



Early Holocene occurrence of thermophilous trees in the Storulvån valley – a study based on pollen analysis

Förekomst av ädellövträd i Storulvådalen under tidig Holocen – en pollenanalytisk studie



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All figures and tables are created by the author unless other is mentioned in the text.

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Sammanfattning

Nya vetenskapliga rön har förändrat synen på klimatet under tidig Holocen. Modern forskning indikerar att isavsmältningen i södra Skanderna skedde tidigare än man trott. Klimatet under tiden efter isavsmältningen var även tillräckligt varmt för att värmeälskande, nemorala trädslag skulle kunna etablera sig i de södra fjälltrakterna. Makrofossiler påträffade i området kring Storulvån i västra Jämtland bekräftar förekomst av *Ulmus glabra*, *Quercus robur* and *Corylus avellana* under Holocens inledande århundraden.

Syftet med studien är att undersöka förekomsten av nemorala trädslag i Storulvåområdet under hela Holocene genom att utvärdera förekomsten av pollen av *Ulmus*, *Quercus*, *Tilia* och *Corylus* i torvlagerföljder. En fråga är huruvida de vanligen låga halterna av pollen av dessa trädslag är tolkningsbara; dvs. går det att avgöra om dessa pollen kommer från lokala individer alternativt bestånd eller om de transporterats ifrån från avlägsna skogar? En myr i Getryggens sydsluttning på norra sidan av Storulvån valdes ut för provtagning och två parallella borkkärnor togs för pollenanalys. Resultaten påvisar pollen från *Quercus*, *Tilia*, *Ulmus* och *Corylus*, huvudsakligen från perioden mellan 7500 och 2800 kalibrerade år före nutid. Om dessa nemorala trädslag har kunnat etablera sig i sluttningen har de växt långt ifrån deras naturliga utbredningsområde och vilket bör ha medfört att deras förmåga att producera pollen har varit nedsatt, om inte periodvis helt förhindrad. De lägsta procentgränser man ibland använder som ett indirekt mått på lokal närvaro måste därför användas med försiktighet. Istället jämförs studiens resultat med liknande pollenstudier och makrofossilstudier som utförts i området. Slutsatsen är att även låga halter av pollen från *Quercus*, *Tilia*, *Corylus* och möjligtvis *Ulmus* kan tolkas som ett resultat av pollenspridning från träd som har vuxit på den klimatiskt gynnsamma sydsluttningen under perioder av fördelaktigt klimat.

Abstract

Recent studies on vegetation history in the Swedish Scandes have altered the view on deglaciation and patterns of vegetation colonization. It is now suggested that the mountains were deglaciated earlier than previously thought and the climate being warm enough to allow thermophilous tree species to establish further north than generally thought. Macrofossil finds from the area around Storulvån in western Sweden confirm that *Ulmus glabra*, *Quercus robur* and *Corylus avellana* have been present during the early Holocene.

The aim of the study is to evaluate occurrences of pollen from thermophilous deciduous tree species in pollen diagrams from the Storulvån area in the southern Scandes where macrofossils from these species have been found and dated. A mire close to the macrofossil site on the southern slope of Mt. Getryggen was selected for the study and two parallel cores were taken for pollen analysis. The results showed recordings of *Quercus*, *Tilia*, *Ulmus* and *Corylus*, mainly between 7500 and 2800 calibrated years before present. The thermophilous tree species have grown in this area on their distributional limits and their pollen productivity has most likely been reduced if not occasionally even impaired. So general lowest pollen percentage limits that have been sometimes used as an indication of local presence must be treated with care, and validation of local presence must be done by other means and through comparison with similar studies and macrofossils. The present results were compared to similar pollen studies performed in the area and the results suggest that here the low pollen shares of *Quercus*, *Tilia*, *Ulmus* and *Corylus*, are in fact local imprints that can be interpreted as originating from trees that grew in the study area. It can be concluded that *Quercus*, *Tilia*, *Corylus* and possibly *Ulmus* most likely have been present on the prosperous south-facing slope during periods of favourable climate.

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Introduction

During the last decade several studies have contributed to an altered view on the tree colonization in the Swedish Scandes after the last ice age (Kullman, 1995; 1998a; 1998b; 2000; Kullman and Kjällgren, 2000; Kullman, 2002; Segerström and von Stedingk, 2003; Kullman, 2004; Bergman et al., 2005; Giesecke, 2005). These studies have revealed that the Scandes were deglaciated earlier than formerly assumed and that the climate was warmer than previously thought during the early Holocene. Since von Post introduced pollen analysis in the early 20th century (von Post, 1918) it has been the main source for interpreting vegetation colonization patterns after the ice age. However, early in the history of pollen analysis Hesselman (1916) remarked on the more difficult parts of using pollen analysis for reconstruction of past climates: how can we distinguish pollen produced by local trees from pollen dispersed from distant forests? In modern studies plant macrofossils therefore have added important information to the palaeological studies and the interpretation of tree colonization patterns (Birks & Birks, 2002; Kullman, 2004; Bergman et al., 2005; Giesecke, 2005).

Already in the beginning of the 20th century the earlier geographical distribution of the thermophilous tree species *Corylus avellana* in Scandinavia was considered to be a clear indication of the climate variation during the Holocene (Nordhagen, 1933). When fossil nutshells from *Corylus avellana* were found outside its natural range it was suggested that during some period of time in the past the summer temperature must have been higher to allow such a geographical spread (Andersson, 1912). In Norway macrofossil evidence for past widespread mixed oak forests were found in places where these thermophilous tree species do not occur today (Nordhagen, 1933). When pollen analysis was performed in the Swedish Scandes pollen of *Tilia cordata*, *Ulmus glabra*, and *Corylus avellana* were found (von Post, 1933). Von Post (1933) concluded that these thermophilous species must have grown during a warmer period on locations with favourable local climate, such as south facing mountain slopes. Andersson (1912) presented such relict locations in the northern part of Sweden for several species that at that time only were found in southern Sweden. One example is from an area in the southern Swedish Scandes, Skalängarna, where Andersson (1912) recorded a 14 m tall *Ulmus glabra* tree, which was interpreted as a remnant from a larger *Ulmus glabra* stand. At Mt. Totthummeln, also in the southern Scandes, a northern outpost population of *Ulmus glabra* has been the subject of more recent research (von Stedingk *et al.*, 2006). The results of this study, based on pollen analysis from Mt Totthummeln and the adjacent Mt. Åre-Björnen, indicate that the *Ulmus glabra* population that grow on the southern slope of Mt. Totthummeln is a relict from a population that established already during the Holocene thermal maximum.

Many modern paleoecological studies from the southern Scandes that focus on tree-line studies, forest development and spruce migration, based on pollen analysis, also display finds of thermophilous trees such as *Quercus robur*, *Tilia cordata*, *Ulmus glabra*, *Corylus avellana*, *Fraxinus excelsior* and *Acer platanoides* (e.g. Bergman et al. 2005; Giesecke, 2005; Segerström & von Stedingk, 2003). These finds can indirectly describe the characteristics of the postglacial climate and the changes over thousands of years since different species have different demands on their environment for establishment, regeneration and growth. However, due to low pollen percentages of these species, below 3 %, these finds are often dismissed as being of long distance origin (Tallantire, 1980). A main objective when reconstructing palaeoclimates is to interpret and evaluate percentages and influx of tree pollen in terms of local presence (Birks, 2003).

The value of pollen studies for interpreting vegetation development has often been debated and the reason for this is the mobility of pollen. Pollen grains recorded at a site may have been transported very long distances and the resulting pollen diagram may display recordings of species that has never been present at the site. Especially at tree-line situations, where the trees are growing at their distribution limit and producing small amounts of pollen, the regional pollen signal may overshadow the local pollen signal (Birks & Birks, 2000). In conclusion, it is hard to determine local presence of a species and to reconstruct past vegetation compositions from pollen analysis alone. Plant macrofossils submit evidence of local presence because, unlike pollen, macrofossils have a very limited distribution from their source. It is however hard to quantify representation of a particular species beyond the basic conclusion of local presence with macrofossil evidence but it enables, together with pollen analysis, reconstruction of vegetation at site scale (Birks & Birks, 2000). So the main practical difference between these two fossil evidences is that the relative pollen frequencies are comparable, while macrofossil presences are not (Faegri & Iversen, 1989). Kullman (1998a, 1998b) performed two macrofossil studies in the subalpine birch forest close to Storulvån tourist station in western Jämtland, a county in the southern Swedish Scandes. In both studies he recovered macrofossils from thermophilous tree species, which were dated and yielded quite extraordinary results. The 1998a study resulted in macrofossil finds from *Alnus incana*, *Alnus glutinosa*, *Quercus robur*, *Ulmus glabra* and *Corylus avellana*. The thermophilous tree remains all dated back to the early Holocene, 8000-8500 BP and an *Alnus glutinosa* cone was almost 7500 years old. The date of *Alnus incana* (8100 BP) is the earliest ever recorded *Alnus incana* macrofossil in the Scandes. In the 1998b study a well-preserved almost 7000-year-old *Tilia cordata* inflorescence was found in a deep vast mire in the same area as the 1998a study.

The aim of the present study is to assess if the thermophilous species persisted during the warm period in the Storulvån valley through evaluation of the early Holocene occurrences of pollen from thermophilous deciduous tree species in pollen diagrams from the southern Scandes. The study is based on a detailed pollen analysis of a peat deposit near the site where macrofossils of *Quercus robur*, *Ulmus glabra* and *Corylus avellana* were found and dated to between 8000-8500 years BP (Kullman, 1998a; 1998b). The main questions that will be addressed are: Is the thermophilous pollen record from a peat deposit close to a known macrofossil location more distinct than records from mires further away? The results of the pollen analysis will be discussed in terms of local presence of thermophilous trees. Did these trees, which grew on their distributional limit, even produce pollen in such amounts that they could be recorded in pollen analysis and if so, could the records be interpreted as local presence? Can a distinction be made in the pollen diagram between local production of pollen and long-distance transport? Can the pollen analysis performed in the study contribute to increased knowledge concerning the quantity of trees that has been present on a site where macrofossils are recovered, i.e. a site where local presence has been confirmed but not quantified?

Material and method

Study site

The area chosen for the study is the Storulvån valley, which is in western part of the county of Jämtland. The Storulvån valley is located in the southern Scandes in western Sweden, on the border to Norway, (Figure 1). Andersson (1912) mentions Jämtland as a county with an intriguing flora due to its bedrock and high amount of favourable southern slopes. The closeness to the prosperous Trondheim fjord and the relatively low mountains also contribute to the wealthy flora in Jämtland (Andersson, 1912).

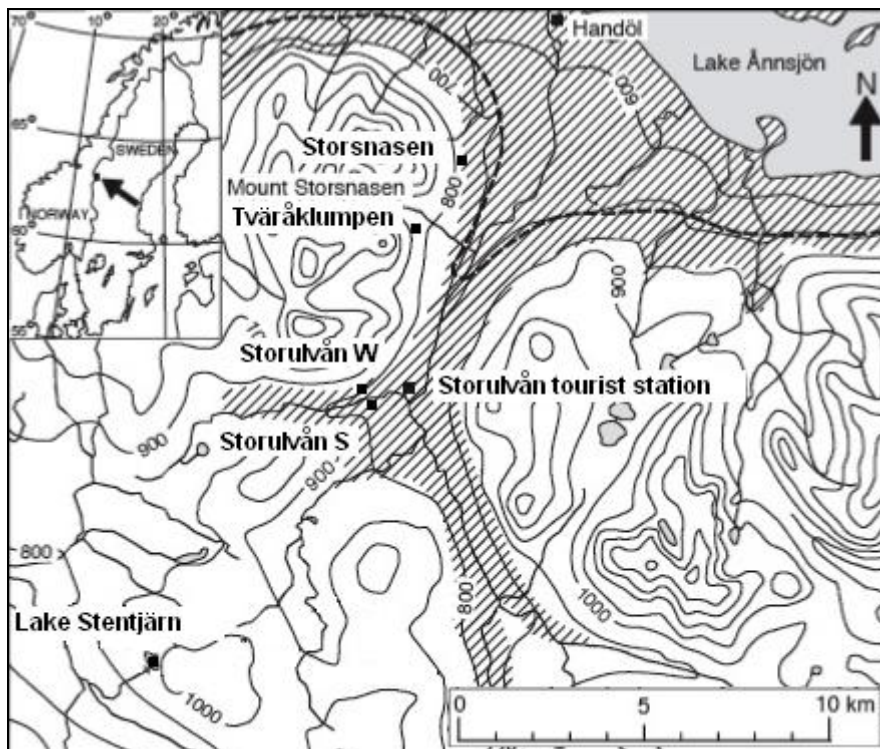


Figure 1. Fennoscandia with the study site, Storulvån W, indicated.

The climate in western Jämtland is oceanic and humid with a mean temperature for January of -8°C , July 11°C and the annual mean is about 1°C (Wastensson *et al.* 1995). The annual precipitation amount is 850 mm and almost half of this falls as snow. Glaciofluvial sediments cover the amphibolite bedrock and the area is rich in peat mires (Lundqvist, 1969). According to Lundqvist (1986) the regional deglaciation occurred *c.* 9100 BP, but more recent studies imply that the deglaciation in the Storulvån area occurred *c.* 10 000 BP (Bergman, 2005).

The study site, Storulvån W, is a small, raised, ombrotrophic mire ($63^{\circ}10'N$, $12^{\circ}21'E$), *c.* 740 m a. s. l., in the sub alpine birch forest (Sjörs, 1956), *c.* 1 km west of the Storulvån Tourist Station. The site is situated in the mountain birch forest zone, which is found between 600 and 800 m. a. s. l. (von Stedingk, 2006), on the south-facing slope of Mount Getryggen. The mire is situated close to the Storulvån creek and is tilting slightly (Figure 2). When examining the peat thickness on the mire it became clear that the depth of the mire varied considerably and the sampling point is in a natural depression where the paludification started and the peat accumulation began.



Figure 2. The sampled mire.

Today the vegetation in the slope that surrounds the mire is dominated by subalpine mountain birch forest including ericaceous shrubs, *Betula nana*, mosses and lichens on the ground layer. A few individuals of *Picea abies* is present close to the tourist station and further north in the valley as a few layering individuals that form a tree line at 765 m a. s. l. *Pinus sylvestris* and *Picea abies* dominate the forests below 600 m a. s. l. further north in the valley (Segerström & von Stedingk, 2003). The species that grow on the mire are presented in table 1. Two parallel 180 cm cores were taken in the deepest part of the mire with a “Russian” corer in August 2007.

Table 1 Species present on the sampled mire and the pollen taxonomical equivalent

Species	Pollen and spore group
<i>Betula nana</i>	<i>Betula</i>
<i>Juniperus communis</i>	<i>Juniperus</i>
<i>Andromeda polifolia</i> , <i>Empetrum nigrum</i> , <i>Vaccinium oxycoccos</i> , <i>V. uliginosum</i> , <i>V. myrtillus</i>	<i>Ericaceae</i>
<i>Calluna vulgaris</i>	- <i>Calluna type</i>
	<i>Rosaceae</i>
<i>Rubus chamaemorus</i>	- <i>Rubus chamaemorus</i>
<i>Potentilla erecta</i>	- <i>Potentilla type</i>
<i>Cirsium palustre</i>	<i>Asteraceae</i>
<i>Equisetum palustre</i>	<i>Equisetum</i>
<i>Selaginella selaginoides</i>	<i>Selaginella</i>
<i>Molinia caerulea</i>	<i>Poaceae</i>
<i>Carex bigelowii</i> , <i>C. rotundata</i> , <i>C. vaginata</i> , <i>Eriophorum vaginatum</i>	<i>Cyperaceae</i>
<i>Sphagnum spp.</i>	<i>Sphagnum</i>

Pollen analysis

Before the core was prepared for pollen analysis it was briefly analysed for changes in degree of humification and larger wood remains. For pollen analysis 36 samples were taken out from

the 180 cm core. One sample was taken every 10 cm from the upper half of the core (0-90 cm) and in the lower half (93-180 cm) on every third cm. The closer sample interval in the lower half was chosen to enable a thorough investigation of the vegetation changes in the older parts of the core. Preparations for analysis included digestion in 5% potassium hydroxide and acetolysis (according to Moore et al. 1991). The samples were stained with safranin and mounted with glycerine on microscopic slides. A total of 500-600 pollen were counted on each level and the identification was made to species level when possible, otherwise to family, genera or pollen type according to the pollen key by Moore et al. (1991). The results were compiled in a pollen diagram using Tilia and TG view, where percentage frequencies were calculated on a total pollen sum including *Cyperaceae*. Spores were also counted and identified to species level if possible, otherwise to family or genera. The resulting pollen diagram (Figure 4) was divided into four periods based on major changes in the pollen recordings.

Radiocarbon dating

From the 111, 149 and 179 cm levels macrofossils, including moss and *Cyperaceae* leaves, were sorted out for ^{14}C AMS (accelerator mass spectroscopy) radiocarbon dating. This selection was made before the pollen analysis was finished so the chosen levels were estimated to give a good understanding of the calibrated age-versus-depth relationship of the core rather than representing specific changes. The age determinations were performed at the Ångström Laboratory in Uppsala. Based on the results from the ^{14}C analysis an age-depth diagram was drawn where the approximate age of different depths can be estimated.

Results and interpretation

Dating

The age of the dated macrofossils are presented in table 2. The results show that peat initiation started at the site between 8000 and 7700 calibrated years before present (cal yr BP). This means that the mire was formed *c.* 2000 years after the regional deglaciation (Bergman, 2005).

Table 2 Radiocarbon dates from Storulvån W.

Laboratory code	Depth (cm)	¹⁴ C age BP	Calibrated age ranges (cal. BP) at 2 σ
Ua-34986	111-112	4700 \pm 40	5310 – 5790
Ua-34987	149-150	5970 \pm 90	6550 – 7200
Ua-34988	179-180	7030 \pm 75	7690 – 7980

Based on the radiocarbon dates (Table 2) an age-versus-depth diagram was created (Figure 3). All radiocarbon dates are plotted as the calibrated age range and an average age-versus-depth curve is drawn.

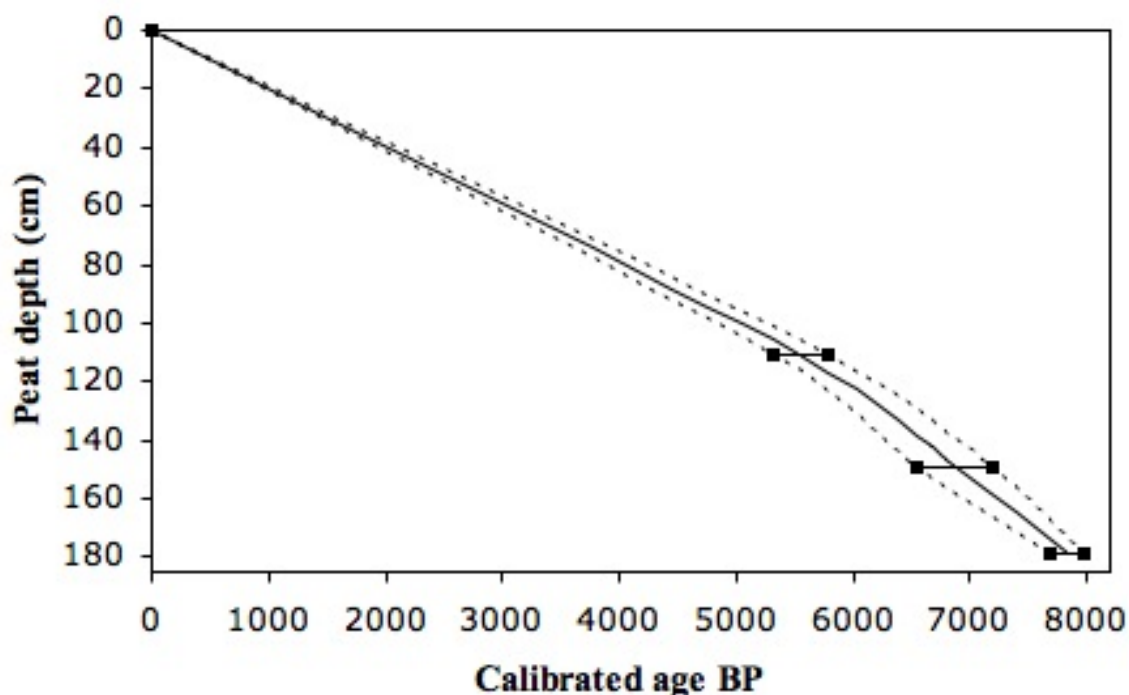


Figure 3. Tentative age-depth curve based on calibrated ¹⁴C dates. The ¹⁴C date intervals are marked with filled squares and the solid horizontal lines represents the interval at each dated level. The dotted lines represent the estimated age range at different depths through the core and the solid line represents the average age (cal yr BP) on which all age estimations will be based.

Vegetation history

Four different periods identified in the pollen diagram (Figure 4) are as follows; (1) the *Alnus* period; (2) the thermophilous period; (3) the *Poaceae* period; and (4) the dwarf shrub period. All age estimations that follow will be based on the tentative age-depth curve (Figure 3). Each period will be presented firstly with a paragraph describing the main changes in the pollen diagram, followed by a paragraph with the vegetation history interpreted from the pollen.

1. The *Alnus* period, 8000-7700 cal yr BP (180-175 cm)

The *Alnus* period is the initial stage of the mire formation. *Alnus* pollen is the most common pollen type, with almost 70 % of the terrestrial pollen in the bottom sample, but the percentage is declining down to 40 % when the period ends at c. 7700 cal yr BP. The proportions of both *Pinus* and *Betula* pollen are at their all-time low percentages at the start of the period with approximately 15 and 5 %, respectively. The *Pinus* percentage increases to 40 % at 7700 cal yr BP and *Betula* increases to 10 %. The only thermophilous pollen type recorded is *Corylus* with almost 1 %. Pollen from *Stachys sylvatica*, *Solanum nigrum*, *Rubus saxatilis*, *Geranium ssp.* and *Sorbus* are found in this period and *Compositae* pollen is recorded with 4 %. At the end of the first period *Selaginella* has a distinct peak. Other pollen types that occur are *Salix* type, *Poaceae* type, *Cyperaceae* type, *Filipendula ulmaria*, *Potentilla* type and *Lycopodium* type.

The peat initiation started about 8000 cal BP in a small depression in the slope close to the Storulvån creek. The depression and the surrounding land was dominated by *Alnus* and became paludified possibly due to a combination of altered external conditions, such as precipitation and temperature, and local hydrological conditions. The depression became more or less waterlogged which turned the site into something resembling a swamp forest. The excess of water thus inhibited the decomposition and lead to the initiation of peat formation. The newly formed swamp forest was probably quite nutrient rich since this type of minerotrophic peatland receives nutrients from the ground water and surface runoff (Charman, 2002). Other than *Alnus*, which is excellent at fixating nitrogen and utilising high levels of nutrients, the vegetation on the newly formed fen was characterised by nutrient demanding species, like *Filipendula*, *Polypodiaceae* and *Selaginella*. As *Alnus* probably grew on the site it is represented by a very high percentage and therefore overshadows pollen from other species that grew in the area. The slopes close to the fen were probably open with some grasses and herbs in the field layer. *Pinus* was present in the valley before the fen was formed (Segerström & von Stedingk, 2003) and probably grew scattered in the slopes close to the fen (Kullman & Kjällgren, 2000). The quantity of *Pinus* was probably quite constant throughout the period but the high *Alnus* proportion shadows the pollen signal from *Pinus*.

Storulvån W

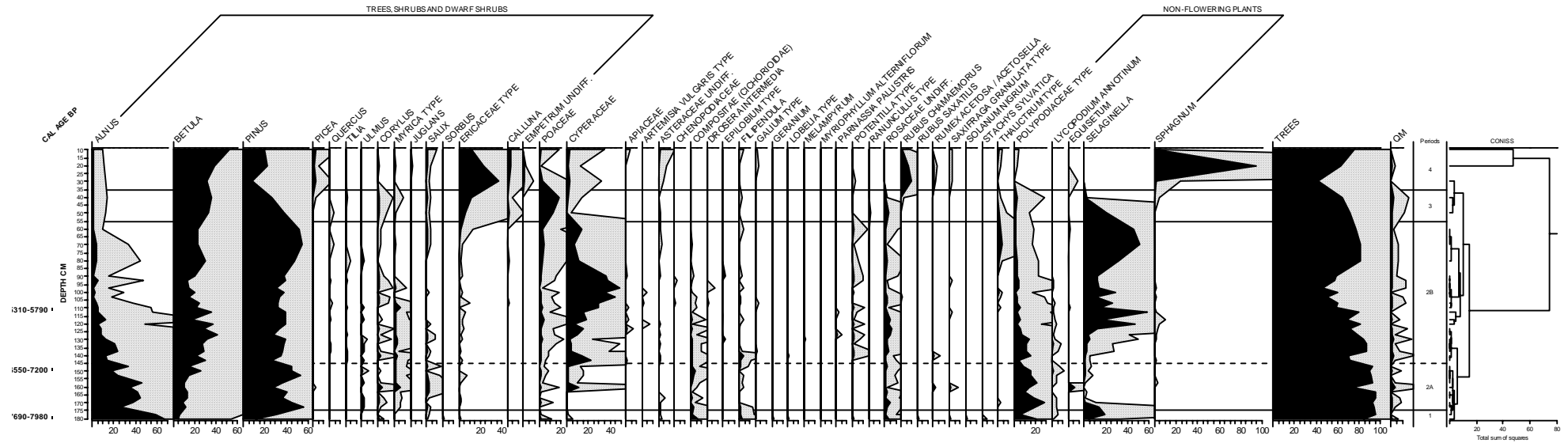


Figure 4. Pollendiagram from Storulvån W. From the left: calibrated ^{14}C dates; depth scale in cm; percentage values of individual pollen taxa and spore types; percentage values for tree pollen and *Quercetum mixtum*; zone division. Black fields represent the percentage of each pollen type and dotted fields represent 10 X exaggeration of percentage values. Pollen and spore types of low proportion and without importance for the discussion are not shown. The zonation is based on CONISS with some adjustments according to occurrence of thermophilous tree species.

2. The thermophilous period, c. 7700-2800 cal yr BP (175-55 cm)

The second period is the longest period and it is in this zone pollen of *Quercus*, *Tilia*, *Ulmus* and *Corylus* are recorded. The period is subdivided into two parts, 2A from 7700 to 6800 cal yr BP and 2B from 6800 to 2800 cal yr BP. This division is based primarily on changes in recordings of pollen from fen vegetation and the lack of *Quercus* and *Tilia* in the first part of the period.

2A: *Ulmus* and *Corylus* are recorded with percentages in general below 1 % but *Corylus* has a peak with almost 5 % at c. 7200 cal yr BP. The proportion of *Alnus* declines from 50 % to 30 % in this part while *Betula* increases from 10 % to 25 %. The *Pinus* percentage starts at 45 % and ends at roughly the same, but varies between 55 % and 30 %. A single *Picea* pollen is recorded at c. 7200 cal yr BP. *Filipendula*, which occurred already in the *Alnus* period, is recorded with percentages around 1 % and *Salix* with 2-4%. Two large pieces of unidentified wood, probably *Alnus* remains, were found between 7400-7500 cal yr BP.

2B: All four of the thermophilous tree species are recorded in period 2B. *Tilia* pollen is recorded from c. 6700 cal yr BP and is thereafter recorded sparsely until c. 3500 cal yr BP. *Corylus* is the most abundant of the four thermophilous species recorded at this site. It varies around 2 % and is recorded at almost every level. *Quercus* is first found at c. 6600 cal yr BP and is recorded with about the same proportions as *Tilia*. *Ulmus* is recorded with low percentages until c. 4000 cal yr BP. The decline of *Alnus* continues; from c. 30 % to 2-3 % at the end of the period. *Betula* peaks with 40 % at c. 6200 cal yr BP after which it declines to c. 20 % of the terrestrial pollen sum. The *Pinus* pollen percentage varies around 35 % and at c. 3500 cal yr BP it peaks with 55 %. Except for a small peak in period 2A at c. 7400 cal yr BP, *Cyperaceae* increases steadily from a few percents at the beginning of period 2B and peaks with 50 % of the terrestrial pollen sum at 4900 cal yr BP. The *Poaceae* share is quite constant around 2-3 % throughout the period.

Single pollen grains from two species of aquatic plants, *Lobelia ssp.* and *Myriophyllum alterniflorum*, occur at c. 6600 cal yr BP and around c. 5000 cal yr BP respectively. *Potentilla* pollen is recorded with percentages around 2 %. *Filipendula* displays a discontinuous curve and declines to less than 1 % above c. 6400 cal yr BP. *Myrica* and *Compositae* are both recorded with continuous curves from the start of period 2B until c. 5000 cal yr BP. *Rosaceae* has a continuous curve above 2 % and peaks at 6050 cal yr BP with 6 %.

When period 2A starts c. 5 cm of peat had accumulated in the depression. The landscape surrounding the site became more open and the swamp forest gradually disappeared from the slopes, indicated by the lowered *Alnus* signal. As more peat accumulated, the depression became oxygen deprived and the vegetation on the fen became dominated by *Polypodiaceae* species, some *Cyperaceae* species and the first *Sphagnum* mosses. *Myrica* probably established close to the wetlands and lakes in the area, fixating nitrogen in nitrogen-poor growing conditions. The vegetation on the slopes surrounding the fen was most likely quite open as inferred by the low *Betula* proportions, but the sub alpine *Betula* was most likely expanding as the *Alnus* swamp forest disappeared. As the number of *Alnus* trees in close vicinity to and on the fen declined in the beginning of period 2A, the share of *Pinus* pollen increased. The amount of *Pinus* in the landscape was plausibly the same as in period 1. *Salix* was also present in the valley but declined in the end of the sub period. *Ulmus* and *Corylus* were possibly growing on the prosperous southern slopes close to the fen. Herbs belonging to the *Compositae* family were present in the area as well as herbs belonging to *Rosaceae*.

At approximately 6800 cal yr BP the peat thickness was *c.* 35 cm and the fen became more dominated by *Cyperaceae*, *Poaceae* and *Selaginella*. The climate at this time was slightly warmer than during the previous periods (Hammarlund *et al.*, 2004), possibly allowing species like *Quercus*, *Tilia*, *Ulmus* and *Corylus* to establish in the area during periods of advantageous climate. *Myrica* decreased on the slope surrounding the mire. *Betula* was thriving in the beginning of period 2B, but declining somewhat after *c.* 6100 cal yr BP. The decline is plausibly not as great as the pollen diagram implies, caused by the high percentage of *Cyperaceae* that grew on the fen and thus shadowing the *Betula* pollen signal. By this time *Alnus* declined from the slopes around the fen, possibly due to the increased peat accumulation and disadvantageous hydrologic conditions. *Alnus* plausibly remained at lower altitudes in the valley below the forest limit close to the creek. Grasses increased, maybe due to the disappearance of *Salix* and *Myrica* shrubs. *Potentilla* and *Rosaceae* were present in the field layer and towards the end of the period *Thalictrum* was also present.

3. The *Poaceae* period, 2800-1800 cal yr BP (55-35 cm)

This period is named after the large peak in *Poaceae* at *c.* 2000 cal yr BP. *Alnus* percentage decreases to its absolute low point and stays low throughout the period. *Pinus* pollen decreases steadily from almost 45 % at *c.* 2800 cal yr BP to 15 % in the end of the period. One *Picea* pollen is recorded at *c.* 2200 cal yr BP. Ericaceous species increase at the beginning of the period. Both *Quercus* and *Tilia* pollen are recorded in this period but with low percentages. *Corylus* on the other hand continues to record higher percentages than the other thermophilous tree species. The *Cyperaceae* pollen percentage declines rapidly in the beginning of the period, but increases slightly after *c.* 2500 cal yr BP. *Selaginella* drops from 35 % to 0 % in this period. The *Rosaceae* type, which has been recorded throughout most of the core with proportions between 1 and 5 %, displays its last occurrence at 2000 cal yr BP.

The fen changed to a bog in this period. In the beginning of the period the bog was nutrient poor and *Selaginella* was decreasing on the fen. Ericaceous species became established on the fen. Grasses increased on the fen and on the surrounding slopes, thus out-competing the herbs that were present earlier. *Betula* was plausibly present in the same extent as earlier but the pollen signal is now stronger as the percentages of *Cyperaceae* and *Pinus* pollen is decreased. *Pinus* was plausibly decreasing in the landscape, due to the lowering of the *Pinus* tree limit around that time, suggested by Kullman and Kjällgren (2000) in a study from the area. The climate was by this time becoming colder again (Hammarlund *et al.*, 2004) and the thermophilous species disappeared from the area.

4. The dwarf shrub period, 1800 cal yr BP-present (35-10 cm)

The period starts with a peak (35 %) in *Ericaceae* pollen. *Calluna* also increases in proportion. *Betula* increases from values around 30 % at the start of the period to about 55 % at the end. *Picea* is recorded continuously with 2 % in this period. *Corylus* is the only thermophilous tree species that is recorded in this period with a single pollen grain at *c.* 1000 cal yr BP. One single *Juglans* pollen grain is recorded at *c.* 1000 cal yr BP. *Salix* is recorded with 1 % at 10 cm.

Sphagnum spores are the totally dominating spore type in this period with almost 100 % of the total spore sum at *c.* 1000 cal yr BP. *Cyperaceae* and *Poaceae* both have low recordings, below 5 %. Some of the herbs, like *Potentilla*, *Rumex* and *Saxifraga*, are again recorded after being absent in period 3. *Rubus chamaemorus* is recorded with percentages above 1 %.

Around 1800 cal yr BP the mire had developed from a fen into a bog. More than 1.5 m of peat had been accumulated to raise the mire above the surroundings and a raised ombrotrophic bog was formed. Since then the *Sphagnum* mosses and *Calluna* dominated the ground and field layer on the bog and ericaceous shrubs colonised the tufts. Since ericaceous shrubs were common in this period some of the *Betula* pollen may have come from *Betula nana*, which also may have established on the bog. *Rubus chamaemorus* indicates nutrient poor conditions. The slopes around the bog were throughout the period dominated by *Betula pubescens* ssp. *czerepanovii* with some *Salix* shrubs. The grasses were not as abundant in this period as in the previous period, which allowed for more herbs to get established. *Picea* was established in the Storulvån area from about 1100-800 cal. BP (Segerström & von Stedingk, 2003) in probably the same quantities as today. The *Pinus* tree line declined during the period (Kullman, 1995) therefore becoming less abundant in the valley.

Discussion

Validating local presence of thermophilous trees through comparison with other studies

To evaluate whether the pollen of *Quercus*, *Tilia*, *Ulmus* and *Corylus* represent local presence in the southern slope of Getryggen nearby the study site the results from the present study are compared to results from the other studies performed in the Storulvån area. Each species will be presented individually and evaluated in terms of local presence. If the *Quercus*, *Tilia*, *Ulmus* and *Corylus* pollen found in the present study are of long-distance origin, the proportions of the thermophilous pollen is not expected to vary across the different studies and the pollen curves should display similar representation for the considered time period. Background pollen values are expected to be similar for all sites in the region (Segerström & von Stedingk, 2003).

Kullman's (1998a) macrofossil study was performed in close vicinity to the present study site, Storulvån W and confirms local presence of *Quercus*, *Ulmus* and *Corylus* at Storulvån (Table 3). The question is what conclusion can be drawn from these results; are these occurrences of thermophilous trees isolated events or have they been growing there several times in the valley during time periods with more favourable climate?

Table 3 Compilation of Kullman's macrofossils (1998a; b)

Age (cal yr BP)	Species	Material dated
8510 ± 50	<i>Ulmus glabra</i>	Leaf
8300 ± 50	<i>Corylus avellana</i>	Nut
8270 ± 50	<i>Corylus avellana</i>	Nut
8030 ± 50	<i>Quercus robur</i>	Leaf

Segerström & von Stedingk (2003) conducted a series of pollen analyses in the Storulvån area (Figure 1). The first analysis, here called Storulvån S (Figure 5), was performed close to Storulvån W, on the fringe of a large mire complex on the southern side of the Storulvån creek. The records cover more or less the entire Holocene. The second analysis, Tväråklumpen, was conducted on a small peat mire 5 km north of Storulvån W and the bottom sample is estimated to 8000-7000 cal yr BP (Figure 5). The third analysis, Storsnasen, comes from a 1.5-hectare peat mire, c. 7 km north of Storulvån W and covers the same time period as Storulvån S (Figure 6). The study sites Storulvån S and Storsnasen are comparable to Storulvån W as they are located at similar altitudes, below the mountain birch forest limit, while Tväråklumpen is located at a higher altitude than Storulvån W. Bergman *et al.* (2005) performed a study at the 7 ha lake Stentjärn, 987 m. a. s. l, 10 km southwest of Mt Getryggen (figure 1), and it also covers the entire Holocene (Figure 6). As Stentjärn is a lake the resulting pollen diagram is not straight forward comparable to Storulvån W. These are the four studies to which the present results will be compared with.

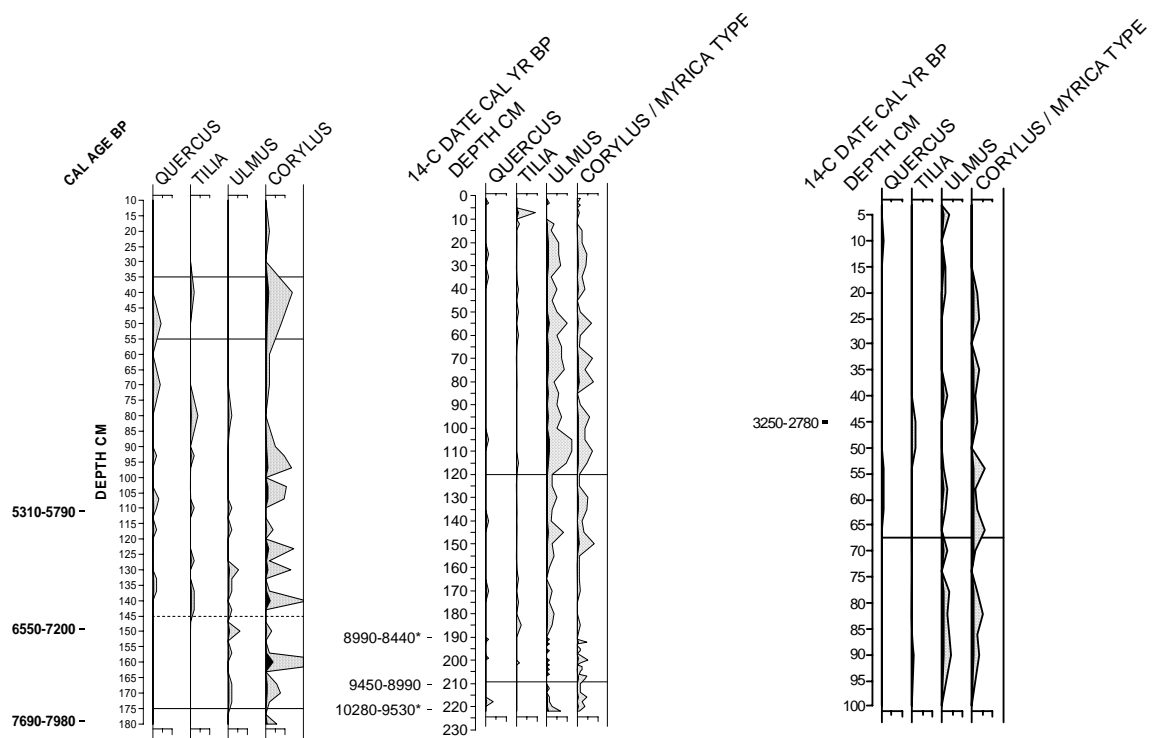


Figure 5. Extractions from the pollen analyses. From the left: Storulvån W, Storulvån S and Tväråklumpen (Segerström & von Stedingk, 2003). Note the different time scales.

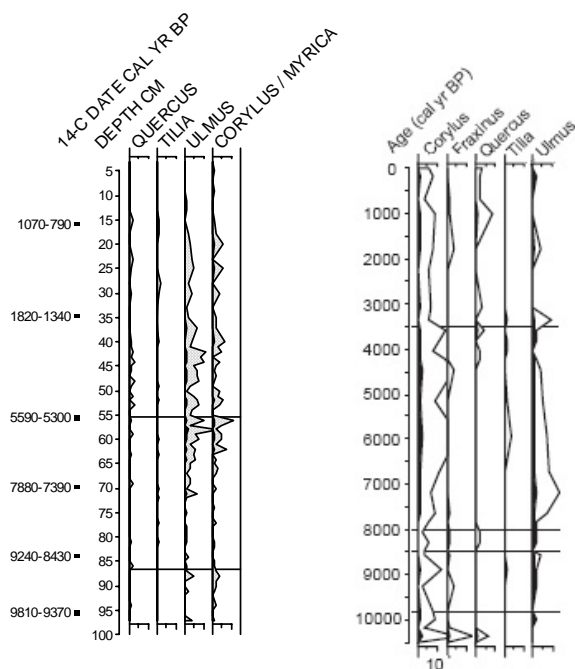


Figure 6. Extractions from pollen analyses. From the left: Storsnasen (Segerström & von Stedingk, 2003) and Stentjärn (Bergman *et al.*, 2005). Note the different time scales.

An additional macrofossil study was performed at the Klocka bog, *c.* 12 km north of Storulvån W, which verifies local presence of *Tilia* in this part of the region (Kullman, 1998b). Lundqvist (1969) performed a pollen analysis at Klocka, which covers the time since *c.* 8500 cal yr BP. The present results will be compared to the studies from Klocka when *Tilia* is discussed.

Quercus

Kullman (1998a) discovered a *Quercus robur* leaf dated to 8030 ± 50 cal yr BP and the climate was obviously warm enough to allow for a tree to establish. The pollen diagram from Storulvån S does not display any records of *Quercus* pollen from this time period and neither does the pollen record from Storsnasen (Segerström & von Stedingk, 2003). The tree that the leaf originated from did probably not produce enough pollen to be recorded at Storulvån S. At Stentjärn there is a small peak in the recording of *Quercus* pollen at approximately the same time as the macrofossil (Bergman *et al.* 2005).

During the millennium that followed after 8000 cal yr BP very few sporadic *Quercus* pollen are recorded at all five study sites, which suggest that *Quercus* were not growing in the area. The first few *Quercus* pollen are recorded at Storulvån W at 6800 cal yr BP in period 2B (Figure 4). During the time period between 6800 and 4500 cal yr BP *Quercus* pollen are recorded frequently at Storulvån W. The representation of *Quercus* pollen in the other four studies, *i.e.* Storulvån S, Tväråklumpen, Storsnasen and Stentjärn, is quite alike which indicate that *Quercus* was not been present at these sites between 6800 and 4500 cal yr BP. The deviant pattern of *Quercus* pollen recordings at Storulvån W suggests local presence. During the remaining part of period 2B, between 4500 and 2800 cal yr BP recordings of *Quercus* pollen are also noted at Stentjärn (Bergman *et al.* 2005).

In the time that corresponds to period 3 and 4, *i.e.* 2800 cal yr BP to present, the recordings of *Quercus* are very few in Segerström & von Stedingk's (2003) study and at Storulvån W. At Stentjärn *Quercus* recorded more or less continuously around 1 % (Bergman *et al.*, 2005).

In conclusion, the recordings of *Quercus* pollen at Storulvån W from 6800-4500 may be a result of local presence, as the recording pattern differs from the other four studies.

Tilia

The earliest records from the beginning of the Holocene (*c.* 10 000 cal yr BP) from the Storulvån valley show few recordings of *Tilia* pollen. No *Tilia* macrofossils were found at Getryggen but the record from Storulvån S displays a small number of *Tilia* pollen from approximately the same time as the *Quercus* macrofossil, around 8000 cal yr BP (Segerström & von Stedingk, 2003), indicating that there may also have been *Tilia* present at Getryggen. At Stentjärn there is also a recording of *Tilia* pollen from approximately 9000 cal yr BP (Bergman *et al.* 2005), that suggests that it may have been a period with more favourable climate around 9000-8000 cal yr BP. At Storsnasen there are few recordings from this time (Segerström & von Stedingk, 2003). The recordings from the time between 8000 and 6800 cal yr BP are quite similar in all five diagrams with none or very few pollen recorded, indicating that the pollen records can be the result of long distance pollen transport.

A *Tilia* inflorescence, dated back to 6980 ± 60 cal yr BP, was found at the Klocka bog (Kullman, 1998b). The pollen analysis from Klocka displays only sporadic recordings of *Tilia* from the time period around 7000 cal yr BP (Lundqvist, 1969), suggesting either that the pollen production of the tree from which the leaf originated from was very low or that there were only a few trees. The record from Storsnasen, which is 5 km south of the Klocka bog, does not display any distinguishable peaks (Segerström & von Stedingk, 2003), however the Klocka bog is probably too far away from Storsnasen catchment area for *Tilia* growing at Klocka to be recorded at Storsnasen.

During the period 2B, *i.e.* 6800 to 2800 cal yr BP, the majority of *Tilia* pollen are recorded at Storulvån W and Stentjärn. The overall recording patterns of the other three sites are similar to each other which could be due to background pollen, and thus suggesting local presence at Storulvån W at times of favourable climate. The remaining time until present the recordings are similar at all sites, except for a larger peak at Storulvån S in the uppermost part of the stratigraphy (Segerström & von Stedingk, 2003), which is difficult to interpret.

In conclusion, the recordings of *Tilia* pollen at Storulvån W in period 2B indicate local presence of *Tilia* trees at Getryggen.

Ulmus

Kullman's (1998a) macrofossil study revealed an *Ulmus glabra* leaf dated to 8510 ± 60 cal yr BP. During this time there are recordings of *Ulmus* pollen in all three diagrams that cover this time around 8500 cal yr BP, *i.e.* Storulvån S, Storsnasen and Stentjärn (Segerström & von Stedingk, 2003; Bergman *et al.*, 2005). The question is whether this is an indication of long distance spread or if *Ulmus* was fairly common in the area at this time. Due to the macrofossil evidence, the latter is more probable.

Ek (2004) performed two pollen analyses about 30 km north-east of Storulvån, one at Mt. Totthummeln, which is close to a known stand of *Ulmus glabra* (Andersson, 1912), and the other one on Mt. Åre-Björnen, 3 km southeast of Mt. Totthummeln. The results (Figure 7) clearly show higher percentages of *Ulmus* pollen in the diagram from Mt. Totthummeln than in the Mt. Åre-Björnen diagram, indicating that the *Ulmus* pollen record from a site close to a known stand of *Ulmus* trees is more distinct than a record from a site further away. The recordings of *Ulmus* occur at almost every level at Mt. Totthummeln, whereas at Mt. Åre-Björnen the recordings are more sporadic. It should also be noted that the proportions of *Ulmus* pollen are not high, but still indicates local presence. Ek's results suggest that the stand of *Ulmus glabra* is possibly a relict from the Holocene thermal optimum.

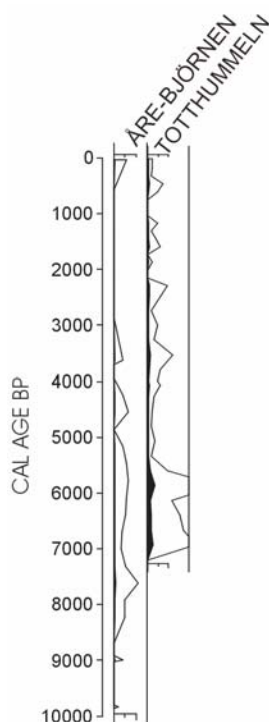


Figure 7. *Ulmus* curves for Mt. Åre-Björnen and Mt. Totthummeln (Ek, 2004)

Storulvån W and Tväråklumpen records the least amount of *Ulmus* pollen in the studies considered here. Storulvån S, Storsnasen and Stentjärn all have continuous *Ulmus* curves (between 0.1-1%), which again leads to the question of local presence in the valley or not. However, based on the results it is hard to give any firm conclusions although it seems likely that the species was present in the valley. In period 3, after 3000 cal yr BP, the *Ulmus* curves decline in percentage in all diagrams, which is an indication of that *Ulmus* probably disappeared from the area.

Corylus

Two *Corylus avellana* nuts were found at Storulvån and dated back to c. 8300 cal yr BP (Kullman, 2008a). At this time very few *Corylus* type pollen are recorded at Storulvån S and Segerström & von Stedingk (2003) have not made a distinction between *Corylus* and *Myrica* pollen, which complicates the interpretation. At Storsnasen and Stentjärn recordings are similar to Storulvån S.

During the thermophilous period between 7700 to 2800 cal yr BP *Corylus* and *Corylus/Myrica* are recorded at most levels in all studies. At Stentjärn the highest share of *Corylus* are recorded with a continuous curve throughout periods 2, 3 and almost the whole fourth period (Bergman *et al.*, 2005). The recordings of *Corylus/Myrica* from Storulvån S are quite similar to the *Corylus* curve from Storulvån W, and based on the latter, suggesting that *Myrica* was more abundant close to Storulvån W than at Segerström and von Stedingk's site. The percentages of *Corylus* is however higher at Storulvån W than Storulvån S during period 2A and the first half of 2B, indicating local presence at times of favourable climate.

In conclusion, the results from Storulvån indicate that the *Corylus* pollen are local and thus *Corylus* may have been present at Storulvån W during the thermophilous period between 7700 and 2800 cal yr BP.

Pollen production of thermophilous trees growing at their distributional limit

The relationship between vegetation composition and the pollen deposited is influenced by the following factors:

- Pollen productivity for the species present
- Pollen dispersal mechanisms
- Basin size of sampling site
- Spatial distribution of vegetation around the sampling site

The pollen productivity varies both between and within species according to the conditions under which a specific individual grows (Faegri & Iversen, 1989). If *Quercus*, *Tilia*, *Ulmus* and *Corylus* have been present in the slope at Mt. Getryggen they would all have grown at their distributional limit, which would have influenced their pollen productivity. Trees that have established on locations close to their distributional limit may have long periods of rest between flowering due to the climate being too cold and/or dry for them to flower (Hicks, 2006), which would also influence the pollen deposition. Results from pollen productivity trials show that there is a difference in pollen productivity estimates (PPE) between specimens of *Juniperus*, *Betula* and *Calluna* growing in the southern Sweden and central Sweden when

compared to a reference pollen type, *Poaceae*. The specimens growing in southern Sweden displayed a higher PPE than specimens growing in the central parts, possibly due to environmental factors (Broström *et al.* 2008). It is known that pollen production is limited by temperature (Hicks, 2006) so it is very likely that the thermophilous trees growing on the slopes around the sampled site produced small amounts of pollen relative to their more southern equivalent.

The results from Broström *et al.* (2008) also revealed that *Quercus* is a species with consistently high PPEs relative to *Tilia* and *Ulmus*, which have consistently low PPEs. *Tilia* pollen may also be underrepresented in the pollen rain due to the fact that it is insect-pollinated (Faegri & Iversen, 1989). *Tilia* produces quite large quantities of pollen but the dispersal mechanisms are not as effective as of those that are strictly wind-pollinated. *Corylus* produces approximately the same amount of pollen as *Ulmus* (Sugita *et al.* 1999). *Pinus* is a high pollen producer and comparative PPE studies show that the PPE for *Pinus* is higher in central Sweden than in southern Sweden compared to the reference pollen type, i.e. the opposite relationship as for *Juniperus*, *Betula* and *Calluna*. A conclusion is that if a species with a low PPE, e.g. *Tilia*, is recorded, even in low percentages, at the same time as local *Pinus* pollen it is likely to be an indication of local presence of, in this case, *Tilia*. In the presented pollen diagram the *Pinus* pollen percentage is consistently high, and results from tree-line studies suggest that *Pinus* was present on the slope (Kullman & Kjällgren, 2000) at the same time as the pollen records of the thermophilous tree species suggest local presence of thermophilous trees. Also, in tree line situations the pollen production is generally low for all species present so the proportion of background pollen is high.

How did the thermophilous tree species reach the valley? Results from Kullman's (1998a; b) macrofossil studies in the area propose that the dispersion of thermophilous tree species is quite fast. It has been suggested that dispersal rates toward extreme geographical range should decelerate and be a time-constant, step-by-step process that proceeds along geographically favourable routes, such as river valleys and coasts (e.g. Birks, 1989). But instead it seems more likely that the species that the macrofossils originated from were dispersed more instantaneous, not much unlike the dispersal of beetles (Kullman, 2002). *Quercus* and *Corylus* are species whose seeds are dispersed generally by animals, such as birds carrying the seeds over long distances (Kullman, 1998a). *Tilia* and *Ulmus*, on the other hand, are generally considered to be wind-dispersed and unable to disperse longer distances. But since the seeds are palatable to birds it is very likely that also these species can be bird-dispersed (Wilkinson, 1997). Higgins *et al.* (2003) emphasize that the apparent morphological dispersal mechanism may not be the vector for long distance transport. However, the resulting long-distance dispersion for e.g. *Tilia* and *Ulmus* is more occasional. Salisbury (1932, quoted in Kullman, 1998a) emphasizes this occasional long-distance dispersal and implies that the thermophilous species concerned here can grow everywhere where the environmental conditions allow. So during times when more favourable climate coincided with occasional bird-dispersion of *Quercus*, *Tilia*, *Ulmus* and *Corylus*, the species established in the Storulvån valley.

Kullman (1998b) confirms that thermophilous trees were present in the Storulvån valley during the Holocene thermal optimum around 9000 cal yr BP. After this warm period the temperatures declined (Bergman *et al.*, 2005) and the thermophilous trees probably disappeared from the area. Around 8000 cal yr BP the climate became warmer again (Bjune *et al.*, 2005) and a peak in the mean July temperature was reached c. 7500-5000 cal yr BP (Hammarlund *et al.*, 2004), corresponding to period 2 in the present diagram, where all four thermophilous species occur.

During the last century the tree-limit in the southern Scandes has been monitored. Due to 19th century warming the tree-limit has ascended 200 m (Kullman & Kjällgren, 2006). Even in the last two decades the climate has changed into warmer and wetter to such a degree that the flora in the mountains is shifting. Frequent monitoring of an area in the southern Scandes, in which the present study site is situated, has revealed multiple, approximately 10-year-old saplings of thermophilous tree species, such as *Quercus robur*, *Ulmus glabra* and *Acer platanoides* (Kullman, 2008). All high-elevational locations are in south- or south-west-facing slopes. Kullman (2008) concluded from this study that only 10-15 years of climatic warming could enable thermophilous species establishing in the mountainous areas considered here. From this it can be concluded that short periods of warming can allow for thermophilous tree species to germinate and grow in the southern Scandes.

Conclusions

It has been confirmed by Kullman (1998a) that *Quercus*, *Ulmus*, and *Corylus* have been present in the Storulvån valley during the early Holocene. Pollen records from the same time period support the conclusion with recordings of *Quercus*, *Tilia*, *Ulmus* and *Corylus* (Bergman, 2005, Segerström and von Stedingk, 2003). The present results suggest that during the time of cooling that followed the summer thermal optimum at 9400 cal BP (Kullman & Kjällgren, 2000) the thermophilous tree species disappeared from the valley. During a warmer period between 7500 and 5000 cal BP *Quercus*, *Tilia*, *Corylus* and *Ulmus* were probably able to establish in the valley due to periods of favourable climate although they never seem to gain any importance, since this location most likely still was at the northern range of their distribution. The recent finds of thermophilous saplings in the area (Kullman, 2008) confirm that these species occasionally can grow at this latitude under good climatic conditions.

When comparing the present results with the pollen analysis from the *Ulmus* stand on Mt Totthummeln (von Stedingk *et al.*, 2006) it is suggested that there have been no large stands of *Ulmus* or other thermophilous trees on the southern slope in Storulvån. Rather there have instead been some individuals colonizing sheltered locations where the local climate allowed germination and growth. Many different factors must have concurred in order for a single tree to grow large enough to produce pollen; first of all the seed had to be transported into the valley.

When performing paleoecological studies on species outside or on the margins of their geographical range it has to be kept in mind that their pollen productivity is likely to be reduced, if not impaired. Therefore, to interpret defined lowest limits for pollen percentages unambiguously as local presence is hazardous. Such values must be regarded with great care; also low percentages can be a sign of local occurrence. Still, occasional records of pollen in a single pollen diagram can be hard to interpret in terms of local presence of a species, but by using a multi-site approach deviant recording patterns can be detected and conclusions concerning local presence can be drawn.

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