BOREAL ENVIRONMENT RESEARCH 13 (suppl. B): 92–106 © 2008
ISSN 1239-6095 (print) ISSN 1797-2469 (online) Helsinki 25 November 2008

Water-extractable organic compounds in different components of the litter layer of boreal coniferous forest soils along a climatic gradient

Sari Hilli[1)2)]*, Sari Stark[1)] and John Derome[1)]

[1)] *Finnish Forest Research Institute, Rovaniemi Research Unit, P.O. Box 16, FI-96301 Rovaniemi, Finland (corresponding author's e-mail: sari.hilli@metla.fi)*
[2)] *Finnish Forest Research Institute, Rovaniemi Research Unit, Salla Office, FI-98900 Salla, Finland*

Received 4 Apr. 2008, accepted 30 Sep. 2008 (Editor in charge of this article: Jaana Bäck)

Hilli, S., Stark, S. & Derome, J. 2008: Water-extractable organic compounds in different components of the litter layer of boreal coniferous forest soils along a climatic gradient. *Boreal Env. Res.* 13 (suppl. B): 92–106.

We investigated the concentrations and stocks of water-extractable carbon (WEC), nitrogen (WEN), phenolics and sugars in the main litter types (tree, dwarf shrub, moss) in boreal forests on two site types (mesic Norway spruce and sub-xeric Scots pine forests) in the south and north boreal climatic zones. WEC, sugar, and phenolic concentrations in the dwarf shrub and tree litter were higher in the north, whereas WEC and phenolic concentrations in the moss litter were higher in the south. Trees, dwarf shrubs, and mosses contributed to a varying extent to soil WEOM in the north and south boreal forests, the trees accounting for a major part of the WEOM in the south, but the understorey dwarf shrubs in the north. WEOM stocks were not predominantly determined by the concentrations of water-extractable compounds in each litter type, but instead by the quantitative proportions of the individual litter types.

Introduction

Water-extractable organic matter (WEOM) constitutes a continuum ranging from small molecular weight and labile compounds (mono- and disaccharides, amino acids and soluble phenols) (Tipping *et al*. 1999, Michalzik *et al*. 2001, Marschner and Kalbitz 2003, van Hees *et al*. 2005) to slowly-degradable carbohydrates and phenolic compounds derived from tannins and lignin (Kalbitz and Kaiser 2008). The chemical composition of the WEOM has an important effect on the degradation and mineralization rates of organic matter (Miltner and Zech 1998, Gallet and Keller 1999, Kalbitz *et al*. 2003). Due to the varying chemical composition of the plant litter among and within plant species, individual plants have different effects on the concentrations and stocks of soil WEOM (Howard and Howard 1980, Kögel-Knabner 2002, Vargas *et al*. 2006). For example, the leaf litter of perennial grasses is rich in carbohydrates, while evergreen shrubs produce litter with high concentrations of phenolic secondary compounds (Vargas *et al*. 2006).

Boreal coniferous forest soils are usually relatively poor in nitrogen (N) (Flanagan and Van Cleve 1983). The understorey vegetation is dominated by plant species containing high concentrations of tannins and other phenolics (Gallet and Lebreton 1995, Kraus *et al*. 2004a, 2004b).

The litter (L) layer in boreal forest ecosystems consists of a mixture of different types of litter, e.g. senescent conifer needles, senescent leaves of deciduous and evergreen dwarf shrubs, and the senescent parts of mosses. The tree species and species composition of the ground vegetation are very important determinants of the chemical composition and quantity of water-extractable carbon (WEC) and N (WEN) (Wardle *et al*. 2003, Don and Kalbitz 2005). However, there is little information available about how the different litter types (e.g. tree needles, higher plants in the ground layer, and mosses) contribute to the fluxes of WEC and WEN, phenolics and sugars in boreal coniferous forests soils. The quantity and chemical composition of the litter accumulating in the L layer depends on the chemical composition of the litter but, over time, the conditions regulating the decomposition processes, such as climate and site fertility, also influence the quality of the litter that accumulates in the L layer (Vucetich *et al*. 2000, Berg and Meentemeyer 2001, Sariyildiz and Anderson 2003, McTiernan *et al*. 2003, Wardle *et al*. 2003, Kirschbaum 2006). Furthermore, although the role of the chemical composition of water-extractable and dissolved carbon in different forest and vegetation types has been investigated (Neff and Hooper 2002, Smolander *et al*. 2005, Kiikkilä *et al*. 2006), we still lack information on the role of different litter components as determinants of the total stocks of WEOM in boreal forests. The role of each type of litter as a source for WEOM should be determined by both the concentration of water-soluble compounds, and the relative proportion of the litter type in the total litter stock.

The objective of the study was to answer the following questions: (1) how do the main litter types (tree, dwarf shrub, and moss litter) in coniferous boreal forests differ in their concentrations of WEC, WEN, soluble phenolics and sugars in sub-xeric Scots pine forests and mesic Norway spruce forests, (2) how important are each of the litter types in determining the stocks of water-soluble compounds in the L layer, and (3) which litter type can be regarded as the most important source of WEOM in boreal forest soils, and does this vary between the sub-xeric and mesic forests or the south boreal and north boreal forests? In order to find answers to these questions we analyzed the concentrations and stocks of WEC, WEN, and extractable phenols and sugars in different types of litter in both sub-xeric and mesic forests situated in the south boreal and north boreal climatic zones in Finland. We hypothesized (1) that WEOM from the litter of the understorey vegetation constitutes a considerable part of the total WEOM in relation to WEOM from the tree litter, and (2) because concentrations are generally used for describing the pools and fluxes of water-soluble compounds, the concentrations should also reflect the stocks of these compounds.

Material and methods

Study area and sampling

The boreal coniferous forest belt, the taiga, is divided in Finland into four climatic zones: hemiboreal, south boreal, middle boreal, and north boreal. We chose six plots situated in the north boreal zone (hereafter referred to as "north") and six plots situated in the south boreal zone (hereafter referred to as "south") for the study (Fig. 1). Eleven of the plots sampled in this study are a part of the EU/Forest Focus and UN-ECE/ICP Forests intensive monitoring network (Raito *et al*. 2001), with one extra plot (the mesic plot in Sodankylä) not belonging to the network. Precipitation (during 1 June–30 Sep. 2002) was determined on nine of the plots using three precipitation collectors (diameter = 20 cm) located in open areas near to the forest plot. The collectors were emptied at 2-week intervals and the volume of rainfall determined by weighing. Precipitation was determined as the average value of the three collectors. On two of the plots measurements made at the nearest weather station of the Finnish Meteorological Institute were used. On the Pallasjärvi sub-xeric plot, the corresponding value from the mesic plot was used. The temperature sum (threshold +5 °C) on the plots was calculated from temperature measurements made at a height of 2 m in the stand. The temperature was recorded at 1-minute intervals with a data logger, and averaged on a daily basis.

The coverage of main plant growth forms is presented in Table 1. The mesic plots (hereaf-

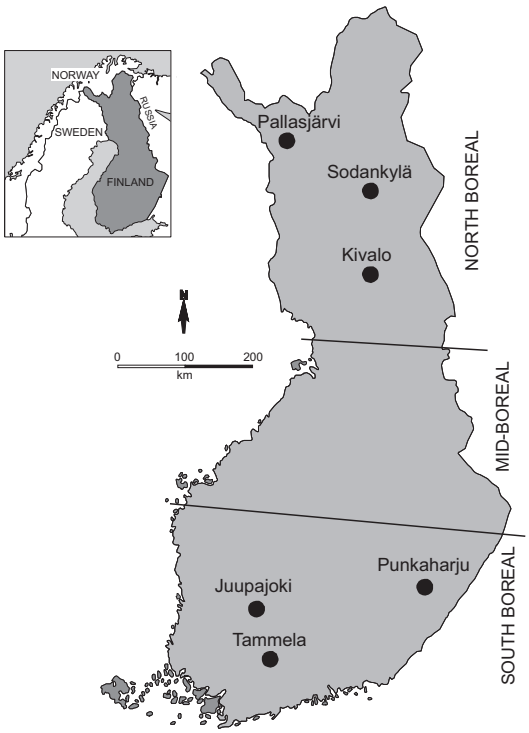

Fig. 1. Location of the intensive-monitoring plots in the north and south boreal zones in Finland.

ter referred to as "mesic") were dominated by Norway spruce (*Picea abies*), and the ground vegetation by mosses and deciduous dwarf shrubs with some herbs and grasses. *Vaccinium myrtillus* formed the most common dwarf shrub species on the mesic plots at Tammela, Punkaharju, Juupajoki, and Kivalo. On the Sodankylä mesic plot, *V. myrtillus* was intermixed with *Vaccinium uliginosum*, whereas on the Pallasjärvi mesic plot, *Empetrum nigrum* was also common. The sub-xeric plots (hereafter referred to as "sub-xeric") were dominated by Scots pine (*Pinus sylvestris*), and the dwarf shrubs by *V. vitis-idea*, which was a common dwarf shrub on all the other sub-xeric plots than on the Punkaharju and Pallasjärvi. On the Punkaharju sub-xeric plot, *V. myrtillus* was more common than *V. vitis-idaea*, and on the Pallasjärvi sub-xeric plot, the ground vegetation was dominated by *Calluna vulgaris*. On the south boreal plots, grasses (e.g. *Solidago virgaurea*, *Melampyrum* sp., *Trientalis europaea*) were much more common than in the north. On the north boreal plots, by contrast, the abundance of lichens (e.g. *Cladonia stellaris*, *C. rangiferina*, *C. arbuscula*) was relatively high (Table 1). In the moss layer, *Pleurozium schreberi* was the most abundant moss species on all the plots except for the mesic plot at Juupajoki, where *Dicranum* sp. were the most abundant. On the mesic plots, *Hylocomnium splendens* was also common.

Organic layer samples were taken in 2002 and 2003, starting in mid July and ending in mid August when the current year litter had still not fallen. Using a rectangular steel frame, intact samples of the forest floor (30 × 30 cm) were removed at regular intervals (7) along four sampling lines at the edge of each 30 × 30 m study plot, resulting in 28 samples for each of the 12 plots, and an overall total of 336 samples. The total area of the squares on each plot was 2.52 m^2. The samples contained the whole organic layer (L, F and H) and all the living ground vegetation (including mosses, dwarf shrubs, etc.). The samples were transported to the laboratory and the L layer was separated into the following fractions: (1) needle litter, (2) coarse tree litter, (3) dwarf shrub litter, (4) moss and lichen litter, and (5) herb and grass litter. The fractions were dried (60 °C) and weighed separately. The dwarf shrub litter fraction was obtained as the sum of the individual dwarf shrub species litter after weighing the litter from all the species individually. Needle and coarse tree litter were combined to form the tree litter fraction. The stocks of moss litter were obtained by separating the dead basal sections of the mosses from the living part, and weighing them. The dry weights and the percentages of each litter type out of the total accumulated litter are presented in Table 2. The total amount of litter in the L layer was taken as the sum of the individual litter fractions (*see* Hilli *et al*. 2008). The amounts of herb, grass, and lichen litter were so small that chemical analyses could not be performed, and these fractions were therefore not included in the chemical analyses.

Physical and chemical analyses

The dry matter content of the initial litter samples was determined by drying a sub-sample for 24 hours in an oven at 105 °C. The organic matter (OM) content was determined as the

Table 1. Site characteristics of the mesic and sub-xeric plots in the north and south boreal zones.

Stand	Lat. N	Elevation (m a.s.l.)	Annual temp. sum d.d. in 2002	Precipit.[1] (mm) bulk deposit.	Stand age (years)*	Site index (H_{100}) (m)	Basal area (m^2 ha^{-1})	Cover percentage			
								Dwarf shrubs	Herbs/ grasses	Mosses	Lichens
Mesic											
Tammela	61°48´	88	1562	526	70	34.7	28.5	38	16	54	0
Punkaharju	61°48´	88	1524	526	70	34.7	28.5	2	8	77	0
Juupajoki	61°51´	177	1510	629	80	28.0	33.2	15	20	64	0
Kivalo	66°20´	252	1073	585	70	17.3	21.6	23	2	92	0.06
Sodankylä	67°42´	240	980**	500**	96	13.4	11.5	31	6	87	2
Pallasjärvi	67°60´	300	889	545	140	10.0	13	15	4	94	0.3
Sub-xeric											
Tammela	60°37´	120	1562	619	60	25.5	21.9	23	18	52	0
Punkaharju	61°46´	99	1524	526	80	26.0	29.4	24	1	80	0
Juupajoki	61°52´	154	1507	629	80	23.6	17.9	31	13	88	0
Kivalo	66°21´	145	1073	587	55	17.9	21.3	38	0.2	81	3
Sodankylä	67°20´	201	980**	500**	80	16.0	18.3	32	0	80	7
Pallasjärvi	67°57´	321	889	550***	90	14.0	12.9	32	0.1	62	14

* 1999.

** measurements made at Sodankylä weather station of the Finnish Meteorological Institute.

*** value from the Pallasjärvi mesic site used.

[1] Mean 1996–2003.

H_{100} = mean stand height (m) at 100 years old.

Table 2. The dry weight of accumulated litter (g m^{-2}) and percentages of the litter types out of the total accumulated litter on each plot (%).

Stand	Dwarf shrub litter		Moss litter		Tree litter		Herb and grass litter		Lichen litter		Other	
	g m^{-2}	Percentage	g m^{-2}	Percentage	g m^{-2}	Percentage	g m^{-2}	Percentage	g m^{-2}	Percentage	g m^{-2}	Percentage
Mesic												
Tammela	12.1	3.1	236	50.6	251	45.9	0	0	0	0.03	1.84	0.42
Punkaharju	0.6	0.2	227	37.0	483	62.9	0.1	0	0	0.01	0.03	0.01
Juupajoki	2.0	0.8	175	49.0	240	48.3	0	0.09	0	0.04	4.67	1.78
Kivalo	51.7	5.8	127	64.0	125	29.7	0	0	0.10	0	2.49	0.45
Sodankylä	19.4	15.8	220	41.2	122	42.1	0	0	0.05	0	2.22	0.85
Pallasjärvi	58.8	22.5	161	48.3	100	27.0	0	0	0.07	0	5.84	2.17
Sub-xeric												
Tammela	15.5	2.6	112	35.6	393	61.6	0	0	0	0	1.41	0.22
Punkaharju	13.5	2.1	161	40.6	324	57.2	0.04	0.01	0	0	0.35	0.07
Juupajoki	23.6	4.3	213	57.7	229	37.8	0	0	0	0	0.85	0.18
Kivalo	44.3	7.4	237	63.6	172	28.8	0	0	0.04	0.1	0.45	0.08
Sodankylä	34.1	17.6	47	15.7	140	64.4	0	0	0.01	2.2	0.35	0.13
Pallasjärvi	54.9	28.5	41	20.1	85	43.1	0	0	0.03	8.1	0.81	0.60

loss in weight on ignition in a muffle furnace at 550 °C for 2 hours.

For the chemical analyses, composite samples were formed by combining the samples from each sampling line into two samples, thus reducing the number of replicates per plot from 28 to eight, resulting in an overall total of 96 samples. The different litter types (moss, dwarf shrub, and tree litter) were kept separate. The dried samples were milled to pass through a 1-mm sieve. The milled samples were analysed using a sequential extraction technique according to Ryan *et al*. (1990) into the following fractions: nonpolar extractives (NPE, waxes, fatty acids and lipids), water-soluble extractives (WSE, e.g. sugars and phenolics), acid-soluble fraction (AS, e.g. cellulose), and acid-insoluble residue (AIR). The results for the WSE fraction only are presented in this paper. Data on the NPE, AS, and AIR fractions will be published elsewhere. In the extraction procedure, 2 (± 0.010) g of dry sample was weighed into a glass fibre thimble (Gerhardt SE33A) and 120 ml of chloroform added. The sample was boiled for half an hour at 62 °C in an extraction device (Soxtherm 2000). The thimble was dried overnight at 50 °C and weighed. The difference in weight before and after extraction was taken as NPE. Water-soluble compounds: the residue was then extracted with 120 ml of distilled water, boiled at 100 °C for one hour. The water extract was cooled and stored in a plastic bottle at –18 °C until analyzed. Chloroform extraction prior to water extraction enhances the extractability, because lipids and fatty acids may retard the dissolution of water-soluble compounds. We used hot water because it dissolves low molecular sugars, phenols and other extractable compounds more effectively than cold water (Cheshire 1979, Angers *et al*. 1988, Ryan *et al*. 1990, Landgraft *et al*. 2006). The following analyses were conducted on the water extracts:

1. The water-extractable phenol concentration was determined by the Folin-Ciocalteu method (Suominen *et al*. 2003), using commercial tannic acid (Ph Eur., VWR BDH Prolabo) as standard (Yu and Dahlgren 2000). Although this method does not produce an accurate quantification of phenolics, it is a

useful indicator of the relative amount of phenolics in ecological studies.

2. The water-extractable sugar concentration was determined according to the method of Wood and Bhat (1988), using (D+)glucose (Ph Eur., Merck) as standard.
3. WEC was determined on a total organic carbon analyser (Shimadzu TOC — 5000 A) after filtering the samples through a 45 μm membrane filter.
4. The total WEN concentration, which includes all forms of soluble N (i.e. NO_3-N, NH_4-N, and extractable organic N), was analyzed by flow injection analysis (FIA 5012) after oxidation of N to NO_3-N with alkaline potassium persulphate (Williams *et al*. 1995).

The results from the chemical analyses were expressed both in concentrations (mg g^{-1} OM) and in stocks per unit soil area (g m^{-2}). The stocks of WEC, WEN, soluble sugars, and soluble phenolics were calculated by multiplying the amount of each litter fraction with the concentration of each water soluble fraction. Concentrations reflect the chemical composition of WEOM, and the stocks per unit area reflect the stocks of different water-extractable compounds in the individual litter fractions.

Data analysis

The Kolmogorov-Smirnov test and normality plots were used to test normality, and the homogeneity of the variances with Levene's test. In the case of unequal variances, square root transformations were used. Differences in the concentrations and stocks of WEC, WEN, phenols and sugars between the different litter types and between the plots, their location in the north or south boreal zone, and between site types (sub-xeric and mesic), were tested with nested ANOVA with plot as a random factor and nested with the location. The normality of the residuals was explored with normal probability plots (Metsämuuronen 2005). The error for evaluating the main effects of site type was calculated as the mean square (MS) of (Site type × Plot (Location) + MS (Error), location as MS (Plot (Location)) + MS (Error), and plot as MS (Site type × Plot (Location)). The interaction between site type, location and plot was calculated as MS (Error), and the interaction between location and site type as MS (Site type × Plot (Location)) + MS (Error). Correlations between annual temperature sum, precipitation, site index H_{100}, elevation, and basal area with water-extractable compounds were calculated with the Pearson correlation test. All the data were analyzed using SPSS 15.0 Software.

Results

Effect of site type and location on litter quality

The concentrations of water-extractable compounds in different litter types are shown in Fig. 2. On the sub-xeric plots, the concentrations of water-extractable sugars and WEC in dwarf shrub litter were higher than in the tree litter, whereas on the mesic plots the differences among the litter types were not as large (Fig. 2A and C). The highest phenolic concentrations were found in the dwarf shrub litter (Fig. 2B), and the highest WEN concentrations in the moss litter (Fig. 2D). However, the concentrations of water-extractable phenolics in the moss litter were very low on both site types.

The concentrations of water-extractable compounds in the different litter types varied both between the mesic and sub-xeric plots and between the north and the south boreal plots (Figs. 2 and 3). In the tree litter, the concentrations of WEN were significantly higher on the mesic than on the sub-xeric plots (ANOVA: $P < 0.001$; Fig. 3A), whereas there were no differences between the site types in the concentrations of WEC, sugars, and phenolics. In the dwarf shrub litter, the WEN concentration was higher on the mesic than on the sub-xeric plots ($P < 0.05$; Fig. 3B). In the moss litter, the concentration of water-extractable phenolics was significantly higher on the mesic than on the sub-xeric plots ($P < 0.05$; Fig. 3C).

In the tree and the dwarf shrub litter, the concentrations of WEC (ANOVA: $P < 0.05$) and sugars ($P < 0.05$) were significantly higher on the north than on the south boreal plots (Fig. 3A and B), whereas there was no effect of location

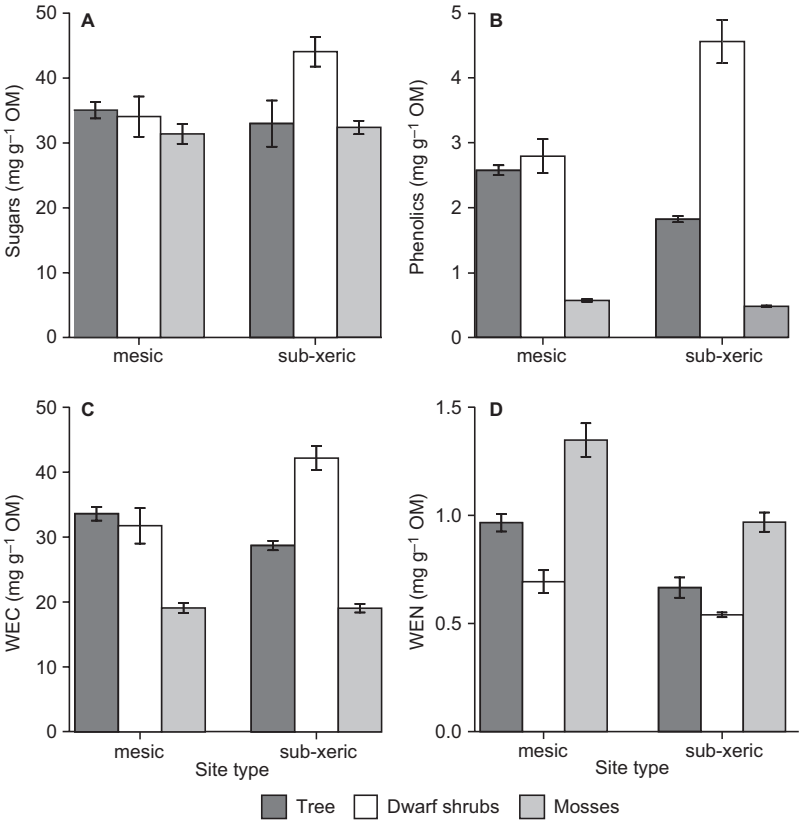

Fig. 2. The mean concentrations (mg g^{-1} OM) of (**A**) sugars, (**B**) phenolics, (**C**) water-extractable carbon (WEC), and (**D**) water-extractable nitrogen (WEN) in tree, dwarf shrub and moss litter on the mesic and sub-xeric plots (data from the south boreal and the north boreal plots combined). N = 6, error bars indicate SE.

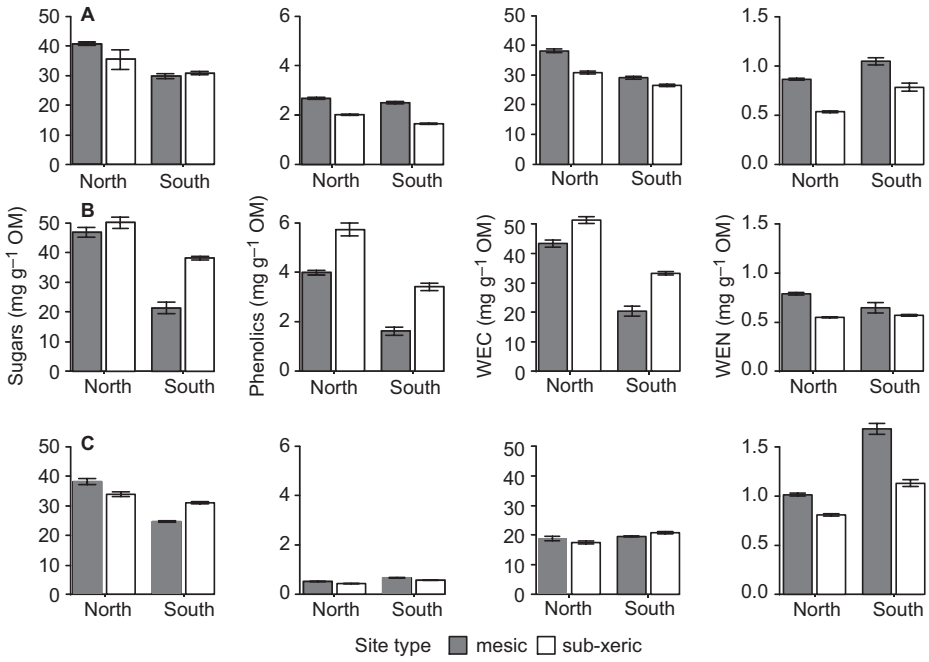

Fig. 3. The mean concentrations (mg g^{-1} OM) of sugars, phenolics, water-extractable carbon (WEC) and water-extractable nitrogen (WEN) in (**A**) tree, (**B**) dwarf shrub and (**C**) moss litter on the mesic and sub-xeric plots in the north and south boreal zones. N = 3, error bars indicate SE.

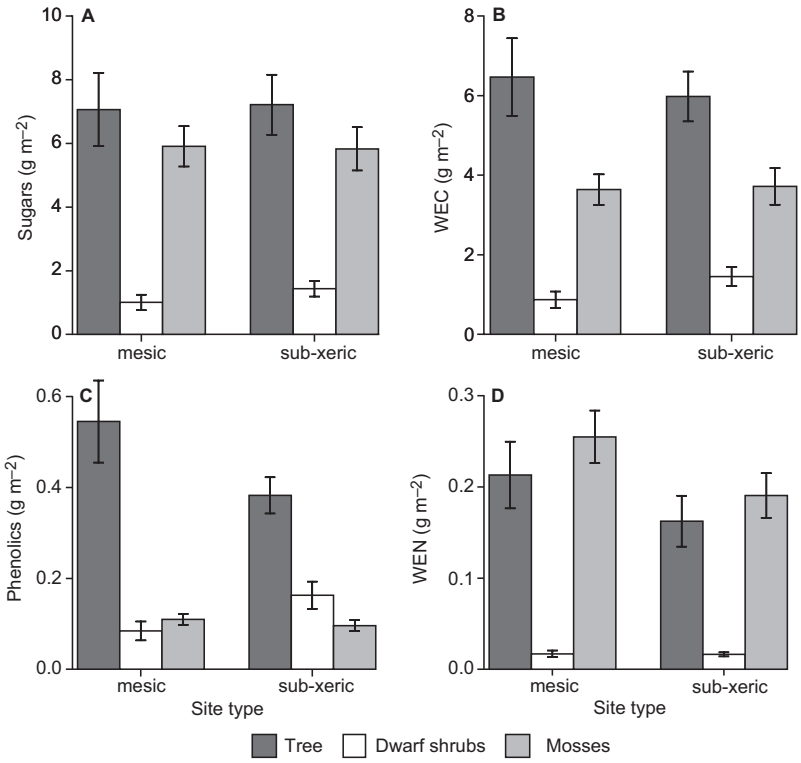

Fig. 4. The mean stocks of (**A**) sugars, (**B**) phenolics, (**C**) water-extractable carbon (WEC), and (**D**) water-extractable nitrogen (WEN) in the tree, dwarf shrub and moss litter on the mesic and sub-xeric plots (data from the south boreal and the north boreal plots combined). $N = 6$, error bars indicate SE.

on the concentrations of WEN or water-extractable phenolics. In the moss litter, on the other hand, the sugar concentrations were significantly higher on the north boreal than on the south boreal plots ($P < 0.05$), whereas the concentrations of WEN ($P < 0.05$) and water-extractable phenolics ($P < 0.05$) were significantly higher in the south than in the north.

Effect of litter type, site type, and location on WEOM stocks in litter

When calculated as stocks on an areal basis, the largest stocks of water-extractable sugars and phenolics, WEC and WEN were found in the tree litter (Fig. 4). The moss litter also had large stocks of water-extractable sugars, WEC and WEN (Fig. 4A, B and D). The quantitative role of each litter type varied between the site types. In the tree and moss litter, the stocks of water-extractable compounds did not vary between the site types, but in the dwarf shrub litter the stocks of water-extractable sugars (ANOVA: $P < 0.05$), WEC ($P < 0.05$) and phenolics ($P < 0.05$) were higher on the sub-xeric than on the mesic plots (Fig. 4A–C).

The stocks of phenolics, WEC, and WEN in the tree litter were significantly higher in the south than in the north on both site types (ANOVA: $P < 0.05$; Fig. 5A), whereas the stocks of sugars, phenolics, WEC, and WEN in the dwarf shrub litter were all significantly lower on the south boreal plots ($P < 0.05$; Fig. 5B). There was no statistically significant influence of the location on the stocks of WEOM in the moss litter (ANOVA: $P > 0.05$; Fig. 5C). However, the role of the location in the stocks of water-extractable sugars in the moss litter varied between the site types (significant site type × location interaction; ANOVA: $P < 0.05$; Fig. 5C). In the south boreal zone, the stock of water-extractable sugars in the moss litter was higher on the sub-xeric than on the mesic plots, whereas in the north the stock of sugars was higher on the mesic than on the sub-xeric plots.

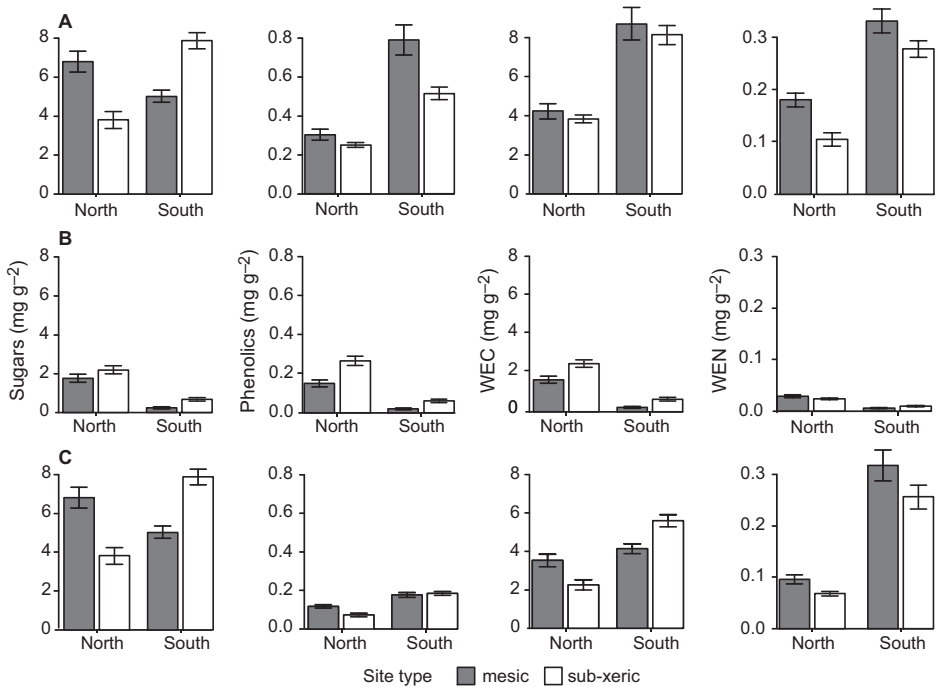

Fig. 5. The mean stocks of sugars, phenolics, water-extractable carbon (WEC) and water-extractable nitrogen (WEN) in (**A**) tree, (**B**) dwarf shrub and (**C**) moss litter on the mesic and sub-xeric plots in the north and south boreal zones. *N* = 3, error bars indicate SE.

Correlations between climatic variables and concentrations and stocks of water-extractable compounds

Annual temperature sum correlated positively with the sugar concentration of the tree litter and the phenolic concentration of the moss litter, and negatively with the sugar and phenolic concentrations of the dwarf shrub litter and sugar concentration of the moss litter (Table 3). We found no correlation between water-extractable compounds and precipitation. Site index (H_{100}) correlated positively with the sugar concentration of the tree litter and the phenolic and WEN concentration in the moss litter, and negatively with the phenolic, sugar and WEC concentration of the dwarf shrub litter and sugar concentration of the moss litter. We also found some correlations between the elevation and basal area of the trees with water-extractable compounds in the different litter types.

Annual temperature sum and site index H_{100} correlated positively with the stocks of water-extractable compounds in the tree litter and negatively with the stocks in the dwarf shrub litter (Table 3). In moss litter the annual temperature sum correlated positively with the stocks of phenolics and WEN. Elevation correlated negatively with the stocks of water-extractable compounds, except for the sugar stocks in the moss litter. Basal area of the trees correlated negatively with the stocks of water-extractable compounds in the dwarf shrub litter, and positively with the stocks of phenolics, WEC and WEN in the tree and moss litter.

Discussion

Concentrations of water soluble compounds in different litter types in the south and north boreal forests

The chemical quality of the different litter types varied significantly between the south and the north boreal forests: in the dwarf shrub and tree

litter, the concentrations of WEC and sugars were significantly higher on the north than on the south boreal sites, whereas in the moss litter the concentrations of WEN and water-extractable phenolics were higher in the south than in the north. The latitudinal variation in the quality of soil organic matter is in line with the findings of some earlier investigations (Neff and Hooper 2002, Sjögersten *et al*. 2003). The importance of different plant growth forms and plant species as determinants of soil organic matter decomposability and, consequently, the rate of soil nutrient cycling in ecosystems, is widely recognized (*see* e.g. Hobbie 1992, Berendse 1994). However, to our knowledge our investigation is the first study to show that the individual plant growth forms (trees, dwarf shrubs, mosses) contribute to the soil WEOM to a varying extent in different climatic zones.

The dissimilarity in litter chemical composition between the south and north boreal forests can be explained by both within-species and between-species differences. The concentrations of phenolics in *V. myrtillus*, the dominant boreal understorey dwarf shrub of mesic and intermediate nutrient rich Norway spruce forests in northern Europe (Arnborg 1990, Hägglund and Lundmark 1997), generally increase with

Table 3. Pearson correlations between the climatic variables and the concentrations and stocks of WEC, WEN, soluble phenolics, and soluble sugars in tree, dwarf shrub, and moss litter. NS = non-significant, * = significant at $P < 0.05$, ** = significant at $P < 0.01$.

	Annual temperature sum	Precipitation	Site index H_{100}	Elevation	Basal area
Concentrations					
Tree litter					
Phenolics	NS	NS	NS	NS	NS
Sugar	0.619*	NS	0.667*	–0.703*	NS
WEC	NS	NS	NS	636*	NS
WEN	NS	NS	NS	NS	NS
Dwarf shrub litter					
Phenolics	NS	NS	–0.602*	0.648*	–0.633*
Sugar	–0.649*	NS	–0.778**	0.721**	–0.696*
WEC	–0.613*	NS	–0.694*	0.657*	NS
WEN	NS	NS	NS	NS	NS
Moss litter					
Phenolics	0.730**	NS	0.859**	–0.580*	0.671*
Sugar	–0.683*	NS	–0.733**	0.657*	–0.662*
WEC	NS	NS	NS	NS	NS
WEN	0.606*	NS	0.653*	NS	0.750**
Stocks					
Tree litter					
Phenolics	0.693*	NS	0.848**	–0.727**	0.617*
Sugar	0.619*	NS	0.667*	–0.703*	NS
WEC	0.809**	NS	0.836**	–0.798**	0.720**
WEN	0.789**	NS	0.853**	–0.752**	0.641*
Dwarf shrub litter					
Phenolics	–0.725**	NS	–0.713**	0.781**	–0.707*
Sugar	–0.816**	NS	–0.832**	0.851**	–0.814**
WEC	–0.807**	NS	–0.801**	0.812**	–0.746**
WEN	–0.812**	NS	–0.838**	0.823**	–0.746**
Moss litter					
Phenolics	0.752**	NS	0.668*	–0.704*	NS
Sugar	NS	NS	NS	NS	NS
WEC	NS	NS	NS	–0.613*	NS
WEN	0.804**	NS	0.751**	–0.690*	0.766**

latitude (F. Martz unpubl. data). Plants growing under nutrient stress and soils with low pH have high concentrations of tannins and other phenolic compounds (Northup *et al*. 1995, Kraus *et al*. 2004b). Due to the lower fertility of soils in the north than in south boreal forests (Tamminen 2000), the concentrations of phenolics can be expected to be higher in the north than in south boreal forests.

In the moss and dwarf shrub litter, the differences between the north and south boreal forests in the concentrations of water-extractable compounds can also be explained by the differences in plant species composition. The evergreen dwarf shrub species *Calluna vulgaris* and *Empetrum nigrum*, which contain high levels of phenolics (Gallet and Lebreton 1995, Wallstedt *et al*. 1997), were more common in the north, especially on the Pallasjärvi and Sodankylä subxeric plots. This could contribute to the higher phenolic concentration of dwarf shrub litter in the north. The higher WEN concentration in dwarf shrub litter on the mesic sites in the north could be explained by the high proportion of *V. myrtillus*, which is rich in N compared to other *Ericaceous* species (Gallet and Lebreton 1995, Wardle *et al*. 2003). The higher concentration of phenolics and WEN in the moss litter on both the sub-xeric and mesic sites in the south may also be explained by the species differences: in the south, where the moss layer consists of both *Pleurozium schreberi* and *Dicranum* species, while in the north it is dominated by *Pleurozium schereberi* (*see* Salemaa *et al*. 2008). Mosses obtain their water and nutrients from atmospheric deposition and, because precipitation contains relatively more N in the south than in the north (Lindroos *et al*. 2007), the supply of N for mosses is probably better on the south boreal than on the north boreal sites.

Besides higher WEN concentration in the spruce litter than in the pine litter, there were no statistically significant differences in the concentrations or stocks of water-extractable compounds in the litter between the spruce and pine. The differences between the mesic and the subxeric site types were minor, except for the concentrations of WEC and phenolics in the dwarf shrub litter, which probably resulted from differences in the species composition, as discussed above. Earlier Smolander and Kitunen (2002) and Strobel *et al*. (2001) showed that tree species appear to have little effect on DOC composition. Therefore, the coniferous tree species do not seem to be an important determinant of the concentrations of WEOM in the L layer, which further highlights the importance of understorey vegetation in the concentrations and stocks of water-extractable compounds in boreal forests. This result supports that of Augusto *et al*. (2003), who suggested that geographical and geological characteristics influence the vegetation and soil chemistry more than tree species.

Higher concentrations of water-extractable compounds in the north than in the south boreal forests could also be explained by differences in the decomposition rates. Plant residues are decomposed more rapidly in warm and moist conditions (Berg *et al*. 1993, Coûteaux *et al*. 1998, McTiernan *et al*. 2003), which may indicate that soluble substrates are released more rapidly in warm conditions, and in more fertile soils (Côte *et al*. 2000). In laboratory and field studies the release of dissolved carbon (DOC) and nitrogen (DON) from organic matter have been found to increase with temperature or soil temperature (Christ and David 1996, Michalzik and Matzner 1999, Neff and Hooper 2002). We found inverse correlation between the annual temperature sum and the sugar, and WEC concentration of dwarf shrub litter and the sugar concentration of moss litter, which could indicate that more of the water-extractable compounds had already been released due to decomposition on the south boreal than on the north boreal sites. Furthermore, the negative correlation with water-extractable compounds and site index H_{100} may reflect higher decomposition rates in fertile conditions. We also found positive correlations between the annual temperature sum and water-extractable compounds, as well as with the site index H_{100}. Litter with a different initial chemical composition decomposes at a different rate even under the same climatic conditions (Wardle *et al*. 2003), and the long-term decomposition processes result in similar amounts of residual material as their end-product (Latter *et al*. 1998). We do not have any information on the chemical quality of fresh litter on our study sites and, therefore, our data do not support a discussion

on whether the differences in the decomposition rates influence the chemical quality of the litter accumulated in the L layer. Based on our results, however, the concentrations and stocks of water-extractable organic compounds in the main litter fractions of boreal forests are determined by a combination of climatic factors, the tree biomass, and the composition and biomass of the understorey vegetation.

Due to differences in the extraction methods used in individual investigations, it is difficult to compare the results of our study with those obtained in other studies carried out in boreal ecosystems. However, our results for the phenol concentrations in the dwarf shrub litter in the L layer (mainly *V. myrtillus* on the mesic sites, and *V. vitis-idea* and *Calluna vulgaris* on the sub-xeric plots, and consisting of both leaf and stem litter) were higher than those reported by Wardle *et al*. (2003) for newly-shed litter of *V. vitis-idaea* (0.8 mg g^{-1}) and lower than that for *V. myrtillus* (70.3 mg g^{-1}). In comparison to Wardle *et al*. (2003), we found higher phenolic concentrations in the total tree litter (needle, branches, cones, bark), but lower in fresh Norway spruce litter, than those reported by Lorenz *et al*. (2000). The concentrations of water-extractable compounds in the moss litter in our study are comparable with those of Wardle *et al*. (2003). Don and Kalbitz (2005) incubated Scots pine and Norway spruce litter for 27 months in the field and reported an extractable DOC (dissolved organic carbon) concentration (corresponding to the WEC concentration in our data) of 13 mg g^{-1} in Norway spruce litter and 9.4 mg g^{-1} in Scots pine litter. These values are lower than our WEC results. The WEC concentration in our study may be higher due to sieving (< 2 mm), drying and extraction with hot water, which are all treatments that enhance the extractability of DOC (dissolved organic carbon) or WEC and DON (dissolved organic nitrogen) (Jones and Willett 2006, Landgraf *et al*. 2006). However, Don and Kalbitz (2005) and Kalbitz *et al*. (2006) suggested that DOC production from needle litter may increase after the mass loss exceeds 20% because of the increasing contribution of lignin-derived compounds in DOC. It is also possible that our values are higher than those reported in other studies due to the later stage of decomposition of the litter. We investigated the total stock of litter in the L layer, which represents tree litter of varying age shed by spruce and pine over a period of several years, and our samples therefore consisted of needles and coarse woody litter in various stages of decomposition.

The contribution of different litter types in the stocks of WEOM

According to our knowledge this is the first time that the concentrations of water-extractable compounds have been calculated into stocks of each of the main litter types in the L layer. Because we dried and weighed each type of litter on each 30 × 30 cm plot, we were able to calculate how much WEC, WEN, water extractable sugars and phenols are present in the dwarf shrub, moss and tree litter per m^2 in the L layer. For example, the concentration of water extractable compounds in the tree litter was higher on the north boreal sites but, because the proportion of tree litter in the total litter stock was considerably higher in the south, the total WEC, WEN and phenolic stocks in the tree litter were also higher in the south. This result was contrary to our hypothesis. The concentrations of different organic compounds do depict the quality of the litter but, in order to assess the role of each type of litter as a determinant of the chemical quality of SOM, it is necessary to know the quantitative proportions of the litter types.

Our finding is interesting especially in the light of the predicted effects of climate warming on soil C cycles, because climatic conditions influence the ground vegetation and, through this, the amount of litter produced by the individual plant species. The negative correlation between the stocks of water-extractable compounds in the dwarf shrub litter and annual temperature sum, site index H_{100} and basal area indicate that the role of dwarf shrubs in litter accumulation is higher on sites with lower productivity, where tree growth is also lower and, therefore, light conditions for the understorey vegetation are better. On the other hand, the positive correlation between the annual temperature sum, site index H_{100} and basal area of the trees and the stocks of water-extractable compounds in the

tree litter suggests that the litter production by the trees increases with site productivity. The climate, vegetation, and decomposition rates form complex interactions with the vegetation (Neff and Hooper 2002, Sjögersten *et al*. 2003). Our results suggest that global change could influence the WEOM in boreal forests by altering the proportion between the tree and the understorey biomass.

Confirming our hypothesis, the litter derived from the ground vegetation constituted a significant part of the WEC stocks in the L layer, demonstrating that, in addition to the tree species, the ground vegetation is an important determinant of the quantity of water extractable compounds in the L layer. The magnitude of the water extractable compounds in the litter of the ground vegetation varied, however, between the north and south boreal zones: the stocks of WEC derived from the dwarf shrub litter were generally higher in the north than in the south, whereas the proportion of WEC in tree litter was higher in the south. Furthermore, the WEC stocks in the moss litter were higher in the south than in the north. Similar trends were found in water-extractable phenolics, sugars and WEN. Due to differences in both the species composition and the chemical composition of the individual types of litter, the stocks of WEOM originate from different plant growth forms in the different climatic zones. For example, although the total stocks of phenolics in WEOM in the L layer on the mesic plots did not differ between the north and the south (*see* Hilli *et al*. 2008), the stock of phenolics in WEOM in the L layer in the south was mainly formed by the tree litter, whereas in the north it was formed by both the dwarf shrub and the tree litter.

In summary, we conclude that (1) the plant growth forms (trees, dwarf shrubs, mosses) contribute to WEOM to a varying extent in different climatic zones: in the north boreal zone, the understorey vegetation is a considerable determinant of the concentrations and stocks of litter WEOM, whereas in the south boreal zone, the tree litter constitutes a considerable proportion of the litter WEOM stocks. (2) The concentrations and stocks of water-extractable organic compounds in the main litter types in the boreal forests are determined by a combination of climatic factors, the tree biomass, and the composition and biomass of the understorey vegetation. (3) WEOM stocks are not only determined by the concentrations of water-extractable compounds in each litter type, but also by the quantitative proportions of the litter types.

Acknowledgements: We are grateful to Reijo Hautajärvi and Pekka Välikangas for organizing the pre-treatment of the samples, and to all the members of staff at the Salla Office, Rovaniemi Research Unit, Finnish Forest Research Institute, who participated in the laborious task of sorting the samples. We thank Dr. Jaana Bäck and Dr. Annamari Markkola for the valuable comments on earlier drafts of the manuscript, Dr. Maija Salemaa and Leena Hamberg for providing background information on the study plots, Petteri Muukkonen for assistance in the field work, and Raimo Pikkupeura for editing the figures. The study was carried out with co-funding provided within the framework of the EU/Forest Focus programme (Regulation (EC) No. 2152/2003). The participation of S.S. was supported by the Academy of Finland (project 108235).

References

Angers D.A., Nadeau P. & Mehuys G. 1988. Determination of carbohydrate composition of soil hydrolysates by high-performance liquid chromatography. *J. Chrom*. 454: 44–449.

Arnborg T. 1990. Forest types in northern Sweden. *Vegetatio* 90: 1–13.

Augusto L., Dupouey J.-L. & Ranger J. 2003. Effects of tree species on understorey vegetation and environmental conditions in temperate forests. *Ann. For. Sci*. 60: 823–831.

Berg B., McClaugherty C. & Johansson M. 1993. Litter mass-loss rates in late stages of decomposition at some climatically and nutritionally different pine sites. Long-term decomposition in a Scots pine forest. VIII. *Can. J. Botany* 71: 680–692.

Berg B. & Meentemeyer V. 2001. Litter fall in some European coniferous forests as dependent on climate: a synthesis. *Can. J. For. Res*. 31: 292–301.

Berendse F. 1994. Litter decomposability — a neglected component of plant fitness. *J. Ecol*. 82: 187–190.

Cheshire M.V. 1979. *The nature and origin of carbohydrates in soils*. Academic Press, London.

Christ M.J. & David M.B. 1996. Temperature and moisture effects on the production of dissolved organic carbon in a spodosol. *Soil Biol. Biochem* 28: 1191–1199.

Côte L., Brown S., Parre D., Fyles J. & Bauhus J. 2000. Dynamics of carbon and nitrogen mineralization in relation to stand type, stand age and soil texture in the boreal mixedwood. *Soil Biol. Biochem* 32: 1079–1090.

Coûteaux M.M., McTiernan K.B., Berg B., Szuberla D., Dardenne P. & Bottner P. 1998. Chemical composition and carbon mineralization potential of Scots pine needles at different stages of decomposition. *Soil Biol.*

Biochem. 30: 583–595.

Don A. & Kalbitz K. 2005. Amounts and degradability of dissolved organic carbon from foliar litter at different decomposition stages. *Soil Biol. Biochem*. 37: 2171–2179.

Flanagan P.W. & Van Cleve K. 1983. Nutrient cycling in relation to decomposition and organic matter quality in taiga ecosystem. *Can. J. For. Res*. 13: 795–817.

Gallet C. & Keller C. 1999. Phenolic composition of soil solutions: comparative study of lysimeter and centrifuge waters. *Soil Biol. Biochem*. 31: 1151–1160.

Gallet C. & Lebreton P. 1995. Evolution of phenolic patterns in plants and associated litters and humus of a mountain forest ecosystems. *Soil Biol. Biochem*. 27: 157–165.

Hilli S., Stark S. & Derome J. 2008. Qualitative and quantitative changes in water-extractable organic compounds in the organic horizon of boreal coniferous forests. *Boreal Env. Res*. 13 (suppl. B): 107–119.

Hobbie S.E. 1992. Effects of plant species on nutrient cycling. *Trends Ecol. Evol*. 7: 336–339.

Howard D.M. & Howard P.J.A. 1980. Effect of species, source of litter, type of soil and climate on litter decomposition. Microbial decomposition of tree and shrub leaf litter 3. *Oikos* 34: 115–124.

Hägglund B. & Lundmark J.-E. 1977. Site index estimations by means of site properties. Scots pine and Norway spruce in Sweden. *Stud. For. Sci*. 138: 1–34.

Jones D.L. & Willett V.B. 2006. Experimental evaluation of methods to quality dissolved organic nitrogen (DON) and dissolved organic carbon (DOC) in soil. *Soil Biol. Biochem*. 38: 991–999.

Kalbitz K. & Kaiser K. 2008. Contribution of dissolved organic matter to carbon storage in forest mineral soils. *J. Plant Nutr. Soil Sci*. 171: 52–60.

Kalbitz K., Kaiser K., Bargholz J. & Dardenne P. 2006. Lignin degradation controls the production of dissolved organic matter in decomposing foliar litter. *Eur. J. Soil Sci*. 57: 504–516.

Kalbitz K., Schwesig D., Schmerwitz J., Kaiser K., Hamaier L., Glaser B., Ellerbrock R. & Leinweber P. 2003. Changes in properties of soil-derived dissolved organic matter induced by biodegradaradation. *Soil Biol. Biochem*. 35: 1129–1145.

Kiikkilä O., Kitunen V. & Smolander A. 2006. Dissolved soil organic matter from surface organic horizons under birch and conifers: Degradation in relation to chemical characteristics. *Soil Biol. Biochem*. 38: 737–746.

Kirschbaum M.U.F. 2006. The temperature dependence of organic-matter decomposition — still a topic of debate. *Soil Biol. Biochem*. 38: 2510–2518.

Kraus T.E.C., Zasoski R.J. & Dahlgren R.A. 2004a. Fertility and pH effects on polyphenol and condensed tannin concentrations in foliage and roots. *Plant Soil* 162: 95–109.

Kraus T.E.C., Zasoski R.J., Dahlgren R.A., Horwath W.R. & Preston C.M. 2004b. Carbon and nitrogen dynamics in a forest soil amended with purified tannins from different plant species. *Soil Biol. Biochem*. 36: 309–321.

Kögel-Knabner I. 2002. The macromolecular organic composition of plant end microbial residues as input to soil organic matter. *Soil Biol. Biochem*. 34: 139–162.

Landgraf D., Leinweber P. & Makeschin F. 2006. Cold and hot water-extractable organic matter as indicators of litter decomposition in forest soils. *J. Plant Nutr. Soil Sci*. 169: 76–82.

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

Lindroos A.J., Derome J. & Derome K. 2007. Open area bulk deposition and stand throughfall in Finland during 2001–2004. *Working papers of Finnish Forest Research Institute* 45: 81–92.

Lorenz K., Preston C.M., Raspe S., Morrison I.K. & Feger K.H. 2000. Litter decomposition and humus characteristics in Canadian and German spruce ecosystems: information from tannin analysis and 13C CPMAS NMR. *Soil Biol. Biochem*. 32: 779–792.

Marschner B. & Kalbitz K. 2003. Controls of bioavailability and biodegradability of dissolved organic matter in soils. *Geoderma* 113: 211–235.

McTiernan K.B., Coûteaux M.M., Berg B., Berg M.P., Calvano de Anta R., Gallardo A., Kratz W., Piussi P., Remacle J. & Virzo De Santo A. 2003. Changes in chemical composition on Pinus sylvestris needle litter during decomposition along a European coniferous forest climatic transect. *Soil Biol. Biochem*. 35: 801–812.

Metsämuuronen J. 2005. *Tutkimuksen tekemisen perusteet ihmistieteissä*. Gummerus kirjapaino Oy, Jyväskylä.

Michalzik B., Kalbitz K., Park J.H., Solinger S. & Matzner E. 2001. Fluxes and concentrations of dissolved carbon and nitrogen — a synthesis for temperate forests. *Soil Biol. Biochem*. 52: 173–205.

Michalzik B. & Matzner E. 1999. Dynamics of dissolved organic nitrogen and carbon in a central European Norway spruce ecosystem. *Eur. J. Soil Sci*. 50: 579–590.

Miltner A. & Zech W. 1998. Carbohydrate decomposition in beech litter as influenced by aluminium, iron and manganese oxides. *Soil Biol. Biochem*. 30: 1–7.

Neff J.C. & Hooper D.U. 2002.Vegetation and climate controls on potential CO_2, DOC and DON production in northern latitude soils. *Global Change Biology* 8: 872–884.

Northup R.R., Yu Z., Dahlgren R.A. & Vogt K.A. 1995. Polyphenol control of nitrogen release from pine litter. *Nature* 377: 227–229.

Raito H., Hamari A., Merilä P., Mäkinen J. & Nöjd P. 2001. Forest condition monitoring under the UN/ECE and EC programmes in Finland. *The Finnish Forest Research Institute*, *Research Papers* 824: 10–33.

Ryan M.G., Melillo J. & Ricca A. 1990. A comparison of methods for determining proximate carbon fractions of forest litter. *Can. J. For. Res*. 20: 166–171.

Salemaa M., Derome J. & Nöjd P. 2009. Response of boreal forest vegetation to the fertility status of the organic layer along a climatic gradient. *Boreal Env. Res*. 13 (suppl. B): 48–66.

Sariyildiz T. & Anderson J.M. 2003. Interactions between litter quality, decomposition and soil fertility: a laboratory study. *Soil Biol. Biochem*. 35: 391–399.

Sjögersten S., Turner B.L., Mahieu N., Condron L.M. & Wookey P.A. 2003. Soil organic matter biochemistry

and potential susceptibility to climatic change across the forest-tundra ecotone in the Fennoscandian mountains. *Global Change Biology* 9: 759–772.

Smolander A. & Kitunen V. 2002. Soil microbial activities and characteristics of dissolved organic C and N in relation to tree species. *Soil Biol. Biochem.* 34: 651–660.

Smolander A., Loponen J., Suominen K. & Kitunen V. 2005. Organic matter characteristics and C and N transformations in the humus layer under two tree species, *Betula pendula* and *Picea abies*. *Soil Biol. Biochem.* 37: 1309–1318.

Strobel B.W., Bruun Hansen H.C., Borggaard O.K., Andersen M.K. & Raulund-Rasmussen K. 2001. Composition and reactivity of DOC in forest floor soil solutions in relation to tree species and soil type. *Biogeochem.* 56: 1–26.

Suominen K., Kitunen V. & Smolander A. 2003. Characteristics of dissolved organic matter and phenolic compounds in forest soils under silver birch (*Betula pendula*), Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). *Eur. J. Soil Sci.* 54: 287–293.

Tamminen P. 2000. Soil factors. In: Mälkönen E. (ed.), *Forest conditions in a changing environment — the Finnish case*, Forestry Sciences Volume 65, Kluwer Academic Publishers, Dordrecht, the Netherlands, pp. 72–86.

Tipping E., Woof C., Rigg E., Harrison A.F., Ineson P., Taylor K., Benham D., Poskitt J., Rowland A.P., Bol R. & Harkness D.D. 1999. Climatic influences the leaching of dissolved organic matter from upland UK moorland soils, investigated by a field manipulation experiment. *Environment International* 25: 83–95.

van Hees P.A.W., Jones D.L.J., Finlay R., Godbold D.L. & Lundström U.S. 2005. The carbon we do not see — the impact of low molecular weight compounds on carbon dynamics and respiration in forest soils: a review. *Soil Biol. Biochem.* 37: 1–13.

Vargas D.N., Bertiller M.B., Ares J.O., Carrera A.L. & Sain C.L. 2006. Soil C N dynamic induced by leaf-litter decomposition of shrubs and perennial grasses of the Patagonian Monte. *Soil Biol. Biochem.* 38: 2401–2410.

Vucetich J.A., Reed D.D., Breymeyer A., Degórski M., Mroz G.D., Solon J., Roo-Zielinska E. & Noble R. 2000. Carbon pools and ecosystem properties along a latitudinal gradient in northern Scots pine (*Pinus sylvestris*) forests. *For. Ecol. Manage.* 136: 135–145.

Wallstedt A., Nilsson M.-C., Odham G. & Zackrisson O. 1997. A method to quantify the alleopathic compound Batatasin-III in extract from Empetrum hermaphroditum using gas chromatography: applied on extracts of leaves from different ages. *J. Chem. Ecol.* 23: 2345–2355.

Wardle D.A., Nilsson M.-C., Zackrisson O. & Gallet C. 2003. Determinants of litter mixing effects in a Swedish boreal forest. *Soil Biol. Biochem.* 35: 827–835.

Williams B.L., Shand C.A., Hill M., O'Hara C., Smith S., Young M.E. 1995. A procedure for the simultaneous oxidation of total soluble nitrogen and phosphorus in extracts of fresh and fumigated soils and litters. *Commun. Soil Sci. Plant Anal.* 26: 91–106.

Wood T.M. & Bhat K.M. 1988. Methods for measuring cellulase activities. In: Wood W.A. & Kellog S.T. (eds.), *Methods in enzymology* vol. 160, Academic Press, San Diego, pp. 87–112.

Yu Z. & Dahlgren R.A. 2000. Evaluation of methods for measuring polyphenols in conifer foliage. *J. Chem. Ecol.* 26: 2119–2140.