



## Deglacial vegetation succession and Holocene tree-limit dynamics in the Scandes Mountains, west-central Sweden: stratigraphic data compared to megafossil evidence

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### Abstract

High-resolution records of plant macrofossils, magnetic susceptibility, and total carbon content, complemented by pollen data, were obtained from a postglacial lake sediment sequence at alpine Lake Stentjärn (987 m a.s.l.), in west-central Sweden. Holocene vegetational and environmental changes were reconstructed from the data, with particular emphasis on the deglacial establishment of terrestrial vegetation and subsequent tree-limit dynamics. A short-lived pioneer flora with *Geum rivale*, *Dryas octopetala*, *Empetrum nigrum*, *Ledum palustre*, *Saxifraga* sp., *Salix* spp., and *Oxyria digyna* established locally following deglaciation at c. 10,500 cal year BP. The pioneer flora was out-competed by establishing *Betula pubescens* and grasses at c. 10,300 cal year BP. Subsequent local expansions of *B. pubescens* at c. 9800 cal year BP and *Pinus sylvestris* at c. 9200 cal year BP were followed by a temporary retraction of the birch tree-limit and a permanent retreat of pine between 8500 and 8000 cal year BP, accompanied by declining aquatic productivity and increasing catchment erosion. A gradual decrease in forest density initiated at c. 6000 cal year BP led to a retreat of the birch tree-limit from the lake catchment at c. 3500 cal year BP, followed by persistence of scattered trees until c. 2000 cal year BP. A mosaic heath vegetation dominated by *Empetrum nigrum* and *Betula nana* developed at c. 3500 cal year BP. Comparison of the stratigraphic data from Lake Stentjärn with records of radiocarbon-dated subfossil wood remains (megafossils) obtained from adjacent areas during recent decades revealed a high level of consistency of the inferred tree-limit variations for *P. sylvestris*, *B. pubescens*, and *Alnus incana*. Chronological control was established by radiocarbon dating of terrestrial macrofossils and geochemical identification of a tephra horizon originating from the Icelandic Askja-1875 eruption. © 2004 Elsevier B.V. All rights reserved.

**Keywords:** tree-limit ecotone; macroscopic plant remains; deglacial plant succession; forest history; palaeoclimate; 8200 cal year BP event

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## 1. Introduction

Past fluctuations of alpine tree-limit ecotones have caught the attention of naturalists for more than a century. Such profound environmental changes have implications for human activities such as occupation history and forestry, as well as for palaeoclimate research and prediction of ecosystem responses to possible future warming (Hofgaard, 1997). Holocene tree-limit dynamics and forest compositional changes in the Scandes Mountains of Sweden and Norway have recently been increasingly considered and debated (e.g. Kullman, 1998a, 2000a; Karlén, 1999; Barnett et al., 2001; Segerström and von Stedingk, 2003; Eide, 2003; Eide et al., 2005), partly motivated by observations of progressively ascending tree-limits during the last century (Kullman, 2001, 2002a). The long-term Holocene vegetation development in the central part of the Scandes is known through radiocarbon dating of subfossil wood remains (megafossils) found above the present-day tree-limit (Lundqvist, 1959; Kullman, 1995, 1998b; Kullman and Kjällgren, 2000), and through regional pollen analytical studies of lake sediments and peat sequences (Lundqvist, 1969). However, as pointed out by Kullman (1998a), Birks and Birks (2000), and Birks (2003), pollen analysis alone is insufficient for reconstruction of Holocene tree-limit fluctuations. Macrofossil analysis stands out as an obligate complement, enabling secure detection of the presence of specific tree species, e.g. as applied in vegetational studies of deglacial nunataks in Scandinavia (Kullman, 2002b). A stratigraphic approach allows details of vegetation history and related environmental changes to be evaluated in a continuous temporal framework at specific sites. Although highly informative in a regional context, alpine megafossil data-sets can be considered, at a local scale, to be temporally and spatially discontinuous (Kullman, 1998c; Aas and Faarlund, 1988, 1996), mainly due to changing preservation conditions (Dubois and Ferguson, 1985). Stratigraphic studies of lake sediments including pollen and plant macrofossil analyses have provided valuable information on Holocene forest dynamics in the northern part of the Scandes (Barnekow, 1999, 2000), complementing and partly deviating from previous megafossil evidence.

Here we present high-resolution plant macrofossil records from an alpine lake site in the western part of the province of Jämtland, west-central Sweden, an area in which an unprecedented set of megafossils has been collected and radiocarbon dated during recent decades (Kullman, 1995; Kullman and Kjällgren, 2000). This megafossil data-set includes almost 250 samples of *Pinus sylvestris*, *Betula pubescens*, and *Alnus incana* collected above the modern altitudinal forest-limit. Our combined palaeoecological and sediment stratigraphic approach enables further details of the Holocene vegetational history in this area to be assessed, such as the vegetational succession preceding the arrival of trees and the response of tree-limit vegetation to abrupt and more gradual climate forcing mechanisms, respectively. Together with corresponding records from a nearby lake at a slightly lower elevation (Hammarlund et al., 2004), these new findings form a basis for an evaluation of the establishment, temporal development, and ultimate retreat of high-altitude forest ecosystems in the Scandes Mountains. Definitions of the terms forest-limit and tree-limit used in this study generally follow Matthews et al. (2001). In summary, the forest-limit is the upper altitudinal limit of continuous forest (maximum 30 m between stems) or stands of trees (minimum 15 trees), and the tree-limit (tree-line) is the upper altitudinal limit of tree clusters or individual trees exceeding 2 m in height.

Alpine and arctic plant communities are sensitive to environmental changes and react more quickly to fluctuations in climate than terrestrial communities of the temperate climate zone. Many species in the alpine/arctic region occur at their distributional limits, which makes them well qualified as proxies for climate reconstructions. For example, the tree-limit in the southern part of the Scandes has ascended by 100–130 m in response to warming during the 20th century (Kullman, 2001), whereas no significant vegetation response has been reported from southern Sweden. The study area is well located for comparison with records of glacier status variations (Karlén et al., 1995; Dahl and Nesje, 1996), lake-level fluctuations (Hyvärinen and Alhonen, 1994; Barnekow, 2000), and tree-limit dynamics (Kullman and Kjällgren, 2000, and references therein) in northern, central and southern Scandinavia. The relative proximity to the Atlantic Ocean is also an important factor as the

local climate has been directly linked to the North Atlantic throughout the Holocene. Negligible human impact on the tree-limit ecotone during most of the Holocene facilitates interpretation of the vegetational records, although limited summer farming may have had an effect during the last c. 1500 years in some parts of the province (Wallin, 1999). Little is known about the extent of reindeer pastoralism, but local studies have shown that its impact on the tree-layer and the tree-limit ecotone has been limited, possibly

with the exception of the last 400 years (Kullman, 1979, 1989a; Kjällgren and Kullman, 1998).

### 1.1. Study area

The Storulvån–Sylarna area is situated in the south central part of the Scandes mountain range (Fig. 1). Details of local bedrock geology and morphology, Quaternary deposits, and regional climate were given by Hammarlund et al. (2004). Lake

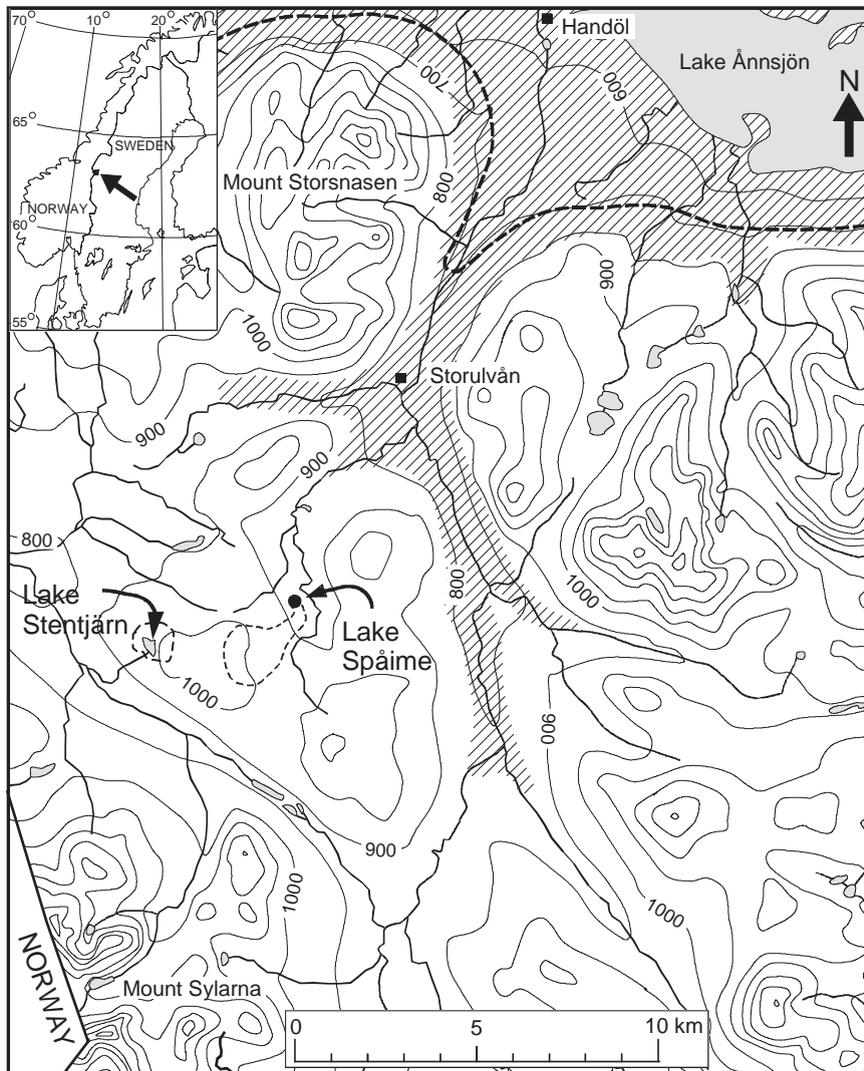


Fig. 1. Map of the Storulvån–Sylarna study area in west-central Sweden. The hatched area indicates the local altitudinal limit of subalpine mountain birch forest (c. 800 m a.s.l.), and the heavy dashed line mark the local forest-limit of *Pinus sylvestris* (c. 720 m a.s.l.). The catchment areas of Lake Stentjärn and Lake Spåime (Hammarlund et al., 2004) are indicated by dashed lines.

Stentjärn (63°06.0' N, 12°14.5' E) measures c. 375×300 m (c. 7 ha) and is situated at 987 m a.s.l. near the summit of Mount Enkälen (Fig. 1). Its maximum water depth is c. 6 m. The catchment area extends across c. 30 ha and is covered mainly by heath vegetation dominated by dwarf-shrubs, willows, grasses, sedges, and herbs. *Betula nana*, *Empetrum nigrum*, and *Vaccinium uliginosum* are among the most common vascular plants (Rafstedt, 1984). A small outlet stream (c. 20 ls<sup>-1</sup>) drains towards the south.

Lake Stentjärn is located in the centre of the c. 8000 km<sup>2</sup> area represented by the megafossil data set used for comparison. This area extends from the low altitude coniferous forest zone to the high alpine zone. Mountain birch (*Betula pubescens* ssp. *czerepanovii* (N.I. Orlova)) forms the local tree-limit and forest-limit at c. 900 and 800 m a.s.l., respectively, although the regional mean tree-limit is situated at c. 925 m a.s.l. Below the mountain birch zone, Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst) dominate the regional coniferous forest, with single tree-sized specimens extending to maximum c. 825 and 875 m a.s.l., respectively. However, krummholz of *Picea* and *Pinus* can be found far beyond their respective tree-limits (Kullman and Kjällgren, 2000). Grey alder (*Alnus incana*) grows in small stands or as isolated individuals within the subalpine mountain birch zone. The field layer in the tree-limit ecotone is dominated by dwarf shrubs such as *Vaccinium myrtillus*, *Empetrum nigrum*, *Betula nana*, *Calluna vulgaris*, and *Juniperus communis* (Rafstedt, 1984; Kullman, 1995).

## 2. Methods

### 2.1. Fieldwork

Multiple, overlapping sediment cores were collected from the lake ice in February 2002. The coring was performed c. 50 m from the southern shore, where the thickest sediments were located and the bottom topography was flat, using Russian corers (Jowsey, 1966; 7.5 and 10 cm diameter, 1 m length). The water depth at the coring point was 4.65 m, and the coring reached a maximum depth of 8.735 m below the water surface (Fig. 2 and Table 1). The 1-m

segments of the 4.085-m sediment profile were carefully wrapped in plastic and transported to the laboratory at Lund University for cold storage and subsequent sub-sampling.

### 2.2. Core correlation and sediment stratigraphic analyses

Overlapping sediment core segments were correlated based on measurement of magnetic susceptibility at 4-mm increments using a Bartington Instruments MS2E1 surface scanning sensor coupled to a Tamiscan-TS1 automatic logging conveyor.

Mineral magnetic parameters and total carbon (TC) content were measured on contiguous sediment samples (2 cm<sup>3</sup>), spanning 1 cm in stratigraphic extension from 8.735 to 8.00 m, 2 cm from 8.00 to 5.66 m, and 3 cm from 5.66 to 4.65 m (sediment surface). Magnetic susceptibility ( $\chi$ ) was

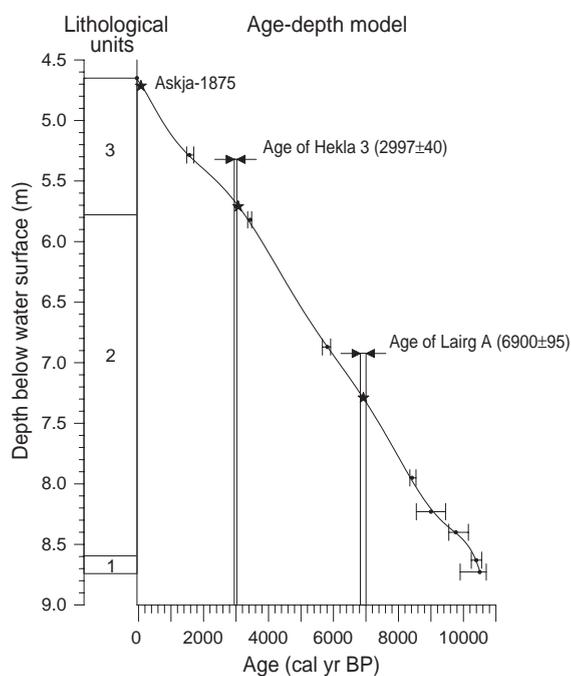


Fig. 2. Lithological subdivision of the Lake Stentjärn sediment sequence and the age-depth model applied, based on radiocarbon dating (horizontal lines with  $2\sigma$  standard deviations; Table 2) and the identification of the Askja-1875 tephra horizon. Stars at 5.71 and 7.29 m depth represent unidentified tephra not used in the age-depth model. Published ages for Hekla-3 (Van den Bogaard et al., 2002) and Lairg A (Pilcher et al., 1996) are indicated with 95.4% confidence intervals. Lithological units are described in Table 1.

Table 1  
Lithostratigraphic description of the sediment sequence from Lake Stentjärn

Lithological units	Depth (m)	Sediment description
3	4.65–5.78	Brown, moss-dominated algal gyttja, lower boundary gradual
2	5.78–8.59	Light brown, slightly silty algal gyttja, lower boundary gradual
1	8.59–8.735	Grey silty gyttja

Depths are related to the water surface.

measured with a Geofyzica Brno KLY-2 air-cored magnetic susceptibility bridge. Samples were then dried at 40 °C, weighed, and ground to powder for determination of TC content, using a Carlo Erba Instruments NC2500 elemental analyzer. The reproducibility is within ±0.5% based on repeated analyses, and the TC data are expressed on a total dry weight basis, as percentages of elemental carbon (Fig. 3).

### 2.3. Chronological methods

AMS radiocarbon dating was carried out on eight samples of macroscopic plant remains and one bulk sediment sample (Table 2). The macrofossil samples were wet-sieved, rinsed in de-ionized water, and dried at 105 °C, followed by standard pre-treatment and analysis at the radiocarbon dating laboratories at Poznań University, Poland, and Lund University, Sweden. The reported radiocarbon ages were converted to calibrated ages based on the IntCal98 calibration data set (Stuiver et al., 1998), using the OxCal vers. 3.5 radiocarbon calibration software.

With guidance from the age–depth model based on the calibrated radiocarbon dates (Fig. 2), five sections within the sediment sequence spanning 200–600 years were screened for cryptotephra horizons in order to refine the chronology. These sections covered approximately 0–200, 2700–3300, 3500–4100, 3900–4500, and 6700–7300 cal year BP, thus possibly containing

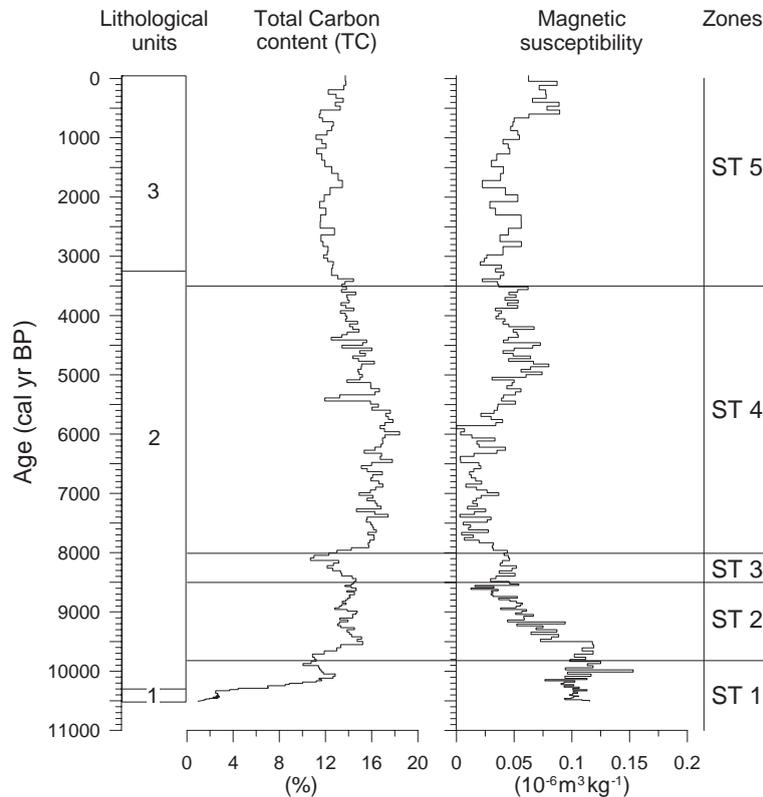


Fig. 3. Total carbon content and magnetic susceptibility in relation to the lithological subdivision of the sediment sequence. Terrestrial vegetation zones are shown for comparison (see Fig. 5).

Table 2  
AMS radiocarbon dates

Lab. No.	Depth (m)	<sup>14</sup> C age (years BP)	Calibrated age, (years BP, 2σ)	Dated material
Poz-2834	5.27–5.30	1660±30	1480–1700	Leaves ( <i>Empetrum</i> )
Poz-2753	5.80–5.84	3215±30	3360–3480	Twigs, leaf fragments ( <i>Betula</i> )
Poz-2752	6.86–6.88	5045±40	5660–5910	Twig ( <i>Salix</i> )
Poz-3306	7.88–7.90	8070±50	8700–9300	Bulk sample (not used for chronology)
Poz-2751	7.94–7.96	7630±40	8350–8540	Mosses, twigs, leaf fragments ( <i>Salix</i> )
Poz-2832	8.22–8.24	8080±130	8550–9450	Twigs, mosses, (0.1 mg C)
Poz-2830	8.38–8.42	8760±45	9550–10150	Twigs, mosses, seeds
Poz-2750	8.62–8.64	9250±50	10240–10560	Leaf fragments, seeds ( <i>Empetrum</i> )
LuA5477	8.72–8.735	9165±120	9900–10700	Cone, bud scales ( <i>Salix</i> )

Depths are related to the water surface.

the Askja-1875, Hekla-3, Kebister, Hekla-4, and Lairg A tephra, respectively. Glassy tephra particles (shards) were detected using the method described by Pilcher et al. (1995). Further details of this procedure including the geochemical identification by electron probe micro-analysis (EPMA) were given by Bergman et al. (2004), and, more generally, by Dugmore et al. (1995) and van den Bogaard and Schmincke (2002).

#### 2.4. Plant macrofossil analysis

Macrofossil analysis was performed on 2 cm contiguous samples from 8.735 to 5.66 m, and on 3 cm contiguous samples from 5.66 to 4.65 m (sediment surface) using standard techniques (Wasylikowa, 1986). The samples were soaked in 5% NaOH overnight followed by wet-sieving through a 250-μm mesh. Sieve residues were examined under a

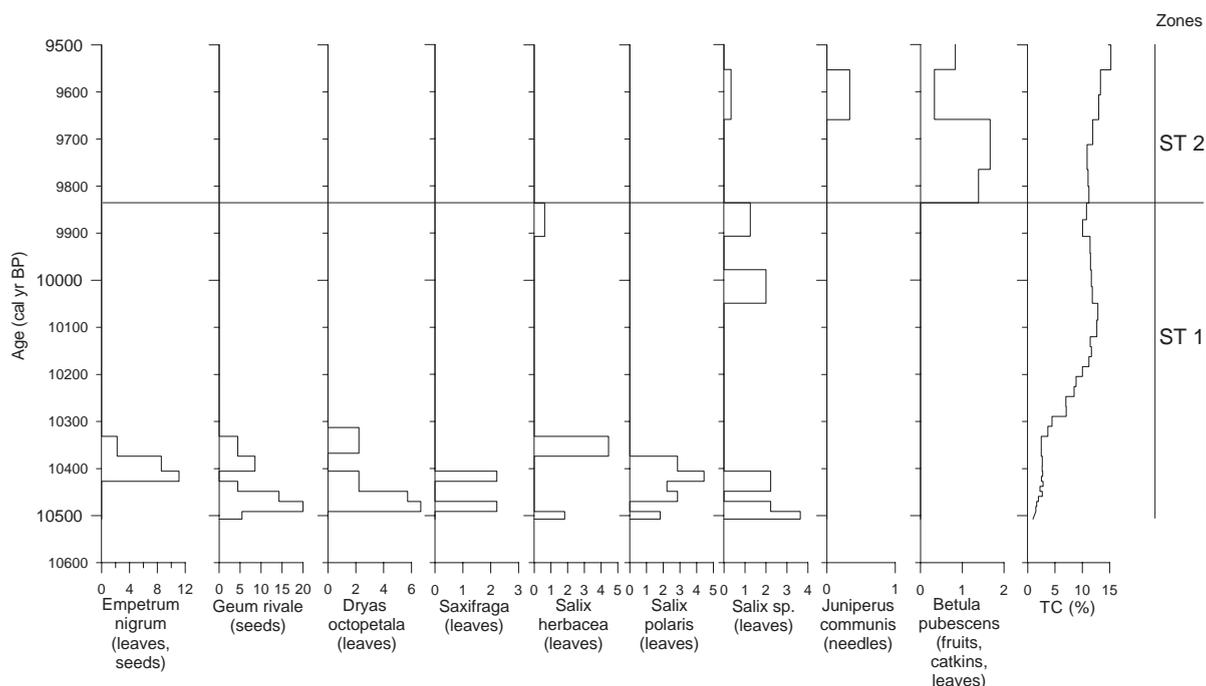


Fig. 4. Pioneer vegetation macrofossil record and TC content. The macrofossil data are expressed as concentration values (total numbers of macroscopic plant remains recorded per 20 cm<sup>3</sup> of sediment).

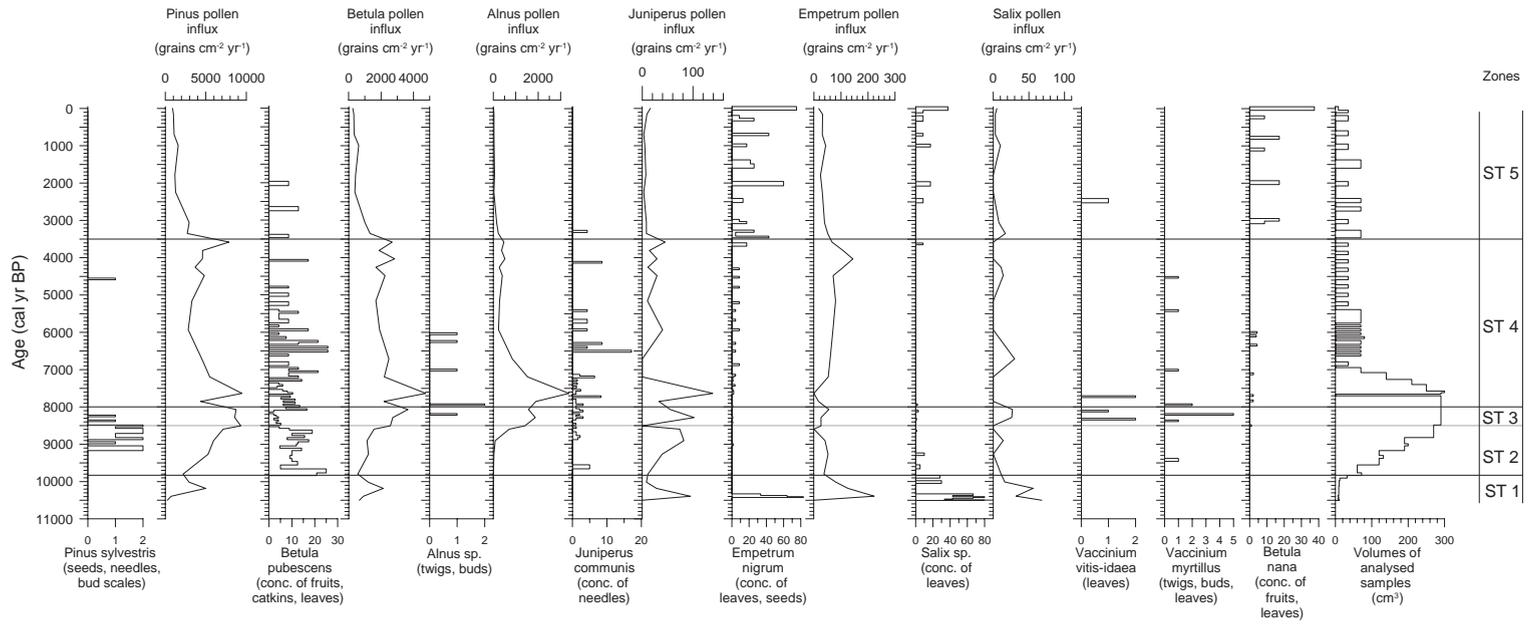


Fig. 5. Composite macrofossil and pollen influx records of selected taxa and sample volumes used for macrofossil analysis. The macrofossil data are expressed as concentration values (numbers of macrofossils per 300 cm<sup>3</sup> of sediment) or as numbers of macroscopic plant remains recorded per sample (infrequent taxa).

binocular microscope at  $\times 50$  magnification, and plant remains were determined to species level where possible following [Bejjerinck \(1947\)](#) and [Tomlinson \(1985\)](#), and by comparison with reference collections. Sample volumes generally ranged from 35 cm<sup>3</sup> in the upper part of the sequence, where fewer core segments could be included due to correlation problems, to a maximum of c. 300 cm<sup>3</sup> in the interval of 7.44–8.14 m. In the lowermost part of the sequence, only one core segment was used for analysis, yielding 10–30 cm<sup>3</sup> per sample ([Fig. 4](#)). Major macrofossil taxa are expressed as concentrations (numbers of plant remains per 20 cm<sup>3</sup> and 300 cm<sup>3</sup> of wet sediment in [Figs. 4 and 5](#), respectively), whereas less frequently recorded taxa are expressed as numbers of macrofossils per sample ([Fig. 5](#)).

### 2.5. Pollen analysis

Pollen samples (2 cm<sup>3</sup>) were prepared according to method A as described by [Berglund and Ralska-Jasiewiczowa \(1986\)](#), complemented by treatment with 40% hydrofluoric acid of samples rich in minerogenic material. *Lycopodium* tablets were added to allow calculation of pollen concentration and influx. A total number of 30 samples were counted, using a Leica microscope at  $\times 400$  and  $\times 1000$  magnification. At least 500 tree pollen grains were counted, except for the two lowermost samples where concentrations were very low. The taxonomy and identification of pollen and spore taxa follow [Florin \(1969\)](#) and [Moore et al. \(1991\)](#), and identifications were confirmed by comparison with pollen reference collections. The pollen diagram was constructed using the TILIA and TILIA GRAPH 2 programs ([Grimm, 1992](#)).

## 3. Results and interpretations

### 3.1. Sediment description and age model

The sediment sequence was classified into three lithostratigraphic units ([Table 1](#)). The lowermost 0.145 m (unit 1) consists of silty gyttja which grades upwards into homogenous, brownish algal gyttja (unit 2). At 5.78 m limnic mosses (*Pseudocalliergon trifarum* and *Scorpidium scorpioides*) appear, and across a 3- to 4-cm interval the algal gyttja changes

into moss-rich gyttja (unit 3), which continues to the sediment surface at 4.65 m.

The age–depth model ([Fig. 2](#)) was based on an 8th degree polynomial curve, adjusted to the mid points of the single standard deviation age intervals of the eight calibrated radiocarbon ages ([Table 2](#)), the tephra horizon at 4.715 m (see below), and the sediment surface at 4.65 m (set to –50 cal year BP). Sediment accumulation rates vary in the range of 0.24–0.61 mm year<sup>-1</sup> with minimum values around 8.50–8.30 m and maximum values below c. 8.60 m (unit 1). The age of the lowermost silty/sandy sediments is consistent with the regional deglaciation age, estimated to 11,000–10,500 cal year BP by [Lundqvist \(1998\)](#).

Three sections within the sediment sequence (0–200, 2700–3300, and 6700–7300 cal year BP) contained rhyolitic tephra glass shards. Samples exhibiting maximum concentrations of tephra particles within the respective sections were subjected to quantitative geochemical analysis, but only the most recent tephra horizon at 4.715 m depth yielded enough EPMA data (J. Bergman, in preparation), enabling a correlation to the Icelandic Askja-1875 eruption ([Fig. 2](#)). The unidentified cryptotephra horizons at 5.71 m and at 7.29 m also exhibited optical characteristics suggesting an Icelandic origin, although correlations to specific eruptions were not possible. However, based on the radiocarbon-inferred age model ([Fig. 2](#)), the interpolated ages of these horizons fall within the published age estimates of the Hekla-3 and Lairg A eruptions, respectively. Cryptotephra horizons originating from these two eruptions have been geochemically identified at a nearby site ([Bergman et al., 2004](#)).

### 3.2. TC content and mineral magnetic susceptibility

Total carbon content is low (<5%) at c. 10,500–10,300, and then increases to a peak (13–14%) at c. 10,100 cal year BP ([Fig. 3](#)). Following declining values between 10,100 and 9900 cal year BP, TC increases from 10% at c. 9800 cal year BP, and stabilizes at values of 13–16% between 9500 and 8400 cal year BP. Around 8400 cal year BP TC decreases (from 14% to 15%), reaching c. 11% at 8200–8100 cal year BP, followed by a rapid recovery to values of 15–16% around 8000 cal year BP. After 8000 cal year BP, TC shows more or less stable, slightly increasing

values (16–18%), until c. 5500 cal year BP when values start to decrease. Around 3400 cal year BP, TC values decrease further, showing limited variation (12–14%) in the remainder of the sequence.

Mineral magnetic susceptibility shows little variability at c. 10,500–9500 cal year BP. Between 9500 and 8500 cal year BP, values decrease constantly, followed by an increase around 8500–8000 cal year BP. Minimum values ( $0\text{--}0.025 \times 10^{-6} \text{ m}^3 \text{ kg}^{-1}$ ) prevail until c. 5900 cal year BP, followed by an increase to  $0.05\text{--}0.075 \times 10^{-6} \text{ m}^3 \text{ kg}^{-1}$  around 5000 cal year BP. Magnetic susceptibility then declines slightly until c. 3500 cal year BP, when values drop to c.  $0.03 \times 10^{-6} \text{ m}^3 \text{ kg}^{-1}$ . Following relatively stable values at c. 3500–1500 cal year BP, a slight increase occurs until the onset of a period with peak values of  $0.075\text{--}0.085 \times 10^{-6} \text{ m}^3 \text{ kg}^{-1}$ , lasting from c. 600 cal year BP to the present.

### 3.3. Vegetation records

The sediment sequence was divided into five zones (ST 1–ST 5), based on general characteristics of the macrofossil, pollen influx, and pollen percentage records of terrestrial plants as described below (Figs. 4–7). Additional details of the macrofossil record are given in Table 3. Pollen concentration data were also used during initial interpretation, but are not shown since the trends and variability of the pollen concentration record closely resemble those of the pollen influx record, as suggested by the linear appearance of the age–depth curve (Fig. 2).

### 3.4. ST 1 (10,500–9800 cal year BP)—Pioneer flora

In spite of the limited amount of material available for macrofossil analysis, a distinctive terrestrial vegetation assemblage characterizes the initial c. 200-year period following deglaciation, as compared to subsequent vegetation zones. Pioneer taxa identified in the macrofossil record include *Geum rivale*, *Dryas octopetala*, *Saxifraga* sp., and *Salix* spp. (including the dwarf forms *Salix herbacea* and *Salix polaris*), followed slightly later by *Empetrum nigrum*, *Oxyria digyna*, *Ledum palustre*, *Salix reticulata*, and *Salix repens* (Fig. 4; Table 3). In addition, a single find of *Potamogeton* may suggest an early establishment of aquatic plants (Table 3). Apart from *Salix* and

*Empetrum*, additional shrub and herb taxa were identified in the earliest spectra of the pollen record. These include *Juniperus*, *Artemisia*, Caryophyllaceae, Chenopodiaceae, *Filipendula*, *Rumex*, *Urtica*, and a single pollen grain of *Ephedra distachya* (Fig. 7). Initially low TC contents of the sediments suggest unstable soils and low aquatic productivity associated with this pioneer vegetation assemblage. The magnetic susceptibility record displays high values throughout ST 1 with relatively little variation compared to TC. This may be caused by high concentrations of fine-grained diamagnetic quartz in the newly deglaciated catchment which depresses the signal, thus cancelling out effects of detrital input by catchment erosion on the susceptibility record.

The remaining part of ST 1 (10,300–9800 cal year BP) is characterized by low amounts of terrestrial macrofossils (Fig. 4) and declining pollen influx values for the majority of the taxa recorded previously (Fig. 6). *Salix* and Caryophyllaceae remain at maximum influx values and *Empetrum* exhibits relatively high, although clearly decreasing values, while distinctly increasing pollen influx values were recorded for *Galium* and Poaceae. *Juniperus* shows declining influx values following an early zone maximum, which is not reflected in the macrofossil record. Hippophaë occurs with peak values slightly before 10,000 cal year BP. *Betula* and *Pinus* influx records also exhibit increasing trends, possibly indicating local presence, although this cannot be confirmed by macrofossil evidence. However, *Betula* pollen influx values exceeding  $1500 \text{ grains cm}^{-2} \text{ year}^{-1}$  may indicate that tree birch was present in the lake catchment at this stage, thus possibly shading out the light-demanding pioneer herbs. Recent studies in northern Fennoscandia (Hicks, 2001) have found *Betula* pollen influx values exceeding  $500 \text{ cm}^{-2} \text{ year}^{-1}$  and  $1500 \text{ cm}^{-2} \text{ year}^{-1}$  to be indicative of tree-limit ecotonal and birch forest conditions, respectively. However, the pollen influx data may be influenced by slight variations in the sediment accumulation rate at this initial stage. A substantial increase in TC content of the sediments (Fig. 3) indicates increasing aquatic productivity, possibly in combination with decreasing catchment erosion. Although magnetic susceptibility values remain relatively high, a general increase in vegetation cover probably took place in the lake catchment. Such an

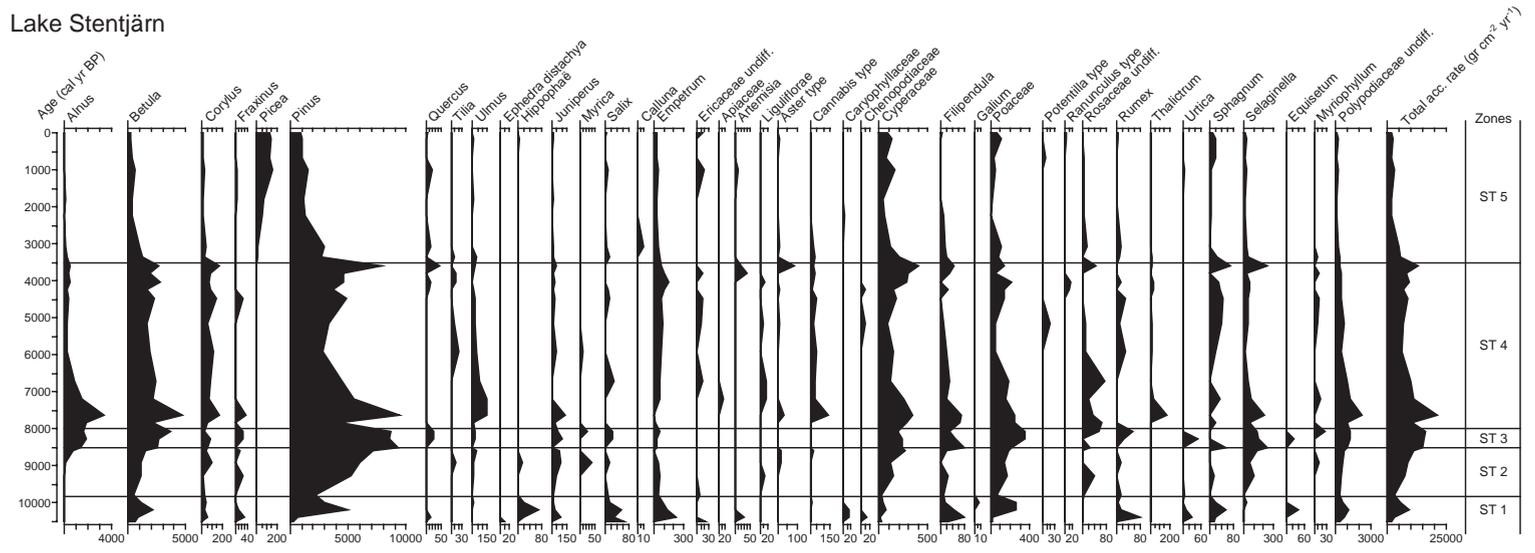


Fig. 6. Pollen and spore influx records from the Lake Stentjärn sediment sequence.

Lake Stentjäm

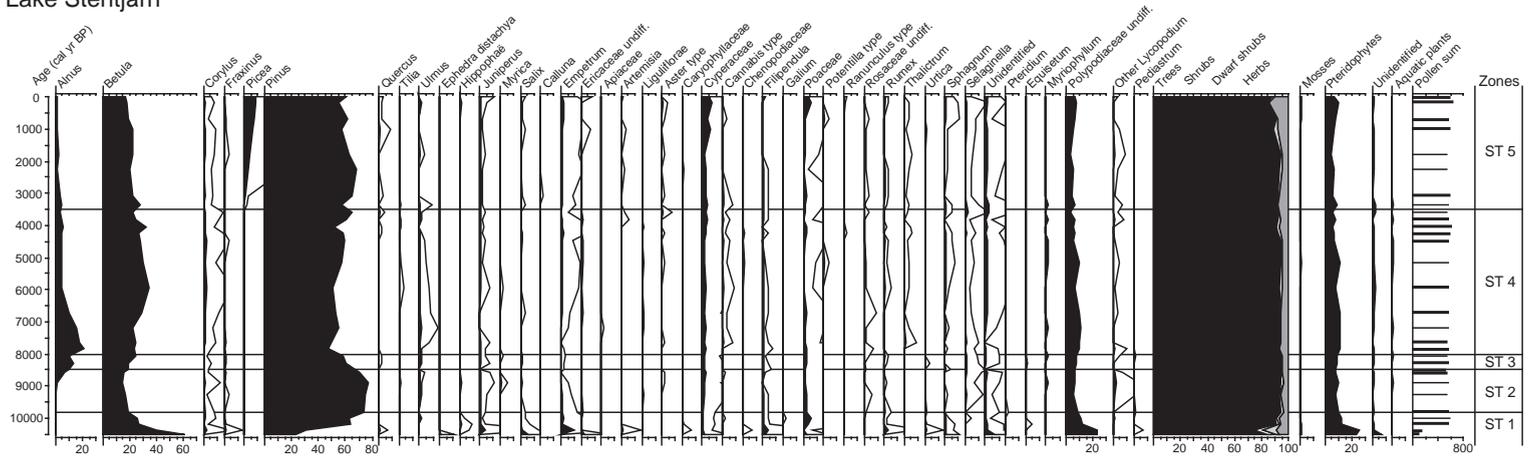


Fig. 7. Pollen and spore percentage records from the Lake Stentjäm sediment sequence.

Table 3

Macrofossil data from Lake Stentjärn not presented in the diagrams

Depth (m)	Zones	Age (cal year BP)	Plant macrofossils not shown in figures
4.65–5.78	ST 5	–50–3200	<i>Pseudocalliergon trifarium</i> , <i>Scorpidium scorpioides</i> (in situ submerged mosses)
5.27–5.30	ST 5	1490–1600	<i>Loiseleuria procumbens</i> leaf
6.78–6.80	ST 4	5600–5650	<i>Potamogeton</i> leaf
6.98–7.00	ST 4	6120–6170	<i>Polytrichum</i> (moss)
7.32–7.34	ST 4	6990–7030	<i>Eriophorum latifolium</i> ,
7.50–7.52	ST 4	7400–7440	<i>Sorbus</i> sp. bud
7.60–7.62	ST 4	7620–7660	Apiaceae seed, <i>Potentilla</i> seed, <i>Carex</i> fruits
7.82–7.84	ST 3	8090–8130	<i>Dryas octopetala</i> shoot, Poaceae seeds, <i>Parnassia palustris</i> seed
7.94–7.96	ST 3	8350–8390	Asteraceae seed
8.12–8.14	ST 2	8770–8820	<i>Apium</i> seed
8.18–8.20	ST 2	8930–8990	Asteraceae seed
8.26–8.28	ST 2	9170–9230	<i>Hylocomium splendens</i> (moss)
8.32–8.34	ST 2	9380–9460	Brassicaceae part
8.34–8.36	ST 2	9460–9550	Asteraceae seed
8.40–8.42	ST 2	9770–9840	<i>Campylium stellatum</i> (moss)
8.46–8.48	ST 1	9980–10050	<i>Polytrichum</i> (moss)
8.60–8.62	ST 1	10330–10370	<i>Salix herbacea</i> leaf, <i>Polytrichum</i> (moss)
8.62–8.64	ST 1	10370–10410	<i>Salix polaris</i> leaf, <i>Polytrichum</i> , <i>Aulacomnium</i> (mosses)
8.64–8.66	ST 1	10410–10430	<i>Saxifraga</i> leaf, <i>Potamogeton</i> seed, <i>Salix reticulata</i> leaf, <i>S. repens</i> leaf, <i>S. polaris</i> leaf, <i>Distichium</i> sp. (moss)
8.66–8.68	ST 1	10430–10450	<i>Ledum palustre</i> leaf, <i>Salix polaris</i> leaf
8.70–8.72	ST 1	10470–10490	<i>Oxyria digyna</i> seed, <i>Saxifraga</i> leaf, <i>Polytrichum</i> (moss)
8.72–8.735	ST 1	10490–10510	<i>Salix polaris</i> leaf, <i>S. herbacea</i> leaf, <i>Polytrichum</i> (moss)

Depths are related to the water surface.

establishment of a soil-stabilizing flora, apparently dominated by grasses, may have also created unfavourable conditions for the pioneer flora.

The low concentrations of macrofossils between 10,300 and 9800 cal year BP (Fig. 4) may be attributed to changes in the sedimentation pattern. Local irregularities in the initial bottom topography of the lake may have led to sediment focusing and trapping of pioneer plant remains, whereas subsequent sediment in-filling resulted in a more uniform deposition of macrofossils on a more even sediment surface. In addition, the supply of terrestrial plant remains probably decreased markedly when soil-stabilizing vegetation established in the catchment.

### 3.5. ST 2 (9800–8500 cal year BP)—*Betula*–*Pinus* forest

At c. 9800 cal year BP, *Betula pubescens* macrofossils are recorded in relatively high concentrations (Fig. 5), indicating continuous presence of tree birch.

This substantial expansion of tree birch probably represents the first establishment of forest at the site, and most likely reflects a regional expansion, as indicated by a synchronous increase in tree birch macrofossils at adjacent Lake Spåime (Hammarlund et al., 2004). At 9100–9200 cal year BP, bud scales and needle fragments of *Pinus sylvestris* appear, reflecting local establishment of the species. Macroscopic remains of *Juniperus communis* and *Vaccinium myrtillus* are also recorded, indicating that the forest was open enough to support a juniper-dominated shrub-layer. Pollen influx values of *Betula* and *Pinus* exhibit generally increasing trends throughout the zone (Fig. 5), which supports the macrofossil interpretation and indicates that the inferred vegetational development was extra-local as well as local. *Corylus*, and *Ulmus* occur in the pollen record (Figs. 6 and 7), although their possible local presence is not supported by macrofossil data from this site. However, macroscopic remains of *Corylus* and *Ulmus* dating to this period have been recorded previously in the area

(Kullman, 1998c). Alder was possibly present in the catchment, as suggested by increasing *Alnus* pollen influx and percentage values at the end of ST 2 (Figs. 6 and 7). *Empetrum* pollen influx values decrease, while *Juniperus* reaches high values towards the end of ST 2. These vegetational data, in combination with a clear decrease in magnetic susceptibility (Fig. 3), suggest that a continuous vegetation cover developed in the lake catchment. The terrestrial field-layer was likely dominated by Poaceae and initially by *Empetrum nigrum*.

### 3.6. ST 3 (8500–8000 cal year BP)—Open *Betula* forest with, *Juniperus* and *Alnus*

At the onset of ST 3 *Betula pubescens* macrofossils decrease markedly (<5 per 300 cm<sup>3</sup> of sediment; Fig. 5), only to regain high values again at the very end of the zone (>20 per 300 cm<sup>3</sup> of sediment). The abrupt decrease in fruit and catkin concentrations of *B. pubescens* may reflect either an actual retreat of tree birch, or a decline in fruit production, supposedly induced by lowered summer temperatures. The disappearance of macroscopic remains of *Pinus sylvestris* at c. 8200 cal year BP probably reflects an effective retreat of the pine tree-limit, possibly leaving only scattered trees in the lake catchment. The first appearance of *Alnus* macrofossils is recorded at the end of ST 3, although pollen influx data may suggest local presence of alder already at the end of ST 2. The expansion of alder (probably *Alnus incana*) may be related to disturbance of the canopy and field layer, since the species is shade intolerant and usually demands bare mineral soils (Kullman, 1992, 1995). Macroscopic remains of *Vaccinium vitis-idaea* and *Betula nana* appear for the first time in the sequence (Fig. 5). Also, a shoot of the light-demanding and cold-tolerant species *Dryas octopetala* was encountered, representing the only specimen in the sequence since the deglaciation. A seed of the wet-meadow element *Parnassia palustris* was also recorded, along with seeds of Poaceae (Table 3). Other macrofossils include *Juniperus*, *Empetrum nigrum*, *Salix* sp., and *Vaccinium myrtillus*. In ST 3, the resolution of the pollen record must be considered too low to allow for a detailed description of changes in pollen assemblages, but the data can still be used to aid interpretation of local and extra-local vegetational changes.

*Betula* pollen influx values are relatively high, and although *Pinus* exhibits maximum pollen influx values at the beginning of ST 3, followed by a decrease until c. 7800 cal year BP (Figs. 5 and 6), *Betula* and *Pinus* pollen percentage values are indicative of a subsequent decline in *Pinus* (Fig. 7), consistent with the macrofossil data. *Alnus* pollen influx values are relatively high, while *Juniperus* shows variable but relatively high values in contrast to most pollen influx records of herbs and shrubs, which generally exhibit low values. However, the total pollen accumulation rate is high, as are the values of Poaceae, Cyperaceae, and *Selaginella* (Fig. 6), possibly suggesting generally elevated pollen influx values due to increased soil erosion. As evidenced by an increase in magnetic susceptibility at c. 8500 cal year BP, followed c. 100 year later by a decrease in TC content (Fig. 3), soil degradation led to increased catchment erosion, likely caused by a shift towards wetter and cooler climatic conditions. The apparent lag between the two records may be explained by an increase in the input of terrestrial organic matter due to soil erosion, initially contributing to relatively high TC values. Patches of dry heath, with only partial vegetation cover, may have developed in wind-exposed settings, dominated by *Vaccinium myrtillus* and *Empetrum nigrum*, macrofossils of which are recorded in ST 3. *Betula nana* was probably also a component of the vegetation, thus it bore some resemblance to the dry heath vegetation type characteristic of modern low/mid-alpine areas. Grasses, sedges, and other cold/wet-adapted elements such as *Selaginella* likely expanded on the slopes and along the shores of the lake.

### 3.7. ST 4 (8000–3500 cal year BP)—*Betula* forest with *Alnus* and *Juniperus*

In ST 4 *Betula pubescens* macrofossils occur frequently until c. 5000 cal year BP, followed by more irregular occurrences (Fig. 5). Macroscopic remains of *Alnus* sp. indicate the local presence of alder. The data do not allow for distinction between *Alnus incana* and *Alnus glutinosa*, although the former seems slightly more probable (e.g. Kullman, 1992, 1995). A single bud scale of *Pinus sylvestris* was recorded at c. 4600 cal year BP. However, it is highly uncertain if this finding indicates a tree-limit

re-advance, as light macrofossils may be transported by wind from lower elevations, e.g. across snow surfaces in winter (e.g. Jackson and Whitehead, 1991). A bud of *Sorbus* sp. was encountered at c. 7300 cal year BP, which indicates the presence of rowan in the catchment (Table 3). *Juniperus* needles occur at high concentrations in ST 4, and juniper was probably common in the half-open birch-dominated forest. The local presence of *Empetrum nigrum*, *Salix* sp., *Vaccinium vitis-idaea*, *Vaccinium myrtillus*, and *Betula nana* is also confirmed by macrofossil data.

Pollen influx values of *Pinus*, *Betula*, and *Alnus* are high, with a zone maximum for *Pinus*, and sequence maxima for *Betula* and *Alnus* at c. 7600 cal year BP (Fig. 6). The increase in *Pinus* pollen influx at 4500–3500 cal year BP may indicate a re-advance of the pine tree-limit, as possibly suggested by the macrofossil record (Fig. 5). Similar increases in pollen influx were observed for *Betula*, and possibly also for *Alnus*, which may indicate a limited expansion induced by favourable climatic conditions. The pollen influx values of these tree taxa decline at the end of ST 4. The total accumulation rate generally exhibits a similar trend as the main tree taxa, with a sequence maximum at c. 7600 cal year BP. Relatively high pollen influx values of *Ulmus*, and to some extent *Corylus*, were recorded throughout the zone, with peak values between 7500 and 7000 cal year BP (Fig. 6). These taxa may have been present in the catchment, and they probably occurred at slightly lower elevations, as proposed by Kullman (1998c). The local presence of *Ulmus* has been confirmed by macrofossils in association with similar pollen influx values in southern Norway (Eide et al., 2005). Rosaceae shows high and fluctuating pollen influx values in the early half of ST 4. As suggested by macrofossil evidence, this pattern may reflect mainly the presence of *Sorbus aucuparia*, which occurs as a subordinate component in the modern mountain-birch zone. Poaceae, Cyperaceae, *Filipendula*, and *Selaginella* all exhibit relatively high pollen influx values in the early part of ST 4, followed by decreasing trends with some fluctuations until c. 4200 cal year BP. Subsequently, Cyperaceae increases to a sequence maximum at c. 3600 cal year BP. *Thalictrum* and *Cannabis* type reach their respective pollen influx maxima at c. 7600 cal year BP. Relatively high values of the latter taxon, which includes *Humulus lupulus*,

may indicate the local presence of hop on moist soils in the vicinity of the lake. The lower part of ST 4 (8000–5500 cal year BP) is characterized by maximum TC content and minimum values of magnetic susceptibility (Fig. 3), indicating high organic productivity, insignificant catchment erosion, and a substantial vegetation cover with well-developed field layers and soils. Sedges probably dominated the telmatic zone of the lake. From c. 5500 cal year BP and onwards, lowered TC contents and increasing magnetic susceptibility indicate increasing rates of soil erosion, which may be related to a successive thinning of the vegetation cover and soil degradation. It is possible that the elevated pollen influx values during the late part of ST 4 (c. 4500–3500 cal year BP) were caused by a shift to late spring snowmelt, or a general increase in soil erosion, as suggested by a small increase in magnetic susceptibility at c. 3900–3500 cal year BP. The vegetation cover in the catchment area was diminishing along with pollen production, but the fluvial transport of pollen to the lake may have increased because of continued melting of semi-perennial snow banks during spring and summer. Vegetation data and lake system records from nearby Lake Spåime support such a development (Hammarlund et al., 2004).

### 3.8. ST 5 (3500 cal year BP–present)—*Empetrum*–*Betula nana* heath

This zone is characterized by a general absence of tree macrofossils and increased frequencies of shrub and dwarf-shrub elements (Fig. 5). However, a few *Betula pubescens* remains were recorded, which suggests that scattered individuals of tree birch prevailed at the elevation of the site at least until c. 2000 cal year BP (cf. Fig. 5). Macroscopic remains of *Empetrum nigrum*, *Salix* sp., and *Betula nana* occur at high concentrations throughout ST 5, indicating a mosaic of heath vegetation similar to the present-day catchment vegetation. A single leaf of *Loiseleuria procumbens*, dating to c. 1500 cal year BP, suggests the presence of this arctic/alpine plant, which probably grew on wind-exposed sites in association with *Arctostaphylos alpinus*. *Vaccinium* also appears to have declined at this stage. Only a single leaf of *Vaccinium vitis-idaea* was recorded in ST 5. The pollen influx records of trees show generally deas-

ing trends or low values, as does the total pollen accumulation rate, in contrast to *Picea* which appears at c. 3500 cal year BP and exhibits a progressive increase (Fig. 6). No macroscopic remains of *Picea* were found at the site, but the species has probably been present in nearby valleys, since the early Holocene (Segerström and von Stedingk, 2003), although single specimens have been recorded at high elevations (Kullman, 1996, 2000b, 2002b). Herb and shrub pollen influx values generally decrease in ST 5, possibly with the exception of Poaceae and Cyperaceae, which display fluctuating values. However, a comparison between pollen influx and percentage data (Fig. 7) reveals that within ST 5, *Empetrum* pollen percentage data seem to correlate better with the macrofossil record than with corresponding pollen influx data. The lake bottom was colonized by mosses (mainly *Pseudocalliergon trifarium* and *Scorpidium scorpioides*) at c. 3200 cal year BP (Table 3). Subsequently, no other aquatic plant remains were recorded. The establishment of aquatic mosses may have affected the total pollen influx, since nearly all taxa exhibit decreasing trends at this stage (Fig. 6). The sediment input probably decreased although the accumulation rate was kept largely constant due to in situ moss growth. It is likely that the introduction of submerged mosses reflects a generally lowered trophic status of Lake Stentjärn in response to the inferred decline in forest vegetation and an associated decrease in nutrient supply from catchment soils. A similar development was recorded following the late-Holocene tree-limit retraction at Lake Spåime (Hammarlund et al., 2004). Aquatic bryophytes are efficient nitrogen-fixers and may out-compete macrophytes in oligotrophic lakes (Karttunen and Toivonen, 1995; Turetsky, 2003). Magnetic susceptibility and TC records exhibit little variation during the last c. 5000 years (Fig. 3), which suggests relatively stable conditions in terms of catchment erosion.

## 4. Discussion

### 4.1. The pioneer vegetational succession

The oldest sediments at Lake Stentjärn were deposited during or immediately after the deglaciation at c. 10,500 cal year BP, and the recorded macrofossil

assemblage has supplied us with a “snapshot” of the terrestrial flora surrounding the site (Fig. 4 and Table 3). The pioneer flora was probably replaced by birch and grass-dominated vegetation within less than 200 years, although the temporal duration of this initial light-demanding plant assemblage cannot be assessed with confidence because of the two lowermost, temporally overlapping, radiocarbon dates. As a “deglaciation flora”, it largely resembles late glacial plant assemblages of southern and western Scandinavia, but with the important difference that these plant communities existed in a glacial climate setting, and as such were cold-adapted. At the onset of the Holocene, these plants were already established locally in the glacial/periglacial landscape, and could expand rapidly into newly deglaciated areas. At the time of deglaciation in the study area, approximately 1000 years after the onset of the Holocene, a mix of cold-adapted and temperate plant species colonized the protocratic soils surrounding Lake Stentjärn. Palaeoecological studies in southern and central Norway (Eide, 2003; Eide, 2005) have revealed broadly similar pioneer macrofossil records, although without *Geum rivale* (Water Avens) and *Ledum palustre* (alt. *Rhododendron tomentosum*; Labrador-tea). The presence of these taxa is interesting from a palaeobiogeographical and climatological point of view. The modern distribution of *Geum rivale* extends across the whole of Scandinavia but it is rare in the northeastern part. It prefers moist and calcareous substrates and may form monocultures on wet meadows in southern Sweden. *Ledum palustre* is a wintergreen shrub, with a modern distribution that mainly extends eastward from eastern Scandinavia and into the lower areas of the northernmost Scandes Mountains, which may suggest that its presence in the study area during the early Holocene was related to warmer summers. As argued by Birks (2003), late glacial pollen assemblages have frequently been considered to lack good modern vegetation analogues, and are hence characterized as “non-analogous”, in contrast to late glacial macrofossil assemblages. This study presents a deglacial plant macrofossil assemblage that is reasonable from an ecological viewpoint, although slightly unorthodox as outlined above, complemented by a pioneer pollen assemblage that makes good vegetational sense. The only “non-analogous” pollen element recorded at this site is a

single *Ephedra distachya* pollen at the base of the sequence (Fig. 6). However, it may have been redeposited from older minerogenic sediments. *Ephedra* type pollen grains recorded in late glacial sediments in Denmark and southern Sweden (Iversen, 1954; Berglund, 1966) were supposedly long-transported from northeastern Europe (e.g. Lundqvist and Bengtsson, 1970).

The seemingly sudden termination of the pioneer flora at c. 10,300 cal year BP (c. 10,500–10,150 cal year BP at  $2\sigma$ , linear interpolation) may be partly related to an increase in sedimentation rate following increased aquatic production. Possibly, the aquatic and terrestrial changes were triggered by an expansion of grasses, and possibly also tree birch, which quickly out-competed light-demanding herbs and dwarf-shrubs (Fig. 4). This process would have also led to stabilization of catchment soils and a general reduction of the input of macrofossils to the lake. These recorded changes in vegetation and lake system proxies, may have been triggered by a climatic shift to cooler and more humid conditions, at c. 10,400–10,100 cal year BP. Such an event has been detected in lake sediment records from the Faroe Islands (Hannon et al., 2003), northern Norway (Björck et al., 2001; Husum and Hald, 2002; Seppä et al., 2002), and the Alps (e.g. Haas et al., 1998; Heiri et al., 2003), but due to the chronological uncertainties, the proxy data presented here cannot be considered as conclusive evidence of such an event.

#### 4.2. Disturbance of the tree-limit vegetation at 8500–8000 cal year BP

The high-resolution plant macrofossil record from Lake Stentjärn reveals clearly lowered concentrations of *Betula pubescens* accompanied by the disappearance of *Pinus sylvestris* at c. 8500–8000 cal year BP (Fig. 5). These changes are correlated to elevated magnetic susceptibility values, followed slightly later by a decrease in TC content (Fig. 3). No apparent changes in sedimentation rate are associated with these variations (Fig. 2). Considering the fact that no tree birch macrofossils originating from lower elevations were recorded in the later part of ST 5 (2000–0 cal year BP), it is worth noting that the *B. pubescens* macrofossil concentrations do not drop to zero in ST 3. This

indicates either a weakened fruit production of tree birch at the elevation of the site or a retreat of *B. pubescens*, probably leaving only scattered trees in the catchment. An increase in openness of the catchment vegetation is indicated by abundant macrofossils of *Vaccinium vitis-idaea* and *Vaccinium myrtillus* and by elevated pollen influx values of grasses, *Salix* and different herb taxa (Figs. 5 and 6). *Pinus sylvestris* probably retreated from the catchment and adjacent areas at c. 8200 cal year BP (Figs. 5 and 7).

It is probable that less-favourable conditions for pine and tree birch were caused primarily by a decrease in mean summer air temperature, although there is no simple and linear relationship between temperature and tree-limits (Körner, 1998). Generally, and at present-day conditions, *Betula pubescens* and *Pinus sylvestris* require mean summer temperatures of 8–10 °C and 9–11 °C, respectively (Iversen, 1954; Aas and Faarlund, 1988), but the climatic requirements differ somewhat depending on the degree of oceanicity. In coastal areas of western Scandinavia slightly higher summer temperatures are required as compared to more continental settings (Odland, 1996). This may suggest that mean summer temperatures fell below 8–9 °C at the elevation of Lake Stentjärn, on the assumption that the tree-limit descended to a level slightly below the lake catchment as indicated by the continuously high pollen influx values of the major tree taxa (Fig. 6). This estimate is in good agreement with a chironomid-inferred reconstruction of mean July air temperature obtained from the sediment sequence of nearby Lake Spåime (Fig. 1), c. 100 m below the study site (Hammarlund et al., 2004). Most likely the vegetational disturbance inferred from the macrofossil record at this stage was related to the transient cooling episode around 8200 cal year BP, which is widely recognized around the North Atlantic (e.g. Alley et al., 1997; von Grafenstein et al., 1998; Hammarlund et al., 2003; Magny et al., 2003). Previous evidence of this cooling has been obtained locally at Lake Spåime (Hammarlund et al., 2004), as well as more regionally in Scandinavian glacio-lacustrine sediments (e.g. Karlén, 1976, 1988; Dahl and Nesje, 1994; Nesje and Dahl, 2001). Vegetational responses supposedly coupled to this event have also been detected in pollen records from south central Norway (Barnett et al., 2001),

northern Sweden (Snowball et al., 2002), central Europe (Tinner and Lotter, 2001), and Estonia (Veski et al., 2004).

At c. 8100–8000 cal year BP the climate recovered, although probably not to conditions resembling those of ST 2, since *Pinus sylvestris* did not fully re-colonize the catchment. As suggested by megafossil evidence from the area (Fig. 7), the pine tree-limit continued to decline subsequent to the recovery of the birch tree-limit at c. 8000 cal year BP. Possibly the long-term Holocene trend of declining seasonality, with associated increases in snow-cover and effective humidity, prevented pine from reclaiming its former tree-limit position. In general, previous palaeoecological studies based on macrofossil analysis (e.g. Barnekow, 1999; Birks, 2003; Eide, 2003; Hammarlund et al., 2004) have not been specifically aimed at detecting short-term climatic perturbations. These studies have generally been based on lower sample volumes and less-detailed temporal resolutions than needed to assess the vegetational responses to such events. However, a macrofossil record from the Torneträsk area in northernmost Sweden may show evidence of a temporary birch tree-limit descent shortly before 8000 cal year BP (Barnekow and Sandgren, 2001).

#### 4.3. Macrofossil representation in subalpine lake sediments

In order to obtain a rough estimate of the macrofossil concentration of modern lake sediments deposited in the zone of mountain-birch forest in the study area, surface sediments of two small lakes were investigated. The lakes are situated at around 810 m a.s.l. in the valley west of Storulvån (Fig. 1). Samples of the uppermost loose sediments, collected near the lake margins, contained surprisingly low concentrations of *Betula pubescens* plant remains (c. 50–60 fruits and catkins per 300 cm<sup>3</sup> of surface sediment). These estimates cannot be considered statistically significant, but the results generally imply that the modern mountain-birch forest surrounding the two lakes, characterized by an average distance between stems of c. 10 m, can be regarded as representing a maximum density of the forests inferred from the stratigraphic data from Lake

Stentjärn. The subalpine forests surrounding the site in ST 2–ST 4 may therefore have been slightly more open in character. However, available macrofossil, megafossil, and pollen data do not allow assessment with any certainty of the actual density of the woodlands that occupied the catchment of Lake Stentjärn during the early and mid Holocene. Whether the reconstructed vegetation can be considered to be of forest density (max 30 m between stems) or more dispersed, as at or slightly below the present-day tree-limit (scattered trees or isolated clusters), is at present beyond the capabilities of these methods. Future, well-controlled tests involving high-volume surface sediment samples from different vegetation settings may provide more detailed insights into this problem, but this is beyond the scope of this study.

#### 4.4. Comparison with megafossil data

Numerous reconstructions of tree-limit dynamics in Fennoscandia have been based on radiocarbon dating of subfossil wood remains (e.g. Eronen, 1979; Hafsten, 1981; Kullman, 1987, 1992, 1996, 2000b; Aas and Faarlund, 1988, 1996; Eronen and Huttunen, 1993; Kvamme, 1993; Eronen and Zetterberg, 1996; Kalela-Brundin, 1996; Selsing, 1996; Zetterberg et al., 1996; Vorren et al., 2003) but none have been based on such extensive compilations of megafossils as available here (Fig. 8). The palaeobotanical results presented by Kullman (1998a,c) and related inferences of an early Holocene climatic optimum and a non-analogous tree flora partly contradict interpretations based on pollen records (e.g. Lundqvist, 1969; Sonesson, 1974; Karlén, 1993; Berglund et al., 1996). However, in this context our stratigraphic data from a site in the same area and at a representative altitude are ideally suited for comparison. As illustrated in Fig. 8, a good temporal correlation is evident between the megafossil data-sets for *Pinus*, *Betula*, and *Alnus*, and corresponding macrofossil records from Lake Stentjärn.

The pine megafossil record is the most extensive data set (161 samples), but the earliest finds of *Pinus* from high altitudes, dating to 11,000–10,500 cal year BP are obviously not reflected in the macrofossil record, since the oldest sediments at Lake Stentjärn

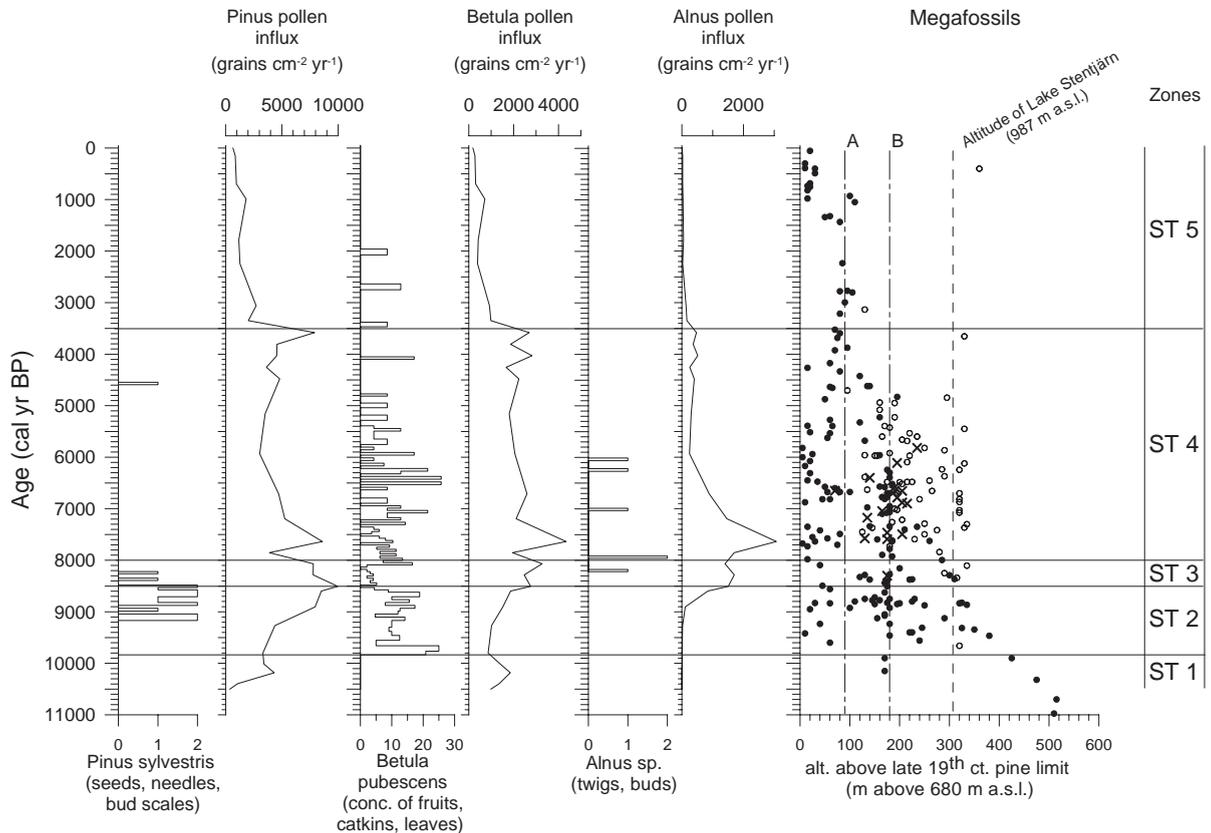


Fig. 8. Comparison between records of macrofossils, pollen influx (this study) and published radiocarbon-dated finds of subfossil wood remains (megafossils) from the study area, plotted against a calendar-year age-scale. The megafossil data sets include 161 samples of *Pinus sylvestris* (Lundqvist, 1959, 1969; Kullman, 1980, 1987, 1988, 1989a,b, 1995; Kullman and Kjällgren, 2000), 64 samples of *Betula pubescens* (Kullman, 1988, 1989a,b, 1995), and 17 samples of *Alnus incana* (Kullman, 1988, 1995), all collected within a continuous mountain area of c. 8000 km<sup>2</sup> (Kullman, 1995). The maximum distance of individual samples from Lake Stentjärn is c. 50 km. Radiocarbon ages of all megafossils were converted to calibrated ages based on the IntCal98 calibration data set (Stuiver et al., 1998), using the OxCal vers. 3.5 radiocarbon calibration software, and age estimates are expressed as most probable intercepts with the calibration curve within 95.4% probability envelopes (Hammarlund et al., 2004). The approximate local limit of *Pinus sylvestris* enclaves (Kullman, 1994; personal communication) at the end of the 19th century (c. 680 m a.s.l. in the study area) is used as a reference level. Note that megafossil elevation values also reflect local differences in the late 19th pine enclave limit. (●) *Pinus sylvestris*; (○) *Betula pubescens*; (x) *Alnus incana*. The vertical lines (labelled A and B) represent approximate enclave-limits in the area of *Alnus incana* and *Betula pubescens* ssp. *czerepanovii*, respectively. The approximate altitude of Lake Stentjärn has been included for comparative purposes.

were deposited at c. 10,500 cal year BP. In addition, no macrofossils matching the elevation of these early pine megafossils can be expected since the maximum elevation of the lake catchment is c. 1020 m a.s.l. (c. 340 m above the 19th century pine enclave-limit; Fig. 8; Kullman, 1994). None of the megafossil samples presented in Fig. 8 were collected in the catchment of Lake Stentjärn and the specimens from Mount Enkälen were all found at lower elevations (Kullman, 1995, pers. comm.). Hence, the few pine megafossils

from very high elevations dating to before c. 9500 cal year BP, which were collected on the slopes or summits of major peaks in the area such as Mount Sylarna (Fig. 1; Kullman and Kjällgren, 2000) may represent scattered individuals in extremely favorable micro-climatic settings. The absence of megafossils from lower elevations at this stage may reflect persistence of remnant dead-ice bodies in the valleys or unsuitable soil conditions. In contrast, the macrofossil evidence from Lake Stentjärn suggests that the

frequently recorded megafossils at a variety of altitudes within ST 2, especially the increased frequency around 9000 cal year BP, represent a regional expansion of pine in the study area.

Although macrofossils of *Betula pubescens* were frequently recorded in ST 2, consistent with data from Lake Spåime (Hammarlund et al., 2004), only a single megafossil of mountain birch dates to this period. This pattern contrasts clearly with zone ST 4, where the two records show excellent agreement. Another obvious discrepancy between the macrofossil and megafossil records can be observed for *Alnus*, as the macrofossil data give evidence of a slightly higher alder tree-limit in ST 3–ST 4 than indicated by the megafossil data set. Apart from possible biases of the megafossil sampling strategy, the observed discrepancies for *Betula* and *Alnus* may be examples of an important shortcoming of the megafossil approach, namely the problem of wood preservation, which seems to have effected the megafossil record in ST 1–ST 2, and probably also in ST 4 (Fig. 8). For obvious reasons, potential megafossils at specific sites or altitudes normally represent few individuals as compared to macrofossil and pollen data. Furthermore, megafossils are dependent on adjacent soil, peat, or lake sediment deposits for preservation (Dubois and Ferguson, 1985; Kullman, 1994, 1995). On steep slopes and rough terrain, peat rarely accumulates, which may result in spatial gaps in the records. In addition, wood of alder and birch decays relatively rapidly as compared to pine wood, and its preservation thus depends to a large extent on “catastrophic” burial in response to soil surface instability (Kullman, 1995). The alder macrofossils recorded at Lake Stentjärn in ST 3 and ST 4, consisting of twigs and buds, most likely represent trees that grew in the lake catchment. Thus, during the phase of alder expansion at c. 8500–6000, the accumulation of peat in the catchment of Lake Stentjärn may have been limited, giving rise to poor preservation conditions for wood of deciduous trees. As the occurrence of *Alnus* can be assumed to have been subordinate as compared to *B. pubescens*, fewer alder megafossil specimens were subsequently recovered compared to mountain birch. However, the available data on past distributions of *Alnus* in the study area still give evidence of a good temporal, if not entirely spatial, correlation

between the three *Alnus* proxy records (Fig. 8), clearly showing the elevated mid-Holocene tree-limit position of alder, thus suggesting that the megafossil record can be used for temporal reconstruction of the *Alnus* distribution in the tree-limit ecotone.

As demonstrated by stratigraphic records from southern Norway (Eide et al., 2005) *Alnus* displays one of the best correlations between pollen influx and macrofossil data, and this is generally supported by megafossil evidence and by the stratigraphic data from Lake Stentjärn, whereas the pollen influx records of *Pinus* and *Betula* are not as clearly related to variations in the other two data sets. Interpretation of pollen data in terms of local, extra-local, and regional presence of pine (Hicks, 1994; Hicks and Hyvärinen, 1999; Birks et al., 1996) and tree birch (Pardoe, 2001) is often complicated. However, the *Pinus* pollen influx record exhibits high values when pine was present locally. This pattern is repeated in the later part of ST 4, when a local re-advance of pine may have taken place. *Betula* pollen data show a relatively weak correlation with the macrofossil record, implying that the pollen signal is either of more extra-local character, or simply compromised by fluctuating proportions of *Betula nana* and *Betula pubescens* pollen. Comparisons with pollen influx data from nearby Lake Spåime (Bergman et al., in prep.) suggest that catchment size and topography, rather than lake size, determines how the local and regional vegetation is mirrored by pollen data. However, because of the high degree of complexity that characterizes the relationship between tree-limit vegetation and pollen deposition (e.g. Pardoe, 2001), additional studies and methodological refinement are needed before more detailed conclusions can be drawn from the present data.

## 5. Conclusions

1. A short-lived pioneer flora with *Geum rivale*, *Dryas octopetala*, *Empetrum nigrum*, *Ledum palustre*, *Saxifraga* sp., *Salix* spp., and *Oxyria digyna* was succeeded by grasses, and possibly *Betula pubescens*, at c. 10,300 cal year BP.
2. Local expansions of *Betula pubescens* (c. 9800 cal year BP) and *Pinus sylvestris* (c. 9200 cal year

BP) were followed by a distinct, temporary tree-limit retraction at c. 8500–8000 cal year BP.

3. The climatically induced changes observed in the terrestrial vegetation are also recorded in the aquatic environment. Lake system proxy records indicate environmental shifts or changes at approximately 8500–8000, 5500, and 3500 cal year BP.
4. A successive decrease in forest density initiated at c. 6000 cal year BP was followed by the complete disappearance of trees from the lake catchment at c. 3500–2000 cal year BP.
5. The generally good agreement between our stratigraphic data and previously published megafossil records demonstrates the possibility to assess the validity of stratigraphic and non-stratigraphic palaeoecological approaches in a tree-limit setting.
6. General conformity between pollen influx and macrofossil data is observed for the major tree taxa, although important discrepancies occur, demonstrating the advantages of a multi-proxy approach when investigating alpine tree-limit fluctuations.
7. Three Holocene tephra horizons of Icelandic origin were detected in the sequence. The youngest tephra was geochemically correlated to Askja-1875. The ages of the two other tephtras (c. 3000 and c. 6900 cal year BP) agree with published ages of the Hekla-3 and Lairg A tephtras.

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