The nature of MIS 3 stadial–interstadial transitions in Europe: New insights from model–data comparisons

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A B S T R A C T

15 abrupt warming transitions perturbed glacial climate in Greenland during Marine Isotope Stage 3 (MIS 3, 60–27 ka BP). One hypothesis states that the 8–16 °C warming between Greenland Stadials (GS) and Interstadials (GI) was caused by enhanced heat transport to the North Atlantic region after a resumption of the Atlantic Meridional Overturning Circulation (AMOC) from a weak or shutdown stadial mode. This hypothesis also predicts warming over Europe, a prediction poorly constrained by data due to the paucity of well-dated quantitative temperature records. We therefore use a new evidence from biotic proxies and a climate model simulation to study the characteristics of a GS–GI transition in continental Europe and the link to enhanced AMOC strength. We compare reconstructed climatic and vegetation changes between a stadial and subsequent interstadial – correlated to GS15 and GI14 (~55 ka BP) – with a simulated AMOC resumption using a three-dimensional earth system model setup with early-MIS 3 boundary conditions. Over western Europe (12°W–15°E), we simulate twice the annual precipitation, a 17 °C warmer coldest month, a 8 °C warmer warmest month, 1300 °C-day more growing degree days with baseline 5 °C (GDD5) and potential vegetation allowing tree cover after the transition. However, the combined effect of frequent killing frosts, ~20 mm summer precipitation and too few GDD5 after the transition suggest a northern tree limit lying at ~50°N during GI14. With these 3 climatic limiting factors we provide a possible explanation for the absence of forests north of 48°N during MIS 3 interstadials with mild summers. Finally, apart from a large model bias in warmest month surface air temperatures, our simulation is in reasonable agreement with reconstructed climatic and vegetation changes in Europe, thus further supporting the hypothesis.

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glacial climate conditions in the North Atlantic region, and possibly, most of the Northern Hemisphere (Cortijo et al., 1997; Curry and Oppo, 1997; Wang et al., 2001; Sánchez Goñi et al., 2002; Hemming, 2004; Weldeab et al., 2007).

A hypothesis for a physical mechanism explaining the above changes during Greenland Stadial to Interstadial (GS–GI) transitions has originally been put forward by Broecker et al. (1985). The Atlantic Meridional Overturning Circulation (AMOC) shifted from a shutdown or weak stadial mode to a strong interstadial mode. Warming in the mid- and high-latitudes of the North Atlantic region is then caused by an enhanced northward oceanic heat flux. This hypothesis is supported by numerous modelling studies in which a pre-industrial, present-day or glacial Atlantic Ocean circulation state is perturbed by positive and negative freshwater fluxes, resulting in climate anomalies that resemble the proxy-based evidence (e.g. Manabe and Stouffer, 1988; Ganopolski and Rahmstorf, 2001; Ganopolski, 2003; Shaffer et al., 2004; Flückiger et al., 2006; Kageyama et al., 2010). However, recent reviews on abrupt glacial climate change (Clark et al., 2007; Clement and Peterson, 2008) highlighted that further validation of this hypothesis requires a better understanding of the continental climate response to GS–GI transitions.

In this paper, we therefore study in detail the climate response to a rapid glacial AMOC resumption over the European continent, using both available terrestrial palaeorecords of environmental change and modelling results. Europe’s proximate position to the core region of ocean circulation change makes it a powerful region to analyse the continental response to DO events and HEs (e.g. Flückiger et al., 2008). Three factors have impeded a thorough study of this crucial issue.

Firstly, well-dated, high-resolution, continuous terrestrial records of abrupt glacial environmental changes in Europe were scarce until very recently (as reviewed among others by Huijzer and Isarin, 1997; Voelker, 2002; Vandenberghe et al., 2004). A number of reasons explains this scarcity, including discontinuous sedimentation, low temporal resolution, poor age control and difficulty to infer quantitative climate information from proxies (Guiot et al., 1989; Kasse et al., 2003; Vandenberghe et al., 2004; Bohncke et al., 2008). Conversely, several such records have been produced in recent years in Europe, though spatio-temporal palaeodata coverage of MIS 3 interval over Europe remains poor (see Table 1b). In Fig. 2b; e.g. Thouveny et al., 1994; Allen et al., 1999; Rousseau et al., 2002; Genty et al., 2003; Kasse et al., 2003; Sirocko et al., 2005; Engels et al., 2008a; Wohlfarth et al., 2008; Margari et al., 2009). Keeping those obstacles in mind, we are nevertheless able to test the ability of a three-dimensional coupled climate model to reproduce reconstructed climatic changes over a GS–GI transition in Europe.
Secondly, previously published model–data comparisons investigating abrupt glacial warming transitions over Europe used atmospheric circulation models which lack a dynamical oceanic component (Renssen and Isarin, 1997; Renssen et al., 2000; Barron and Pollard, 2002; Pollard and Barron, 2003). These studies could not address the role of AMOC shifts in abrupt climate change. Rather, they tried to reproduce as closely as possible the reconstructed climate and vegetation changes across Europe during the Younger Dryas cold episode (Renssen and Isarin, 1997; Renssen et al., 2000) and cold and mild intervals during MIS 3 (Barron and Pollard, 2002; Pollard and Barron, 2003). The latter studies found that MIS 3 interstadials were probably characterised by mild, near-present-day summer temperatures and relatively humid conditions over large parts of Europe, as also indicated by biotic proxies (e.g. Coope et al., 1997). However, Alfano et al. (2003) could not align these climatic conditions with the absence of evidence of forest growth northwards of ~50° N (Huntley et al., 2003). Moreover, assuming that MIS 3 was characterised by two climate states only, Barron and Pollard (2002) and Alfano et al. (2003) compared their simulations to low-resolution records of either interstadials or stadials defined locally and mostly with poor chronological constraints (e.g. van der Hammen et al., 1967; Schlüchter et al., 1987; Kolstrup, 1991; Vandenbergh, 1985; Huijzer and Vandenbergh, 1998; van der Hammen et al., 1967; Caspers and Freund, 2001; Engels et al., 2008a).}

proxies (Coope et al., 1997; Bos et al., 2001; Helmens et al., 2007). To consistently compare model results and palaeorecords, one should look at variables that characterise seasonality (Flückiger et al., 2008). This is exemplified by reviews of glacial abrupt climate change by Renssen and Bogaart (2003) and Denton et al. (2005), suggesting that warming in the North Atlantic region from GS to GI was stronger in winter than in summer. Flückiger et al. (2008) confirmed that, in their model, strongest warming in the North Atlantic region took place in winter, whereas spring warming dominated on the Eurasian continent. Since biota are mostly sensitive to temperature changes during the growing season, limited summer warming may help explain why compelling evidence of warming between stadials and interstadials remained elusive from the terrestrial palaeoclimate archive of Europe.

In the present study, we aim to circumvent these shortcomings of previous studies by performing a model–data comparison over Europe using seasonal climate variables to which biota are physiologically sensitive (presented by Van Meerbeeck et al., 2010, hereinafter referred to as VM2010). New, high-quality terrestrial palaeoclimate records covering the GS15–GI14 transition time span (around 55 ka BP) are compared to a rapid glacial AMOC resumption simulated with the LOVECLIM atmosphere–ocean–vegetation model under early-MIS 3 boundary conditions. Our transient experiment includes a freshwater scenario designed to mimic an HE and a subsequent ice rafting decline near the end of a stadial.

We selected the GS15–GI14 transition for three reasons. First, lasting about 5 ka in Greenland, GI14 was probably long enough for biota and geomorphology to respond to warming (soil formation, species migration, etc.). Therefore, the likelihood of GI14 being represented in high-resolution palaeoenvironmental records is reasonably high. Second, despite an age range beyond the current limit of reliable 14C-dating, chronology of this transition is regionally relatively well constrained with the North Atlantic Ash Zone 2 tephra (deposited at ~ 56 ka BP) being contemporaneous with early parts of GS15 (Austin et al., 2004). Third, this study is a contribution to the RESOLUTION project (Wohlfarth et al., 2007), in which the GS15–GI14 transition was selected as a key period.

2. Methods
2.1. Model

We used the three-dimensional coupled earth system model of intermediate complexity LOVECLIM 1.0 (Driesschaert et al., 2007). In this study, we only use three coupled components, namely the atmospheric ECBilt and oceanic CLIO components, and the vegetation module VECODE.

ECBilt is a quasi-geostrophic, T21 spectral model, with three vertical levels (Opsteegh et al., 1998). Due to its spectral resolution corresponding to a horizontal ~ 5.6° × ~ 5.6° resolution, its surface topography is simplified. Its parameterisation scheme allows for fast computing and includes a linear longwave radiation scheme. ECBilt contains a full hydrological cycle, including a simple bucket model for soil moisture over continents, and computes synoptic variability associated with weather patterns. Precipitation falls in the form of snow when surface air temperatures fall below 0 °C. CLIO is a primitive-equation three-dimensional, free-surface ocean general circulation model coupled to a thermodynamical and dynamical sea-ice model (Goosse and Fichefet, 1999). CLIO has a realistic bathymetry, a 3° × 3° horizontal resolution and 20 vertical levels. The free-surface of the ocean allows introduced freshwater fluxes to change sea level (Tartarinville et al., 2001). In order to bring precipitation amounts in ECBilt–CLIO closer to observations, a negative precipitation–flux correction is applied over the Atlantic and Arctic Oceans. This flux is reintroduced in the North Pacific. The climate sensitivity of LOVECLIM 1.0 to a doubling of atmospheric CO₂ concentration is 1.8 °C, associated with a global radiative forcing of 3.8 W m⁻² (Driesschaert, 2005). The dynamic terrestrial vegetation model VECODE computes the surface fraction of each land grid cell covered by herbaceous plants, trees and desert fractions (Brockin et al., 1997) and is coupled to ECBilt through the surface albedo (Driesschaert, 2005).

LOVECLIM 1.0 produces a reasonably realistic modern climate (Driesschaert, 2005) and an LGM climate generally consistent with data (Roche et al., 2007). Nevertheless, in a control climate forced with pre-industrial boundary conditions, a systematic warm bias of annual mean surface air temperatures of globally about +2 °C compared to a 1971–2000 climatology is found in the model (Driesschaert, 2005). Important for a model–data comparison focusing on Europe, is that the warm bias on this continent is concentrated on peak summer in present-day climate. This is indicated by a difference of regionally up to +8 °C versus ~ 0 °C for the warmest, respectively coldest 30-day period of the year between our present-day simulation using 1961–1990 forcings and the measured 1961–1990 climatology. Finally, it is noteworthy that previous modelling efforts of glacial climate change using this or earlier versions of LOVECLIM compared their glacial simulations to a simulated pre-industrial climate to make a first order reduction of
the systematic warm bias (e.g. Roche et al., 2007; Flückiger et al., 2008). We follow this method and compare reconstructed and simulated temperature anomalies to present-day.

2.2. Experimental design

For a full description of the experimental design of the transient simulation of glacial abrupt warming under realistic MIS 3 boundary conditions, the reader is referred to VM2010. Here we briefly summarise its setup.

The model was run to equilibrium under constant climate forcings characteristic of stadials during MIS 3 (called MIS 3-sta) by Van Meerbeeck et al. (2009). The following forcings were used to simulate the MIS 3-sta climate state: (1) atmospheric greenhouse gases (GHGs) and dust concentrations — 200 ppmv CO₂, 450 ppbv CH₄, 220 ppbv N₂O and 0.8 times the LGM dust forcing calculated by Claquin et al. (2003) — typical of MIS 3 stadials (2) a best-estimate MIS 3 ice sheet topography, (3) orbital parameters between 56 ka BP and 54.6 ka BP were taken fromBerger (1978). The MIS 3 ice sheet topography and the LGM dust forcing values, now kept constant at 56 ka BP values — 211 ppmv CO₂, 494 ppbv CH₄, 257 ppbv N₂O and 0.9 times LGM dust forcing of Claquin et al. (2003). In addition, a freshwater flux of +0.07 Sv (1 Sv = 1 Sverdrup = 10⁶ m³ s⁻¹) was imposed on the sea surface over the mid-latitudes of the North Atlantic and +0.08 Sv over the Nordic Seas (see VM2010). We kept the other forcings unchanged. While the small differences in GHGs and dust concentrations did not modify the climate significantly, the freshwater forcing caused a strong reduction in the AMOC strength.

From this point, we started a 1400-year transient simulation, applying realistic transient forcings for (1) atmospheric CO₂, CH₄ and N₂O concentrations (Indermühle et al., 2000; Flückiger et al., 2004); (2) radiative forcing from atmospheric dust concentrations; (3) orbital parameters between 56 ka BP and 54.6 ka BP were taken from Berger (1978). The MIS 3 ice sheet topography and the LGM land—sea mask were unchanged. The freshwater flux was first kept constant at 0.15 Sv for 400 more years, then increased for 400 years to 0.21 Sv over the mid-latitude North Atlantic and decreased to 0.04 Sv over the Nordic Seas and finally decreased to ~0.2 Sv equally distributed between the two areas for the rest of the simulation. The positive freshwater flux of 0.25 Sv in total was imposed to obtain a cold state with nearly shutdown AMOC. This cold state (model years 1201–1300) was designed to mimic GS15 which coincided with HE5.2 (Rashid et al., 2003). Subsequently, the negative flux would accelerate AMOC recovery into a moderate state with slightly more vigorous AMOC than in MIS 3-sta. The moderate state (model years 1701–1800) should mimic the warmest part of GI14 in Greenland, with a simulated annual mean surface air temperatures warming from the cold to the moderate state of 10 °C there (see Supplementary e-information for a thorough model evaluation).

The timing of the transient forcing scenario was aligned with the GS15—GI14 transition age on the ss09sea time scale, thus heralding a simulated rapid glacial warming transition occurring at ~55.2 ka BP (NorthGRIP-Members, 2004). If the experiment were aligned to the GICC05 time scale, the transition would move to ~54.3 ka BP. However, only the timing of orbital forcing is independent from the ss09sea time scale in our experiment and thus modestly change when aligning the experiment to GICC05 (Berger, 1978). Therefore, the ~900-year time shift of the GS15—GI14 transition between the two time scales should not result in significant differences in simulated climate or ocean circulation.

2.3. Palaeodata

We compare the simulated climate of the cold state and the moderate state to the terrestrial records from Europe that register glacial abrupt environmental changes during the GS15—GI14 transition. For such records to be included in our analysis, at least one radiocarbon, U/Th or OSL date calculated to lie within the time interval 56—48 ka BP must have been published (Aside from GS15 and GI14, this interval includes the short and low amplitude GS14 and GI13, which may not have been distinguished from GI14 in Europe.) Furthermore, that date/those dates may not be formally rejected in subsequent publications. Though by no means a guarantee that the reconstructed interval contains the GS15—GI14 transition, this protocol was adopted within the RESOLuTION project to acknowledge the time-varying expression of individual transitions in Europe during MIS 3 (e.g. Allen et al., 1999; Sánchez Goñi et al., 2008). One exception to the protocol is made for the Lago Grande di Monticchio record from southern Italy, which provides a detailed chronology based on annual varve counts to calculate accumulation rates or, where laminations cannot be distinguished, apply the calculated rates from those varves (Allen et al., 1999). Additional confidence in the Monticchio chronology is provided by a tephra layer — an in situ at depth core, dating to accumulation age 56.25 ka BP — which was ⁴⁰Ar/³⁹Ar dated to 56 ± 4 ka BP. In this record, the interval surrounding a <200 year warming transition dated to ~50 ka BP has been matched to the GS15—GI14 interval (Allen et al., 2000).

Following the above protocol of data inclusion, 17 records of climatic and vegetation change in Europe are found, though with widely varying chronological reliability (see Table 1a and Fig. 2). The most reliable chronology is found in the Kleegrunen cave speleothem record of the Austrian Alps, in which the GS15—GI14 transition has been accurately dated to ~54.5 ± 0.25 ka BP using U/Th dating (see Fig. 1b; Spötl et al., 2006). In second place are three marine cores from the continental margin of Iberian Peninsula, offering continuous high resolution SST records as well as simultaneous pollen assemblage changes reflecting the temporal evolution of vegetation on land (see e.g. Sánchez Goñi et al., 2008). In third place is the Monticchio record, followed by the radiocarbon-dated, continuous high-resolution pollen record from the Greek island Lesvos. In this record, the chronology for the GI14 interval is relatively well constrained with deposition of the ‘green tuff’ tephra layer ⁴⁰K/³⁹Ar dated to 51–45 ka BP (see Margari et al., 2009, and references therein). In fifth place is the chironomid record from the Eiffel Maar lake where sedimentation was (nearly) continuous throughout the last glacial—interglacial cycle (Engels et al., 2008a). The grey scale stack record, distinctly correlated with δ¹⁸O in the Greenland ice cores, together with 6 AMS radiocarbon dates, provides a relatively reliable chronology of the rapid warming transition (Sirocko et al., 2005). The other records — mainly representing an interstadial — have been at least radiocarbon dated to a 56–45 ka BP interval, which is unreliable since most ages lie beyond the dating limit of about 47 ka BP. Nevertheless, for the Vrugum, Oerel, Nochten, Netherlands, Füramoos, Niederweningen and Gossau sites (see Table 1a) we converted published ¹³C-dates into calendar years and estimated to which GI the recorded interval could correspond (not shown). For Nochten and Sokli, OSL dates within the 56–45 ka BP interval provide additional chronological constraints, although dating uncertainties remain too large to ascribe the recorded interstadial(s) to the GI14 time interval. Of special concern is the Reichwalde site, for which preliminary OSL dates suggest an interval older than GS15—GI14. Therefore, although often used in this manuscript, the climate reconstructions pertaining to the Reichwalde interstadial should be considered with caution when comparing to the other records and
to the model results. For the remaining records, we follow the age interpretation given for the respective publications (see Table 1a and Fig. 2) and use these records in our comparison under the assumption that registered stadial or interstadial climate and vegetation is representative for early-MIS 3.

3. Comparison of simulated and reconstructed d stadial and interstadial climate in Europe

To investigate if Europe’s palaeoenvironmental archive supports the AMOC resumption hypothesis, we compare reconstructed near-surface climatic and vegetation changes between intervals correlated to GS15 and GI14 with simulated changes between the cold and the moderate state over the land area stretching from 35° N to 72° N and 12° W to 50° E. The 17 terrestrial sites with relevant proxy records are found in Table 1a and a summary of the reconstructed palaeo-environment is shown in Table 3. Table 1b consists of 17 terrestrial sites with relevant proxy records in Table 1a with the exceptions of Brindisi, Italy, similar geographic setting as the correspondingly numbered climatologies are referred to as present-day. These stations lie in Konstanz, Germany, where 1973–1990 climatologies at 17 meteorological stations (except for Konstanz, Germany, where 1973–2002 is used) hereinafter the climatologies are referred to as present-day. These stations lie in similar geographic setting as the correspondingly numbered terrestrial sites of Table 1a with the exceptions of Brindisi, Italy, lying ~650 m lower than the Lago Grande di Monticchio and Innsbruck, Austria, lying nearly 1500 m lower than Kleebrugnen cave. To compare the latter record to the 1961–1990 climatology, we apply a temperature lapse rate of 0.6 °C/100 m for MAAT and 0.7 °C/100 m for the mean temperature of the warmest month (MTWM) to correct for the elevation difference between Kleebrugnen cave and Innsbruck. This lapse rate has been estimated from the climatological difference in monthly surface air temperatures (Klein Tank et al., 2002) between Innsbruck (582 m) and Sonnblick (3109 m). By contrast, we computed mean temperature of the coldest month (MTCM) anomalies for the Monticchio record to the Brindisi climatology by simply adding 4 °C to the reconstructed MTMCM. The rationale is that present-day MTMCM are 4 °C for Monticchio, respectively 8.4 °C for Brindisi, with up to 4 °C of the difference explained by height difference.

Arguably poor data coverage of Europe does not restrict the model–data comparison, because our model’s coarse spatial resolution allows inferences at sub-continental scale at best. Moreover, by evaluating simulated seasonal and annual temperature anomalies to present-day climate (Section 3.1), GDD5 (Section 3.2), precipitation (Section 3.3) and vegetation (Section 3.4) to the records, we obtain a detailed picture of the climatic response of Europe to the GS15–GI14 transition. Finally, we analyse sub-continental scale climatic changes by dividing Europe into three latitudinal bands and two longitudinal blocks (see Table 2), and then compare the model results with regional climate reconstructions.

Table 2
Simulated seasonality across Europe in the cold state and the moderate state. Temperatures are in °C, GDD5 amounts in °C/day and June–July–August precipitation sum in mm.

<table>
<thead>
<tr>
<th></th>
<th>Northern Europe</th>
<th>Middle Europe</th>
<th>Southern Europe</th>
<th>Western Europe</th>
<th>Eastern Europe</th>
</tr>
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<td><strong>°E</strong></td>
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<td>–12 to 50</td>
<td>–12 to 50</td>
<td>–12 to 15</td>
<td>15 to 50</td>
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<tr>
<td><strong>°N</strong></td>
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<td>45 to 55</td>
<td>35 to 45</td>
<td>35 to 72</td>
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<td>13.4</td>
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<td>–0.8</td>
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<td>moderate state</td>
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<td>10</td>
<td>18.9</td>
<td>10.3</td>
<td>7.4</td>
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<td>8.3</td>
<td>5.5</td>
<td>9.9</td>
<td>8.2</td>
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<td>2.4</td>
<td>–6.2</td>
<td>–14.1</td>
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<tr>
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<td>–3.1</td>
<td>8.7</td>
<td>4.2</td>
<td>–6.2</td>
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<td>11</td>
<td>8.2</td>
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<td><strong>Coldest month SAT</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
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<td>–2.0</td>
<td>–14.8</td>
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<tr>
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<td>–9.7</td>
<td>5.5</td>
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<tr>
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<tr>
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<td>24</td>
<td>2</td>
<td>17</td>
<td>34</td>
<td>5</td>
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<tr>
<td>% years with killing frosts Pinus/Picea</td>
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<td>% years with killing frosts Quercus</td>
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<td>34.3</td>
</tr>
<tr>
<td>moderate state</td>
<td>28.9</td>
<td>7.1</td>
<td>0.0</td>
<td>0.0</td>
<td>16.2</td>
</tr>
<tr>
<td>moderate-cold</td>
<td>–14.0</td>
<td>–35.0</td>
<td>–0.8</td>
<td>–10.3</td>
<td>–18.1</td>
</tr>
<tr>
<td>% years with killing frosts O. Europaea</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>cold state</td>
<td>34.3</td>
<td>90.3</td>
<td>32.7</td>
<td>40.5</td>
<td>58.2</td>
</tr>
<tr>
<td>moderate state</td>
<td>47.8</td>
<td>57.0</td>
<td>5.1</td>
<td>7.6</td>
<td>46.5</td>
</tr>
<tr>
<td>moderate-cold</td>
<td>13.5</td>
<td>–33.3</td>
<td>–27.6</td>
<td>–32.9</td>
<td>–11.7</td>
</tr>
</tbody>
</table>
3.1. Near-surface temperatures

3.1.1. Palaeodata

Despite scant evidence of GS15–GI14 warming in Europe, we enumerate several sites showing increased interstadial temperatures (Table 2). A direct warming signal is found in the pollen-inferred 2–4 °C MTCM rise at Monticchio (Allen et al., 1995). Also, a MAAT rise of >3 °C is reconstructed for the Kleegruben cave record, where the presence of a temperate glacier covering the surface area above the cave during both stadial and interstadial gives additional evidence for daily maximum SATs above 0 °C during summer (Spötl et al., 2006). Disappearance of periglacial features as well as pollen- and chironomid-based reconstructions indicates increasing temperatures for multiple sites in eastern Germany (Huijzer and Isarin, 1997; Kasse et al., 2003; Bohncke et al., 2008). A semi-quantitative MTWM reconstruction based on chironomid assemblages suggests a clear summer warming in the Oberwinkler Maar record of W Germany (Engels et al., 2008a). The retreat of the Scandinavian Ice Sheet for Sokli (N Finland) provides indirect evidence of warming (Helmens et al., 2007, 2009) based on multiple proxy-records. Finally, three marine pollen records from around the Iberian Peninsula (Sánchez Goñi et al., 2008; Margari et al., 2009) provide further evidence for climate warming during the interstadial.

Several other quantitative temperature reconstructions exist for GS15–GI14 in Europe. Six MTWM and four min.Tsummer reconstructions from central European records suggest summer temperatures of 9–16 °C for GI14 (see Tables 1a and 2). Based on several different proxies, summer temperatures are relatively well

<table>
<thead>
<tr>
<th>Site #</th>
<th>GI/GS</th>
<th>MTCM</th>
<th>MTWM</th>
<th>min.Tsummer</th>
<th>MAAT</th>
<th>Precip.</th>
<th>Environment/vegetation (+indicator species)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>GI14</td>
<td></td>
<td></td>
<td>~39 to ~36</td>
<td>+</td>
<td></td>
<td>Increased annual snow accumulation</td>
</tr>
<tr>
<td>2</td>
<td>GI14?</td>
<td>10 to 14</td>
<td>10 to 13</td>
<td>Near-present-day</td>
<td></td>
<td></td>
<td>Shrub tundra (Salix, Betula nana, Juniperus, Ericales, Caryophyllaceae, Rumex-Oxyria, Artemisia, Chenopodiaceae, Polygonum viviparum)</td>
</tr>
<tr>
<td>3</td>
<td>GI147</td>
<td>Warm</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Betula – Pinus vegetation (also Junipers, Salix, Populus, Ulmus, Quercus; thermophilous Hedera &amp; Viscum)</td>
</tr>
<tr>
<td>4</td>
<td>GI14?</td>
<td>~27 to ~2</td>
<td>9 to 14</td>
<td>&gt;4 to 14</td>
<td>Treeless shrub tundra (B. nana, Juniperus, Ranunculus)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>GI147</td>
<td>~20</td>
<td>8 to 10</td>
<td>Permafrost</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>GI16/15/14?</td>
<td>~20</td>
<td>15 to 18</td>
<td>12 to 14</td>
<td>Shrub tundra (Betula, B. nana, Ranunculus subgen. Batrachium), constant lake level</td>
<td></td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>GI13/14?</td>
<td>~13 to ~11.5</td>
<td>7 to 11</td>
<td>Subarctic to boreal open forest landscape (Pinus, Betula)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>GI14/137</td>
<td></td>
<td></td>
<td>Tundra</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>GI14–137</td>
<td></td>
<td></td>
<td>Warmer temperatures and/or bottom-water anoxia and/or increase in trophic level, Betula only tree</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>GI14–127</td>
<td>~12 to ~5</td>
<td>12 to 13</td>
<td>2.2 to 6.4</td>
<td>Atlantic forest (Betula, Pinus, deciduous Quercus) amplitude 41%</td>
<td></td>
<td></td>
</tr>
<tr>
<td>11</td>
<td>GI14–13</td>
<td>~20 to ~9</td>
<td>8 to 11</td>
<td>Cold, oligotrophic lake, Betula only tree</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>GI14</td>
<td>0</td>
<td>&lt;0</td>
<td>Picea, Salix, Larix, Betula; forest tundra low AP%</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>13</td>
<td>GI14</td>
<td>+</td>
<td>12</td>
<td>Area covered by temperate glacier in GS15 &amp; GI14</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>14</td>
<td>GI14–137</td>
<td></td>
<td>Mild</td>
<td>Close to obliquity max.; strong summer warming steppic plants (heaths &amp; sedges; Artemisia)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>GI14</td>
<td>+</td>
<td>12</td>
<td>Atlantic forest (Quercus, Pinus) amplitude 23%</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>16</td>
<td>GI14</td>
<td>~7.7 to ~7.3</td>
<td>+</td>
<td>Close to obliquity max.; strong summer warming Grass and heath land (Artemisia, Chenopodiaceae)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>17</td>
<td>GI14</td>
<td>+</td>
<td>+Winter</td>
<td>Mediterranean forest AP 42–79.4% (Olea, deciduous Quercus, Pinus, Juniperus, Labiatae)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>18</td>
<td>GI14</td>
<td>+</td>
<td>12</td>
<td>Mediterranean forest (evergreens &amp; deciduous Quercus) Close to precession max.; drier winters, attenuated summer warming Semi-desert (Artemisia, Chenopodiaceae, Ephedra)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>19</td>
<td>GI15</td>
<td>~80</td>
<td></td>
<td>Grassland-steppe AP 2.6–26.7% (Graminae, Artemisia, Chenopodiaceae)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note: GS/GI numbers with ‘?’ or ‘??’ if the publication on the original chronology considers (inter-)stadial correlation unreliable, respectively unlikely correct. Preliminary OSL dates from the Reichwalde interstadial point to a likely older age than early-MIS 3.
constrained to 3–10 °C below present-day (Fig. 3c). δ18O measurements on tooth enamel from the mammoth site of Niederweningen (Switzerland) suggest MAAT of ~4 °C below present-day (Tütken et al., 2007). Furthermore, mean temperature of the coldest month (MTCM) reconstructions on Coleopteran assemblages from Niederweningen (Coope, 2007), NW Germany (Behre et al., 2005) and The Netherlands (Huijzer and Vandenberghe, 1998) all suggest interstadial MTCM in the order of 10 °C below present-day (Fig. 3e). Finally, presence of Fagus trees in Georgia points to relatively mild winter and summer conditions there (Arslanov et al., 2007).

3.1.2. Simulated temperatures

In the moderate state, mild westerly winds bring frequent winter thawing episodes to much of south-western Europe, thereby precluding the build-up of a snow pack and preventing extremely low winter temperatures (Table 2). In other regions, snow cover is restricted to the coldest months (not shown), which under early-MIS 3 boundary conditions still leads to coldest month temperatures 10–15 °C below present-day values (see Fig. 3e). Conversely, warmest month SATs over Europe are regionally even warmer in the moderate state than in the present-day simulation, except over the ice sheet (Fig. 3c). Higher than present-day sensible
heat fluxes at the earth’s surface — as a result of enhanced summer insolation — increase summer temperatures in the moderate state. In the cold state, a strong wintertime westerly jet advects very cold air masses eastwards, thus increasing continentality in most places and thereby keeping winter temperatures extremely low — mostly 15–25 °C below present-day values (see Fig. 3f) — and extending the duration of snow cover (not shown). This is because the air masses are transported over sea ice before reaching Europe instead of over open water in the moderate state. Over all but south-western Europe, longer winter snow cover in turn causes spring to be delayed and autumn to be advanced in the year by several weeks, effectively reducing annual mean SATs compared to the moderate state. In summer, finally, air masses advected to Europe remain cooler than at present due to cold surface waters of the North Atlantic Ocean, the Nordic Seas and the Mediterranean Sea. This keeps warmest month temperatures 5–10 °C below those of the moderate state (Table 2), thus mostly well below present-day (Fig. 3d).

3.1.3. Model—data comparison

The inferred stadial to interstadial summer and annual warming of at least 3 °C in central Europe is in qualitative agreement with simulated summer warming of 6–7 °C, respectively annual mean SAT rise of 8 °C, see Table 2. Furthermore, the MAAT anomalies to present-day for the interstadial in Switzerland (about −4 °C; Fig. 3a) and for the stadial in eastern Germany (about −14 °C, Fig. 3b) are in good quantitative agreement with simulated regional anomalies. Also, interstadial MTCM anomalies of between about −15 °C and −8 °C in northern Germany, the Netherlands and Switzerland (Fig. 3e) corroborate simulated coldest month temperatures of −10 °C over middle Europe. Further, a rise in simulated MTCM for southern Europe is supported by the warming seen in the Monticchio record. Lastly, summer temperatures reconstructed in northern Finland support near-present-day simulated warmest month SATs east of the Scandinavian Ice Sheet. However, despite reducing the warm bias of our model by looking at anomalies to present-day, simulated warmest month temperatures are still largely overestimated compared to reconstructed MTWM in western and central Europe, except just south of the ice sheet (Fig. 3c). With reconstructed interstadial MTWM anomalies to present-day of −9 °C in the Netherlands and −7 °C in Switzerland, compared to +3 °C or more in this region in the model, this means a residual warm bias of up to 10–12 °C regionally in western Europe.

3.2. Growing degree-days

With simulated summer SATs that clearly overestimate MTWM in most cases, we need a summer climate variable less sensitive to the warm bias of the model. Following VM2010, we analyse the accumulated temperatures over the thermal growing season — i.e. when daily mean SATs are at least 5 °C — also known as growing degree days (GDD5), to further constrain seasonality changes from GS15 to GI14. Since GDD5 is essential for plant growth and is taxon specific, past GDD5 values can be inferred from palaeobotanical records (e.g. Allen et al., 1999; Wagner-Cremer et al., 2010).

We compare simulated GDD5 to GDD5 ranges inferred from palaeobotanical records (Fig. 4) following the methods of Laurent et al. (2004) — except for the Monticchio record, for which GDD5 was estimated by Allen et al. (1999), also from pollen assemblages. Laurent et al. (2004) divided 320 plant taxa found in Europe into bioclimatic affinity groups. This division is based on monthly mean values of eight climatic variables, including GDD5. Based on the geographical distribution of each bioclimatic affinity group, Laurent et al. (2004) provide 5% and 95% extreme ranges of the GDD5. We estimated GDD5 ranges of fifteen pollen records of GI14 and five of

Interstadial min. GDD5 / moderate state GDD5

Interstadial max. GDD5 / moderate state GDD5

Stadial min. GDD5 / cold state GDD5

Stadial max. GDD5 / cold state GDD5

Fig. 4. Pollen-inferred minimum (top panels) and maximum (bottom panels) GDD5 envelopes for the interstadial correlated to GI14 (left panels) and the stadial correlated to GS15 (right panels) vs simulated GDD5 in the cold state (left panels) and moderate state (right panels) over Europe.
GS15 and use the resulting envelopes (Fig. 4) to further constrain the model results. We show the proxy-based 5% (or minimum, Fig. 4a and b) and 95% (or maximum Fig. 4c and d) GDD5 limits separately.

Direct evidence of GS15–GI14 warming during the growing season from proxy-based GDD5 only found in the Monticchio record, with a rise of ~1820 °C-day. Besides this, range shifts do suggest interstadial GDD5 may have been higher. Most compelling is the marine pollen record from southern Portugal with an increase in minimal and maximal GDD5 of 1270 °C-day and 1590 °C-day, respectively. We calculated the same increase of minimal GDD5 in the Lesvos pollen record, suggesting that the growing season warmed up in southernmost Europe as Mediterranean trees appeared in the records (Sánchez Goñi et al., 2008; Margari et al., 2009). An interstadial minimum GDD5 of 1380 °C-day based on Fagus pollen in the Dziguta river section, Georgia (Arslanov et al., 2007), indicates a possibly warmer growing season in other parts of southern Europe as well. In eastern Germany and northern Finland, the stadial environments were characterised by frozen, barren soil (Nochten and Reichwalde), whereas the interstadial environment was a lake surrounded by shrub tundra vegetation in both cases (Kasse et al., 2003; Helmens et al., 2007; Bohncke et al., 2008). This replacement may point to a rise in growing season temperatures into the interstadial with an ecosystem requiring at least 570 °C-day around Reichwalde and 530 °C-day around Sokli. Whereas most pollen records suggest a minimum GDD5 of 530–570 °C-day in both the stadial and the interstadial, maximum values vary widely, from 1970 °C-day to 4690 °C-day. This leads to a strong variation in envelope size between records (i.e. excluding the Monticchio record). The tightest constraints for interstadial GDD5 envelopes are inferred for the Lesvos (1230 °C-day range), the Dziguta river section (1270 °C-day range) and the Niederweningen (1440 °C-day range) records.

With a GDD5 anomaly of 500–1500 °C-day in the moderate state compared to the cold state, we find that all minimum and nearly all maximum GDD5 constraints from vegetation were met by the model (see Fig. 4 and Table 2). In particular, the GDD5 rise of ~1500 °C-day in southern Europe is quantitatively consistent with the Monticchio record. However, in some regions, GDD5 values are overestimated, as suggested by a maximum of 1970 °C-day for the Niederweningen record versus simulated GDD5 over central Europe of ~2250 °C-day. Also in south-eastern Europe we simulate GDD5 amounts of at least 2800 °C-day, whereas the inferred maximum was 2650–3060 °C-day in that region. In contrast, the best fit between model and data was found in western Europe southwards of ~45°N (Fig. 4).

An important reason for including GDD5 as a constraint to compare our simulations to data is a smaller warm bias compared to MTWM. A simple calculation for middle Europe demonstrates this: (1) the total MTWM warm bias in the moderate state (~present-day bias + additional warm bias) amounts to ~10–20 °C; (2) for a ~6 month long growing season (beginning of April until end of October), a uniform GDD5 bias would yield an excess of ~1800–3600 °C-day; (3) with a simulated 2270 °C-day (Table 2), and pollen data suggesting at least ~560 °C-day (Fig. 4, top left panel), subtracting the uniform GDD5 bias would yield unrealistically low values of 0–470 °C-day. Thus, the temperature bias of the thermal growing season must be < ~9.5 °C and therefore smaller than the total MTWM bias.

3.3. Precipitation

Only qualitative inferences on precipitation increases in Europe from the stadial to the interstadial have been published (see Table 3). From the pollen records of GI14 from off-shore southern Portugal (Sánchez Goñi et al., 2008) and Lesvos, Greece (Margari et al., 2009), an increase of winter precipitation was inferred. In Georgia, a wet interstadial was inferred from the presence of Fagus and Abies pollen (Arslanov et al., 2007). Conversely, steppic plants dominating the stadial vegetation around the Iberian Peninsula (Sánchez Goñi et al., 2008) and in Lesvos (Margari et al., 2009) indicate that less precipitation was available along the western and southern European seaboard. However, a preliminary quantitative precipitation reconstruction using pollen data from marine core MD01-2348 from the Bay of Biscay indicates an annual sum of ~600–800 mm during GI14 in western France. Furthermore, a GS15–GI14 rise of ~0.4–~0.6 actual/potential evapotranspiration ratio (a proxy for soil moisture availability for plants) in the Monticchio record (Allen et al., 1999) in combination with a rise in MTCM and GDD5 suggests a substantial increase in precipitation.

In the model, precipitation increased from the cold to the moderate state in western, southern and most of eastern and northern Europe (Fig. 5). This increase was mostly concentrated in...
winter and spring (Table 2). Over most of Europe, <15% of the simulated annual sum of precipitation occurred in summer (June, July and August), compared to >65% during winter and spring.

Although the above-published records do not provide quantitative constraints on stadial—interstadial changes in annual precipitation, a clear qualitative agreement between model and data is achieved. The simulated ~475 mm—~700 mm (or ~50%) increase over western Europe agrees well with the inferred relatively dry climate of GS15 in the data. Similarly, the simulated transition from semi-arid (250–500 mm) to sub-humid (500–1000 mm) conditions would quantitatively resemble the reconstructed increase in humidity in western France and southern Italy.

3.4. Vegetation

3.4.1. Palaeodata

Enhanced vegetation cover was expected for GI14 in W and S Europe as precipitation and temperatures increased after the stadial. Four pollen records confirm this, showing aorestation of the western and southern European seaboard (at least south of ~45°N; Fig. 6). In these records, open Mediterranean (consisting of e.g. Quercus, Olea and Pinus) and temperate forests replaced stadial semi-desert or steppe-like vegetation (Table 3). Similarly, Atlantic forest characterised by deciduous Quercus and Pinus replaced heaths and sedges between 40°N and 45°N. Finally, the appearance of vegetation (shrub tundra) in N Finland and E Germany in GI14 (Section 3.2) suggests improving circumstances for plant growth.

Additional information is available for the vegetation cover during GI14. Firstly, in the Dziguta river section pollen record from Georgia, Fagus and Abies pollen suggest the presence of warm temperate forest in the region (Arslanov et al., 2007). Second, in and around the Alps, four records contain arboreal pollen (Schlüchter et al., 1987; Müller et al., 2003; Preusser and Schlüchter, 2004; Furrer et al., 2007). This implies some forestation or at least a proximal location of the edge of forested land at around 48°N in the lowest valleys of the Alps. The dominating taxa point to forest tundra with dispersed presence of Betula, Picea, Pinus and Larix. Third, shrub tundra was inferred from pollen records from Oerel (Behre et al., 2005), Oberwinkler Maar (with presence of tree birch; Engels et al., 2008a), Nochten (Bos et al., 2001) and Reichwalde (Böhncke et al., 2008) in Germany, and Sokli (Helmens et al., 2007). In contrast, the Vrångum record from Denmark (Kolstrup, 1991) contains pollen from trees and thermophilous plants. If the latter record represents the same interstadial as in the others, there seems to have been no simple meridional gradient in climax vegetation in areas south of the Fennoscandian Peninsula. Finally, Pinus and Betula pollen found in the Sokli record may imply that the northern edge of boreal forest was located within several hundred kilometres to the south(-east) (Bos et al., 2009).

3.4.2. Simulated potential vegetation

We do not see the transition from steppe-like vegetation to Mediterranean or temperate forest in SW Europe in the model (Fig. 6b). In the model, forest cover dominated the W European seaboard in both the cold and the moderate state (Fig. 6a). Contrarily, in E Europe, barren soil and grassland covered a larger surface area in the cold state, implying a domination of polar or cold desert, grassland and steppe biomes. In the moderate state, polar desert retreated northward to the ice sheet edge, thus making way for a grass-dominated land cover with some open forest in the south-east.

3.4.3. Model—data comparison

The coarse horizontal resolution and simplified topography of the atmospheric model combined with a very simple parameterisation of the vegetation model preclude a direct comparison of local vegetation cover. Rather, the primary motivation for coupling VECODE to ECBilt-CLIO in this study is to include the albedo feedback of large-scale vegetation shifts on glacial climate. With respect to MIS 3, an equator-ward shift of mid- and high-latitude biomes is expected in a colder than present-day climate. This includes the

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expansion of polar desert and tundra in the Northern Hemisphere (e.g. Van Meerbeeck et al., 2009), which increases the surface albedo and thus further cools climate (Harvey, 1988).

Nonetheless, some general vegetation trends on sub-continental scale simulated by VECODE are supported by the above-mentioned reconstructions. Firstly, we correctly simulate the regional retreat of polar desert around the Scandinavian Ice Sheet and its replacement by shrub tundra. Secondly, the northerward advance of the northern tree edge is seen in E Europe. Thirdly, we could tentatively associate the presence of tree pollen in the Dziguta record with signs of forest expansion further south in the model. Finally, forest cover is found in W Europe in the moderate state. However, the model does not realistically simulate vegetation changes associated to the GS15–GI14 transition in W Europe. Western European tree cover was overestimated in the cold state especially, whereas climate was perhaps too cold and arid to sustain temperate forest. To conclude, according to our model, neither (overestimated) temperatures in Europe in the cold state nor annual precipitation appear to be limiting for tree growth. We will return to this problem in Section 4.2.

4. Discussion

4.1. Environmental changes in Europe in response to an AMOC resumption during the GS15–GI14 transition

The presented model-data comparison of environmental changes in response to the GS15–GI14 transition reveals that reconstructions largely support simulated rapid warming induced by an AMOC resumption under early-MIS 3 boundary conditions. The simulated rise in annual mean, winter and growing season temperatures as well as the increased annual precipitation sum qualitatively, and in several cases also quantitatively resemble the terrestrial paleoclimate archive of stadial-interstadial changes in Europe. Assuming that the recorded stadial and interstadial occurred before, respectively after ~55 ka BP (see Fig. 1a), Europe’s main climatic response to the GS15–GI14 transition might have been the following:

Firstly, a relatively uniform temperature rise across central Europe was inferred from several proxies and is seen in the model (Fig. 3). Reconstructed stadial MAAT and MTWM were possibly 4–8 °C, respectively 3–5 °C below interstadial values. Qualitatively, this corresponds well with simulated annual mean SAT rise of around 8 °C and warmest month SAT rise of 7 °C. Despite only a winter warming signal between GS15 and GI14 being available from eastern Germany (i.e. rising above ~20 °C in Nochten and Reichwalde, the latter record suffering from a conspicuous chronology; Table 3), we tentatively infer an even larger winter warming over central Europe as MAAT increased more than MTWM. With coldest month SAT rise of 12 °C in Middle Europe, the model is (qualitatively) consistent with this inference. Furthermore, it fits the prediction that stadial to interstadial warming around the North Atlantic should be more clearly seen outside summer if induced by an AMOC resumption (Denton et al., 2005; Flückiger et al., 2008).

Secondly, palaeoecological records across Europe point to local or regional warming of the growing season and of the winter (Table 3), which is also seen in our simulation with a GDD5 increase of 500–1400 °C-day (Table 2) and with a 6–14 °C warming of the coldest 90-day period of the year (not shown). Direct evidence of a warmer growing season comes from thermophilous plant taxa found in pollen records of southern-most and south-eastern Europe. In addition, indirect evidence is found in eastern Germany and northern Finland, where shrub tundra replaced polar deserts (and glaciation by the Scandinavian Ice Sheet). Evidence of winter warming comes from the ~3 °C reconstructed MTMC rise in southern Italy and the appearance of temperate and Mediterranean forest south of ~48°N, respectively ~40°N in the interstadial. This suggests MTMC higher than ~15 °C between 40°N and 48°N or above ~12 °C in northern Switzerland (Coope, 2007) and ~2 °C in south-western Iberia and Lesvos (following Leroy and Arpe, 2007).

Thirdly, data and model are in agreement with another prediction of AMOC-induced warming, namely an enhanced hydrological cycle over Europe during interstadials (e.g. Claussen et al., 2003). With up to 80% higher annual precipitation sums over Europe in the moderate state than the cold state, the model is consistent with inferred substantial precipitation rise at least over southern Europe.

4.2. Climatic limitation of tree growth during early-MIS 3 stadials and interstadials

We will now give some suggestions why modelling studies have not been able to reconcile mild summer temperatures and enhanced precipitation during MIS 3 interstadials over Europe with the absence of forest north of 50°N (e.g. Alfano et al., 2003). At the same time, we assess why our model overestimates interstadial, and especially stadial tree cover, and would do so even if the warm bias were removed. Then we provide suggestions on which were the strongest climatic factors limiting tree growth in Europe. We only focus on climatic factors, although many non-climate related factors were possibly as/more limiting for tree growth. Some are sunshine duration, wind erosion, CO2-limitation, soil properties and grazing by large mammals (Bohncke et al., 2008; Johnson, 2009; Prentice and Harrison, 2009).

4.2.1. Limiting factors for tree growth in the model and suggested improvements

In our model, potential tree cover fraction of every grid cell is only a function of annual mean SAT and annual precipitation, thus discarding seasonality (Brovkin et al., 1997). In a cold climate, tree cover increases mainly with higher temperatures in VECODE. In other words, annual mean temperature is the main limiting factor, whereas in a warm and dry climate, the annual precipitation sum is most limiting. However, the bioclimatic classification of vegetation was parameterised by Brovkin et al. (1997) to produce tree cover mimicking present-day distribution. In glacial climate states, an increased annual temperature range – inferred from the model and palaeorecords of Europe during the registered early-MIS 3 stadial and interstadial, e.g. in the Monticchio record – may have shifted vegetation to more cold tolerant species than are present nowadays in regions with equal annual mean temperatures. An example is the southwards extension of tundra and cold tolerant trees as Betula in central Europe (Fig. 6). Furthermore, plants require water during their active period, not during their dormant phase. Therefore, at equal annual mean temperatures potential evaporation rates must have risen in the growing season, shifting vegetation to more drought-resistant taxa. This is for instance indicated by the presence of Artemisia in the pollen records of southern Europe during GS15, or in Sokli and Reichwalde during GI14 (Table 3). In summary, during early-MIS 3 stadials and interstadials, the main climatic limiting factors were seasonal, rather than annual.

Acknowledging the importance of seasonality in driving vegetation changes, Alfano et al. (2003) drove a more sophisticated vegetation model with systematically modified winter and summer season length, annual, winter and summer temperatures and precipitation fields from two MIS 3 equilibrium states run with a high resolution atmospheric model equilibrium. In doing this, they tried to mimic stadial and interstadial vegetation using the best combination of these variables. Although some scenarios
allowed a closer match over the northern part of Europe, these then caused a mismatch between simulated and reconstructed vegetation in southern Europe (Alfano et al., 2003). Even when increasing precipitation with temperature no satisfactory match with data of Huntley et al. (2003) was reached. Clearly, the seasonal climatic factors investigated by Alfano et al. (2003) were not sufficient to explain the discrepancy between mild summers and forest absence in northern parts of western and central Europe.

We propose that the three strongest (seasonality related) climatic limiting factors for tree survival and growth in Europe may have been killing frost frequencies (discussed in detail in Appendix), GDD5 and summer moisture availability (here crudely approximated by the June–July–August precipitation sum). The motivations for this selection are based on tree physiology and are twofold. First, killing frosts – lethal (intracellular) frost damage in plants especially during spring, since they then cannot complete their life cycle – impede survival of tree populations if their recurrence period is shorter than the time needed for a seedling to attain adulthood and produce its offspring. Because minimum generation times of trees characterising typical forest types in Europe – boreal, temperate mixed or broadleaf deciduous and Mediterranean forest – are at least 10 years (Young and Young, 1956); a killing frost occurring at least once every 10 years out of ten impedes survival. Second, the minimum daily mean temperature for growth lies around 5 °C for many extra-tropical tree species (e.g. Kauppi and Posch, 1985; Prentice et al., 1992; Solantie, 2004). Like the minimum temperature for plant growth, the minimum summer precipitation needed by trees is taxon-specific, and depends amongst others on transpiration rate (Boisvenue and Running, 2006). Nevertheless, both minimum requirements are relatively uniform among species associated with the same plant functional type (Laurent et al., 2004). Taking the reasoning in consideration, we calculated each threshold value for three forest types (i.e. boreal, temperate and Mediterranean) for the cold and the moderate state. Boreal forest trees are represented by Betula, Picea and Pinus sylvestris, temperate mixed and broadleaf deciduous forest by deciduous Quercus, and Mediterranean forest by Olea europaea. Note that, to our knowledge, too little information is available on the frost hardiness of boreal forest tree species in Europe to formulate robust threshold temperatures as done for temperate mixed or broadleaf deciduous and Mediterranean forest tree types (Appendix Table A.1). Therefore, we do not include killing frost frequencies in boreal forest in our calculations of climatic limiting factors for tree growth.

4.2.2. Calculated GDD5, summer precipitation and killing frost limitation of tree growth

Mapping these three limiting factors for the moderate state (two for boreal forest), we find that in Europe, potential growth of boreal forest is generally inhibited north of 50°N between ~10°W and ~30°E (Fig. 7a). It is primarily due to little summer precipitation. Conversely, further east, boreal tree growth is mostly not inhibited (apart from the Arctic). Furthermore, the northward extent of temperate broadleaf deciduous forest is limited to 50°N over all of Europe. Westwards of 30°E, summer precipitation is limiting, whereas eastwards of 30°E killing frosts are limiting (Fig. 7c). Finally, Mediterranean trees, which are more drought resistant but less frost hardy, cannot grow northwards of 40°N to the east of ~30°E, and northwards of 44°N between ~10°E and ~30°E mainly because of killing frosts (Fig. 7e).

In the cold state, the two/three factors are limiting in more places for the three forest types (Fig. 7b, d and f), such that (1) GDD5 would prevent tree growth north of ~45°N for Mediterranean forest and ~55°N for boreal and broadleaf deciduous forest in Europe; (2) killing frosts are too frequent for survival temperate forest north of 45°N, except west of ~10°E, and everywhere except southern-most Europe for Mediterranean forest; finally (3) summer precipitation further restricts forests to (south-)western Europe.

4.2.3. Can MIS 3 stadial and interstadial vegetation in Europe be explained by the suggested limiting factors?

An arguably better match between simulated and reconstructed potential vegetation arises here than when comparing the output of our vegetation model to data (see Fig. 6). The left panels on Fig. 7 show that the interstadial distribution of records containing arboreal pollen corresponds reasonably well with the area where tree growth is inhibited neither by killing frosts, nor by GDD5 nor by summer precipitation in the moderate state (i.e. shaded white in Fig. 7). 9 records out of 13 containing pollen of trees associated with boreal forest and all records containing oak or olive tree pollen are found in locations where the model allows their growth or survival.

As the northernmost site with open forest in western Europe was around 48°N in a low valley of the Swiss Alps (Preussner and Schlüchter, 2004) and with tree birch surviving up till 50.2°N (Oberwinkler Maar; Engels et al., 2008a), the calculated 50°N northern limit of potential boreal forest seems realistic. Furthermore, several pollen records suggest the presence of boreal forest in the Baltic countries and Poland during at least several MIS 3 interstadials, including the interstadial registered in the Sokli record (e.g. Molodkov et al., 2007; Bos et al., 2009). Potential growth of boreal forest in the area south-east of the ice sheet is, then, in agreement with these reconstructions. Finally, our calculations also allow co-existence of different tree types where found in the pollen records (e.g. on Lesvos).

For the stadial, no pollen records suggest forest cover, but two features of stadial-interstadial vegetation change may be explained by the three limiting factors (Table 3 and right panels of Fig. 7). First, the absence of Mediterranean forest and dominance of steppic plants in Lesvos during the stadial support arid and colder conditions in the cold state in south-eastern Europe (Fig. 7f). Second, if representing the GS15 interval, the absence of vegetation from the eastern German pollen record of Reichwalde is consistent with colder growing seasons, because most herbaceous plants require at least 530 °C-day, except for some cold-adapted grasses and shrubs (see Fig. 7b; Prentice et al., 1992; Laurent et al., 2004).

Remaining discrepancies between predicted potential tree growth limitation and vegetation data – besides an overestimation of the ice sheet size we use in the model (see e.g. Helmens et al., 2007; Molodkov et al., 2007) – require further explanation.

Firstly, Pinus and/or Betula pollen in pollen records of the Netherlands, eastern Germany and western Denmark possibly point to a northern limit of tree growth at 50°N in western and central Europe. However, the latter record – which even contains Populus, Quercus and Ulmus pollen – may not at all have been registering an early-MIS 3 interstadial according to Kolstrup (1991). An older age for this ~48 14C ka BP dated record is further supported by absence of thermophilous plants from the Oerel record 2° to the south and of temperate trees from any record up to 10° further south. Rather, this record probably registered a period with more favourable glacial or interglacial climate (Kolstrup, 1991).

Secondly, Abies pollen in the Dziguta record (Arslanov et al., 2007) suggests at least 40 mm summer precipitation, which is more than twice the simulated sum over much of south-eastern Europe. One reason for the discrepancy is that the model likely underestimates convective precipitation in mountainous areas due to a strongly simplified surface topography. Another is that soil moisture in summer may have been high enough in the river valley due to snow-melt.
Thirdly, for similar reasons water availability was possibly sufficient during summer in northern Germany and the Netherlands, despite seasonally deficient precipitation. Reasons may be the proximity of large river systems draining snow-melt during interstadials (van Huissteden et al., 2001) or the accumulation of melt-water in a nearby thaw lake (Bohncke et al., 2008). Indications of large enough melt-water supply to the low lying parts of western Europe comes from the presence of *Betula* and/or *Betula nana* pollen in nearly all records pollen records north of 45°N, as these plants require snow cover to insulate them from the coldest winter temperatures (Jonasson, 1981). By contrast and in agreement with simulated summer drought, presence of *Artemisia* and other steppic plants in the Nochten and Reichwalde pollen records, means eastern Germany might have been covered by steppe (following Subally and Quézel, 2002) rather than shrub tundra, supporting summer drought and annual mean SATs well above 0 °C (see Table 2) in Middle Europe.

Note that the summer precipitation threshold calculated with LOVECLIM model output should be considered with caution, as the computation of moisture balance on land is highly simplified in ECBilt. Despite the fact that our model–data comparison suggests moisture availability in the growing season to be a likely important limiting factor on tree growth, the summer precipitation threshold maps on Fig. 7 may look quite different in other models. Therefore, more robust conclusions may be drawn by reproducing these calculations in simulations run with earth system models of higher complexity.

4.3. Model limitations in simulating the GS15–GI14 transition and recommendations

4.3.1. How realistic are the simulated AMOC shutdown and resumption?

Although our transient AMOC shutdown and resumption simulation is forced with realistic early-MIS 3 boundary conditions, several assumptions limit our confidence in the conclusions made from the model-data comparison. Two limitations specific to our experimental design are discussed in this section (A third limitation is elucidated in Supplementary e-information section S.2).

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Firstly, we forced the model with a freshwater scenario representing a traditional Heinrich event — including a European precursor event following Grouset et al. (2000) — and a subsequent decline in ice rafting/melting. However, HE5.2, defined in the Labrador Sea much later than the six others of the last glacial (Heinrich, 1988; Rashid et al., 2003), is absent from some records that include the traditional events (Hemming, 2004). If the coldest glacial North Atlantic stadial SSTs resulted from an AMOC shutdown, and HE5.2 did not produce sufficient melt-water to shut it down, then a tempered SST response is expected. Consequently, the GS15–GI4 warming magnitude would be reduced compared to a transition after a full AMOC shutdown (Flückiger et al., 2008). As in many North Atlantic records, SSTs were less depressed during GS15 than during GS13 or GS9, we infer that the impact of HE5.2 was indeed reduced, or limited to regions north of 40° N. Moreover, SST warming during the GS13–GI12 and GS9–GI8 transitions was twice larger at 37° N and 42° N, compared to ~33% larger at 45° N (Sánchez Goñi et al., 2008) and but nearly equal at 59° N (van Kreveld et al., 2000). With more constraints on ice rafting during HE5.2, a more detailed freshwater scenario could be used to perturb the AMOC than done in this study. Such constraints are, however, not available at present.

Secondly, 80% of the warming in Greenland is achieved within ~100 years across the simulated transition — in part due to the negative freshwater flux at the end of the simulated stadial — which is still much slower than a few decades at most, as inferred from Greenland ice cores (NorthGRIP-Members, 2004; Steffensen et al., 2008). Moreover, though generally reduced IRD fluxes towards the end of GS15 after HE5.2 (e.g. Rasmussen and Thomsen, 2004) indicate reduced iceberg calving, we do not know if the Northern Hemisphere ice sheets resumed growth immediately after an HE leading to reduced freshwater flux to the surface ocean (Clark et al., 2007). Therefore, we cannot verify whether the negative freshwater forcing we applied to accelerate the AMOC resumption is realistic.

4.3.2. Does our simulated rapid glacial warming transition represent the GS15–GI14 specifically?

Despite the above limitations, our simulated warming transition produces many of the essential inferred climatic changes during the GS15–GI14 transition (see Section 3). However, as the simulation has been set up using boundary conditions for an early-MIS 3 transition from a stadial perturbed by a Heinrich event, it could represent many aspects of other transitions as well, such as the transition between GS13 — coinciding with HE5 — and GI12. Although GI12 lasted about half as long as GI14, Greenland temperature rise over the transition was very similar (Huber et al., 2006).

A considerable decline in Northern Hemisphere summer insolation (20–30 W m⁻²) between the onset of GI14 and that of GI12 is expected to lead to cooler glacial summer temperatures during GI12. Interestingly, this is not seen in data, neither in Greenland (Huber et al., 2006), nor over Western Europe (Sánchez Goñi et al., 2008). Rather, the obliquity was near a maximum during GI14 and GI12 while the precession index decreased to a minimum (Berger, 1978). According to Sánchez Goñi et al. (2008) maximum obliquity translated into stronger aforesaturation during interstadials north of 40° N compared to GI8 or GI17–16. In contrast, southward of 40° N summer climate was more sensitive to precession change. With a higher precession index compared to GI8 or GI17–16, they found a reduced extent of Mediterranean forest (~5% of vegetation) during GI14 southwards in Western Europe. In view of the similar vegetation response to insolation changes between GI12 and 14, but a different response during GI8, an interesting study could be to perform a transient simulation setup with boundary conditions prevailing at around 38 ka BP and a similar freshwater scenario to represent HE4.

4.3.3. Uncertainties on the size of the Scandinavian Ice Sheet and its impact on climate in early-MIS 3

The size of the Scandinavian Ice Sheet during MIS 3 was probably overestimated in our experiment. We know that, at some points during MIS 3, parts of Scandinavia were not ice covered (e.g. Mangerud et al., 1981; Helmens et al., 2000). However, to our knowledge, no reconstruction of entire ice sheet consistent with these findings existed until most recently. Helmens and Engels (2009), amongst others, reconstructed an ice sheet covering essentially northernmost Sweden during early-MIS 3. By contrast, in our experiment — setup before new reconstructions became available — the ice sheet configuration follows that by Helmens et al. (2007). The ice sheet thus covers all of Scandinavia, except south-eastern Finland. Our configuration stands between two recent efforts to simulate MIS 3 climate with the coupled general circulation model CCSM3, both using a larger Scandinavian Ice Sheet than reconstructed by Helmens and Engels (2009). Kjellström et al. (2010) use the ‘small’ ice sheet as prescribed by Barron and Pollard (2002), covering mostly Norway and Sweden. Merkel et al. (2010) set up their experiment with a 35 ka BP ice sheet configuration consistent with the ICE-5G reconstruction, being even larger than ours.

As the Scandinavian Ice Sheet extent is probably too large in our experiment, its impact on Europe’s climate may well be overestimated, e.g. strong, local biases in temperature (Barron and Pollard, 2002). Notably, (1) enhanced surface albedo and higher elevation of ice covered grid cells reduce local temperatures by up to ~10 °C or more, especially in summer; (2) part of this cooling would be transferred to adjacent regions; and (3) cold temperatures above the ice sheet would facilitate atmospheric blocking, resulting in modified wind patterns, heat and moisture transport over Scandinavia and surrounding regions (as suggested by Helmens et al., 2007). Clearly, reconstructions such as that of Helmens and Engels (2009) remain to be implemented in realistic MIS 3 climate simulations to correct for those biases.

4.3.4. Warm summer temperature bias in LOVECLIM

The unrealistically high warmest month SATs simulated across Europe, especially western and south-eastern Europe are the consequence of a 20–75% reduction in soil moisture in summer. This warm bias is largely caused by a +25 W m⁻² (earth surface) sensible heat flux anomaly between the moderate state and present-day, induced by enhanced summer insolation (+35 W m⁻² at the top of the atmosphere) around 56 ka BP, in turn leading to anomalously strong atmospheric warming (Van Meerbeeck et al., 2009). The anomalously large sensible heat flux can further be attributed to a more often blocked atmospheric circulation pattern over Europe, reducing advective summer precipitation (Renssen et al., 2000). The latter leads to dryer soils in our model, since the bucket-style soil module does not allow replenishment by horizontal moisture flow. Therefore, the dryer summers are, the higher the expected summer temperature bias.

The additional 10–12 °C local warmest month (i.e. warmest 30-day period of the year) SAT bias in the moderate state would have been reduced to 5–6 °C if July SAT were analysed instead. It is thus tempting to compare simulated July SAT anomalies, rather than the simulated warmest month SAT anomalies, with the reconstructed MTWM anomalies. However, to be consistent, one should then compare reconstructed MTWM anomalies with simulated January SAT anomalies. By doing this, a 5–10 °C warm bias arises between modelled and reconstructed peak winter temperatures. Since those
MTCM and MTWM were estimated from assemblages of biotic species sensitive to the annual temperature range between the very coldest (due to limited cold/frost hardiness) and warmest temperatures (for growth), coldest and warmest month SATs give a better approximation than January or July (VM2010). Furthermore, with MTCM and MAAT anomalies in reasonable agreement with simulated coldest month, respectively annual mean SAT anomalies, it appears that the warm bias is only amplified in summer. Finally, we find that the warm bias is mostly concentrated on peak summer, since the warm bias is much reduced in terms of thermal growing season temperature, which is ~3 °C colder over Europe in the moderate state than in the present-day state (The latter temperature anomaly is based on 400–800 °C-day lower GDD5 in the moderate than the present-day state.).

A more physically consistent way of tempering simulated glacial summer temperatures would be to improve the soil module in our model by implementing a representation of permafrost. This has been done for the ECHAM atmospheric module in our model by implementing a representation of glacial summer temperatures would be to improve the soil module in our model by implementing a representation of permafrost. This has been done for the ECHAM atmospheric module in our model by implementing a representation of permafrost. This has been done for the ECHAM atmospheric module in our model by implementing a representation of permafrost. This has been done for the ECHAM atmospheric module in our model by implementing a representation of permafrost.

4.3.5. Improving terrestrial climate constraints on simulations of abrupt glacial warming

Aside from more refined modelling experiments, future studies of the response of the terrestrial environment to abrupt glacial warming transitions would greatly benefit from publications of reliably dated palaeoclimate reconstructions based on fast migrating plants and animals that are sensitive to summer duration, precipitation and warming changes such as given by Sánchez Goñi et al. (2008) or Margari et al. (2009). In addition, reliable quantitative proxies on winter temperatures (such as given by Allen et al., 1999) and duration (for instance duration of snow cover) could shed a light on the amplitude of the average annual temperature cycle. Models should then be used to further analyse interannual variability. Specifically, interpreting climate signals registered by those proxies in terms of the variability of summer precipitation, growing degree days and possibly, constraints on the frequency of cold waves — including killing frosts — and heat waves would greatly improve our understanding of the physiological stress inflicted on biota during abrupt climate change.

5. Conclusions

We compared glacial abrupt warming over Europe simulated with the LOVECLIM earth system model to the geological archive of palaeoenvironmental changes during the Greenland Stadial 15 – Greenland Interstadial 14 (GS15–GI14) transition. As a ~10 °C MAAT GS15–GI14 warming occurred in Greenland, a nearly synchronous warming of several degrees is seen over the European continent, as supported by terrestrial and marine pollen records in southern Italy, respectively off the coast of France and Portugal, as well as by a speleothem record from the Austrian Alps. This warming transition was accompanied by a simulated 50–100% precipitation increase over the North Atlantic region, in qualitative agreement with ice core and pollen data.

Europe’s climatic response to the GS15–GI14 transition may have had a distinct seasonal imprint, as suggested by palaeoclimate reconstructions and model results. Simulated seasonality changes in Europe include (1) a rise of coldest month and warmest month temperatures by at least ~3 °C and regionally up to ~17 °C across the continent, with a larger warming magnitude during winter; (2) a warmer growing season, with GDD5 increasing by 600–1400 °C-day; and (3) a concentration of the precipitation increase outside the three climatological summer months (i.e. June–July–August), the rest of the year receiving more than 85% of the annual sum.

These model results fit the available constraints from proxy data fairly well, apart from unrealistically high-simulated warmest month temperatures, which resulted in an overestimation of stadial and interstadial potential vegetation in terms of tree cover. In the moderate state, tree cover dominated the landscape of western Europe in most places, while in the cold state, it was restricted between 40°N and 55°N. In contrast, pollen records show no evidence of tree growth in Europe during stadials, and forests were probably restricted to latitudes south of 50°N during interstadials.

We propose three climatic limiting factors for tree growth in MIS 3, all related to seasonality. These are (1) frequent killing frost, especially in eastern and northern Europe; (2) GDD5 amounts below a critical threshold, mostly limiting tree growth north of 55°N; and (3) too little summer precipitation in many places. Using a coarse-resolution model, we show that these three factors alone may have limited growth of boreal, temperate and Mediterranean forest to the regions where evidence was found. This may also partly explain the over-estimation of forest cover in previous model simulations focusing on abrupt glacial warming transitions, as these model studies did not consider these three factors (e.g., Alfano et al., 2003). As our model can only reproduce climate on sub-continental scale at most, many smaller scale processes limiting tree growth are not investigated in this study. We thus argue that our understanding of the vegetation response to GS–GI transition would benefit from a higher resolution study which uses a dynamical vegetation model incorporating the discussed three limiting climatic factors. Furthermore, a better representation of soil moisture content could significantly reduce the systematic warm summer temperature bias of our model while possibly also increasing summer precipitation in early-MIS 3 simulations. However, our model results provide a relatively simple, physically possible and physiologically relevant explanation of why no evidence of forest growth during MIS 3 interstadials, despite summer temperatures of ~14 °C at around 50°N.

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Appendix

A.1. Calculating killing frost frequencies

In this study, killing frost frequencies have been calculated as a physiological stress factor on tree growth following the method described in VM2010. Here, a summary of the method suffices. Threshold temperatures for survival of trees typical of two forest types found in Europe at present-day were found in literature, namely broadleaf deciduous forest (typified by Quercus petraea and Quercus robur) and finally Mediterranean forest (typified by O. europaea). Only species-specific coldest threshold temperatures were used for the killing frost types depicted in Table 1. With these thresholds, we calculated the number of years containing killing frost at each grid cell over Europe for the two forest types in the cold and moderate climate states. Note that killing frosts are calculated both within and outside the growing season, following the rules depicted in Table A.1.

Table A.1
Killing frost frequencies: daily minimum temperature threshold definitions.

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*Killing frost temperature (Tkf) in growing season (gs), no prior frost (nof – at least 30 days with Tmin > 0 °C); **Tkf in gs with prior mild frost (mf – at least one day in last 34 days with –5 °C < Tmin < 0 °C); ***Tkf outside gs with prior mf; ****Tkf for December, January and February.

Fig. A.1 depicts calculated killing frost frequencies, minimum GDD5 and minimum JJA precipitation.

Fig. A.1: Potential tree growth limitation for boreal, broadleaf deciduous and Mediterranean forest in Europe in the present-day simulation by the percentage of years with killing frosts (ykf), minimum GDD5 (GDD5) and minimum JJA precipitation (pp).


A.2. Calculated present-day killing frost frequencies, GDD5 and minimum JJA precipitation

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A.3. Additional references


Appendix. Supplementary data

Supplementary data related to this article can be found online at doi:10.1016/j.quascirev.2011.08.002.
References


