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Impact of CO_2 and climate on Last Glacial Maximum vegetation – a factor separation

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Abstract

Differences between glacial and pre-industrial potential vegetation patterns can conceptually be attributed to two factors: firstly to differences in the climate, caused by a strong increase in ice masses and the radiative effect of lower greenhouse gas concentrations, and secondly to differences in the ecophysiological effect of lower glacial atmospheric CO_2 concentrations. The synergy emerging from these effects when operating simultaneously can be interpreted as sensitivity of the effect of enhancing physiologically available CO_2 on shifting vegetation to climate warming. Alternatively and equally valid, it can be viewed as sensitivity of climatically induced vegetation changes to differences in physiologically available CO_2. A first complete factor separation based on simulations with the MPI Earth System Model indicates that the pure climate effect mainly leads to a contraction or a shift in vegetation patterns when comparing glacial with pre-industrial simulation vegetation patterns. Globally, a reduction in fractional coverage of most plant functional types is seen – except for raingreen shrubs which strongly benefit from the colder and drier climate. The ecophysiological effect of CO_2 appears to be stronger than the pure climate contribution for many plant functional types – in line with previous simulations. The ecophysiological effect of lower CO_2 mainly yields a reduction in fractional coverage, a thinning of vegetation and a strong reduction in net primary production. The synergy appears to be as strong as each of the pure contributions locally. For tropical evergreen trees, the synergy appears strong also on global average. Hence this modelling study suggests that for tropical forests, an increase in CO_2 has, on average, a stronger ecophysiological effect in warmer climate than in glacial climate. Alternatively, areal differences in tropical forests induced by climate warming can, on average, be expected to be larger with increasing concentration of physiologically effective CO_2.

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1 Introduction

During the Last Glacial Maximum some 21 000 years ago, large parts of Northern America and Northern Europe were covered by ice masses, and the atmospheric concentration of greenhouse gases was lower than today. Global glacial climate was considerably colder and drier, and global vegetation patterns were different from those today. Tropical forests were presumably reduced in their extent (Crowley, 1995) with tropical rainforest being replaced by tropical seasonal forest in tropical lowlands and by xerophytic woods in tropical highlands (Elenga et al., 2000) or by savannah and tropical grassland, mainly in Latin and South America (Marchant et al., 2009). Boreal and temperate forests regressed equatorwards with a compression and fragmentation of the forest zones (Prentice et al., 2000; Tarasov et al., 2000) covering a much smaller fraction than today.

Differences between glacial and present-day potential vegetation were diagnosed by vegetation models with input from climate models (e.g. Claussen and Esch, 1994; Kutzbach et al., 1998) or by coupled climate–vegetation models where vegetation was assumed to be a function of climate in terms of moisture, temperature and insolation (e.g., Kubatzki and Claussen, 1998; Jahn et al., 2005; Roche et al., 2007). Numerous coupled and uncoupled simulations (Levis and Foley, 1999; Harrison and Prentice, 2003; Crucifix et al., 2005; Prentice et al., 2011; Woillez et al., 2011) highlighted the role of ecophysiological effects of differences in atmospheric CO_2 concentration. In an atmosphere with reduced CO_2, photorespiration increases so that net productivity is reduced. As a second indirect effect, plants increase their stomatal conductance and their number of stomata, thereby affecting their transpiration and water-use efficiency. Subsequently, not only the dispersion of plants changes, but also the ratio between C3 and C4 plants shifts. Simulations of glacial vegetation which take changes in the climate and the ecophysiological CO_2 effect into account draw the same qualitatively similar picture: a strong reduction of forests in mid and high northern latitudes was attributed to the colder climate and the presence of ice sheets where the ecophysiological effect

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adds to this reduction. In the tropics, the ecophysiological effect of low CO_2 appears to be the dominant factor. Globally, a shift to more open vegetation with enhanced fraction of grass coverage under reduced CO_2 is seen in the models and, consistently, a strong reduction in simulated global net primary production.

So far, few modelling studies have analysed the relative contribution of the climate and ecophysiological effects of CO_2 to differences between glacial and present-day potential vegetation (e.g. Harrison and Prentice, 2003; Crucifix et al., 2005; Prentice et al., 2011; Woillez et al., 2011). A systematic factor separation, i.e. an analysis of pure contributions of ecophysiology and of climate and of synergies of these effects on the difference between glacial and present-day potential vegetation has not been done. Therefore, this problem is reassessed. A global dynamic vegetation model, JSBACH, coupled to the atmospheric general circulation model ECHAM6 is used with sea-surface temperature and sea-ice patterns taken from an earlier simulation with the ECHAM5-MPIOM atmosphere–ocean model. Factors and synergies are computed, and the results are compared with values computed from recent simulations by Woillez et al. (2011).

2 Models and model set up

This study focusses on atmosphere–vegetation interaction. Sea-surface temperature and sea ice conditions are prescribed from separate simulations for pre-industrial and glacial climate, respectively. This implies that feedbacks between vegetation dynamics and ocean dynamics on glacial–interglacial climate dynamics are assumed to be much smaller than atmosphere–vegetation and atmosphere–ocean feedbacks. Furthermore, atmospheric CO_2 concentration is prescribed. Hence the carbon exchange between vegetation and atmosphere can evolve only with this constraint.

In this study, the MPI-ESM, the Earth System model developed at the Max Planck Institute for Meteorology in Hamburg, is used with the atmospheric model ECHAM6 (Stevens et al., 2012) and the land surface model JSBACH (Raddatz et al., 2007, Brovkin et al., 2009, Reick et al., 2012). The JSBACH model simulates fluxes of energy, water, momentum, and CO_2 between land and atmosphere. The modelling concept is based on a tiled (fractional) structure of the land surface. Each land grid cell is divided into tiles covered with eight plant functional types (PFTs), i.e. tropical evergreen trees, tropical deciduous trees, extratropical evergreen trees, extratropical deciduous trees, raingreen shrubs, deciduous shrubs, C3 grasses, C4 grasses, and 2 types of bare surface (seasonally bare soil and permanently bare ground, i.e. deserts). Tiles which are excluded from vegetation dynamics (anthropogenic land cover, inland water, crops, etc.) are not taken into account in this study. The C3 and C4 photosynthetic pathway for autotrophic respiration and photosynthesis processes are based on the model by Farquhar et al. (1980) for C3 plants and Collatz et al. (1992) for C4 plants. The version of JSBACH used here does not consider nitrogen limitation in plant growth. The simulated vegetation dynamics is based on the assumption that competition between different PFTs is determined by their relative competitiveness expressed in annual net primary productivity (NPP), bioclimatic limits, as well as natural and disturbance-driven mortality (Brovkin et al., 2009).

The sea-surface temperatures for pre-industrial climate and glacial climate were prescribed by using results of earlier simulations with the ECHAM-5–MPI-OM model system at T31 resolution for the atmosphere while the oceanic model MPI-OM (Jungclaus et al., 2006) was run at approximately 3° resolution with 40 vertical layers. The atmosphere–ocean simulations, which were initialized with boundary conditions defined within the Paleoclimate Modeling Intercomparison Project-2 (PMIP-2; Braconnot et al, 2007), were run some 2000 yr to reach equilibrium (Mikolajewicz, personal communication, 2012; the model system is described in Mikolajewicz et al., 2007).

The boundary conditions and forcing for the simulations done in this study are summarized in Table 1. These include glacial ice sheet topography and coastlines according to Peltier (2004) and orbital parameters according to Berger (1978). To explore the differences between climatic effects and ecophysiological CO_2 effects on glacial and pre-industrial potential vegetation pattern, four simulations were set up: CTRL and

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CTRL-R refer to pre-industrial climate, where for CTRL-R the physiologically available CO_2 was set at glacial level of 185 ppm. Simulations LGM and LGM-E refer to glacial climate, where for LGM-E, the physiologically effective CO_2 was set at pre-industrial level of 280 ppm. This set up is similar to the experimental design used by Woillez et al. (2011). Woillez et al. (2011) used however atmospheric CO_2 concentrations of 310 ppm, a value representative for industrial, non-equilibrium climate of the 20th century.

Simulations in this study were run at T31 (i.e. approximately $3.8^{\circ} \times 3.8^{\circ}$) resolution with 19 vertical levels. The model simulated 300 yr to reach equilibrium between atmospheric and vegetation dynamics. For the first 200 yr of the simulation vegetation dynamics were accelerated by a factor of 3. The results shown in this study have been taken from the last 100 yr of the simulation with synchronous coupling of atmospheric and vegetation dynamics.

Figure 1 shows the fractional coverage of each grid cell with woody vegetation (i.e. tree, shrubs) as estimated by Brovkin et al. (2009) based on satellite data by Hansen et al. (2007) (upper figure) and as computed from the MPI-ESM simulation for present-day climate (lower figure). For comparability, both, data and model account for the historical land use. Comparison of the observed and simulated woody fraction reveals that the main patterns are well reproduced. The model tends to overestimate woody cover partly due to climate biases of the atmosphere model in Africa and partly due to a tendency of the vegetation model to simulate tree encroachment in dry regions (Central Asia, Australia) where, according to Brovkin et al. (2009), the disturbances are underestimated in the model. The model underestimates woody coverage in Alaska and, to some degree, at high northern latitudes. There, disturbance of vegetation due to wind break is presumably too large. For detailed regional comparison of the present-day tree cover and bare ground distribution, see evaluation of the vegetation cover in the historical simulation of the MPI-ESM in the Climate Model Intercomparison Project 5 (Brovkin et al., 2012).

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3 Simulation results

3.1 Glacial temperature and precipitation

The MPI-ESM simulates a near-surface (2 m) air temperature for pre-industrial climate of 13.7 °C on global average and 8.2 °C on average over land. Simulated global mean precipitation is 2.78 mm d^{-1}. These values are in good agreement with recent estimates of near-surface land temperature of some 8 °C in the 19th century and 8.9 °C in the 20th century (Rohde et al., 2011) and estimates of present-day precipitation of 2.62–2.78 mm d^{-1} (Hantel, 2005).

For the Last Glacial Maximum, the MPI-ESM yields 8.6 °C and 2.49 mm d^{-1} for global mean near-surface air temperature and precipitation, respectively. A glacial cooling of 5.1 °C and a reduction of global precipitation by some 10 % is in good agreement with the range of results of other simulations in the Paleoclimate Modeling Intercomparison Project (PMIP) (Braconnot et al., 2007). Moreover, the pattern of differences between glacial and pre-industrial climate simulated by MPI-ESM agrees with the pattern reported by PMIP (see Figs. 2a, b and 3a, b). Noteworthy exceptions include tropical Africa where the MPI-ESM simulates a moderate increase in precipitation for LGM climate, whereas the ensemble mean of the PMIP-2 reveals some decrease.

3.2 Glacial vegetation

Figure 4 depicts the differences in global area covered by the PFTs between glacial and pre-industrial climate. In line with previous simulations, the MPI-ESM yields a decrease in areas of tropical trees (by some 20 %) and of extratropical trees (by some 45 %). The desert area increases by 36 %. The area covered by grassland decreases by some 40 %, while the area covered by shrubs increases by approximately 57 %.

A detailed comparison between simulated glacial and pre-industrial vegetation (see also Selent, 2012) shows that the northern and the southern margin of tropical evergreen trees is shifted towards the equator (Fig. 5a). The fractional coverage of tropical

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evergreen trees in the inner tropics increases, including the area of the Indonesian shelf which can be occupied by vegetation due to lower sea level during the Last Glacial Maximum. Tropical deciduous trees are reduced almost everywhere (Fig. 5b). Extratropical evergreen and deciduous trees (Fig. 5c, d) are regressed southward, and extratropical evergreen trees replace extratropical deciduous trees in large parts of Europe. In turn, extratropical deciduous trees replace extraptropical evergreen trees in Siberia around 60° N. Interestingly, extratropical evergreen trees and, to a much smaller extent extratropical deciduous trees, move into the tropics and outweigh tropical trees in some regions. Raingreen shrubs (Fig. 5e) are more widespread in the glacial tropics and are found in areas which in pre-industrial climate are covered by tropical trees. Hence, raingreen (or tropical and subtropical) shrubs benefit from the glacial climate in the MPI-ESM. Deciduous shrubs (Fig. 5f) are shifted southward over Eurasia, and are nearly extinct in Northern America, but the sum of all areas covered by deciduous shrubs remains nearly the same in glacial and pre-industrial climate. Grassland generally decreases. C3 grass (Fig. 5g) is pushed southward by the ice masses. On average, C3 grassland is reduced in all northern continents, although it is still the dominant PFT in the western part of Northern America and the Northern Siberia and southern part of South America (not shown). It is increased in the southern tropics. C4 grass (Fig. 5h) is reduced in almost all areas.

How do these results compare with reconstruction and previous simulations of glacial vegetation? The regression of forests in the high northern latitudes and the expansion of bare ground is qualitative agreement with reconstruction (Prentice et al., 2000; Tarasov et al., 2000) and simulations by Claussen and Esch (1994), Harrison and Prentice (2003), Kutzbach et al. (1998), Levis and Foley (1999), Roche et al. (2007), Woillez et al. (2011). In the western part of Northern America grasses prevail, and the different tree types in the eastern part of Northern America is found as in reconstructions by Prentice et al. (2000) and in simulations by Harrison and Prentice (2003), Kutzbach et al. (1998), Woillez et al. (2011). In Europe a mixture of evergreen trees and deciduous trees is simulated, but in southern and eastern part of Europe with a large fraction

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of C3 grasses. This seems to be comparable to the simulations by Kutzbach et al. (1998), Roche et al. (2007), Woillez et al. (2011). Reconstructions by Bigelow et al. (2003) indicate that most of Europe was covered by open shrubland. In this study, an increase in deciduous shrubs is found, but shrubs are not the dominant type in glacial Europe. The strong reduction of Siberian forest in glacial climate agrees with reconstructions by Bigelow et al. (2003) and simulations by Claussen and Esch (1994), Crucifix et al. (2005), Harrison and Prentice (2003), Kutzbach et al. (1998), Roche et al. (2007), Woillez et al. (2011). The reduction of trees and grasses, hence the more open vegetation, in Central Asia is comparable to the expansion of semi deserts found by Crucifix et al. (2005) and Roche et al. (2007). East Asia remains to be covered by forests as seen in simulations by Claussen and Esch (1994), Crucifix et al. (2005), Harrison and Prentice (2003), Kutzbach et al. (1998), Roche et al. (2007). The small decrease of tropical evergreen forest in the MPI-ESM agrees with the results by Woillez et al. (2011). However in contrast to the latter study, the MPI-ESM simulates an increase in tropical evergreen forest in the inner tropics. This seems to be at variance with reconstructions by Crowley (1995) and Marchant et al. (2009). Presumably, this difference can partly be attributed to the green bias of the MPI-ESM in these regions and the moderate increase in glacial precipitation over tropical Africa which is not found in the ensemble mean of the PMIP-2 simulations. The comparison of the extent of shrubs is difficult due to the fact that explicit values for shrubs are not given. Nevertheless, the increase of shrub area at the expense of tropical trees in southern South America and South Africa clearly reflects a change to more drought-tolerant vegetation types as seen in Crucifix et al. (2005), Harrison and Prentice (2003), Levis and Foley (1999), and Woillez et al. (2011) and reconstructed for Latin and South America by Marchant et al. (2009). In contrast, the expansion of grasses in the tropics and extratropics, found by Levis and Foley (1999), Harrison and Prentice (2003), Crucifix et al. (2005), and Woillez et al. (2011), is missing in the MPI-ESM. However in the MPI-ESM, C3 grass is still the dominant PFT in Siberia and southern part of South America in glacial climate where trees prevail in pre-industrial climate. Likewise, the

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ratio between C4 and C3 grasses increases which is in qualitative agreement with Crucifix et al. (2005). Finally the simulated increase in deserts, i.e. bare ground, is reported from reconstructions by Prentice et al. (2000) and by previous simulations.

Regarding NPP, the MPI-ESM simulates a decrease from some 57.9 $\mathrm{Gt\,C\,yr^{-1}}$ of NPP in pre-industrial climate to some 31.2 $\mathrm{Gt\,C\,yr^{-1}}$ in glacial climate. These values agree well with results by Crucifix et al. (2005) of 57.5 $\mathrm{Gt\,C\,yr^{-1}}$ and 36.6 $\mathrm{Gt\,C\,yr^{-1}}$, for pre-industrial and glacial climate, respectively.

In summary, the MPI-ESM recaptures many aspects of glacial vegetation pattern, such as the reduction in fractional coverage by trees and the shift to more open vegetation and bare ground in the extratropics and subtropics, found in reconstructions and previous simulations. The reduction in tropical tree coverage seems to be underestimated and there is no expansion of grass as seen in earlier simulations.

3.3 Factors and synergies

Which factors can the vegetation differences between glacial and pre-industrial climate be attributed to – the colder and drier climate and the more wide-spread ice masses or the ecophysiological effect of lower atmospheric CO_2 concentrations? To answer this question, the difference between vegetation patterns are analysed using the factor separation by Stein and Alpert (1993). The pure contribution f_C due to differences in climate, including differences in ice sheet and land–sea distribution, and the pure contribution f_E due to ecophysiological CO_2 effects read for each PFT:

$$f_C = A(\text{LGM-E}) - A(\text{CTRL}) \quad \text{(1a)}$$

$$f_E = A(\text{CTRL-R}) - A(\text{CTRL}) \quad \text{(1b)}$$

where A is the areal coverage by the PFT under consideration.

The synergy f_{CE} between factors f_C and f_E is:

$$\begin{aligned} f_{CE} &= A(\text{LGM}) - A(\text{CTRL}) - f_C - f_E \\ &= A(\text{LGM}) - A(\text{LGM-E}) - A(\text{CTRL-R}) + A(\text{CTRL}) \quad \text{(1c)} \end{aligned}$$

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Please note that the factors differ, if not the pre-industrial climate, but the climate of the Last Glacial Maximum is used as reference state, e.g. $g_C = A(\text{LGM-E}) - A(\text{LGM})$, $g_E = A(\text{CTRL-R}) - A(\text{LGM})$. But the synergy is the same, regardless of whether the simulation CRTL is used as reference state or the simulation LGM, i.e. $g_{CE} = f_{CE}$ with

$$\begin{aligned} g_{CE} &= A(\text{CTRL}) - A(\text{LGM}) - g_C - g_E \\ &= A(\text{CTRL}) - A(\text{LGM-E}) - A(\text{CTRL-R}) + A(\text{LGM}) \end{aligned} \tag{1d}$$

Differences in climate, including the difference in area available for vegetation growth, result in a reduction of the areal coverage of all PFT, except for raingreen shrubs (Fig. 6). In addition, the pure contribution in climate leads to a shift of vegetation pattern. This is valid for most PFTs in most regions. As an example differences in tropical evergreen trees (TET) are presented in Fig. 7. Tropical evergreen trees are reduced at their northern and southern margins. This reduction which can be attributed to the bioclimatic temperature limits of TET is partly compensated by an increase in fractional coverage in the inner tropics, including an expansion of trees onto newly available land due to lower sea level. The pure contribution of climate effects favours the existence of C3 grasses at the expense of C4 grasses in most subtropical areas.

The pure contribution due to the ecophysiologcial effect of lower CO_2 reduces the areal coverage of almost all PFTs (Fig. 6). Noteworthy exceptions are: tropical deciduous trees (TDT) seem to benefit from a lower CO_2 (in some regions in Africa north of the Equator and in Australia, not shown). This could be caused, however, by the retreat of tropical evergreen trees in these regions. Also C4 grass benefits from a reduction in atmospheric CO_2 concentration on average over all areas covered by C4 grass. In many tropical areas, however, coverage by C4 grass decreases which is a consequence of the fact that in JSBACH, trees are always the dominant PFT in comparison with grass, i.e. grass coverage can increase only in areas where tree coverage is reduced.

The ecophysiological CO_2 effect leads to a strong reduction in NPP (Fig. 8). Not only the pattern, but also the difference between pre-industrial and glacial global NPP are very similar in the CTRL-R and the LGM simulations. Globally, NPP reaches some 57.9 $Gt C yr^{-1}$ in the CTRL simulation, 32.0 $Gt C yr^{-1}$ in the CRTL-R simulation, 55.5 $Gt C yr^{-1}$ in the LGM-E simulation and 31.2 $Gt C yr^{-1}$ in the LGM simulation. Consistently, the carbon stored in terrestrial biosphere is reduced between pre-industrial and glacial climate (not shown), and this is mainly caused by the ecophysiological CO_2 effect. Hence, even if there is some increase in the fractional coverage by tropical trees in South America (Fig. 5a), for example, the glacial tropical forest appears to be thinner or more open.

Do the differences in vegetation coverage triggered by the climate and ecophysiological CO_2 effect sum up? For most PFTs, they approximately do on global scale. Figure 6 shows that the synergy between the climate and the ecophysiological CO_2 effect is considerably smaller than at least one of the pure contributions. A globally weak synergy does not imply that the synergy is weak locally. In most cases (not shown), the synergy can be as strong as the pure contributions at grid scale. Tropical evergreen trees stand out as, on global average, their synergy is largest and is approximately as large as the pure contributions of the climate and the ecophysiological CO_2 effect. Figure 7c reveals that the synergy is positive not everywhere, but positive values dominate.

What does the synergy cause? To a large extent, synergy for tropical evergreen trees (Fig. 7c) occurs in regions where no differences in the spatial pattern of other PFTs (Fig. 5) can be found. Obviously, competition between PFTs can hardly be the main source of synergy, rather synergy is linked to the physiology of each PFT. In the Farquhar model, net primary production is a nonlinear function of temperature and CO_2 which indicates that the ecophysiological CO_2 effect on net primary production depends on temperature and vice versa, the temperature effect on net primary production is a function of ecophysiologically available CO_2. In fact, Prentice et al. (2011) and Woillez et al. (2011) already mention that the ecophysiological CO_2 effect on the distribution of vegetation varies with climate.

By rearranging Eq. (1c) it becomes obvious that the synergy is the sensitivity of the ecophysiological CO_2 effect to climate. The synergy can formally be interpreted as the difference between the ecophysiological effect of enhanced CO_2 in warm climate and

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in cold climate, i.e.

$$f_{CE} = A(\mathrm{CTRL}) - A(\mathrm{CTRL\text{-}R}) - (A(\mathrm{LGM\text{-}E}) - A(\mathrm{LGM})) \tag{2a}$$

For tropical evergreen trees, f_{CE} is positive, i.e. A(CTRL) – A(CTRL-R) is larger than A(LGM-E) – A(LGM). This implies that the ecophysiological effect of enhanced CO_2 is stronger in warm than in cold climate. For C4 grass, for example, the opposite conclusion can be drawn. In this case, the synergy is negative; hence the ecophysiological effect of enhanced CO_2 decreases with warmer climate.

The alternative and equally valid interpretation can also be derived from Eq. (1c). The synergy measures the difference between the pure climate effect on vegetation changes under high and low physiologically effective CO_2, i.e.

$$f_{CE} = A(\mathrm{CTRL}) - A(\mathrm{LGM\text{-}E}) - (A(\mathrm{CTRL\text{-}R}) - A(\mathrm{LGM})) \tag{2b}$$

Again, as an example, this difference is positive on global average for tropical evergreen trees, i.e. the shifts and contraction of tropical evergreen forests between warm and cold climate are larger under high physiologically available CO_2.

How do these results compare with the simulations by Woillez et al. (2011)? A direct comparison is difficult as Woillez et al. (2011) use different PFTs than in this study. They differentiate between tropical, temperate and boreal trees, and they do not assign a PFT for shrubs. To facilitate comparison, we combine tropical evergreen and deciduous trees and raingreen shrub to tropical woody plants, extratropical evergreen and deciduous trees and deciduous shrubs to extratropical woody plant, and C3 and C4 grasses to grasses. The PFTs in the study by Woillez et al. (2011) are summed up to tropical trees, extratropical trees (comprising temperate and boreal trees) and grasses. Furthermore, we compare global areal coverage and global foliage projective coverage which are not the same variables, but they are closely related. Furthermore, Woillez et al. (2011) used values of atmospheric CO_2 concentration of 310 ppm and 185 ppm for present-day and glacial climate, respectively. Hence the range of CO_2 changes is roughly 30 % larger than the range used in the present study, and stronger

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CO_2 effects – radiative and ecophysiological effects – can be expected. Finally, Woillez et al. (2011) used off-line vegetation simulations, i.e. they neglected feedbacks between atmosphere and vegetation dynamics. Hence any comparison is of qualitative nature only.

Figure 9 reveals similarities and discrepancies between the simulations by Woillez et al. (2011) and the present study. Factors and synergy of tropical woody plants agree qualitatively. The pure climate effect tends to increase the fractional coverage by tropical woody plants – in this study due to the strong increase in shrubs. The pure ecophysiological effect causes a strong decrease. The synergy is positive. The fractional coverage of extratropical woody plants decreases. The strong reduction in extratropical trees due to the pure climate effect in the simulation by Woillez et al. (2011) is not recaptured in this study. The climatically induced reduction is attributed to a strong reduction in boreal, rather than temperate, trees which could be a consequence of the strong positive bias in present-day boreal tree coverage in the model of Woillez et al. (2011). Only if high northern latitudes are extensively covered by trees in interglacial climate, than the expansion of ice masses in high northern latitudes can cause large differences in boreal tree coverage. Factors and synergy of grass coverage strongly differ between studies. All factors, including synergy, indicate an increase in grass coverage in the study by Woillez et al. (2011), while the climate and CO_2 effect lead to a reduction in grass coverage with a small negative synergy in the present study. This difference can presumably be attributed to two points. First, the strong reduction in boreal tree coverage likely provides favourable conditions for grass expansion in the simulations by Woillez et al (2011). Second, and presumably more important, the desert area in glacial climate is by some 8×10^6 km^2 larger than in the control climate in the simulations by Woillez et al. (2011). In the present study the difference in desert area is nearly 16×10^6 km^2, i.e. almost twice as large (see Fig. 4).

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4 Summary and conclusions

Differences between glacial and pre-industrial potential vegetation patterns have been attributed to differences in the climate, caused by a strong increase in ice masses and the radiative effect of lower greenhouse gas concentrations, and in the ecophysiological effect of lower atmospheric CO_2 concentrations. Most studies so far have highlighted the role of the climate and the ecophysiological effect, but little attention has been paid to the synergy, the feedback between the pure climate contribution and the pure ecophysiological contribution. Woillez et al. (2011) mention that "the relative impact of glacial and CO_2 is not simply additive", but they do not quantify this impact.

In this study, the MPI-Earth System Model (MPI-ESM) has been used to reassess the problem and to quantify the synergy via factor separation. The MPI-ESM in the version used in this study is able to simulate most aspects of glacial versus pre-industrial potential vegetation pattern found in reconstructions and previous simulations. This includes the reduction in fractional coverage by trees and the shift to more open vegetation and bare ground in the extratropics and subtropics. The reduction in tropical tree coverage, however, seems to be underestimated in this study, and there is no expansion of grass as seen in other simulations. The strong reduction in NPP found here agrees with previous simulations and estimates from reconstructions.

In line with previous simulations, the ecophysiological effect of CO_2 is stronger than the pure climate contribution for many PFTs, including tropical evergreen trees. By and large, the pure climate effect leads to a contraction or a shift in vegetation pattern and, globally, to a reduction in fractional coverage – except for raingreen shrubs which strongly benefit from the colder and drier climate. The ecophysiological effect of lower CO_2 mainly yields a reduction in fractional coverage and a strong reduction in NPP. Hence the ecophysiological CO_2 effect is the larger factor with respect to thinning of glacial forests.

The synergy can be interpreted as a measure of the difference in the ecophysiological CO_2 effect between different climate states or, alternatively, a measure of the

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difference in the pure climate effect on vegetation shifts under different physiologically effective CO_2 values. This finding has interesting implications. For tropical forests, the synergy is positive on average, i.e. the ecophysiologcial effect of enhanced CO_2 seems to be larger in interglacial, warmer climate than in glacial, colder climate. Alternatively, climatically induced changes in tropical forests will, on average, be larger with increasing concentration of physiologically effective CO_2. Both interpretations seem to be a robust model-based result, found in this study and in simulations by Woillez et al. (2011). For grass, this study and the study by Woillez et al. (2011) differ: this study predicts a negative synergy, Woillez et al. (2011) a positive synergy.

These conclusions are valid, of course, only within the limits of the validity of the models used. Anthropogenic land use and land-cover change which have been altering biogeophysical and biogeochemical processes for centuries and changing concentrations in nutrients such as nitrogen are not considered in this study. These processes would very likely modify the picture. Furthermore, it is not clear from just two pairs of simulations whether the synergy changes monotonically with climate.

Finally, attribution of processes to feedbacks and synergies is a modelling problem, and one of the complications of comparing different models is the difference in PFTs used in the models. For example, the IBIS model used by Levis and Foley (1999) and the ORCHIDEE model used by Woillez et al. (2011) do not consider shrub as a separate PFT, and their result in expansion of grasses in tropics is not directly comparable with the MPI-ESM which simulate a shift from trees to shrubs in this region. Another complication arises from different approaches to calculate fractions of PTFs and desert (bare soil) in the models. For example, the desert fraction in MPI-ESM depends on the leaf area indexes of PFTs. Low glacial CO_2 concentration leads to reduced NPP for all PFTs, and therefore, to decreased vegetation area and increased desert fraction. The foliage projective cover (FPC) used by ORCHIDEE to determine the PFT fractions is based on a weighted function of canopy of PFT individuals, and sensitivity of FPC to the changed climate and CO_2 concentration in LGM is different from the approach used in MPI-ESM. These conceptual differences among the models limit the value of

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model-to-model intercomparison. A more harmonized analysis of model performance is highly desirable but goes beyond the scope of the given paper.

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Table 1. Boundary conditions and forcing used in the simulations referred to as CTRL, CTRL-R, LGM-E, LGM in this study. Ice sheet, topography and coast line are taken from Peltier (2004), orbital parameters from Berger (1978). These conditions are chosen according to the PMIP-2 protocol (Braconnot et al., 2007).

		CTRL	CTRL-R	LGM-E	LGM
Ice sheets, topography, coast line		Modern		ICE-G5	
Trace gases	Physiologically effective CO_2	280 ppm	185 ppm	280 ppm	185 ppm
	Radiative effective CO_2	280 ppm		185 ppm	
	CH_4 (ppbv)	760 ppb		350 ppb	
	N_2O	270 ppb		200 ppb	
Insolation	Solar constant	1365 ($W m^{-2}$)			
	Eccentricity	0.016724		0.018994	
	Obliquity	23.446°		22.949°	
	Angular precession	102.04°		114.42°	

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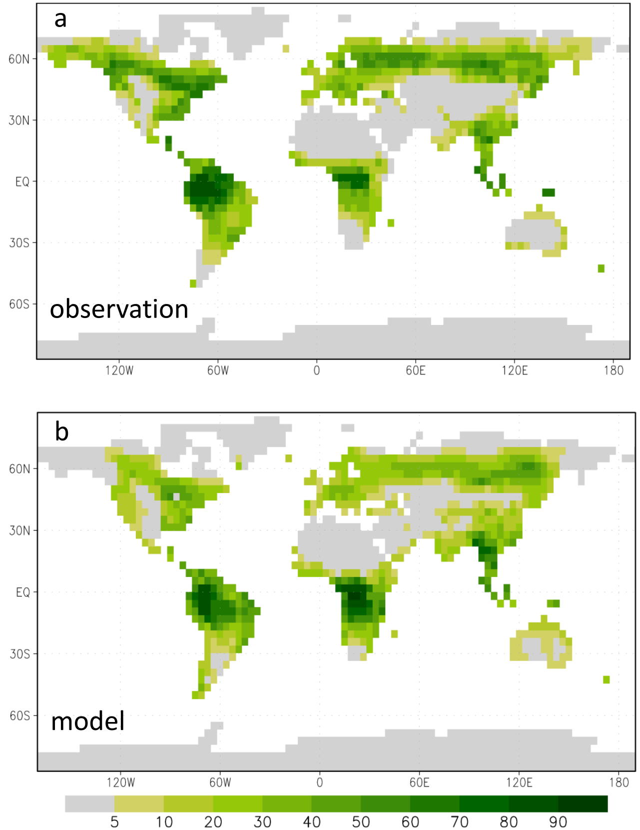

Fig. 1. (a) Present-day tree and shrub cover based on MODIS data by Hansen et al. (2007) averaged on the MPI-ESM grid (figure taken from Brovkin et al., 2009). **(b)** Simulated tree and shrub cover in the control simulation (modified to account for historical deforestation).

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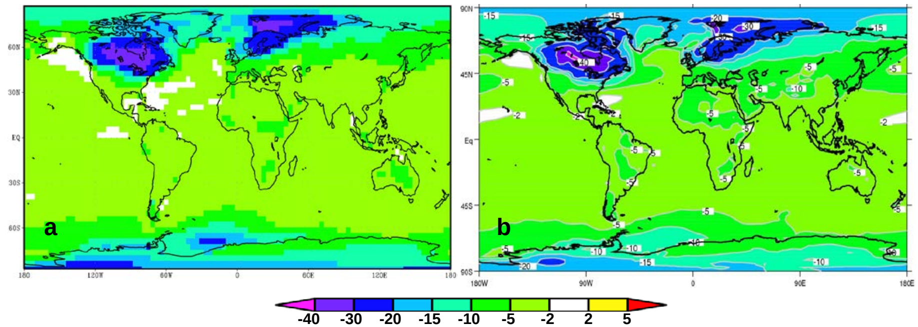

Fig. 2. Changes in 2 m air temperature (in K) between simulations of the climate of the Last Glacial Maximum and of pre-industrial climate. **(a)** Difference between the LGM and the CTL simulation, **(b)** Difference of the ensemble mean of the atmosphere-ocean-vegetation model simulations of PMIP-2 (Braconnot et al., 2007). **(b)** is taken from http://pmip2.lsce.ipsl.fr.

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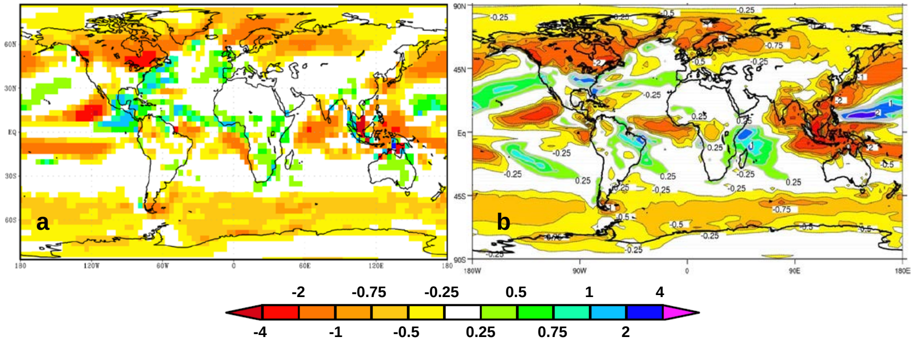

Fig. 3. Same as Fig. 2, except for changes in annual mean precipitation (in $\mathrm{mm\,d^{-1}}$).

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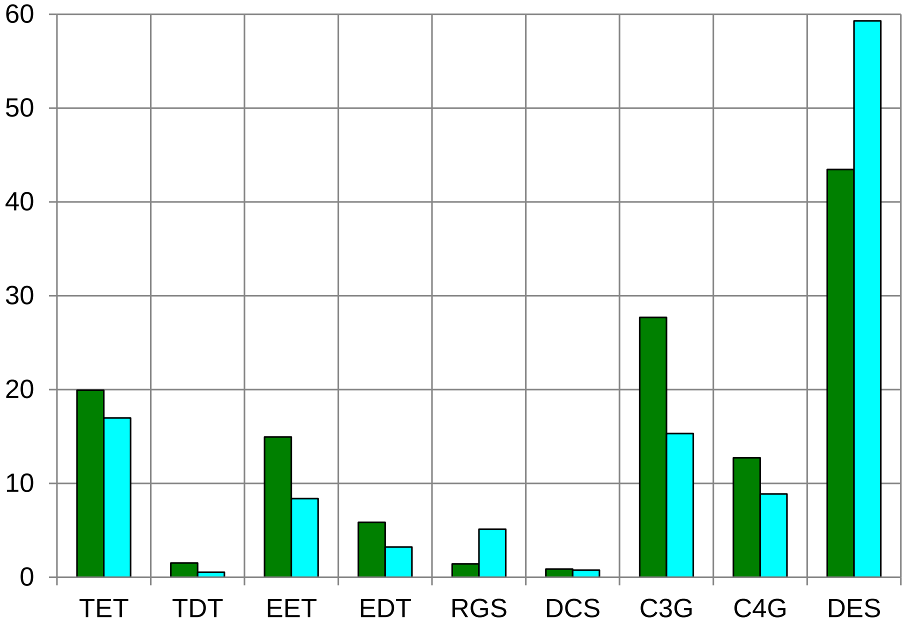

Fig. 4. Area (in 10^6 km^2) covered by different PFTs and bare ground for pre-industrial climate (dark green columns) and glacial climate (blue columns). The PFTs are tropical evergreen trees (TET), tropical deciduous trees (TDT), extratropical evergreen trees (EET), extratropical deciduous trees (EDT), raingreen shrubs (RGS), deciduous shrubs (DCS), C3 grass (C3G), C4 grass (C4G), bare ground (DES).

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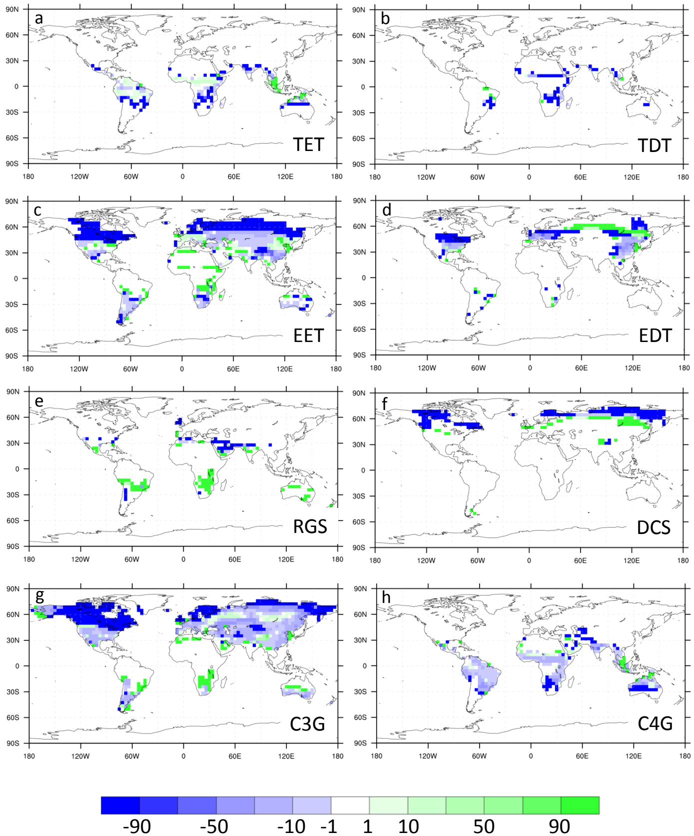

Fig. 5. Differences fractional coverage (given in % coverage of each grid cell) between glacial and pre-industrial vegetation patterns for each PFT (for acronyms see Fig. 4).

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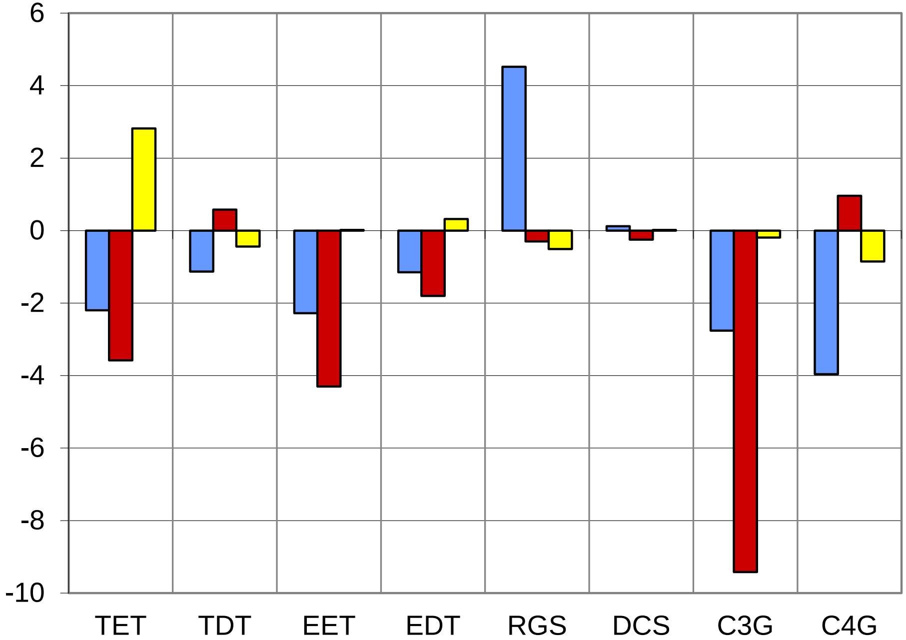

Fig. 6. Changes in global areal coverage (in 10^6 km^2) for different PFTs (for acronyms see Fig. 4). Blue columns refer to the pure contribution of changes climate, including differences in ice sheet and land-sea distribution, to differences between glacial and pre-industrial potential coverage by each PFT. Brown columns refer to the pure contribution due to the ecophysiological effect of different CO_2 concentration in glacial and pre-industrial climate. Yellow columns depict the synergy between the pure contributions.

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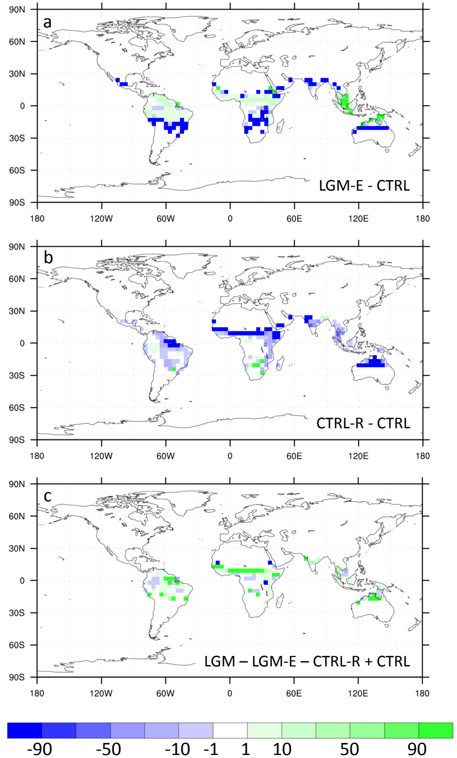

Fig. 7. Differences between glacial and pre-industrial vegetation patterns in terms of fractional coverage by tropical evergreen trees. **(a)** Differences due to the pure climatic effect, **(b)** differences due to the pure ecophysiological CO_2 effect, **(c)** differences due to the synergy between climatic and ecophysiological effects.

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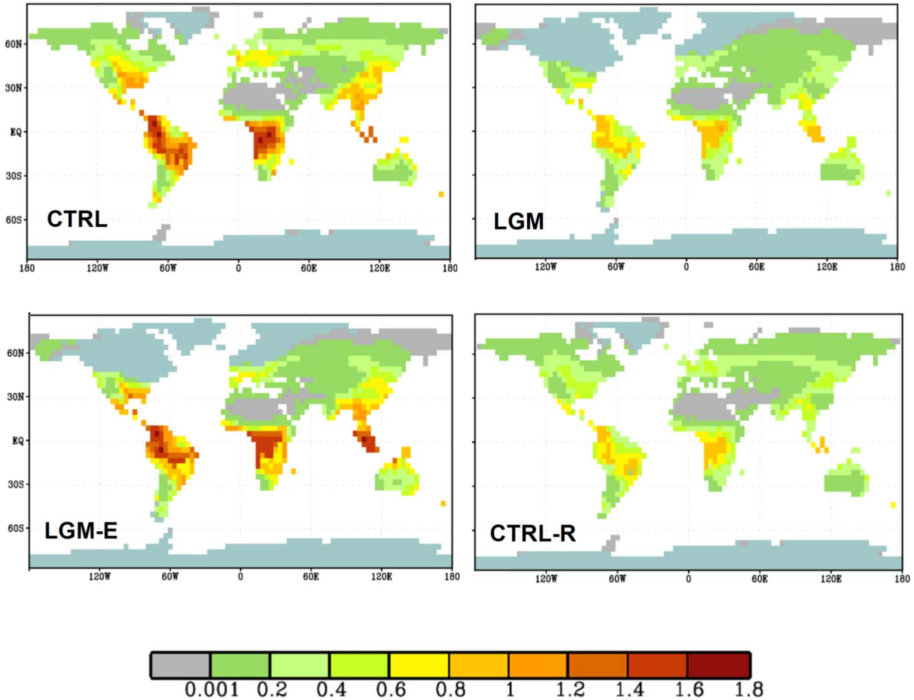

Fig. 8. Net primary production (NPP) (in $kg\,m^{-2}\,yr^{-1}$) for different simulations of pre-industrial climate (CRTL), climate of the Last Glacial Maximum (LGM), climate of the Last Glacial Maximum, but with physiologically effective CO_2 of 280 ppm as in pre-industrial climate (LGM-E), and pre-industrial climate, but with physiologically effective CO_2 of 185 ppm as in glacial climate (CTRL-R).

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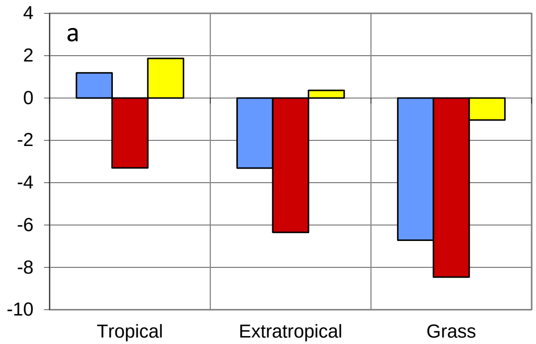

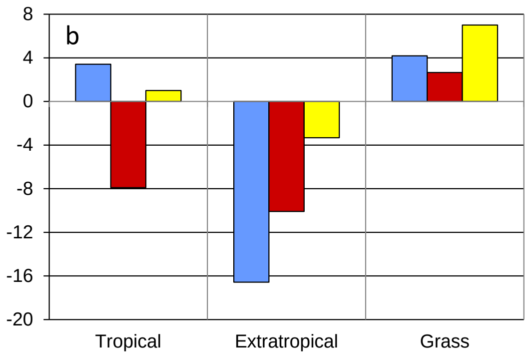

Fig. 9. Same as Fig. 6, except that in the upper part **(a)**, aggregated PFTs are depicted. Tropical: tropical woody PFT = tropical evergreen and deciduous trees and raingreen shrubs, Extropical: extratropical woody PFT = evergreen and deciduous trees and deciduous shrubs, Grass: C3 and C4 grass. In the lower part **(b)**, factors and synergies are shown for the global foliage coverage (in 10^6 km^2) for tropical tree, combined temperate and boreal trees and grass in the study by Woillez et al. (2011).

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