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ORIGINAL PAPER

Wetland development, permafrost history and nutrient cycling inferred from late Holocene peat and lake sediment records in subarctic Sweden

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Abstract Permafrost in peatlands of subarctic Sweden is presently thawing at accelerated rates, which raises questions about the destiny of stored carbon and nutrients and impacts on adjacent freshwater ecosystems. In this study we use peat and lake sediment records from the Stordalen palsa mire in northern Sweden to address the late Holocene (5,000 cal BP-present) development of the mire as well as related changes in carbon and nutrient cycling. Formation, sediment accumulation and biogeochemistry of two studied lakes are suggested to be largely controlled by the development of the mire and its permafrost dynamics. Peat inception took place at ca. 4,700 cal BP as a result of terrestrialisation. Onset of organic sedimentation in the adjacent lakes occurred at ca. 3,400 and 2,650 cal BP in response to mire expansion and permafrost aggradation, respectively. Mire erosion, possibly due to permafrost decay, led to redeposition of peat into one of the lakes after ca. 2,100 cal BP, and stimulated primary productivity in the other lake at ca. 1,900–1,800 cal BP. Carbonate precipitation appears to have been suppressed when acidic poor fen and bog (palsa) communities dominated the catchment mire, and permafrost-induced changes in hydrology may further have affected the inflow of alkaline water from the catchment. Elevated contents of biogenic silica and diatom pigments in lake sediments during periods of poor fen and bog expansion further indicate that terrestrial vegetation influenced the amount of nutrients entering the lake. Increased productivity in the lake likely caused bottom-water anoxia in the downstream lake and led

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to recycling of sediment phosphorous, bringing the lake into a state of self-sustained eutrophication during two centuries preceding the onset of twentieth century permafrost thaw. Our results give insight into nutrient and permafrost dynamics in a subarctic wetland and imply that continued permafrost decay and related vegetation changes towards minerotrophy may increase carbon and nutrient storage of mire deposits and reduce nutrient fluxes in runoff. Rapid permafrost degradation may on the other hand lead to widespread mire erosion and to relatively short periods of significantly increased nutrient loading in adjacent lakes.

Keywords Wetland development · Permafrost history · Nutrient cycling · Peat and lake sediments · Late Holocene · Subarctic Sweden · Carbon and nutrient accumulation

Introduction

Lakes are strongly influenced by input of organic matter and nutrients from surrounding landscapes and play an important role in catchment carbon budgets. This is because allochthonous organic carbon from the catchments can be mineralised in lake waters and emitted to the atmosphere as carbon dioxide or methane, can be transported further downstream or be stored in lake sediments (Cole et al. 2007). Permafrost in peatlands of northern Sweden is presently thawing (Christensen et al. 2004), and organic carbon stored in frozen peat is expected to be released at an increasing rate from the mires and transported to streams and lakes. However, because permafrost ecosystems may be in disequilibrium with rising temperatures (Halsey et al. 1995), contemporary lake studies may fail to capture long term effects of climate change. In this respect, stratigraphic records from peatlands and adjacent lakes have obvious advantages as they include the temporal perspective in their stratigraphy (Kokfelt et al. 2009).

Northern Fennoscandia is characterised by widespread peatlands and lakes that have accumulated carbon since the early Holocene (Sonesson 1974). Two fundamentally different types of peatland ecosystems with regard to hydrology and nutrient sources are distinguished: minerotrophic fens and ombrotrophic bogs. Fens host vegetation receiving water and nutrients from both atmospheric sources and from water that has been in contact with the mineral soil, whereas bogs host vegetation dependent on atmospheric sources and internal recycling exclusively (Malmer and Nihlgård 1980). 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 hydrosere (a succession from an aquatic to a terrestrial ecosystem), a change to a drier climate regime (Svensson 1988), or physical separation from the groundwater due to permafrost aggradation and upheaval of the mire surface (Vardy et al. 1998). Poor fens, intermediate between rich fens and bogs, are poor in vascular plants and are usually dominated by *Sphagnum*. Changes in trophic state of peatlands could substantially impact not only internal dynamics of carbon cycling and closely linked cycles of nitrogen, phosphorous and silica, but also the nutrient dynamics of adjacent lakes. Past and present changes in lake systems are frequently interpreted as results of external forcing, such as changes in climate and catchment vegetation and soil processes, affecting internal lake structure and functioning (Battarbee 2000). By combining studies of lake sediment records with peatland stratigraphy in the drainage area, impacts of catchment processes on lakes can be assessed.

In both lakes and mires, nitrogen (N) is supplied from the groundwater, catchment runoff and from the atmosphere (Limpens et al. 2006; Lampert and Sommer 2007). In contrast, biologically available phosphorous (P) and dissolved silica (DSi) is supplied from non-atmospheric sources exclusively. Inflow from the catchment (Hurley et al. 1985) and sediment recycling (Conley et al. 1988) are the most important sources in lakes. Hence, changes in the trophic status of connected peatlands imply potentially changing dynamics of P and Si. However, while several studies have focused on N and P dynamics in peatlands (Limpens et al. 2006; Walbridge and Navaratnam 2006), corresponding Si dynamics are insufficiently understood. Recently, Struyf and Conley (2009) have highlighted the lack of knowledge of silica biogeochemistry in wetlands as a major gap in our understanding of Si dynamics. In this context, subarctic and arctic peatlands attract special attention. They comprise some of the most important terrestrial C sinks in the world (Gorham 1991), many of which are dominated by silica-rich plants such as sedges and grasses and are characterised by soils rich in biogenic silica (BSi; Struyf and Conley 2009).

In this study, we use peatland and lake sediment sequences to investigate the late Holocene (5,000 cal BP–present) mire development and C, N and BSi dynamics of the subarctic Stordalen Mire in northern Sweden, previously investigated during the International Biological Programme (Sonesson 1980). Bryophyte assemblages and elemental data obtained from a peat succession of a permafrost peat mound (palsa), together with pigment, macrofossil and elemental data obtained on sediment sequences from two adjacent lakes, provide evidence of mire development, permafrost dynamics and elemental accumulation rates. Using these records as a case study, we address aspects of carbon and nutrient cycling related to the vegetation dynamics of the mire to show the existence of physical and biogeochemical impacts on adjacent lakes.

Study site

The Stordalen Mire (N 68°21′, E 19°03′, 350 m a.s.l) is located 10 km east of Abisko in northern Sweden (Fig. 1). The mire is surrounded by sub-alpine birch forest and is situated in the discontinuous permafrost zone where permafrost at low elevations primarily occurs in peatlands. The area has a mean annual temperature around 0.7°C and a low annual precipitation of approximately 300 mm (Alexanderson et al. 1991). Fen peat formed in the area since the early Holocene (Sonesson 1974), and peat deposition was initiated at Stordalen around 6,000 cal BP (Sonesson 1972). The maximum lateral expansion of bog communities was probably reached as late as ca. 300 cal BP (Malmer and Wallén 1996). Today, a large peat plateau containing permafrost dominates the central part of the mire and is characterised by hummock/hollow microtopography, predominantly with bog communities, dominated by *Empetrum hermaphroditum* Hagerup, *Betula nana* L., *Rubus chamaemorus* L., *Eriophorum vaginatum* L., *Dicranum elongatum* Schleich., *Sphagnum fuscum* Klinggr. and lichens. More peripheral parts of the mire are dominated by poor, permafrost-free fen areas with mainly *Eriophorum angustifolium* Honck., *Carex rostrata* Stokes, *Sphagnum lindbergii* Schimp. and *Sphagnum riparium* Ångstr. and by isolated palsas in the northeastern part of the mire.

The mire is bordered by lakes to the northwest and southeast (Fig. 1). Lake Villasjön to the southeast is relatively large (0.17 km^2) and shallow (maximum depth 1.3 m) with a lake water pH around 6.5. It

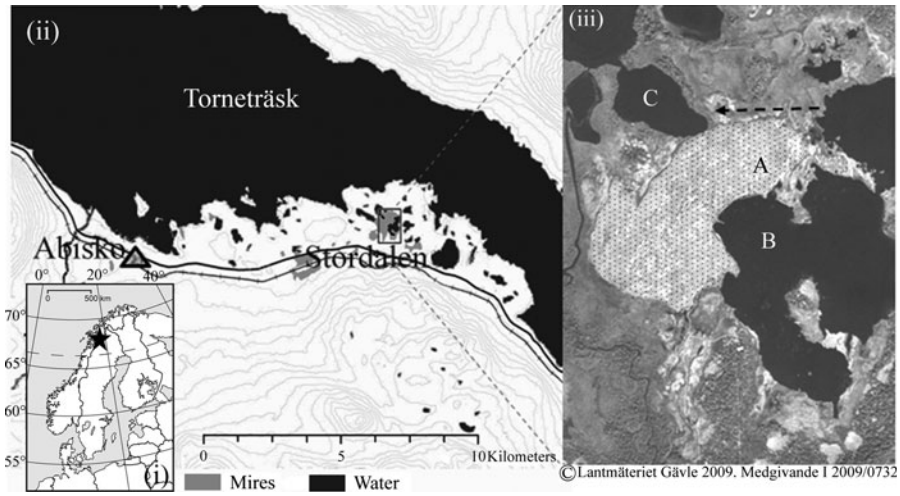

Fig. 1 Map of the study site showing its location in northern Sweden (i). The local setting near Abisko is seen in (ii) and an aerial photograph shows a close-up of the Stordalen Mire (iii). Stratigraphic records were obtained from the northeastern part of the Stordalen Mire (**a**), the western part of Lake Villasjön (**b**), and the north central part of Lake Inre Harrsjön (**c**). The arrow indicates drainage from Lake Villasjön to Lake Inre Harrsjön and the hatched area indicates the approximate extent of the central peat plateau

drains Lake Inre Harrsjön through a fen area north of the central peat plateau (Fig. 1). Lake Inre Harrsjön to the northwest is a smaller lake (0.02 km^2) with a maximum depth of 5 m and a pH of approximately 7.0. The relatively high pH reflects the occurrence of carbonate-containing bedrock in the drainage area (Lindström et al. 1985). Groundwater recharge occurs from two springs south and northeast of the lake, with pH values between 6.5 and 7.0. In contrast, runoff from the mire is acidic with a pH below 4 in plateau areas and between 4 and 4.5 in fen areas (Nilsson 2006).

Materials and methods

Peatland sequence

A peatland sequence was collected from the north-eastern part of the mire in September 2003. The coring site (Fig. 1) was a recently thawed palsa, surrounded by carpet vegetation dominated by *S. lindbergii*. The site was chosen because permafrost had recently disappeared, as indicated by the surface vegetation which resembled that of palsas with species such as *D. elongatum, Sphagnum fuscum, Empetrum hermaphroditum, Andromeda polifolia* L., *Vaccinium uliginosum* L., *Betula nana* and *Rubus chamaemorus*. A 230 cm profile was recovered using a Russian corer with a diameter of 10 cm, and a monolith sampler for the top 66 cm. Individual cores were wrapped in plastic and returned to the lab in sealed PVC tubes and stored at 4°C. The cores were described and the degree of humification estimated visually. Correlation was based on lithostratigraphic characteristics and aided by magnetic susceptibility, measured at 4 mm intervals using a Bartington Instrument MS2EI magnetic susceptibility high-resolution surface scanning sensor coupled to a TAM-ISCAN automatic logging conveyor. The sequence was sectioned at every 0.5 cm down to a depth of 15 cm and thereafter at 1-cm intervals.

The chronology of the peatland sequence was based on ^{210}Pb radioisotope analysis of the top 10 cm (Kokfelt et al. 2009) while radiocarbon dating was applied to 11 samples from the deeper part (ESM 1, Fig. 2). Radiocarbon ages were converted to calendar year intervals at the 95.4%

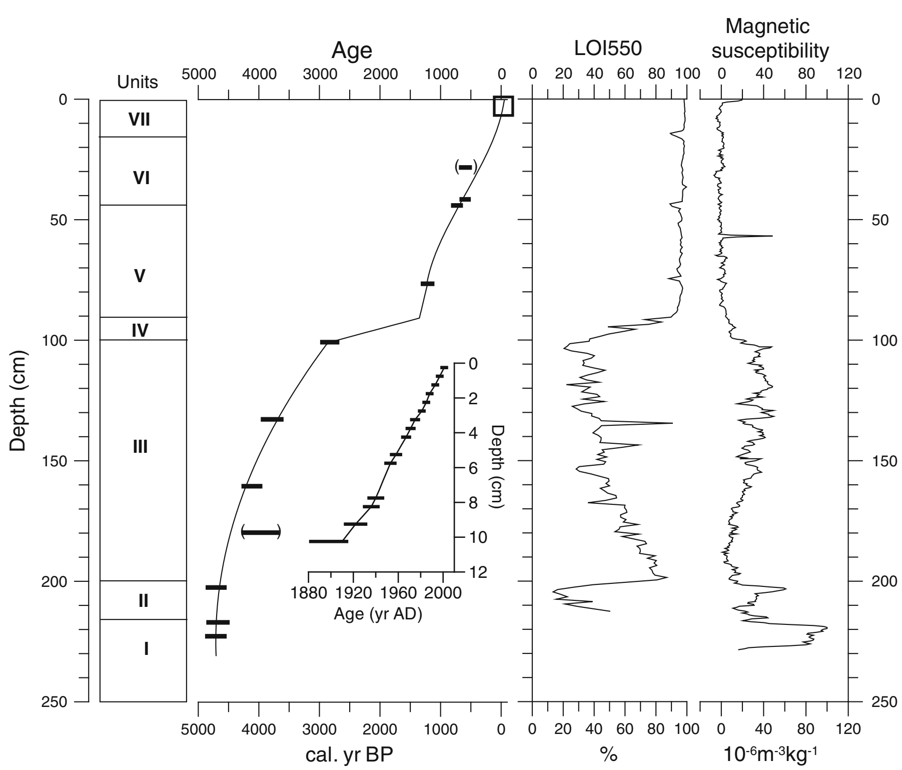

Fig. 2 Stratigraphy of the peat profile (see also ESM 2), ^{210}Pb ages (AD; inset diagram after Kokfelt et al. 2009), radiocarbon ages (ESM 1) and derived age model together with records of organic matter content (LOI) and magnetic susceptibility. For radiocarbon dates calibrated age ranges corresponding to the double standard deviation are shown. Radiocarbon dates not used for the age-model are marked by brackets. Roman numerals as referred in the text; VII: *D. elongatum* (palsa) peat, VI: *S. lindbergii* peat, V: Sedge-*Drepanocladus* peat, IV: Transition layer, III: Organic rich silt, II: Boundary layer from silt to continuous deposition of organic-silt and peat, I: Silt

confidence level using the IntCal04 calibration dataset (Reimer et al. 2004). Two radiocarbon dates were omitted when constructing the age-depth model (Fig. 2): one (LuS 6262) as considered slightly too old and one showing an anomalously young age (LuS 6265). The age-depth relationship was constructed by using second and third degree polynomials through the dates above 90 cm and below 100 cm, respectively. These two depths encompass the transition from mineral-rich to mineral-poor peat (unit IV, Fig. 2). The boundaries of this transition layer are more clearly reflected in the records of loss-on-ignition (LOI) and magnetic susceptibility than in the lithological description (ESM 2). Linear interpolation of the depth-age model was applied between 90 and 100 cm.

Samples of 1 cm 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 semi-quantitatively reported as abundances of 1–5 (ESM 3). *Drepanocladus exannulatus* s. lat. is a systematically critical group as acknowledged by many authors. The forms in unit III to part of unit V resemble both *D. purpurascens* and tiny forms of *D. procerus,* but resemble *D. schulzei* in the upper part of unit V and VI (Nyholm 1954–1965). All these forms are referred to as *D. exannulatus* s. lat. For further information on the systematics and ecology of *D. trichophyllus* in the Abisko area, see Sonesson (1966). Some finds of *Sphagnum* in unit III resembled *Sphagnum squarrosum*, but are here referred to as unidentified *Sphagnum* (indet.) because the identification is uncertain.

Organic matter content was estimated based on loss-on-ignition (LOI) analysis by igniting samples at 550°C for 4 h after drying at 105°C overnight. Total carbon (TC) and nitrogen (TN) contents were determined by combustion of oven-dried and homogenized samples using a Costech ECS 4010 elemental analyzer. BSi content was analysed by alkaline extraction of 30 mg of peat in 1% Na_2CO_3 solution during 3 h, as no simultaneous dissolution of DSi was observed from minerals in the BSi analysis during initial sequential extractions of randomly selected samples along the depth gradient. Elemental C/N and C/BSi ratios were converted into atomic ratios by multiplication with 1.167 and 2.34, respectively. C, N and BSi accumulation rates were calculated from the sedimentation rate, dry-weight bulk densities and dry-weight percentages of the respective elements.

Lake Inre Harrsjön sediment sequence

In January 2005 a 3.85-m long sediment sequence was recovered from Lake Inre Harrsjön (Fig. 1) at 3.5 m water depth. A freeze corer was used for the uppermost 0.84 m and a 10-cm Russian corer for deeper levels. The freeze core technique provides two parallel sequences (a- and b-side). Both were sampled and analyzed, but only the a-side was dated. Correlation between the two parallel frozen sequences as well as correlation between the freeze core sides and the uppermost Russian core segment was based on water and carbon content records. Correlation between individual Russian core segments was based on prominent lithostratigraphic changes.

The freeze core was subsampled frozen at 0.25 (0–25 cm, a-side), 0.5 (0–80 cm, b-side) or 1-cm (80–84 cm, b-side) sections. Russian core segments were stored at 4°C and sectioned at room temperature in 1 cm sections. All freeze core samples and a set of subsamples of the Russian core samples were freeze-dried, homogenised and used for determination of C, N and BSi contents and pigment analysis. Subsamples were kept cold and dark prior to analysis in order to preserve organic matter quality for pigment analysis. Remaining material from Russian core segments was wet sieved (250 μm) and used for extraction of macroscopic plant remains for radiocarbon analysis, whereas corresponding material from the freeze core was picked directly from the freeze-dried samples. As the amount of material from the top of the freeze core was insufficient for carbonate analyses, a complementary sediment sequence covering the upper 26 cm was retrieved in March 2004 using a gravity corer, subsampled in 0.5-cm sections in the field and correlated to the freeze core based on organic matter variability.

The chronology of the sediment sequence (Fig. 3) was based on ^{210}Pb radioisotope analysis of the uppermost section (Kokfelt et al. 2009) in combination with 12 radiocarbon dates deeper in the sequence (ESM 1; Skog 2007). Bayesian modelling (Bronk Ramsey 2008) enabled integration of stratigraphic information with prior calibrated radiocarbon distributions (Reimer et al. 2004) to generate new posterior age intervals with considerably narrower date ranges

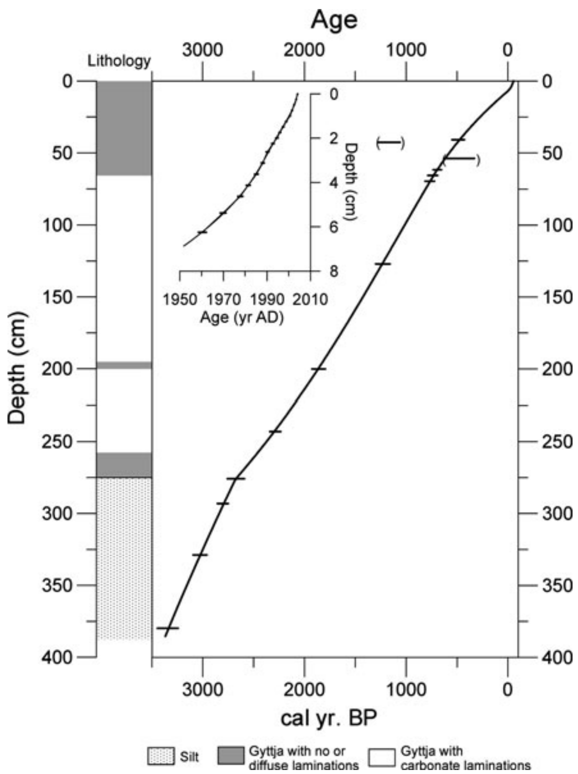

Fig. 3 Lake Inre Harrsjön ^{210}Pb ages (AD; inset diagram after Kokfelt et al. 2009), radiocarbon dates (ESM 1) and derived age model from the sediment sequence. Age-ranges obtained by Bayesian modeling are shown for radiocarbon dates used for the age-model. For the two rejected radiocarbon dates (marked by brackets) calibrated ranges corresponding to the double standard deviation are shown. Stratigraphic zonation (HS1-HS3) was based on visual inspection of the geochemical records and lithology

(Fig. 3). For the stratigraphic analysis of the sequence the procedure outlined in Blockley et al. (2007) was followed. One boundary at the transition from silt to gyttja was inserted at 275 cm. Two dates were excluded; LuS 6781, obtained on *Campylium stellatum* moss remains, was obviously too old, and LuS 7073 was excluded based on the P_Sequence algorithm (Blockley et al. 2007).

Calcium carbonate content ($CaCO_3$) was estimated based on percentage weight loss (LOI) at 925°C of samples previously ignited at 550°C. For analysis of organic C and total N content freeze-dried samples were transferred to silver capsules and carbonates were removed by reaction with 10% HCl. After drying at 65°C the residual material was analysed at the Department of Forest Ecology, Umeå, using a Europa Scientific elemental analyzer unit (ANCA-NT system, solid/liquid preparation module; Ohlsson and Wallmark 1999). The BSi content was determined according to Conley and Schelske (2001). C, N, BSi and $CaCO_3$ accumulation rates were calculated from the sedimentation rate, dry-weight bulk densities and dry-weight percentages of the respective components. Phosphorous in the form of vivianite in the sediment was registered visually in the freeze-dried samples, based on the bright blue colour of the mineral when oxidized. For pigment analysis, freeze-dried sediment samples were analysed as described in Reuss and Conley (2005).

Lake Villasjön sediment sequence

In January 2005 a 355-cm sediment sequence was retrieved from the northwestern part of the lake at a water depth of 1.3 m, using a Russian corer with a diameter of 10 cm. Following correlation of core segments based on the magnetic susceptibility surface scanning, the sequence was subsampled in 2 (1–94 cm) or 3 cm (94–355 cm) sections. 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.

Due to a large amount of redeposited peat components in the gyttja, terrestrial plant remains were deliberately avoided for the establishment of a chronology of the Lake Villasjön sediment sequence. Instead, radiocarbon dates were obtained from aquatic mosses that were assumed to have grown in the lake, although we were aware of potential reservoir effects. Radiocarbon dating was conducted on five samples of aquatic mosses (*Scorpidium scorpioides* and *Drepanocladus trichophyllus*) picked out from wet-sieved sediment samples (ESM 1). Only the lowermost radiocarbon date (LuS 7327) in the organic-rich clay was obtained on a terrestrial macrofossil, as no aquatic mosses were found here. An increase in magnetic susceptibility and decrease in organic matter content (LOI550) in the top 15 cm of the sequence is considered to be an effect of increased soil erosion caused by a nearby railway construction around the turn of the last century. The increase in magnetic susceptibility was therefore, assigned an age of 50 cal BP (Fig. 4).

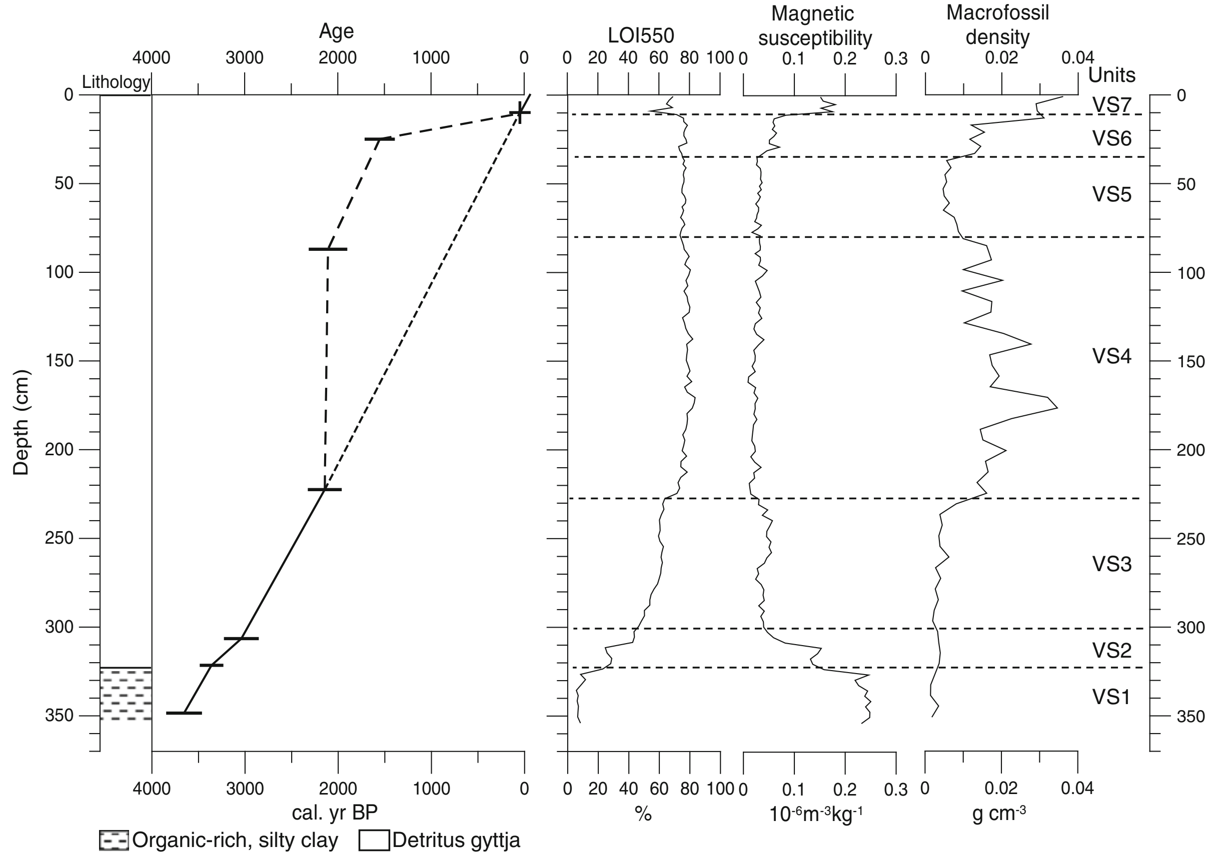

Fig. 4 Lake Villasjön radiocarbon dates (ESM 1) with double standard deviations and derived age model of the sediment sequence (dashed line), a theoretic age model assuming constant sediment accumulation rates (finely dashed line), together with records of organic matter content (LOI), magnetic susceptibility and macrofossil density. Stratigraphic units (VS1-VS7) are based on visual inspection of the records and lithology. In VS4 remains of *D. trichophyllus, D. revolvens, C. stramineum* and *Sphagnum fuscum, Ericaceae* spp. and *Carex* spp. were identified

The content of organic matter was determined by LOI at 550°C. The amount of coarse organic detritus (macroscopic plant remains) was quantified by wet sieving of fresh sediment samples through a 250-µm mesh. Sieve residues were oven-dried at 65°C and weighed, followed by calculation of plant macrofossil densities (g cm^{-3}).

Results

Peatland sequence

A number of different sediment and peat types were distinguished in the peatland sequence (Fig. 2, ESM 2 and ESM 3), with the contents of C, N and BSi and their respective atomic C/N and C/BSi ratios shown in Fig. 5. The lowermost organic-rich layer (unit II, 4,700–4,600 cal BP) contains the aquatic moss *D. trichophyllus*. Unit III consists of medium-humified organic-rich silt with unidentified *Sphagnum* remains (some resembling *S. squarrosum*) and sporadic occurrences of *S. lindbergii* and *D. exannulatus* s. lat.. Above follows a thin layer (unit IV) of low-medium humified peat, containing sporadic sedge shoots, frequent wood fragments and a rapidly increasing organic matter content. This so-called transition layer between organic-rich silt and almost purely organic peat represents a relatively large time span between ca. 2,800 and 1,350 cal BP. The peat in unit V is dominated by sedges (probably *Eriophorum* sp.) and *D. exannulatus* s. lat., followed by *S. lindbergii* peat in unit VI. Two dates at the transition between the sedge-*Drepanocladus* and

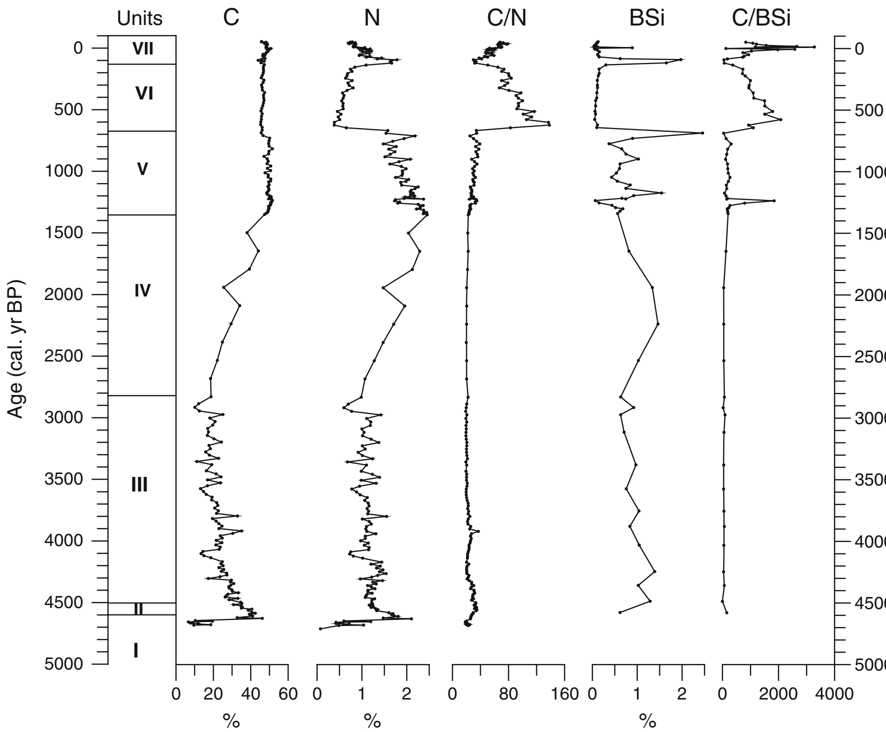

Fig. 5 Total organic carbon (C), total nitrogen (N) and biogenic silica (BSi) percentages, together with atomic C/N and C/BSi ratios shown against time for the peatland sequence

S. lindbergii peat, which marks the transition from fen to poor fen yielded average ages of 730 and 595 cal BP. Here we refer to a transition age of 700 cal BP. After ca. 120 cal BP *D. elongatum* (palsa) peat accumulated (unit VII), composed of taxa typical of permafrost peatlands. In the lowermost part of unit VII a mixture of *D. elongatum*, *S. lindbergii* and *Polytrichum strictum* dominates the moss layer, but after ca. 35 cal BP *D. elongatum* dominates.

Lake Inre Harrsjön sediment sequence

The sediment sequence consists of laminated silt below 275 cm and gyttja above. The latter exhibits occasional calcareous laminations especially between 258 and 64 cm (Fig. 3). A distinct black organic-rich layer occurs at 200–194 cm and two layers of grey silty gyttja at 262–260 cm. Vivianite was observed in the gyttja between 275 and 44 cm (ca. 2,650–500 cal BP).

Three stratigraphic zones (HS1-HS3) were based on major lithological and geochemical changes (Fig. 6). The lowermost laminated silt in HS1 is characterised by rapid silt deposition. The transition from silt to homogenous gyttja in HS2 at ca. 2,650 cal BP is rather abrupt. HS2 is characterised by the presence of carbonate laminations, except in two intervals between ca. 2,650 and 2,450 cal BP and between ca. 1,900 and 1,800 cal BP. The deposits in these two intervals have different characters with respect to colour and texture, but they also show similarities as both layers have elevated BSi and diatoxanthin contents and relatively low accumulation of $CaCO_3$ (ESM 4). Except for the two homogenous gyttja layers, the sediments of HS2 contain carbonate laminations and low BSi and diatoxanthin contents. Because microscopic examination revealed almost complete absence of carbonates of biogenic origin, the carbonate laminations are assumed to originate from precipitation of $CaCO_3$ during times of relatively high pH and alkalinity. $CaCO_3$ accumulation rates increase continuously from ca. 2,500 to ca. 1,250 cal BP (ESM 4). Between ca. 1,250 and 850 cal BP $CaCO_3$ accumulation rates decrease slightly together with the C/N ratio, whereas the C/N ratio decreases rapidly between ca. 850 and 700 cal BP. The uppermost zone HS3 beginning at ca. 700 cal BP is variable and shows a generally low but variable C/N ratio in the range of 14.7–18. The $CaCO_3$ content fluctuates, whereas the $CaCO_3$ accumulation rate shows a generally decreasing trend but with a marked increase during the last few decades.

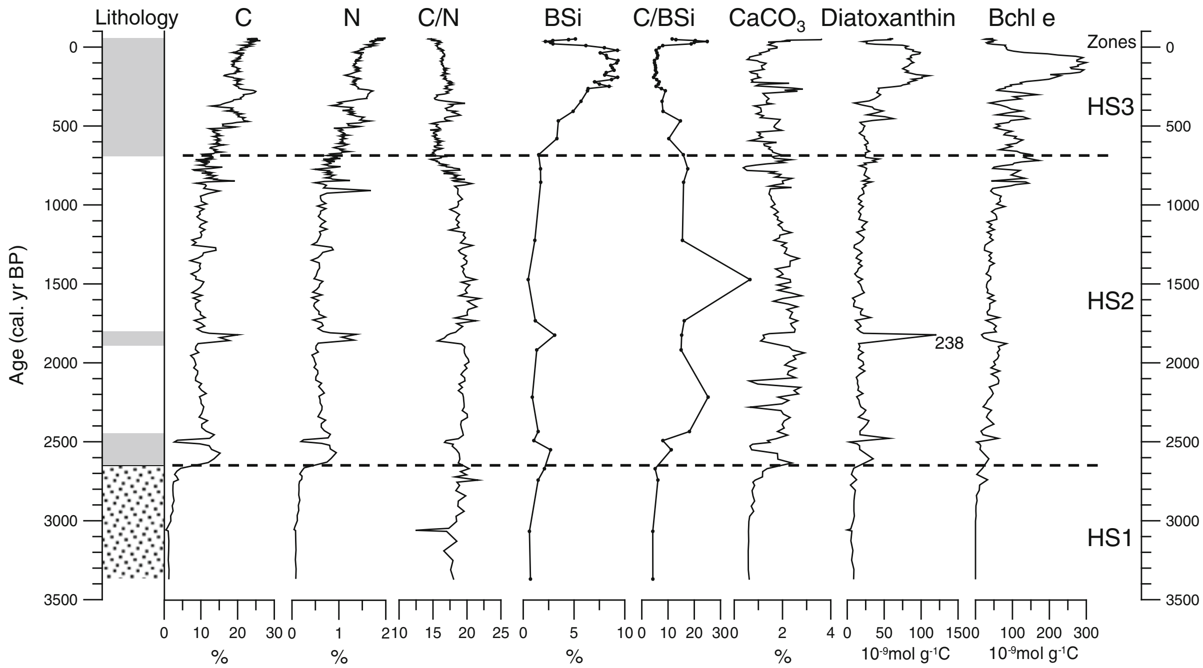

Fig. 6 Total organic carbon (C), total nitrogen (N), calcium carbonate ($CaCO_3$) and biogenic silica (BSi) percentages together with atomic C/N and C/BSi ratios and pigment concentrations against time for the Lake Inre Harrsjön sediment sequence. Stratigraphic zonation (HS1–HS3) was based on visual inspection of the geochemical records and lithology

The BSi accumulation rate increases and reaches a maximum of 5.5 g m^{-2} $year^{-1}$ (ESM 4) simultaneous with a maximum content of the pigments diatoxanthin (diatoms) and bacterial chlorophyll e (anoxygenic phototrophic bacteria) in the sediment organic matter between ca. 200 and 0 cal BP (AD1950; Fig. 6). BSi accumulation rates decrease again towards a minimum ca. AD1975 and increase again towards the present (ESM 4).

Lake Villasjön sediment sequence

Seven stratigraphic units (VS1-VS7) were defined (Fig. 4). The lowermost unit (VS1) consists of organic-rich silty clay followed by 323 cm of detritus gyttja (VS2-VS7), of which the lower and upper parts (VS2 and VS7) exhibit elevated silt content and hence magnetic susceptibility values. The macrofossil density record reveals elevated contents at 227–80 cm and above 35 cm (VS4 and VS6 and VS7).

Dating of the lowermost transition to gyttja indicate that organic sedimentation was initiated ca. 3,400 cal BP. The layer (VS4) rich in terrestrial macrofossils at 227–80 cm is interpreted as reworked peat, deposited after ca. 2,100 cal BP. The layer contains remains of mosses (*D. trichophyllus, Drepanocladus revolvens, Calliergon stramineum* and *Sphagnum fuscum*) and vascular plants *Ericaceae* spp. and *Carex* spp. originating in the mire.

All radiocarbon dates obtained on aquatic mosses (ESM 1) are potentially too old due to a reservoir effect caused by dissolution of carbonate bedrock in the catchment (MacDonald et al. 1987). On the other hand, the good chronological order of the two lowermost dates LuS 7327 on terrestrial plant remains and LuS 7327 on aquatic mosses assumed to have grown in the lake, may suggest a relatively insignificant reservoir age caused by this effect. The reservoir effect on the uppermost two radiocarbon dates above the reworked peat layer may however, have been successively enhanced, as the lake DIC pool used by aquatic mosses during photosynthesis was probably influenced or even dominated by carbon originating in the reworked peat deposited in VS4.

Two alternative age models tentatively based on centered calendar-age intervals have to be considered as theoretically possible. The sediment accumulation rate may have remained largely constant throughout the late Holocene (Fig. 4). Alternatively, and perhaps more likely, the sedimentation rate was significantly higher during periods of elevated macrofossil density. The true sedimentation pattern after ca. 2,100 cal BP thus probably lies somewhere in between these two hypothetical extremes.

C, N and BSi accumulation rates

C, N and BSi accumulation rates and atomic C/N and C/BSi ratios from the peatland and Lake Inre Harrsjön sequences are shown in Table 1 and ESM 4. The highest average accumulation rates of C and N were found in the sedge-*Drepanocladus* peat (unit V), and the highest average BSi accumulation rates were found in the silty fen peat (unit III). The transition between the sedge-*Drepanocladus* peat (unit V) and the *S. lindbergii* peat (unit VI) is characterised by a decrease in average accumulation rates of C, N and in particular in BSi and increased atomic C/N and C/BSi ratios (Fig. 5, ESM 4, Table 1). Following relatively low values in the *S. lindbergii* peat (unit VI) C, N and BSi accumulation rates increase in the palsa peat (unit VII). Accumulation rates in Lake Inre Harrsjön are grouped into three different categories; during silt deposition and during periods of gyttja deposition with and without carbonate laminations (Table 1). Average accumulation rates of all elements were at their highest during the silt deposition phase. The gyttja periods with carbonate laminations are characterised by higher average C and N accumulation rates, whereas the accumulation rate of BSi was higher when carbonate laminations are absent.

Discussion

The stratigraphic records provide insight into aspects of the structural development and permafrost dynamics of the Stordalen Mire and adjacent lakes, as well as nutrient cycling and biogeochemical links between the mire and Lake Inre Harrsjön (Fig. 7).

Late Holocene mire development and permafrost dynamics

Inception of peat deposition at the Stordalen Mire has been dated at ca. 6,000 cal BP (Sonesson 1972) in the southern part of the mire and at ca. 4,700 cal BP in the northern part (this study), as a result of terrestrialisation of a dynamic open water area. This interpretation is based on the occurrence of rapidly deposited silt below the organic-rich deposits. Around this time a relatively continental climate with warm summers prevailed in the region, promoting retraction of glaciers (Snowball and Sandgren 1996), lowered lake levels and expansion of pine-birch forest (Barnekow 2000).

Table 1 Average accumulation rates of C, N, BSi and atomic C/N and C/BSi ratios from units in the peatland sequence and from the lake inre harrsjön sediment record

	C g m^{-2} $year^{-1}$	N g m^{-2} $year^{-1}$	BSi g m^{-2} $year^{-1}$	C/N Atomic ratios	C/BSi
Peatland sequence					
Unit VII: *D. elongatum* bog/palsa peat	43.6	0.9	0.3	56	1,165
Unit VI: *Sph. lindbergii* poor fen peat	17.6	0.3	0.05	85	1,135
Unit V: Sedge-*Drepanocladus* fen peat	51.4	2.1	0.6	29	271
Unit IV: Transition layer	5.4	0.3	0.2	21	68
Unit III: Organic-rich silt	39.1	1.9	1.5	25	54
Lake inre harrsjön					
Gyttja without carbonate laminations[a]	13.2	0.9	3.5	14	7
Gyttja with carbonate laminations[b]	17.4	1.1	2.6	16	18
Silt	25.2	1.6	14.3	18	5

[a] 2,650–2,450 cal BP and 700 cal BP-present

[b] 2,450–700 cal BP. The grey minerogenic double layers (ca. 2,500 cal BP) and the black homogenous gyttja (ca. 1,900–1,800 cal BP) not included

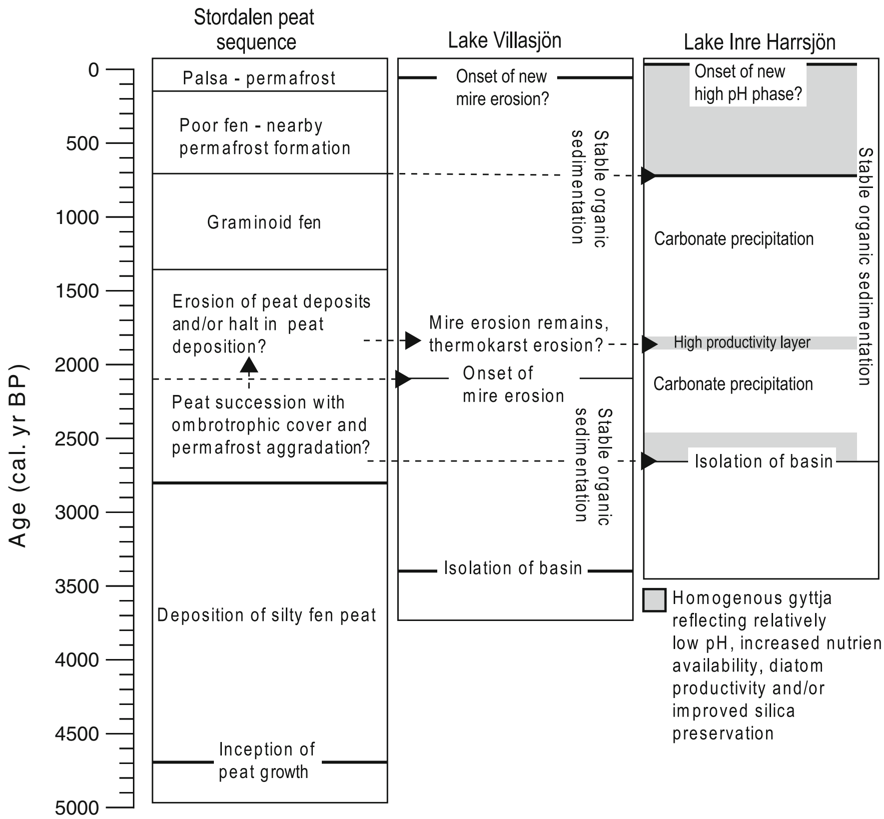

Fig. 7 A syntheses of events inferred from the peatland sequence and the lake sediment records. Dashed arrows indicate tentative relations between records

The peatland sequence investigated reflects hydrosere, with successively diminishing influence of groundwater and catchment runoff and less nutrient-demanding vegetation types. Hydrosere may well occur without any change in climate, but the transition from one step in the succession to another is more rapid if triggered by external factors such as changes in temperature and precipitation (Charman 2002) or permafrost aggradation (Vardy et al. 1998). The deposition of organic-rich silt ca. 4,700–2,800 cal BP indicates that the water flow through the vegetation was strong enough to carry silt in suspension. The low peat accumulation rate at ca. 2,800–1,350 cal BP (unit IV) may reflect post-depositional erosion and/or ceased deposition. Further, the occurrence of wood in this transition layer (unit IV) potentially indicates relatively drier conditions and/or the presence of hummocks with dwarf shrubs. Such hummocks may have been a result of permafrost aggradation but it should be emphasized that this interpretation remains speculative, as the unidentified wood remains may also have originated from shrubs or dwarf shrubs in fen habitats. The peat stratigraphy above the transition layer reflects a succession from a sedge-dominated fen vegetation cover to a poor fen community dominated by *S. lindbergii* around 700 cal BP (unit VI). *S. lindbergii* carpets frequently occur around palsas (Sonesson 1970a; Oksanen and Kuhry 2003), and are possible indicators of permafrost in the near vicinity, as observed at the sampling site today. The upper palsa peat layer (unit VII) gives a minimum age of permafrost aggradation at the sampling site of 120 cal BP. The upper poor fen/bog stratigraphy resembles the record obtained by Sonesson (1970b, 1974) from a palsa mire approximately 500 m east of the Stordalen site. Here poor fen communities were represented by a peat layer dominated by *S. lindbergii, C. stramineum* and *D. exannulatus* s. lat. from a depth of 48 cm. Ombrotrophic palsa peat was found only in the upper 5 cm, pointing to a relatively recent permafrost aggradation phase, consistent with data obtained from the peat sequence investigated here (120 cal BP). Malmer and Wallén (1996) reported ages around 250 and 400 cal BP for the formation of ombrotrophic peat at Stordalen, presumably indicating permafrost aggradation. Several dates thus fall within the Little Ice Age, which in the Torneträsk area was initiated ca. 850 cal BP (Grudd et al. 2002).

Both the Lake Villasjön and the Lake Inre Harrsjön basins were probably parts of a larger and hydrologically dynamic, deltaic environment until they developed into lakes with stable organic sedimentation at ca. 3,400 and 2,650 cal BP, respectively. This interpretation is supported by the minerogenic character of the underlying sediments and by the presence of silt in the peatland deposits during the same time. Vertical and lateral mire expansion may have contributed to the earlier onset of stable organic sedimentation at the upstream, shallow Lake Villasjön as compared to Lake Inre Harrsjön. The initiation of organic sedimentation in Lake Villasjön around 3,400 cal. BP is thus considered as a result of mire expansion and coincides with the retraction of boreal pine-birch forest from the Abisko Valley and reformation of nearby mountain glaciers (Snowball and Sandgren 1996; Barnekow 2000).

The onset of stable organic sedimentation in the Lake Inre Harrsjön basin ca. 2,650 cal BP may have been caused by permafrost aggradation in the central peat plateau, leading to upheaval of the peatland surface as well as the underlying silt. The development of permafrost probably led to expansion of poor fen *Sphagnum* communities and/or ombrotrophic hummocks that caused more acidic runoff to the lake. A lowered lake-water pH due to this mechanism would explain the lack of carbonate laminations in the gyttja of Lake Inre Harrsjön at ca. 2,650–2,450. More solid evidence of this mechanism is present in younger parts of the analysed records, where poor fen (*S. lindbergii*) formation ca. 700 cal BP largely coincides with the disappearance of carbonate laminations in Lake Inre Harrsjön. Permafrost aggradation may also have led to diversion of the inflow of alkaline groundwater that maintains a high pH and carbonate precipitation in the lake at present.

The limited occurrence (10 cm) of peat in the peatland sequence dated at ca. 2,800–1,350 cal BP indicates a significant halt in deposition or erosion around the sampling site leading to a hiatus. A subsequent erosion phase is indicated by 1.4 m of redeposited peat after ca. 2,100 cal BP in the adjacent Lake Villasjön sediment sequence. The redeposited peat contains a mixed assemblage of peat derived from fen and bog habitats. Abundant remains of the ombrotrophy indicator *S. fuscum* recorded together with minerotrophic fen species potentially represent different stages in a peatland succession. *S. fuscum* is frequently found in permafrost settings in mires (Oksanen 2002). The presence of *S. fuscum* in the reworked peat in Lake Villasjön in combination with the low accumulation rate in the peatland sequence, strengthens the hypothesis of an early permafrost aggradation phase after ca. 2,650 followed by block and/or wind erosion processes after ca. 2,100.

The absence of an erosion layer in Lake Inre Harrsjön, only a few hundred meters downstream of Lake Villasjön, probably indicate spatial differences in mire communities and processes. The dark, homogenous fine-detritus gyttja in Lake Inre Harrsjön at ca. 1,900–1,800 cal. BP may however, also be connected to permafrost-induced peat erosion, which likely resulted in increased delivery of dissolved and particulate organic matter. This process may have mobilized nutrients in the peat and made them available for primary producers in the lake, and would explain the high content and accumulation rate of BSi and the elevated content of the diatom pigment diatoxanthin in the organic matter of this layer. It is possible that the dark homogeneous gyttja layer in Lake Inre Harrsjön and the erosion layer of Lake Villasjön have been deposited simultaneously taken into account the possible reservoir effects on the radiocarbon dates from Lake Villasjön.

The increase in $CaCO_3$ content of the Lake Inre Harrsjön sediments after the ca. AD1980 probably indicates increased inflow of alkaline water together with a recent phase of renewed mire erosion. These changes were most likely brought about by the onset of the recent permafrost degradation phase at Stordalen (Christensen et al. 2004).

The inferred permafrost history at Stordalen is largely consistent with the development at other Fennoscandian sites, where multiple permafrost aggradation phases are dated to ca. 2,700 cal BP and to after ca. 600 cal BP (Oksanen 2006; Zuidhoff and Kolstrup 2000). The earliest dated permafrost aggradation phase in Fennoscandia slightly precedes a period of generally cold and variable climate conditions as indicated by Swedish records of pine from ca. 2,550 to 1,950 cal BP (Grudd et al. 2002). This period is characterised by highly variable tree-ring data, including both minimum and maximum ring widths and inferred summer temperatures of the entire 7,400 year record. With respect to permafrost aggradation, it is however, even more important to note that the sample density is very low during this period. Cold winters may have resulted in increased pine tree and seed mortality (Kullman 2007) and hence a relatively low pine tree-line (Kullti et al. 2006). Winters might also have been very windy. Cold winters in combination with a severe winter wind regime promoting snow-drift are favourable for palsa formation (Seppälä 1986). The onset of this anomalous period at ca. 2,550–1,950 cal BP post-dates the earliest potential permafrost aggradation phase at Stordalen at ca. 2,650 cal BP, but encompasses evidence of erosion and relocation of peat deposits within the mire. A vivid wind regime may even have favoured erosion of palsa deposits due to scouring by ice-crystals (Seppälä 2003).

Aspects of nutrient cycling and impacts on adjacent lakes

Several lines of evidence in this study indicate that a mixture of different mechanisms relating to catchment development, climate and internal lake processes have interacted to explain the Late Holocene development of Lake Inre Harrsjön. The similar timing between the expansion of *Sphagnum* in the mire, the increase in BSi and absence of carbonate laminations in the sediments of Lake Inre Harrsjön around 700 cal BP indicate a tight hydrological connection between the mire and the lake. Particularly, the results stress the importance of mire vegetation dynamics controlling catchment nutrient fluxes, lake water pH and internal nutrient recycling.

Our results showed higher C-accumulation rates in bog deposits (unit VII) than in poor fen deposits (unit VI) despite the lower nutrition level. This is possibly due to the high degree of decomposition in the dry and aerated palsa peat where C is allocated into a “fast” metabolic pool dominated by DOC, such as organic acids exudated from the roots of vascular plants (Olsrud 2004). Some organic acids are capable of mobilizing P from litter (Ström 1997) and efficient recycling of nutrients due to this mechanism may have resulted in high C-sequestration rates of dwarf shrubs on the palsa. It should however, be emphasized that C-accumulation rates of dry ombrotrophic parts may vary significantly (Oksanen 2005) dependent on the surface structure and vegetation density.

Strategies for nutrient uptake as well as C and nutrient accumulation rates of poor fen and bog vegetation types differ significantly. Bog communities are *sensu stricto* isolated from water and nutrients in contact with the mineral soil, and are thus unable to take up any nutrients available there. Poor *Sphagnum* fen communities on the other hand have access to nutrients, but create an acidic and nutrient-poor environment that is unsuitable for most vascular plants (van Bremen 1995). Their ability to suppress vascular plant growth combined with the low capacity of *Sphagnum* to accumulate nutrients may lead to an incomplete usage of nutrients originating either from upland sources or mineralised from nutrient-rich peat layers. The Stordalen Mire is located in a rain shadow with low annual precipitation. Recycling under such conditions may lead to longer water residence time and to high nutrient concentrations in the pore waters of minerotrophic peat. These dissolved nutrient pools can subsequently be transported to downstream lakes during rain events or melting of winter snow. In this way nutrients may escape retention by terrestrial vegetation and stimulate primary productivity of adjacent lakes. In response to expanding poor fen and bog communities from ca. 700 cal BP, this process probably induced increased productivity in Lake Inre Harrsjön as indicated by the increase in BSi content. Mineralisation in a *Sphagnum* deposit is, however, hampered by the low rate of decomposition and the mire may thus have acted as a slow nutrient-releasing buffer, constraining primary productivity. These circumstances might explain the initially slow and gradual increase in Si deposition in the lake sediments after poor fen and/or bog development at ca. 700–500 cal BP. Despite fundamental differences in ecosystem functioning between poor fens and bogs, any of these two ecosystem types potentially caused similar impacts on the adjacent lakes by promoting relocation of nutrients from the mire to the lakes.

The potential stabilising effect of permafrost on the buried nutrient-rich peat deposits complicates this hypothesis, as leaching do not occur from permanently frozen pools. Shallow layers of palsa peat above *S. lindbergii* peat in nearby areas (Sonesson 1974 and this study) indicate that permafrost-free wet *Sphagnum* carpets may have been relatively extensive until the recent past (i.e. within the last few centuries), which may have enabled nutrient mineralisation and leaching from the mire.

Periods of lowered lake-water pH are indicated by the absence of carbonate laminations in parts of the Lake Inre Harrsjön sediment record. These periods coincide with expansion of poor fen and bog communities and are probably related to the generally low pH of these ecosystems. Halsey et al. (1997) showed that the influence of poor fens was larger relative to bogs due to greater through-flow in the poor fens. However, mechanisms in bog environments may also lead to acidification of adjacent lakes. The elevated production of organic acids by vascular plants together with aerated decay probably contributes to the low pH in the dry ombrotrophic areas at Stordalen, and acidic runoff may have improved the preservation of BSi in the lake sediments (Flower 1993). The increase in BSi content may therefore, partly reflect acid runoff from the mire during poor fen and bog expansion.

The elevated BSi level recorded in the upper part of the Lake Inre Harrsjön sediment sequence is mainly attributed to increased primary productivity due to increased nutrient fluxes from the catchment. In addition, recycling phosphorous from the sediments may have been important. Phosphorous is labile in sediments. It binds readily to iron oxides under oxic conditions but large fluxes may escape under reducing conditions (Lampert and Sommer 2007). The presence of the iron phosphate mineral vivianite in the sediments prior to ca. 500 cal BP, indicate abundant phosphorous. The apparent absence of vivianite after ca. 500 cal BP, on the other hand, indicates that anoxic conditions developed in the bottom waters. Reducing conditions may have dissolved P from sediments and stimulated diatom productivity in the surface water, such as reflected by the elevated diatoxanthin concentration. The development of anoxia is supported by the high abundance of anoxygenic phototrophic bacterial pigments (bacterial chlorophyll e) after ca. 200 cal BP. Peak values of diatoxanthin, bacterial chlorophyll e and BSi at ca. 200–0 cal BP (AD1950) are thus considered to reflect seasonal anoxia in the bottom waters, with nutrient fluxes from the sediments leading to a state of self-sustained eutrophication. Accordingly, the short-lived but significant decrease in BSi around AD1975, may reflect a period of oxidized conditions at the lake bottom.

Catchment vegetation development may have provided an additional control on the lake-sediment silica content, consistent with recent observations of increased Si supply to lakes in response to reduced plant cover (Conley et al. 2008, Street-Perrot et al. 2008). A similar relationship between major shifts from fen to poor fen/bog vegetation communities and changing nutrient conditions of adjacent lakes seems likely as described in the present study. Therefore, if permafrost degradation causes continued expansion of fen vegetation at the expense of poor fen and bog vegetation, more nutrients will be retained by vegetation, which may lead to reduced nutrient fluxes from the mire.

Conclusions

Bryophyte assemblages and deposition of organic-rich silt indicate permafrost-free conditions in the mire before ca. 2,800 cal BP. Permafrost is inferred to have occurred during two periods; ca. 2,650–2,100 cal BP and after ca. 700 cal BP. Palsa formation developed at the coring site at ca. 120 cal BP. A period of intense erosion, possibly as a result of thermokarst processes and wind erosion, was initiated at ca. 2,100 cal BP and resulted in considerable losses of peat from the mire.

The absence of carbonate laminations in Lake Inre Harrsjön at ca. 2,650–2,450 and after ca. 700 cal BP indicates acidification of mire runoff in response to permafrost aggradation and development of poor fen and bog communities. 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 water. A short-lived period with greatly enhanced lake productivity at ca. 1,900–1,800 cal BP is possibly related to mire erosion.

The accumulation rate of BSi was significantly larger in fen peat as compared to peat dominated by poor fen/bog communities. Leaching of BSi from peat deposits, in particular during periods of poor fen/bog dominance in the mire, may have contributed to increased lake productivity, although increased P and N loading from the catchment may have been equally important.

An increase in terrestrial nutrient fluxes after the transition from a fen to poor fen/bog communities at ca. 700 cal BP likely resulted in bottom water anoxia and P release from the sediments, which initiated a state of self-sustained eutrophication after ca. 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 peat deposits but reduce nutrient fluxes in runoff to adjacent lakes. Rapid permafrost degradation may however, lead to widespread erosion and relocation of mire deposits and to relatively short periods of significantly increased nutrient loading to adjacent lakes.

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