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Climate reconstruction from pollen and $\delta^{13}\text{C}$ records using inverse vegetation modeling – Implication for past and future climates

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Abstract. An improved inverse vegetation model has been designed to better specify both temperature and precipitation estimates from vegetation descriptions. It is based on the BIOME4 vegetation model and uses both vegetation $\delta^{13}\text{C}$ and biome as constraints. Previous inverse models based on only one of the two proxies were already improvements over standard reconstruction methods such as the modern analog since these did not take into account some external forcings, for example CO_2 concentration.

This new approach makes it possible to describe a potential “isotopic niche” defined by analogy with the “climatic niche” theory. Boreal and temperate biomes simulated by BIOME4 are considered in this study. We demonstrate the impact of CO_2 concentration on biome existence domains by replacing a “most likely biome” with another with increased CO_2 concentration. Additionally, the climate imprint on $\delta^{13}\text{C}$ between and within biomes is shown: the colder the biome, the lighter its potential isotopic niche; and the higher the precipitation, the lighter the $\delta^{13}\text{C}$.

For paleoclimate purposes, previous inverse models based on either biome or $\delta^{13}\text{C}$ did not allow informative paleoclimatic reconstructions of both precipitation and temperature. Application of the new approach to the Eemian of La Grande Pile palynological and geochemical records reduces the range in precipitation values by more than 50% reduces the range in temperatures by about 15% compared to previ-

ous inverse modeling approaches. This shows evidence of climate instabilities during Eemian period that can be correlated with independent continental and marine records.

1 Introduction

Accurate and reliable paleoclimate reconstructions are crucial for evaluating the abilities of climate models to simulate future climates under different forcing scenarios. Early data-model comparisons were restricted to qualitative analyses because available paleoclimatic reconstructions that derived from data, such as pollen assemblages or stable isotope records, were only qualitative and could not be simulated by climate models. Quantitative reconstructions of paleoenvironmental parameters offer a more directly comparable and robust opportunity to evaluate climate model sensitivities. Such quantitative reconstructions were developed in the 1970s by the introduction of the so-called transfer function (Imbrie and Kipp, 1971).

On continents, the first quantitative estimates of paleoclimate were based on various versions of the modern analog method of pollen assemblages. They allowed great advances in understanding past climate on terrestrial surfaces (Bartlein et al., 1986; Guiot et al., 1989; Howe and Webb III, 1983; Overpeck et al., 1985; Sabatier and Van Campo, 1984; Webb III and Bryson, 1972); however, these reconstruction methods were based on assumptions which are not all valid. First, any past pollen assemblage is assumed to be well approximated by the modern analog, but glacial assemblage



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(and possibly others) lack good modern analogues. Second, plant-climate interactions are assumed to remain constant throughout time. Implicitly this assumes that these interactions are independent of changes in atmospheric CO_2 (Cowling and Sykes, 1999), whereas a number of physiological and palaeoecological studies (Farquhar, 1997; Polley et al., 1993) have shown that plant-climate interactions are sensitive to atmospheric CO_2 concentration. Therefore, mechanistic vegetation models that account for ecophysiological processes have been used to resolve these problems (Guiot et al., 1999; Wu et al., 2007). The models simulate the natural vegetation (biome) that would grow in prescribed climatic conditions (climatic niche) under specific temporal and spatial forcings (CO_2 concentration, insolation, soil type and texture, elevation, etc.). Some vegetation models include an isotopic fractionation routine with which they simultaneously simulate the associated $\delta^{13}\text{C}$. The paleoclimatic approach consists of inverting such models, i.e. estimating past climate, which is an input of the model, based on a comparison between data and model outputs. Comparison is applied to either biomes and plant assemblages (Guiot et al., 2000; Wu et al., 2007) or to the $\delta^{13}\text{C}$ of vegetation (Boom et al., 2002; Hatté and Guiot, 2005). The comparison process is either empirical (Boom et al., 2002) or based on a statistical inverse modeling procedure (Guiot et al., 2000). Since extra-tropical biomes are mainly functions of temperature, inverse modeling of biomes is highly dependent on temperature, whereas inverse modeling of $\delta^{13}\text{C}$ is related to precipitation.

In the paleoclimate context, a key issue is to approximate vegetation $\delta^{13}\text{C}$ by measuring the sediment $\delta^{13}\text{C}$, which provides unique evidence of the original vegetation isotopic composition. Vegetation $\delta^{13}\text{C}$ undergoes isotopic shift during pedogenesis and fossilization, thus sediment $\delta^{13}\text{C}$ is rarely identical to original vegetation $\delta^{13}\text{C}$. The magnitude of this isotopic shift differs greatly based on fossilization conditions, ranging from negative to positive values, but always within the $\pm 2\%$ range (see for example Balesdent et al., 1993; Nguyen Tu et al., 2004; Poole et al., 2004; Van Bergen and Poole, 2002). Vegetation modeling with isotopic fractionation simulation may be able to address this geochemical issue.

In this study, we present the approach using palynological and isotopic data as constraints for inverse vegetation modeling. We first look at relationships between temperature, precipitation and $\delta^{13}\text{C}$ under different atmospheric CO_2 concentrations within a biome and between biomes. We then apply inverse modeling to the Eemian of La Grande Pile palynological record to illustrate how (to which extent) this method addresses both geochemical and paleoclimatological questions.

2 Data and method

2.1 La Grande Pile data

La Grande Pile is located in Eastern France, south of Les Vosges mountain, at $47^\circ 40' \text{N}$, $6^\circ 30' \text{E}$, 330 m a.s.l. The annual precipitation is 1000 mm and mean annual temperature is 9.5°C with a seasonal range of about 18°C between the warmest and the coldest months ($18.5\text{--}0.5^\circ\text{C}$). The GPXXI core studied in this paper was retrieved at the Grande Pile site at the same time as those investigated by Woillard (1978).

Pollen preparation, analysis and treatment were performed for the Rousseau et al. (2006a) study; further details are available therein. Based on pollen assemblages and the definition of Prentice et al. (1992) updated by Bigelow et al. (2003) and Kaplan et al. (2003), Rousseau et al. (2006a) assigned every pollen sample to the most likely biomes.

Total nitrogen, organic carbon and carbon stable isotope were measured on bulk samples (Rousseau et al., 2006a). Based on the C:N ratio, samples suspected to result from a mixture of algal and superior vegetation were rejected.

2.2 Inverse vegetation modeling

Simulations were performed with the BIOME4 vegetation model (Kaplan, 2001; Kaplan et al., 2002) using an inverse modeling procedure derived from Guiot et al. (2000) and Hatté and Guiot (2005).

We performed two sets of simulations. The first characterized the climatic and isotopic niches of some boreal and temperate biomes and defines relationships between mean annual temperature, annual precipitation and $\delta^{13}\text{C}$. The second was designed to reconstruct past climate from the La Grande Pile Eemian by combining palynological and geochemical studies.

We decided to simulate environmental conditions relevant to the establishment and growth of boreal and temperate biomes identified today and during the last Interglacial (De Beaulieu and Reille, 1992; Guiot et al., 1993; Rousseau et al., 2006a; Woillard, 1978) at La Grande Pile. Focusing on only one location (rather than on a geographical gradient) allows us to restrict our discussion on modeling implication to the influence of climate on both vegetation and stable isotope composition. Indeed, side parameters like latitude, longitude and altitude, which may all impact simulated biome and indirectly reconstructed climatic parameters, remain constant in this work. Furthermore, considering similar interglacial climatic periods (modern and Eemian) allows us to consider degradation conditions as roughly similar.

2.2.1 BIOME4 vegetation model

BIOME4 is a process-based terrestrial biosphere model (Kaplan, 2001; Kaplan et al., 2002) modified from BIOME3 (Haxeltine and Prentice, 1996) which includes an isotopic fractionation routine. This routine was improved by Hatté

and Guiot (2005) to account for external forcing dependence of parameters involved in isotopic fractionation. Model inputs include latitude, soil textural class, and monthly climate (temperature, precipitation and insolation) data. The model can be run for any site with complete climatic and soil data. BIOME4 considers 13 potential Plant Functional Types (PFTs), representing the major bioclimatic types and growth forms of terrestrial plants. A proper combination of PFTs determines a particular biome among 28 potential ones. BIOME4 uses a coupled carbon and water flux scheme to determine, by iterative calculation, the maximum leaf area index (LAI) which maximizes the net primary production (NPP) for any given PFT based on soil water balance, canopy conductance, photosynthesis, respiration and phenological state. Competition among PFTs is simulated by using the optimal NPP of every PFT as an index of competitiveness. BIOME4 determines the dominant, co-dominant, and grass-dominant (if different) PFTs. It then determines the output biome from the successful PFTs, the corresponding NPP, respiration, gross primary production (GPP=NPP minus respiration), and LAI. Fractionations by C3 and C4 plants are computed using a model modified from Lloyd and Farquhar (1994). The mean annual isotopic fractionation is estimated by weighting monthly fractionation of C3 and C4 in all PFTs by the respective NPP. BIOME4 then allocates the isotopic fractionation to the output biome, weighted according to the NPP of each PFT.

This model accounts for physiological adaptation of plant to environmental changes by simulating the stomates closure, but, as all vegetation models that can be used in paleoclimatological studies does not account for plants genetic evolution.

2.2.2 Inverse modeling procedure

We follow the procedure of Guiot et al. (2000), based on a Monte-Carlo sampling of monthly precipitation and monthly temperature in a pre-defined range (Metropolis-Hastings algorithm, Hastings, 1970). For each run, five parameters are randomly varied until minimizing the difference between observed and predicted $\delta^{13}\text{C}$. They are (i) January temperature, (ii) July temperature, (iii) January precipitation, (iv) July precipitation (the temperature and precipitation of the other months are calculated by sinusoidal interpolation between January and July), and (v) $1/S^2$, the inverse residual variance, also called the precision of the estimates. $1/S^2$ illustrates model and inversion precision. The percentage of sunlight for each month, which is also an input of BIOME4, is estimated by linear regression from temperature and precipitation of the same month as described by Guiot et al. (2000). An improvement for future works could be to accommodate monthly changes in the incoming solar irradiance due to altered orbital parameters according to the concerned period. Meanwhile, $\delta^{13}\text{C}$ is also calculated for each run and compared to the target value to check the quality of the fit. Agree-

ment between the inferred parameters and targets is computed only when the simulated biome matches the target and is evaluated using the following equation:

$$\text{LH} = -\frac{(\delta^{13}\text{C}_o - \delta^{13}\text{C}_s)^2}{S^2} \quad (1)$$

where subscripts o and s correspond to target and simulated values, respectively.

Generally, convergence is achieved after several thousands of model runs (20 000 runs typically last ca 1 hour on a current office computer). Modeling results consist of probability distributions (from which a 95%-confidence interval can be computed) of the five input parameters from which mean annual precipitation and temperature are evaluated.

For the first set of simulations, which aimed to characterize biome isotopic niche, we set S^2 to a constant value (equal to 1) to avoid adding noise to the precision of the estimated niche. We further set a LH threshold of -0.2 (uncertainty on $\delta^{13}\text{C}$ lower than 0.45‰). A LH under this threshold means that the target $\delta^{13}\text{C}$ cannot be reached within the target biome. The corresponding simulation is thus rejected.

For the second set of simulations, which aimed to reconstruct past climate from La Grande Pile palynological and geochemical data, we set a LH threshold at -0.5 (uncertainty on $\delta^{13}\text{C}$ lower than -0.7‰) to encompass both uncertainties from the physical measurement (lower than $\pm 0.15\text{‰}$) and from the geochemical correction (lower than $\pm 0.5\text{‰}$). This choice matches the ability of BIOME4 to reconstruct target $\delta^{13}\text{C}$ with a precision better than 0.6‰ (Hatté and Guiot, 2005).

2.2.3 Input vector for inverse vegetation modeling

First set of simulations (biome isotopic niche)

For each inverse modeling simulation, an input vector was defined which specified one of the boreal or temperate biomes available within BIOME4. These biomes include erect dwarf-shrub tundra (DShTund), high and low-shrub tundra (ShTund), cold evergreen forest (EgTaig), cold deciduous forest (DeTaig), cool evergreen needleleaf forest (CoCoFo), cool mixed forest (CoMxFo), cool-temperate evergreen needleleaf and mixed forest (CIMxFo), temperate grassland (TeGr1) and temperate deciduous broadleaf forest (TeDeFo).

The BIOME4 input vector also included parameters characterizing latitude, longitude, altitude ($47^\circ 44' \text{N}$, $6^\circ 30' 14''$, 330 m a.s.l.) and soil type and texture, which are defined according to the Food and Agriculture Organization (FAO) present time grid and vary according to the target biome (from that grid we estimated typical values for each biome). Atmospheric CO_2 concentration was specified at one of four levels (220, 260, 300 and 360 ppm – from glacial to modern value) and atmospheric $\delta^{13}\text{C}$ was set constant at -6.8‰ by reference to a mean MIS5.5 value recently obtained by

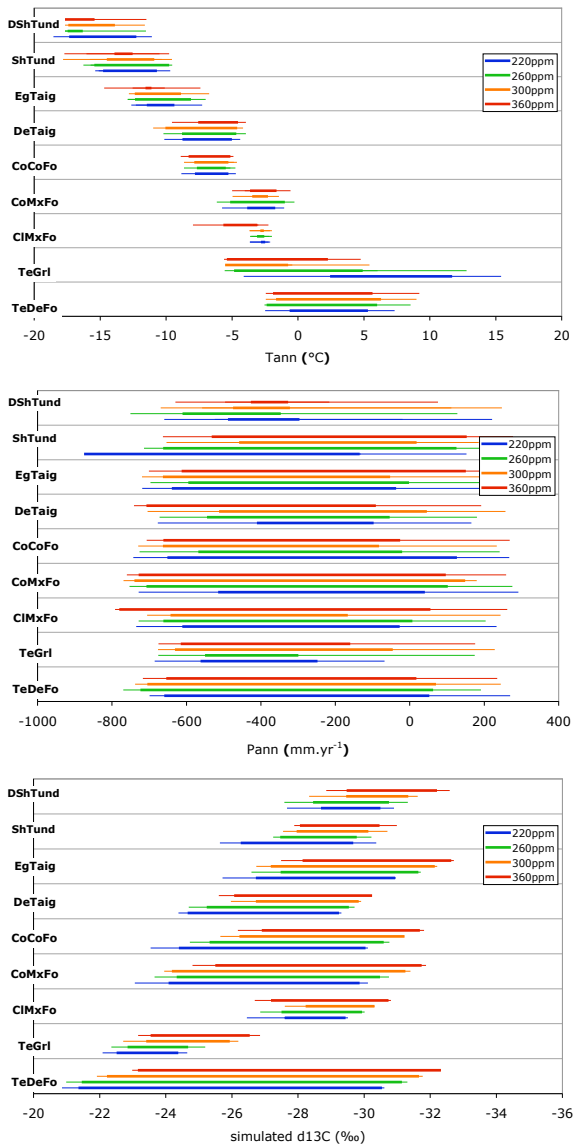


Fig. 1. Climatic and isotopic niches for nine temperate and boreal biomes.

This shows potential domains in terms of mean annual temperature (a – upper panel), annual precipitation (b – middle panel) and mean $\delta^{13}\text{C}$ (c – lower panel, please note that the x-axis of c-panel is inverse) for erect dwarf-shrub tundra (DShTund), high and low-shrub tundra (ShTund), cold evergreen forest (EgTaig), cold deciduous forest (DeTaig), cool evergreen needleleaf forest (CoCoFo), cool mixed forest (CoMxFo), cool-temperate evergreen needleleaf and mixed forest (CIMxFo), temperate grassland (TeGrl) and temperate deciduous broadleaf forest (TeDeFo). Four atmospheric CO_2 concentrations are shown here: 220 ppm (blue line), 260 ppm (green line), 300 ppm (orange line) and 360 ppm (red line). Bold lines are for median values whereas fine lines are for 2-sigma uncertainties. Precipitation and temperature are shown as anomalies relative to modern reference values (9.5°C of mean annual temperature and 1000 mm yr^{-1} of annual precipitation).

Schmitt and Fischer (2005). Likewise, in each run $\delta^{13}\text{C}$ was set at one of 10 target values within the interval $[-36\text{‰}; -21\text{‰}]$. Since this range is much larger than the natural range, most of target $\delta^{13}\text{C}$ values are not realistic and cannot be simulated. This will necessarily exhibit the whole array of potential isotopic niches for each of the considered biomes.

Second set of simulations (Eemian climate of La Grande Pile)

For each level, an input vector was constructed which defined (1) target biomes as the two with the highest scores achieved by the biomisation procedure (further information in Rousseau et al., 2006a), (2) the vegetation $\delta^{13}\text{C}$ based on measured $\delta^{13}\text{C}$, (3) the atmospheric CO_2 concentration based on the Petit et al. (1999) record interpolated to the timescale of La Grande Pile, (4) the isotopic composition of atmospheric CO_2 , set constant at -6.8‰ (Schmitt and Fischer, 2005), (5) latitude, longitude, altitude and (6) soil type and texture.

3 Results and discussion

3.1 Potential isotopic niche

The niche theory (Grinnell, 1917; Grinnell, 1924) makes it possible to describe the relationships between the biomes and their environment. In any environmental space (for example, the 2-D precipitation – temperature space), the distribution areas that are relevant to the establishment and growth of any biome can be represented. The “potential environmental space” fills the whole space described by these two variables, while only the area called “realized environmental space” exists in the real world (Austin, 1985). By analogy, an “isotopic space” can be described where the “potential isotopic niche” is the whole possible distribution of $\delta^{13}\text{C}$ that might relate to a biome and the “realized isotopic niche” is the range that effectively exists. Since our simulation does not account for species competition but considers each biome independently, the isotopic range shown in this study is the potential niche, not the realized one.

Figure 1 shows the existence domains for nine of the biomes that grow and have grown in La Grande Pile. These domains are defined by mean annual temperature, annual precipitation and $\delta^{13}\text{C}$. Figure 1a clearly illustrates one of the parameters at the origin of biome definition: a strong relationship prevails between the biomes progression and the annual mean temperature. Conversely, the biome is not determined by annual precipitation (Fig. 1b). All biomes simulated here can grow under a very wide range of precipitation regimes that almost totally overlap. Figure 1c shows the potential isotopic ranges of the nine biomes. Isotopic niche is finite and encompasses ranges of 3.6 to 10.9‰-units. Even with more or less overlap, potential isotopic value follows a gradient (except for TeDeFo). This relationship between

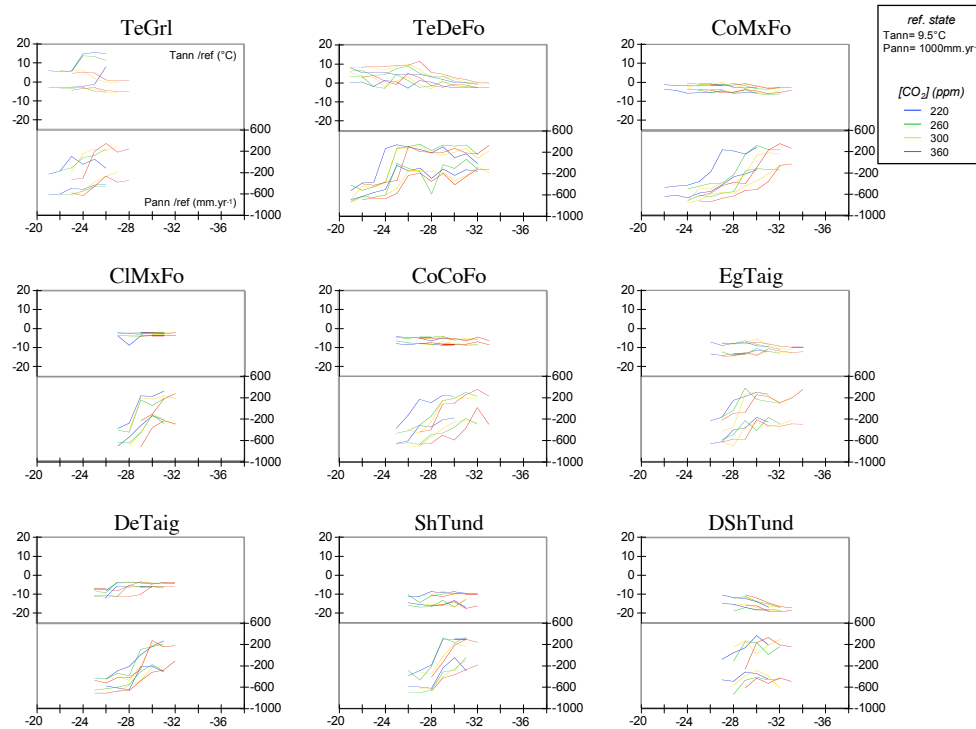


Fig. 2. Relationship between potential $\delta^{13}\text{C}$ and precipitation or temperature for nine temperate and boreal biomes, with an enlargement for CoMxFo and TeGrl in Fig. 2b.

Minimum and maximum limits of potential domains of existence are shown here for nine biomes (see Fig. 1 for legend). Four atmospheric CO_2 concentrations (220 ppm: blue, 260 ppm: green, 300 ppm: orange, 360 ppm: red) are considered. Precipitation and temperature are shown as anomalies relative to modern reference values (9.5°C of mean annual temperature and 1000 mm yr^{-1} of annual precipitation).

$\delta^{13}\text{C}$ and biome has to be compared to the one linking biome and temperature. Biomes with cold environmental niche show the lightest isotopic range. Our results highlight another key point: the validity of isotopic fractionation modeling within BIOME4 is supported by the observed CO_2 dependence of isotopic niche. Isotopic niche shifts toward more negative values under higher CO_2 concentration. This is in agreement with the results of Feng and Epstein (1995) that show $\delta^{13}\text{C}$ depletion of about 2‰ for 100 ppm increase of CO_2 and in agreement with other studies that show similar results (Garten and Taylor, 1992; Pasquier-Cardin et al., 1999; Van De Water et al., 2002). The implications for vegetation under future climate conditions are also illustrated. Some biome niches move according to CO_2 level. If potential niches of biomes under different CO_2 concentration remain roughly the same or at least greatly overlap, clear discrepancies exist for the most likely niches (median values in bold line in Fig. 1). As an example, at a mean annual temperature of 6.5°C , two major biomes coexisted under 220 ppm: CIMxFo and CoMxFo. They were replaced by TeGrl and CoMxFo when concentrations were increased to 360 ppm. Likewise, TeGrl requires mild temperature (mean annual temperature of 12 to 20°C) to grow under 220 ppm of CO_2 ; the temperature range expands 4 to 9°C under 300 ppm

of CO_2 . This illustrates the likely consequences of human-induced CO_2 increases for vegetation replacement in the near future.

Figure 2 and its enlargement for CoMxFo and TeGrl in Fig. 3 present $\delta^{13}\text{C}$ distributions within a single biome and their relationship to precipitation and temperature for four different CO_2 concentrations. No correspondence between $\delta^{13}\text{C}$ and mean annual temperature within a biome is clearly expressed. Conversely (with the exception of TeDeFo which remains unexplained), a clear correlation between $\delta^{13}\text{C}$ and annual precipitation is shown here: high precipitation implies lower $\delta^{13}\text{C}$. The pattern of the precipitation/ $\delta^{13}\text{C}$ relationship reveals a stress state expressed in the stable isotope signature. Heavy (less negative) $\delta^{13}\text{C}$ is associated with a low precipitation regime corresponding to a stressful environment. The precipitation range allowing plant growth with heavy $\delta^{13}\text{C}$ is very narrow compared to the potential precipitation range associated with a lighter (more negative) $\delta^{13}\text{C}$.

It appears that CO_2 concentration change does not imply a supplementary stress, since precipitation and temperature potential ranges remain roughly the same size. A slight shift toward milder conditions is evident only for lower CO_2 concentrations.

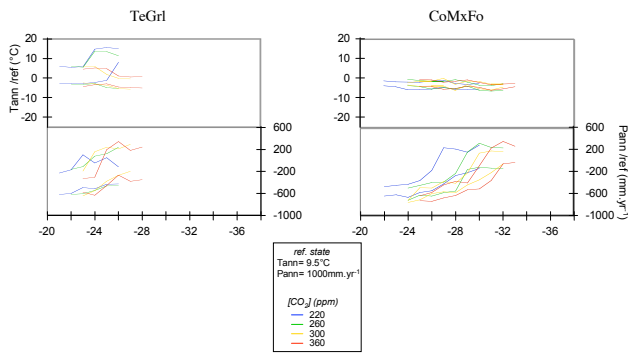


Fig. 3. Measured $\delta^{13}\text{C}$ bracketed by the potential isotopic niches of targeted biomes.

Background color is associated with the simulated biome: green for TeDeFo, orange for CoMxFo, blue for EgTaig. Pink squares are for measured $\delta^{13}\text{C}$ (error is of ca 0.1‰ according to level). Bold blue lines are for min and max limits of the potential isotopic niche associated with the output biome (CO_2 variations are considered).

In summary, we have identified a rough gradient of $\delta^{13}\text{C}$ between biomes (the colder the biome, the lighter its potential isotopic niche) and within each biome (the higher the precipitation, the lighter the $\delta^{13}\text{C}$).

3.2 Contribution to organic geochemistry

With each biome being defined by a potential isotopic niche, it is possible in some cases to specify the impact of plant organic matter degradation on the original isotopic composition. Indeed, a $\delta^{13}\text{C}$ of sediment organic matter outside of the potential isotopic niche of the associated biome obviously results in an isotopic shift linked to organic matter degradation. Measured $\delta^{13}\text{C}$ are shown in Fig. 4 bracketed by the potential isotopic niche of the associated biome under the specified CO_2 concentration simulated during this experiment. Few points are plotted off the potential range. The highest levels represent depleted values compared to the potential isotopic niche of the associated biome whereas $\delta^{13}\text{C}$ from the lowest levels are enriched. In humid environments, a classical degradation moves $\delta^{13}\text{C}$ towards enriched values for the highest levels, whereas degradation of the lowest levels induces depleted $\delta^{13}\text{C}$ values. These lowest levels have been effectively characterized by an orange color (Rousseau et al., 2006a) that is likely associated with better preservation of carbohydrates due to sulfurization. Carbohydrates are isotopically heavier than average organic matter. Better preservation of carbohydrates induces enriched organic matter $\delta^{13}\text{C}$. Apart from levels undergoing specific and local degradation, the isotopic shift deduced from the highest levels (regular degradation in a humid environment) can be applied along the series to retrieve the original isotopic signature. Indeed, since this series records interglacial climate (a relatively stable climate), quite similar degradation

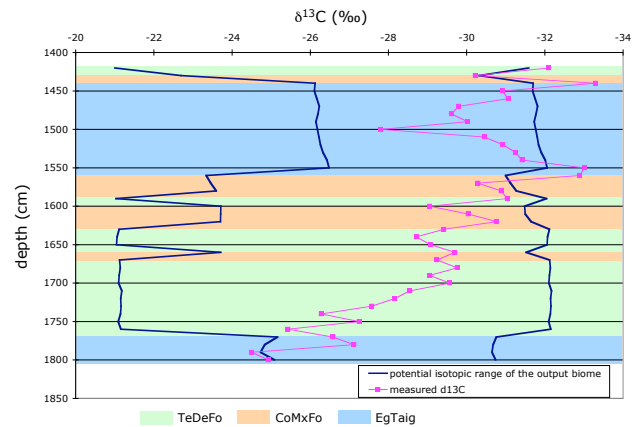


Fig. 4. Interest of double constraints inverse modeling

This is a zoomed version of Fig. 2 for cool mixed forest (CoMxFo) and temperate grassland (TeGr) under 260 ppm of atmospheric CO_2 . Panels on the left (a) show the potential climatic domain that can be reconstructed from inverse modeling of the biome only. This is the white area and is equal to the whole potential climatic niche: 1100 and 850 mm yr^{-1} ranges for precipitation and 7 and 20°C ranges for temperature, for CoMxFo and TeGr respectively. Panels on the right (b) show the potential climatic domain that can be reconstructed using inverse modeling with the double constraint. $\delta^{13}\text{C}$ with an uncertainty of $\pm 0.5\text{‰}$, which is much higher than physical measurement uncertainty, allows us to greatly restrict the white area. In case of CoMxFo under 260 ppm CO_2 , precision increases by a factor of 2.75 and 1.2 for precipitation and temperature respectively. For TeGr, precision increases by a factor of 1.3 for both precipitation and temperature.

conditions can be assumed throughout this period, and the degradation-induced isotopic shift can be assumed to be constant. The applied correction will leave isotopic signatures within the range of the potential isotopic niches. Moreover to further study the La Grande Pile record, we enlarge the $\delta^{13}\text{C}$ uncertainty range to make it encompass both physical measurement error and diagenesis derived isotopic shift

Briefly, for particular levels, isotopic inverse modeling contributes to better specification of degradation pathways by (1) defining the lower limit of the isotopic shift and (2) highlighting particular degradation pathways.

3.3 Contribution to paleoclimatology

A benefit for understanding paleoclimatology based on the double constraint inverse model is illustrated in Fig. 5 by a forest biome, Cool Mixed Forest (CoMxFo), and a grassland biome, Temperate Grassland (TeGr). It shows that coupling both inverse modeling approaches based on pollen derived biome and sediment $\delta^{13}\text{C}$ greatly improves estimates ranges of both reconstructed temperature and precipitation. On the leftmost panels (Fig. 5a, c), the white space indicates the potential climatic niche of CoMxFo and TeGr. The extent of this niche is about 7°C to 20°C in mean annual temperature

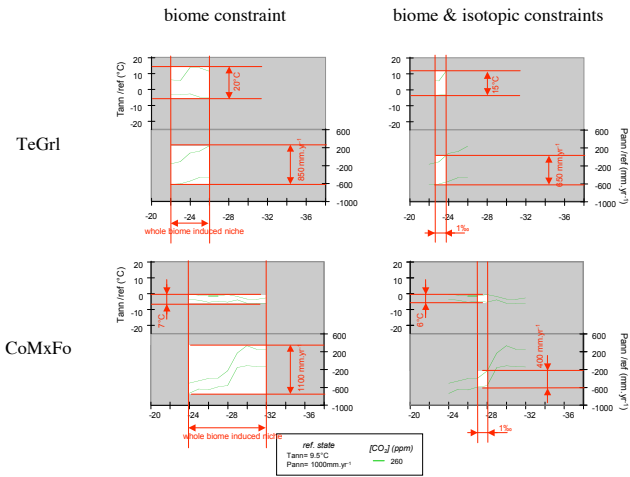


Fig. 5. Temperature and precipitation reconstruction at La Grande Pile during the Eemian period.

Mean annual temperature and annual precipitation reconstructed by biome(s) and $\delta^{13}\text{C}$ inverse modeling are shown here. They are bracketed by the domain that encompasses both potential climatic niches of both most likely biomes (bold lines).

and 1100 to 850 mm yr^{-1} in annual precipitation. Constraining the reconstruction using only the biomes, the estimated niche is relatively well specified in temperature but extremely large in precipitation. We demonstrated a strong relationship between $\delta^{13}\text{C}$ and precipitation; therefore, adding $\delta^{13}\text{C}$ to the biome as a constraint would greatly reduce the potential precipitation range. On Fig. 6b, d, $\delta^{13}\text{C}$ is defined with 1‰ uncertainty. 1‰ is significantly larger than current instrumental error, which remains below 0.2‰. 1‰ of possible variation thus encompasses both instrumental error and at least part of the degradation induced-isotopic shift. Crossing the potential climatic niche of CoMxFo/TeGr1 and $\delta^{13}\text{C}$ results in a shorter range of about 6°C/15°C for mean annual temperature and of 400/650 mm yr^{-1} for annual precipitation. An estimate of annual precipitation for CoMxFo considering $\delta^{13}\text{C}$ as a constraint is about a third of the original value obtained by the single biome constraint. Similar results are obtained under other atmospheric CO_2 concentrations and for others biomes (Fig. 2).

As a rationale, our method requires processing of both palynological and geochemical records. This induces that an upstream error that can be derived from an inadequate handling of one or both records would be perpetuated through the inverse modeling procedure. As an example, inadequate procedure prior geochemical measurements (Gauthier and Hatté, 2008) or the presence of absence of a single pollen grain of a single taxon in the pollen counts can cause a change in the biome that is identified by the biomisation technique. Improvements for future studies would be to use the abundance of plant functional types identified in the pollen spectra (PFT-scores) instead of biomes (Davis et al., 2003).

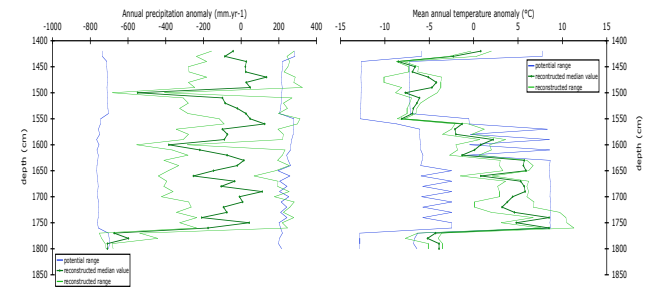


Fig. 6. Atlantic and Grande Pile Eemian paleoclimatic records. The left panel shows *N. pachyderma* $\delta^{18}\text{O}$ recorded in the MD95-2042 core (37°48' N 10°10' W 3146 m) for the Eemian period (Shackleton et al., 2002). The middle and right panels present the mean annual precipitation and annual temperature in La Grande Pile during the Eemian period, reconstructed by biome(s) and $\delta^{13}\text{C}$ inverse modeling. Median values are bracketed by their 95%-confidence intervals. Bars underline cold events recognizable in both marine and continental records. Data are presented versus the age model described in Rousseau et al. (2006b).

In summary, the description of reconstructed precipitation is greatly improved (by more than a factor of two) by biome and $\delta^{13}\text{C}$ inverse modeling.

3.4 Application on Eemian of La Grande Pile

Considering our previous geochemical results and the assumption that for time periods under similar climatic conditions degradation can be assumed to be roughly constant, we decided to apply a -1% degradation isotopic shift throughout the studied period (estimated original $\delta^{13}\text{C}$ = measured $\delta^{13}\text{C}$ + 1‰). Nevertheless, to account for this induced uncertainty, the LH threshold was set at -0.5 (corresponding to a $\delta^{13}\text{C}$ deviation of on average 0.7‰) instead of -0.2 .

Results are shown in Fig. 6. Mean annual temperature and annual precipitation reconstructed by biome(s) and $\delta^{13}\text{C}$ inverse modeling are presented bracketed by the combined domain of potential climatic niches of both of the most likely pollen-derived biomes. This figure clearly demonstrates the added value of the double constraints inverse vegetation model. Precipitation reconstruction would have remained constant and not informative ($[-600; +200 \text{ mm yr}^{-1}]$ in precipitation anomaly) for the whole studied period with biome as the single constraint. Precision increases by more than a factor of two and even reaches a factor of four by considering both isotopic fractionation and biome as combined constraints. Furthermore, reconstructed temperature ranges are often specified by a factor two for the same period.

This improvement within paleoclimatic reconstructions allows us to highlight important climatic shifts that have previously been recognized in marine records (McManus et al., 1994, 2002; Shackleton et al., 2002) but have been only poorly documented in continental records. Figure 6 illustrates some cooling events identified in both oceanic and

continental records. Heinrich Event 11 (Heinrich, 1988) is then marked by a very dry (about 300 mm yr^{-1}) and relatively cold period (mean annual temperature of 2°C). An initial 5°C cooling event at 117–116 ka can be linked to the sea surface cooling C26 recorded in the central North Atlantic. This cooling is contemporaneous with a 200 mm yr^{-1} precipitation decrease. After 115 ka, a progressive cooling in mean annual temperature is recorded, followed 1000 to 2000 years later by a decrease in precipitation by ca 400 mm yr^{-1} . A sudden cooling at 109 ka followed 2000 to 3000 years later by a sharp decrease of mean annual precipitation of ca 500 mm yr^{-1} . Decreased temperature with a stationary precipitation regime leads to longer wet winters. For the middle latitudes, this conjunction of low temperature with high precipitation likely mirrors a similar situation further north that would have been favorable to ice-sheet extension. Ice build-up agrees with climate modeling that shows northern hemisphere ice volume growth starting ca 115 ka with a maximum at ca 108 ka (Sanchez-Goni et al., 2005). A climatic improvement is recorded as 108 ka by a sharp increase of mean annual precipitation by ca 500 mm yr^{-1} and a slight warming. This milder climate, which lasted until 104 ka, was recognized as a Brörup period. This is in agreement with travertine growth that very rapidly accumulated in Germany around 106–105 ka (Frank et al., 2000). Paleoclimatic interpretation in a global context is further developed in Rousseau et al. (2006a).

4 Conclusions

The inverse biome vegetation modeling, constrained by both $\delta^{13}\text{C}$ and pollen, allows us to better specify both temperature and precipitation estimates from vegetation description than was previously done with single constraint inverse modeling. Two major applications of this new approach are presented. First, it makes it possible to define potential isotopic niches of temperate and boreal biomes. This exhibits a relationship between $\delta^{13}\text{C}$ and external forcing such as temperature, precipitation and CO_2 concentration. CO_2 increase thus induces replacement of a biome by another in a prescribed (Tann, Pann) space and high precipitation implies light $\delta^{13}\text{C}$. Second, application to paleoclimate enables us to reduce the uncertainty in the temperature estimates and to divide it by a factor of two to four for precipitation estimates. Paleoclimatic reconstruction carried out at La Grande Pile for the Eemian period thus provides evidence for climatic oscillations that is correlated with independent marine and continental records. This method of evaluating the precision of the reconstruction is much more satisfying here as it is based on the true tolerance of the vegetation to its environment and not simply on the statistical error of the transfer function which mainly depends on the data available for the calibration.

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