If winter decomposition results from biological activity, such differences must be accounted for when predicting warming effects on decomposition. Also, what happens to climate variability or snow depth, and thus the frequency of freeze-thaw events, may determine future decomposition more than will mean temperature increase.

Despite the attention given to warming effects on decomposition in tundra, no studies exist with the intra-annual resolution necessary to assess the significance of winter-time decomposition in these ecosystems. However, decomposition during winter and spring thaw could account for a large proportion of total litter decomposition in tundra ecosystems. Measurements of respiration under the snowpack in Siberia suggest that significant biological activity occurs in tundra soils even when they are frozen (Zimov et al. 1993). Because soils are frozen for much of the year, winter-time respiration could account for a relatively large proportion of total annual respiration, even though respiratory rates might be slow relative to those in summer. In laboratory incubations of tundra soil, the majority of net N mineralization results from conditions of soil freezing and thawing, rather than of constant soil temperatures, consistent with the pulse of soil net N mineralization observed in early spring in some tundra ecosystems (Kielland 1990). How respiration responds to such freeze-thaw cycles is unknown.

In this study, we compared winter and summer mass and N dynamics of decomposing leaf litter in Alaskan tussock tundra to determine whether significant decomposition occurs during winter. We focused on N because it limits primary production in this ecosystem (Shaver & Chapin 1986). In

addition, we compared these dynamics between surface and buried litter and among litters buried in microsites that differ in temperature and moisture. In general, laboratory incubations have shown that decomposition and N mineralization in tundra systems increase exponentially with temperature and exhibit moisture optima slightly below average field conditions (Flanagan & Veum 1974; Marion & Black 1986; Nadelhoffer et al. 1991). These studies are consistent with a number of field and laboratory studies in temperate ecosystems showing that rates of decomposition and litter and soil respiration increase exponentially with increasing temperature (e.g., Wiant 1967; Reiners 1968; Kucera & Kirkham 1971; Edwards 1975). We determined whether *in situ* decomposition varied with temperature and moisture as expected from these previously observed patterns.

We compared decomposition in three common microsites associated with the tussock-forming sedge *Eriophorum vaginatum* and the mosses *Hylocomium splendens* and *Sphagnum* spp. because they exist as discrete patches dominated by one species or genus. *Eriophorum* tussocks are significantly warmer than surrounding intertussock areas since their growth habit elevates them above the permafrost and surrounding vegetation and increases their exposure to radiation (Heal et al. 1978; Chapin et al. 1979). Because of the sensitivity of moss growth to moisture (Busby et al. 1978; Clymo & Hayward 1982; Murray et al. 1989), mosses require particularly wet conditions that may impede decomposition due to anaerobiosis (Clymo & Hayward 1982). We thus hypothesized that decomposition would be more rapid in *Eriophorum* tussocks than in moss mats because of more favorable temperature and moisture conditions.

Methods

We conducted the study in gently sloping upland tussock tundra near Toolik Lake, Alaska (68°38′ N, 149°34′ W, elevation 760 m). We determined the relative abundance of *Eriophorum vaginatum, Hylocomium splendens*, and *Sphagnum* spp. (mainly *S. balticum* and *S. warnstorfii*, L. C. Johnson personal communication) visually. The percent cover of these species was estimated in 400-cm^2 quadrats placed every meter along 10 20-m transects spaced 10 m apart and running parallel to the slope. In 1991, we measured summer (June 26-August 12) mean soil temperature at 10 cm below the moss surface in five replicate randomly chosen microsites downslope of the area in which we estimated percent cover. A datalogger (Campbell CR10, Campbell Scientific, Logan UT) recorded hourly and daily means of one-minute measurements made with copper-constantan thermocouples. We measured soil moisture gravimetrically at 5–10 cm depth in five replicate cores from randomly chosen

microsites in early August 1991 and early July 1992. We measured pH in slurries (5:1 soil:0.1 N NaCl) from six replicate randomly chosen cores from each microsite collected in mid-July 1991.

Nutrient availability was assessed in all microsites using ion-exchange resins (Giblin et al. 1994). We constructed 25-cm^2 resin bags by placing 7 ml of acid-washed (10% HCl) anion or cation exchange resins (Dowex 50W-X8 20–50 mesh H^+ or 1-X8 20–50 mesh Cl^-, respectively) into acid-washed nylon stockings and sewing the end shut. We randomly placed six replicate anion and cation resin bags at 5–10 cm depth in *Hylocomium* and *Sphagnum* moss mats and *Eriophorum* tussocks along a 50-m transect in mid-June 1992 (perpendicular to the slope and just downslope from where we measured percent cover). At the end of July 1992, we replaced those resin bags with fresh resin bags that we harvested the following spring (mid-June 1993).

After each harvest, resins were frozen until extraction. We extracted the resins by rinsing them in a soil sieve with deionized water, placing them in a pre-leached 30 ml syringe with Whatman #1 filter paper in the bottom, and dripping 100 ml of 2 N NaCl (in 0.1 N HCl) over the resins (Giblin et al. 1994). We analyzed the extracts for NH_4^+, NO_3^-, and PO_4^- colorimetrically on a Lachat QuickChem Autoanalyzer (Lachat Instruments, Milwaukee WI), and compared ion accumulation among sites and between seasons using repeated-measures ANOVA with season as a repeated measure.

We measured decomposition by enclosing ~5 g of weighed, air-dried *Betula papyrifera* leaf litter in 100-cm^2 bags made of 1-mm nylon mesh. We used litter collected near Fairbanks, Alaska rather than locally available tundra litter because *B. papyrifera* litter was readily available in large quantities and has N and carbon (C) chemical fractions similar to those of the local birch species (*B. nana*; Chapin & Kedrowski 1983; Chapin & Shaver 1988; Chapin & Kedrowski, unpublished). On 22 June 1991, we placed litter bags at 5–10 cm below the moss surface in *Hylocomium* or *Sphagnum* moss mats, in *Eriophorum* tussocks, or on the surface of *Hylocomium* moss mats along the 50-m transect where we deployed ion-exchange resins. Every five m along the transect, we placed litter bags in the five nearest microsites of each type. We harvested 10 randomly chosen litter bags from each microsite in mid-August 1991, mid-June 1992, late July 1992, mid-June 1993, and mid-August 1993 (51, 361, 404, 720, and 782 days after deployment, respectively). Spring harvests occurred as soon as soils thawed to the depth of the litter bags.

We dried (65 °C) and weighed harvested litter to determine the percent of the original mass remaining. We ground harvested litter using a Wiley Mill followed by a ball mill and determined % C and % N using a Carlo-Erba NA 1500 Nitrogen Analyzer (Carlo Erba Instruments, Milan, Italy). We determined N content by multiplying % N by total dry mass of litter from each bag.

In addition, we determined % C and % N on a subsample of initial litter. An additional subsample of initial litter was analyzed for % acid-insoluble mass at the Center for Water and the Environment (Natural Resources Research Institute, University of Minnesota, Duluth MN) according to forest-products techniques (Ryan et al. 1989). Although the acid-insoluble fraction undoubtedly contains other recalcitrant C fractions besides lignin, for ease we will refer to this fraction as lignin.

Results

Hylocomium, Sphagnum, and *Eriophorum* comprise 7.7 (S.E. = 1.0), 11.4 (S.E. = 1.6), and 21.9 (S.E. = 1.8) % of cover, respectively. Overall, the microsites associated with these species were wet, acidic, cold, and low in nutrient availability, as is typical of tussock tundra soils (Table 1; Nadelhoffer et al. 1992). As expected, the microsites differed in moisture and temperature. *Sphagnum* mats were nearly twice as wet as *Hylocomium* mats and *Eriophorum* tussocks (two-way ANOVA, $F_{2,24} = 13.45$, $P < 0.001$), but years did not differ in moisture within microsites, nor was there a significant year by microsite interaction. Temperature differed significantly among microsites, with *Eriophorum* tussocks 4 °C warmer than the moss mats (one-way ANOVA, $F_{2,12} = 50.69$, $P < 0.001$). However, microsites did not differ in pH (one-way ANOVA, $F_{2,15} = 1.36$, $P = 0.29$) or in nutrient accumulation on ion-exchange resins (repeated-measures ANOVA, $F_{2,15} = 1.36$, $F_{2,14} = 1.67$, and $F_{2,15} = 1.66$, for NH_4^+, NO_3^-, and PO_4^-, respectively, $P > 0.1$). Significantly more PO_4^- accumulated on resins during winter than during summer ($F_{1,15} = 29.50$, $P < 0.001$). Initial C:N, % N, and % lignin of the *Betula papyrifera* litter were 60.5, 0.78, and 17.7, respectively.

Litter mass remaining was always significantly lower in the spring than the preceding fall regardless of microsite (Figure 1, Tukey HSD, $P < 0.001$). By contrast, litter lost mass during the first growing season after deployment, but did not lose significant mass during either of the two subsequent growing seasons in any microsite (Tukey HSD, $P > 0.1$). Microsites differed significantly at all harvests except the first one (ANOVA for each date separately, $F_{3,36} = 2.05$, $F_{3,36} = 19.82$, $F_{3,36} = 18.78$, $F_{3,34} = 26.19$, and $F_{3,32} = 3.21$ for 51, 361, 404, 720, and 782 d, respectively, $P < 0.001$ in all significant cases) because mass remaining was significantly higher on the surface than below at all dates (Tukey HSD, $P < 0.001$). Buried litter bags did not differ from one another (Tukey HSD, $P > 0.1$) until the final harvest (782 d) when litter bags buried in *Eriophorum* microsites had significantly less mass remaining than those buried in *Hylocomium* microsites (Tukey HSD, $P < 0.05$).

Table 1. Physical characteristics of microsites. Different letters within a row indicate significant differences among sites (Tukey's HSD, $\alpha = 0.05$). Values are means (S.E.).

Parameter	Microsite		
	Hylocomium	*Sphagnum*	*Eriophorum*
Temperature (°C)	2.9 (0.5)[a]	2.7 (0.2)[a]	7.0 (0.3)[b]
Soil moisture (% dry mass)			
1991	411 (40)[a]	719 (24)[a]	431 (34)[a]
1992	450 (46)[a]	862 (159)[a]	529 (57)[a]
Nutrient accumulation on resins (μmol ion bag^{-1})			
NH_4^+			
Summer	5.56 (0.42)	6.98 (0.59)	6.22 (0.84)
Winter	5.53 (0.32)	7.00 (1.34)	5.88 (0.44)
NO_3^-			
Summer	0.25 (0.15)	0.08 (0.01)	0.16 (0.09)
Winter	0.21 (0.05)	0.19 (0.02)	0.13 (0.01)
PO_4^-			
Summer	0.17 (0.10)	0.03 (0.01)	0.21 (0.09)
Winter	0.55 (0.10)	0.52 (0.14)	1.00 (0.39)
pH	3.5 (0.1)	3.5 (0.1)	3.3 (0.1)

As with mass, litter lost N during the winter. Absolute N content decreased significantly during each winter (Figure 2, Tukey HSD, $P < 0.01$), increased significantly during the first summer (Tukey HSD, $P < 0.01$), and did not change during the second summer (Tukey HSD, $P > 0.1$). The litter N content did not differ among microsites, including the surface ($F_{3,183} = 0.09, P > 0.1$).

Discussion

After the first summer, all of the mass loss occurred during winter, when soils were mostly frozen, rather than during summer, the time of presumed greatest biological activity. Although other studies have demonstrated significant litter mass loss during winter (Bleak 1970; Gosz et al. 1973; Lousier & Parkinson 1975; McBrayer & Cromack 1980; Hågvar & Kjøndal 1981), ours is the first to find that, after the first summer, litter mass loss occurred entirely during the months outside of the growing season. The most likely explanations for our results are either that (1) significant decomposition occurs during winter when soils are frozen, or (2) freeze-thaw cycles cause most of the mass loss from litter in tundra, resulting in leaching and/or particulate loss of organic matter during snow melt and spring runoff over the permafrost. The lower

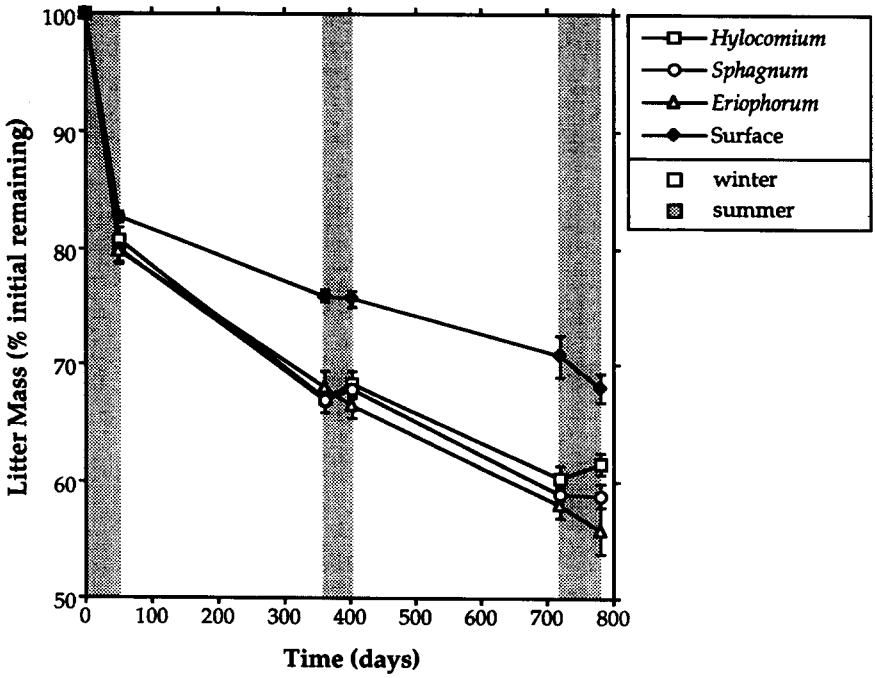

Figure 1. Mass of *Betula papyrifera* leaf litter buried in 3 different microsites (*Hylocomium* or *Sphagnum* moss mats or *Eriophorum* tussocks) or placed on the moss surface. Values are means, bars are standard errors.

mass loss of the surface litter over winter may have resulted from its being subject to less water flow during runoff than the buried litter. Whether organic matter was lost from litter bags in particulate or dissolved form has important implications. Particulate organic matter would likely decompose further *in situ*, whereas dissolved organic matter would be more readily transported to aquatic systems.

Differences in moisture and temperature did not translate into strong differences in decomposition among microsites. Although we did not measure surface temperatures, they are generally warmer than soil temperatures during the growing season in permafrost tundra (Hinzman et al. 1991). Thus, the two warmest microsites had the lowest (surface) and highest (*Eriophorum*) decomposition rates. By contrast, in northern England Heal et al. (1978) observed more rapid rates of decomposition in *Sphagnum* mats than in *Eriophorum* tussocks, which they attributed to moisture limitation of decomposition in tussocks, which were slightly drier than the tussocks in our study. The overall differences that we observed among buried microsites were surprisingly small since Flanagan & Veum (1974) found that *in situ* respiration

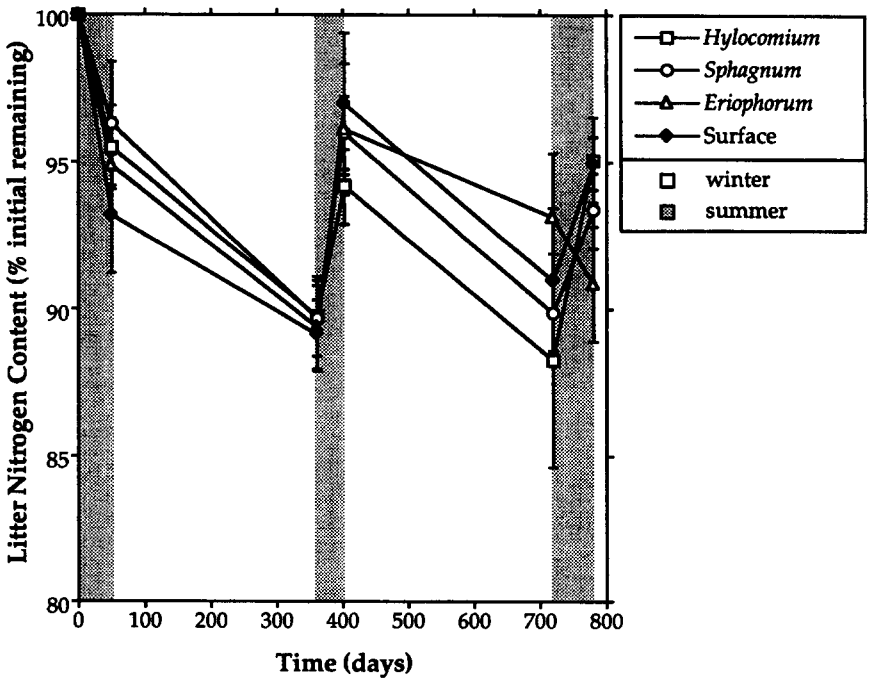

Figure 2. N content of *Betula papyrifera* leaf litter buried in 3 different microsites (*Hylocomium* or *Sphagnum* moss mats or *Eriophorum* tussocks) or placed on the moss surface. Values are means, bars are standard errors.

of *Betula papyrifera* litter responded exponentially to increased temperature within the range we measured in the microsites and was optimal at 300% moisture, sharply declining at higher moisture contents. However, others have found soil respiration to be fairly insensitive to changes in temperature between 3 and 10 °C, within the range found among the microsites studied here (Nadelhoffer et al. 1991; but see Hobbie, in press).

The litter N dynamics that we observed differ strikingly from those observed in temperate systems. Many litter types incubated in different temperate ecosystems all showed that after a short (1–2 month) initial period of leaching, litter immobilized N for 1–2 years, then began a period of net N release (e.g., Gosz et al. 1973; Staaf & Berg 1981; Melillo et al. 1982; Pastor et al. 1987; Melillo et al. 1989). By contrast, in our study, litter N content never rose above 100% of the initial N content, but instead declined during each winter, and increased during the first summer. The absolute increase in litter N that we observed during summer suggests that microbial activity and N immobilization was associated with the litter despite the lack of mass loss. This is reasonable, because, assuming a 40% microbial efficiency and a

microbial C:N ratio of 15 (Paul & Clark 1989), the observed N immobilization requires only 1.3% of the initial mass to be lost. We hypothesize that N immobilization occurs slowly during summer because of low soil temperatures. As with mass loss, net N release occurs each spring when thawing of frozen and lysed microbial cells allows leaching of N during runoff, a time of presumably low microbial activity and N assimilation. Others have found an increase in water-soluble sugars and amino acids following freezing and thawing of soils (Ivarson & Sowden 1970).

We found that the seasonal N dynamics of tundra litter resemble those of tundra soil (Chapin et al. 1988; Kielland 1990), being characterized by freeze-thaw release and summer immobilization of N. If the N released from litter during spring thaw is mineralized or taken up by plants in organic form (Read 1991; Chapin et al. 1993), then our results imply that N availability to plants is greatest at snow melt, when soil temperature is lowest. Thus, tight cycling of N in tundra ecosystems requires active root growth (Shaver & Billings 1975) and nutrient uptake (Chapin & Bloom 1976) by tundra plants at low temperatures before appreciable aboveground growth occurs.

Alternatively, if N is released from litter during spring thaw but is unavailable to plants or soil microbes because of low soil temperatures, it may be transported from terrestrial to aquatic ecosystems. This interpretation is consistent with the observation that tundra lakes and streams receive most inputs of terrestrial dissolved organic C and N during and immediately following snow melt (Whalen & Cornwell 1985; Peterson et al. 1992). Furthermore, the dissolved organic matter entering Toolik Lake early during spring runoff has a labile component that strongly increases lake bacterial respiration and production (Kling 1995). Such losses of N from the terrestrial to the aquatic system may contribute to the strong N limitation of terrestrial primary production observed in tussock tundra.

Whether the wintertime mass and N loss that we observed resulted from physical or biological processes has implications for how tundra C and N cycling will respond to future warming and should be the focus of further research. Winter mass loss resulting from respiration could increase significantly with climate warming. Arctic regions are expected to warm more in winter than in summer (Maxwell 1992). Furthermore, soils may warm more relative to surface temperatures in winter than in summer (Kane et al. 1992). However, if winter mass loss is not respiratory, but results from particulate or dissolved organic losses associated with spring thaw, predicting the response of mass loss to warming becomes more complicated. Particulate organic matter will likely decompose *in situ*, where its decomposition rate may be sensitive to soil warming. However, dissolved organic matter may only be mineralized after it is transported to aquatic ecosystems. Therefore,

knowledge of how climate change will alter spring run-off and whether C lost from litter is ultimately mineralized in terrestrial or aquatic ecosystems may be necessary for predictions to be accurate.

Our results also have important implications for future changes in tundra N availability resulting from global warming. Assuming that subfreezing winter temperatures and warmer summer temperatures will characterize the future tundra climate (Maxwell 1992), N availability may actually decline with global warming, if warmer summer temperatures increase summer N immobilization that is subsequently leached and potentially lost during spring thaw and runoff. Future research should focus on increasing the intra- and inter-seasonal resolution of measurements of litter and soil C and N dynamics. Furthermore, we need to determine whether winter C and N losses result primarily from biological or physical processes as well as the fate of C and N released from litter (e.g., mineralization or transport from terrestrial to aquatic ecosystems as dissolved or particulate organic matter).

Acknowledgments

We thank Chris Lund, Megan McGlinchey, and Laurie Tucker for help in the field, Hailin Zhong for technical assistance, Carla D'Antonio, John Harte, and Wayne Sousa for comments on a previous version of the manuscript, and Mary Firestone for helpful discussion. Brad Dewey and John Pastor provided lignin analysis. This research was supported by NSF pre-doctoral and NASA global change fellowships and an NSF Doctoral Dissertation Improvement Grant (BSR 91-22791) to SEH and NSF grant (BSR 87-05323) to FSC.

References

Bleak AT (1970) Disappearance of plant material under a winter snow cover. Ecology 51: 915–917

Busby JR, Bliss LC & Hamilton CD (1978) Microclimate control of growth rates and habitats of the boreal forest mosses, *Tomenthypnum nitens* and *Hylocomium splendens*. Ecol. Monogr. 48: 95–110

Chapin FS III & Bloom A (1976) Phosphate absorption: adaptation of tundra graminoids to low temperature, low-phosphorus environment. Polar Biol. 2: 37–52

Chapin FS III, Fetcher N, Kielland K, Everett KR & Linkins AE (1988) Productivity and nutrient cycling of Alaskan tundra: Enhancement by flowing soil water. Ecology 69: 693–702

Chapin FS III & Kedrowski RA (1983) Seasonal changes in nitrogen and phosphorus fractions and autumn retranslocation in evergreen and deciduous taiga trees. Ecology 64: 376–391

Chapin FS III, Moilanen L & Kielland K (1993) Preferential use of organic nitrogen for growth by a non-mycorrhizal arctic sedge. Nature 361: 150–153

Chapin FS III & Shaver GR (1988) Differences in carbon and nutrient fractions among arctic growth forms. Oecologia 77: 506–514

Chapin FS III, Van Cleve K & Chapin MC (1979) Soil temperature and nutrient cycling in the tussock growth form of *Eriophorum vaginatum*. J. Ecol. 67: 169–189

Clymo RS & Hayward PM (1982) The ecology of *Sphagnum*. In: Smith AJE (Ed) Bryophyte Ecology (pp 229–289). Chapman and Hall, London

Coxson DS & Parkinson D (1987) Winter respiratory activity in Aspen woodland forest floor litter and soils. Soil Biol. Biochem. 19: 49–59

Edwards NT (1975) Effects of temperature and moisture on carbon dioxide evolution in a mixed deciduous forest floor. Soil Sci. Soc. Am. Proc. 39: 361–365

Flanagan PW & Veum AK (1974) Relationships between respiration, weight loss, temperature, and moisture in organic residues on tundra. In: Holding AJ, Heal OW, Maclean SF Jr. & Flanagan PW (Eds) Soil Organisms and Decomposition in Tundra (pp 249–277). Tundra Biome Steering Committee, Stockholm

Giblin AE, Laundre JA, Nadelhoffer KJ & Shaver GR (1994) Measuring nutrient availability in arctic soils using ion exchange resins: a field test. Soil Sci. Soc. Amer. J. 58: 1154–1162

Gosz JR, Likens GE & Bormann FH (1973) Nutrient release from decomposing leaf and branch litter in the Hubbard Brook forest, New Hampshire. Ecol. Monogr. 43: 173–191

Hågvar S & Kjøndal BR (1981) Decomposition of birch leaves: dry weight loss, chemical changes, and effects of artificial acid rain. Pedobiologia 22: 232–245

Heal OW, Latter PM & Howson G (1978) A study of the rates of decomposition of organic matter. In: Heal OW & Perkins DF (Eds) Production Ecology of British Moorlands and Montane Grasslands (pp 136–159). Springer-Verlag, Berlin

Hinzman LD, Kane DL, Gieck RE & Everett KR (1991) Hydrologic and thermal properties of the active layer in the Alaskan Arctic. Cold Reg. Sci. Technol. 19: 95–110

Hobbie SE (In press) Temperature and plant species control over litter decomposition in Alaskan tundra. Ecol. Monogr.

Ivarson KC & Sowden FJ (1970) Effect of frost action and storage of soil at freezing temperatures on the free amino acids, free sugars and respiratory activity of soil. Can. J. Soil Sci. 50: 191–198

Kane DL, Hinzman LD, Woo M & Everett KR (1992) Arctic hydrology and climate change. In: Chapin FS III, Jefferies RL, Reynolds JF, Shaver GR & Svoboda J (Eds) Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective (pp 35–57). Academic Press, San Diego

Kielland K (1990) Processes controlling nitrogen release and turnover in arctic tundra. PhD, University of Alaska, Fairbanks

Kling GW (1995) Land-water interactions: the influence of terrestrial diversity on aquatic ecosystems. In: Chapin FS III & Körner C (Eds) Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences (pp 297–310). Springer-Verlag, Berlin

Kucera CL & Kirkham DR (1971) Soil respiration studies in tallgrass prairie in Missouri. Ecology 52: 912–915

Lousier JD & Parkinson D (1975) Litter decomposition in a cool temperate deciduous forest. Can. J. Bot. 54: 419–436

Marion GM & Black CH (1986) The effect of time and temperature on nitrogen mineralization in arctic tundra soils. Soil Sci. Soc. Amer. J. 51: 1501–1508

Maxwell B (1992) Arctic climate: potential for change under global warming. In: Chapin FS III, Jefferies RL, Reynolds JF, Shaver GR & Svoboda J (Eds) Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective (pp 11–34). Academic Press, San Diego, California, USA

McBrayer JF & Cromack K Jr (1980) Effect of snow-pack on oak-litter breakdown and nutrient release in a Minnesota forest. Pedobiologia 20: 47–54

McKane RB, Rastetter EB, Shaver GR, Nadelhoffer KJ, Giblin AE, Laundre JA & Chapin FS III (In preparation) Analysis of the effects of climate change on carbon storage of arctic tundra.

Melillo JM, Aber JD, Linkins AE, Ricca A, Fry B & Nadelhoffer KJ (1989) Carbon and nitrogen dynamics along the decay continuum: Plant litter to soil organic matter. Plant Soil 115: 189–198

Melillo JM, Aber JD & Muratore JF (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63: 621–626

Murray KJ, Harley PC, Beyers J, Walz H & Tenhunen JD (1989) Water content effects on photosynthetic response of *Sphagnum* mosses from the foothills of the Philip Smith Mountains, Alaska. Oecologia 79: 244–250

Nadelhoffer KJ, Giblin AE, Shaver GR & Laundre JA (1991) Effects of temperature and substrate quality on element mineralization in six arctic soils. Ecology 72: 242–253

Nadelhoffer KJ, Giblin AE, Shaver GR & Linkins AE (1992) Microbial processes and plant nutrient availability in arctic soils. In: Chapin FS III, Jefferies RL, Reynolds JF, Shaver GR & Svoboda J (Eds) Arctic Ecosystems in a Changing Climate: An Ecophysiological perspective (pp 281–300). Academic Press, San Diego

Oechel WC, Hastings SJ, Vourlitis G, Jenkins M, Riechers G & Grulke N (1993) Recent change of Arctic tundra ecosystems from a net carbon dioxide sink to a source. Nature 361: 520–523

Pastor J, Stillwell MA & Tilman D (1987) Little bluestem litter dynamics in Minnesota old fields. Oecologia 72: 327–330

Paul EA & Clark FE (1989) Soil microbiology and biochemistry. Academic Press, San Diego

Peterson BJ, Corliss TL, Kriet K & Hobbie JE (1992) Nitrogen and phosphorus concentrations and export for the upper Kuparuk River on the North Slope of Alaska in 1980. Hydrobiologia 240: 61–69

Read DJ (1991) Mycorrhizas in ecosystems. Experientia 47: 376–391

Reiners WA (1968) Carbon dioxide evolution from the floor of three Minnesota forests. Ecology 49: 471–483

Ryan MG, Melillo JM & Ricca A (1989) A comparison of methods for determining proximate carbon fractions of forest litter. Can. J. For. Res. 20: 166–171

Shaver GR & Billings WD (1975) Root production and root turnover in a wet tundra ecosystem, Barrow, Alaska. Ecology 56: 401–410

Shaver GR, Billings WD, Chapin FS III, Giblin AE, Nadelhoffer KJ, Oechel WC & Rastetter EB (1992) Global change and the carbon balance of arctic ecosystems. BioScience 61: 415–435

Shaver GR & Chapin FS III (1986) Effect of fertilizer on production and biomass of tussock tundra, Alaska, U.S.A. Arct. Alp. Res. 18: 261–268

Skogland T, Lomeland S & Goksøyr J (1988) Respiratory burst after freezing and thawing of soil: experiments with soil bacteria. Soil Biol. Biochem. 20: 851–856

Staaf H & Berg B (1981) Accumulation and release of plant nutrients in decomposing Scots pine needle litter. Long-term decomposition in a Scots pine forest II. Can. J. Bot. 60: 1561–1568

Townsend AR, Vitousek PM & Holland EA (1992) Tropical soils could dominate the short-term carbon cycle feedbacks to increased global temperatures. Climatic Change 22: 293–303

Whalen SC & Cornwell JC (1985) Nitrogen, phosphorus, and organic carbon cycling in an arctic lake. Can. J. Fish. Aquat. Sci. 42: 797–808

Wiant HV (1967) Influence of temperature on the rate of soil respiration. J. Forest. 65: 489–490

Zimov SA, Semiletov IP, Davidov SP, Voropaev IV, Prosyannikov SF, Wong CS & Chan Y-H (1993) Wintertime CO_2 emission from soils of northeastern Siberia. Arctic 46: 197–204