Available online at www.sciencedirect.com

SCIENCE DIRECT®

Global and Planetary Change 49 (2005) 47–62

GLOBAL AND PLANETARY CHANGE

www.elsevier.com/locate/gloplacha

Last interglacial atmospheric CO_2 changes from stomatal index data and their relation to climate variations

Mats Rundgren*, Svante Björck, Dan Hammarlund

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

Received 10 October 2004; accepted 18 April 2005

Abstract

A high-resolution atmospheric CO_2 reconstruction based on stomatal index data obtained from *Betula* and *Quercus* leaf fragments extracted from the Danish Hollerup lake sediment section provides a unique insight into last interglacial CO_2 dynamics. According to pollen stratigraphic correlations the CO_2 record covers the first c. 7400 years of the Eemian, as palaeobotanically defined in northwestern Europe. The first c. 3000 years of the reconstruction are characterised by centennial to millennial CO_2 variability in the interval 250–290 ppmv, while the remaining part of the record is generally more stable with slightly higher values (290–300 ppmv). According to pollen stratigraphic correlations this shift in CO_2 dynamics is coincident with the end of the early Eemian climatic optimum in northwestern Europe. Pollen data from this region indicate that early Eemian CO_2 instability may be linked to vegetation succession following deglaciation in Europe, but vegetation dynamics on other northern continents were probably also important. In addition, palaeoceanographic records from the Nordic seas indicate an influence of oceanic processes on the reconstructed Eemian CO_2 evolution. A 300-year period of rapid CO_2 oscillations immediately before the establishment of stable conditions is synchronous with a dry and cool event previously inferred from proxy data from the same sediment sequence, suggesting that this was a climatic event of regional or global significance. The presented CO_2 reconstruction is in general agreement with previous ice core and stomatal-based CO_2 data, although a larger variability compared with Vostok ice core data is evident. This may be explained partly by the different resolution of the two records and the inherent smoothing of ice core gas records.
© 2005 Elsevier B.V. All rights reserved.

Keywords: CO_2; last interglacial; Eemian; climate; stomata; leaves

1. Introduction

Data from the Antarctic Vostok ice core have revealed that atmospheric carbon dioxide plays an important role as an amplifier of climatic changes over glacial–interglacial time scales (Fischer et al.,

* Corresponding author. Tel.: +46 46 2227856; fax: +46 46 2224830.

E-mail address: mats.rundgren@geol.lu.se (M. Rundgren).

0921-8181/$ - see front matter © 2005 Elsevier B.V. All rights reserved.
doi:10.1016/j.gloplacha.2005.04.002

1999; Petit et al., 1999; Raynaud et al., 2000; Shackleton, 2000; Mudelsee, 2001). The deduced sequence of events is that a change in orbital parameters affecting summer insolation at high northern latitudes directly influences temperature conditions at Earth's surface. Reorganization of the global carbon cycle caused by this initial temperature change then leads to amplification of the temperature response through a change in the atmospheric concentration of CO_2 (and methane). The temperature change resulting from this positive feedback is most pronounced at high northern and southern latitudes and therefore an important control of global ice volume. The Vostok ice core has allowed detection of the link between atmospheric greenhouse gases and climate over the past four glacial–interglacial cycles and a new ice core drilled at Dome C in Antarctica will extend this over three more cycles (EPICA community members, 2004).

Human activity has recently introduced a new role for atmospheric CO_2 in the climate system; burning of fossil fuels and the resulting rapid CO_2 increase has made atmospheric CO_2 into an important forcing factor that is itself not influenced by climate. This situation is unique to the last 150–200 years, although it has been suggested that human activities (agriculture and forest clearance) already started to impact on atmospheric CO_2 concentrations 8 kyr ago (Ruddiman, 2003). The latter proposition is partly based on the observation that the Holocene CO_2 evolution is different from those of earlier interglacials. Like the Holocene, the three previous interglacials began with a pronounced CO_2 peak (Petit et al., 1999). However, following a decline over c. 3 kyr, Holocene CO_2 concentrations started an increasing trend that, with minor oscillations, continued up to the onset of industrialisation (Indermühle et al., 1999), a feature not seen in previous interglacials. The CO_2 evolution following the early maximum was not identical between earlier interglacials but, according to the Vostok record, there was in no case a reverse trend towards higher CO_2 concentrations.

The study of proxy records from previous interglacials is important to increase our understanding of interglacial climate dynamics without human interference and it may also help us to identify anthropogenic influence during the Holocene. The penultimate interglacial, approximately corresponding to marine isotope stage (MIS) 5e dated to c. 130–116 ka (Kukla et al., 2002), offers the possibility to study interglacial climate records from a wide array of archives and regions at relatively high resolution. Prior to MIS 5e, terrestrial interglacial records become more sparse and fragmented and temporal resolution generally becomes lower for all types of archives. Moreover, the last interglacial has been a major focus of interest within palaeoclimate research over the last decade, an interest spurred by indications of marked interglacial instability in a Greenland ice core (GRIP members, 1993). Although ambiguous (Grootes et al., 1993; North Greenland Ice Core Project Members, 2004), these data were the starting point of an intensive search for evidence of rapid climate changes in marine and terrestrial records. So far, the resulting data tend to suggest that the last interglacial was less stable than the Holocene, at least at high northern latitudes (e.g., Fronval et al., 1998), but it is not known what role CO_2 may have played for this relative instability.

Because of the low ice accumulation rate at Vostok, the last interglacial section of this CO_2 record is of low resolution (Petit et al., 1999), with wide age distribution of the enclosed air. As a consequence of diffusion through the firn layer during enclosure, air bubbles in interglacial sections of this core have an age distribution of c. 300 years (Barnola et al., 1991). In addition, the dating uncertainty, estimated to be ± 10 kyr in the relevant interval (Petit et al., 1999), makes it difficult to directly relate the Vostok CO_2 record to palaeoclimatic records. Of the alternative CO_2 proxies available, the stomatal frequency method is the most direct and also has the capability to reconstruct CO_2 dynamics at the century scale (Royer, 2001; Rundgren and Beerling, 2003). It has previously been applied to leaves of last interglacial age and yielded results in general agreement with Vostok data (Rundgren and Bennike, 2002). The method rests on the inverse relationship between stomatal frequency of terrestrial plant leaves and CO_2 partial pressure as revealed by historic data sets and controlled experiments (Woodward, 1987; Woodward and Bazzaz, 1988). The level of atmospheric CO_2 determines the number of cells that develop into stomata and this is set during the early stages of leaf development. Consequently, the number of stomata relative to the sum of stomata and epidermal cells, usually referred to as stomatal index (SI), constitutes a reliable proxy for atmospheric CO_2 (Beerling, 1999; Royer, 2001).

Here, we present a CO_2 reconstruction of centennial resolution for the first 7400 years of the last interglacial in northwestern Europe (the Eemian) based on SI measurements on *Betula* and *Quercus* leaves extracted from a lake sediment section at Hollerup in Denmark. Because of its high resolution, this study provides a unique insight into the CO_2 dynamics of the first half of the Eemian. The sediment sequence has previously been subject to an extensive multi-proxy study (Björck et al., 2000). Consequently, our CO_2 data can be directly compared with local and regional records of climatic and hydrologic conditions, which enables detection of possible interactions between CO_2 and northern hemispheric climate.

2. Site, stratigraphy and chronology

The investigated lake sediment sequence, which is overlain by glaciofluvial and glacial deposits associated with the Weichselian glaciation, is exposed in a disused diatomaceous earth pit (56°24′23″, 9°50′46″) on the northern edge of the Gudenå river valley, c. 500 m south of Hollerup farm between Ulstrup and Langå in eastern central Jylland, Denmark (Fig. 1). Its macro flora and fauna was first studied by Hartz and Østrup (1899) and later palynological investigations (Jessen and Milthers, 1928; Andersen, 1965, 1966) revealed a pollen stratigraphy typical for the Eemian of northwestern Europe. Björck et al. (2000) carried out a detailed multi-proxy study of the Hollerup sequence involving sedimentology, geochemistry and analyses of stable isotopes, diatoms and mineral magnetics and they interpreted their results in terms of lake development and hydrologic and climatic changes.

Björck et al. (2000) identified five lithologic units in the lake sediment sequence at Hollerup (Fig. 2). The basal and coarse minerogenic sediments of unit 1 are overlain by the highly calcareous unit 2 showing a gradual transition to the more organic-rich unit 3. The carbonate content decreases upwards in unit 3, at the same time as diatoms become an important component of the sediment. The uppermost part of unit 3 shows clear indications of disturbance and the boundary to unit 4 is very distinct. Unit 4 is dominated by diatomite. The lacustrine sequence ends with the minerogenic sediments of unit 5, which are of variable grain size.

Our CO_2 reconstruction is based on a new series of sediment samples collected at Hollerup in October 1999. Resampling of the sequence was necessary to obtain a sufficient number of leaf fragments for stomatal frequency analysis. All lithologic units and most subunits described by Björck et al. (2000) were easily identified in a section exposed in the same wall as previously studied. Units 2–5 as described by Björck et al. (2000) were found to com-

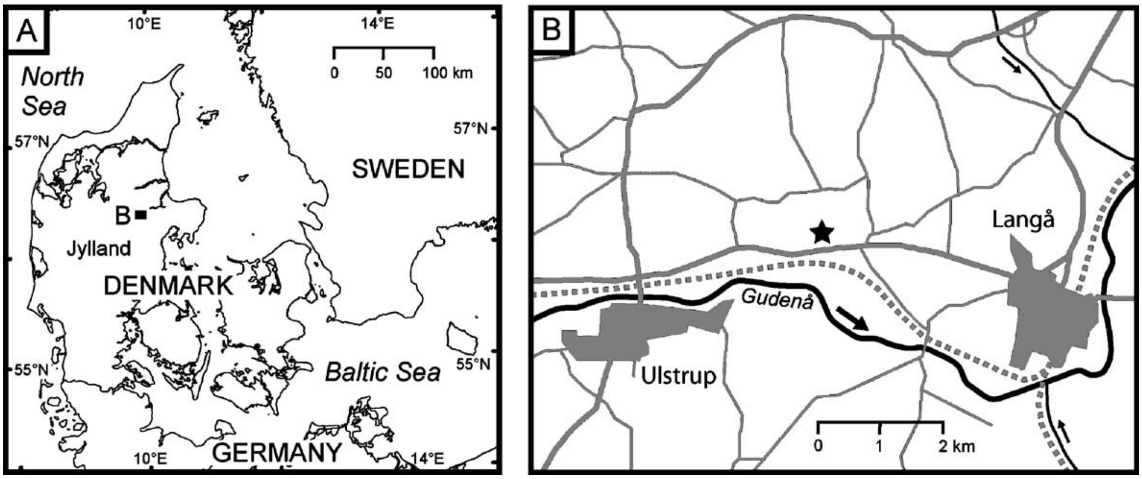

Fig. 1. (A) Map of Denmark and neighbouring countries. The area covered by the map in 'B' is indicated by a black rectangle. (B) Map showing the location of the Hollerup site (marked by a star) on the northern edge of the Gudenå river valley. Roads (full lines) and railways (dashed lines) are shown in grey.

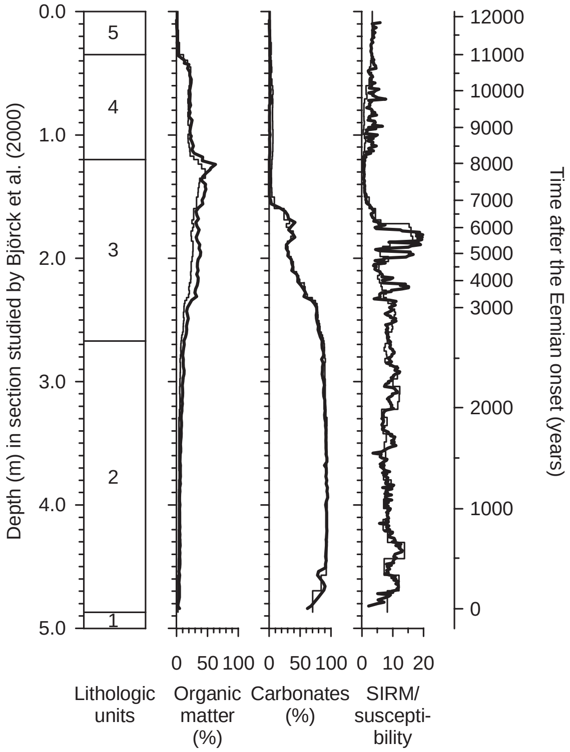

Fig. 2. Correlated loss-on-ignition and mineral magnetic records for the Hollerup section studied by Björck et al. (2000) (thick lines) and the new section sampled for the present investigation (thin lines). SIRM=Saturation isothermal remanent magnetization. Also shown are the lithologic units described in the text and by Björck et al. (2000). The chronology shown was constructed by Björck et al. (2000) based on pollen stratigraphic correlations to the partly laminated lake sediment sequence at Bispingen in northern Germany (Müller, 1974).

prise 4.54 m in the new section compared with 4.87 m in the previous study. Taking into account lithologic boundaries, 99 samples covering 3–12 cm vertical intervals were taken contiguously through units 2–5 and a detailed correlation to the previously studied sequence was made through analysis of loss on ignition and mineral magnetic parameters (Fig. 2). This enabled us to apply the chronology of Björck et al. (2000), which is based on pollen stratigraphic correlations to the partly annually laminated lake sediments at Bispingen in northern Germany (Müller, 1974). According to these correlations, units 2–4 in the section at Hollerup constitutes a complete Eemian sequence covering c. 11 kyr (Fig. 2). Following the recommendations by Kukla et al. (2002), we make a distinction between the "last interglacial" and "Eemian" and restrict the term "Eemian" to sites in northwestern Europe with a palaeobotanically defined period of temperate forests (e.g. Hollerup). The "last interglacial" is used for corresponding warm periods registered in other regions and by other proxies; the beginning and end of these may not be synchronous with those of the Eemian in northwestern Europe. For example, the beginning of the last interglacial in the marine record (MIS 5e) is dated to c. 130 ka, i.e. 3–4 kyr before the development of temperate Eemian forests in northwestern Europe (Kukla et al., 2002; Shackleton et al., 2003).

3. Methods

3.1. Laboratory methods

Sample volume, as measured by displacement of water, ranged from 260 to 1570 cm^3 (mean = 894 cm^3). Samples were disaggregated overnight in a 5% NaOH solution, which was found not to be harmful to the leaf fragments, and carefully washed through sieves with 0.25 and 0.50 mm mesh size. Subsequently, all leaf fragments were picked out using a stereomicroscope.

Leaf fragments were determined to species using a reference collection of leaves of northwest European trees and literature on leaf cuticle morphology (Westerkamp and Demmelmeyer, 1997). Fragments of *Betula pendula*, *Quercus petraea* and *Quercus robur* were analysed for stomatal index and density in epifluorescent light (UV filter, 330–380 nm) at a magnification of ×600; a graticule in one of the eyepieces facilitated counting of stomata and epidermal cells. Following the recommendations of Poole and Kürschner (1999), counts were restricted to interveinal areas and not conducted along leaf margins. Stomatal index was calculated as $SI = [SD/(SD + ED)] \times 100$, where SD is the stomatal density (mm^{-2}) and ED is the epidermal cell density (mm^{-2}) (Salisbury, 1927). When possible, seven counts were made distributed over the lower, stomata-bearing surface of all *Betula* and *Quercus* leaf fragments. Based on these measurements a mean SI value was calculated for each fragment and subsequently a sample mean value was calculated for each taxon and used in the CO_2 calibration.

3.2. CO_2 calibration

Our CO_2 reconstruction is based on SI data obtained from *B. pendula*, *Q. petraea* and *Q. robur*. Of these species, CO_2 calibration data sets have previously been developed for *B. pendula* (combined *B. pendula*/*B. pubescens* data set; Wagner et al., 1999, 2002, 2004) and *Q. petraea* (Kürschner et al., 1996) and used in CO_2 reconstruction from fossil leaves. Calibration data are currently not available for *Q. robur*, but a stomatal response in this species is known from both herbarium studies and CO_2 experiments (Woodward, 1987; Woodward and Bazzaz, 1988; Beerling and Chaloner, 1993). The response is very similar to that of *Q. petraea* (Van Hoof, 2004), allowing the *Q. petraea* calibration to be applied also to the more abundant *Q. robur* leaves. Past CO_2 concentrations were estimated using inverse (linear) regression (Draper and Smith, 1981) applied to the *B. pendula* (Wagner et al., 2002) and *Q. petraea* (Kürschner et al., 1996) data sets. Regression details are as follows: *B. pendula*/*B. pubescens*: $n=64$, intercept$=36.152$, slope$=-0.085$, and $r^2=0.78$ and *Q. petraea*: $n=82$, intercept$=38.648$, slope$=-0.074$, and $r^2=0.51$.

The low level of leaf preservation for the other broad-leaved tree species recorded (*Alnus glutinosa* and *Carpinus betulus*) prevented their use in CO_2 reconstruction. Although stomatal frequency response to CO_2 changes has been shown for some conifer species (Royer, 2001; Kouwenberg et al., 2003), no attempt was made at utilizing the recorded needles of *Pinus sylvestris* and *Picea abies*. This was mainly because these leaf records end around the same stratigraphic level as that of *B. pendula* and therefore would not extend our CO_2 reconstruction. In addition, no modern training sets are available for *P. sylvestris* and *P. abies*.

4. Results and interpretations

4.1. Leaf record

Leaf fragments of five broad-leaved tree species and two conifers were identified from 78 of the 99 Hollerup samples and, in general, there is a good correspondence between the leaf and pollen records (Fig. 3). *Betula pendula* and *Quercus robur* are the most frequent species, both with respect to the number of samples and total number of leaf fragments.

B. pendula leaves are present in high concentrations already at the base of the sequence, at the same time as *Betula* pollen percentages are at their maximum. The two lowermost leaf samples represent the basal part of unit 2, which is characterised by a high content of sand, gravel and pebbles (Björck et al., 2000). This suggests deposition in a more near-shore environment compared to the samples above, which may explain the relative abundance of leaf fragments (and pollen). The following interval of low *Betula* pollen percentages (<10%) is characterised by low numbers or absence of *B. pendula* leaf fragments. A second interval with relative abundance of *B. pendula* fragments begins at 2.41 m, around a level where pollen percentages begin to increase again. This interval ends at 1.69 m and the uppermost birch fragment is recorded at 1.41 m. While the leaf record ends in unit 3, *Betula* pollen percentages above 10% are found also in parts of units 4–5.

The *Quercus* leaf record corresponds to an interval of high *Quercus* pollen percentages. The pollen record peaks, however, below the leaf record, which indicates that *Quercus* was present at the site before the first leaf is recorded in the sediments. *Q. robur* occurs continuously between 4.21 and 2.32 m with a pronounced peak at 2.93–2.41 m, while *Q. petraea* is represented only by single fragments at a few levels in the lower part of the sequence. There is no counterpart in the pollen record to the observed maximum in *Q. robur* leaf fragments. Therefore, this maximum is likely to reflect a change in the depositional environment, e.g. a change in lake level (see Section 5.3), rather than a change in vegetational composition. The end of the maximum is coincident with a decline in *Quercus* pollen percentages and values stay below 10% for the remaining part of the sequence.

In addition to single fragments in the lower part, an interval of high concentrations of *Alnus glutinosa* leaf fragments is found between 0.60 and 0.35 m and marks the end of the Hollerup leaf record. These high concentrations occur in the uppermost part of unit 4, which is characterised by relatively high minerogenic content and sand lenses (Björck et al.,

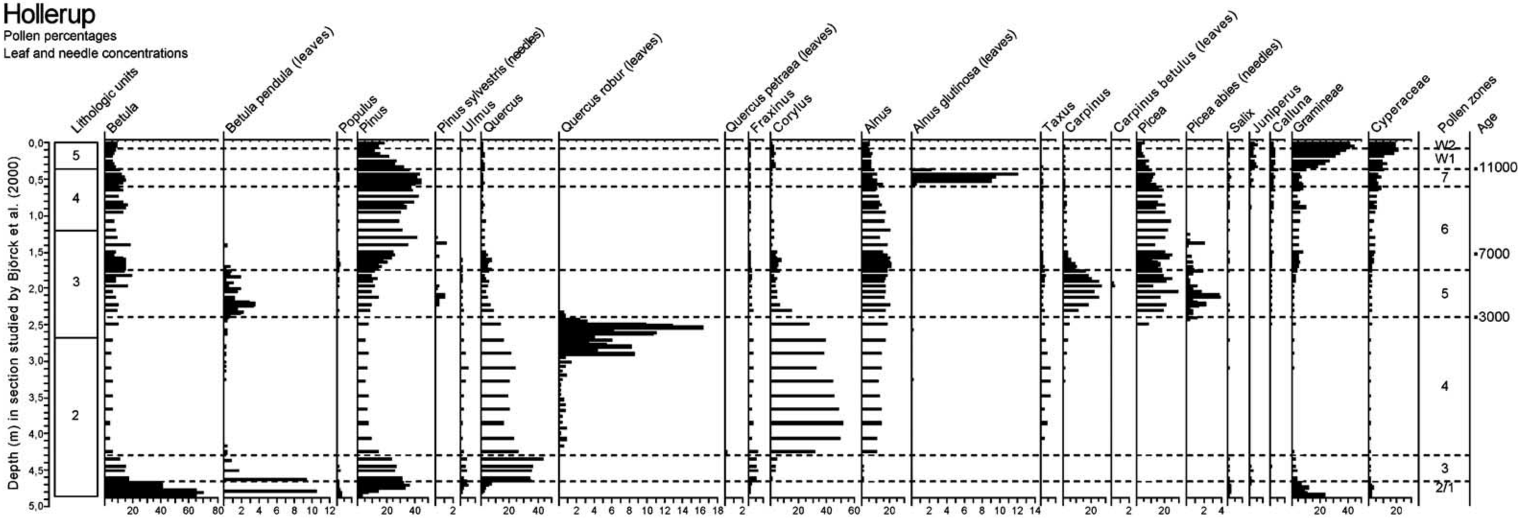

Fig. 3. Pollen and leaf/needle stratigraphies of the Hollerup lake sequence. Pollen data (percentages) are based on Andersen's (1965, 1966) analysis and presented according to the correlations made by Björck et al. (2000). Only the most abundant taxa are shown. Leaf and needle data (concentrations; number of fragments in 100 cm^3 of sediment) were obtained from a new series of samples correlated to the sequence studied by Björck et al. (2000) based on data presented in Fig. 2. The indicated pollen zones were defined by Andersen (1965, 1966) and age estimates are according to Björck et al. (2000). See text for description of lithologic units.

2000). This suggests that the abundance of leaf fragments in these samples partly results from increased soil erosion and it may also explain the poor preservation of the leaf material. *Carpinus betulus* was only identified in two samples in the mid part of the sequence (1.99–1.90 m) and this occurrence is consistent with the pollen record. Also needles of *Pinus sylvestris* and *Picea abies* were recorded in the mid part at 2.23–1.28 and 2.46–1.20 m, respectively. *P. sylvestris* needles were only found in unit 3, although relatively high *Pinus* pollen percentages are seen already in the lower part of unit 2. The samples with the highest needle concentrations coincide with peaks in the pollen record, but no pine needles were found in samples corresponding to the peaks in pollen percentages in unit 4. The first *P. abies* needles were recorded shortly above the first occurrence of *Picea* pollen. As for *Pinus*, no needles were found in unit 4 despite relatively high pollen percentages. This may reflect less favourable conditions for preservation of needles (and leaves) in the diatomite.

4.2. CO_2 reconstruction

Reconstructed CO_2 values for each sample and species are presented in Fig. 4A together with running

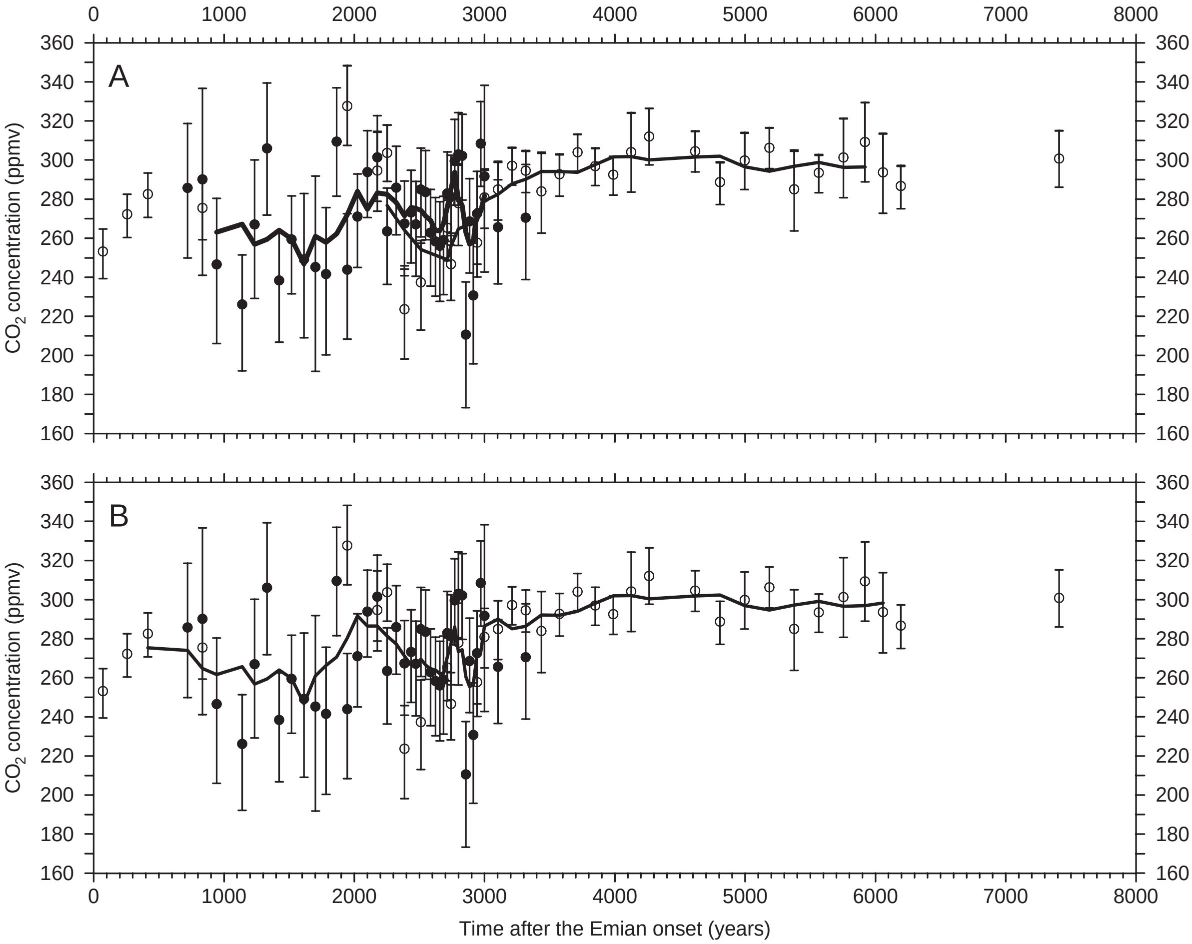

Fig. 4. Reconstructed atmospheric CO_2 concentrations, with 95% confidence intervals, based on stomatal index data obtained from *Betula pendula* (open circles) and *Quercus robur*/*Quercus petraea* (full circles) leaf fragments preserved in the Hollerup lake sediment sequence. (A) Smoothed taxon-specific CO_2 records (five-point running mean values) for *B. pendula* (thin line) and *Q. robur*/*Q. petraea* (thick line). (B) Smoothed composite CO_2 record (five-point running mean values). Chronology is according to Björck et al. (2000).

mean values to emphasize trends in the data. The entire data set spans the first c. 7400 years of the Eemian. Confidence intervals for the reconstructed CO_2 values are generally more narrow for *Betula*, which reflects the higher coefficient of determination ($r^2=0.78$) of the modern training set used for calibration ($r^2=0.51$ for *Quercus*).

In general, *Betula* and *Quercus* CO_2 estimates for the same samples overlap within their 95% confidence intervals. The species-specific records show good agreement both in their trends and absolute CO_2 levels in the main interval where they overlap, i.e. approximately 1900–3300 years after the Eemian onset (Fig. 4A). A CO_2 decrease is recorded by both *Betula* and *Quercus* between c. 2000 and 2700 years, followed by an overall increase ending around 3000 years after the onset of the Eemian. The more well-resolved *Quercus* record indicates, however, that the period c. 2700–3000 years after the start of the Eemian was characterised by large-scale CO_2 shifts rather than a unidirectional increase and each high and low during this dynamic interval is supported by several data points. This non-random character of the CO_2 record clearly indicates that the change in depositional environment suggested to be responsible for the high input of *Quercus* leaves around this time did not involve redeposition of leaves. Continuous sedimentation over this interval is further supported by the gradual character of sedimentary boundaries and loss-on-ignition and mineral magnetic records (Fig. 2; Björck et al., 2000). Because of the good agreement observed between *Betula* and *Quercus* data, the two data sets were combined to form a composite CO_2 record covering the first c. 7400 years of the Eemian. A mean CO_2 value was calculated for samples with both taxa present and this was used as input for the smoother displayed to illustrate trends in the data (Fig. 4B).

The CO_2 record may be divided into two main parts: an unstable period covering the first c. 3000 years followed by more stable conditions over the next 3000 years (Fig. 4B). According to the reconstruction, the first c. 2700 years were characterised by centennial to millennial CO_2 changes within the range of 250–290 ppmv. An initial CO_2 increase from c. 255–275 ppmv was followed by a c. 25 ppmv decrease in the period c. 600–1600 years after the Eemian onset. Then CO_2 levels increased again from c. 250 ppmv to reach around 290 ppmv c. 2000 years after the beginning of the Eemian. A CO_2 decrease (c. 290–260 ppmv) is indicated for the next c. 700 years. As noted above, these centennial to millennial changes were followed by more rapid CO_2 oscillations within the range of c. 255–285 ppmv between c. 2700 and 3000 years after the onset of the Eemian. In the subsequent relatively stable period, which apparently lasted at least until c. 7400 years after the Eemian onset, CO_2 concentrations of c. 290–300 ppmv are reconstructed. A c. 1000-year gap in the record between the two youngest samples makes it, however, difficult to definitively claim CO_2 stability for the entire interval.

5. Discussion

5.1. Comparison with the Vostok CO_2 record

It is difficult to temporally relate our Eemian CO_2 reconstruction to the CO_2 record from Vostok; there are uncertainties associated with absolute dating of both the air bubbles contained in Antarctic ice and the leaf fragments preserved in the Danish lake sediments. On the one hand, age determination of Vostok ice samples relies on glaciological modelling and for the last interglacial dating uncertainty is estimated to c. ±10 kyr (Petit et al., 1999). In addition, there is the uncertainty associated with estimating the ice-age/gas-age difference (Barnola et al., 1991). On the other hand, the age of the Hollerup sediments is beyond the limit of radiocarbon dating and application of other radiometric methods has proved to be problematic (Kronborg and Mejdahl, 1989; Israelson et al., 1998). Although the pollen-based Hollerup chronology is relatively well constrained, it is not an independent and absolute chronology. To enable direct comparison with Vostok CO_2 data, this floating chronology needs to be fixed relative to that of the Vostok record.

It has long been noted that Eemian pollen diagrams from northwestern and central Europe display a characteristic succession of trees, suggesting a very uniform vegetational development in the region (Jessen and Milthers, 1928; Zagwijn, 1996; Cheddadi et al., 1998). Therefore, correlation is straightforward between sites and pollen zones are considered to be more or less synchronous within the region, with age differences for zone boundaries estimated to be no more than 200–500 years (Zagwijn, 1996). The Hollerup pollen stratigraphy includes all of the zones established for the Eemian in NW Europe and therefore constitutes a complete Eemian sequence (Andersen, 1965, 1966; Zagwijn, 1996). As indicated by the partly annually laminated sediments at Bispingen in northern Germany, the Eemian in northwestern Europe (and Hollerup) lasted approximately 11 kyr (Müller, 1974). This NW European pollen-stratigraphic framework constitutes an important component in the establishment of a temporal relation between the Hollerup CO_2 reconstruction and the Vostok CO_2 record.

In the Vostok record, maximum interglacial CO_2 levels are reached already c. 129–128 ka, immediately following glacial–interglacial transition and at the same time as δD data reflect culminating Antarctic air temperatures (Fischer et al., 1999; Petit et al., 1999). Detailed analysis of the isotopic composition (δ^{18}O) of atmospheric O_2 trapped in the Vostok ice core has shown that these maxima of Antarctic temperature and atmospheric CO_2 were reached several thousand years before minimum $\delta^{18}O_{atm}$ values were attained (Sowers et al., 1991). Because $\delta^{18}O_{atm}$ is considered a proxy for δ^{18}O of seawater and hence global ice volume, this indicates that melting of northern hemisphere ice sheets was significantly delayed relative to warming in Antarctica and atmospheric CO_2 increase. Thus, deglacial warming in Antarctica preceded warming in the northern hemisphere and the high CO_2 concentrations early in the interglacial are likely to have promoted melting of the northern ice sheets. The important points here are that deglaciation in northern Europe post-dated the early CO_2 maximum and that peak interglacial sea levels were reached 6–7 kyr after the CO_2 peak (Sowers et al., 1991).

As suggested by its complete Eemian pollen record, sedimentation in the Hollerup basin started within a few hundred years of the onset of the Eemian in northwestern Europe. This is likely to have occurred shortly after local deglaciation, as shown by the relative importance of non-arboreal pollen taxa, e.g. grasses (Gramineae), in the lowermost samples (Fig. 3). The rapid rise in lake level at Hollerup documented for the first 500 years (Björck et al., 2000) may be partly a result of the Eemian marine transgression, leading to higher ground-water levels in coastal areas. This is supported by the pollen-analysed marine sequence at Ristinge Klint in southern Denmark reflecting an onset of marine conditions 300–365 years after the beginning of the Eemian and a culmination of saline conditions around the start of the *Carpinus* zone, c. 3000 years into the Eemian (Kristensen et al., 2000). Taking into account the 6–7 kyr lag of global sea level behind the CO_2 peak identified in the Vostok record, this suggests that sedimentation in the Hollerup basin started approximately 3–4 kyr after the early interglacial CO_2 maximum recorded at Vostok. This estimate is consistent with data from the Netherlands showing that maximum interglacial sea levels in the North Sea area were reached in the first part of the *Carpinus* pollen zone, 3–4 kyr after the onset of the Eemian (Zagwijn, 1996). Moreover, it is in accordance with current estimates of the onset of the Eemian in northwestern Europe (c. 126 ka; Kukla et al., 2002; Shackleton et al., 2003).

Fig. 5 shows the Hollerup CO_2 reconstruction together with the Vostok CO_2 record with a tentative c. 3.5 kyr lag of the start of sedimentation at Hollerup relative to the early interglacial Vostok CO_2 maximum. Taking into account their difference in resolution, the two records display similar millennial-scale trends. This gives credibility to the attempted matching of the records and no other reasonable lag times result in a better visual fit. The matching shown in Fig. 5 is further consistent with an onset of the Eemian in NW Europe around 126 ka and a possibly slightly delayed start of sedimentation in the Hollerup basin. It is clear from Fig. 5 that the Hollerup reconstruction has a larger variability than the Vostok record. Such a difference between ice core and stomatal-based CO_2 records is a commonly observed feature (McElwain et al., 2002; Wagner et al., 2002; Rundgren and Björck, 2003; Kouwenberg et al., 2005) that may partly reflect the inherent smoothing of ice core gas records caused by diffusion during bubble close-off (Van Hoof, 2004). The Vostok CO_2 record itself does, however, also show considerable variability. Taking into account the wide age distribution of air bubbles (c. 300 years; Barnola et al., 1991) and the estimated accuracy of the gas measurements $\pm$2–3 ppmv; Petit et al., 1999), this suggests a larger century-scale CO_2 variability during the last interglacial compared with the Holocene (Indermühle et al., 1999).

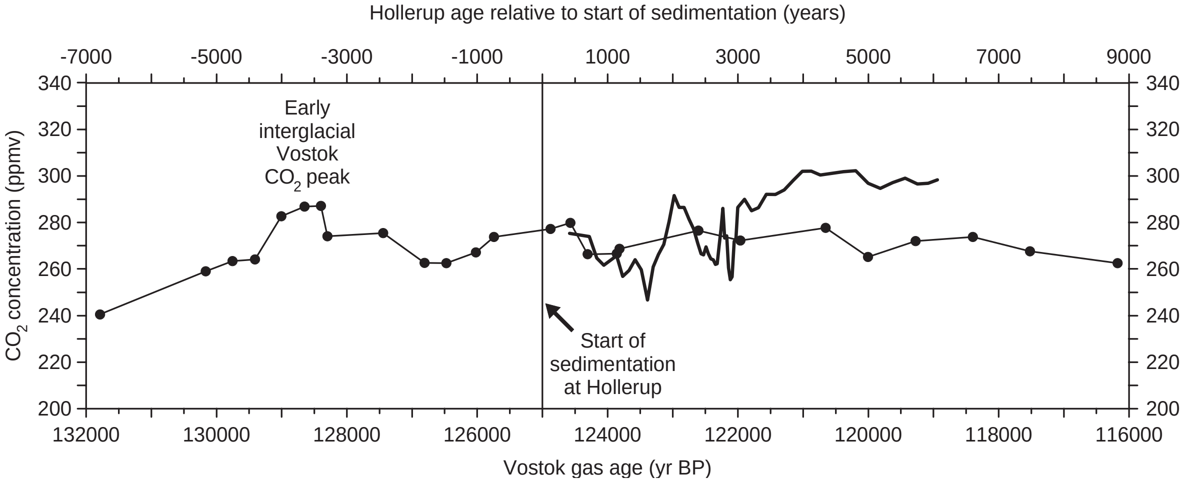

Fig. 5. Tentative matching of the Vostok CO_2 record (Petit et al., 1999) and Hollerup CO_2 reconstruction (five-point running mean values). The proposed matching takes into account the 6–7 kyr lag of peak interglacial sea levels relative to the early interglacial CO_2 peak in Vostok indicated by $\delta^{18}O_{atm}$ measurements on atmospheric O_2 trapped in the Vostok core (Sowers et al., 1991) and the 3–4 kyr delayed attainment of maximum interglacial sea levels in the North Sea area relative to the onset of the Eemian in northwestern Europe (Zagwijn, 1996; Kristensen et al., 2000).

The consistently higher stomatal-based CO_2 estimates relative to ice core data in the second half of the overlapping interval (Fig. 5) could be explained partly by the coarse resolution of the Vostok record. The fact that these estimates almost exclusively are derived from one species (*Betula pendula*; Fig. 4) may, however, indicate that the apparent offset is an effect of inadequate CO_2 calibration, but this is not supported by the first half of the Hollerup record showing good agreement between *Betula* and *Quercus* CO_2 estimates.

5.2. CO_2 evolution during the last interglacial

As pointed out by Ruddiman (2003), the Holocene CO_2 evolution differs from that of previous interglacials by showing a reverse trend towards higher concentrations following an initial CO_2 peak. In the three preceding interglacials the early maximum was followed by either a more or less continuous declining trend or a period of relative stability (Fischer et al., 1999; Petit et al., 1999). The latter applies to the last interglacial. Maximum values attained during the early CO_2 peak also vary among interglacials. For example, the higher resolution record from Taylor Dome (Indermühle et al., 1999; Smith et al., 1999) indicates that maximum early-interglacial concentrations were c. 20 ppmv lower during the Holocene compared with last interglacial Vostok values. These divergent CO_2 signatures among interglacials are likely to originate in differences in both orbital configuration and the dynamics of carbon exchange between the atmosphere and the major carbon reservoirs (the ocean and terrestrial biosphere). If correct, our reconstruction suggests that parts of the second half of the last interglacial were characterised by CO_2 levels similar to, or even higher than, those recorded during the initial peak. This would call in question the anomalous character of the Holocene CO_2 evolution invoked by Ruddiman (2003) to claim human interference with climate early in the present interglacial. However, with regard to the difficulties associated with comparing ice core and stomatal-based data, the indicated return to high CO_2 levels remains tentative as long as no high-resolution, well-dated record is available for the entire last interglacial.

5.3. The role of CO_2 in Eemian climate dynamics

5.3.1. CO_2 stability transition c. 3000 years after the Eemian onset

The most conspicuous feature of the Hollerup CO_2 record is the transition from an early period characterised by CO_2 variability at millennial and centennial scales to a relatively stable CO_2 regime c. 3000 years after the Eemian onset (Fig. 4). This transition coincides with a marked change in the Hollerup pollen stratigraphy, i.e. the boundary between pollen zones 4 and 5 (Fig. 3). This distinct change from an assemblage characterised by *Corylus* and *Taxus* to one characterised by *Carpinus* and *Picea* is typical for sites throughout northwestern Europe (Zagwijn, 1996; Turner, 2002). A corresponding transition to a *Carpinus*-dominated zone is evident in Eemian pollen diagrams from sites all over northern, central and western Europe and coincides with the end of the climatic optimum as defined by maximum Eemian summer temperatures in all these regions (Litt et al., 1996; Zagwijn, 1996; Aalbersberg and Litt, 1998; Rioual et al., 2001; Klotz et al., 2003). According to pollen-based transfer functions, this transition is also associated with a change to more continental conditions as indicated by generally lower reconstructed January temperature and annual precipitation values at sites in France, Germany and Poland (Field et al., 1994; Cheddadi et al., 1998; Rioual et al., 2001). These low winter temperature estimates are challenged, however, by reconstructions based on the climate indicator species approach (pollen, plant macrofossils and Coleoptera) suggesting relatively high winter temperatures and high annual precipitation in central and northwestern Europe during the *Carpinus* phase (Litt et al., 1996; Zagwijn, 1996; Aalbersberg and Litt, 1998; Klotz et al., 2003). This discrepancy may in part be explained by a lack of adequate present-day analogues for certain Eemian pollen assemblages. In particular, the composition of the Eemian *Carpinus*-dominated forests appears to have been different from that found in eastern Europe today and this difference may be attributed partly to divergent tree migration patterns during the Eemian and Holocene (Cheddadi et al., 1998; Klotz et al., 2003).

Because the expansion of *Carpinus* and *Picea* in northwestern Europe constitutes the last in a series of rapid tree migration waves during the early Eemian, the millennial and centennial CO_2 variability recorded for the first 3000 years (Fig. 4) may be linked to vegetation dynamics in Europe following deglaciation. Vegetation succession on other northern continents should, however, also be expected to have contributed to the CO_2 evolution shown by the Hollerup record. In addition, the CO_2 variability during the first three millennia may be related to a generally more unstable climate compared with the subsequent *Carpinus* phase, as indicated by proxy records reflecting conditions in the Hollerup basin and its catchment (Fig. 6). These records may, however, not be of regional significance, but a climatically more variable early Eemian is indicated also in other European records (Cheddadi et al., 1998; Rioual et al., 2001). This is consistent with a relatively stable end of the last interglacial in northern Greenland, as suggested by recent ice core data (North Greenland Ice Core Project Members, 2004).

The last interglacial appears to have been fairly stable in the midlatitudinal North Atlantic (McManus et al., 1994; Cortijo et al., 1994; Adkins et al., 1997), while periods of rapid oceanic changes have been documented from the Nordic seas (Cortijo et al., 1994; Sejrup et al., 1995; Fronval and Jansen, 1996; Fronval et al., 1998). A recent study of foraminiferal faunas in two cores taken off the Faroe Islands shows a delayed increase in sea surface temperatures (SST) at the beginning of the last interglacial north of the Iceland–Scotland Ridge relative to areas south of the ridge (Rasmussen et al., 2003). During the initial phase of this two-step warming, the NE Atlantic site experienced maximum interglacial temperatures. After c. 3 kyr SSTs began to increase in the Nordic seas and attained maximum interglacial levels 3–5 kyr later, while temperatures were still high in the NE Atlantic. Rasmussen et al. (2003) assumed that the beginning of MIS 5e in their cores is synchronous with the onset of the Eemian in northwestern Europe and correlated the initial phase of warming in the NE Atlantic with the Eemian climatic optimum recorded prior to the *Carpinus* pollen zone (e.g., Zagwijn, 1996). This correlation is, however, not consistent with current estimates of the relation between MIS 5e and the Eemian based on detailed isotopic and pollen studies on marine cores suggesting that the onset of the Eemian post-dated the beginning of MIS 5e with 3–4 kyr (Kukla et al., 2002; Shackleton et al., 2003). If this view is accepted, the Eemian climatic optimum would rather correspond to the second, c. 3 kyr long, interglacial warming step of Rasmussen et al. (2003) when SSTs in the Nordic seas increased to their maximum. Thus, this SST increase would coincide with the first c. 3 kyr of CO_2 insta-

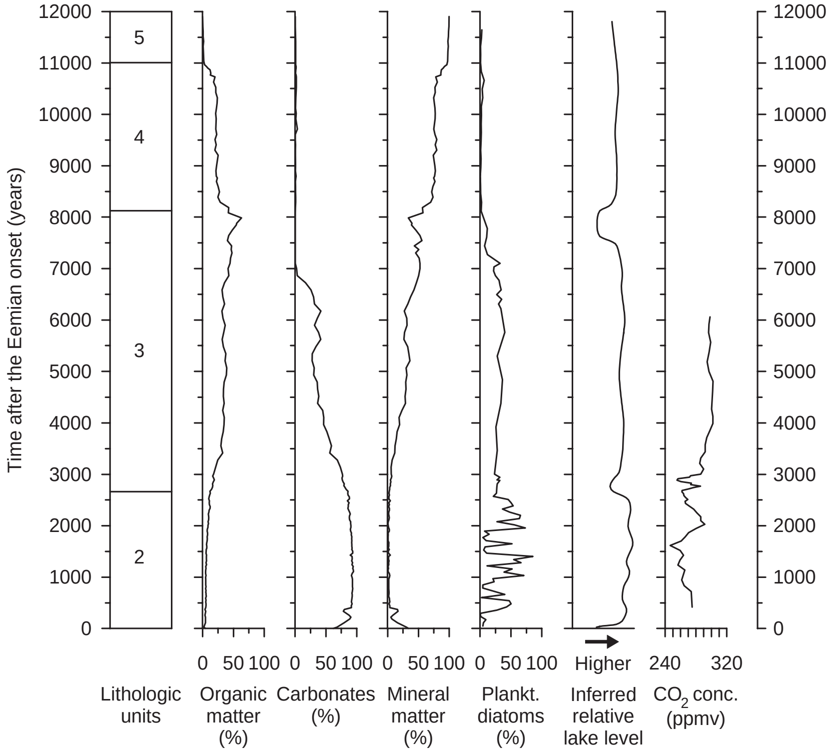

Fig. 6. Palaeohydrologic, palaeoclimatic and CO_2 data from the Hollerup lake sediment sequence. Inferred relative lake levels, lithologic units and all proxy records except CO_2 are from Björck et al. (2000). CO_2 data were correlated to the sequence studied by Björck et al. (2000) based on data presented in Fig. 2. Chronology is according to Björck et al. (2000). See text for description of lithologic units.

bility in the Hollerup reconstruction and the later part of that record characterised by relatively stable and high CO_2 levels would correspond to a period of high and fairly stable temperatures in the Nordic seas (and NE Atlantic). Such a correlation is consistent with an oceanic influence on atmospheric CO_2 through changes in SST and thereby CO_2 solubility. However, despite efforts to link marine and terrestrial records from the Nordic Sea region (Wastegård et al., 2005), the chronological relationship between MIS 5e and the Eemian remains uncertain.

5.3.2. Rapid CO_2 oscillations c. 2700–3000 years after the Eemian onset

The interval of rapid CO_2 oscillations recorded c. 2700–3000 years after the Eemian onset and immediately prior to the above discussed establishment of stable CO_2 conditions is synchronous with a short phase of inferred low lake levels in the Hollerup basin (Fig. 6; Björck et al., 2000). This hydrologic event was interpreted to reflect a brief period of dry and cool conditions possibly linked to the termination of the early Eemian Baltic Sea–White Sea connection and an associated increased influence of continental air masses (Björck et al., 2000). This proposition is, however, contested by molluscan evidence presented by Funder et al. (2002) showing that water transport through the White Sea–Baltic seaway was too limited to support the Baltic branch of the North Atlantic current often invoked to explain pronounced oceanic conditions in northern Europe during the Eemian (Zagwijn, 1996; Kristensen et al., 2000; Björck et al., 2000; Rioual et al., 2001). According to Funder et al. (2002), early Eemian oceanic conditions are more likely to reflect the larger extent and more vigorous ventilation of the Baltic.

The dry and cool event identified by Björck et al. (2000) may have been important for the previously discussed rapid expansion of *Carpinus* in Europe. In the Hollerup sequence, the expansion of *Carpinus* is coincident with the arrival and rapid expansion of *Picea* (Fig. 3; Andersen, 1965, 1966) and these pollen stratigraphic features occur at around the same level as the important sediment change evidenced by, e.g., the onset of a marked decline in carbonate content c. 3000 years into the Eemian (Fig. 6; Björck et al., 2000). This suggests that soil acidification caused by *Picea* establishment may have been responsible for the *Carpinus* expansion. As proposed by Björck et al. (2000), the establishment of *Picea* may, in turn, have been favoured by the short dry and cool period immediately prior to the *Carpinus* expansion. Although soil processes and *Carpinus* establishment may have been closely linked at Hollerup, this is unlikely to have been the general rule as indicated by the different relative timing of *Carpinus* and *Picea* arrival shown by European pollen diagrams. In accordance with Eemian climate reconstructions discussed above (Litt et al., 1996; Zagwijn, 1996; Aalbersberg and Litt, 1998; Rioual et al., 2001; Klotz et al., 2003), this points to a dominant climatic control of the *Carpinus* expansion throughout northwestern and central Europe, possibly through the short dry and cool event identified by Björck et al. (2000). As indicated by its associated highly dynamic CO_2 regime (Fig. 4), this climatic event may have been of regional or even global significance.

It was speculated by Björck et al. (2000) that the dry and cool event c. 2700–3000 years into the Eemian was synchronous with one of two brief last interglacial periods of decreased water temperature and altered circulation in the easternmost North Sea area (Seidenkrantz et al., 1995; Seidenkrantz and Knudsen, 1997; Knudsen et al., 2002). Foraminiferal fauna and isotope data suggest that this period was characterised by a drastically weakened North Atlantic drift allowing southward penetration of arctic waters, which is supported by repeated interglacial cooling episodes recorded also further north in the Nordic seas (Sejrup et al., 1995; Fronval and Jansen, 1996; Fronval et al., 1998). This indicates an oceanic origin of the rapid CO_2 oscillations seen in the Hollerup reconstruction but, because the duration and age of this early to mid interglacial marine event is not well constrained, it is difficult to link it directly to the cool and dry event recorded at Hollerup. Moreover, a dominant oceanic origin of these CO_2 oscillations may not be consistent with their high frequency.

6. Conclusions

A c. 7400-year atmospheric CO_2 reconstruction based on stomatal index data obtained from *Betula* and *Quercus* leaves preserved in a lake sediment sequence from the last interglacial at Hollerup, Denmark is in general agreement with previous ice core and stomatal CO_2 data for the same period, although a larger variability compared with Vostok ice core data is evident. The first c. 3000-year period of the reconstruction is characterised by centennial to millennial CO_2 variability in the interval 250–290 ppmv, while CO_2 concentrations during the following 3000 years are generally more stable and slightly higher (290–300 ppmv). Rapid CO_2 oscillations are reconstructed for a period of c. 300 years immediately before the establishment of stable conditions.

Pollen stratigraphic correlation allows the CO_2 reconstruction to be relatively dated and compared with Eemian climate records from a large part of Europe. The transition to more stable CO_2 conditions coincides with the end of the early Eemian climate optimum in northern, central and western Europe. Pollen records from these regions indicate that early Eemian CO_2 instability may be linked to vegetation succession following deglaciation in Europe, but vegetation dynamics on other northern continents are also likely to be important. Moreover, CO_2 instability during the first 3000 years may reflect a relatively unstable early Eemian climate as indicated by proxy records from Hollerup and other European sites. Comparison with foraminiferal data from the NE Atlantic and Nordic seas suggests that oceanic processes may also have contributed to the early Eemian CO_2 evolution indicated by the Hollerup record through the influence of sea surface temperature on CO_2 solubility. The rapid CO_2 oscillations recorded c. 2700–3000 years after the Eemian onset are synchronous with a dry and cool event previously inferred from Hollerup proxy data, suggesting that this was a climatic event of regional or global significance. This event may correspond to one of a series of brief cooling episodes recorded in the easternmost North Sea and Nordic seas.

Acknowledgements

Friederike Wagner and Wolfram M. Kürschner kindly supplied the CO_2 calibration data for *B. pendula/B. pubescens* and *Q. petraea*. Maria Agardh is thanked for sieving the sediment samples and Ole Bennike for supplying the original used for Fig. 1A. We are also grateful to the two referees, Friederike Wagner and Jean Nicolas Haas, for their helpful comments. This study was financially supported by the Swedish Research Council (grant to M.R.).

References

Aalbersberg, G., Litt, T., 1998. Multiproxy climate reconstructions for the Eemian and Early Weichselian. Journal of Quaternary Science 13, 367–390.

Adkins, J.F., Boyle, E.A., Keigwin, L., Cortijo, E., 1997. Variability of the North Atlantic thermohaline circulation during the last interglacial period. Nature 390, 154–156.

Andersen, S.T., 1965. Interglacialer og interstadialer i Danmarks kvartær. Et overblik. Meddelelser fra Dansk Geologisk Forening 15, 486–506.

Andersen, S.T., 1966. Interglacial vegetational succession and lake development in Denmark. The Palaeobotanist 15, 117–127.

Barnola, J.-M., Pimienta, P., Raynaud, D., Korotkevich, Y.S., 1991. CO_2–climate relationship as deduced from the Vostok ice core: re-examination based on new measurements and on a re-evaluation of the air dating. Tellus 43B, 83–90.

Beerling, D.J., 1999. Stomatal density and index: theory and application. In: Jones, T.P., Rowe, N.P. (Eds.), Fossil Plants and Spores: Modern Techniques. The Geological Society, London, pp. 251–256.

Beerling, D.J., Chaloner, W.G., 1993. The impact of atmospheric CO_2 and temperature change on stomatal density: observations from *Quercus robur* lamma leaves. Annals of Botany 71, 231–235.

Björck, S., Noe-Nygaard, N., Wolin, J., Houmark-Nielsen, M., Hansen, H.J., Snowball, I., 2000. Eemian lake development, hydrology and climate: a multi-stratigraphic study of the Hollerup site in Denmark. Quaternary Science Reviews 19, 509–536.

Cheddadi, R., Mamakowa, K., Guiot, J., de Beaulieu, J.-L., Reille, M., Andrieu, V., Granoszewski, W., Peyron, O., 1998. Was the climate of the Eemian stable? A quantitative climate reconstruction from seven European pollen records. Palaeogeography, Palaeoclimatology, Palaeoecology 143, 73–85.

Cortijo, E., Duplessy, J.C., Labeyrie, L., Leclaire, H., Duprat, J., van Weering, T.C.E., 1994. Eemian cooling in the Norwegian Sea and North Atlantic Ocean preceding continental ice-sheet growth. Nature 372, 446–449.

Draper, N.R., Smith, H., 1981. Applied Regression Analysis, second ed. Wiley, New York. 709 pp.

EPICA community members, 2004. Eight glacial cycles from an Antarctic ice core. Nature 429, 623–628.

Field, M.H., Huntley, B., Müller, H., 1994. Eemian climate fluctuations observed in a European pollen record. Nature 371, 779–783.

Fischer, H., Wahlen, M., Smith, J., Mastroianni, D., Deck, B., 1999. Ice core records of atmospheric CO_2 around the last three glacial terminations. Science 283, 1712–1714.

Fronval, T., Jansen, E., 1996. Rapid changes in ocean circulation and heat flux in the Nordic Seas during the last interglacial period. Nature 383, 806–810.

Fronval, T., Jansen, E., Haflidason, H., Sejrup, H.P., 1998. Variability in surface and deep water conditions in the Nordic seas during the last interglacial period. Quaternary Science Reviews 17, 963–985.

Funder, S., Demidov, I., Yelovicheva, Y., 2002. Hydrography and mollusc faunas of the Baltic and the White Sea–North Sea seaway in the Eemian. Palaeogeography, Palaeoclimatology, Palaeoecology 184, 275–304.

GRIP members, 1993. Climate instability during the last interglacial period recorded in the GRIP ice core. Nature 364, 203–207.

Grootes, P.M., Stuiver, M., White, J.W.C., Johnsen, S., Jouzel, J., 1993. Comparison of oxygen isotope records from the GISP2 and GRIP Greenland ice cores. Nature 366, 552–554.

Hartz, N., Østrup, E., 1899. Danske diatoméjord-aflejringer og deres diatoméer. Danmarks Geologiske Undersøgelser II 9, 1–80.

Indermühle, A., Stocker, T.F., Joos, F., Fischer, H., Smith, H.J., Wahlen, M., Deck, B., Mastroianni, D., Tschumi, J., Blunier, T., Meyer, R., Stauffer, B., 1999. Holocene carbon-cycle dynamics based on CO_2 trapped in ice at Taylor Dome, Antarctica. Nature 398, 121–126.

Israelson, C., Björck, S., Hawkesworth, C.J., Noe-Nygaard, N., 1998. Uranium-series isotopes from Eemian lake deposits, Hollerup, Denmark. Bulletin Geological Society of Denmark 44, 73–179.

Jessen, K., Milthers, V., 1928. Interglacial fresh-water deposits in Jutland and northwest Germany. Danmarks Geologiske Undersøgelser II 48, 1–379.

Klotz, S., Guiot, J., Mosbrugger, V., 2003. Continental European Eemian and Early Würmian climate evolution: comparing signals using different quantitative reconstruction approaches based on pollen. Global and Planetary Change 36, 277–294.

Knudsen, K.-L., Seidenkrantz, M.-S., Kristensen, P., 2002. Last interglacial and early glacial circulation in the northern North Atlantic Ocean. Quaternary Research 58, 22–26.

Kouwenberg, L.R., McElwain, J.C., Kürschner, W.M., Wagner, F., Beerling, D.J., Mayle, F.E., Visscher, H., 2003. Stomatal frequency adjustment of four conifer species to historical changes in atmospheric CO_2. American Journal of Botany 90, 610–619.

Kouwenberg, L., Wagner, R., Kürschner, W.M., Visscher, H., 2005. Atmospheric CO_2 fluctuations during the last millennium reconstructed by stomatal frequency analysis of *Tsuga heterophylla* needles. Geology 33, 33–36.

Kristensen, P., Gibbard, P., Knudsen, K.L., 2000. Last interglacial stratigraphy at Ristinge Klint, South Denmark. Boreas 29, 103–116.

Kronborg, C., Mejdahl, V., 1989. Thermoluminescence dating of Eemian and Early Weichselian deposits in Denmark. Quaternary International 3/4, 93–99.

Kukla, G.J., Bender, M.L., de Beaulieu, J.-L., Bond, G., Broecker, W.S., Cleveringa, P., Gavin, J.E., Herbert, T.D., Imbrie, J., Jouzel, J., Keigwin, L.D., Knudsen, K.-L., McManus, J.F., Merkt, J., Muhs, D.R., Müller, H., Poore, R.Z., Porter, S.C., Seret, G., Shackleton, N.J., Turner, C., Tzedakis, P.C., 2002. Last interglacial climates. Quaternary Research 58, 2–13.

Kürschner, W.M., van der Burgh, J., Visscher, H., Dilcher, D.L., 1996. Oak leaves as biosensors of Late Neogene and Early Pleistocene paleoatmospheric CO_2 concentrations. Marine Micropaleontology 27, 299–312.

Litt, T., Junge, F.W., Böttger, T., 1996. Climate during the Eemian in north-central Europe—a critical review of the palaeobotanical and stable isotope data from central Germany. Vegetation History and Archaeobotany 5, 247–256.

McElwain, J.C., Mayle, F.E., Beerling, D.J., 2002. Stomatal evidence for a decline in atmospheric CO_2 concentration during the Younger Dryas stadial: a comparison with Antarctic ice core records. Journal of Quaternary Science 17, 21–29.

McManus, J.F., Bond, G.C., Broecker, W.S., Johnsen, S., Labeyrie, L., Higgins, S., 1994. High-resolution climate records from the North Atlantic during the last interglacial. Nature 371, 326–329.

Mudelsee, M., 2001. The phase relations among atmospheric CO_2 content, temperature and global ice volume over the past 420 ka. Quaternary Science Reviews 20, 583–589.

Müller, H., 1974. Pollenanalytische Untersuchungen und Jahresschichtenzählungen an der Eemzeitlichen Kieselgur von Bispingen/Luhe. Geologisches Jahrbuch A21, 149–169.

North Greenland Ice Core Project Members, 2004. High-resolution record of northern hemisphere climate extending into the last interglacial period. Nature 431, 147–151.

Petit, J.R., Jouzel, J., Raynaud, D., Barkov, N.I., Barnola, J.-M., Basile, I., Benders, M., Chappellaz, J., Davis, M., Delaygue, G., Delmotte, M., Kotlyakov, V.M., Legrand, M., Lipenkov, V.Y., Lorius, C., Ritz, C., Saltzman,, Stievenard, M., 1999. Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. Nature 399, 429–436.

Poole, I., Kürschner, M., 1999. Stomatal density and index: the practice. In: Jones, T.P., Rowe, N.P. (Eds.), Fossil Plants and Spores: Modern Techniques. The Geological Society, London, pp. 257–260.

Rasmussen, T.L., Thomsen, E., Kuijpers, A., Wastegård, S., 2003. Late warming and early cooling of the sea surface in the Nordic seas during MIS 5e (Eemian interglacial). Quaternary Science Reviews 22, 809–821.

Raynaud, D., Barnola, J.-M., Chappellaz, J., Blunier, T., Indermühle, A., Stauffer, B., 2000. The ice core record of greenhouse gases: a view in the context of future changes. Quaternary Science Reviews 19, 9–17.

Rioual, P., Andrieu-Ponel, V., Rietti-Shati, M., Batterbee, R.W., de Beaulieu, J.-L., Cheddadi, R., Reille, M., Svobodova, H., Shemesh, A., 2001. High-resolution record of climate stability in France during the last interglacial period. Nature 413, 293–296.

Royer, D.L., 2001. Stomatal density and stomatal index as indicators of paleoatmospheric CO_2 concentration. Review of Palaeobotany and Palynology 114, 1–28.

Ruddiman, W.F., 2003. The anthropogenic greenhouse era began thousands of years ago. Climatic Change 61, 261–293.

Rundgren, M., Bennike, O., 2002. Century-scale changes of atmospheric CO_2 during the last interglacial. Geology 30, 187–189.

Rundgren, M., Beerling, D., 2003. Fossil leaves: effective bioindicators of ancient CO_2 levels? Geochemistry, Geophysics, Geosystems 4 (7), 1058. doi: 10.1029/2002GC000463.

Rundgren, M., Björck, S., 2003. Late glacial and early Holocene variations in atmospheric CO_2 concentration indicated by high-resolution stomatal index data. Earth and Planetary Science Letters 213, 191–204.

Salisbury, E.J., 1927. On the causes and ecological significance of stomatal frequency, with special reference to the woodland flora. Philosophical Transactions of the Royal Society (London) B216, 1–65.

Seidenkrantz, M.-S., Knudsen, K.-L., 1997. Eemian climatic and hydrographical instability on a marine shelf in northern Denmark. Quaternary Research 47, 218–234.

Seidenkrantz, M.S., Kristensen, P., Knudsen, K.-L., 1995. Marine evidence for climatic instability during the last interglacial in shelf records from northwest Europe. Journal of Quaternary Science 10, 77–82.

Sejrup, H.P., Haflidason, H., Klitgaard Kristensen, D., Johnsen, S., 1995. Last interglacial and Holocene climatic development in the Norwegian Sea region: ocean front movements and ice-core data. Journal of Quaternary Science 10, 385–390.

Shackleton, N.J., 2000. The 100,000-year ice-age cycle identified and found to lag temperature, carbon dioxide, and orbital eccentricity. Science 289, 1897–1902.

Shackleton, N.J., Fernanda Sánchez-Goňi,, Pailler, D., Lancelot, Y., 2003. Marine isotope substage 5e and the Eemian interglacial. Global and Planetary Change 36, 151–155.

Smith, H.J., Fischer, H., Wahlen, M., Mastroianni, D., Deck, B., 1999. Dual modes of the carbon cycle since the last glacial maximum. Nature 400, 248–250.

Sowers, T., Bender, M., Raynaud, D., Korotkevich, Y.S., Orchardo, J., 1991. The $\delta^{18}O$ of atmospheric O_2 from air inclusions in the Vostok ice core: timing of CO_2 and ice volume changes during the penultimate deglaciation. Paleoceanography 6, 679–696.

Turner, C., 2002. Formal status and vegetational development of the Eemian interglacial in northwestern and southern Europe. Quaternary Research 58, 41–44.

Van Hoof, T., 2004. Coupling between atmospheric CO_2 and temperature during the onset of the Little Ice Age. PhD Thesis, Laboratory of Palaeobotany and Palynology Utrecht University, The Netherlands. LPP contribution series, 18.

Wagner, F., Bohncke, S.J.P., Dilcher, D.L., Kürschner, W., van Geel, B., Visscher, H., 1999. Century-scale shifts in Early Holocene atmospheric CO_2 concentration. Science 284, 1971–1973.

Wagner, F., Aaby, B., Visscher, H., 2002. Rapid atmospheric CO_2 changes associated with the 8200-years-B.P. cooling event. Proceedings of the National Academy of Sciences 99, 12011–12014.

Wagner, F., Kouwenberg, L.R., van Hoof, T.B., Visscher, H., 2004. Reproducibility of Holocene atmospheric CO_2 records based on stomatal frequency. Quaternary Science Reviews 23, 1947–1954.

Wastegård, S., Björck, S., Greve, C., Rasmussen, T.L., 2005. A tephra-based correlation between the Faroe Islands and the Norwegian Sea raises questions about chronological relationships during the last interglacial. Terra Nova 17, 7–12.

Westerkamp, C., Demmelmeyer, H., 1997. Leaf Surfaces of Central European Woody Plants. Gebrüder Borntraeger, Berlin. 558 pp.

Woodward, F.I., 1987. Stomatal numbers are sensitive to increases in CO_2 from pre-industrial levels. Nature 327, 617–618.

Woodward, F.I., Bazzaz, F.A., 1988. The responses of stomatal density to CO_2 partial pressure. Journal of Experimental Botany 209, 1771–1781.

Zagwijn, W.H., 1996. An analysis of Eemian climate in Western and Central Europe. Quaternary Science Reviews 15, 451–469.