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Climate and CO_2 modulate the C_3-C_4 balance and $\delta^{13}C$ signal in simulated vegetation

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Abstract

Fossil pollen data and $\delta^{13}C$ measurements from cores collected in peatbogs or lakes have shown major changes in the terrestrial vegetation during Late Quaternary. Although the effect of climate on the C_3-C_4 balance has been discussed for 50 years, the impact of a low atmospheric CO_2 during the Last Glacial Maximum (LGM) was emphasized recently and conflicting evidence exists. In this paper, we use a physiologically-based biome model (BIOME4) in an iterative mode to simulate vegetation response to changing mean climate conditions and atmospheric CO_2 partial pressure (p_{CO_2}). In particular, we investigate the transition from LGM to present conditions in two sites which changed from either a C_4- or a C_3-dominated vegetation to the opposite pole, respectively at Kuruyange (Burundi) and Lingtaï (Central Loess Plateau, China). The response of the C_3-C_4 balance and $\delta^{13}C$ signal in the simulated vegetation are investigated. The results show that the vegetation is primarily sensitive to temperature and p_{CO_2}. Rainfall impacted the simulated variables below a threshold which decreased with higher p_{CO_2}. Climate and p_{CO_2} interacted differently between the two sites showing indirect effects on the $\delta^{13}C$ signal. Moreover, the plant functional types (PFTs) differed in their composition and in their response between the two sites, emphasizing that the competition between C_3 and C_4 plants cannot be hardly considered as a simple binary scheme. Our results confirm the advantages of using process-based models to understand past vegetation changes and the need to take account of multiple drivers when the C_3-C_4 balance is reconstructed from a palaeo-$\delta^{13}C$ signal.

1 Introduction

Evidence of the relative influence of climate and p_{CO_2} on the balance between C_3 and C_4 plants come from two sources essentially. The first type of evidence derives from current patterns which indicate that C_4 plants abound more in warm and dry conditions. Meanwhile, meta-analysis and experiments in controlled conditions have

led to mixed results with respect to the competitive advantage of C_4 species at low CO_2 concentration (Wand et al., 1999; Ward et al., 1999, p_{CO_2}). C_4 species are less sensible to photorespiration than C_3 plants (Sage, 2004) and can tolerate low p_{CO_2}. The second type of evidence derives from the analysis of $\delta^{13}C$ signal along cores. Because they discriminate ^{13}C differently during photosynthesis, C_3 and C_4 species have different carbon isotopic composition ($\delta^{13}C$), and hence leave different isotopic signal in paleorecords. Sequences of $\delta^{13}C$ sampled along cores are routinely used to the reconstruct C_3-C_4 balance, i.e. the proportion of C_4 for instance in the vegetation (Gu et al., 2003; Wang et al., 2008) which we note r_{C_4}. Meanwhile, pollen assemblages can be used to reconstruct climatic parameters and p_{CO_2} and their changes through time (Guiot, 1994; Guiot et al., 2000).

Different patterns of $\delta^{13}C$ during the transition from the Last Glacial Maximum (LGM) to Holocene led to various conclusions regarding the relative influence of climate and CO_2 on the C_3-C_4 balance (Aucour et al., 1999; Huang et al., 2001; Gu et al., 2003). Large changes occurred in climatic conditions and in the chemical composition of the atmosphere. The concentration of atmospheric CO_2 gradually increased from 180 ppmv to 270 ppmv, which alone could induce vegetation changes (Cole and Monger, 1994; Jolly and Haxeltine, 1997; Street-Perrott et al., 1997). Samples from the intertropical African highlands revealed high values of $\delta^{13}C$ during the LGM ($>-18‰$), and low during the late Holocene (Aucour and Hillaire-Marcel, 1994; Aucour et al., 1999, $-28.5<\delta^{13}C<-19.5‰$). These variations were consistent with pollen records taken in peatbogs or lakes which revealed a shift in the C_3-C_4 balance at the end of the LGM, from grasslands with C_4 species to montane forests with a majority of C_3 trees (Jolly et al., 1997).

Accumulated evidence moderated this view and several studies concluded that climate was the main control on the abundance of C_4 plants (Huang et al., 2001; Gu et al., 2003; Zhang et al., 2003; Liu et al., 2005a). The comparison of $\delta^{13}C$ sequences in lakes of South America revealed opposed trends (Huang et al., 2001). The authors concluded that differing trajectories originated from differing local climatic conditions,

since all sites shared the same p_{CO_2} (Huang et al., 2001). At a regional/continental scale, aridity appeared as the dominant control on the C_3-C_4 balance (Schefusz et al., 2003). Reported $\delta^{13}C$ sequences from central China reveal lower values during the LGM than during late Holocene (Gu et al., 2003; Wang et al., 2008). This trend was interpreted as an increase of the abundance of C_4 species in time in response to warmer conditions (Zhang et al., 2003) or increased monsoon intensity with higher temperature and rainfall (Liu et al., 2005a).

The reconstruction of the C_3-C_4 balance in empirical studies is based on a linear model between the $\delta^{13}C$ and r_{C_4} (e.g. Gu et al., 2003): $\delta^{13}C = r_{C_4} \times \delta^{13}C_{C_4} + (1 - r_{C_4}) \times \delta^{13}C_{C_3}$ where $\delta^{13}C_{C_4}$, and $\delta^{13}C_{C_3}$ are the values of $\delta^{13}C$ of the C_3 and C_4 poles, the most commonly used values being −26 and −13‰ (Deines, 1980), respectively. However, climate and p_{CO_2} have direct effects on r_{C_4} and on $\delta^{13}C_{C_3}$ and $\delta^{13}C_{C_4}$ as well (Wang et al., 2008). The carbon isotopic ratio of C_3 plants increases with decreasing water availability for instance. This trend has been evidenced along rainfall gradient (Liu et al., 2005b; Wang et al., 2008). In C_4 plants, the response of $\delta^{13}C$ to water stress depends on the degree of leakiness. C_4 plants tolerate low ratio of intercellular to atmospheric p_{CO_2} ratio ($\frac{c_i}{c_a}$) during warm hours, whereas stomatal conductance of C_3 strongly decreases under water stress.

The purpose of this work is to simulate the C_3-C_4 balance in various conditions of climate and atmospheric CO_2 to investigate their respective influence. We use a process-based equilibrium model to simulate the Net Primary Production of the vegetation as well as the respective values of $\delta^{13}C$ in C_3 and C_4 in designed climatic scenarii. We use the model outputs to study the relationships between climate and p_{CO_2} and two features of the simulated vegetation that are the proportion of C_4 NPP (C_3-C_4) and the carbon isotope composition of the bulk vegetation ($\delta^{13}C$). Namely, we consider two sets of climatic conditions and p_{CO_2} that correspond to the current climate and to LGM conditions and investigate the responses to the two types of forcings in two contrasted sites located in the highlands of equatorial Africa and on the central Loess plateau in

China.

2 Methods

2.1 Site selection

We chose to focus on sites differing in current and past climatic conditions and vegetation in addition of being located in areas where reconstructions of paleoclimate have been previously conducted. Two sites were selected for comparison, one located in intertropical Africa (Kuruyange) and one located on the loess plateau in China (Lingtaï).

Kuruyange lies in the interlacustrine highlands in Central Africa (Burundi) in the current altitudinal range of montane forests. These forests are present in the area as fragments of broad-leaved forest inbetween cultivated and grazed land (Jolly et al., 1997). In Kuruyange as in intertropical Africa overall, the local vegetation was essentially composed of cold grasses and scrub during the LGM (Hamilton, 1982; Bonnefille and Riollet, 1988; Vincens, 1991; Taylor, 1992; Jolly and Haxeltine, 1997). After ca. 10–11 kyr BP, it was progressively replaced by a tropical montane forest (Coetzee, 1967; Hamilton, 1972; Taylor, 1990, 1993; Bonnefille et al., 1991, 1995; Vincens, 1991; Jolly et al., 1994). In pollen records, Poaceae and Cyperaceae, including C_4 species, are abundant at the LGM. After 10 kyr BP, the grasses tend to disappear from records, whereas C_3 trees become more abundant.

Lingtaï lies on the Loess plateau in central China. The vegetation in the area is a mixed forest of temperate coniferous and broad-leaved trees and many grass species. Studies of $\delta^{13}C$ in core sequences showed that C_4 plants were absent of the vegetation at the LGM which was mostly steppe and desert vegetation (Yu et al., 2000). During the Holocene, C_4 plants became more abundant (Gu et al., 2003; Wang et al., 2008).

2.2 Current and past climate

Climatic data were extracted from the 10×10′ grids published by New et al. (2002) considering the nearest grid point from sites location. Monthly precipitations in mm/month, mean temperatures in °C, and mean sunshine in % of day length were taken at (−3.583°, 29.750°, 1850 m a.s.l.) for Kuruyange in Burundi, and (35.083°, 107.583°, 1180 m a.s.l.) for Lingtaï in China.

Annual precipitation and mean annual temperature were respectively 1370 mm, 18.0°C for Kuruyange, and 600 mm, 10.2°C for Lingtaï. Kuruyange has a typical equatorial climate with consistent monthly temperatures throughout the year, three warm and dry months during summer and high rainfall from September to May (Fig. 1). Climatic parameters were estimated respectively about 4±2°C and 40±10% lower at the LGM in the area (Bonnefille et al., 1990; Bonnefille and Chalié, 2000).

Lingtaï has a continental climate with a cold and dry winter and low rainfall concentrated in summer. The climate on the Loess plateau is largely controlled by the East Asian Monsoon (EAM) system (Balsam et al., 2004). Estimates of mean annual temperature anomaly at the LGM range between −7 and −10°C in northern and central China compared to current conditions, and −4 and −6°C in southern areas (Zheng et al., 1998). Rainfall was between 400 and 600 mm lower in the regions under the current influence of the EAM (Zheng et al., 1998).

2.3 Simulated climate and p_{CO_2}

We used the model to analyse the C_3-C_4 balance response to various conditions of p_{CO_2} and climate. In order to deal with realistic distributions of climate parameters, climatic conditions were derived from the actual current climate observed in the two sites. Soil parameters were obtained from the FAO database. Cloudiness was kept constant in all simulations. We conducted two types of simulations with either constant p_{CO_2} or constant temperature and rainfall distributions.

First, current distributions of temperature and precipitation were modified to adjust

the mean annual temperature $\left(\overline{T}\right)$ and annual rainfall (P_a) to chosen values, while keeping the overall shape of the distributions. These simulations therefore reflect changes in annual values, not seasonality although the amplitude of the distribution changed. For a given change in temperature, $\Delta\overline{T}$, monthly means were adjusted as $T_i^{'} = T_i + \Delta T$, where T_i is the mean temperature of month i. Monthly rainfall were modified in a similar way. For a given change in precipitation, ΔP_a, monthly means were adjusted as $P_i^{'} = (1 + \frac{\delta P}{P_a})P_i$, where P_i is the amount of precipitation of month i and P_a is the annual amount of precipitation. We ran the model at two different values of p_{CO_2}:

1. the LGM level (180 ppmv, Monnin et al., 2001),
2. the current level CO_2 (360 ppmv).

Second, we studied the influence of p_{CO_2} under fixed climatic conditions. Responses to p_{CO_2} were simulated in each site under the current climatic conditions and under estimated conditions at the LGM as described in the previous section. p_{CO_2} was changed gradually from 180 to 540 ppmv.

2.4 Model description

The BIOME4 model (Kaplan et al., 2002) is a process-based equilibrium model for terrestrial vegetation of the BIOME family (Prentice et al., 1992; Haxeltine and Prentice, 1996). The inputs fed in the model are monthly temperatures, rainfalls and cloudiness, absolute minimal temperatures, soil textures, latitude, atmospheric pressure through altitude and p_{CO_2}. Incoming solar radiation is calculated using current orbital parameters and average albedo. The model uses a two-layers description of soil, with different textures and depths. Run-off is evaluated, but lateral fluxes are not redistributed. Routines are included to approximate additional risks due to canopy fire and snow.

The models simulates 13 Plant Functional Types (PFT, Table 1). These PFTs are primarily constrained by absolute bioclimatic tolerance limits, such as the minimal sup-

ported number of growing days over 5°C. These constraints determine whether the NPP of a given PFT is calculated or not. A photosynthesis-based growth procedure then optimizes the NPP and the optimal Leaf Area Index (LAI) for each of the potentially present PFTs under local climatic conditions. This calculation is based on a coupling between water and carbon fluxes in the plant (Haxeltine et al., 1996). Ten PFTs out of 13 are exclusively C_3, one is exclusively C_4, and two may use either pathway (Table 1). Water fluxes in the model depend on water availability in local soil and evapo-transpiration of soil and plants. Plant evapo-transpiration is controlled by the stomatal conductance of the PFTs which integrates to canopy conductance. In turn, the stomatal conductance controls $\frac{c_i}{c_a}$ and thus the concentration of CO_2 available for photosynthesis.

Revisions of BIOME4 by Hatté and Guiot (2005) mostly concerned three aspects of photosynthesis and carbon isotopic discrimination depending on PFTs' pathways (see Hatté and Guiot, 2005, for details). The model of carbon isotopic discrimination originally followed Lloyd and Farquhar (1994) and produced estimates of Δ_A which is the total discrimination against $^{13}CO_2$ during carbon assimilation, i.e. from the atmosphere to the photosynthetates. Hatté and Guiot (2005) first imposed a lower limit on the $\frac{c_i}{c_a}$ ratio for C_3 PFTs to avoid situations of stomatal closure. Second, the revised version takes into account the photosynthetic pathway of all potentially present PFTs – not only of the dominant, and weights isotopic fractionation by NPP which allows to take the stored carbon into account. Both pathways are taken into account in PFTs that can be either C_3 or C_4. Third, refined isotopic fractionation during photosynthesis is simulating by taking temperature influence into account.

We studied two response variables obtained from the model outputs in the different scenarii: the fraction of NPP that is produced by C_4 photosynthesis: $r_{C_4} = \frac{\sum_{C_4} \mathrm{NPP}}{\sum \mathrm{NPP}}$ where the sum is on the three PFTs that are obligate or facultative C_4 in the numerator and on all PFTs in the denominator (Table 1), and the carbon isotopic ratio, $\delta^{13}C$, at the bulk vegetation level. $\delta^{13}C$ was obtained form the simulated values of Δ_A as $\delta^{13}C = \frac{\delta_{atm} - \Delta_A}{1 + \Delta_A}$

where δ_{atm} is the atmospheric value which was fixed at −8‰.

3 Results

Change in r_{C_4} and $\delta^{13}C$ from the LGM to current conditions

The proportion of C_4 NPP (r_{C_4}) was 6% in the vegetation simulated at Kuruyange and 0% at Lingtaï under mean LGM conditions (Table 2). Starting from mean LGM conditions, the change in r_{C_4} was positive at the two sites, and lower at Kuruyange (+14%) than Lingtaï (+23%). However, the change in r_{C_4} was highly sensible to incertitude in climatic parameters at Kuruyange, and showed negative values down to −22% at the upper bound of the climatic parameters. Starting from average LGM conditions, $\delta^{13}C$ decreased by −3.2‰ at Kuruyange and increased by +1.9‰ at Lingtaï (Table 2). The signs of the change were consistent over the complete range of climatic parameters at the two sites.

Response to climate at fixed p_{CO_2}

The proportion of C_4 NPP (r_{C_4}) and the carbon isotopic composition of the vegetation ($\delta^{13}C$) showed overall the same responses to temperature and precipitation in the two sites (Fig. 2 and 3). Changes in rainfall had weak effects on r_{C_4} and $\delta^{13}C$. The response of $\delta^{13}C$ to temperature was hardly linear in the two sites and less variable at Kuruyange than at Lingtaï. At Kuruyange, the response was hardly dependent of rainfall, except in cases of large decrease in rainfall ($\Delta P_a < -500$ mm, Fig. 2a and 2b). The surface response was rough and more contrasted in Lingtaï and water limitation occurred below −300 mm (Fig. 2b and 2d).

Positive temperature changes implied increasing r_{C_4}, but no C_4 NPP was simulated in cases of strong negative changes in mean annual temperature, whatever the change in rainfall or p_{CO_2} (Fig. 2). The maximal simulated value of r_{C_4} was 45% at Kuruyange

CPD
5, 1187–1213, 2009

in the current condition of p_{CO_2} (Fig. 2a), and 61% in the LGM condition (Fig. 2c). These numbers were respectively 43% and 85% in Lingtaï (Fig. 2b and 2d). The range of simulated $\delta^{13}C$ was (−33, −23)‰ at Kuruyange in the current condition of p_{CO_2} (Fig. 2a), and (−30, −18)‰ in the LGM conditions (Fig. 2c). At Lingtaï, these ranges were respectively (−35, −23)‰ (Fig. 2b) and (−31, −19) (Fig. 2d).

CO_2- and temperature-induced change

In the following section, we focus on the responses of r_{C_4} and $\delta^{13}C$ to p_{CO_2} and temperature. We investigate two different sets of climatic conditions:

1. the current climatic conditions of rainfall and temperature ($\Delta\overline{T}$=0 and ΔP_a=0, Fig. 1),
2. the average LGM conditions at Kuryange: $\Delta\overline{T}$=−4°C, ΔP_a=−350 mm (Bonnefille et al., 1990; Bonnefille and Chalié, 2000), and at Lingtaï: $\Delta\overline{T}$=−6°C, ΔP_a=−400 mm (Zheng et al., 1998).

The proportion of C_4 NPP (r_{C_4}) and the carbon isotopic composition of the vegetation ($\delta^{13}C$) both responded negatively to increase in p_{CO_2} (Fig. 4a and 4b). The two sites showed low simulated values of r_{C_4} in the climatic conditions of the LGM, whatever the p_{CO_2}. At Kuruyange, the simulated responses of $\delta^{13}C$ were similar in the two sets of climatic conditions (Fig. 4a). On the contrary, transition from the LGM climate to the current climate at Lingtaï induced an increase in $\delta^{13}C$ (Fig. 4) whatever the p_{CO_2} (Fig. 4b).

The change in $\delta^{13}C$ from the mean LGM to the current conditions can be decomposed in one variation due to climate and one to p_{CO_2}. Quantitatively, $\delta^{13}C$ decreased by −3.2‰ in Kuruyange (Table 2). The variation due to an increase in p_{CO_2} under constant climate was between −3.5 (current conditions) and −4.6‰ (LGM conditions), whereas the change due to the transition from the LGM to the current climate only was

between +0.3 (at current p_{CO_2}) and +1.4‰ (at LGM p_{CO_2}). In Lingtaï, $\delta^{13}C$ increased by +1.9‰ (Table 2). Climate and p_{CO_2} interacted less than in Kuruyange, so that the change due to increasing p_{CO_2} was −4.1‰, and the change due to the transition in climatic conditions was +6.7‰ (Fig. 4b).

Positive temperature change increased in r_{C_4} and $\delta^{13}C$ in all simulations (Fig. 4c and 4d). The increase was steeper in r_{C_4} in Kuruyange compared to Lingtaï. As seen in Fig. 2, no C_4 photosynthesis occurred below −5°C of temperature change at Kuruyange in both sets of tested conditions (Fig. 4c). At Lingtaï, the threshold on r_{C_4} was lower (≈−7°C, Fig. 4d).

Response of the PFTs

We studied in detail the contribution of the different PFTs to the response profile of r_{C_4} and $\delta^{13}C$ to temperature. The response of the different PFTs to temperature (Fig. 5) reveal the effect of abrupt changes in the composition of the vegetation in PFTs on r_{C_4} and $\delta^{13}C$, as seen also on the Figs. 2 and 3.

In the current conditions, tree PFTs had the highest NPP (tet, tft, tee, cot, Fig. 5a) in Kuruyange, followed by the tropical grass type (tog) and the woody desert type (wde). Major changes in the composition in PFTs occurred at values of $\Delta\overline{T}$ around −4, −2, 2 and 5°C. The temperate and tropical grass types coexisted for $\Delta\overline{T}$ values between −4 and −2°C. In Lingtaï, the simulated NPPs were dominated by the "temperate deciduous tree" type (ted, Fig. 5b), the "temperate grass type" (teg) and the "woody desert type". Majors changes occurred above 1°C where the "conifer tree" type became productive, below −2°C where the "boreal tree" types (bet, bdt) replaced the "temperate deciduous tree" type.

Increased p_{CO_2} from the LGM to the current level had a fertilization effect on all PFTs (Fig. 5). This effect led to decreased r_{C_4} and increased $\delta^{13}C$ (Fig. 5).

4 Discussion

This study demonstrated interacting effects of climate and p_{CO_2} on the balance between C_3 and C_4plants, and on the resulting $\delta^{13}C$ signal in vegetation using simulation. Our study evidenced that climate had a prevailing effect over CO_2 on the C_3-C_4 balance. Temperature was the most limiting factor on C_4 NPP at the two studied sites, while the influence of rainfall was lower and differed across the sites. These results agree with studies of palaeosequences in central China (Gu et al., 2003; Zhang et al., 2003; Liu et al., 2005a) and in central America (Huang et al., 2001). Our results also show that changes in p_{CO_2} affected the C_3-C_4 balance, although more weakly, and implied changes in the vegetation $\delta^{13}C$ signal. In another simulation study Jolly and Haxeltine (1997) concluded that change in p_{CO_2} level alone could drive large vegetation changes.

The overall responses of the C_3-C_4 balance to simulated climatic conditions were the same between the two sites, but the changes simulated in response to the transition from the LGM to the current conditions highly differed. Namely, the simulated balance at Kuruyange was between +20% and −22%, thus showing high sensitivity to the incertitude in climatic parameters. Palaeodata indicate that the proportion of C_4 plants was higher at the LGM than in more recent records (Jolly et al., 1997; Aucour et al., 1999). Our results thus suggest that the anomaly in mean temperature at the LGM was probably closer to the estimated upper bound ($\Delta\overline{T}=-2^{\circ}C$, Bonnefille et al., 1990) than to the lower ($\Delta\overline{T}=-6^{\circ}C$). At Lingtaï, the proportion of C_4 plants increased from the LGM to the current conditions, despite incertitude in climatic parameters, which corresponded to observations in core sequences (Gu et al., 2003; Wang et al., 2008).

The climatic conditions impacted $\delta^{13}C$ differently across the two sites as a result of a double control of climate on the vegetation $\delta^{13}C$. First, a change from LGM climatic conditions to the current ones favored a higher proportion of C_4 plants. The change in the C_3-C_4 balance induced an increase in the bulk $\delta^{13}C$ which could be compensated

by changes in the $\delta^{13}C$ values of the C_3 pole (Boom et al., 2002; Wang et al., 2008), and of the C_4 pole to a lesser extent. This second effect was stronger in Lingtaï than in Kuruyange. In Kuruyange, p_{CO_2} had stronger influence on $\delta^{13}C$ than in Lingtaï. The relative influence of climate and p_{CO_2} at the two sites relates to the current distribution of temperature and rainfall, the seasonality of which was conserved in the simulations. In Kuruyange, climatic conditions are less stressful than in Lingtaï where winter temperatures and rainfall are low. The effect of changing the mean annual temperature and total rainfall therefore induced a stronger response in $\delta^{13}C$ at the chinese site compared to the african site.

The decrease of $\delta^{13}C$ at Kuruyange and increase at Lingtaï during the transition from the LGM to the current conditions were in agreement with changes observed in cores from Kuryange (Aucour et al., 1999) and Lingtaï (Gu et al., 2003). The simulated change was lower in absolute value than the observed change at the two sites. Our purpose here was not to reconstruct the $\delta^{13}C$ signal obtained in cores but to identify trends and effects of climate and p_{CO_2}. We used a process-based model that simulates the isotopic discrimination in the living vegetation (Kaplan et al., 2002). Adjustments to the model output need to be taken into account if one wants to approach values recorded in cores (Wang et al., 2008). The total organic content (TOC) of cores yields larger $\delta^{13}C$ values than the ^{13}C signal in the vegetation (Liu et al., 2005a) which is better estimated using *n*-alkanes (Boom et al., 2002; Wang et al., 2008). Here the model simulated the $\delta^{13}C$ signal of the vegetation which is thus closer to that measured in *n*-alkanes.

The influence of climate and p_{CO_2} on the $\delta^{13}C$ value of C_3, and C_4 plants to a lesser extent highlights the need for controlling this effect when reconstructing the C_3-C_4 balance. The drier conditions at the LGM induce a trend to higher $\delta^{13}C$ in C_3 plants, as found currently along rainfall gradients (Liu et al., 2005b; Wang et al., 2008). Meanwhile, a lower p_{CO_2} also implies a higher $\delta^{13}C$ (Lloyd and Farquhar, 1994). These effects add to the bioclimatic constraints limiting the potentially present PFTs with potential direct effects on the proportion of C_4 plants. Also pedogenesis effects increase

the $\delta^{13}C$ of the soil organic matter with depth (Wang et al., 2008), whereas on a longer time scale, diagenesis depletes the organic matter in ^{13}C to a small extent (Meyers, 1994). These effects thus enforce the need for correcting the $\delta^{13}C$ of the C_3 and C_4 poles when reconstructing the C_3-C_4 balance (Wang et al., 2008).

The balance turns to the advantage of C_3 plants at high temperature and rainfall when p_{CO_2}increases. For the C_4 PFTs, the simulated catalytic activity of RuBisCO is independent of the ambient CO_2 concentration (Haxeltine et al., 1996). CO_2 interferes only with the Light Use Efficiency to reduce photosynthesis rates at low intercellular concentrations. On another hand, both effects are accounted in the computation of C_3 photosynthesis rates. With increasing concentration of CO_2, these effects are reduced and C_3 PFTs become more competitive. The domain of living conditions is reduced for C_4 plants.

The analysis of the PFTs response showed that changes in their composition corresponded to important changes in the r_{C_4} response to temperature. The selection of potential PFTs in the model is essentially based on temperature constraints (mean temperature of the coldest month; absolute minimal temperature, number of days over 0 or 5°C) and snow cover. Hence, the list of present PFTs changes with temperature, as shown in Table 1. Local productivity peaks are linked with differential productivities of the PFTs, and to a succession of different PFTs in the domain of simulation. The study of present PFTs is then essential for a given site.

The competitiveness of C_4 versus C_3 plants improved in conditions of water stress, as indicated by large percentages of C_4 NPP. Two effects can be called upon: C_4 PFTs may be supported by their lower canopy conductance and/or lower evapotranspiration rates (Haxeltine et al., 1996). At low atmospheric CO_2 levels, the simulated surfaces reveal the high sensitivity of C_4 PFTs to climate. The evolution of the different PFTs shows that the observed excursions were due to strong variations in the NPP values of the present PFTs. In the model formulation, evapotranspiration depends on the canopy conductance, which is inversely proportional to the diffusion gradient of CO_2 between the atmosphere and the intercellular air (Haxeltine and Prentice, 1996). Therefore,

increased p_{CO_2} tends to reduce evapotranspiration. Consequently, the PFTs are more tolerant to low annual rainfall.

5 Conclusions

Biome models based on physiological processes allow us to disentangle the impact of the climate and CO_2 on ecosystems known to have been very sensitive in the past. Among these constraints, the atmospheric CO_2 is strongly implied in the fundamental process of photosynthesis. Therefore, it seems that a biogeographical approach of the vegetation is insufficient to describe its evolution. Nowadays, C_4 plants are rather known to be located at low altitude, under warm climatic conditions, in sub-desert or even desert areas, whereas C_3 plants are found at higher altitude, under cooler conditions. The C_3-C_4 balance seems to fit an intuitive altitudinal or thermic gradient. In the present study, p_{CO_2}, as well as the climate, have important effects on this balance. Vegetation modelling is necessary to apprehend the evolution of the vegetation, since it allows a mechanistic approach taking account of natural processes.

Vegetation modelling can contribute to simulate the coexistence of various C_3 and C_4 poles. Then, a new contribution of vegetation modelling could be the estimation of $\delta^{13}C$ for peculiar PFTs. This could provide a better reconstruction of the C_3-C_4 balance and allow comparisons between data and modelling results .

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Table 1. Characteristics of Plant Functional Types (PFT) in BIOME4 (Haxeltine et al., 1996). Phe.: phenology; E, evergreen; S, summergreen; R, raingreen; g_C: maximal value for minimum canopy conductance; E_{max}: maximum value of supported daily transpiration rate; value of sw below which raingreen leaves drop; value of sw above which raingreen leaves appear; R_{top}: fraction of roots in top soil layer, 30 cm from Jackson et al. (1996); LL: expected leaf longevity in months; GDD5: annual growing degree-days (GDD) above base temperatures of 5 and 0°C required for full leaf out; P.P.: photosynthetic pathway, C_3, C_4, or both.

Label	Type	Phe.	g_C	E_{max}			R_{top}	LL	GDD_5	GDD_0	P.P.
tet	Tropical evergreen tree	E	0.5	10			0.69	18			C_3
tdt	Tropical drought-deciduous tree	R	0.5	10	0.5	0.6	0.70	9			C_3
tee	Temperate broadleaved evergreen tree	E	0.2	4.8			0.67	18			C_3
ted	Temperate deciduous tree	S	0.8	10			0.65	7	200		C_3
cot	Cool conifer tree	E	0.2	4.8			0.52	30			C_3
bet	Boreal evergreen tree	E	0.5	4.5			0.83	24			C_3
bdt	Boreal deciduous tree	S	0.8	10			0.83	24	200		C_3
teg	Temperate grass	R	0.8	6.5	0.2	0.3	0.83	8		100	C_3/C_4
trg	Tropical grass	R	0.8	8	0.2	0.3	0.57	10			C_4
wde	Woody desert type	E	0.1	1			0.53	12			C_3/C_4
tsh	Tundra shrub	E	0.8	1			0.93	8			C_3
che	Cold herbaceous type	S	0.8	1			0.93	8		25	C_3
lfo	Lichen/forb	E	0.8	1			0.93	8			C_3

Table 2. Simulated C_3-C_4 balance (r_{C_4}, the proportion of C_4 Net Primary Production, NPP) and $\delta^{13}C$ of the vegetation at Kuruyange (Burundi) and Lingtaï (China) in the conditions of the Last Glacial Maximum (LGM: p_{CO_2}=180 ppmv; Kuryange: $\Delta\overline{T}$=−4±2°C, ΔP_a=−450±250 mm; Lingtaï: $\Delta\overline{T}$=8±2°C, ΔP_a=−500±100 mm) and in the current conditions (p_{CO_2}=360 ppmv; $\Delta\overline{T}$=0°C, ΔP_a=0 mm). The numbers in the square brackets indicate the simulated values using the extreme values of the climatic parameters.

	Kuruyange		Lingtaï	
	r_{C_4} (%)	$\delta^{13}C$ (‰)	r_{C_4} (%)	$\delta^{13}C$ (‰)
LGM	6 [0, 36]	−26.7 [−28.0, −23.4]	0 [0, 6]	−28.0 [−29.7, −27.4]
Current	20	−29.9	23	−26.1
Δ	+14 [+20, −22]	−3.2 [−1.9, −6.5]	+23 [+23, +17]	+1.9 [+3.6, +1.3]

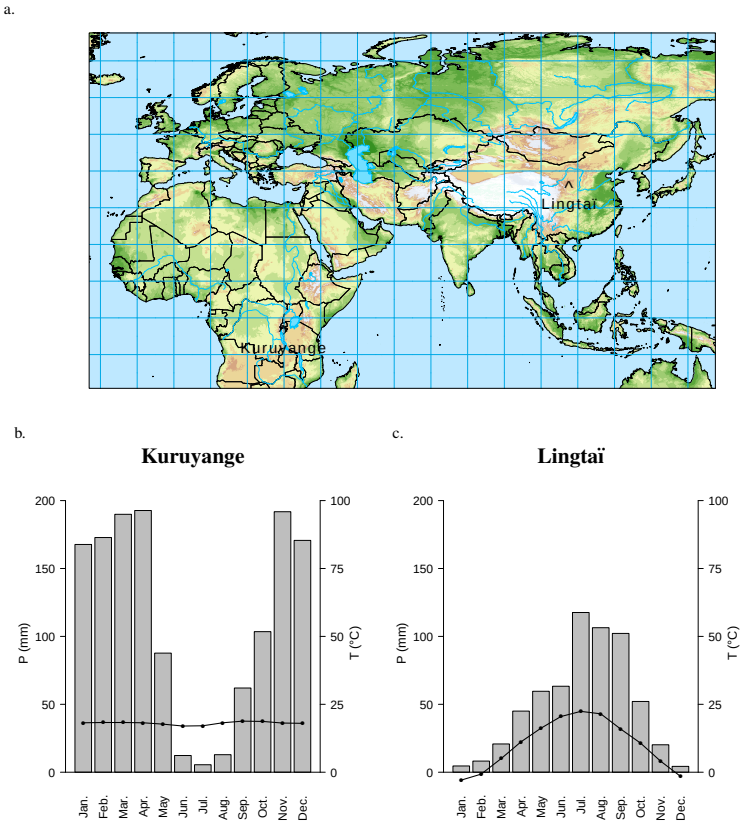

Fig. 1. (a) Location of the two study sites: Kuruyange in the intertropical highlands of Burundi, and Lingtaï on the Loess Plateau in central China; **(b)** Climatic diagram of Kuruyange (Burundi, mean annual temperature, $\overline{T}$=18.1°C, annual rainfall amount, P_{ann}=1380 mm); **(c)** Climatic diagram of Lingtaï (China, mean annual temperature, $\overline{T}$=10.2°C, annual rainfall amount, P_{ann}=600 mm), data taken from New et al. (2002).

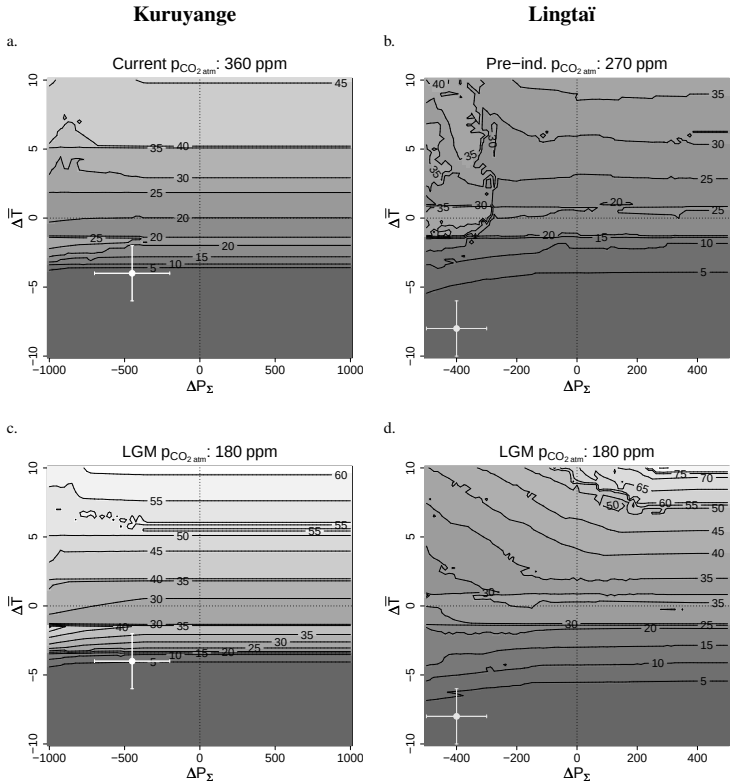

Fig. 2. Percentage of total NPP produced by C_4 photosynthetic as predicted by BIOME4 at Kuruyange (Burundi, **a** and **c**) and Lingtaï (China, **b** and **d**). $\Delta\overline{T}$, ΔP_a represent the simulated changes in mean annual temperature and annual rainfall with regards to the current values. Two cases of p_{CO_2} are presented: current level (360 ppm in a and c), and Last Glacial Maximum level (LGM, 180 ppm in b and d). Dashed lines indicates the current climatic conditions ($\Delta\overline{T}$=0, ΔP_a=0). The asterisk corresponds to climatic parameters during the LMG.

CPD
5, 1187–1213, 2009

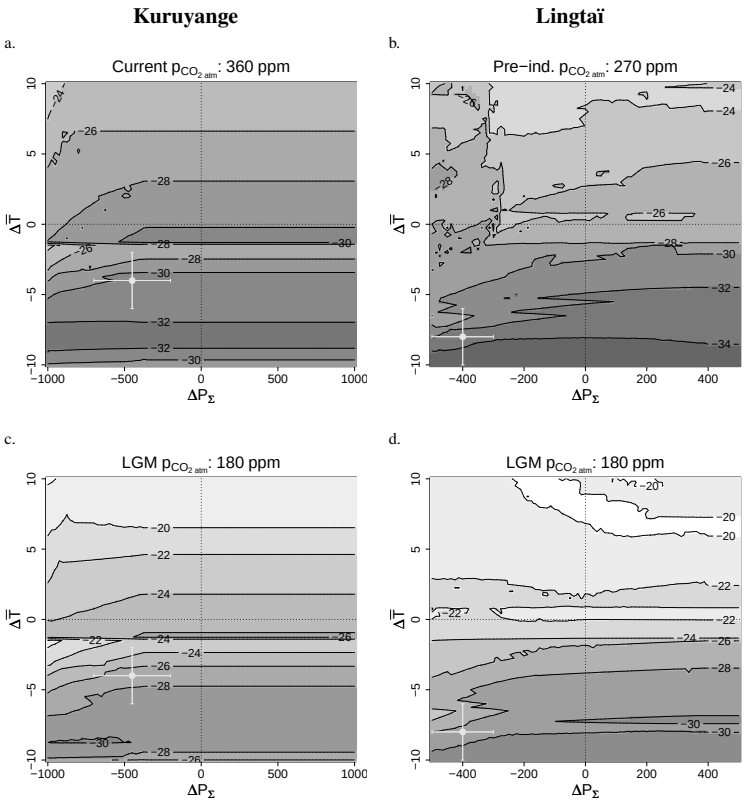

Fig. 3. Carbon isotope fractioning in predicted vegetation at Kuruyange (Burundi, **a** and **c**) and Lingtaï (China, **b** and **d**). $\Delta\overline{T}$, ΔP_a represent the simulated changes in mean annual temperature and annual rainfall. Two cases of p_{CO_2} are presented: current level (360 ppm in a and c.), and Last Glacial Maximum level (LGM, 180 ppm in b and d). Dashed lines indicates the current climatic conditions ($\Delta\overline{T}$=0, ΔP_a=0). The asterisk corresponds to climatic parameters during the LMG.

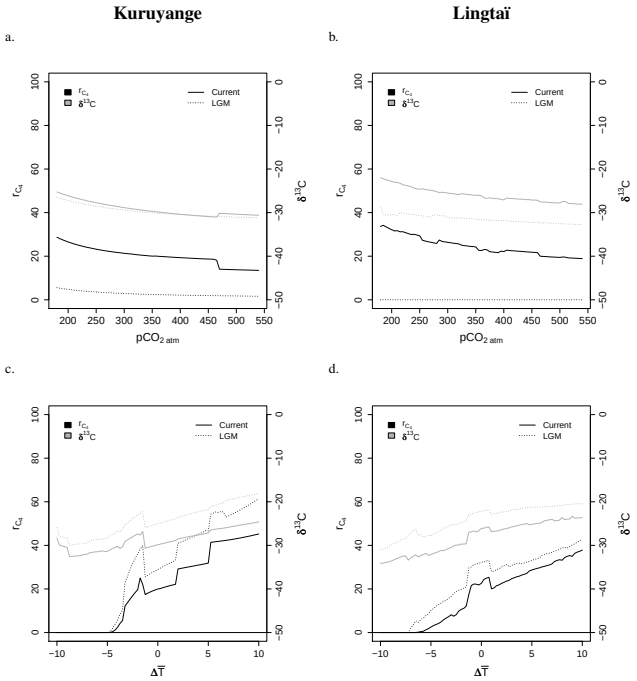

Fig. 4. Top: Response profile of the percentage of C_4 NPP (r_{C_4}, black lines) and carbon isotope fractioning ($\delta^{13}C$, gray lines) to p_{CO_2} in the simulated vegetation at Kuruyange (Burundi, **a**) and Lingtaï (China, **b**). Thick solid and dotted lines correspond respectively to the current climatic conditions at the site ($\Delta\overline{T}$=0, ΔP_a=0) and the mean LGM climatic conditions. Bottom: Response profile of the percentage of C_4 NPP (r_{C_4}, black lines) and carbon isotope fractioning ($\delta^{13}C$, gray lines) to temperature in the simulated vegetation at Kuruyange **(c)** and Lingtaï **(d)**. $\Delta\overline{T}$ represents the simulated change in mean annual temperature. Thick solid and dotted lines correspond to the current p_{CO_2} and rainfall at the site and the mean LGM climatic conditions.

CPD
5, 1187–1213, 2009

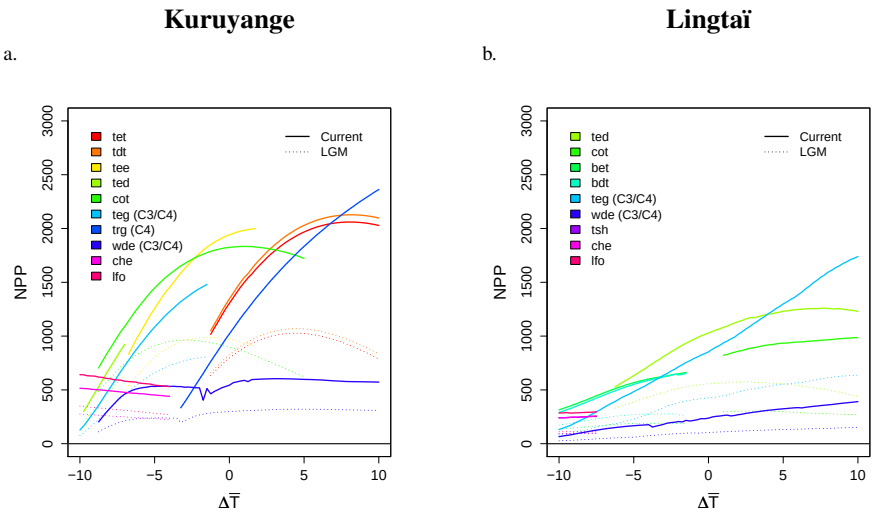

Fig. 5. NPP response profile to temperature of the simulated PFTs at Kuruyange (Burundi, **a**) and Lingtaï (China, **b**). Thick solid and dotted lines correspond to the current p_{CO_2} and rainfall at the site and the mean LGM climatic conditions. The PFTs are labeled according to Table 1: tet, tropical evergreen tree; trt, tropical drought-deciduous tree; tbe, temperate broadleaved evergreen tree; tst, temperate deciduous tree; ctc, cool conifer tree; bec, boreal evergreen tree; bst, boreal deciduous tree; teg, temperate grass; tog, tropical grass; wde, woody desert type; tsh, tundra shrub; che, cold herbaceous type; lfo, lichen/forb.