Available online at www.sciencedirect.com

SCIENCE DIRECT®

Palaeogeography, Palaeoclimatology, Palaeoecology 211 (2004) 107–126

PALAEO

www.elsevier.com/locate/palaeo

Eemian to early Würmian climate dynamics: history and pattern of changes in Central Europe

Stefan Klotz[a,*], Ulrich Müller[b], Volker Mosbrugger[a],
Jacques-Louis de Beaulieu[c], Maurice Reille[c]

[a] *Institut für Geowissenschaften, Universität Tübingen, Sigwartstr. 10, 72076 Tübingen, Germany*
[b] *Lamont-Doherty Earth Observatory, P.O. Box 1000, 61 Route 9W, Palisades, NY 10964-1000, USA*
[c] *Laboratoire de Botanique historique et Palynologie, C.N.R.S., No. 404, Faculté des Sciences et Techniques St. Jérôme, F-13397 Marseille Cedex 13, France*

Received 9 April 2003; received in revised form 17 March 2004; accepted 27 April 2004

Abstract

High-resolution pollen records from the northern alpine foreland are used to evaluate the patterns of climate change during the period between the late Eemian Interglacial (marine oxygen isotope stage OIS 5e) about 115 ky ago and the end of the St. Germain II (OIS 5a, Dansgaard–Oeschger interstadial D/O IS21) about 75 ky ago. For the quantitative climate interpretation of the fossil pollen assemblages, we compare two different methods, a modern analogue technique and a mutual climatic range approach. The results not only reveal major climatic changes at the transition to stadials and interstadials, but also indicate short-term oscillations which are followed by an almost full return to the preceding climate conditions, and components of gradual trends resembling saw-tooth structures. Based on the pollen data, the climate reconstructions suggest that the optimum in St. Germain II (OIS 5a, D/O IS21) in winter temperatures was about 0.8 to 1.4 °C and in summer temperatures about 0.7 to 1.2 °C warmer than the optimum in St. Germain I (OIS 5c, D/O IS22 to IS24). The severe and short-time Montaigu cold event (iceberg discharge event C23) clearly divided St. Germain I into two thermal periods. Thus, St. Germain Ia (D/O IS24) preceding the Montaigu event is slightly more favourable than the following St. Germain Ic (D/O IS23). Since several climate oscillations occurred during these interstadials, they show only limited stability. With respect to the stadial periods, the results reveal a coherent pattern for all records. Winter temperatures during Melisey II (OIS 5b, C21) are about 1 to 4 °C lower than those during Melisey I (OIS 5d, C24). As regards short-term climate changes during Melisey I and Melisey II, consistent amelioration episodes may be distinguished during these intervals.

Keywords: Climate change; Early Würmian; Palaeoclimate reconstruction; Interstadial; Stadial; Pollen; Pleistocene

---

1. Introduction

The climate history from the late Eemian at about 115 ky ago to the early Würmian is of particular interest since the period is characterised by the transition from interglacial to glacial conditions with the occurrence of a series of oscillations which may be of

---

* Corresponding author. Tel.: +49-7071-2973081; fax: +49-7071-295217.
E-mail address: stefan.klotz@uni-tuebingen.de (S. Klotz).

0031-0182/$ - see front matter © 2004 Elsevier B.V. All rights reserved.
doi:10.1016/j.palaeo.2004.04.009

relevance to understand future climate change (Bond et al., 1993; Van Andel and Tzedakis, 1996). Mainly controlled by feedback mechanisms within the coupled climate system, these considerable and sometimes rapid shifts are well documented in polar regions from several high-resolution oxygen-isotope records, for example the Greenland ice cores GRIP (Dansgaard et al., 1993; Johnsen et al., 1995) and GISP2 (Grootes et al., 1993), or the Antarctic ice core of Vostok (Jouzel et al., 1987). Since the magnitudes of the measured climate variations are considerably larger than predicted from direct orbital forcing, various other processes have been proposed to be responsible for such amplifications. Particularly, the roles of the oceanic thermohaline circulation, ice-sheet response, ice-shelf destruction, sea-level changes, freshwater flux, and variations in greenhouse gas concentrations are suggested as potentially important factors (Broecker, 2000; Buggisch and Walliser, 2001). Whereas most of the palaeoclimate results derived from ice-core data or deep-sea drillings concern changes in ocean currents and general atmospheric flow, continental climate dynamics may also have been affected by other factors such as land-sea distribution or mountain ranges controlling air mass flow. Therefore, quantitative climate analyses of continental time series are essential for an understanding of the spatial patterns of Quaternary climate change, for the comparison between oceanic and terrestrial climate signals and thus for an understanding of the coupling between oceans, atmosphere, and biosphere. Furthermore, quantitative continental palaeoclimate data also can be used for validating General Circulation Models (GCM).

Concerning the reconstruction of the European late-Pleistocene climate, most valuable information is provided by fossil biological proxies such as plant or insect remains which sensitively reflect ecological changes through space and time. Particularly, pollen records are recognised to be reliable to document the marked climate changes during the transition from the last interglacial into the early Würmian (Tzedakis et al., 1997). Depending on biostratigraphy, several characteristic episodes of the early Würmian have been distinguished across Europe and roughly correlated with deep-sea oxygen-isotope stages (Woillard, 1978; Grüger, 1979; Mangerud, 1989; Behre, 1989). Mostly, these episodes were referred to as the Melisey I stadial (OIS 5d) which is followed by the St. Germain I interstadial (OIS 5c), the Melisey II stadial (OIS 5b) and the St. Germain II interstadial (OIS 5a). According to more recent investigations (Broecker, 1998; Sanchez Goni et al., 2000; Kukla, 2000; Shackleton et al., 2002), however, these correlations have to be examined critically since the marine climate development has been found to lead terrestrial changes during some periods. In order to take these results into account, this study correlates the biostratigraphic units with the more strictly defined Dansgaard–Oeschger (D/O) events and iceberg discharge events (Bond et al., 1993).

Previous terrestrial palaeoclimate studies applied different quantitative reconstruction methods based on pollen or multi-proxy approaches, each of which has their own merits and limitations. Only a few of these studies, however, have used several methods contemporaneously in order to compare the reconstructed climate signals (Guiot et al., 1993; Klotz, 1999; Klotz et al., 2003). With respect to early Würmian climate development, estimates from previous studies provide information that suggests that the climate deterioration from the Eemian into the Melisey I is about 11 to 14 °C in mean annual temperature, and linked with a reduction in precipitation of more than 500 mm (Guiot et al., 1989; Pons et al., 1992; Forsström and Punkari, 1997; Cheddadi et al., 1998). Other studies from northern Europe conclude that the decrease in winter temperatures was about 12 °C and in summer temperatures about 3 to 10 °C (Frenzel, 1991a; Zagwijn, 1996; Aalbersberg and Litt, 1998). With regard to the important and unsolved question about early Würmian climate characteristics in the Melisey I and II as well the St. Germain I and II, however, the information provided by most of the studies is sparse. Furthermore, some fundamental discrepancies occur between most of the investigations, leaving the discussion still open. For example, some reconstructions for Les Echets/France and Grande Pile/France (Guiot et al., 1989; Guiot, 1990) suggests that the climate optimum of St. Germain I is similar or slightly cooler but shows comparable humidity than St. Germain II. Other studies suggest higher moisture during St. Germain II (Fauquette et al., 1999). According to analyses of the record from Gröbern/North-East Germany (Hoffmann et al., 1998), winter temperatures during Melisey I and Melisey II are about 6 °C higher than those reconstructed from some western French pollen sites (Cheddadi et al., 1998). Moreover, at Gröbern mean annual temperatures during these periods are estimated to be considerably higher than those obtained from other palynological studies (Guiot, 1987; Fauquette et al., 1999).

Considering these discrepancies, the aim of this paper is to provide a detailed analysis of early Würmian climate characteristics concerning (a) the general climate development, (b) the comparison of Melisey I and Melisey II, (c) the comparison of St. Germain I and St. Germain II, and (d) the stability of these interstadials and stadials. For comparative reconstructions, we use two different methods which are applied to four high-resolution early Würmian pollen records in the northern alpine foreland of France and Germany. The climate development is reconstructed on the basis of the parameters of mean temperature of the coldest (MTC) and warmest (MTW) month as well as of mean annual precipitation (MAP), all of which are representing major limiting factors for plant occurrences (Woodward, 1987).

2. Pollen records analysed

The early Würmian pollen records studied are Les Echets (De Beaulieu and Reille, 1984; 1989), Jammertal (Müller, 2000), Füramoos (Müller et al., 2003), and Samerberg (Grüger, 1979) which are situated in western and central Europe in the foreland of the Alps (Fig. 1). They are at an altitude between 200 and 662 m a.s.l., ranging from 45°50′ N to 48°3′ N and from 4°59′ E to 12°12′ E (Table 1). The Les Echets mire is situated northeast of Lyon in the southwest part of the Dombes Plateau, lying in a closed basin which was created by Pre-Würmian glacier erosion. The Jammertal and adjacent Füramoos sites are located in the

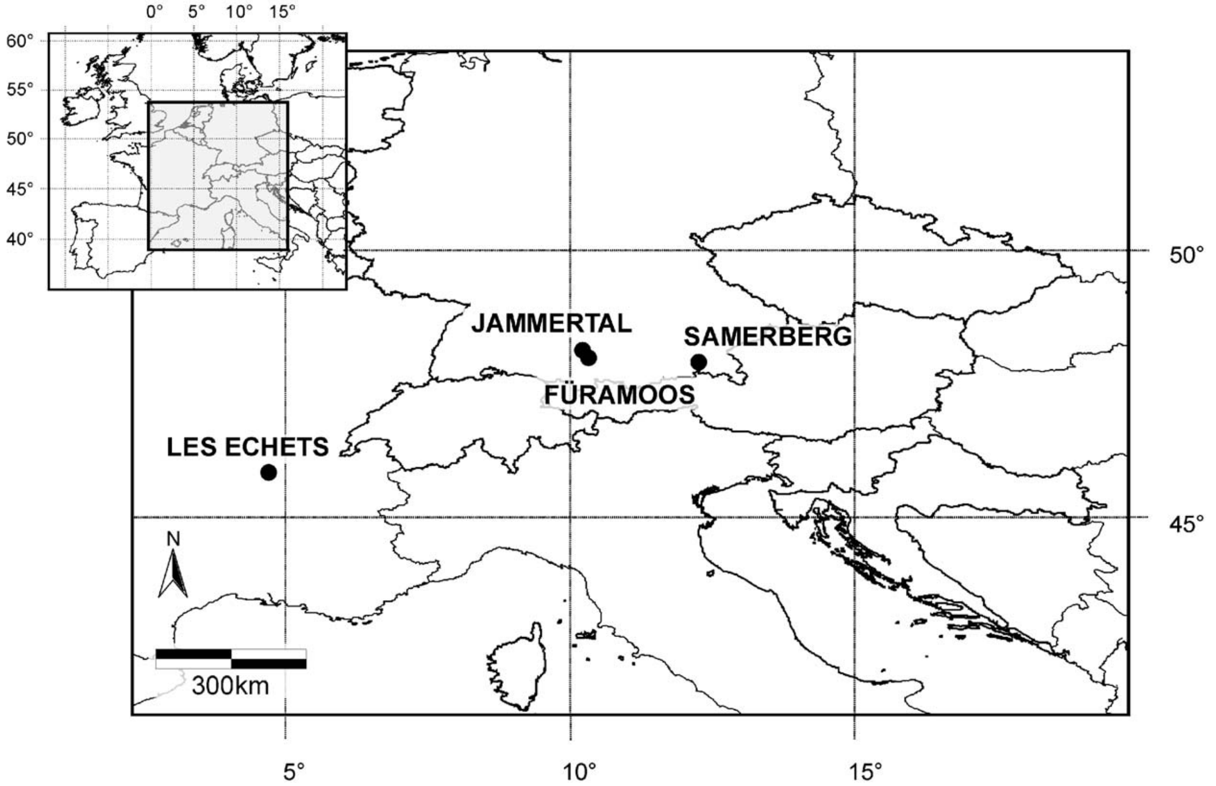

Fig. 1. Location map of the four sites studied in the alpine foreland.

Table 1
Site information for the pollen records included in the study

Name	Elevation (m a.s.l.)	Latitude (°)	Longitude (°)	MTC (°C)	MAT (°C)	MTW (°C)	MAP (mm)	Pollen Analysis
Les Echets	200	45°50′ N	4°59′ E	1.90	10.50	19.70	900	De Beaulieu and Reille (1984)
Jammertal	578	48°3′ N	9°32′ E	– 1.40	8.10	17.30	838	Müller (2000)
Füramoos	662	47°55′ N	9°57′ E	– 0.80	8.50	17.80	964	Müller et al. (2003)
Samerberg	660	47°45′ N	12°12′ E	– 2.80	6.70	15.70	1172	Grüger (1979)

Present-day climate data are represented by the mean temperature of the coldest (MTC) and warmest month (MTW) and the mean annual temperature (MAT) in °C and the mean annual precipitation (MAP) in mm.

southwest of Germany within small subglacial basins which are bordered by terminal moraines of the Rissian Rhine glacier. Similarly for Les Echets, Jammertal and Füramoos, these locations were unglaciated during the Würmian. The Samerberg site which is situated in southeast Germany at the fringe of the northern Alps in a basin deepened in large Pleistocene deposits, was glaciated at least during the last glacial maximum. In contrast to the other records, the Samerberg pollen record represents a composite where biostratigraphy, sedimentologic proxies (i.e. grain size, changes in colour), as well as additional pollen samples have been used to derive a complete sequence (Grüger, 1979). On the basis of biostratigraphy and inferred from vegetation history, similar pollen zones have been identified in all records during the late Eemian and the early Würmian, taking into account the more continental influence to the east of the study area.

Consistently with the classification used by Aalbersberg and Litt (1998), three main vegetation periods during the late Eemian have been distinguished in all the pollen sequences. During the first phase, *Carpinus* is the most common thermophilous species accompanied by *Corylus*, *Quercus*, *Ilex*, and *Buxus* in the west and *Corylus*, *Picea*, and *Abies* are more prominent in the east of the study area. This vegetation pattern reflects a climate which is characterised by warm conditions and a high degree of oceanicity. During the second phase, *Picea* and *Pinus* dominated woodland coincided with reduced proportions of *Abies*, indicating an increase of continental conditions at this time. Finally, during the termination of the Eemian interglacial, the vegetation was dominated by *Pinus*, *Picea*, *Betula*, and nonarboreal taxa.

During the subsequent Würmian stadial Melisey I (OIS 5d, C24), remarkable environmental changes with major deforestation occurred. Steppe assemblages rich in Poaceae, *Artemisia* and accompanying *Pinus* and *Betula*, support the view of open steppe-tundra-like ecosystems. During the following Würmian interstadial St. Germain I (OIS 5c, D/O IS22 to IS24), a partial return to warm conditions is observable from the pollen floras. In comparison to the *Carpinus* phase of the late Eemian interglacial, however, the proportions of thermophilous taxa are diminished, especially to a greater extent at the more easterly sites. Since some characteristic climate oscillations occurred during St. Germain I, a subdivision of this interstadial is feasible. The first phase St. Germain Ia (D/O IS24) is characterised by the remarkable spread of *Quercus*, *Corylus* and *Carpinus* at Les Echets (De Beaulieu and Reille, 1984). At the more northern and eastern sites of Jammertal (Müller, 2000), Füramoos (Müller et al., 2003) and Samerberg (Grüger, 1979), however, this thermal episode is less pronounced in the pollen records. Nevertheless, a change from tundra-steppe vegetation to *Pinus* or *Picea* dominated woodlands accompanied by minor percentages of *Quercus*, *Corylus* and *Carpinus* is recorded. At Samerberg, a higher proportion of thermophilous species can be found than at Jammertal and Füramoos, possibly indicating its proximity to plant refuges. Following St. Germain Ia, all the pollen records consistently record a noticeable climate deterioration which is mainly characterised by the decline of thermophilous trees at Les Echets and of *Picea* at the more northern and eastern sites. At all sites, a considerable expansion of *Pinus*, *Betula*, and, to a lesser extent, NAP, can also be noticed. This abrupt cooling is addressed as the Montaigu event (Woillard,

1978) or St. Germain Ib (C23) and is most pronounced at Les Echets. Subsequent to St. Germain Ib, all pollen records indicate a recovery of woodland during St. Germain Ic (D/O IS22 and IS23). At Les Echets, the vegetation succession is characterised by the spread of *Pinus*, *Quercus*, *Corylus*, *Carpinus*, *Fagus*, *Picea* and a final re-expansion of *Pinus*. At Jammertal, Füramoos and Samerberg, however, the thermophilous taxa reached only minor proportions. There, after an initial spread of *Pinus*, *Picea* became the dominant taxon until the re-expansion of *Pinus* at the end of St. Germain Ic. The Melisey II stadial (OIS 5b, C21) following St. Germain I is documented by a considerable increase in NAP, especially in Poaceae and *Artemisia*. *Pinus* and *Betula*, however, are still abundant. In comparison to Melisey I, the proportion of some NAP such as *Artemisia* is higher in all records during Melisey II, suggesting open steppe-like ecosystems and more continental climate conditions. Vegetation development following Melisey II is characterised by a re-expansion of *Pinus* and *Betula*, commencing in the St. Germain II interstadial (OIS 5a, D/O IS21). During St. Germain II, deciduous taxa such as *Quercus*, *Corylus* or *Carpinus* become dominant at Les Echets whereas they are hardly present at the more easterly sites. Since coniferous woods mainly composed of *Picea* and *Pinus* are abundant there, the northern boundary of deciduous trees is located somewhere between Les Echets and Füramoos (Grüger, 1979; Müller, 2000). When compared to St. Germain I, at all sites the proportions of pollen from thermophilous trees are somewhat higher during St. Germain II, possibly reflecting more favourable thermal conditions. Towards the end of the period, colder conditions are indicated by increased proportions not only of NAP but also of *Pinus*, *Betula* or *Picea*. Finally, the following stadial period is characterised by a strong increase in NAP, especially Poaceae, *Artemisia* and Cyperaceae, suggesting a considerable climate deterioration.

3. Methods used for palaeoclimate analysis

For the climate interpretation of Late Pleistocene pollen records, a number of reconstruction methods have been developed so far which may be classified into numerical approaches (e.g. Bartlein et al., 1986; Guiot, 1987, 1990; Prentice et al., 1991; Huntley, 1992; Peyron et al., 1998; Klotz, 1999) and mutual climate range approaches (e.g. Iversen, 1944; Grichuk, 1969; Atkinson et al., 1986; Mosbrugger and Utescher, 1997; Fauquette et al., 1999; Klotz and Pross, 1999; Pross et al., 2000). Both types of approaches are based on the taxonomic and evolutionary assumption that the climatic preferences of fossil plants are similar to those of their nearest living relatives. Numerical approaches establish a relationship between present-day climate parameters and the proportions of pollen in modern pollen assemblages that are collected in different environments. In order to obtain palaeoclimate information on the basis of fossil pollen floras, the same relationship between climate and relative pollen abundance is assumed to be valid in the past. In contrast, mutual climate range approaches determine the climatic ranges of the tolerances of fossil floras by means of the present-day ranges of tolerances of the plants which are represented in the fossil assemblages. Since the methodologies and the underlying calibration data bases used, as well as the preconditions of application are quite different for the numerical and mutual climatic range approaches, the application of the two techniques to the same pollen records may provide different results. In combination, however, the weaknesses of both approaches can be avoided.

Concerning the applicability of the numerical approaches, important limitations occur when no or very few present-day analogues are available for fossil pollen floras. This problem exists for instance for some typical Eemian vegetation types such as *Carpinus* forests accompanied by *Ilex* (Cheddadi et al., 1998), steppe vegetation with an abundance of Chenopodiaceae, *Corylus*-dominated forests (Frenzel, 1968, 1991b; Guiot, 1987; Pons et al., 1992; Guiot et al., 1993), or *Taxus*-dominated phases as during the Eemian of southern Germany (Grüger, 1979). For these vegetation types, either present-day analogues do not exist, or they have not yet been sampled. In addition, climate reconstructions with numerical approaches may be significantly influenced by taphonomic effects. In contrast, when using mutual climate range methods, in general the climate resolution is very poor if the fossil flora has a low diversity, thus leading to climate reconstructions with very broad ranges. Additionally, even a small alteration in the composition of a fossil flora from one assemblage to the next may largely affect the climate reconstruction. If so, a more abrupt climate development may result than with numerical approaches. It may also be considered a weakness of the mutual climate range approach that the relative abundance of pollen, which contains climatic relevant information, remains unconsidered. This, however, implies that the mutual climatic range approaches are less affected by taphonomic effects (Mosbrugger and Utescher, 1997).

In order to reduce the deficiencies of any palaeoclimate interpretation resulting from the use of a single approach, we applied one method from each approach, namely the "modern analogue vegetation types" as a representative of the numerical approach and the "probability mutual climatic spheres" belonging to the mutual climate range approach (Klotz, 1999; Klotz and Pross, 1999; Pross et al., 2000).

3.1. Modern analogue vegetation types

The modern analogue vegetation type (MAV) approach which is described in detail by Klotz (1999) and Klotz et al. (2003) is a numerical method that is based on the best-fit selection of modern surface samples (10 analogues are chosen) for a given fossil pollen assemblage with respect to composition and relative abundances of taxa. The use of proportions as a selection criterion for modern analogue methods is well established (Guiot, 1987, 1990). However, proportions may sometimes be altered taphonomically. Additionally, fossil pollen floras and modern analogues may differ only with respect to some less abundant taxa but which may be of ecological significance for the palaeoclimatic interpretation. These deficiencies can be reduced when the dominant plant compositions are identified on the basis of pollen floras and used as an additional selection criterion. In the MAV-method, this is realised by the assignment of vegetation types to fossil and modern pollen floras. Vegetation types such as xeric shrub forests or subalpine spruce forests are characterised by a specific combination of dominant and associated plant species. Thereby, for a given vegetation type, dominant plants are essential elements which have to be present at every observation, whereas associated plants must not. In contrast to broad-scale biomes which are also used as a selection criterion (Peyron et al., 1998), vegetation types reflect a more specific vegetation composition and, thus, are more closely related to regional environmental patterns.

According to this concept, each fossil pollen flora and modern pollen flora out of 2653 surface samples (Huntley, personal communication; Guiot, 1990; Peyron et al., 1998) are assigned to the most similar modern vegetation type of 108 modern European and adjacent Asian vegetation types (Aichinger, 1967; Ellenberg, 1986) which reflect the major ecological environments through the sampling area. The procedure of assignment is feasible in our study since the taxa which define the various vegetation types are largely represented in the pollen floras. Vegetation types as described by Aichinger (1967) and Ellenberg (1986) are characterised by a plant list and frequencies of these plants provided by the present-day observation of in how many cases a plant occurs in a specific vegetation type. Associated plants are thus rated with values between 0 and 1 and dominant plants which determine the fundamental climatic and ecological requirements of the flora with 1. We have used this characterisation in order to select that vegetation type with the highest affinity to a given (fossil or modern) pollen flora. For this, similarity coefficients based on Euclidean distances are calculated between all vegetation types and the pollen flora for which all plants present are rated with 1. Finally, the quantitative palaeoclimate reconstruction for a fossil pollen assemblage is based on the best-fit selection of those modern surface samples which are of the same vegetation type and similar with respect to the relative proportions of the fossil plants. The similarity in relative proportions is calculated on the basis of a weighted ln-transformed squared Euclidean distance (Klotz et al., 2003). Palaeoclimate data are then calculated on the basis of the nearest climate station data which are extrapolated to the modern surface sample sites, the procedure of which is described in detail by Peyron et al. (1998) and by Guiot (1991).

3.2. Probability mutual climatic spheres

The probability mutual climatic spheres (PCS) which is described in detail by Klotz (1999), Klotz and Pross (1999), Pross et al. (2000) and Klotz et al. (2003), are based only on the presence/absence of plants in fossil assemblages and are independent of the existence of modern analogue floras. The method generally quantifies the climatic requirements of a fossil flora by means of the climatic requirements of the present-day nearest living relatives of the fossil plants. By correlating modern climate data on a 0.5°∗0.5° latitude/longitude grid (New et al., 1999) with the present-day potential distribution areas of 205 plants occurring in Europe and adjacent Asia (Walter and Straka, 1970; Krüssmann, 1977a,b; Jalas and Suominen, 1989; Meusel and Jäger, 1992), basic information about the climatic requirements of these plants is obtained. Since the distribution of plants depends not only on single climate parameters, we analysed the climate preferences of these 205 plants with respect to two parameter-combinations, i.e. winter/summer temperatures and annual temperature/annual precipitation. For example, in the case of winter/summer temperatures, a diagram of all combinations of parameter values that occur within the distribution area of a plant is plotted, describing its winter/summer temperature sphere (two-dimensional). In this way, the winter/summer temperature spheres are determined for all 205 present-day plants. The mutual winter/summer temperature sphere of a fossil flora can then be calculated by overlapping the individual spheres of those plants, the pollen of which occur in the pollen flora with a relative abundance above 0.5% (delimiting their presence). To make the palaeoclimate calculations easier, however, the mutual ranges (one-dimensional) of winter and summer temperatures are determined from this mutual winter/summer temperature sphere.

Next, within these ranges probability intervals can be calculated for which the actual palaeoclimate conditions are assumed. This calculation is based on the use of a multitude of synthetically generated floras (Klotz, 1999; Klotz and Pross, 1999, Pross et al., 2000). A synthetic flora is composed exactly of those of the 205 plants at a given geographical co-ordinate, whose potential distribution areas cover that location. In total, 9555 synthetically floras have been generated, being equally distributed across Europe and adjacent Asia. For all 9555 synthetic floras, mutual ranges have been calculated in the way described before, representing the basis for determining the probability intervals of a fossil flora. For this, the calculated mutual climatic range of a fossil flora, for example that of winter temperature, is compared to all mutual ranges of winter temperature derived from the synthetic floras. Those synthetic floras which show mutual ranges of winter temperature similar to that of the fossil flora (with a maximum 5% deviation) are supposed to indicate comparable climatic requirements. Since the present-day winter temperature data are available for all selected synthetic floras, the distribution pattern of the actual temperature values can be statistically analysed. It can be observed that the distribution of the actual temperature values is restricted to a smaller interval when compared to the reconstructed mutual ranges of the selected synthetic floras. Obviously, the selected synthetic floras show closer defined winter temperature preferences, which are thus considered to represent the probability interval. For a concise graphical presentation of the results of the reconstruction, however, only the average value of the upper and lower limits of the probability intervals are shown.

3.3. Reliability of the methods

To test the reliability of both methods, they are applied to pollen surface samples and synthetic floras, respectively, for which the actual climate is known. Thus, it is possible to estimate the deviation between the reconstructed and the actual climate. Correspondingly, MAV is applied to all 2653 modern pollen spectra and then the deviations between the reconstructed and the actual climate data are analysed statistically. For MAV correlation coefficients of 0.9 for MTC (root mean square error 2.6 °C, mean average absolute error 2.1 °C), 0.81 for MTW (1.8 °C, 1.3 °C), and 0.78 for MAP (169 mm, 107 mm) between actual climate data and estimates are obtained. The use of vegetation types as an additional selection criterion represents an advance in palaeoclimate reconstruction since previous studies yielded correlation coefficients of only 0.7 for MTC (Pons et al., 1992) or less than 0.78 for several temperature parameters (Cheddadi et al., 1998). Similarly, the simulation procedure is applied to PCS to predict the climate for all 9555 synthetic floras and to compare the results with the actual climate data. For PCS, correlation coefficients of 0.95 for MTC (root mean square error 2.5 °C, mean average absolute error 1.7 °C) and MTW (1.6 °C, 1.1 °C) and 0.86 for MAP (170 mm, 104 mm) between actual grid climate data and estimates are obtained. These tests indicate that both methods are potentially suitable for accurate palaeoclimate reconstructions (in respect of the root mean square errors of 2.6 and 2.5 °C for MTC, 1.8 and 1.6 °C for MTW, and 169 and 170 mm, as calculated on the basis of MAV and PCS).

4. Results

The late Eemian to early Würmian climate development is estimated for Les Echets, Jammertal (Fig. 2), Füramoos and Samerberg (Fig. 3) using both methods, MAV and PCS. As there is no absolute time control available for these profiles, biostratigraphical zones as defined in the original publications are correlated with each other and with the GRIP δ^{18}O-curve and chronology (Johnsen et al., 1992; Dansgaard et al., 1993). The correlation of the pollen zones with the GRIP data is based on unequivocal climate signals, lithostratigraphy and event stratigraphy, additionally considering the succession of events. For a better representation of the climate development, units of climate phases (cp) are used as indicated in Figs. 2 and 3. On the basis of the reconstruction results with MAV, 95% and 70% confidence intervals have been calculated for all climate parameters, indicating that the maximum deviation of MTC is 2.6 °C (95%) and 1.3 °C (70%), of MTW is 1.2 °C (95%) and 0.7 °C

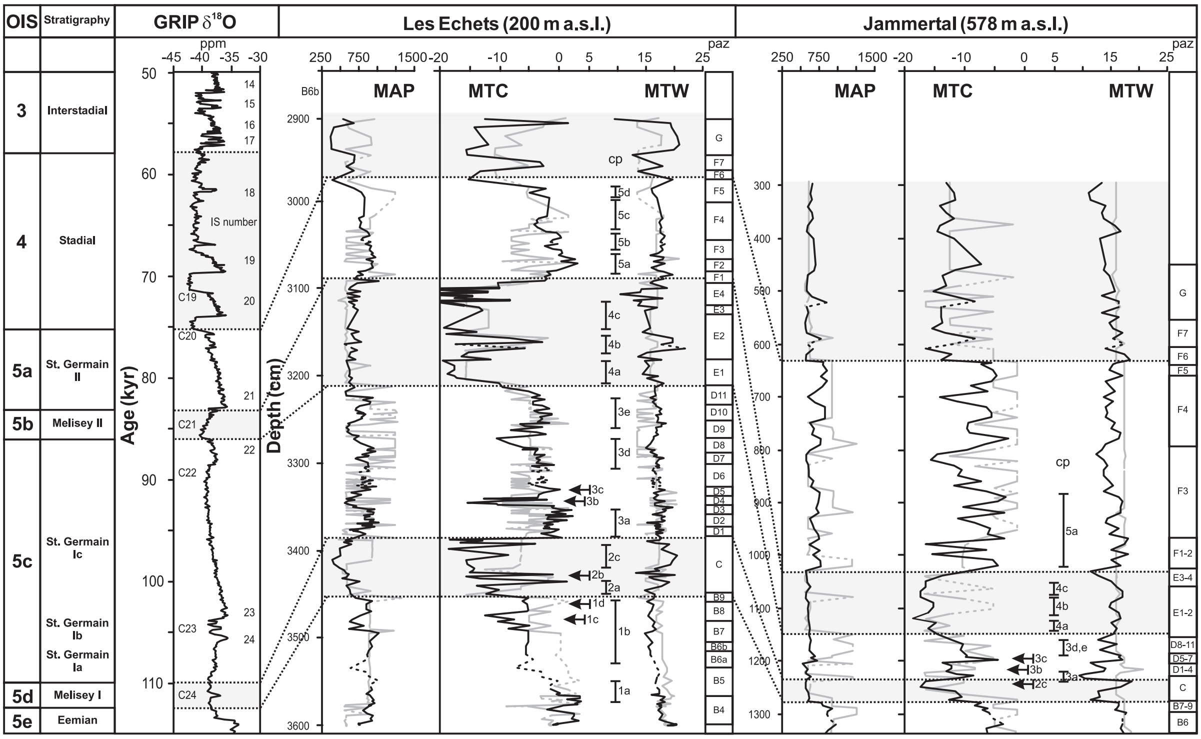

Fig. 2. Reconstructed mean temperature of the coldest (MTC) and warmest month (MTW) in °C and mean annual precipitation (MAP) in mm with the modern analogue vegetation types (black line), and the average of the upper and lower limit of the probability intervals with the probability mutual climatic spheres (grey line) for Les Echets and Jammertal. Dashed grey lines are plotted with regard to the results of PCS in case of significant deviations to the results of MAV when applying a *t*-test with a significance level of 5% ($p = 0.05$). Dashed black lines are plotted with regard to the results of MAV in the case when no reliable modern analogues are available (if the weighted ln-transformed squared Euclidean distance is larger than 1.3, which corresponds to an average estimation error in the pollen proportions of about 0.5% to 1.3% for all 43 taxa of the modern surface samples). PAZ represent biostratigraphical units of pollen floras, cp represents climate phases as used in the text. Major GRIP oxygen-isotope excursions during the period considered are indicated by Dansgaard–Oeschger interstadials IS14 to IS24 and cold spell events C19 to C24.

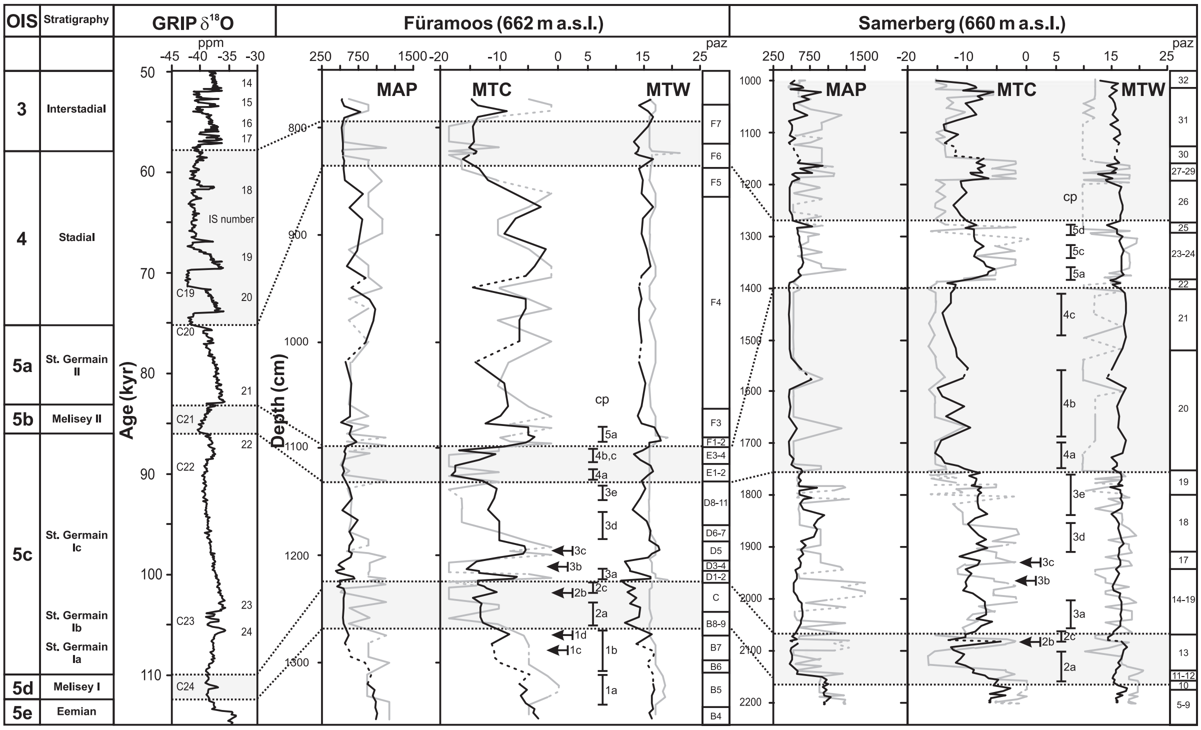

Fig. 3. Reconstructed mean temperature of the coldest (MTC) and warmest month (MTW) in °C and mean annual precipitation (MAP) in mm with the modern analogue vegetation types (black line), and the average of the upper and lower limit of the probability intervals with the probability mutual climatic spheres (grey line) for Füramoos and Samerberg.

(70%), and of MAP is 97 mm (95%) and 51 mm (70%).

In general, Figs. 2 and 3 indicate that the reconstructed mean climate values from MAV and PCS are mostly quite similar. Some significant deviations, however, become obvious for MTC and MAP during the warm episodes. These discrepancies are most likely linked with specific vegetation patterns that are interpreted differently by both methods and which will be discussed below. With respect to the general climate development, MTC shows an overall higher variability than MTW and MAP, especially during cold periods, whereas the variability of MAP is higher during warm episodes.

4.1. Late Eemian

During the *Carpinus* phase of the Eemian interglacial (OIS 5e), the reconstructions from MAV and PCS are quite different from each other since MAV reveals decreasing winter temperatures whereas PCS suggests a climate amelioration after an initial decline of temperatures (cp1a). This pattern is documented, for example, at Les Echets (3580 to 3535 cm profile depth) or Füramoos (1345 to 1310 cm profile depth). The discrepancy in the reconstruction results from MAV and PCS can be explained by a lack of suitable modern analogue pollen spectra (Cheddadi et al., 1998) for MAV, whereas PCS is believed to be sufficiently representative to reconstruct this interval (Klotz et al., 2003). According to PCS, during the climatic optimum of the *Carpinus* phase maximum winter temperatures varied between 0 and 3.2 °C (Les Echets, 200 m a.s.l. and Füramoos, 662 m a.s.l) and summer temperatures between 18.2 and 19.6 °C (Les Echets and Jammertal, 578 m a.s.l.), concomitant with a maximum precipitation of about 1200 mm. These findings are confirmed by the study of Rioual et al. (2001) whose analyses for the Ribains maar sequence also suggest a short warming event at the end of the

Eemian. There, the warming is indicated by the rise of *Picea* and the increase of sediment loss on ignition, and may also be supported by the occurrence of the diatom *Stephanodiscus minutulus*. A similar pattern is proposed by Ponel (1995) on the basis of coleopteran appearances at Grande Pile, and by Zagwijn (1983, 1996) on the basis of pollen. Following this mild suboceanic to oceanic period during the *Carpinus* phase, a gradual attenuation of thermal conditions is similarly suggested by both methods which can be seen, for example, at Les Echets (3535 to 3450 cm, cp1b) and Füramoos (1310 to 1275 cm, cp1b). Based on MAV, for which suitable modern analogues are available, during the *Picea*–*Pinus* phase a climate deterioration (cp1c) is first evidenced by an average decline of winter temperatures of 5 °C and of precipitation of 140 mm for all sites. A subsequent return to warmer conditions (cp1d) is suggested mainly by the reduction of *Betula* and NAP. Whereas both methods consistently yield an average increase of winter temperatures of 3.3 °C and of precipitation of 120 mm for all sites during this final warming, absolute winter temperatures reconstructed with PCS are about 4 °C higher than according to MAV. This discrepancy can be explained by the occurrence of some pollen of thermophilous plants which have low percentages and thus have no dominant influence on the reconstruction using MAV, but are fully considered by PCS.

4.2. Melisey I stadial

The transition from the last interglacial (OIS 5e) to the Melisey I stadial (OIS 5d, C24) is characterised by a marked climatic cooling. Both methods indicate a decrease in winter temperatures to an average minimum of about −13 °C, a decrease in summer temperatures to 14 °C and in precipitation to 590 mm. This climate deterioration can be correlated with the C24 cold event documented in the GRIP data at 113 to 110 ky, which is linked to iceberg discharges into the central North Atlantic (Fig. 2). Consistently for all pollen records, a similar pattern of climate evolution can be determined across Melisey I which is well evident at Les Echets (3450 to 3385 cm), Füramoos (1250 to 1230 cm) and Samerberg (2150 to 2070 cm). At first, continentality is intensified as winter temperatures fall to an average minimum of about −15 °C accompanied by stable or even increasing summer temperatures of about 2.3 °C (cp2a). Afterwards, an intra-Melisey I amelioration can be observed across the study area which is mostly documented by a rise in winter temperatures (cp2b). The warming is reflected in the pollen floras by a slight rise in the proportions of thermophilous taxa and is most conspicuous at Les Echets and Samerberg. Towards the end of the stadial, another reduction in winter temperatures with mostly stable or decreasing summer temperatures can be observed (cp2c).

4.3. St. Germain I

The considerable climate amelioration at the onset of St. Germain Ia (OIS 5c, D/O IS24) is heralded mainly by the successive spread of *Betula*, *Pinus*, and thermophilous broad-leaved trees which is most pronounced at Les Echets (3385 to 3350 cm, cp3a). There, similarly for MAV and PCS winter temperatures rise to a maximum of 2.2 °C, summer temperatures to 18.5 °C and precipitation to 1050 mm (Fig. 2). With respect to the more easterly sites of Jammertal, Füramoos and Samerberg (cp3a), however, thermal conditions are reconstructed to be colder as compared to Les Echets. Average winter temperatures only rise to about −7 °C and summer temperatures to 14.8 °C when using MAV, but are 3 °C higher according to PCS (Fig. 3). This can be recognised, for example, at Füramoos (1221 to 1219 cm). The discrepancy between the results of MAV and PCS for the easterly sites can be explained by the occasional presence of pollen of thermophilous plants such as *Carpinus*, *Corylus* or *Ulmus* which considerably affect the reconstruction with PCS.

Following the St. Germain Ia, the Montaigu cooling event (Woillard, 1978) or St. Germain Ib (C23) is similarly recorded (cp3b) at Les Echets (3346 to 3339 cm based on climate reconstructions, and 3354 to 3333 cm based on pollen floras), Jammertal (1225 to 1205 cm), Füramoos (1216 to 1206 cm), and Samerberg (1993 to 1945 cm). It corresponds to a short-term expansion of NAP, *Pinus* and *Betula* concordant with a reduction of thermophilous species. For all pollen records, an average winter temperature of −13.5 °C and summer temperature of 14.8 °C is provided by both methods. In addition to this rise in continentality, the conditions also became drier during this cooling episode.

Subsequently, during St. Germain Ic (D/O IS22 and IS23) a rapid shift to climatically favourable conditions is documented in the pollen records by the spread of *Betula* and *Pinus* and the re-immigration of thermophilous species such as *Quercus*, *Corylus* and *Carpinus*. Whereas these plants dominate the pollen assemblages at Les Echets (3333 to 3300 cm), they only accompany coniferous pollen assemblages with *Betula* at the easterly sites. With respect to plant immigration history, the climatic optimum occurs at an early stage of St. Germain Ic (cp3c). Referring to MAV, the coldest month is 0 °C at Les Echets and about −5.4 °C at the eastern sites and the warmest month is 18.3 °C at Les Echets and 17 °C at the eastern sites. PCS again provides maximum winter temperatures which are about 3 °C higher for Jammertal, Füramoos and Samerberg than those reconstructed by MAV. The discrepancy in the reconstruction by MAV and PCS again can be attributed to the occasional occurrence of *Corylus*, *Fagus*, *Quercus* and *Taxus* pollen which may indicate suitable thermal conditions but which were hardly contributing to the total spectrum and thus are largely ignored in the MAV method. After the climatic optimum, St. Germain Ic is characterised by a continuous decline in thermal conditions and precipitation. The transition to the cooling C22 is similarly depicted by all pollen records (cp3d), for example at Les Echets (3300 to 3265 cm based on climate reconstructions and 3300 to 3250 cm based on pollen floras), Füramoos (1189 to 1157 cm) and Samerberg (1905 to 1857 cm). At the end of St. Germain Ic (D/O IS22), the final partial climatic return (cp3e) is reflected by an attenuated re-expansion of some thermophilous species at Les Echets (3249 to 3229 cm), Jammertal (1180 cm), Füramoos (1070 to 1040 cm) and Samerberg (1837 to 1755 cm). According to MAV, the increase in winter temperatures varies between 9 °C at Les Echets, 4.5 °C at Samerberg, 1.4 °C at Jammertal and Füramoos, and is about 2 °C in summer temperatures and 200 mm in precipitation. This oscillation in late St. Germain Ic is also in accordance with the GRIP δ^{18}O data.

4.4. Melisey II stadial

The climate development during early Melisey II (OIS 5b, C21) is well defined by a strong expansion of NAP, especially Poaceae and *Artemisia*, indicating open steppe-like ecosystems and more continental climate conditions. According to both methods, average winter temperatures experience significant changes with a decrease at all sites to a minimum of −17 °C, summer temperatures to 15 °C and precipitation to 525 mm (cp4a). The reconstructed low values of the average winter temperatures can mainly be attributed to the occurrence of low diversity pollen floras which occasionally include *Alnus*, *Betula*, *Pinus*, *Artemisia*, Cyperaceae, Ericaceae and Poaceae. Succeeding, an intra-stadial amelioration (cp4b) with a higher oceanicity occurs at Les Echets (3178 to 3146 cm), Jammertal (1110 to 1090 cm), Füramoos (1110 to 1105 cm), and Samerberg (1670 to 1495 cm). Both methods indicate an increase in winter temperature by about 8 °C on average and a rise in precipitation by about 100 mm. The reconstructed climate amelioration may be on the one hand an effect of reworked pollen. On the other hand, the amelioration is evident in all four pollen records and thus may indicate the actual existence of a warming during Melisey II. Subsequently, winter temperatures decline again to a minimum of −16 °C which is about 1 °C higher than at the beginning of the stadial (cp4c). Similarly, summer temperatures and precipitation return to values characteristic of the early stadial.

4.5. St. Germain II

Very strong environmental changes occur at the transition from Melisey II to St. Germain II (OIS 5a, D/O IS21) since *Pinus*, *Quercus*, *Corylus* and *Carpinus* expand rapidly. Although the history of re-immigration and spread is similar for all sites, the proportions of the thermophilous broad-leaved trees with up to 90% at Les Echets clearly exceed those at other sites which show a maximum of 19% (De Beaulieu and Reille, 1984). The shift to warm suboceanic to oceanic conditions at the early stage of St. Germain II is revealed by MAV with an increase in winter temperatures to about 3 °C at Les Echets and −4 to −5.3 °C at the other sites (cp5a). Summer temperatures are 19.7 °C at Les Echets and 16 to 17.7 °C at the other sites. The warming also coincides with an increase in precipitation of above 700 mm. PCS yields temperatures about 2 to 3 °C warmer and precipitation 200 mm higher for the eastern sites than estimated by MAV.

During the middle and upper part of St. Germain II, the reconstructions for Füramoos and Jammertal show mostly irregular variations. Possibly, these effects are caused by re-worked pollen rather than by strong climate changes. For this interval, we therefore focus on the records at Les Echets and Samerberg where further characteristic episodes can be distinguished and correlated with the GRIP δ^{18}O data. This concerns a first slight cooling followed by a partial return to favourable conditions (cp5b) which is, however, only represented at Les Echets (3065 to 3032 cm). No similar pattern is recorded in the GRIP δ^{18}O data, which possibly indicates regional differences in the climate evolution between Les Echets and GRIP.

Subsequently, a pronounced cooling–warming cycle (cp5c) becomes obvious at Les Echets (3030 to 2991 cm) and Samerberg (1350 to 1320 cm) which can be correlated with the GRIP δ^{18}O data for the period between 78.7 and 76 ky on the basis of the climate development. With respect to the pollen assemblages, *Carpinus* occurs with more than 40% at Les Echets during this episode, whereas the maximum is 1% at Samerberg. Concerning the reliability of the climate reconstructions, MAV may underestimate temperature parameters at Les Echets for this period because available modern analogues originate only from eastern Europe. Hence, PCS should more accurately reflect climate change in this case. For Samerberg, however, the MAV reconstruction is thought to describe the climate development reliably. At Les Echets, the deterioration (78.7 to 77.5 ky in GRIP) as reconstructed with PCS occurs with a shift in the coldest month to -8.2 °C and in the warmest month to 16.9 °C (Fig. 2). At Samerberg, MAV indicates an average cooling of the coldest month to -9 °C and of the warmest month to 16.5 °C, accompanied by a slight lowering of precipitation (Fig. 3). The ensuing warming (77.5 to 76 ky in GRIP) is characterised only by an attenuated return to previous conditions.

Towards the end of St. Germain II, a rapid and short-term climate oscillation (cp5d) is documented at Les Echets (2985 to 2980 cm) and Samerberg (1310 to 1280 cm), climatically corresponding to the GRIP oxygen-isotope excursions between 76 and 75.5 ky. Based on MAV, the initial cooling occurs with an average decline in temperature of the coldest month of 3.3 °C associated to a reduction in the warmest month of 1.6 °C. The final recovery in thermal conditions is associated with an increase in winter temperatures by 2.3 °C on average.

Finally, the end of St. Germain II is clearly recorded by a strong decline in pollen of thermophilous species and conifers and by an increase of NAP, especially Poaceae and *Artemisia*. This climate deterioration is obvious at Les Echets (2970 cm) and Samerberg (1270 cm) and climatically correlates with the rapid decline in the GRIP oxygen-isotope data at the end of D/O IS21 (75.5 ky). During the transition to the subsequent stadial (C20), winter temperatures fall to -15 to -16 °C, summer temperatures to 9 to 15 °C and precipitation to about 490 mm, as reconstructed by both methods.

5. Discussion

The numerical reconstructions of climate change from four pollen records covering the late Eemian to St. Germain II are largely consistent. In addition, environmental signals recorded in the ice and pollen records show good agreement, but the pollen records suggest a greater climatic variability.

5.1. Melisey I versus Melisey II

The abrupt shifts into Melisey I and Melisey II within 140 to 1900 years (Johnsen et al., 1992; Adkins et al., 1997; Allen et al., 1999; Rioual et al., 2001) are indicated by significant changes in oxygen-isotope ratios. According to the GRIP data the transition to stadial conditions in Greenland is linked to a reduction of mean annual surface temperature by 4 to 7 °C (Johnsen et al., 1989). More detailed information is provided by our palaeoclimate reconstructions for continental Europe based on fossil pollen floras using MAV and PCS.

Comparably for Melisey I and Melisey II, the climate development at the beginning of the stadials is determined by a considerable decline in winter and summer temperatures, succeeded by a phase of increased continentality which is evident in all pollen records by further declining winter but increasing or stable summer temperatures (across cp2a to cp2c and cp4a to cp4c). These findings are in accordance with studies of Frenzel (1967, 1973) and are also consistent to reconstructions by Guiot et al. (1993) based on beetle remains from Grande Pile, and to data provided by Rioual et al. (2001) for the Ribains maar pollen profile. There is, however, an inconsistency in our data regarding the development of continentality when comparing the western and the eastern sites. At the most western location, Les Echets, the degree of continentality becomes higher during this climatic development than at the other sites. This implausible pattern may be explained mainly by methodological problems. Since vegetation at Les Echets is more diverse than at the other sites, especially during glacial times, changes in vegetation can be interpreted more sensitively in terms of climate change. During the phase of increasing continentality, the reconstructions for all pollen records also indicate an interruption by an intra-stadial amelioration (cp2b). This fluctuation might be caused by re-deposited pollen but may also represent an actual warming episode. The observed climate change with decreasing winter and summer temperatures which is followed by increasing continentality may be related directly to oceanic and atmospheric processes. Due to the abrupt cut-off of the North Atlantic thermohaline circulation (e.g. Mangerud et al., 1979; Keigwin et al., 1994; Björck et al., 2000; McManus et al., 2002) caused by increased freshwater influx from precipitation or melting ice (Mikolajewicz and Maier-Reimer, 1994), the continental European climate experienced a reduced heat transport by westerlies from the warm Gulf Stream. Thus, sea ice build-up would increase, leading to higher albedo and cooling in winter and summer on the adjacent landmasses. Related to the southward displacement of the North Atlantic Drift by more than 10° latitude when compared to its position during the Eemian (Behre, 1989), a southward movement of the Arctic front (Knudsen et al., 2002), the build-up of the Scandinavian ice sheet and a stable high pressure zone could have developed, resulting in stronger dryness on the continent. Because of lower cloudiness, summer temperatures could have increased in the course of the stadial whereas winter temperatures may have dropped further, leading to an increased continentality. With a re-initiation of the thermohaline circulation, again enhanced oceanicity results at the transition to the subsequent interstadial.

Based on the reconstructions of MAV and PCS, however, also significant differences between Melisey I and Melisey II can be determined. During Melisey II winter temperatures are 1 to 4 °C lower then during Melisey I, but summer temperatures are 1 °C higher (Fig. 4). A similar difference between Melisey I and II is observed in northwest European pollen records

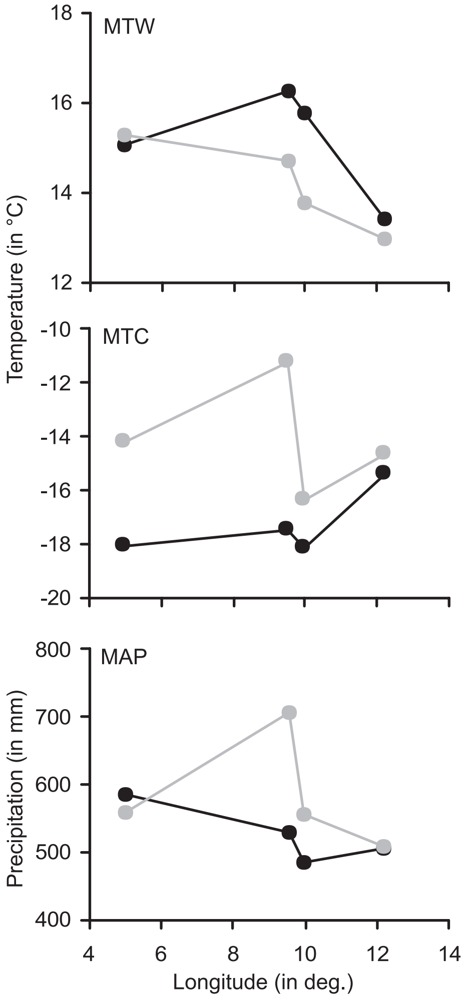

Fig. 4. Reconstructed average mean temperature of the coldest (MTC) and warmest month (MTW) in °C and mean annual precipitation (MAP) in mm, based on the modern analogue vegetation types and probability mutual climatic spheres (by averaging values) for Melisey I (grey line) and Melisey II (black line) across the study area. The dots indicate the locations of the sites with respect to latitude, from W to E with Les Echets, Jammertal, Füramoos and Samerberg.

(Aalbersberg and Litt, 1998) but which show a higher oceanicity. Especially at Gröbern/Germany (Hoffmann et al., 1998), winter temperatures were found to be even 6 °C higher than reconstructed for several western European pollen sites (Cheddadi et al., 1998; Klotz et al., 2003).

Whereas our results are in good agreement with the GRIP and North Atlantic oxygen-isotope data (Keigwin et al., 1994), insolation signals at higher latitudes indicate summer input during Melisey II to be considerable higher than during Melisey I (Berger, 1978; Herterich and Berger, 1993). Although this may explain the first Würmian stadial to be favourable for initial ice-sheet growth and ice accretion as observed (Labeyrie et al., 1987; Forsström and Punkari, 1997), the enhanced cold climate conditions which are documented for Melisey II thus must have been caused by other factors. It is suggested by the coupled LLN climate model used by Herterich and Berger (1993) that a larger ice sheet may have extended to the south during Melisey II with a lower mean height when compared to Melisey I, finally causing an increased continentality.

5.2. St. Germain I versus St. Germain II

Documented, for example, by the GRIP chronology, the warming into full temperate conditions in St. Germain I (D/O IS22 to IS24) and St. Germain II (D/O IS21) occurred over a few centuries. On continental Europe, the replacement of steppe biomes by forests also substantiates that the biosphere reacted very rapidly to these fluctuations (Adams et al., 1999). Similarly for both interstadials, the shift to the temperate optimum at the beginning of each period (cp3a and cp5a) is characterised by an increase in winter temperatures of up to 17 °C and in summer temperatures of up to 6 °C at all sites. This pattern is associated with a considerable rise in humidity with precipitation about 450 mm higher than before. The general climate development during the interstadials is then characterised by a more gradual decline of temperature parameters comprising a series of cooling and warming episodes (cp3a to cp3e and cp5a to cp5d), similarly to the saw-tooth structure documented in the GRIP δ^{18}O data. When comparing the different climatic optimum phases during St. Germain I attributed to IS23 and IS24, the MAV and PCS reconstructions suggest that St. Germain Ia (cp3a) is slightly colder and more continental than St. Germain Ic (cp3c) at Jammertal (1230 to 1200 cm) and Füramoos (1221 to 1189 cm). This difference is mainly caused by the fact that winter temperatures are about 2.6 °C cooler in St. Germain Ia as compared to St. Germain Ic, whereas moisture remains comparable. In contrast to these results, marine and ice-core data suggest similar or even warmer conditions during St. Germain Ia as compared to Ic (Jouzel et al., 1987; Martinson et al., 1987), but which are consistent with our results for Les Echets and Samerberg. The discrepancy between our estimates favouring either St. Germain Ia or Ic for the climatic optimum may actually be unravelled when the migration history of the plants is considered. At Les Echets and Samerberg, the vegetation during the beginning of St. Germain Ic shows a specific pattern with a large expansion of thermophilous taxa, especially *Corylus*, *Quercus* and *Fraxinus*, indicating more favourable thermal conditions. In contrast, at Jammertal and Füramoos which are far away from glacial refugia a considerable migration lag during the short time of St. Germain Ia could have prevented the full expansion of thermophilous taxa (Müller, 2000). In conclusion, the real climate conditions during the St. Germain Ia are possibly better recorded at Les Echets and Samerberg than at Füramoos and Jammertal. At Les Echets, St. Germain Ia is about 2.5 °C warmer in winter than St. Germain Ic, but summer temperature and moisture are comparable in St. Germain Ia and Ic. A similar pattern with higher winter temperatures during St. Germain Ia is observed at Samerberg.

The question of the climatic differences between St. Germain I and St. Germain II has been discussed in various studies. On the basis of North Atlantic marine δ^{18}O data (Keigwin et al., 1994), St. Germain II is considered to be somewhat warmer than St. Germain I although North Atlantic deep-water production is slightly reduced. This observation is confirmed by the deciduous and evergreen *Quercus* pollen abundances in a marine pollen record off the Iberian margin (Sanchez Goni et al., 2000) and by pollen-based analyses at Grande Pile (Guiot et al., 1989). In contrast, GRIP δ^{18}O ratios suggest mean annual surface temperatures to be similar during both interstadials. Likewise, other reconstructions for northwest European records (Aalbersberg and Litt, 1998; Hoffmann et al., 1998) estimate winter and summer temperatures during St. Germain I and II to be mostly similar.

The palaeoclimate analysis of the pollen records used in our study, however, suggests climatic differences between both interstadials. At Les Echets (3360 to 3349 cm, cp3a), during St. Germain I maximum winter temperatures of 2.2 °C and summer temperatures of 18.5 °C are reconstructed whereas St. Germain II at Les Echets (3072 to 3060 cm, cp5a) is characterised by maximum winter temperatures of 3 °C and summer temperatures of 19.7 °C. Maximum precipitation is about 1050 mm during both interstadials. A similar pattern is provided by the palaeoclimatic analyses of the more easterly sites, although they show conspicuously lower winter temperatures when compared to Les Echets. Whereas for St. Germain I average winter temperatures of − 5.4 °C and summer temperatures of 17 °C are estimated, St. Germain II winter temperatures are reconstructed to be 1.4 °C and summer temperatures to be 0.7 °C higher. As a result, St. Germain I may thus be considered somewhat more continental and slightly colder than St. Germain II.

When compared to the present-day situation, the palaeoclimate results reveal also stronger gradients in winter temperatures across the study area during both interstadials (Fig. 5). This phenomenon may be explained either by changes in atmospheric circulation patterns or by migration lags of vegetation largely influencing the climate reconstructions. However, St. Germain Ic and St. Germain II were long enough to allow the spread of thermophilous taxa towards the eastern sites as documented by the pollen records used in this study. Hence, the stronger gradient must actually have been caused by atmospheric changes inducing higher continentality in the east. The following scenario provides a simple explanation for this pattern. During the interstadials, sea-levels are about 40 m below present-day values. Together with the southward displacement of the Gulf Stream this leads to a cooling as compared to the Eemian optimum and present (Behre, 1989), and increases continentality. As confirmed by our study, this effect is most accentuated at localities east of Les Echets. In addition, the modelling study of Herterich and Berger (1993) indicates a stronger reduction of the global ice volume during St. Germain II than during I, and this is especially true for the Scandinavian ice sheet which exists during St. Germain I and II (Forsström and Punkari, 1997). A smaller Scandinavian ice sheet may explain the somewhat higher winter and summer temperatures during St. Germain II.

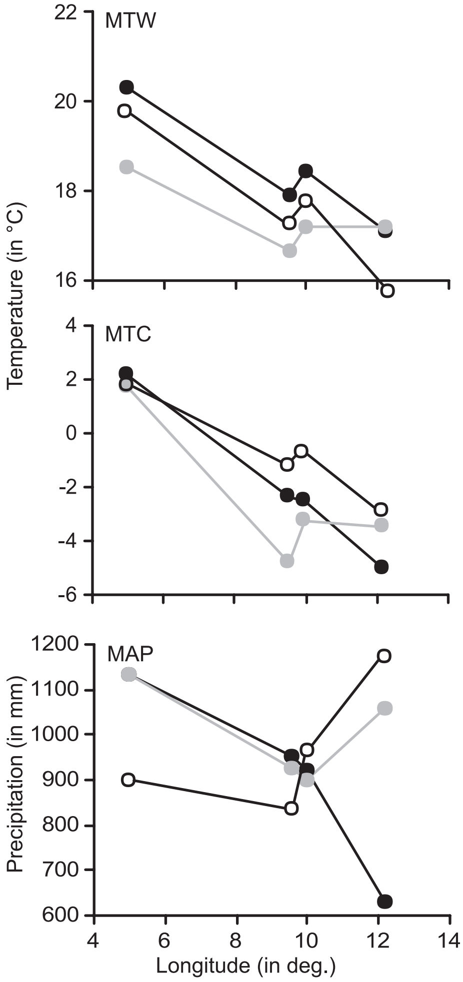

Fig. 5. Reconstructed average mean temperature of the coldest (MTC) and warmest month (MTW) in °C and mean annual precipitation (MAP) in mm, based on the modern analogue vegetation types and probability mutual climatic spheres (by averaging values) for St. Germain I (grey line) and St. Germain II optimum (black line) across the study area. The dots indicate the locations of the sites with respect to latitude, from W to E with Les Echets, Jammertal, Füramoos and Samerberg. Framed circles represent present-day values.

5.3. Stability of the stadials and interstadials

Most major climate oscillations documented in the GRIP ice core are also detected in our palaeoclimate analyses of the central European pollen records. There are, however, also discrepancies, for example, a short-term climate amelioration during Melisey II which is consistently revealed by the pollen records but is not documented in the GRIP oxygen isotope data. This observation indicates that terrestrial archives may show local or regional patterns in climate evolution which are not reflected in the global trends.

During Melisey I, the existence of a short-time climate amelioration (cp2b) is indicated by the palaeoclimate reconstructions for Les Echets (3435 to 3427 cm), Jammertal (1270 cm), Füramoos (1234 cm) and Samerberg (2085 cm). During this event, winter temperatures increase at all sites by 7.5 °C in average and decreased by 9 °C, concomitant to an oscillation in summer temperatures of 2 °C. For Les Echets and Samerberg, for which a shorter migration lag of vegetation as compared to Jammertal and Füramoos can be assumed (Müller, 2000), maximum temperatures during this warming are comparable to those of interstadial St. Germain Ia. The intra-Melisey I amelioration is also documented at about 111 ky ago by the GRIP and Vostok ice-core data (Johnsen et al., 1995; Jouzel et al., 1987) as well as by maximum δ^{13}C ratios in a western North Atlantic core (Keigwin et al., 1994) suggesting an advanced North Atlantic Deep Water production. During Melisey II, a climate amelioration (cp4b) with higher oceanicity occurs at Les Echets (3178 to 3146 cm based on the climate reconstructions, but is hardly visible in the pollen flora), Jammertal (1110 to 1090 cm), Füramoos (1110 to 1105 cm) and Samerberg (1670 to 1495 cm). The oscillation is characterised by an increase in winter temperatures by 8.4 °C on average and in precipitation by 120 mm. In contrast to the intra-Melisey I warming which is followed by even harsher climate conditions than preceding, the short-term warming during Melisey II may indicate a trend to the succeeding more favourable thermal conditions during St. Germain II interstadial. The GRIP record, however, does not reflect this excursion between IS21 and IS22 (Johnsen et al., 1995). In conclusion, considering the climate development during Melisey I and II, our findings suggest these stadials to be largely stable, although each of them appears to be interrupted by a short warming event.

Consistent with other pollen records across Europe such as Grande Pile (Woillard, 1978) or Tenaghi Philippon (Tzedakis, 1993), the pollen records used in this study also allow the analysis of the Montaigu cooling event (De Beaulieu and Reille, 1984). Our reconstructions suggests a short-term reduction in winter temperatures (cp3b) for all sites with an average of 9.7 °C, reduced summer temperatures by 2 °C and precipitation by 400 mm. This climate deterioration is even more pronounced than the intra-Eemian cooling detected in pollen records from the northern alpine foreland (Klotz et al., 2003). The Montaigu event is similarly documented by the GRIP oxygen-isotope data between IS23 and IS24 but can be seen, too, in a western North Atlantic core with minimum δ^{13}C ratios indicating NADW suppression comparable to full-glacial conditions (Keigwin et al., 1994).

With regard to questions about the stability of the climate during St. Germain I and II, in addition to the Montaigu event our analyses of the St. Germain I and II using MAV show characteristic climate patterns strikingly resembling the saw-tooth structure described by Bond et al. (1993). This can be observed during St. Germain I from peak warming (cp3a) until the transition into Melisey II (cp3e) at Les Echets (3360 to 3210 cm), Jammertal (1200 to 1160 cm), Füramoos (1198 to 1131 cm) and somewhat less distinctly at Samerberg (2046 to 1745 cm). In addition, the early thermal optimum (cp3c) and the late partial recovery (cp3e) of climate during St. Germain Ic can be correlated with IS23 and IS22 in the GRIP record. Comparable to the GRIP ice-core data between IS21 and IS19, our climate reconstructions for St. Germain II show a similar saw-tooth structure (cp5a to cp5d) at Les Echets (3067 to 2890 cm) and Samerberg (1365 to 1270 cm). For Jammertal and Füramoos, however, such a structure is not observed which can, in turn, be explained by the proximity of Les Echets and Samerberg to the main distribution areas of thermophilous taxa which may produce more stable climate reconstructions. All in all, our findings indicate that the interstadials St. Germain I and II are not very stable, at least in continental Europe but show saw-tooth structures. The origin of the series of coolings, especially of the Montaigu event, may be similar to that of the intra-Eemian climate deterioration. This would imply that a decrease in the density of Norwegian Sea surface waters induced by an input of fresh water, or a temperature increase, could have reduced deep-water formation in the Norwegian Sea within a few decades (Bryan, 1986; Cortijo et al., 1994). In addition to a more westerly position of the North Atlantic Current (Larsen et al., 1995; Bauch et al., 1999), this would have allowed the penetration of subarctic waters towards the south and a southward displacement of the polar front (Seidenkrantz et al., 2000; Sanchez Goni et al., 2000).

6. Conclusions

The comparative use of different reconstruction methods for analysing late Eemian to early Würmian climate dynamics allows us to detect some of its main characteristic patterns. The modern analogue technique and mutual climate sphere technique complement each other because they have different bases.

At first, it can be observed that the reconstructed terrestrial climate signals for all pollen profiles are in good agreement with the GRIP data, although reconstructed winter temperatures show a higher variability. This may be explained by the fact that the GRIP data represent only annual average data. Next, winter temperatures show a more pronounced variability then summer temperatures, implying during cooling periods an increase in seasonality which is accompanied also by a drop in mean annual precipitation. With regard to geography, generally a higher continentality for the more eastern pollen profiles is reconstructed. Further, the results reveal that the stadials experience a higher climate variability than the interstadials, although oscillations are not as frequent as during the interstadials. All in all, our findings suggest that neither stadials nor interstadials are very stable in continental Europe.

With a more detailed view on the climate development based on the four pollen sites along the northern alpine foreland, some major climate differences between each of the stadials and the interstadials can be distinguished. Our climate analysis suggests that the climate of Melisey II is cooler than that of Melisey I in winter. This climatic pattern may be the result of a larger ice-sheet extension to the south during Melisey II, although the global ice volume is reduced as compared to Melisey I. Moreover, our palaeoclimate analyses suggest the possible existence of amelioration episodes during Melisey I and Melisey II evidenced by a considerable rise in winter and summer temperatures concomitant to a somewhat increased precipitation. Whereas the amelioration during Melisey I is also documented in the Greenland ice core-data, no such warming is found there during Melisey II. Concerning the early Würmian interstadials, the St. Germain II optimum is characterised by slightly warmer winters and summers than the St. Germain I optimum. In view of the climate differences between St. Germain Ia and Ic, the climate during St. Germain Ia is reconstructed to be warmer in winter than in St. Germain Ic, but summer temperatures and moisture are comparable. Further, periods with cooler climate conditions are detectable during the interstadials St. Germain I and St. Germain II. They may either show a saw-tooth structure with a series of coolings and warmings, or they may represent sharp and severe climate deteriorations such as the Montaigu event during St. Germain I. In order to test these results, further detailed investigations based on different proxies and climate modelling studies are needed.

Acknowledgements

We thank Prof. E. Grüger for providing the Samerberg pollen data and Prof. B. Huntley for providing modern pollen spectra for climatic analyses. We also thank A. Micheels for technical assistance. We thank the reviewers Prof. H.J.B. Birks and Prof. B. Frenzel for their very valuable suggestions on our manuscript.

References

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

Adams, J., Maslin, M.A., Thomas, E., 1999. Sudden climate transitions during the Quaternary. Progress in Physical Geography 23, 1–36.

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.

Aichinger, E., 1967. Pflanzen als forstliche Standortsanzeiger. Österr Agrarverlag, Wien. 227 pp.

Allen, J.R.M., Brandt, U., Brauer, A., Hubberten, H.W., Huntley, B., Keller, J., Kraml, M., Mackensen, A., Mingram, J., Negendank, J.F.W., Nowaczyk, N.R., Oberhänsli, H., Watts, W.A., Wulf, S., Zolitschka, B., 1999. Rapid environmental changes in southern Europe during the last glacial period. Nature 400, 740–743.

Atkinson, T.C., Briffa, K.R., Coope, G.R., Joachim, M.J., Perzy, D.W., 1986. Climatic calibration of Coleopteran data. In: Berglund, B.E. (Ed.), Handbook of Holocene Palaeoecology and Palaeohydrology. Wiley, New York, pp. 851–858.

Bartlein, P.J., Prentice, I.C., Webb III, T., 1986. Climatic response surfaces from pollen data for some eastern North American taxa. Journal of Biogeography 13, 35–57.

Bauch, H.A., Erlenkeuser, H., Fahl, K., Spielhagen, R.F., Weinelt, M.S., Andruleit, H., Heinrich, R., 1999. Evidence for a steeper Eemian than Holocene sea surface temperature gradient between Arctic and sub-Arctic regions. Palaeogeography, Palaeoclimatology, Palaeoecology 144, 95–117.

Behre, K.E., 1989. Biostratigraphy of the Last Glacial period in Europe. Quaternary Science Reviews 8, 25–44.

Berger, A., 1978. Long-term variations of daily insolation and Quaternary climatic changes. Journal of the Atmospheric Sciences 35, 2362–2367.

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

Bond, G.C., Broecker, W., Johnsen, S., McManus, J., Labeyrie, L., Jouzel, J., Bonani, G., 1993. Correlations between climate records from North Atlantic sediments and Greenland ice. Nature 365, 143–147.

Broecker, W.S., 1998. The end of the present interglacial: how and when? Quaternary Science Reviews 17, 689–694.

Broecker, W.S., 2000. Abrupt climate change: causal constraints provided by the paleoclimate record. Earth-Science Reviews 51, 137–154.

Bryan, F., 1986. High-latitude salinity effects and interhemispheric thermohaline circulation. Nature 323, 304–310.

Buggisch, W., Walliser, O.H., 2001. Erdgeschichte und Klimageschichte. In: Huch, M., Warnecke, G., Germann, K. (Eds.), Klimazeugnisse der Erdgeschichte. Springer, Berlin, pp. 17–49.

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., Weering van, T.C.E., 1994. Eemian cooling in the Norwegian Sea and North Atlantic Ocean preceding continental ice sheet growth. Nature 372, 446–449.

Dansgaard, W., Johnsen, S.J., Clausen, H.B., Dahl, J.D., Gundestrup, N.S., Hammer, C.U., Hvidberg, C.S., Steffensen, J.P., Sveinbjornsdottir, A.E., Jouzel, J., Bond, G., 1993. Evidence for general instability of past climate from a 250-kyr ice-core record. Nature 364, 218–220.

De Beaulieu, J.L., Reille, M., 1984. A long Upper Pleistocene pollen record from Les Echets, near Lyon, France. Boreas 13, 111–132.

De Beaulieu, J.L., Reille, M., 1989. The transition from temperate phases to stadials in the long upper Pleistocene sequence from Les Echets (France). Palaeogeography, Palaeoclimatology, Palaeoecology 72, 147–159.

Ellenberg, H., 1986. Vegetation Mitteleuropas mit den Alpen. Ulmer, Stuttgart. 989 pp.

Fauquette, S., Guiot, J., Menut, M., de Beaulieu, J.L., Reille, M., Guenet, P., 1999. Vegetation and climate since the last interglacial in the Vienne area (France). Global and Planetary Change 20, 1–17.

Forsström, L., Punkari, M., 1997. Initiation of the last glaciation in northern Europe. Quaternary Science Reviews 16, 1197–1215.

Frenzel, B., 1967. Die Klimaschwankungen des Eiszeitalters. Vieweg and Sohn, Braunschweig. 291 pp.

Frenzel, B., 1968. Grundzüge der pleistozänen Vegetationsgeschichte Nord-Eurasiens. Franz Steiner, Wiesbaden. 326 pp.

Frenzel, B., 1973. Climatic Fluctuations of the Ice Age. Press of Case Western Reserve University, Cleveland. 306 pp.

Frenzel, B., 1991a. Das Klima des Letzten Interglazials in Europa. Paläoklimaforschung 1, 51–78.

Frenzel, B., 1991b. Über einen frühen letzteiszeitlichen Eisvorstoß des Rheingletschers in das deutsche Alpenvorland. In: Frenzel, B. (Ed.), Klimageschichtliche Probleme der letzten 130000 Jahre. Fischer, Stuttgart, pp. 377–400.

Grichuk, V.P., 1969. In: Neishtadt, M.I. (Ed.), An attempt to Reconstruct Certain Elements of the Climate of the Northern Hemisphere in the Atlantic Period of the Holocene. Golotsen, Moscow, pp. 41–57.

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.

Grüger, E., 1979. Spätriss, Riss/Würm und Frühwürm am Samerberg in Oberbayern-ein vegetationsgeschichtlicher Beitrag zur Gliederung des Jungpleistozäns. Geologica Bavarica 80, 5–64.

Guiot, J., 1987. Late Quaternary climatic change in France estimated from multivariate pollen time series. Quaternary Research 28, 100–118.

Guiot, J., 1990. Methodology of the last climatic cycle reconstruction in France from pollen data. Palaeogeography, Palaeoclimatology, Palaeoecology 80, 49–69.

Guiot, J., 1991. Structural characteristics of proxy-data and methods for quantitative climate reconstructions. Paläoklimaforschung 6, 271–284.

Guiot, J., Pons, A., de Beaulieu, J.L., Reille, M., 1989. A 140,000-year continental climate reconstruction from two European pollen records. Nature 338, 309–313.

Guiot, J., de Beaulieu, J.L., Cheddadi, R., David, F., Ponel, P., Reille, M., 1993. The climate in western Europe during the last Glacial/Interglacial cycle derived from pollen and insect remains. Palaeogeography, Palaeoclimatology, Palaeoecology 103, 73–93.

Herterich, K., Berger, A., 1993. Modelling the last ice-age cycle with 2-D climate models. Palaeogeography, Palaeoclimatology, Palaeoecology 103, 107–116.

Hoffmann, M.H., Litt, T., Jäger, E.J., 1998. Ecology and climate of the early Weichselian flora from Gröbern (Germany). Review of Palaeobotany and Palynology 102, 259–276.

Huntley, B., 1992. Pollen-climate response surfaces and the study of climate change. In: Gray, J. (Ed.), Applications of Quaternary Research. Quaternary Proceedings, vol. 2, pp. 91–99.

Iversen, J., 1944. *Viscum*, *Hedera* and *Ilex* as Climate Indicators. Geologiska Föreningen i Stockholm Förhandlingar 66, 463–483.

Jalas, J., Suominen, J. (Eds.), 1989. Atlas Florae Europaeae. Distribution of vascular plants in Europe. Nymphaeaceae to Ranunculaceae, vol. 8. Committee for Mapping the Flora of Europe and Societas Biologica Fennica Vanamo, Helsinki. 261 pp.

Johnsen, S.J., Dansgaard, W., White, J.W.C., 1989. The origin of Arctic precipitation under present and glacial conditions. Tellus 41B, 452–468.

Johnsen, S.J., Clausen, H.B., Dansgaard, W., Fuhrer, K., Gundestrup, N., Hammer, C.U., Iversen, P., Jouzel, J., Stauffer, B., Steffensen, J.P., 1992. Irregular glacial interstadials recorded in a new Greenland ice core. Nature 359, 311–313.

Johnsen, S.J., Clausen, H.B., Dansgaard, W., Fuhrer, K., Gundestrup, N., Hammer, C.U., Tauber, H., 1995. The Eem stable isotope record along the GRIP ice core and its interpretation. Quaternary Research 43, 117–125.

Jouzel, J., Lorius, C., Petit, J.R., Genthon, C., Barkov, N.I., Kotlyakov, V.M., Petrov, V.M., 1987. Vostok ice core: a continuous isotope temperature record over the last climatic cycle (160000 years). Nature 329, 403–408.

Keigwin, L.D., Curry, W.B., Lehman, S.J., Johnsen, S., 1994. The role of the deep ocean in North Atlantic climate change between 70 and 130 kyr ago. Nature 371, 323–325.

Klotz, S., 1999. Neue Methoden der Klimarekonstruktion-angewendet auf quartäre Pollensequenzen der französischen AlpenTübinger Mikropaläontologische Mitteilungen, vol. 21. Tübingen. 169 pp.

Klotz, S., Pross, J., 1999. Pollen-based reconstructions in the European Pleistocene: the modified indicator species approach as a tool for quantitative analysis. Acta Palaeobotanica. Supplementum 2, 481–486.

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.

Krüssmann, G., 1977a. Handbuch der Laubgehölze. Verlag Paul Parey, Band I, Berlin und Hamburg. 486 pp.

Krüssmann, G., 1977b. Handbuch der Laubgehölze. Verlag Paul Parey, Band I, Berlin und Hamburg. 486 pp.

Kukla, G., 2000. The last interglacial. Science 287, 987–989.

Labeyrie, L.D., Duplessy, J.C., Blanc, P.L., 1987. Variations in mode of formation and temperature of oceanic deep waters over the past 125000 years. Nature 327, 477–482.

Larsen, E., Sejrup, H.P., Johnsen, S.J., Knudsen, K.L., 1995. Do Greenland ice cores reflect NW European interglacial climate variations? Quaternary Research 43, 125–132.

Mangerud, J., 1989. Correlation of the Eemian and the Weichselian with deep sea oxygen isotope stratigraphy. Quaternary International 3, 1–4.

Mangerud, J., Sonstegaard, E., Sejrup, H.P., 1979. Correlation of the Eemian (interglacial) stage and the deep-sea oxygen-isotope stratigraphy. Nature 277, 189–192.

Martinson, D.G., Pisias, N.G., Hays, J.D., Imbrie, J., Moore Jr., T.C., Shackleton, N.J., 1987. Age dating and the orbital theory of the Ice Ages: development of a high-resolution 0 to 300 000-year chronostratigraphy. Quaternary Research 27, 1–29.

McManus, J.F., Oppo, D.W., Keigwin, L.D., Cullen, J.L., Bond, G.C., 2002. Thermohaline circulation and prolonged interglacial warmth in the North Atlantic. Quaternary Research 58, 17–21.

Meusel, H., Jäger, E.J. (Eds.), 1992. Vergleichende Chorologie der zentraleuropäischen Flora. Fischer, Jena. 688 pp.

Mikolajewicz, U., Maier-Reimer, E., 1994. Mixed boundary conditions in OGCMs and their influence on the stability of the models conveyor belt. Journal of Geophysical Research 99, 22633–22644.

Mosbrugger, V., Utescher, T., 1997. The coexistence approach—a method for quantitative reconstructions of Tertiary terrestrial palaeoclimate data using plant fossils. Palaeogeography, Palaeoclimatology, Palaeoecology 134, 61–86.

Müller, U., 2000. A Late-Pleistocene pollen sequence from the Jammertal, south-western Germany with particular reference to location and altitude as factors determining Eemian forest composition. Vegetation History and Archaeobotany 9, 125–131.

Müller, U., Pross, P., Bibus, E., 2003. Vegetation response to rapid climate change in Central Europe during the past 140,000 yr based on evidence from the Füramoos pollen record. Quaternary Research 59, 235–245.

New, M., Hulme, M., Jones, P., 1999. Representing twentieth century space–time climate variability: I. Development of a 1961–1990 mean monthly terrestrial climatology. Journal of Climate 12, 829–856.

Peyron, O., Guiot, J., Cheddadi, R., Tarasov, P., Reille, M., de Beaulieu, J.L., Bottema, S., Andrieu, V., 1998. Climatic reconstruction in Europe for 18,000 yr B.P. from pollen data. Quaternary Research 49, 183–196.

Ponel, P., 1995. Rissian, Eemian and Würmian Coleoptera assemblages from La Grande Pile (Vosges, France). Palaeogeography, Palaeoclimatology, Palaeoecology 114, 1–41.

Pons, A., Guiot, J., de Beaulieu, J.L., Reille, M., 1992. Recent contributions to the climatology of the last glacial–interglacial cycle based on French pollen sites. Quaternary Science Reviews 11, 439–448.

Prentice, I.C., Bartlein, P.J., Webb III, T., 1991. Vegetation and climate change in eastern North America since the Last Glacial Maximum. Ecology 72, 2038–2056.

Pross, J., Klotz, S., Mosbrugger, V., 2000. Reconstructing palaeotemperatures for the Early and Middle Pleistocene based on plant fossils: a modern approach to an old technique. Quaternary Science Reviews 19, 1785–1799.

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

Sanchez Goni, M.F., Turon, J.L., Eynaud, F., Shackleton, N.J., Cayre, O., 2000. Direct land/sea correlation of the Eemian, and its comparison with the Holocene: a high-resolution palynological record off the Iberian margin. Geologie en Mijnbouw 79, 345–354.

Seidenkrantz, M.S., Knudsen, K.L., Kristensen, P., 2000. Marine late Saalian to Eemian environments and climate variability in the Danish shelf area. Geologie en Mijnbouw 79, 335–343.

Shackleton, N.J., Chapman, M., Sanchez Goni, M.F., Pailler, D., Lancelot, Y., 2002. The classic marine isotope substage 5e. Quaternary Research 58, 14–16.

Tzedakis, P.C., 1993. Long-term tree populations in northwest Greece through multiple Quaternary climatic cycles. Nature 364, 437–440.

Tzedakis, P.C., Andrieu, V., de Beaulieu, J.L., Crowhurst, S., Follieri, M., Hooghiemstra, H., Magri, D., Reille, M., Sadori, L., Shackleton, N.J., Wijmstra, T.A., 1997. Comparison of terrestrial and marine records of changing climate of the last 500,000 years. Earth and Planetary Science Letters 150, 171–176.

Van Andel, T.H., Tzedakis, P.C., 1996. Palaeolithic landscapes of Europe and environs, 150,000–25,000 years ago; an overview. Quaternary Science Reviews 15, 481–500.

Walter, H., Straka, H., 1970. Arealkunde. Floristisch-historische Geobotanik Ulmer, Stuttgart. 478 pp.

Woillard, G.M., 1978. Grand Pile peat bog: a continuous pollen record for the last 140000 years. Quaternary Research 9, 1–21.

Woodward, F.I., 1987. Climate and Plant Distribution. Cambridge Univ. Press, Cambridge. 173 pp.

Zagwijn, W.H., 1983. Sea-level changes in The Netherlands during the Eemian. Geologie en Mijnbouw 62, 437–450.

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