Dissertationes Forestales 112

Carbon dynamics in peatlands under changing hydrology: Effects of water level drawdown on litter quality, microbial enzyme activities and litter decomposition rates

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Academic dissertation

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Title: Carbon dynamics in peatlands under changing hydrology: Effects of water level drawdown on litter quality, microbial enzyme activities and litter decomposition rates

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ABSTRACT

Pristine peatlands are carbon (C) accumulating wetland ecosystems sustained by a high water level (WL) and consequent anoxia that slows down decomposition. Persistent WL drawdown as a response to climate and/or land-use change directly affects decomposition: increased oxygenation stimulates decomposition of the “old C” (peat) sequestered under prior anoxic conditions. Responses of the “new C” (plant litter) in terms of quality, production and decomposability, and the consequences for the whole C cycle of peatlands are not fully understood. WL drawdown induces changes in plant community resulting in shift in dominance from *Sphagnum* and graminoids to shrubs and trees. There is increasing evidence that the indirect effects of WL drawdown via the changes in plant communities will have more impact on the ecosystem C cycling than any direct effects.

The aim of this study was to disentangle the direct and indirect effects of WL drawdown on the “new C” by measuring the relative importance of 1) environmental parameters (WL depth, temperature, soil chemistry) and 2) plant community composition on litter production, microbial activity, litter decomposition rates and, consequently, on the C accumulation. This information is crucial for modelling C cycle under changing climate and/or land-use. The effects of WL drawdown were tested in a large-scale experiment with manipulated WL at two time scales and three nutrient regimes. Furthermore, the effect of climate on litter decomposability was tested along a north-south gradient. Additionally, a novel method for estimating litter chemical quality and decomposability was explored by combining Near infrared spectroscopy with multivariate modelling.

WL drawdown had direct effects on litter quality, microbial community composition and activity and litter decomposition rates. However, the direct effects of WL drawdown were overruled by the indirect effects via changes in litter type composition and production. Short-term (years) responses to WL drawdown were small. In long-term (decades), dramatically increased litter inputs resulted in large accumulation of organic matter in spite of increased decomposition rates. Further, the quality of the accumulated matter greatly changed from that accumulated in pristine conditions. The response of a peatland ecosystem to persistent WL drawdown was more pronounced at sites with more nutrients.

The study demonstrates that the shift in vegetation composition as a response to climate and/or land-use change is the main factor affecting peatland ecosystem C cycle and thus dynamic vegetation is a necessity in any model applied for estimating responses of C fluxes to changes in the environment. The time scale for vegetation changes caused by hydrological changes needs to extend to decades. This study provides grouping of litter types (plant species and part) into functional types based on their chemical quality and/or decomposability that the models could utilize. Further, the results clearly show a drop in soil temperature as a response to WL drawdown when an initially open peatland converts into a forest ecosystem, which has not yet been considered in the existing models.

Keywords: boreal peatlands, carbon cycle, decomposition, litter quality, litter inputs, microbial enzyme activity, NIRS, water level drawdown

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Thank you - Kiitos - Děkuji.
We finally made it!

Helsinki, November 2010, Petra Straková

LIST OF ORIGINAL ARTICLES

The thesis is based on the following articles which are referred to in the text by Roman numerals. The articles are reproduced with the kind permission from the publishers: Springer Science + Business Media (**I** and **V**) and Elsevier (**IV**). The articles **II** and **III** are the author versions of the submitted manuscripts.

I **Straková, P.**, Anttila, J., Spetz, P., Kitunen, V., Tapanila, T. & Laiho, R. 2010. Litter quality and its response to water level drawdown in boreal peatlands at plant species and community level. Plant and Soil 335, 501-520.
doi: 10.1007/s11104-010-0447-6

II **Straková, P.**, Niemi, R. M., Freeman, C., Peltoniemi, K., Toberman, H., Heiskanen, I., Fritze, H. & Laiho, R. Litter type affects the activity of aerobic decomposers in a boreal peatland more than site nutrient and water level regimes. Manuscript.

III **Straková, P.**, Penttilä, T., Laine, J. & Laiho, R. Disentangling direct and indirect effects of water level drawdown on above and belowground plant litter decomposition: Consequences for accumulation of organic matter in boreal peatlands. Manuscript.

IV **Vávřová, P.**, Penttilä, T. & Laiho, R. 2009. Decomposition of Scots pine fine woody debris in boreal conditions: Implications for estimating carbon pools and fluxes. Forest Ecology and Management 257, 2, 401-412.
doi: 10.1016/j.foreco.2008.09.017

V **Vávřová, P.**, Stenberg, B., Karsisto, M., Kitunen, V., Tapanila, T. & Laiho, R. 2008. Near Infrared Spectroscopy for characterization of plant litter quality: Towards a simpler way of predicting C turnover in peatlands? In: Vymazal, J. (ed.), Wastewater treatment, plant dynamics and management in constructed and natural wetlands. Springer Science + Business Media, Dordrecht. p. 65-87. ISBN 978-1-4020-8234-4.
doi: 10.1007/978-1-4020-8235-1_7

AUTHOR'S CONTRIBUTION

P. Straková, nee Vávřová, compiled the summary part of this doctoral thesis.

Articles **I-V**: P. Straková had the main responsibility for the experimental set up (except for the FWD decomposition experiment in **IV** that was initiated before P. Straková joined the research team). She was responsible for most of the field and laboratory work: collection and preparation of the litter materials and their chemical and NIRS analyses, measurements of microbial enzyme activities and litter decomposition rates; and all the data analyses, models constructions and simulations (except for the annual litter inputs simulation in **IV**). She was the main writer in all papers.

Data on the litter inputs utilized in **I** and **III** come from Anttila (2008), data on the microbial community composition utilized in **II** come from Peltoniemi (2010).

TABLE OF CONTENTS

1 INTRODUCTION

1.1 Background

Pristine peatlands, or mires, represent a wide variety of wetlands where organic matter has been accumulating as peat, partly decomposed plant material of which about half is carbon (C). With an estimated area of 4 million km^2 peatlands constitute only about 3% of the Earth's land area, from which the largest proportion (approximately 85%) is located in the northern boreal and subarctic zone (Joosten and Clarke 2002). In spite of their small land cover in global scale, northern peatlands act as large C reservoirs with global importance.

The accumulation of atmospheric C in peatlands as peat has been achieved by a long-term imbalance between net primary production and decomposition caused by high water level (WL) and consequent anoxia, with decomposition being slower than the production (Clymo 1984). Though the imbalance is relatively small, which in the long term translates into only 2-16% of the net primary production of a peatland ecosystem depositing as peat (Päivänen and Vasander 1994), peatlands have succeeded in storing about 30% of the global soil C pool with their estimated reservoir of 455 Pg (10^{15} g) (Gorham 1991). This equals more than 50% of the atmospheric C pool (Gorham 1991). The C sink function of a peatland is labile, however, and sensitive to variations in environmental conditions (Bubier et al. 2003, Aurela et al. 2004, 2007, Roulet et al. 2007, Chivers et al. 2009).

Changes in peatland functioning may follow from climate change and/or changes in the land-use. In both cases, WL drawdown may be a major effect launching several other factors (Gitay et al. 2001) but the impacts on the peatland functioning are not well understood. Lowered WL and the consequent increase in oxygen availability in the surface peat accelerate rates of organic matter decomposition. This might reduce the peatland C sink function, and eventually turn it into a source of C into the atmosphere. However, earlier studies gave contradictory results on the response of peatland C sink functioning to lowered WL (Sakovets and Germanova 1992, Minkkinen and Laine 1998, Minkkinen et al. 1999, Minkkinen et al. 2002). Site fertility (peatland type) and climatic conditions (temperature sum) may account for part of the variation in the outcomes (Minkkinen and Laine 1998, Minkkinen et al. 1999, Ojanen et al. 2010).

Climate change scenarios predict higher temperatures and more frequent summer droughts in northern latitudes (Houghton et al. 2001, Good et al. 2006, IPCC 2007), which would result in WL drawdown in boreal peatlands. Understanding the ecological mechanisms controlling peatland response to changes in their hydrology is crucial for predicting potential feedbacks on the global C cycle. This study mainly focuses on the hydrological effects on the "new C" in peatlands: C inputs via litter production and C release via litter decomposition.

1.2 Role of plant litter in the C cycle of peatlands

Atmospheric C is bound into plant biomass during photosynthesis, and may be temporarily stored there in the form of living plants (Fig. 1). Senescent plants or their parts are eventually deposited as litter on the soil surface, and root litter and root exudates under the surface. Litter is physically broken into small particles and biochemically degraded, primarily under oxic conditions on the soil surface or in the oxic peat layer. Large proportion of the carbon bound in litter is thus released back to the atmosphere as CO_2. Part of the organic material that gets deposited into the anoxic water-saturated zone below the water level is decomposed to produce methane (CH_4). If there is an imbalance between the rates of litter production and decomposition the incompletely decomposed litter accumulates as peat, resulting in long-term C storage. Plant litter production and decomposition are thus the key processes in element cycling and C balance of a peatland.

Decomposition is mainly carried out by soil mesofauna and microbes (bacteria and fungi) that use litter as their energy source, and mediated by extracellular enzymes produced by microbes to convert complex substrates into smaller compounds that they can assimilate. Decomposition rates are controlled by a hierarchy of interacting physical, chemical and biotic factors (Laiho 2006). Climate, determining decomposition rates at a broad (regional) scale, mainly sets the general limits of decomposition through physiological restrictions on the activities of decomposing organisms (Heneghan et al. 1999). In the boreal and temperate zones, decomposition rates generally increase from cold to warm and from dry to moist conditions, as demonstrated with many litter types (Palosuo et al. 2005) in the validation of the Yasso decomposition model (Liski et al. 2005). Chemical quality of the substrate and/or site specific factors, such as microtopography and fertility, then determine the rates at which the organisms can operate within these restrictions (Coûteaux et al. 1995, Berg and Meentemeyer 2002).

The aerobic decomposition of organic matter to CO_2 is faster and more energetically-profitable for the decomposers compared to the anaerobic decomposition of organic matter to CH_4 (e.g., Blodau et al. 2003, 2004). Even though peatlands are based on sequestration

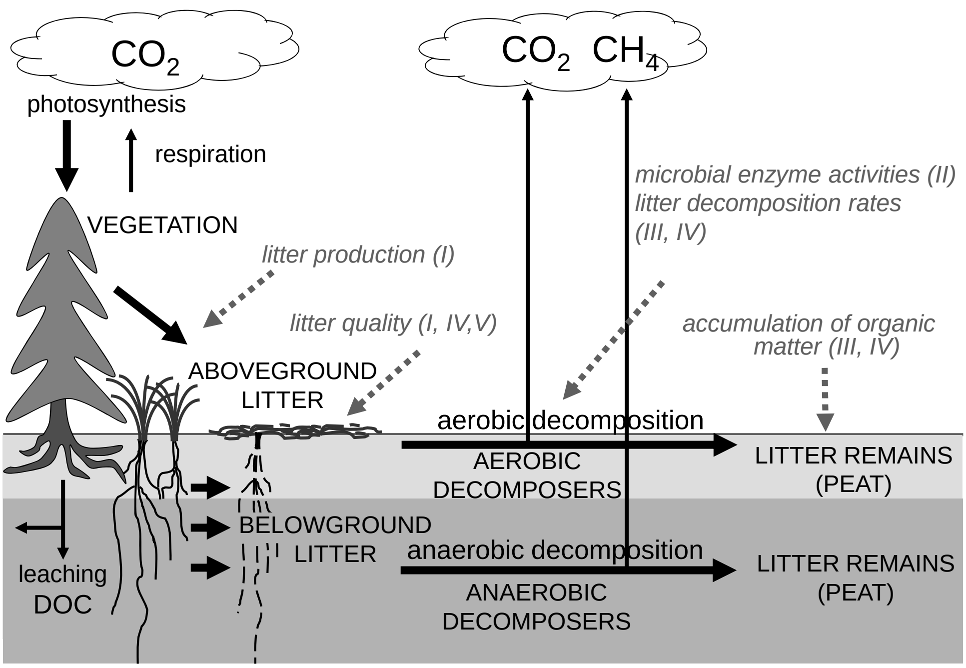

Figure 1. Simplified view of carbon (C) flows in peatlands (full arrows). This study focused on water level drawdown effects on selected components of the C flow (dotted arrows, with Roman numerals referring to the particular articles).

of organic matter in the anoxic layer, most of the C fluxes take place in the relatively thin oxic layer near the surface. In the oxic surface layer of peatlands, the rates of litter decomposition may not in fact generally differ from those found in mineral soil sites for the same litter types (Coulson and Butterfield 1978, Moore et al. 2002). In peatlands the C accumulation mainly depends on the extent to which the aerobic decomposition proceeds before the litter material gets deposited in the anoxic layer, and/or on the limit value of prevailing litters, which is the level of accumulated mass loss at which decomposition either continues at a very low rate or possibly stops (Berg et al. 2010).

1.3 Water level drawdown impacts on peatlands

Persistent lowering of the WL promotes several changes in peatland environmental conditions (Laiho et al. 2006) that may have direct effects on decomposition. Decreased water content in the surface peat and increased soil aeration may stimulate decomposition. Increased peat compaction and drop in temperature may, in turn, slow down decomposition. Direct effects of WL drawdown on the current vegetation cover include changes in nutrient concentrations because of changes in nutrient availability or root functioning. However, any direct effects may be overruled by the indirect effects through changes in vegetation composition (Dorrepaal et al. 2005). These effects have not yet been thoroughly evaluated.

Litter decomposition is a crucial factor in the C cycle of peatlands, and shifts in vegetation composition, particularly in terms of the dominant plant functional types (PFTs, Box 1996) or growth forms, may result in overall shifts in litter quality and decomposability (Hobbie et al. 2000, Saleska et al. 2002, Quested et al. 2003). Plant litters with high concentration of nutrients and simple sugars (sedge litter, herbs; typical of pristine peatlands) decompose faster than those with high lignin concentration (woody litter of shrubs and trees; typical of drained peatlands), while moss decomposition rates are in general low (e.g., Hobbie 1996, Thormann et al. 2001, Bragazza et al. 2007).

Litter input, i.e. amount of litter produced per specific time period and area, is another crucial factor for estimating C pools and fluxes. At the community level, litterfall consists of inputs of several litter types. Overall litter quality at the community level may be defined as a function of the litter quality of individual litter types and their relative inputs (Dukes and Hungate 2002, Finzi and Schlesinger 2002). Changes in relative inputs of different litter types in response to WL drawdown may have the greatest effect on the overall litter quality in various ecosystems, including peatlands (Kemp et al. 1994, Weatherly et al. 2003, Dorrepaal et al. 2005, Henry et al. 2005).

In oxic peatland conditions aerobic bacteria and fungi are the most important and effective decomposers of organic matter (Peltoniemi 2010 and references therein). The structure of the peatland microbial community varies with the vegetation community (Borgå et al. 1994, Fisk et al. 2003, Thormann et al. 2004, Jaatinen et al. 2007, 2008), and it has been shown that such changes in peatland hydrology that affect the vegetation community also induce adaptation in the microbial communities (Jaatinen et al. 2007, Peltoniemi et al. 2009). Such adaptations are then reflected in the change of microbial enzyme activities (Fenner et al. 2005, Toberman et al. 2010). This may be induced directly through the physical environment (e.g., oxygen availability, Freeman et al. 2001) and indirectly by altering the litter quality (Laiho 2006). The patterns of microbial community adaptation may vary according to site nutrient levels and change over time since the hydrological change (Jaatinen et al. 2007, Peltoniemi et al. 2009).

The changes in vegetation and microbial community composition and activity following WL drawdown may be translated to changes in litter decomposition rates at the community level and the amounts of accumulating organic matter, and may thus affect the C storage potential of peatlands. Although it is generally known which mechanisms play a role in the C cycle of peatlands, far less is known about their relative importance, and their impact on the peatlands under changing climate and/or land-use.

2 AIMS OF THE STUDY

The aim of this study was to disentangle the direct and indirect effects of WL drawdown on the peatland C cycle by measuring the relative importance of environmental parameters (WL depth, temperature, soil chemistry) and vegetation community composition (litter type composition and/or litter chemical quality) on litter production, microbial activity, litter decomposition rates and, consequently, on the C accumulation. The climatic effect was included in a sub-study on decomposition of fine woody debris (FWD) along a north-south climatic gradient. Furthermore, a novel method for estimating litter chemical quality and decomposability was explored by combining Near infrared spectroscopy (NIRS) with multivariate modelling. The study consists of five research articles, which had the following specific aims (see also Fig. 1).

I To determine the quality (chemical composition) of litter types typical of boreal peatland sites with varying nutrient and WL regimes. To disentangle the direct and indirect effects of WL drawdown on litter quality (plant species and community level), and to discuss a possible role of such effects on the peatland C cycle.

II To disentangle the direct and indirect effects of WL drawdown on the activity of aerobic microbial decomposers, and to link the activity to the microbial community composition, litter quality and litter decomposition rates.

III To determine decomposition rates of the litter types typical of boreal peatland sites with varying nutrient and WL regimes. To disentangle the direct and indirect effects of WL drawdown on litter decomposition rates (plant species and community level), and to describe accumulation rate of organic matter at the different WL regimes.

IV To determine decomposition rates of FWD in pine-dominated boreal peatland forests along a north-south climatic gradient, and to link the rates to the variation in litter quality and environmental conditions.

V To test the ability of NIRS to characterize the chemical composition of a variety of plant litters, typical of boreal peatland sites with varying nutrient and WL regimes, by developing NIRS-calibrations for N and several C fractions potentially affecting decomposition dynamics in peatlands.

This is the first study to analyze the impact of both short-term (years) and long-term (decades) WL drawdown that may be caused by the predicted climate change and/or forestry drainage. Research was done at three nutrient regime levels: bog, oligotrophic fen and mesotrophic fen; and extended from south boreal to north boreal and hemiboreal conditions.

3 MATERIALS AND METHODS

A short description of the materials and methods used in this study is given below, further information can be found in **I–V**.

3.1 Study sites

The effects of WL drawdown on quality and production (**I**), microbial activity (**II**) and decomposition rates (**III**) of numerous litter types, typical of boreal peatland sites, were tested in a large-scale experiment with manipulated WL at two time scales and three nutrient regimes in a raised box complex Lakkasuo in Central Finland (Fig. 2, Table 1). To include the climatic effect, decomposition of FWD (**IV**) was studied at three peatland sites drained for forestry in climatically different parts of the boreal vegetation zone: north boreal (Northern Finland), south boreal (Southern Finland), and hemiboreal (Estonia) (Fig. 2; Table 1). *Sphagnum* moss litter from additional six sites was used in **V**, but as the litter origin was not of particular importance in that study, those sites are not described in any detail.

3.1.1 Lakkasuo

Lakkasuo included three study sites with differing nutrient regimes: bog (ombrotrophic, i.e. precipitation-fed, nutrient-poor), oligotrophic fen (minerotrophic, i.e. additionally groundwater-fed, more nutrient-rich), and mesotrophic fen (minerotrophic, nutrient-rich). Each of those consisted of a pristine control plot, a plot with short-term, c. 4 years, water level drawdown (STD), and a plot with long-term, c. 40 years, water level drawdown (LTD) (Fig. 2, Laine et al. 2004). Within each specific site, all plots supported the same vegetation community and had similar soil composition and structure before the WL drawdown. Together, these plots formed a gradient from a wet pristine peatland to a drying system and finally towards a peatland forest ecosystem (Laiho et al. 2003).

The WL in the manipulated plots was lowered by ditching. LTD had been achieved with practical-scale drainage for forestry, and STD with new ditches for this experimental purpose. In the STD plots, the average WL was 10 (bog) to 20 (fen) cm deeper than in the corresponding pristine plots, which is close to the estimate given by Roulet et al. (1992) for the short-term impact of climate change on WL in northern peatlands. In the LTD plots, the average WL was 15 (bog) to 40 (fen) cm deeper than in the pristine plots. It is assumed that the initial post-drainage drop in WL was close to that observed in the STD plots, and that the further lowering was caused by increased evapotranspiration by the tree stands (Sarkkola et al. 2010).

Short-term WL drawdown had a minor effect on vegetation composition. In long-term, however, WL drawdown had resulted in conversion of an open peatland dominated by *Sphagnum* and graminoids into a forest ecosystem dominated by pine and birch (**I**). The vegetation change was associated, besides a decrease in WL, with a drop in pH and increase in nutrient concentration of surface peat (**I**, **III**).

Table 1. General description of the study sites. Weather parameters are averages for periods 1961–1990 and/or 1991–2005 (the longest period available for the hemiboreal site).

Site	Coordinates	m a.s.l.	Mean annual air T (°C)	Annual air T sum (d.d. > 5°C)	Precipitation (mm year $^{-1}$)
North boreal	66°21' N, 26°37'E	180	-0.2/0.8	865/927	538/598
Lakkasuo	61°47' N, 24°18'E	150	3.0/n.e.	1160/n.e.	709/n.e
South boreal	61°22' N, 25°07'E	115	3.4/4.3	1239/1295	601/618
Hemiboreal	58°59' N, 25°27'E	78	n.e./4.8	n.e./1421	n.e./725

a.s.l., above see level; d.d.; degree days; n.e., not estimated for the given period; T, temperature

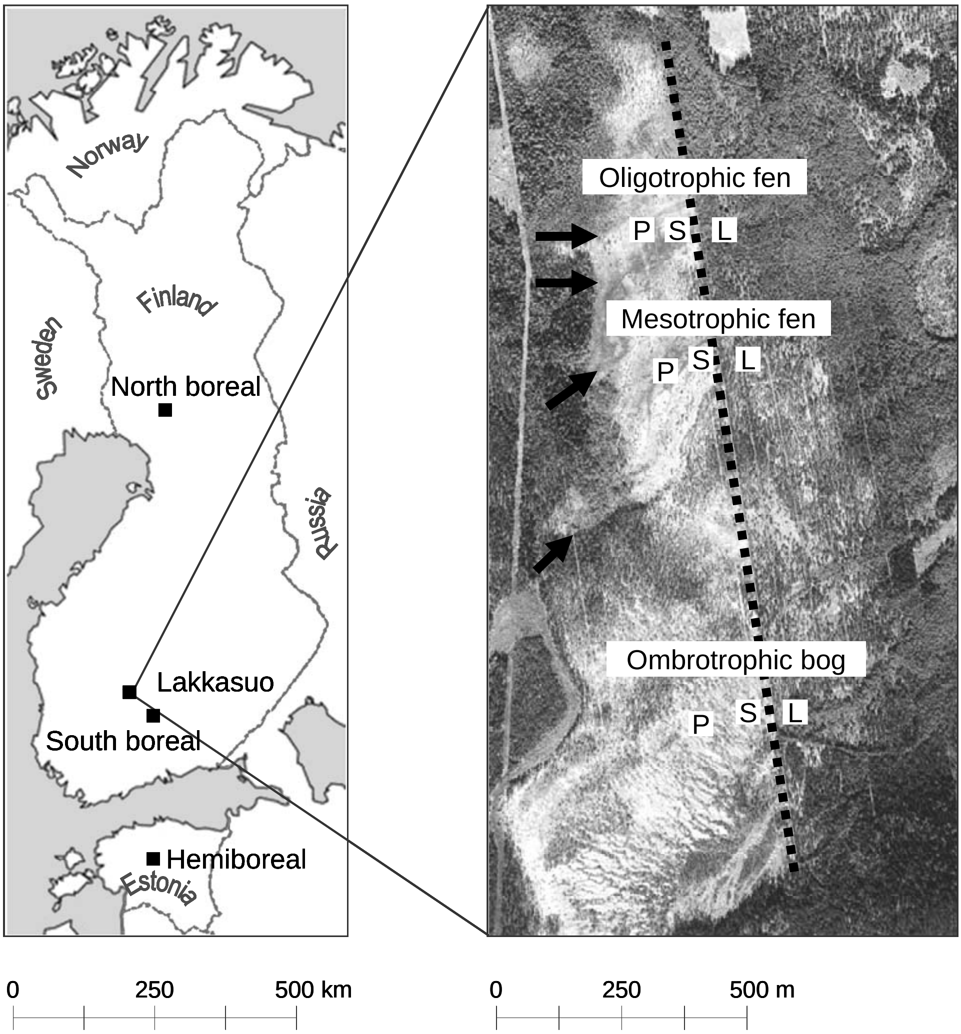

Figure 2. Map showing the locations of the study sites, with air-photo of the Lakkasuo site with marked study plots (different nutrient and water level (WL) regimes). The arrows show the inflow points of water feeding the mire, and the dotted line shows the position of the main drainage ditch (long-term WL drawdown). P, pristine; S, short-term WL drawdown; L, long-term WL drawdown.

3.1.2 Sites along the north-south climatic gradient

The north boreal site was situated in Rovaniemi at the Kivalo Research Forest of the Finnish Forest Research Institute. This site served as the northern extent for defining FWD decomposition rates in the boreal climate. The site was originally a treed minerotrophic mire. It was drained for forestry in 1933.

The south boreal site, situated in Padasjoki at the Vesijako Research Forest of the Finnish Forest Research Institute, served as the main experimental site for defining FWD decomposition rates, with the longest period of monitoring and two plots representing different initial (pre-drainage) nutrient regimes: ombrotrophic and minerotrophic. The mire was drained for forestry in 1915.

The hemiboreal site was situated at Väätsa, Central Estonia. This site served as the southern extent in the boreal climate. The site was originally a rich fen and was drained for forestry in 1959. Due to the southern location and the initial site type, the site was considered to represent high availability of N and P, and, potentially, the highest mass loss rates within the boreal zone.

3.2 The litter material

In the study site Lakkasuo, litter production (inputs) at plant species and part level was measured from all vegetation layers: tree, shrub, herb and moss (**I**, Anttila 2008). Litter production was expressed as dry mass produced per m^2 and year.

Litter types that reflected the dominant species at the different nutrient and WL regimes as well as different plant groups with distinctive chemical composition (**I**) were collected for studies **I-III** and **V**. Some of the litters were present at all the nutrient and WL regimes, and could be used to evaluate the direct effect of WL drawdown on litter quality and production (**I**), microbial activity (**II**) and decomposition rates (**III**), including a possible change in litter quality at the litter type level. The other litter types were typical of certain nutrient and WL regimes (Appendix 1 in **III**) and thus reflected the indirect effects. Vascular plant litter was collected by harvesting senescent leaves, needles or dead branches from living plants, moss litter by cutting 3-5 cm thick litter layer beyond the living moss with scissors (thus, excluding both the upper green and the lower, already decomposing, layers). Belowground parts of sedges and shrubs were harvested from plants that were collected at the study sites and cultivated in containers filled with expanded clay and fertilized water during one vegetation season. Tree roots were harvested from young trees cultivated at a tree-nursery.

Scots pine *(Pinus sylvestris)* is a common tree species in Eurasian boreal and temperate forests with considerable litter inputs into the forest floor. Although the proportion of FWD in aboveground litterfall is much smaller than that of foliar litter (Laiho et al. 2003), FWD may be of great importance regarding the C cycle and storage in forest ecosystems. FWD of two size classes were collected at the three sites along the north-south climatic gradient (**IV**).

Each litter type was air-dried at the room temperature (20 °C) to constant mass (about 92-94% dry mass) and gently mixed. Sub-samples were withdrawn to determine initial litter quality and dry mass content (**I**, **IV**).

3.3 Litter quality

3.3.1 "Wet chemistry" methods

The chemical analyses were selected to divide the litter into organic chemical fractions that are considered to decompose at different rates (Berg et al. 1982) and to include parameters potentially regulating the decomposition rates, based on the earlier studies (e.g., Berg and Ekbohm 1991, Limpens and Berendse 2003, Bragazza et al. 2007, Turetsky et al. 2008).

The characterization was done at differing levels, from fairly rough fractionation to individual compound level (**I, IV**). The properties measured were extractable substances (dichloromethane-, acetone-, ethanol- and water-solubles), cellulose, holocellulose (sum of cellulose and hemicelluloses), composition of hemicelluloses and uronic acids (arabinose, galactose, galacturonic acid, glucose, glucuronic acid, mannose, rhamnose, xylose), lignin, CuO oxidation phenolic products (acetosyringone, acetovanillone, ferulic acid, 4-hydroxyacetophenone, 4-hydroxybenzaldehyde, 4-hydroxybenzoic acid, p-coumaric acid, syringe aldehyde, syringic acid, vanillic acid, vanillin) that derive from lignin and concentrations of C, nitrogen (N), phosphorus (P), potassium, magnesium, manganese, calcium and ash.

The methods included stepwise extraction for the gravimetric determination of extractable substances (Ryan et al. 1990, Wieder and Starr 1998); sodium chlorite method (Quaramby and Allen 1989) for the determination of holocellulose; acid methanolysis or hydrolysis followed by gas chromatography (GC) for the concentrations of cellulose and hemicelluloses (Sundberg et al. 1996, 2003); acid hydrolysis for the determination of Klason lignin and acid soluble lignin (Ehrman 1996); degradative alkaline CuO oxidation method (Hedges and Ertel 1982) for the information about the composition of the lignin fraction.

3.3.2 Near infrared spectroscopy (NIRS)

The methods involved in characterization of litter quality and decomposability are costly and/or time consuming and therefore unlikely to be used routinely for large sample sets applied in complex ecological studies. NIRS (780-2500 nm) is an established analytical technique which offers the potential for accurate, quick and inexpensive characterization of various organic materials. Organic samples absorb NIR radiation mainly by C-H, N-H, and O-H bonds. The nature and number of bonds present in a sample, and thus the amount of radiation that might be absorbed, is determined by the chemical composition of the sample. Therefore, the NIR spectrum reflected back from a sample contains information about its chemical composition. Direct interpretation of NIR spectra is difficult. However, NIRS can be used as an indirect method that estimates characteristics (chemical composition, decomposition rates, etc.) of samples by comparing their spectra with spectra of samples whose characteristics are already known (i.e., have been measured by an established laboratory method; calibration data).

The litters analyzed by the "wet chemistry" methods were additionally analyzed by NIRS and models were constructed for the relationships between the spectra and the detailed chemical composition of the litters (**V**) and their decomposition rates. The spectra were obtained from dried and milled samples with a FieldSpec Pro FR spectroradiometer (ASDI Colorado). The NIR spectrum of a sample consisted of 100 averaged scans. Reflectance (R) was transformed to absorbance (A) using $A = \log(1/R)$.

3.4 Litter decomposition rates

Litter decomposition rates were determined in the natural environment: each specific litter type was decomposing at the plot where it had been produced and collected (except for tree roots that originated from a tree-nursery) and in conditions where it would naturally decompose (**III**, **IV**). The litterbag method was used, which, in spite of some known sources of inaccuracy (Taylor 1998, Domisch et al. 2000, Kurz-Besson et al. 2005), is the most useful and widely used method for determining mass loss rates of different materials *in situ*. The mesh size of the nylon bags used was 1 x 1 mm to prevent physical losses of the material but to allow small mesofauna typical of the sites (Silvan et al. 2000) to enter the bags. Incubation periods presented in here are 1-2 years for Lakkasuo (**III**); and 1-4, 1-3 and 1-2 years for the south boreal, north boreal and hemiboreal site on the climatic gradient, respectively (**IV**). The samples originate from ongoing long-term studies. The experiments are designed for 10-year monitoring of litter decomposition.

After each recovery, litterbags were transported to a laboratory where the content was cleaned by removing all materials that had penetrated the bags, and weighed to determine the remaining “fresh” mass. Subsamples were taken from some litterbags for measurements of microbial activity (**II**) and community composition (**II**, Peltoniemi 2010). Dry mass content of the “fresh” samples was determined by drying two subsamples at 105 °C overnight. Decomposition rates were expressed as dry mass loss after each incubation period (**III, IV**).

3.5 Microbial community

In oxic peatland conditions, aerobic bacteria and fungi are the most important and effective decomposers of organic matter (Peltoniemi 2010 and references therein). To capture for the active microbial community, the analyses were based on ribosomal RNA extracted from the litters (**II**, Peltoniemi 2010). RNA is more short-lived compared to DNA and thus represents only the microorganisms that were living and active at the time of sampling. The microbial community data are a subset of a more extensive study on the microbial communities in the sites (Peltoniemi 2010).

Microbial activity was characterized by the activities of several extracellular enzymes involved in mineralization of organic C, N, P and sulphur (S) (**II**). The enzymes involved in C acquisition included α-glucosidase, ß-glucosidase, cellobiosidase, ß-xylosidase, chitinase (also N acquiring enzyme) and phenol oxidase; in N acquisition alanine-aminopeptidase and leucine-aminopeptidase; in P acquisition phosphomonoesterase and phosphodiesterase; and in S acquisition arylsulphatase.

The enzyme activities were measured under 1) “laboratory” (buffer regulated pH of a reaction mixture, incubation temperature was higher than in the field) and 2) “natural” (no buffer used in the assay, incubation temperature was as low as in the field) conditions. The first approach gives information about the *potential* enzyme activities and especially the quantity of active enzyme (Kang and Freeman 1999) while the second one more closely reflects the *actual* natural processes, including possible litter type- or environment- related differences in pH and their influence on enzyme activities. The outcomes may vary between the two approaches (Freeman et al. 1995). The assays were performed in two laboratories, both having extensive experience with the given approach (e.g., Freeman et al. 2001, Vepsäläinen et al. 2001).

3.6 Environmental parameters

This section describes measurements of environmental parameters that were tested in this study as potential predictors of variation in litter decomposition rates.

WL was continuously recorded at all pristine and LTD plots of the study site Lakkasuo using Ott (Kempten, Germany) WL recorders. Position of the decomposing litter relative to the WL was estimated based on those continuous measurements, and monthly measurements at the exact locations where litterbags were installed (**III**).

Temperature was monitored using temperature loggers iButtons (Maxim, USA) at the exact locations where the studied litter was decomposing, and in the air at 2 m above the soil surface. Daily mean temperatures and the cummulative temperature sums over 0 ºC threshold for the specific incubation periods were calculated from these local measurements (**III**, **IV**). Daily variation in temperature was calculated as standard deviation of the temperature records within a day (**III**). If the local data were not available for some site and period, data from the closest weather station were used (**IV**).

Precipitation data were obtained from the closest weather stations (**III**, **IV**). Monthly precipitation for the summer months, annual summer precipitation sums and summer precipitation sums for the specific incubation periods were calculated for each site on the climatic gradient (**IV**).

Potential evapotranspiration (PET) was calculated for the sites on the climatic gradient (**IV**) using the Thornthwaite water balance method (Thornthwaite 1948), which is based on an empirical relationship between potential evapotranspiration and mean air temperature. Precipitation minus potential evapotranspiration (PREC-PET) values were used to estimate the monthly site water balance. Positive values indicated that precipitation exceeded PET while negative values indicated possible site moisture deficiency.

Soil samples were collected from the 0-30 cm surface peat layer using a box sampler (**III**, **IV**). The peat-cores were cut into 10-cm layers, and element concentrations were analyzed as for the litter materials.

To capture for purely environmental effects on decomposition pine cellulose was used as a standard material (**III**). Unlike common litter which quality may be changed as a response to WL drawdown (**I**), cellulose had identical chemical composition at all nutrient and WL regimes. Mesh bags with cellulose strips were installed at the same locations as the litterbags and the mass loss rates were measured for the same periods as that for litters.

3.7 Data analyses

Multidimensional ordination methods were applied for data analyses (**I, II, IV**) due to multiple intercorrelated variables in the data (Lepš and Šmilauer 2003). Variation within the datasets was first explored by indirect gradient analyses (PCA, DCA), followed by direct gradient analyses (RDA, CCA) to quantify the relationships between litter quality, litter inputs, microbial enzyme activity and community composition, litter and cellulose decomposition rates and environmental factors. The choice of test (linear (PCA, RDA) or unimodal (CCA) response model) was based on the heterogeneity of the response variable data, i.e. the extent of response variable turnover, in each case. This was evaluated using DCA (Lepš and Šmilauer 2003). Standardized values of litter quality parameters (**I, IV**) and activities of microbial extracellular enzymes (**II**) were used in the analyses to eliminate the scale effect. The ordinations were performed using Canoco for Windows version 4.5 (ter Braak and Šmilauer 2002).

Grouping of litter types (plant species and part) into PFTs was based on PCA analysis of litter chemical quality, and verified by cluster analysis that was conducted using Euclidean distance for dissimilarity measures and Ward´s clustering method (**I**). Correlations between the different litter quality parameters (**IV**, **V**) were estimated by Pearson's coefficient.

Direct effects of WL drawdown and site nutrient regime on litter quality were tested by PCA/RDA using common litter (litter types present at all nutrient and WL regimes). Direct effects of WL drawdown, site nutrient regime and incubation period on microbial activity (**II**), cellulose and/or litter decomposition rates (**III, IV**) were tested by analysis of variance (ANOVA) using common litter. The cluster analysis, correlation analysis and ANOVA were performed using Statistica for Windows version 6.1 (StatSoft 2003).

Models were constructed to identify factors controlling the variation in litter mass loss and to quantify their effects (**III**, **IV**). Because of the hierarchical data structure, a mixed (multilevel) model approach was used (Goldstein 1995). Models were constructed using MLwiN software (Rasbash et al. 2004), which estimates the fixed and random parameters simultaneously. The restricted iterative generalized least square (RIGLS) method was applied. The significance of the variables was evaluated based on their parameter standard error (parameter value should be at least twice its SE), which was also used to group different litter types into PFTs based on their decomposition rates (**III**). The value of −2×log-likelihood was used to compare models of increasing complexity. The factors included in the final models were selected based on the amount of explained total variation in litter mass loss and the value of −2×log-likelihood. The goodness of fit was further evaluated based on residuals.

Simple decomposition rate coefficients were estimated for the different litter types (**III, IV**) using the exponential decay function (Olson 1963)

$$Y_t = Y_0 \, e^{-kt} \qquad (1)$$

where Y_t = mass remaining at time t (%), Y_0 = mass remaining at time 0 (here always 100%), k = decomposition rate constant, and t = time (days). The function was fit using nonlinear regression with least squares estimation by Gauss-Newton method that computes exact derivatives, using SYSTAT 10 for Windows. The goodness of fit was evaluated based on residuals.

To estimate litter quality (**V**) and decomposition rates by NIRS models were build by partial least squares (PLS) regression (Esbensen 2002, Martens and Naes 1991) using The Unscrambler, version 9.2, software package (Camo Process AS; Oslo, Norway). In this sudy the PLS models used spectral absorbances at all wavelengths as the X-matrix, and a chemical property or mass loss rate as the Y-variable. Spectral data pre-processing may strongly influence the prediction performance of calibration models (e.g., Gillon et al. 2004), so a number of pre-processing options (see **V** for details) was investigated. For each quality parameter (1) a general model calibrated for various litter types and (2) a more specific model calibrated for FWD only were compared. The r^2 values, root mean square error of calibration (RMSEC) and root mean square error of prediction (RMSEP) were mainly used for estimating the accuracy of the models. RMSEC tells how well the calibration model fits the calibration data, while RMSEP shows the accuracy of prediction on independent (extracted) samples. RMSEC/P is expressed in the same units as the dependent variable so it indicates the error in the same units as the Y.

RMSEC/P is calculated as follows:

$$\text{RMSEC/P} = \sqrt{\frac{1}{\mathrm{I}}\sum_{i=1}^{\mathrm{I}}(\hat{y}_i - y_i)^2} \tag{2}$$

where
$\hat{y}_i$ = predicted value of the *i*th observation
y_i = measured value of the *i*th observation
I = number of observations in the calibration set.

A good model should have (1) high correlation coefficient, (2) low RMSEC, low RMSEP, and a small difference between RMSEC and RMSEP, and (3) a relatively low number of factors in order to avoid inclusion of signal noise in the models.

3.8 Simulations of organic matter accumulation

To describe accumulation rate of organic matter at the different WL regimes (**III**), the measured litter mass loss rates (**III**) were applied to litter inputs (**I**).

To estimate the magnitude of the C fluxes of FWD relative to the better known needle litter fraction, simulated annual FWD and needle inputs (described in **IV**) were decomposed using the *k* values determined in **IV** and published *k* values (Berg and McClaugherty, 2003), respectively. On an *a posteriori* basis, the FWD *k* value was applied to the harvesting residue branches. The first-year litter cohort was decomposed for 60 years, the second for 59, and so forth. The cumulative differences between inputs and decomposition losses for each year were summed up to represent organic matter accumulation from the different fractions during the 60-year simulation period (**IV**).

4 RESULTS AND DISCUSSION

There are three main factors that influence decomposition dynamics *in situ*: (1) quality of litter as the substrate for decomposing organisms, (2) the type and abundance of the decomposers, and (3) the environmental conditions (e.g., temperature, moisture, oxygen and nutrient availability, pH) under which the decomposers live and assimilate the litter (Belyea 1996, Laiho 2006). This study focuses on the effects of persistent WL drawdown on litter decomposition at plant species (i.e. affected mainly by the environmental changes) and community level (i.e. additionally affected by the changes in vegetation community composition) at sites with different nutrient regimes (peatland types) and at different time scales (years and decades after the persistent WL drawdown).

4.1 Litter quality varied between litter types: implications for litter decomposability

Relatively clear grouping into growth forms (non-graminoid foliar litters, graminoids, woody litters, mosses) was found among the different litter types, based on their chemical composition (**I**). Non-graminoid foliar litters were rich in nutrients and extractives, and woody litters had a high Klason lignin concentration. Noteworthy, the graminoids were closer to woody litters than to the non-graminoid foliar litters. *Sphagnum* species were characterized by rather high concentration of p-hydroxyphenols (CuO oxidation phenolic products) and other components captured as soluble lignin and Klason lignin fraction (**I**).

Growth form may, to relatively large extent, predict the variation in litter decomposability (**III**, Hobbie 1996, Hobbie et al. 2000, Preston et al. 2000, Dorrepaal et al. 2005, Bragazza et al. 2007). Generally, foliar litters decompose fast while woody litters and mosses decompose slowly. Within these simplified growth form categories, there may still be such variation in litter quality that affects the decomposition rates (**III**, **IV**, Bragazza et al. 2007, Turetsky et al. 2008). Broad-leaf foliar litters had higher concentration of nutrients and polar extractives (e.g. soluble carbohydrates) and experienced fairly higher decomposition rates compared to needle-leaved foliar litters with higher concentration of nonpolar extractives (e.g. fats, oils, waxes) (**III**, Hobbie et al. 2000, Preston et al. 2000, Dorrepaal et al. 2005). Within the group of *Sphagnum* mosses, species of sections Acutifolia and Sphagnum (typical of hummocks and/or lawns) had a higher cellulose concentration compared to those of section Cuspidata (typical of hollows and/or lawns) which had high concentration of hemicellulose. Cellulose degradation starts somewhat later than the degradation of hemicellulose (Berg and McClaugherty 2003) and thus, the higher cellulose:hemicellulose ratio may be associated with slower decomposition of the hummock *Sphagnum* species (**III,** Johnson and Damman 1991, Limpens and Berendse 2003, Turetsky et al. 2008). Morphological differences between the different FWD size classes of the same plant species were reflected as surprisingly clear differences in litter quality that might contribute to differences in their decomposability (**IV**). Possible explanation might be the different proportion of bark and wood: the FWD size class with lower diameter has a higher proportion of bark, which has lower concentration of holocellulose and greater concentrations of nutrients and lignin compared to wood (Hyvönen et al. 2000, Ganjegunte et al. 2004).

Though no single chemical parameter could predict the variability in decomposition dynamics associated with such different materials as included in this study (see also Bragazza 2007), reasonably well predictions were possible with few chemical parameters, even in such a large dataset (**III**). Concentrations of total extractives and N (positive correlation with mass loss), Klason lignin and p-hydoxyphenols (lignin-like compounds, negative correlation with mass loss) accounted for about 40% of the total variation in aboveground litter mass loss. This gives the general characteristic of a substrate that the decomposers prefer to utilize: rich in nutrients, with high proportion of easily degradable compounds relative to the recalcitrant fraction.

4.2 Direct effects of WL drawdown were overruled by the indirect effects

WL drawdown had direct effects on litter quality at the species (litter type) level (**I**), microbial community composition (Peltoniemi 2010) and activity (**II**) and litter decomposition rates (**III**). However, the direct effects were minor compared to the indirect effects via changes in litter type composition and litter production (**I-III**; see also Fig. 3). This resulted in large accumulation of organic matter at the long-term drained plots, in spite of increased decomposition rates of the litter.

Sphagnum mosses that produce litter with low decomposability (Hobbie et al. 2000, Dorrepaal et al. 2005, Cornelissen et al. 2007) were typical of pristine conditions and following short-term WL drawdown (Fig. 4, **I**). Mosses other than *Sphagnum* species, mostly *Pleurozium schreberii*, whose litter quality did not generally differ much from that of Sphagna, increased their abundance after the long-term WL drawdown. Graminoid and forb litter typical of the pristine fens was continuously replaced by shrub, and finally tree litter (leaves, needles, branches, cones). Such changes in the relative abundance of different litter types then result in changes of litter quality (Fig. 6 in **I**) and decomposition rates (Fig. 3 in **III**) at the community level. This supports the postulate of Dorrepaal et al. (2005) and Aerts et al. (2009) that the direct effects of environmental changes on species-level litter traits may be overruled by the indirect effects via changes in the relative abundance of growth forms. Together, these results indicate that the direct impacts of climate change and/or forestry drainage on a peatland functioning are minor compared to the indirect effects via the shift in plant species and, consequently, litter type composition (see Fig. 3).

It is noteworthy that besides the increased soil aeration (direct effect of WL drawdown), environmental conditions for decomposition are in long-term further changed via the vegetation changes (indirect effect of WL drawdown, see Fig. 3). This study shows a drop in temperature associated with the site forestation, possibly due to tree canopy shading and evaporative cooling effect of trees. We did not find any negative effect of such decrease in temperature on litter decomposition rates (cf. Dorrepaal et al. 2009). The temperature effect was possibly overruled by other effects, i.e. litter type and soil characteristics, as those also changed following WL drawdown. Also, litter represents the youngest, most easily decomposable organic matter that has low temperature sensitivity but its response to temperature may increase as decomposition proceeds (Karhu et al. 2010).

Further, increased litter inputs (**I**) serve as increased source of nutrients and easily-metabolizable energy for decomposers that may enhance decomposition of recalcitrant materials (i.e. peat, woody litters; priming effect hypothesis, Bingeman et al. 1953). Moreover, the litter layer might (together with increasing tree canopy) serve as protection against UV-B radiation having negative effects on litter decomposers (Gehrke et al. 1995, Duguay and Klironomos 2000), as well as insulation keeping favourable moisture conditions. Such effects were not explicitly measured in this study and thus cannot be separated from the direct effects of WL drawdown.

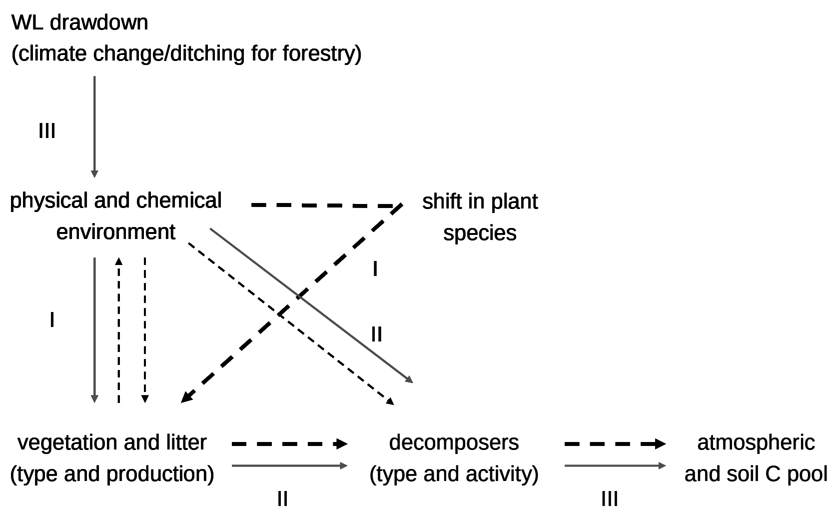

Figure 3. Schematic view of WL drawdown effects on C flow in peatlands. Direct effects of WL drawdown (full arrows) are overruled by indirect effects via shift in plant species composition (dotted arrows). Roman numerals refer to the particular articles of this thesis.

4.3 Accumulation of organic matter increased following long-term WL drawdown in spite of increased decomposition rates

In long-term, dramatically increased litter inputs (**I**) resulted in large accumulation of organic matter in spite of increased decomposition rates (**III**), see Fig. 4. This emphasizes the significance of litter production: if the inputs are high, organic matter accumulates at a site despite the high litter decomposability (**III, IV**).

The C balance of a drained peatland depends on 1) the rate of decomposition of the ‘‘old C’’ (peat accumulated before the WL drawdown), and 2) the rates of inputs and decomposition of the ‘‘new C’’ (litter produced by the changed vegetation after the WL drawdown) under the new environmental conditions (Laiho 2006). If the accumulation (inputs – decomposition losses) of the new organic matter exceeds the decomposition losses from the old peat, the peatland will remain a sink of C. If not, then the peatland will become a source of C to the atmosphere. The estimated annual C loss via heterotrophic soil respiration ranged from 145-670 g m^{-2} in boreal forestry-drained peatlands (Ojanen et al. 2010). The annual C inputs via litter production estimated in this study ranged from 190 to 200 g m^{-2} for the forestry-drained (LTD) plots, and from such inputs 110-130 g m^{-2} remained after 2 years. Considering that relatively large proportion of the measured litter losses (10-30%) may still be retained in the soil (Domish et al. 2000), it seems that a drained peatland may, under certain conditions defined mainly by the site nutrient regime (Ojanen et al. 2010), still act as a sink of atmospheric C. Our assumptions are based on 2-year decomposition data only, however. Longer-term decomposition results are needed to validate the further behaviour of the accumulated organic matter at the different WL regimes. Also, the measured “old C” loss may not include the possible priming effect of litter inputs on peat decomposition, as litter was removed from the sites before each measurement (Ojanen et al. 2010).

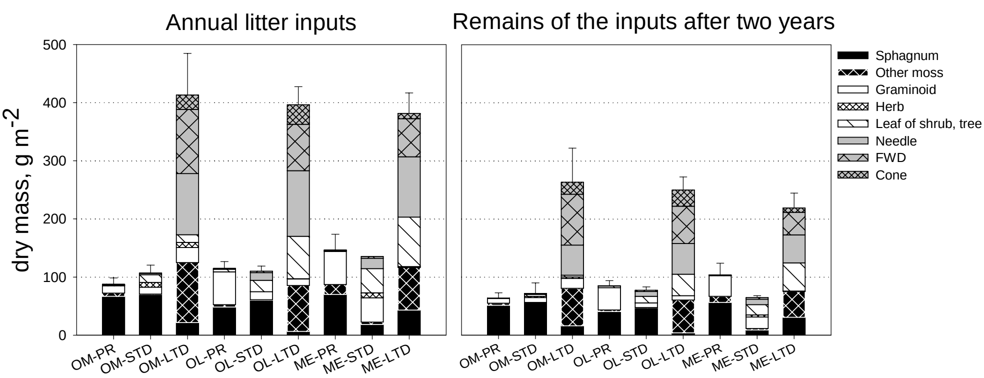

Figure 4. Annual litter inputs (**II**) vs. remains of the inputs after two years of decomposition (**III**). The error bars show standard errors for the total litter remains per given nutrient and water level (WL) regime. WL regimes: LTD, long-term WL drawdown; PR, pristine; STD, short-term WL drawdown. Site nutrient regimes: ME, mesotrophic fen (minerotrophic); OL, oligotrophic fen (minerotrophic); OM, bog (ombrotrophic). FWD, fine woody debris (twigs, branches, bark).

The composition and quality of the accumulated organic matter varied between the pristine and long-term drained conditions (Fig. 4, **III**). In the pristine plots, litter remains after 2 years of decomposition consisted mainly of *Sphagnum* and graminoid litter with initially high content of holocellulose-comprising sugars and CuO oxidation phenolic products (**I**) and low to moderate decomposability (**III**). Following short- term WL drawdown, composition of litter remains did not change at the bog. At fens relative proportions of graminoid and *Sphagnum* litter remains decreased, while that of tree and shrub woody and foliar litter increased. Following long-term WL drawdown, litter remains consisted mainly of woody litter with initially high lignin content, C:N, lignin:N, C:P and low decomposability; foliar litter of trees and shrubs with initially high content of nutrients and easily extractable compounds and high decomposability; and forest moss, mainly *Pleurozium schreberi*, with initially high content of holocellulose-comprising sugars and lignin and moderate decomposability (**I**, **III**).

Based on the variation in litter quality we could, to rather large extent, predict further decomposition rates of the newly accumulated organic matter (**III**, **IV**) if the environmental conditions did not change. However, litter will eventually get deposited into waterlogged conditions in the pristine plots and there the environmental effect on decomposition will overwhelm the litter type effects. Longer-term decomposition results are thus needed to validate the further behaviour of the accumulated organic matter at the different WL regimes.

4.4 The effects of WL drawdown were more pronounced in long-term when the indirect effects gained dominance

The effects of WL drawdown on the site environment, vegetation communities and microbial decomposers were more pronounced in long-term (decades) relative to short-term (years) (**I-III**, Peltoniemi 2010). The short-term changes reflect transient conditions where the direct effects of WL drawdown are dominant: improved conditions for aerobic decomposition are linked with unchanged or lowered amounts of organic matter inputs (**I**), most likely facilitating a net C loss from the soil. In contrast, the long-term changes reflect a longer-lasting situation as the ecosystem becomes adapted to the new conditions and the indirect effects of WL drawdown gain dominance: the increased litter inputs (**I**) may at least partly compensate for the increased rates of peat decomposition (**III**, Ojanen et al. 2010). So far, too few studies have considered the long-term aspect.

4.5 The effects of WL drawdown were more pronounced at sites with more nutrients

At the different sites (peatland types), the response of the site environment, vegetation communities and microbial decomposers to persistent WL drawdown is pronounced with different strength (**I-III**, Laine et al. 1995, Peltoniemi 2010). At the fens, the changes mostly appeared already after the short-term WL drawdown, while at the more nutrient-limited bog they were expressed only in the long-term.

Site nutrient regime had direct effects on litter quality and inputs at the species (litter type) level (**I**), microbial community composition (Peltoniemi 2010) and activity (**II**) and litter decomposition rates (**III**). The direct effects were again minor compared to the indirect effects that reflect the variation in vegetation communities between the different peatland types, and all the site effects were smaller than the effects of WL drawdown (**I-III**, Peltoniemi 2010).

The site effects seem to vary between the different processes. Environmental conditions for decomposition are generally more favourable at minerotrophic (fen) sites compared to ombrotrophic (bog) sites, as showed by decomposition of cellulose (**III**) and peat (Minkkinen et al. 2007, Ojanen et al. 2010). However, microbial activity and decomposition rates of litter tended to be higher at bog (**II, III**). Peat (old C) and cellulose may behave differently from litter (new C). Such different behaviour is also reflected in the climatic response (**IV**). Still, site differences in litter decomposition were partly explained by the surface peat N and P concentration (**III**, **IV**).

4.6 Accelerated decomposition along the north-south climatic gradient was associated with increased temperature and precipitation

The results on FWD decomposition in drained peatlands on the climatic gradient from the north boreal (Northern Finland) to hemiboreal (Central Estonia) conditions showed that mass loss rates overall increased from north to south (**IV**). Temperature and moisture are generally the limiting factors for decomposition in the boreal and temperate zones (Palosuo et al. 2005). In our sites, both temperature and precipitation increased southwards (Table 2 in **IV**), and it is thus difficult to separate their effects. Temperature, as indicated by air T sums over the incubation period, showed a smaller effect on FWD mass loss than precipitation in the model analysis (not shown). Sites characterized by a cold climate still experience significant mass loss (Moore 1983), partly since snow cover moderates temperatures in the litter layer (Hardy et al. 2001) and partly due to the presence of microbial communities active under low temperatures (Schmidt and Lipson 2004).

The single weather-based variable most related to FWD mass loss was summer precipitation minus PET sum (PREC-PET), which combined the effects of both summer precipitation and mean air T. The best results were obtained when sums of positive PREC-PET values, that indicate moisture surplus, were used in the models. PET and precipitation, as well as actual evapotranspiration (AET) which incorporates these two variables, have also been shown to correlate with foliar litter mass loss across a wide range of climatic conditions (Berg et al. 1993, Johansson 1994, Berg et al. 2000, Gholz et al. 2000, Berg and Meentemeyer 2002).

In contrast to our results on FWD decomposition, Minkkinen et al. (2007) found the heterotrophic soil respiration from old organic matter to be highest in the north (see also Bringmark and Bringmark 1991). The north boreal site experiences longer periods with soil temperature at 5 cm below the soil surface higher than 0 °C during the winter because of better insulation by the snow cover, and this may play a significant role in soil respiration, but obviously not in the decomposition of FWD on the soil surface. The number of days with soil T > 0 °C during winter did not affect FWD mass loss, results not shown. The microbial communities decomposing peat seem to respond differently to variation in environmental conditions, such as winter temperatures or soil nutrient regimes, compared to those decomposing FWD in the forest floor. Dalias et al. (2001) found that a substrate initially decomposing at a higher temperature was in later stages degraded more slowly than the same substrate initially degraded at a lower temperature. As FWD was still a continuously changing substrate, the effects of climate on its decomposition may change with time.

4.7 Implications for soil C modelling

This study demonstrates that the shift in vegetation composition as a response to climate and/or land-use change is the main factor affecting the peatland ecosystem C cycle (**I-III**). Thus, dynamic vegetation is a necessity in any models applied for estimating responses of C fluxes to changes in environmental conditions. It is noteworthy that the time scale for vegetation changes caused by hydrological changes needs to extend to decades.

The study provides detailed chemical characterization of plant litters typical of boreal peatland sites (**I, IV**) with their decomposition rates (**III, IV**), and offers grouping of litter types (plant species and part) into PFTs based on the chemical quality (**I**) and/or decomposability (**III**) that the models could directly utilize. Of the existing models, the dynamic global vegetation model LPJ-Why (Wania et al. 2009), and the ecosystem-level models by Zhang et al. (2002) and Bauer (2004) cover the minimum requirement of PFT and/or litter type separation quite well. However, model development for simulating vegetation community level successional dynamics of ecohydrology-vegetation interactions could benefit from grouping provided by this study that is based on the real (measured) plant litter characteristics.

Overall, the role of the changing vegetation in the C cycling following a persistent lowering of the water level has been largely neglected in previous research. Changes in vegetation community composition may affect the decomposition process in several ways: via shifts in litter types and their chemical quality (**I, III**), but also via interactions (either positive or negative) between different litter types when decomposing as mixtures (Gartner and Cardon 2004), and via the specific conditions and decomposer communities that develop under certain vegetation (e.g., Nilsson et al. 2008, Laganière et al. 2010). Since the vegetation of fens and bogs responds differently to WL drawdown it is likely that the implications to soil functioning will also differ.

The changes in litter type composition (**I**) will eventually result in a 2-layer, or 2-compartment, structure in the oxic surface peat; atop the "old peat" layer consisting of a continuum of decomposition products from the pre-WL drawdown litter types, a layer of the "new litter" will be introduced (see also Laiho 2006). The two layers or compartments may be very different, as shown by the litter quality data (**I**). The old peat compartment may only decompose, and this may be enhanced by priming effect of the new compartment (Bingeman et al. 1953). The new compartment is a dynamic system where both inputs and decomposition take place. As a consequence, interpretation of CO_2-exchange studies gets more complicated. Only few studies separated gas fluxes from decomposing peat and decomposing fresh litter (Minkkinen et al. 2007, Jaatinen et al. 2008, Mäkiranta et al. 2008, Ojanen et al. 2010). The increase in the rate of decomposition of the old peat may be a more critical parameter than the C exchange of the litter layer that may, however, have a major contribution to the net CO_2 efflux (Laiho et al. 2008) and will mask any changes in the soil C balance unless the quantity of the litter inputs is known and accounted for.

Simulations of a peatland ecosystem responses to climate change presented in this study are based on WL drawdown only. The expected increase in air temperature (Houghton et al. 2001, Good et al. 2006, IPCC 2007) and further localized warming via lowered albedo associated with forestation of an initially open land (Betts 2000) are not included here, though these factors are proposed to have substantial effects on ecosystem C cycle (Betts 2000, Dorrepaal 2009). Contrary to such expectations, however, results of this study clearly show a drop in temperature associated with the site forestation, possibly due to tree canopy shading and evaporative cooling effect of trees. In the existing models the possible lowering of soil temperature as the long-term response of a peatland ecosystem to climatic warming has not yet been considered.

4.8 NIRS as an alternative method for estimating litter quality and decomposability

NIRS proved to be an accurate and fast method for the estimation of plant litter quality (**V**) that might be highly relevant for decomposition and C dynamics in peatlands (**I-IV**). Models constructed for specific litter types (or PFTs) seem to yield better predictions than models combining different litter types if the dataset is large and varied enough to yield significant correlations between NIR spectra and the chemical properties (**V**).

The accuracy of the calibrations (Table 7.4 and Figs. 7.2-5 in **V**) was generally among the best results obtained in published studies on plant litters or biomass (e.g., Jofre et al. 1992, Gillon et al. 1999, Bouchard et al. 2003, Stenberg et al. 2004), organic soils (Coûteaux et al. 2003) as well as mineral soils or mineral soil-chemical-organic materials mixtures (Chang and Laird 2002, McCarty et al. 2002 Coûteaux et al. 2003, Terhoeven-Urselmans et al. 2006). Few of the quality parameters were not estimated well with NIRS (Table 7.4, Figs. 7.2 and 7.5 in **V**). The reason might be a possible inaccuracy of the reference methods, and/or low variation in the measured parameter within the dataset.

Litter decomposition rates cannot be detected directly with NIRS, but could be detected indirectly because of their strong relationship to initial litter quality (**III**, **IV**). The predictions made here for several litter types performed somewhat better for the 1-year mass loss compared to accumulated mass loss after 2 years (Fig. 5), probably due to increased role of site environment on litter mass loss in the second year of decomposition (**IV**). Still, the mass loss predictions were very satisfactory and might be widely applied in ecological studies.

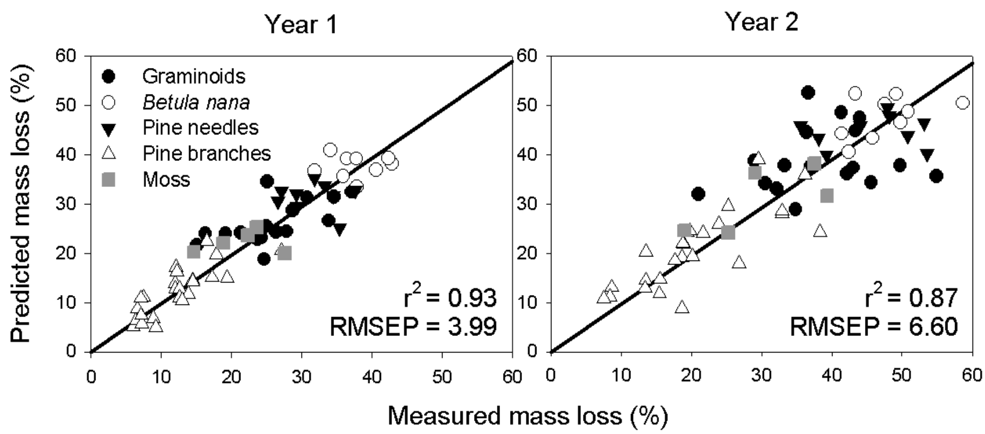

Figure 5. NIRS models predicting litter mass loss rates.

5 CONCLUSIONS

The study demonstrates that the direct effects of changing climate and/or land-use on decomposition and C accumulation in peatlands are in long-term (decades) overruled by the indirect effects via changes in vegetation community composition. Even though plant litter decomposition rates increase following WL drawdown, the accumulation of new organic matter still increases due to dramatically increased litter inputs. The accumulation seems to even exceed the decomposition of the old peat at nutrient-poor sites. Boreal peatlands under changing climate and/or land-use may thus still act as a sink of atmospheric C, but the quality (chemical composition) of accumulated C will greatly differ from that accumulated in pristine conditions, suggesting differences in its further behaviour.

The response of a peatland ecosystem to persistent WL drawdown is more pronounced in long-term (decades) relative to short-term (years), and varies between the different peatland types, being stronger at fens compared to bogs.

This study was designed to fill some critical gaps in our knowledge of the C cycle in peatlands under changing hydrology (Laiho 2006). The findings may be summarized as following:

- The environmental changes induced by WL drawdown (increased soil aeration, peat compaction, drop in temperature and pH) have small effects on litter decomposition compared to the indirect effects via the shift in the structure of vegetation communities.
- After short-term WL drawdown, changes in the amounts and quality of litter inputs are minor. After long-term WL drawdown, however, litter inputs dramatically increase due to increased tree litter inputs, and this lead to a change of litter quality at the community level (more lignified, but also more extractives, nutrients) and high accumulation of the organic matter at the sites.
- At the community level, decomposition rates increase following WL drawdown. The study provides data that enable a direct testing and reparameterization of the existing decomposition models (e.g., Liski et al. 2003, Zhang et al. 2002) with measured inputs and mass loss rates for different litter types with known organic composition. Combined with models for heterotrophic soil respiration (e.g., Ojanen et al. 2010), the whole C cycle of peatlands might be modelled to test whether drainage or climate change will lead to a site being a source or sink of C.
- Results of this study clearly show a drop in temperature associated with the site forestation, possibly due to tree canopy shading and evaporative cooling effect of trees. In the existing models the possible lowering of soil temperature as the long-term response of a peatland ecosystem to climatic warming has not yet been considered.
- NIRS was tested as a “cheap and fast” method for predicting litter quality and decomposition rates. The predictions were generally very satisfactory and showed a good potential for their wide use in ecological studies.

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