



## Vegetation dynamics and climate variability during the Holsteinian interglacial based on a pollen record from Dethlingen (northern Germany)

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### ABSTRACT

To better understand the environmental variability during the Holsteinian interglacial, we have palynologically analyzed a new core from Dethlingen, northern Germany, at a decadal resolution. Our data provide insights into the vegetation dynamics and thus also climate variability during the meso- to telocratic forest phases of the interglacial. Temperate mixed forests dominated the regional landscape throughout the Holsteinian. However, changes in the forest composition during the younger stages of the interglacial suggest a climatic transition towards milder conditions in winter. The strong presence of boreal floral elements during the older stages of the Holsteinian interglacial suggests a high seasonality. In contrast, during the younger stages the development of sub-Atlantic and Atlantic floral elements suggests increasingly warm and humid climatic conditions. Peak warming during the younger stage of the Holsteinian is marked by the maximum pollen abundances of *Buxus*, *Abies*, and *Quercus*. Although the vegetation dynamics suggest a general warming trend throughout the Holsteinian interglacial, abrupt as well as gradual changes in the relative abundances of temperate plants indicate considerable climatic variability. In particular, two marked declines in temperate taxa leading to the transient development of boreal and sub-temperate forests indicate short-term climatic oscillations that occurred within full interglacial conditions. The palynological signatures of these two regressive phases in vegetation development differ with regard to the expansion of pioneer trees, the abundances and rates of change of temperate taxa, and the presence of frost-sensitive taxa. These differences point to different mechanisms responsible for the individual regressive phases. Assuming a correlation of the interglacial at Dethlingen with Marine Isotope Stage (MIS) 11, our data suggest that temperate forests prevailed in northern Germany during the younger parts of MIS 11c.

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### 1. Introduction

The study of past interglacials can significantly contribute to improving the prediction of future climate change and its potential impact on the biotic and abiotic environment (e.g., EPICA, 2004; Tzedakis et al., 2004, 2009; Müller et al., 2005; Brauer et al., 2007; Jouzel et al., 2007; Pross et al., 2009). In this context, the Holsteinian interglacial has received considerable attention owing to its presumed correlation to MIS 11 (e.g., Reille et al., 2000; de Beaulieu et al., 2001; Tzedakis et al., 2001), which, with regard to orbital forcing, represents one of the closest palaeoclimatic

analogues for the present interglacial (e.g., Loutre and Berger, 2003; Ruddiman, 2005).

Based on the available climate information from continental archives, the Holsteinian represents a long interglacial (~ 15–16 ka; Müller, 1974) that is characterised by the development of mixed temperate forests in central and northwestern Europe (e.g., Erd, 1970; Turner, 1970; Müller, 1974; Kukla, 2003; Nitychoruk et al., 2005). Pollen-based temperature reconstructions from central European records suggest an overall warming trend. This trend, which is particularly reflected in July temperatures (from 17.5 to 19.7 °C), resulted in warmer conditions than today during the younger stages of the Holsteinian (Kühl and Litt, 2007). The above mentioned studies indicate long-lasting mild climatic conditions during the Holsteinian. However, earlier palynological studies have suggested the presence of climatic instabilities lasting for several

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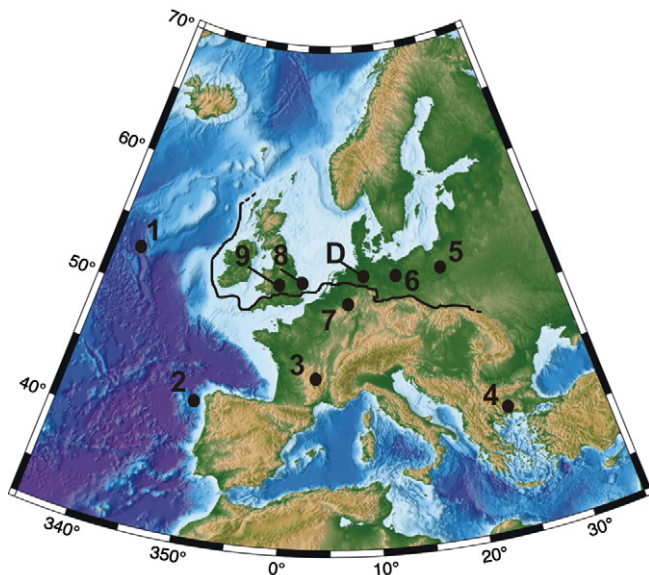
centuries as reflected by two intervals with abrupt shifts in forest composition associated with the development of pioneer vegetation (Müller, 1974; Kukla, 2003). These two phases have been identified at numerous sites in central and northwestern Europe, such as in England (West, 1956; Turner, 1970; Coxon, 1985; Thomas, 2001), Germany (Müller, 1974; Diehl and Sirocko, 2007), and Poland (Krupiński, 1995; Bińka and Nitychoruk, 1995, 1996; Bińka et al., 1997; Nitychoruk et al., 2005). However, the lack of high-resolution data has yet precluded deeper insights into the vegetation and climate dynamics of these phases. As a consequence, the mechanisms responsible for the regressive phases in vegetation development have remained unclear (Kukla, 2003).

Owing to the formation of numerous lakes after the melting of the Elsterian ice-sheet (Ehlers et al., 1984), the region of Lüneburger Heide in northern Germany is characterised by a number of partially annually laminated sedimentary archives of Holsteinian age (Benda and Brandes, 1974). Sedimentological investigations for mining purposes have been carried out on several diatomite deposits of the Lüneburger Heide region (Benda and Brandes, 1974), including Dethlingen (Benda et al., 1984). In this context, palaeoclimate studies were carried out on the sites of Munster–Breloh (Müller, 1974), Hetendorf (Meyer, 1974), Ober–Ohe (Gistl, 1928; Selle, 1954), and Wiechel (Benda, 1974). The potential for annual time-control, the good preservation of palynomorphs, and the possibility to crosscheck results on a regional scale make these archives well suited for the analysis of short-term climate and vegetation variability during the Holsteinian interglacial.

In light of the above, we describe the vegetation dynamics during the Holsteinian interglacial based on a decadal-scale-resolution record of terrestrial palynomorphs from a new core retrieved at Dethlingen, northern Germany.

## 2. Materials and methods

The Dethlingen site is located in the Lüneburger Heide region within the lowlands of northern Germany (10° 08' E, 52° 57' N, 65 m a.s.l., see Fig. 1). Dethlingen is surrounded by several basins that



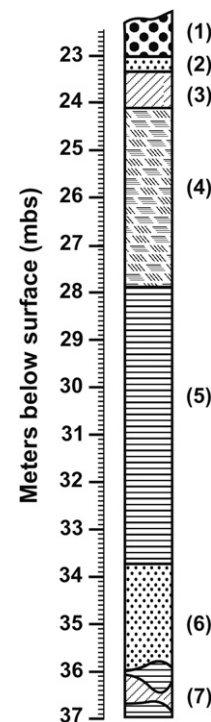
**Fig. 1.** Map indicating the location of Dethlingen and other sites mentioned in the text. The black line indicates the southern limit of the Elsterian ice-sheet (after Ehlers and Gibbard, 2004). (D) Dethlingen; (1) core M23414; (2) core MD01-2447; (3) Praclaux; (4) Tenaghi Philippon; (5) Biala Podlaska; (6) Gröbern-Schmerz; (7) Döttingen; (8) Hoxne and Marks Tey; (9) Quinton.

contain Holsteinian lacustrine deposits, such as Munster–Breloh, Hetendorf, Wiechel, and Ober–Ohe (Benda and Brandes, 1974).

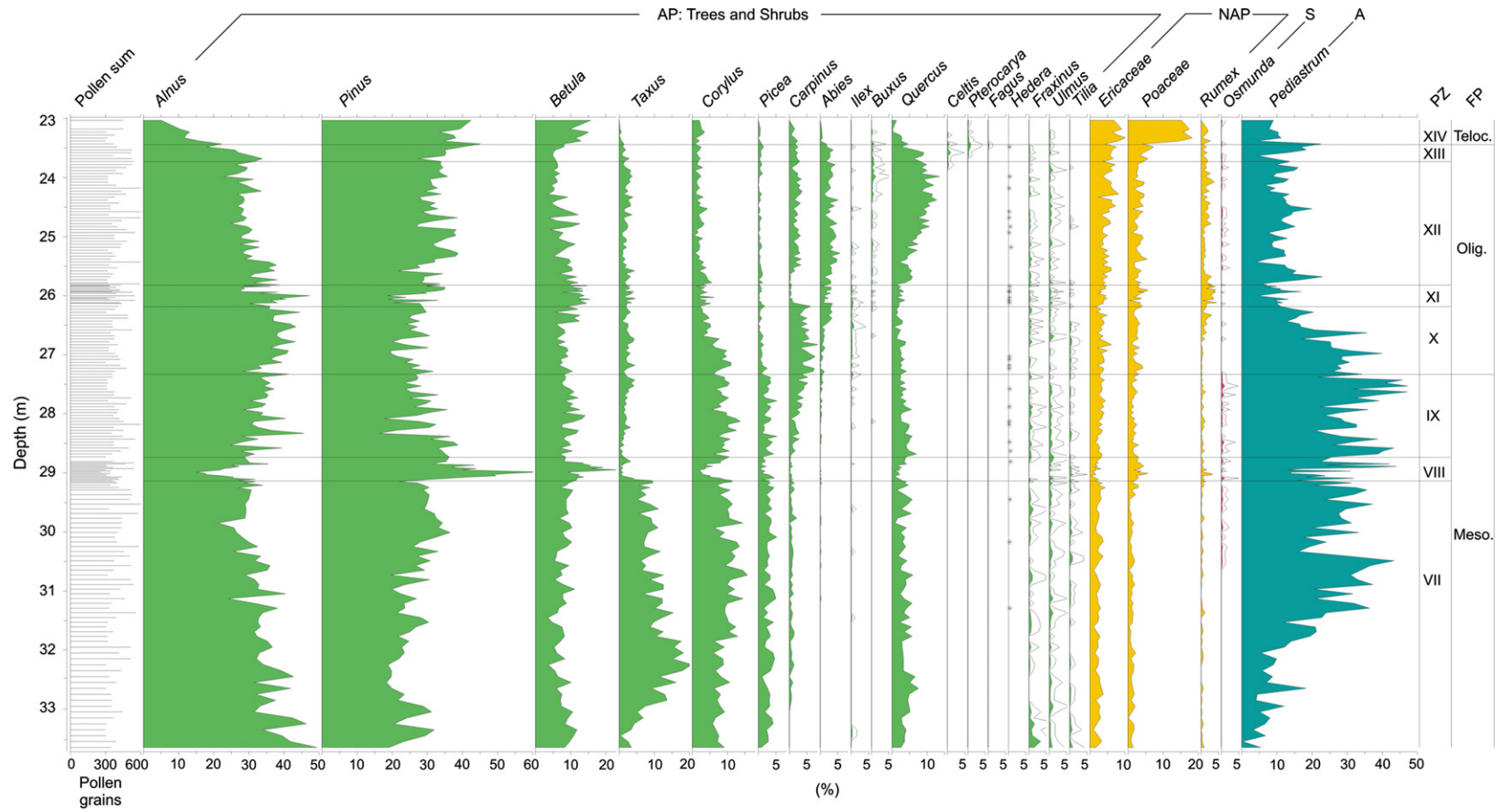
The Dethlingen core was retrieved in 2004 and comprises organic-rich lake sediments between 37 and 23 m depth below the present-day soil surface (mbs; Fig. 2). The lower part of the core (37–27.80 mbs) consists of a laminated diatomite with an intercalated, c. 2 m thick sand layer between 35.90 and 33.68 mbs. This interval is overlain by non-laminated diatomaceous sediments (27.80–24.10 mbs) and diatomaceous mud with increasing sand content (24.10–23 mbs). The lake sediments are topped by glacial gravel and sand that have been attributed to the Saalian glaciation (Benda et al., 1984). In this study, we exclusively focus on the interval between 33.68 and 23 mbs in order to avoid potential sediment unconformities and reworking that may have resulted from the deposition of the 2-m thick sand layer (Fig. 2).

Pollen samples were taken at intervals of between 5 and 10 cm; subsequently, dynamic phases in vegetation development were sampled every 1–2 cm. The thickness of individual samples varied between 0.5 cm for the non-laminated part of the core and the dynamic intervals, and 1 cm for the laminated part of the core. Based on varve counting of the Dethlingen core the sample spacing yields a decadal-scale-resolution, i.e., c. 40–60 years between samples for the laminated diatomite, a mean of c. 75 years (min. 45 years; max. 130 years) for the non-laminated diatomite, and 10–15 years for the dynamic intervals. Each sample integrates c. 5–10 years for the dynamic intervals and c. 10–15 years for the rest of the core.

The preparation of pollen samples followed standard palynological techniques including sediment freeze-drying, weighing, treatment with HCl (10%), NaOH (10%), HF (40%), heavy-liquid separation with  $\text{Na}_2\text{WO}_4 \times 2\text{H}_2\text{O}$ , acetolysis, and slide preparation using glycerine jelly. In total, 196 samples were analyzed using a Zeiss Axioskop light microscope at 400 $\times$  magnification. An average of 407 pollen grains (excluding pollen from aquatics,



**Fig. 2.** Lithology of the Dethlingen core. (1) Gravels and sand; (2) Sand; (3) Diatomaceous mud; (4) Non-laminated diatomite; (5) Laminated diatomite; (6) Sand; (7) Re-deposited diatomite, partially laminated.



**Fig. 3.** Pollen record of the Holsteinian interglacial at Dethlingen. Percentages of selected tree, shrub, and herb taxa plotted against core depth (meters below the present-day soil surface). The total number of pollen grains per sample (excluding aquatics and spores) and sample depth are indicated. Percentages of *Osmunda* and *Pediastrum* are calculated relative to the main pollen sum. Pollen zones have been adopted from the Holsteinian pollen stratigraphy of Munster–Brelah following Müller (1974). (AP) Arboreal Pollen; (NAP) Non-arboreal pollen; (S) Spores; (A) Algae; (PZ) Pollen Zone; (FP) Forest phase; (Meso.) Mesocratic phase; (Olig.) Oligocratic phase; (Teloc.) Telocratic phase.

**Table 1**

Summary of pollen zones (pz) characteristics, vegetation dynamics, infested forest types, and forest phases for each individual pollen zones. Pollen zones have been adopted from the Holsteinian pollen stratigraphy of Munster–Breloh (Müller, 1974).

PZ	Characteristics	Vegetation dynamics	Forest type	Forest phase
XIV	(+) Ericaceae, Poaceae, herbs (↑) <i>Pinus</i> , <i>Betula</i> (↓) <i>Quercus</i> , <i>Alnus</i> , <i>Picea</i> , <i>Carpinus</i> , <i>Abies</i>	• maximum forest opening (↑) pioneer trees (↓) temperate taxa (↓) evergreen taxa	Transition to open vegetation	Telocratic
XIII	(+) <i>Pterocarya</i> , <i>Fagus</i> , <i>Celtis</i> , <i>Buxus</i> (↑) <i>Pinus</i> , <i>Betula</i> , Ericaceae, herbs (↓) <i>Quercus</i> , <i>Alnus</i> , <i>Abies</i> , <i>Taxus</i>	(↓) temperate taxa (↑) pioneer trees	Mixed temperate with atlantic taxa and slight forest opening	Oligocratic
XII	(+) <i>Quercus</i> , <i>Buxus</i> , <i>Abies</i> (↑) Ericaceae, herbs (↓) <i>Alnus</i>	(↑) temperate taxa (↑) forest opening	“	“
XI	(+) <i>Betula</i> , <i>Ilex</i> , <i>Hedera</i> (↑) Ericaceae, herbs (↓) <i>Carpinus</i> , <i>Abies</i>	(↑) pioneer trees (↑) forest opening (↓) temperate taxa	Sub-temperate with forest openings	“
X	(+) <i>Carpinus</i> , <i>Ilex</i> (↑) <i>Abies</i> , herbs (↓) <i>Corylus</i> , <i>Picea</i>	(↓) temperate taxa (↑) evergreen taxa (↑) pioneer trees	Mixed temperate with atlantic taxa	“
IX	(+) <i>Corylus</i> , <i>Picea</i> , <i>Quercus</i> , Ericaceae (↑) <i>Carpinus</i> (↓) <i>Pinus</i>	(↑) temperate taxa (↓) pioneer trees	Mixed temperate with boreal taxa	Mesocratic
VIII	(+) <i>Pinus</i> , <i>Betula</i> , Poaceae (↓) <i>Taxus</i> , <i>Corylus</i> , <i>Alnus</i> , <i>Picea</i> , <i>Quercus</i> , Ericaceae	(↑) pioneer trees (↑) forest opening (↓) temperate taxa	Boreal with forest openings	“
VII	(+) <i>Taxus</i> , <i>Picea</i> , <i>Corylus</i> , <i>Quercus</i>	• maximum of temperate taxa	Mixed temperate with boreal taxa	“

Symbols: (+) characteristic taxa; (↑) increase; (↓) decrease.

spores, and algae) were counted per sample; the minimum counting sum was always above 300 pollen grains per sample. The percentages of aquatics, spores, and algae were calculated relative to the pollen sum of terrestrial taxa.

### 3. Results

#### 3.1. Biostratigraphic age assignment

The Dethlingen pollen record (Fig. 3) exhibits an early, prominent *Taxus* phase accompanied by *Picea* and a subsequent *Carpinus*–*Abies* phase associated with the occurrence of *Buxus*, *Pterocarya*, and *Fagus*. This succession of taxa is characteristic for Holsteinian pollen records from central and northwestern Europe (Erd, 1970; Turner, 1970; Müller, 1974; Linke and Hallik, 1993; Bińka and Nitychoruk, 1995, 1996; Geyh and Müller, 2005; Diehl and Sirocko, 2007). Hence, based on this biostratigraphy, the Dethlingen record can be firmly assigned to the Holsteinian interglacial.

#### 3.2. Palynostratigraphy of the Dethlingen record

The palynoflora at Dethlingen as depicted in Fig. 3 is dominated by *Alnus* and *Pinus*, which together account for more than 60% of the terrestrial pollen sum throughout the record. In association with the prominent occurrence of *Carpinus* and the virtual absence of *Fagus* (Fig. 3), this pattern is characteristic for the lowland vegetation during the Holsteinian in central Europe (Erd, 1970; Linke and Hallik, 1993; de Beaulieu et al., 2001). The vegetation succession shows a high degree of similarity to that of the nearby site of Munster–Breloh (Müller, 1974). Therefore, the pollen zonation from Munster–Breloh as developed by Müller (1974) has been adopted with minor modifications (Fig. 3). The pollen zones (PZ) VII–XIV of Müller (1974), which cover most of the Holsteinian interglacial, are recorded at Dethlingen. Pollen zones I–VI,

reflecting the onset of the Holsteinian (Meyer, 1974), are obscured by sediment reworking below 33.68 mbs that resulted from the deposition of the sand layer (see Section 2). The development of the palynoflora during the pollen zones identified at Dethlingen (Fig. 3) is briefly described below, whereas a summary of the characteristics of each pollen zone is given in Table 1.

##### 3.2.1. PZ VII (33.68–29.15 mbs)

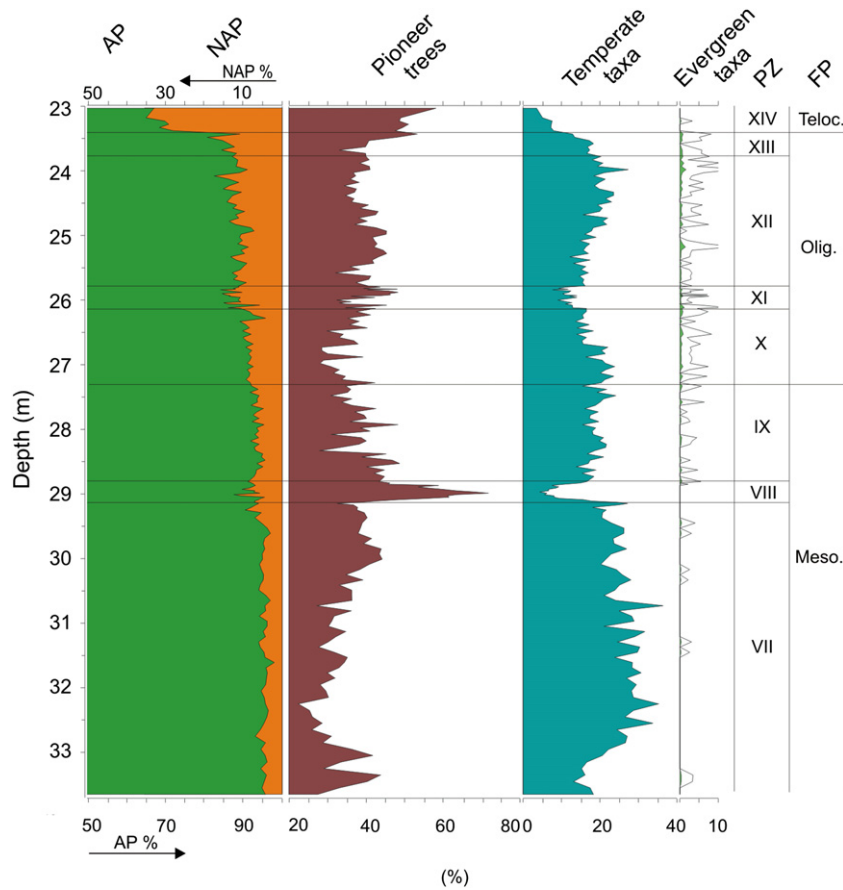
The lowermost part of the record from Dethlingen can be correlated to PZ VII from Munster–Breloh. This zone is characterised by a strong increase in *Taxus* from ~2% to an average of ~10% (with maximum percentages as high as ~20%). *Picea* and *Corylus* are also characteristic taxa, accounting for 3–5% and 10%, respectively. *Betula* (up to 10%), *Quercus* (up to 5%), and Ericaceae (3–5%) are also abundant. *Carpinus*, mixed oak forest elements such as *Fraxinus*, *Ulmus*, and *Tilia*, as well as Poaceae and *Rumex* are present in this zone, albeit in low abundances.

##### 3.2.2. PZ VIII (29.15–28.73 mbs)

The onset of PZ VIII is clearly marked by the abrupt decline in pollen of temperate taxa and the increase in pollen of pioneer trees (*Pinus* and *Betula*), grasses, and herbs. The decline of temperate taxa is clearly reflected in the curves of *Taxus*, *Corylus*, and *Quercus* (Fig. 3). The abundance of *Picea*, *Alnus*, and Ericaceae pollen also declines. This zone has been described as the older regressive phase in vegetation development at Munster–Breloh, with peak abundances of *Pinus* and *Betula* (Müller, 1974).

##### 3.2.3. PZ IX (28.73–27.28 mbs)

This zone is characterised by the increase in percentages of *Corylus*, *Quercus*, *Picea*, and Ericaceae pollen to levels attained prior to the regressive vegetation phase of PZ VIII. *Taxus*, however, remains at much lower percentages throughout the remainder of the Dethlingen record. *Alnus*, which is the dominant tree pollen of



**Fig. 4.** Percentages of selected groups of taxa plotted against depth (meters below the present-day soil surface). (i) Pioneer trees, including *Pinus* and *Betula*; (ii) Evergreen taxa, including *Buxus*, *Ilex*, and *Hedera*; (iii) Temperate taxa, including the evergreen taxa of group (ii) and *Abies*, *Acer*, *Carpinus*, *Celtis*, *Corylus*, *Fagus*, *Fraxinus*, *Ostrya*, *Pterocarya*, *Quercus*, *Taxus*, *Tilia*, and *Ulmus*. Pollen zones have been adopted from the Holsteinian pollen stratigraphy of Munster–Breloh following Müller (1974). (AP) Arboreal Pollen; (NAP) Non-arboreal pollen; (PZ) Pollen Zone; (FP) Forest phase; (Meso.) Mesocratic phase; (Olig.) Oligocratic phase; (Teloc.) Telocratic phase.

PZ IX, shows a slight increase towards the top of the zone, whereas relative *Pinus* pollen abundances gradually decline. The zone shows an increase of *Carpinus* percentages, the regular presence of *Abies* and the sporadic occurrence of *Ilex* and *Hedera* pollen.

#### 3.2.4. PZ X (27.28–26.18 mbs)

During this zone, *Corylus* and *Picea*, which are both characteristic for PZ VII–IX, decline to very low pollen percentages (<3 and ~1%, respectively). *Carpinus* reaches peak values and *Abies* exhibits an increase with maximum abundances occurring in the upper part of the zone. Pollen grains from *Ilex* are almost permanently present. *Alnus* percentages reach their maximum, and *Betula* percentages increase towards the top of the zone. Pollen Zone X also marks the upper limit for the regular presence of *Tilia*; higher up in the record, pollen of this taxon occur only sporadically. In contrast, pollen of herbs, such as *Rumex*, increase in abundance during this zone and are subsequently frequently recorded until the end of the Holsteinian interglacial.

#### 3.2.5. PZ XI (26.18–25.78 mbs)

This pollen zone comprises the younger regressive phase in vegetation development as described at Munster–Breloh (Müller, 1974). The onset of PZ XI is marked by the abrupt decline in *Carpinus*. Smaller declines in *Abies* and *Alnus* can be also observed; the latter, however, reaches an abundance peak during the middle part of the zone. *Betula* pollen percentages increase (max. 18%), whereas *Pinus* percentages remain nearly stable and even exhibit a transient

decline during the lower part of PZ XI (Fig. 3). As in PZ X, *Quercus*, *Taxus*, and *Picea* remain at low levels. Remarkably, the evergreen taxa *Ilex*, *Buxus*, and *Hedera* are not affected during this regressive phase. The abundances of Ericaceae, Poaceae, and *Rumex* pollen as well as of a variety of herb taxa increase, leading to non-arboreal pollen (NAP) percentages as high as 16% (Fig. 4).

#### 3.2.6. PZ XII (25.78–23.78 mbs)

This zone is marked by the increase in *Quercus* pollen percentages to peak values throughout the Dethlingen record; *Abies* percentages reach 5%. The percentages of *Carpinus* pollen also increase, but do not reach the level attained prior to the regressive phase of PZ XI. *Buxus* is recorded frequently, whereas *Ilex* pollen occurs only sporadically. Finally, *Pinus*, Ericaceae, and a variety of NAP exhibit a slight increasing trend throughout PZ XII, while *Alnus* gradually declines (Fig. 3).

#### 3.2.7. PZ XIII (23.78–23.38 mbs)

This zone shows the first occurrence of *Pterocarya*, *Fagus*, and *Celtis*. *Buxus* pollen remains frequent. However, the abundances of pollen of other temperate trees such as *Quercus*, *Abies*, but also *Alnus*, decline strongly. *Pinus* and *Betula* pollen increase towards the end of the zone, whereas Poaceae percentages increase only gradually.

#### 3.2.8. PZ XIV (23.38–23.03 mbs)

The percentages of Ericaceae and Poaceae pollen increase strongly, reaching up to 10% and 18%, respectively. Conifer taxa such

as *Abies* and *Taxus*, most of the deciduous trees (including *Alnus*, *Carpinus*, and *Quercus*), and evergreen taxa (*Ilex*, *Buxus*, and *Hedera*) decline to minimum values during PZ XIV, whereas *Pinus* pollen remains dominant and *Betula* further increases, reaching values of up to 15%.

## 4. Discussion

### 4.1. Vegetation dynamics and climate variability

The Dethlingen pollen record reflects a mixed temperate forest that was temporarily replaced by boreal (during PZ VIII) and sub-temperate forests (during PZ XI) (see Table 1). These two short phases, described as older and younger regressive phases in vegetation development, are discussed in detail in Section 4.2.

The forest in the lower and middle part of the record (i.e., PZ VII–IX) is marked by constant abundances of temperate trees and shrubs (~20–25%; Fig. 4), such as *Taxus*, *Corylus*, *Quercus*, and *Carpinus* (Fig. 3), suggesting temperate climatic conditions (Dahl, 1998). However, the occurrence of *Picea* (Fig. 3), which has a competitive advantage when growing in climates with a rapid transition between winter and summer (Dahl, 1998), suggests increased seasonality during the older stages of the Holsteinian. The temperate fern *Osmunda* is present especially in the upper parts of PZ VII–IX (Fig. 3). Based on the distribution and ecology of *Osmunda regalis* during the present interglacial in Europe (e.g., Birks and Paus, 1991; Dahl, 1998; Landi and Angiolini, 2008), we may assume that this interval was characterised by high humidity and soil moisture, and a mean temperature of the coldest month above  $-4^{\circ}\text{C}$ . During the younger stages of the Holsteinian interglacial (i.e., PZ X–XIII), sub-Atlantic and Atlantic taxa reached the surroundings of the Dethlingen palaeolake and became part of the mixed temperate forest. This interval is characterised by the development of the *Carpinus–Abies* phase after the decline of *Picea* (Fig. 3) and the expansion of evergreen taxa (Fig. 4). Such vegetation changes point to a climatic transition towards warm or mild winter conditions with increased humidity (Turner, 1970) and higher precipitation (e.g., Zagwijn, 1996). During this interval (PZ X–XIII), the mixed temperate forest is characterised by considerable variability in vegetation dynamics in comparison to the older stages of the Holsteinian interglacial. Forest openings gradually expand after PZ X, as reflected by an increase of NAP from 8 to 15% (Fig. 4). Furthermore, variability in the abundances of the temperate taxa is indicated by gradual changing trends (Fig. 4). At first, during PZ X, a declining phase of the temperate taxa is concurrent with an increase in *Betula* and *Alnus* (Fig. 3). This trend reaches a minimum in the abundances of temperate taxa during the prominent younger regressive phase in vegetation development (PZ XI; Fig. 4). After this regressive phase, the temperate taxa exhibit an increase during PZ XII that is associated with maximum percentages of *Quercus*, *Abies*, and *Buxus* (Fig. 3). *Buxus* has present-day thermal limits of  $0^{\circ}\text{C}$  in January and  $17^{\circ}\text{C}$  in July, and requires, similar to *Abies*, high precipitation rates to grow (Zagwijn, 1996). Therefore, the increase in these temperate taxa suggests that the warmest conditions were reached during the later stages of the Holsteinian, with the peak warmth being accompanied by very high humidity. In the upper part of PZ XII the temperate taxa decline as they also do during PZ XIII. Finally, the mixed temperate forest is replaced by pioneer trees (*Pinus* and *Betula*) growing in open habitats (PZ XIV; Table 1). During this uppermost pollen zone the temperate taxa reach minimum values of ~6.5%, whereas pioneer trees and NAP increase, accounting for ~50–60% and ~30–35% of the pollen sum, respectively (Fig. 4).

The vegetation succession at Dethlingen as described above reflects the trajectory from the mesocratic, oligocratic, to the telocratic forest phase of a glacial–interglacial cycle (Birks, 1986;

Andersen, 1994; Birks and Birks, 2004). The mesocratic phase is characterised by the development of temperate forests, the absence of shade-intolerant species (e.g., *Juniperus*), and productive lakes (Birks, 1986; Andersen, 1994). These characteristics are prominent within PZ VII–IX, which show the highest percentages of temperate taxa (Table 1; Fig. 4) associated with an expansion of shade-tolerant taxa (e.g., *Corylus*; Fig. 3). At the same time, maximum percentages of *Pediastrum* as well as high diatom productivity point to elevated trophic conditions in the Dethlingen palaeolake. The oligocratic phase has been described as a retrogressive interglacial phase characterised by decreasing forest cover, declining biomass and lake productivity (Birks, 1986; Andersen, 1994). This forest phase is represented at Dethlingen by PZ X–XIII coinciding with the *Carpinus–Abies* phase (Table 1). During that time, the increased percentages of NAP suggest a slight forest opening around Dethlingen, whereas a decline in lake productivity is mirrored by decreasing *Pediastrum* abundances in PZ X (Fig. 3). According to the correlation of the Holsteinian interglacial with the Hoxnian (England) and Mazovian (Poland) interglacials (Geyh and Müller, 2007), the *Carpinus–Abies* phase of the Holsteinian is recognisable across central and northwestern Europe. Comparable slight forest openings occurred during the *Carpinus–Abies* phase of the Hoxnian (local PZ HolIII; e.g., Turner, 1970; Coxon, 1985; Thomas, 2001) and the Mazovian (local PZ 7; e.g., Bińka et al., 1997). Thus, the slight forest opening at Dethlingen does not result from a change in local environmental conditions, but rather represents a supraregional signal marking the forest development during the oligocratic phase.

The causes of vegetation changes during the oligocratic phase have been attributed to impoverishment of soils (Andersen, 1994). It is conceivable that such an impoverishment resulted from an increased limitation of P relative to N often associated with reductions in litter decomposition rates and changes in the microbial assemblages (e.g., Wardle et al., 2004). As the vegetation succession during the oligocratic phase is not climatically driven, the opening of the forest and the decline in arboreal pollen (AP) percentages at Dethlingen (Fig. 4) can indeed coincide with the warmest temperatures and the very humid conditions as reflected by the peak abundances of *Buxus*, *Abies*, and *Quercus* (PZ XII; Fig. 3). Although *Quercus* is usually a prominent forest element of the mesocratic phase (Birks, 1986), it reaches its maximum abundance during the oligocratic phase of the Holsteinian in central Europe. The tree was able to take advantage of the warm climate in combination with the opening of the forests as it is less shade-tolerant than *Corylus* and also more tolerant than *Carpinus* when growing on poor soils (Birks, 1986; Ellenberg, 1988). Finally, the telocratic phase, which is generally characterised by declining temperatures and increasingly open vegetation during the terminal stage of interglacials (Birks, 1986; Andersen, 1994), is represented in the uppermost part of the Dethlingen record (PZ XIV; Table 1), indicating a transition towards glacial conditions.

In summary, the overall vegetation composition as reflected by the development of mixed temperate forests at Dethlingen suggests a general prevalence of mild climatic conditions during the Holsteinian. The expansion of sub-Atlantic and Atlantic floral elements during the younger parts of the interglacial (i.e., PZ X–XIII; Table 1) and the decline of boreal elements that characterise the older stages of the interglacial (i.e., PZ VII–IX; Table 1) suggest warmer winters and increased humidity. However, both abrupt and gradual changes in the abundances of the temperate plant taxa point to considerable climatic variability during the Holsteinian interglacial.

### 4.2. Short-term regressive phases

The Holsteinian pollen record from Dethlingen exhibits two prominent regressive phases in vegetation development (PZ VIII

and XI). Based on varve counts from palaeolake sediments from the Lüneburger Heide region, both the two phases have a duration of c. 300 years (Müller, 1974). Although they are marked by a short-term forest opening with the expansion of pioneer trees and a decline of temperate taxa (Table 1), a close inspection reveals strong differences between the two phases. These differences relate to the magnitude of the expansion of pioneer trees, the occurrence of specific taxa with regard to their frost tolerance, and the rates and intensity of vegetation changes.

#### 4.2.1. Older regressive phase (PZ VIII)

The older regressive phase in vegetation development is clearly defined by the abrupt decline in temperate taxa and the pronounced increase in pioneer trees (Fig. 4). The percentages of temperate taxa decline to the lowest value (4.5%) throughout the temperate stage of the interglacial. Pioneer tree abundances reach peak values of 72% at the expense of the temperate taxa. The declines of *Taxus* and *Corylus* (Fig. 3), which are sensitive to severe and prolonged frost (e.g., Tallantire, 2002; Thomas and Polwart, 2003) suggest particularly low winter temperatures during this regressive phase. In addition, considering the coeval decline in *Picea* (Fig. 3), which tolerates low winter temperatures, a climatic shift towards drier conditions is also plausible.

A clear distinction of two sub-phases within PZ VIII can be made based on the succession of pioneer trees. *Pinus* peak abundances are recorded during the declining stage of the temperate taxa, whereas the expansion of *Betula* coincides with the onset of the recovery of temperate taxa during the middle part of PZ VIII (Fig. 3). This suggests that the expansion of *Pinus* represents the primary vegetation response to the cooling (and possibly drying), whereas the expansion of *Betula* would mark the onset of subsequent warming, with this tree expanding as a pioneer during the forest recovery.

#### 4.2.2. Younger regressive phase (PZ XI)

The younger regressive phase in vegetation development punctuates a gradual decline in temperate taxa that started in PZ X (Fig. 4). Although this phase is marked by a final abrupt decline and a short recovery, it seems to be centred within a long-term vegetation change that includes the time covered by PZ X–XII. During this interval, the percentages of temperate taxa decrease to ~8% (Fig. 4). The phase is marked by the abrupt decline in *Carpinus* and *Abies* (Fig. 3). The expansion of pioneer trees is mainly reflected by an increase in *Betula*; *Pinus*, in contrast, even shows a declining trend. The considerable changes in *Alnus* (Fig. 3) suggest fluctuations in the palaeolake level.

With regard to low temperature tolerance, pollen grains of several winter frost-sensitive taxa such as *Ilex*, *Buxus*, *Hedera*, and *Abies* occur throughout the younger regressive phase (Fig. 3). *Abies* and *Hedera* cannot tolerate mean winter temperatures below  $-4^{\circ}\text{C}$  and  $-2^{\circ}\text{C}$ , respectively, whereas *Ilex* and *Buxus* require mean winter temperatures above  $0^{\circ}\text{C}$  (Iversen, 1944; Zagwijn, 1996). It is therefore unlikely that the younger regressive phase was related to a substantial decline in mean winter temperatures, particularly given that *Buxus* seems to start immigrating at the onset of PZ XI (Fig. 3). The presence of winter frost-sensitive taxa together with the minimum of temperate taxa possibly suggests a lack of summer warmth, although changes in precipitation or other factors cannot be excluded.

#### 4.2.3. Comparison of the regressive phases

The two regressive phases in vegetation development (PZ VIII and XI) are both characterised by the replacement of temperate forest by pioneer trees, although this process is much more pronounced during the older regressive phase. The rates of vegetation change and the presence of frost-sensitive taxa provide

information on further differences between the two phases. They suggest that an abrupt onset of severe climatic conditions related to low winter temperatures, probably in combination with drier conditions, took place during the older regressive phase. In contrast, the younger regressive phase is possibly part of a long-term gradual trend of decreasing and subsequently increasing summer warmth.

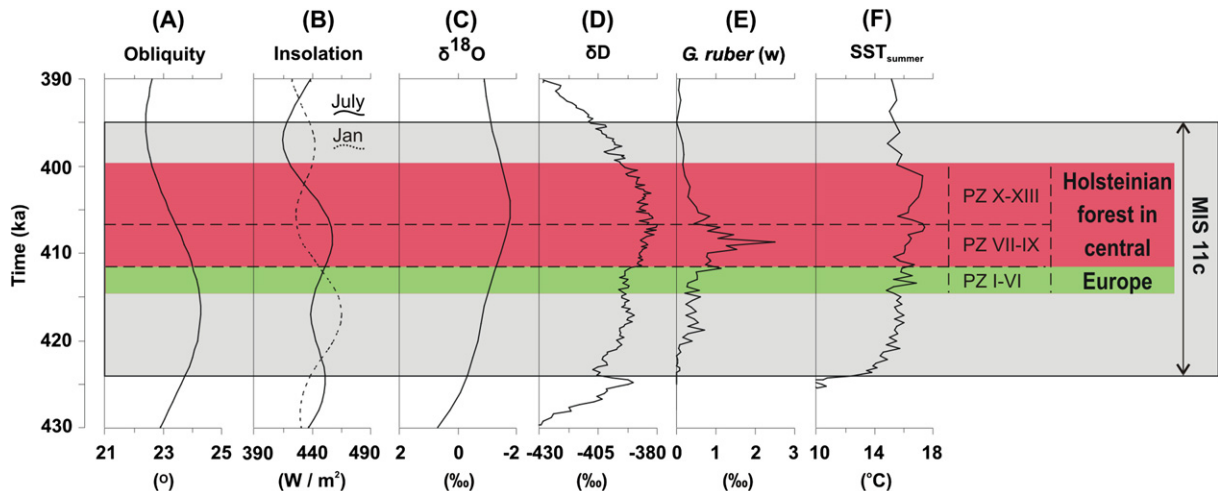
The comparison of Holsteinian pollen records from central and northwestern Europe provides information on the distribution of the two regressive phases. The older phase, identified by increased NAP and pioneer tree abundances before the establishment of the *Carpinus–Abies* phase of the Holsteinian interglacial, is detected in numerous records from central and northwestern Europe, e.g., Munster–Breloh (Müller, 1974) and Döttingen (Diehl and Sirocko, 2007) in Germany; Hoxne (West, 1956; Coxon, 1985), Marks Tey (Turner, 1970), and Quinton (Thomas, 2001) in England; and around Biała Podlaska in Poland (e.g., Krupiński, 1995; Bińka and Nitychoruk, 1995, 1996; Bińka et al., 1997) (Fig. 1). The younger regressive phase, however, which is associated with a decline in *Carpinus* and an expansion of pioneer trees within the *Carpinus–Abies* phase, has so far only been clearly evidenced in records from northwestern Germany, e.g., at Munster–Breloh (Müller, 1974), Gröbern–Schmerz (Eissmann, 2002), and Döttingen (Diehl and Sirocko, 2007) (Fig. 1). It seems possible that the occurrence of evergreen taxa during the younger regressive phase and the lack of high-resolution Holsteinian pollen data have yet precluded its detection in records from other geographic regions. Therefore, high-resolution pollen analyses are needed to better constrain its distribution in central and northwestern Europe.

Although the two regressive phases have been known for decades, their triggering mechanisms have remained poorly understood. Causes that have been proposed include fire or animal grazing (Turner, 1970) and volcanism (Diehl and Sirocko, 2007). However, given the nature of the vegetation changes and the supraregional distribution of the regressive phases, they may well have resulted from climate oscillations (Müller, 1974; Kukla, 2003). Such a scenario is strongly supported by our data. However, because the Dethlingen record indicates that the two phases exhibit different characteristics, it appears likely that they have been caused by different triggering mechanisms. The signature of the older phase is reminiscent of the imprint of the Holocene 8.2 kyr cold event on the vegetation in central and northern Europe (see e.g., Tinner and Lotter, 2001, 2006; Veski et al., 2004); thus, a relationship to a meltwater-forced slowdown of the North Atlantic circulation appears possible. However, as the phase took place ~6000 years after the onset of the Holsteinian interglacial (Müller, 1974), it remains to be explained how it could have been triggered within a period of low ice volume. Hence, a decrease in solar activity, as it has also been suggested for the 8.2 kyr and other events in the North Atlantic (Bond et al., 2001; Muscheler et al., 2004), may also be a possible explanation for the older regressive phase.

The younger regressive phase, in contrast, appears to be related to long-term, gradual changes in vegetation dynamics during the younger stages of the Holsteinian (PZ X–XII). Based on the duration of the pollen zones at Munster–Breloh (Müller, 1974), these long-term changes occurred over c. 4000 years. The trend in temperate taxa abundances and the long duration of the gradual changes suggest a connection to orbital forcing. However, the mechanism triggering such a short-term regressive phase under changing orbital boundary conditions remains unclear.

### 4.3. The Holsteinian interglacial and MIS 11

The absence of long, continuous terrestrial records in northwestern Europe and the lack of reliable absolute dates have led to



**Fig. 5.** Orbital parameters and climate proxy records plotted against time (ka) for MIS 11. (A) Obliquity and (B) Insolation at 65°N (Berger and Loutre, 1991); (C) SPECMAP curve (Imbrie et al., 1984) as proxy for global ice volume; (D) Deuterium ( $\delta D$ ) composition of ice from EPICA Dome C (Jouzel et al., 2007) as temperature proxy; (E) relative abundance of *G. ruber* (w) and (F) planktic foraminiferal-derived summer SST at Site M23414 (Fig. 1) in the North Atlantic (Kandiano and Bauch, 2007) plotted after the age model of Helmke et al. (2008). Grey area corresponds to MIS 11c according to SPECMAP (Imbrie et al., 1984). Green and red bars mark the suggested intervals of Holsteinian boreal and temperate forests, respectively, in central Europe (see Section 4.3 for details); pollen zones have been adopted from the Holsteinian pollen stratigraphy of Munster–Breloh following Müller (1974) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

conflicting views on the chronostratigraphic position of the Holsteinian interglacial (e.g., Reille et al., 2000; de Beaulieu et al., 2001; Tzedakis et al., 2001; Geyh and Müller, 2005). There is an ongoing debate as to whether the Holsteinian correlates with MIS 9 (Rowe et al., 1997; Eissmann, 2002; Geyh and Müller, 2005; Degering and Krbetschek, 2007; Meijer and Cleveringa, 2009) or MIS 11c (e.g., Turner, 1998; Rowe et al., 1999; Reille et al., 2000; Grün and Schwarcz, 2000; Tzedakis et al., 2001; Kukla, 2005; Nitychoruk et al., 2005, 2006; Müller and Pross, 2007; Preece et al., 2007; Ashton et al., 2008; Pawley et al., 2009). Moreover, studies on the British Isles of interglacial deposits displaying a Hoxnian/Holsteinian vegetational and faunal development may include stratigraphic units corresponding to sub-stages of both MIS 9 and 11 (Dowling and Coxon, 2001; Scourse, 2006; Roe et al., 2009). Circumventing the complexities connected to the stratigraphic position of terrestrial records for the Holsteinian interglacial, a land–sea correlation off Iberia (Fig. 1; Desprat et al., 2005) has provided the opportunity to directly compare the marine isotope record to terrestrial vegetation changes. These data support a correlation of the Holsteinian interglacial to MIS 11c. Given the significance of this direct land–sea correlation, we propose to place the Holsteinian interglacial forest development in central Europe into the chronological frame of MIS 11c (i.e., 423–395 ka BP) as proposed by SPECMAP (Fig. 5c; Imbrie et al., 1984).

Data from Antarctic ice cores indicate that peak warmth occurred towards the end of MIS 11c in contrast to more recent interglacials, including MIS 9, for which early peak warmth and continuous cooling are typical (Fig. 5d; EPICA, 2004; Jouzel et al., 2007). As already discussed in Section 4.1, the Holsteinian vegetation succession indicates peak warmth during the younger part of the interglacial, which is in agreement with the warming trend of MIS 11c rather than MIS 9.

Based on annually laminated sediment records from the Lüneburger Heide region (northern Germany), the Holsteinian interglacial forests in central Europe lasted for ~15–16 ka (Meyer, 1974; Müller, 1974), which is similar to the duration of the Holsteinian climatic optimum at Lake Ossówka (Poland)(Nitychoruk et al., 2005). However, the duration of MIS 11c has been estimated to be roughly twice as long, i.e., ~28 ka (Imbrie et al., 1984). If the spread of Holsteinian forests started with the onset of MIS 11c, the

end of the terrestrial interglacial would have been at ~408 ka BP. Such a scenario would, however, be inconsistent with the summer insolation maximum in the northern hemisphere (65° N; Berger and Loutre, 1991) and the climatic optimum of MIS 11c in the North Atlantic, which is centred between 416 and 398 ka BP (de Abreu et al., 2005; Kandiano and Bauch, 2007; Helmke et al., 2008). It therefore seems that in contrast to southern Europe, where Holsteinian forests spread soon after Termination V as documented off Iberia (Desprat et al., 2005), Holsteinian forests in central Europe expanded later, i.e., in the second half of MIS 11c, after 415 ka BP (Fig. 5).

In the following, we attempt to justify this scenario considering that the Atlantic heat transport is a key driving mechanism for European climate (e.g., Broecker, 1997; von Grafenstein et al., 1999). The pioneer boreal forests in central Europe have most probably expanded in response to the strengthening of the oceanic heat transport to the North Atlantic after 415 ka BP (Dickson et al., 2009). This forest phase prevailed for c. 3000–4000 ka (PZ I–VI; Meyer, 1974) before it was replaced by a temperate forest (PZ VII–XIII). The prevalence of temperate forests (PZ VII–XIII; Fig. 5) was most likely associated with the peak expansion of warm surface-water advection into the polar North Atlantic notably in the younger stages of MIS 11c (Bauch et al., 2000; Helmke and Bauch, 2003). The mesocratic forest phase (PZ VII–IX) is most probably related to the warming in the North Atlantic between ~411 and 407 ka as inferred by the relative abundance peak of *Globigerinoides ruber* (w) at Site M23414 (Fig. 5e; Kandiano and Bauch, 2007; Helmke et al., 2008). Hence, this forest phase coincides with the summer insolation maximum (Fig. 5b; Berger and Loutre, 1991), low global ice volume (Fig. 5c; Imbrie et al., 1984), and highest temperatures in Antarctica during MIS 11c (Fig. 5d; Jouzel et al., 2007). As already mentioned in Section 4.1, the oligocratic forest phase (PZ X–XIII) reflects peak warming during the younger Holsteinian. If correct, the maximum expansion of the summer-warmth-requiring trees during this interval, such as *Quercus* and *Buxus* (Fig. 3), was related to the continuously increasing summer sea surface temperature (SST) in the North Atlantic (Fig. 5f; Kandiano and Bauch, 2007; Helmke et al., 2008). In addition, the maximum expansion of evergreen trees (Fig. 4), such as *Buxus* and *Ilex*, was favoured by the decreasing seasonality as inferred by the decline in summer



insolation and the increase in winter insolation during that time (Fig. 5b; Berger and Loutre, 1991). The decline of the Holsteinian forest (upper PZ XII–XIII) in central Europe should hence be placed after ~401 ka BP when the North Atlantic summer SST declined (Fig. 5f; Kandiano and Bauch, 2007; Helmke et al., 2008); the telocratic phase (PZ XIV) should coincide with the summer insolation minimum at ~397 ka BP (Fig. 5b) that also terminated the interglacial vegetation successions in Praclaux, France and Tenaghi Philippon, Greece (Müller and Pross, 2007).

## 5. Conclusions

A new high-resolution palynological record from Dethlingen, northern Germany, provides evidence for climatic variability during the Holsteinian interglacial. Our data suggest decreasing seasonality and increasing warmth and precipitation towards the younger stages of the interglacial. The nature and tempo of this climatic change supports a correlation of the Holsteinian interglacial with MIS 11c, as the latter, in contrast to MIS 9, shows peak warmth at the end of the warm period. Considering that the Atlantic heat transport strongly influences vegetation development in central Europe, it is conceivable that the 15-ka-long period of Holsteinian forest development in central Europe is coeval with the second half of MIS 11c.

The temperate stage of the Holsteinian interglacial was interrupted by two short (c. 300 years long) regressive phases of vegetation development characterised by boreal and sub-temperate forests. The decline in temperate taxa and the expansion of pioneer trees during these phases, along with the observation that these phases occur supraregionally across central and northwestern Europe, suggest climatic forcing as the underlying mechanism. With regard to the pollen signatures of the two phases, it seems plausible that they were caused by different triggering mechanisms. For the older phase, a slowdown of the North Atlantic circulation and/or decreasing solar activity are the most likely driving forces.

Our results underscore the need to elucidate the causes of the two vegetation regressive phases in order to better understand the effect of potentially analogous abrupt events during the present interglacial. The high-resolution Dethlingen pollen record provides a significant contribution in this direction; its interpretation will be further refined through future investigations of additional high-resolution, multi-proxy data and the development of a varve chronology with annual time resolution.

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