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Edvardsson, Johannes

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PO Box 117
221 00 Lund
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Johannes Edvardsson

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Abstract

Dendrochronological analysis was applied to subfossil remains of Scots pine (*Pinus sylvestris* L.) buried in South Swedish peat deposits. By cross-dating Swedish bog-pine ring-width (RW) chronologies with corresponding material from North-west Germany, three Swedish RW chronologies were assigned absolute ages and yielded continuous, dated chronologies over the periods 5284-3728 BC and 2668-1108 BC. The obtained cross-match between RW chronologies from regions separated by 500-700 km is remarkably strong, which indicates that large-scale climate dynamics had a significant impact on bog-tree growth variability during the Holocene Thermal Maximum (HTM), a relatively warm and dry period generating favourable growth conditions on peatlands over large parts of North-west Europe. Nine additional RW chronologies, each about 200 years in length, were developed from pine, oak (*Quercus robur* L.) and alder (*Alnus glutinosa* L.). Most of these RW chronologies were dated by radiocarbon (^{14}C). An approach combining bog-tree RW, replication and mean-age data, with peat stratigraphic records was explored to provide information about local hydrology, depositional history and peatland development. Registration of growth position of individual trees allowed assessment of the spatial dynamics of tree populations in response to hydrological changes and peatland development. Major bog-tree establishment and degeneration phases reflect changes in bog-surface wetness, often in response to climate-controlled groundwater fluctuations. Tree establishment phases coincide with stratigraphic layers of increased peat humification locally, and periods of increasing temperatures and widespread lake-level lowering regionally in southern Sweden. When conditions become more humid at the end of the HTM, increased lateral peatland expansion was recorded. This process could be studied in detail based on trees buried in the marginal zone of a peatland. An independent test of the hypothesis that bog-tree growth variability is controlled by effective moisture was performed by comparing RW data with tree-ring carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotope records. Variations in the isotopic records confirm that growth depressions coincided with moister atmospheric conditions and reveal a lag of about three years in the growth response with respect to the isotopic signals, likely due to slow hydrologic response in the peatlands. This thesis demonstrates the usefulness of the South Swedish subfossil bog-tree material as a climate proxy with particular potential for decadal- to centennial-scale reconstructions of humidity fluctuations. It also demonstrates that subfossil bog-trees in combination with peat stratigraphy can be used for detailed reconstructions of peatland development and local groundwater variability, which are also highly relevant in a long-term regional palaeoclimatic context.

Key words: Dendrochronology, Subfossil trees, Raised bog, Palaeohydrology, Palaeoclimatology, Peatland development, Scots pine, The Holocene.

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Johannes Edvardsson

Department of Geology, Quaternary Sciences, Lund University,
Sölvegatan 12, SE-223 62 Lund, Sweden

This thesis is based on four papers listed below as Appendices I-IV. Paper I has been published in Dendrochronologia. Paper II has been published in Journal of Quaternary Science. Papers III and IV are unpublished manuscripts.

Appendix I: Edvardsson, J., Leuschner, H.H., Linderson, H., Linderholm, H.W., Hammarlund, D. 2012. South Swedish bog pines as indicators of Mid-Holocene climate variability. Dendrochronologia 30, 93–103.

Appendix II: Edvardsson, J., Linderson, H., Rundgren, M., Hammarlund, D. 2012. Holocene peatland development and hydrological variability inferred from bog-pine dendrochronology and peat stratigraphy – a case study from southern Sweden. Journal of Quaternary Science 27, 553–563.

Appendix III: Edvardsson, J., Poska, A., Van der Putten, N., Rundgren, M., Linderson, H., Hammarlund, D. Late-Holocene expansion of a South Swedish peatland and its impact on marginal ecosystems – evidence from dendrochronology, peat stratigraphy and palaeobotanical data. Manuscript.

Appendix IV: Edvardsson, J., Edwards, T.W.D., Linderson, H., Hammarlund, D. Climate forcing of growth depression in subfossil South Swedish bog pines inferred from stable isotopes. Manuscript

Contents

1. Introduction

1.1 Importance of bog-tree dendrochronology and peat-stratigraphic studies

The impact of current and future climate change on ecosystems and society is a key issue requiring advanced knowledge about the forcing mechanisms that control climate variability. In recent decades, improved dating methods and palaeoclimatic methodology have enabled more accurate and detailed climate and ecosystem reconstructions, and have thus increased our understanding of climate dynamics during the last interglacial, referred to as the Holocene (Mayewski *et al.,* 2004; Wanner *et al.,* 2008). Despite this, there are still very few detailed and reliable records of hydrological variations in the past. This is mainly due to the absence of direct precipitation proxies applicable to natural climate archives. Peatlands, especially raised bogs, generate valuable long-term archives reflecting climatic and hydrological changes of the past (Aaby, 1976; Barber, 1981; Charman *et al.,* 2009). Peatlands are globally important landscape elements covering approximately 4 million km^2 across Eurasia and North America (MacDonald *et al.,* 2006), and net carbon sinks with a considerable impact on atmospheric carbon dioxide (CO_2) and methane (CH_4) concentrations. Consequently, peatlands are of significant importance for the global carbon (C) budget as stored carbon is available for exchange with the atmosphere (Korhola, 1994; MacDonald *et al.,* 2006; Yu *et al.,* 2010; Limpens *et al.*, 2011). It is therefore essential to improve our understanding of interactions between internal and external factors affecting peatland development, hydrology and carbon budget to advance our knowledge about climate variability during the Holocene.

Dendrochronological analysis of trees found in peatlands can yield valuable knowledge about the duration, magnitude and frequency of hydrological events of the past (Hupp, 1988; Schweingruber, 1996; Leuschner *et al.,* 2002). In areas where hydrology is the main factor controlling annual growth, trees can respond with abrupt growth variations, changing wood density, formation of scars or new roots if the hydrological conditions change rapidly (Schweingruber, 1996; Eckstein *et al.,* 2009). Trees growing in areas affected by hydrological changes can therefore provide valuable information about ecological conditions, for instance, groundwater fluctuations, channel migration patterns, growth rate of organic soils and effects of drainage or damming. Growth dynamics of trees growing on bogs usually differ from those on solid ground by being highly dependent on the depth and variability of the water table beneath the root system (Boggie, 1972; Frelechoux *et al.,* 2000; Vitas and Erlickyte, 2007; Eckstein *et al.,* 2009). High groundwater tables generate unfavourable growth conditions as a result of several physical, chemical, and biological processes, of which perhaps the most important is the reduced availability of nutrients in the saturated zone (Boggie, 1972; Mannerkoski, 1991; Vitas and Erlickyte, 2007). Groundwater lowering in peatlands typically results in enchanted tree growth because of increased availability of nutrients in the unsaturated zone (Penttila, 1991), but also invasion of trees due to improved growth conditions on drier peat surfaces (Frelechoux *et al.,* 2000; Leuschner *et al.,* 2002; Eckstein *et al.,* 2009). Consequently, moister conditions would lead to groundwater table rises towards the bog surface, which results in an even shallower unsaturated zone (Schouwenaars, 1988; Hunt *et al.,* 1999). In most cases a thinning of the unsaturated zone would cause stress and growth reductions in bog trees due to lack of oxygen for respiration and formation of toxic compounds (Boggie, 1972; Schouwenaars, 1988; Linderholm, 2001). Studies of subfossil bog trees from Germany show that tree establishment phases often took place in parallel at different peat bogs, indicating that regional climate variability controlled bog-surface wetness and therefore bog-tree population dynamics (Leuschner *et al.,* 2002; Eckstein *et al.,* 2009). Several studies have found a strong link between groundwater variability and bog-tree population dynamics (Leuschner *et al.,* 2002; Sass-Klaassen and Hanraets, 2006; Eckstein *et al.,* 2009). It can therefore be assumed that bog tree ring-width (RW) chronologies provide information about hydrological changes associated with regional climate change and variability on an annual to decadal scale.

During the last hundred years, extensive peat-stratigraphic studies have been conducted in southern Sweden (von Post and Granlund, 1926).

Land use and exploitation are widespread in the region, and since the beginning of last century peat has been used as an energy resource and to improve planting soils, as a result of which large quantities of subfossil wood have been exposed. Due to the extensive peat-stratigraphic studies conducted and the availability of easily accessible subfossil trees, southern Sweden was selected as study area. Initial studies of subfossil bog trees, performed, for example, by Pilcher *et al.* (1977, 1984) and Leuschner *et al.* (1987, 1992), were primarily based on oak (*Quercus robur* L.). However, Scots pine (*Pinus sylvestris* L.) is the most commonly found tree species on peat bogs in southern Sweden (Rydin *et al.,* 1999). Pine usually invades open and exposed sites rapidly after disturbances such as drainage, deforestation, fire or insect invasion (Zackrisson, 1977; Frelechoux *et al.,* 2000; Eckstein *et al.,* 2010). Pine has also frequently occurred at Swedish bogs during the Holocene and subfossil remains are often found in bogs used for peat mining. Several initial studies in north-western Europe show that there is great potential in the subfossil bog-pine material, in terms of climatic, hydrological, palaeoecological and archaeological surveys (e.g. Leuschner *et al.,* 2007; Eckstein *et al.,* 2009, 2010, 2011; Pilcher *et al.,* 1995; Turney *et al.,* 2006, Lageard *et al.,* 2000; Moir *et al.,* 2010; Gunnarson, 1999, 2008; Appendices I–IV).

The ultimate aims of this PhD project were: (1) to develop new bog-tree chronologies from southern Sweden and to investigate their potential for palaeoclimatic and palaeohydrological interpretations; (2) to provide detailed reconstructions of peatland development and hydrological variability, using an approach combining dendrochronological analysis of subfossil bog trees and peat-stratigraphic data. The reconstructions of peatland development and past hydrological variability will provide useful knowledge to other research areas where topics such as the role of peatlands in the global carbon cycle and Holocene climate variability are investigated.

1.2 Historical overview

Due to anaerobic conditions, the preservation potential in peatlands is exceptional, and in combination with an environment sensitive to climate change this makes peatlands excellent palaeoclimatic and palaeobotanical archives. Since the early twentieth century, palaeobotanic and climatic research based on plant macrofossils, pollen grains and variations in degree of peat decomposition has been performed in the Nordic countries (Birks and Seppä, 2010). However, it was often horizons of tree trunks and stumps in the peat-stratigraphic sequences that initially caught many researchers attention (Birks and Seppä, 2010; Nielsen and Helama, 2012). These tree horizons clearly represent periods of changed environmental conditions, and back in 1829 Heinrich Dau published a paper describing layers of pine trunks and other trees in Danish peat deposits (Birks and Seppä, 2010). These pine horizons were mysterious and gained much public attention, so the Royal Danish Academy of Sciences offered a prize for solving the enigma of why pine once became established on numerous Danish peat bogs before vanishing (Birks and Seppä, 2010; Nielsen and Helama, 2012). In 1841 Johannes Japetus Smith Steenstrup (1813–1897) published a peat-stratigraphical study in which tree horizons were classified on the basis of species composition; they were believed to reflect changes in temperature and humidity during the postglacial period (Birks and Seppä, 2010). The following year, Steenstrup's theory was awarded the prize, and he can actually be regarded as one of the fathers of Holocene palaeoecology and climate research because of his findings (Birks and Seppä, 2010; Nielsen and Helama, 2012). Christian Theodor Vaupell (1821–1862) was another Danish pioneer with a special interest in the development of bog forests and vegetative reproduction, and he studied buried bog trees and their relation to different natural processes (Nielsen and Helama, 2012).

In Norway, Alex Blytt (1843–1898) investigated layers of wood and changes in peat decomposition. The basic idea of Blytt (1876) was that conditions of plant growth and humification at the bog surface were controlled by climate. In Sweden, Rutger Sernander (1866–1944) carried on the methods introduced by Blytt, analysing peat-stratigraphical changes and tree remains on lake bottoms (Birks and Seppä, 2010). Sernander (1890, 1893) associated dark peat layers containing wood material with periods of continental climate, whereas less humified layers were connected to humid periods. Based on his own and Blytt's research, Sernander developed a schematic model for postglacial climate

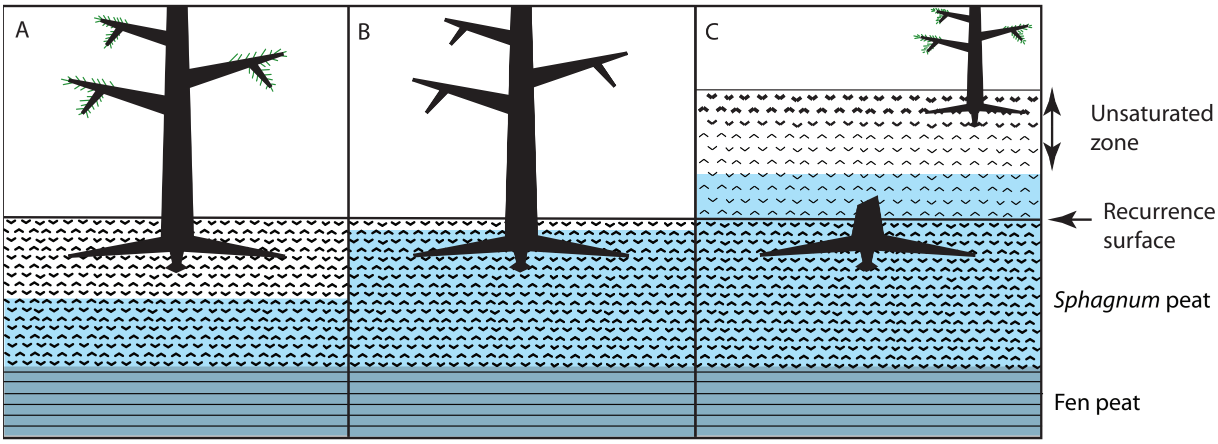

Figure 1.(A) When the groundwater level in a raised bog is lowered trees can get established on the bog surface. Relatively dry conditions also generate a higher degree of peat decomposition as more oxygen (O) can be involved in the degradation process. (B) A groundwater elevation can cause bog-tree growth depressions and die-off phases when the volume of the unsaturated zone decreases. (C) A groundwater elevation also increases the growth rate of the peat and wet-shifts can sometimes be seen as recurrence surfaces in peat-stratigraphic sequences. Due to the anaerobic conditions in the peat bogs, stumps and trunks can be preserved for thousands of years in the peat.

change, known as the Blytt-Sernander scheme, which has been used by many generations of Quaternary geologists and palaeobotanists (Birks and Seppä, 2010). During the early twentieth century palaeoclimatological research was improved significantly when pollen analysis was introduced by Lennart von Post (1884–1951), and changes in species composition detected in the new palaeorecords were assumed to reflect climate variability (von Post, 1924, 1930). Systematic surveys of peat deposits were carried out by the Geological Survey of Sweden, which contributed to detailed knowledge of peat distribution and properties over large parts of Sweden (von Post and Granlund 1926). Granlund (1932) showed peat-stratigraphical shifts, referred to as recurrence surfaces (Fig. 1), and demonstrated at least five abrupt changes assumed to be synchronous with colder and wetter conditions during the Holocene. Recurrence surfaces can be seen as sharp boundaries from dark peat with a high degree of humification to less humified peat formed when bog-surface conditions rapidly became wetter (Granlund, 1932; Borgmark and Wastegård, 2008; Rundgren, 2008). In studies by e.g. Aaby (1976) and Barber (1981) they were able to link peat-stratigraphical shifts to climate changes. Barber (1981) showed that peat stratigraphy could be used to reconstruct past climate variability and that the changes did not appear to be cyclic. However, climate reconstructions based on peat stratigraphy most often show variations in bog-surface wetness (BSW), a parameter closely related to variations in effective precipitation (precipitation minus evaporation), described by e.g. Charman *et al.* (2006, 2009). Over the last few decades BSW records from ombrotropic peatlands have been common in palaeoclimatic literature (e.g. Langdon and Barber, 2005; Mauquoy *et al.,* 2008). These climate reconstructions are commonly based upon peat humification, pollen data, plant macrofossils and testate amoebae (Swindles *et al.,* 2012). BSW in north-west Europe is most likely controlled by precipitation reinforced by temperature and it might therefore be a mixed temperature and precipitation signal in the data (Charman *et al.,* 2004, 2009).

Although horizons with wood material in peat deposits were discovered over a century ago, and their fundamental characteristics as indicators of changes in BSW at an early stage were understood, it was not until the 1970s and 1980s that the material began to be analysed in more detail (e.g. Pilcher *et al.,* 1977, 1984; Leuschner *et al.,* 1987, 1992). Since the establishment of dendrochronology (Douglass, 1921, 1941), considerable improvements of time series from various tree species have become possible. Initially, the time series were used for dating of archaeological materials. However, annual-growth rings from trees have proved to be a valuable source in palaeoclimatic research as trees, especially those growing close to their limit of distribution, normally produce growth rings providing climate information of annual resolution (Fritts, 1976; Schweingruber, 1988; Cook and Kairiukstis, 1990). Over the last couple of decades RW chronologies, density records, and stable isotope records developed from tree rings have been a valuable palaeoclimatic source and has resulted in significant results regarding climate reconstructions over the last centuries to millennia (e.g. Briffa *et al.,* 1990; Esper *et al.,* 2002; IPPC, 2007). Depending on what limits the tree growth, the chronologies developed from tree rings can be used as proxy data for e.g. temperature, precipitation or hydrology. Most often temperature is the main growth-limiting factor at high latitude or altitude, whereas precipitation limits growth in dry regions (Fritts, 1976; Schweingruber, 1996). Apart from being highly valuable for absolute dating and climate reconstructions, tree-ring chronologies have become important tools for the development of the radiocarbon (^{14}C) calibration curve, as annual growth rings are excellent archives of atmospheric radiocarbon concentrations (Becker, 1993; Friedrich *et al.,* 2004; Kromer, 2009).

Initially, dendrochronological studies of subfossil bog trees focused on oak trees, and multi-millennial chronologies have been developed in e.g. Germany (Leuschner *et al.,* 1987, 1992, 2002) and Ireland (Pilcher *et al.,* 1977, 1984; Baillie and Brown, 1988). It was expected that the trees growing in very moist conditions would mainly be affected by local hydrological conditions and not regional climate. However, Leuschner *et al.* (1987; 2002) used RW chronologies, replication and mean-age records from bog oaks to show that water-level fluctuations were the major factor affecting annual growth and tree establishment on bogs, and that these changes were synchronous between different peat bogs. Relatively dry bog-surface conditions enabled bog-tree establishment (Fig. 1) and the annual growth of the trees indicated water-table fluctuations in the bogs after tree establishment. When the water table was lowered the annual tree increment increased, and when the water level rose the growth was depressed. Over the last few decades major investigations of subfossil bog pines have been carried out in e.g. north-western Germany (Leuschner *et al.,* 2007; Eckstein *et al.,* 2009, 2010, 2011), Ireland (Pilcher *et al.,* 1995; Turney *et al.,* 2006), Great Britain (Lageard *et al.,* 1995, 2000; Moir *et al.,* 2010; Moir, 2012) and Lithuania (Pukienė, 1997). In Sweden, dendrochronological studies of subfossil trees have mainly been based on wood preserved in dry mountain regions or lake sediments (Briffa *et al.,* 1990; Grudd *et al.,* 2002; Gunnarson *et al.,* 2003). Systematic studies of trees buried in peat bogs in Sweden started relatively recently and are so far restricted to a few sites in central and northern Sweden (Gunnarson, 1999, 2008) and southern Sweden (Edvardsson, 2006, 2010, Edvardsson *et al.*, 2011, Appendices I–IV).

2. Study area and sites

2.1 Study area and present-day conditions

The study sites are located in upland areas in the provinces of Skåne and Småland in southern Sweden (Fig. 2A). The distance between the southern and northernmost sites (Viss Mosse and Hällarydsmossen) is about 200 km. The region is dominated by crystalline bedrock types of gneiss and granitic composition, generally covered by sandy tills (Malmberg Persson, 2000). Since deglaciation of the area, which took place from south to north between 15,000 and 14,000 cal BP (years before AD 1950) (Lundquist and Wohlfarth, 2001), numerous lakes and peat bogs have been formed in topographic depressions. Mean annual temperature is 5–7 °C, mean annual precipitation varies from 500 to 1000 mm (350 to 500 mm per year during growth season), and the length of the tree-growth season varies from 180 to 240 days per year (Nilsson, 1990).

2.2 Site descriptions

The major part of the presented data in Appendices I to IV originates from three peat bogs: Viss Mosse, Hällarydsmossen and Åbuamossen (Fig. 2). Trees and peat sequences have also been sampled at other sites; so far these data have been used for comparisons, or have not been published yet.

Viss Mosse (55°51´N, 13°49´E) is a raised bog in central Skåne located approx. 173 m a.s.l. on the bedrock ridge of Linderödsåsen (Fig. 2D, 3A-B, E). The bog is about 2 km^2 and is one of the most southerly raised bogs in Sweden (Malmberg Persson, 2000). Due to extensive peat mining since the early twentieth century, removal of 2–4 m of *Sphagnum* peat has exposed numerous stumps and trunks of pine, alder and oak.

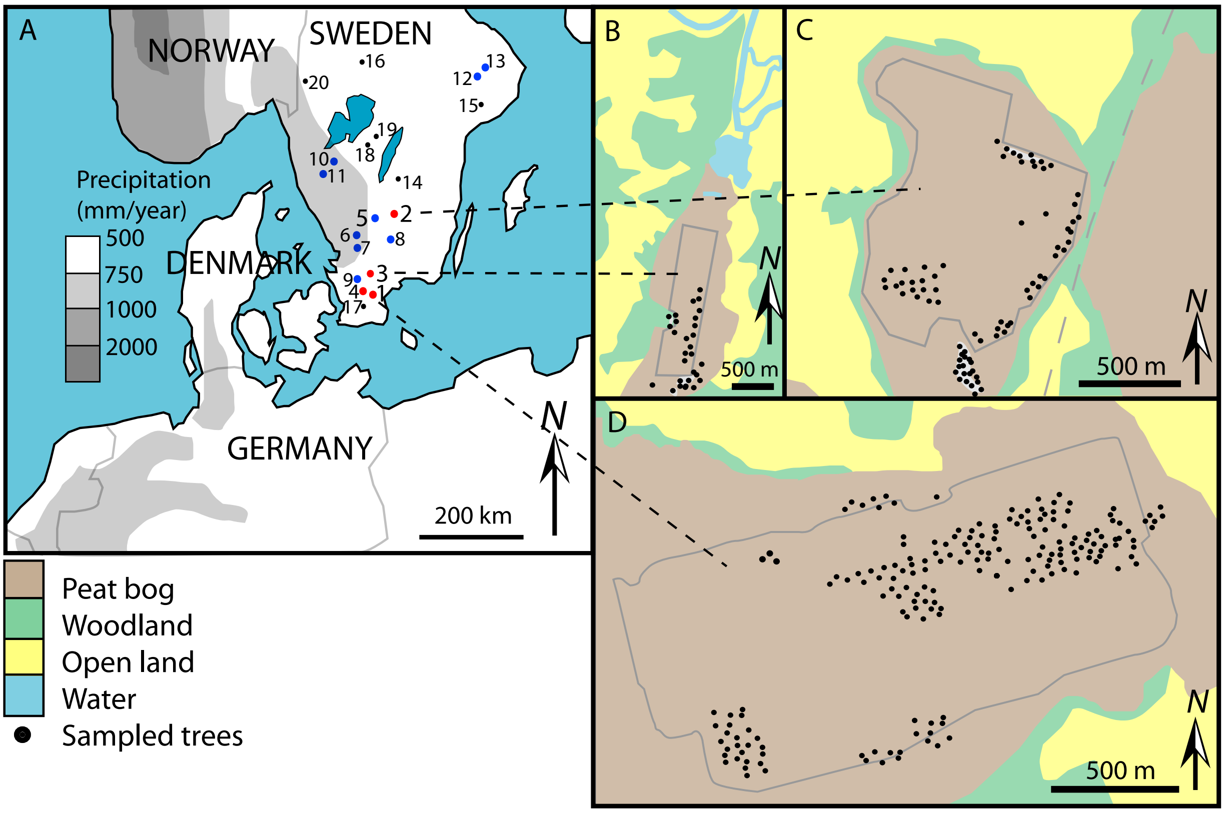

Figure 2. (A) The study area in southern Sweden and location of studied peat bogs and other locations discussed in the text. The red dots are peat bogs where subfossil trees have been collected: Viss Mosse (1), Hällarydsmossen (2), Åbuamossen (3) and Stass Mosse (4). The blue dots show locations where recent trees have been sampled: Store Mosse (5), Saxnäs Mosse (6), Hästhults Mosse (7) Buxabygds Mosse (8), Fäjemyr (9), Mycklemossen (10), Skogaryd (11), Norunda (12) and Skytorp (13). The black dots show other sites discussed: Anebymossen (14), Hanvedsmossen (15) and Bredmossen (16; Linderholm et al., 2002), Lake Bysjön (17; Digerfeldt, 1988), Lake Igelsjön (18; Hammarlund et al., 2003), Lake Flarken (19; Seppä et al., 2005), Kortlandamossen (20; Borgmark and Wastegård, 2008). (B) Åbuamossen, (C) Hällarydsmossen and (D) Viss Mosse. Locations of wood samples are shown by the black dots. The grey lines show present peat-mined areas.

Hällarydsmossen (57°20´N, 14°35´E) is located approx. 215 m a.s.l. in the central part of Småland (Fig. 2C, 3C–D). The area around the bog, which is roughly 2.5 km^2 in size, is dominated by coniferous forest in an undulating morphology with numerous lakes and bogs. Hällarydsmossen has been subjected to peat mining, and an estimated 4 m of *Sphagnum* peat has been removed from above the layer where the pine material was collected. The pine horizon is underlain by 1.7–3.7 m of organic deposits, consisting of 0.2–0.8 m of *Sphagnum* peat resting on more than 1.2 m of carr peat and gyttja.

Åbuamossen (56°19´N, 13°55´E) is a roughly 2.4 km^2 raised bog in north-east Skåne located approx. 75 m a.s.l. in an area with several lakes connected by the river Helge Å (Fig. 2B). Due to the river north of the bog, the catchment area of Åbuamossen is much larger than for Viss Mosse and Hällarydsmossen, both located in isolated basins. The pine material is located in *Sphagnum* peat overlying fen peat and gyttja.

Additional studies of subfossil trees have been made at Stass Mosse (55°54´N 13°45´E) in central Skåne, whereas recent bog pines have been sampled at Store Mosse (57°14´N, 13°55´E), Buxabygds Mosse (56°48´N, 14˚13´E), Saxnäs Mosse (56˚51´N, 13˚27´E), Hästhults Mosse (56°42´N, 13°29´E), Fäjemyr (56˚16´N, 13°33´E) and Mycklemossen (58°21´N, 12°10´E) (Fig. 2A).

3. Methods

3.1 Fieldwork

During fieldwork campaigns between 2006 and 2012 cross-sections (Fig. 4A) were collected with a chainsaw from a total of 574 trunks and stumps from subfossil trees from the peat bogs of Viss Mosse, Hällarydsmossen and Åbuamossen (Fig.

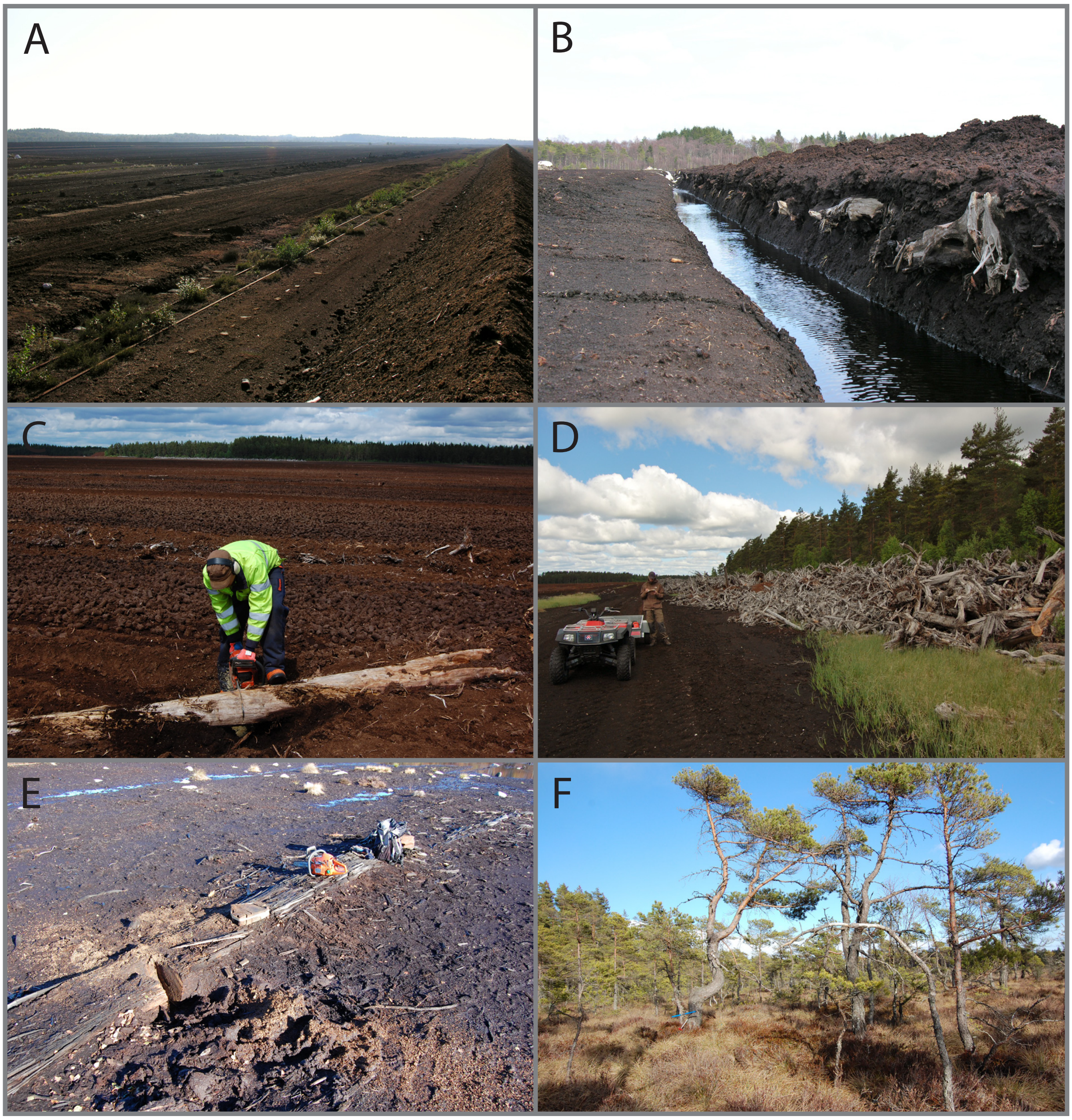

Figure 3. (A) Large amounts of subfossil bog trees can be found in peat bogs where extensive peat mining is in progress. Between 2 and 4 m of peat has been removed from the surface of the Viss Mosse bog, with the result that thousands of trees preserved in peat have been exposed. In total, 247 trees were sampled at Viss Mosse. (B) Stump horizon at Viss Mosse containing in situ pine trees. These trees were growing at the bog surface between 7200 and 6500 years ago. (C) Fieldwork at Hällarydsmossen, where 129 pine trees were sampled. The ring-width (RW) sequence from this specific tree covers the period between 3851 and 4038 BC (photo by R. Åkesson). (D) To enable continued peat mining tree trunks and stumps are moved to piles around the bogs. A total of 81 trunks were sampled from deposits around the Hällarydsmossen bog. (E) Oak tree sampled at Viss Mosse. The tree grew on a till hummock offering stable and relatively dry conditions before the bog expanded and buried the trunk about 3000 years ago. (F) Tree coring at Saxnäs Mosse. In total, 145 pine trees growing on thick peat deposits were sampled at six South Swedish raised bogs.

2B-D). Apart from these, 88 additional samples were collected from the peat bog Stass Mosse. The exact growth position of *in situ* trees was obtained with handheld GPS and marked on maps during fieldwork. The expression *in situ* is used in a broder sense an includes rooted tree stumps, but also trunks from fallen trees. Information about morphology, the presence of pith, bark, fire marks (Fig. 4B) or other damage and sampling distance from the roots was recorded for each sample. To improve our understanding of bog-tree growth dynamics, 145 recent bog pines were sampled at Store Mosse, Buxabyds Mosse, Hästhults Mosse, Saxnäs Mosse, Fäjemyr and Mycklemossen (Fig. 2A). These trees were sampled with an increment corer.

Peat cores were taken with a Russian peat sampler (5 and 7 cm in diameter and 1 m in length) at Viss Mosse, Hällarydsmossen, Stass Mosse, Store Mosse, Buxabygds Mosse, Hästhults Mosse and Saxnäs Mosse. The total thickness of the remaining organic layers, defined as the distance from the present-day bog surface to the mineral soil, was measured with a probe along transects or where most of the trees were found.

3.2 Development of RW chronologies

In order not to dry out the subfossil tree samples, they were stored at 4 °C after fieldwork. To avoid deformation of annual rings soft samples were frozen during surface preparation. The surfaces of the cross-sections were prepared by cutting several radii with razor blades, and chalk was applied to enhance the appearance of ring borders and cell structures. Ring-width (RW) series of individual radii were created based on measurement of annual rings with a precision of 0.01 mm, using a LINTAB measuring table connected to a stereomicroscope and a computer using the TSAP (Rinn, 1996) and CATRAS (Aniol, 1983) software. In order to identify wedging rings and possible measuring errors, at least two radii, separated by 90° or more if possible, were measured for each sample. Two statistical tests were applied to evaluate similarities between individual RW series; Coefficient of parallel run and *t*-value. Coefficient of parallel run, also referred to as Gleichlaeufigkeit, measures the year-to-year agreement between two series based on the sign of agreement (Eckstein and Bauch, 1969). The *t*-value (Baillie and Pilcher, 1973) compares the actual difference between two means in relation to the variation in the data. In dendrochronology, these statistical analyses are common when assessing the significance of correspondence between two RW series, a process generally referred to as cross-dating or cross-matching. First, the two or more radii from individual samples were cross-dated, and if matching, they were averaged into a RW series for each tree. Subsequently, the RW series from all individual trees were cross-dated against each other. In general, *t*-values that exceed 3.5 are quoted as significant (Wigley *et al.,* 1987), and all cross-matches between samples yielding *t*-values above 4 as well as significant coefficient of parallel run ($p<0.01$) were visually examined. The individual RW series for which cross-dating was satisfactorily established were then averaged into site records, also referred to as master chronologies.

In the next step, the cross-dating and measurement quality, as well as the strength of the master chronologies, were evaluated using the software COFECHA (Holmes, 1983), which is a helpful tool in order to detect possible measuring errors, missing rings and outliers. Segments with correlation values beneath the critical confidence level 0.3281 ($p<0.1$) in COFECHA were corrected or removed before all samples were cross-dated to form corrected site records (master chronologies).

Standardization, also referred to as detrending of RW data is a correction process that minimizes the influence of non-climatic RW variations and trends related to e.g. age, height within the stem and geometry (Fritts, 1976; Cook and Kairiukstis, 1990). During the standardization process non-climatic trends are removed from the measured RW series, which are then transformed into dimensionless RW indices (Fritts, 1976; Cook and Kairiukstis, 1990). These series were thereafter cross-dated into standardized RW chronologies. The analysed trees often showed growth trends with narrow rings during both juvenile and adolescent stages (Fig. 4F), and therefore various flexible methods were used for the standardization. The standardized data shown in Appendices I–IV are based either on a 67% flexible spline function or on the Friedman variable span smoother (Friedman, 1984) and mainly processed with the software ARSTAN_41d (Cook and Krusic, 2006). To highlight the low-frequency patterns of variability the RW chronologies have been smoothed either with a 10 to 30 year Gaussian-weighted filter or a 20-year low-pass filter spline. Further analyses of RW data were made using e.g. AutoSignal (AISN, 1999), TREND and v-show (Riemer, 1994).

To assess the reliability of the chronologies, i.e. how well RW series from individual trees agree with a theoretical population chronology, the expressed population signal (EPS) was calculated, mostly with a 30-year window and a 25-year overlap using the ARSTAN software. The EPS is dependent on the

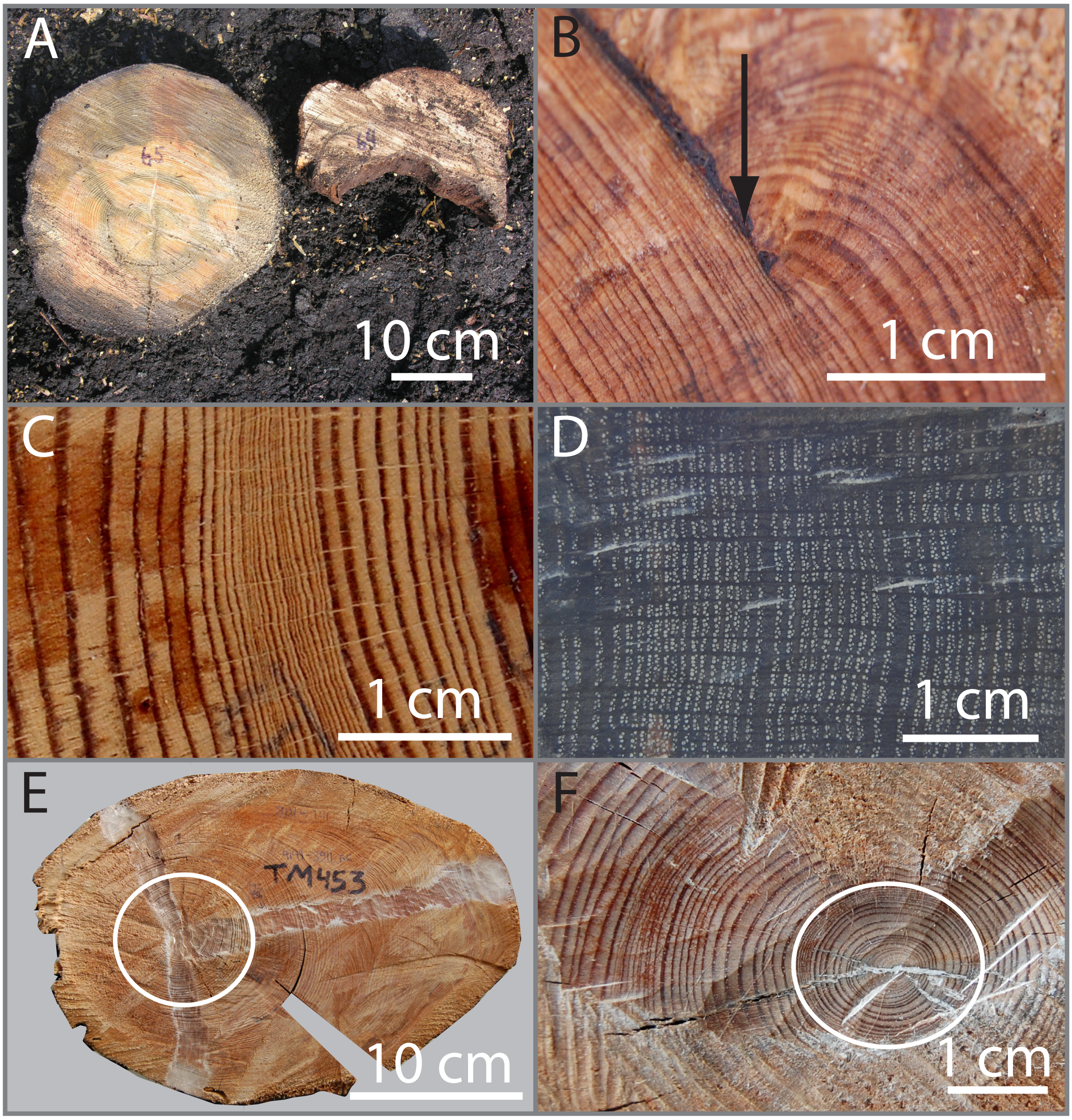

Figure 4. Cross-sections and annual growth rings from subfossil trees that exhibit different growth patterns and characteristics. (A) Two cross-sections from Scots pine (Pinus sylvestris L.*) sampled at Viss Mosse. The left sample contains a complete ring sequence from pith to bark corresponding to 5078–4970 BC. The right sample has been degraded after death. The growth rings correspond to the period 4872–4716 BC, but approximately 50–70 rings towards the centre and another 10–20 of the outermost rings are expected to be eroded away. (B) RW sequence from a pine tree found in the Hällarydsmossen bog. The fire scare, shown by the arrow, is absolutely dated to 4420 BC. (C) Abrupt growth depression visible in a pine tree from the Åbuamossen bog. The growth depression is probably resulted by a period of extremely wet bog-surface conditions between 1288 and 1270 BC. (D) RW sequence from a bog oak (Quercus robur* L.*). (E) Eccentric pine-stem cross-section characteristic for a bog trees growing on unstable soils. The innermost 70 annual rings are circular, whereas something happens about 4070 BC that generates more unstable conditions forcing the tree to form reaction wood. (F) About 30 narrow annual rings (inside the circle) around the pith, indicating unfavourable conditions during tree establishment.*

number of overlapping RW series and their mutual conformity. The limit at which the RW records were considered as reliable and well replicated was set to EPS ≥ 0.85 (Wigley *et al.*, 1984). Finally, cross-dating tests against absolutely and radiocarbon-dated RW chronologies were made to assign ages to the new chronologies. The RW chronologies were also dated by radiocarbon, either as an independent control of the absolutely dated chronologies or to give an age to undated chronologies.

3.3 Peat-stratigraphic studies

Peat sequences were retrieved from Viss Mosse, Hällarydsmossen, Stass Mosse, Store Mosse, Buxabyds Mosse, Hästhults Mosse and Saxnäs Mosse. The peat cores from Hällarydsmossen were only examined in the field, whereas cores from the other sites were analysed further in the laboratory. In order to prevent the peat samples from drying out and deforming, the cores were stored in plastic tubes at 4 °C between fieldwork and laboratory studies. Different stratigraphic units were identified from visible variations in the degree of humification, peat colour and species content. Most cores were sliced into 2–3 cm segments used for further analysis. To measure the content of organic material, loss on ignition (LOI) analysis was performed (Heiri *et al.,* 2001). Organic bulk density (OBD) was measured to improve and evaluate the initial visual classification of variations in peat humification, as well as the borders between different stratigraphic units.

3.4 Radiocarbon dating

Radiocarbon (^{14}C) was used to date wood samples and peat. The samples were dated using accelerator mass spectrometry (AMS) at the Radiocarbon Dating Laboratory, Lund University. Calibration and age modelling of radiocarbon dates were performed with the OxCal 4.1 software (Bronk Ramsey, 2001). *D_Sequence* analysis (Bronk Ramsey *et al.,* 2001) was used to improve the accuracy and to tie different radiocarbon dates from wood samples to narrower intervals on the IntCal09 calibration dataset (Reimer *et al.,* 2009). The method is based on the non-linear relationship between radiocarbon and calendar ages. By fitting a sequence of radiocarbon dates, with known intervals between them, on the radiocarbon calibration curve it is possible to tie the radiocarbon dates and reduce the margin of error. The intervals are determined by counting the exact number of annual growth rings between each radiocarbon-dated wood sample. In a similar way, but with depth intervals between samples instead of counted years, *P_Sequence* analysis (Bronk Ramsey, 2008) was used to develop stratigraphic age-depth models. The ages used for the dated samples are the calculated mean values (μ) from the *R_Date*, *D_Sequence* or *P_Sequence* probability curves, and the margins of error are the uncertainties at the 95.4% probability level.

3.5 Pollen and macrofossil analyses

Pollen samples were prepared and analysed using standard equipment and following methods described by Berglund and Ralska-Jasiewiczowa (1986). *Lycopodium* spores were added to calculate pollen concentration (Stockmarr, 1971). At least 1000 terrestrial pollen grains were counted at each sampled level. Pollen data were expressed as percentages of the total terrestrial pollen sum. Counts of spores, algae, charcoal and other microfossils were calculated as percentages of the total terrestrial pollen sum. Macrofossil were treated and analysed following methods described by Van der Putten *et al.* (2004). Pollen and macrofossil diagrams were constructed using the TILIA and TGView software (Grimm, 2007).

3.6 Stable isotope analysis

Wood samples were separated under magnification using a scalpel. Individual wood samples were finely ground in a mill, washed, and freeze-dried. Subsamples of freeze-dried whole-wood powder were loaded into tin cups and analysed for $^{13}C/^{12}C$ ratio on CO_2 gas in the University of Waterloo Environmental Isotope Laboratory. The remaining material was processed to isolate α-cellulose by sequential elimination of non-cellulose components through solvent extraction, delignification, and alkaline hydrolysis (Sternberg, 1989). Separate subsamples of freeze-dried α-cellulose were loaded into tin cups for analysis of $^{13}C/^{12}C$ and $^{18}O/^{16}O$ ratios on CO_2 and CO gas, respectively. The isotopic results are expressed as conventional $\delta^{13}C$ and $\delta^{18}O$ values, representing deviation in permil (‰) from the VPDB and VSMOW standards.

3.7 Wavelet and spectral analyses

To assess possible periodicities in the RW data, spectral analysis was performed on chronologies from each study site, using a range of different spectral analysis models. Wavelet analysis was also performed to visualize the temporal stability of the detected cycles over the time-span of each chronology. The Sysat software package AutoSignal (AISN, 1999) was used for both spectral and wavelet analyses. Further wavelet analyses were made in order to assess whether detected cycles occurred temporarily or remained stable over time using software provided by the University of Colorado (Torrence and Compo, 1998).

4. Summary of papers

4.1 Appendix I

Edvardsson, J., Leuschner, H.H., Linderson, H., Linderholm, H.W., Hammarlund, D. 2012. South Swedish bog pines as indicators of Mid-Holocene climate variability. Dendrochronologia 30, 93–103.

Subfossil Scots pine (*Pinus sylvestris* L.) from two raised bogs in southern Sweden, Hällarydsmossen and Viss Mosse, initially yielded two new floating ring-width (RW) records covering 1112 and 646 years respectively. By cross-dating with bog-pine chronologies from the Lower Saxony area in Germany, the south Swedish records were assigned absolute ages. The two dated chronologies could thereafter be linked to a 1492-year continuous chronology spanning the period 5219–3728 BC.

The cross-match between the RW chronologies from regions in southern Sweden and north-west Germany, separated by 500–700 km, is remarkably strong and the correlation both positive and significant ($p<0.01$). This indicates that large-scale climate dynamics had a significant impact on the annual growth of bog pines during the Holocene Thermal Maximum (HTM), a period characterized by relatively warm and dry conditions (Seppä *et al.,* 2005; Renssen *et al.,* 2009). The climatic conditions during the HTM are believed to have generated relatively dry bog-surface conditions which should have favoured tree growth and facilitated the establishment of new bog trees. As a result of this, bog-pine distribution reached a maximum in both southern Sweden and north-western Germany during the HTM. Finally, a comparison was made between RW chronologies developed from recent pine trees from four south-central Swedish raised bogs: Store Mosse, Anebymossen, Hanvedsmossen and Bredmossen. The results show that more coherent climatic conditions controlled the growth of bog pines during previous warm periods such as HTM compared to current conditions.

A compilation of lake-level data by Yu and Harrison (1995) shows that a gradual northward expansion of summer drought across northern Europe was initiated about 7000 BC, and conditions were drier than at present, especially at c. 5000 BC (Hammarlund *et al.,* 2003; Seppä *et al.,* 2005). The regionally representative lake-level reconstruction by Digerfeldt (1988) supports the hypothesis that the establishment and spread of pine across the studied peat bogs in southern Sweden was a response to drier conditions and lowered groundwater levels. However, local population dynamics were also influenced by peatland ontogeny and competition, as shown by differences in replication and mean-tree age between the Swedish and German bog-pine populations. This study demonstrates the usefulness of the Swedish subfossil bog-pine material as a climate proxy, with particular potential for decadal- to centennial-scale reconstructions of humidity fluctuations. The study also shows that the growth conditions for peatland trees evidently have changed from the mid-Holocene to the present.

4.2 Appendix II

Edvardsson, J., Linderson, H., Rundgren, M., Hammarlund, D. 2012. Holocene peatland development and hydrological variability inferred from bog-pine dendrochronology and peat stratigraphy – a case study from southern Sweden. Journal of Quaternary Science 27, 553–563.

An approach combining dendrochronological and peat-stratigraphic data was explored for its potential to provide information on the local hydrological and depositional history at a peat bog, forming the basis for a regional palaeohydrological analysis. Dendrochronological analysis was applied to 155 subfossil pine trees buried in Viss Mosse, a raised bog in southern Sweden. A 726-year RW chronology was developed and assigned an absolute age of 5284–4559 BC (7233–6508 cal BP) through cross-dating with German bog-pine chronologies, whereas two short additional RW records were radiocarbon dated, yielding age spans of 8081–7896±88 cal BP (6132–5947±88 BC) and 7415–7186±74 cal BP (5466–5237±74 BC), respectively. The 4.4 m continuous stratigraphic sequence collected at Viss

Mosse shows seven distinct units and a normal hydroseral succession from a lake to a raised bog. Dry bulk density was measured in the *Sphagnum* peat and provides information on variations in peat humification, which can be used as a proxy for local bog-surface wetness, but also for regional climatic conditions if similar changes are observed in peat sequences at different sites (Aaby, 1976; van Geel, 1978; Barber *et al.,* 1994). The density of the peat increases at the stratigraphical level where the pine material was encountered, which clearly shows that surface conditions became drier during the period when the pine trees established the bog.

Registration of growth positions of individual *in situ* trees allowed assessment of the spatial dynamics of the pine population in response to hydrological changes and peatland ontogeny. An annually resolved tree-replication record reveals several establishment and degeneration phases, probably reflecting fluctuations in bog-surface wetness. A major establishment phase at 7200–6900 cal BP reflects the onset of a period of lowered groundwater level, also indicated by increased peat humification. This local development is consistent with regional temperature records based on pollen (Seppä *et al.,* 2005), lake-level reconstructions (Digerfeldt, 1988) and peat-stratigraphic data (Borgmark and Wastegård, 2008). In combination with the material from Hällarydsmossen (Appendix I), absolutely dated RW and replication data covering the period 5284–3728 BC were obtained for comparison to bog-oak replication data from Germany (Leuschner *et al.,* 2002) and Ireland (Turney *et al.,* 2006), as well as bog pines from north-western Germany (Eckstein *et al.,* 2011). The main bog-pine woodland phase in southern Sweden is largely coincident with the corresponding phase on peat bogs in north-western Germany, described by Eckstein *et al.* (2011). In addition, Turney *et al.* (2006) observed peaks in Irish bog and lake-edge tree populations at about 8000, 7300 and 6200 cal BP consistent with onsets of establishment phases in the Swedish replication record. The end of the studied Swedish woodland phase is synchronous with a wet shift seen as a recurrence surface in several Swedish raised bogs (Borgmark and Wastegård, 2008; Rundgren, 2008).

This study demonstrates that subfossil bog-pine populations provide annually to decadally resolved reconstructions of local groundwater variability, which are highly relevant in a long-term palaeoclimatic context. It also shows great potential for peatland development reconstructions by using subfossil bog-tree dendrochronology in combination with peat stratigraphy.

4.3 Appendix III

Edvardsson, J., Poska, A., Van der Putten, N., Rundgren, M., Linderson, H., Hammarlund, D. Late-Holocene expansion of a South Swedish peatland and its impact on marginal ecosystems – evidence from dendrochronology, peat stratigraphy and palaeobotanical data. Manuscript.

A multi-proxy approach combining dendrochronological analysis of subfossil trees, peat stratigraphic sequences and palaeobotanical data, was used to reconstruct long-term development of the peat bog Viss Mosse (Appendices I–II), and to assess the impacts of the well-known regional climate transition during the mid- to late Holocene on lateral peatland expansion. Samples from oak, ash (*Fraxinus excelsior* L.), alder (*Alnus glutinosa* L.) and pine found in different stratigraphic contexts were analysed, which in combination with pollen and macrofossil data gave detailed information about tree population dynamics. These data, in combination with radiocarbon-dated stratigraphic sequences gave detailed information about the development and expansion of the bog.

Trees growing at till hummocks in the central part of the bog were overgrown by peat between 8000 and 7500 cal BP, whereas pine trees growing at the bog surface during the HTM were overgrown by peat between 7000 and 5900 cal BP. The period between 5000 and 3000 cal BP shows a lateral bog expansion during which trees east and north of the bog become overgrown by peat. Radiocarbon dated *in situ* trunks show that alders were growing in a marginal fen between 4800 and 4200 cal BP before the expanding bog buried and preserved them. Several oaks, ashes and alders reflect a continuous bog expansion towards the north and east. These trees were buried in peat about 3300 cal BP. About 3200 cal BP, large oak trees were growing on a till hummock offering relatively dry and stable substrate. Trunks from these trees were preserved when the till hummock was overgrown by peat about 3000 years ago. None of the RW chronologies offers a continuous record over the entire studied period. However, by combining these results with peat accumulation records, pollen and macrofossil data a continuous reconstruction of the bog development during the mid- to late Holocene was possible.

Improved understanding of the lateral expansion of peatlands is important as newly formed fens are considerable sources of methane (CH_4) and peatlands affect the global carbon (C) budget (e.g. Korhola, 1994; MacDonald *et al.,* 2006; Yu *et al.,* 2010). The results show that *in situ* bog trees can successfully be used as a valuable complement to radiocarbon-dated basal peat samples during studies of lateral bog expansion. Apart from giving an approximate age of tree burial in different areas of a peatland, the RW data also provide information about periods of hydrological stress. Tree-ring records, in combination with peat stratigraphy, macrofossil and pollen data, enabled a detailed reconstruction of a phase of lateral expansion coincident with the transition during the mid- to late Holocene, often referred to as the Neoglacial transition (Nesje *et al.,* 1991; Jessen *et al.,* 2005; Wanner *et al.,* 2008). This transition is associated with moister conditions, which would accelerate peatland development and generate wetter bog-surface conditions unfavourable for bog-tree growth. Widespread peatland expansions in the Northern Hemisphere have previously been noted during the period 5000–3000 cal BP and dated using basal peat samples (e.g. Korholoa *et al.,* 2010). The advantage of using dated subfossil trees may be that events in different parts of the bog can be connected and water-level fluctuations prior the peatland expansion can be detected and dated.

4.4 Appendix IV

Edvardsson, J., Edwards, T.W.D., Linderson, H., Hammarlund, D. Climate forcing of growth depression in subfossil South Swedish bog pines inferred from stable isotopes. Manuscript.

It has not been possible to determine exactly to what extent different environmental factors such as temperature and moisture influence the annual growth of bog trees during the mid-Holocene. This is mainly due to the absence of natural analogous tree-covered peat bogs in north-west Europe today (Lindbladh *et al.,* in review). Therefore, independently developed and complementary proxy records are needed to improve our understanding of how various climate-related factors influenced the growth variability of these trees. Isotope dendrochronology was applied to test whether moisture was the main growth-limiting factor for trees on north-west European peatlands during the mid-Holocene, and to explore the temporal response information $\delta^{13}C$ and $\delta^{18}O$ isotope data can add to RW series from subfossil bog trees. Two tree-ring sequences associated with well-marked episodes of growth depression were analysed isotopically. The analysed trees originate from two raised bogs, Hällarydsmossen and Åbuamossen, having different hydrology and catchment size to probe the isotopic signals.

Under natural conditions, atmospheric moisture regime plays a dominant role in the carbon-isotope labelling of terrestrial plant matter, reflecting the need for plants to continuously balance the uptake of carbon dioxide from the air against the loss of water vapour through transpiration. Environmental factors such as temperature, soil moisture deficit, irradiance, and cloudiness also appear to influence discrimination against ^{13}C (Edwards *et al.,* 2000; Gagen *et al.,* 2011; Seftigen *et al.,* 2011), yet robust inverse correlations are commonly observed between variations in $\delta^{13}C$ and growth season relative humidity (RH) in the annual rings of trees in various climates (Lipp *et al.,* 1991; Sidorova *et al.,* 2008), as predicted by the model of Farquhar *et al.* (1989). Varying RH, similarly, exerts pronounced effects on $\delta^{18}O$ variability in tree-ring cellulose through the preservation of evaporative-enrichment signals from leaf waters, in addition to potential signals from changes in the $\delta^{18}O$ of water taken up by the tree (Roden *et al.,* 2000; Edwards *et al.,* 2008). Although other factors may have had some influence. The probability that atmospheric relative humidity is a common driver of variability in both oxygen- and carbon-isotope labelling of the bog pines at the two sites is supported by the existence of similar positive correlations between the cellulose $\delta^{13}C$ and $\delta^{18}O$ records for both Hällarydsmossen and Åbuamossen, as well as weaker, but still positive correlations between whole-wood $\delta^{13}C$ and cellulose $\delta^{18}O$. Hence, all three isotopic series appear to be proxy moisture records.

Table 1. Author contribution to Appendices I–IV

	Appendix I	**Appendix II**	**Appendix III**	**Appendix IV**
Fieldwork	J. Edvardsson H. Linderson	J .Edvardsson H. Linderson	J. Edvardsson D. Hammarlund M. Rundgren H. Linderson A. Poska N. Van der Putten	J. Edvardsson H. Linderson
Sample preparation (wood and peat)	J. Edvardsson	J. Edvardsson	J. Edvardsson M. Rundgren A. Poska N. Van der Putten	J. Edvardsson
Tree-ring analysis	J. Edvardsson	J. Edvardsson	J. Edvardsson	J. Edvardsson
Peat-stratigraphic analyses	J. Edvardsson	J. Edvardsson D. Hammarlund M. Rundgren	M. Rundgren D. Hammarlund J. Edvardsson	-
Pollen analyses	-	-	A. Poska	-
Macrofossil analyses	-	-	N. Van der Putten H. Linderson	-
Stable isotopes, sample prep.	-	-	-	T.W.D. Edwards J. Edvardsson D. Hammarlund
Data interpretation	J. Edvardsson H.H. Leuschner H. Linderson D. Hammarlund H.W. Linderholm	J. Edvardsson H. Linderson D. Hammarlund M. Rundgren	J. Edvardsson M. Rundgren D. Hammarlund A. Poska N. Van der Putten H. Linderson	J. Edvardsson T.W.D. Edwards D. Hammarlund
Manuscript preparation	J. Edvardsson D. Hammarlund H.W. Linderholm H.H. Leuschner H. Linderson	J. Edvardsson D. Hammarlund M. Rundgren H. Linderson	J. Edvardsson A. Poska D. Hammarlund M. Rundgren N. Van der Putten	J. Edvardsson T.W.D. Edwards D. Hammarlund

The comparison between growth variability, based on RW analysis, and tree-ring $\delta^{13}C$ and $\delta^{18}O$ records provides improved understanding of how hydrology and climate variability influenced tree growth at two bogs in southern Sweden during the mid- and late Holocene. The main conclusion is that variations in the isotopic records confirm that growth depressions at both sites coincided with moister atmospheric conditions, as indicated by lower whole-wood $\delta^{13}C$ and cellulose $\delta^{13}C$ and $\delta^{18}O$ values. The results also reveal a characteristic lag of about three years in the tree-growth response with respect to the isotopic signals at each site, likely due to a relatively slow rise in the local water table in response to wetter climate.

5. Synthesis of dendrochronological and peat-stratigraphic results from south Swedish peat bogs

During fieldwork campaigns between 2006 and 2012 cross-sections from 662 subfossil trees were sampled with a chainsaw at the peat bogs Viss Mosse, Hällarydsmossen, Åbuamossen and Stass Mosse. Of these 587 were pines, 40 oaks, 1 ash, and 34 alders. So far, 574 trees from the peat bogs Viss Mosse (247), Hällarydsmossen (129) and Åbuamossen (198) have been analysed. In total, 74% of these trees have been dated using dendrochronology or radiocarbon and form the framework of Appendices I–IV. In total, 251 of the analysed trees from Viss Mosse, Hällarydsmossen and Åbuamossen were

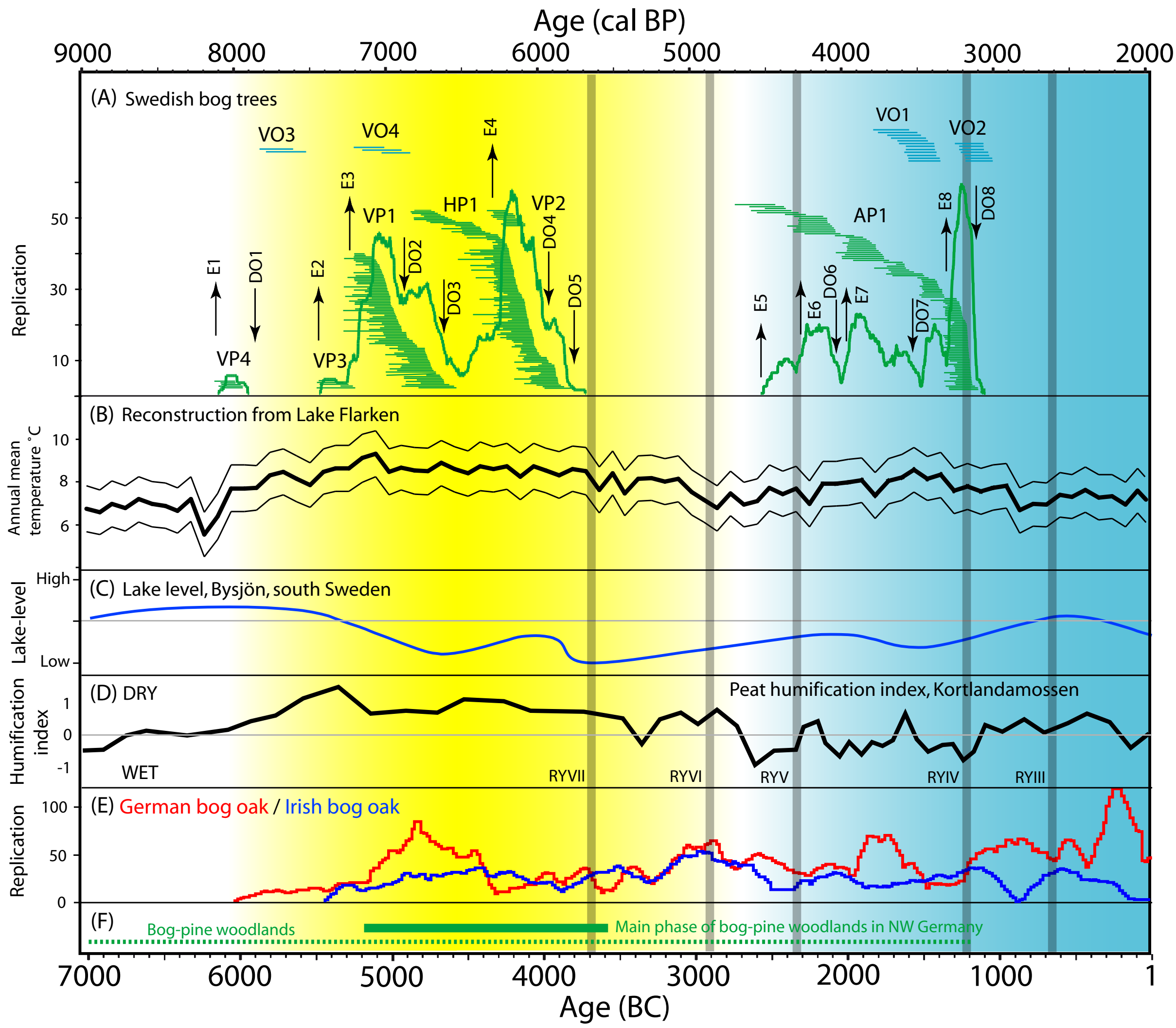

Figure 5. (A) Temporal distribution of South Swedish bog pine (green lines) and bog oak (blue lines), the chronology codes corespond to those in Table 2. The green curve show pine replication. Tree establishment phases (E1–E8) and die-off phases (DO1–8) are discussed in the text. (B) Temperatures as inferred from the pollen-based reconstruction from Lake Flarken (Seppä et al., 2005). (C) Lake-level reconstruction from Lake Bysjön, southern Sweden (Digerfeldt, 1988). (D) Humification index from the raised bog of Kortlandamossen (Borgmark and Wastegård, 2008). (E) Bog-oak replication in continental Europe (red curve) and Ireland (blue curve; Leuschner et al., 2002), and (F) the temporal distribution of bog-pine tree-ring records from Lower Saxony, Germany (Eckstein et al., 2011). The South Swedish and German bog-pine records cluster during a common period within the Holocene Thermal Maximum (HTM, highlighted in yellow), a period with generally low lake levels and high temperatures. The blue field shows the transition towards moister conditions, sometimes referred to as the Neoglacial transition (Nesje et al., 1991). Recurence surfaces (RYVII-III) are shown by the grey lines (Borgmark and Wastegård, 2008; Rundgren, 2008).

found *in situ*, whereas the remaining trees were moved from their primary growth position to enable continued peat mining. Dated RW chronologies spanning 5618 calendar years have been developed, but due to overlap between different chronologies the total number of years covered by annual RW data is about 3800 years and the absolutely dated chronologies cover 3117 years (Fig. 5).

5.1 Interpretations of the tree-ring data

Depending on whether the sampled trees have grown on the bog surface or on till hummocks in the bog, the RW and replication data might be interpreted differently. Most of the subfossil wood material consists of pine trees that have grown on the bog surface. Growth variations of these trees have been linked to hydrological changes that generated

Table 2. Information about the RW chronologies used in: Appendices I–IV, for comparison with the metrological data, and for spectral and wavelet analyses. The table shows abbreviated site name, chronology code, tree species, number of trees used in each chronology, length of the chronologies, the period each chronology covers, the period with EPS above 0.85, and series inter-correlation.

Site / Code	Species	Trees (n) / Length (years)	Total period / EPS>0.85	Series inter-correlation	Appendix (I–IV)
Subfossil material (BC ages)					
Åbua / ÅP1	Pine	159 / 1560	2668-1108 / 2480-1150	0.548	(I), IV
Hällaryd / HP1	Pine	117/ 1112	4839-3728 / 4730-3830	0.498	I
Viss / VP1	Pine	91 / 726	5284-4559 / 5220-4670	0.473	(I), II, (III)
Viss / VP2	Pine	10 / 308	4236-3929 / 4200-4060	0.411	III
Viss / VP3	Pine	4 / 221	5467-5247±74 * / -	0.370	II, (III)
Viss / VP4	Pine	7 / 186	6133-5948±88 * / 6070-6045	0.541	II, (III)
Viss / VO1	Oak	15 / 326	1725-1399 / 1700-1460	0.596	III
Viss / VO2	Oak	9 / 207	1282-1076±113 * / 1245-1105	0.555	III
Viss / VO3	Oak	2 / 242	5837-5596±66 * / -	0.528	III
Viss / VO4	Oak	3 / 292	5189-4898±112 */ -	0.469	III
Stass / SMP1	Pine	10 / 437	2266-1830±105 *	-	-
Recent material (AD ages)					
Store / SP1	Pine	31 / 159	1850-2008 / 1910-2008	0.519	I
Aneby / AnP1	Pine	21 / 118	1846-1996 / 1900-1996	0.539	I, **
Bred / BrP1	Pine	21 / 191	1789-1996 / 1840-1997	0.632	I, **
Hanved / HvP1	Pine	23 / 186	1800-1996 / 1830-1996	0.614	I, **
Buxa / BP1	Pine	21 / 227	1785-2011 / 1925-2011	0.530	-
Hästhult / HaP1	Pine	25 / 144	1868-2011 / 1960-2011	0.506	-
Saxnäs / SaP1	Pine	20 / 141	1871-2011 / 1915-2011	0.451	-
Myckle / MP1	Pine	7 / 109	1903-2011 / 1940-2011	0.514	-
Fäjemyr / FP1	Pine	11 / 140	1872-2011 / 1935-2011	0.502	-

*Uncertainty due to radiocarbon dating. **Previously published in Linderholm *et al.* (2002)

altered bog surface conditions. If many trees from different parts of a bog exhibit homogeneous growth patterns, it is an indication that growth conditions have been similar across the bog (Fig. 6). If RW records from a location can then be cross-dated with chronologies from other sites, as in Appendix I, this suggests that there is a large-scale climate signal in the data. As for the RW data, replication records can be connected to surface conditions on the bogs. Increasing tree replication, as found about 5200 BC (Establishment phase 3 (E3), Fig. 5A, E and F) suggest that conditions simultaneously became more favourable at bogs over a large region. At the same time one should keep in mind that the preservation conditions of the trees play an important role. For trees that have grown on the bog, roots and stumps are usually preserved in accumulating peat. However, the preservation of trees grown in relatively dry locations around a bog can be non-existent for millennia, and replication of these trees therefore indicates that preservation conditions have changed. This implies that the replication series for pine trees in Appendices I–II and oak trees in Appendix III should be interpreted differently. The pine trees were favoured by dry conditions during the HTM and therefore became numerous, while the oak trees were present but not preserved until the bog expanded due to moister climate conditions. Therefore, the population dynamics of bog-pines have in general served as a hydrological proxy related to climate-driven variations affecting bog-surface wetness and tree growth (Eckstein *et al.,* 2009; Appendices I–II). Establishment (E) and die-off phases (DO) (Figs. 5–9) in bog-tree populations can provide information on changes in bog-surface wetness, hydrology and climate on a decadal to centennial time scale. The bog-pine RW chronologies, on the other hand, show variations on an annual to decadal scale (Figs. 7–9). However, it is still difficult to separate temperature and precipitation signals as the effective precipitation also depends on temperature.

5.2 Palaeohydrological and climatic interpretations

Hydrology and groundwater levels within peat bogs reflect long-term changes between dry and moist climatic conditions. As water table fluctuations in bogs are largely controlled by climate, RW data, tree replication, mean-age records, germination

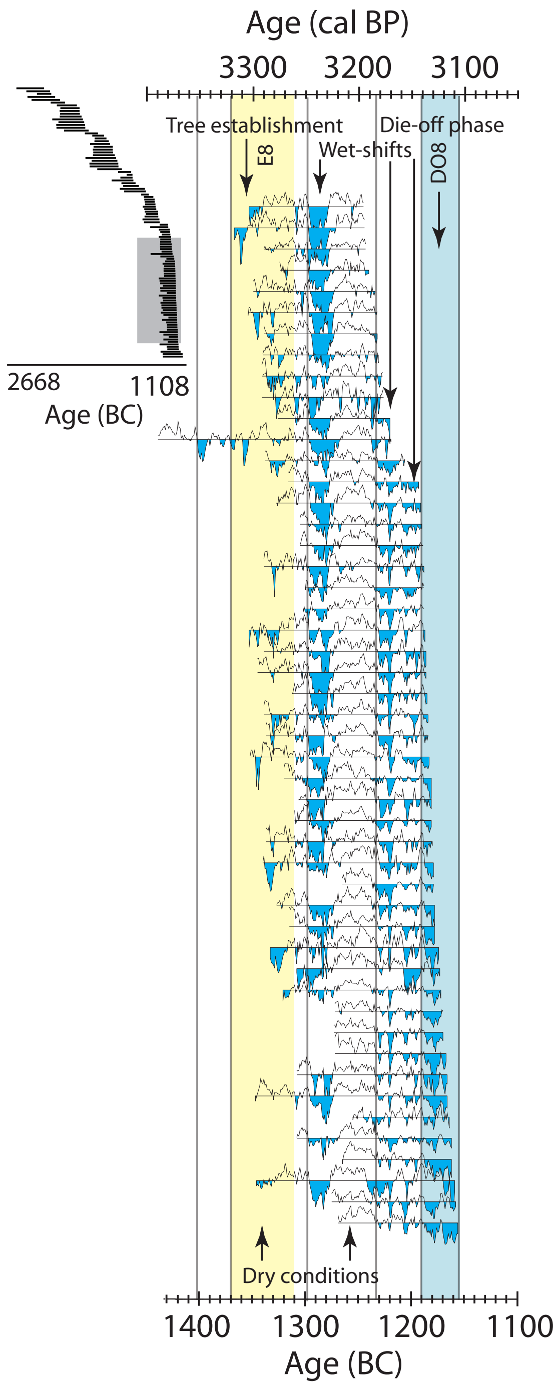

Figure 6. The RW chronology from Åbuamossen covers the period 2668–1108 BC. The figure shows RW variations for individual trees over the period 1430–1154 BC, corresponding to the grey box on the overview image to the left. The trees germinated within a relatively short period (about 60 years, E8 shown in yellow) and most trees died abruptly within a 35-year period (DO8, shown in blue). The establishment and die-off phase was interpreted as rapidly changing growth conditions on the bog due to initially dryer and finally wetter bog-surface conditions. The growth conditions changed on several occasions while the trees were growing, which can be interpreted as short-lasting hydrological events shown as wet-shifts or dry conditions.

and die-off phases etc. can be used for climate reconstructions (Leuschner *et al.,* 2002; Eckstein *et al.,* 2009; Appendices I–III). The dated south Swedish RW chronologies presented in Appendices I–IV covers large parts of the period between 8100 and 3000 cal BP (Fig. 5A), and can therefore be used for palaeohydrological and climate reconstructions over the mid- to late Holocene.

The oldest dated trees included in the south Swedish bog-tree material germinated at Viss Mosse around 8100 cal BP (Appendices II–III), which is immediately after the well-known 8200 cal BP cold event (e.g. Alley *et al.,* 1997; Mayewski *et al.,* 2004). A pollen-based temperature reconstruction from Lake Flarken, southern Sweden (Figs. 2 and 5), shows a prominent cooling during this cold event (Seppä *et al.,* 2005), and isotopic records from the nearby Lake Igelsjön (Fig. 2) indicate lowered temperature, increased effective moisture and elevated lake levels about 8200 cal BP (Hammarlund *et al.,* 2003, 2005). However, the succeeding millennia were dominated by significantly warmer and drier climatic conditions and are commonly referred to as the Holocene Thermal Maximum (HTM) (e.g. Seppä *et al.,* 2005; Renssen *et al.,* 2009). In general, HTM is associated with relatively high atmospheric temperatures and dry conditions, probably caused by orbitally forced high summer insolation (Snowball *et al.,* 2004; Renssen *et al.,* 2009). In Denmark, summer temperatures were approximately 3 °C warmer than present between 6700 and 5400 cal BP (Brown *et al.,* 2011) and pollen-based reconstructions by Seppä *et al.* (2005) and Antonsson and Seppä (2007) show similar patterns in southern Sweden. Sediment-based lake-level reconstructions from Lake Bysjön (Fig. 2) show relatively low lake levels in southern Sweden during the HTM (Digerfeldt, 1988; Fig. 5). In Scandinavia HTM is usually dated to somewhere between 8000 and 4500 cal BP (Snowball *et al.,* 2004; Seppä *et al.,* 2009).

The initial pine-tree establishment at Viss Mosse, during the onset of the HTM (Appendices II–III), was followed by a widespread bog-pine woodland phase at both Viss Mosse (Fig. 7) and Hällarydsmossen (Fig. 8) between c. 7200 and 5600 cal BP (Appendices I–II). This is largely coincident with the main woodland phase on peat bogs in north-west Germany, 7150–5550 cal BP,

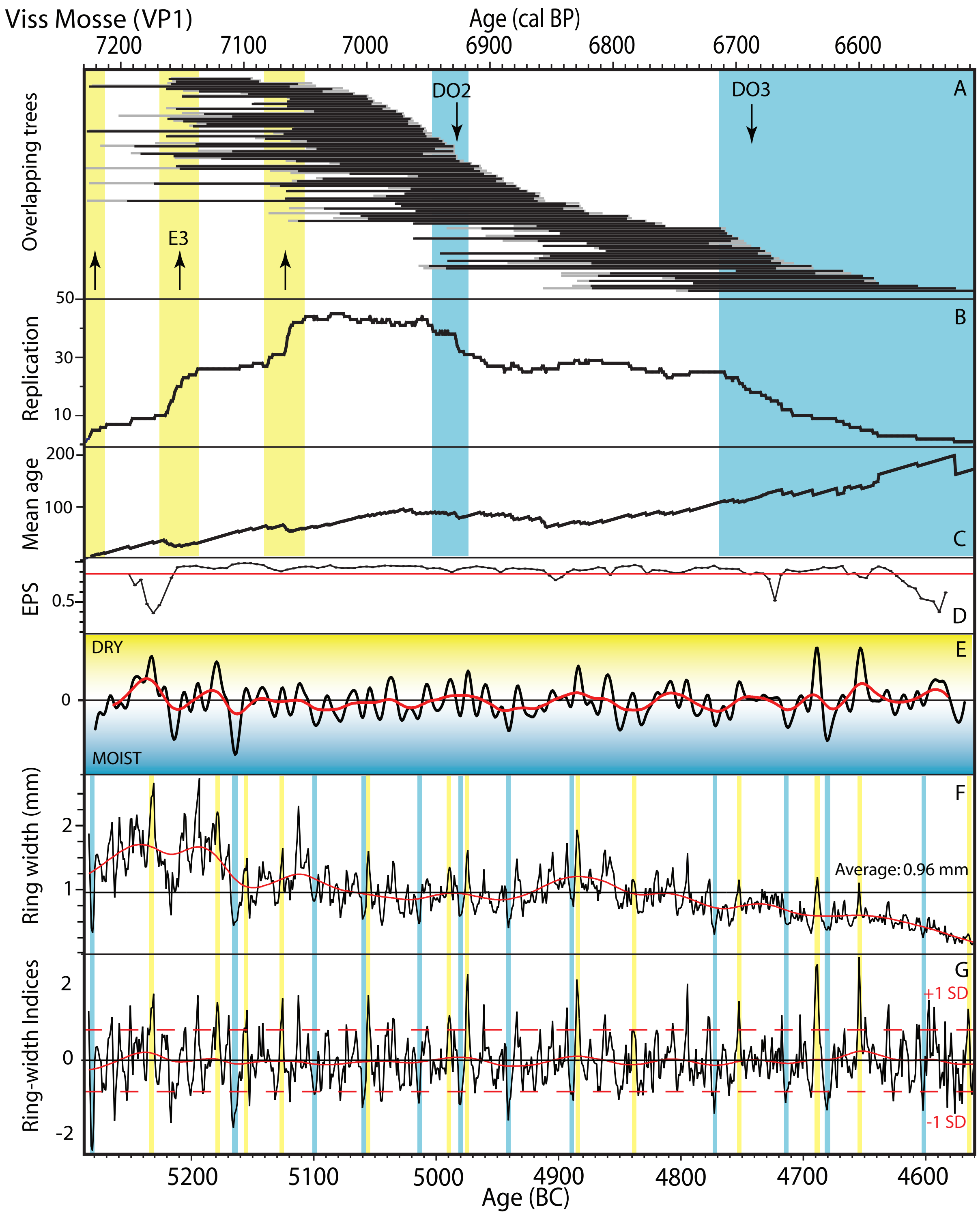

Figure 7. (A) The 726-year main chronology from Viss Mosse based on 86 pine samples (Appendix II). The horizontal black lines represent individual trees and the grey extensions are estimated years to germination and death. The material is sorted by ending years. Establishment and die-off phases are shown as yellow and blue fileds, respectively. (B) Sample replication. (C) Mean age of samples. (D) Expressed population signal (EPS) calculated with a 30-year window moved with 25-year overlaps. (E) RW indicies smoothed with a 10 (black curve) to 30 year (red curve) Gaussian-weighted filter. (F) Averaged RW chronology (mm). (G) Averaged and standardized RW chronology (dimensionless indices). The smooth red curves in F and G are 20-year low-pass filter splines highlighting the low-frequency patterns of variability. The blue fields are periods of 3 years in a row or longer with depressed growth (RW indices below –1 standard deviation (SD)), and the yellow fields are periods of elevated growth (RW indices above +1 SD).

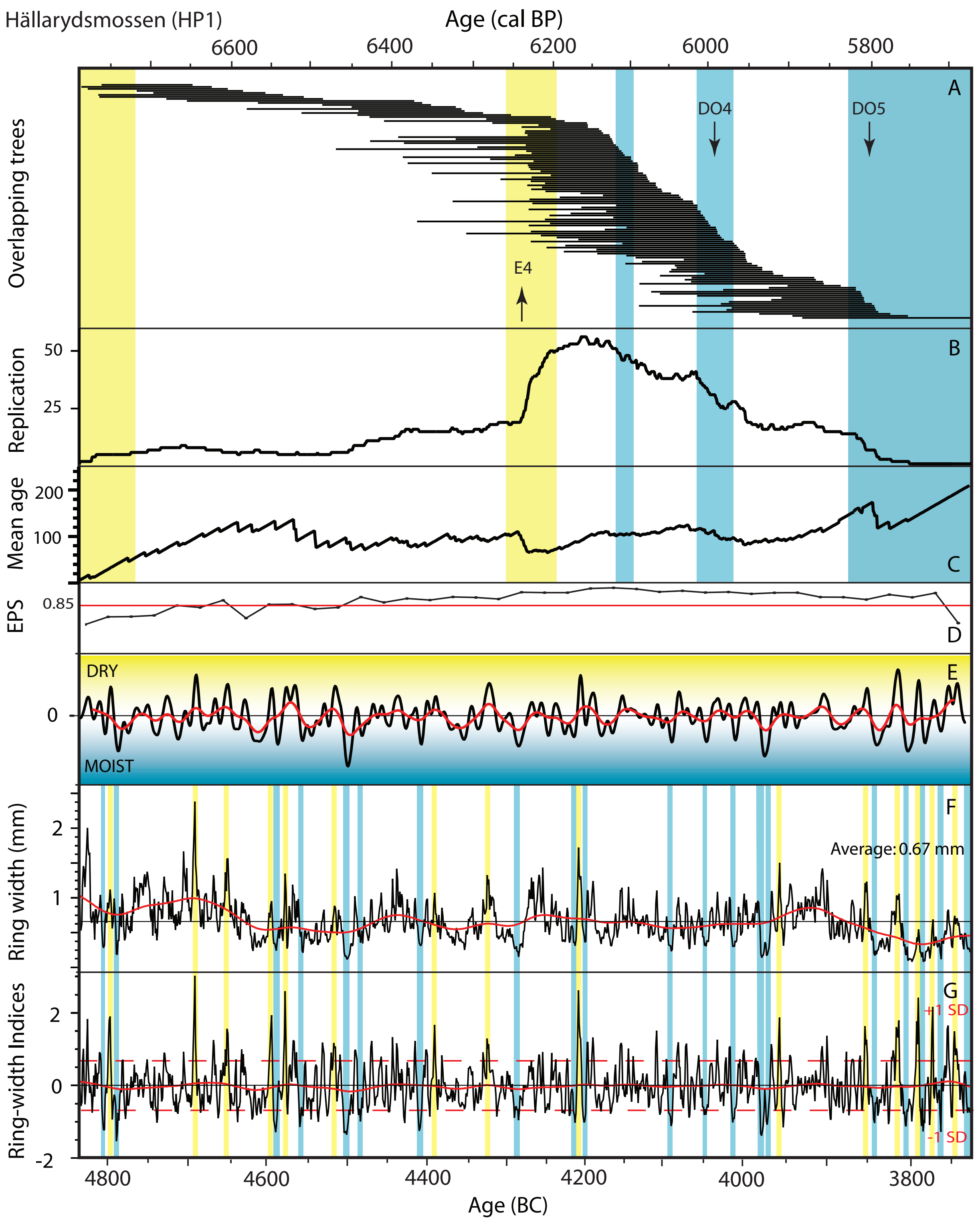

Figure 8. (A) The 1112-year main chronology from Hällarydsmossen based on 117 pine samples (Appendix I). The horizontal black lines represent individual trees sorted by ending years. Establishment and die-off phases are shown as yellow and blue fileds, respectively. (B) Sample replication. (C) Mean age of samples. (D) Expressed population signal (EPS) calculated with a 30-year window moved with 25-year overlaps. (E) RW indicies smoothed with a 10- (black curve) to 30-year (red curve) Gaussian-weighted filter. (F) Averaged RW chronology (mm). (G) Averaged and standardized RW chronology (dimensionless indices). The smooth red curves in F and G are 20-year low-pass filter splines highlighting the low-frequency patterns of variability. The blue fields are periods of 3 years in a row or longer with depressed growth (RW indices below –1 standard deviation (SD)), and the yellow fields are periods of elevated growth (RW indices above +1 SD).

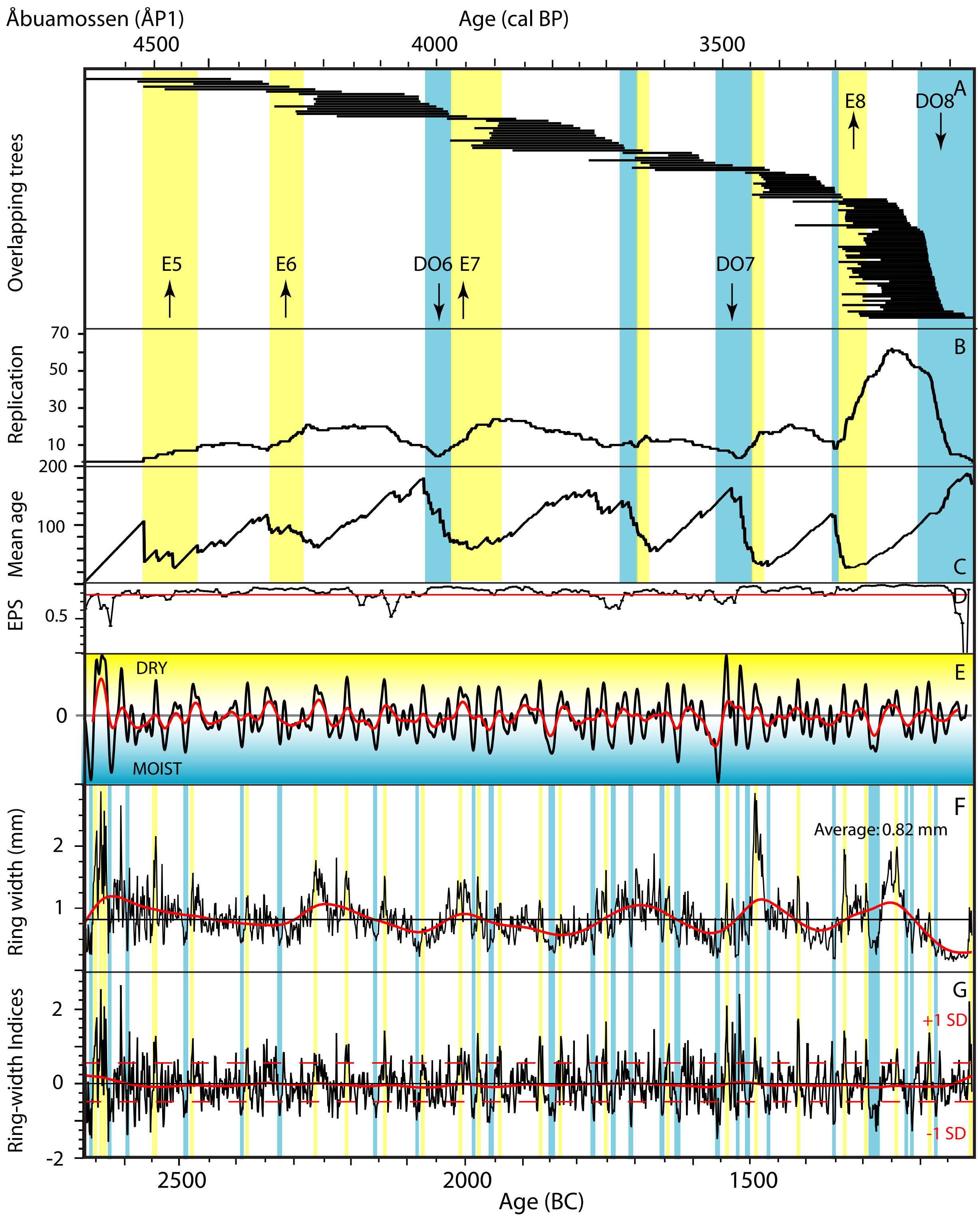

Figure 9. (A) The 1561-year main chronology from Åbuasmossen based on 159 pine samples (Appendix IV). The horizontal black lines represent individual trees sorted by ending years. Establishment and die-off phases are shown as yellow and blue fileds, respectively. (B) Sample replication. (C) Mean age of samples. (D) Expressed population signal (EPS) calculated with a 30-year window moved with 25-year overlaps. (E) RW indicies smoothed with a 10- (black curve) to 30-year (red curve) Gaussian-weighted filter. (F) Averaged RW chronology (mm). (G) Averaged and standardized RW chronology (dimensionless indices). The smooth red curves in F and G are 20-year low-pass filter splines highlighting the low-frequency patterns of variability. The blue fields are periods of 3 years in a row or longer with depressed growth (RW indices below –1 standard deviation (SD)), and the yellow fields are periods of elevated growth (RW indices above +1 SD).

described by Eckstein *et al.* (2011). The surprisingly strong cross-match between the RW chronologies from southern Sweden and north-west Germany (Appendix I) indicates that large-scale climate dynamics had a significant impact on the annual growth of bog pines during the HTM. Peaks in Irish bog and lake-edge replication records at 8000, 7300, 6200 and 3200 cal BP (Turney *et al.,* 2006) are consistent with onsets of establishment phases (E1, 2, 3 and 8 in Fig. 5A) detected in the Swedish pine replication records. A comprehensive study of bog oaks from Germany, the Netherlands and Ireland, in which replication and mean-age records were compared shows clear similarities in tree-population dynamics over large areas indicating that similar climatic conditions were forcing the bog-tree growth over large parts of north-western Europe during HTM (Leuschner *et al.,* 2002). The termination of the mid-Holocene bog-pine phases in both Sweden and Germany is synchronous with a wet shift seen as a recurrence surface in several Swedish raised bogs (Fig 5; Borgmark and Wastegård, 2008; Rundgren, 2008). An abrupt wet-shift would result in groundwater rise and wetter bog-surface conditions, generating a bog tree die-off phase and increased peat growth preserving dead trees (Fig. 1). In summary, then, it is possible to conclude that the relatively warm and dry conditions during the HTM caused decreased bog-surface wetness, and thus more favourable conditions enabling bog-tree establishment and increased tree growth.

The HTM was followed by a transition phase towards moister and colder conditions, often referred to as the Neoglacial transition (Nesje *et al.,* 1991; Wanner *et al.,* 2008). This late Holocene transition is evident on a hemispherical scale in numerous proxy records and is believed to be driven by changes in orbital insolation patterns (Bradley, 2003; Korhola *et al.,* 2010). A multi-proxy study from south-central Sweden dated this transition phase to 4600 and 3400 cal BP (Jessen *et al.,* 2005). The $\delta^{18}O$ record from Lake Igelsjön (Fig. 2) indicates moister conditions and a significant lake level rise between 4450 and 3350 cal BP (Hammarlund *et al.,* 2003), and temperature reconstructions based on pollen from Lake Flarken (Fig. 2) show that the annual mean temperature was lowered by almost 2 °C between 4500 and 2000 cal BP (Seppä *et al.,* 2005). Also the lake-level reconstruction from Lake Bysjön further south in Sweden suggests moister conditions with rising lake levels between 5000 and 2500 cal BP (Fig. 5; Digerfeldt, 1988). Due to increasingly moister conditions accelerating lateral peatland expansion has been recorded at numerous sites in the Northern Hemisphere (Korhola *et al.,* 2010; Weckstöm *et al.,* 2010). These conditions should have generated an increasingly difficult environment for bog trees to establish and grow in.

The dated tree material from Åbuamossen (Appendix IV) and Stass Mosse grew in a raised-bog environment during this transitional phase, while the oaks and alders from Viss Mosse (Appendix III) grew in fens or the marginal zone next to the bog. It is therefore not appropriate to make direct comparisons of tree-growth dynamics between these coniferous and deciduous tree populations. The pine trees from Åbuamossen and Stass Mosse show highly different growth patterns, which is probably due to differences in both size and hydrology of the two bogs. Stass Mosse is just 0.4 km^2 in size and located in a relatively deep basin (>5 m). The bog is probably hydrologically influenced by a groundwater-supplying adjacent glacifluvial deposit. The trees from Stass Mosse were unusually old when they died, in some cases >400 years, but the correlation is weak to non-existent between most of them and they exhibit poor growth and numerous missing rings. It is therefore likely that the prevailing growth conditions on Stass Mosse were so severe that local hydrological variations in the bog often affected the tree growth to a greater extent than regional climatic variations. Therefore, the following discussion is primary based on results from Åbuamossen (Figs. 2B, 9 and Appendix IV). The RW chronology from Åbuamossen has been absolutely dated to 2668–1108 BC (4617–3057 cal BP) from statistical and visual comparisons with the Lower Saxony bog oak master chronology (Leuschner *et al.,* 1987). The tree-establishment phase, between c. 4600 and 3050 cal BP, is largely coincident with a minor lake-level lowering (Digerfeldt, 1988) and temperature rise (Seppä *et al.,* 2005) (Fig. 5).

No clear population-dynamic similarities were found during the HTM when tree-replication data from southern Sweden and wet and dry periods reconstructed from west-central Swedish subfossil trees (Gunnarson, 2008) were compared. In contrast, replication data from Åbuamossen show several similarities when establishment phases (E6 and E7, Fig. 5) fit with periods of low lake levels from 2400–2200 and 2100–1800 BC, and die-off phases (DO6–8, Fig. 5) correspond to periods with high lake levels, 2200–2100, 1700–1500 and 1100–900 BC (Gunnarson, 2008). It is not possible to conclude from this observation alone that the south Swedish bog pines were governed by a more northern Scandinavian than western European climate regime after c. 2500 BC. However, the mid- to late Holocene transition seems to have caused a shift about 2000 BC causing lack of agreement between e.g. continental and Irish mean-age chronologies (Leuschner *et al.,* 2002). It is therefore likely that this shift could have caused less agreement between south Swedish and continental bog-tree populations as well. The subsequent die-off event (DO8; Fig. 5) was accompanied by degeneration of German bog-pine populations, as well as by rising lake levels and increased peat humification in southern Sweden, the latter identified as recurrence surface IV (Borgmark and Wastegård, 2008; Rundgren 2008; Fig. 5).

There is an almost 20-year-long growth depression around 1280 BC (3230 cal BP) in the Åbuamossen RW chronology (Figs. 4C, 6, 9 and Appendix IV). There are recurrence surfaces in peat-stratigraphies in Halland, south-west Sweden, indicating a rapid change from dry to moist conditions around 3200 cal BP (Björck and Clemmensen, 2004). Simultaneously, lake levels started to rise (Digerfeldt, 1988; Hammarlund *et al.,* 2003) and temperatures decreased (Bond *et al.,* 2001). The trees recovered temporarily before a massive die-off phase between 1200 and 1150 BC (3150–3100 cal BP) when nearly all trees died (DO8; Figs. 5 and 9), probably due to moister conditions and rising groundwater levels. The lack of dated subfossil bog-pines younger than 3000 years in Sweden and Germany indicates unfavourable growth conditions, most likely as a result of increased bog-surface wetness. This development is consistent with several palaeoclimate records from southern Sweden, indicating decreased summer temperature, increased effective precipitation and stronger westerlies during the last 3–4 millennia of the Holocene (Hammarlund *et al.,* 2003; Seppä *et al.,* 2005; Jessen *et al.,* 2005; De Jong *et al.,* 2009).

5.3 Peatland development reconstructions

In combination, detailed dendrochronological analysis of subfossil bog trees and peat-stratigraphical studies provide improved temporal precision and enhanced conceptual understanding of both peatland development and climate variability on local to regional scales (Appendices II–III). The reconstructions presented in these two appendices, combining tree-ring, peat and palaeobotanical data, improved the understanding of peatland development, especially spatially, as groundwater fluctuations could be connected to stand dynamics and tree-growth variability. The sensitivity of individual trees to variations in bog-surface wetness enables reconstruction of groundwater fluctuations with annual to decadal resolution in different parts of peatlands. Peat humification records covering a large part of the Holocene can be successfully complemented by annually resolved RW chronologies. Appendices II and III can be viewed as a continuous study of the period 8000-3000 cal BP and the development of the Viss Mosse bog in relation to climate and hydrology. The HTM offered relatively dry bog-surface conditions enabling widespread pine establishment whereas the moister condition following HTM made the raised bog expand laterally (Fig. 10). According to Korhola *et al.* (2010) and Weckström *et al.* (2010) the most intensive lateral expansion of northern peatlands occurred between 5000 and 3000 cal BP, coincident with the expansion that buried the deciduous trees growing around Viss Mosse (Fig. 10, Appendix III).

The reconstructed development of the Åbuamossen bog (Appendix IV, Edvardsson unpublished data) is based on bog-pine dendrochronology and peat-stratigraphic studies (Thelaus and Holmquist, 1994). In the south-eastern part of the bog, which corresponds to the area where the majority of tree samples have been collected, there is a >2 m thick succession of sedge peat containing alders. On top of the sedge peat is about 0.4 m *Sphagnum* peat in which the pine trees were found. Another 2 to 2.5 metres of the *Sphagnum* peat is estimated to have been lost as a result of peat mining on the bog. In the northern part of Åbuamossen there is gyttja overlain by reed peat. This shows that the northern part of the bog was a lake in contact with the river system further north.

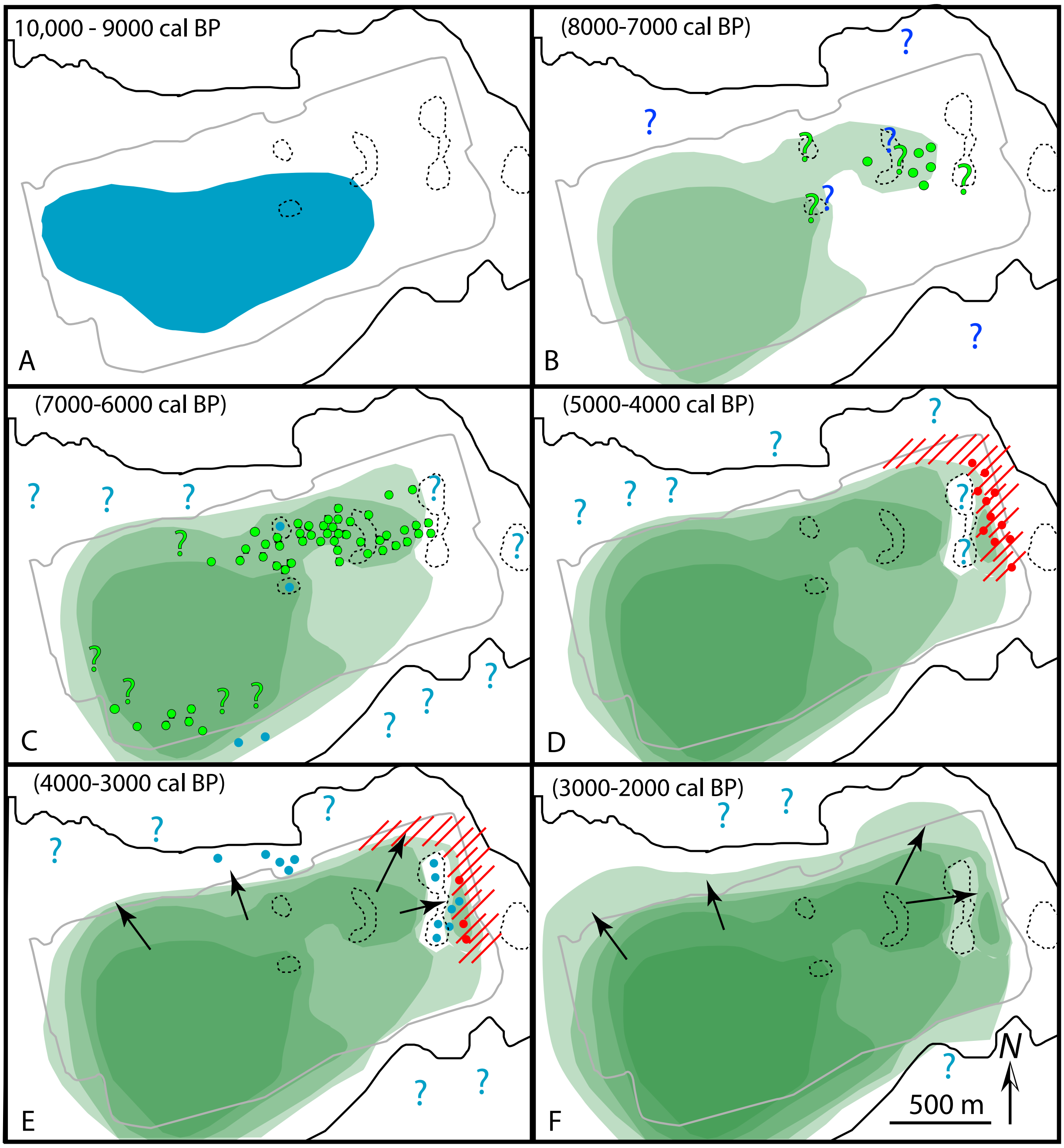

Figure 10. Reconstruction of the development of Viss Mosse 10,000–2000 cal BP based on dated in situ bog trees, peat stratigraphy, pollen and macrofossil analysis (Appendices II–III). The blue area (A) shows the approximate extent of the lake based on the distribution of algal gyttja. The green areas in B-F represent parts of the peatland where a bog environment has developed, the arrows show the direction of the expansion and the color darkens as the depth increases. Green dots represent areas of dated in situ pine trees, whereas the green question marks show possible pine population areas. Blue dots represent areas of dated in situ oak trees, whereas the blue question marks show possible oak-population areas. Even though few oak trunks have been found, the pollen data confirm the presence of oak during the entire HTM. However, the oak trees were probably growing on drier areas around the bog and therefore not preserved before periods of increased bog expansion between 4000 and 3000 cal BP (E and F). The red lines show fen areas and the red dots show where radiocarbon-dated in situ alders have been found. The black line shows the contemporary distribution of the bog, whereas the grey line shows the boundary of the peat-mining area.

Through natural succession the area has become a raised bog. Pine trees began to establish on the bog at least 4600 years ago and spread northward as the growth conditions became more favourable. The pine population was most extensive between 1300 and 1100 BC (Figs. 9 and 11), and covered most of the excavated area. On several occasions the pine trees exhibit extremely suppressed growth (Figs. 4A,

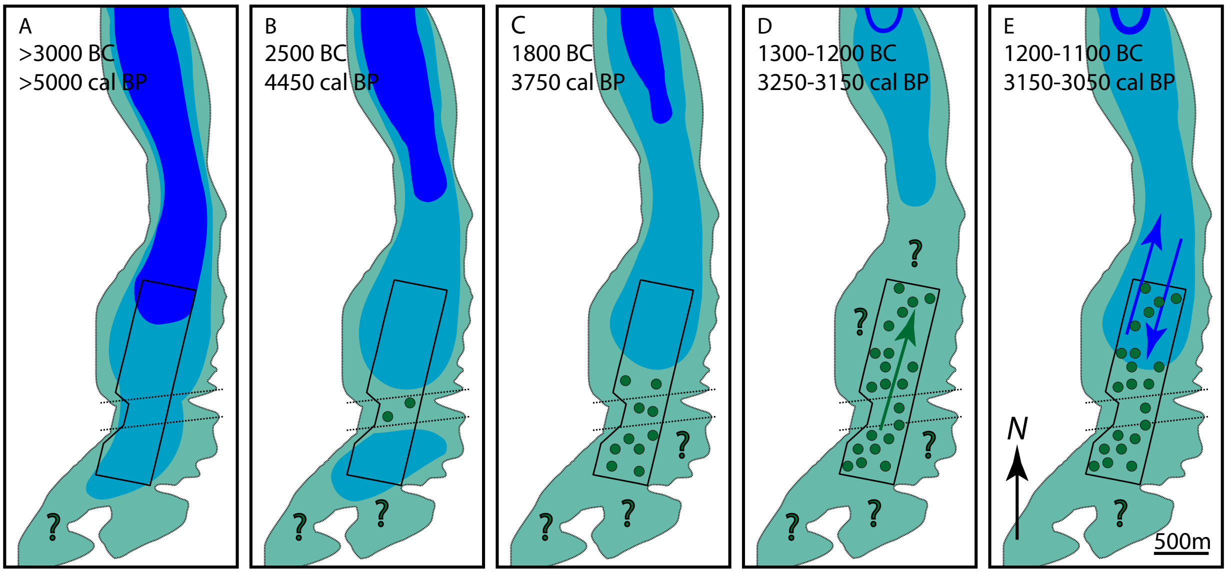

Figure 11. Reconstruction of the development of Åbuamossen. The reconstruction is based on 159 absolutely dated pine trees covering the period 2668–1108 BC and peat-stratigraphic data. (A) The dark blue area corresponds to the maximum extent of a lake that existed in the area and is based on the distribution of gyttja layers beneath the bog. The bright blue areas in A–E represent parts of the bog where the groundwater table was too close to the bog surface for the establishment of trees. The green dots show established pine trees and green arrows the direction of tree spread. The two dotted lines represent a moraine ridge through the bog which probably divided the area into two hydrological systems, an isolated southern part and a northern part directly affected by the river Helge Å. (D) According to the replication record (Fig. 9), the pine population was most widespread between 1300 and 1100 BC. (E) However, the impact of rising water levels and increasing influence of the river (shown by the blue arrows) caused much stress in trees (Figs. 4C and 6) and an abrupt extinction (DO8; Figs. 5 and 9). The black border shows the area used for peat mining.

6, 9 and Appendix IV) and the entire population died during a relatively short period of time (Figs. 6 and 11). The extinction of the pine trees is consistent with the transition towards moister and colder conditions (Nesje *et al.,* 1991; Wanner *et al.,* 2008), which probably caused rising water levels in the bog and the river in the north. A complicating factor is the moraine ridge that runs through the bog, probably causing different hydrological conditions in its southern and northern parts. Hydrological variations were probably more extreme in the north as this area should be more affected by the river Helge Å.

6. Ongoing studies and future challenges

Overall, the results from Appendices I to IV show that climate-controlled moisture variability is closely related to bog-surface wetness and thereby bog-tree growth dynamics. However, it has not been possible to determine exactly to what extent different environmental factors such as temperature and moisture influenced the annual growth of bog trees in the past. This is mainly due to the absence of natural analogous tree-covered peat bogs in north-west Europe today. For example, the pine material presented in Appendices I–II consists of numerous 250–300-year-old trees, >40 cm in diameter, whereas the bog pines growing on nearby bogs today are on average 105 years old and 16 cm in diameter (Edvardsson unpublished data; Lindbladh *et al.,* in review). Corresponding environments with oak trees growing on thick organic soils like those at Viss Mosse (Appendix III), or in Germany and Ireland, described by e.g. Leuschner *et al.* (2002), cannot be found either. It is therefore difficult to make direct comparisons between past and present bog-tree populations.

Another complicating factor is that it is difficult to separate precipitation and temperature signals in the data when the effective precipitation, i.e. precipitation minus evaporation, also depends on the temperature. Instead, most palaeohydrological data reflect changes in the balance between precipitation and evaporation, observed e.g. as water-level fluctuations in peat bogs or lakes. Initial tests using stable isotope analysis ($\delta^{13}C$ and $\delta^{18}O$) of RW series showing abrupt environmental changes confirmed that moisture was an important growth-regulating factor for bog trees in the past (Appendix IV). However, other independent and complementary records are needed to improve our understanding of how various climate-related factors influenced bog-tree growth in the past. To shed further light on this, studies were conducted in which RW chronologies from recent bog pines were correlated with metrological data, and spectral and wavelet analysis were performed to test whether there are detectable cycles in the RW data.

6.1 Comparison of recent bog-pine growth variability and metrological data

In total, 145 living pine trees were sampled at Store Mosse, Buxabygds Mosse, Saxnäs Mosse, Hästhults Mosse, Fäjemyr and Mycklemossen (Fig. 2 and Table 2). These trees were studied with the aim of increasing our understanding of the influence of temperature and precipitation for bog-tree growth dynamics. The RW chronologies developed from material collected at Store Mosse (SP1), Buxabygds Mosse (BP1), Saxnäs Mosse (SaP1) and Hästhults Mosse (HaP1) were used for comparison with metrological data obtained from SMHI (Sveriges meteorologiska och hydrologiska institut). The RW chronologies were compared with monthly values of precipitation and temperature measured at the weather station outside Växjö, 35–70 km east or south-east of the four bogs. The RW chronologies were developed, statistically controlled and standardized following the procedure described in the methods section and Appendix II. The correlation tests were performed using DendroClim 2002 (Biondi and Waikul, 2004), a statistical software for analysis of climate and tree-growth relationships. Initially, correlation tests were performed between RW indices, monthly precipitation and temperature data starting with August of the previous year and ending with November of the current year. The tests were performed on complete standardized chronologies, residual chronologies and periods assessed as reliable (EPS ≥ 0.85, Table 2). The results discussed below are based on standardized chronologies and a common period 1920–2008, over which all the chronologies were considered reliable. Under these conditions all chronologies showed significant correlation ($p<0.05$) against temperature for two to four months before or during the growth period (Table 3). However, correlation with precipitation showed no common pattern among the four bog-pine chronologies

The hydrological response of peat bogs is believed to be slow, and water-table changes noticeable in the unsaturated zone in a raised bog might therefore be delayed. Hydrological delays in peat bogs depend on factors such as the location of the bog surface, which varies depending on how much water is being stored in the bog, slow water transport through soils towards the bog or precipitation falling as snow. A

Table 3. Correlation tests between RW chronologies from Buxabygds Mosse (BP1), Hästhults Mosse (HaP1), Saxnäs Mosse (SaP1) and Store Mosse (SP1) and total monthly precipitation and average monthly temperature. The period 1920–2008 was used for all correlations presented. Correlation between RW – temperature (T) and RW – precipitation (P) are displayed only if significance level corresponding to p<0.05 is reached.

Period	**BP1**	**HaP1**	**SaP1**	**SP1**
August (previous yr)	-	*P -0.23*	-	-
September (previous yr)	-	*P -0.17*	-	-
October (previous yr)	-	-	-	-
November (previous yr)	-	-	-	-
December (previous yr)	*T 0.20*	-	-	*T 0.22*
January	-	-	-	-
February	-	-	T 0.26	-
March	-	-	T 0.32	-
April	-	-	-	T 0.22
May	-	T 0.31	-	-
June	T 0.33	T 0.32/P -0.25	T 0.23	T 0.22
July	-	-	-	T 0.18
August	T 0.22/P -0.25	-	P -0.22	-
September	-	-	-	-
October	-	-	-	-

study by Linderholm *et al.* (2002) showed that pine trees growing on peatlands in Sweden are influenced by growth-season temperature and precipitation, but also by varying groundwater tables caused by climate variability over several years. Bog-tree chronologies may therefore display a multiple-year climate signal, especially in terms of precipitation. To investigate this hypothesis further, tests were made where the total precipitation over longer periods, up to three years, were correlated with RW data (Table 4). Interestingly, the highest significant correlations between precipitation and RW data from Buxabygds Mosse (BP1) and Saxnäs Mosse (SaP1) were obtained against total rainfall for the previous year, or the previous two years (Table 4). The results show that multi-year total precipitation can have a significant negative impact on the annual growth of bog pines. Similar results have been demonstrated in an ongoing study by A. Hansson, containing water-flow rates from Rörvik south of Store Mosse compared with RW chronologies from the bog. So far, the study shows significant negative correlation between RW and the total water flow from the bog drainage area during the previous 3–4-year period. These results show that there is a hydrological delay effect in many peat bogs that might explain the lag effect detected when RW and isotopic records were correlated (Appendix IV). Similar tests were made where the average temperature for periods of between two and six months were correlated with RW data. However, this investigation only confirmed the previous findings of the importance of temperature before and during the growing season.

On several occasions, tree establishment at the four bogs coincided with major drainage projects during the early 1900s in areas adjacent to the bogs (Fig. 12; Axbom, 2012). Also, studies based on dendrochronology and aerial photographs show increased bog-tree establishment during this period at other nearby bogs (Linderholm and Leine, 2004). The increase in tree establishment on raised bogs over the last 100–150 years may depend on a combination of factors. Land-use changes and drainage projects, in combination with warmer climate probably favoured the bog pines. It may also be that we are seeing a slow recovery of bog trees after the Little Ice Age (LIA). The cold and humid climate that prevailed during the LIA (Mann *et al.,* 2009) might have caused too unfavourable conditions for tree growth on the south Swedish raised bogs. However, the many extensive drainage projects that have been conducted in southern Sweden makes the analyses of recent bog trees somewhat more uncertain. At the same time they also shows that the drier bog-surface conditions favour bog-tree establishment.

Other factors causing bog-tree establishment might be precipitation containing increasing amounts of nutrients fertilizing the bogs. Nitrogen (N) deposition, for instance, has increased over the last few decades and has previously been reported as a fertilizer increasing the growth of pine trees

Table 4. Correlation tests between standardized RW chronologies from Buxabygds Mosse (BP1), Hästhults Mosse (HaP1), Saxnäs Mosse (SaP1), Store Mosse (SP1) and total precipitation (Precip.) for the periods January to October (J–O), January to December previous year (Prev. yr), January to October in combination with previous year (J–O+Prev. yr), January to October together with total amount of precipitation during the previous two years (J–O+2 Prev. yrs), average temperature (Temp.) over two to six month periods. The letters show the relevant months. The period 1920–2008 was used during all correlation tests. Correlation values are displayed only if significance level corresponding to p<0.05 is reached.

Period	BP1	HaP1	SaP1	SP1
Precip. J–O	-0.21	-0.17	-0.20	-
Precip. Prev. yr.	-0.18	-	-0.27	-
Precip. J–O+Prev. yr	-0.30	-0.20	-0.30	-
Precip. J–O+Prev. 2 yrs	-0.25	-0.18	-0.32	-
Temp. JF	-	-	0.18	-
Temp. JFM	-	-	0.24	-
Temp. JFMA	-	-	0.25	-
Temp. FM	-	-	0.32	-
Temp. FMAMJ	0.18	-	0.36	0.22
Temp. AM	-	0.24	0.20	0.20
Temp. AMJ	0.20	0.35	0.27	0.27

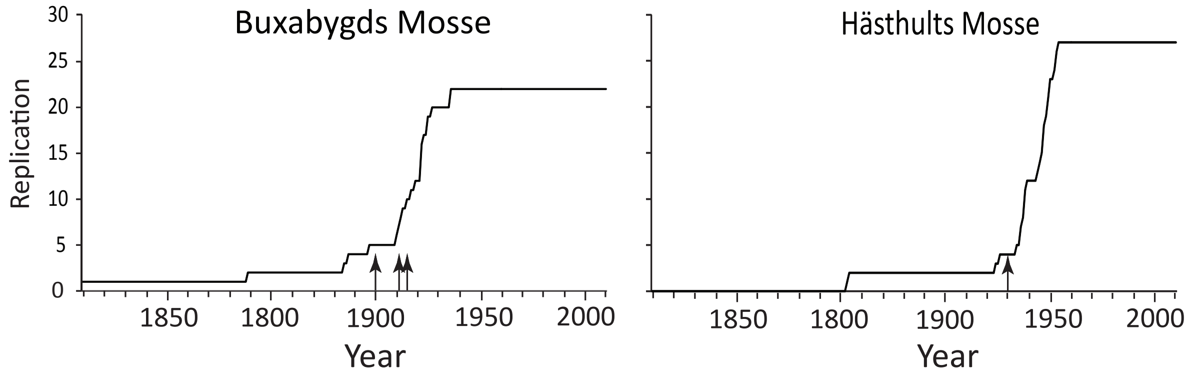

Figure 12. Replication records from Buxabygds Mosse and Hästhults Mosse. The arrows indicate the year in which major drainage projects were implemented around the bogs. Extensive tree establishment occurred almost immediately after ditching, probably due to drier surface conditions in the two bogs.

(Valinger, 1992; Saarsalmi *et al.,* 2012). However, there are several hypotheses about the production of *Sphagnum* in response to N enrichment and the importance of different factors in relation to each others (Limpens *et al.,* 2011). This makes it difficult to predict the response of the bog trees. Although, N usually have a positive effect on tree growth, it is possible that bog trees respond differently depending on how various species of *Sphagnum* mosses react.

It is not possible to directly transfer the results from recent to subfossil bog trees, as even a visual comparison between the two groups indicates that these trees have grown under different conditions. As mentioned above, the recent trees that were found in the area are considerably smaller than the subfossil trees described in Appendices I to IV. There are several reasons behind this, for instance the relatively warm and dry climate during the mid-Holocene offered a better bog-tree growth environment and the peat bogs were probably not as hydrologically complex since they were not as old and deep as at present. Overall, however, the comparison between RW and metrological data demonstrates that moisture is a growth-limiting factor, in terms of both annual growth and tree establishment. The comparison also shows that hydrological lag effects may occur, which is also discussed in Appendix IV.

6.2 Cycles detected in bog-tree RW chronologies – preliminary results from spectral and wavelet analyses

In another attempt to advance our knowledge of factors affecting the growth variability of bog trees, spectral and wavelet analyses were used to identify potential occurrences of periodicities in RW chronologies. Initial tests were made on RW chronologies from seven peat bogs (Edvardsson *et*

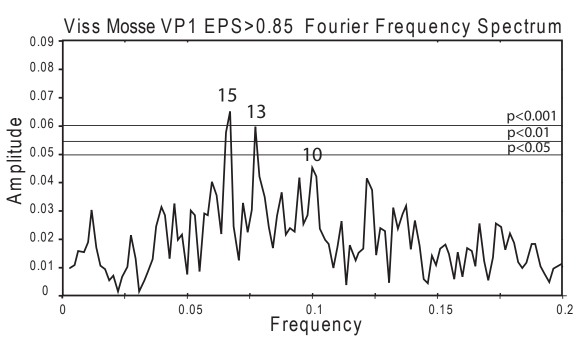

Figure 13. Power spectra using Tukey-Hanning window on the standardized RW chronology from Viss Mosse. Horizontal lines indicate significance level, p<0.05, p<0.01 and p<0.001. The numbers indicate the length in years of the three most significant spectral peaks.

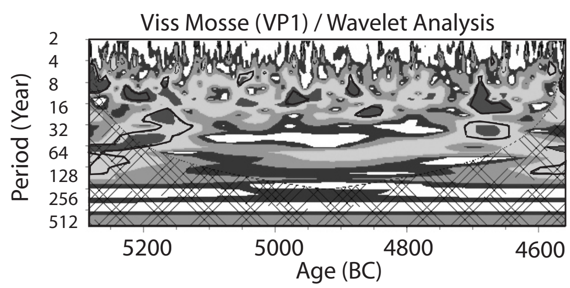

Figure 14. Wavelet analysis of the standardized Viss Mosse RW chronology. The detected c. 13- and 15-year cycles appear to be present during most of the 726-year period. Solid black lines indicate significant areas at the p<0.05 level. The cross-hatched region is the cone of influence where edge effects are present.

Table 5. *Cycles detected based on spectral analysis of bog tree RW chronologies. Significant cycles (number of years) found with the Tukey-Hanning and Multi-taper window for periods when RW chronologies achieve EPS>0.85. In brackets are the cycles that were found when the whole RW chronologies were analysed.*

Code	**Tukey-Hanning**		**Multi-taper**	
	Cycles p>0.001	**Cycles p>0.01**	**Cycles p>0.001**	**Cycles p>0.01**
Subfossil material				
ÅP1	35.0, 26.8, 17.1 (34.9, 17.0)	-	35.0, 31.0, 26.6, 17.1, 16.0, 10.6 (33.2, 30.6, 26.9, 17.0, 16.1, 10.6)	11.3
HP1	(62.2)	62	12.5, 10.7 (18.8, 17.7, 12.2)	64.4, 27.3 (61.8)
VP1	15.0 (15.1, 12.9)	12.9	14.9, 13.9, 12.9 (17.3, 15.1, 13.0)	
VP2	-	12.1 (11.5)	10.1	12.8 (18.1)
VP3	-	21.4	22, 60.5	-
VP4	-	-	-	15.5
VO1	(15.3, 9.0)	15.1, 9.0 (7.8)	(15.5, 7.1)	15.1
VO2	-	-	-	(23.0)
VO3	-	(21.4)	(22.0)	-
VO4	-	-	(73.0, 16.2)	-
Recent material				
SP1	-	14.0 (15.0)	14.1, 9.9	-
AnP1	-	(20.9)	-	-
BrP1	26.3 (29.7)	-	26.3 (29.9)	-
HvP1	18.4 (18.4)	(30.4)	27.8	18.6
BP1	(37.2, 15.4)	-	(15.1)	-
HaP1	-	-	(36.0)	-
SaP1	-	(14.9)	13.9 (15.3)	-
MP1	-	-	-	-
FP1	-	(18.9)	-	-

al., 2011). The analysis presented in Edvardsson *et al.* (2011) has been repeated with updated and several new chronologies. In total, 19 RW chronologies developed from material collected at 12 peat bogs have been used. The RW data were treated in a similar manner to that described in Appendix II. The results from the spectral analysis below (Table 5) were calculated using a Tukey-Hanning window (Blackman and Tukey 1958), and to evaluate the spectra further and test the significance of detected spectral peaks the multi-taper method was used as well (Thomson, 1982). Wavelet analysis was also performed to visualize the temporal stability of the detected cycles over the entire time-span of each chronology. The AutoSignal software (AISN, 1999) was used for both spectral and wavelet analyses. Further wavelet analyses were made using software provided by the University of Colorado (Torrence and Compo, 1998). Each chronology was studied separately in its total length and for periods with EPS values above 0.85 (Table 2). Chronologies spanning more 600 years were also divided into 300-year sequences that underwent analyses identical to the complete chronologies.

Cycles that affect climate and moisture variability, as well as cycles that cause groundwater fluctuations, such as lunar cycles (O'Brien and Currie 1993), were expected to be found in the analysed chronologies. Several highly significant cycles were found using the spectral analysis (Table 5). The roughly 13- and 15-year cycles detected in e.g. the Viss Mosse chronology (Fig. 13) were seemingly stable over time (Fig. 14). The 15-year cycle is interesting as it was detected in various chronologies from pine, oak, subfossil and recent material (Table 5). Temperature variability observed in Norway identifies periods of warming and cooling in the entire northern North Atlantic with a cyclicity of about 15 years (Yndestad, 2006), and Moron *et al.* (1998) described a 13- to 15-year oscillation cycle in North Atlantic sea-surface temperature. However, the 13-year cycle can also be linked to a 9–13-year periodicity in solar irradiance, which is thought to influence global sea-surface temperatures (White *et al.,* 1997). As solar and lunar cycles are believed to affect groundwater levels they should be encountered in RW chronologies from bog trees. Both 11- and 22-year cycles were detected in the RW data, possibly related to solar cycles. Other detected cycles between 18 and 19 years might be related to the 18.6-year lunar nodal cycle (O'Brien and Currie 1993). Multi-decadal variability connected to long-term changes in sea-surface temperature with a period of 62 years has been identified by e.g. Fischer and Mieding (2005). The 60–62-year cycle, which is observed with different significance level in two chronologies, could therefore be related to internal dynamics of the climate system, such as the meridional overturning of the North Atlantic and/or the Atlantic Multidecadal Oscillation (Goldenberg *et al.,* 2001; Knight *et al.,* 2005; Wanner *et al.,* 2008). These cycles may affect precipitation patterns over Fennoscandia, which in turn would affect the water level in the peat bogs.

Consistent cycles in both modern and subfossil RW chronologies from bog pines at several sites in southern Sweden may indicate coherent responses of tree populations to large-scale climate variability throughout the mid- and late Holocene. The nature of these cycles is still unclear, but external forcing mediated by atmospheric circulation dynamics in the North Atlantic region, solar and lunar cycles may be involved. Cycles related to internal hydrological dynamics of the individual peat deposits may also be involved, which complicates the interpretations.

6.3 Radiocarbon dating of subfossil bog trees

Dendrochronology and radiocarbon (^{14}C) dating are two valuable and complementary dating methods applicable to subfossil wood remains from Holocene peat deposits. Tree-ring chronologies can provide precise dating and be site-specific, whereas radiocarbon can be used globally due to the fast mixing of CO_2 in the atmosphere. However, the radiocarbon technique requires calibration by an independently developed dating tool because the radiocarbon production and the distribution among carbon reservoirs varied in the past, leading to fluctuations in the atmospheric radiocarbon concentration (Kromer, 2009). Tree-ring chronologies are important tools for the development of the radiocarbon calibration curve as annual growth rings are excellent archives of atmospheric radiocarbon (Becker, 1993; Friedrich *et al.,* 2004; Kromer, 2009). The cellulose in annual growth rings is a direct sample of the atmospheric radiocarbon concentration of the year the ring was formed, and the information can be stored over several millennia in subfossil wood. The most extensive RW chronology used to improve the radiocarbon calibration curve is the Hohenheim chronology (Friedrich *et al.,* 2004) which

Table 6. Radiocarbon dates obtained from absolutely dated RW chronologies. The last column shows calibrated radiocarbon ages following defined sequence analysis. Uncertainties are at the 95.4% significance level.

Lab. No.	**Radiocarbon Age (^{14}C BP)**	**Calibrated age (cal BP)**	**Absolute age (BC / BP)**	**D-seq. age (cal BP)**	**(years) Offset**	**Chronology (Appendix)**
LuS 8255	3750±50	4108±177	1966 / 3915	4005±38	90	ÅP1 (IV)
LuS 8256	3555±50	3839±137	1746 / 3695	3785±38	90	ÅP1 (IV)
LuS 8257	3420±50	3697±135	1626 / 3575	3665±38	90	ÅP1 (IV)
LuS 8258	3315±50	3551±136	1464 / 3413	3503±38	90	ÅP1 (IV)
LuS 8259	3125±50	3334±115	1394 / 3343	3433±38	90	ÅP1 (IV)
LuS 8260	3030±50	3220±142	1164 / 3113	3203±38	90	ÅP1 (IV)
LuS 8642	5768±50	6558±118	4649 / 6598	6582±64	–16	HP1 (I)
LuS 8643	5603±50	6390±91	4435 / 6384	6368±64	–16	HP1 (I)
LuS 8644	5330±55	6113±163	4209 / 6158	6142±64	–16	HP1 (I)
LuS 8645	5266±55	6054±133	4068 / 6017	6001±64	–16	HP1 (I)
LuS 9450	3275±50	3511±119	1615 / 3564	3524±63	–40	VO1 (III)
LuS 9451	3205±50	3454±105	1515 / 3464	3424±63	–40	VO1 (III)
LuS 9452	3145±50	3360±109	1415 / 3364	3324±63	–40	VO1 (III)
UU-1*	6170±45	7090±148	5204 / 7153	7179±48	26	VP1 (I–II)*
UU-2*	6175±40	7062±113	5175 / 7124	7150±48	26	VP1 (I–II)*
UU-3*	6230±45	7132±126	5055 / 7004	7030±48	26	VP1 (I–II)*
UU-4*	5995±35	6838±95	4815 / 6764	6790±48	26	VP1 (I–II)*
UU-5*	5835±40	6624±119	4695 / 6644	6670±48	26	VP1 (I–II)*
UU-6*	5830±45	6621±119	4655 / 6604	6630±48	26	VP1 (I–II)*

*Previously described in Edvardsson (2006) contributed to an important part of the radiocarbon calibration over the entire Holocene and has been used for the IntCal09 calibration data set (Reimer *et al.,* 2009).

In total, 54 subfossil wood samples and 20 peat samples were radiocarbon-dated to give RW chronologies and undated trees an approximate calendar age, to date stratigraphic boundaries and to develop age-depth models for peat-stratigraphic sequences (Appendices II–III). In total, 19 of these radiocarbon dates (Table 6) were obtained from trees included in RW chronologies which subsequently were absolutely dated (Appendix I). However, six radiocarbon dates, all from Åbuamossen, show an offset of about 90 years after *D_Sequence* analysis (Bronk Ramsey *et al.,* 2001), which are older than the margin of error suggests using the uncertainties at the 95.4% significance level (Table 6). The recorded offset between radiocarbon and tree-ring ages was unexpected as the Holocene part of the calibration curve has been based on absolutely dated samples from tree-ring chronologies (Friedrich *et al.,* 2004). Similar age offsets have been detected during dating of raised bog deposits (Kilian *et al.,* 1995) and development of a bog-oak chronology from the Netherlands (E. Jansma, unpublished data). One hypothesis tested by Vestin *et al.* (2012) is that old carbon can be respired from soils and get mixed in the atmosphere, affecting the isotopic composition of the trees. This is an ongoing project where combined radiocarbon dating has been done of CO_2 respired from soils, tree-rings of known ages, and soil samples from different depths. Preliminary results show that old carbon can respire from soils, but despite this, no age difference was found between absolutely dated tree rings around the bomb peak (Levin and Kromer, 2004) and corresponding radiocarbon ages. In the initial tests, the 1964 annual rings from the six locations, Åbuamossen, Skogaryd, Mycklemossen, Norunda, Skytorp and Fäjemyr, were analysed (Fig. 2A). The 1964 annual ring was chosen as the ability to detect a possible age offset around the bomb peak was considered to be the most likely. Further studies using longer tree-ring sequences containing five annual rings are planned.

6.4 Complicating factors in bog-tree dendrochronology and future prospects

So far, studies where bog tree establishment and die-off phases have been compared to Holocene climate variability (Appendix I; Leuschner *et al.,* 2002, etc.), studies where peat-stratigraphic variations have been compared with the occurrence of bog trees (Appendices II–III; Eckstein *et al.,* 2011), studies where variations in tree growth and stable isotopes have been compared (Appendix IV), and studies where tree growth has been compared with metrological data all show that moisture or bog-surface wetness has a major impact on the occurrence of bog trees and bog-tree growth dynamics. Despite this, many unresolved issues remain. Neither bog-tree RW chronologies nor peat humification records offer a direct precipitation proxy applicable to natural climate archives, as bog-surface wetness depends on both precipitation and temperature-controlled evaporation.

The local hydrological conditions in bogs have a crucial role in bog-tree establishment and growth dynamics. However, local groundwater changes might not be driven by climate, but still affect bog-surface conditions. The climatic conditions at the nearby bogs Åbuamossen and Stass Mosse should have been close to identical during the period 4200–3800 cal BP. Despite this, the trees from these two bogs have completely different growth patterns and cannot be cross-dated to each other. This can be explained by the influence of local hydrological variations, due to different geological and hydrological conditions. The hydrology of a bog may also vary over time as a result of bog development, increasing peat thickness, and possible changes of the in- or outlets of the bog basin. Therefore, studies from several locations are required to exclude site-specific changes. This would increase the possibilities to separate site-specific and climate-related changes detected in the RW chronologies. To increase our understanding of the climatic conditions in different locations and during different periods of the Holocene, bog-tree chronologies from new regions would need to be constructed. These chronologies could be compared with the Swedish, German and Irish bog-pine materials which are under development. To increase our understanding of what controlled bog-tree growth during the mid-Holocene, studies where large mature trees, growing in shallow peat deposits in slightly warmer environments than southern Sweden offers would also be desirable.

There are also positive and negative feedback effects that can influence aspects such as the establishment and degeneration of bog trees. The tree cover itself may for instance generate drier bog-surface conditions due to increased evapotranspiration or an improved nutrient status of the bog through aeration and increased peat decomposition (Moir *et al.,* 2010). The trees would benefit from such a development, which constitutes a positive non-climate-controlled feedback effect. Simultaneously, it is possible to speculate whether the increasing weight of hundreds of trees may lower the bog surface towards the groundwater table, which would inhibit tree growth. Also, the presence of trees in relation to the natural succession of bogs is of importance; widespread tree establishment cannot reasonably take place before the bog surface reaches above the groundwater table. However, these problems can be solved by having material from multiple locations.

Due to constantly wet conditions bogs trees develop more horizontal root systems than trees growing on solid ground. It may therefore be that extreme and rapid groundwater reductions initially cause severe growth conditions. However, tolerant species such as Scots pine have two root systems, one at the surface and another reaching deeper and able to adapt to sinking groundwater tables (Schweingruber, 1996). This has the consequence that tree growth usually increases although the groundwater lowering is extreme and caused by large-scale drainage. However, there can be a lag of a few years during which the roots adapt to the new conditions before the growth increase is visible. Root systems of bog trees are often well preserved and offer a possibility to study secondary changes and adaptations to environmental changes (Eckstein *et al.,* 2009). There is still much left to do in this area that could provide valuable information about droughts and groundwater reductions. This would also shed light on whether the extended growth increases visible in RW chronologies (Figs. 7–9) result from prolonged periods of dry bog-surface conditions.

Extensive additional bog-tree chronologies are needed to cover the entire HTM. It may become possible to connect the two oldest radiocarbon-dated chronologies from Viss Mosse (VP3 and VP4) to the main chronology (VP1) as further trees are recovered due to continuous peat mining at the bog (Fig. 5). Data in progress from Åbuamossen (ÅP1) cover the transition towards the late-Holocene. However, an extensive gap of 1060 years still remains between ÅP1 and the Hällarydsmossen (HP1) chronology. An even greater challenge is to bridge the gap between these subfossil data, ending at 1108 BC (3050 cal BP), and the older end of the presently existing pine reference chronology for southern Sweden starting about 930 AD. Such an effort would provide extremely valuable palaeoclimatic information and allow significant progress in the ability to date archaeological material.

7. Conclusions

From the discussion in this synthesis and the results presented in Appendices I to IV, it is possible to draw the following conclusions:

- Extensive new bog-tree RW chronologies from southern Sweden have been developed, of which the most valuable are the absolutely dated pine chronologies covering over 3100 years during the mid-Holocene. The long-distance cross-match and the positive significant correlation with the German bog-pine chronologies show that there are large-scale climate signals in the data, at least in the absolutely dated RW chronologies, allowing palaeoclimatic and palaeohydrological interpretations from the tree-ring data. This enables detection of subtle and short-lasting hydrological changes, whereas the peat-stratigraphic records offer a valuable view of the long-term development of the study sites. The replication and mean-age records also provide palaeohydrological information, although on decadal to centennial time scales.
- The combination of detailed dendrochronological analysis of subfossil bog trees and peat-stratigraphical records provides improved reconstructions of peatland development, especially spatially, as groundwater fluctuations can be connected to stand dynamics and tree-

growth variability. The sensitivity of individual trees to variations in bog-surface wetness enables reconstruction of groundwater fluctuations with annual to decadal resolution in different parts of peatlands. This approach also offers increased temporal precision and enhanced conceptual understanding of climate variability on both local and regional scales.

- *In situ* bog trees can be successfully used as a complement to radiocarbon-dated basal-peat samples in studies of lateral bog expansion. Apart from giving an age of tree burial in different areas of a peatland, the RW data also offer information about periods of hydrological stress affecting tree growth before death.
- Variations in the isotopic records ($\delta^{13}C$ and $\delta^{18}O$) confirm that growth depressions coincided with moister atmospheric conditions. The data also reveal a characteristic lag in the growth response with respect to the isotopic signals, likely due to relatively slow rise in the local groundwater table in response to a wetter climate. A similar lag effect was also found in data from two of the recent bog-pine populations when precipitation of the previous years was correlated with RW data.

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"Last but not least" is the usual saying. Now it happens to be that a couple of those who are left are quite small. Edwine and Wilhelmina, you will always be the most valuable and important to me. The last thanks go to my dear wife Helena, thank you for always putting up with me. It must be hard to live with and plan a future with someone always thinking about what might have happened in a peatland in the middle of nowhere 7000 years ago. If the sun refused to shine, I would still be loving you. When the mountains crumble to the sea, there will still be you and me.

Svensk sammanfattning

Vi lever i en tid då klimatförändringar är en fråga som engagerar, men det krävs en djupare förståelse för hur och varför vårt klimat har förändrats för att möjliggöra realistiska förutsägelser om framtiden. Efterhand som olika metoder för att rekonstruera klimatförändringar har förfinats, och nya dateringsmetoder har utvecklats, så har förståelsen för hur klimatet förändrats över tid och precisionen för när förändringar skett förbättrats. Trots detta är det förvånansvärt lite vi vet om till exempel hydrologiska förändringar under holocen (den pågående mellanistid som inleddes för cirka 11 700 år sedan). Detta beror främst på avsaknaden av proxydata i de naturliga klimatarkiven som direkt relaterar till nederbörd.

Många trädarter producerar årsringar som kan användas för att spåra förändringar i den miljö där träden har vuxit. Om ett träds tillväxt begränsas av en eller flera klimatrelaterade faktorer kan dess årsringar användas för att rekonstruera hur och när klimatet har ändrats. Genom att mäta bredden på årsringar går det att skapa ringbreddsserier med årlig tidsupplösning. Dessa kan sedan statistiskt och visuellt jämföras och sammanlänkas till långa tidsserier (en procedur som inom dendrokronologin vanligen benämns som korsdatering). Tidsserierna, som här kommer att benämnas som trädringskronologier, kan ibland nå tusentals år tillbaka i tiden. Trädringskronologier kan användas för att rekonstruera till exempel temperatur, nederbörd och hydrologi, samt datera händelser då träd skadats av exempelvis bränder, insekter, miljöförändringar, slutningsprocesser eller mänsklig påverkan.

Torvmossar utgör biotoper som är känsliga för miljöförändringar. Torvlagerföljder kan användas för att rekonstruera vegetations- och klimatförändringar över tusentals år. Den syrefattiga miljön i torvmossar genererar en fantastisk bevarandepotential för exempelvis mossor, växter och trädrester. I en torvlagerföljd kan bland annat skiftningar hos den flora som vuxit på mossen och variationer hos torvens nedbrytningsgrad studeras. Dessa förändringar kan återspegla olika klimatväxlingar som påverkat växtligheten och miljön på mossen under dess utveckling. Ibland kan lager innehållande stubbar och stammar från storvuxna träd påträffas. Dessa lager är tydliga indikationer på att de hydrologiska förhållandena dramatiskt ändrats. Relativt varma och/eller torra perioder generar grundvattensänkningar som medför torrare ytförhållanden på mossarna. Detta medför bättre möjligheter för trädetablering och starkare tillväxt hos redan etablerade träd på mossarna.

De huvudsakliga syftena med detta arbete har varit att: (1) utveckla långa trädringskronologier från subfossila sydsvenska torvmosseträd och undersöka materialets potential för paleohydrologiska och paleoklimatologiska tolkningar och; (2) göra detaljerade rekonstruktioner av torvmossars utveckling och paleohydrologi genom att kombinera dendrokronologisk analys av subfossila mosseträd med torvstratigrafisk data. Detaljerade rekonstruktioner av torvmossars utveckling kan ge värdefulla kunskaper som är användbara inom andra områden, till exempel där frågor rörande den globala kolcykeln och holocen klimatutveckling undersöks.

Den trädart som mest frekvent påträffas i sydsvenska torvmossar, och därför utgör huvuddelen av detta arbete, är tall (*Pinus sylvestris* L.). Även ek (*Quercus robur* L.) och al (*Alnus glutinosa* L.) har dock påträffats och därför använts då trädringskronologier har konstruerats. För att datera de svenska mossetallarna, samt testa till vilken grad deras tillväxt har reglerats av lokala hydrologiska variationer i förhållande till mer regionala klimatrelaterade förändringar, så jämfördes de svenska mossetallkronologierna med liknande material från nordvästra Tyskland. De svenska och tyska kronologierna kunde korsdateras och korrelationen mellan dem var signifikant. De absolut daterade tallkronologierna täcker perioderna 5284-3728 f.Kr. och 2668-1108 f.Kr. och visar på att relativt likartade parametrar begränsade trädens tillväxt över stora delar av nordvästra Europa under mitten av holocen. Enligt tidigare gjorda studier så var årsmedeltemperaturen cirka 2-3 °C varmare och vattenståndsnivåerna i sjöar i södra Sverige lägre än dagens. Detta medförde även sänkta grundvattennivåer och torrare förhållanden på torvmossarna i både Tyskland och Sverige, vilket gynnade mossetallarna som snabbt etablerades under denna period.

Den torvmosse som undersökts mest ingående i detta arbete är Viss mosse som är belägen på Linderödsåsen i Skåne. Totalt 247 träd från mossen har analyserats och 162 av dessa har daterats med hjälp av tyska och danska kronologier samt kol-14-metoden (^{14}C). Trädringsdata över cirka 2700 år under mellersta holocen och torvstratigrafiska studier från olika delar av mossen, har tillsammans möjliggjort en detaljerad rekonstruktion av områdets utveckling från sjö till högmosse. Individuella träds etablering, tillväxtdynamik och död länkades till den plats på mossen där de vuxit. Detta möjliggjorde detaljerade rekonstruktioner av vattenståndsförändringar under trädens levnad, samt en kartläggning av mossens spatiala utbredning och tillväxt.

Direkta jämförelser mellan de trädpopulationer som vuxit på mossar under mellersta holocen och de träd som växer på dagens högmossar bör undvikas. Under mellersta holocen växte storvuxna tallar på de Sydsvenska mossarna, ofta med diametrar på över 40 cm och ibland var träden mer än 300 år gamla då de dog. Levande tallpopulationer på skånska och småländska högmossar har undersökts. Dessa träd mätte i snitt 16 cm i diameter och hade en genomsnittlig ålder på cirka 100 år. Denna relativt enkla iakttagelse visar på att de rådande förhållandena inte är de samma som de för 3000-7000 år sedan. Under denna period fanns det även rikligt med ek på många mossar, främst på kontinenten, men även i södra Sverige. Även detta visar på tydliga skillnader mellan nutida och dåtida torvmossar. För att få stöd för hypotesen om att trädtillväxten på mossarna under mitten av holocen begränsades av hydrologiska förändringar, så har analyser av stabila syre- ($\delta^{18}O$) och kolisotoper ($\delta^{13}C$) från trädringar gjorts. Denna studie visar på att tillväxten hos träden minskade efterhand som det blev blötare. Studien visar även på att träden inte reagerade direkt då klimatet förändrades. Det dröjde nämligen cirka tre år innan trädtillväxten följde de klimatförändringar som kol- och syreisotoperna påvisade. Denna fördröjning kan troligen förklaras av en långsam hydrologisk respons i torvmossarna. Detta påstående styrks av jämförelser mellan nederbörddata och tillväxt hos levande mossetallar.

Resultat från detta doktorandprojekt visar på att dendrokronologiska och torvstratigrafiska data i kombination kan användas för detaljerade rekonstruktioner av torvmossars utveckling, expansion och hydrologi. Det stora material av subfossila tallar som påträffats i sydsvenska torvmossarna kan därför med fördel användas för paleoklimatologiska och paleohydrologiska rekonstruktioner som kan ge ökad förståelse om hur vårt klimat förändrats över tid.

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Appendix A

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Lindbladh, M., Fraver, S., Edvardsson, J., Felton, A. Past forest composition, structures and processes – How paleoecology can contribute to forest conservation. In review.

Edvardsson, J., Poska, A., Hammarlund, D., Linderson, H. Rundgren, M., Van der Putten, N., Hansson, A. Late-Holocene peatland expansion and tree succession at Viss mosse, southern Sweden, inferred from subfossil trees and peat stratigraphy. Submitted to TRACE.

Selected conference abstracts:

Edvardsson, J., Hammarlund, D., Linderson, H., Rundgren, M. 2012. Subfossil Swedish bog-pines as indicators of mid-Holocene palaeohydrology and climate. 14th International Peat Congress, Stockholm, Sweden.

Edvardsson, J., Hammarlund, D., Linderson, H., Rundgren, M. 2012. Subfossil bog trees as indicators of palaeohydrology, climate and peatland development. LUCCI, Örenäs slott, Sweden.

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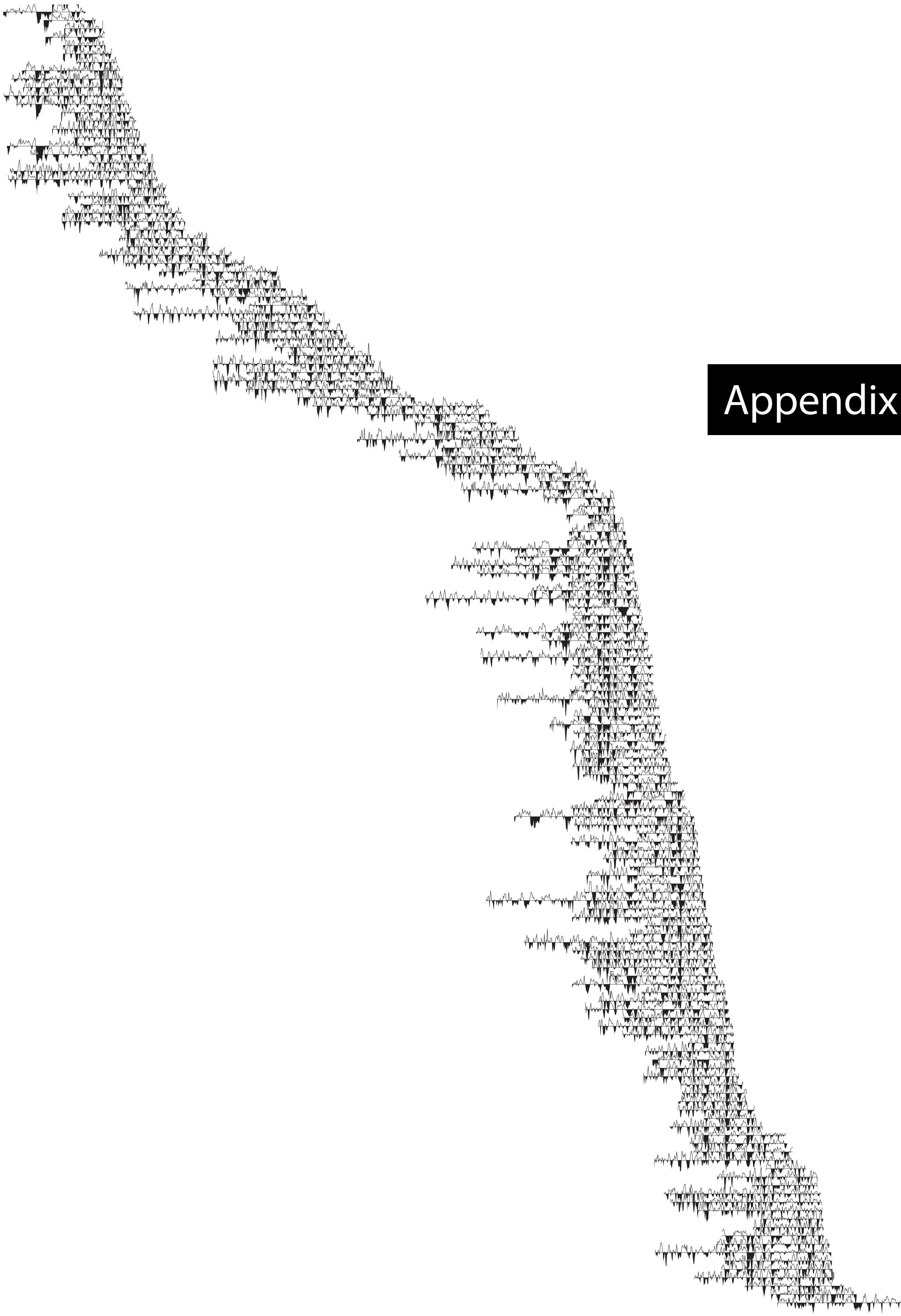

Appendix I

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South Swedish bog pines as indicators of Mid-Holocene climate variability

Johannes Edvardsson[a,*], Hanns Hubert Leuschner[b], Hans Linderson[a], Hans W. Linderholm[c], Dan Hammarlund[a]

[a] Quaternary Sciences, Department of Earth and Ecosystem Sciences, Lund University Sölvegatan 12, SE-223 62 Lund, Sweden
[b] University of Goettingen, Albrecht-von-Haller-Institute, Department of Palynology and ClimateDynamics, Untere Karspüle 2, 37073 Goettingen, Germany
[c] Department of Earth Sciences, University of Gothenburg, Box 460, 405 30 Gothenburg, Sweden

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ABSTRACT

Dendroclimatic investigations of subfossil Scots pine (*Pinus sylvestris*) from two raised bogs in southern Sweden yielded a continuous floating 1492-year long tree-ring record. By cross-dating with bog-pine chronologies from Lower Saxony, Germany, the South Swedish record was assigned an absolute age of 5219–3728 BC. The cross-match between ring-width chronologies from these two regions, separated by 500–700 km, is remarkably strong and the correlation positive, which indicates that large-scale climate dynamics had a significant impact on the growth of bog pines during the Holocene Thermal Maximum (HTM) when bog-pine distribution reached a maximum in both regions. However, local population dynamics were also influenced by peatland ontogeny and competition, as shown by differences in replication and mean tree age between the Swedish and German records. Comparisons with chronologies developed from modern bog pines in southern Sweden indicate that more coherent climate was controlling pine growth on natural peatlands during warm periods in the past. This study demonstrates the usefulness of Swedish subfossil bog-pine material as a climate proxy, with particular potential for decadal- to centennial-scale reconstructions of humidity fluctuations.

Introduction

Scots pine (*Pinus sylvestris* L.) is a tree species commonly found on peat bogs in southern Sweden (Rydin et al., 1999), and it usually invades open and exposed sites rapidly after disturbances like drainage, deforestation, fire or insect invasion (Zackrisson, 1977; Freléchoux et al., 2000; Eckstein et al., 2010). Growth dynamics of trees growing on bogs usually differ from those on solid ground by being highly dependent on the depth and variability of the water table beneath the root system (Boggie, 1972; Freléchoux et al., 2000; Vitas and Erlickytë, 2007; Eckstein et al., 2009). High groundwater tables generate unfavourable growth conditions as a result of several physical, chemical, and biological processes, of which perhaps the most important is reduced availability of nutrients in the saturated zone (Boggie, 1972; Mannerkoski, 1991; Vitas and Erlickytë, 2007). Groundwater lowerings in peat deposits commonly lead to enhanced tree growth because of the increased availability of nutrients in the unsaturated zone (Penttilä, 1991), but also invasion of trees due to improved germination on drier peat surfaces (Freléchoux et al., 2000). Consequently, increased effective precipitation on peat bogs where the groundwater table is close to the surface results in an even shallower unsaturated zone (Schouwenaars, 1988; Hunt et al., 1999), which in most cases leads to stress and growth reductions in trees growing on the peat surface (Boggie, 1972; Leuschner et al., 2002; Linderholm et al., 2002; Eckstein et al., 2009). Given the strong link between groundwater fluctuations and the growth and establishment of trees on bogs, it can be assumed that ring-width records provide information on inter-annual to decadal-scale hydrological changes associated with regional climate change and variability in the past (Leuschner et al., 2002; Sass-Klaassen and Hanraets, 2006; Eckstein et al., 2009). Studies of establishment and degeneration phases in bog-tree populations may also provide information on changes in bog-surface wetness, hydrology and climate on the centennial time scale (Gunnarson, 2002).

Previous studies have demonstrated that bog pines are of limited use as high-resolution climate proxies, mainly because of weak correlation between ring-width patterns and observed meteorological parameters. Moreover, correlations between tree-ring records between neighbouring sites, or even within a single site, may be low. For example, negative correlations were observed between trees growing on the same peat bog in Lithuania (Pukiene,

* Corresponding author. Tel.: +46 46 222 39 59; fax: +46 46 222 48 30.
E-mail address: johannes.edvardsson@geol.lu.se (J. Edvardsson).

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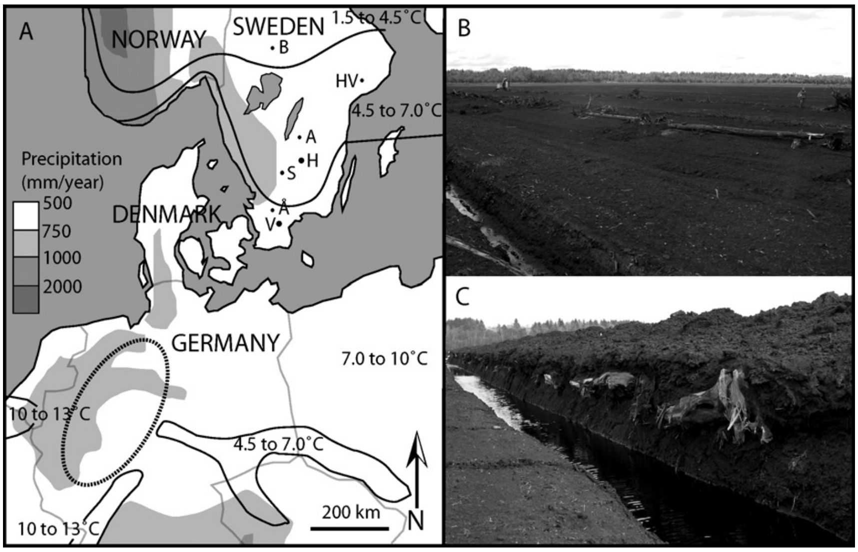

Fig. 1. (A) Locations of South Swedish bog-pine sites presented or discussed in this paper. Subfossil material has been obtained from Viss mosse (V) (Edvardsson, 2010; this study), Åbuamossen (Å) (Edvardsson, 2010) and Hällarydsmossen (H) (this study), whereas the modern material was obtained from Store mosse (S) (Edvardsson unpublished) and the previously published Anebymossen (A), Hanvedsmossen (HV) and Bredmossen (B) (Linderholm et al., 2002). Most of the German bog-pine material originates from the area inside the dotted circle. Annual mean precipitation (mm/year) is shown with shaded fields and average mean temperature with black lines (Wright, 1993). (B) Trunks and stumps exposed at the excavated surface of Hällarydsmossen. About 4 m of *Sphagnum* peat was removed during peat cutting before the stump horizon was reached. (C) Stump horizon with in situ pine stumps visible in a drainage ditch at Viss mosse.

1997), suggesting that shifts in bog-surface wetness are often caused by site-specific ontogeny, and thus weakly related to regional climate dynamics (Väliranta et al., 2007). However, in a regional study in Sweden, Linderholm et al. (2002) found that while the correlation with temperature and precipitation is lower for bog pines than for pines growing on neighbouring dry mineral soils, tree-ring chronologies from the former category exhibit substantially stronger correlations between sites. Furthermore, robust, long-distance correlations between subfossil bog tree-ring chronologies from Germany, Netherlands and Ireland demonstrate that spatial coherence in growth variability is related to large-scale climate variability (Leuschner, 1992; Leuschner et al., 2002, 2007; Eckstein et al., 2009).

Major investigations of subfossil pine and oak (*Quercus robur*) from peat bogs have been carried out in northwestern Germany (Leuschner et al., 1987, 2002, 2007; Eckstein et al., 2008, 2009, 2010) Ireland (Pilcher et al., 1995), Great Britain (Lageard et al., 1995, 2000) and Lithuania (Pukiene, 1997). In Sweden, dendrochronological studies of subfossil trees have mainly been based on wood preserved in dry mountain regions or lake sediments (Briffa et al., 1990; Grudd et al., 2002). Systematic studies of trees buried in peat bogs started relatively recently and are so far restricted to a few sites in central and northern Sweden (Gunnarson, 1999, 2008; Gunnarson et al., 2003) and some preliminary data from southern Sweden (Edvardsson, 2006, 2010).

The main aim of this study is to explore the potential of bog-pine tree-ring records from southern Sweden as indicators of spatial and temporal patterns of humidity variability during the Holocene. We present updated material from Viss mosse (Edvardsson, 2010), which, together with a new record from Hällarydsmossen, form a continuous 1492-year chronology. The absolute age of this new chronology, spanning 5219–3728 BC, was established through cross-dating against well-dated bog-pine chronologies from Lower Saxony, Germany (Eckstein et al., 2009; Leuschner, unpublished data). This new chronology provides novel insight into decadal- to centennial-scale climate variability during the Holocene Thermal Maximum (HTM), a period of relatively warm and dry summers dated to c. 6050–2450 BC (c. 8000–4400 cal. BP) in southern Sweden (Jessen et al., 2005; Seppä et al., 2005; De Jong et al., 2009).

Methods

Study sites and fieldwork

During fieldwork campaigns on six different peat bogs in 2006, 2008 and 2009, about 500 disks from subfossil pine trees were collected with a chainsaw. In total, 209 of these were from the two peat bogs Viss mosse and Hällarydsmossen (Fig. 1).

Viss mosse is located on the bedrock ridge Linderödsåsen in central Scania, southern Sweden (173 m a.s.l., 55°51′N, 13°49′E). It is c. 2 by 1 km in size and one of the most southerly raised bogs in Sweden (Malmberg Persson, 2000). Extensive peat excavation and removal of 2–4 m of *Sphagnum* peat during recent decades has exposed numerous stumps and trunks of mature pine trees with the root level generally c. 0.7 m above the base of the *Sphagnum* peat. These deposits are underlain by a sequence of c. 1 m of carr peat and various types of gyttjas on top of the mineral soil.

Hällarydsmossen is located in the central part of Småland (215 m a.s.l., 57°20′N, 14°35′E), c. 200 km north of Viss mosse. The area around the bog, which is c. 1.8 by 1.4 km in size, is dominated by coniferous forest in an undulating morphology with numerous lakes and bogs. Similarly to Viss mosse, Hällarydsmossen has been subjected to peat excavation, and an estimated 4 m of *Sphagnum* peat has been removed from above the layer where the pine material was collected. The pine horizon is underlain by 1.7–3.7 m of organic deposits, consisting of 0.2–0.8 m of *Sphagnum* peat resting on more than 1.2 m of carr peat and gyttja.

At Viss mosse, a total of 80 cross-sections of in situ stumps and trunks were sampled. In total, 129 cross-sections were collected at Hällarydsmossen, of which 48 were sampled from in situ pines, while the remaining 81 were taken from trees removed from their primary growth positions to enable further peat cutting at the bog surface. In the latter cases the exact stratigraphic positions of the trees are unknown. Information on morphology, sampling distance from the roots, presence of pith, bark, fire marks, damages and other anomalies was recorded for each sample. Trees with less than 60 annual rings or obvious non-climatic disturbances were excluded due to limited possibilities for cross-dating.

Development of tree-ring chronologies

In order not to dry out and deform the wood, all samples were stored at 4 °C prior to measurement. The surfaces of the disks were prepared by cutting several radii with razor blades, and to enhance the appearance of ring and cell structures chalk was applied. Ring-width series of individual samples were measured with a precision of 0.01 mm, using the CATRAS software (Aniol, 1983). Further notations about e.g. specific rings in which insect burrows and fire scars appear were made during the measuring process. In order to identify wedging rings and possible measuring errors, at least two radii, separated by 90° or more, were measured for each sample.

Initially, two statistical tests were applied to evaluate similarities between individual tree-ring series; Gleichlaeufigkeit (Glk) and Students *t*-test. Glk (coefficient of parallel run) is a measure of the year-to-year agreement between two series based on the sign of agreement, expressed in percentage (Eckstein and Bauch, 1969). The *t*-test (Baillie and Pilcher, 1973) compares the actual difference between two means in relation to the variation in the data. In dendrochronology, these statistical analyses are common when assessing the significance of correspondence between two tree-ring series, a process generally referred to as cross-dating or cross-matching. First, the two or more radii from individual samples were cross-dated, and if matching, they were averaged into a ring-width series for each tree. Subsequently, the ring-width series form all individual trees were cross-dated against each other. In general, *t*-values that exceed 3.5 are quoted as significant (Wigley et al., 1987), and all cross-matches between samples yielding *t*-values above 4 as well as significant ($p < 0.01$) Glk values were visually examined. The individual tree-ring series for which cross-dating was satisfactory established, based on statistical and visual examination, were then averaged into site records, also referred to as master chronologies.

In the next step, the cross-dating and measurement quality, as well as the strength of the master chronologies from each site, were evaluated using the software COFECHA (Holmes, 1983), in order to detect possible missing rings, measuring errors and outliers. Segments with correlation values beneath the critical confidence level 0.3281 ($p < 0.1$) in COFECHA were corrected or removed before all samples were cross-dated to form site records (master chronologies).

Standardization of tree-ring data is a correction which minimises non-climatic ring-width variations related to e.g. age, height within the stem and geometry. During the standardization process non-climatic trends are removed from the measured ring-width series, which then become transformed into dimensionless tree-ring indices (Fritts, 1976). As several trees showed growth trends with narrow rings during both juvenile and adolescent stages as opposed to the negative exponential trend, commonly observed in ring-width series, a flexible method was used in the standardization. All individual tree-ring series were standardized with a 67% flexible spline using the software ARSTAN_41d (Cook and Krusic, 2005). To assess the reliability of the chronology, i.e. how well ring-width series from individual trees agree with a theoretical population chronology, the expressed population signal (EPS) was calculated throughout the chronology using ARSTAN. The EPS is dependent on the number of overlapping series and their mutual conformity. The limit at which the chronology was considered as reliable was set to EPS ≥ 0.85 (Wigley et al., 1984).

Development of replication and mean tree age records

Together with replication data, mean tree age data are valuable for reconstruction of population dynamics, particularly germination and die-off events (Leuschner et al., 2002). A replication record was developed by counting the number of overlapping samples year-by-year, and a mean tree age record was created by calculating the average age of all overlapping samples during each individual year. As the inner- and outermost rings sometimes were absent the start and end years were adjusted before the mean age and replication records were developed. The number of missing annual rings to germination depends on the height above root level at which the samples were taken. As the general growth rate of the bog pines was low, 20 years per meter were added for trunks. The number of missing rings to pith and bark was estimated both in the field and during the ring-width measurements. For samples where the outermost rings were absent, the offset to death was estimated from the number of annual rings in the sapwood. Complete samples contained on average 70 annual rings in the sapwood. In general, relatively fast-growing trees showed fewer annual rings than 70, whereas relatively slow-growing trees in some cases had more than 100 annual rings in the sapwood. In some cases evaluations were made in the field by ring counting on stumps or roots below the sampled disks.

Statistical analysis and correlation tests

Initially, the two statistical tests described above were used to evaluate similarities between individual tree-ring records developed from different sites. In addition, the Pearson correlation coefficient *r* (Rodgers and Nicewander, 1988), which measures the correlation between two variables, was calculated. The Pearson correlation coefficient is widely used as it measures the strength of linear dependence between two variables. Finally, the stability of the cross-dating and correlations over time was tested using step-wise moving of a 100-year window in 50-year steps to assess how Glk, *t*- and *r*-values change over time.

Results

Site records

Based on 44 trees, a ring-width site record spanning 646 years was developed from Viss mosse, and another site record based on 117 trees and spanning 1112 years was developed from Hällarydsmossen (Fig. 2). The remaining samples from the two sites (36 from Viss mosse and 12 from Hällarydsmossen) could not be cross-dated and were thus rejected. The high rejection rate (45%) in the Viss mosse material is likely a result of a wide age distribution with several temporal outliers and non-detectable missing rings.

Dating of the Swedish tree-ring records

The two individual Swedish site records were both assigned absolute ages by cross-dating with a German bog-pine chronology, based on subfossil material, from Lower Saxony (Eckstein et al., 2009; Leuschner, unpublished data). This dating procedure (Table 1), indicates that the two Swedish site records overlap with each other. However, there was no significant statistical cross-match between the Viss mosse and the Hällarydsmossen records, most likely a result of relatively few and ageing trees at Viss mosse during this 265 years period of overlap (4839–4574 BC). In this

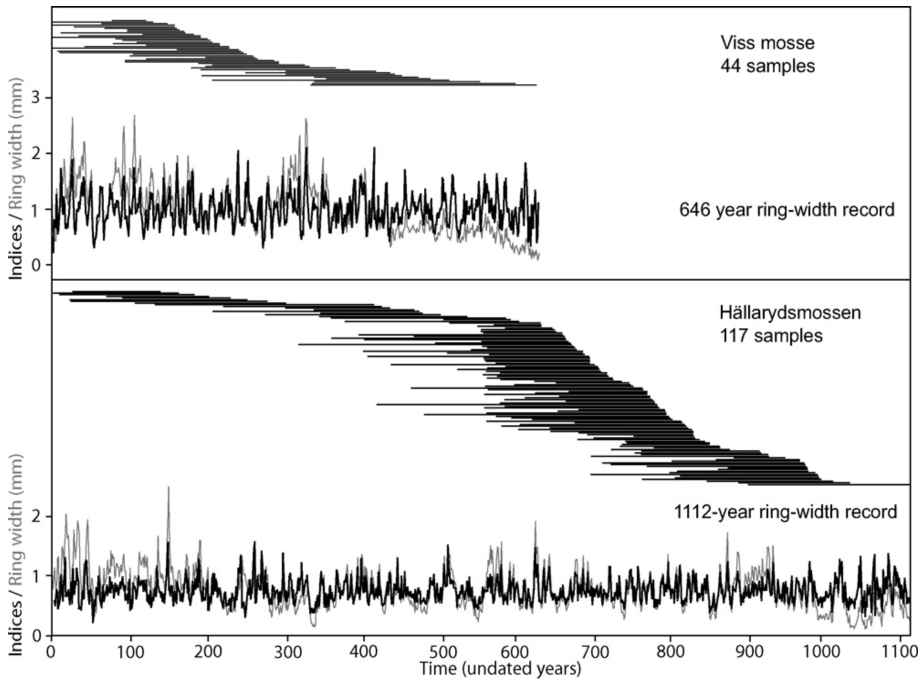

Fig. 2. Subfossil bog-pine tree-ring records from Viss mosse and Hällarydsmossen, southern Sweden, plotted against total incremental age of the respective records. Individual trees are represented by black horizontal bars, the lengths of which represent their numbers of measured annual rings, with their positions determined by dendrochronological cross-dating. The thin grey curves represent averaged, raw ring-width data (mm) while the black curves are dimensionless ring-width indices based on detrending of individual samples with a 67% spline.

overlap period the Viss mosse record matches with the German chronology, although the cross-match is weak (*t*-value 3.4, Glk 58 $p < 0.5$, $r = 0.16$). During the very same period the Hällarydsmossen record exhibits a more convincing match with the German chronology (*t*-value 4.9, Glk 62 $p < 0.01$, $r = 0.30$). The overall cross-match with the German chronology for the period of overlap improves when the two Swedish records are combined (*t*-value 7.8, Glk 68 $p < 0.01$, $r = 0.26$). Together, the Viss mosse and Hällarydsmossen records were combined into a continuous 1492-year south Swedish bog-pine chronology, based on 161 samples, covering the period 5219–3728 BC (Table 1 and Fig. 3).

EPS-values above 0.85 for the composite Swedish bog-pine chronology were obtained during the period of 5186–3859 BC, with a drop below 0.85 around 4550 BC (Fig. 3). The same cross-dating procedure was performed against e.g. the German bog-oak chronology (Leuschner et al., 2002). These comparisons gave identical age determinations, only with a lower, but still significant cross-match statistics (*t*-value: 5.2, Glk: 55 $p < 0.5$).

Growth variability

Several periods of consecutive years of growth depressions and elevations were observed in the Swedish bog-pine chronology (Fig. 3B) and synchronous changes in the individual ring-width series (Fig. 4). In total, 19 periods, three years or longer, of weak growth (−1 standard deviation (SD)) were recorded. The high variability during the final years of the chronology (Fig. 3), i.e. after 3850 BC, is most likely a result of few overlapping samples (also indicated by EPS-values below 0.85), and this part is not considered in the discussion. The most extended periods of growth depression began at 5164, 4939, 4503, 4410, 3986 and 3980 BC, of which the one initiated at 4503 BC was the longest, lasting for 9 years (Fig. 3B). In total, 26 periods of three consecutive years or more with above-average growth (+1 SD) were recorded. Among these, the ones initiated at 4883, 4596, 4213 and 4161 BC were the most prominent (Fig. 3B). In general, the below-average growth periods lasted longer (5–8 years) than the above-average growth periods (3–5 years).

South Swedish mean-age and replication data

The replication record shows peaks at c. 5070 and 4210 BC, and the lowest values were recorded at c. 4550 BC (Fig. 3E). A distinct germination phase took place at c. 4300 BC when the bog-pine population seems to have more than doubled within a century. Over the period 5205–4300 BC, the replication fluctuates between five and 25 samples. At c. 4300–4100 BC favourable growth conditions prevailed at Hällarydsmossen but after c. 4150 BC a prolonged decline was observed, with some minor population increases around 4095 and 3940 BC and abrupt decreases at c. 4050, 4010 and 3850 BC.

Table 1
Statistical cross-match and correlation results for our new South Swedish tree-ring records compared to the subfossil bog-pine chronology from northwestern Germany (Eckstein et al., 2009; Leuschner, unpublished data) expressed as *r* (Pearson correlation coefficient), *t*-value and Gleichlaeufigkeit, Glk. In all three cases the Glk data are significant at the $p > 0.01$ level. The overlaps (number of years) between the Swedish records and the German chronology are also shown, as well as inferred age spans.

Tree-ring records	*r* (Pearson CC)	*t*-Value	Glk	Overlap	Age (BC)
Viss mosse	0.28	6.9	60 ($p < 0.01$)	646	5219–4574
Hällarydsmossen	0.36	11.2	61 ($p < 0.01$)	1112	4839–3728
Combined chronology	0.33	13.6	62 ($p < 0.01$)	1492	5219–3728

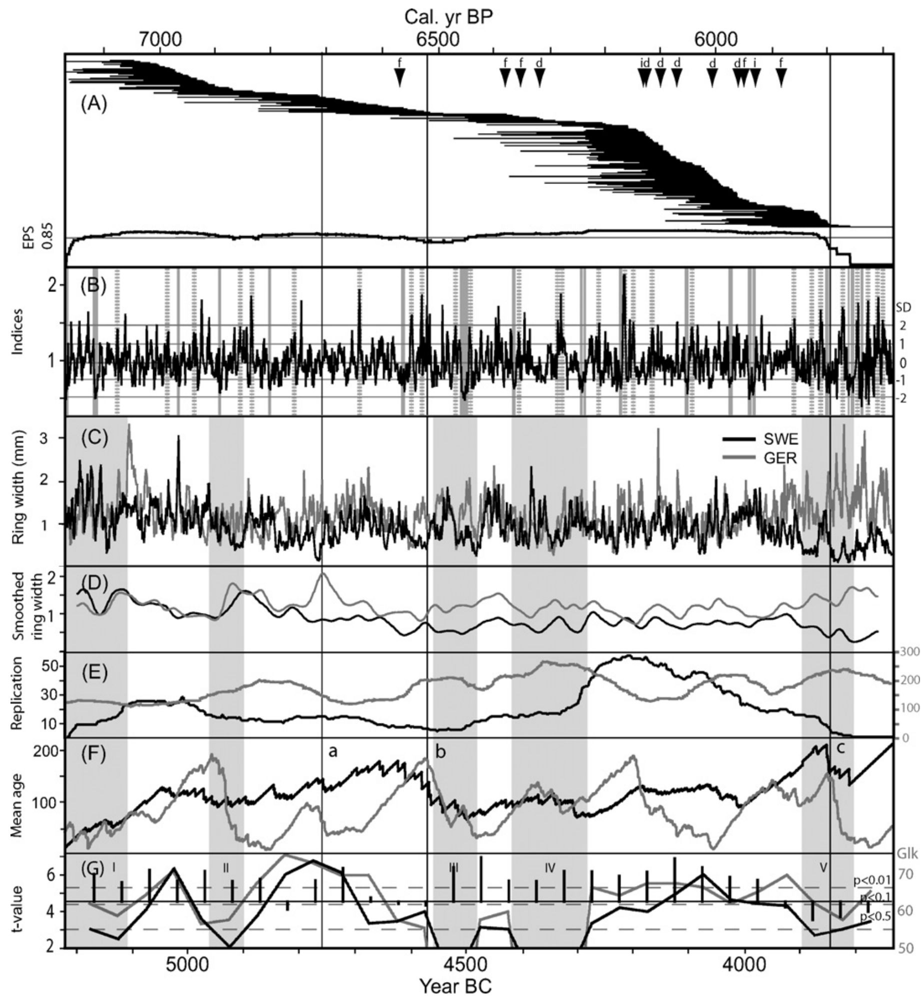

Fig. 3. (A) 161 subfossil trees from South Sweden were used to construct a 1492-year chronology. Individual trees are represented by black horizontal bars, the lengths of which represent their numbers of measured annual rings, with their positions determined by dendrochronological cross-dating. Disturbance events are shown with arrows, indicating samples affected by fire (f), post-mortem degradation (d) and insect burrows (i). The curve shows the evolving EPS and the grey line represents the level required (0.85) for a particular part of the chronology to be considered reliable. (B) The black curve is the chronology based on individual samples standardized with a 67% spline (dimensionless indices). Periods of three years in a row or longer with weak (−1 standard deviation (SD)) growth are highlighted with grey bands and corresponding periods of strong growth (+1 SD) are highlighted with hatched bands. The grey lines show the SD values. (C) Comparison between the averaged ring-width chronologies from southern Sweden (black) and Germany (grey) (Eckstein et al., 2009; Leuschner, unpublished data). (D) Ring-width records from Sweden (black) and Germany (grey) smoothed with a 30-year filter. (E) The Swedish (black) and German (grey) replication records. Note the different scales (Swedish values to the left and German to the right). (F) Mean age records from southern Sweden (black) and Germany (grey) showing average ages of all overlapping samples during each year. The lines labelled a–c indicate parallel drops in average age of the Swedish and German material. (G) Statistical comparison between the Swedish and German chronologies based on stepwise moving of a 100-year window along the time series. The black and grey lines represent observed changes in *t*-values and Glk, respectively. The significance levels of the Glk are shown with hatched lines. Five periods with *t*-values below 3 are highlighted with vertical grey zones (I–V). The bar graphs show correlation values (*r*) between 0.5 and −0.5, and the black horizontal line represents 0.

A germination period occurred at c. 5220–5100 BC, followed by relatively stable conditions. Clear drops in mean age occurred at c. 4575, 4300, 4010 and 3850 BC (Fig. 3F). After 4000 BC no substantial germination was observed and the remaining trees increased in age before they finally died.

Cross-match and correlation variability

The observed patterns of cross-match and correlation between the Swedish and German chronologies, based on a stepwise moving-window test, are shown in Fig. 3G. During five discrete periods, centred at 5100, 4915, 4550, 4350 and 3900 BC (labelled I–V in Fig. 3), there was no significant cross-match between the Swedish and German chronologies. However, the correlation remained positive during four of these periods. The periods without significant cross-match are characterized by relatively low sample depths (1–15) and evolving EPS values close to 0.85. EPS values below 0.85 were recorded during parts of periods I, III and V (Fig. 3).

Discussion

The subfossil Swedish material

Based on knowledge of present-day bog-pine ecology, the observed growth variability of our new Swedish chronology (Figs. 3B and 4) likely reflects climate-related hydrological variations within the bogs. Accordingly, periods of enhanced bog-pine growth in general reflect lowerings of the groundwater table as a result of dry and/or warm conditions with reduced precipitation and/or increased evaporation. Growth depressions on the

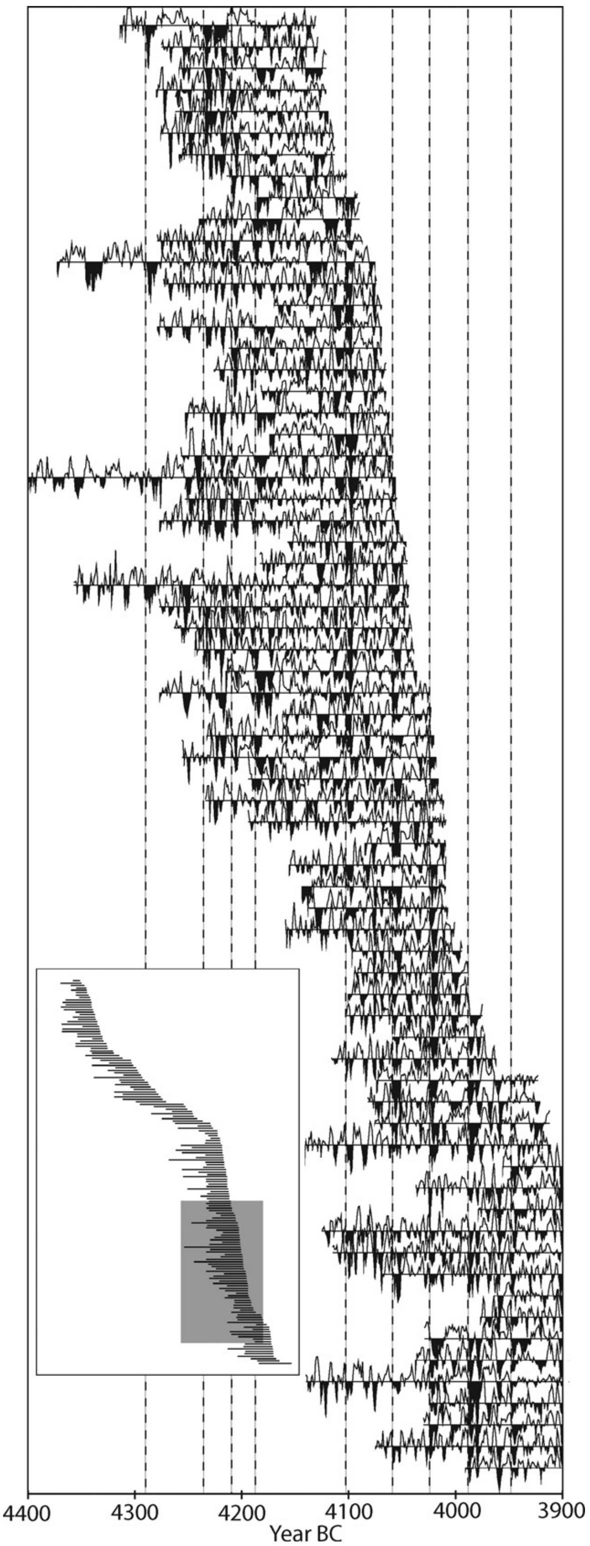

Fig. 4. Example of growth variability patterns observed for individual samples spanning the period 4400–3900 BC of the new 1492-year Swedish bog-pine chronology. The shaded area on the insert marks the selected part of the chronology. Periods with ring-width indices below average are highlighted in black and onsets of nine distinct and parallel growth depressions are indicated by vertical dotted lines.

other hand are associated with relatively high groundwater tables, most likely related to colder and/or wetter conditions. Most of the individual trees used in the Swedish bog-pine chronology display similar growth variability and synchronous growth depressions (Fig. 4) indicating changes affecting the entire pine population. Strong common signals among the majority of the cross-dated samples emphasize the strength of subfossil bog pines as indicators of climate and humidity reconstructions.

The mean age and replication records, based on the South Swedish material, provide information on population dynamics at the study sites. The mean-age record shows improving conditions for bog-pine growth and a trend of ageing trees from c. 5200 to c. 4600 BC when the sampled pines were on average c. 160 years old. Decreases in mean age caused by dying trees took place around 4770, 4570, 4010 and 3850 BC (Fig. 3F). However, the decrease in mean age at c. 4300 BC (Fig. 3F) is not a die-off event, since the replication record shows a strong germination phase at this stage, with more than a doubling of sample depth. Hällarydsmossen was probably covered by a relatively dense pine forest around 4200 BC, followed by a general decline in forest cover without any notable reproduction. The growth rate of *Sphagnum* peat is clearly influenced by shifts in the precipitation–evaporation balance, and peat initiation events in mid-Sweden have been coupled to climatic shifts to colder and/or wetter conditions (Rundgren, 2008). Opposite, the net growth of peat decreases during relatively warm and/or dry periods. According to Charman (2007), millennial-scale water-table changes in peatlands are controlled mainly by precipitation rather than temperature. Frequent signs of post-mortem degradation and insect burrows were observed on trees that grew on Hällarydsmossen at c. 4200–4000 BC (Fig. 3A) when the growth conditions were especially favourable as indicated by the replication record (Fig. 3E). This confirms relatively dry surface conditions at this stage, with slower peat accumulation and prolonged exposure of dead wood to decay processes. Relatively dry peat-surface conditions are also indicated by fire scars in samples from Hällarydsmossen at 4613, 4420, 4400, 3996 and 3931 BC (Fig. 3A).

Regional comparison between subfossil bog-pine chronologies

The long-distance cross-match and the positive correlation between the bog-pine chronology from northwestern Germany (Eckstein et al., 2009; Leuschner, unpublished data) and our new chronologies from southern Sweden are noteworthy. This strengthens the hypothesis of Leuschner et al. (2002), based on bog-oak records from continental Europe and Ireland, that large-scale climate dynamics influenced peatland tree growth in northwestern Europe during the mid-Holocene. The generally warm and dry climate mode during the HTM (Renssen et al., 2009) was apparently characterized by spatially coherent sub-decadal-scale variability that provided stronger impacts on bog-pine growth and more limited influences from local hydrology. The comparison of smoothed ring-width records (30-yr filter) from Sweden and Germany also show apparent similarities on the decadal to centennial scale, especially at c. 5200–4800 BC and c. 4500–4100 BC (Fig. 3D), although, in general, the correlation is weaker ($r = 0.18$) than the one based on annually resolved data.

During five periods the cross-match on the centennial scale between the Swedish and German chronologies is insignificant (labelled I–V in Fig. 3G), of which the longest (IV) lasted for c. 225 years, 4445–4220 BC (*t*-value: 3.4, Glk: 58 $p < 0.5$, $r = 0.32$). Low replication often reduces the cross-match statistics, as evident in periods I, II, III and V when EPS values are close to or partly below the 0.85 limit. However, the correlation remained positive during all except the final period with insignificant cross-match and reached negative values around 4600 and 4800 BC. Other possible

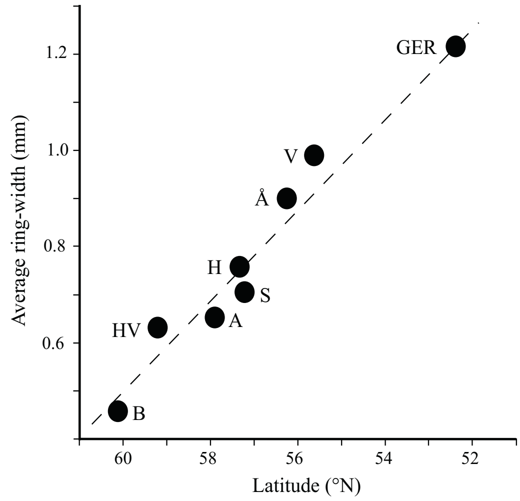

Fig. 5. Average ring-width of bog pines expressed as a function of latitude. The data are based on subfossil material from Lower Saxony in Germany (GER) (Eckstein et al., 2009; Leuschner, unpublished data), Viss mosse (V), Åbuamossen (Å) (Edvardsson, 2010) and Hällarydsmossen (H). Data obtained on modern material shown for comparison were derived from Store mosse (S), together with data from Anebymossen (A), Hanvedsmossen (HV) and Bredmossen (B) (Linderholm et al., 2002). Locations of sites are shown in Fig. 1.

reasons for periods with insignificant cross-match statistics might be anomalously cold and/or wet climatic conditions in any of the two regions, which may have resulted in elevated groundwater levels, reduced tree growth and increased impact of local groundwater variability. For example, apart from generally low replication values, periods II and III could reflect transient wet periods with dying trees as indicated by distinct decreases in average ring-width (Fig. 3C). Within most of period IV, however, mean age and replication increased in both regions, indicating improving conditions for bog-pine growth (Fig. 3E and F). Towards the end of period IV the low correlation could be related to increased abundance of juvenile trees, possibly in combination with a large-scale climate regime shift. Similar correlation shifts have been observed in oak records from northern Europe (Kelly et al., 2002). The periods of general agreement on the centennial scale are noteworthy, suggesting that both regions experienced relatively continental conditions with warm summers and cold/dry winters. This may be the result of displacement of the westerlies to more northerly positions, allowing continental air masses to penetrate further west.

The average ring width decreases over time in the Swedish bog-pine data, although this is more likely related to site-specific conditions than climate. The average ring width of the bog-pine records were 0.74 mm at Hällarydsmossen, 1.00 mm at Viss mosse and 1.22 mm in the German material, showing a north-south gradient with thinner annual rings at the more northerly sites. Also, the subfossil material from Åbuamossen (Edvardsson, 2010), with an average ring width of 0.89 mm, matches this pattern, and the modern bog-pine material shows even lower values (0.44–0.70 mm), providing further evidence of the north-south gradient in growth rate (Fig. 5). A similar trend of thinner tree rings at more northerly sites along a latitudinal gradient has previously been reported by Naurzbaeva et al. (2004). Slightly lower average temperatures northwards (Fig. 1) generate shorter growth seasons and less evaporation, which results in wetter bog-surface conditions and decreased bog-pine growth rate. Apart from this, regionally different precipitation patterns may have had an influence on the observed growth patterns.

Comparisons with modern bog-pine material

The cross-match and correlation data obtained on the subfossil material presented here were compared to corresponding data from four peat bogs with living pine trees in southern Sweden (Fig. 1), three previously published chronologies from Hanvedsmossen, Anebymossen and Bredmossen (Linderholm et al., 2002) and a 159-year chronology from Store mosse (Edvardsson, unpublished data). The Store mosse chronology was developed from 35 pine trees growing on peat exceeding 2 m in depth on an intact raised-bog surface. The four chronologies were statistically and visually compared based on methods identical with those used for the subfossil material. The cross-match and correlation between the two northern sites Bredmossen and Hanvedsmossen are convincing (196 year overlap, t-value 7.2, Glk 62 $p < 0.1$, $r = 0.58$), otherwise the common signals were weak. Comparison of the records from Hanvedsmossen and Anebymossen, which are separated by c. 320 km, exhibits a t-value of 3.9, a Glk 65 ($p < 0.01$), and $r = 0.34$. The Store mosse chronology did not show any statistically significant cross-match, but positive correlation (r-values between 0.34 and 0.58), against the other site chronologies even though it is located only c. 70 km from Anebymossen. These comparisons demonstrate that the common growth signals and cross-matches between modern bog-pine populations located c. 70–400 km apart (Fig. 1) are weaker than between the subfossil records, which are developed on material from sites separated by 500–700 km. However, the modern chronologies are relatively short, only about 200 years, which affects the t-values. Correlation tests yielded positive r-values between the four modern chronologies, which are slightly higher than between the subfossil ones. Modern bog-tree material may often show growth patterns reflecting strong influences from e.g. drainage and peat cutting. Increased human impact on peat deposits in the region has been recorded during the last 4000 years (Linderholm and Leine, 2004) while human impact was probably negligible before c. 4000 BC, although the bogs from which the modern records were obtained are relatively undisturbed. The convincing long-distance cross-match between the mid-Holocene bog-pine chronologies from Sweden and Germany may therefore indicate a more coherent climate control of pine growth across large parts of northern Europe during the HTM than at present.

Stand dynamics of Swedish and German bog-pine populations

It is likely that different environmental conditions influenced stand dynamics of subfossil pine populations on the Swedish and German peat bogs, respectively. On the German bogs, the pine populations were commonly exposed to competition with other tree species, mainly oak, birch (*Betula bubescens*) and alder (*Alnus glutinosa*) (Eckstein et al., 2010), whereas the Swedish bog pines probably had a dominant position with limited competition from other tree species. Remains of birch and alder were found at Viss mosse and Hällarydsmossen, but in limited numbers and often in stratigraphic positions indicating that these trees grew on the bogs prior to the investigated pine material. Another difference is the general stratigraphic position of the pine horizons in Swedish and German peat sequences. Pine layers in German bogs are often located at the transition between fen peat and *Sphagnum* peat (Leuschner et al., 2007; Eckstein et al., 2010), while the material at Viss mosse, Hällarydsmossen and Åbuamossen (Edvardsson, 2010) was found within the *Sphagnum* peat. Frenzel (1983) and Anderson et al. (2003) suggest that fen-peat transitions in German bogs were diachronous and mainly affected by local site conditions. However, studies by Eckstein et al. (2009, 2010) on subfossil pine populations in transition layers show synchronous tree population dynamics at different sites, which indicates that growth changes were forced by climate variability rather than site-specific ontogeny.

The establishment of pine populations on German bogs was probably confined to the restricted ecological niche at the fen-bog transition zone, generally too wet, acidic and nutrient-poor for species such as oak. Disturbances involving broad-leaved trees could also have enabled germination events of pine on German bogs, whereas establishment phases on Swedish bogs were mainly related to decreases in bog-surface wetness. Fen-bog transitions on German peatlands were generally more long-lasting prior to c. 3000 BC, which resulted in extended establishment phases for bog pines (Eckstein et al., 2009).

A comparison between Swedish and German mean-age records show no clear common population dynamics apart from some synchronous drops in mean age at c. 4770, 4570 and 3850 BC (labelled a, b and c in Fig. 3F), possibly caused by shifts to wetter conditions. Mean ages in both regions increased over the period of 5200–4950 BC, which indicates improved or stable conditions. The German mean age record shows larger variability than the Swedish, possibly as a result of stronger competition between species. No common trends were detected in the respective replication records (Fig. 3E). Hence, the divergent population dynamics may reflect a combination of different competition situations and site-specific peatland ontogeny.

In contrast, mean-age records obtained from Irish and continental bog oaks (Fig. 6) show clear common trends during the mid-Holocene (Leuschner et al., 2002). Therefore, improved growth conditions may have resulted in similarities in large-scale population dynamics of bog oaks and enabled establishment of pine populations on areas previously too wet and unfavourable for both species (Fig. 6). The temporal distribution of bog-pine populations may reflect large-scale dynamics in a more accurate way than population dynamics as there are few similarities between the mean age and replication records from Sweden and Germany. The comparisons of modern bog-pine records indicate that tree growth was affected by local hydrological changes during recent centuries, while the noteworthy long-distance cross-match and correlation between Swedish and German subfossil chronologies in combination with their largely similar temporal distributions (Fig. 6) demonstrate forcing by large-scale climate dynamics during the HTM.

Long-term palaeoclimatic implications

Our new tree-ring chronology demonstrates that pine occurred frequently on peat bogs in southern Sweden during the HTM, at least during the interval of almost 1500 years represented by the combined site records (c. 5200–3750 BC). As indicated by the compilation of lake-level data by Yu and Harrison (1995), a gradual northward expansion of summer drought across northern Europe was initiated around 7000 BC, and conditions were drier than at present, especially at c. 5000 BC (Hammarlund et al., 2003; Seppä et al., 2005). As shown in Fig. 6, the regionally representative lake-level reconstruction by Digerfeldt (1988) supports the hypothesis that pine established and spread across the studied sites in southern Sweden as a response to drier conditions and lowered groundwater levels. This is also consistent with the presence of pine at Åbuamossen at c. 2150–1200 BC (Edvardsson, 2010) during a period of relatively low lake levels (Fig. 6). Peat initiation periods in South-central Sweden have been dated to 7700–6000 BC (9500–8000 cal. BP) and 4000–3500 BC (6000–5500 cal. BP), and attributed to increased precipitation associated with increased influence of westerly winds (Rundgren, 2008). The first of these peat initiation periods coincides with absence of Swedish bog pines, and the second corresponds well with the degeneration phase observed at Hällarydsmossen (Fig. 3A and E).

The high abundance of pine trees at the two Swedish sites studied here coincides with maximum occurrence of bog pines in Germany (Eckstein et al., 2009; Leuschner, unpublished data). Together with the long-distance dendrochronological cross-match and positive correlation between the two regions, this indicates generally favourable conditions for tree growth on bogs across large parts of Europe during the HTM. The regional coherence of climate dynamics during the HTM is also evidenced by broadly similar long-term trends in lake-level data from southern Sweden (Digerfeldt, 1988; Hammarlund et al., 2003) and central Europe (Magny, 2004). Lowered lake-levels as a result of relatively dry conditions were likely associated with decreased wetness on peatlands and improved growth conditions for bog pines in both regions, such as at c. 5000 BC (Fig. 6). While pine colonized bogs in southern Sweden as a result of reduced bog-surface wetness, this regional decrease in effective precipitation enabled pine to establish on fen peat in settings that were generally too wet for oak in northwestern Germany (Eckstein et al., 2009).

Interestingly, contrary to the successful cross-match with the German material, attempts failed to cross-match the South Swedish chronology against the 7400-year pine chronology from the Torneträsk area in northernmost Sweden (Grudd et al., 2002). There are several likely explanations to this, e.g. the vastly different seasonal climate in northern Sweden, different growth responses in the Torneträsk material which is derived from pines growing on mineral soils, and probably even more important, different atmospheric circulation patterns in southern and northern Sweden during the HTM. Further evidence of such a distinction, perhaps related to a generally more oceanic climate in northern Fennoscandia during the early Holocene (Hammarlund et al., 2002, 2004; St. Amour et al., 2010), is provided by absence or scarcity of subfossil pine material older than c. 4000 BC at sites in west-central Sweden (Gunnarson et al., 2003).

The lower frequency of massive stump horizons younger than c. 2000 BC (Fig. 6), indicates a shift to colder, wetter and more unfavourable growth conditions for bog pines in northwestern Europe. This transitional phase, which is sometime referred to as the neoglaciation (Nesje et al., 1991; Holzhauser et al., 2005), was probably caused by a major rearrangement of atmospheric circulation patterns in the North Atlantic region, which led to decreased summer temperature, increased effective precipitation and stronger westerlies (Hammarlund et al., 2003; Seppä et al., 2005; De Jong et al., 2009). In southern Sweden this transition to more unstable climatic conditions at the end of the HTM has been dated to 2650–1450 BC with two distinct, step-wise shifts centred at c. 2450 BC and c. 1950 BC, respectively, superimposed on the cooling trend (Jessen et al., 2005; De Jong et al., 2009). As shown in Fig. 6, the transitional phase is accompanied by rising lake levels and successively less coherent population dynamics of continental and Irish bog-oak populations (Leuschner et al., 2002), the latter providing further evidence of increased regional climate variability. Based on plant macrofossil analysis of peat deposits in Denmark and northern Germany, Barber et al. (2004) recorded significant shifts to increased bog-surface wetness at c. 1400 BC, broadly coinciding with the youngest know subfossil bog-pine records in Germany and southern Sweden.

Conclusions and future prospects

A 1492-year tree-ring chronology developed from South Swedish subfossil bog pines was absolutely dated to 5219–3728 BC by cross-dating with a bog-pine chronology from northwestern

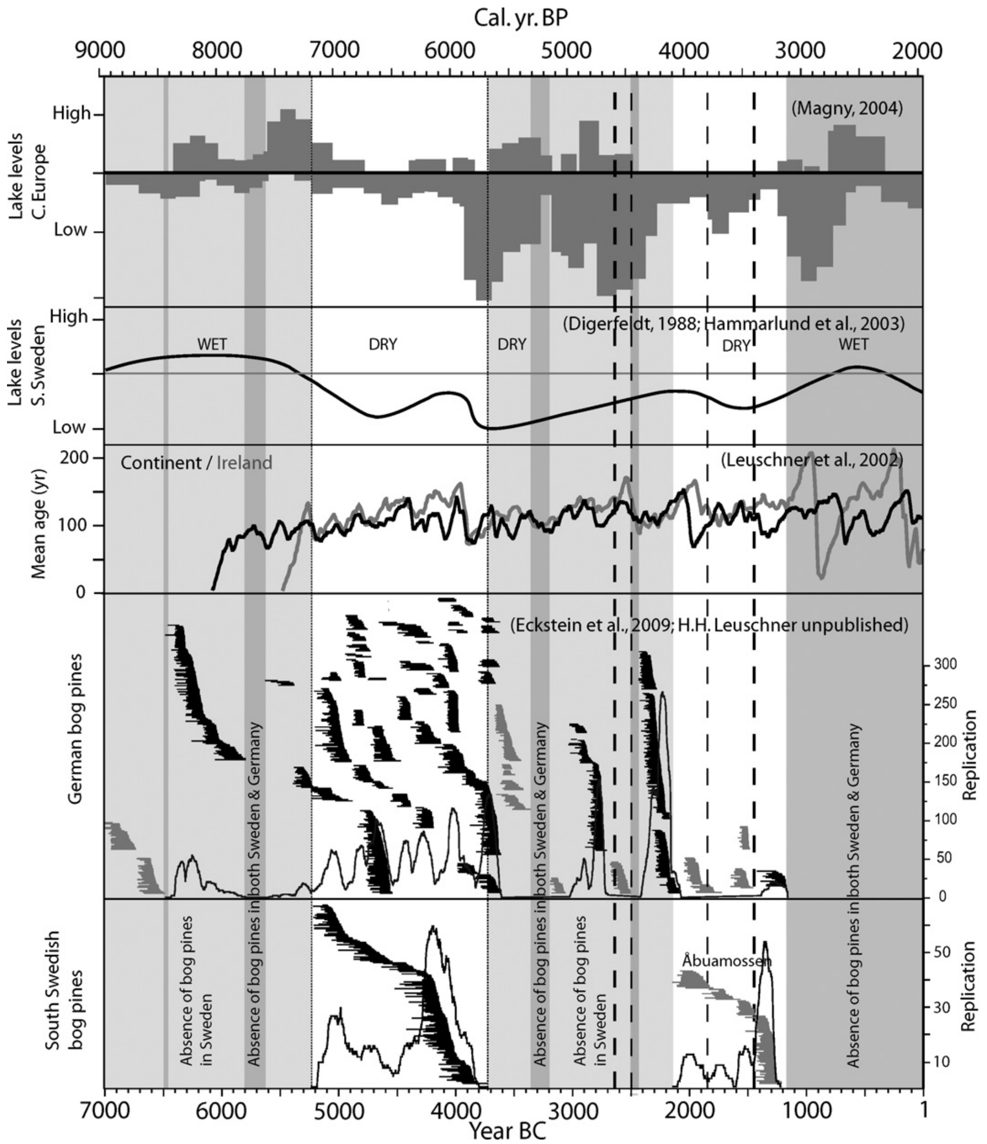

Fig. 6. Comparison of lake-level fluctuations in central Europe (Magny, 2004) and southern Sweden (Digerfeldt, 1988; Hammarlund et al., 2003), mean age variations of bog oaks in continental Europe and Ireland (Leuschner et al., 2002), and the temporal distribution of bog-pine tree-ring records from Lower Saxony, Germany (Eckstein et al., 2009; Leuschner, unpublished data) and southern Sweden (this study; Edvardsson, 2010). The South Swedish and German bog-pine records cluster during a common period within the Holocene Thermal Maximum (HTM) and broadly coincide with maximum correlation between population dynamics of continental and Irish bog oaks, as well as with generally low lake levels. Periods of absence or low coverage of bog-pine records are highlighted in grey. Samples from absolutely dated bog-pine records are shown in black and radiocarbon-dated records are grey. The period within heavy dashed lines (2650–1450 BC) represents the transitional end of the HTM in southern Sweden, within which two distinct shifts towards colder and wetter conditions occurred (thin dashed lines), centred at c. 2450 BC and c. 1950 BC, respectively (Jessen et al., 2005).

Germany. Notably strong cross-match statistics together with a positive correlation between the chronologies provide evidence of coherent, large-scale climate dynamics influencing pine growth on bogs across large parts of northwestern Europe during the HTM.

Warm and/or dry summer conditions are generally more favourable for tree growth on bogs in the relatively maritime climate regime that characterizes southern Sweden and northern Germany. Long-distance cross-match and correlation are therefore more likely during periods of relatively low effective precipitation when established pine populations are probably influenced to a larger extent by regional climate variations than by local hydrological changes. This hypothesis gains support from the generally poor cross-match between modern Swedish bog-pine chronologies. No subfossil bog-pine tree-ring records younger than c. 1200 BC are presently known from Germany or southern Sweden, but ongoing work strives to extend and complement existing records as a basis for more detailed climate reconstructions. Additional bog-pine records based on large numbers of subfossil trees are needed to cover the entire HTM and the transition into the neoglacial period. Deeper knowledge of growth-controlling factors is also necessary to fully understand the observed variations in cross-match statistics between distant populations. Further studies of potential impacts of e.g. flooding, drought and winter precipitation on bog-pine growth variability are also needed. Snow-rich winters may for instance result in wet bog surfaces during spring and early summer, which most likely creates unfavourable bog-pine growth conditions. However, preliminary tests on the Store mosse data did not show any clear relations. Continued studies of both living and subfossil bog pines are therefore needed to fully understand the mechanisms behind observed changes in growth variability and their exact relations to, temperature, precipitation and local hydrology.

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Appendix II

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Holocene peatland development and hydrological variability inferred from bog-pine dendrochronology and peat stratigraphy – a case study from southern Sweden

JOHANNES EDVARDSSON,* HANS LINDERSON, MATS RUNDGREN and DAN HAMMARLUND
Quaternary Sciences, Department of Geology, Lund University, Sölvegatan 12, SE-223 62 Lund, Sweden

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ABSTRACT: Dendrochronological analysis was applied to subfossil remains of Scots pine (*Pinus sylvestris* L.) buried in a South Swedish peat deposit. In combination with peat stratigraphy, this approach was explored for its potential to provide information on the local hydrological and depositional history at the site, forming the basis for a regional palaeohydrological analysis. A 726-year ring-width chronology was developed and assigned an absolute age of 7233–6508 cal a BP (5284–4559 BC) through cross-dating with German bog-pine chronologies, whereas two short additional records of older ages were radiocarbon dated. Registration of growth positions of individual trees allowed assessment of the spatial dynamics of the pine population in response to hydrological changes and peatland ontogeny. Annually resolved growth variability patterns in the pine population reveal several establishment and degeneration phases, probably reflecting fluctuations in bog-surface wetness. A major establishment phase at 7200–6900 cal a BP reflects the onset of a period of lowered groundwater level, also indicated by increased peat humification, and a development consistent with regional temperature and lake level reconstructions revealed from other proxies. This study demonstrates that subfossil bog-pine populations may provide annually to decadally resolved reconstructions of local groundwater variability, which are highly relevant in a long-term palaeoclimatic context. Copyright © 2012 John Wiley & Sons, Ltd.

KEYWORDS: Holocene thermal maximum; palaeohydrology; Scots pine; subfossil trees.

Introduction

The impact of ongoing and future climate change on ecosystems and society is a crucial issue that requires understanding of the climate system, natural climate variability and its forcing mechanisms. Although improved palaeoclimate methodology and more accurate dating methods have resulted in more reliable and detailed reconstructions, and thereby advanced our understanding of climate dynamics during the present (Holocene) interglacial (Mayewski *et al.*, 2004; Wanner *et al.*, 2008), a number of issues remain. For example, it is surprising how little we know about past hydrological changes. This is partly because of the lack of direct precipitation proxies applicable to natural climate archives. Instead, most palaeohydrological data reflect changes in the precipitation–evaporation balance as manifested in, for example, water levels in lakes and bogs, and it is often difficult to separate the effect of temperature on evaporation from the precipitation signal in this type of data. Moreover, because of relatively slow deposition, palaeohydrological records based on lake sediments and peat rarely provide better than multi-decadal to centennial resolution.

Since the last deglaciation large continental areas have become covered by peatlands. There are approximately 400 million hectares of peatlands covering ca. 3% of Earth's land surface (Strack, 2008). About 90% of these peatlands are located in the northern hemisphere (Strack, 2008), and peatlands cover ca. 15% of Sweden (Borgmark and Wastegård, 2008). As peatlands cover significant land areas and constitute one of the largest terrestrial carbon reservoirs (Smith *et al.*, 2004), improved understanding of the dynamics and hydrology of peatlands is required to enable accurate reconstructions of Holocene climate variability and predictions of future climate change.

Raised bogs are lens-shaped peat deposits with their centres rising above the surroundings, and bog-surface wetness depends primarily on precipitation, temperature and evaporation. Peat-forming plants (typically *Sphagnum* mosses) depend for their nutrients and moisture on atmospheric precipitation and thus are sensitive to climate change (Aaby, 1976). Variations in effective moisture and groundwater tables of peat deposits are reflected by changes in species composition and peat humification, which therefore can be used for reconstructions of bog-surface wetness (Aaby, 1976; van Geel, 1978; Barber *et al.*, 1994). In Sweden, the potential of peat-stratigraphic records has been explored by von Post and Granlund (1926), and the degree of peat humification was found to be a useful proxy for variations in bog-surface wetness by Granlund (1932). These studies were based on extensive peatland surveys, revealing visible transitions from more to less humified peat, termed recurrence surfaces, which were believed to reflect large-scale shifts in effective moisture during the Holocene (Granlund, 1932; Aaby, 1976). Relatively warm and dry conditions result in enhanced humification, while peat formed during cold and wet periods is less influenced by decomposition processes (Mitchell and Ryan, 1997). Following recent development of more accurate and quantitative methods, *Sphagnum* humification data from ombrotrophic peatlands may now at best provide decadally resolved palaeohydrological records over the mid- to late Holocene (Barber *et al.*, 2004; Charman, 2007).

Series of annual growth rings in trees have proved to be a valuable source in palaeoclimatic research (Fritts, 1976; Schweingruber, 1988; Cook and Kairiukstis, 1990). Trees growing at or close to their limits of distribution are more likely to be sensitive to climate and their rings provide quantitative climate information of annual resolution (Cook and Kairiukstis, 1990). Scots pine (*Pinus sylvestris* L.) is a tree species

*Correspondence: J. Edvardsson, as above.
E-mail: johannes.edvardsson@geol.lu.se

commonly found on the drier parts of ombrotrophic bogs in Sweden (Zackrisson, 1977; Rydin *et al.*, 1999), indicating that it grows close to its physiological limit in this environment. Pine often invades open sites after disturbances such as climate change, drainage, deforestation, fire or insect invasion (Zackrisson, 1977; Frelechoux *et al.*, 2000; Eckstein *et al.*, 2010), and pine populations have been established repeatedly on many Scandinavian peat bogs during the Holocene (Lundqvist, 1969; Gunnarson *et al.*, 2003). Recurring pine establishment phases are therefore likely to reflect past shifts to drier bog-surface conditions, which in turn may be closely related to Holocene climate variations.

Because tree growth on peat bogs is highly dependent on the depth to, and fluctuations of, the water table beneath the root system (Boggie, 1972; Frelechoux *et al.*, 2000; Vitas and Erlickytë, 2007), growth dynamics of bog trees may differ from trees on surrounding solid ground. Elevated groundwater levels commonly generate unfavourable growth conditions as a result of several physical, chemical and biological processes (Boggie, 1972; Vitas and Erlickytë, 2007). Together these factors produce an environment where tree growth is strongly inhibited by lack of oxygen, accumulation of CO_2, reduction of Fe and formation of toxic compounds (Vitas and Erlickytë, 2007). Additional detrimental effects are a thinning of the unsaturated zone from which the roots receive nutrients (Schouwenaars, 1988; Hunt *et al.*, 1999; Linderholm, 2001; Eckstein *et al.*, 2011) and dying inundated roots (Eckstein *et al.*, 2011). This often results in growth reductions detectable in ring-width records obtained from bog trees (Boggie, 1972; Leuschner *et al.*, 2002; Linderholm *et al.*, 2002; Eckstein *et al.*, 2009). Therefore, synchronous growth reductions have been attributed to periods of relatively high groundwater levels. In contrast, lowered groundwater levels in peat bogs may trigger increased tree growth and phases of tree germination. Tree settlements are often observed only in the marginal parts of raised bogs, mainly because groundwater levels generally are lower in these situations (Rydin *et al.*, 1999; Frelechoux *et al.*, 2000). However, during drier periods more widespread establishment appears to take place. If the bog continues to grow, these trees may become buried and preserved as stump horizons.

Major investigations of subfossil pine and/or oak (*Quercus robur* L.) from peat bogs have previously been carried out in north-western Germany (Leuschner, 1992; Leuschner *et al.*, 2002, 2007; Eckstein *et al.*, 2009, 2010, 2011) Ireland (Pilcher *et al.*, 1995; Turney *et al.*, 2006), Great Britain (Lageard *et al.*, 1995, 2000; Moir *et al.*, 2010) and Lithuania (Pukiene, 1997). In Sweden, dendrochronological studies of subfossil trees have mainly been based on wood preserved in lake sediments (Briffa *et al.*, 1990; Grudd *et al.*, 2002; Gunnarson *et al.*, 2003; Gunnarson, 2008). Systematic studies of trees buried in Swedish raised bogs started relatively recently and are so far restricted to a few sites in the central and northern parts of the country (Gunnarson, 1999, 2008) and work in progress at sites in southern Sweden (Edvardsson, 2006, 2010; Edvardsson *et al.*, 2012).

The aim of this study is to demonstrate how peat stratigraphy and dendrochronology in combination can provide detailed records of local climatic and environmental change, in particular through spatial analysis of bog-pine tree-ring records. Annually resolved palaeohydrological data obtained from dendroclimatic analysis of populations of bog trees preserved in peat deposits can contribute to regional-scale Holocene climate reconstructions based on other, commonly less highly resolved palaeoclimate records.

Material and methods

Site description and fieldwork

This study is based on material from Viss mosse (55°51′N, 13°49′E; Fig. 1), a raised bog located on the bedrock ridge Linderödsåsen, southern Sweden (ca. 173 m a.s.l.). The local bedrock is composed mainly of orthogneiss with dykes of dolerite, covered by ca. 5 m of sandy till with a shallow morphology (Malmberg Persson, 2000). The area was deglaciated at ca. 15 000 cal a BP, and ridges, drumlins and eskers in the area indicate a deglaciation towards the north-east (Malmberg Persson, 2000). The bog is situated in a depression surrounded by slightly undulating topography (Fig. 1), and the basin lacks obvious natural in- and outflows. Runoff from the marginal fen passes through an artificial ditch towards the south-west but probably occurred as diffuse seepage in the past. The peat deposit covers about 2 km^2 and its catchment area is ca. 6 km^2. Initial peat excavation at Viss mosse started around 1910 and due to extensive peat cutting during recent decades numerous stumps and trunks are exposed at the present surface of the bog (Fig. 2).

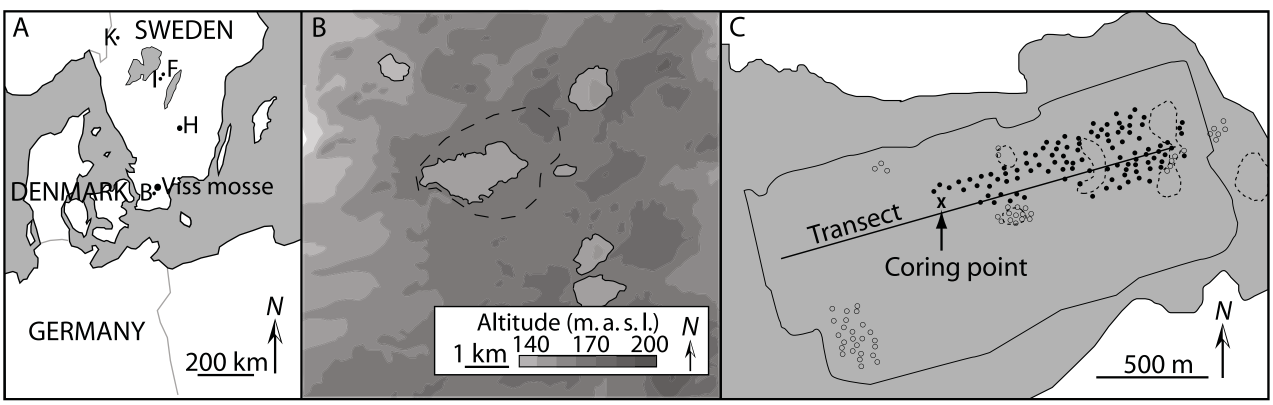

Figure 1. (A) Location of the peat bog Viss mosse, southern Sweden. Other sites discussed are indicated: Hällarydsmossen (H; Edvardsson *et al.*, 2012), Lake Bysjön (B; Digerfeldt, 1988), Lake Igelsjön (I; Hammarlund *et al.*, 2003), Lake Flarken (F; Seppä *et al.*, 2005) and Kortlandamossen (K; Borgmark and Wastegård, 2008). (B) Topographic setting of the study site and adjacent peat bogs. The catchment of Viss mosse (ca. 6 km^2) is indicated by the dashed line. (C) Locations of samples collected at the site; 102 *in situ* trees (black dots) and 53 trees removed from their original growth positions and collected at wood deposits (open circles). The shading indicates the distribution of peat, the cross shows the point where the stratigraphic sequence was recovered (Fig. 5), the straight line represents the transect across the bog (Fig. 6), the solid contour line shows the area of peat excavation and the dotted contour lines show protruding till hummocks.

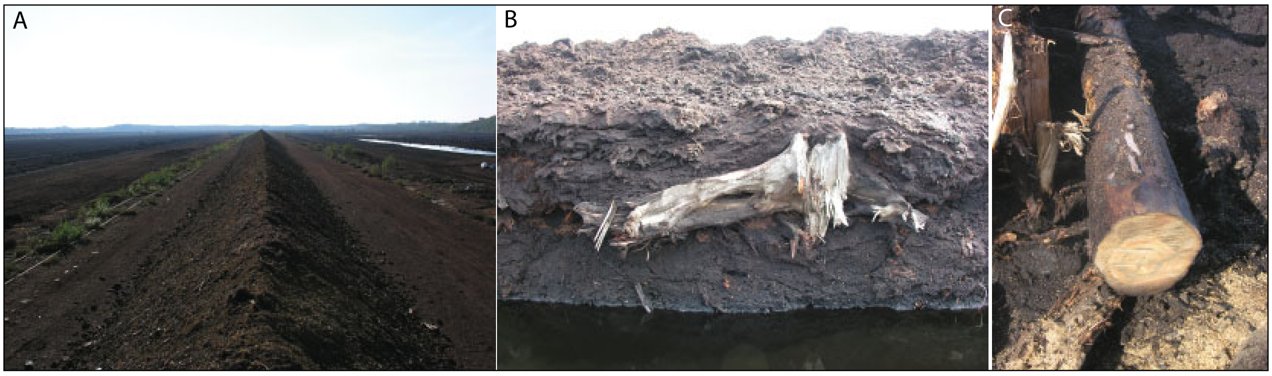

Figure 2. (A) View towards the west over Viss mosse from a ridge of excavated peat. (B) *In situ* pine stump in a drainage ditch. The trees are rooted in *Sphagnum* peat. (C) A well-preserved pine trunk, the ring sequence of which covers the period 7026–6919 cal a BP (5077–4970 BC). This figure is available in colour online at wileyonlinelibrary.com/journal/jqs.

During fieldwork campaigns in 2006, 2009 and 2010, cross-sections from subfossil pine trees were collected with a chainsaw (Fig. 2). In total 155 samples were collected, 102 of which were obtained from *in situ* trees or stumps and trunks that could be traced to their exact growth positions. The remaining 53 samples were collected from nearby deposits of stumps and trunks removed from their growth positions on the bog during recent years in order to facilitate commercial peat excavation. The exact growth positions of *in situ* trees were obtained with a handheld GPS device. Information about morphology, presence of pith, bark, fire marks or other damages, together with sampling distance from the roots was recorded for each sample. Trees with fewer than 50 annual rings were considered unlikely to cross-date and were therefore excluded.

Overlapping peat and sediment cores were obtained from a nearly complete succession in the central part of the bog (Fig. 1), using a 1-m-long Russian peat sampler, 5 cm in diameter, to provide a representative peat stratigraphy for comparison with the dendrochronological data. To get an impression of the total thickness of the organic layers and the morphology of the till surface beneath, depths to the mineral soil were measured with a probe along transects across the bog.

Measurements and data analysis

Development of ring-width records

In order not to dry out and deform the wood, all samples were stored at 4°C prior to preparation and measurements. The surfaces of the cross-sections were prepared by cutting several radii with a razor blade, and chalk was applied to enhance the appearance of ring borders and cell structures. Ring-width (RW) series of individual radii were created based on measurement of annual rings with a precision of 0.01 mm, using a LINTAB measuring table connected to a stereomicroscope and a computer using the TSAP (Rinn, 1996) and CATRAS (Aniol, 1983) softwares. To identify wedging rings and possible measuring errors, at least two radii, separated by 90° or more if possible, were measured for each sample. Two statistical tests were applied to evaluate similarities between individual RW series; coefficient of parallel run and *t*-value. The coefficient of parallel run, also referred to as Gleichläufigkeit (Eckstein and Bauch, 1969), measures the year-to-year agreement between two series based on the sign of agreement. The *t*-value (Baillie and Pilcher, 1973) compares the actual difference between two means in relation to the variation in the data. These statistical analyses are commonly used in dendrochronology for assessment of significance of correspondence between individual RW series, a process generally referred to as cross-dating or cross-matching (Baillie and Pilcher, 1973; Fritts, 1976). First, the two or more radii from individual samples were cross-dated, and if matching, they were averaged into an RW series for each tree. Subsequently, the RW series from all individual trees were cross-dated against each other. In general, *t*-values exceeding 3.5 are considered significant (Wigley *et al.*, 1987), and all cross-matches between samples yielding *t*-values above 4, as well as significant coefficient of parallel run ($P < 0.01$), were visually examined. The individual RW series for which cross-dating was satisfactorily established based on statistical and visual examination were thereafter averaged into preliminary test records.

In the next step, the cross-dating and measurement quality, as well as the strength of the test records, were evaluated using the software COFECHA (Holmes, 1983), which is a tool for detection of possible missing rings, measuring errors and outliers. Segments with correlation values beneath the critical confidence level 0.3281 ($P < 0.1$) in COFECHA were corrected or removed before all samples were cross-dated to form corrected site records, also referred to as master chronologies.

Standardization of tree-ring data is a correction process that minimizes the influence of non-climatic RW variations and trends related to, for example, age, height within the stem and geometry (Fritts, 1976; Cook and Kairiukstis, 1990). During the standardization process non-climatic trends are removed from the measured RW series, which then become transformed into dimensionless RW indices (Fritts, 1976; Cook and Kairiukstis, 1990). These series were thereafter cross-matched into standardized RW records. Several standardization methods were applied to the material. However, as the trees often showed growth trends with narrow rings during both juvenile and adolescent stages as opposed to the negative exponential trend commonly observed in RW series (Cook and Peters, 1997), a flexible method was used for the standardization. The standardized data shown here are based on the Friedman variable span smoother (Friedman, 1984) processed with the software ARSTAN_41d (Cook and Krusic, 2006). The alpha value was set to 7 to preserve long-term variability in the RW data (Friedman, 1984), and to highlight the low-frequency patterns of variability in all RW records a 20-year low-pass filter spline was used (Cook and Peters, 1981).

To assess the reliability of the chronologies, i.e. how well RW series from individual trees agree with a theoretical population chronology, the expressed population signal (EPS) was calculated with a 30-year window and a 25-year overlap using ARSTAN. The EPS is dependent on the number of overlapping series and their mutual conformity. The limit at which the RW records were considered as reliable and well replicated was set to EPS ≥ 0.85 (Wigley *et al.*, 1984). Finally, cross-dating tests between the developed RW records from Viss mosse were made against absolutely and radiocarbon-dated RW chronologies to assign ages to the material.

Development of replication and mean tree-age records

In combination, tree-replication and mean-age records are valuable for reconstruction of population dynamics, particularly for detection of germination and die-off events (Leuschner *et al.*, 2002). A replication record was developed by counting the number of overlapping samples year by year, and a mean-age record was created by calculating the average age of all overlapping samples during each individual year. As the inner- and outermost rings were sometimes absent due to post-mortal degradation, the germination and death years were adjusted prior to the development of mean-age and replication records. As the number of missing annual rings to germination also depends on the height above root level at which the samples were taken, and as the general growth rate of the investigated bog pines was low, 10 years per metre was added for trunks. For samples where the outermost rings were absent, the offset to death was estimated based on the average number of annual rings (72) in the sapwood, the brighter coloured and water-conducting outer part of the tree stem (Fritts, 1976), of intact trees. In some cases evaluations could be made in the field by ring counting on stumps or roots below the sampled cross-sections.

Radiocarbon dating

In cases where precise calendar ages could not be determined by cross-dating with available RW chronologies, approximate calendar ages were obtained by radiocarbon dating of annual rings from one or several samples included in the RW records. The radiocarbon-dated subsamples spanned 11 consecutive years and were separated by 100 annual rings. The samples were dated at the Lund University Radiocarbon Dating Laboratory, and calibrated radiocarbon ages (years before present, cal a BP, with present defined as AD 1950) were obtained based on the IntCal09 radiocarbon calibration dataset (Reimer *et al.*, 2009) and the OxCal 4.1 calibration software (Ramsey, 2009). Defined sequence analysis (Ramsey *et al.*, 2001) was used to minimize the calibrated age intervals for the ^{14}C-dated RW series. The method is based on the non-linear relationship between radiocarbon and calendar ages by fitting a sequence of radiocarbon dates with known intervals between them on the radiocarbon calibration curve. The ages used for the dated chronologies are the calculated mean values (μ) from the defined sequence probability curves. A bulk peat sample, 1 cm^3 in volume, from the sampled stratigraphic sequence was also radiocarbon dated. All presented margins of error are the uncertainties at the 95.4% probability level.

Stratigraphic analyses

Stratigraphic variations in general and peat humification changes in particular were used to place the analysed trees in a palaeohydrological context. The 4.4-m-long stratigraphic sequence was inspected visually and the thickness of each observed layer was measured. Individual layers were identified based on visual changes in colour and texture as well as variations in the content of macroscopic plant remains. In the *Sphagnum* peat, samples were taken at intervals of 10 or 5 cm, taking stratigraphic boundaries into account, and their wet weights and volumes were measured. Drying at 105°C for 24 h followed by additional weighing allowed calculation of dry bulk density, a physical parameter commonly used as a proxy for peat humification (Chambers *et al.*, 2011). Supplementary information on the stratigraphy and spatial extent of the peat deposits and underlying sediments was obtained from a detailed peat inventory at the site performed by M. Thelaus and B. Holmquist (1994, unpublished report).

Results

Ring-width records

Three RW records, V1, V2 and V3, were developed, the most extensive of which (V1) was based on cross-matching of 86 pine trees and covers 726 years (Fig. 3). Two shorter and supplementary RW records were based on five trees each and cover 186 and 230 years, respectively (Fig. 4). Cross-matches between the remaining 59 samples were either too weak or absent. The high rejection rate (38%) in the material is probably a result of a wide age distribution with several temporal outliers. Among the trees used in the three records, 63 were *in situ*, whereas the remaining 33 had been removed from their original growth positions.

Main chronology (V1)

Material used for construction of the main chronology from Viss mosse (V1) has previously been assigned absolute ages through cross-dating against bog-pine chronologies from Lower Saxony, Germany (Edvardsson *et al.*, 2012). The present and updated chronology is extended from 646 to 726 years and covers the period 7233–6508 cal a BP (5284–4559 BC). The cross-match tests between the updated V1 chronology and the German bog-pine chronology (Eckstein *et al.*, 2009; H. H. Leuschner, unpublished data) yield a *t*-value of 7.4 and a coefficient of parallel run of 61 ($P < 0.01$) for the 726-year overlapping sequence.

In total, 99 years with depressed growth (RW indices below -1 SD) and 107 years of elevated growth (RW indices above $+1$ SD) were recorded. The longest observed period of suppressed growth starts at 7113 cal a BP (5164 BC) and covers six years, whereas the longest periods of elevated growth cover four years each and start at 7103, 6832 and 6637 cal a BP (5154, 4883 and 4688 BC), respectively. The mean RW of the trees included in the V1 chronology is 0.96 mm.

Supplementary chronologies (V2 and V3)

The two shorter RW records (V2 and V3), covering 186 and 230 years, respectively, could not be connected to the main chronology or cross-dated with other available chronologies. These two records were therefore radiocarbon dated (Table 1), yielding age spans of 8081–7896 $\pm$ 88 cal a BP (6132–5947 $\pm$ 88 BC) and 7415–7186 $\pm$ 74 cal a BP (5466–5237 $\pm$ 74 BC) for V3 and V2, respectively.

The mean RW of the V2 and V3 records are 1.25 and 1.13 mm, respectively. As a result of few overlapping trees (1–5) the quality of the RW data was considered unsuitable for detailed analyses. However, the temporal distribution of the material is of interest for the peatland development and for the regional palaeohydrological synthesis.

Sediment and peat stratigraphy

The stratigraphic succession collected at Viss mosse shows seven distinct stratigraphic units (Fig. 5). Basal grey medium

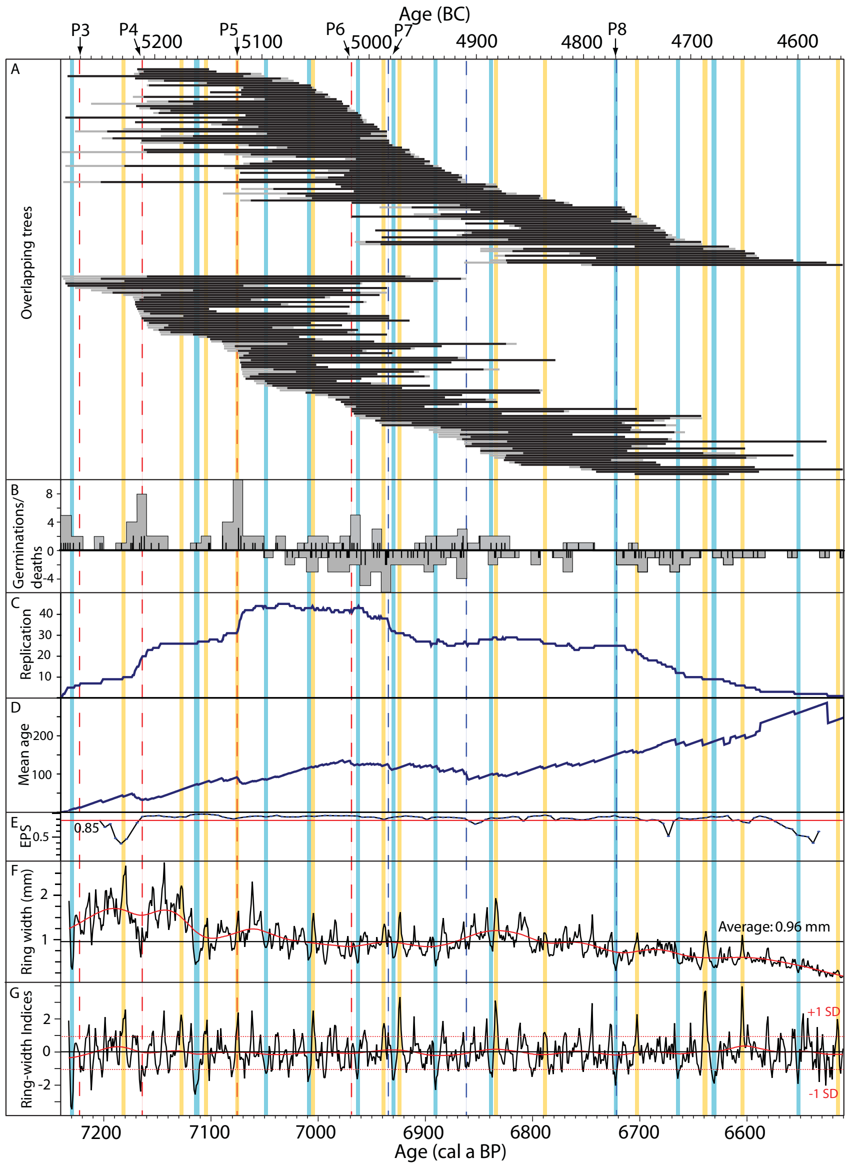

Figure 3. (A) The 726-year main chronology (V1) from Viss mosse based on 86 pine samples. The horizontal black lines represent individual trees and the grey extensions are estimated years to germination and death. The material is sorted after ending and starting years (upper and lower panels, respectively). (B) The black bars show numbers of germinating and dying trees each year and the grey boxes represent germination and die-off during consecutive 10-year intervals. (C) Sample replication. (D) Mean age of samples. (E) Expressed population signal (EPS) calculated with a 30-year window moved with 25-year overlaps. (F) Averaged ring-width (RW) chronology (mm). (G) Averaged and detrended RW chronology (dimensionless indices). The smooth red curves in F and G are 20-year low-pass filter splines highlighting the low-frequency patterns of variability. The blue fields are periods of 3 years in a row or longer with depressed growth (RW indices below −1 SD), and the yellow fields are periods of elevated growth (RW indices above +1 SD). Germination and die-off events as illustrated in Fig. 7 and discussed in the text (P3–P8) are indicated by arrows and dashed red and blue lines, respectively.

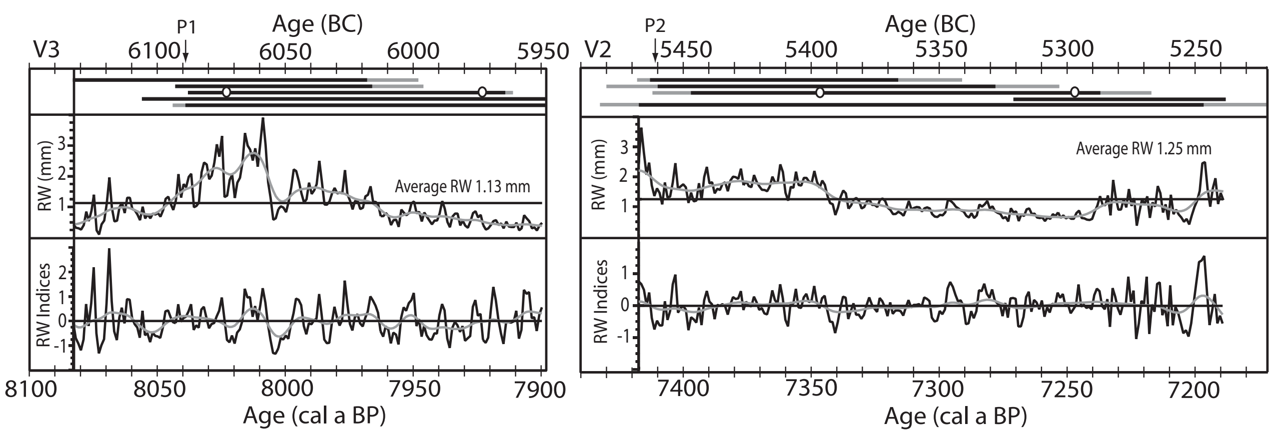

Figure 4. Two groups of five pine samples each were used to construct supplementary ring-width (RW) chronologies from Viss mosse: V3 (186 years) and V2 (230 years). The horizontal black lines (upper panels) represent individual trees and the grey extensions are estimated years to germination and death. The material is sorted after ending years. The middle panels show the averaged RW chronologies (mm) and the lower panels show the detrended and averaged RW chronologies (dimensionless indices). The smooth grey curves are 20-year low-pass filter splines highlighting the low-frequency patters of variability. Based on radiocarbon dating (open circles in upper panels) the V3 chronology starts at 8081 ± 88 cal a BP and the V2 chronology starts at 7415 ± 74 cal a BP. Period 1 (P1) is the first observed event with several trees germinating at the site and period 2 (P2) is the first observed event with several trees found germinating *in situ* on the bog surface.

Table 1. Radiocarbon dates obtained from the RW records V2 and V3. The last column shows calibrated radiocarbon ages following defined sequence analysis. Uncertainties are at the 95.4% significance level.

Lab. no.	Ring no.	Radiocarbon age (^{14}C a BP)	Calibrated age (cal a BP/BC)	D-seq. age (cal a BP/BC)
LuS9564	68 ± 5 (V2)	6400 ± 55	7306/5357 ± 125	7347/5398 ± 74
LuS9565	168 ± 5 (V2)	6345 ± 55	7293/5344 ± 125	7247/5298 ± 74
LuS9566	58 ± 5 (V3)	7170 ± 65	8014/6065 ± 149	8023/6074 ± 88
LuS9567	158 ± 5 (V3)	7110 ± 60	7919/5970 ± 132	7923/5974 ± 88

sand (4.40–4.35 m below the bog surface) is followed by laminated silty clay gyttja with dark laminations (4.35–4.10 m), grey clay gyttja (4.10–4.02 m), olive-green algal gyttja (4.02–3.70 m), dark-brown detritus gyttja (3.70–3.55 m), reed peat (3.55–3.40 m) and *Sphagnum* peat (3.40–0 m). The radiocarbon date at 3.38 m (LuS9873; 6855 ± 55) gives an age of 7705 ± 118 cal a BP for the initiation of *Sphagnum* peat deposition (Fig. 5). Dry bulk density was measured in the *Sphagnum* peat and provides information on variations in peat humification. Densities vary between 0.07 and 0.17 g cm^{-3} (Fig. 5), with maximum values (average 0.16 g cm^{-3}) recorded at 2.60–2.30 m. The average density of the entire *Sphagnum* peat layer is 0.13 g cm^{-3}. The pine-stump horizon is located at 2.70–2.30 m, with the base of the roots in general located ca. 0.5 m above the transition between the reed peat and the *Sphagnum* peat.

Discussion

Stratigraphy and long-term peatland development

Precipitation and temperature-controlled evaporation are fundamental factors influencing hydrology and surface wetness of raised bogs and therefore important for bog dynamics (Aaby, 1976; Barber *et al.*, 1994). However, because water supply and runoff systems are unique for every peatland, climatic interpretations may differ significantly, even between nearby records from similar precipitation and temperature regimes. Groundwater variability at Viss mosse is essentially governed by precipitation and evaporation without any influence of major rivers or lakes (Fig. 1).

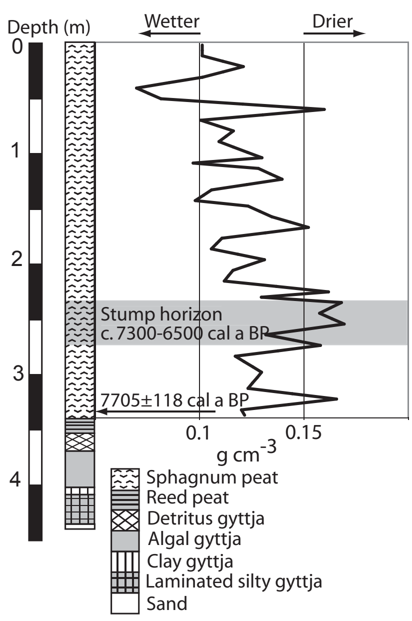

Figure 5. The stratigraphy from the central part of Viss mosse (see Fig. 1C) reflects a succession from an open lake to a raised bog. The curve represents bulk density variations (g cm^{-3}) in the *Sphagnum* peat (uppermost 3.4 m). The location of the stump horizon (shaded zone representing the period when the majority of the analysed pine trees grew on the bog) corresponds to relatively dry bog-surface conditions.

The basin in which the Viss mosse bog is situated is probably a dead-ice depression formed during the deglaciation of the area, and the peat sequence recovered shows a normal hydroseral succession from a lake to a raised bog (Fig. 5). The sand layer at the base of the sequence probably dates to the period following the deglaciation when the basin was occupied by a lake with sparse catchment vegetation (Figs 6 and 7A). The overlying organic sediments reflect increased aquatic productivity and successive infilling of the basin during favourable climatic conditions in the Late Weichselian and the early Holocene. The layer of clay gyttja indicates a temporary return to elevated catchment erosion and low lake productivity, probably linked to colder conditions. This is a pattern often observed in South Swedish lake-sediment stratigraphies (Hammarlund and Keen, 1994; Hammarlund *et al.*, 1999), indicating that this layer was deposited during the Younger Dryas stadial ending abruptly at ca. 11 650 cal a BP (Walker *et al.*, 2009). If so, the overlying algal gyttja was formed during the earliest millennia of the Holocene. Because the layer of algal gyttja represents deposition in an open water environment, its spatial distribution is a robust indicator of the minimum extent of open water during the early Holocene lake stage (Fig. 7A). After becoming overgrown by a fen, an ombrotrophic environment with *Sphagnum* peat deposition became established around 7700 cal a BP. The absolutely dated *in situ* trees at Viss mosse are located at a stratigraphic level corresponding to ca. 7200–6500 cal a BP according to cross-dating of the trees.

The degree of humification in the *Sphagnum* peat can be used as a proxy for local bog-surface wetness, but also for regional climatic conditions if similar changes are observed at different sites. The studied stump horizon is situated at a level where the degree of humification increases (Fig. 5), which indicates that the establishment of the trees coincided with a period of relatively dry bog-surface conditions. However, the unsaturated zone was probably still relatively shallow, as indicated by horizontally spreading roots in all samples with preserved root systems. This conclusion is supported by the relatively low average growth rate, 0.96 mm a^{-1}. As evidenced by the V1 chronology the most widespread tree establishment took place at ca. 7200–6500 cal a BP, during the early part of the Holocene Thermal Maximum (HTM), a period of relatively warm and dry summers dated to ca. 8000–4400 cal a BP in southern Sweden (Jessen *et al.*, 2005; Seppä *et al.*, 2005; De Jong *et al.*, 2009). Above the stump horizon, the peat humification record shows some rapid changes but a general trend towards decreasing peat density. The exceptional preservation of the wood material suggests that it was relatively rapidly incorporated into the *Sphagnum* peat. This clearly indicates wetter bog surface conditions during the termination

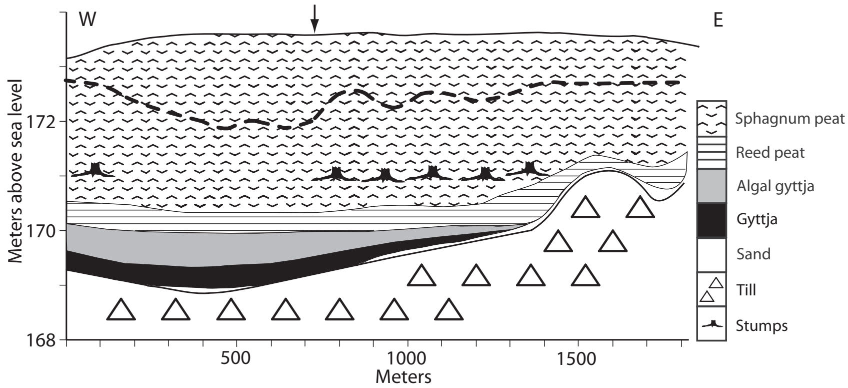

Figure 6. Transect across Viss mosse from west to east (see Fig. 1C) based on probe measurements and a peat inventory by M. Thelaus and B. Holmquist (1994, unpublished report). The original bog surface is approximated, whereas the dashed line shows the excavated surface in 1994. The present (2010) surface following continued peat excavation is in general level with the stump horizon. The stratigraphic sequence (Fig. 5) was recovered ca. 30 m north of the point indicated by the arrow.

of the Viss mosse woodland phase and most of the remaining part of the Holocene. Because of the low hydraulic gradient, a shift to a cooler/wetter climate would have led to an earlier water-level rise in the central, flatter part of the bog than in the marginal zone (Ingram, 1982). This is evidenced by the generally later establishment and earlier degeneration of trees growing in the central part of the bog (Fig. 7). Together, these observations strengthen the assumption that hydrology was the

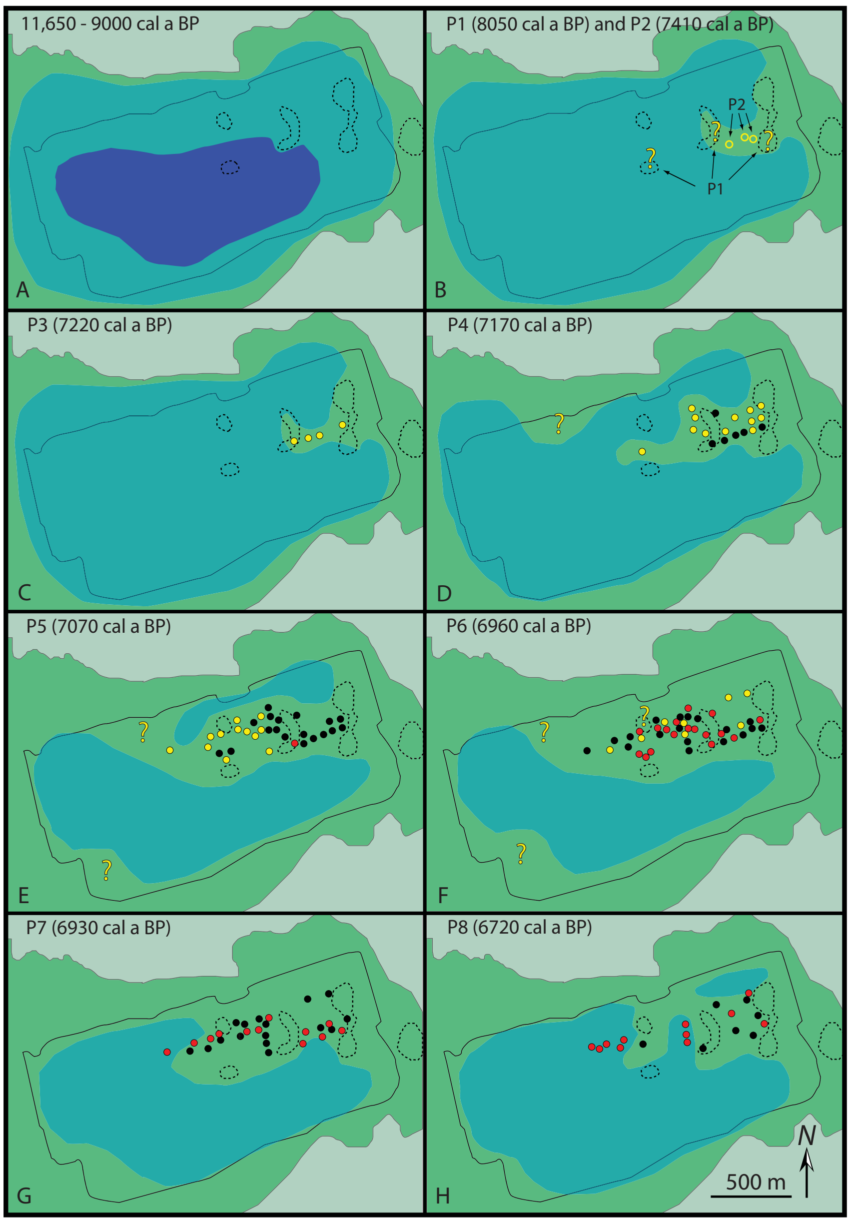

Figure 7. Reconstruction of the development of Viss mosse during the period 11 650–6600 cal a BP based on 63 dated *in situ* trees and the peat stratigraphy (Figs 1, 3–6). The dark blue area (A) shows the maximum extension of the lake based on the distribution of algal gyttja (Thelaus and Holmquist, 1994). The light blue areas in A–H represent parts of the peatland where the groundwater table was too close to the surface for trees to establish. Yellow dots represent germinating trees, black dots established and mature trees, and red dots trees showing suppressed growth, degeneration and die-off. The question marks show possible positions of germinating trees based on *ex situ* material collected nearby, and the open circles represent radiocarbon-dated *in situ* trees. P1–8 correspond to the periods highlighted in Figs 3 and 4.

main growth-controlling and limiting factor at the site, and that the RW and replication records can be used for palaeohydrological reconstruction.

Tree-growth variability and stand dynamics

There are at least two possible causes of tree establishment on peat bogs: natural responses to rising peat surfaces and expanding unsaturated zones in raised bogs (peatland ontogeny), or lowered groundwater tables reflecting climate change or human activity. Once established, there are several feedback processes, both positive and negative, affecting the bog trees. The tree cover itself may lead to a lowering of the groundwater table through increased evapotranspiration or an improved nutrient status of the bog through aeration and increased peat decomposition (Moir *et al.*, 2010), which the trees would benefit from. At the same time the increasing weight of the trees could lower the bog surface towards the groundwater table, which would deteriorate their growth conditions.

The RW index records provides annually to decadally resolved data on hydrological variability at the site. Growth variations detected in the majority of the overlapping individual RW series can be linked to site-representative fluctuations of the groundwater table beneath the roots. The V1 chronology shows in total 99 synchronous growth depressions (−1 SD), of which 12 lasted for 3 years or more, indicating repeated short-lived wet phases. Many of these wet phases affected the tree growth over 3–10 years and were sometimes followed by elevated growth. Similarly, 107 rapid and 13 prolonged periods, 3 years or longer, with strong growth (+1 SD) were observed (Fig. 3).

The dating of germination, growth depressions, growth elevations and death (Figs 3 and 4), in combination with the recorded growth positions of the trees (Fig. 1C) and the stratigraphic succession (Figs 5 and 6), allows a detailed spatial reconstruction of stand dynamics of the pine population linked to hydrological variability (Fig. 7). Moreover, the degree of synchroneity between individual trees can be assessed based on growth patterns in different parts of the peatland. Eight periods referred to as P1–P8 (Figs 3, 4 and 7) were used to illustrate major establishment and degeneration phases (Fig. 7).

Based on radiocarbon dating of the V3 chronology (Fig. 4) the first tree establishment took place at 8081 ± 88 cal a BP (P1, Figs 4 and 7), possibly in response to warming and decreased effective moisture following the 8200 cal a BP cold event (Hammarlund *et al.*, 2003; Seppä *et al.*, 2005). Although the oldest dated trees were not found *in situ*, their 18% greater average RW compared with the V1 chronology indicates that these pioneer trees grew on a small till hummock (Fig. 7B), offering drier and more suitable conditions for germination, compared with other parts of the bog. Similar establishment patterns on protruding areas of mineral soil prior to bog surface invasion have previously been observed by Eckstein *et al.* (2010). Three pine trees included in the V2 chronology (Fig. 4) were found *in situ* and provide a radiocarbon-based age of the first definite tree establishment on the bog surface of 7415 ± 74 cal a BP (P2, Figs 4 and 7B). The oldest dendrochronologically dated *in situ* tree germinated at ca. 7235 cal a BP and was followed by other trees in the following years (P3, Figs 3 and 7C). Growth conditions appear to have improved over the following centuries with establishment phases in the north-eastern part of the bog around 7170, 7070 and 6960 cal a BP (P4, P5 and P6, Figs 3 and 7). This development, as illustrated in Fig. 7, may be related to centennial-scale hydrological changes in the region. In general, the bog-pine establishment reflects decreased bog-surface wetness, as supported by increased peat humification in the stump horizon (Fig. 5). The initial spread of trees until ca. 7050 cal a BP may therefore be linked to decreased effective moisture, and maximum replication numbers indicate that the bog was most densely forested and growth conditions most favourable in the period 7070–6930 cal a BP (Fig. 3C). The first phase of stress and growth depression in several trees was recorded around 6930 cal a BP (P7, Figs 3 and 7G). Thereafter, only minor germination phases took place in the eastern part of the bog until ca. 6700 cal a BP. In general, the period after ca. 6720 cal a BP (P8, Figs 3 and 7) was dominated by prolonged degeneration of trees and growth depressions, most likely a result of less favourable growth conditions caused by increased bog-surface wetness.

Relations to other climate records from northern Europe

The temporal distribution of the wood material from Viss mosse provides evidence of climatically controlled establishment phases of bog-pine populations in southern Sweden during the onset and first half of the HTM (Fig. 8). The significant cross-match and positive correlation between the V1 chronology and similar records from Germany (Edvardsson *et al.*, 2012) also provide evidence of the large-scale climatic forcing of bog-pine populations in northern Europe, a phenomenon worth examining in the light of other palaeoclimatic evidence.

In several cases, centennial-scale lake-level fluctuations during the Holocene have been found to be synchronous on a regional scale (Digerfeldt, 1988; Magny, 2004). A pollen-based temperature reconstruction from Lake Flarken, southern Sweden (Fig. 1), shows a prominent, transient cooling during the well-known 8200 cal a BP cold event (Seppä *et al.*, 2005).

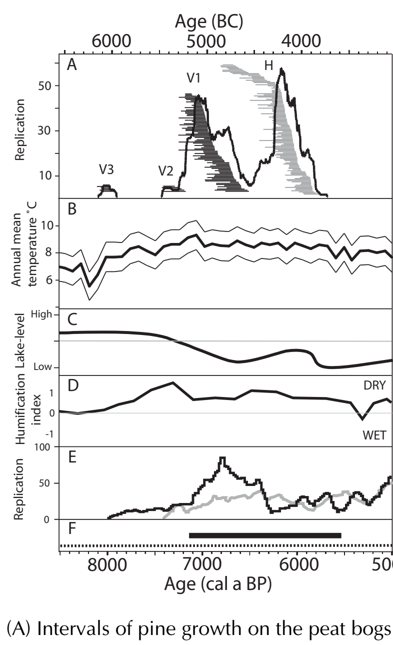

Figure 8. (A) Intervals of pine growth on the peat bogs of Viss mosse (V1–3; this study), and Hällarydsmossen (H; Edvardsson *et al.*, 2012). These establishment phases coincide with relatively high temperatures as inferred from the pollen-based reconstruction from Lake Flarken (B; Seppä *et al.*, 2005), generally low lake levels according to data from Lake Bysjön (C; Digerfeldt, 1988), and predominantly dry surface conditions on the raised bog Kortlandamossen (D; Borgmark and Wastegård, 2008). Replication data obtained from populations of German (E, black curve; Leuschner *et al.*, 2002) and Irish bog oak (E, grey curve; Turney *et al.*, 2006), as well as bog pine (F; Eckstein *et al.*, 2011) from north-western Germany, are shown for comparison.

Isotopic records from nearby Lake Igelsjön (Fig. 1) also indicate lowered temperature, increased effective moisture and elevated lake levels during this event (Hammarlund *et al.*, 2003, 2005). In contrast, the succeeding millennia were dominated by significantly warmer and drier climatic conditions (Seppä *et al.*, 2005; Renssen *et al.*, 2009), consistent with increased peat humification at Kortlandamossen in Värmland, south-central Sweden (Borgmark and Wastegård, 2008). The initial germination of pine trees at Viss mosse occurred around, or slightly after, 8100 cal a BP, immediately following the 8200 cal a BP cold event (Fig. 8). In close agreement with data from Germany, the subsequent increase in tree replication (Fig. 8A) is coincident with the onset of the HTM, when the climate of southern Sweden became generally dry and relatively stable (Hammarlund *et al.*, 2003; Seppä *et al.*, 2005). According to Brown *et al.* (2011), summer temperatures in Denmark were up to ca. 3°C warmer than at present at 6700–5400 cal a BP, with maximum values around 6500 cal a BP. Pollen-based reconstructions by Seppä *et al.* (2005) and Antonsson and Seppä (2007) show broadly similar patterns in southern Sweden. These relatively warm and dry climatic conditions can be assumed to have led to decreased bog-surface wetness, and hence to more favourable conditions for tree growth and widespread germination phases on peat bogs. The ca. 800-year main period of tree growth on Viss mosse falls within the first half of the HTM when lake levels were generally low in southern Sweden (Digerfeldt, 1988; Fig. 8), largely consistent with similar, but more highly resolved lake-level records from central Europe (Magny, 2004).

There are also similarities between Swedish and German bog-pine population dynamics on annual to decadal time-scales. Eckstein *et al.* (2009) observed an establishment phase at 7170 cal a BP (5220 BC), which coincides with P4 at Viss mosse (Figs 3 and 7). Also the prolonged decline at Viss mosse, which began after some years of inhibited growth at ca. 6720 cal a BP (P8, Fig 3), coincides with a die-off event at 4770 BC at several German sites (Eckstein *et al.*, 2009). At centennial scale, establishment and degeneration patterns at Viss mosse are in agreement with the German (Leuschner *et al.*, 2002) and Irish bog-oak replication records (Turney *et al.*, 2006), which indicates improved growth conditions during the first half of the HTM, especially around 7000 cal a BP (Fig. 8).

A widened perspective on Holocene palaeohydrology in southern Sweden is provided by considering the slightly younger bog-pine chronology from Hällarydsmossen (Edvardsson *et al.*, 2012) (Figs 1 and 8), which overlaps with the V1 chronology and extends the dated record to the middle of the HTM. Together, the four chronologies from the two sites cover 1973 years between 8100 and 5600 cal a BP. The main woodland phase at Viss mosse and Hällarydsmossen, 7200–5600 cal a BP (Fig. 8), is largely coincident with the corresponding main woodland phase on peat bogs in north-western Germany, 7150–5550 cal a BP, described by Eckstein *et al.* (2011). In addition, Turney *et al.* (2006) observed peaks in Irish bog and lake-edge tree populations at about 8000, 7300 and 6200 cal a BP, consistent with onsets of establishment phases in our Swedish replication record (Fig. 8). The end of the Viss mosse–Hällarydsmossen woodland phase is synchronous with a wet shift seen as a recurrence surface in several Swedish raised bogs (Borgmark and Wastegård, 2008; Rundgren, 2008) and with the termination of the main bog-pine woodland phase in north-western Germany (Eckstein *et al.*, 2011). Several wet shifts have also been recorded in peat sequences in south-eastern Scotland (Langdon *et al.*, 2003). The two earliest of these, at 6650 and 5850 cal a BP, coincide with the end of bog-tree phases at Viss mosse and Hällarydsmossen. These similarities indicate coherent centennial- to millennial-scale climate dynamics across large parts of north-western Europe during the HTM.

Future challenges

Most palaeohydrological data reflect changes in the precipitation–evaporation balance, and it is difficult to separate the effect of temperature on evaporation from the precipitation signal. The same applies to the RW data presented here. As discussed above, hydrology is the dominant growth-limiting factor, but bog-surface wetness depends on both precipitation and temperature-controlled evaporation. A more detailed assessment of these relationships needs to be based on calibration of modern RW series against meteorological data.

Additional bog-tree records are needed to cover the entire HTM. It may become possible to connect the two radiocarbon-dated chronologies (V2 and V3) to the V1 chronology if further trees are recovered as peat cutting continues at Viss mosse. Data in progress from another south Swedish site cover an additional Holocene period of ca. 1550 years (4600–3050 cal a BP). However, an extensive gap still remains between this record and the Hällarydsmossen chronology (Edvardsson *et al.*, 2012). Another challenge is to bridge the gap between these subfossil data, ending at ca. 3050 cal a BP, and the older end of the presently existing pine reference chronology for southern Sweden at 930 AD. Such an effort would provide extremely valuable palaeoclimatic information as well as significant progress in our ability to date archaeological material.

Conclusions

The combination of detailed dendrochronological analysis of bog-pine material and peat stratigraphical studies provides increased temporal precision and enhanced conceptual understanding of climate variability on both local and regional scales. Reconstructions of peatland development can be improved, especially spatially, as groundwater fluctuations can be connected to stand dynamics and tree-growth variability. The sensitivity of individual trees to variations in bog-surface wetness enables reconstruction of groundwater fluctuations with annual to decadal resolution in different parts of peatlands. As shown by the present data, low-resolution peat humification records covering a large part of the Holocene can be successfully complemented by annually resolved RW chronologies, in this case over three periods spanning more than 1100 years. The V1 chronology from Viss mosse, 7233–6508 cal a BP (5284–4559 BC), extends the absolutely dated South Swedish bog-pine chronology backwards in time and the two radiocarbon-dated chronologies are even older. These records demonstrate that the north-eastern part of the bog was forested during a period of at least 1600 years (8100–6500 cal a BP), and stand dynamics during this period can be linked to more widespread variations in effective moisture in the area. The year-by-year variability in the main RW chronology must be closely linked to regional climate dynamics, as evidenced by the strong cross-match with German bog-pine chronologies. The replication and mean-age records also provide valuable palaeohydrological information, although on decadal to centennial time scales. In contrast, the RW records, compared with, for example, radiocarbon-dated stratigraphic sequences, are of annual resolution, which enables detection also of subtle and short-lasting hydrological changes of palaeoclimatic relevance.

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Abbreviations. EPS, expressed population signal; HTM, Holocene Thermal Maximum; RW, ring-width.

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Appendix III

Late-Holocene expansion of a South Swedish peatland and its impact on marginal ecosystems – evidence from dendrochronology, peat stratigraphy and palaeobotanical data

Johannes Edvardsson[a*], Anneli Poska[b], Nathalie Van der Putten[a], Mats Rundgren[a], Hans Linderson[a] and Dan Hammarlund[a]

[a] *Quaternary Sciences, Department of Geology, Lund University, Sölvegatan 12, SE-223 62 Lund, Sweden*

[b] *Department of Physical Geography and Ecosystem Science, Lund University, Sölvegatan 12, SE-223 62, Lund, Sweden*

*** Corresponding author. Tel.: +46 46 222 39 59; fax: +46 46 222 48 30, E-mail address: johannes.edvardsson@geol.lu.se**

Abstract

In this study, a reconstruction of the long-term development and lateral expansion of a South Swedish peat bog was performed by using a multi-proxy approach including dendrochronology, peat stratigraphy and macrofossil and pollen analyses. By combining mapping of cross-dated subfossil trees with radiocarbon dated peat sequences, a new approach to reconstruct lateral peat expansion was explored. Apart from providing approximate ages of tree burial episodes, the ring-width records offer information on hydrological variations prior to the bog expansion. New bog-oak and alder chronologies are presented and their potential for local to regional environmental interpretations is examined. Our detailed reconstructions of the development of the peat deposit and associated changes in the distribution of vegetation communities provide increased insight into peatland responses to climate change at the end of the Holocene Thermal Maximum and during the following transition phase towards moister conditions (5000-3000 cal a BP).

Keywords: *Lateral bog expansion, Bog oak, Pollen analysis, Macrofossil analysis*

1. Introduction

Peatlands are globally important landscape elements, covering approximately 4 million km^2 across Eurasia and North America (MacDonald *et al.,* 2006). Improved understanding of forcing mechanisms behind changes in peatland ecosystems is urgent in order to predict future climate change (IPCC, 2007), as e.g. carbon stored in peatlands can be made available for exchange with the atmosphere due to environmental changes (Korhola, 1994; MacDonald *et al.,* 2006; Weckström *et al.,* 2010; Yu *et al.,* 2010). Peat deposits, and especially raised bogs can provide long-term archives of climate and vegetation dynamics (Aaby, 1976; Barber *et al.,* 1994), and their histories are influenced by a combination of internal and external forcing mechanisms (Robichaud and Bégin, 2009). Variations in effective moisture, related to temperature and/or precipitation, affect the hydrology and vegetation of peatlands. Records of plant communities and peat humification can therefore be used for reconstruction of past climate driven changes in bog-surface wetness (Granlund 1932; Aaby, 1976; van Geel, 1978; Barber *et al.,* 1994; Rundgren, 2008).

Often peatland studies are based on single stratigraphic sequences from the central parts, offering the thickest peat layers. However, as newly formed minerotrophic fens are considerable sources of methane (CH_4) (MacDonald *et al.,* 2006), marginal peat deposits also need to be investigated. Studies based on basal peat dates along transects have been performed by e.g. Robichaud and Bégin (2009), Korhola (1994), Korhola *et al.* (2010) and Weckström *et al.* (2010), and some of these show periods of rapid lateral expansions, with mire fronts advancing several meters per year.

Peat deposits commonly offer excellent preservation conditions for plant material, such as pollen grains, plant macrofossils and wood remains, based on which changes in local vegetation and hence climate can be inferred. Pollen records provide information on local to regional vegetation changes (Huntley and Birks, 1983; Bradshaw and Lindbladh, 2005), whereas plant macrofossil records primarily reflect local vegetation dynamics and offer higher taxonomic precision (Dudová *et al.,* 2012). Periods of relatively warm and dry climatic conditions may sometimes allow trees to establish on peat bogs and tree horizons buried in peat deposits are clear indications of past episodes of decreased bog-surface wetness (Leuschner *et al.,* 2002; Eckstein *et al.,* 2009; Edvardsson *et al.,* 2012a, b). Pioneer studies describing layers of wood in Scandinavian peat deposits and their relationships to climate change were performed already 150 years ago, as reviewed by Birks and Seppä (2010) and Nielsen and Helama (2012). Since the establishment of dendrochronology in the early 20th century (Douglass, 1921) considerable methodological improvements have taken place, and annually resolved ring-width records are now frequently used in palaeoclimatology (Fritts, 1976; Cook and Kairiukstis, 1990). Studies based on subfossil bog trees from southern Sweden have so far focused on the large quantities of Scots pine (*Pinus sylvestris* L.) that are frequently encountered in this region (Edvardsson 2010; Edvardsson *et al.,* 2012a, b). However, initial dendrochronological studies of subfossil bog trees were mainly focused on oak (*Quercus robur* L.), and multi-millennial chronologies have been developed in Germany (Leuschner *et al.,* 1987, 2002) and Ireland (Pilcher *et al.,* 1977, 1984). Oak trunks buried in peat deposits also occur in southern Scandinavia and the material offers great potential, as shown by Christensen *et al.* (2007) who developed extensive Danish bog oak chronologies which together cover about 5000 years from 6132 BC to 430 AD.

In connection with an on-going dendroclimatic study of subfossil bog-pine populations from ombrotrophic peat deposits in southern Sweden (Edvardsson *et al.,* 2012a, b), well-preserved trunks of oak, ash (*Fraxinus excelsior* L.) and alder (*Alnus glutinosa* L.) were found at the peat bog Viss Mosse. These deciduous trees probably represent a forest ecosystem that occurred in the marginal parts of the peat deposit and which was buried by lateral expansion of the peat bog in response to a transition to colder and moister climatic conditions at the end of the Holocene Thermal Maximum (HTM). Here we present tree-ring records based on oak and alder in combination with new and updated chronologies based on the pine population that grew in the central part of the bog during the HTM. Peat stratigraphic records, including pollen and plant macrofossil data, are used to provide supportive information on the peatland development and to place the subfossil wood material in the context of long-term vegetation dynamics. The aim of the study is to provide a well-dated, spatial and temporal visualisation of the late Holocene lateral expansion of a South Swedish peat bog, to assess the impacts of climate change on bog-tree species and population dynamics, and to evaluate the potential of the new bog-oak material for continued studies. The reconstruction of the lateral expansion of Viss Mosse may also provide useful knowledge to other research areas where topics such as the role of peatlands in the global carbon cycle and Holocene climate variability are investigated.

2. Material and methods

2.1 Site description and fieldwork

Viss Mosse (55°51´N, 13°49´E) is a South Swedish raised bog located on the bedrock ridge Linderödsåsen (approx. 173 m a.s.l.) (Fig. 1). The bog is about 2 km^2 and subject to extensive peat mining since early 20th century. During fieldwork campaigns in 2010, 2011 and 2012 trunks from subfossil deciduous trees were found from which cross sections were collected with a chainsaw. Samples from 40 oaks, 1 ash, and 29 alders were obtained. In total 43 of these trees were found *in situ*, whereas the remaining trees were moved from their primary growth position to enable further peat cutting at the bog surface (Fig. 2). Here, the expression *in situ* is used in a broader sense and includes rooted stumps, but also trunks from fallen trees. Apart from the deciduous trees, 172 pine trees were sampled. Most of these were described by Edvardsson *et al.* (2012b). The growth positions of *in situ* trees were obtained with a handheld GPS and marked on a map during fieldwork (Fig. 1). Information about morphology, presence of pith, bark, fire marks or other damages and sampling distance from the roots was recorded for each sample.

Peat cores were taken adjacent to sampled trunks with a Russian peat sampler (7 cm in diameter and 1 m in length) at three locations from the eastern area where most of the deciduous trees were found (Fig. 1C). Distances between the coring points and their relative altitude were measured and to get an impression of the total thickness of the organic layers distance from the present-day bog surface to the mineral soil was measured with a probe.

2.2 Development of ring-width records

In order not to dry out and deform the soft deciduous tree samples, all the wood material was stored at 4 °C after fieldwork and frozen during surface preparation. The surfaces of the discs were prepared by cutting several radii with razor blades. Ring-width (RW) series of individual radii were created based on measurement of annual rings with a precision of 0.01 mm, using a LINTAB measuring table connected to a stereomicroscope and a computer using the TSAP (Rinn, 1996) and CATRAS (Aniol, 1983) softwares. In order to identify wedging rings and possible measuring errors, at least two radii were measured for each sample. Two statistical tests were applied to evaluate similarities between individual RW series; Coefficient of parallel run (Eckstein and Bauch, 1969) and Students *t*-test (Baillie and Pilcher, 1973). In dendrochronology, these statistical analyses in combination with visual comparisons are common when assessing the significance of correspondence between two RW series and generally referred to as cross-dating. First, the radii from individual samples were cross-dated, and if matching, they were averaged into RW series from individual trees. Subsequently, the RW series from all trees were cross-dated against each other and series where cross-dating was satisfactory established (Wigley *et al.,* 1987) were then averaged into site records, also referred to as master chronologies.

In the next step, the cross-dating and measurement quality, as well as the strength of the master chronologies, were evaluated using the software COFECHA (Holmes, 1983). Segments with correlation values beneath the critical confidence level 0.3281 ($p<0.1$) in COFECHA were corrected or removed. To minimise the influence of non-climatic variations and trends, the RW series were standardized (detrended) and transformed into dimensionless RW indices (Fritts, 1976; Cook and Kairiukstis, 1990). The standardization process was performed using Friedman's variable span smoother (Friedman, 1984) in the software ARSTAN_41d (Cook and Krusic, 2006). To highlight the low-frequency patterns of variability the standardized RW chronologies were sometimes smoothed with a 10-year Gaussian-weighted filter.

To assess the reliability of the RW records the expressed population signal (EPS) was calculated using ARSTAN, and the limit at which the records were considered as reliable and well replicated was set to EPS ≥ 0.85 (Wigley *et al.,* 1984). Finally, cross-dating tests between the developed RW records from Viss Mosse were made against absolutely and radiocarbon-dated RW chronologies to assign ages to the material.

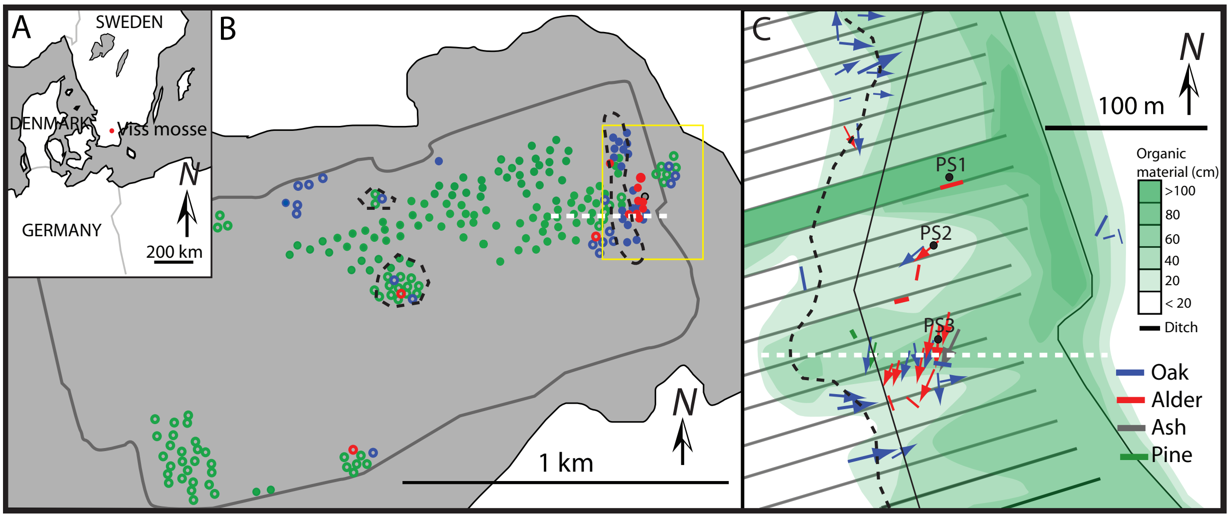

Figure 1. (A) The location of the peat bog Viss Mosse, southern Sweden (red dot). (B) Locations of sampled trees, with dots representing in situ trees and circles representing trees removed from their original growth positions (green = pine, blue = oak, red = alder, grey = ash). Till hummocks are shown with dashed black lines. The yellow square represents the area enlarged to the left, whereas the grey border shows the area used for peat mining and the shaded area represents to total extension of the bog. (C) Close-up of the eastern part of the bog and the till hummock shown in Fig 7. Locations and directions of in situ tree trunks (arrowheads point towards the top of the trees), depth of remaining organic deposits and coring points (PS1, PS2 and PS3). The transect shown in Fig. 7 is indicated by the white dashed lines in Fig. 1B and 1C.

2.3 Peat stratigraphic analyses

The three peat sequences (PS1, PS2 and PS3) were stored in plastic tubes at 4 °C between fieldwork and laboratory studies. Stratigraphic units were identified based on visible differences in peat composition and degree of humification. Thereafter, the cores were sliced into 2 cm segments with some exceptions when 3 cm slices were taken to avoid crossing boundaries between stratigraphic units. Loss on ignition (LOI) and organic bulk density (OBD) (Heiri *et al.*, 2001) were determined on the samples to support the initial classifications of variations in peat humification and stratigraphic units.

2.4 Radiocarbon dating

Wood and peat samples were dated by radiocarbon (^{14}C) to give the RW records approximate calendar ages and to develop age-depth based peat accumulation records. The samples were dated using accelerator mass spectrometry (AMS) at the Radiocarbon Dating Laboratory, Lund University. Calibration and modelling was performed with the OxCal 4.1 software (Bronk Ramsey, 2001). For wood *D_Sequence* analysis (Bronk Ramsey *et al.*, 2001) and for peat, *P_Sequence* analysis (Bronk Ramsey, 2008) were used to improve the accuracy and to tie different radiocarbon dates to more narrow intervals on

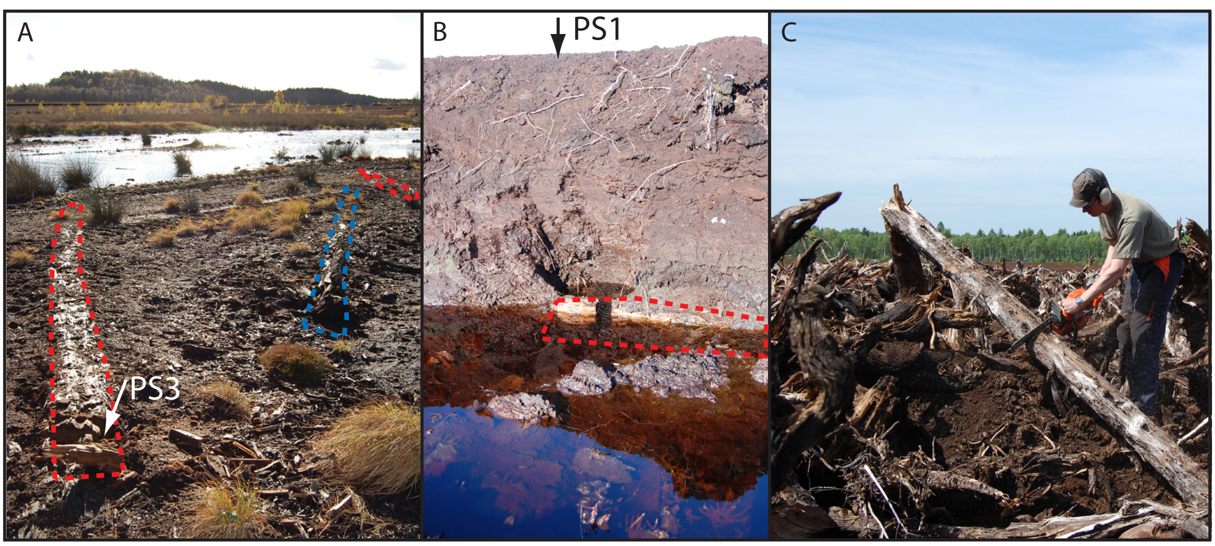

Figure 2. (A) In situ trunks of alder (red dashed lines) and oak (blue dashed lines) found at the excavated peat surface. The arrow shows the coring point for PS3. (B) The longest core (PS1) was collected from a remnant peat bank following more extensive peat mining of the surrounding peat. The alder trunk in the ditch shows the stratigraphic level where most oaks and alders were found. (C) Deposits of stumps and trunks removed from their original growth positions, the RW records of which were mainly used to improve the quality of the tree-ring records.

the IntCal09 radiocarbon calibration dataset (Reimer *et al.,* 2009), The ages used for the dated samples are the calculated mean values (μ) from the *R_Date*, *D_Sequence* or *P_Sequence* probability curves, and the margins of error are the uncertainties at the 95.4% probability level.

In total, 33 wood samples and 13 peat samples were radiocarbon dated. As most of the oak samples cross-date among each other only two or three samples from each oak record (10 samples in total) were needed to date 29 oak trees. As the alders were difficult to cross-date 23 radiocarbon dates from 21 individual trunks were obtained. The three peat cores were sampled close to stratigraphic boundaries and dated to place the wood material in a stratigraphic context and to assess the bog development on a centennial to millennial time scale.

2.5 Pollen and plant macrofossil analyses

Samples for pollen analysis, 1 cm^3 in volume, were taken at 2 cm intervals from PS3 whereas the upper part of PS1 was sampled at every 5 cm. Pollen sample preparation followed the standard acetolysis method (Berglund and Ralska-Jasiewiczowa, 1986). *Lycopodium* spores were added to calculate pollen concentrations (Stockmarr, 1971). At least 1000 terrestrial pollen grains (*Arboreal Pollen* (AP) + *Non-Arboreal Pollen* (NAP)) were counted at each level using a microscope. Pollen, spores, algae, charcoal and other microfossils were calculated as percentages of the total terrestrial pollen sum. Local pollen assemblage zones (LPAZ) were determined using binary splitting by the sum-of-squares method with the PSIMPOLL 4.10 program and the significance of the determined zones was tested using a broken-stick model (Bennett, 1996).

Seven samples, with a thickness of 1 cm and a volume of 10-15 cm^3, were taken for plant macrofossil analysis. Five samples were taken every 10 cm from the PS3, corresponding to the levels at and below the tree trunks, while two samples from PS1 were taken at levels above the trees. Each fresh sample was weighed and the volume was determined by immersion in a known volume of water. The samples were soaked overnight in 5% NaOH and washed through a 250 μm sieve. Macrofossils retained on the sieve were stored in a known volume of water, in this way a subsample of a known volume could be obtained in order to quantify the main peat components (Janssens, 1983; Van der Putten *et al.,* 2004). The samples were systematically examined using a stereomicroscope, and seeds, fruits and other non-dominant remains were picked out and counted in the complete samples. The absolute number of each taxon was calibrated for a standard sample volume. Both pollen and macrofossil diagrams were compiled using the TILIA and TGView software (Grimm, 2007). Ages of the pollen and macrofossil samples were calculated from the radiocarbon based age-depth models.

3. Results

3.1 Ring-width records

Four oak RW records (OR1, OR2, OR3 and OR4) were developed based on 29 trunks. OR1 and OR2 contain two and three samples respectively, and were radiocarbon dated to 7786-7545±66 and 7138-6847±112 cal a BP (Table 1). The 326-year OR3 record was developed from 15 samples (Fig. 3), eight of which were found *in situ* in the eastern or northern parts of the bog on up to 0.6 m of organic deposits. The material was absolutely dated to 1725-1399 BC by means of cross-dating against a Danish bog-oak chronology (Christensen *et al.,* 2007), consistent with a radiocarbon-based age of 3634-3308±63 cal a BP. There is also a cross-match between OR3 and the ash tree from same part of the bog. OR4 was constructed from nine *in situ* trees found on a till hummock in the eastern part of the bog and was dated by radiocarbon to 3231-3035±113 cal a BP (Fig. 3; Table 1).

One RW record from alder (AR1), containing five trees was constructed and dated to 4541-4293±38 cal a BP (Table 1). Due to non-significant cross-matches no other well-replicated and qualitative alder RW records were obtained. Therefore, 21 individual trunks were dated by radiocarbon (Tables 1 and 2), of which AR2 yielded a precise age of the death of the tree above PS3 (Figs. 2A and 5; 3328±78 cal a BP), which is in agreement with the uppermost peat sample (3332±114 cal a BP).

The majority of the pine material from Viss Mosse (PR1, PR2 and PR3) has previously been described by Edvardsson *et al.* (2012b). PR1 and PR2 were dated by radiocarbon to 8081-7896±88 and 7415-7186±74 cal a BP, respectively, and PR3 was absolutely dated to 5284-4559 BC (7233-6508 cal a BP) by cross-dating against

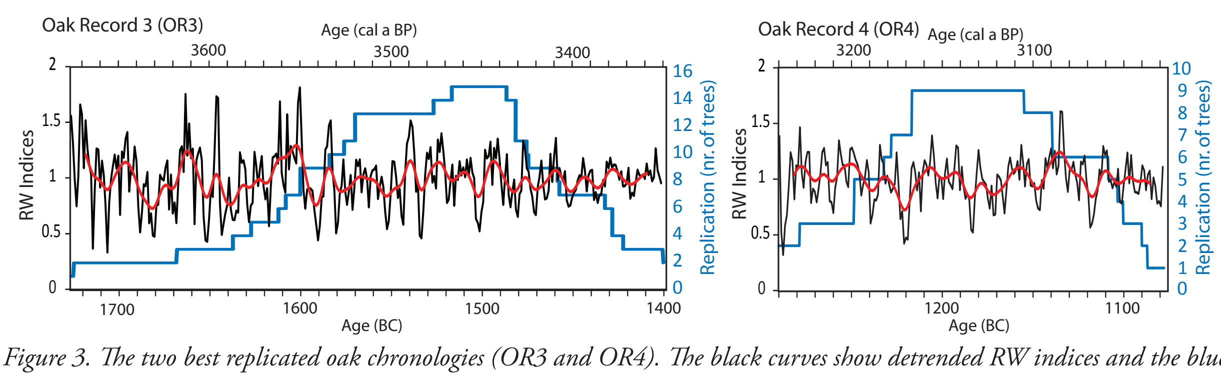

Figure 3. The two best replicated oak chronologies (OR3 and OR4). The black curves show detrended RW indices and the blue curves show tree replication. To highlight the low-frequency patterns of variability the RW chronologies were smoothed with a 10-year Gaussian-weighted filter (red curves). OR3 was absolutely dated using a Danish bog-oak chronology (Christensen et al., 2007) and OR4 was dated by radiocarbon (age ± 113 years).

Table 1. Radiocarbon dating of RW-records.

Sample no.	Gap (no. yrs)	Lab. no.	Radiocarbon age (^{14}C a BP)	Calibrated age (cal a BP)	*D*_seq. age (cal a BP/BC)
Oak Record 1 (OR1)					
TM719		LuS 10254	6945±55	7801 ± 126	7744 / 5795 ± 66
TM719	100	LuS 10255	6790±55	7630 ± 106	7644 / 5695 ± 66
Oak Record 2 (OR2)					
TM692		LuS 10252	6190±60	7100 ± 152	7112 / 5163 ± 112
TM692	200	LuS 10253	6080±55	6976 ± 181	6909 / 4960 ± 112
Oak Record 3 (OR3)					
TM646		LuS 9450	3275±50	3511 ± 119	3525 / 1576 ± 63
TM623	100	LuS 9451	3205±50	3454 ± 105	3425 / 1476 ± 63
TM623	100	LuS 9452	3145±50	3360 ± 109	3325 / 1376 ± 63
Oak Record 4 (OR4)					
TM645		LuS 9447	3055±50	3231 ± 150	3182 / 1233 ± 113
TM645	100	LuS 9448	2920±50	3070 ± 172	3082 / 1133 ± 113
TM655	50	LuS 9449	2815±50	2929 ± 138	3032 / 1083 ± 113
Alder Record 1 (AR1)					
TM625		LuS 10185	4050±50	4613±195	4473 / 2524 ± 38
TM624	28	LuS 9455	3990±50	4537±245	4445 / 2496 ± 38
TM626	62	LuS 10186	3855±50	4260±159	4383 / 2434 ± 38
TM624	38	LuS 9456	3865±50	4285±135	4345 / 2396 ± 38
TM658	10	LuS 10187	3930±50	4351±169	4335 / 2386 ± 38
TM687	32	LuS 10188	3900±50	4332±177	4303 / 2354 ± 38
Alder Record 2 (AR2)					
TM622		LuS 9453	3305±50	3545 ± 138	3463 / 1514 ± 78
TM622	100	LuS 9454	3070±50	3238 ± 155	3363 / 1414 ± 78

Table 2. Radiocarbon dating of alders.

Sample no.	Ring no.	Lab. no.	Radiocarbon age (^{14}C a BP)	Calibrated age (BC)	Calibrated age (cal a BP)
TM629	21±5	LuS 10184	3910±50	2387±178	4336±178
TM494	165±5	LuS 10189	6380±50	5352±123	7301±123
TM614	145±5	LuS 10190	3190±50	1467±142	3416±142
TM627	35±5	LuS 10191	4065±50	2668±195	4647±195
TM628	50±5	LuS 10192	3815±50	2299±163	4248±163
TM632	125±5	LuS 10193	3940±50	2432±141	4381±141
TM636	10±5	LuS 10194	4030±55	2636±227	4585±227
TM643	135±5	LuS 10195	3150±50	1415±108	3364±108
TM653	25±5	LuS 10196	2990±45	1222±165	3171±165
TM663	105±5	LuS 10197	3270±45	1552±112	3501±112
TM674	113±5	LuS 10198	6865±60	5762±119	7711±119
TM675	70±5	LuS 10199	6840±50	5738±99	7687±99
TM685	170±5	LuS 10200	3940±55	2407±171	4356±171
TM686	140±5	LuS 10201	3840±50	2306±160	4255±160
TM689	90±5	LuS 10202	3150±50	1415±108	3364±108

German bog-pine chronologies (Edvardsson *et al.*, 2012b). PR1 and PR3 were reworked here to encompass seven and 90 trees, respectively. A new 296-year RW record (PR4) was developed from 11 samples, covering the period 4236-3941 BC (6185-5890 cal a BP). This chronology was cross-dated against an absolutely dated pine chronology from Hällarydsmossen (Edvardsson *et al.*, 2012a).

3.2 Peat stratigraphy and peat accumulation

The most complete peat sequence is based on two overlapping peat cores, 187-cm in length and referred to as PS1 (Fig. 4). The two shorter sequences, 46 cm and 60 cm, respectively, are referred to as PS2 and PS3. In total, eight stratigraphic units were identified (Fig. 4). Rapid increases in peat accumulation were recorded between 5000 and 4000 cal a BP in all three peat sequences.

Table 3. Radiocarbon dating of the peat samples.

Depth (cm)	Lab. no.	Radiocarbon age (^{14}C a BP)	Calibrated age (cal a BP)
Peat sequence 1 (PS1)			
183-182	LuS 9693	7520±55	8306±107
167-166	LuS 9694	3635±50	3985±152
162	LuS 10035	3780±50	4189±199
115-114	LuS 9695	2875±50	3034±167
102	LuS 10034	2870±50	3012±150
76	LuS 10033	2480±50	2542±179
15-14	LuS 9696	1885±50	1820±112
Peat sequence 2 (PS2)			
43-42	LuS 9697	8125±50	9038±247
32	LuS 10036	5155±50	5873±127
5-4	LuS 9698	3420±50	3697±135
Peat sequence 3 (PS3)			
48-47	LuS 9699	7130±55	7942±107
35	LuS 10037	4110±50	4637±188
3-2	LuS 9700	3120±50	3332±114

3.3 Pollen and plant macrofossil data

Thirty pollen samples and seven plant macrofossil samples from the two peat sequences PS1 and PS3, respectively, were analysed (Fig. 5). Age-depth models developed from PS1 and PS3 gave the analysed samples comparable ages. Based on terrestrial pollen data, three statistically significant local pollen assemblage zones (LPAZ, referred to as V1–V3) were identified (Fig. 5).

Throughout the lower zone (V1), which covers the period 7500-3300 cal a BP, both boreal and nemoral tree taxa are present. Alder was the dominating tree species (20-40%) with a maximum around 5000 cal a BP. Pine, hazel (*Corylus*) and birch (*Betula*) were subdominant (10%), whereas oak and lime (*Tilia*) were present in the area but at lower abundances. The macrofossil data from the corresponding period are clearly dominated by alder. A shift from alder root remains to alder above-ground remains occurred around 4500 cal a BP. Leaf remains of birch are present from c. 4000 cal a BP. The amount of charcoal is generally low (<5%) except for two distinct peaks corresponding to c. 4600 cal a BP and 4000-3600 cal a BP, respectively.

In the middle zone (V2), which covers the period between 3300 and 2800 cal a BP, birch is clearly the dominating tree species with values reaching 30%. Alder is present with values around 20%, whereas pine and oak appear at lower frequencies. Sedges (*Cyperaceae*) occur with values up to 20%. Macrofossils of alder are present but at lower concentrations than in the previous zone (Fig. 5). Besides leaf remains, additional above-ground birch remains such as seeds and female catkins occur after 3300 cal a BP. At that time, a clear shift in the main peat components occurs, to high amounts of monocots, *Sphagnum* section *Acutifolia* and epidermis of *Eriophorum vaginatum*.

In the upper zone (V3), which covers the period between 2800 and 1500 cal a BP, the dominating tree species are birch, alder and hazel (c. 20%), whereas oak and pine are present at frequencies around 5%. Heather (*Calluna*) shows increasing frequencies. The amount of *Sphagnum* spores increases throughout the zone and a charcoal peak occurs at c. 2300 cal a BP (Fig. 5).

4. Discussion

4.1 General peatland development

During the early Holocene a lake existed in the topographic depression occupied by Viss Mosse, and a previously published stratigraphic sequence from the central part of the bog shows a normal hydroseral succession from a lake to a raised bog (Edvardsson *et al.,* 2012b). The lake developed into a wetland where till hummocks, consisting of boulder-rich till, formed small solid-ground islands where trees and shrubs could establish. During archaeological excavations on till hummocks in the central parts of the bog flint tools have been found, dating to about 9000 cal a BP (L. Larsson and A. Sjöström, personal communication), which shows that these islands were repeatedly visited by humans. In the central parts of the bog, *Sphagnum* mosses dated to 7700 cal a BP show that a raised bog started to develop about 8000 years ago (Edvardsson *et al.,* 2012b).

Between 8000 and 6000 cal a BP pine trees established across large parts of the bog (Fig. 6). These trees grew on several meters of peat. Alders were growing in the wet marginal zone of the bog, while oak trees were probably growing on till hummocks in the bog or in its surroundings. Pollen data show that tree species such as birch, hazel and lime were present in the area (Fig. 5). The peat stratigraphy together with pollen and macrofossil data show that the easternmost bog area was characterised by the seasonal presence of open ponds and that peat accumulation rates were low. Aquatic plants tolerating short drought periods (e.g. *Rumex aquaticus*, *Typha*, *Sparganium* and *Alisma palntago-aquatica*) grew in open water bodies, whereas adjacent waterlogged areas were dominated by sedges (*Cyperaceae*) and ferns (*Polypodiaceae*) (Fig. 7B). Well-preserved *in situ* trunks show that numerous alders established in the eastern part about 4800 cal a BP and grew there for more than

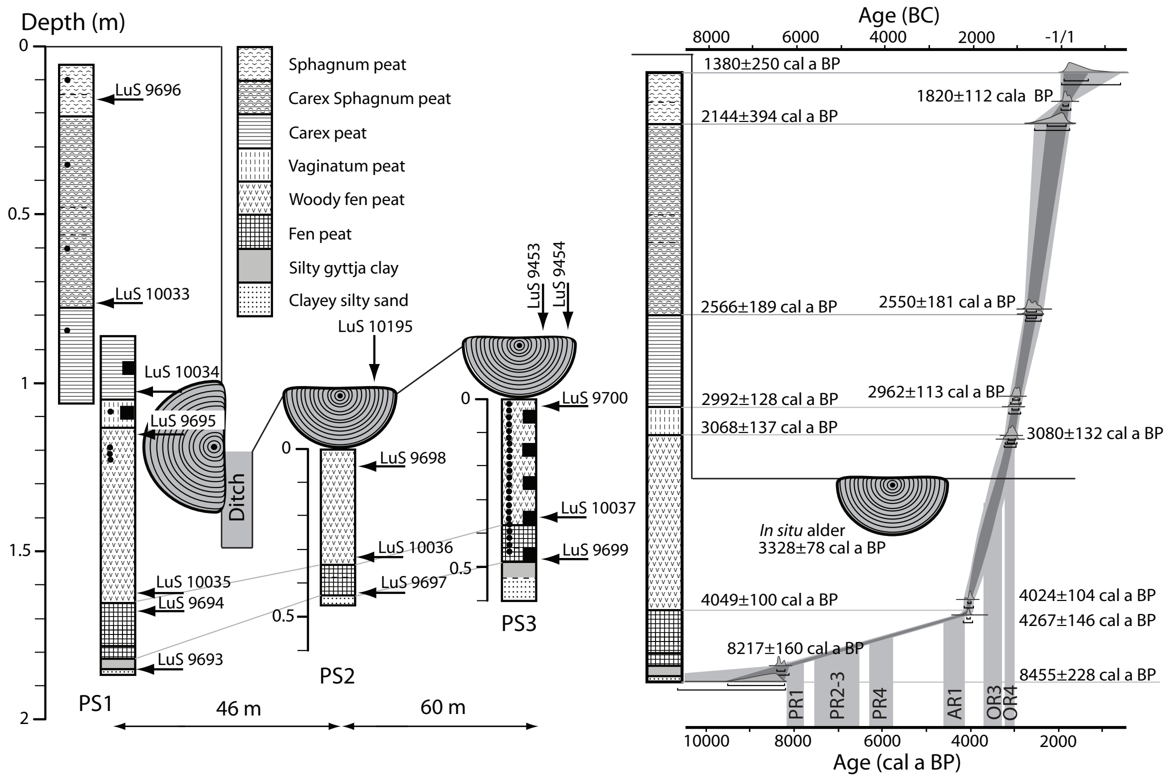

Figure 4. The three analysed peat sequences (PS1, PS2 and PS3) from Viss Mosse. The arrows show depths where samples for radiocarbon dating were taken and corresponding Lab. no. (Table 1-3). The black line shows the surface of the peat bog after mining. The age-depth model is based on depths and radiocarbon ages from PS1. The ages shown represent stratigraphic boundaries and peat samples following P_Sequence analysis (Bronk Ramsey, 2008) in OxCal 4.1 (Bronk Ramsey, 2001). Periods dominated by different tree species according to the dated RW records are shown beneath the age-depth model, the abbreviations indicate the chronology representing the main part of the wood material.

500 years, which is also supported by the pollen and macrofossil data (Figs. 5 and 7C). The upland areas were dominated by mixed broadleaved forests composed of lime, hazel, oak, elm (*Ulmus*) and ash with presence of boreal taxa such as birch and pine. The amount of pine and lime clearly decreased from about 5000 cal a BP onwards and the forest composition shifted to increased dominance of oak.

Dated *in situ* trunks show that oak was growing in the northern part of the bog, and that oak, alder and ash were growing together in the eastern fen area at about 3800 cal a BP (Fig. 7D). Several radiocarbon dated alders of approximately the same age were also found in the fen area. The pollen data indicate a decrease in alder, presence of ash and hazel and an increase in birch. Layers containing high amounts of charcoal indicate fire events at or close to the sampled area of the peat bog at about 4600, 3600 and 2300 cal a BP (Fig. 5), although, no fire scars have been observed on the sampled trunks of oak and alders. The fire at about 3600 cal a BP was followed by a rapid increase in birch pollen frequency, probably due to establishment of birch next to the bog. The pollen record also shows decreasing frequencies of oak and alder immediately after the inferred fire. According to the tree-replication data (Figs. 3 and 6), the oak population was not affected by the fire as a phase of tree establishment is recorded between 3600 and 3500 cal a BP. This is in agreement with previous studies of Eckstein *et al.* (2009) showing that fires on peat bogs do not significantly affect the tree populations. However, the influence of fires can be expected to be negligible in the fen due to permanently wet conditions. It is therefore likely that the fires never reached the trees, but were rather located to the west on the bog or in the woods to the east of the fen.

The youngest dated tree population (OR4 and one alder) established on a till hummock between the eastern fen and the raised bog area (Fig. 7E). These trees were growing on relatively thin organic soils. The pollen data indicate an increase in oak at about 3000 cal a BP, although no trunks or macrofossils have been found. About 3000 years ago conditions shifted from minerotrophic to a more ombrotrophic state and the eastern fen area was transformed into a *Carex-Sphagnum* dominated raised bog environment. The pollen record shows a shift towards more open vegetation with less trees and shrubs (Fig. 5). The conditions became more acidic as the thickness of the peat deposit increased and typical raised-bog species such as heather (*Calluna*) and *Sphagnum* established (Figs. 5 and 7F). In general, aquatic plants and ferns (*Polypodiaceae*) decreased, while more acid-tolerant taxa such as birch (*Betula pubescens*) and sedges (*Cyperaceae*) remained. The species composition in the upland areas shifted as well, from a rich mixed broadleaved forests to an oak- and hazel-dominated forest with reduced amounts of elm, ash and lime.

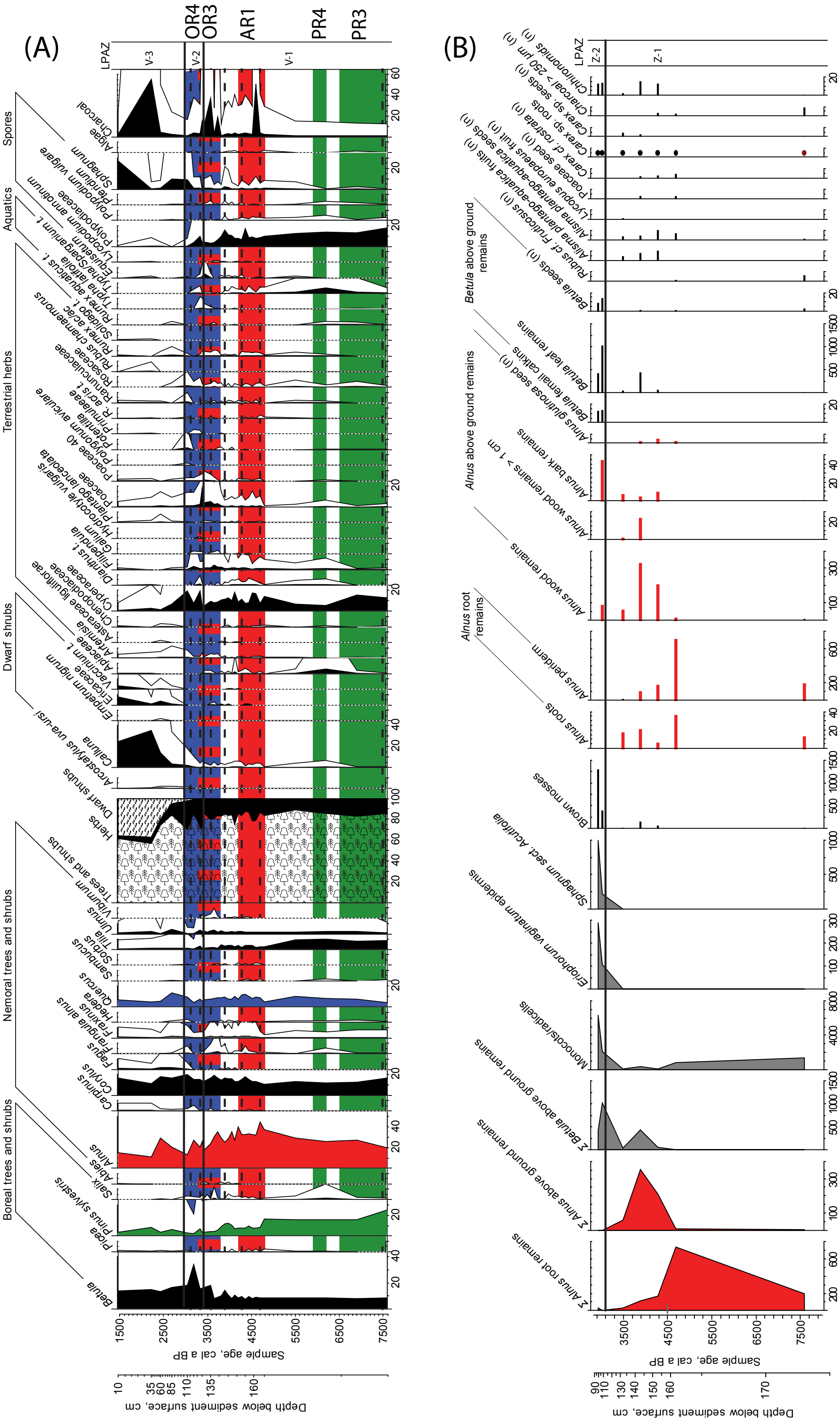

Figure 5. (A) Pollen diagram based on samples from PS1 and PS3. Ages are estimated from the age-depth model (Fig. 4). The filled curves represent percentage frequencies and the hollow curve a x10 exaggeration of the horizontal scale. Solid lines mark the zone boundaries of LPAZ (V1-3), the dotted lines indicate levels analysed for macroscopic plant remains. The coloured areas represent periods dominated by different species of subfossil tree remains (green = pine, red = alder, blue = oak). (B) Record of macroscopic plant remains based on samples from PS1 and PS3. Absolute numbers of each taxon are shown, except for Carex sp. root remains where the dots refer to presence only. Note different abundance scales for some taxa. Taxa that are represented by curves show the main peat components and summarise in some cases the taxa also represented by bars. For taxa marked with (n), the total numbers of plant remains in each sample are shown, while for the remaining taxon quantifications based on 20 ml subsamples are provided. The horizontal line indicates the boundary between the two lower pollen zones (V1 and V2).

4.2. Lateral bog expansion

The oldest discovered trees were found in the central part of the bog, while the younger material was found closer to the marginal zone. Given that the wood material is very well preserved, it can be assumed that the peat burial process was relatively fast. Reconstructing the lateral expansion of the peatland should therefore be possible by using dated *in situ* trees preserved within the peat. Apart from giving approximate ages of tree-burial in the peat, the tree-ring data provide valuable information on the conditions in the area before the trees died.

The dated samples of pine, oak and alder from till hummocks in the central part of the bog were overgrown by peat between 8000 and 7500 cal a BP (Figs. 6 and 7A), whereas pine trees growing on the bog surface during the mid-Holocene were overgrown by peat between 7000 and 5900 cal a BP (Figs. 6 and 7A). The average age of the oldest pine trees was relatively low, c. 125 years and the average RW relatively wide, 1.15 mm a^{-1}, indicating that these trees were growing under relatively dry and stable conditions. In comparison, the dated *in situ* trees that grew between 7400-5900 cal a BP established on relatively thick layers of peat in the central and northern parts of the bog had an average age of c. 190 years and an average growth rate of 0.95 mm a^{-1}. The latter group was preserved in *Sphagnum* peat likely due to vertical peat growth (Fig. 7A-C). Several meters of peat beneath these pines show that most of the Viss Mosse depression was already filled by relatively thick layers of peat prior to 5900 cal a BP. No *in situ* trees older than 5900 cal a BP have been detected outside the yellow line in Figure 7A. It can therefore be assumed that the preservation conditions outside this area were poor and that peat growth mainly occurred vertically. However, a different peat accumulation pattern was recorded after c. 5000 cal a BP, when lateral peat expansion and tree burial towards the east and north started (Fig. 7A). Radiocarbon dated *in situ* trunks show that alders growing in the eastern fen area were buried about 4200 cal a BP (Fig. 7C). Some of these alders were unusually old and large (diameter >30 cm, trunks >10 m in length) and in some cases more than 200 annual growth rings were recorded. Many alders show initially strong growth, but suffered from depressed growth conditions during their final 100-120 years, probably due to the rapidly growing woody fen peat. After the death of the alders, about 4200 cal a BP, conditions were probably too wet for tree establishment during the following 700 years as no wood material from this period has been found (Fig. 6).

Cross-dated oak trunks from the period 3600-3300 cal a BP have been found in both the northern and eastern parts of the bog (Figs. 1 and 7D). Alders, ashes and oaks were buried in fen peat about 3300 cal a BP when the fen area expanded, whereas the oak trees in the north were buried by a northward lateral bog expansion. Large oak trunks, up to 17 m long and >40 cm in diameter have been preserved on the till hummock in the eastern part of the bog. These trees were growing at about 3200 cal a BP on relatively dry and stable substrate (Fig. 7E) and were preserved when the till hummock was overgrown by peat about 3000 years ago. The average growth rate of the OR4 trees was in general higher than that of the neighbouring oaks in the fen area (OR3), 1.28 mm a^{-1} compared to 0.97 mm a^{-1}. Interestingly, the oak trees growing in fen peat could be cross-dated against Danish bog oaks (Christensen *et al.*, 2007), whereas the oak trees on the till hummocks only could be dated by radiocarbon. The annual growth variability of the two oak populations may therefore have been limited by different factors, with the trees found in the fen peat responding more strongly to water-level variations than the trees growing at the till hummock. No trees younger than 3000 years have been found, although younger populations may be preserved in the remaining peat deposits to the north and east.

4.3 Regional palaeoclimatic implications

The analysed peat succession covers the Holocene Thermal Maximum (HTM) and the transition to the

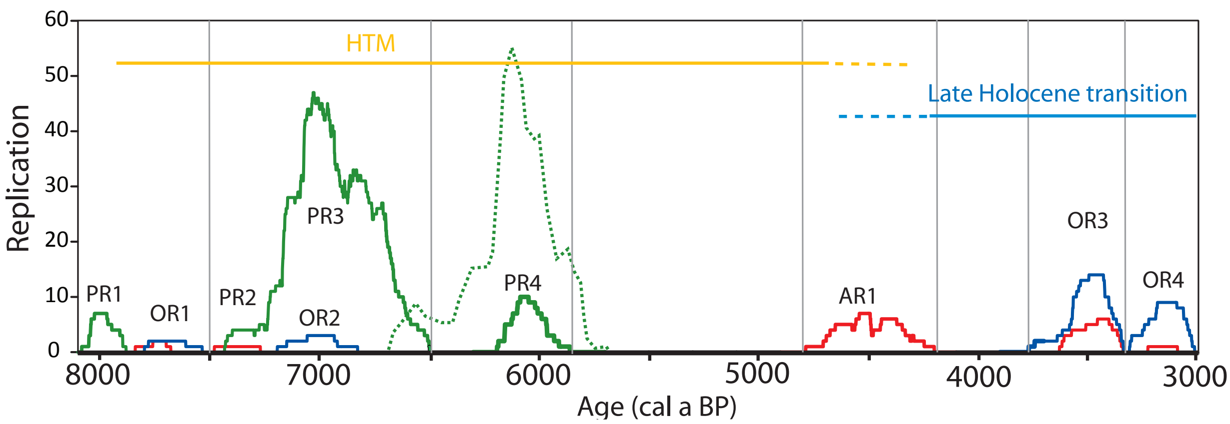

Figure 6. Temporal distributions of dated tree remains from Viss Mosse (green = pine, blue = oak, red = alder). The dotted curve shows the distribution of pine samples from Hällarydsmossen (Edvardsson et al., 2012a) as discussed in the text. The lines above show the approximate lengths of periods discussed. PR1 and OR2 represent tree populations that grew on till hummocks in the central part of the bog. PR3, PR4 and the Hällarydsmossen pines were growing on the surface of the two raised bogs. AR1 represent a population which grew in a fen area east of the raised bog, OR3 and several alders also grew in this area. OR4 grew on a till hummock east of the bog. OR3 and OR4 were preserved as the bog expanded laterally and buried these tree populations.

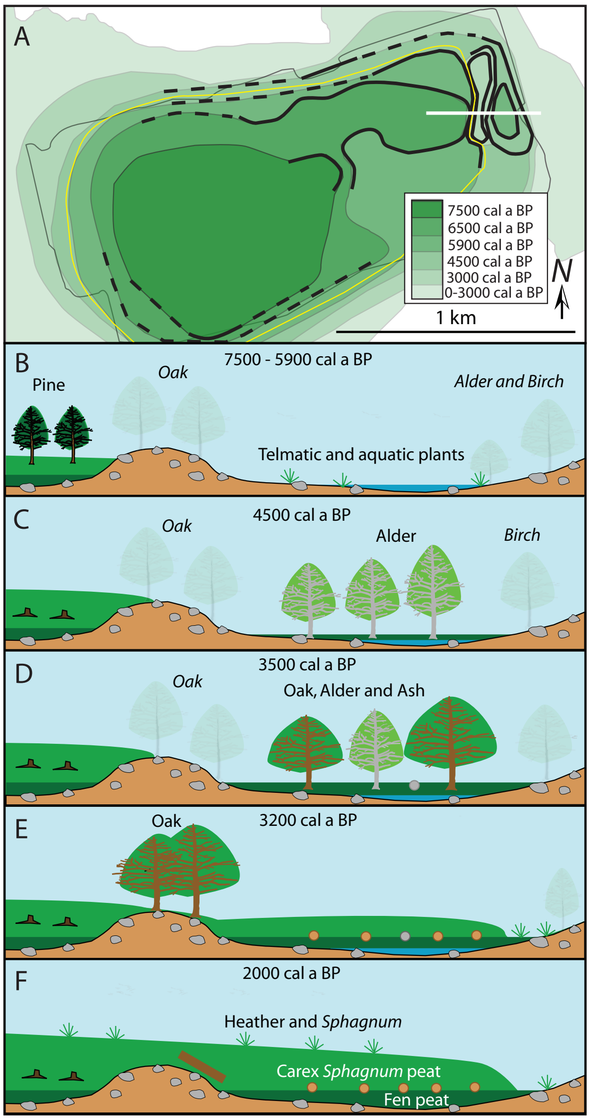

Figure 7. (A) Lateral expansion of Viss Mosse based on dated in situ trees. The ages show when trees were buried by peat in different parts of the bog. The solid lines shows the outermost boundary where the dated trees with corresponding ages were found. The dashed lines show where dated trees were found, but these trees may have been moved from their original growth positions. The yellow line show the approximate size of the bog 5900 cal a BP, as discussed in the text. (B-F) Bog development along the transect shown as a white line in the uppermost panel. The transparent trees (species names in italics) represent conditions as inferred from the pollen record.

late Holocene. The HTM was a period of relatively warm and dry conditions associated with orbitally forced high summer insolation (Snowball *et al.*, 2004; Renssen *et al.*, 2009). This period, which is dated to c. 8000-4500 cal a BP in Fennoscandia (Snowball *et al.*, 2004; Seppä *et al.*, 2009) offered relatively dry bog surface conditions enabling widespread pine establishment in southern Sweden (Fig. 6). The HTM was followed by a shift to moister and colder conditions, often referred to as the Neoglacial transition (Nesje *et al.*, 1991; Wanner *et al.*, 2008). In South-central Sweden this transition phase has been dated to between 4600 and 3400 cal a BP by Jessen *et al.* (2005). Temperature reconstructions based on pollen show that the mean annual temperature decreased by almost 2 °C between 4500 and 2000 cal a BP (Seppä *et al.*, 2005) and lake-level reconstructions suggest a lake-level rise between 5000 and 2500 cal a BP (Digerfeldt, 1988). The replication record from Viss Mosse reflects tree-population dynamics related to the shift from the HTM to the late Holocene (Fig. 6). During the HTM, pine established on the bog surface, but trees in the marginal zone of the bog were not preserved due to low peat accumulation rates. Following the shift towards wetter conditions no trees established on the bog surface and trees growing in the marginal zone were preserved due to increasing peat accumulation and lateral peatland expansion (Figs. 6-7)

Increased lateral expansion of peatlands has been observed in the Northern Hemisphere between 5000 and 3000 cal a BP (Korhola, 1994; Korhola *et al.*, 2010; Weckström *et al.*, 2010), consistent with the increased peat accumulation rate and the lateral expansion recorded at Viss Mosse (Figs. 4 and 7A). A significant rise in atmospheric CH_4 concentrations has been recorded over the last 5000 years (Blunier *et al.*, 1995; MacDonald *et al.*, 2006), and has sometimes been linked to the contemporary increase in lateral expansion of peatlands (Korhola *et al.*, 2010).

4.4 Concluding remarks

As demonstrated by the present study, reconstructions of Holocene peatland development and lateral expansion can successfully be obtained by combining dendrochronology, radiocarbon dated peat sequences, plant macrofossil and pollen analyses. The RW data obtained provided additional information on groundwater fluctuations and cross-dating of trees from different parts of the peat bog enabled mapping of the lateral expansion in different sectors. The multi-proxy approach improved the reconstruction of the site development and provided a more complete picture of spatial and temporal vegetation in a changing environment. For example, the pollen data indicate the local presence of oak and pine during a longer period than covered by the RW chronologies, suggesting the possibility of extending the oak and pine chronologies from Viss Mosse. The alder material was unsuitable for dendrochronological analyses, but the dated trunks provided valuable information on the bog development in the marginal zone. The oak material exhibits strong common growth signals and can be developed further. Additional comparisons of oak RW records obtained from wet and dry areas of peat bogs could increase our understanding of growth limitations in bog-oak populations that lack modern analogues, hence providing enhanced precision in palaeohydrologic reconstructions.

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Appendix IV

Climate forcing of growth depression in subfossil South Swedish bog pines inferred from stable isotopes

Johannes Edvardsson[a], Thomas W.D. Edwards[b], Hans Linderson[a] and Dan Hammarlund[a]

[a] *Quaternary Sciences, Department of Geology, Lund University, Sölvegatan 12, SE-223 62 Lund, Sweden*

[b] *Department of Earth and Environmental Sciences, University of Waterloo, Waterloo, ON N2L 3G1, Canada*

*** Corresponding author. Tel.: +46 46 222 39 59; fax: +46 46 222 48 30, E-mail address: johannes.edvardsson@geol.lu.se**

Abstract

Comparison between bog-tree growth variability, based on ring-width (RW) analysis, and tree-ring carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotope records provides increased understanding of how hydrologic and climatic variability influenced bog pine *(Pinus sylvestris* L.) growth at two sites in southern Sweden during the mid- and late Holocene. Ring sequences from two subfossil trees collected at raised bogs with different hydrology and catchment size were analysed isotopically to probe the isotopic signals associated with periodic bog-wide episodes of growth depression. Variations in the isotopic records confirm that growth depression at both sites coincided with moister atmospheric conditions, as indicated by lower whole-wood $\delta^{13}C$ and cellulose $\delta^{13}C$ and $\delta^{18}O$ values. The data also reveal a characteristic lag of about three years in the growth response with respect to the isotopic signals at each site, likely due to relatively slow rise in the local water table in response to wetter climate.

Keywords: *Dendrochronology, Carbon isotopes, Oxygen isotopes, Peat bog, The Holocene.*

1. Introduction

Multi-millennial ring-width (RW) chronologies based on subfossil bog trees have been developed at various sites across northwestern Europe, initially from bog oaks (e.g. Pilcher *et al.,* 1977; Leuschner *et al.,* 1987), and more recently from bog pines (e.g. Pilcher *et al.,* 1995; Leuschner *et al.,* 2007; Eckstein *et al.,* 2009; Moir *et al.,* 2010; Edvardsson *et al.,* 2012a). Variability in the thickness of the unsaturated zone of the peat deposits, related to variations in local effective moisture, is believed to have been the primary factor controlling establishment, degeneration and growth variability of trees over time within individual bogs (Leuschner *et al.,* 2002; Eckstein *et al.,* 2009; Edvardsson *et al.,* 2012b). However, the existence of long-distance cross-correlation between bog-tree RW chronologies described by Edvardsson *et al.* (2012a) suggests that regional temperature fluctuations also influenced growth variability.

A characteristic feature of site-specific RW chronologies developed from subfossil bog pines is the existence of periodic multi-year intervals of suppressed growth. Although reduction in tree growth rates because of a rise in the water table is commonly invoked to explain bog-wide growth depressions (Boggie, 1972; Leuschner *et al.,* 2002), confirmation of this mechanism has been hampered by the absence of corresponding data obtained on modern bog-pine populations for comparison (Lindbladh *et al.*, in review). A range of processes coupled to thinning of the unsaturated zone may contribute to growth depression, including lack of oxygen for respiration, accumulation of CO_2, formation of toxic compounds (Schouwenaars, 1988; Linderholm, 2001), and dying inundated roots (Eckstein *et al.,* 2011). Here we report the results of a pilot study aimed to test this 'drowning hypothesis' using carbon and oxygen isotope data obtained from bog-pine tree-ring sequences spanning well-marked growth depressions at two sites in southern Sweden.

2. Material and methods

2.1 Sites and wood material

Samples of well-preserved subfossil Scots pine (*Pinus sylvestris* L.) from two raised peat bogs in southern Sweden were selected for analysis (Fig. 1). Mining of peat at the two sites has exposed hundreds of subfossil pine trees. Collection of samples using a chainsaw yielded 129 discs from Hällarydsmossen (57°20´N, 14°35´E) and 198 discs from Åbuamossen (56°19´N, 13°55´E). Hällarydsmossen is situated in a small headwater catchment, while Åbuamossen is in hydrologic contact with a major river and thus has a much larger effective catchment area than Hällarydsmossen (Fig. 1). The trees at Hällarydsmossen were found in highly humified *Sphagnum* peat resting on more than 120 cm of sedge peat and gyttja, which indicates establishment during a period of relatively dry bog-surface conditions. The analysed trees had an average of 172 measured growth rings and the oldest trees exceeded 360 years in age and 40 cm in diameter, bark excluded. Based on 117 trees, a 1112-year RW chronology spanning 4840-3728 BC was developed (Edvardsson *et al.,* 2012a). At Åbuamossen, 159 trees were used to construct a 1560-year RW chronology spanning 2668-1108 BC (Edvardsson, 2010; unpublished data). These trees were found above *c.* 40 cm of *Sphagnum* peat overlying *c.* 200 cm of sedge peat. The analysed trees had on average 156 measured growth rings and the oldest trees exceeded 320 years in age and 40 cm in diameter, bark excluded. The Hällarydsmossen RW chronology was assigned absolute ages by cross-dating against German bog-pine chronologies (Eckstein *et al.,*

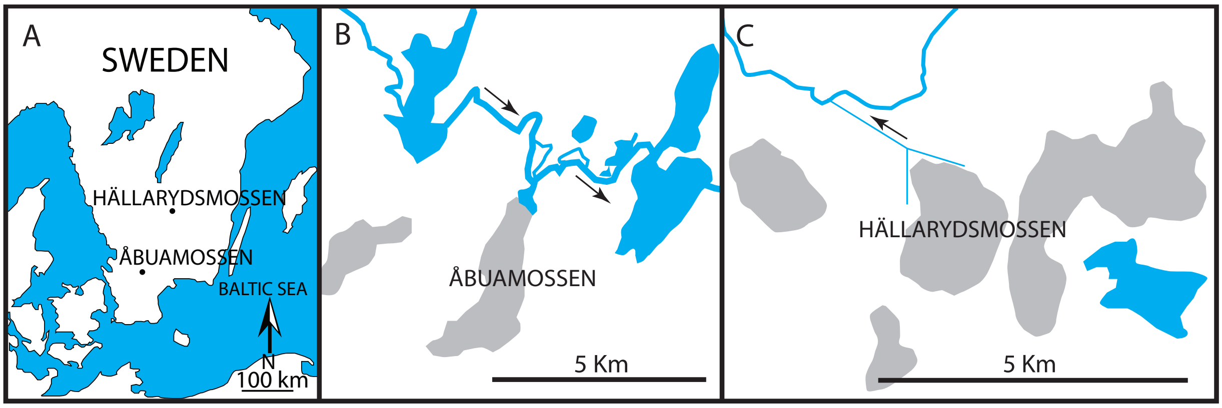

Figure 1. (A) Location of the peat bogs Hällarydsmossen and Åbuamossen, southern Sweden. (B) Åbuamossen (56°19´N, 13°55´E) is influenced by the river Helge å with a drainage basin upstream the site of c. 2000 km², whereas (C) Hällarydsmossen (57°20´N, 14°35´E) is located in a c. 15 km² headwater catchment within the Lagan River drainage basin. Peat deposits are shown as shaded areas and lakes and rivers are indicated in blue.

2009; Edvardsson *et al.,* 2012a), and the Åbuamossen chronology was cross-dated against a German bog-oak chronology (Leuschner *et al.,* 1987). No pine populations of corresponding ages and dimensions exist on peat bogs in southern Sweden today, which precludes direct comparison of RW data against meteorological records.

One tree at each site capturing a well-marked episode of bog-wide growth depression, identified in all sampled trees spanning the episode, was chosen for isotopic investigation. The two analysed tree-ring sequences each span 75 years and are both characterized by initially undisturbed, relatively strong tree growth, followed by abrupt growth depression, and finally a recovery back to the initial growth rate (Fig. 2). To avoid potential juvenile effects in the isotope records (Gagen *et al.,* 2011a), the selected trees each contained more than 40 annual rings prior to the analysed period. Wood samples were separated under magnification using a scalpel. The majority of samples (43) comprised three annual rings, whereas eight samples required either two (4) or four (4) annual rings to avoid crossing a transition between strong and depressed tree growth.

Individual wood samples were finely ground in a Retsch MM200 mixer mill, washed into test tubes using de-ionized water, and freeze-dried. Subsamples (≈0.1 mg) of freeze-dried whole-wood powder were loaded into tin cups and analysed for $^{13}C/^{12}C$ ratio (expressed as $\delta^{13}C_{WOOD}$) on CO_2 gas by EA-CF-IRMS (Carlo Erba CN Elemental Analyser interfaced to an Isochrom Continuous Flow Isotope Ratio Mass Spectrometer) in the University of Waterloo Environmental Isotope Laboratory. The remaining material was processed to isolate α-cellulose by sequential elimination of non-cellulose components through solvent extraction, delignification, and alkaline hydrolysis (Sternberg, 1989). Separate subsamples (≈0.1 mg) of freeze-dried α-cellulose were loaded into tin cups for analysis of $^{13}C/^{12}C$ ($\delta^{13}C_{CELL}$) on CO_2 gas, as for the whole-wood analysis, and $^{18}O/^{16}O$ ratios ($\delta^{18}O_{CELL}$) were determined on CO gas produced by high-temperature pyrolysis. The isotopic results are expressed as conventional $\delta^{13}C$ and $\delta^{18}O$ values, representing deviation in permil (‰) from the VPDB and VSMOW standards.

2.2 Correlation tests

Several different correlation tests were performed to assess possible controls on tree growth during the two investigated periods. The three isotope records developed from each bog-pine tree ($\delta^{13}C_{WOOD}$, $\delta^{13}C_{CELL}$, $\delta^{18}O_{CELL}$) were first correlated against six different RW series: three from each sampled tree at annual resolution (Annual RW_{Sample} – total ring, Annual EW_{Sample} – early wood, Annual LW_{Sample} – late wood); one multi-tree

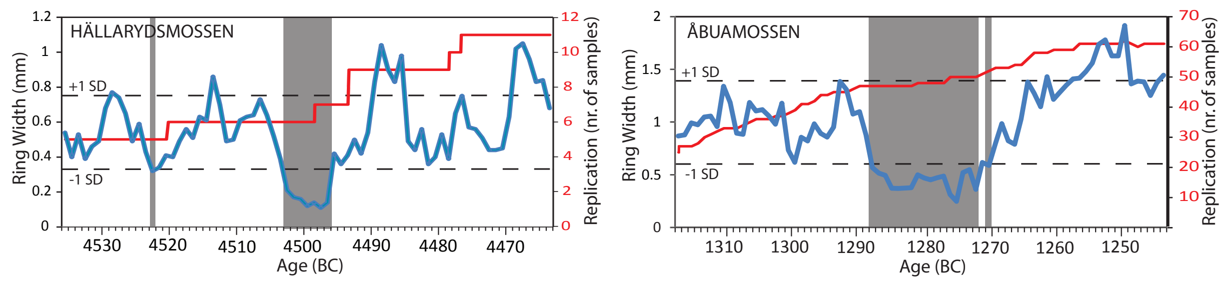

Figure 2. Average ring-width (RW) chronologies over the analysed periods from the two sites. The RW pattern from Hällarydsmossen (left panel) between 4536 and 4464 BC exhibits an eight-year growth depression around 4500 BC. The RW pattern from Åbuamossen (right panel) between 1318 and 1243 BC exhibits a c. 20-year growth depression around 1280 BC. The scales at the right show variations in tree replication (red curves) over the two periods, respectively. The shaded areas are years with depressed growth (RW less than -1 standard deviation).

site chronology at annual resolution (Annual RW_{Chron}); and two series composited over the same multiple ring increments as used for the isotopic analysis (Composite RW_{Sample}, Composite RW_{Chron}), representing the sample and the site population, respectively. Correlation tests with standardized index chronologies were also performed, but to maintain common units for all RW data, the results shown and discussed here are based on raw and averaged RW measurements in millimetres (mm). Additional lagged correlation tests between the isotopic records and selected RW parameters were also performed to probe for potential lags between the isotopic and growth responses of the trees.

3. Results

3.1 Hällarydsmossen

The six RW records and the three isotope records from Hällarydsmossen are shown in Figure 3, and the results of the correlation tests are shown in Tables 1 and 2. In all cases the strongest correlation between the two RW chronologies (Annual RW_{Chron} and Composite RW_{Chron}) and isotope records from Hällarydsmossen was obtained when the isotope records were shifted three years forward in time, and the highest *r* value was obtained when $\delta^{13}C_{CELL}$ was correlated with Composite RW_{Chron} following a three-year shift (Table 2).

Table 1. Pearson correlation coefficient (r) between RW and isotope data from Hällarydsmossen. Correlation values are shown when significance corresponding to (p<0.1) was achieved, and with asterisks (*) when highly significant correlation (p<0.01) was reached.

	Annual RW_{Chron}	**Annual EW_{Sample}**	**Annual LW_{Sample}**	**Annual RW_{Sample}**	**Composite RW_{Sample}**	**Composite RW_{Chron}**
$\delta^{13}C_{WOOD}$	0.37*	0.38*	0.29	0.38*	0.43*	0.40*
$\delta^{13}C_{CELL}$	0.29	0.39*	-	0.35*	0.39*	0.32*
$\delta^{18}O_{CELL}$	-	0.23	-	-	-	-

Table 2. Pearson correlation (r) between isotope data shifted in one-year steps along the Annual RW chronology from Hällarydsmossen and the Composite RW chronology (in italics). Correlation values are shown when significance corresponding to (p<0.1) was achieved, and with asterisks (*) when highly significant correlation (p<0.01) was reached.

	-5	**-4**	**-3**	**-2**	**-1**	**0**	**+1**	**+2**	**+3**	**+4**	**+5**
$\delta^{13}C_{WOOD}$	-	-	-	-	0.25	0.37*	0.48*	0.55*	0.58*	0.55*	0.49*
$\delta^{13}C_{CELL}$	-	-	-	-	-	0.29	0.43*	0.55*	0.61*	0.60*	0.52*
$\delta^{18}O_{CELL}$	-	-0.21	-0.24	-	-	-	0.21	0.33*	0.42*	0.38*	0.23
$\delta^{13}C_{WOOD}$	-	-	-	*0.22*	*0.31**	*0.40**	*0.48**	*0.56**	*0.61**	*0.56**	*0.52**
$\delta^{13}C_{CELL}$	-	-	-	-	*0.22*	*0.32**	*0.44**	*0.55**	*0.65**	*0.58**	*0.53**
$\delta^{18}O_{CELL}$	-	*-0.23*	*-0.23*	-	-	-	*0.24*	*0.36**	*0.44**	*0.33**	*0.21*

Table 3. Pearson correlation coefficient (r) between RW and isotope data from Åbuamossen. Correlation values are shown when significance corresponding to (p<0.1) was achieved, and with asterisks (*) when highly significant correlation (p<0.01) was reached.

	Annual RW_{Chron}	**Annual EW_{Sample}**	**Annual LW_{Sample}**	**Annual RW_{Sample}**	**Composite RW_{Sample}**	**Composite RW_{Chron}**
$\delta^{13}C_{WOOD}$	0.50*	-	-	-	-	0.52*
$\delta^{13}C_{CELL}$	0.55*	-	-	0.23	0.24	0.57*
$\delta^{18}O_{CELL}$	0.58*	-	-	0.21	0.21	0.60*

Table 4. Pearson correlation (r) between isotope data shifted in one-year steps along the Annual RW chronology from Åbuamossen and the Composite RW chronology (in italics). Correlation values are shown when significance corresponding to (p<0.1) achieved, and with asterisks (*) when highly significant correlation (p<0.01) been reached.

	-5	**-4**	**-3**	**-2**	**-1**	**0**	**+1**	**+2**	**+3**	**+4**	**+5**
$\delta^{13}C_{WOOD}$	0.41*	0.41*	0.43*	0.44*	0.47*	0.50*	0.52*	0.52*	0.52*	0.51*	0.53*
$\delta^{13}C_{CELL}$	0.37*	0.39*	0.42*	0.45*	0.49*	0.55*	0.58*	0.59*	0.58*	0.58*	0.58*
$\delta^{18}O_{CELL}$	0.40*	0.42*	0.40*	0.46*	0.51*	0.58*	0.63*	0.65*	0.68*	0.70*	0.69*
$\delta^{13}C_{WOOD}$	*0.43**	*0.43**	*0.44**	*0.47**	*0.50**	*0.52**	*0.53**	*0.53**	*0.54**	*0.53**	*0.53**
$\delta^{13}C_{CELL}$	*0.39**	*0.41**	*0.43**	*0.48**	*0.53**	*0.57**	*0.59**	*0.60**	*0.61**	*0.60**	*0.59**
$\delta^{18}O_{CELL}$	*0.43**	*0.43**	*0.42**	*0.48**	*0.54**	*0.60**	*0.64**	*0.67**	*0.71**	*0.70**	*0.70**

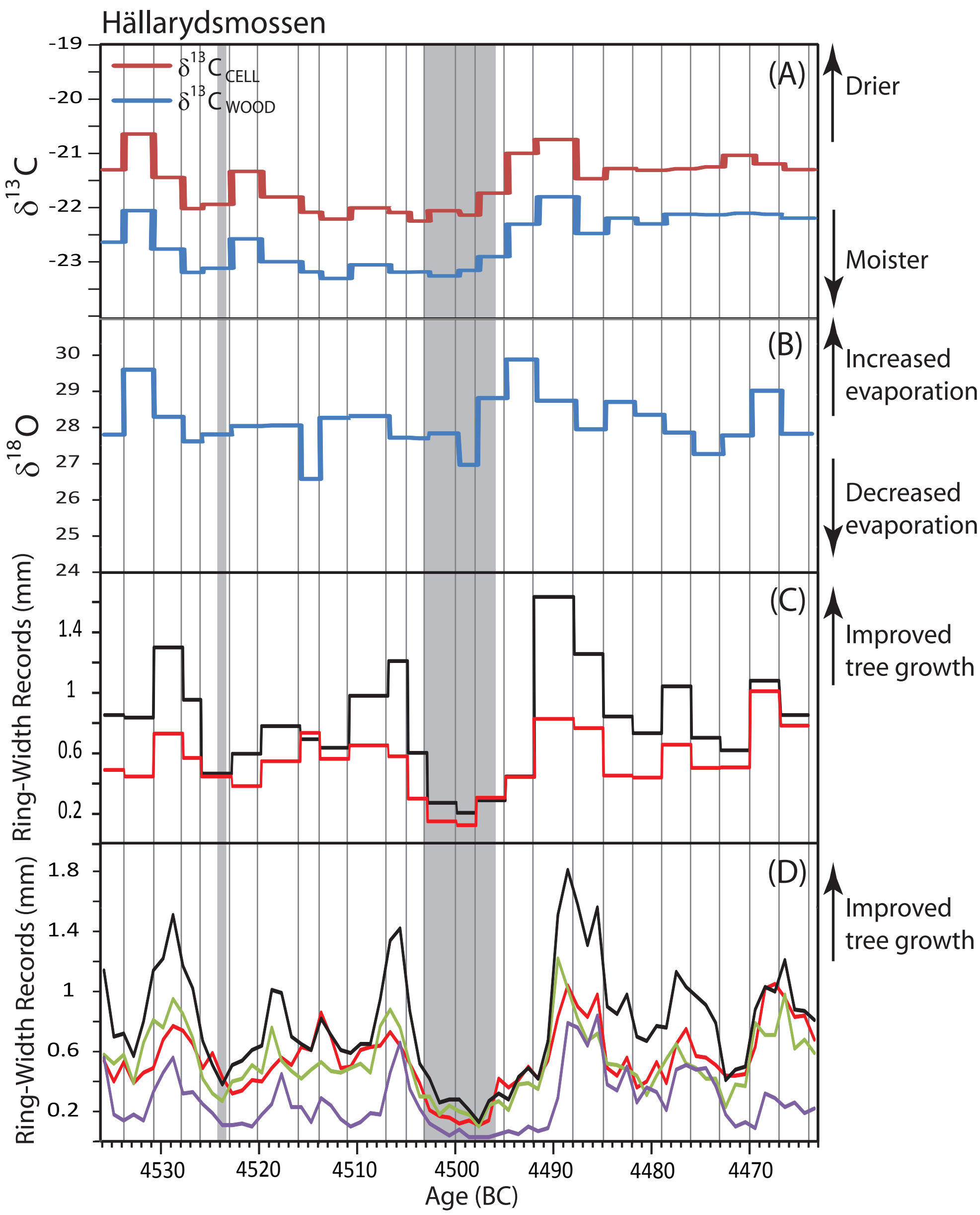

Figure 3. Stable-isotope and ring-width (RW) records from Hällarydsmossen. (A) Carbon-isotope data obtained on wood cellulose ($\delta^{13}C_{CELL}$) and whole-wood material ($\delta^{13}C_{WOOD}$). (B) Cellulose oxygen-isotope data ($\delta^{18}O_{CELL}$). (C) Composite RW record (Composite RW_{Sample}) obtained on the tree analysed for stable isotopes (black) and averaged RW chronology (Composite RW_{Chron}) based on 5-11 trees (Fig. 2) using the same multiple ring increments (red). (D) Different tested RW series with annual resolution from the analysed tree; averaged RW chronology (Annual RW_{Chron} - red), early-wood record (Annual EW_{Sample} - green), late-wood record (Annual LW_{Sample} - purple), and total ring (RW_{Sample} - black). The vertical lines show increments of annual growth rings analysed for stable isotopes. Shaded zones represent years with depressed growth (RW less than -1 standard deviation).

3.2 Åbuamossen

The six RW records and three isotope records from Åbuamossen are shown in Figure 4, and the results of the correlation tests are shown in Table 3 and 4. The correlation between the two RW chronologies (Annual RW_{Chron} and Composite RW_{Chron}) and isotope records from Åbuamossen increased when the isotope records were shifted forward in time, with maximum r values obtained for shifts in the range between two and five years (Table 4). The strongest correlation (r) between a RW and isotope record was obtained when $\delta^{18}O_{CELL}$ was correlated with Composite RW_{Chron} following a three-year shift, yielding an r value of 0.71 ($p<0.01$) (Table 4).

4. Discussion

Atmospheric moisture regime typically plays a dominant role in the carbon-isotope labelling of terrestrial plant matter under natural conditions, reflecting the need for plants to continuously balance the uptake of carbon dioxide from the air against the loss of water vapour through transpiration. Such environmental factors as temperature, soil moisture deficit, irradiance, and

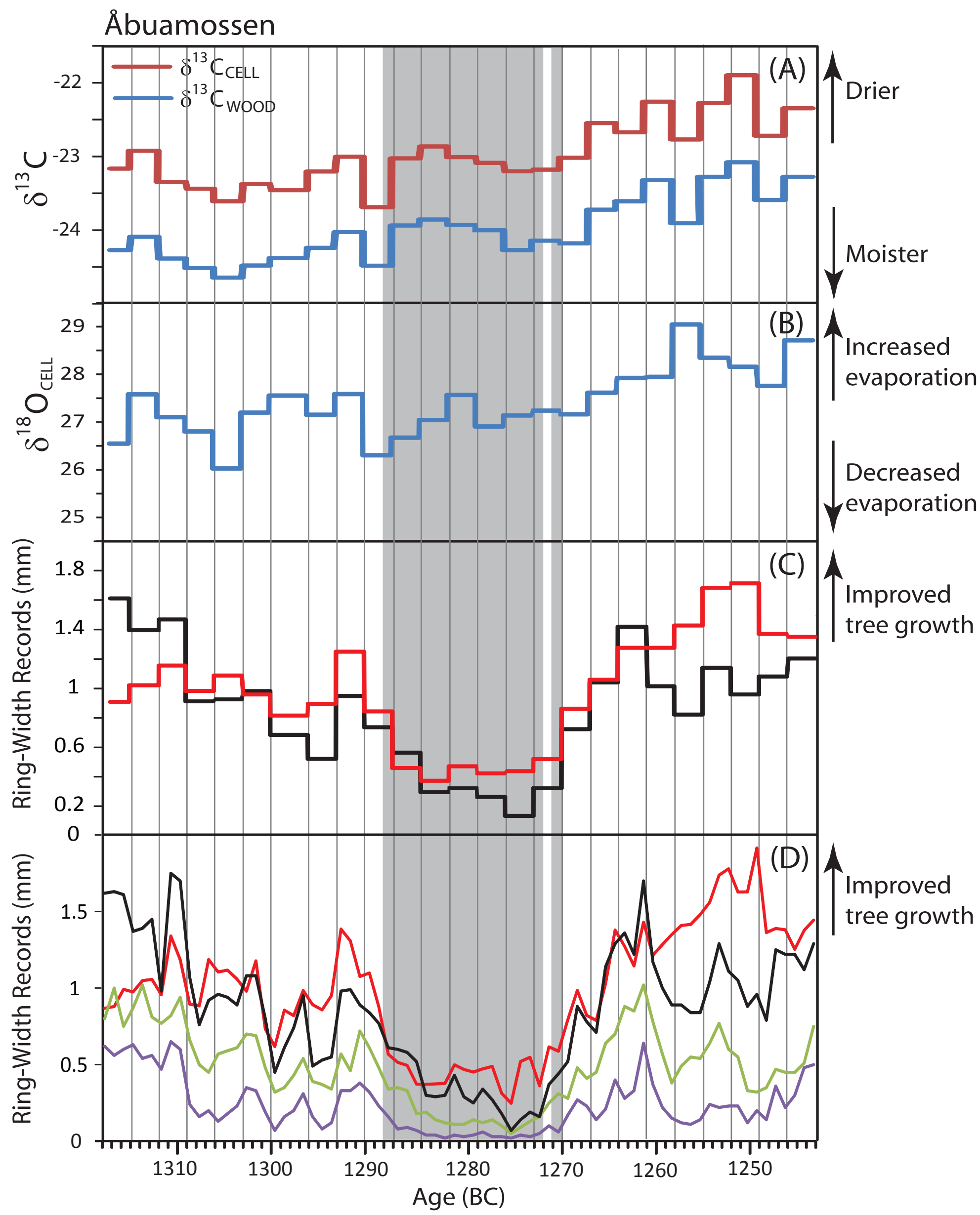

Figure 4. Stable-isotope and ring-width (RW) records from Åbuamossen. (A) Carbon-isotope data obtained on wood cellulose ($\delta^{13}C_{CELL}$) and whole-wood material ($\delta^{13}C_{WOOD}$). (B) Cellulose oxygen-isotope data ($\delta^{18}O_{CELL}$). (C) Composite RW record (Composite RW_{Sample}) obtained on the tree analysed for stable isotopes (black) and averaged RW chronology (Composite RW_{Chron}) based on 30 to 60 trees (Fig. 2) using the same multiple ring increments (red). (D) Different tested RW series with annual resolution from the analysed tree; averaged RW chronology (Annual RW_{Chron} - red), early-wood record (Annual EW_{Sample} - green), late-wood record (Annual LW_{Sample} - purple), and total ring (RW_{Sample} - black). The vertical lines show increments of annual growth rings analysed for stable isotopes. Shaded zones represent years with depressed growth (RW less than -1 standard deviation).

cloudiness also appear to influence discrimination against ^{13}C under some conditions (Edwards *et al.*, 2000; Gagen *et al.*, 2011b; Seftigen *et al.*, 2011), yet robust inverse correlations are commonly observed between variations in $\delta^{13}C$ (both whole wood and cellulose) and growth season relative humidity in the annual rings of trees in various climates (Lipp *et al.*, 1991, 1996; Hemming *et al.*, 1998; Sidorova *et al.*, 2008), as predicted by the model of Farquhar *et al.* (1989). Varying relative humidity, similarly, exerts pronounced effects on $\delta^{18}O$ variability in tree-ring cellulose through the preservation of evaporative-enrichment signals from leaf waters, in addition to potential signals from changes in the $\delta^{18}O$ of water taken up by the tree (Edwards and Fritz, 1986; Roden *et al.*, 2000; Edwards *et al.*, 2008). Although other factors may have had some influence, the probability that atmospheric relative humidity is a common driver of variability in both oxygen- and carbon-isotope labelling of the bog pines at the two sites is supported by the existence of similar positive correlations between the $\delta^{13}C_{CELL}$ and $\delta^{18}O_{CELL}$ time-series for both Hällarydsmossen (r = 0.77) and Åbuamossen (r = 0.60), as well as the weaker, but also positive correlations between $\delta^{13}C_{WOOD}$ and $\delta^{18}O_{CELL}$ (r = 0.76 at Hällarydsmossen; r = 0.48 at Åbuamossen). Hence, all three isotopic series appear to be proxy moisture records.

The existence of positive correlations between RW and isotopic records from our two study sites is consistent with the hypothesis that peatland tree growth is limited by excess effective moisture, likely through associated rise in the water table and thinning of the unsaturated zone, which inhibits root respiration (Boggie, 1972; Linderholm *et al.,* 2002). In general, $\delta^{13}C_{CELL}$, $\delta^{13}C_{WOOD}$ and $\delta^{18}O_{CELL}$ exhibit low values during and/or slightly before the recorded growth depressions, followed by increasing trends that broadly coincide with the subsequent increases in RW (Fig. 3 and 4). In the following discussion, $\delta^{13}C$ refers to the respective $\delta^{13}C_{CELL}$ records.

The $\delta^{13}C$ and $\delta^{18}O$ records from Hällarydsmossen (Fig. 3) reflect an onset of moister conditions at about 4531 BC followed by decreased tree growth a few years later, i.e. between 4526 and 4523 BC. Minor changes in the $\delta^{13}C$ records are recorded over the following decade, but generally moist conditions appear to dominate prior to 4495 BC. As both the $\delta^{13}C$ and the $\delta^{18}O$ records show extended minima prior to and during the onset of the period with depressed tree growth (4503-4496 BC), conditions can be assumed to have been increasingly moist. Thereafter, the isotopic records suggest a change towards drier conditions between c. 4498 and 4492 BC. The response in tree growth is not immediate, but the overall response agrees with the hypothesis that tree growth is limited by moisture. During the last decades the isotope records exhibit no major changes while RW shows substantial variations, although no years with RW values of less than 1 standard deviation were recorded.

The isotopic records from Åbuamossen reach minimum values around 1305 BC, accompanied by decreasing RW, followed by slight increases until 1290 BC (Fig. 4). Temporary decreases in the isotopic records occurred at 1290 BC, followed by relatively stable isotopic values until 1267 BC. However, the isotopic excursions at 1290 BC coincide with the onset of the RW-inferred growth depression that lasted for about two decades. This growth depression is visible in all individual trees indicating that the detected wet shift affected the entire bog-pine population. The isotopic records shift to elevated values at 1267 BC, a few years after the onset of increasing RW, although the latter increase continued until at least 1264 BC, well after the isotopic responses, perhaps as a result of root adaptation or slowly improving growth conditions. Over the two last decades the Åbuamossen isotopic records show that conditions became increasingly drier. The trend in the averaged RW chronologies corresponds to the isotopic records, while the isotopically analysed tree had difficulties to recover.

4.1 A possible delay in tree-growth response

The correlation (r) between RW and the isotopic records increases when the latter are moved c. three years forward in time, which indicates a lagged response of tree growth compared to the isotopic labelling of wood cellulose at major shifts between moisture regimes at the investigated peat bogs. This lag effect is less clear at Åbuamossen than at Hällarydsmossen, where the increase of the correlation in percentage terms is considerably larger. However, the resolution is not annual in the isotopic records, which precludes assignment of exact years to the recorded shifts. It is also worth noting that the duration of the RW-based growth responses considered here as compared to the total length of the respective RW records probably has an influence on the correlation tests. The 18-year growth depression at Åbuamossen represents 24% of the analysed time series, as compared to 9 years (12%) at Hällarydsmossen. This difference may to some extent explain the more equally distributed correlation matrix with a less distinct increase in r values following a forward shift of Composite RW_{Chron} at the former site. Statistical evaluations of the RW chronologies (not shown) demonstrate that autocorrelation cannot explain this phenomenon. The lag effect observed in the RW data may therefore be attributed to delayed adjustments of water tables in the bogs in response to changing atmospheric conditions.

Hydrological delays in peat deposits may reflect several processes, such as the location of the bog surface, which varies depending on how much water is stored in the bog, slow water transport through the surrounding mineral soils of precipitation falling as snow. A study by Linderholm *et al.* (2002) showed that pine trees growing on peatlands in Sweden were directly influenced by temperature and precipitation, but also by groundwater fluctuations caused by climate variability over several years. Peat soils are also compressible and changes in water content may result in volumetric fluctuations detectable as variations in the surface elevation (Price and Schlotzhauer, 1999). Bog surfaces, for example, may be lowered in response to groundwater draw-down during periods of relatively warm and dry conditions, and widespread bog surface lowerings have been observed in southern Sweden since the 1970s (Franzén, 2006). Some of these scenarios would initially result in relatively unchanged thickness of the unsaturated zone. As a result, growth conditions for bog trees may remain largely constant until the bog-surface and water table stabilize and the unsaturated zone adjusts to the altered hydrologic regime. This could explain the delayed growth response of the bog pines compared to the isotopic responses, which are more directly related to atmospheric moisture conditions. However, delayed hydrologic effects may well be highly site-specific due to differences in size of the catchment, shape of the basin or thickness of the peat deposit. The Hällarydsmossen bog is situated in a relatively small and topographically constrained basin, while Åbuamossen is connected to a much larger catchment area (Fig. 1). The signals detected in the isotopic records from Hällarydsmossen can therefore be expected to reflect more local variations than the corresponding records from Åbuamossen. The stronger correlation between the composite RW records and $\delta^{18}O_{CELL}$ is likely a result of the large catchment area of Åbuamossen, which probably propagates more regional and hence less variable $\delta^{18}O$ signal to the bog-pine population. The RW response at Åbuamossen is also more rapid and the improvement in correlation with the isotopic records, expressed in percentages, is less significant following a three-year shift as compared to Hällarydsmossen.

Another possible explanation for the observed lag effect may be storage of carbohydrates in the trees. However, studies by e.g. Treydte *et al.* (2007) show that conditions during previous years do not strongly influence cellulose $\delta^{13}C$ and $\delta^{18}O$ records obtained on pine trees. On the other hand, the bog trees analysed here have grown under substantially wetter conditions. Further studies are therefore needed to assess the importance of potential carry-over effect in the bog pines in response to remobilized carbohydrate reserves as compared to hydrologically induced delays of tree growth.

These initial results show that (1) effective moisture is an important factor influencing growth of bog-pine populations, with prolonged wet periods leading to suppressed growth due to rising water tables, (2) variations in RW of bog pines in response to altered hydrologic conditions of peat deposits are delayed by c. three years as compared to $\delta^{13}C$ and $\delta^{18}O$ records reflecting ambient atmospheric moisture conditions, (3) differences in lag effects between isotopic signals and RW records may be related to catchment conditions of peat bogs. However, further studies based on longer isotopic time series of higher resolution and replication are required to fully understand the relation between bog-tree growth and moisture variability in peat bogs.

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