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**Climate
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Impact of CO$_2$ and climate on the Last Glacial Maximum vegetation: results from the ORCHIDEE/IPSL models

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Abstract. Vegetation reconstructions from pollen data for the Last Glacial Maximum (LGM), 21 ky ago, reveal lanscapes radically different from the modern ones, with, in particular, a massive regression of forested areas in both hemispheres. Two main factors have to be taken into account to explain these changes in comparison to today's potential vegetation: a generally cooler and drier climate and a lower level of atmospheric CO$_2$. In order to assess the relative impact of climate and atmospheric CO$_2$ changes on the global vegetation, we simulate the potential modern vegetation and the glacial vegetation with the dynamical global vegetation model ORCHIDEE, driven by outputs from the IPSL_CM4_v1 atmosphere-ocean general circulation model, under modern or glacial CO$_2$ levels for photosynthesis. ORCHIDEE correctly reproduces the broad features of the glacial vegetation. Our modelling results support the view that the physiological effect of glacial CO$_2$ is a key factor to explain vegetation changes during glacial times. In our simulations, the low atmospheric CO$_2$ is the only driver of the tropical forests regression, and explains half of the response of temperate and boreal forests to glacial conditions. Our study shows that the sensitivity to CO$_2$ changes depends on the background climate over a region, and also depends on the vegetation type, needleleaf trees being much more sensitive than broadleaf trees in our model. This difference of sensitivity leads to a dominance of broadleaf types in the remaining simulated forests, which is not supported by pollen data, but nonetheless suggests a potential impact of CO$_2$ on the glacial vegetation assemblages. It also modifies the competitivity between the trees and makes the amplitude of the response to CO$_2$ dependent on the initial vegetation state.

1 Introduction

During the Last Glacial Maximum (LGM), 21 ky ago, the environmental conditions on the Earth's surface were very different from today. The climate was much colder, North America and Fennoscandia were covered by high ice-sheets, and the level of atmospheric CO$_2$ was only 185 ppm (Monnin et al., 2001). Pollen data reveal that the vegetation was also radically different from the modern potential vegetation. In all the following sections, we will always consider vegetation changes looking backward in time, i.e. at the LGM compared to present-day. At high latitudes, boreal and temperate forests regressed and migrated southward, replaced by tundra and grassland (Prentice et al., 2000; Tarasov et al., 2000; Ray and Adams, 2001; Harrison and Prentice, 2003). Subtropical deserts expanded and tropical forests were partly replaced by savanna and tropical grasslands, but did not completely disappear (Colinvaux et al., 1996, 2000; Marchant et al., 2009). These vegetation reconstructions have been widely used to reconstruct past climate conditions in terms of temperature and precipitations (e.g. Peyron et al., 1998; Tarasov et al., 1999; Farrera et al., 1999; Wu et al., 2007). Many of these studies considered that the climate was the only driver of vegetation changes in the past. However, the atmospheric level of CO$_2$ effects plant-climate interactions (Prentice and Harrison, 2009). It has an impact on photosynthetic rates but also on stomatal conductance and water-use efficiency. Under low CO$_2$ conditions, plants increase their stomatal conductance and their number of stomata to maintain a sufficient intake of CO$_2$. Consequently, evapo-transpiration increases and so does the loss of water (Cowling and Sykes, 1999). These physiological changes effect the climatic range in which a given ecosystem is sustainable. As a result, temperature and precipitation reconstructions from pollen data based on modern vegetation distribution may be biased.

In eastern Africa, glacial conditions led to the development of cool grasslands and xerophytic shrubs at the expense of the tropical montane forest. This forest regression used to be interpreted as the result of a cooler and drier climate over the region. Jolly and Haxeltine (1997) used the vegetation model BIOME3 (Haxeltine and Prentice, 1996) to test the relative impact of precipitation, temperature, and CO_2 on vegetation changes at the Kashiru site (Burundi), where a well-dated and high resolution pollen record is available for data-model comparisons. With a present-day CO_2 atmospheric concentration, a cooling of 6.5 °C is required to match the data and drive the transition from forest to shrubs in the model. Precipitation is not a limiting factor. But when CO_2 is decreased to 190 ppm, montane forest is replaced by shrubs even under present-day climate. This result demonstrated that the previous estimation from paleovegetation of a 6 °C LGM cooling in this region may be largely overestimated. This 6 °C cooling on land appeared as inconsistent with the LGM reconstructed sea-surface temperatures in the Indian Ocean, indicating temperatures only 0 to 4 °C cooler than present. Taking the CO_2 effect into account resolves this discrepancy between the reconstructions. Cowling et al. (2001) also used BIOME3 and studied the impact of the LGM conditions on another tropical forest, the Amazonian forest. They applied hypothetical temperature and precipitation anomalies (from 0 to −10 °C and from 0 to −60 %, respectively, relatively to modern values) and tested different atmospheric CO_2 levels, from 360 to 180 ppm. Even for extreme LGM conditions, changes in biomes were not very strong, but the leaf area index (LAI) was significantly decreased. They showed that the LAI was much more effected by the decrease in CO_2 than by the decrease in precipitation: a 20 % decrease in precipitation under modern CO_2 reduces the mean LAI by only 11 %, whereas a decrease in CO_2 from 360 to 220 ppm leads to an LAI decrease of 34 %. With the same model, Harrison and Prentice (2003) confirmed that atmospheric CO_2 plays a major role in tropical regions and showed that it is also a key parameter to explain the global reduction of forests during glacial times. They forced the BIOME4 model (Kaplan et al., 2003) with climatic LGM anomalies from different General Circulation Models (GCMs) superimposed to a modern climatology. Under an LGM climate and modern CO_2, tropical forests remain as extensive as today, whereas temperate and boreal forests regress, replaced by tundra. When the physiological effect of low CO_2 is taken into account, the extent of temperate and boreal forests is further reduced, and in the Tropics drought-tolerant vegetation develops at the expense of tropical forests. It also appears that low CO_2 favours deciduous forests at the expense of evergreen forests. Using a statistical method similar to Sykes et al. (1999) to measure dissimilarity between two biomes map, they found the effect of the decrease in atmospheric CO_2 to be on average 19 % of the effect of the climate change in the northern extra-tropics, and 49 % in the Tropics. Crucifix et al. (2005) obtained different results in their simulation of the glacial vegetation with the HadSM3_TRIFFID atmosphere-ocean-vegetation model. With this model, low CO_2 accounts for two thirds of the reduction in the biosphere carbon stock between preindustrial and the LGM, but changes in the dominant vegetation type were mainly driven by changes in climate. Moreover, the broadleaved/needleleaved competition was not significantly effected by the level of CO_2. Similarly, experiments with the global vegetation model LPJ for a few sites in Europe showed a significant impact of the glacial CO_2 on the LAI, but not on the vegetation composition (Ramstein et al., 2007).

These few studies clearly show that the effect of low CO_2 concentration on vegetation should be taken into account when reconstructing past climate from pollen data. This has recently been done by Wu et al. (2007), who re-evaluated LGM temperature and precipitation for Eurasia and Africa via an inverse modelling method using pollen data and the BIOME4 vegetation model. The new climate reconstruction obtained by this method is less cold and less dry than the previous estimations. The LGM climate simulated by GCMs being usually too warm compared to paleoreconstructions not taking the low CO_2 level into account (Pinot et al., 1999 for the Tropics and Kageyama et al., 2001, 2006; Ramstein et al., 2007 for Europe), the revised interpretation of data set carried out by Wu et al. (2007) revealed that models were not that wrong and LGM climate was probably not as cold as previously thought (Ramstein et al., 2007).

Only few modelling studies have actually explored the relative contribution of climate and CO_2 to the changes in vegetation type and structure at the LGM. Most of them use equilibrium biogeography models of the BIOME family, and this lack of diversity in the models makes it difficult to assess how much the results depend on the vegetation model chosen. We wanted to check the robustness of previous studies with a completely different model and chose the dynamical global vegetation model ORCHIDEE (Krinner et al., 2005). The model is forced off-line by outputs from the atmosphere-ocean general circulation model (AOGCM) IPSL_CM4_v1 (Marti et al., 2010) to simulate the global LGM vegetation cover. The use of vegetation fractions in ORCHIDEE instead of biomes allows to look more accurately to vegetation changes, which might be unnoticed otherwise with the BIOME family models, providing only one single biome over a grid-cell. We impose different climates and CO_2 levels in order to evaluate: (i) the impacts of these two most important forcing conditions for the vegetation, and (ii) how they combine. Our study offers a more detailed analysis than previous studies, with various different variables (area occupied, vegetation fraction, LAI, NPP). The layout of this paper is as follows. Section 2 describes the vegetation model ORCHIDEE, the AOGCM, and the climatic forcings used in this study. Section 3 presents the global vegetation simulated by ORCHIDEE for present-day and full glacial conditions.

Table 1. Surface types in ORCHIDEE and abbreviations used in this paper.

PFT	abbreviation
Bare soil	Bare soil
Tropical broadleaf evergreen trees	TrBE
Tropical broadleaf raingreen trees	TrBR
Temperate needleleaf evergreen trees	TempNE
Temperate broadleaf evergreen trees	TempBE
Temperate broadleaf summergreen trees	TempBS
Boreal needleleaf evergreen trees	BoNE
Boreal broadleaf summergreen trees	BoBS
Boreal needleleaf summergreen trees	BoNS
C3 grass	C3
C4 grass	C4

A brief qualitative model-data comparison for these two periods assesses the potential biases of the model. Then in Sect. 4 we analyse the relative impact of climate and CO_2 in terms of vegetation cover, LAI, and net primary productivity (NPP) changes and examine if the background climate has an impact on the sensitivity of vegetation to CO_2 changes. In Sect. 4.3, we investigate the role of dynamics and competitivity vs. photosynthesis, which to our knowledge had never been done so far. We discuss the results and conclusions in Sect. 5.

2 Material and methods

2.1 The ORCHIDEE dynamical global vegetation model

ORCHIDEE (Krinner et al., 2005) is a dynamic global vegetation model which simulates the distribution of ten natural plant functionnal types (PFT) and bare soil (see Table 1) as a result of climatic forcings and competitivity.

The different PFTs can coexist on every grid-cell, but grass cannot grow below trees. ORCHIDEE is run at the same spatial resolution as the forcing fields. The model includes three coupled submodels: a surface vegetation atmosphere transfer model (SVAT) called SECHIBA (Ducoudré et al., 1993; de Rosnay and Polcher, 1998), a module which simulates the phenology and carbon dynamics of the terrestrial biosphere (STOMATE), and a dynamical vegetation model inspired from LPJ (Sitch et al., 2003). This dynamical module simulates the competitive processes such as light competition, sapling establishment, or tree mortality. In this study, ORCHIDEE is forced off-line either by IPSL_CM4 outputs or by the CRU time series. In the case of IPSL_CM4 forcings, we use the high-frequency outputs (time step = 6 h) for the following variables: temperature, precipitation, specific humidity, wind, surface pressure, and short-wave and long-wave radiations. In the case of CRU forcings, we use the monthly values and activate the weather generator of ORCHIDEE, described in Krinner et al. (2005).

2.2 The IPSL_CM4 model and the climatic forcings

The IPSL_CM4_v1 AOGCM includes LMDz.3.3, the atmospheric component, with resolution of $96 \times 72 \times 19$ in longitude $\times$ latitude $\times$ altitude and a regular horizontal grid, and ORCA2, the ocean module, with an irregular horizontal grid of 182×149 points and 31 depth levels. Sea-ice is dynamically simulated by the Louvain-La-Neuve sea-Ice Model (LIM), and the coupling is performed thanks to the OASIS coupler. LMDz includes ORCHIDEE, but in the climatic simulations used here, STOMATE and LPJ were not interactive. Land, land-ice, ocean, and sea-ice can coexist on the same grid-cell of LMDz.

The AOGCM is used to simulate the climate of the 20th century (PRES) and the climate of the LGM. The LGM climate is the IPSL PMIP2 LGM run (see LGMb in Kageyama et al., 2009 for details; and Braconnot et al., 2007, and http://pmip2.lsce.ipsl.fr/ for the PMIP2 project). The glacial boundary conditions are as follows: ICE-5G ice-sheet reconstruction for the ice-sheets (Peltier, 2004); CO_2, CH_4, and N_2O levels set to 185 ppm, 350 ppb, and 200 ppb, respectively, (Monnin et al., 2001; Dallenbach et al., 2000; Flückiger et al., 1999); and orbital parameters for 21 ky BP (Berger, 1978), following the PMIP2 protocol. Since interactive dynamic vegetation is unavailable with this version of IPSL_CM4, vegetation is fixed to its present-day distribution, including agriculture, and the LAI is prescribed monthly, using present-day values. It can be noticed that for some regions, the presence of agriculture leads to a vegetation not so different from the LGM one: Europe, for instance, is covered by agricultural grass, which can be considered as close to the steppic vegetation present at the LGM. The simulated climate is cooler by $-4.2\,°C$ in global annual mean temperature. The cooling is stronger over the continents than over the oceans, especially in the high-latitudes of the Northern Hemisphere where it reaches more than $-20\,°C$ over the ice-sheets, due to the combined albedo and altitude effect, and also the sea-ice and snow albedo effect (Fig. 1 and Laîné et al., 2009). The climate is also globally drier, with a decrease in global mean annual precipitation of 8 %. The pattern of precipitation changes is heterogeneous, with a strong decrease of more than 80 % over the ice-sheets because of the orography effect and the strong cooling, up to 70 % in Central America, 50 % in Indonesia, and between 20 and 40 % in China and Siberia. Local increases of precipitation exist, over Amazonia (+15 %), North America south of the Laurentide ice-sheet, southern and equatorial Africa, and over the Iberian Peninsula (Fig. 2).
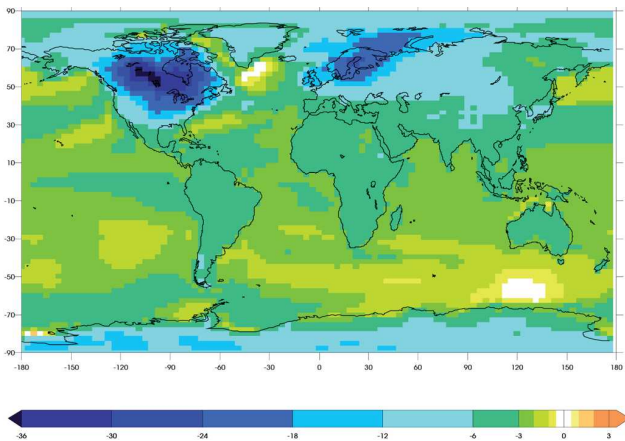
Fig. 1. Difference in mean annual temperature (°C) between present-day and LGM (LGMP-CTRLP) simulated by the IPSL_CM4_v1 GCM.
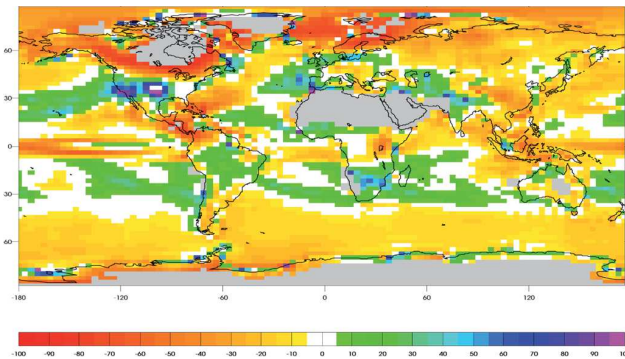

Fig. 2. Difference in annual precipitation (%) between present-day and LGM (LGMP-CTRLP) simulated by the IPSL_CM4_v1 GCM. Grey areas are regions for which annual precipitation is lower than $100\,\mathrm{mm.yr}^{-1}$.

2.3 Experimental design

Four different runs (Table 2) were performed with OR-CHIDEE off-line to test the relative impact of CO_2 and climate on the global vegetation.

Each run is preceeded by a spinup phase as follows: the simulation starts from bare ground, and ORCHIDEE is run for 500 yr with the forcing in climate and CO_2 of the given experiment. The climatic forcing is the 6 h output from the AOGCM and therefore includes simulated interannual variability. We have chosen the period 1930–1980 (see Table 2) for the control simulation because we wanted a modern vegetation, not a pre-industrial one, as climate reconstructions based on pollen assemblages are calibrated on present-day climate. This period roughly corresponds to a plateau in the increasing trend of global mean temperature. The pertinent variables are saved to drive the soil carbon submodel for

Table 2. Names and characteristics of the ORCHIDEE off-line runs.

Name	climatic forcings	CO_2 level for photosynthesis
CTRLP	years 1930 to 1980 of the 20th century simulation (PRES), repeated 6 times	310 ppm
CTRLG	years 1930 to 1980 of the 20th century simulation (PRES), repeated 6 times	185 ppm
LGMP	1000 yr of LGM climate	310 ppm
LGMG	1000 yr of LGM climate	185 ppm

10 000 yr, so that equilibrium of the carbon stocks is reached. The whole model is then run for another 50 yr to achieve the spinup. The four simulations start at the last year of their respective spinup. The whole model is run for another 300 yr for CTRLP and CTRLG, repeating the forcing of the spinup phase. For LGMP and LGMG we used the whole 1000 yr timeseries from IPSL_CM4 (see Table 2). All simulations present stable vegetation distribution during this last period of simulation. The results presented in the following sections are averages of the last 10 yr of each simulation.

The vegetation simulated for present day (CTRLP) presents some biases (see Sect. 3.1), which can be partly corrected using a more realistic climatology such as the Climate Research Unit (CRU) data (New et al., 2002) (see Sect. 3.1 for a more detailed comparison). To take into account the climatic biases of the IPSL model for the LGM period as well, we tested two different anomaly procedures. In the first case, to obtain the LGM forcing we used the CRU timeseries as the basis onto which the mean monthly climatic anomaly between the IPSL LGM and the mean monthly CRU climate is added, thus keeping the CRU interannual variability. In the second case, we used the IPSL LGM climate corrected by the mean bias between the CRU and the modern climate simulated by the AOGCM. The broad vegetation patterns obtained with these two methods or without correction are quite similar (not shown). At global scale, the broad vegetation pattern obtained with these two methods are quite similar (not shown). The simulated LGM vegetation appears less dependent on the climatic forcing than the present-day one: with or without corrections with an anomaly procedure, the change in climate is strong enough to drive a major forest regression in any case. For that reason, we chose to keep outputs from the IPSL model as forcing fields for all simulations, even for present day. This simplifies the forcing procedure and will also allow us to compare our results with future fully coupled atmosphere-ocean-vegetation runs. This first set of simulations is completed with static simulations, in order to evaluate the role of dynamics and competitivity (see Sect. 4.3).
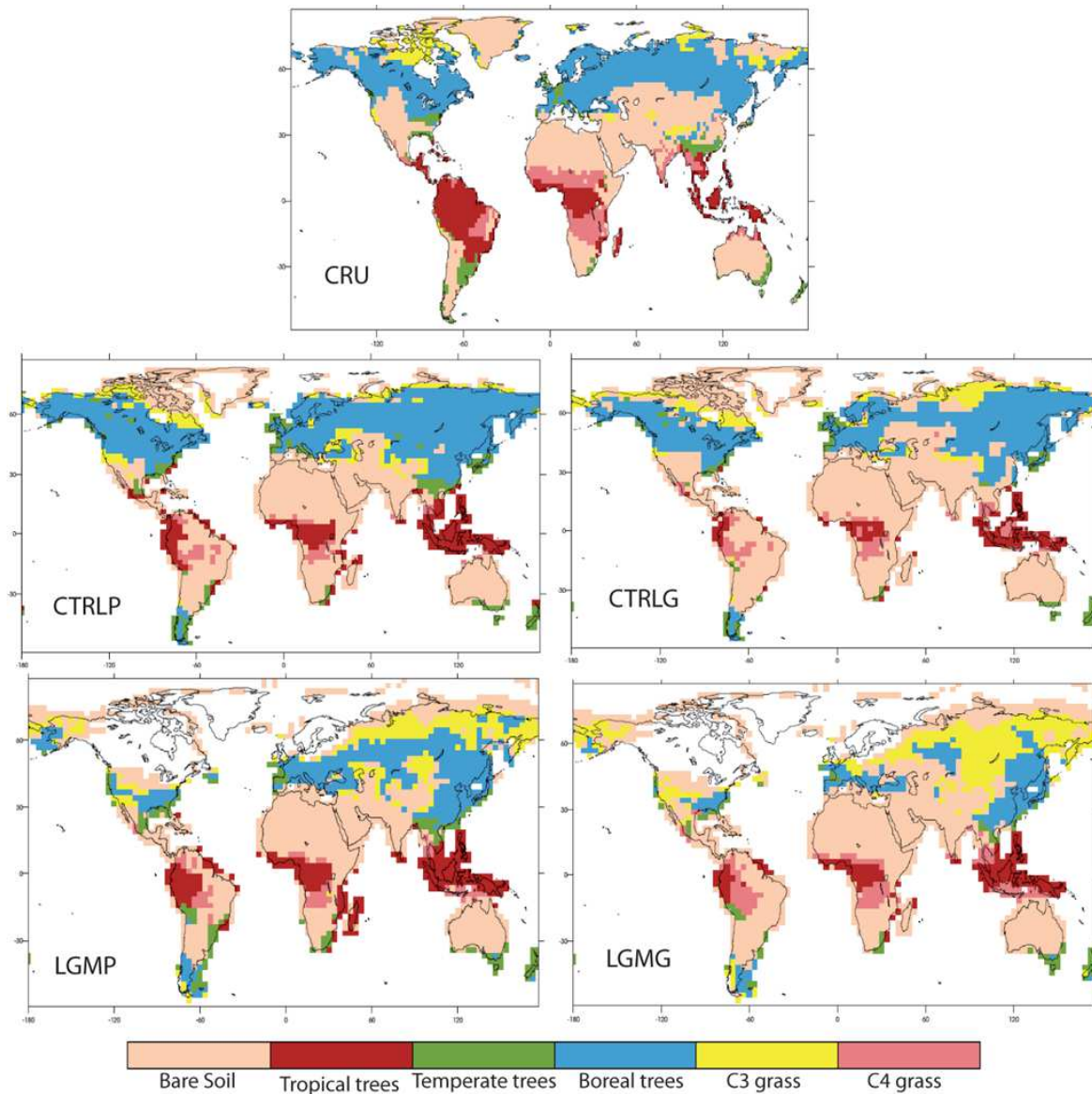
Fig. 3. Dominant PFT type simulated by ORCHIDEE forced off-line by monthly CRU data (CRU) or by high-frequency outputs of the IPSL_CM4_v1 GCM for present-day climate (CTRLP and CTRLG) and LGM climate (LGMP and LGMG). Abbreviations: see Table 2. For each grid-cell we consider the fraction of bare soil, C3 and C4 grasses, and the sum of the tree PFT fractions of a given tree type (tropical, temperate, and boreal). The dominant type is the one occupying the greatest cell fraction, without considering its absolute value.

3 Simulated vegetation for present day and LGM

3.1 Present day potential vegetation

Figure 3 presents the dominant vegetation type simulated in CTRLP. The detailed repartition and fractions of the different PFTs are given on Fig. 4. The biases in this potential modern vegetation are due to the climatic forcing and/or to the vegetation model itself. Tropical forests are correctly represented over Indonesia and equatorial Africa, but are underestimated over the Amazon basin. The bare ground fraction over India, South America and Africa is overestimated. This is mainly due to a lack of precipitation over these regions in the IPSL model (Marti et al., 2010) and is corrected when we force ORCHIDEE with CRU data (Fig. 5). For mid to high latitudes, the location of temperate forests is well represented (Fig. 4), but their density is underestimated. They dominate only in small regions, in western Europe, the east coast of North America, southern China, Japan and South America (Fig. 3). They are mainly composed of broadleaf trees, which represent more
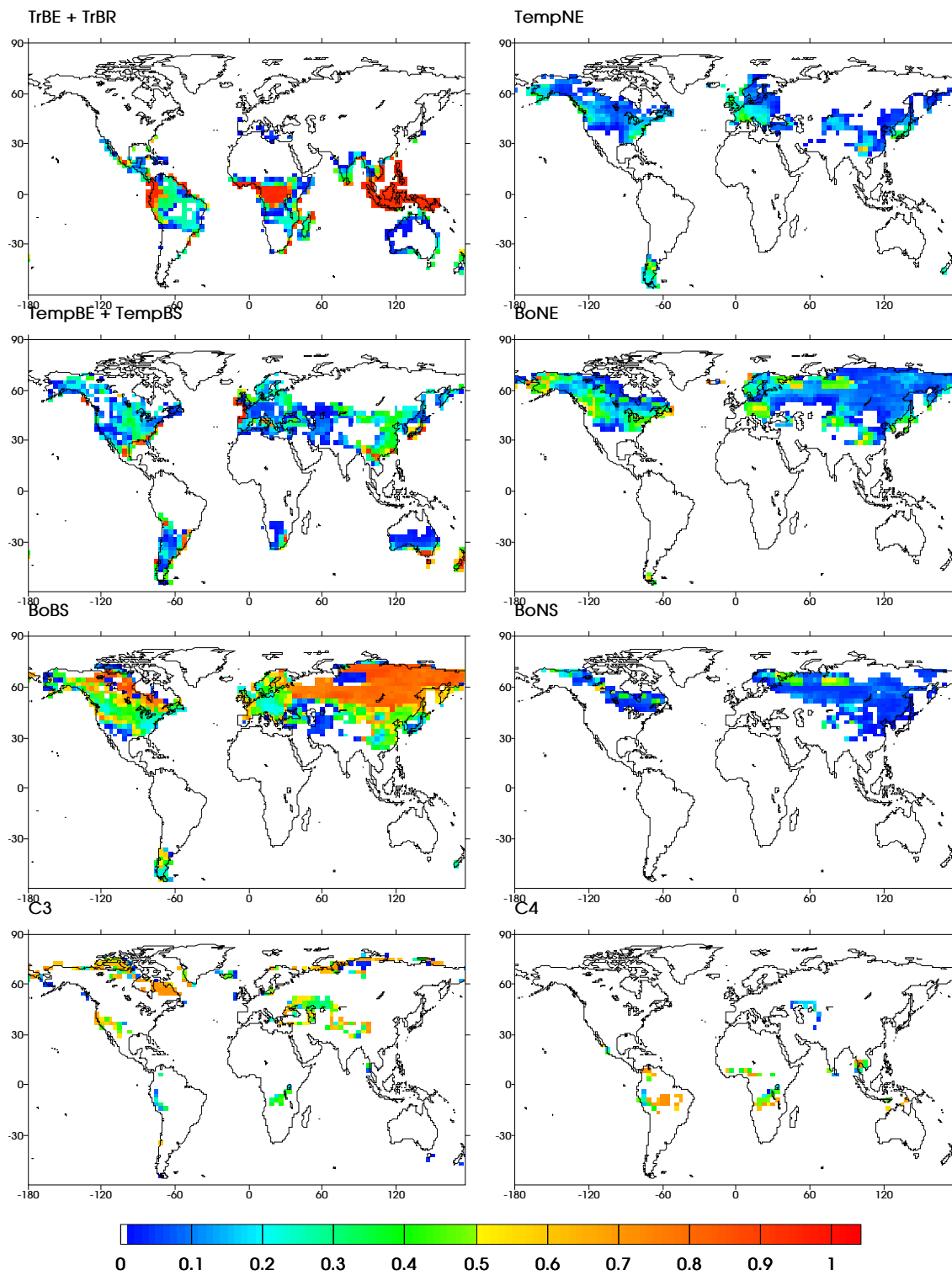
Fig. 4. Fractions of vegetation (annual maximum, in % of grid-cell) simulated by ORCHIDEE in CTRLP (present-day climate and modern CO_2 for photosynthesis). Abbreviations: see Table 1.
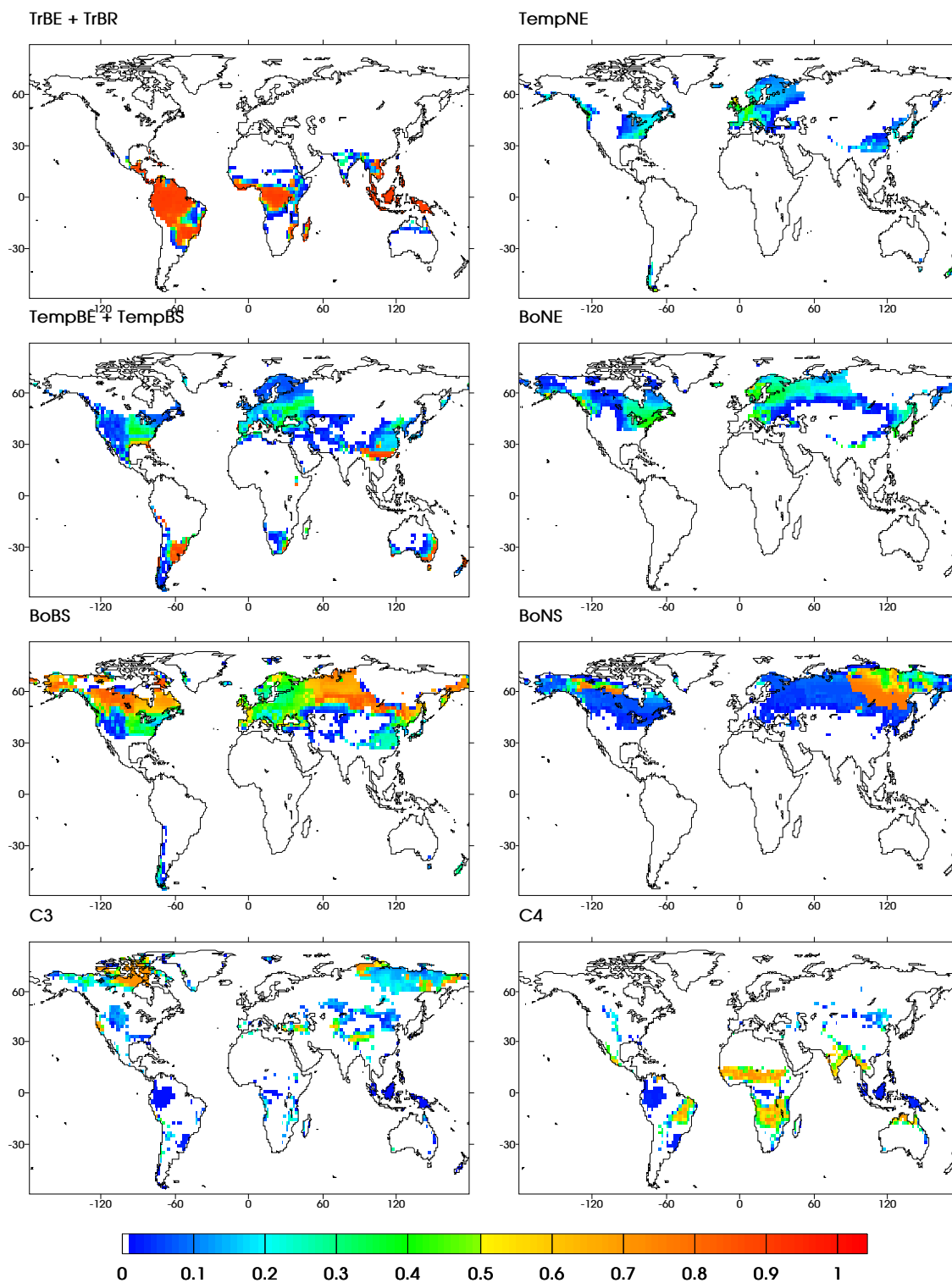
Fig. 5. Fractions of vegetation (annual maximum, in % of grid-cell) simulated by ORCHIDEE forced off-line by monthly CRU timeseries. Abbreviations: see Table 1.
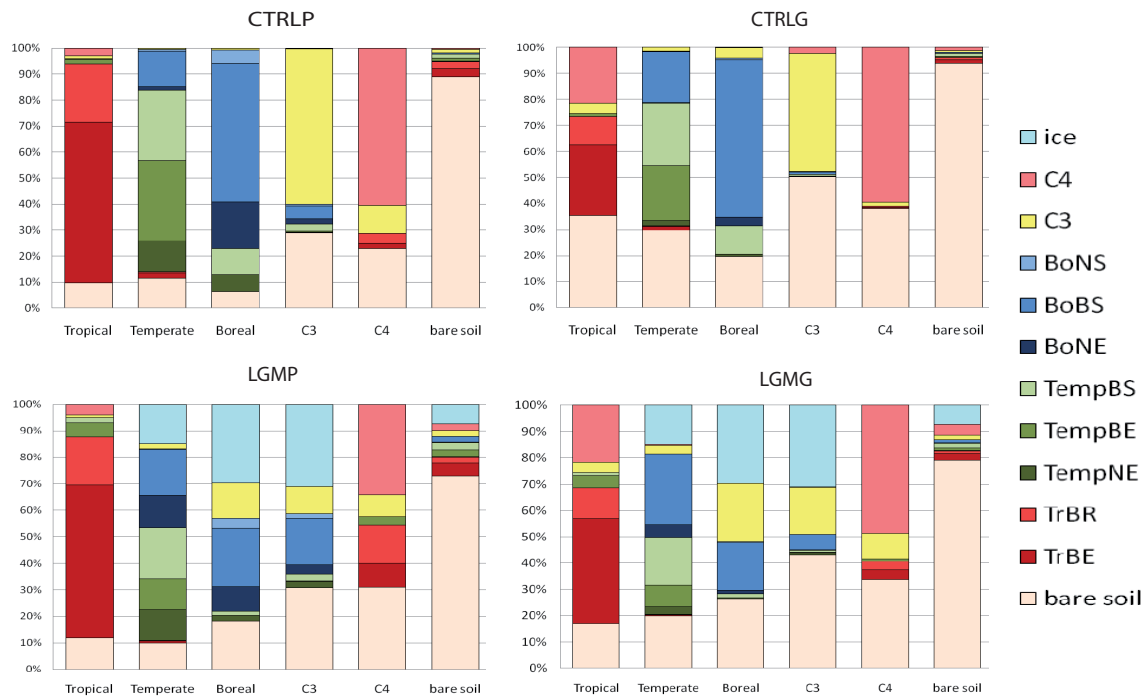
Fig. 6. Detail of the PFT composition in the area of dominance of tropical forests, temperate forests, boreal forests, C3 and C4 grasses, and bare soil in CTRLP. We keep this same area as the reference for CTRLG, LGMP, and LGMG. Abbreviations: see Table 1.

than 50 % while TempNE (temperate needleleaf evergreen trees, cf. Table 1 for the acronyms describing the PFTs) only represent about 10 % of the total area where temperate trees are dominant (Fig. 6). On the contrary, boreal forests are overestimated: they dominate almost everywhere above 40° N (Fig. 3) and the treeline is too far north, above 70° N. The composition of this boreal forest is biased in favour of deciduous broadleaf trees, as the fraction of BoBS exceeds 50 %, and BoNE and BoNS represent only about 30 % of the total surface (Fig. 6). The development of boreal PFTs might be favoured by a cold bias in IPSL_CM4, but ORCHIDEE has a tendency to overestimate BoBS anyway. This bias is still present when using the CRU data set (Fig. 5). The over-prediction of this PFT in boreal forets is a bias already present in LPJ (Sitch et al., 2003), but has been accentuated in the version of ORCHIDEE used in this study, for presently undetermined reasons. Grasses (C3 and C4) are largely underestimated, partly because of a bias not yet understood in ORCHIDEE, and partly because of the climatic forcing. In particular, the lack of C4 grass over Africa and India is corrected with CRU (Fig. 5). C3 grass remains underestimated at high latitudes of the Northern Hemisphere, a bias which can be attributed to the persistent overestimation of trees shading the grass. A more detailed model-data comparison for present-day has already been done in Krinner et al. (2005) and even if the ORCHIDEE model has evolved since this publication, one can refer to

this paper for a finer assessment of the model biases. Here, our aim was to point out the main biases that the reader should keep in mind for the analysis of the LGM results.

3.2 Glacial vegetation

We briefly compare the vegetation obtained in LGMG (Figs. 3 and 7) with reconstructions based on pollen data to evaluate the performance of ORCHIDEE in its simulation of the glacial vegetation. The computation of the surfaces takes into account the fraction of land on each grid-cell.

The area where tropical forests are present is slightly decreased from 35×10^6 km^2 in CTRLP to 31×10^6 km^2 in LGMG, and their surface of global foliage projective cover is reduced to 10×10^6 km^2 (14×10^6 km^2 in CTRLP) (Fig. 8). The global foliage projective cover represents the ground fraction covered by a PFT and results from the number of trees, i.e. their crown area, which depends on the biomass of an individual tree type and their leaf area index (LAI, in m^2 m^{-2}). This limited regression can be explained by the fact that the simulated tropical forests are already underestimated for present-day. The expansion of tropical forests on the new area available because of a lower sea-level accounts for less than 0.5×10^6 km^2 of their global foliage projective cover in LGMG and can be neglected. Tropical
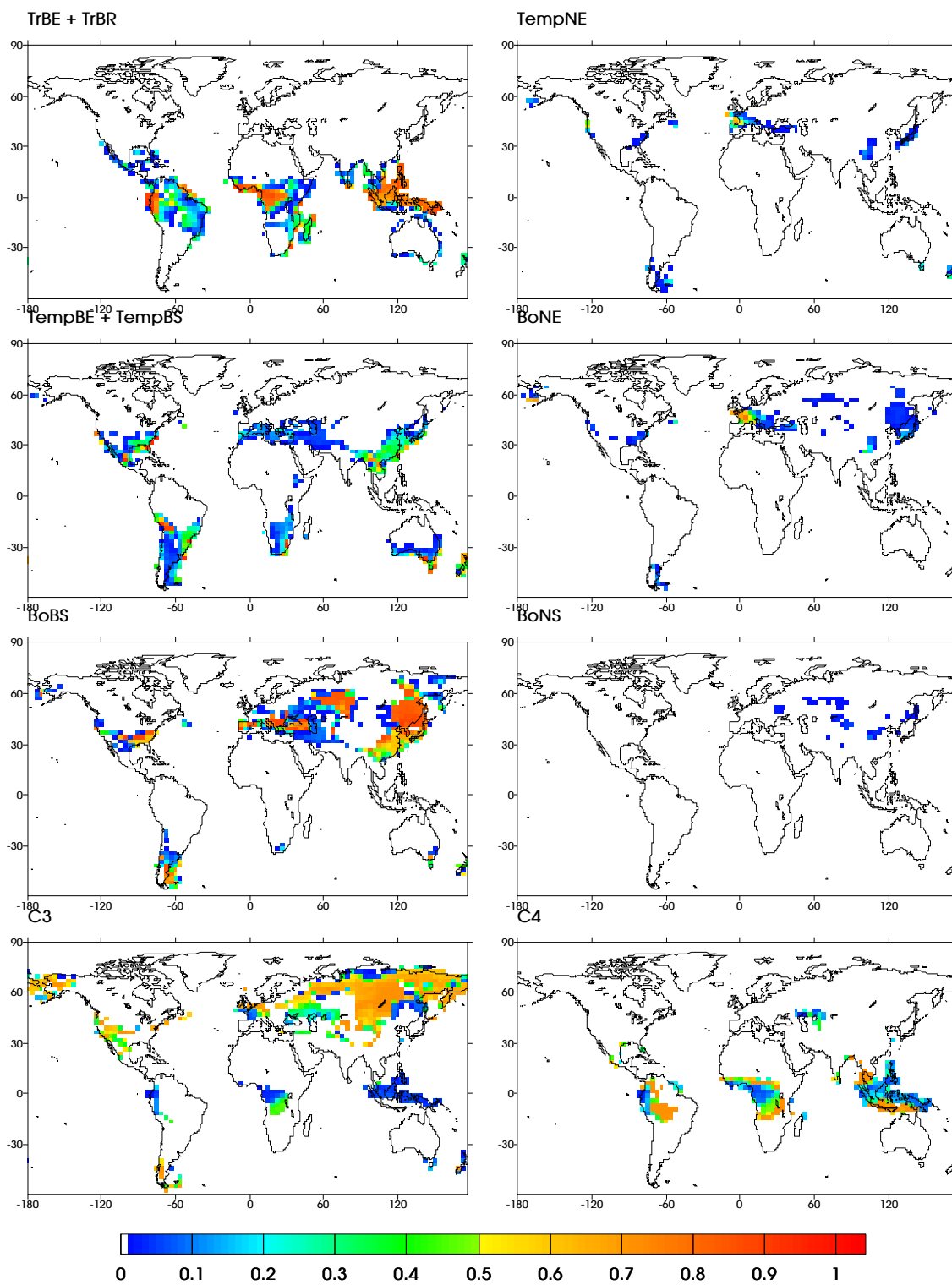
Fig. 7. Fraction of vegetation (annual maximum, in % of grid-cell) simulated by ORCHIDEE in LGMG (LGM climate and LGM CO$_2$). Abbreviations: see Table 1.
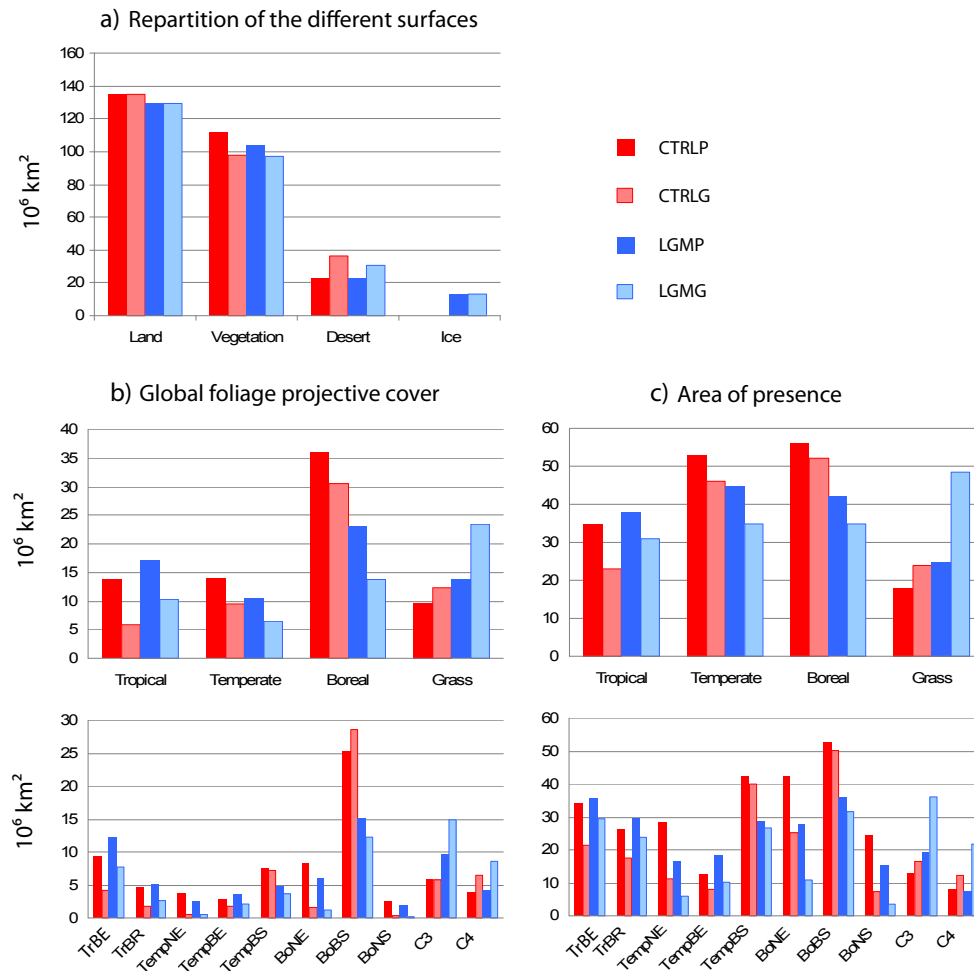
Fig. 8. **(a)** Repartition of the different surfaces: "Land" is the area available for vegetation (and therefore does not comprise the land area covered by ice); "Vegetation" is the area where the fraction of total vegetation is above 1 %; "Desert" is the area where the bare soil fraction exceeds 99 %; and "Ice" is the surface of the Laurentide and Fennoscandian ice-sheet present in LGMP and LGMG. **(b)** Area of annual maximum global foliage projective cover (10^6 km^2). **(c)** Area of presence (10^6 km^2) for the different PFTs. A PFT is considered to be present on a grid-cell when its fraction exceeds 1 %. The area of presence is thus greater than the surface really covered by a PFT. CTRLP: present climate and modern CO_2; CTRLG: present climate and glacial CO_2; LGMP: LGM climate and modern CO_2; LGMG: LGM climate and glacial CO_2. Tropical: TrBE + TrBR; Temperate: TempNE + TempBE + TempBS; Boreal: BoNE+BoBS+BoNS; Grass: C3 + C4. Abbreviations: see Table 1.

forest subsists in Amazonia, and still dominates in equatorial Africa and Indonesia (Fig. 3), but the fraction of trees is decreased by about 10–20 % (Fig. 7 vs. Fig. 4). A survival of tropical forests is in agreement with data (Colinvaux et al., 1996, 2000 for the Amazonian forest; and Kershaw et al., 2001 for South-East Asia). Grasses are underestimated in South America, where data show steppe and cool grass shrublands in the south-east of Brazil for instance (Marchant et al., 2009). However, the LGM is often missing in pollen reconstructions of the lowland tropical forests, indicating dry and erosive climatic conditions (Ledru et al., 1996, 1998). The high bare ground fraction simulated by ORCHIDEE over South America at LGM is thus less problematic than

it is for present-day. Similarly, pollen data show the presence of steppe in southern Africa (Prentice et al., 2000) where OR-CHIDEE simulates only bare soil. However, the model succeeds in simulating grass and small tree fractions over the region of the African Great Lakes, in agreement with the reconstruction of steppe and xerophitic scrubs by Prentice et al. (2000).

Temperate and boreal forests regress (Fig. 4 vs. Fig. 7) and are replaced by C3 grass, which becomes the dominant PFT over most parts of Eurasia and in the west of North America (Fig. 3), in agreement with data indicating the development of grassland and/or tundra vegetation in these zones (Prentice et al., 2000; Tarasov et al., 2000).

Beringia is also mboxoccupied by grass, in agreement with the reconstructions from Bigelow et al. (2003). A mixture of temperate and boreal forests (TempBS and BoBS) persists in South China, and Japan is covered by BoBS. The presence of forests in these two regions is in agreement with data, but their composition disagrees: the reconstruction from Prentice et al. (2000) shows temperate deciduous forests in Japan and temperate conifer forests in South China. ORCHIDEE also simulates a dense forest of BoBS on the Pacific coast of Siberia in disagreement with data, which show taiga only locally, according to Prentice et al. (2000). Forests are also still present on the east coast of North America and in western Europe, whereas pollen data indicate that grasslands were actually prevalent in southern Europe (Prentice et al., 2000). Köhler et al. (2005) had the same bias over western Europe when simulating the glacial vegetation with the LPJ-DGVM, as well as Harrison and Prentice (2003) with BIOME4. This discrepancy may be the sign that the glacial climate simulated by IPSL_CM4 over western Europe is too warm and wet and maybe closer to an interstadial state than to the LGM state, since oak forests were present over the Iberian Peninsula during interstadials (Sánchez-Goñi et al., 2000; Naughton et al., 2007). This is also true in terms of Atlantic Meridonal Overturning circulation, which is stronger in the LGM run than in the CTRL run (see Swingedouw et al., 2009). For North America, the reconstruction by Williams et al. (2002) confirms the presence of forest, but with dominant needleleaf trees, while ORCHIDEE simulates a broadleaf forest. On the whole, the global foliage projective cover of temperate and boreal forests regress from 50×10^6 km^2 in CTRLP to 20.4×10^6 km^2 in LGMG (Fig. 8). The growing of the northern ice-sheets explains a loss of 2.41 and 5.16×10^6 km^2 for BoNE and BoBS, respectively.

The simulated glacial vegetation is broadly consistent with data, the main discrepancy being a large underestimation of grass in the southern hemisphere, a bias already present in CTRLP, as mentionned in the previous section. The lack of needleleaf PFTs will be discussed in Sect. 4.3. Our purpose is not to present a more quantitative model-data comparison here. In the present work, our goal is to focus on identifying the parameters the simulated vegetation is sensitive to.

4 Relative impact of glacial climate and CO$_2$

The large vegetation changes simulated in LGMG compared to CTRLP result from both the change in climate and the decrease of the pCO$_2$ from 310 to 185 ppm. In order to evaluate their relative impact, we now compare the changes in vegetation cover, mean annual maximum LAI, and net primary productivity (NPP) in the four simulations CTRLP, CTRLG, LGMP and LGMG. For the vegetation cover, we will consider two variables: the surface of global foliage projective cover, as in the previous section, and the surface of presence

of a PFT. A PFT is considered to be present when it occupies more than 1% of a grid-cell. This variable reflects broadly the area where a PFT can grow. It is interesting to differenciate these two variables because the amplitude of change in response to climate change is not necessarily the same. We focus on forests because grasses cannot grow below trees in ORCHIDEE. It is the forest disappearance which can allow their expansion and therefore is a necessary condition for their changes.

4.1 Impact of the LGM climate change

We first compare the impact of climate change under present CO$_2$, and in Sect. 4.1.4 we will briefly compare the differences due to the climate change under glacial CO$_2$.

4.1.1 Tropical forests

The cooler climate at LGM does not effect tree growth, and glacial climate only actually favours the development of tropical forests: in LGMP compared to CTRLP, the global foliage projective cover of tropical PFTs (TrBE and TrBR) increases from 14×10^6 km^2 to 17×10^6 km^2 (Fig. 8). Both Amazonian and African forests expand, as well as the tropical Indonesian forest, which benefits from the lower sea-level (Figs. 3 and 9). However, as mentionned in Sect. 3.2, this last effect is negligible. Here, tropical forests benefit from an extension of the area where tropical trees can be present, from 35×10^6 km^2 to 38×10^6 km^2 (Fig. 8), but also from a slight increase of the mean LAI, from 5.4 to 5.6 for TrBE and from 4.9 to 5.3 for TrBR (Fig. 10). The forests become more productive, and their mean NPP increases by about 20 % (Fig. 11). The LAI increase is in agreement with the modelling results from Harrison and Prentice (2003) and Cowling et al. (2001). As suggested by Cowling et al. (2001), these results can be explained by the fact that the decrease in temperature during the LGM (Fig. 1) reduces evapo-transpiration (not shown), which improves water-use efficiency by the trees. Moreover, the slight increase of precipitation over the Amazon basin (Fig. 2) and the west of central Africa also favours tree growth. The Indonesian forest is not effected by the precipitation decrease (-50 %, see Fig. 2), which shows that precipitation is not a limiting factor in this region.

4.1.2 Temperate forests

Glacial climate leads to a large regression of temperate forests, mainly due to the cold temperatures: the global foliage projective cover drops from 14×10^6 km^2 in CTRLP to 10×10^6 km^2 in LGMP (Fig. 8). Part of this regression is simply due to the presence of the ice-sheets, which occupies 15 % of the area dominated by temperate trees in CTRLP (Fig. 6). Boreal PFTs invade part of this former dominance area, essentially at the expense of TempBS and TempNE, and occupy about 30 % of this zone (15 % in CTRLP, see
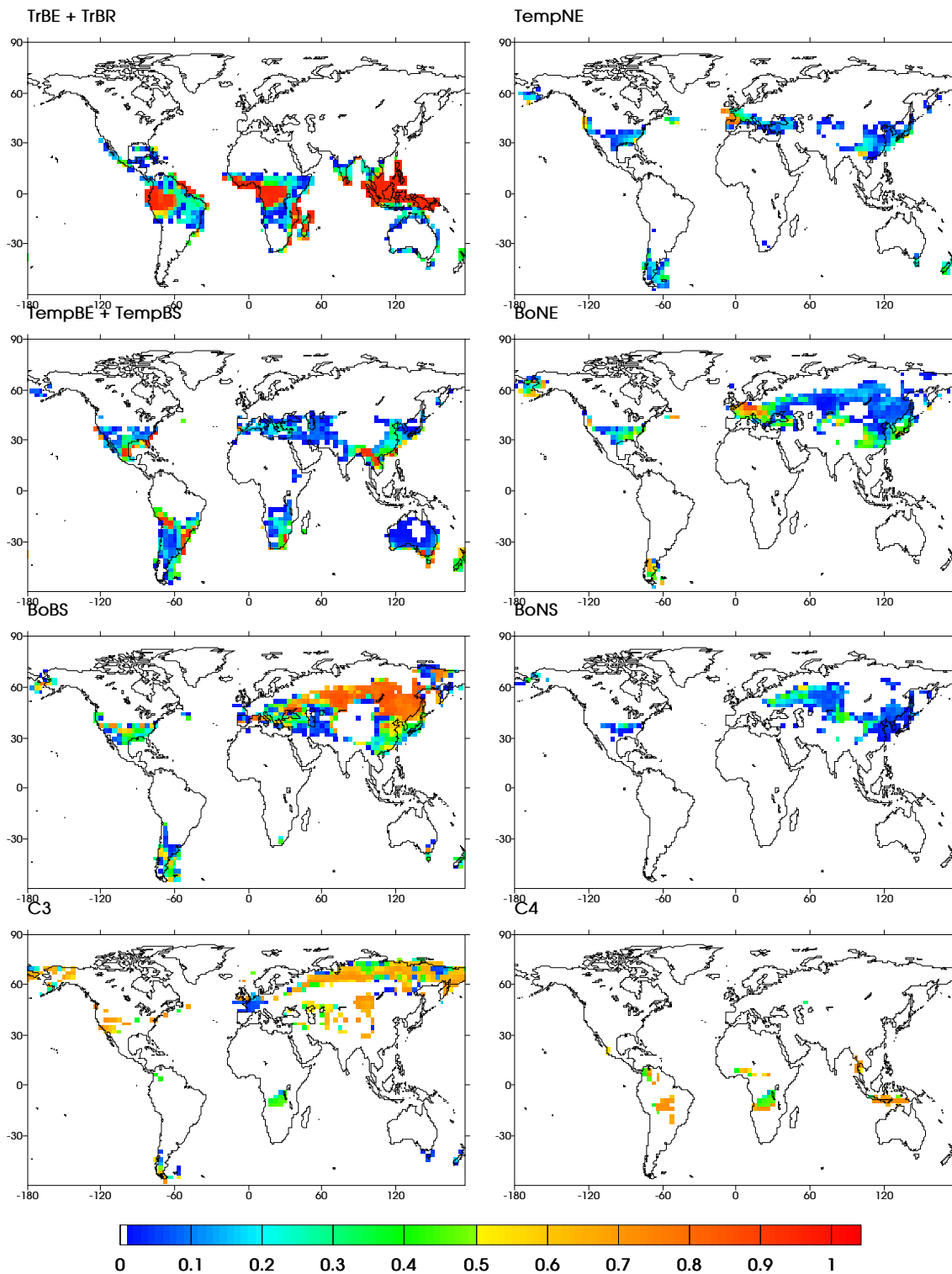
Fig. 9. Fraction of vegetation (annual maximum, in % of grid-cell) simulated by ORCHIDEE in LGMP (LGM climate and modern CO$_2$ for photosynthesis). Abbreviations: see Table 1.
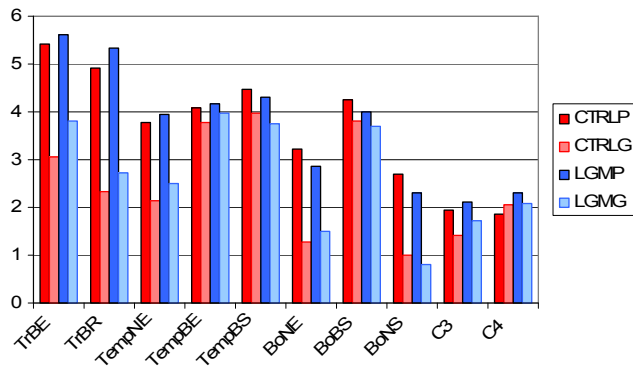
Fig. 10. Global mean annual maximum leaf area index (LAI) ($m^2 \, m^{-2}$). The LAI is averaged on the grid-cells where the fraction of the PFT exceeds 1 %. Abbreviations: see Table 1 for the PFTs and Table 2 for the simulations.
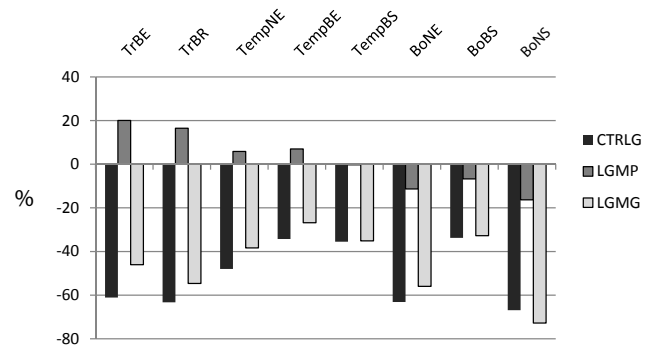

Fig. 11. Relative changes in the global mean annual net primary productivity (NPP) in CTRLG, LGMP and LGMG in % compared to CTRLP. The NPP is averaged on the grid-cells where the fraction of the PFT exceeds 1 %. Abbreviations: see Table 1 for the PFTs and Table 2 for the simulations.

Fig. 6). Temperate broadleaf PFTs regress over Eurasia and northern America, migrate towards lower latitudes and dominate in southern China, southern Atlantic coast of North America and South America (Fig. 9). In western Europe, TempNE migrate towards the north of the Iberian Peninsula, where they still represent 60–70 % (Fig. 9). Globally, the surface of presence decreases from $53 \times 10^6 \, \mathrm{km^2}$ in CTRLP to $45 \times 10^6 \, \mathrm{km^2}$ in LGMP, despite a slight expansion for TempBE ($+5.6 \times 10^6 \, \mathrm{km^2}$) (Fig. 8). If the area where temperate PFTs can survive under the drier and colder LGM climate is reduced, there is no huge change in productivity per m^2 and in LAI in their new living areas in LGMP compared to CTRLP. The mean NPP remains close to CTRLP: +5 % for tempNE, +7 % for TempBE, and no changes for TempBS (Fig. 11). Changes in the mean LAI are small: +5 % for TempNE, +2 % for TempBE, and −4 % for TempBS (Fig. 10).

4.1.3 Boreal forests

The global foliage projective cover of boreal forests decreases from $36 \times 10^6 \, \mathrm{km^2}$ in CTRLP to $23 \times 10^6 \, \mathrm{km^2}$ in LGMP (Fig. 8). The area where they are present decreases from $56 \times 10^6 \, \mathrm{km^2}$ to $41 \times 10^6 \, \mathrm{km^2}$ (Fig. 8), partly because of the development of the ice-sheets, which occupy about 30 % of their dominance area in CTRLP (Fig. 6). Due to the cooling by several °C at the high latitudes of the Northern Hemisphere, boreal trees cannot survive in these regions and the northern tree line in Eurasia shifts from 70° N to 60° N and from 70° N to 40° N in North America (Fig. 3 and 9). C3 grasses expand over areas abandoned by trees. Parts of the area occupied by boreal forests in CTRLP are simply replaced by bare soil, as in the south of the Laurentide ice-sheet, on the Arctic coast of Siberia and in Alaska, and the bare ground fraction over the dominance area of boreal forest in CTRLP increases from 7 % to 20 % (Fig. 6). However, an important boreal forest, dominated by BoBS

(70–80 %, see Fig. 9) remains across Eurasia. The mean LAI decreases slightly from 3.1 to 2.7 for BoNE, 4.2 to 3.9 for BoBS, and 2.6 to 2.2 for BoNS (Fig. 10). The mean NPP decreases for all boreal PFTs (−11 %, −6 %, and −16 % for BoNE, BoBS, and BoNS, respectively, see Fig. 11), indicating that the living conditions in the area they occupy are less favourable than in CTRLP, except in western Europe for BoNE, where its fraction reaches about 70 % (Fig. 9).

4.1.4 Is the response to the LGM climate robust under low CO_2 ?

We now compare the simulated vegetation in CTRLG (Fig. 12) and LGMG (Fig. 7), to assess the impact of glacial climate under low CO_2. Temperate and boreal forests regress in the Northern Hemisphere, replaced by C3 grass, but the amplitude of this regression is larger under low CO_2: the loss of global foliage projective cover between LGMG and CTRLG is $19.1 \times 10^6 \, \mathrm{km^2}$ ($16.4 \times 10^6 \, \mathrm{km^2}$ between LGMP and CTRLP), which represent a decrease of 48 % (32 %), respectively. The low CO_2 does not prevent tropical forests to increase in response to the glacial climate: from $5.9 \times 10^6 \, \mathrm{km^2}$ in CTRLG to $10 \times 10^6 \, \mathrm{km^2}$ in LGMG (Fig. 8).

4.2 Impact of CO_2 under LGM climate

4.2.1 Tropical forests

When the physiological effect of low CO_2 is taken into account (LGMG compared to LGMP), tropical forests regress: their global foliage projective cover is reduced to $10 \times 10^6 \, \mathrm{km^2}$ ($17 \times 10^6 \, \mathrm{km^2}$ in LGMP, see Fig. 8). Their area of presence loses $7 \times 10^6 \, \mathrm{km^2}$ compared to LGMP, and their mean NPP decreases by about 50 % (Fig. 11). The mean LAI is only 3.8 for TrBE and 2.7 for TrBR (Fig. 10),
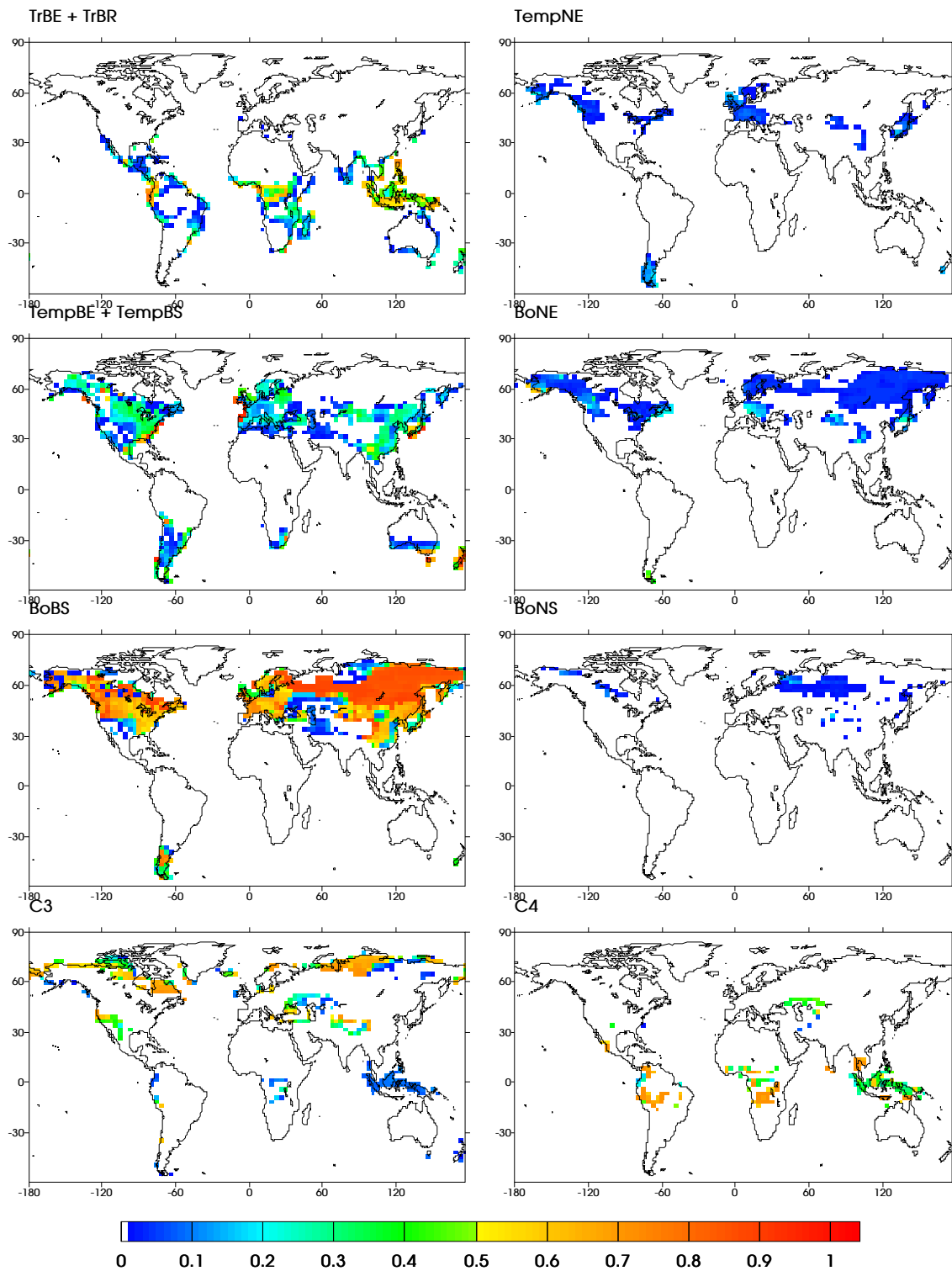
Fig. 12. Fraction of vegetation (annual maximum, in % of grid-cell) simulated by ORCHIDEE in CTRLG (present-day climate and glacial CO_2 for photosynthesis). Abbreviations: see Table 1.

i.e. a decrease of 29 % and 44 %, respectively, compared to CTRLP. This decrease is stronger than the one obtained by Harrison and Prentice (2003) (only 6 %), but is of the same order of magnitude as the 34 % obtained by Cowling et al. (2001) over the Amazonian basin. The forest shifts towards a more open ecosystem: the bare ground fraction over the area dominated by tropical forests in CTRLP reaches about 18 % (10 % in CTRLP) and the C4 grass fraction about 20 % (less than 5 % in CTRLP, see Fig. 6), a development allowed by the regression of trees.

4.2.2 Temperate forests

In LGMG, the global foliage projective cover of temperate forests decreases to 6×10^6 km^2 (Fig. 8). The reduction caused by the physiological effect of low CO$_2$ is of the same order of magnitude as the reduction caused by climate alone, and the response to low CO$_2$ represents 54 % of the response of vegetation to glacial conditions. CO$_2$ mostly impacts TempNE, which almost completely disappear outside western Europe (Fig. 7): they can be found only on 6×10^6 km^2 (16×10^6 km^2 in LGMP, see Fig. 8). Their mean LAI decreases from 3.9 in LGMP to only 2.5 in LGMG (Fig. 10), and the mean NPP is reduced by 38 % compared to CTRLP (Fig. 11). The impact on broadleaf PFTs is less strong, the mean LAI does not change much, and their relative global foliage projective cover in LGMG is close to LGMP (Figs. 10 and 8). This difference of sensitivity between needleleaf and broadleaf vegetation to CO$_2$ is discussed in Sect. 4.3.

4.2.3 Boreal forests

The physiological effect of glacial CO$_2$ has a strong impact on boreal forests, especially for the needleleaf types, which are more sensitive than broadleaf PFTs as previously observed for the temperate PFTs. The mean LAI decreases from 2.7 in LGMP to only 1.4 in LGMG for BoNE, from 2.2 to 0.7 for BoNS, and from 3.9 to 3.6 for BoBS (Fig. 10). This strong decrease in LAI leads to the almost complete disappearance of BoNS. BoNE subsist significantly only in western Europe. The needleleaf PFTs are replaced by BoBS on the east coast of North America (Fig. 7 vs. Fig. 9). BoBS also increase in the Mediterranean region and on the west coast of South China. The boreal forest present across central Eurasia in LGMP is fragmented, but BoBS still cover an important fraction of the Pacific coast of Eurasia (Fig. 7). The global projective cover of boreal forests in LGMG regresses to 14×10^6 km^2 (Fig. 8), and C3 grasses widely expand across Eurasia, to occupy a surface of 15×10^6 km^2 (10×10^6 km^2 in LGMP, see Fig. 8). Over the area dominated by boreal PFTs in CTRLP, the fraction of bare ground occupies more than 30 % in LGMG, and the fraction of C3 grass about 20 %, vs. 20 and 12 %, respectively, in LGMP (Fig. 6). Boreal forests appear to be as sensitive as the tem-

perate ones to the decrease in CO$_2$: the impact of imposing the glacial climate represents 58 % of the total reduction in global foliage leaf cover, and the impact of glacial CO$_2$ represents the remaining 42 %, with huge differences depending on the phenology. For BoNS and BoNE, the glacial CO$_2$ impact is responsible for 80 % and 70 %, respectively, of their decrease, but only for 20 % for BoBS.

4.2.4 Impact of LGM CO$_2$ for a modern background climate

As seen in the previous section, CO$_2$ is a major factor to explain vegetation changes at the LGM. But would such a decrease in CO$_2$ have the same consequences under modern climate conditions? In order to answer this question, we now briefly consider vegetation changes between CTRLG and CTRLP (Fig. 12 vs. Fig. 4).

The area of presence decreases for all the tree PFTs in CTRLG compared to CTRLP (Fig. 8), but the percentage of relative decrease between these two simulations is not the same as between LGMG and LGMP. For TrBE and TrBR, the decrease is less than 20 % with a glacial climate in background, and more than 30 % under a modern climate (Fig. 14). For TempNE the response is similar for both climates, but for BoNE the decrease is much stronger in LGM climatic conditions than in modern climate (-60 % vs. -40 %, respectively, see Fig. 14). The global response to a pCO$_2$ decrease in terms of area of presence therefore depends on the background climate and initial vegetation. However, the response of the global foliage projective cover is different. In particular, for BoBS the global foliage projective cover actually increases from 25×10^6 km^2 in CTRLP to 28×10^6 km^2 in CTRLG (Fig. 8), despite the decrease in area of presence. This can be explained by the difference of sensitivity between broadleaf and needleleaf PFTs. In CTRLG, TempNE and BoNE strongly regress and BoBS can replace them in North America, Europe, and Siberia, where they were already present in CTRLP but limited by the presence of the needleleaf PFTs. This expansion compensates the global reduction of the geographical area corresponding to the climatic range appropriate for them when pCO$_2$ equals 185 ppm. This compensation does not occur in glacial climate since the surface occupied by needleleaf PFTs is already reduced by the change in climate and BoBS can replace them only on smaller regions. The initial state and the dynamics of vegetation are thus important factors to understand the response of global vegetation to changes in CO$_2$ in ORCHIDEE. For this reason, the interpretation of the changes in the surface of presence or global foliage projective cover is not straightforward.
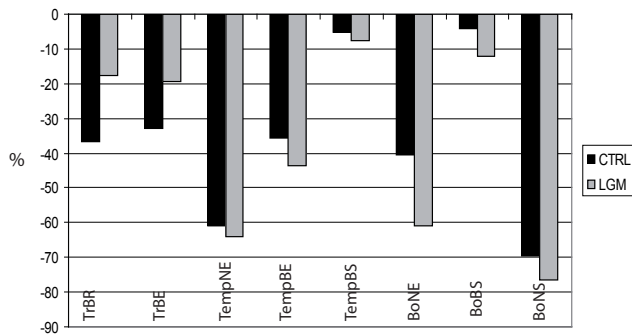
Fig. 13. Percentage of change in the area of presence of the tree PFT (fraction exceeds 1 %) when the CO₂ is decreased from 310 to 185 ppm and the background climate is kept constant to CTRL present or LGM. Abbreviations: see Table 1.

Fig. 14. Percentage of change in the area of presence of the tree PFT (fraction exceeds 1 %) when the CO₂ is decreased from 310 to 185 ppm and the background climate is kept constant to CTRL present or LGM. Abbreviations: see Table 1.
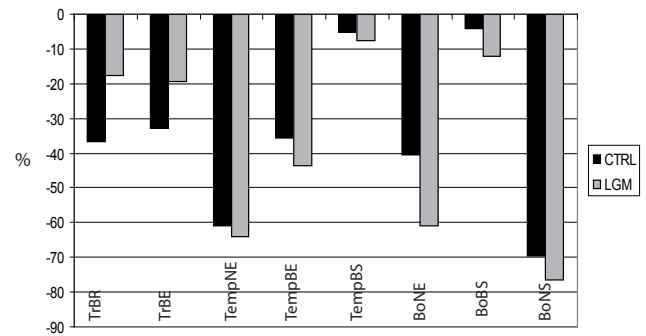
4.3 Impact of dynamics and competitivity

To evaluate the impacts of dynamics and competitivity vs. LAI and NPP, we perform 20 static runs (in which the vegetation fraction is not allowed to change along the run) to test the response of some PFTs considered separately. We chose to consider only five tree PFTs: TrBE, TempNE, TempBS, BoNE, and BoBS. The simulations were designed as follows:

– present climate: we consider the area where a given PFT is present in CTRLP, and impose on this zone a coverage of 100 % of this PFT. Since the bioclimatic limits of a PFT are not taken into account when the vegetation dynamics is not activated, this procedure ensures that the coverage of the chosen PFT is not applied over a senseless region. Then we impose a present climate and 310 or 185 ppm of atmospheric CO₂

– LGM climate: same method, but we consider the area where a given PFT is present in LGMP

The names and characteristics of the 20 simulations are summarized in Table 3.

Each simulation is run for 30 yr without activation of the vegetation dynamics. Trees adjust their productivity to the climate and CO₂ conditions. We compare the mean annual NPP over the last ten years of a run. The results presented in Fig. 15 show that the decrease of the global mean NPP in response to the decrease in CO₂ is very similar under a modern climate or a LGM climate. This decrease is about 60–70 % for TrBE, TempNE, and BoNE, and 35–40 % for TempBS and BoBS. This confirms the higher sensitivity of needleleaf PFTs compared to broadleaf PFTs even when there is no competition between species. However, this similar response in global average hides important spatial differences. As can be seen on Fig. 15, the mean annual NPP decrease depends on the region. For BoNE, the decrease is around 40 % in central Europe in modern climate, but

Table 3. Names and characteristics of the static runs. Abbreviations for PFT coverage: see Table 1.

Name	PFT coverage	climate	CO₂ level for photosynthesis (ppm)
TrBEP310/TrBEP185	TrBE	modern	310/185
TempNEP310/TempNEP185	TempNE	modern	310/185
TempBSP310/TempBSP185	TempBS	modern	310/185
BoNEP310/BoNEP185	BoNE	modern	310/185
BoNSP310/BoNSP185	BoNS	modern	310/185
TrBE310/TrBEG185	TrBE	glacial	310/185
TempNEG310/TempNEG185	TempNE	glacial	310/185
TempBSG310/TempBSG185	TempBS	glacial	310/185
BoNEG310/BoNEG185	BoNE	glacial	310/185
BoNSG310/BoNSG185	BoNS	glacial	310/185

more than 90 % in Siberia. For BoBS, the decrease is more important in the region of the Caspian Sea than in Alaska (45 to 60 % vs. 20 %, respectively) for CTRL climate. Similar results are obtained under the LGM climate. This dependence on the region means that the sensitivity to CO₂ decrease actually depends on the climatic conditions on a given grid-cell. Thresholds appear in some areas, for instance in Siberia for BoNE, where their productivity becomes negligible under modern climate and 185 ppm of CO₂. These results agree with observations regarding the response of trees to the *p*CO₂ increase over the last century. Different tree species have increased their water-use efficiency, but the amount of change depends on the climatic conditions of each considered region (e.g. Waterhouse et al., 2004).

To summarize, the decrease in CO₂ globally reduces the viability zone for a PFT, and in the new area where the PFT can survive its productivity is decreased. But the impact of CO₂ is spatially variable and depends on the background
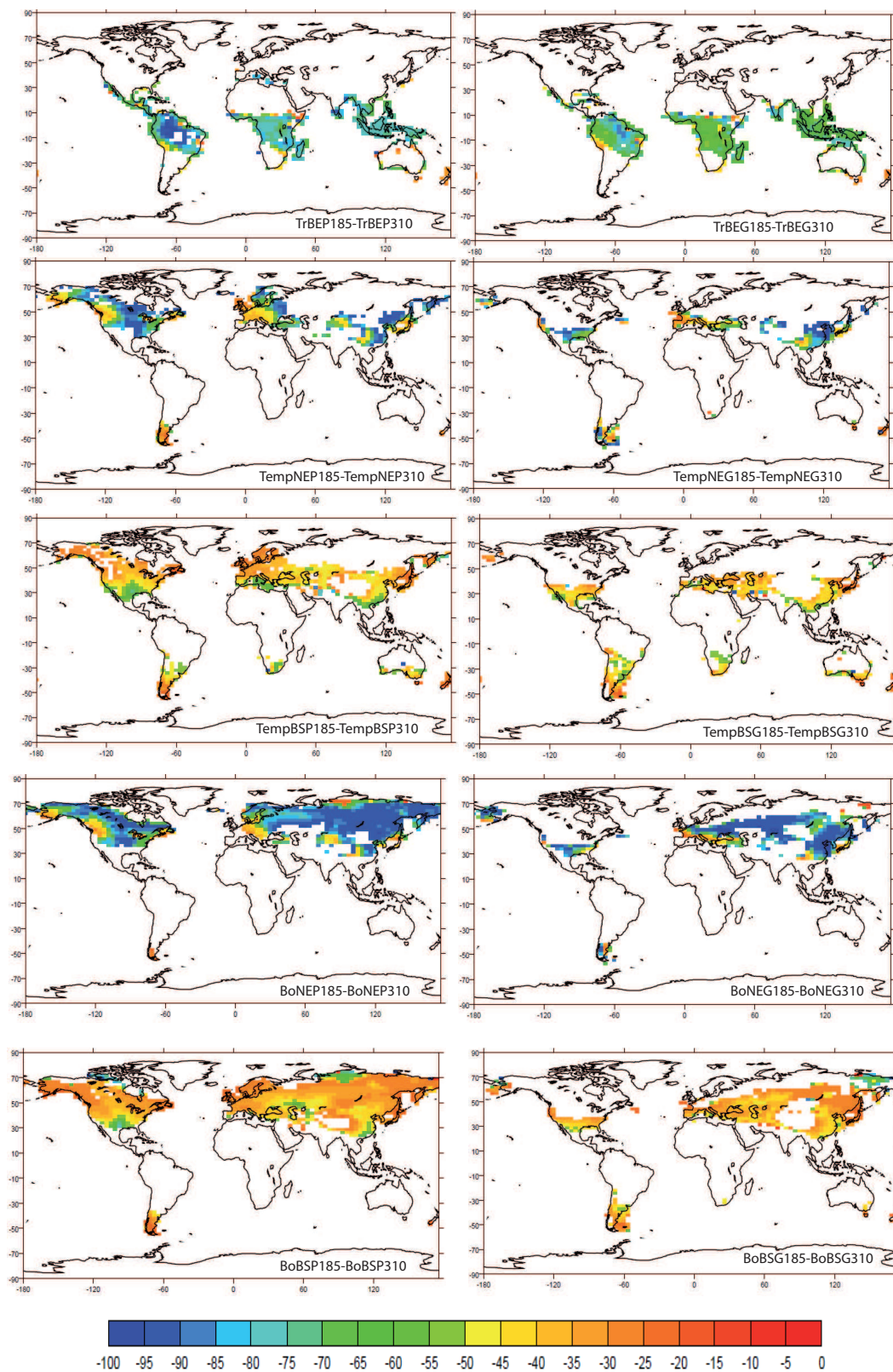
Fig. 15. Changes in annual NPP (in %) in the fixed vegetation runs when CO$_2$ is decreased from 310 to 185 ppm with a CTRL (left column) or LGM (right column) climate in background. Names of the simulations: see Table 3.

climate over the region considered. The relative change in the global mean NPP is very similar under modern or LGM climate because a given PFT always occupies the same climatic range, even if it is at different geographical locations. Depending on the global climate, the corresponding geographical area is more or less extended but always large enough for all the different sustainable climatic conditions to be represented. As a result, on global mean we find the same relative impact.

However, these results may depend on the climatic forcing. Indeed, if a PFT is on the limit of viability over a great part of the area occupied, it will respond more strongly to the CO_2 decrease than it would have done under more favourable climatic conditions. It would be interesting to investigate more precisely the link between climatic conditions and the amplitude of the response to CO_2 changes and to test the impact of another present or LGM climate on the sensitivity of the results. We leave this point to a further study, but the fact that needleleaf PFTs are more sensitive than broadleaf PFTs to the CO_2 decrease under both modern and LGM climate is in favour of the robustess of this result in ORCHIDEE.

5   Discussion and conclusions

The results from this study confirm that the physiological effect of low CO_2 plays a major role in vegetation changes during glacial times and should be taken into account in climate reconstructions based on pollen data.

In terms of global foliage projective cover, low glacial CO_2 is the only driver of the regression of tropical forests during the LGM, and the change in climate actually mitigates this effect. Our result is in agreement with Jolly and Haxeltine (1997) who found that the change in CO_2 was sufficient to explain changes in montane vegetation in tropical Africa, as mentioned in the introduction. It also agrees with the results of Harrison and Prentice (2003). For temperate and boreal forests, the CO_2 represents respectively 54 % and 41 % of the regression. Schematically, a decrease in CO_2 reduces the zone where a tree PFT can grow, and reduces the mean LAI and NPP over the remaining sustainable area. The magnitude of the impact depends on the region and also on the PFT type, broadleaf PFTs being less sensitive than needleleaf ones, for both temperate and boreal types. This difference modifies the competitivity between the PFTs, driving changes in the composition of forests, where broadleaf PFTs become dominant. This different response of needleleaf and broadleaf PFTs in ORCHIDEE can be explained by the different parameterization of the physiological effect of CO_2 for these two types. The CO_2 level has an impact on stomatal conductance, and on the rate of the carboxylation (Krinner et al., 2005), which is greater for broadleaf than for needleleaf PFTs. The rate of carboxylation effects assimilation, which both depends upon and has an impact on stomatal conductance. The pCO_2 also modifies the optimal temperature

for photosynthesis. However, the needleleaf PFTs in ORCHIDEE are probably too sensitive to CO_2 changes. Indeed, the reconstruction of the LGM forests on the Atlantic coast of America for instance show that needleleaf trees were actually dominant (Williams et al., 2002), contrary to our results from ORCHIDEE (Fig. 7). Similarly, in Japan the landscape was occupied by a cool mixed forest (Prentice et al., 2000), while we obtain more than 70 % of BoBS in ORCHIDEE in LGMG.

The overestimation of the productivity and competitivity of BoBS compared to the other tree PFTs might effect the sensitivity of the results. On the one hand, the overestimation of BoBS in CTRLP may lead to an exaggerate forest regression at LGM compared to present-day, but on the other hand the lower sensitivity of BoBS to the CO_2 decrease in LGMG may on the contrary underestimate this regression. However, these possible biases do not effect our conclusions on the important role of the CO_2 decrease to explain the regression and/or change of composition of forests at the LGM compared to present-day. They also do not effect our conclusion on the importance of the initial state (Sect. 4.2.4) and the fact that the response to CO_2 depends on the background climate (see Sect. 4.3).

The increase in competitivity of C4 plants relative to C3 at low CO_2 levels, thanks to their particular photosynthetic pathway, is a well-known fact (Ehleringer and Bjorkman, 1977), but to our knowledge no experimental study of the possible different responses between C3 species to low CO_2 concentrations has been undertaken. Such a study would be useful to evaluate the accuracy of the amplitude in the response of vegetation models to decrease in atmospheric CO_2, and to improve the parameterizations. The pCO_2 also has an impact on the concentration of stomata (Woodward and Bazzaz, 1988), but this is not taken into account in ORCHIDEE.

To summarize, vegetation changes during glacial times depend on several factors:

- Change in climate effects the geographical area where a PFT can grow.

- The decrease in CO_2 reduces the extension of the sustainable zone for a given PFT and its productivity in this zone. The CO_2 impact depends on the local climatic conditions.

- Dynamics: the PFTs in ORCHIDEE have different sensitivities to pCO_2. Changing the CO_2 also changes their competitivity. In particular, needleleaf are less competitive than broadleaf at low CO_2 level, and broadleaf PFTs actually expand in areas previously occupied by needleleaf PFTs.

The relative impact of glacial climate and CO$_2$ is not simply additive, given the many feedbacks at stake. The response of vegetation to a given climate depends on its atmospheric CO$_2$ level, and the sensitivity of vegetation to a given CO$_2$ change depends on both the former and the actual climate reached under that CO$_2$ level. As a result, the dynamical vegetation response to abrupt climate changes such as during Dansgaard-Oeschger or Heinrich events will not only depend on their climatic amplitude but also on the period in which they occur, since the atmospheric CO$_2$ level was not constant throughout the last glacial period. We can expect the vegetation to be more sensitive to cooling or drying at a low CO$_2$ level. Considering the fact that different species will have different sensitivities to a given climate change, the vegetation response will also depend on the floristic composition before the abrupt event: the strong regression of a particularly sensitive species will allow a more resistant one to expand even if the new climate, alone, is not so favourable to it. On longer time-scales, the timing of the progressive development of a glacial vegetation after an interglacial period should also depend on the rate of atmospheric CO$_2$ decrease.

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