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Kokfelt, Ulla

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Ulla Kokfelt

Avhandling

Att med tillstånd från Naturvetenskapliga Fakulteten vid Lunds Universitet för avläggande av filosofie doktorsexamen, offentligen försvaras i Geologiska Institutionens föreläsningssal Pangea, Sölvegatan 12, fredagen den 2 april 2009 kl. 14.00.

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Abstract

This thesis assesses aspects of the wetland development, permafrost dynamics and associated changes in carbon and nutrient cycling of the Stordalen Mire in northern Sweden. Various ecological and biogeochemical analyses of one peat and two lake sediment sequences were conducted, including analyses of organic matter and carbonate content, mosses, diatoms, testate amoebae, pigments, carbon and nitrogen and their stable isotopes, near infrared spectroscopy and biogenic silica. Results revealed that the structural development of the mire occurred during the later part of the Holocene. Peat inception was dated at 4700 cal BP and onset of organic sedimentation in two adjacent lake basins occurred at 3400 and 2650 cal BP. Fen peat accumulated until minimum 2800 cal BP, and after c.2650 cal BP an early permafrost aggradation phase likely caused frost heave and significant changes in the wetland structure and hydrology. Peat is largely missing in the examined core between 2800 and 1350 cal BP, reflecting either environmental stress causing a decrease/cease of peat accumulation and/or erosion of previously formed peat. An increased content of redeposited peat in one of the lakes after c.2100 cal BP, points to mire erosion caused by permafrost decay. A high nutrient/productivity layer in the other lake between 1900 and 1800 cal BP may have been related to the same event in the mire. Sedge peat accumulated from 1350 cal BP. Renewed permafrost aggradation is indicated indirectly around 700 cal BP and directly 120 cal BP from changes in peat building vegetation. Fen peat and transitions between dominating mire vegetation communities were characterized by frequent diatoms and high nutrient concentrations. Permafrost phases were associated with poor fen and bog formation, and thus considerably more acidic conditions in the mire as compared to pH conditions when richer fen communities dominated. This development resulted in more acidic runoff to adjacent lakes and affected carbonate precipitation there. Further, poor catchment retention of nutrients during poor fen/bog stages, probably caused increased fluxes of nutrients out of the system, stimulating primary lake productivity in adjacent lakes. Increased lake productivity in turn caused increased oxygen consumption for decomposition at the lake bottom, and thus anoxic conditions. Thereby an increased flux of phosphorous from the sediment triggered a state of self-sustained eutrophication during two centuries, preceding the onset of 20th century permafrost thaw.

Proxy indications of peat surface moisture conditions and lake-water TOC concentration dynamics during the last 100 years were reconstructed by means of testate amoebae assemblages in peat and near infrared spectroscopy and the carbon isotopic composition of lake sediment bulk organic matter. These results revealed a close connection with decadal trends of total annual and summer precipitation as well as single years with anomalously high precipitation, especially in the late summer. The proxy data could thus not be directly linked to monitored trends in active layer thickness.

Key words: subarctic Sweden, palsa mire development, permafrost history, peat, lake sediments, carbon and nutrient cycling

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Ulla Kokfelt

Quaternary Sciences, Department of Geology, GeoBiosphere Science Centre,
Lund University, SE-223-62 Lund, Sweden.

This thesis is based on four papers (appendices I-IV), which will be referred to by their roman numeral (I-IV). The papers are appended at the end of the thesis.

Appendix I: Karlsson, J., Christensen, T.R., Friborg, T., Förster, F., Hammarlund, D., Jackowicz-Korczynski, M., Kokfelt, U., Roehm, C. & Rosén, P.: Quantifying the relative importance of lake emissions in the carbon budget of a subarctic catchment. *Manuscript.*

Appendix II: Kokfelt, U., Rosén, P. , Schoning, K., Christensen, T.R., Förster, J., Karlsson, J., Reuss, N., Rundgren, M., Callaghan, T.V., Jonasson, C. & Hammarlund, D. (2009): Ecosystem responses to increased precipitation and permafrost decay in subarctic Sweden inferred from peat and lake sediments. *Global Change Biology*, doi: 10.1111/j.1365-2486.2009.01880.x.

Appendix III: Kokfelt, U., Reuss, N., Struyf, E., Sonesson, M., Rundgren, M., Skog, G., Rosén, P. & Hammarlund, D.: Late Holocene wetland development, permafrost history and nutrient cycling inferred from peat and lake sediment records in subarctic Sweden. Submitted to *Journal of Paleolimnology*.

Appendix IV: Kokfelt, U., Struyf, E. & Randsalu, L.: Diatoms in peat - opportunist vegetation in a changing environment. Submitted to *Soil Biology and Biochemistry*.

The authors contribution to papers

Paper I: I contributed to initial data selection, interpretations and discussions and was the main person responsible for the age model and the carbon accumulation rate data from the lake. I was also active during several stages of improving the manuscript.

Paper II: I developed the idea for this paper, was the main person responsible for the dating and participated in fieldwork. I wrote most parts of the paper. All authors contributed however to the manuscript.

Paper III: The background idea for this paper was developed by Dan Hammarlund and Torben Christensen. I participated in the fieldwork and was the main person responsible for all radiocarbon dating and for the age model on the peat sequence. Lake age models were developed together with Dan Hammarlund and Göran Skog. I was the main person responsible for organic matter, carbonate, carbon and nitrogen analyses on the peat sequence and on the Lake Inre Harrsjön sediment sequence, and for calculation of accumulation rates. I developed the paper and wrote most parts. All authors contributed however to the manuscript.

Paper IV: I developed the idea for this paper together with Eric Struyf and we jointly wrote the paper. Linda Randsalu conducted all diatom analysis. I participated in the fieldwotk.

CONTENTS

Appendices

1. Introduction

Resolving ecosystem responses and feedbacks to climate change has become a recurrent issue to many fields of research throughout the few last decades. Anthropogenic emissions are responsible for rising concentrations of carbondioxide and methane in the atmosphere, and there is broad consensus that these emissions are and will be responsible for higher global temperatures and changing precipitation patterns (IPCC 2007). Such statements and predictions increase the need to understand the effects of ongoing and predicted climate change on ecosystems and their carbon balance. Carbon stored in different terrestrial, limnic and oceanic reservoirs are important as these, under certain conditions, can be emitted to the atmosphere and further amplify climate change.

Carbon storage in peat-forming wetlands and lakes is of a considerable size. Peat-forming wetlands and lakes are widespread in the northern hemisphere and have accumulated vast amounts of carbon since deglaciation. It is estimated that up to 455 Pg (= 10^{15} g) or *c.*30% of the world pool of soil carbon is stored in northern peatlands (Gorham 1991). Lakes are estimated to store 19-27 Pg of carbon in the boreal region and are, in Finland, considered to store the second largest carbon stocks after peatlands (Kortelainen et al. 2004). Many boreal and arctic peatlands are underlain by permafrost, which serve as a stabilizing factor for these deposits. Permafrost in such settings exerts a primary control on hydrology (Oksanen & Kuhry 2003). Therefore vegetation, carbon and nutrient cycling will be affected, if permafrost thaws (e.g. Christensen et al. 2004).

Lowland permafrost in the discontinuous permafrost zone is restricted to palsa mires (Johansson et al. 2006a). Palsas or peat plateaus are morphological peat forms elevated above the surrounding wetter fen areas (Seppälä 1986). Sparse vascular plant cover on poor fen surfaces promotes snowdrift that in this way may be exposed in the winter. A thin snow-cover is critical for the formation of embryo palsas (Seppälä 1986) as this allows for winter-cold to penetrate deep into the peat. Once ice has formed deep enough to survive summer temperatures, due to the insulating capacity of dry *Sphagnum*, volumetric expansion causes the surface to be slightly elevated above the surrounding carpet vegetation. This may allow hummock-species to colonise and further increase micro-topographic differences. Thereby snowdrift is enhanced from elevated parts the following winter, where the cold again penetrates the barren ground, and a self-sustaining process, leading to further aggradation of permafrost, is initiated. Elevation of the peat surface and presence of permafrost beneath, create a poor environment, favouring the growth of ombrotrophic vegetation communities, i.e. vegetation that depends exclusively on water and nutrient supply from the atmosphere and internal recycling (e.g. Sjörs 1948; Malmer & Nihlgård 1980). Palsas have a cyclic nature; because of growth they reach a certain level where the surface cracks open, heat penetrates to the frozen core, and the palsa collapses (e.g. Zuidhoff & Kolstrup 2000). Such a development may result in block-erosion to leave a collapse scar or a thermokarst pond, often the only remains of the palsa. The ever evolving dynamics of this landscape type and the heterogeneity of palsa mires with their dry palsa surfaces, wet fen areas and scattered ponds, make them fascinating and also important, for example as they support a diverse bird life (Luoto et al. 2004a).

The optimal mean annual temperature interval for palsas is -5 to -3°C (Luoto et al. 2004b) but they exist at higher mean annual temperatures, as in parts of northern Fennoscandia, where the distribution of lowland permafrost is closely related to the precipitation shadow, east of the Scandes Mountains (Luoto et al. 2004b). Both low snow cover during the winter and dry peat surfaces during the summer are important parameters for the existence of permafrost (Seppälä 1986), but other factors such as short summers and vegetation cover may also be decisive for the presence or absence of permafrost (Johansson et al. 2006a).

In the Torneträsk area in northern Sweden, the mean annual temperature has been just

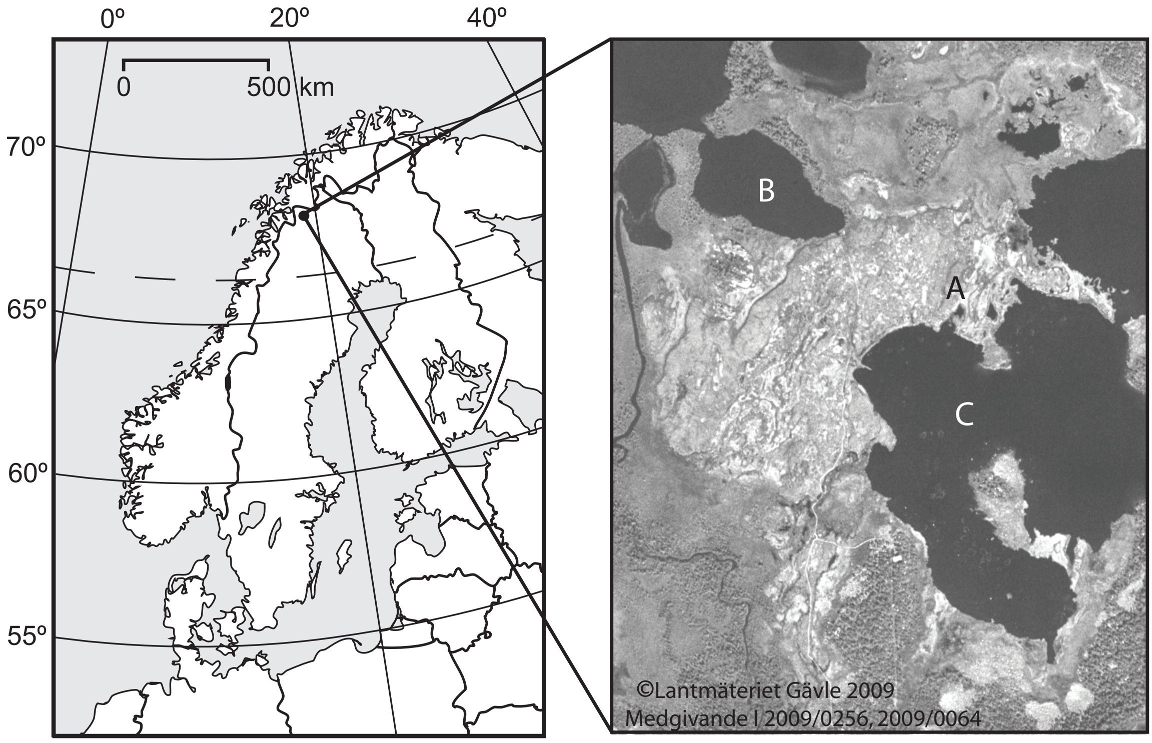

Figure 1. *Map showing the position of the Stordalen Mire in northernmost Sweden. The right picture shows an aerial photograph of the mire with the three sampling locations: A) the Stordalen peat core, B) Lake Inre Harrsjön and C) Lake Villasjön.*

below or around 0˚C for the last century (Johansson et al. 2008) and palsa mires in the area are therefore close to their limit of existence (Åkerman & Malmström 1986). Whereas this is unfortunate with regards to the potential loss of this landscape type in the area, it allows the existence of very sensitive ecosystems, where many aspects of short term effects of natural and/or human induced climatic variability can be studied.

The Stordalen Mire in northern Sweden (Fig. 1) has been subject to research since the early 1950s (reviewed by Bäckstrand 2008). During the International Biological Program (IBP) 1970-1974, which aimed to derive basic information on the productivity of the tundra area of the world, research activities at Stordalen were intensified. The site was chosen as representative for a subarctic ombrotrophic mire on permafrost (Sonesson 1980). A large number of publications have since emerged from studies on the mire, and have provided a firm foundation for the understanding of how this ecosystem functions. Recently, Bäckstrand (2008) reviewed the last 50 years of activities at the mire, activities that are part of the comprehensive research tradition on the subarctic environment, centered around the Abisko Scientific Research Station (ANS).

Over the last decade there has been increased focus on how the thawing of permafrost influences ecology, vegetation, hydrology and greenhouse gas emissions from the mire (Christensen et al. 2004; Malmer et al. 2005; Johansson et al. 2006b). These parameters are tightly connected, as the presence or absence of permafrost controls the vegetation, that in turn, to a large extent, controls greenhouse gas emissions to the atmosphere (Joabsson et al. 1999; Ström & Christensen 2007). Decades of intensive and multifaceted research on the functioning of the subarctic landscape and its sink and source functions of different compartments, led Christensen and co-authors (2007) to create a modern carbon budget integrated over the catchment, to determine a holistic understanding of carbon cycling in the landscape. Many wild cards in the budget were described as poorly established, for example the carbon export to lakes and streams and their carbon accumulation. It has been recognized that only around 50% of the terrestrial carbon exported to inland-waters reach the ocean (Cole et al. 2007), and that inland waters such as lakes and streams, act as mineralisation sites of terrestrial exported organic carbon (Karlsson et al. 2007), and as conduits of CO_2 and CH_4 to the atmosphere (Kling et al. 1991; Cole et al. 1994; Algesten et al. 2004). Even low productive clear water lakes may be net heterotrophic (Karlsson 2001). This means that more carbon is respired in the lake than taken up by lake producers, resulting in lake waters super-saturated with respect to CO_2. Hence, where mires act as net sinks of carbon (here disregarding calculations of radiative forcing potentials due to emission of methane), streams and lakes are estimated to be the most important sources of carbon to the atmosphere from the sub-arctic landscape (Christensen et al. 2007). Quantifying the amount of carbon being exported from terrestrial ecosystems to lakes and streams, in order to integrate inland waters in the global carbon cycle, is a major challenge and focus of recent research (e.g. Cole et al. 2007; Karlsson & Giesler 2008).

The sink or source function of a terrestrial ecosystem is typically measured by eddy covariance or chamber measurement techniques, as the balance between fluxes (photosynthesis versus respiration) to and from the atmosphere (e.g. Johansson et al. 2006b). Measurements of this net ecosystem exchange (termed NEE) quantifies the carbon flux in and out of a system, where a positive value denotes a net source to the atmosphere and a negative value denotes a net sink from the atmosphere to the terrestrial system. However, NEE measurements typically overestimate the sink function of terrestrial ecosystems (Roulet et al. 2007), as losses to the aquatic environment are not accounted for. Therefore, carbon accumulation rates of different vegetation types, as well as the export of carbon to lakes and streams and the temporal variability of this export in relation to climate and catchment changes, are important to understand and quantify.

Because the distribution of permafrost can be in disequilibrium with rising temperatures (Halsey et al. 1995), contemporary studies are unlikely to capture the full impacts of ongoing climate change. Therefore, stratigraphic records from peatlands and their adjacent lakes are important, as they include the temporal perspective in their stratigraphy.

In this thesis, stratigraphic records obtained on peat and lake sediment sequences from the Stordalen Mire and adjacent lakes are used to identify different aspects of ecosystem dynamics relation to internal and external forcing on decadal to millennial timescales. The longer perspective focuses on wetland development, permafrost history and carbon and nutrient cycling over the last *c.*5000 years. In a short perspective, the focus is to understand recent ecosystem variability inferred from peat and lake sediment cores in relation to climate and permafrost dynamics over the last century. The ultimate goal is to add to the understanding of how future climate change may alter the mires and lakes, and their carbon and nutrient cycling in this subarctic landscape.

1.1 Aims, objective and research questions

The general aim of this thesis was to use peat and lake sediment records to analyse aspects of the Holocene development of the Stordalen Mire and adjacent lakes, permafrost history and temporal changes in carbon and nutrient cycling. A further aim was to test high-resolution stratigraphical peat and lake sediment records covering the last 100 years, against time series of temperature and precipitation since 1913 and active layer thickness data since 1978, in order to examine to which extent these reflect monitored changes in permafrost decay.

More specific obejectives and research questions were to:

- Date peat inception at Stordalen and the onset of organic sediment deposition in adjacent lakes.

- Date indications of permafrost aggradation and degradation in the mire.

- Determine the long term storage capacity of carbon, nitrogen and biogenic silica in peat and lake sediments.

- Reconstruct recent changes in soil moisture conditions using testate amoebae.

- Assess past changes in the carbon export based on quantitative and qualitative approaches.

- Describe lake ecosystem responses to changes in catchment, climate and permafrost.

2. Study area

2.1 The Torneträsk area and Stordalen

The Torneträsk area is situated in northern Sweden at 68°N (Fig. 1), in the Scandes mountain range. The geology of the area is characterized by nappes consisting of partly carbonaceous meta-sediments, overthrusting the crystalline basement (Lindström et al. 1985). The mountains, with peaks up to 1000 m a.s.l., create a precipitation shadow to the east, resulting in an annual precipitation of only *c.*300 mm (1961-1991) around the village of Abisko (Alexandersson et al. 1991). The mean annual temperature fluctuates just below and sometimes above 0°C (Johansson et al. 2008), with the temperature variability of the 20th Century broadly corresponding to the general northern Hemisphere temperature development (e.g. Hurrell 1996; Moberg et al. 2005). Sub-alpine birch forest, lakes and peatlands characterize the lowlands around the large lake Torneträsk, where the tree-line reach an altitude of 600-800 m a.s.l. (Barnekow 1999).

The Stordalen Mire (N 68°21′, E 19°03′; Sonesson 1980) is a palsa mire located 10 km east of Abisko, Sweden, *c.*200 km north of the Arctic Circle (Fig. 1). The mire is situated in the discontinuous permafrost zone where permafrost in low elevations primarily occurs in peatlands (Johansson et al. 2006a). A peat plateau containing permafrost dominates the central part of the mire, and is characterized by hummock/hollow microtopography, predominantly with bog communities. More peripheral parts of the mire are dominated by poor fen areas with permafrost below palsas. A recent shift towards increased coverage of wet minerotrophic communities documented by Malmer et al. (2005) was related to a change in the surface structure of the mire due to disintegrating and melting permafrost (Christensen et al. 2004).

The central mire is bordered by lakes to the west and east (Fig. 1). The relatively large (0.17 km^2) and shallow (maximum depth 1.3 m) Lake Villasjön to the east, with a pH around 6.5, drains through a wetter area north of the central and permafrost-dominated part of the mire, flowing into Lake Inre Harrsjön. Lake Inre Harrsjön to the west is a small lake (0.02 km^2) with a maximum depth of 5 m and a pH of *c.*7.0. The relatively high pH reflects the occurrence of carbonate-containing bedrock in the drainage area (Lindström et al. 1985). Downstream, the lake is connected to a system of lakes to the west and northwest. Also, inflow from two springs to the south and northeast of Lake Inre Harrsjön has been observed. These have pH values between 6.5 and 7.0. In contrast, runoff from the mire is acidic with a pH around 4 in the plateau area and up to 4.5 in the poor fen areas (Nilsson 2006).

2.2 Holocene environmental and climate development

Holocene environmental and climate development in Northern Fennoscandia and in the Abisko region is well constrained by various studies. Pollen analytical studies (Sonesson 1974; Berglund et al. 1996; Barnekow 2000; Barnekow & Sandgren 2001; Bigler et al. 2002) give an overall consistent picture of

Holocene vegetation zones. After deglaciation *c.*10000 cal BP the area was dominated by open vegetation with *Hippophaë rhamnoides, Juniperus communis, Salix* and *Betula*. A few hundred years later, open *Betula* woodlands with *Salix* and ferns established. At 8800 cal BP *Juniperus communis* expanded to form a thick under-storey in the *Betula* woodland (Bigler at al. 2002). *Pinus* arrived in the area at 7500-7600 cal BP when a strong oceanic influence prevailed with warm and moist conditions (Hammarlund et al. 2002). Optimum conditions for pine and the maximum extent above the present tree-line existed at 6300-4500 cal BP (Barnekow 1999), when oceanic influence weakened, and precipitation decreased (Hammarlund et al. 2002). Pine declined, initially at high altitudes *c.*4500 cal BP, but a gradual retreat from the whole region, also at low altitudes, continued until *c.*2800 cal BP, causing dominance of sub-alpine birch-woodlands (Barnekow 1999). After *c.*2800 cal BP the climate has been characterized by great variability. The extensive tree-ring series presented by Grudd et al. (2002) reveal a very variable period between 2550 and 1950 cal BP. During this period the pine tree-line was suppressed (Kullti et al. 2006) and the first evidence for permafrost formation in Fennoscandia has been dated (Oksanen 2006). A cold period corresponding to the Little Ice Age (LIA) was initiated at *c.*850 cal BP (Grudd et al. 2002) and lasted until the end of the last century, when summer temperatures rose (Holmgren & Tjus 1996). The present day climate around Abisko is characterized by relatively warm summer conditions that have led to an increasing thickness of the active layer in soils above permafrost (Åkerman & Johansson 2008). Recent research indicates that similar warm or warmer summers occurred *c.*1200, 950, 550 and 200 cal BP and that the Medieval Warm Period (MWP) was probably significantly warmer during April to October than today (Grudd 2008).

3. Material and methods

3.1 Fieldwork, core correlations and sampling

Peat and lake sediment cores were retrieved for stratigraphic analyses during fieldwork in September 2003, March 2004 and January 2005. The second winter-fieldwork session in January 2005 became necessary, as the first set of lake sediment cores retrieved in March 2004 unfortunately disappeared during transport from Abisko to Lund. They arrived two years later. The new winter fieldwork in 2005 however resulted in improved sampling of the Lake Inre Harrsjön surface sediments with a freeze corer, and was thus a net advantage to the project. One peat core and two lake sediment sequences were retreived (Fig. 1). Photographs of the three coring sites and their sediments are shown in Figure 2. The peat sequence (A) was cored in September 2003 using a monolith corer for the uppermost 66 cm and a Russian corer (10 cm) for deeper levels. In January 2005 the two lakes: Lake Inre Harrsjön (B) and Lake Villasjön (C) were cored using a Russian corer (Jowsey 1966) with a diameter of 10 cm. The uppermost sediment sequence in Lake Inre Harrsjön was sampled using two different methods: a Kajak gravity corer (Renberg 2008) and a freeze corer (Renberg 1981). Correlations between individual cores were based on a combination of organic matter, carbon and water content, magnetic susceptibility records or on significant lithological changes.

3.2 Dating and chronologies

Reliable chronologies are important for comparison of records and for calculation of long term accumulation rates. In this thesis chronologies are based on radiometric dating (^{14}C and ^{210}Pb) and in the case of Lake Inre Harrsjön also on Bayesian modelling (Appleby & Oldfield 1978; Appleby 2001; Reimer et al. 2004; Skog 2007; Blockley et al. 2007; Bronk Ramsey 2008).

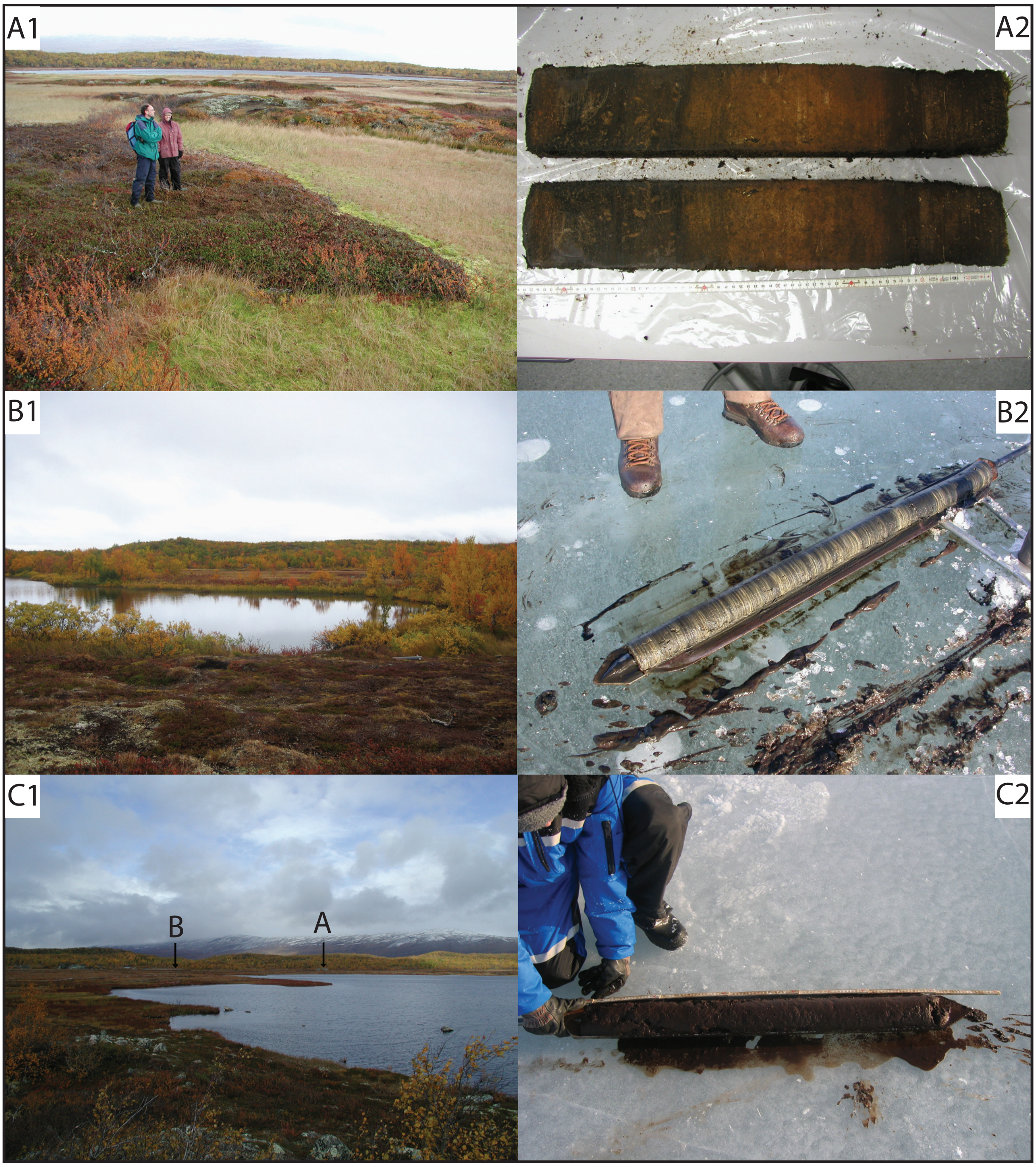

Figure 2. *Pictures from the three sampling sites (A, B and C also refers to Fig. 1) and of their sediments. A1: The coring site for the peat core; A2: the upper peat core (0-66 cm, surface to the right); B1: Lake Inre Harrsjön with palsa surfaces in the foreground and wetter fen areas in the background; B2: example of the carbonate laminated gyttja from the lake (photo: D. Hammarlund); C1: Lake Villasjön. Arrows indicate the location of Lake Inre Harrsjön and the sampling location for the peat core; C2: example of the homogenuous organic sediments (gyttja) from the lake.*

The chronologies of the peat sequence and of the Lake Inre Harrsjön sediment sequence were based on a combination of ^{210}Pb dating of the uppermost sediments combined with ^{14}C dates on plant remains from deeper levels (paper II and III). The chronology of the Lake Villasjön sediment sequence was based on ^{14}C dating, exclusively (paper II).

3.3 Magnetic susceptibility

Magnetic susceptibility is the degree of magnetisation of a material in response to an applied magnetic field (Evans & Heller 2003). In sediments this parameter reflects the content of particles that can be magnitised. Stratigraphic changes in the magnetic properties of sediments are often used to aid correlation between cores.

Magnetic susceptibility on the peat core was measured at 4 mm intervals using a Bartington Instrument MS2EI magnetic susceptibility high-resolution surface scanning sensor, coupled to a TAMISCAN automatic logging conveyor. On samples from Lake Villasjön dry-weight-corrected magnetic susceptibility data were obtained on individual fresh subsamples using a Geofyzica Brno KLY-2 air-cored magnetic susceptibility bridge, followed by oven-drying at 40°C and weighing to permit the calculation of mass-specific SI units.

3.4 Loss-on-ignition

The organic matter content in peat and sediment samples was estimated based on loss-on-ignition (LOI) analysis (Bengtsson & Enell 1986) by igniting samples at 550°C for 4 hours after drying at 105°C overnight. Calcium carbonate content ($CaCO_3$) in the Lake Inre Harrsjöns sediments was estimated based on further weight loss at 925°C.

3.5 Elemental and stable isotope analyses

Elemental concentrations in combination with bulk densities and linear sedimentation rates can be used to calculate accumulation rates per year and area of elements. Temporal changes in carbon (C) and nitrogen (N) contents of sediments and in their ratio (C/N) together with stable isotope variability of sediment organic matter, are in palaeoecological and palaeolimnological studies applied to analyse changes in for example productivity, the relative amount of allochthonous versus autochthonous organic matter in sediments, nutrient limitation, sediment diagenesis or as a source of information on changes in trophic state (e.g. Meyers & Teranes 2001; Talbot 2001).

In the peat, total carbon (TC) and nitrogen (TN) contents were determined by combustion of oven-dried and homogenized samples using a Costech ECS 4010 elemental analyzer. Elemental C/N ratios were converted into atomic ratios by multiplication with 1.167 (Meyers & Teranes 2001). In samples from Lake Inre Harrsjön TOC, TN and δ^{13}C and δ^{15}N were analyzed on samples of freeze-dried lake sediment that were transferred to silver capsules. Potential trace amounts of carbonate were removed by reaction with 10% HCl. Samples were dried at 65°C, and measured at the Department of Forest Ecology, Umeå, using a continuous flow IRMS (20-20 Stable Isotope Analyser, Europa Scientific Ltd, Crewe, UK) interfaced with an elemental analyzer unit (ANCA-NT system, solid/liquid preparation module, Europa Scientific) (Ohlsson & Wallmark 1999). Atomic TOC/TN ratios are reported and isotopic results are given in (δ-notation (δ= [(R_{sample}/R_{std}-1) x 1000], where R=^{13}C/^{12}C or ^{15}N/^{14}N) with respect to international standards (V-PDB and AIR). The analytical precision was better than 0.4‰ for δ^{13}C, 0.3‰ for δ^{15}N, 0.7% for C and 0.1% for N.

3.6 Pigments

Pigments are often the only remaining evidence of primary producers in lake sediments and may provide important information on community changes of phototrophic communities in lakes (Leavitt and Hodgson 2001; Reuss et al. submitted). However, pigments are easily degraded by light, heat and oxygen and the presence of pigments in lake sediments also provide information on preservation conditions (Leavitt and Hodgson 2001; Leavitt 1993). Pigments specific of anoxygenic phototrophic bacteria can provide evidence on at least temporal anoxic conditions in bottom waters (e.g. Villa et al. 1998; Pfennig 1989).

For analyses of pigments, freeze-dried sediment samples were extracted in 100% acetone spiked with Sudan II as an internal standard overnight at -20°C. Samples were filtered (0.45 µm) and diluted to 80% acetone with milli-Q water. Diluted samples were stored at 4°C in the autosampler for a maximum of 7 hours before analysis by high performance liquid chromatography (HPLC). The run method was a modification of (Wright et al. 1991) as described in (Reuss & Conley 2005). Pigment concentrations are presented as mol pigment per gram organic carbon.

3.7 Near infrared spectroscopy

Near infrared spectroscopy (NIRS) analyses were applied on lake sediment samples in order to reconstruct past variations in lake water TOC concentrations (Rosén 2005). The analyses were performed using a NIR System 6500 instrument (FOSS NIR Systems INC., Silver Spring, MD, USA). The spectra from 400-2500 nm were recorded at 2 nm intervals giving 1050 data points per sample. For the numerical analyses the multivariate statistical software SIMCA-P 10.0 (Umetrics AB, SE-907 19 Umeå, Sweden) was used. To infer past changes in lake-water TOC concentration based on NIRS data, a model based on a 100-lake calibration set from northern Sweden was used. The 4-component PLS model between NIRS of surface sediment and contemporary TOC concentration of ambient lake water shows a R^2cv of 0.61 and a root mean squared error of prediction (RMSEP) of 1.6 mg l^{-1} (11% of the gradient).

3.8 Testate amoebae

Testate amoebae are protozoa with a single cell enclosed within a shell, commonly used to reconstruct peat surface moisture variability and water table fluctuations (Booth 2002; Charman et al. 2007). For analyses, sub-samples of 1 cm^3 were taken for analyses of testate amobae assemblages for the reconstruction of hydrological changes near the peat surface. Sample treatment and taxonomy followed Grosspietsch (1958) and Charman et al. (2000). 150-200 specimens were counted in each sample. A European training set for the relationship between testate amoebae assemblages and water table position was applied (Charman et al. 2007). Testate amoebae live in the uppermost part of the peat and the assemblages are mainly controlled by growing season moisture conditions in the peat, and are used to reconstruct the depth down to the water table (e.g. Charman et al. 2007).

3.9 Bryophytes

Mosses are important components in mire vegetation. They may be highly specialized to grow in environments where it can be difficult for many vascular plants to thrive. *Sphagnum* mosses even engineer the environment, by creating acid conditions and thereby slowing down decomposition processes, causing retention of nutrients in litter (Van Bremen 1995). Identification of mosses present in peat, together with the overall structure and composition of the peat building community, provide an important first hand indication of ecology and nutrient status.

For bryophyte analyses 1 cm thick peat samples of 1 cm^3 from 40 levels were sieved through a 125 µm mesh and the residue was examined for bryophyte remains. Bryophytes were identified to the lowest possible taxonomic level following Nyholm (1954-1965) and are semi-quantitatively reported as abundances of 1-5.

3.10 Biogenic silica

Biogenic (BSi) is frequently analysed in lake sediment studies as a proxy for diatom productivity (Conley et al. 1993). Biogenic silica pools and dynamics within wetlands are on the other hand rarely analysed and thus poorly understood. Recently, Struyf and Conley (2008) highlighted the lack of knowledge of silica biogeochemistry in wetlands as a major gap in our understanding of Si dynamics. In this thesis BSi was measured both in lake sediments and in peat.

The BSi content in lake sediments was determined by alkaline extraction of 30 mg of freeze-dried sediment in 1% Na_2CO_3 solution, over a 5 hour period with sub-samples taken at 3, 4 and 5 hours and neutralized as adapted by Conley and Schelske (2001). The extracts were analysed for dissolved silica (DSi), plotted against time and the y-intercept was considered to be the BSi content corrected for simultaneous dissolution of silica from minerals.

BSi content in peat was analysed by alkaline extraction of 30 mg of peat in 1% Na_2CO_3 solution during 3 hours, as no simultaneous dissolution of silica was observed from minerals in the BSi analysis during initial sequential extractions of randomly selected samples along the depth gradient. Elemental C/BSi ratios were converted into atomic ratios by multiplication with 2.34.

3.11 Diatoms

Diatoms are uni-cellular photosynthesizing organisms, with a siliceous shell, the frustule, where silica is deposited in an amorphous hydrated form, usually referred to as biogenic (BSi) or amorphous silica (ASi). Frustules are usually well preserved in sediments and can be used as indicators of past environmental conditions.

Diatom preparation was carried out using standard methods including digestion with 30% H_2O_2 as described by Battarbee (1986) and Renberg (1990). Cleaned diatom samples were dried onto coverslips and permanently mounted onto microscope slides using Zrax (R.I. ~1.7+). At least 300 diatom valves were counted along random transects in each sample using an Olympus BX41 light microscope at 1000X under oil immersion using phase-contrast optics, although only 50 specimens could be found in samples 5 and 46. In samples with abundant diatoms the quantitative method for determining a representative sample count described by Pappas & Stoermer (1996) was used in order to establish that enough valves had been counted. Krammer & Lange-Bertalot (1986-1991) was the main taxonomic reference. Diatom data were expressed as relative abundances (i.e. % of total diatoms) and only taxa with a relative proportion of >1% were included in the analysis.

3.12 Macrofossil density

The amount of coarse organic detritus (macroscopic plant remains), here termed the macrofossil density, may give an indication of erosion rates from the mire and was quantified by wet sieving of fresh sediment samples of 50-200 cm_3 through a 250µm mesh. Sieve residues were oven-dried at 65°C and weighed followed by calculation of plant macrofossil densities (g cm^{-3}).

3.13 Accumulation rates

C, N, BSi and $CaCO_3$ accumulation rates were calculated based on sediment accumulation rates as inferred from the respective age models, dry-weight bulk densities and dry-weight percentages of the respective elements.

4. Summary of papers

4.1 Paper I

Karlsson, J, Christensen, T. R., Friborg, T., Förster, F., Hammarlund, D., Jackowicz-Korczynski, M., Kokfelt, U., Roehm, C.& Rosén, P.: Quantifying the relative importance of lake emissions in the carbon budget of a subarctic mire. Manuscript.

The sink or source function of a terrestrial ecosystem is often referred to as the balance between fluxes (photosynthesis versus respiration) to and from the atmosphere. This parameter is termed the net ecosystem exchange or NEE, and is measured with chamber or eddy co-variance tower techniques. However, such measurements are unable to account for vertical losses of organic carbon to aquatic environments, where up to 50% of the exported material may be mineralized and lost back to the atmosphere (Algesten et al. 2004). The NEE thus typically overestimates the sink function of terrestrial ecosystems (Roulet et al. 2007). This paper aims at solving this problem for the catchment of the Lake Inre Harrsjön in the Stordalen Mire, where estimates of NEE are available, by integrating fluxes to and from the Lake Inre Harrsjön in the terrestrial carbon budget.

The results revealed that respiration in the lake exceeded photosynthesis by 90%. This means that the lake is clearly net heterotrophic, therefore supersaturated with respect to CO_2, and thus a net source of carbon to the atmosphere. The terrestrial export of carbon from the catchment to the lake was calculated as the sum of the carbon emitted to the atmosphere from the lake (as CO_2 and CH_4), the export of carbon from the lake (DIC and OC) and the carbon accumulation in the sediment. The calculated terrestrial carbon export to the lake was then subtracted from terrestrial NEE estimates, to give a new estimate of the present day sink function of the terrestrial ecosystem. The carbon budget for the year 2005 revealed that the export of carbon from the terrestrial ecosystem was equivalent to 20% of the terrestrial NEE, and that 53% of this carbon was returned to the atmosphere as gas exchange from the lake surface, corresponding to *c.*5 g m^{-2} yr^{-1} of carbon for the total catchment area including the lake. Very large inter annual variability in NEE estimates however prevented the development of a conceptual model for the carbon export to lake relative to the terrestrial NEE. The carbon export to the lake since the late 1970s was reconstructed based on a near infrared spectroscopy (NIRS) reconstruction of lake water concentrations of total organic carbon (TOC) and an estimated runoff from the mire during the same period. A reconstructed increase in the export of carbon to the lake occurred in a period where permafrost decay has been documented in the adjacent mire, and the increase in carbon export was considered at least partly to originate from consequent releases of carbon stocks there. The study clearly demonstrates the importance of including lakes in terrestrial carbon budgets and their potential impact on future climate change.

4.2 Paper II

Kokfelt, U., Rosén, P. , Schoning, K., Christensen, T.R., Förster, J., Karlsson, J., Reuss, N., Rundgren, M., Callaghan, T.V., Jonasson, C.& Hammarlund, D.: Ecosystem responses to increased precipitation and permafrost decay in sub-arctic Sweden inferred from peat and lake sediments. Global Change Biology, doi: 10.1111/j.1365-2486.2009.01880.x

Recent accelerated decay of discontinuous permafrost at the Stordalen Mire in northern Sweden has been attributed to increased temperature and snow depth, and has resulted in expansion of wet minerotrophic areas, leading to significant changes in carbon cycling. In order to track these changes through time and evaluate potential forcing mechanisms, this paper analysed a peat succession and a lake sediment sequence from a lake in the mire, providing a high resolution record for the last 100 years, and compared these with monitored climate changes and active layer thickness data. The peat core was analysed for testate amoebae to reconstruct changes in peatland surface moisture conditions and water table fluctuations. The lake sediment core was analysed by near infrared spectroscopy (NIRS) to infer changes in the total organic carbon (TOC) concentration of the lake-water, and changes in $\delta^{13}C$ and C, N and $\delta^{15}N$ to track changes in the dissolved inorganic carbon (DIC) pool and the potential influence of diagenetic effects on sediment organic matter, respectively.

The results revealed major shifts towards increased peat surface moisture and TOC concentration of the lake-water occurred around 1980, one to two decades earlier than a temperature driven-increase in active layer thickness. Comparison with monitored temperature and precipitation from a nearby climate station (ANS) indicates that this change in peat surface moisture is related to June-September (JJAS) precipitation and that the increase in lake-water TOC concentration reflects an increase in total annual precipitation. A significant depletion in ^{13}C of sediment organic matter in the early 1980s probably reflects the effect of a single or a few consecutive years with anomalously high summer precipitation, resulting in elevated dissolved inorganic carbon content of the lake water, predominantly originating from increased export and subsequent respiration of organic carbon from the mire. Based on these results, it was not possible to link proxy data obtained on peat and lake-sediment records directly to permafrost decay. Instead our data indicate that increased precipitation in general and anomalously high rainfall during summers had an impact on the mire and the adjacent lake ecosystem. It was therefore proposed that effects of increased precipitation should be considered when evaluating potential forcing mechanisms of recent changes in carbon cycling in the subarctic.

4.3 Paper III

Kokfelt, U., Reuss, N., Struyf, E., Sonesson, M., Rundgren, M., Skog, G., Rosén, P & Hammarlund, D.: Wetland development, permafrost history and nutrient cycling inferred from peat and lake sediment records in subarctic Sweden. Submitted to Journal of Paleolimnology.

Contemporary studies are unable to encompass the full consequences of ongoing climate change. One reason for this is that permafrost distribution may be in disequilibrium with rising temperatures (Halsey et al. 1995). Therefore, past examples of permafrost aggradation and degradation and impacts on adjacent lakes based on peat and lake studies are optimal, as they archive the temporal perspective over thousands of years in their stratigraphy. In this paper, two lake sediment cores and one peat core covering the Late Holocene time period (after *c.*5000 cal BP) were analysed. Analyses included detailed chronologies based on ^{14}C, ^{210}Pb dating and Bayesian modelling, C, N and BSi content and accumulation rates, phototrophic pigments, loss-on-ignition at 550 and 925°C, revealing the content of organic matter and $CaCO_3$ respectively, bryophytes, magnetic susceptibility and macrofossil density. The aim of the paper was to outline aspects of the Stordalen Mire development and to date indications of permafrost aggradation and degradation. Furthermore, links between the mire and adjacent lakes were assessed.

The results presented indicate a strong control of mire development and permafrost dynamics on the formation, sediment accumulation and biogeochemistry of the adjacent lakes. Organic sedimentation was initiated *c.*3400 cal BP in the eastern lake and *c.*2650 cal BP in the western lake. The latter largely coincided with the lower boundary of a condensed peat layer dated to between *c.*2800 and 1350 cal BP, and together this is interpreted as indications of permafrost aggradation in the mire. A *c.*1.4 m thick layer of re-worked peat deposited in the eastern lake after *c.*2100 cal BP further indicates that peat, previously deposited in the mire, was eroded and at least partly re-located to the adjacent lake. Macrofossils from the layer of reworked peat show that the eroded peat had been succeeded by an ombrotrophic peat cover, probably underlain by permafrost. The carbonate precipitation and thus lake pH appeared to have been controlled by the presence or absence of *Sphagnum* in the catchment mire. Initiation of the poor fen/bog communities present in the mire today was dated at *c.*700 cal BP, but indications of an older bog formation phase, which likely took place sometime between 2650 and 2100 cal BP, were found in the macrofossil content of the sediments of Lake Villasjön.

Elevated contents of biogenic silica and diatom pigments in the sediments of the western lake, during periods of poor fen and bog expansion in and over the adjacent mire, indicate indicate that terrestrial vegetation influenced not only lake pH, but also the amount of nutrients entering the lake from the catchment. Decreased retention by terrestrial vegetation with a low nutrient accumulation potential, may thus have caused an increased transfer of nutrients below the *Sphagnum* cover to the lake, and stimulated primary productivity there. As a result of increased productivity in the lake, bottom water anoxia developed, and led to recycling of phosphorous from the sediments. This development in the lake resulted in a state of self-sustained eutrophication during two centuries preceding the onset of 20th Century permafrost thaw.

4.4 Paper IV

Kokfelt, U., Struyf, E. & Randsalu, L.: Diatoms in peat - opportunist vegetation in a changing environment. Submitted to Soil Biology and Biochemistry.

Changes in hydrology and ambient temperature can induce rapid changes in wetland vegetation communities. Factors such as hydroseral succession, permafrost dynamics or external forces (climate, human interference) may relatively fast disturb prevailing mire vegetation, whereby a new dominating vegetation assemblage can develop, specialized to optimize growth under the altered environmental conditions. In the interface from one vegetation type to another, the old vegetation may be suppressed, die out or even start to decay, and some time may pass until a new mire vegetation is fully established.

In this study, we used a combination of ignition residue, BSi and diatom analysis from a well-studied peat sequence to demonstrate that diatoms may thrive during such transitions, to create isolated and shallow peat layers with significantly elevated silica and nitrogen storage. In this way nutrients, that could otherwise be lost during mineralization and subsequent runoff, are kept in the ecosystem. The diatom assemblages in the peat were in particular dominated by *Pinnularia* and *Eunotia* species with different ecological affinities, reflecting wetness conditions, acidity and nutrient availability during the time of growth. The diversity was greatest in the fen peat where *Eunotia* species were prevalent. Diatoms were rare in the poor fen and bog peat but very abundant in the interface between these peat-units where the aerophilic hummock species *Pinnularia rupestris* became dominant. The results presented in this paper results give new insight into the functioning of diatoms in boreal wetlands, and imply that diatom occurrence could increase in today´s rapidly changing boreal wetlands, which could induce significant changes in nutrient cycling.

5. Discussion

5.1 Mire development and permafrost history

Analyses, preferably of multiple peat sequences, are frequently used to describe permafrost development in peatlands (Kuhry & Turunen 2006). In this thesis there is one peat sequence in combination with two sediments sequences from lakes bordering the peatland, used for the same purpose. Although it can obviously be questioned how well one peat core represent the mire development, there are also some potential advantages to this approach: the spatial variation of peat forming plant communities in mires may be significant, and thus accordingly also the variability found and dated in peat cores. Sediments accumulated in lakes are on the other hand likely to reflect an integrated catchment signal, including major changes in mire development. The consistent linkage between events recorded in the peat and in the sediments from the two adjacent lakes (paper III) strengthened conclusions concerning aggradation and degradation of permafrost, the structural development of and erosion in the mire. A synthesis of the Stordalen mire development and permafrost history, based on the obtained palaeo-records outlined in paper III, is summarized in Figure 3.

The inferred permafrost development was similar to what is known from previous research in Fennoscandia. The earliest evidence of permafrost aggradation in Fennoscandia dates to *c.*2700-2400 cal BP (Oksanen 2005; 2006). This period occurs slightly later than a change to colder/wetter conditions after 2800 cal BP (van Geel 1996), but largely coincides with

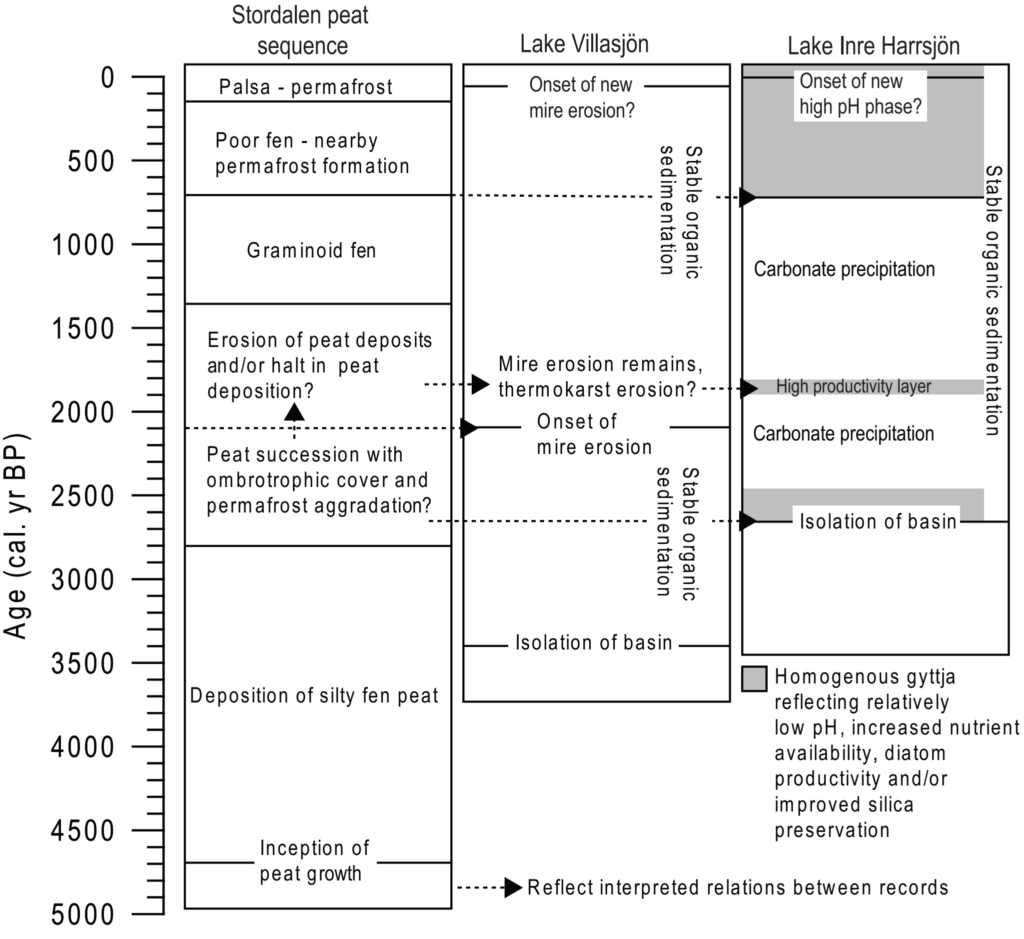

Figure 3. *A synthesis of events in the peat and lake sediment records.*

indications of a period with generally cold and highly variable climate conditions, as indicated by e.g. Swedish records of pine in the interval from *c.*2550-1950 cal BP (Grudd et al. 2002). The period is characterized by highly variable tree-ring width, including both minimum and maximum ring widths and inferred summer temperatures of the entire 7400 year record. With respect to permafrost aggradation, it is however even more important to note that in the same time interval, the sample density is very low which implies a relatively low pine tree-line during this time interval (Kullti et al. 2006). This may indicate that winter conditions were very severe with low temperatures resulting in increased pine tree and seed mortality (Kullman 2007). Winters might also have been very windy. Cold winters, in combination with a severe winter wind regime promoting snow-drift, will have served as favourable for palsa formation (Seppälä 1986). The onset of the variable and severe period from *c.*2550-1950 cal BP post-dates the earliest inferred permafrost aggradation phase at Stordalen at *c.*2650 cal BP, but encompasses evidence of erosion and relocation of peat deposits within the mire. An intensified wind regime will even have favoured erosion of palsa-deposits due to scouring by ice-crystals (Seppälä 2003). The presence of permafrost was also indicated during the Little Ice Age *c.*700 cal BP and *c.*120 cal BP, from changes in the peat building vegetation.

Changes in peat forming vegetation in the sequence (paper III), are apparently closely related to Northern Hemisphere climate patterns. In Northern England and northwest Europe the compilation of numerous peat stratigraphies have been used to infer regional bog surface wetness changes (Hughes et al. 2000; Barber et al. 2003). Interestingly, reported changes to wetter conditions around 4400, 2700, 1400 and 700 cal BP are remarkably close to the dating of major stratigraphical changes in the Stordalen peat record around 4700, 2800, 1350 and 700 cal BP, pointing to a dynamic mire environment, reacting rapidly to changing climate conditions.

5.2 Carbon accumulation

Paper I and III presented quantitative estimates of the export of carbon to Lake Inre Harrsjön, and long term carbon accumulation of different peat types and of the organic sediments in Lake Inre Harrsjön. The calculated average long term accumulation rate of organic carbon (OC) in the organic lake sediments (gyttja) from this thesis of *c.*15 g m^{-2} yr^{-1} was similar to the estimate obtained by Christensen et al. (2007) of 13 g OC m^{-2} yr^{-1}. The estimated average sink strength of the mire today is estimated at 22 g OC m^{-2} yr^{-1} (Christensen et al. 2007). This number corresponds to former estimated long term accumulation rates of carbon in peat during the last 700 years of 20 g OC m^{-2} yr^{-1} (Malmer & Wallén 2004), but is significantly lower than the average carbon accumulation rate of peat of *c.*35 g OC m^{-2} yr^{-1} obtained from the peat core (paper III). A simple comparison between the average ambient carbon accumulation rate of peat (*c.*35 g OC m^{-2} yr^{-1}) and the carbon accumulation in a condensed transition layer between 2800 and 1350 cal (*c.*5 g OC m^{-2} yr^{-1} BP; paper III) reveal that the sink strength of the mire was lowered with up to *c.*85% in this period relative to the surrounding periods of ambient peat deposition. This lowering of the sink strength probably resulted from increased decomposition, decreased or ceased uptake of atmospheric carbon by mire vegetation and/or widespread erosion as result of permafrost degradation. The the amount of organic material simply being relocated from storage in the mire to storage in the Lake Villasjön, has not been quantified. An interesting and important issue for future studies, will be to examine whether the phase of low peat accumulation after *c.*2800 cal BP, can also be found in other permafrost mires in the region.

5.3 Ecosystem functioning and nutrient cycling

Changes in ecosystem functioning and varying behavior of different nutrient cycles are central to any consideration of possible impacts of future climate change on boreal and subarctic peatlands. Two fundamentally different types of peatland ecosystems with regard to mineral nutrition can be distinguished: minerotrophic fens and ombrotrophic bogs (Sjörs 1948). Fens host vegetation receiving water and nutrients from both atmospheric sources and from ground-water, which has been directly or indirectly in contact with the mineral soil, whereas bogs host vegetation dependent on atmospheric sources and internal recycling exclusively (e.g. Sjörs 1948; Malmer & Nihlgård 1980). Poor fens, intermediate between rich fens and bogs, are poor in vascular plants but are usually dominated by *Sphagnum* (Van Bremen 1995). Transitions from fen to bog ecosystems may occur due to any change causing isolation of the plant cover from the nutrient-rich groundwater (Hughes 2000), such as hydroseral succession, a change to a drier climate regime (e.g. Svensson 1988; Almquist-Jacobson and Foster 1995), or physical separation from the groundwater due to permafrost formation and upheaval of the mire surface (Vardy et al. 1998). Hydroseral succession may on the other hand be rapidly reversed when permafrost dynamics are involved; degrading permafrost may lead to thaw subsidence or erosion, both processes resulting in wetter conditions and a return to minerotrophic vegetation communities. Consequent changes in trophic status of peatlands could substantially impact, not only on internal dynamics of carbon cycling and closely linked cycles of nitrogen, phosphorous and silica, but also the nutrient dynamics of adjacent lakes.

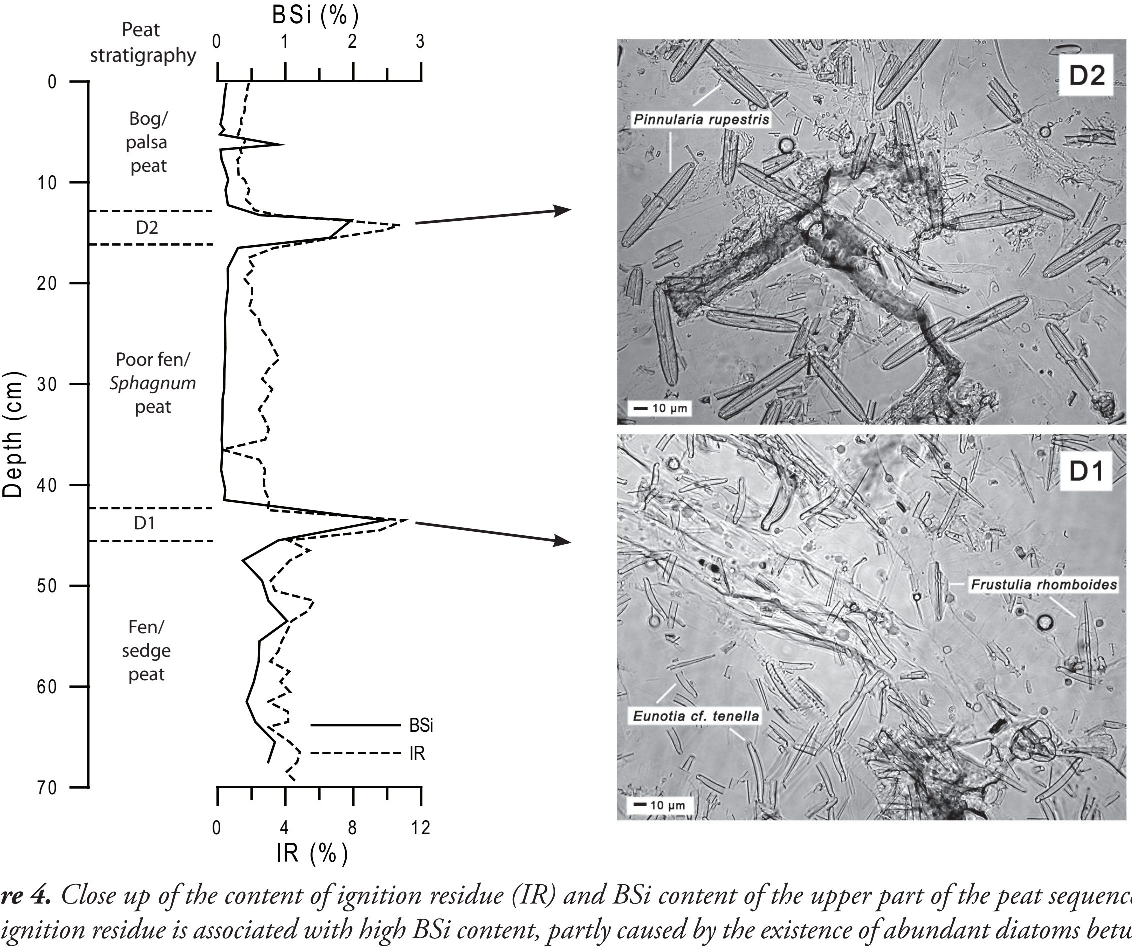

Figure 4. *Close up of the content of ignition residue (IR) and BSi content of the upper part of the peat sequence. A high ignition residue is associated with high BSi content, partly caused by the existence of abundant diatoms between major peat units. These layers are characterized by a relatively low species diversity.*

Lake Inre Harrsjön provides an interesting example of how a lake ecosystem may respond to changes in the nutrient status of the catchment vegetation. A similar timing between the expansion of poor fen and bog communities in the mire and increasing productivity and lower lake water pH of Lake Inre Harrsjön (paper III), indicated a tight hydrological connection between the catchment and the lake. A mixture of different mechanisms relating to catchment development, climate and internal lake processes likely interacted to explain these circumstances. These mechanisms included: more acidic run-off from the catchment, differences in nutrient retention potential between various mire vegetation types (poor fen/bog versus fen), increased nutrient fluxes to the lake and phosphorous re-cycling from the lake sediments, caused by productivity-driven bottom water anoxia.

Paper IV addressed a currently poorly understood aspect of peatland biogeochemistry and ecology, that in the future may provide new insights into carbon and nutrient cycling in peatlands, especially during times of transition. Abundant diatoms were found in fen peat and at transitions between peat build by both poor and rich mire vegetation types (Fig. 4). The diatom species diversity decrease significantly in these layers indicating that certain species are particularly adapted to survive under conditions where ambient vegetation is surpressed. Mostly *Pinnularia* and *Eunotia* species were found. The results provide an intruiging picture of diatoms as an opportunistic type of uni-cellular vegetation, with the potential to retain nutrients during periods of environmental stress.

5.4 Implementing the lake allochtony concept in palaeolimnology

Within limnology, it is broadly recognized that allochthonous organic carbon (OC) provides an important source for food-webs in lake ecosystems (e.g. Pace et al. 2004; Karlsson et al. 2007), and that mineralisation of allochthonous OC may cause lake-water CO_2 super-saturation (e.g. Algesten et al. 2004). Lakes are in general net sources of carbon to the atmosphere (Kling et al. 1991; Cole et al. 1994; Kortelainen et al. 2004), and are important to include in carbon budgets of terrestrial catchments (Christensen et al. 2007; Cole et al. 2007) as 30-80% of total OC transported to freshwater systems is lost to the atmosphere (Algesten et al. 2004). The recognition of these mechanisms does not appear to be broadly applied in palaeolimnology, and there seem to be some gaps between the sciences of limnology and palaeolimnology. However, the lake allochtony concept potentially opens up for important insight to the understanding and interpretation of certain palaeo-proxies from lake sediments, such as stable and radioactive carbon isotopes (paper II and III). A first approach to these applications is summarized in the following.

5.4.1 Lake allochtony and implications for the age of aquatic DIC reservoirs

Allochthonous OC is mineralised in lakes, causing these to be super-saturated with respect to CO_2. The origin, amount and age of this allochthonous OC ought to have a significant influence on radiocarbon dates obtained on organic matter produced in the lake. Dissolved inorganic carbon (DIC) resulting from mineralisation of allochthonous OC will reflect the age of the allochthonous OC. Accordingly, if in-lake primary producers (e.g. aquatic mosses) assimilate such DIC during photosynthesis, resulting radiocarbon ages will be too old. This offset is termed a reservoir age. In Quaternary sciences it is well established that radiocarbon dates from aquatic organisms as a rule are relatively too old, but the mechanisms used to describe the off-set from “true” ages differ from the mechanism given above. In marine environments a reservoir age of minimum 400 years is routinely subtracted radiocarbon ages obtained on marine organisms, but reservoir ages up to several thousand years are possible dependent on factors such as sea-ice cover, oceanic ventilation and upwelling of “old” water (e.g. Bradley et al. 1999; Kokfelt 2003).

Significant reservoir ages are also reported from lakes. When bulk sediments or material containing OC from in-lake producers are dated, and compared to dates obtained on terrestrial plant remains from the same samples, consistently too old ages are obtained (MacDonald et al. 1987; Barnekow et al. 1998). Mechanisms to explain these old ages are typically hard-water effects due to calcareous bedrock in the catchment, contamination from old organic matter, slow exchange rates of CO_2 at the lake surface or inwash of old inorganic carbon residues such as e.g. graphite or coal (MacDonald et al. 1987; Lowe & Walker 1997; Barnekow et al. 1998). However, as a result of the limnological research on lake allochtony, with the recognition that the DIC pool of lakes is controlled by terrestrial organic matter being mineralised in the water-column, effects of mineralised allochthonous OC need to be added to the line of mechanisms explaining reservoir ages in lakes. Also, slow exchange rates of CO_2 at the lake surface (e.g. Lowe and Walker 1997) possibly need to be re-evaluated as a valid explanation altering the DIC reservoir of lakes, as the exchange of carbon between lakes and the atmosphere apparently may be thought of as more or less unidirectional out of the lake.

This line of argument relates directly to some results and interpretations presented in this thesis (paper III). In contrast to Lake Inre Harrsjön where radiocarbon dates were obtained directly on terrestrial plant remains, the same were deliberately avoided for the establishment of the Lake Villasjön chronology. The sediments in Lake Villasjön contain frequent erosion remains from peat originating in the mire, probably representing a broad age range. Instead, to construct a chronology there, radiocarbon dates were obtained from aquatic mosses that were assumed to have grown directly in the lake, although we were aware that an age offset compared to real ages would be impossible to avoid (MacDonald et al. 1987). The aquatic mosses were carefully picked and identified, and all but one radiocarbon date (in the lowermost core part, before onset of organic sediments) from this lake are based on the aquatic mosses *Drepanocladus trichophyllus* and *Scorpidum scorpioides*. As these may well have assimilated DIC from mineralised eroded peat, radiocarbon dates obtained here are probably all more or less too old. An estimate of the age of the DIC reservoir used by the mosses for aquatic photosynthesis can theoretically be qualitatively estimated from the catchment peat core analysed and presented in the same paper (III). A low-accumulation layer, at least partly reflecting erosion of mire deposits, with a lower age of *c.*2800 cal BP potentially provides a maximum age of the allochthonous OC that was eroded into in Lake Villasjön. If therefore allochthonous OC with an age of 700 to 0 years (the hypothesised maximum and minimum ages for the erosion material at the start of the erosion event) contributed to the source for the aquatic DIC, in turn used for photosynthesis by aquatic mosses, the reservoir age of the DIC pool originating here, will have averaged the age of the eroded material. According to this line of reasoning, it is considered likely, that the obtained age of *c.*2100 cal BP (based on dating of aquatic mosses), dating the deposition of the 1.4 m thick erosion layer in Lake Villasjön, is too old. If so, the deposition of the erosion layer and the deposition of a conspicuous fine-detritus gyttja with a high nutrient content in Lake Inre Harrsjön *c.*1900-1800 cal BP (based on terrestrial plant remains), may actually have been caused by the same event in the mire.

5.4.2 Lake allochtony and implications for the interpretation of $\delta^{13}C$ of sediment organic matter

As described for ^{14}C, the lake allochtony concept may also have implications for the interpretation of variations in $\delta^{13}C$ of sediment organic matter (paper II).

Pathways of allochthonous OC in lakes are manifold. Allochthonous OC may either be consumed by grazing organisms, used as substrate and be respired by bacteria, heterotrophic and mixotrophic algae and used for aquatic photosynthesis, flocculate and sediment or be further exported out of the system, either downstream or to the atmosphere. Flocculation is an important mechanism that changes the hydrodynamic properties of the particles and their sinking abilities (Droppo 2001; Von Wachenfeldt & Tranvik 2008). As flocculation and grazing of the organic carbon pool does not result in any carbon isotope fractionation, the influence of these processes will lead to preservation of the $\delta^{13}C$ signature of allochthonous carbon in the sediments. This is not the case for mineralised allochthonous OC. Depending on the amount of DIC supplied relative to consumption by photosynthesis the mineralization of allochthonous carbon will tend to decrease or keep $\delta^{13}C$ values low if the lacustrine DIC pool is continuously replenished, allowing ample ^{13}C discrimination during aquatic photosynthesis. In the opposite scenario, insufficient replenishment of the DIC pool during periods of lower allochthonous input, will lead to a gradual enrichment in ^{13}C of the residual DIC pool and associated ^{13}C-enrichment of sediment organic matter.

A straight forward relationship between TOC concentrations and $\delta^{13}C$ can however not be assumed. This is so because the two parameters reflect fundamentally different parameters. $\delta^{13}C$ of sediment organic matter reflects the carbon isotope composition of the total organic (through grazing and burial) and inorganic (through photosynthesis) carbon pools of the lake water, whereas NIRS data reflect TOC concentrations in the water column. Concentrations in the water column can be buffered by dilution even though the total carbon pool increases. This interpretation was applied in paper II, in order to explain $\delta^{13}C$ variability and reconstructed changes in lake-water TOC concentrations in Lake Inre Harrsjön during the last 100 years.

5.5 Assessing variations in C-export to lakes using lake sediment records

Increasing active layer thickness together with increased temperatures during the summer potentially lead to increased production of dissolved organic carbon (DOC) (Olsrud 2004; Frey & Smith 2005) and run-off may export this DOC to aquatic environments (paper II). Degradation of permafrost may lead to erosion of peat deposits (paper III) and expansion of wet minerotrophic areas dominated by graminoids (Christensen et al. 2004). Both permafrost decay mechanisms (increased active layer thickness and erosion) thus potentially lead to increased export of OC from terrestrial to aquatic sites. Estimations of changes in the export of to lakes are central to the present day carbon budget of the mire, but are notoriously difficult to reconstruct. Past lake water TOC concentrations can be reconstructed by applying near infrared spectroscopy on lake sediments, but transforming these concentrations into carbon export, further requires knowledge of run-off rates (paper I). In the paper I and II, two different approaches to assess the recent (last 30-100 years) carbon export to Lake Inre Harrsjön quantitatively and qualitatively, were presented.

In both studies the basis was a reconstruction of past lake water TOC concentrations based near infrared spectroscopy (NIRS). However, whereas in paper I the export was directly quantified by multiplication with reconstructed run-off rates from the mire, a qualitative approach was applied in paper II. Here, the TOC reconstruction was evaluated together with $\delta^{13}C$ variability of sediment organic matter and the regional climate development based on instrumental records from ANS. Both studies indicated a net increase in the export of organic carbon the lake since the 1970s, and further that the reconstructed increase in lake water TOC concentrations probably underestimates the actual increase in carbon export. In this way, paper I reconstructed an increase in carbon export *c.*6% higher than the reconstructed increase in lake water TOC concentration (difference between approximate regression estimates 1970-2004). In paper II it was (based on carbon isotopic indications) argued that the increase in lake water TOC concentrations underestimated the increase in carbon export, because of dilution due to higher summer and annual precipitation in the same period.

How much of the inferred increase in carbon export is caused by run-off rates, carbon stocks released from thawing permafrost or increased DOC production in the active layer, is unclear. Recent findings from Finland, emphasized the importance of longer lasting dry periods (e.g. in the 1960s, 1970s and mid 1990s), preceding periods of increased rainfalls (e.g. the early 1980s and after the late 1990s), for carbon flux dynamics (Lepistö et al. 2008), possibly because of higher decomposition rates and DOC production in the peat during dry periods.

6. Conclusions and outlook

Taken together, the studies reported in this thesis demonstrate the strength of multi-proxy stratigraphical studies, to address very different aspects of ecosystem behavior and functioning.

Firstly, this thesis has improved our understanding of the Holocene development of the Stordalen Mire and of peat accumulation, carbon and nutrient cycling and interactions with surrounding freshwater systems. The onset and end of transition periods are archived in sediment records, and may aid projections of consequences caused by continued permafrost degradation. In paper III it was demonstrated, that permafrost degradation, may cause large scale relocation of peat deposits into adjacent basins and/or boost productivity of connected freshwaters for a short period of time. In a longer time perspective is was argued that the trophic status of mire vegetation, may influence nutrient availability of adjacent lakes. Assessing ecology and ecosystem functioning is nescessary to concieve such mechanisms fully.

Secondly, the potential for applying stratigraphical studies to address recent changes in ecosystems was demonstrated. Reconstructions of changes in soil moisture variations, water table fluctuations and carbon export dynamics may for example capture ecosystem variability in response to climate, that cannot or have not been obtained by contemporary measurements. One example is the monitoring of soil moisture above permafrost, an integrated part of the circumpolar active layer monoitoring program CALM (Brown 2001). Soil moisture is an important parameter controlling the thermal conductivity of the peat both during the thawing and freezing season, and a potential is recognised in applying testate amoebae to reconstruct soil moisture changes above permafrost. Reconstructions of water table changes above permafrost likely provide further essential information on permafrost conditions, as discussed in paper II. Calibration studies should however be conducted to strengthen conclusions based on such data.

Thirdly, the strength of stratigraphical studies to assess aspects of biogeochemical cycling in mire communities, was demonstrated in paper IV. The new insight in the formation and apparent predictability of nutrient hotspots in soils formed by poor vegetation, have implications for the understanding of ombrotrophic vegetation communities on permafrost. It should thus for example be examined how effecient nutrients in such pools, situated within the rooting depth of vascular plants, can be mobilised and utilised.

Based on this thesis the following more specific conclusions have been made:

- Peatland inception at Stordalen was dated at *c.*4700 cal BP. Bryophyte assemblages and high minerogenic content of peat indicate permafrost-free conditions in the mire until at least *c.*2800 cal BP. The presence of permafrost in the mire is indicated during two periods; *c.*2650-2100 cal BP and after *c.*700 cal BP. The latest phase of permafrost aggradation at the coring site was dated at *c.*120 cal BP. A period of intense erosion, likely as a result of thermokarst and wind erosion processes, was initiated at *c.*2100 cal BP and resulted in translocation of a considerable amount of peat from the mire into Lake Villasjön.

- Acidification of Lake Inre Harrsjön

is indicated by the absence of carbonate laminations at *c.*2650- 2450 and since *c.*700 cal BP. These conditions are considered to be a result of the development of poor fen and bog communities in the mire, probably related to permafrost. Simultaneous increases in lake productivity were possibly controlled by a combination of reduced ability of terrestrial vegetation to retain nutrients and by P-fluxes from the sediment during periods of oxygen deficit in the bottom waters of the lake. A short-lived period of very high lake productivity at *c.*1900-1800 cal BP is possibly related to mire erosion.

- The accumulation rate of BSi was significantly larger in peat dominated by fen than by poor fen/bog communities, and partly reflected the presence of abundant diatoms. Leaching of biogenic silica from peat deposits and/or decreased retention by mire vegetation, in particular during periods of poor fen/bog dominance in the mire, may have contributed to increased lake productivity, but increased P and N loading from the catchment will have been as important.

- An initial increase in terrestrial nutrient fluxes resulted in bottom water anoxia leading to P release from the sediments. This brought about a state of self-sustained eutrophication after *c.*200 cal BP. Lowered lake-water pH, during periods of acidic runoff from poor fen/bog communities, may have caused more favourable conditions for the preservation of BSi in the lake sediments.

- Continued permafrost decay and related vegetation changes towards minerotrophy may increase C and nutrient storage in mire deposits, but reduce nutrient fluxes in run-off to adjacent lakes. However, rapid permafrost degradation may lead to widespread erosion and relocation of mire deposits and to relatively short periods of significantly increased nutrient loading to adjacent lakes.

- Changes in peat surface moisture variations and lake water TOC concentrations over the last century predominantly reflect summer and annual precipitation variability.

- Fen peat and transition layers between major peat building vegetation communities were dominated by shallow layers, rich in nutrients and diatoms.

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8. Svensk sammanfattning

Holocena ekosystemförändringar orsakade av klimat- och permafrostdynamik i Stordalen, Abisko

Nordliga torvmarker utgör viktiga sänkor för atmosfäriskt kol. Det uppskattas att ca 30% av det kol som globalt är lagrat i jordmåner finns i denna typ av torvmarker. Sjöar lagrar också betydande mängder kol, men dessa fungerar främst som viktiga källor för atmosfäriskt kol till följd av effektiv nedbrytning av det organiska material som transporteras dit från omgivningen. I nordliga torvmarker spelar förekomsten av permafrost en viktig roll för dessa ekosystems hydrologi och ekologi och därmed också för deras kolbalans. Det har påvisats att permafrosten i torvmarker i norra Sverige för närvarande håller på att smälta, och därför är mycket av dagens forskning fokuserad på att förstå vilka konsekvenser detta har för kolbalansen i dessa ekosystem.

I denna avhandling har torv och sjösediment från Stordalen i norra Sverige använts för att rekonstruera denna torvmarks utveckling och permafrostdynamik i syfte att analysera hur ändringar i torvmarken har påverkat ekosystemen i angränsande sjöar, samt att öka förståelsen for hur flöden och ackumulation av kol och näringsämnen har varierat i en föränderlig miljö. De metoder som har använts inkluderar radiometrisk datering, bestämning av glödförlust, analys av mossor, diatoméer, skalamöbor, pigment, kol, kväve, biogent kisel, stabila isotoper samt när-infraröd spektroskopi (NIRS).

Resultaten från undersökningen visar att torvmarken främst utvecklades i sen-holocen tid. Början på tillväxten daterades till ca 4700 cal BP (år före nutid), och början på den organiska sedimentationen i två angränsande sjöar daterades till 2650 respektive 3400 cal BP. Resultaten från torven visar även att kärrtorv ackumulerade fram till ca 2800 cal BP, varefter en tidig permafrostfas sannolikt förorsakade frosthävning och stora förändringar i torvmarkens struktur och hydrologi. Torv saknas i princip helt i den analyserade sekvensen mellan 2800 och 1350 cal BP, vilket antingen avspeglar miljömässig stress och/eller torverosion. Ett ökat innehåll av omlagrad torv i en av sjöarna efter ca 2100 cal BP stöder hypotesen om omfattande torverosion, vilken sannolikt orsakades av smältande permafrost. En kort och högproduktiv period i Inre Harrsjön ca1900 cal BP kan också ha samband med denna fas i torvmarkens utveckling. Kärrtorv ackumulerades från ca 1350 cal BP. Indirekta indikationer på en ny permafrostperiod finns efter ca 700 cal BP, och direkta indikationer för detta finns ca 120 cal BP baserat på ändringar i den torvbildande vegetationen. Kärrtorv och torv avsatt i samband med omfattande förändringar i torvmarksvegetationens sammansättning karakteriseras av ett rikt innehåll av diatoméer och näringsämnen. Permafrostfaser är associerade med utveckling av fattigkärr och mosse-miljöer, vilket resulterade i lägre pH i torvmarken jämfört med perioder då rikkärr dominerade. Denna utveckling kommer även till uttryck i sedimenten i en av de undersökta sjöarna i form av att bildningen av kalklager upphör. Näringsflödena till en av sjöarna tycks också ha varit påverkade av vilken vegetation som dominerade på torvmarken, och dessa flöden var sannolikt högre under perioder då fattigkärr och/eller mosse-vegetation dominerade. Ökade näringsflöden till sjön ökade produktionen där, vilket i resulterade i syrefattiga förhållanden nära bottnen. De syrefattiga förhållandena ledde i sin tur till recirkulering av fosfor från sedimenten, vilket resulterade i eutrofiering under en period på ca 200 år.

Rekonstruktioner av förändringar i fuktighet i torvytan och koncentrationen av organiskt kol i sjövatten under de senaste 100 åren uppvisar främst samband med variationer i mängden årlig nederbörd och sommarnederbörd. Det var inte möjligt att direkt koppla dessa rekonstruktioner till variationer i det aktiva lagrets tjocklek.

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