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Dynamics of dissolved carbon and nitrogen in decomposing boreal mor and peat as affected by enchytraeid worms

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Academic dissertation

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ABSTRACT

Export of dissolved organic carbon and nitrogen (DOC and DON) from terrestrial ecosystems to watercourses has increased in the boreal zone. However, the effects of decomposing material and soil food webs on the release rate and quality of DOC and DON are poorly known. The objective of this study was to quantify the release of carbon (C) and nitrogen (N) from mor and peat, which are the most common organic soil types in the boreal zone. The impact of soil fauna on the release processes was also estimated. Decomposition products were divided into intermediate products (DOC and DON) and mineralised end products, i.e. carbon dioxide (CO_2-C) and ammonium (NH_4^+-N). The release of C and N into the soil solution, extractable pools, and CO_2-C efflux were measured. DOC and DON were further divided into high molecular weight (HMW) and low molecular weight (LMW) fractions.

Carbon release was slightly different in each soil type. In absolute terms, the peat released less C and in relative terms more DOC than mor. Enchytraeids worms (*Cognettia sphagnetorum*) affected the quantity and composition of the decomposition products by enhancing mineralisation and the release of HMW-DOC.

In the slightly decomposed peat, the net release of N occurred in the form of DON, whereas the other soil types mainly released NH_4^+-N. The slightly decomposed peats are typically located close to water bodies, in the topmost soil layer, where the water discharge is the highest. Therefore, the slightly decomposed peats might have an important role in controlling the quality and quantity of N export.

The results were used to further develop the decomposition model ROMUL to account for DOC and DON processes and the division between intermediate and end products. The parameterisation and structure of the model was analysed by means of the GLUE (Generalised Likelihood Uncertainty Estimation) method, and several simultaneously measured variables, which is novel in this research field.

Keywords: dissolved organic compound, soil water, adsorption, biodegradation, mineralisation, ROMUL

ACKNOWLEDGEMENTS

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Finally, my dearest thanks to Bastian, and children Siiri, Kaisu and Simo, for enriching my life. You did your best to scatter my focus but, *endlich mal*, here I am!

Turku, September 2018

Mari Lappalainen

LIST OF ORIGINAL ARTICLES

This thesis is based on the following papers, which are referred to in the summary by their Roman numerals. Articles are reproduced with the kind permission of publishers.

I Laurén, A., Lappalainen, M., Saari, P., Kukkonen, J.V.K., Koivusalo, H., Piirainen, S., Setälä, H., Sarjala, T., Bylund, D., Heinonen, J., Nieminen, M., Palviainen, M., Launiainen, S., Finér, L. (2012). Nitrogen and carbon dynamics and the role of enchytraeid worms in decomposition of L, F and H layers of boreal mor. Water, Air and Soil Pollution 223: 3701-3719. https://doi.org/10.1007/s11270-012-1142-4

II Lappalainen, M. Kukkonen, J.V.K., Setälä, H., Piirainen, S. Sarjala, T., Koivusalo, H., Finér, L., Palviainen, M., Launiainen, S., Laurén, A. (2018). Release of carbon in different molecule size fractions from decomposing boreal mor and peat as affected by Enchytraeid worms. Water, Air and Soil Pollution 229: 240. https://doi.org/10.1007/s11270-018-3871-5

III Lappalainen, M., Kukkonen, J.V.K., Piirainen, S., Sarjala, T., Setälä, H., Koivusalo, H., Finér, L., Laurén, A. (2013). Nitrogen release in decomposition of boreal mor and peat as affected by enchytraeid worms. Boreal Environment Research 18: 181-194. http://www.borenv.net/BER/pdfs/ber18/ber18-181.pdf

IV Laine-Kaulio, H., Koivusalo, H., Komarov, A.S., Lappalainen, M., Launiainen, S., Laurén, A. (2014). Extending the ROMUL model to simulate the dynamics of dissolved and sorbed C and N compounds in decomposing boreal mor. Ecological Modelling 272: 277-292. https://doi.org/10.1016/j.ecolmodel.2013.09.026

Author's contribution

Paper **I**: Mari Lappalainen was responsible for the planning and implementation of the laboratory experiment, statistical analyses and wrote the manuscript together with Ari Laurén – the co-authors contributed to the article via work related to the experimental design and to manuscript revisions.

Papers **II** and **III**: Mari Lappalainen was responsible for the planning and implementation of the laboratory experiments, for the data analysis and the writing of the manuscripts. Co-authors contributed to the work by commenting on the manuscript and the experimental set-up.

Paper **IV**: Mari Lappalainen was the principal expert in the application and interpretation of the experimental results in the modelling work. Without the experimental results, the construction of the model would not have been possible. Lappalainen actively participated in the manuscript writing. Other co-authors supported the work with modelling techniques and by commenting on the manuscript.

TABLE OF CONTENTS

ABBREVIATIONS

C_{mic}	C in microbial biomass, method: fumigation extraction, TOC analyser
CO_2-C	Carbon dioxide, method: closed chamber method with an infrared gas analyser
DOC	Dissolved organic carbon in soil solution; method: Rhizon sampler with 0.1 µm cut-off, TOC analyser
$DOC_{size1–7}$	Relative molecule size of DOC, method: HPLC analysis, size decreasing from size 1 to size 7
DON	Dissolved organic nitrogen; calculated as DON = $TN_{sol} - (NH_4^+\text{-}N_{sol} + NO_3^-\text{-}N_{sol})$
LMW-DOC	Low molecular weight DOC, method: ultrafiltration through 1 kDa membrane, TOC analyser
LMW-DON	Low molecular weight DON, method: ultrafiltration through 1 kDa membrane, calculated as LMW-DON = $TN_{sol\ <1kDa} - (NH_4^+\text{-}N_{sol} + NO_3^-\text{-}N_{sol})$
NH_4^+-N_{ex}	Extractable ammonium nitrogen, method: K_2SO_4 extraction, filtering with 0.45 µm cut-off, FIA analysis
NH_4^+-N_{sol}	Ammonium nitrogen in soil solution, method: Rhizon sampler with 0.1 µm cut-off, FIA analysis
N_{mic}	N in microbial biomass, method: fumigation extraction, FIA analysis
NO_3^--N_{ex}	Extractable nitrate nitrogen, method: K_2SO_4 extraction, filtering with 0.45 µm cut-off, FIA analysis
NO_3^--N_{sol}	Nitrate nitrogen in soil solution, method: Rhizon sampler with 0.1 µm cut-off, FIA analysis
OC	Organic carbon
OC_{ex}	Extractable organic carbon, method: K_2SO_4 extraction, filtering with 0.45 µm cut-off, TOC analyser
ON	Organic nitrogen
ON_{ex}	Extractable organic nitrogen, K_2SO_4 extraction, calculated as $ON_{ex} = TN_{ex} - (NH_4^+\text{-}N_{ex} + NO_3^-\text{-}N_{ex})$
TC	Total carbon, method: CHN analyser
TN	Total nitrogen, method: CHN analyser
TN_{ex}	Extractable total nitrogen, method: K_2SO_4 extraction, filtering with 0.45 µm cut-off, FIA analysis
TN_{sol}	Total nitrogen in soil solution, method: Rhizon sampler with 0.1 µm cut-off, FIA analysis

1. INTRODUCTION

1.1 C and N fluxes and pools

Decomposition products and decomposers

Organic matter (OM) decomposition is the primary factor controlling the carbon (C) and nutrient balance in forest ecosystems (e.g. Paul 2016). Most of the nitrogen (N) in boreal forest soils is bound to dead organic matter, and a smaller part to living roots, microbes and fauna (Schulten and Schnitzer 1998). Under aerobic conditions, decomposition releases carbon dioxide (CO_2) to the atmosphere and a small proportion of the total C and N becomes dissolved in the soil solution, mainly as dissolved organic C (DOC), dissolved organic N (DON) and ammonium (NH_4^+-N) (Berg and McClaugherty 2003). Gaseous N fluxes, typically through denitrification, have a negligible role in the N balance of acid, nitrate-poor boreal forest soils (Regina et al. 1996; Paavolainen and Smolander 1998; Korhonen et al. 2013).

The process by which organic molecules gradually disintegrate into smaller compounds and finally into CO_2-C and NH_4^+-N is referred to as biodegradation (Kalbitz et al. 2003a; Kiikkilä et al. 2006). In this study, CO_2-C and NH_4^+-N are considered as the end products and DOC and DON as the intermediate products of the decomposition process. Soil microbes are known as the primary decomposers of organic matter. In addition to microbes, soil fauna play an important but less studied role in the decomposition and mineralisation processes. Soil fauna, such as protozoans, nematodes, microarthropods and enchytraeid worms, enhance the release of C and N by fragmenting organic matter into smaller particles and by grazing upon both living and dead microbes and other soil fauna, thereby stimulating mineralisation and increasing the solubility of organic compounds (Setälä and Huhta 1991; Briones et al. 1998; Bardgett and Chan 1999; Laakso and Setälä 1999; Gajda et al. 2017). In the absence of soil fauna, nutrients in the microbial biomass become immobilised until the growth of the microbial population becomes restricted by the availability of C and N in the soil (Park et al. 2002). Functionally, the most influential soil animals in boreal upland and peatland forest soils are the enchytraeid worms (Laakso and Setälä 1999; Silvan et al. 2000), of which more than 95% are comprised of one species, *Cognettia sphagnetorum* (Vejdovsky) (Nurminen 1967: Abrahamsen 1972). Based on genetic studies, the species taxonomy has recently been revised, including changes in nomenclature (Martinsson et al. 2015). In this summary, the previous species name is used to maintain the consistency between the summary and the original articles.

Mobilisation of decomposition products

Dissolved decomposition products released into the soil solution potentially move further on into runoff, which transports the dissolved compounds into streams. Nitrification may turn NH_4^+-N into the more mobile nitrate (NO_3^--N). In boreal forested catchments, a remarkable share of N and C is exported to watercourses as DOC and DON (Ahtiainen and Huttunen 1999; Perakis and Hedin 2002; Mattsson et al. 2003; Kortelainen et al. 2006; Sarkkola et al. 2009; Rasilo et al. 2015), which are important energy and nutrient sources for heterotrophic microbes (Münster et al. 1999; Qualls and Richardson 2003). Thus, terrestrial DOC and DON can increase the productivity of aquatic microbiota, which in turn leads to deterioration in the quality of surface waters. Transport of DOC and dissolved N in the soil is affected by adsorption and biodegradation, with the effect depending on the compound structure; NH_4^+-N is adsorbed more effectively than DON, especially in the organic soil horizon (Qualls 2000; Vandenbruwane et al. 2007). Therefore, the net transport of N decreases when biodegradation turns DON into NH_4^+-N.

The degradability of organic matter is related to its origin and decomposition stage (Kiikkilä et al. 2014). Fresh litter and root exudates are the main source of labile DOC in the soil (Yano et al. 2000; Kalbitz et al. 2003a; Kiikkilä et al. 2006; Fischer et al. 2007), and refractory DOC compounds typically originate from highly decomposed organic matter and microbial metabolites (Kalbitz et al. 2003b). During decomposition, DOC becomes enriched in aromatic structures and is, therefore, higher in molecular weight (Kalbitz et al. 2003b; Hagedorn and Machwitz 2007). Thus, low-molecular-weight (LMW) organic compounds are often considered mostly labile, whereas high-molecular-weight (HMW) organic compounds, when not originating from fresh litter, consist mainly of refractory compounds with low biodegradability (Marschner and Kalbitz 2003). The export of the labile fraction is likely to be small because its half-life is in the order of a few days (Kalbitz et al. 2003a), which is a considerably shorter time than the typical residence time of soil water in forested catchments, which varies from several months to years (Lepistö 1994). According to previous studies (e.g., Kalbitz et al. 2003a; van Hees et al. 2005; Kiikkilä et al. 2006), the proportion of labile DOC in the total DOC pool in the soil varies considerably. The size of the labile pool can change rapidly due to fast turnover (Kiikkilä et al. 2014), as also to physico-chemical sorption and complex-forming processes that retain the labile fraction in the organic soil (Müller et al. 2009). The presence of easily degradable DOC can promote the decomposition of more refractory compounds, which is referred to as the priming effect (Lindén et al. 2014). In addition, soil fauna enhances biodegradation from refractory pools (Fox et al. 2006; Briones et al. 2007), although less is known about their relative importance in affecting the release of DOC and DON in the labile and refractory fractions in different types of organic soils.

1.2 Simulation of the C and N dynamics

Modelling needs

Decomposition of organic matter evidently represents the largest influx of DOC and dissolved N in the soil solution. Therefore, it has an important role in catchment scale C and nutrient dynamics. Quantification of decomposition is a prerequisite for understanding the mechanisms of DOC and DON export to watercourses and for developing realistic process-based models for DOC and dissolved N transport. Many process-based models have been built to simulate the release of C and N from organic matter but only a few can account for the intermediate decomposition products.

The starting point for modelling in this study was the ROMUL model by Chertov et al. (2001). ROMUL mimics the decomposition process in boreal upland forests with medium to low fertility, where decomposition occurs principally in the mor layer. The visible sublayers; litter (L), fermentation (F) and humus (H) represent the various stages of decomposition, as fresh litter gradually disintegrates and transforms into humified OM. ROMUL follows first-order kinetics, and temperature, moisture and the quality of the OM control the release and transfer rates (Chertov et al. 2001). The model calculates the mass loss of OM and the loss of N content in the L, F and H stores during decomposition. ROMUL has been applied in many forest ecosystem studies at the stand to catchment scales (e.g. Kellomäki and Väisänen 1997; Matala et al. 2003; Laurén et al. 2005; 2007; Yurova and Lankreijer 2007; Laurén et al. 2008; Chertov et al. 2009; Ge et al. 2010; Komarov and Shanin 2012; Shanin et al. 2013).

Decomposition models are often developed to calculate total C and N balances or greenhouse gas fluxes. In ROMUL, for instance, the end product of decomposition for C is CO_2, while the quality of N is undefined and is designated as the total amount of N available for vegetation (Chertov et al. 2001). When combined with a solute transport model, a decomposition model should include in more detail defined C and N compounds, as was demonstrated by Laurén et al. (2005) for example, where ROMUL was extended by fractioning the N into NH_4^+-N and DON, and then the value of the fractionation parameter was calibrated against measured data on NH_4^+-N and DON loads from a forest catchment. Laurén et al. (2005) showed that decomposition was among the most important processes for the N balance and N fluxes. They showed that released N in N-limited environment was mainly immobilised in the soil and vegetation, with minor leaching losses occurring with water flow. However, in the model by Laurén et al. (2005), vegetation was assumed to uptake both NH_4^+-N and DON, although DON did not degrade into NH_4^+-N in the model. Furthermore, the transport of C was not included in their solute transport scheme. The results of Laurén et al. (2005) demonstrate that without measurements of the largest N fluxes, the validation of the modelled N balance will contain large uncertainties. Improvements in model development and validation require data that enable a separate quantification of the main N fluxes. When modelling the export of DOC and N from terrestrial systems to watercourses, it is important to simulate the biodegradation processes of both C and N compounds because adsorption and other stabilisation processes, as well as the consecutive net transport, vary between different C and N compounds (e.g. Kalbitz and Kaiser 2008; Müller et al. 2009). Moreover, it is essential to distinct labile dissolved organic compounds with fast biodegradation rates and refractory compounds with slow biodegradation rates.

The computation scheme describing decomposition processes will inevitably contain a large number of parameters introducing a problem of parameter identifiability. This problem can be managed with uncertainty estimation procedures together with specifically designed experiments which may isolate individual processes (Kirchner 2006; Laine-Kaulio 2011).

1.3 Aims of the study

General

As a consequence of the increasing requirements for surface water protection, there is a critical need to investigate the dynamics of DOC and DON. Simulation of the decomposition processes by modelling provides considerable advantages in terms of upscaling and generalisations of the empirical results. Therefore, the needs and aims of modelling are emphasised in this study; to obtain the required C and N release data to support development of the decomposition model ROMUL with special emphasis on facilitating the use of the decomposition model in solute-transport applications. Furthermore, as DOC export links the terrestrial and aquatic systems, the results of this study can be used to examine the ecosystem C balance.

Firstly, the differences in decomposition between the various sublayers of mor were studied experimentally (paper **I**). Secondly, the experimental part of the study was extended to cover different boreal organic materials. The C release rates from different mor and peat materials together with the implications for DOC export are reported in paper **II**. Nitrogen dynamics in various mor and peat materials as affected by enchytraeid worms are reported in paper **III**. Thirdly, the experimental results from paper **I** were further refined into a process-based understanding using mathematical modelling (paper **IV**). Finally, the overall results are discussed, and conclusions are made in this summary based on the original papers, considering the use of experimental results in the decomposition model parameterisation. The research topics that need further investigation and development are indicated. In conclusion, the results are considered in the context of C and N export from boreal forested catchments to streams.

Experimental part

The requirements of model development and parameterisation are addressed in the experimental part of the study (papers **I-III**), where the aim is to quantify the C and N release rates from the most common organic soil layers/types in boreal coniferous forests, i.e. mor and peat, by means of laboratory incubation. The impact of enchytraeids, the most important soil fauna group in these types of organic soils, is quantified. Based on existing knowledge, it is hypothesized that (i) the differences between the decomposing materials are reflected in the release of intermediate and end products, so that the less decomposed and more fertile materials release more decomposition end products and labile intermediate products, and that (ii) the presence of enchytraeids enhance the overall release of C and N.

Modelling Part

In paper **IV,** an extended version of the ROMUL model was developed to simulate the dynamics of DOC and dissolved N compounds for one mor humus type. To describe the internal dynamics of the decomposition of boreal forest mor, experimental results (paper **I**) following the structure of the ROMUL by Chertov et al. (2001) were used. The objectives of paper **IV** were: (i) to further develop the ROMUL model including the dynamics of the intermediate and end products of C and N in the model, and (ii) to apply the model to decomposing mor samples under the conditions of a controlled experiment. To achieve these aims, new computation routines were added to ROMUL that (i) divide the released total C (TC) and N (TN) into their intermediate and end products, (ii) simulate the biodegradation of the intermediate decomposition products and (iii) simulate the adsorption/desorption of the dissolved C and N compounds on the soil particle surfaces. The resulting model was parameterised and evaluated against data using the Generalised Likelihood Uncertainty Estimation (GLUE) procedure (Beven and Binley 1992).

2. MATERIAL AND METHODS

2.1 Conceptualisation of C and N processes in the experiments

Controlled laboratory experiments were arranged to eliminate N uptake by vegetation, root exudation, plant-microbe-interactions and C and N leaching, as well as the effects of varying moisture and temperature conditions on decomposition. When leaching and vegetation functions were excluded, decomposition processes increased the end product in the soil; the NH_4^+-N pool. Therefore, the rate of change in the NH_4^+-N pool together with the release of CO_2-C reflects the decomposition rate of OM. The intermediate products, i.e. DOC and DON, increase from decomposition but simultaneously decrease due to biodegradation, which is why the net changes in the DOC and DON pools do not directly reflect the rate of decomposition. The schematic model of the C and N pools and fluxes in the experiments and the sampling methods used are demonstrated in Fig. 1. Conceptually, the measured C fractions are assumed to be nested in the following way: TC includes undecomposed organic matter, C in microbial biomass (C_{mic}), extractable organic C (OC_{ex}), DOC and dissolved inorganic C (DIC). OC_{ex} includes both the extractable adsorption pool and DOC. Methane (CH_4^+-C) flux was assumed to be negligible due to good aeration in the soil samples. The measured N pools were nested in a similar way: TN contains all N including undecomposed dead organic matter, N in microbial biomass (N_{mic}), extractable N (TN_{ex}) and N in the soil solution (TN_{sol}). TN_{ex} includes N compounds both in soil solution and adsorbed on the surfaces of soil material. During the incubation, denitrification and the production of N_2 and nitrous oxide (N_2O) were assumed to be negligible because of aerobic decomposition conditions, a very small NO_3^--N pool and low soil pH.

The mass changes in the C and N compound pools were used to describe the decomposition process. Because of the relatively short incubation time, in comparison to the time required for the conversion of fresh litter into humus, the change in the compound pools was assumed to be linear with respect to time, in line with Eq. 1 in paper **I**.

2.2 Study sites and soil sampling

Soil sampling for the laboratory experiments was conducted in Sotkamo, eastern Finland, located within the middle boreal forest zone. Intact soil samples of six organic soil types, representing the most common types in Finland (medium and low-fertility mor, slightly and highly decomposed *Carex-Sphagnum* peat, and slightly and highly decomposed *Sphagnum* peat), were collected. Mor humus forms the organic horizon in typical upland forest types, which are Mesic and Sub-xeric heath forests (Tomppo 2000). *Sphagnum*-dominated peat represents 49% and *Carex*-dominated peat 37% of the peatlands in Finland (Virtanen et al. 2003).

The sampling sites for the medium (**I-III**) and low-fertility (**II-III**) mor were in the adjoining catchments of Kangasvaara and Kangaslampi, respectively (63°51’N /28°58’E, Finér et al. 1997). In Kangasvaara, the C and N pools and fluxes have been intensively studied using experimental (e.g. Piirainen et al. 1998; 2002; Finér et al. 2003; Palviainen et al. 2005) and modelling approaches (e.g. Laurén et al. 2005; 2007). The long-term (1981-2010) mean annual air temperature is 2.3 °C, mean monthly temperature varies from -10.7 °C (January) to 16.4 °C (July), and mean annual precipitation is 591 mm, with approximately 200 mm of snowfall (Pirinen et al. 2012). The mean annual soil temperature at the topmost soil layer varies from 3.8 °C to 4.9 °C (Palviainen et al. 2004), the depth of snow cover from 72 cm to 92 cm, and maximum depth of soil frost from 3 to 24 cm (Finér et al. 1997). The ground vegetation cover is classified as a medium-rich, *Vaccinium myrtillus* type vegetation in Kangasvaara and as the *Empetrum vaccinium* type in Kangaslampi (Cajander 1949). The forest at both sites is old-growth Norway spruce (*Picea abies* (L.) Karsten) mixed mainly with Scots pine (*Pinus sylvestris* L.). This site type creates a mor-type forest floor with distinct L, F and H layers above a mineral haplic podsol profile (FAO 1988). During soil sampling for experiment **I**, a visual identification established that the thickness of the mor in Kangasvaara ranged from 3 to 5 cm, the L layer comprised 0.5-2 cm, the F layer 2-3 cm and the H layer 0.5 cm. During soil sampling for **II** and **III,** the thickness of the mor layer in Kangasvaara was observed to range from 5-9 cm and, from 3-5 cm in Kangaslampi.

The drained pine bogs in the adjoining catchments of Koivupuro and Suopuro (63°52'N /28°39'E, Ahtiainen and Huttunen 1999) were used for sampling the *Carex-Sphagnum* and *Sphagnum* peat (**II** and **III**). The peat layer depth was 1-5 m in Koivupuro and 1.5-2 m in Suopuro. The dominant tree species in the catchments was Scots pine, and the ground vegetation cover was the dwarf-shrub type (Cajander 1949).

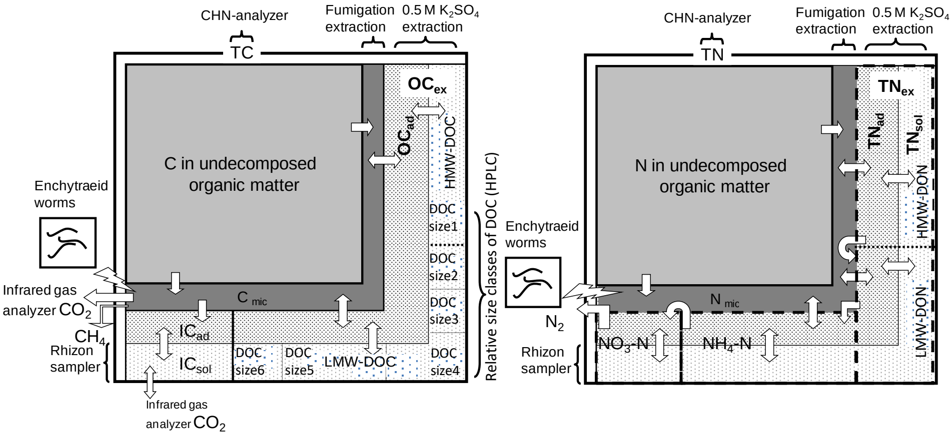

Figure 1. A schematic model of the carbon (C) and nitrogen (N) pools and fluxes in the incubation experiments. The model describes the nested structure of the different pools: Total carbon (TC) contains C in undecomposed dead organic matter, microbial C (C_{mic}), extractable organic C (OC_{ex}) and dissolved organic C (DOC). Furthermore, OC_{ex} includes organic carbon (OC) adsorbed on soil particles (OC_{ad}) and DOC. The number of relative size classes of DOC, based on chromatographic techniques (HPLC), varies according to the soil material. The dissolved organic pool is divided into high molecular weight (HMW) and low molecular weight (LMW) pools. The N pools are nested similarly to C pools. Adapted from paper **I**.

A total of 24 soil samples were collected for the first experiment (**I**), and a total of 48 soil samples for the experiment reported in papers **II** and **III**, which included eight laboratory replicates for each of the organic materials, i.e. sublayers L, F, and H (**I**), and six organic soil types (**II** and **III**). Aboveground living vegetation was carefully removed, and a cylindrical core from the organic layer was cut into the shape of a plastic soil container (diameter 20 cm, height 20 cm). After visual identification, the L, F and H layers were placed in separate containers (**I**). Due to the thin sublayers in the site used for experiment **I** and the thin organic layer in the low-fertility upland site (papers **II** and **III**), the samples of these materials were constructed from several layers placed into the container layer by layer until the thickness of the sample was approximately 10 cm. The thicker sample was required to facilitate soil solution sampling during the incubation experiment. The procedure was considered to cause less soil disturbance than would be caused by homogenisation of the soil material (Tamminen and Mälkönen 1999). The peat samples were collected from the 0-20 cm surface layer to represent slightly decomposed peat (H3-H4 on the von Post (1922) scale of decomposition) and from the underlying layer (down to approx. 40 cm deep) to represent highly decomposed peat (H6-H7 on the von Post scale). The composition and texture of the peat was checked visually and microscopically. In these experiments, replicates of the soil types were not taken in order to ensure that the variation within each soil type was low. This was important since the data was used in the parameterisation of an application of a decomposition model where quantification of the C and N release rates was needed.

Parallel soil samples of each soil material were collected for the analyses of the basic soil characteristics and the extractable contents. Additional mor material was collected for extraction of enchytraeid worms (Fig. 2), which were later used to inoculate the containers in the incubation experiment. Prior to the worm extraction, the soil was stored at 4 °C. The main procedures in the experiments are shown in Fig. 3.

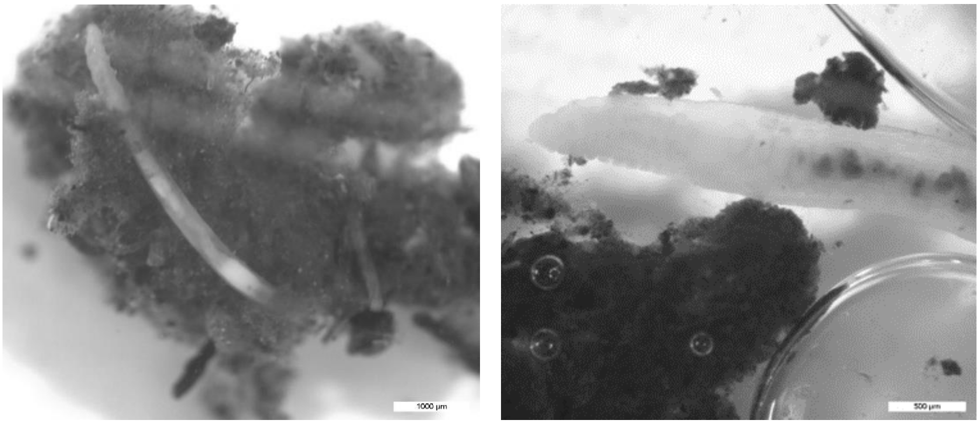

Figure 2. Enchytraeid worms used in incubations (photo: Mari Lappalainen).

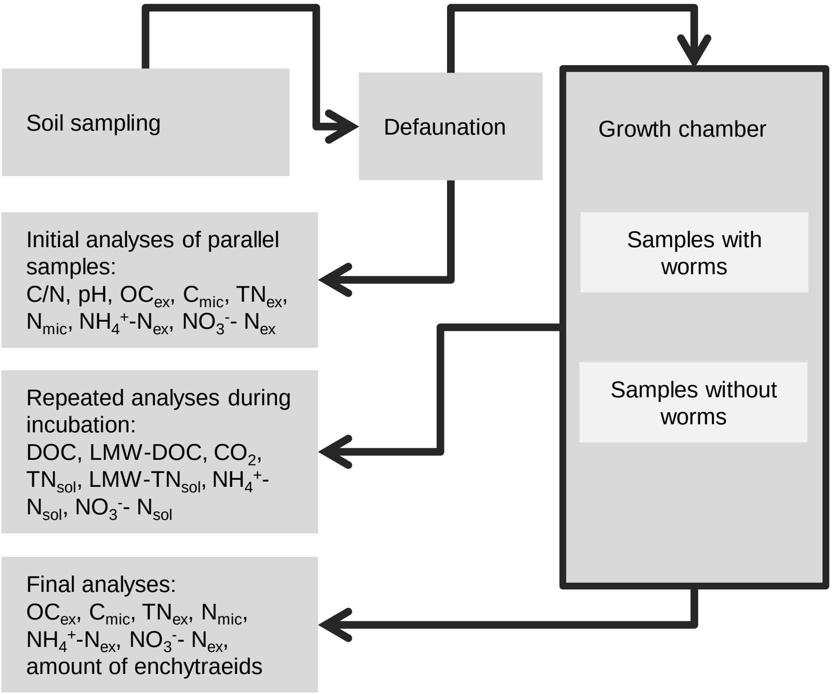

Figure 3. The main procedure of the experiments, adapted from **II**.

2.3 Incubation environment and soil analyses before the incubation

Before initiating the experiment, soil meso- and macrofauna in the soil containers were killed by successively freezing the soil containers to -20 °C and then thawing the containers twice (Setälä et al. 1988). In addition to the decaying roots in the soil samples, the defaunation treatment probably caused a momentary C and N flush from the soil, which was considered in the statistical analysis by omitting the first measurements and thereafter considering the rate of change in the C and N pools (see Section 2.6). After defaunation, the water content of the soil in the containers was adjusted to correspond to field capacity and the containers were placed in a dark growth chamber (GR77, Conviron Controlled Environments Ltd., Canada) with a constant temperature of 15 °C and a relative humidity of 80%. The incubation temperature was set to the typical summertime topsoil temperature in the study area (Palviainen et al. 2004).

One half of the containers, i.e., four replicates for each soil type (or organic sublayer in paper **I**), were inoculated with enchytraeids to determine the impact of soil fauna on decomposition. These worms had been extracted from additional mor material by means of the wet funnel method (O’Connor 1962). About 50 individuals per container were inoculated at the beginning of the incubation and a further 50 worms were added monthly to ensure the continuous presence of an enchytraeid population in the containers. The number of enchytraeids inoculated during the experiment (per container) corresponded to a total of approx. 8,000 individuals m^{-2}, or 0.1 g m^{-2} in terms of the dry mass of worms; representing typical *Cognettia* -population densities in field conditions in these kind of sites (Räty and Huhta 2004). The total number of enchytraeids in the soil containers was determined at the end of the incubation. The remaining containers were left as controls.

The characteristics of the organic materials (C/N, pH, and the contents of extractable C and N compounds) at the beginning of the incubation experiment were determined by destructive analyses from parallel samples. TC and TN contents in the materials were determined using a CHN analyser (CHN-2000, LECO Corporation, USA). The soil pH was measured from a suspension of soil in H_2O (1:2 v:v). Extractable C and N compounds were extracted from the parallel soil samples by means of a 0.5M potassium sulphate (K_2SO_4) extraction. Nitrogen compounds were analysed by flow injection analysis (FIA-Star 5020 Analyzer, FOSS TECATOR). Carbon compounds were analysed using a total organic carbon analyser (TOC 5000A, Shimadzu Scientific Instruments, Inc., USA). The microbial biomass C and N content was determined by means of the fumigation-extraction method (Brookes et al. 1985; Vance et al. 1987; Sparling et al. 1990), described in detail in paper **I**. The extracts were filtered through a 0.45 µm filter before further analyses. The basic characteristics of the organic materials are reported in Table 1.

Table 1. Basic characteristics of the studied organic soil materials (I-III) given as means ± SDs (n=8, except for C/N and pH; n=4). Medium-fertility mor (1) was studied in sublayers L, F, and H in paper **I**.

Soil type	C/N	pH	Water content (vol-%)[a]	Bulk density (kg m^{-3})[a]	Loss on ignition (%)[a]
Mor					
(1) medium fertility	39±0.6	3.82±0.04	33±3	87.2±17.9	95.3±0.5
L	30±0.7	3.95±0.01	39±3	61.6±7.1	94.2±1.7
F	31±1.1	3.63±0.03	41±4	93.9±10.5	90.7±2.3
H	46±2.3	3.49±0.01	45±3	172.8±34.9	58.6±18
(2) low fertility	43.9±2.9	3.76±0.04	39±5	94.8±6.9	93.6±1.9
Carex-Sphagnum peat					
(3) slightly decomposed	37.7±0.6	3.72±0.02	47±7	59.8±4.4	97.6±0.3
(4) highly decomposed	40.0±0.6	3.83±0.01	74±4	145±13.2	98.5±0.2
Sphagnum peat					
(5) slightly decomposed	41.6±2.1	3.84±0.01	76±5	75.7±5.5	98.0±0.7
(6) highly decomposed	38.0±1.0	3.80±0.00	76±8	127±5.2	98.6±0.3

[a] value measured at the end of the incubation

2.4 Sampling and analyses during the experiment

During the incubation period of 112 days (paper **I**) or 154 days (**II** and **III**), soil solution samples were regularly collected from the containers by means of suction samplers (MacroRhizon with syringe, Eijkelkamp, The Netherlands); the mean pore size of the sampler tip was 0.1 µm. The soil solution collected through samplers with a 0.1 µm pore size results in a smaller cut-off in filtering compared to the frequently used 0.45 µm cut-off. Therefore, the measured DOC and DON pools can be slightly lower than the respective standard filtered DOC and DON pools. However, the small pore size in the sampler enables soil solution sampling in drier conditions and was, therefore, suitable for this study. Two sampling tips were inserted vertically into each container. In each sampling event, approx. 100 ml of soil solution was collected over a 2-3 day period. The mass of each soil solution sample was determined before further analysis. The sampling was repeated six times (**I**) or eight times (**II** and **III**) at 2-6-week intervals, with the shortest intervals at the beginning of the experiment. Evaporation loss from the soil samples and water removed by the soil solution sampling were compensated once a week by the addition of deionised water into the containers.

The soil solution samples were analysed in two parts. First part was filtered (Amicon Stirred Cell model 8400, Millipore Corporation, USA, pressure 1.5-2 bar) through an ultrafiltration membrane with a nominal molecular weight limit of 1 kDa. The ultrafiltered fraction represents the LMW fraction of the dissolved compounds. The second part remained unfiltered. DOC was determined from both the filtered and the unfiltered samples (TOC-5000A). The relative molecular-size distributions of DOC and LMW-DOC were determined by means of size-exclusion chromatography analysis (HPLC, Aglient Technologies, USA) with wavelength of 254 nm. Six (paper **I**) or seven (paper **II**) different relative molecular-size classes were distinguished with the size decreasing from class 1 to class 6 (**I**) or 7 (**II**). The comparison of size classes in the DOC and LMW-DOC samples revealed that class 1 (**I**) and classes 1 and 2 (**II**) were missing from the LMW-DOC fraction. Thus class 1 (**I**) or classes 1 and 2 (**II**) represent the high molecular-weight DOC (HMW-DOC), and the other classes represent LMW-DOC.

Dissolved total N (TN_{sol}), NH_4^+-N_{sol} and NO_3^--N_{sol} were determined from the unfiltered solutions (FIA-Star 5000 Analyzer); LMW-TN_{sol} was analysed from the ultrafiltered samples. The DON content was calculated as the difference between the TN_{sol} and the inorganic N contents in the solution. Similarly, LMW-DON corresponds to the difference between LMW-TN_{sol} and inorganic N. However, the LMW-DON pool was small; the LMW-DON concentration in 73% of the solution samples was below 0.1 mg l^{-1} (the detection limit of TN_{sol}) (**III**). The concentration of NO_3^--N_{sol} was below the detection limit (0.01 mg l^{-1}) in 12% (**I**) or in 30% (**III**) of the analysed samples, and for those samples a value equal to half of the detection limit was used in the subsequent calculations.

The CO_2 efflux from the soil containers was measured following each soil solution sampling (**I**) or just before each soil solution sampling (**II**) by means of the static chamber method with an infrared gas analyser (ADC LCA-2, the ADC Bioscientific Ltd., UK). The equipment and setup are described in **I-II**. The CO_2 concentration (ppm) in the air was recorded by saving 4-6 readings at 10-second intervals, and the gas flux was calculated from the linear change in CO_2 concentration during the closure. The CO_2-C measurements represent instantaneous CO_2-C flux from the soil containers. The cumulative CO_2-C release, which is comparable to the collected soil solution data, was calculated by assuming a constant CO_2-C release rate between measurements. This is reasonable since the soil temperature and moisture were kept constant during the experiment. Because soil solution sampling removes some of the biodegradable DOC, it may potentially decrease the observed CO_2-C release. However, the total sampled DOC represented only 1-4% of the total CO_2-C loss during the incubation, and therefore the soil solution sampling is assumed to have had a negligible effect on the CO_2-C release rate.

2.5 Soil analyses at the end of the experiment

At the end of the experiment, the fresh volume and the mass of the soil in the containers were measured, and the soil was cut vertically into four equal sections. The mass of the first section was determined before and after drying at 105 °C to determine the volumetric water content. The dried section was further used to determine the loss on ignition (LOI) at 550 °C. The second section was cut horizontally into 5 cm thick slices, out of which enchytraeids were extracted by means of the wet funnel method. The extraction process was also carried out on the containers without worm inoculations in order to verify the absence of worms. The third section was used for the analyses of K_2SO_4-extractable compounds and microbial C and N. The fourth section was stored for potential further analyses.

2.6 Data processing and statistical methods

The experimental setup was based on the assumption that the net release of C and N compounds on the time scale of the experiment would be constant over time and could thus be described by means of a linear model. The conditions in the growth chamber remained constant and the incubation time was short enough to allow only a small fraction of the total organic matter to decompose. In the experiments, the measured maximum cumulative mass loss via CO_2-C flux was 3% (**I**) or less (**II**) of the initial dry mass (Fig. 3 in paper **I**, Fig. 2 in paper **II**). Therefore, the bias in the release rates due to decreasing OM mass was evidently small. At the beginning of the experiments, the content of NH_4^+-N_{sol} in mor (Fig. 2 in papers **I** and **III**) and the content of LMW-DOC in peat rapidly decreased (Fig. 2 in paper **II**). This could have resulted from strong microbial assimilation after the nutrient flush caused by the preparation of the soil samples for the experiment. Therefore, data from the first sampling date (**I**) or first two sampling dates (**II** and **III**) were excluded from all statistical analyses. As the aim was to quantify the release/accumulation rates of decomposition products, the nutrient flush at the beginning could be disregarded.

After standardising the measured compound quantities by dry organic mass and taking into account the quantities removed in the soil solution samplings, the release rates ($\mu g\ g^{-1}\ day^{-1}$) were calculated by means of mixed linear models (see Eq. 1 in papers **I-III** for dissolved compounds and CO_2-C efflux, and see Eq.2 in papers **I-III** for extractable compounds). A positive release rate refers to an increasing compound pool. Data processing and statistical methods are described in more detail in papers **I-III**. Statistical significance of the release rate of each compound was tested using the t test and the results are reported with 95% confidence intervals for each layer and treatment. Differences at the $p<0.05$ level were considered significant. The statistical analyses were performed with SPSS (IBM SPSS Statistics for Windows, Version 20.0. Armonk, NY: IBM Corp.).

2.7 Model development, parameterisation and evaluation

Development

Here L, F and H describe the decomposition stages in ROMUL, whereas soil samples in different decomposition stages in study **I** are referred as slightly, intermediately and highly decomposed mor materials. This distinction allows to follow the different phases of decomposition process: for example, a slightly decomposed material may contain F and H material in addition to L matter in ROMUL. The original ROMUL model (Chertov and Komarov 1997; Chertov et al. 2001; Komarov et al. 2003) computes organic matter loss and the release of N from L, F and H materials. In paper **IV** the model was extended by adding algorithms for (i) fractionation the released TC and TN into their intermediate decomposition products and end products, (ii) biodegradation of the intermediate decomposition products into the end products, and (iii) adsorbtion/desorbtion of the C and N compounds between the dissolved and sorbed phases.

The extension uses the output of the original ROMUL as forcing data. Therefore, only the extended part is described here. The extended model involves ten new types of stores that represent the dissolved and sorbed phases of the modelled C and N compounds; it also has a new fictitious store for CO_2-C (Fig. 4). The fractionation of the released C into CO_2-C, and the HMW and LMW fractions of organic carbon (OC), was conducted in two steps. First, the C was fractioned into OC in relation to CO_2-C both in the dissolved and sorbed phases (Eq. 1 in **IV**). Then, the fractionation of OC into the HMW and LMW pools was calculated in both the dissolved and sorbed phases (Eq. 2 in **IV**). Released TN was fractionated similarly into organic N (ON) in the HMW- and LMW-fractions and NH_4^+-N, in both the dissolved and sorbed phases (Eq. 3 in **IV**).

The biodegradation of the intermediate decomposition products of C and N was assumed to follow the first-order decay and so the same decay rate constants were used in the dissolved and sorbed phases. The adsorption of all soluble C and N compounds was performed via a first-order, reversible, kinetic reaction, assuming that the adsorption equation describes and combines all the physical and chemical sorption reactions of the molecules. Microsoft Excel with Visual Basic was used in programming the model.

Model parameterisation and evaluation

To manage the equifinality problem and the parameter identifiability issue, the GLUE procedure was applied in parameterization and evaluation of the model (described in more detail in **IV**). In this procedure, the parameters of the original part of ROMUL were kept constant following Chertov et al. (2001), while the parameters in the extension part were allowed to vary.

In GLUE, the model is run repeatedly with different possible parameter combinations, where the prior values for each parameter were sampled from a uniform distribution with a given range. The model result included several variables that were comparable to the laboratory experiments conducted in study **I**. The modelled results for each comparable variable were evaluated against the measured data using a subjectively chosen, predefined likelihood measures, and thereafter these were merged to produce a combined goodness of fit measure for the whole run. The run was accepted if all the predefined criteria were met.

The accepted runs produced the uncertainty intervals for the model result, while the posterior distribution of the accepted parameter values represents the sensitivity of the model to its parameters and the identifiability of parameter values. The parameter sensitivity was evaluated using the two-sample Kolmogorov–Smirnov test (Beven 2008 as cited in Salazar et al. 2011, described in more detail in **IV**) to compare the prior parameter distributions with the posterior distributions.

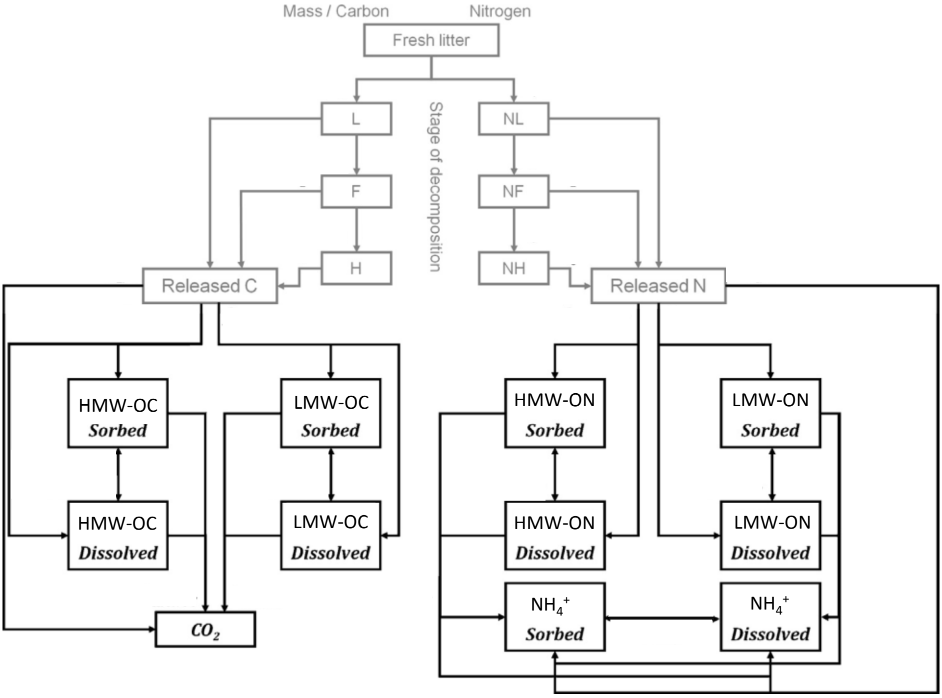

Figure 4. Flow-chart of the ROMUL model (grey) and the extensions made in the present study (black). For a full description of ROMUL, see Chertov et al. (2001). Adapted from **IV**.

3. RESULTS

3.1 Release of C and N from different soil types and sublayers of mor

Carbon

The majority of the released C was released as CO_2-C in all sublayers of mor (**I**) and in all soil types (**II**). The highest rate of C release was observed in mor and in the slightly decomposed *Sphagnum* peat (soil types 1, 2, and 5 in Fig. 2, **II**). More C was released from the L layer than from the F and H layers of mor (**I**). The lowest rate of C release was found in the highly decomposed peats (soil types 4 and 6 in Fig. 2, **II**) for both DOC and CO_2-C. Soil type affected how the released C was partitioned between DOC and CO_2-C. DOC increased at a rate of 3-7% (**I**) or 3-5% (**II**) of the corresponding CO_2-C release rate in mor. In peat, 5-9% of the C release occurred in the form of DOC; except in the slightly decomposed *Sphagnum* peat, where only 2% was released as DOC (**II**).

In all sublayers of mor and in all soil types, the net release of DOC consisted mainly of HMW-DOC. The largest relative molecular-size class (class 1) of DOC in **II** was found only in peat and the changes in the class were small in comparison with those in the other size classes. Due to the high release in class 2, the proportion of the HMW fraction (classes 1-2) in the DOC pool increased during the incubation in almost all soil types (**II**). The release in class 2 represented 62-70% of the total DOC release; except in the slightly decomposed *Sphagnum* peat, where the release was slightly higher in the LMW fraction (classes 3-7). It should be noted that the release of LMW-DOC was negligible from highly decomposed peat samples. The initial DOC pool, especially the HMW fraction, was larger in peat than in mor.

The rate of C accumulation into microbial biomass was substantial during the incubation of the different sublayers of mor, contributing 10-20% of the release rate of CO_2-C (**I**). In the second experiment, the medium fertile mor with enchytraeids showed similar accumulation (**II**). The intermediate C decomposition products (OC_{ex}) decreased during the incubation (**I** and **II**). The amount of DOC increased concurrent with the decrease in the OC_{ex} pool, thereby indicating changes in the distribution between the adsorbed and solution OC pools.

Nitrogen

The largest amount of NH_4^+-N_{sol} was released from mor (soil types 1 and 2 in Fig. 3, **III**) in the presence of enchytraeids. In these soils and in the highly decomposed peat (soil types 4 and 6 in Fig. 3, **III**), approx. 80% of the TN_{sol} was released in the form of NH_4^+-N_{sol}. In contrast, the release was mainly in the form of DON in mor without worms and in slightly decomposed peat with and without worms (soil types 3 and 5 in Fig. 3, **III**). As a whole, the estimated rate of NH_4^+-N_{sol} release was an order of magnitude lower than the release rate of NH_4^+-N_{ex}, except for mor without worms and for the slightly decomposed peat with and without worms, where no net release of NH_4^+-N_{sol} was detected (**III**). In the mor sublayers, the proportion of NH_4^+-N_{sol} from the NH_4^+-N_{ex} was highest in the L layer, between 0.2 and 0.3 (**I**). The degree of decomposition had a significant impact on N release rates from the mor sublayers. The calculated release rates in the TN pools both in extracted and soil solution pools, and in mineral N pools were all significantly higher in the L layer than in the F and H layers (Fig. 4 in **I**). The release rate of NO_3^--N_{sol} was negligible when compared with other N compounds (**I** and **III**).

Of the intermediate N products of decomposition, the ON_{ex} pool decreased in all soil types and layers, more rapidly in the mor L layer than in the F and H layers (Fig. 4 in **I**). Released DON was mainly in the form of HMW-DON as the LMW-DON pool decreased or remained unchanged during the experiment, with the exception of slightly decomposed *Sphagnum* peat (soil type 5 in Fig. 3, **III**), where the LMW-DON pool increased marginally. Both the initial DON pool and the proportion of dissolved N in extractable N pool was largest in peat.

3.2 Role of enchytraeids in the release of C and N

Enchytraeids enhanced the decomposition in the mor soil types. In mor, enchytraeids enhanced the release of CO_2-C by 31-43% and the release of DOC by 46-77%. Enchytraeids changed the quality of total DOC by increasing the release rates especially in HMW-DOC (size class 1 in **I** and size class 2 in **II**). There was a tendency for a smaller decrease of OC_{ex} in the presence of enchytraeids, but the effect was significant only in low fertility type mor (soil type 2 in Fig. 3, **II**).

The rate of NH_4^+-N_{ex} and NH_4^+-N_{sol} release in mor, especially in the L layer was clearly higher in the presence of enchytraeids (Fig. 4 in **I**). The enhanced mineralization of N was also reflected in the LMW-DON pool, which decreased in the presence of worms in mor (Fig. 3 in **III**). In the absence of worms there was practically no net mineralization of N (Figs. 3 and 4 in **III**).

During the incubation, the number of enchytraeids changed from approx. 8,000 individuals m^{-2} to over 20,000 individuals m^{-2} in peat (**II-III**) and over 70,000 individuals m^{-2} in mor (**I-III**).

3.3 Extension of ROMUL: Parameterisation and identifiability

The original ROMUL and its parameters were kept unchanged, and therefore input to the extension part of the model depended only on the L, F and H fractions, ash and N contents and moisture conditions in the sample (as described in **IV)**. For the GLUE analysis a suitable range for parameter prior values was searched using large number of test runs with a target of finding at least 100 acceptable runs. C-related parameters proved to be critical in finding acceptable runs even though the prior value range of the C-related parameters were restricted more than the prior value range of the N-related parameters. The main difference between C- and N- simulation was connected to the gaseous efflux of CO_2-C; it was difficult to find acceptable parameter combinations for the dissolved C compound concentrations, the quantity of released CO_2-C and the total amount of OC at the end state. The desired 100 acceptable runs was easiest to obtain for the highly decomposed mor material, and most difficult for the slightly decomposed material. The main difference between the materials was the distribution between labile and refractory matter.

The model applications for slightly, intermediately and highly decomposed materials showed sensitivity to different parameter subsets each (**IV:** Table A1, A2). The intermediately decomposed mor application indicated sensitivity to the smallest parameter set, whereas the slightly decomposed mor indicated sensitivity to the largest set of parameters. A simultaneous sensitivity examination of all three materials showed that the model was insensitive only to the first-order rate coefficients of LMW-OC and LMW-ON between the dissolved and sorbed phases, and to the initial fraction of the H material in the simulation of the N processes. In all cases the model was sensitive to two C-related parameters: the distribution coefficient of HMW-OC between the dissolved and sorbed phases, and the initial fractions of the L, F and H matter in the modelled samples. On the other hand, the model was sensitive to the following N-related parameters: fractions of HMW- and LMW-ON in TN, the distribution coefficients of NH_4^+-N and HMW-ON between the dissolved and sorbed phases, and the decay rate constant of HMW-ON (**IV**).

The GLUE analysis revealed the best identifiability for the distribution coefficient of HMW-OC, for the distribution coefficient of NH_4^+-N and for the distribution coefficient and decay rate constant of HMW-ON, indicated as a clear difference between the parameter prior and posterior values. An overall evaluation revealed that particular parameter combinations rather than specific values were required for the most plausible model results.

3.4 Extension of ROMUL: Model structure

The simulated results followed the measured dynamics in dissolved C compounds for the slightly, intermediately and highly decomposed mor, except for LMW-DOC where the simulated deviated from the measurements. Although the simulated LMW-DOC fitted within the range of measurements, it showed different dynamics than the measurements. The modelled CO_2-C flux was close to the measured average when computing the intermediately decomposed material, whereas the modelled flux deviated from the measurements most when computing the highly decomposed material.

There was a reasonably good fit between the modelled and measured dynamics of dissolved N fraction in the model applications for slightly, intermediately and highly decomposed mor. However, the comparison of the measured and simulated end-state of OC_{ex} and TN_{ex} pools was not unambiguous. The simulated values were higher than the measured averages in slightly, intermediately and highly decomposed mor, even though simulated variations overlapped the measured ones. In the end-state the simulated OC_{ex} was close to the highest allowed variation, whereas the simulated TN_{ex} was close to the average allowed variation. In the applications it was necessary to allow a wide range of variation in the end-state of OC_{ex} and TN_{ex} pools to produce plausible results in the dissolved fractions. Overall, there were difficulties to produce coherent results simultaneously for all measured C and N pools.

4. DISCUSSION

4.1 C and N dynamics in the experiments

Decomposition of organic matter is an important process in nutrient cycling in forests, an elementary factor in the ecosystem greenhouse gas balance and significant for nutrient transport to watercourses. The advantage of a laboratory decomposition experiment is that it permits nutrient leaching and root uptake to be excluded, thereby allowing quantification of the accumulation/release rates of decomposition products more explicitly. Accordingly, laboratory experiments create a good starting point for the development and parameterisation of process-based simulation models. The experimental results showed that decomposition rates of boreal mor clearly follow the degree of decomposition of organic matter (**I**); the fresh L layer released more NH_4^+-N and CO_2-C than the more decomposed F and H layers. Irrespective of the soil material, the CO_2-C efflux represented the largest C flux in the experiments (**I-II**). Enchytraeids especially enhanced the release of the decomposition end products.

Decomposition at a similar incubation temperature (15 °C) was studied by Park et al. (2002) using sieved temperate deciduous forest floor material. They found rates of CO_2-C, DON and DOC release similar to the rates measured from the L layer in this study (**I**). However, the highest release rates of DOC and CO_2-C for the mor as a whole were clearly lower than Park et al. (2002). On one hand, this reflects the differences in the organic matter quality; while on the other hand, the soil disturbance caused by sieving might have enhanced decomposition in Park et al. (2002). The rate of NH_4^+-N_{sol} release from mor with worms was similar to the rates reported by Park et al. (2002), although the release of DON was only 10% or less as compared with the results of Park et al. (2002). Persson and Wirén (1995) used destructive sampling and KCl extraction in their incubation experiment to study decomposition of a boreal coniferous forest floor material, and the NH_4^+-N_{ex} values in the L layer (**I**) were comparable to their results.

The results of this study are not directly comparable to field measurements as living vegetation and microbe-vegetation interactions were excluded from the experiments and the seasonal variability in environmental conditions was omitted. The net N release rates of boreal forest soils estimated in the field vary greatly within and between studies: 0-110 kg N $ha^{-1}a^{-1}$ (Persson et al. 2000), 28-45 kg N $ha^{-1}a^{-1}$ (Kjønaas and Wright 1998), 4-104 N $ha^{-1}a^{-1}$ (Andersson et al. 2002) and 18-139 kg N $ha^{-1}a^{-1}$ (Matson et al. 1992; Devito et al. 1999). As estimated in paper **I** by means of general temperature response function $f(T)=Q_{10}^{(T-b)/10}$ (Jansson and Karlberg 2001), the annual N release per hectare under field conditions at the site of this study was 24 kg $ha^{-1}a^{-1}$ for NH_4^+-N_{ex} and 4.2 kg $ha^{-1}a^{-1}$for NH_4^+-N_{sol}, using N release rates from the experiment (**I**), the thickness and bulk density values of the L, F and H layers, a 10-year dataset of air temperature (T) measured at Kangasvaara, and assuming Q_{10} equal to 3 and b equal to 15 (Persson and Wirén 1995). Based on field lysimeters and soil N pools, Piirainen (2002) calculated that 32 kg total N was mineralised annually at Kangasvaara, which is close to the estimate calculated in **I**.

The estimated CO_2-C release rate in the experiments was lower than what is measured from boreal mor layers under field conditions (Widén and Majdi 2001; Pumpanen et al. 2003; Kolari et al. 2004; Niinistö et al. 2004), but closer to rates measured in the laboratory (Andersson et al. 2000; Andersson and Nilsson 2001). In the field, CO_2-C flux is reported to vary from 43 to 461 mg m^{-2} h^{-1} in typical growing season conditions, whereas in experiment

I, it was only 29 mg $m^{-2}h^{-1}$. As stated in **I**, the difference can be explained by the absence of roots and root exudates in the laboratory. Root respiration and biodegradation of root exudates, as well as the possible priming effect by root exudates, can contribute to more than half of the observed CO_2-C flux from the soil (Kolari 2010).

The rate of net change in the intermediate product pools (DOC, DON, OC_{ex} and ON_{ex}) does not directly represent the rate of decomposition because the pools are continuously decreased by biodegradation and filled by decomposition. As the decrease in the OC_{ex} and ON_{ex} pools in **I-III** during the incubation demonstrated, biodegradation of extractable organic compounds is important in the decomposition process. Part of the organic compounds in dead organic matter are directly mineralised into end products, CO_2-C and NH_4^+-N, although a portion are first decomposed into the intermediate product pool (Fig. 5). The significance of the intermediate product pathway in decomposition can be estimated by evaluating the results against biodegradation rates (e.g. Kiikkilä et al. 2006, see Fig. 6 in **I**), although the estimation includes considerable uncertainty as the biodegradation estimate is sensitive to the division of organic compounds between the labile and refractory fractions.

The dominance of CO_2-C in total C release was expected given the aerobic incubation conditions and an incubation temperature that represents summertime conditions. At lower temperatures, the proportion of DOC can be higher (Moore et al. 2008). The partitioning of C release into DOC and CO_2-C is also controlled by substrate quality. As noted in **II**, the proportion of DOC of the total amount of released C is higher in peat than in mor. The highest proportions of DOC were released from the highly decomposed peats and the slightly decomposed *Carex-Sphagnum* peat, with the released DOC consisting mainly of HMW compounds. Older organic materials, where lignin-derived compounds comprise a high proportion of DOC, typically release larger relative amounts of DOC than younger materials (Hansson et al. 2010). In general, the initial DOC pools were larger in peat as well. Furthermore, the initial DON pool and the proportion of dissolved N in the total extractable N pool were larger in peat than in mor. In the decomposition of slightly decomposed peat, DON was the main fraction of the released dissolved N. Combined with a large storage of organic matter in peat, the results suggest that C and N are more susceptible to leaching from peatlands than from upland soils. This correlates with Kortelainen et al. (2006) and Sarkkola et al. (2009; 2012) who reported higher leaching of DOC and N in peatlands than in upland-dominated headwater catchments.

The quality of the organic matter is known to control the decomposition rate (Prescott 2010), but its contribution to the quality of the released compounds is not well known. The highest rate of DOC release, mainly in the HMW fraction, was found in mor and in the slightly decomposed peat types, and the highest rates of mineralisation (CO_2-C production) were measured for mor and the slightly decomposed *Sphagnum* peat (**II**). As expected, the lowest release rates of DOC and CO_2-C were found in the highly decomposed peats.

Low amounts of LMW compounds were to be expected due to the absence of inputs of fresh organic matter and root exudates and the rapid turnover of the LMW organic compounds (e.g. Kalbitz et al. 2003a; Kiikkilä et al. 2006). In general, the content of the LMW-DOC pool is typically very low even though the flux through this pool can be high (van Hees et al. 2005). The decrease rate of the DOC pool in the smallest size classes in **I** indicate that biodegradation was faster than the entry of DOC. Therefore, detecting the temporal changes in the labile pools would probably require more frequent sampling than conducted in this study.

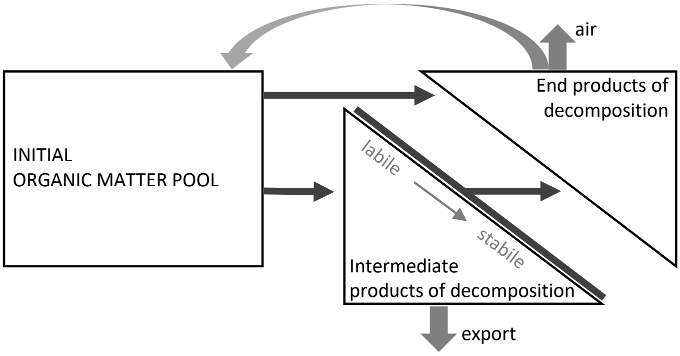

Figure 5. Simplified pathways of mineralisation from the organic matter pool to end products directly and through intermediate products. Part of the intermediate products are exported from the soil to streams. End products are mainly immobilised in the soil and in new organic matter or released to the atmosphere.

The molecular size classification method (LMW and HMW fractions) used to estimate the labile and refractory pools of organic compounds was employed in this study as it describes all DOC and DON, rather than only measuring some known compounds. If the living vegetation with fresh inputs of litter and root exudates were present, a division of DOC according to molecular weight would be too simplistic, and other methods would need to be considered (e.g. Stockmann et al. 2013).

As mentioned in **II**, the positive correlation between DOC and CO_2 release found in this study has been observed in earlier work (e.g. Neff and Hooper 2002; Moore et al. 2008), although a lack of correlation has also been reported (e.g. Park et al. 2002; Hagedorn and Machwitz 2007). The correlation between the release rates of DOC and CO_2-C indicates that the increase in the DOC pool originated from biological decomposition processes rather than from increased solubility from the adsorbed organic C pool through physical and chemical processes. It is recognised that the role of vegetation must be included in ecosystem level computation. An experiment quantifying the links between fresh C inputs, root associated microbes and the decomposition process should be the subject of future research. In addition, variability in environmental conditions should be included in future studies, as it affects DOC and DON production, biodegradation and transport and thus causes changes in the quantity and quality of these compounds.

In general, the increase in NH_4^+-N_{ex} was large compared to the increase in NH_4^+-N_{sol} in the experiments. This suggests that most of the released NH_4^+-N was adsorbed to soil particles or microorganisms attached to the particle surfaces (**III**). In contrast, the ON_{ex} pool decreased despite an increasing DON pool. The decrease in ON_{ex} is most likely explained by mineralization; the majority of the decreasing ON_{ex} appears to be transformed into NH_4^+-N_{ex}. The differences in DON release between the soil types were relatively small. The opposite changes in NH_4^+-N_{sol} between the slightly and highly decomposed peats may be explained by the degree of decomposition; the slightly decomposed peat had a clearly larger initial ON_{ex} pool, which consisted of complex molecules with a high sorption capacity (Stevenson and

Cole 1999), and therefore NH_4^+-N_{sol} in slightly decomposed peat can be effectively immobilised by sorption. As suggested in **III**, the positive rate of NH_4^+-N_{ex} release in the slightly decomposed peat indicates that there occurred N mineralization in the slightly decomposed peat too, but that the released NH_4^+-N was adsorbed on organic matter.

Altogether, the quantitative changes in the extractable compound pools were notably greater than the corresponding changes in soil solution pools, which indicates large changes in the adsorbed pools. It is still unclear whether biodegradation, for example, occurs at similar or dissimilar rates for dissolved and adsorbed forms. Therefore, both the extractable and soil solution pools, in their labile and refractory fractions, should be monitored in the future to provide a better understanding of C and N dynamics in the soil.

Enchytraeids

Enchytraeids increased mineralisation (NH_4^+-N_{sol}, NH_4^+-N_{ex} and CO_2-C release) in mor, but the effect of the worms on extractable organic compound pools was not that clear. This suggests that enchytraeids enhanced mineralization from sources other than the extractable organic compound pool, e.g. by processing dead organic matter into a more available form for microbes (Cole et al. 2000) and by excreting N-rich compounds (Didden 1993). Recent findings connected to the taxonomic changes of *C. sphagnetorum*, which define the species to be a complex of at least four cryptic species, indicate that there is still a need for further research on the feeding ecology of the worm at the species level (Gajda et al. 2017). Earlier it was shown that enchytraeids (*C. sphagnetorum*) can increase mineralization of N and C, as well as the release of dissolved organic matter (Briones et al. 1998; Cole 2000; 2002; van Vliet et al. 2004), but the effect of enchytraeids on N dynamics depends on environmental conditions and resource quality (Haimi and Siira-Pietikäinen 2003). According to Setälä and Huhta (1991), soil fauna, with enchytraeids the main group, increased the amount of NH_4^+-N_{ex} in incubated organic soil samples. In the current study, the smaller effect of enchytraeids on C release in peat was probably related to the lower population density. In all the soils in this study, the majority of worms were found in the topmost layer, and the density of worms corresponded to the numbers found in nature. In the mor and peat soils, *C. sphagnetorum* density (the majority live close to the soil surface) can vary from a few thousand up to more than 100,000 individuals m^{-2} (> 1 g m^{-2} in dry mass) (Didden 1993; Räty and Huhta 2004).

The most evident effect of enchytraeids on DOC release occurred in the HMW fraction, which may have resulted from enhanced degradation of solid organic matter and from enhanced mineralisation of LMW-DOC. The mineralisation of LMW-DOC has been observed to result in the accumulation of the refractory HMW-DOC in the soil (Kalbitz et al. 2003b, Hagedorn and Machwitz 2007). As stated in **II**, the explanations for the findings in this experimental setup remain speculative. Mineralisation probably explained the decrease in the extractable organic C pool, indicating a favourable source of C for microbes. The smaller decrease in the extractable pool in the presence of enchytraeids suggests that the presence of worms may have stimulated the microbes to utilise C from organic matter as well. This may have resulted from microbial activity in the guts and faeces of enchytraeids (Cole et al. 2000). No direct effect of the enchytraeids on the C or N in the microbial biomass (**I-III**) was found. After Hedlund and Augustsson (1995), enchytraeids can either increase or decrease the microbial biomass, depending on the intensity of grazing. The increase is enabled by both the stimulated activity of decomposer microbes and by enhanced dispersal of fungal propagules by the worms.

4.2 Modelling

The release of CO_2 and N is accounted for in ROMUL by calculating the first-order decomposition rates from the L, F and H pools separately. In addition, first-order kinetics is used to transfer mass and N from the L to F and from the F to H pools enabling quantification of the whole decomposition succession gradient from fresh litter to stable humus (Chertov et al. 2001). As the environmental conditions were kept constant in the current study, the variation in the decomposition rates relates directly to differences in the decomposing materials and thus enables the use of the results in model development.

The extended ROMUL model was able to simulate the biodegradation and sorption processes of dissolved organic C and N compounds (**IV**). The simulated dynamics of the modelled C and N compounds conformed to the measured dynamics in all applications, with an obvious contradiction between the modelled and simulated dynamics in LMW-DOC. As stated in **IV**, other approaches (than first-order decay) should be tested to provide different simulations of LMW-DOC dynamics in future applications; the biodegradation of soil OM has been observed to have a non-linear manner, which indicates that there might be better ways than first-order decay to describe the biodegradation processes (Schimel and Weintraub 2003). Further testing of the model with new data is important, as is noted in **IV,** to reveal other unjustifiable process descriptions or simplifications in the model. In the extension part, the released compounds are either sorbed or degraded into smaller molecules, and thus the model does not, for instance, account for the transition from the LMW fraction to the HMW fraction, although organic compounds retained in the soil may become enriched with aromatic structures increasing their molecular weight (Kalbitz et al. 2003b; Hagedorn and Machwitz 2007). Structural changes in the molecules affect the sorptivity and thereby further affect the modelled processes.

The assumption that the proportions of the LMW and HMW fractions are the same in the sorbed and dissolved phases was used in **IV**. This was due to the restricted data available for the dissolved phase. However, the adsorption onto soil particles is likely to differ between the LMW and HMW compounds and the compounds may replace each other on the sorption sites depending on the quality of the soil material (e.g., Han et al. 2016). Labile, litter-derived LMW compounds adsorb more easily than older HMW compounds in the organic soil layer (Fröberg et al. 2007; Müller et al. 2009). If LMW compounds replace adsorbed HMW compounds, it can increase the portion of HMW-DOC in the soil solution. Yet, the use of different parameter values in the dissolved and sorbed phases would increase the number of model parameters, which easily leads into an over-parameterisation of the model. Considering the equifinality problems that have already arisen because of the current number of parameters, the use of different fractioning for the C and N compounds in the dissolved and sorbed phases, for example, would require that a subset of parameter values would need to be fixed (**IV**).

Like the original ROMUL, the extension omits or only implicitly accounts for some of the stores or processes of decomposition, such as microbes that are included in the total organic store. In addition, changes in the observed C and N stores describe only net changes between the sampling intervals of the incubation. Changes that occur in a shorter time scale, e.g. the rapid microbial consumption of the most labile fraction, or the separate inflows and outflows of the various types of storage, are not described in a physically consistent manner in ROMUL (**IV**).

As stated in **IV**, data on the extractable pools represent the vague part of the measurements from the modelling point of view. The extraction method appeared not to produce precise estimates for the initial and end state compound stores. Therefore, a large degree of variation in the total size of the C and N pools was allowed in the GLUE analysis. Determination of the extractable stores is challenging as depending on the extraction method, estimates of varying magnitude for the different compounds are produced (e.g. Qualls 2000; Haney et al. 2001; Zsolnay 2003; Rennert et al. 2007; Hilli et al. 2008). For methodological reasons, the extracted pool typically includes relatively more labile OM than the dissolved pool (Fröberg et al. 2003; Rennert et al. 2007); the sampling of a soil solution reveals the dissolved concentrations in the largest pores, whereas the extract washes the compounds also from smaller pore spaces. However, K_2SO_4 extraction is generally considered convenient method for estimation of the potentially soluble OM (Rennert et al. 2007).

Because the model evaluation was based on a single dataset, measured in a stable environment without living vegetation, the model is not validated for use in other conditions. The rates of decomposition in the original ROMUL model are based on laboratory experiments under constant conditions with missing living vegetation as well (Chertov et al. 2001). Thus, data including a wider range of abiotic and biotic factors are necessary for the validation of the model under other conditions (**IV**).

As described in **IV**, critics state that the outcome of the GLUE method (Beven and Binley 1992) is statistically not valid because the parameterisations and simulation results are evaluated by means of subjectively defined likelihood measures (e.g. Stedinger et al. 2008). However, the use of various likelihood measures means that the GLUE method can be applied to complex mechanistic environmental models (e.g. Beven and Freer 2001; Beven et al. 2008). In **IV**, the GLUE was found to be useful, especially, for the quantification of the model’s sensitivity to changes in the uncertain parameter values. The subjectively defined likelihood measures enabled consideration of uncertainties in the data. The uncertainties corresponded to high variation in the measured concentrations of sample replicates. The GLUE procedure enabled meaningful comparison of the measurements and the modelling outcome, focusing on the structural compatibility and parameter identifiability of the model, as well as on the critical points in the underlying measurements (**IV**). As demonstrated in **IV**, utilisation of uncertainty estimation procedures is important when dealing with incomplete and uncertain data in process-based modelling. The advantage of using uncertainty estimation procedures in ecological modelling has been demonstrated also by Wetterstedt and Ågren (2011), who applied GLUE in a litter decomposition study with data on litter respiration rates that exhibited a high degree of variability.

4.3 Implications for the export of C and N

It is important to integrate decomposition models with solute transport models due to the connection between terrestrial and aquatic ecosystem C balance (e.g. Cole et al. 2007; Jonsson et al. 2007; Tranvik et al. 2009; Battin et al. 2008; Rasilo et al. 2015). Terrestrial C, which reach surface waters often in dissolved form, can play an essential role in regional C balance, as demonstrated by Downing (2010) and Einola et al. (2011). Huotari et al. (2011) showed that terrestrially fixed C emissions from a boreal lake can cover up to 10% of total ecosystem productivity within a catchment. In contrast to C, N transport from a boreal forest is less remarkable because of the closed N cycle and the high demand by plants and microbes (e.g. Piirainen 2002; Piirainen et al. 2002; Korhonen et al. 2013).

Despite the small N transport from a forest, the terrestrial N fluxes can be large, which should be included in a simulation of the catchment N balance. Laurén et al. (2005) demonstrated that without measuring the largest N fluxes, large uncertainties occur when the modelled N balance is validated against N load data. The extended version of ROMUL and its evaluation against the detailed decomposition data increases the understanding of the complex C and N interactions during decomposition.

Combining a decomposition model with a solute transport model needs the simultaneous consideration of C and N release, and the quality, sorption and biodegradation of the compounds, which are simulated in the extended version of ROMUL. Yet, ROMUL is applicable in forested upland sites in a boreal or temperate climate only (Chertov et al. 2001). Modelling decomposition in peatlands would require other approach because of the anaerobic environment that affect the decomposition process and cause CH_4 and N_2O emissions (e.g. Zhang et al. 2002). Because peatlands are connected to high C exports (e.g. Kortelainen et al. 2006, Laudon et al. 2011), it is important to link peat decomposition with combined decomposition-solute transport models. In addition, the use of models describing preferential flow is necessary when simulating subsurface water flows and solute transport in forested areas (e.g. Laine-Kaulio 2011). A complete approach for a boreal forested catchment thereafter includes modelling plant nutrient uptake and the microbial C and N use, together with flow and solute transport. There are advanced OM decomposition models (e.g. Chertov et al. 2001) and subsurface water solute transport models (e.g. Šimůnek et al. 2008), although models that describe both the decomposition processes and solute transport of OM are still few (e.g. Laurén et al. 2005) and are missing a description of the detailed fractions of organic C and N.

The experiments showed the impact of enchytraeids, which could be added into model applications as suggested in **I** by combining the results with information of temporal enchytraeid population dynamics. The decomposition rate for the low-population period (summer droughts) should be closer to the treatment without enchytraeids and increase towards the levels of the treatment with enchytraeids when the population increases towards the autumn (Nurminen 1967). Furthermore, forest management practices can cause a temporary decrease in the enchytraeid population (Huhta 1976; Siira-Pietikäinen et al. 2001), which should be accounted for in the modelling as well.

The proportion of the surface water C that originates from terrestrial systems can be an essential factor in the catchment C balance. As stated in **I,** it is necessary to consider the quality of the intermediate products of decomposition that are susceptible to further adsorption, biodegradation and transport in order to simulate both catchment scale C and N fluxes and leaching to water streams. Lepistö (1994) reported the mean residence time of water in a small boreal forested catchment to be eight months, which is significantly longer than the half-life of the labile OC and ON fractions (Kalbitz et al. 2003a; Kiikkilä et al. 2006). This means that even though up to 15% of the DOC released through decomposition was in the form of LMW-DOC in the current experiments, it is likely that only a minor share of it could reach the watercourse and the majority would instead be converted into CO_2-C by biodegradation. Thus, HMW-DOC becomes enriched in the export towards the water body and the LMW-DOC found in the watercourses, therefore, must originate mainly from areas close to the watercourse, which are often peatlands. From more remote areas, LMW compounds can be exported to surface waters only through preferential flow paths during intensive subsurface stormflow events (e.g. Laine-Kaulio 2011).

The “Numerical discussion” in paper **II** shows how the experimental results can be simply upscaled to reflect DOC quality and quantity in watercourses. Combining the results with existing literature including data regarding the average properties of head water catchments in Central Finland (Korkalainen et al. 2007), and a biodegradation equation with parameters (Kalbitz et al. 2003a), transport time, role of biodegradation in the transport and the DOC export load to watercourse can be produced. By means of more complex initial information, such as water flow path characteristics of the catchment, hydraulic characteristics, soil types, and experimental parameters, more precise computational remarks can be obtained (Palviainen et al. 2016). The calculation in **II** indicates that enchytraeids can increase the DOC export load from 14 to 20 ha^{-1} yr^{-1}. Assuming 0.1 g m^{-2} enchytraeids in dry mass (i.e. 1 kg ha^{-1}), the result emphasises the magnitude of impact of these small worms on DOC export. The calculation shows how the decomposing materials i.e. mor and peat, and the proportion of the C released as CO_2, LMW-DOC and HMW-DOC, play an important role in DOC export to water courses, and ultimately in the ecosystem C balance. Enchytraeid worms can substantially enhance DOC leaching from terrestrial ecosystems to watercourses.

5. CONCLUSIONS

This study estimated net decomposition for the most common boreal organic soil types and separately for the L, F and H layers of boreal mor, and also examined the influence of enchytraeids on the release rates. The results indicated that both the quality of organic material and the presence of enchytraeids control the rate of C and N release and the quality of the decomposition products in the boreal forest floor. The novelty of the study is the description of the dissolved organic compounds as intermediate decomposition products, which are then partitioned into LMW and HMW fractions. The proportion of the HMW fraction increased during decomposition. Based on the combined results of the experiments and modelling, it is evident that the intermediate products in the adsorption pool biodegrade effectively, and the role of soil animals and other biotic factors is important in this process. Enchytraeids enhanced the decomposition, which was seen as increased release of NH_4^+-N, CO_2-C and DOC in mor soil types. Therefore, it is reasonable to suggest that a functional terrestrial soil fauna can extend its impact from the soil to aquatic environments, which affects the C balance at the ecosystem level as well. Furthermore, if the enchytraeid population density changes in the future, e.g. due to climate change, it will influence the C and N dynamics in the soil.

The results suggest that the higher DOC and DON leaching observed in peatlands results from higher relative DOC and DON release in peat than in mor. Because several types of mor and peat both exist in boreal forested catchments, the C and N release rates for the two types of mor and the four types of peat provided in this study will enable a more realistic description of decomposition outputs. This will enhance modelling and allow upscaling of the results from a soil-sample scale to catchment scales. The positive correlation between the DOC and CO_2-C release rates indicates a biological control of DOC release in organic soil layers. However, because the proportion of intermediate products in total decomposition is also affected by ambient soil conditions, the abiotic controls of decomposition, such as temperature and soil moisture, should be subjects for further study.

The extended version of the ROMUL model, within the framework of this study, was found to be capable of simulating the biodegradation and sorption processes of C and N compounds. The simulated temporal dynamics followed the measured dynamics of all dissolved compounds with the exception of LMW-DOC. The variation was large in the experimental results, and neither statistical examination nor process-based modelling could explain the variation when all measured variables were investigated at the same time. This poses a challenge for model development but addresses the necessity to measure different processes simultaneously when developing large ecosystem models that combine terrestrial and aquatic systems. The GLUE procedure was able to incorporate the variation and uncertainty in the measurements and parameter values in the modelling results, and to assess the parameter identifiability and structural compatibility of the model in the presence of uncertainty. Additional data and the means to fix a subset of parameter values are necessary to enhance the identifiability of parameter values and to enable further analyses of the model structure. Determining credible estimates for the extractable pools is particularly important because the simulation results are controlled by these pools together with the L, F and H composition of the mor material. Uncertainty in the estimates of the extractable pools reflects the complexity of the organic compound structures and the large variability of the OM surfaces where these molecules are sorbed. To improve the model, the impact of abiotic factors, as well as the interactions between living vegetation, the soil food web and organic matter should be investigated. If linked with models on subsurface flow and solute transport, the model could provide an up-to-date description of the solute transport of C and N compounds in boreal forest soils.

REFERENCES

Abrahamsen, G. (1972). Ecological study of *Enchytraeidae* (*Oligochaeta*) in Norwegian coniferous forest soils. Pedobiologia 12: 26-82.

Ahtiainen, M., Huttunen, P. (1999). Long-term effects of forestry managements on water quality and loading in brooks. Boreal Environment Research 4: 101-114.

Andersson, S., Nilsson, S.I. (2001). Influence of pH and temperature on microbial activity, substrate availability of soil-solution bacteria and leaching of dissolved organic carbon in a mor humus. Soil Biology and Biochemistry 33: 1181-1191. https://doi.org/10.1016/S0038-0717(01)00022-0

Andersson, S., Nilsson, I., Saetre, P. (2000). Leaching of dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) in a mor humus as affected by temperature and pH. Soil Biology and Biochemistry 32: 1-10. https://doi.org/10.1016/S0038-0717(99)00103-0

Andersson, C., Berggren, D., Nilsson, I. (2002). Indices for nitrogen status and nitrate leaching from Norway spruce (*Picea abies* (L.) Karst.) stands in Sweden. Forest Ecology and Management 157: 39-53. https://doi.org/10.1016/S0378-1127(00)00651-4

Bardgett, R.D., Chan, K.F. (1999). Experimental evidence that soil fauna enhance nutrient mineralization and plant nutrient uptake in montane grassland ecosystems. Soil Biology and Biochemistry 31: 1007-1014. https://doi.org/10.1016/S0038-0717(99)00014-0

Battin, T.J., Luyssaert, S., Kaplan, L.A., Aufdenkampe, A.K., Richter, A., Tranvik, L.J. (2008). The boundless carbon cycle. Nature Geoscience 2: 95-100. https://doi.org/10.1038/ngeo618

Berg, B., McClaugherty, C. (2008). Plant litter, decomposition, humus formation, carbon sequestration. 2nd ed. Springer-Verlag, Berlin Heidelberg. 338 p. ISBN: 978-3-540-74922-6

Beven, K. (2008). Environmental Modelling: An Uncertain Future? Routledge, London. 328 p. ISBN: 978-0-415-46302-7

Beven, K., Binley, A. (1992). The future of distributed models: model calibration and uncertainty prediction. Hydrological Processes 6: 279-298. https://doi.org/10.1002/hyp.3360060305

Beven, K., Freer, J. (2001). Equifinality, data assimilation, and uncertainty estimation in mechanistic modelling of complex environmental systems using the GLUE methodology. Journal of Hydrology 249: 11-29. https://doi.org/10.1016/S0022-1694(01)00421-8

Beven, K., Smith, P., Freer, J. (2008). So just why would a modeller choose to be incoherent. Journal of Hydrology 354: 15-32. https://doi.org/10.1016/j.jhydrol.2008.02.007

Briones, M.J., Ineson, P., Poskitt, J. (1998). Climate change and *Cognettia sphagnetorum*: effects on carbon dynamics in organic soils. Functional Ecology 12: 528-535. https://doi.org/10.1046/j.1365-2435.1998.00218.x

Briones, M.J., Ostle, N.J., Garnett, M.H. (2007). Invertebrates increase the sensitivity of non-labile soil carbon to climate change. Soil Biology and Biochemistry 39: 816-818. https://doi.org/10.1016/j.soilbio.2006.09.007

Brookes P.C., Landman A., Pruden G., Jenkinson D.S. (1985). Chloroform fumigation and the release of soil nitrogen: A rapid direct extraction method to measure microbial biomass nitrogen in soil. Soil Biology and Biochemistry 17: 837-842. https://doi.org/10.1016/0038-0717(85)90144-0

Cajander, A.K. (1949). Forest types and their significance. Acta Forestalia Fennica 56: 1-72.

Chertov, O.G., Bhatti, G.S., Komarov, A.S., Mikhailov, A.V., Bykhovets, S.S. (2009). Influence of climate change, fire and harvest on the carbon dynamics of black spruce in Central Canada. Forest Ecology and Management 257 (3): 941-950. https://doi.org/10.1016/j.foreco.2008.10.038

Chertov, O.G., Komarov, A.S. (1997). SOMM: A model of soil organic matter dynamics. Ecological Modelling 94: 177-189. https://doi.org/10.1016/S0304-3800(96)00017-8

Chertov, O.G., Komarov, A.S., Nadporozhskaya, M., Bykhovets, S.S., Zudin, S.L. (2001). ROMUL - A model of forest soil organic matter dynamics as a substantial tool for forest ecosystem modelling. Ecological Modelling 138: 289-308. https://doi.org/10.1016/S0304-3800(00)00409-9

Cole, L., Bradgett, R.D. & Ineson, P. (2000). Enchytraeid worms (Oligochaeta) enhance mineralization of carbon in organic upland soil. European Journal of Soil Science 51: 185-192. https://doi.org/10.1046/j.1365-2389.2000.00297.x

Cole, L., Bardgett, R.D., Ineson, P., Hobbs, P.J. (2002). Enchytraeid worm (Oligochaeta) influences on microbial community structure, nutrient dynamics and plant growth in blanket peat subjected to warming. Soil Biology and Biochemistry 34: 83-92. https://doi.org/10.1016/S0038-0717(01)00159-6

Cole, J.J., Prairie, Y.T., Caraco, N.F., McDowell, W.H., Tranvik, L.J., Striegl, R.G., Duarte, C.M, Kortelainen, P., Downing, J.A., Middelburg, J.J., Melack J. (2007). Plumbing the global carbon cycle: integrating inland waters into the terrestrial carbon budget. Ecosystems 10 (1): 172-185. https://doi.org/10.1007/s10021-006-9013-8

Devito, K. J., Westbrook, C. J., Schiff, S. L. (1999). Nitrogen mineralization and nitrification in upland and peatland forest soils in two Canadian Shield catchments. Canadian Journal of Forest Research 29: 1793-1804. https://doi.org/10.1139/x99-148

Didden, W.A.M. (1993). Ecology of terrestrial Enchytraeidae. Pedobiologia 37: 2-29.

Downing, J.A. (2010). Emerging global role of small lakes and ponds: little things mean a lot. Limnetica 29: 9-23.

Einola, E., Rantakari, M., Kankaala, P., Kortelainen, P., Ojala, A., Pajunen, H., Mäkelä, S., Arvola, L. (2011). Carbon pools and fluxes in a chain of five boreal lakes: a dry and wet year comparison. Journal of Geophysical Research: Biogeosciences 116: G03009. https://doi.org/10.1029/2010JG001636

FAO. (1988). Food and Agriculture Organization FAO/UNESCO Soil Map of the World (revised legend). World Resources Report 60, Rome. Reprinted as Technical Paper 20, 1989. ISRIC, Wageningen. 138 p.

Fischer, H., Meyer, A., Fischer, K., Kuzyakov, Y. (2007). Carbohydrate and amino acid composition of dissolved organic matter leached from soil. Soil Biology and Biochemistry 39: 2926-2935. https://doi.org/10.1016/j.soilbio.2007.06.014

Finér, L., Ahtiainen, M., Mannerkoski, H., Möttönen, V., Piirainen, S., Seuna, P., Starr, M. (1997). Effects of harvesting and scarification on water and nutrient fluxes. A description of catchment and methods, and results from the pretreatment calibration period. Finnish Forest Research Institute, Research Papers 648. 38 p. ISBN 951-40-1575-4.

Finér, L., Mannerkoski, M., Piirainen, S., Starr, M. (2003). Carbon and nitrogen pools in an old-growth, Norway spruce mixed forest in eastern Finland and changes associated with clear-cutting. Forest Ecology and Management 174: 51-63. https://doi.org/10.1016/S0378-1127(02)00019-1

Fox, O., Vetter, S., Ekschmitt, K., Wolters, V. (2006). Soil fauna modifies the recalcitrance-persistence relationship of soil carbon pools. Soil Biology and Biochemistry 38: 1353-1363. https://doi.org/10.1016/j.soilbio.2005.10.014

Fröberg, M., Berggren Kleja, D., Hagedorn, F. (2007). The contribution of fresh litter to dissolved organic carbon leached from a coniferous forest floor. European Journal of Soil Science 58: 108-114. https://doi.org/10.1111/j.1365-2389.2006.00812.x

Gajda, L., Gorgón, S., Urbisz, A. (2017). Food preferences of enchytraeids. Pedobiologia 63: 19-36. https://doi.org/10.1016/j.pedobi.2017.06.002

Ge, Z.M., Zhou, X., Kellomäki, S., Wang, K.Y., Peltola, H., Väisänen, H., Strandman, H. (2010). Effects of changing climate on water and nitrogen availability with implications on the productivity of Norway spruce stands in southern Finland. Ecological Modelling 221: 1731-1743. https://doi.org/10.1016/j.ecolmodel.2010.03.017

Hagedorn, F., Machwitz, M. (2007). Controls on dissolved organic matter leaching from forest litter grown under elevated atmospheric CO_2. Soil Biology and Biochemistry 39: 1759-1769. https://doi.org/10.1016/j.soilbio.2007.01.038

Haimi, J., Siira-Pietikäinen, A. (2003). Activity and role of enchytraeid worm *Cognettia sphagnetorum* (Vejf.) (Oligochaeta: Enchytraeidae) in organic and mineral forest soil. Pedobiologia 47: 303-310.

Han, L., Sun, K., Jin, J., Xing, B. (2016). Some concepts of soil organic carbon characteristics and mineral interactions from a review of literature. Soil biology and Biochemistry 94: 107-121. https://doi.org/10.1016/j.soilbio.2015.11.023

Haney, R.L., Franzluebbers, A.J., Hons, F.M., Hossner, L.R., Zuberer, D.A. (2001). Molar concentration of K_2SO_4 and soil pH affect estimation of extractable C with chloroform fumigation-extraction. Soil Biology and Biochemistry 33: 1501-1507. https://doi.org/10.1016/S0038-0717(01)00065-7

Hansson, K., Berggren Kleja, D., Kalbitz, K., Larsson, H. (2010). Amounts of carbon mineralized and leached as DOC during decomposition of Norway spruce needles and fine roots. Soil Biology and Biochemistry 42: 178-185. https://doi.org/10.1016/j.soilbio.2009.10.013

Hedlund K., Augustsson A. (1995). Effects of enchytraeids grazing on fungal growth and respiration. Soil Biology and Biochemistry 27: 905-909. https://doi.org/10.1016/0038-0717(95)00016-8

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 Environment Research 13: 107-119.

Huhta, V. (1976). Effects of clear-cutting on numbers, biomass and community respiration of soil invertebrates. Annales Zoologici Fennici 13: 63-80.

Huhta V., Wright D.H., Coleman D.C. (1989). Characteristics of defaunated soil. I. A comparison of three techniques applied to two different forest soils. Pedobiologia 33: 415-424.

Huotari, J., Ojala, A., Peltomaa, E., Nordbo, A., Launiainen, S., Pumpanen, J., Rasilo, T., Hari, P., Vesala, T. (2011). Long-term direct CO_2 flux measurements over a boreal lake: five years of eddy covariance data. Geophysical Research Letters 38: L18401. doi:10.1029/2011GL048753

Jansson, P.-E., Karlberg, L. (2001). Coupled heat and mass transfer model for soil-plant-atmosphere systems. Royal Institute of Technology, Department of Civil and Environmental Engineering, Stockholm. 321 p.

Jonsson, A., Algesten, G., Bergström, A.K., Bishop, K., Sobek, S., Tranvik, L.J., Jansson, M. (2007). Integrating aquatic carbon fluxes in a boreal catchment carbon budget. Journal of Hydrology 334 (1-2): 141-150.

Kalbitz, K., Kaiser, K. (2008). Contribution of dissolved organic matter to carbon storage in forest mineral soils. Journal of Plant Nutrition and Soil Science 171: 52-60. https://doi.org/10.1002/jpln.200700043

Kalbitz, K., Schmerwitz, J., Schwesig, D., Matzner, E. (2003a). Biodegradation of soil-derived dissolved organic matter as related to its properties. Geoderma 113: 273-291. https://doi.org/10.1016/S0016-7061(02)00365-8

Kalbitz, K., Schwesig, D., Schmerwitz, J., Kaiser, K., Haumaier, L., Glaser, B., Ellerbrock, R., Leinweber, P. (2003b). Changes in properties of soil-derived dissolved organic matter induced by biodegradation. Soil Biology and Biochemistry 35: 1129-1142. https://doi.org/10.1016/S0038-0717(03)00165-2

Kellomäki, S., Väisänen, H. (1997). Modelling the dynamics of the forest ecosystem for climate change studies in the boreal conditions. Ecological Modelling 97: 121-140. https://doi.org/10.1016/S0304-3800(96)00081-6

Kiikkilä, O., Kitunen, V., Smolander, A. (2006). Dissolved soil organic matter from surface horizons under birch and conifers: Degradation in relation to chemical characteristics. Soil Biology and Biochemistry 38: 737-746. https://doi.org/10.1016/j.soilbio.2005.06.024

Kiikkilä, O., Kanerva S., Kitunen V., Smolander A. (2014). Soil microbial activity in relation to dissolved organic matter properties under different tree species. Plant and Soil 377: 169-177. http://dx.doi.org/10.10/s11104-013-1988-2

Kirchner, J.W. (2006). Getting the right answers for the right reasons: linking measurements, analyses, and models to advance the science of hydrology. Water Resources Research 42: W03S04. https://doi.org/10.1029/2005WR004362

Kjønaas, O. J., Wright, R. F. (1998). Nitrogen leaching from N limited forest ecosystems: the MERLIN model applied to Gårdsjön, Sweden. Hydrology and Earth System Sciences 2: 415-429. https://doi.org/10.5194/hess-2-415-1998

Kolari, P., Pumpanen, J., Rannik, Ü., Ilvesniemi, H., Hari, P., Beringer, F. (2004). Carbon balance of different aged Scots pine forests in southern Finland. Global Change Biology 10: 1106-1119. https://doi.org/10.1111/j.1529-8817.2003.00797.x

Kolari, P. (2010). Carbon balance and component CO2 fluxes in boreal Scots pine stands. Dissertationes Forestales 99. 43 p. https://doi.org/10.14214/df.99

Komarov, A.S., Chertov, O.G., Zudin, S.L., Nadporozhskaya, M., Mikhailov, A.V., Bykhovets, S., Zudina, E., Zoubkova, E. (2003). EFIMOD 2 – a model of growth and cycling of elements in boreal forest ecosystems. Ecological Modelling 170: 373-392. https://doi.org/10.1016/S0304-3800(03)00240-0

Komarov, A.S., Shanin, V.N. (2012). Comparative analysis of the influence of climate change and nitrogen deposition on carbon sequestration in forest ecosystems in European Russia: simulation modelling approach. Biogeoscience 9: 1-14. https://doi.org/10.5194/bg-9-4757-2012

Korhonen, J.F.J., Pihlatie, M., Pumpanen, J., Aaltonen, H., Hari, P., Levula, J., Kieloaho, A.-J., Nikinmaa, E., Vesala, T., Ilvesniemi, H. (2013). Nitrogen balance of a boreal Scots pine forest. Biogeoscience 10: 1083-1095. https://doi.org/10.5194/bg-10-1083-2013

Korkalainen, T., Laurén, A., Kokkonen, T. (2007). A GIS-based analysis of catchment properties within a drumlin field. Boreal Environment Research 12: 289-500.

Kortelainen, P., Mattsson, T., Finér, L., Ahtiainen, M., Saukkonen, S., Sallantaus, T. (2006). Controls on the export of C, N, P and Fe from undisturbed boreal catchments, Finland. Aquatic Sciences 68: 453-468. https://doi.org/10.1007/s00027-006-0833-6

Laakso, J., Setälä, H. (1999). Sensitivity of primary production to changes in the architecture of belowground food webs. Oikos 87: 57-64. https://doi.org/10.2307/3546996

Laine-Kaulio, H. (2011). Development and analysis of a dual-permeability model for subsurface stormflow and solute transport in a forested hillslope. Aalto University publication series. Doctoral Dissertations 71. 166 p. ISBN: 978-952-60-4245-9

Laudon, H., Berggren, M., Ågren, A., Buffam, I., Bishop, K., Grabs, T., Jansson, M., Köhler, S. (2011). Patterns and dynamics of dissolved organic carbon (DOC) in boreal streams: the role of processes, connectivity, and scaling. Ecosystems 14: 880-893. https://doi.org/10.1007/s10021-011-9452-8

Laurén, A., Finér, L., Koivusalo, H., Kokkonen, T., Karvonen, T., Kellomäki, S., Mannerkoski, H., Ahtiainen, M. (2005). Water and nitrogen processes along a typical water flowpath and streamwater exports from a forested catchment and changes after clear-cutting: a modelling study. Hydrology and Earth System Sciences 9 (6): 657-674.

Laurén, A., Koivusalo, H., Ahtikoski, A., Kokkonen, T., Finér, L. (2007). Water protection and buffer zones: how much does it cost to reduce nitrogen load in a forest cutting? Scandinavian Journal of Forest Research 22 (6): 537-544. https://doi.org/10.1080/02827580701614487

Laurén, A., Sikanen, L., Asikainen, A., Koivusalo, H., Palviainen, M., Kokkonen, T., Kellomäki, S., Finér, L. (2008). Impacts of logging residue and stump removal on nitrogen export to astream: a modelling approach. Scandinavian Journal of Forest Research 23 (3): 227-235.

Lepistö A. (1994). Areas contributing to generation of runoff and nitrate leaching as estimated by empirical isotope methods and TOPMODEL. Aqua Fennica 24(2): 103-120.

Lindén A., Heinonsalo J., Buchmann N., Oinonen M., Sonninen E., Hilasvuori E. Pumpanen, J. (2014). Contrasting effects of increased carbon input on boreal SOM decomposition with and without presence of living root system of *Pinus sylvestris* L. Plant and Soil 377: 145-158. https://doi.org/10.1007/s11104-013-1987-3

Marschner, B., Kalbitz, K. (2003). Controls of bioavailability and biodegradability of dissolved organic matter in soils. Geoderma 113: 211-235. https://doi.org/10.1016/S0016-7061(02)00362-2

Martinsson, S., Rota, E., Erséus, C. 2015. Revision of Cognettia (Clitellata, Enchytraeidae): reestablishment of *Chamaedrilus* and description of cryptic species in the *sphagnetorum* complex. Systematics and Biodiversity 13: 257-277. https://doi.org/10.1080/14772000.2014.986555

Matala, J., Hynynen, J., Miina, J., Ojansuu, R., Peltola, H., Sievänen, R., Väisänen, S., Kellomäki, S. (2003). Comparison of a physiological model and a statistical model for prediction of growth and yield in boreal forests. Ecological Modelling 16: 95-116. https://doi.org/10.1016/S0304-3800(02)00297-1

Matson, P.A., Gower, S.T., Volkman, C., Billow, C., Grier, C.C. (1992). Soil nitrogen cycling and nitrous oxide flux in a Rocky Mountain Douglas-fir forest: effects of fertilization, irrigation and carbon addition. Biogeochemistry 18: 101-117. https://doi.org/10.1007/BF00002705

Mattsson, T., Finér, L., Kortelainen, P., Sallantaus, T. (2003). Brook water quality and background leaching from unmanaged forested catchments in Finland. Water, Air, and Soil Pollution 147: 275-297. https://doi.org/10.1023/A:1024525328220

Moore, T.R., Paré, D. Boutin, R. (2008). Production of dissolved organic carbon in Canadian forest soils. Ecosystems 11: 740-751. https://doi.org/10.1007/s10021-008-9156-x

Müller, M., Alewell, C., Hagedorn, F. (2009). Effective retention of litter-derived dissolved organic carbon in organic layers. Soil Biology and Biochemistry 41: 1066-1074. https://doi.org/10.1016/j.soilbio.2009.02.007

Münster, U., Salonen, K., Tulonen, T. (1999). Decomposition. In: Keskitalo, J., Eloranta, P. (eds.), Limnology of humic waters Backhuys Publishers, Leiden, The Netherlands. pp. 225-264. ISBN 90-5782-029-3

Niinistö, S., Silvola, J., Kellomäki, S. (2004). Soil CO_2 efflux in boreal pine forest under atmospheric CO_2 enrichment and air warming. Global Change Biology 10: 1363-1376. https://doi.org/10.1111/j.1365-2486.2004.00799.x

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(9): 872-884. https://doi.org/10.1046/j.1365-2486.2002.00517.x

Nurminen, M. (1967). Ecology of enchytraeids (Oligochaeta) in Finnish coniferous forest soil. Annales Zoologici Fennici 4: 147-157.

O’Connor, F.B. (1962). The extraction of Enchytraeidae from soil. In: Murphy, P.W. (ed.). Progress in Soil Zoology. Butterworth, London. pp. 279–285.

Paavolainen L., Smolander A. (1998). Nitrification and denitrification in soil from a clear-cut Norway spruce (*Picea abies*) stand. Soil Biology and Biochemistry 30: 775-781. https://doi.org/10.1016/S0038-0717(97)00165-X

Palviainen, M., Finér, L., Kurka, A.-M., Mannerkoski, H., Piirainen, S., Starr, M. (2004). Decomposition and nutrient release from logging residues after clear-cutting of mixed boreal forest. Plant and Soil 263: 53-67. https://doi.org/10.1023/B:PLSO.0000047718.34805.fb

Palviainen, M., Finér, L., Piirainen, S., Starr, M. (2005). Changes in above- and below-ground biomass and nutrient pools of ground vegetation after clear-cutting of a mixed boreal forest. Plant Soil 275: 157-167. https://doi.org/10.1007/s11104-005-1256-1

Palviainen, M., Laurén, A., Launiainen, S., Piirainen, S. (2016). Predicting the export and concentrations of organic carbon, nitrogen and phosphorus in boreal lakes by catchment characteristics and land use: A practical approach. Ambio 45(8): 933-945. https://doi.org/10.1007/s13280-016-0789-2

Park, J.H., Kalbitz, K., Matzner, E. (2002). Resource control on the production of dissolved organic carbon and nitrogen in a deciduous forest floor. Soil Biology and Biochemistry 34: 813-822. https://doi.org/10.1016/S0038-0717(02)00011-1

Paul, E. A. (2016). The nature and dynamics of soil organic matter: Plant inputs, microbial transformations, and organic matter stabilization. Soil Biology and Biochemistry 98: 109-126. https://doi.org/10.1016/j.soilbio.2016.04.001

Perakis S.S., Hedin L.O. (2002). Nitrogen loss from unpolluted American forests mainly via dissolved organic compounds. Nature 415: 416-419. https://doi.org/10.1038/415416a

Persson, T., Rudebeck, A., Jussy, J. H., Colin-Belgrand, M., Priemé, A., Dambrine, E., Karlsson, P. S., Sjöberg, R. M. (2000). Soil nitrogen turnover, mineralization, nitrification and denitrification in European forest soils. In: Schulze, E.D. (ed.). Carbon and nitrogen cycling in European forest ecosystems. Ecological studies (Analysis and Synthesis) 142. Springer, Berlin, Heidelberg. pp. 297-311. https://doi.org/10.1007/978-3-642-57219-7_14

Persson, T., Wirén, A. (1995). Nitrogen mineralization and potential nitrification at different depths in acid forest soils. Plant and Soil 168-169: 55-65. https://doi.org/10.1007/BF00029313

Piirainen, S., Finér, L., Starr, M. (1998). Canopy and soil retention of nitrogen deposition in a mixed boreal forest in eastern Finland. Water, Air, and Soil Pollution 105: 165-174. https://doi.org/10.1023/A:1005052030998

Piirainen, S. (2002). Nutrient fluxes through a boreal coniferous forest and the effects of clear-cutting. Finnish Forest Research Institute, Research Papers 859. 50 p. ISBN 951-40-1839-7

Piirainen, S., Finér, L., Mannerkoski, M., Starr, M. (2002). Effects of forest clear-cutting on carbon and nitrogen fluxes through podzolic soil horizons. Plant and Soil 239: 301-311. https://doi.org/10.1023/A:1015031718162

Pirinen, P., Simola, H., Aalto, J., Kaukoranta, J.-P., Karlsson, P., Ruuhela, R. (2012). Climatological statistics of Finland 1981–2010. Finnish Meteorological Institute. Reports 2012:1. Helsinki. 96 p. ISBN: 978-951-697-765-5

Potila H., Sarjala T. (2004). Seasonal fluctuation in microbial biomass and activity along a natural nitrogen gradient in a drained peatland. Soil Biology and Biochemistry 36: 1047-1055. https://doi.org/10.1016/j.soilbio.2004.02.014

Prescott, C.E. (2010). Litter decomposition: what controls it and how we can alter it to sequester more carbon in forest soils? Biogeochemistry 101: 133-149. https://doi.org/10.1007/s10533-010-9439-0

Pumpanen, J., Ilvesniemi, H., Perämäki, M., Hari, P. (2003). Seasonal patterns of soil CO_2 efflux and soil air CO_2 concentration in a Scots pine forest: comparison of two chamber techniques. Global Change Biology 9: 371-382. https://doi.org/10.1046/j.1365-2486.2003.00588.x

Qualls, R. (2000). Comparison of the behavior of soluble organic and inorganic nutrients in forest soils. Forest Ecology and Management 138: 29-50. https://doi.org/10.1016/S0378-1127(00)00410-2

Qualls, R. G., Richardson, C. J. (2003). Factors controlling concentration, export, and decomposition of dissolved organic nutrients in the Everglades of Florida. Biogeochemistry 62: 197-229. https://doi.org/10.1023/A:1021150503664

Rasilo, T., Ojala, A., Huotari, J., Starr, M., Pumpanen, J. (2015). Concentrations and quality of DOC along the terrestrial-aquatic continuum in a boreal forested catchment. Freshwater Science 34(2): 440-455. https://doi.org/10.1086/680682

Regina, K., Nykänen, H., Silvola, J., Martikainen, P.J. (1996). Fluxes of nitrous oxide from boreal peatlands as affected by peatland type, water table level and nitrification capacity. Biogeochemistry 35: 401-418. https://doi.org/10.1007/BF02183033

Rennert, T., Gockel, K.F., Mansfeldt, T. (2007). Extraction of water-soluble organic matter from mineral horizons of forest soils. Journal of Plant Nutrition and Soil Science 170: 514-521. https://doi.org/10.1002/jpln.200625099

Räty, M. Huhta, V. (2004). Communities of Enchytraeidae (Oligochaeta) in planted birch stands as compared with natural forests in central Finland. Biology and Fertility of Soils 40: 413-420. https://doi.org/10.1007/s00374-004-0791-x

Salazar, O., Casanova, M., Kätterer, T. (2011). The impact of agroforestry combined with water harvesting on soil carbon and nitrogen stocks in central Chile evaluated using the

ICBM/N model. Agriculture, Ecosystems & Environment 140: 123-136. https://doi.org/10.1016/j.agee.2010.11.019

Sarkkola, S., Koivusalo, H., Laurén, A., Kortelainen, P., Mattsson, T., Palviainen, M., Piirainen, S., Starr, M. Finér, L. (2009). Trends in hydrometeorological conditions and stream water organic carbon in boreal forested catchments. Science of the Total Environment 408: 92-101. https://doi.org/10.1016/j.scitotenv.2009.09.008

Sarkkola S., Nieminen M., Koivusalo H., Laurén A., Kortelainen P., Mattsson T., Palviainen M., Piirainen S., Starr S. Finér L. (2012). Trends in concentrations and export of nitrogen in boreal forest streams. Boreal Environment Research 17: 85-101.

Schimel, J.P., Weintraub, M.N. (2003). The implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: a theoretical model. Soil Biology and Biochemistry 35: 549-563. https://doi.org/10.1016/S0038-0717(03)00015-4

Schulten H.-R., Schnitzer M. (1998). The chemistry of soil organic nitrogen: a review. Biology and Fertility of Soils 26: 1-15. https://doi.org/10.1007/s003740050335

Setälä, H., Haimi, J., Huhta, V. (1988). A microcosm study on the respiration and weight loss in birch litter and raw humus as influenced by soil fauna. Biology and Fertility of Soils 5: 282-287. https://doi.org/10.1007/BF00262132

Setälä H., Huhta V. (1991). Soil fauna increase *Betula pendula* growth: Laboratory experiments with coniferous forest floor. Ecology 72: 665-671. https://doi.org/10.2307/2937206

Shanin, V.N., Komarov, A.S., Khoraskina, Yu.S., Bykhovets, S.S., Linkosalo, N., Mäkipää, R. (2013). Carbon turnover in mixed stands: modelling possible shifts under climate change. Ecological Modelling 251: 232-245. https://doi.org/10.1016/j.ecolmodel.2012.12.015

Siira-Pietikäinen, A., Pietikäinen, J., Fritze, H., Haimi, J. (2001). Short-term responses of soil decomposer communities to forest management: clear felling versus alternative forest harvesting methods. Canadian Journal of Forest Research 31: 88-99. https://doi.org/10.1139/cjfr-31-1-88

Silvan, N., Laiho, R., Vasander, H. (2000). Changes in mesofauna abundance in peat soils drained for forestry. Forest Ecology and Management 133: 127-133. https://doi.org/10.1016/S0378-1127(99)00303-5

Šimůnek, J., van Genuchten, M.Th. (2008). Modeling nonequilibrium flow and transport processes using HYDRUS. Vadose Zone Journal 8: 782-797. https://doi.org/10.2136/vzj2007.0074

Smolander, A., Kurka, A., Kitunen, V., Mälkönen, E. (1994). Microbial biomass C and N, and respiratory activity in soil of repeatedly limed and N- and P-fertilized Norway spruce stands. Soil Biology and Biochemistry 26: 957-962. https://doi.org/10.1016/0038-0717(94)90109-0

Sparling, G.P., Feltham, C.W., Reynolds, J., West, A.W., Singleton, P. (1990). Estimation of soil microbial C by a fumigation-extraction method: Use on soils of high organic matter content, and a reassessment of the k_{EC}-factor. Soil Biology and Biochemistry 22(3): 301-307. https://doi.org/10.1016/0038-0717(90)90104-8

Stedinger, J.R., Vogel, R.M., Lee, S.U., Batchelder, R. (2008). Appraisal of the generalized likelihood uncertainty estimation (GLUE) method. Water Resources Research 44: W00B06. https://doi.org/10.1029/2008WR006822

Stevenson, F.J., Cole, M.A. (1999). Cycles of soils: Carbon, nitrogen, phosphorus, sulphur, micronutrients, 2nd ed. John Wiley & Sons Inc., New York, USA. 448 p. ISBN: 978-0-471-32071-5

Stockmann, U., Adams, M.A., Crawford, J.W., Field, D.J., Henakaarchchi, N., Jenkins, M., Minasny, B., McBratney, A.B., de Courcelles V.R., Singh, K., Wheeler, I., Abbott, L., Angers, D.A., Baldock, J., Bird, M., Brookes, P.C., Chenu, C., Jastrow, J.D., Lal, R., Lehmann, J., O'Donnell, A.G., Parton, W.J., Whitehead, D., Zimmermann, M. (2013). The knowns, known unknowns and unknowns of sequestration of soil organic carbon. Agriculture, Ecosystems and Environment 164: 80-99. https://doi.org/10.1016/j.agee.2012.10.001

Tamminen, P., Mälkönen, E. (eds.). Näytteenotto metsämaan ominaisuuksien määrittämistä varten. Metsäntutkimuslaitoksen tiedonantoja 729. 54 p. ISBN 951-40-1676-9

Tomppo, E. (2000). Kasvupaikat ja puusto. In: Reinikainen, A., Mäkipää, R., Vanha-Majamaa, I., Hotanen, J.-P. (eds.). Kasvit muuttuvassa metsäluonnossa. Tammi, Helsinki. pp. 60-83. ISBN: 951-31-1963-7

Tranvik, L.J., Downing, J.A., Cotner, J.B., Loiselle, S.A., Striegl, R.G., Ballatore, T.J., Dillon, P., Finlay, K., Fortino, K., Knoll, L.B., Kortelainen, P., Kutser, T., Larsen, S., Laurion, I., Leech, D.M., McCallister, S.L., McKnight, D.M., Melack, J.M., Overholt, E., Porter, J.A., Prairie, Y., Renwick, W.H., Roland, F., Sherman, B.S., Schindler, D.W., Sobek, S., Tremblay, A., Vanni, M.J., Verschoor, A.M., von Wachenfeldt, E. Weyhenmeyer, G.A. (2009). Lakes and reservoirs as regulators of carbon cycling and climate. Limnology and Oceanography 54(6): 2298-2314. https://doi.org/10.4319/lo.2009.54.6_part_2.2298

Vandenbruwane, J., De Neve, S., Qualls, R. G., Sleutel, S., & Hofmen, G. (2007). Comparison of different isotherm models for dissolved organic carbon (DOC) and nitrogen (DON) sorption to mineral soil. Geoderma 139: 144-153.

Vance, E.D., Brookes, P.C. & Jenkinson, D.S. (1987). An extraction method for measuring soil microbial biomass C. Soil Biology & Biochemistry 19(6): 703-707.

van Hees, P.A.W., Jones, D.L., 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 Biology & Biochemistry 37: 1-13.

van Vliet P.C.J., Beare M.H., Coleman D.C., Hendrix P.F. (2004). Effects of enchytraeids (*Annelida*: *Oligochaeta*) on soil carbon and nitrogen dynamics in laboratory incubations. Applied Soil Ecology 25: 147-160. https://doi.org/10.1016/j.apsoil.2003.08.004

Virtanen, K., Hänninen, P., Kallinen, R.-L., Vartiainen, S., Herranen, T. & Jokisaari, R. (2003). Suomen turvevarat 2000. Summary: The Peat Reserves of Finland in 2000. Geological Survey of Finland, Report of Investigation 156. 101 p. ISBN 951-690-844-6

von Post, L. (1922). Sveriges geologiska undersöknings torvinventering och några av dess hittills vunna resultat. Svenska Mosskulturföreningens Tidskrift 37: 1-27.

Wetterstedt, J., Ågren, G. (2011). Quality or decomposer efficiency – which is most important in the temperature response of litter decomposition? A modelling study using the GLUE methodology. Biogeosciences 8: 477-487. https://doi.org/10.5194/bg-8-477-2011

Widén, B., Majdi, H. (2001). Soil CO_2 efflux and root respiration at three sites in a mixed pine and spruce forest: seasonal and diurnal variation. Canadian Journal of Forest Research 31: 786-796. https://doi.org/10.1139/x01-012

Yano, Y., McDowell, W.H., Aber, J.D. (2000). Biodegradable dissolved organic carbon in forest soil solution and effects of chronic nitrogen deposition. Soil Biology & Biochemistry 32: 1743-1751.

Yurova, A.Yu., Lankreijer, H. (2007). Carbon storage in the organic layers of boreal forest soils under various moisture conditions: a model study for Northern Sweden sites. Ecological Modelling 204: 475-484. https://doi.org/10.1016/j.ecolmodel.2007.02.003

Zhang, Y., Li, Z., Trettin, C.C., Li, H., Sun, G. (2002). An integrated model of soil, hydrology, and vegetation for carbon dynamics in wetland ecosystems. Global Biogeochemical Cycles 16 (4): 1061. https://doi.org/10.1029/2001GB001838

Zheng, C., Bennett, G.D. (2002). Applied Contaminant Transport Modeling, 2nd ed. John Wiley & Sons Inc., New York. 656 p. ISBN: 978-0-471-38477-9