Plant and Soil **262:** 215–227, 2004.

Decomposition of mountain birch leaf litter at the forest-tundra ecotone in the Fennoscandian mountains in relation to climate and soil conditions

Sofie Sjögersten[1,2] & Philip A. Wookey[1]
[1] *University of Uppsala, Department of Earth Sciences, Villavägen 16, S-752 39 Uppsala, Sweden.* [2] *Corresponding author**

Received 17 January 2003. Accepted in revised form 4 November 2003

Key words: decomposition, ecotone, fennoscandia, litter, mountain birch

Abstract

Litter decomposition is a key process in terrestrial ecosystems, releasing nutrients, returning CO_2 to the atmosphere, and contributing to the formation of humus. Litter decomposition is strongly controlled both by climate and by litter quality: global warming scenarios involving shifts in vegetation communities are therefore of particular interest in this context. The objective of the present study was to quantify the role of climatic environment and underlying substrate chemistry for the decomposition of standard mountain birch (*Betula pubescens* Ehrh. spp. *czerepanovii*) leaf litter at four sites, spanning the forest-tundra ecotone, in the Fennoscandian mountain range. Litter quality effects were thus held constant, but the study incorporated systematic changes in (i) latitude/altitude, (ii) 'continentality', and (iii) vegetation community at each site, together with (iv) experimental manipulation of temperature using passive warming systems. The study was undertaken during a 3 year period, and forms part of a broader investigation of forest-tundra ecotone dynamics in the Fennoscandian mountains. Our results showed (1) higher decomposition rates in forest sites compared to tundra, (2) that the difference between the two vegetation communities was most pronounced at the more maritime sites, and (3) that chemistry of litter remaining after the three years experiment varied according to site and vegetation community (e.g. at the most southerly site, more lignin had decomposed at tundra communities compared with the forest). (4) Surface temperature explained 58% of the variation in mass loss at forest sites; at tundra sites, however, we hypothesise that litter moisture content was the more important factor. (5) Experimental warming lent weight to this hypothesis by reducing rates of mass loss: this reduction was likely the result of surface soil drying, an artefact of the warming treatment. We conclude that a replacement of tundra by forest would likely accelerate litter decomposition both via changes in surface and near-surface temperature and moisture regimes, although the strength of this response will vary between maritime and continental parts of the mountain range.

Introduction

Litter decomposition plays a fundamental role in ecosystem nutrient cycling processes, is a key component of the global C cycle, and culminates in the formation of humus and other recalcitrant soil organic matter fractions (Swift et al., 1979; Melillo et al., 1989; Aber and Melillo, 1991; Rutigliano et al., 1996; Aerts, 1997; Scott and Binkley, 1997; Latter et al., 1998). There is currently great interest in the potential impacts of climate warming on high latitude ecosystems and the implications of such changes for the global carbon (C) cycle (Robinson and Wookey, 1997; Goulden et al., 1998; Christensen et al., 1999; Hobbie et al., 2000; Oechel et al., 2000; Hobbie et al., 2002). High latitude ecosystems accumulate large amounts of C as surface litter and soil organic matter (SOM) due to slow decomposition (Swift et al., 1979; Cherkinsky, 1996). Most litter types seem to reach a stage where mass loss decreases to a minimum as a result of humification processes, and this results in accumulation of recalcitrant organic compounds in soil (Berg et al.,

*FAX No: +44 (0)1330 823303. E-mail: sstu@ceh.ac.uk

1996; Latter et al. 1998). The initial litter chemistry is of great importance in controlling both short and long-term decomposition rates (Melillo et al., 1982; Aber et al., 1990; Berg et al., 1996; Pérez- Harguindeguy et al., 2000; Quested et al. 2002), but on a regional scale the climate dominates the patterns of mass-loss rates (Dyer et al., 1990; Aerts 1997). The relative importance of climate varies between ecosystems, but in high latitude ecosystems climate is generally considered the primary limiting factor, and there is evidence that even a small increase in temperature could enhance decomposer activity and release of CO_2 from organic matter in these soils (Lloyd and Taylor, 1994; Coûteaux et al., 1995; Kirschbaum, 1995; Rustad et al., 2000; Sjögersten and Wookey, 2002).

Shifts in the distribution of major vegetation zones have been suggested in response to increased temperature (Emanuel et al., 1985; Kittel et al., 2000; White et al., 2001). At high latitudes the most striking vegetation transition is the boreal forest-tundra ecotone: here changes in ecosystem processes – such as litter production as well as soil C dynamics and respiration – may occur over short distances in relation to above ground vegetation and microclimate (Krosshavn et al., 1992; Raich and Schlesinger, 1992; Körner, 1998; Sjögersten and Wookey, 2002; Sjögersten et al., 2003). The mountain birch forest-tundra ecotone area in Abisko (Swedish Lapland), for example, has been responsive to increased temperatures both during the 20th century, as well as during earlier parts of the Holocene (Holmgren and Tjus, 1996; Barnecow and Sandgren, 2001). The rate and extent of such responses may, however, be strongly dampened by processes such as herbivory of tree seeds and/or seedlings (Olofsson, 2001 (PhD thesis); Stark et al., 2002), competition during seedling recruitment, cryoturbation, and the interrelationships between vegetation and snow distribution near the ecotone (Josefsson, 1990 (PhD thesis); Walsh et al., 1994; Källgren and Kullman, 1998).

The current study is part of a broader project investigating the dynamics of the mountain birch forest-tundra ecotone in response to environmental change in Fennoscandia (the EU 'DART' project: http://www.durham.ac.uk/DART). Two accompanying studies have demonstrated greater accumulation of labile organic compounds and lower soil respiration in tundra areas compared to nearby mountain birch forest (Sjögersten and Wookey, 2002; Sjögersten et al., 2003). We have attributed these differences primarily to more favourable climate within the mountain birch forest, rather than to soil organic matter (SOM) quality at the sites, despite some indications of higher SOM quality within the birch forest.

On the basis of these observations we developed the hypothesis that decomposition of a standardised litter material (*Betula pubescens* Ehrh. spp. *czerepanovii* (Orlova) Hämet-Ahti leaf litter) would be more rapid within the mountain birch forest compared to open tundra heath, and that the structure of the forest canopy would influence the decomposition rates. The Fennoscandian mountain range is ideal to test this hypothesis since the ecotone area, and especially the structure of the mountain birch forest, varies with latitude and with continentality. In addition to the natural latitudinal and altitudinal gradients along the mountain range and across the ecotone area, we deployed a warming treatment to address the more direct short-term impact of warming on litter decomposition. Further, we also compared summer and winter season litter decomposition rates since different physical and biological processes act upon the decomposing litter during different seasons.

Materials and methods

Field sites

The three main study areas were Dovrefjell (Sør-Tröndelag, Norway), Abisko (Norrbotten, Sweden) and Joatka (Finnmark, Norway); a fourth secondary site was established at Vassijaure (close to Abisko) (Figure 1). These areas in the Fennoscandian mountain range form a gradient in both latitude and continentality: Dovrefjell is the most southerly and maritime, and Finnmarksvidda the most northerly and continental (Table 1). The study sites are situated in the mountain birch (*B. pubescens* Ehrh. Ssp. *czerepanovii* (Orlova) Hämet-Ahti) - tundra ecotone. The main species in the tundra heath are as are *Empetrum hermaphroditum, Vaccinium uliginosum, V. vitis-idea*, and *Betula nana*, lichens and bryophytes (and additionally in Dovrefjell, *Arctostaphylos uva-ursi*). Mesic areas within the mountain birch forest have comparable understorey vegetation, tending towards a greater cover of *V. myrtillus*. The structure of the mountain birch forest at the four sites differs considerably, with denser forests at the two most maritime sites, especially at Dovrefjell. Also, the understorey vegetation is taller within the forest sites at Dovrefjell and Vassijaure.

Table 1. Summary environmental information on the four field sites in the Fennoscandian mountains

Site	Location	Elevation (m a.s.l.)	Slope	Monthly mean temperature		Continentality[a]	Precipitation (mm)	Other information
				Coldest (°C)	Warmest (°C)			
Dovrefjell	62°18′N, 9°37′E	1000-1100	10° Facing NW	-7.9 (Jan)	10.2 (june)	14.3	473	Alpine tree-line, sharp transition between tundra and birch forest (ca. 50 m). Bedrock in the arena is composed of gneisses.
Vassijaure	68°25′N 18°10′E	450-500	Facing NE	-11.9 (Jan)	11.0 (July)	21.5	848	Sub-Arctic tree-line. Undulating precambrian bedrock.
Abisko	68°21′N 18°49′E	520-600	8° Facing NW	-11.9 (Jan)	11.0 (July)	21.5	304 [b]	Sub-Arctic/alpine tree-line, transition over ca. 3–4 km. Hummocky till deposits, bedrock mainly hard-scale.
Joatka	69°45′N 23°59′E	420-500	8° facing NE (tundra) SW (forest)	-14.0 (Feb)	11.0 (July)	24.9	354	Arctic tree-line, prevailing tundra above 400 m a.s.l., discontinuous birch woodlands. Undulating plateau, precambrian bedrock.

[a] Gorzinsky's continentality index $K = 1.7 \times A \times \sin\theta^{-1} - 20.4$ (A = annual temperature range, θ = latitude angle
[b] (Alexandersson et al., 1991)

Figure 1. Map of Scandinavia showing locations of field sites, i.e. Dovrefjell, Vassijaure, Abisko and Joatka.

The sites are mesic and the soils are predominantly thin spodosols (principally orthods) developed within well drained medium to coarse-grained till deposits. The organic horizon is generally thinner in forest soil than in tundra and tends to be less dense, more fibrous and largely lacking humic layers: detailed soil profile descriptions can be found in Sjögersten et al. (2003).

Experimental design

In June 1998 we established four experimental sites at each main study area, spanning the mountain birch-tundra ecotone. Two of these sites have a mountain birch canopy (one at lower altitude and one at higher, denoted 'Lower Forest' and 'Upper Forest', respectively) and two sites represent open tundra at different altitudes (subsequently denoted 'Lower Tundra' and 'Upper Tundra'). Ten experimental plots were established at each site with five 1 × 1 m control plots and five plots which were randomly assigned an experimental warming treatment using hexagonal open top chambers (OTCs) 1.5 m diameter and 0.5 m height, and contructed with 3 mm thick polycarbonate sheet (Marion et al., 1997; Hollister and Webber, 2000). The experimental site at Vassijaure was established in 1999 and was set up to strengthen the continentality gradient incorporated in the study with a more maritime site close to the Abisko site. These two sites have the same Gorzinski continentality index (Table 1)

but Vassijaure has more than double the precipitation compared to Abisko. In contrast to the other three sites, OTCs were not deployed at Vassijaure, and only five untreated plots at each of one tundra and one forest site were established: litter bags here were placed out in 1999, with parallel bags also at the Abisko sites, while the major study was initiated in 1998 (see below). Soil temperature data were collected year-round at all three main sites on an hourly basis using TinyTag data-loggers with thermistor probes at 5 cm depth. Soil water content was measured with a ThetaProbe and hand-held ThetaMeter.

All litterbags were made using a standard *Betula pubescens* spp. *czerepanovii* leaf litter material to enable a comparison of the decomposition process between the areas: In this way decomposition rates (mass loss and chemical changes) were considered a 'bioassay'. Litter was collected from the ground surface in June 1998 (1999 for the parallel study at Abisko and Vassijaure) at the Lower Forest site in Abisko. Last years litter was separated from older litter based upon colour and tensile strength. We chose not to wait until we could collect fresh litter since that would have significantly shortened our study period. Our litter at time 0 was therefore already 9 months old since senescence and had undergone a winter season (the implications of which are discussed subsequently). The litterbags were distributed to their locations in July 1998 (and, for the Vassijaure/Abisko comparison, also in 1999) and 15 litterbags were pinned to the surface of each plot (1800 in total), using wooden toothpicks. Litterbags were made using inert nylon, of l mm mesh size, and contained ca. 0.5 g of air-dried *Betula pubescens* leaf litter (the exact initial mass was recorded for each individual bag), subsamples were taken for conversion to oven-dry mass. We sampled three litterbags from each plot on five occasions: spring 1999, autumn 1999, spring 2000, autumn 2000, and autumn 2001. Litterbags placed at Vassijaure and Abisko in 1999 were collected in July in both 2000 and 2001.

After sampling, the litterbags were stored at 2 °C for 1–2 weeks, prior to carefully opening the bags and separating the original birch litter from ingrown vegetation and invertebrates. Mass loss was estimated by weighing the oven-dried (80 °C) litter remains. In addition to mass estimates, initial litter material and selected final samples (only from Upper Tundra and Lower Forest sites from Dovrefjell, Abisko and Joatka) from 2001 were analysed for total carbon, nitrogen, soluble sugars, non-cellulosic polysaccharides (NCP), α-cellulose and lignin content. The carbon and nitrogen was analysed on a Leco CHNS-932 element analyser. The soluble sugars as well as NCP were determined colorimetrically, NCP were first hydrolyed from the litter material using 2M TFA (Fry 1988). α-cellulose content was determined by purification using acetic acid: nitric acid for simultaneous delignification and removal of non-cellulose polysaccharides, the samples were thereafter washed and weighed (Brendel et al., 2000). Lignin content was analysed by the acetyl bromide and perchloric acid procedure, with subsequent determination of lignin content by spectrophotometry (Iiyama and Wallis, 1988).

Statistical analysis

We used repeated-measures analysis of variance (ANOVA) to test for effects of the different sites, warming treatment, and time. Where significant effects were indicated we used Tukey's HSD (Honest Significant Difference) for means separation (P-values cited in text). To test the correlation between mass loss and chemical composition we used General Linear Models, simple and multiple regression analyses. All percent data were arcsin transformed to meet the normality assumption in ANOVA and linear regression. Statistical analyses were performed using STATISTICA (StatSoft, 1995).

Results

Surface temperatures were, in most cases, higher at forest sites ($F = 11.1$, $P < 0.01$) (Table 2). No significant difference between Dovrefjell, Abisko and Joatka was detected for mean annual temperature (MAT), but 2000 July surface temperature varied significantly ($F = 36.3$, $P < 0.001$) between sites with the highest temperatures in Joatka and the lowest in Dovrefjell. The open top chambers (OTCs) generally increased surface temperature ($F = 10.6$, $P < 0.01$) (Table 2) at all sites.

Mass remaining

Decomposition varied significantly over time and was generally highest over the first year, and after three years of decomposition in the field ca. 50 to 60% of the original mass remained (Figure 2, Table 3). The mass lost from litter during the summer season of 1999 and 2000, averaged for the three main

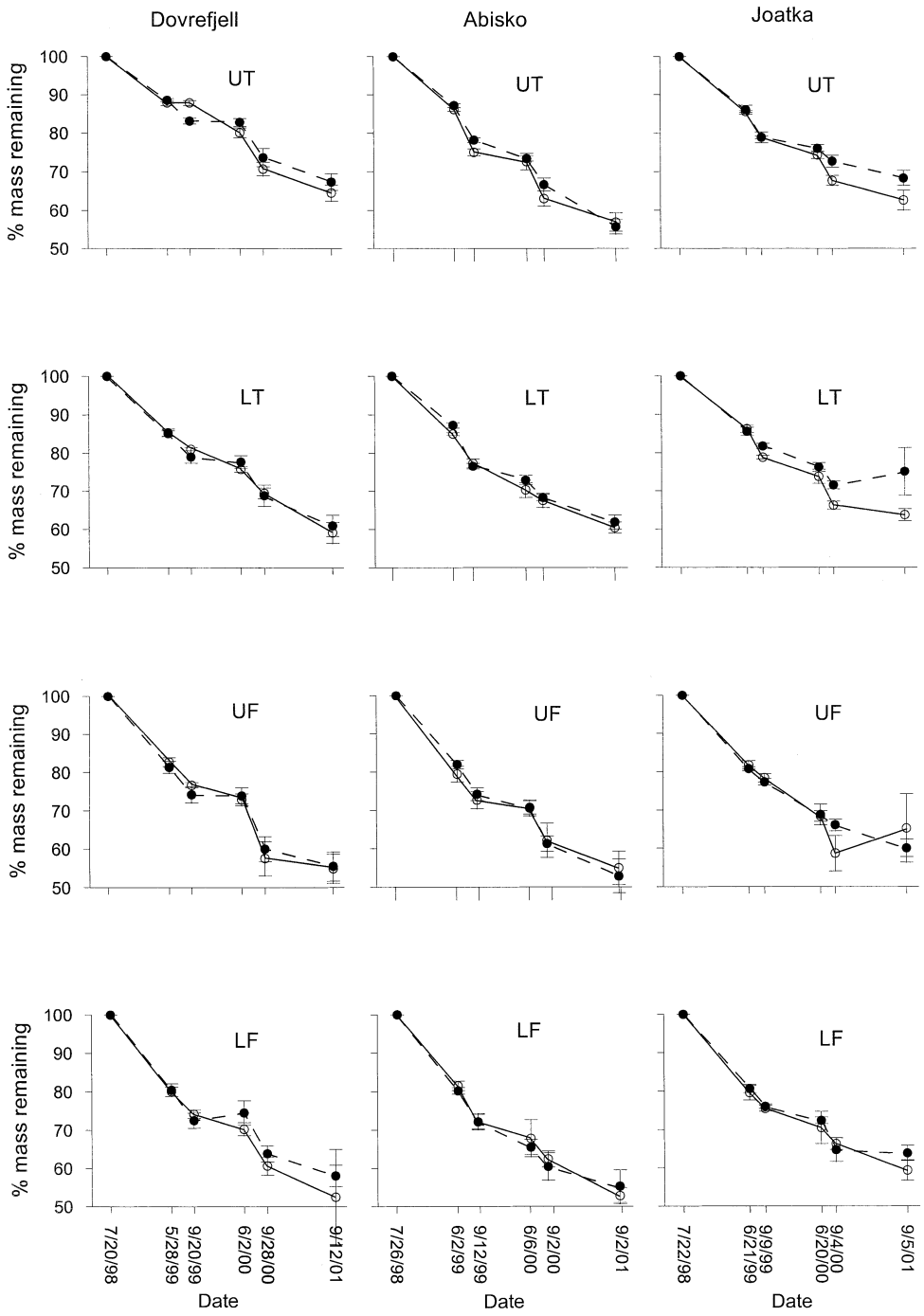

Figure 2. Litter decomposition measured as mass loss over time from control and OTC plots at three locations across the forest tundra ecotone. UT - Upper Tundra, L T - Lower Tundra, UF- Upper Forest, LF - Lower Forest; ○ Control ● OTC treatment.

sites, was 6.6 and 7.6%, respectively. The winter (i.e., September–May) mass loss was 3.8% on average.

No difference in final litter mass remaining was detected between Dovrefjell and Abisko (57.6 and 56.3%, respectively) at the end of the experiment, but at the Joatka site final mass remaining (62.9%) was significantly (Table 3) greater than in the other two sites. No significant difference in mass remaining

Table 2. Micrometerological data, unshielded surface temperature data presented as mean annual temperatures (MAT) from 1999 and 2000, and July average temperatures from 2000 (calculated from hourly means). At Vassijaure only mean July temperature was available. C = control (unwarmed) plots, OTC = warmed (Open-Top Chamber) plots, nd = no data, – = no equivalent sites were established

Site treatment	Dovrefjell			Abisko			Joatka			Vassijaure	
	1999 MAT	2000 MAT	2000 July	1999 MAT	2000 MAT	2000 July	1999 MAT	2000 MAT	2000 July		
Upper tundra C	1.1	0.9	9.5	nd	0.8	12.9	−0.2	1.0	14.3	9.4	9.5
Upper forest C	2.0	1.4	9.5	1.5	nd	nd	nd	2.3	14.6	–	–
Lower tundra C	1.1	1.1	10.1	0.1	0.9	12.7	−0.4	1.5	15.0	–	–
Lower forest C	2.4	2.9	10.6	1.4	2.2	12.6	nd	2.4	14.2	13.4	12.6
Upper tundra OTC	2.2	1.9	11.1	nd	2.1	13.7	nd	2.2	16.8	–	–
Upper forest OTC	2.6	2.9	10.2	nd	1.6	12.6	nd	2.1	15.2	–	–
Lower tundra OTC	2.4	2.4	11.4	nd	0.8	7.7	nd	nd	nd	–	–
Lower forest OTC	nd	3.0	10.3	nd	nd	nd	nd	2.2	15.4	–	–

was detected between Abisko and Vassijaure. Regression analysis revealed no relationship between total mass remaining (measured in September 2000) and July average temperature at the tundra sites. At the forest sites, however, 58% of the variation in mass remaining between sites could be explained by the July mean temperature (Figure 3), with a negative relationship between rate of decomposition and temperature. Despite more rapid decomposition at the southerly sites, no significant regression between mean annual temperature and mass remaining was found.

During the three years of decomposition in the field we have seen a clear pattern of lower mass remaining in forest sites compared to tundra (Table 3, Figure 2). At the last sampling date in September 2001 the average mass remaining was 62.6, 55.8, 62.5 and 55.0% (average for all three main sites) at the Upper Tundra, Upper Forest, Lower Tundra and Lower Forest sites, respectively. At Vassijaure, 73.3 and 65.1% of original mass remained after two years, at tundra and forest sites, respectively. The largest differences in mass remaining between forest and tundra sites were detected after two years of decomposition at the two most maritime sites, i.e. Dovrefjell and Vassijaure (10.1, 8.2, 0.6 and 1.5% difference, at Dovrefjell, Vassijaure, Abisko and Joatka, respectively).

The OTC treatment gradually reduced the decomposition rates over time, compared with control plots, and final mass remaining was significantly higher in the warmed plots, 60.7 and 57.2% for warmed and control plots, averaged for the three main areas (Table 3, Figure 2). The impact of the OTC treatment upon mass remaining was largest at Dovrefjell and Joatka, while the effect at the Abisko sites was rather small (5.7, 4.7 and 0.2% mass remaining, respectively).

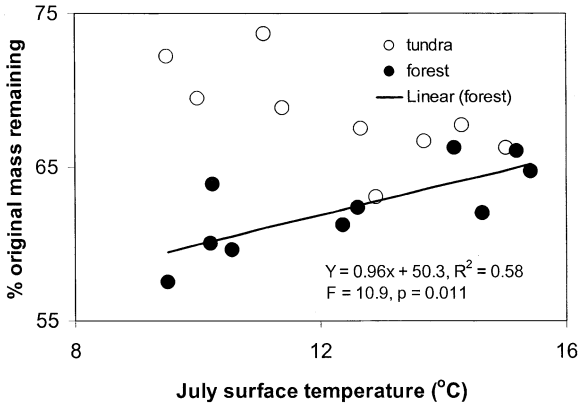

Figure 3. Linear regression between mass remaining (measured in Sept 2000) and mean July temperature for 2000 after two years decomposition in the field at Dovrefjell, Abisko and Joatka, at tundra and forest sites.

Chemical composition after three years

The initial leaf litter chemistry, and after three years, is presented in Table 5. Both in the initial litter, and in the litter remaining after three years, cellulose was the most abundant component, followed by lignin, non-cellulosic polysaccharides (NCPs) and sugars. After three years of field decomposition overall concentration of total C, cellulose, lignin, NCP and soluble sugar concentrations in litter did not differ signific-

Table 3. ANOVA, all effects summary table, for litter bag mass remaining (conversely, lost) during the course of the experiment. Effects: Area (Dovrefjell, Vassijaure, Abisko, Joatka), Site (tundra, forest), Treatment (unwarmed control, OTC), Time (July 1998–September 2001)

Effect	df	F	*P*-level
Area	2	13.21	<0.0001
Site	3	45.92	<0.0001
Treatment	1	7.47	0.0075
Time	5	4098	<0.0001
Area × Site	6	3.54	0.0034
Area × Treatment	2	0.62	0.54
Site × Treatment	3	0.41	0.74
Area × Time	10	8.75	<0.0001
Site × Time	15	5.07	<0.0001
Treatment × Time	5	3.13	0.0087
Area × Site × Treatment	6	0.69	0.66
Area × Site × Time	30	1.58	0.028
Area × Treatment × Time	10	1.47	0.15
Site × Treatment × Time	15	1.10	0.35
Area × Site × Treatment × Time	30	0.73	0.86

antly from initial concentrations. By contrast, N concentration had increased and lignin-to-N and C-to-N ratios decreased significantly (Table 4 and 5).

Generally, overall C and N concentrations were significantly lower at tundra sites, lignin and cellulose concentrations did not differ significantly between vegetation type, while concentrations of NCP and soluble sugars were significantly higher at tundra sites compared to forest sites (Table 4 and 5). The compound/element-specific decomposition (Table 6 and 7; giving the % of the original absolute amount remaining), accounting for the variable overall rates of mass-loss between sites, was not significantly different for lignin, cellulose and NCP, although significantly higher amounts of soluble sugar remained in the litter. For all compound groups the largest relative mass loss was at forest sites (Table 7). For lignin decomposition (Table 4 and 5) at the three main areas, a significant reversed pattern between the forest and tundra sites was noted, with the highest loss of lignin recorded at the Upper Tundra site at Dovrefjell and the Lower Forest site at Joatka. Sugar concentrations varied significantly between areas (Table 5). The highest concentration of sugars was found at Joatka, followed by Abisko and Dovrefjell.

Both the greatest and the smallest proportional reductions in C and N content were found at the

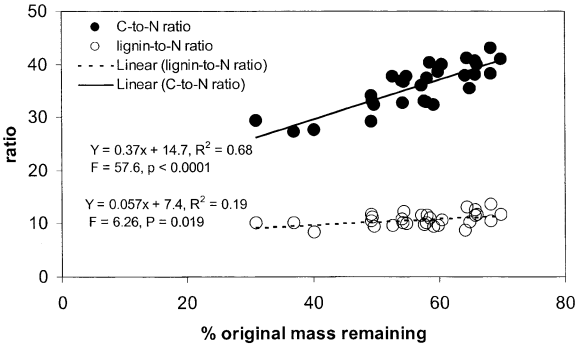

Figure 4. Linear regression between C-to-N and lignin-to-N ratios and mass remaining after three years decomposition in the field at Dovrefjell, Abisko and Joatka (measured in Sept 2001).

Dovrefjell forest and tundra sites, respectively (Table 6 and 7), whilst the differences between forest and tundra sites at Abisko and Joatka were much less pronounced. The final C-to-N ratios varied significantly between different areas ($F = 9.69$, $P < 0.001$) and vegetation communities ($F = 20.93$, $P < 0.001$): generally, litter C-to-N ratios increased with latitude and were higher in litter decomposing in tundra environments compared to forest (Table 4). The difference in C-to-N ratios comparing tundra to forest was clearest at Dovre (37.3 and 29.2), while at Abisko the difference was less clear (37.2 compared with 32.4), and at Joatka this was minimal (39.2 and 38.2). A significant positive regression ($R^2 = 0.68$, $F = 57.55$, $P < 0.001$) was noted between final leaf litter C-to-N ratios and final mass remaining, as well as with lignin-to-N ratios ($R^2 = 0.19$, $F = 6.26$, $P < 0.05$) (Figure 4).

Discussion

Betula pubescens Ehrh. ssp. *czerepanovii* leaf litter decomposition rates reported here are relatively high (with ca. 60% original mass remaining after three years, averaged over the three study sites) relative to other litter types in similar environments (Cornelissen, 1996). The most rapid mass loss occurred during the short summer period, but continued decomposition during the winter (in the broad sense, September–May), although considerably slower, contributed significantly to overall mass loss due to the length of this season (Figure 2). Assuming the 3.8% mass lost during the winter period 1999/2000 was representative, winter decomposition would account for 11.4% mass loss over three winters, i.e. 20% of the

Table 4. Chemical composition of *Betula pubescens* ssp. *czerepanovii* leaf litter after three years decomposition in the field at Dovrefjell, Abisko and Joatka (Figure 1). Mass remaining, expressed as % of original, (± SE) and mean concentration of lignin, α-cellulose, Non-cellulosic polymers (NCP), soluble sugars, C and N, and C-to-N and lignin-to-N ratios. Analysis of initial material was conducted using pooled samples (three pseudo-replicates), otherwise $n = 5$

Site	Mass remaining (% original)	Lignin (mg g^{-1})	Cellulose (mg g^{-1})	NCP (mg g^{-1})	Sugars (mg g^{-1})	C (mg g^{-1})	N (mg g^{-1})	C:N	Lignin:N
Initial (June 98)	100	171 (11)	462 (3.0)	76.0 (3.0)	32.0 (2.0)	490.5 (5.9)	9.9 (0.53)	49.8	17.3
Dovrefjell UT	64.4 (2.7)	123 (2.4)	464 (9.6)	75.8 (2.2)	36.2 (1.5)	484.7 (3.3)	13.1 (0.56)	37.4	10.4
Dovrefjell LF	40.6 (5.0)	163 (7.4)	485 (20.6)	71.0 (4.1)	30.8 (0.8)	495.3 (3.3)	17.1 (0.73)	29.2	9.5
Abisko UT	56.9 (2.4)	150 (4.9)	460 (8.4)	78.6 (4.4)	40.2 (2.2)	492.8 (2.9)	13.3 (0.56)	37.2	11.3
Abisko LF	52.7 (2.1)	160 (5.9)	482 (9.3)	71.0 (2.1)	38.4 (1.2)	487.8 (3.3)	15.1 (0.43)	32.4	10.6
Joatka UT	62.6 (2.6)	145 (4.2)	493 (3.0)	73.6 (3.0)	62.2 (2.0)	492.2 (4.4)	12.6 (0.29)	39.2	11.6
Joatka LF	63.8 (2.0)	136 (7.6)	485 (11.8)	65.2 (1.6)	52.4 (2.5)	510.1 (4.1)	13.3 (0.23)	38.3	10.3

Table 5. ANOVA all effects (SS1) summary table of litter chemistry (see Table 4) over time (initial compared to after three years decomposition), between areas (Dovrefjell, Abisko, and Joatka) and vegetation (tundra and forest).

Compound	Effect	df	F	*P*-level	Effect	df	F	*P*-level
Lignin	Time	1	2.12	0.16	Area	2	3.53	0.046
					Veg	1	3.26	0.084
					Area × Veg	2	5.19	0.014
Cellulose	Time	1	0.41	0.53	Area	2	1.67	0.21
					Veg	1	1.52	0.23
					Area × Veg	2	1.18	0.32
NCP	Time	1	0.23	0.64	Area	2	1.89	0.17
					Veg	1	8.31	0.0084
					Area × Veg	2	0.19	0.89
Soluble sugars	Time	1	1.13	0.26	Area	2	88.5	<.0001
					Veg	1	13.9	0.0011
					Area × Veg	2	2.44	0.17
C	Time	1	0.09	0.77	Area	2	6.52	0.0056
					Veg	1	6.66	0.017
					Area × Veg	2	5.31	0.013
N	Time	1	6.17	0.019	Area	2	7.69	0.002
					Veg	1	30.5	<.0001
					Area × Veg	2	5.37	0.012
C-to-N	Time	1	9.81	0.004	Area	2	9.69	0.0009
					Veg	1	20.9	0.0001
					Area × Veg	2	4.60	0.021
Lignin-to-N	Time	1	29.23	<0.0001	Area	2	1.81	0.19
					Veg	1	5.37	0.029
					Area × Veg	2	0.17	0.84

Table 6. Relative decomposition (expressed as percentage remaining in the litter) of lignin, α-cellulose, non-cellulosic polymers (NCP), soluble sugars, C and N of *Betula pubescens* ssp. *czerepanovii* leaf litter decomposed in the field at Dovrefjell, Abisko and Joatka, and at forest and tundra sites, after three years. Mean values (± SE) are shown. $n = 5$ Relative decomposition $= 100 - 100*(\frac{([C]_i \times m_i) - ([C]_{i+3} \times m_{i+3})}{[C]_i \times m_i})$ $[C]_i$ = initial concentration; m_i = initial weight; $[C]_{i+3}$ = concentration after three years; m_{i+3} = weight after three years

Site	Mass loss (% orig. remaining)		Lignin		Cellulose		NCP		Sugars		C		N	
Dovrefjell UT	64.4	(2.73)	52.2	(1.4)	66.3	(2.5)	65.6	(2.1)	74.8	(4.6)	65.1	(2.0)	86.5	(1.3)
Dovrefjell LF	40.6	(5.0)	38.2	(3.9)	42.0	(4.0)	38.4	(6.8)	39.2	(5.7)	40.9	(5.1)	69.0	(6.7)
Abisko UT	56.9	(2.41)	50.1	(2.9)	56.6	(2.2)	58.6	(3.3)	71.2	(4.1)	57.1	(2.5)	76.0	(1.0)
Abisko LF	52.7	(2.09)	49.0	(0.6)	55.2	(3.0)	49.2	(1.2)	63.4	(3.4)	52.5	(2.0)	80.4	(3.1)
Joatka UT	62.6	(2.59)	53.3	(3.5)	66.7	(2.6)	60.5	(2.8)	121.3*	(4.8)	62.8	(2.7)	79.3	(2.1)
Joatka LF	63.8	(2.00)	47.3	(3.7)	62.1	(1.8)	50.9	(2.7)	97.6	(8.0)	61.8	(3.0)	79.8	(3.2)
Mean			48.7	(1.4)	58.7	(1.8)	54.4	(2.0)	79.3	(5.2)	57.3	(1.8)	78.8	(1.5)

*Note: a value greater than 100% original mass suggests that soluble sugars have been immobilised in this litter material from the underlying substrate

Table 7. ANOVA all effects (SS1) summary table for relative decomposition (see Table 6) of lignin, α-cellulose, non-cellulosic polymers (NCP), soluble sugars, C and N of *Betula pubescens* ssp. *czerepanovii* leaf litter decomposed in the field at Dovrefjell, Abisko and Joatka, at forest and tundra sites, after three years

Compound	Effect	df	F	*P*-level
Lignin	Area	2	1.32	0.29
	Veg	1	8.50	0.0078
	Area × Veg	2	2.75	0.085
Cellulose	Area	2	7.40	0.0033
	Veg	1	19.7	0.0002
	Area × Veg	2	10.7	0.0005
NCP	Area	2	0.35	0.51
	Veg	1	30.6	<0.0001
	Area × Veg	2	4.87	0.017
Sugars	Area	2	48.1	<0.0001
	Veg	1	23.5	<0.0001
	Area × Veg	2	3.16	0.061
C	Area	2	4.82	0.018
	Veg	1	16.0	0.0006
	Area × Veg	2	9.06	0.0013
N	Area	2	0.10	0.91
	Veg	1	2.09	0.16
	Area × Veg	2	6.65	0.0053

total mass loss. These data underscore the importance of year-round studies of soil organic matter dynamics, even in cold environments, as discussed by Hobbie et al. (2000). Our data disagree, however, with the suggestion by Hobbie and Chapin (1996) that winter processes would dominate mass loss from litter in arctic and subarctic environments. Moody et al. (2001) reported that mass loss rates of *Betula pubescens* Ehrh. ssp. *czerepanovii* litter after a 14 month study in Abisko were ca. 35% (65% original mass remaining). As a consequence of the delayed litter sampling in the current study, it is likely that between 5–10% mass had already been lost from the litter material over the winter period prior to sampling. As a result of this, the total mass loss from litter fall to the last collection in 2001 would be larger than figures reported here, probably in the range 55–50% original mass remaining. However, most of the initial mass loss would have been attributed to leaching of soluble compounds (e.g. certain phenols and sugars) rather than active microbial decomposition. The use of 'old' litter material, may partially explain the unexpected accumulation of soluble sugars in the litter material over the experiment (Table 5): If the litter was depleted from soluble sugar due to leaching during winter prior to collection, over time small amounts of sugar might have been introduced to the litter material by fungi tissue.

In forest sites the higher mass loss (7.1% compared with tundra sites), lower concentrations of NCP and soluble sugars, higher relative decomposition of lignin, cellulose, NCP and sugars, in combination with the lower C-to-N ratios in remaining litter, suggest that the forest environment, in general, was more favourable for decomposition than the tundra (Figure 2, Tables 2, 4 and 6). Higher decomposition rates at forest sites were also observed in a parallel study in Abisko where forest soils were noted to respire at rates ca. 30% higher than tundra soils (Sjögersten and

Wookey, 2002). These data, combined, concur with the generally thicker organic horizons found at tundra sites compared with forest, together with the accumulation of relatively labile carbon (as measured by solid-state ^{13}C NMR) in tundra soils (Sjögersten et al., 2003). The contrasting physical structure of the forests are a likely cause of the less pronounced difference in decomposition rates between forest and tundra at the two more continental sites (i.e., Abisko and Joatka), where tree density was low (< 1250 trees ha^{-1}). The denser forests at Dovrefjell and Vassijaure (the latter with ca. 3200 trees ha^{-1}), by contrast, produce a more sheltered environment that differs strikingly from the adjacent tundra heaths. Additionally, smaller inputs of birch litter at forest sites in Abisko and Joatka will likely influence the quality of the underlying substrate (litter/SOM) to a lesser degree than they do at Dovrefjell and Vassijaure. Since underlying substrate chemistry is pivotal for decomposition of carbon-rich fresh litter material (Chadwick et al., 1998; Lindahl, 2001, PhD thesis; Quested et al., 2002) this could also contribute to the reduced differential in decomposition rates between forest and tundra at Abisko and Joatka compared to Dovrefjell and Vassijaure.

The slower rates of decomposition recorded at tundra sites compared with forests may be linked to the lower overall litter quality of the dominant plant species (dwarf shrubs, mosses and lichens), and lower soil N content/availability there compared to forest (as indicated by the higher final N concentration in litter decomposing at the forest sites, Table 5). More or less subtle differences in the species composition, biomass, metabolic rates and population turnover of the decomposer communities in forest and tundra environments may occur in response both to the contrasting climate and resources (litter/SOM) (Robinson, 2002). In nearby tundra heath, fungal biomass was found to increase slightly in response to enhanced temperatures (Ruess et al., 1999), but in a parallel study we observed that forest soils respired at higher rates compared to tundra, despite lower microbial biomass in the forest (Sjögersten and Wookey, 2002). The presence of key functional groups, such as lignin decomposing basidiomycetes, likely plays a greater role for decomposition rates than microbial biomass *per se*, although data to confirm this assertion is lacking from these environments (Robinson, 2002).

Litter decomposition at forest and tundra sites is differentially responsive to physical environmental factors. At the forest site a negative regression between mass loss and July temperature ($R^2 = 0.58$) suggests summer temperature to be a major controlling factor (Figure 3), especially since no significant relation between mean annual temperature and mass loss was found. At the tundra sites no similar regression was found, indicating that, for example, litter moisture might assume greater significance at these sites, where litter material is more exposed to direct insolation and desiccation by wind. The poorer substrate quality at tundra sites could also affect the temperature sensitivity of the decomposition process (Chadwick et al., 1998; Robinson, 2002). In fact, the *negative* regression between mass loss and temperature at the forest sites is counter-intuitive, and the explanation likely lies in a co-variation between temperature and litter moisture content: In the forest, surface desiccation may be associated with higher temperatures, resulting in reduced decomposition rates. If litter moisture content was held constant across a range of temperatures we would anticipate that a classical direct relationship between temperature and decomposition would result, as documented by Hobbie et al. (1996) in their microcosm study of the decomposition of tundra plants. The generally lower decomposition rates found in the OTC treatment compared with the control plots (Table 2, Figure 2) were probably also caused by increased surface dryness. Reduced soil moisture content within the chambers, due to increased evapotranspiration and partial exclusion of precipitation around the edges, has been documented previously (Sjögersten et al., 2003). Indeed Robinson et al. (1995) also observed reduced rates of litter decomposition in experimental warming treatments involving polyethylene tents (which also resulted in surface-soil drying). A pivotal issue, therefore, is whether or not natural summer warming is also associated with increased surface drying (Oechel et al;, 2000). It is important to emphasise here that tundra environments are highly variable in moisture conditions (Bliss and Matveyeva, 1992; Wookey, 2002), and in mesic/dry systems, in particular, water deficits in the upper soil and litter layers may limit the extent of increased decomposition in relation to climate warming. The strong influence of moisture availability on surface decomposition rates, as well as soil respiration rates, has been demonstrated in several studies in similar environments (Berg et al., 1975; Rosswall et al., 1975; Robinson et al., 1995; Latter et al., 1998; Sjögersten and Wookey, 2002), and increased evaporation and surface dryness in relation to increased air and soil temperature must be taken into consideration when discussing rates of litter decomposition in a warmer world. It is worth noting,

however, that the significant contribution to annual mass loss from the autumn, winter and spring periods observed in this study is likely to be temperature-dependent, since litter moisture content should be less limiting during these periods.

The contrasting patterns in lignin decomposition between the most southerly and the most northerly site suggest that process rates differ across the forest tundra ecotone in the two areas. Similar results have been found in a study of soil C chemistry at these sites, where contrasting concentrations of alkyls, O-alkyls and aromatics were found across the ecotone (Sjögersten et al., 2003). The variation in final lignin concentrations and SOM chemistry could be explained by contrasts in the structure/composition of the microbial community, in response to the structure of the forest at the three areas. Thus there may be a more active population of litter decomposing basidiomycetes, at the sites with high lignin decomposition (Baldock et al., 1995, 1997; Steffen et al., 2000). The more rapid lignin decomposition at the Upper Tundra site at Dovrefjell than at the Lower Forest suggests, however, that the carbon accumulation noted in the organic horizon at tundra sites is not simply related to slower decomposition due to the harsher climate at these sites. Furthermore, a lower degree of lignin transformation in SOM at Abisko and Joatka, compared to Dovrefjell, is indicated by lower concentrations of carboxyls, that result from lignin degradation, in SOM at these sites (Kögel-Knabner, 1993; Sjögersten et al., 2003).

We conclude that vegetation cover (i.e., mountain birch forest compared to tundra heath) greatly influences litter decomposition, with generally higher decomposition rates and lower C accumulation in forest soils (in spite of greater litter inputs in forest). Shifts in the tree-line in these regions in response to climate change (or other factors, such as changing grazing intensity and land management practices) therefore have the potential to alter soil C dynamics, possibly reducing C storage in tundra soils as they become forested, and influencing nutrient cycling significantly (Sjögersten and Wookey, submitted). Our results suggest, therefore, that great care should be taken when modelling C fluxes in this ecotone region, since decomposition rates vary significantly at the meso- (individual ecotone) and macro-scales (latitude/continentality gradients). A more detailed understanding of the underlying processes that control the magnitude and nature of the decomposition processes are also needed, especially relating to the structure and functional characteristics of the decomposer communities. Our data also highlight the need for better regional predictions of surface energy and water budgets, since temperature and water regimes are not independent, but both play a key role in decomposition processes.

Acknowledgements

We thank the European Commission IVth Environment and Climate Framework Programme, the Swedish Royal Academy of Sciences, Svenska Sällskapet for Antropologi och Geografi, Uppsala University Linné Fonden, and Sernanders Resestipendium for funding this work. We are grateful for laboratory and field assistance from Katrin Sjögersten, Marie Nilsson, Karin Luthbom, Per Thermaenius, Pär Eriksson, and Dr Robert Baxter. We also thank Dr Helen Quested and Professor Else Kolstrup for constructive comments on the manuscript.

References

Aber J D and Melillo J M 1991 Terrestrial Ecosystems. Saunders College Publishing, Philadelphia.

Aber J D, Melillo J M and McClaugherty C A 1990 Predicting long-term patterns of mass-loss, nitrogen dynamics, and soil organic matter formation from initial fine litter chemistry in temperate forest ecosystems. Can. J. Bot. 68, 2201–2208.

Aerts R 1997 Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: A triangular relationship. Oikos 79, 439–449.

Alexandersson H, Karlstöm C and Larsson-McCann S 1991 Temperaturen och Nederbörden i Sverige: 1961–1990 Referensnormaler. SMHI Meteorologi Rapport No. 81, SMHI (Sveriges meteorologiska och hydrologiska institut). Norrköping.

Baldock J A and Preston C M 1995 Chemistry of carbon decomposition processes in forests as revealed by solid-state carbon-13 nuclear magnetic resonance. *In* Carbon Forms and Function in Forest Soils. Eds. W W McFee, J M Kelly pp. 89–117. Soil Science Society of America, Inc, Madison WI.

Baldock J A, Oades J M, Nelson P N, Skene T M, Golchin A and Clarke P 1997 Assessing the extent of decomposition of natural organic materials using solid state ^{13}C NMR spectroscopy. Austral. J. Soil Res. 35, 1061–1083.

Barnekow L and Sandgren P 2001 Palaeoclimate and tree-line changes during the Holocene based on pollen and plant macrofossil records from six lakes at different altitudes in northern Sweden. Rev. Paleobot. Palynol. 117, 109–118.

Berg B, Kärenlampi L and Veum A K 1975 Comparison of decomposition rates measured by means of cellulose. *In* Fennoscandian tundra Ecosystems, Part 1, Plants and Microorganisms. Ed. F E Wielgolaski pp. 261–267. Springer-Verlag, Berlin.

Berg B, Ekbohm G, Johansson M B, McClaugherty C, Rutigliano F and DeSanto 1996 Maximum decomposition limits of forest litter types: A synthesis. Can. J. Bot. 74, 659–672.

Berg B 2000 Litter decomposition in northern forest soils. For. Ecol. Manage. 133, 13–22.

Bliss L C and Matveyeva N 1992 Circumpolar Arctic Vegetation. *In* Arctic Ecosystems in a Changing Climate - an Ecophysiological Perspective. Eds. F S Chapin III, R L Jefferies, J F Reynolds, G R Shaver and J Svobod. pp. 59–89. Academic Press, San Diego.

Brendel O, Iannetta P P M and Stewart D 2000 A rapid and simple method to isolate pure alpha-cellulose. Phytochem. Analyses 11, 7–10.

Chadwick D R, Ineson P, Woods C and Piearce T G 1998 Decomposition of *Pinus sylvestris* litter in litter bags: Influence of underlying native litter layer. Soil Biol. Biochem. 30, 47–55.

Cherkinsky A B 1996 ^{14}C dating and soil organic matter dynamics in Arctic and Subarctic ecosystems. Radiocarbon 38, 241–245.

Cornelissen J H C 1996 An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. J. Ecol. 84, 573–582

Coûteaux M, Bottner P and Berg B 1995 Litter decomposition, climate and litter quality. TREE 10, 63–66.

Dyer M L, Meentemeyer V and Berg B 1990 Apparent controls of mass loss rates of leaf litter on a regional scale: Litter Quality vs. Climate. Scand. J. For. Res. 5, 311–323.

Emanuel W R, Shugart H H and Stevenson M P 1985 Climate change and broad-scale distribution of terrestrial ecosystem complexes. Climat. Change 7, 29–43.

Fry S 1988 The Growing Plant Cell Wall: Chemical and Metabolic Analysis. pp. 97–120. Longman Scientific & Technical, Harlow, UK.

Goulden M L, Wofsy S C, Harden J W, Trumbore S E, Crill P M, Gower S T, Fries T, Daube B C, Fan S M, Sutton D J, Bazzaz F A and Munger J W 1998 Sensitivity of boreal forest carbon balance to soil thaw. Science 279, 5348, 214–217.

Hobbie S E 1996 Temperature and plant species control over litter decomposition in Alaskan tundra. Ecol. Monogr. 66, 503–522.

Hobbie S E and Chapin F S III 1996. Winter regulation of tundra litter carbon and nitrogen dynamics. Biogeochemistry 35, 327–338.

Hobbie S E, Schimel J P, Trumbore S E and Randerson J R 2000 Controls over carbon storage and turnover in high-latitude soils. Glob. Change Biol. 6, 196–210.

Hobbie S E, Nadelhoffer K J and Högberg P 2002 A synthesis: The role of nutrients as constraints on carbon balance in boreal and arctic regions. Plant Soil 242, 163–170.

Hollister R D and Webber P J 2000 Biotic validation of small open-top chambers in a tundra ecosystem. Glob. Change Biol. 6, 835–842.

Holmgren B and Tjus M 1996 Summer air temperatures and tree-line dynamics at Abisko. Ecol. Bull. 45, 159–169.

Iiyama K and Wallis A F A 1988 An improved acetyl bromide procedure for determining lignin in woods and wood pulps. Wood Sci. Technol. 22, 271–280.

Kittel T G F, Steffen W L and Chapin F S III 2000 Global and regional modelling of Arctic-boreal vegetation distribution and its sensitivity to altered forcing. Glob. Change Biol. 6, 1–18.

Kögel-Knabner I 1993 Biodegradation and humification processes in forest soils. *In* Soil Biochemistry, Vol. 8. Eds. J-M Bollag and G Stotzky. pp. 101–137. Marcel Dekker, New York.

Körner C 1998 A re-assessment of high elevation tree-line positions and their explanation. Oecologia 115, 445–459.

Latter F M, Howson G, Howard D M and Scott W A 1998 Long-term study of litter decomposition on a Pennine peat bog: which regression? Oecologia 113, 94–103.

Lindalh B 2001 Nutrient cycling in boreal forests – A mycological perspective. Studies on phosphorus translocation within and between mycelia of saprotrophic – and mycorrizal fungi. Acta Universitatis Agriculturae Sueciae Silvestria 214.

Lloyd J and Taylor J A 1994 On the temperature dependence of soil respiration. Funct. Ecol. 8, 315–323.

Marion G M, Henry G H R, Freckman D W, Johnstone J, Jones G, Jones M R, Lévesque E, Molau U, Mølgaard P, Parsons A N, Svoboda J and Virginia R A 1997 Open-top designs for manipulating field temperature in high latitude ecosystems. Glob. Change Biol. 3, 20–32.

Melillo J M, Aber J D and Muratore J F 1982 Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63, 621–626.

Melillo J M, Aber J D, Linkins A E, Ricca A, Fry B and Nadelhoffer K J 1989 Carbon and nitrogen dynamics along the decay continuum – plant litter to soil organic matter. Plant Soil 115, 189–198.

Moody S A, Paul N D, Björn L O, Callaghan T V, Lee J A, Manetas Y, Rozema J, Gwynn-Jones D, Johanson U, Kyparissis A and Oudejans A M C 2001 The direct effects of UV-B radiation on *Betula pubescens* litter decomposing at four European field sites. Plant Ecol. 154, 29–36.

Oechel W C, Vourlitis G L, Hastings S J, Zulueta R C, Hinzman L and Kane D 2000 Acclimation of ecosystem CO_2 exchange in the Alaskan Arctic in response to decadal climate warming. Nature 406, 978–981.

Olofsson J 2001 Long Term Effects of Herbivory on Tundra Ecosystems. Doctoral Dissertation. Umeå University.

Osono T and Takeda H 2001 Organic chemical and nutrient dynamics in decomposing beech leaf litter in relation to fungal ingrowth and succession during 3-year decomposition processes in a cool temperate deciduous forest in Japan. Ecol. Res. 16, 649–670.

Pérez-Harguindeguy N, Díaz S, Cornelissen J H C, Vendramini F, Cabido M and Castellanos A 2000 Chemistry and toughness predict leaf litter decomposition rates over a wide spectrum of functional types and taxa in central Argentina. Plant Soil 218, 21–30.

Quested H M, Press M C, Callaghan T V and Cornelissen J H C 2002 The hemiparasitic angiosperm *Bartsia alpina* has the potential to accelerate decomposition in sub-arctic communities. Oecologia 130, 88–95.

Robinson C H and Wookey P A 1997 Microbial ecology, decomposition an nutrient cycling. *In* The Ecology of Arctic Environments. Eds. S J Woodin and M Marquis. pp. 41–68. Special Publication Number 13 of The British Ecological Society. Blackwell Science, Oxford.

Robinson C H 2002 Controls on decomposition and soil nitrogen availability at high latitudes. Plant Soil 242, 65–81.

Rosswall T, Veum A K and Kärenlampi L 1975 Plant litter decomposition at Fennoscandian tundra sites. *In* Fennoscandian Tundra Ecosystems, Part 1, Plants and Microorganisms. Ed. F E Wielgolaski. pp. 268–278. Springer-Verlag, Berlin.

Rustad L E, Cambell J L, Marion G M, Norby R J, Mitchell M J, Hartley A E, Cornelissen J H C, Gurevitch and GCTE-NEWS 2001 A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126, 543–562.

Scott N A and Binkley D 1997 Foliage litter quality and annual net N mineralization: comparison across North American forest sites. Oecologia 111, 151–159.

Sjögersten S and Wookey P A 2002 Climatic and resource quality controls on soil respiration across the forest-tundra ecotone in Swedish Lapland. Soil Biol. Biochem. 34, 1633–1646.

Sjögersten S and Wookey P A (submitted) The role of soil organic matter quality and physical environment for nitrogen mineraliz-

ation at the forest tundra ecotone in Fennoscandia. Arc. Antarct. Alp. Res.

Sjögersten S, Turner B L, Mahieu N, Condron L M and Wookey P A 2003 Soil organic matter biochemistry and potential susceptibility to climatic change across the forest tundra ecotone in the Fennoscandian mountain range. Glob. Change Biol. 9, 759–772.

Stark S, Strömmer R and Tuomi J 2002 Reindeer grazing and soil microbial processes in two suboceanic and two subcontinental tundra heaths. Oikos 97, 69–78.

StatSoft 1995 STATISTICA Volume 1 – General Conventions and Statistics 1 (2nd Edition). StatSoft, Tulsa.

Steffen K T, Hofrichter M and Hataka A 2000 Mineralisation of ^{14}C-labelled synthetic lignin and lignolytic enzyme activities of litter-decomposition basidiomycetous fungi. Appl. Microb. Biotechnol. 54, 819–825.

Swift M J, Heal O W and Anderson J M 1979 Decomposition in Terrestrial Ecosystems. Blackwell Scientific Publications, Oxford.

Trofymow J A, Moore T R, Titus B, Prescott C, Morrison I, Siltanen M, Smith S, Fyles J, Wein R, Camir T C, Duschene L, Kozak L, Kranabetter M and Visser S 2002 Rates of litter decomposition over 6 years in Canadian forests: influence of litter quality and climate. Can. J. For. Res. 32, 789–804.

Walsh S J, Butler D R, Allen T R and Malanson G P 1994 Influence of snow patterns and snow avalanches on the alpine treeline ecotone. J. Veget. Sci. 5, 657–672.

White A, Cannell M G R and Friend A D 2000 The high-latitude terrestrial carbon sink: A model analysis. Glob. Change Biol. 6, 227–245.

Wookey P A 2002 Tundra. *In* Encyclopedia of Global Environmental Change, Volume 2, The Earth System: biological and ecological dimensions of global environmental change. Eds. H A Mooney and J G Canadell. pp. 593–602. John Wiley & Song Ltd, Chichester.

Section editor: R.M. Boddey