

## Reply to Review Comments

We thank the anonymous referee and Ashley Ballantyne for their thoughtful comments and for their time and effort to review this manuscript. Original review comments are given in black, our answer in red, and new or revised text added to the manuscript in blue fonts. A revised version in track change mode is attached to this reply.

### Anonymous Referee #1

In the manuscript “20th – century changes in carbon isotopes and water-use efficiency: Tree-ring based evaluation of the CLM4.5 and LPX-Bern models” Keller et al. present the implementation of a carbon isotope scheme in two global models as well as their performance with respect to simulated spatial patterns and decadal trends. The model results are compared to two different datasets, tree-ring records and bulk leaf delta 13C data. This study is a valuable contribution to ongoing efforts on the implementation of carbon isotopes in global vegetation models. The overall approach as well as the results are presented in an adequate and clear manner.

Thank you.

My main criticism is on the conclusions that are drawn from these results. Some parts of the discussion will be subject to revision. More detailed comments are listed below.

We will address your points below.

Abstract The abstract is a nice summary and contains all important aspects of the paper. However, I disagree with the last sentence. Suggesting “fundamental problems associated with the prescribed relationship between conductance and assimilation” is rather provocative and not supported by the results of this study. This relationship is strongly supported by observations (see e.g. Wong 1979 and also De Kauwe et al. 2013, Global Change Biology; papers cited in this study) and consequently used in most global models. I.e. it would indeed be a fundamental problem in our understanding of plant physiology. If this thought is brought up at such a prominent position in the paper, it needs to be better discussed and corroborated later in the manuscript, see below.

The sentence is revised to read: “The results suggest that the down-regulation of  $c_i/c_a$  and of photosynthesis by nitrogen limitation is possibly too strong in the standard setup of CLM4.5 or there may be problems associated with the implementation of conductance, assimilation, and related adjustment processes to long-term environmental changes.”

We agree that the relationship is experimentally well-established. Yet, it remains controversial whether and how the relationship between conductance and assimilation changes under changing environmental conditions, particularly those now addressed in the model experiments such as the monotonic increase in atmospheric CO<sub>2</sub> over the past 170 years (Miner et al., 2016).

Introduction The introduction starts with a nice overview on the application of isotopes in the Earth System, which is a good motivation for this study. Following this part, the connection between carbon isotopes and plant physiological behavior is pointed out. The introduction closes with a very clear outline of the goals of this study.

Thank you.

Methods Page 4: the listing of all PFTs seems a bit unnecessary to me. It is enough to mention the classifiers (phenology, photosynthetic type, etc.). Alternatively, one could provide a table showing the different PFTs and their main attributes in the appendix, but I don't think this is necessary for this manuscript.

Done. PFT listing is deleted.

I would appreciate some more information on the carbon and nitrogen pools mentioned on the same page, in brief. How do they communicate? On what time scales?

Done. The following text is added: "Vegetation comprises fifteen different PFTs, which are classified into three different phenological groups: evergreen, seasonal-deciduous, and stress-deciduous. Fourteen of these PFTs follow the C3 photosynthetic pathway (11 tree, 2 grasses and crops) and one the C4 path (warm grasses). Altogether, 20 carbon and 19 nitrogen pools per PFT represent carbon (C) and nitrogen (N) in vegetation. C and N are tracked for leaf, live stem, dead stem, live coarse root, dead coarse root, and fine root pools and corresponding storage pools representing, respectively, short-term and long-term storage of non-structural carbohydrates and labile nitrogen.

Decomposition of fresh litter material (including C and N) into progressively more recalcitrant forms of soil organic matter is represented as a cascade of transformations between decomposing coarse woody debris, litter, and soil organic matter pools. Depending on the C:N ratios of involved pools and the amount of carbon lost by respiration, each transformation can generate either a source or a sink of new mineral nitrogen.

Steps that result in an uptake of mineral nitrogen (e.g., immobilization fluxes) are subject to rate limitation, depending on the availability of mineral nitrogen and the sum of nitrogen demands from immobilization, photosynthesis, nitrification, and denitrification. If mineral N is less than the sum of these demands, fluxes are downregulated in order to match N supply. We note that the "Relative Demand" downregulation in CLM4.5 has recently been shown to be inaccurate in several tropical (Zhu et al., 2016b), tundra (Zhu et al., 2016a), and grassland (Zhu et al., 2017) systems. In addition to the cycling of nitrogen within the plant - litter - soil organic matter system, CLM represents external sources, including atmospheric deposition and biological nitrogen fixation. CLM also represents other N sinks not included in this budgeting, including leaching and losses in fire."

There is an abrupt jump from leaf level photosynthesis (the models by Farquhar and Collatz) to the canopy level (GPP). Please add a short sentence explaining how photosynthesis is scaled to the canopy level. However, I think it would make more sense to explain this (p.4, lines 14-19) after equation 6, and not in the general description of the model.

Done. The following text is added:

"The maximum rate of carboxylation at 25°C varies with an assumed static foliage nitrogen concentration and specific leaf area and is a PFT specific parameter. It is assumed that leaf nitrogen and sunlight decrease exponentially with cumulative leaf area index from the canopy top to bottom. Accordingly, the carboxylation rate and other photosynthesis parameter decrease exponentially within the canopy. Leaf level photosynthesis is scaled to the canopy level by integration over the total leaf area. This is done separately for sunlit and shaded leaves and by considering the exponential scaling."

In addition, rather than describing the stomatal model in words on page 6 and showing the Equation in the discussion (Eq. 14), I would show the equation at this point. Please make sure that its original source is cited and that the notation is consistent: here you use “ca” for atmospheric CO<sub>2</sub>, later in Equation 14 “CO<sub>2</sub>” is used.

Done. Equation 14, now Eq. 7, moved to method section as requested. Reference to (Ball et al., 1987) is added.

Equation 6: Could this equation be double-checked? In my understanding the last term of this equation should be the overall resistance, i.e.  $1/(1.6 \cdot g_s) + 1/(1.4 \cdot g_b)$ , which differs from the term here.

Done. Equation is correct and given as implemented in CLM.

Conductance,  $g$ , and resistance  $r$ , are inversely related. The boundary layer,  $g_b$ , and stomatal,  $g_s$ , conductance of H<sub>2</sub>O is related to the boundary layer,  $r_b$ , and stomatal,  $r_s$ , resistance of H<sub>2</sub>O by:

$$g_b = 1/r_b \text{ and } g_s = 1/r_s.$$

Total resistance is the sum of individual resistances. For H<sub>2</sub>O the total resistance is:

$$r = r_b + r_s$$

For CO<sub>2</sub>, diffusive transport is slower than for H<sub>2</sub>O as the molecular mass of CO<sub>2</sub> is higher than of H<sub>2</sub>O. Thus, resistance is larger for CO<sub>2</sub> than for H<sub>2</sub>O (by a factor of 1.6 for stomatal, molecular diffusion and by a factor 1.4 assumed for the boundary layer). It holds for the total resistance of CO<sub>2</sub>:

$$r_{\text{CO}_2} = 1.6 r_s + 1.4 r_b = 1.6/g_s + 1.4/g_b$$

*Rearranging yields for the conductance:*

$$g_{\text{CO}_2} = 1/r_{\text{CO}_2} = 1 / (1.6/g_s + 1.4/g_b) = g_s g_b / (1.6 g_b + 1.4 g_s)$$

Please also check the equation on page 6 l.13, including the unit for conductance.

Done. Equation and units correct. Conductance is usually related to the mixing ratio and given in units of mol m<sup>-2</sup> s<sup>-1</sup>. In the submitted manuscript, conductance is related to the partial pressure of the gas and given in units mol m<sup>-2</sup> s<sup>-1</sup> Pa<sup>-1</sup>). To avoid confusion and for consistency with the notations used to describe LPX, we redefined  $c_i$  and  $c_a$  to represent CO<sub>2</sub> concentrations instead of CO<sub>2</sub> partial pressure. This required some small adjustments at various places in the method section.

The information on the LPX-Bern model is quite detailed and in some parts unnecessary. Again, the information on the PFTs can be shortened. E.g. for this paper it is not relevant what PFTs grow on peatland. Descriptive text elements such as “The CO<sub>2</sub> flux from the atmosphere to the stomatal cavity is proportional to the CO<sub>2</sub> difference between the atmosphere and the stomatal cavity ( $c_a - c_i$ )” are not needed and can be seen from the Equations (e.g. Eq.8) or are physical principles.

Done. The list of PFTs is deleted for natural non-peatland areas. The PFTs for peatland are still mentioned as discrimination is set constant for sphagnum moss to 30 permil and is following the C3 path for C3 graminoids. This is of some relevance for the simulated δ13C signature of vegetation and GPP as shown in Figure 4 and the global terrestrial isotopic budget as given in Figure 1 and Table 2.

The sentence on the CO<sub>2</sub> flux is deleted as requested. In addition the following sentence is deleted: “Tree PFTs and fires are excluded from the agricultural cell fraction.”

The stomatal control as simulated in LPX is poorly described. It is stated that  $c_i/c_a$  is set to 0.8 for non-water stressed conditions. That reads as if  $c_i/c_a$  is constant whenever there is enough water, even under low light, high VPD etc. Further, it is not really clear how this optimization works. Is it an optimization in the sense of Cowan & Farquhar 1977? If yes, the original reference should be cited. If not, it would be good to either elaborate this aspect or cite another study at this point where it is explained in more detail.

Done. Yes,  $c_i/c_a$  is set to 0.8 whenever there is enough water supply from soils. Note that the photosynthesis-conductance routines are solved on a daily time step in LPX.

The model description of LPX has been revised and mirrors now in its structure the description of CLM4.5. The description of photosynthesis and conductance is expanded and the nitrogen cycle is briefly described. The previous text is replaced by: “Photosynthesis and stomatal control in LPX is described by (Haxeltine and Prentice, 1996a) as summarized elsewhere (Keel et al., 2016;Sitch et al., 2003). The equations for water supply from soil and transpiration, assimilation, and canopy conductance are solved simultaneously by varying the ratio  $c_i/c_a$ , also termed  $\lambda$ , to yield self-consistent values for these properties.

Total day time net photosynthesis,  $A_{dt}$ , is modeled following (Collatz et al., 1991;Collatz et al., 1992) which is a Farquhar model (Farquhar et al., 1980) generalized for global modeling purposes (for details, see (Haxeltine and Prentice, 1996b) ).  $A_{dt}$  is a function of incoming radiation, temperature, day length, and atmospheric CO<sub>2</sub> partial pressure and  $\lambda$ .  $A_{dt}$  is computed from a formulation which gives a gradual transition between light-limited and Rubisco-limited rate of photosynthesis. The amount of photosynthetically active radiation absorbed by the entire canopy increases with the modelled leaf area index following Beer’s law and is used to compute the light-limited photosynthesis rate. The N content and Rubisco activity of leaves are assumed to vary seasonally and with canopy position in a way to maximize  $A_{dt}$ .

Canopy conductance,  $g_c$ , is linked to  $A_{dt}$  through

$$g_c = g_{min} + 1.6 A_{dt} / (c_a (1-\lambda)) \quad (9)$$

where  $g_{min}$  is a PFT specific minimum canopy conductance.

Daily transpiration of water is calculated for each PFT as the minimum of a plant- and soil limited supply function ( $E_{supply}$ ) and the demand for transpiration  $E_{demand}$ .  $E_{supply}$  is the product of root-weighted soil moisture availability and a maximum water supply rate that is equal for all PFTs.  $E_{demand}$  is calculated following the empirical relation between evaporation efficiency and surface conductance of (Monteith, 1995):

$$E_{demand} = E_{eq} \alpha_m (1-\exp(-g_c \phi/g_m)) \quad (10)$$

where  $E_{eq}$  is the equilibrium evaporation rate, dependent on temperature and radiation,  $g_m$  and  $\alpha_m$  are empirical parameters,  $g_c$  is the canopy conductance, and  $\phi$  the fraction of present foliage area to ground area (i.e., projected leaf area). Eq. 10 is solved for  $E_{demand}$  using the non-water-stressed potential canopy conductance which is calculated using Eq. 9 and a fixed ratio  $\lambda$  to compute  $A_{dt}$ .  $\lambda$  is

set equal to 0.8 following Sitch et al. (2003) to approximate non-water-stressed conditions and as a starting value for the iterative computation of carbon assimilation and transpiration under water shortage. In case of water-stressed conditions when  $E_{demand}$  exceeds  $E_{supply}$ , canopy conductance and photosynthesis are down-regulated;  $E_{demand}$  is set to  $E_{supply}$  and Eq. 10 is solved for  $g_c$ . Knowing  $g_c$  and  $c_a$ ,  $\lambda$  is varied in the photosynthesis module until the following relationship is satisfied:

$$A_{dt}(\lambda) = ((g_c - g_{min})/1.6) c_a (1-\lambda) \quad (11)$$

NPP is downregulated on the daily model time step if N-demand exceeds N-availability from the inorganic soil nitrogen pools. Daily NPP is integrated over a year and allocated annually to vegetation. Thus, in contrast to CESM there is no immediate feedback of nitrogen limitation on isotopic discrimination on a daily time scale, but there is a long-term feedback by annual changes in vegetation structure and, in turn, photosynthesis and carbon assimilation.”

Are the two models forced with two different meteorological datasets? CRUNCEP and CRU TS3.23? Is there a reason for this? And could that affect the results in some way?

Yes, the two models are forced by two different, though closely related, products for technical reasons. CLM4.5 is run with a sub-hourly time step, while a daily time step is used in LPX.

This does not affect our conclusions and differences in these data products cannot explain differences in simulated discrimination and iWUE, as we explain below.

CRU NCEP (<https://www.earthsystemgrid.org/dataset/ucar.cgd.cesm4.CRUNCEP.v4.html>) is used to force CLM4.5. CRU NCEP is a combination of two existing datasets ([ftp://nacp.ornl.gov/synthesis/2009/frescati/model\\_driver/cru\\_ncep/analysis/readme.htm](ftp://nacp.ornl.gov/synthesis/2009/frescati/model_driver/cru_ncep/analysis/readme.htm)): The CRU TS.3.2 0.5°x0.5° monthly climatology covering the period 1901 to 2009 and the NCEP reanalysis 2.5°x2.5° 6 hours time step beginning in 1948.

The CRU TS3.2 climatology offers a good spatial resolution but only monthly mean fields are available which is a too low resolution for CLM4.5. On the other hand NCEP reanalysis has a temporal resolution of 6 hours and is compatible with the CLM4.5 time step. But the spatial resolution is low and precipitation of such reanalysis is known to be less reliable than CRU data based on station data.

As evident from Figure 9 and 10 of the manuscript, the influence on changes in climate on the change in discrimination and iWUE is small, except in semi-arid regions. But to more comprehensively address the reviewers' question, we further investigated the potential impact of using two different data products. The CRU NCEP data used to force CLM4.5 are interpolated on the 1°x1° LPX grid and integrated to monthly values. This re-gridded CRU NCEP data are then used in LPX. LPX results for both climate input data, CRU NCEP and CRU-TS3.22, are compared. We investigated two cases, the standard model setup where climate is changing transiently and the factorial setup with “constant climate”. Difference in simulated changes in discrimination and iWUE are small for both cases (Figure R1).

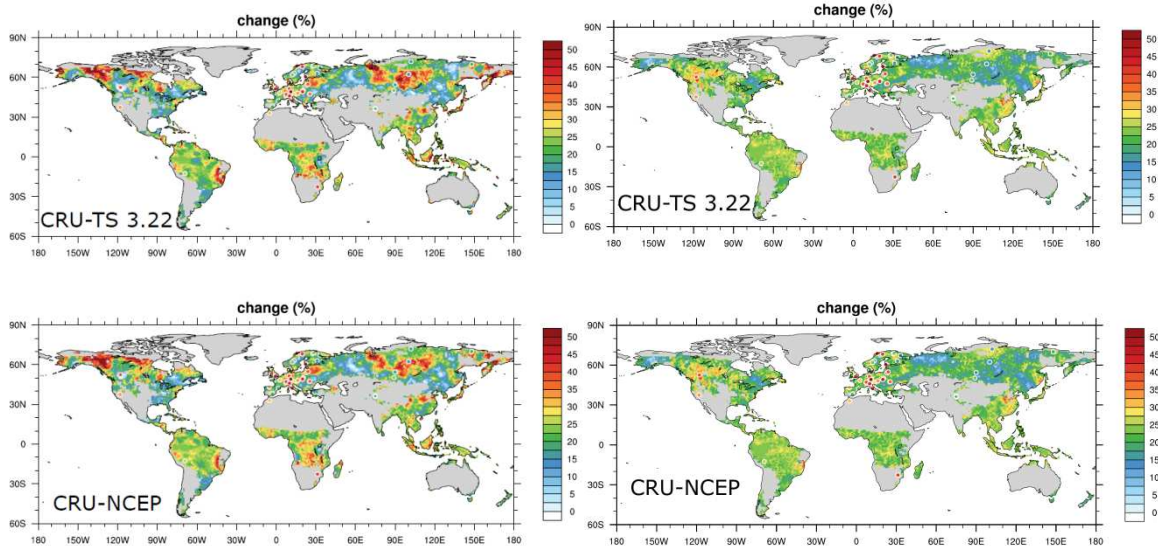


Figure R1: Century-scale changes in iWUE (%) of C3 trees as simulated by LPX forced by (a) the CRU-TS3.22 (top panels) and the CRU-NCEP climatology (bottom panel). The left panels show results obtained with the standard model setup including transient climate and CO<sub>2</sub> forcing. The right panels show results obtained by keeping climate constant. In both setups, the influence of the different climate input data on results is very small. Changes are based on decadal means (1990 minus 1900). Changes in iWUE as calculated from d13C tree-ring data are shown by colored circles. The upper left panel is shown as the bottom panel of Figure 11 in the originally submitted manuscript.

The following text is added to the section describing the climate forcing data: “The two models are forced with two slightly different climate data sets as CLM4.5 is run on a sub-hourly time step, while a daily time step is used in LXP. CRU NCEP, used to force CLM4.5, is a combination of the CRU TS3.2 monthly climatology (resolution of 0.5°x0.5°) and the NCEP reanalysis product with a time step of six hours (2.5° x2.5°). The results of the factorial runs, presented later, suggest generally a small influence of this difference in forcings on simulated discrimination and iWUE. We further investigated the potential impact of using two different climate data products. The CRU NCEP data are interpolated on the 1° x1° LPX grid and integrated to monthly values for use in LPX. LPX is run with the modified CRU NCEP and, as usual, with CRU-TS3.22 in the standard model setup where climate is changing transiently and the factorial setup with “constant climate” (cCLIM). Difference in simulated changes in discrimination and iWUE are small for both cases. In conclusion, the large model differences, presented in the result section, are not caused by differences in climate input data.”

Just for clarification: when referring to delta 13C forcing (e.g. p.8, l.21) it would be clearer to write atmospheric delta 13C.

Done. The term forcing is not used anymore for prescribed atmospheric CO<sub>2</sub> and <sup>13</sup>C in the manuscript.

The sentence “An empirical convective boundary layer parameterization (Monteith, 1995) couples the carbon and water cycle” does not make sense to me. Please explain why the convective boundary layer couples the water and carbon cycle. To me it would be more helpful to read how the leaf boundary layer is treated in the model, as it directly affects your calculations (see Eq. 6). In general, when describing the models I recommend putting more emphasis on the calculation of

variables that are directly used for later calculations or referred to in the Results section (e.g. calculation of the leaf boundary layer, are there differences in how soil water stress affects  $g_s$  or  $A_n$ ?). This will certainly be of greater interest to the reader than a list of PFTs that occurs in every land surface model in a similar form.

Done. Please see our reply to the comments above on stomatal controls.

Page 8: not everyone is familiar with the discrimination model by Lloyd & Farquhar 1994. Please mention the key differences between the two models here (Lloyd & Farquhar 1994 and Farquhar 1989). The fact that the two formulations give similar trends is an interesting aspect but it is a little bit hidden in the Methods section. Lines 14 – 20 are better moved to the discussion and can be extended. I think it would be good to be more precise here: what processes are not considered in the discrimination formulation and what does that change or not change? For instance, why is the agreement with leaf  $\delta^{13}C$  worse when the more complex model is used? Why does it not change the trend? Discussing such aspects may not be the focus of this study but it would be a valuable contribution to the discussion on how isotopes are (or should be) considered in global models.

Done. Text moved to discussion section and expanded as requested:

“In applications with the predecessor of LPX (Joos et al., 2004; Scholze et al., 2008)  $\delta^{13}C$  was implemented following (Scholze et al., 2003) with discrimination modeled following (Lloyd and Farquhar, 1994). Here, we adjusted the discrimination formulations and use instead the simpler formulations of (Farquhar et al., 1989) for consistency with CLM4.5 and with the computation of  $iWUE$  from tree-ring  $\delta^{13}C$  measurements. We note that our conclusions do not depend on this choice. LPX yields similar 20<sup>th</sup>-century changes in discrimination and  $iWUE$  for both formulations. However, simulated  $\delta^{13}C$  of carbon assimilated by C3 trees is generally less negative (by about 2 permil) when applying the (Lloyd and Farquhar, 1994) formulation and agreement with leaf  $\delta^{13}C$  is less favorable.

The difference between the two implementations arises from additional processes considered in the approach of (Lloyd and Farquhar 1994) and different parameter choice. Here, fractionations associated with the diffusion of  $CO_2$  from the stomatal cavity to the cell wall, entrance of  $CO_2$  in solution at the cell wall, and transport within the cell, as well as photorespiration are neglected. The discriminations by the first three processes are set to be constant in the earlier implementation following (Scholze et al., 2003), neglecting a minor temperature dependency associated with the carboxylation by PEP-c (Lloyd and Farquhar 1994). The discrimination associated with respiration varies with atmospheric  $CO_2$  and the photocompensation point, but is small. In addition,  $b$ , the discrimination during photosynthetic fixation, is set to 27 in this study and to 27.5 in the earlier implementation. Overall, the consideration of the additional processes and the difference in  $b$  result in an approximately constant offset between the two implementations. This highlights that absolute values of discrimination depend on uncertain model parameters. Agreement or disagreement between leaf and model data (or tree ring and model data) concerning absolute levels of  $\delta^{13}C$  (Figure 5 and 6) may not be interpreted as an indication of the performance of the conductance/photosynthesis module.”

Results Overall, this section is nicely written and clearly structured.

Thank you.

Model results are compared to a study by Carvalhais et al. 2014. It would be good to provide a bit more detail here. Do you mean aboveground and belowground vegetation carbon? How was vegetation carbon estimated in the study by Carvalhais et al. 2014? **Done.** Estimates of total vegetation carbon, including below and aboveground biomass, were derived by Carvalhais et al. 2014 from a collection of estimates for pan-tropical regions and for northern and temperate forests based on radar remote-sensing retrievals. Above- and below-ground biomass uncertainty for the tropical regions was propagated from errors in measurements, allometric relations, sampling and predictions. In the Northern Hemisphere, estimates accounted for uncertainties in the BIOMASAR GSVdata, wood density data and biomass compartment data. Herbaceous carbon is estimated from GPP data products. See the original publication for a more detailed description and references.

The following text is added to the manuscript: “Estimates of total vegetation carbon, including below and aboveground biomass, were derived by Carvalhais et al., 2014 from a collection of estimates for pan-tropical regions and for northern and temperate forests based on radar remote-sensing retrievals.”

Section 3.3: Results and Discussion are mixed here. It would be better to focus on the Results and discuss uncertainties in section 4. Just a thought: Why not taking PFT-specific model output? One could only take the corresponding PFT of the simulations that matches the PFT of the measured species. Up to the authors.

We prefer to keep the text on the caveats and uncertainties related to the tree ring data-model comparison at the beginning of section 3.3. This is important information for the reader and we feel allows the reader to better put the results into perspective. In response to the comment, the sentence “Differences in the rooting depth, water transport systems, root-to-leaf distance, leaf morphology, or in irradiance (sunlit versus shadow) affect discrimination.” is deleted and we added the following text in the discussion section:

“The influence of rooting depth, water transport systems, root-to-leaf distance, leaf morphology, and irradiance (sunlit versus shadow) on discrimination is neglected. Although, these factors may affect discrimination and reported isotopic differences within a species, even growing at the same site, can be as large or even larger as those between species (McCarroll and Loader, 2004; Leuenberger, 2007).”

We prefer to use grid-cell average model output instead results for individual PFTs. As explained in section 3.3., differences in  $\delta^{13}\text{C}$  are reported for different species. In addition, differences within a species, even growing at the same site, can be as large or even larger as those between species. Differences in the rooting depth, water transport systems, root-to-leaf distance, leaf morphology, or in irradiance (sunlit versus shadow) affect discrimination. Further, the models as applied here use generic PFTs and not individual species.

The authors suggest that there is a stronger downregulation of stomatal conductance by water stress in LPX than in CLM4.5 in some regions. Here, it would be helpful to provide some possible explanations. Is it because water stress in LPX is stronger due to the climate forcing, the way soil moisture is simulated, or due to a stronger stomatal response to water stress?

Differences in the applied climate forcing are not responsible for the stronger downregulation of stomatal conductance in CLM compared to LPX (see Figure R1 and related discussion above).



Soil moisture and stomatal conductance are coupled and influence each other in both models in a non-linear way hampering somewhat a firm attribution of signals to these two processes. The available results suggest that the primary reason for the difference in modeled 20<sup>th</sup> century changes in discrimination and iWUE is rooted in the different parameterizations of the photosynthesis-conductance coupling in the two models.

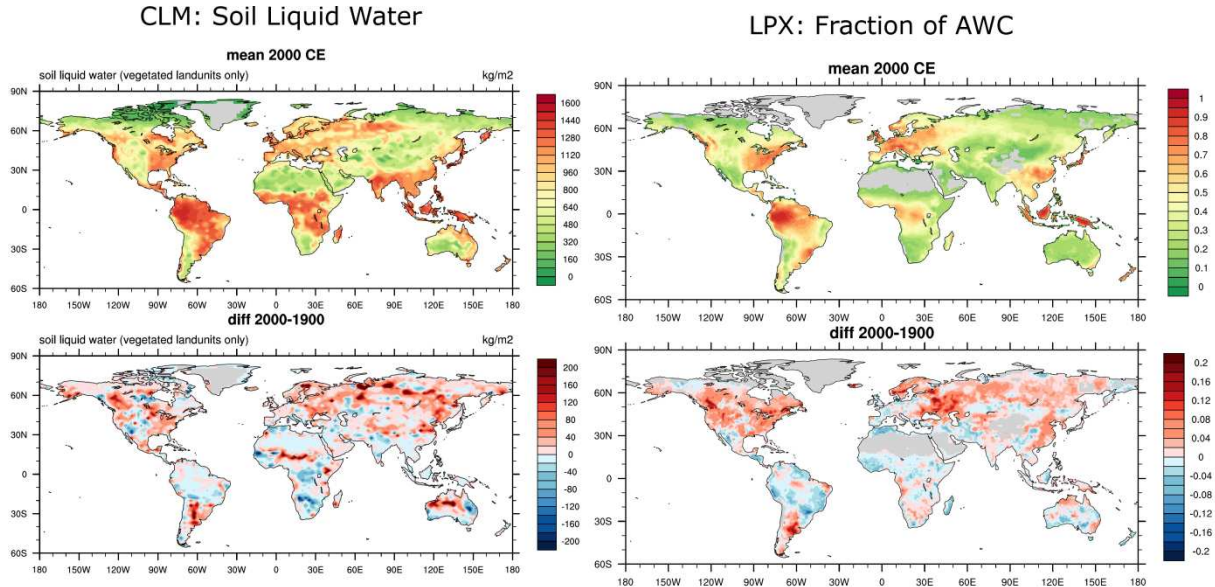


Figure R2: Soil moisture (top) and 20<sup>th</sup> century changes (bottom) as simulated for CLM4.5 (left) and LPX (right) with the standard model setup. Changes are based on decadal means (1990 minus 1900). For CLM, soil liquid water content in  $\text{kg m}^{-2}$  and its change (1990 minus 1900) is shown. For LPX, the water-filled fraction of the available water holding capacity in the top soil layer and its change is displayed.

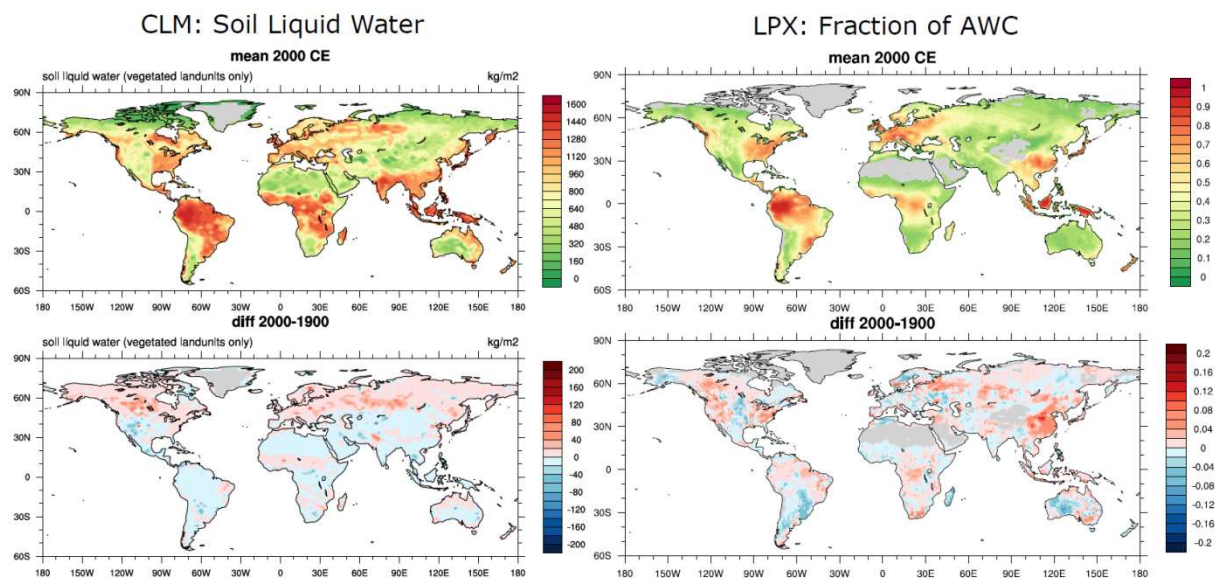


Figure R3: As figure R2, but with a model setup where climate is kept constant.

A primary input to soil moisture is precipitation, which is similar in both models. Patterns of soil moisture are similar in both models (Figure R2, top).

20<sup>th</sup> century changes in soil moisture are small in the factorial simulations where climate is kept constant (Figure R3, bottom). For the standard model setup, changes in soil moisture simulated by CLM and LPX are also small in large parts of Europe and Asia, where most of our tree-ring data are located. Despite these small changes in soil moisture, large differences in discrimination and iWUE changes are found between the two models in these simulations and regions (see Figure 9, 10, 11).

This is in line with the conclusion stated in the manuscript at the end of section 3.4 (p15, l33-35): “This suggests that the simulated decrease in discrimination and in  $c_i/c_a$  in the CLM4.5 runs is mainly linked to increasing CO<sub>2</sub> and a corresponding downregulation of  $c_i/c_a$  (Eq. 6). The downregulation in CLM4.5 is larger than suggested by the tree-ring records.”

The following text is added to the manuscript at the end of section 3.4: “Soil moisture and stomatal conductance are coupled and influence each other and in turn discrimination. 20<sup>th</sup> century changes in soil moisture are small in the factorial simulations where climate is kept constant. For the standard model setup, changes in soil moisture simulated by CLM and LPX are also small in large parts of Europe and Asia, where most of our tree-ring data are located. Despite these small changes in soil moisture, large differences in discrimination changes are found between the two models in these simulations and regions (Figure 9). This suggests that the primary reason for the model-model difference in simulated 20<sup>th</sup> century changes in discrimination is rooted in the different parameterizations of the photosynthesis-conductance coupling.”

Discussion This section contains many interesting thoughts, but its structure is not very clear. If it was divided in several subsections as it is the case for the results section, it would be easier to find certain aspects the reader is interested in.

Done. Subsections are introduced in the discussion section. These mirror the presentation of results.

The subsection titles are:

1. “Isotopic signatures, pools and fluxes of the global land biosphere”
2. “ $\delta^{13}\text{C}$  in leaves of C3 plants: modern distribution”
3. “20<sup>th</sup> century changes in carbon isotopes and water use efficiency of C3 plants”
4. “Consistency of a constant  $c_i/c_a$  with previous studies”

In addition, Discussion and Conclusions are now separated into two sections.

p. 17, l.14-18: This paragraph can be expanded. As mentioned before, the differences between the discrimination model used here, and a more complex one (e.g. Lloyd & Farquhar, 1994), as well as possible implications for the simulated absolute values of discrimination and its trends can be discussed in more detail.

Done. The paragraph is expanded and the following text is added: “The influence of rooting depth, water transport systems, root-to-leaf distance, leaf morphology, and irradiance (sunlit versus shaded) on discrimination is neglected. However, these factors may affect discrimination. Reported isotopic differences within a species, even growing at the same site, can be as large or even larger as those between species (McCarroll and Loader, 2004; Leuenberger, 2007).”

As mentioned above, the difference between the two isotopic discrimination models and implications are now explained in the discussion (subsection on  $\delta^{13}\text{C}$  in leaves of C3 plants.) See our response to the earlier comment on this point for the new text

p. 18: The question that the reader will have is: why does CLM4.5 simulate such a strong trend in iWUE? The authors provide two possible explanations: 1) the downregulation of photosynthesis by nitrogen, and 2) an inadequate relationship between simulated stomatal conductance and assimilation. The first one is described well and is supported by other recent studies. In this context it would be helpful to know how the fdreg factor in Equation 6 changes over time, and whether it affects the relationship between  $A_n$  and  $g_s$ .

The downregulation by nitrogen does not directly affect  $g_s$  for the carbon assimilation calculation. It affects the amount of GPP that is allocated to the carbon pools. The following text is added to the method section 2.1.2, where discrimination for CLM4.5 is described, to make this point explicitly: “In other words, plants photosynthesize carbon at a potential, nitrogen unlimited rate. Photosynthesis  $a_n$  and, in turn, stomatal conductance  $g_s$  are not directly affected by nitrogen limitation.”

The paragraph in the discussion section on p17, bottom has been reformulated. The original text “In CLM4.5, photosynthesis for isotopic discrimination is downregulated immediately, on the subhourly time step of the model, by limited nitrogen availability in CLM4.5 (Eq. 6). This can lead to a depression of assimilation in the isotope calculation during times of high assimilation.” is changed to read:

“Regarding nitrogen limitation, photosynthesis for isotopic discrimination is downregulated immediately, on the subhourly time step of the model, by limited nitrogen availability in CLM4.5 (Eq. 6). This can lead to a depression of assimilation in the isotope calculation during times of high assimilation. As explained in the method section, photosynthesis of carbon and stomatal conductance for water is computed, unlike for discrimination, without nitrogen limitation. Instead, the allocation of gross primary productivity to carbon pools is downregulated under nitrogen limitation). This downregulation is on annual average generally less than 20% in forested regions and 20<sup>th</sup> century changes in downregulation are generally small (within  $\pm 2\%$ ) in areas with tree ring data.”

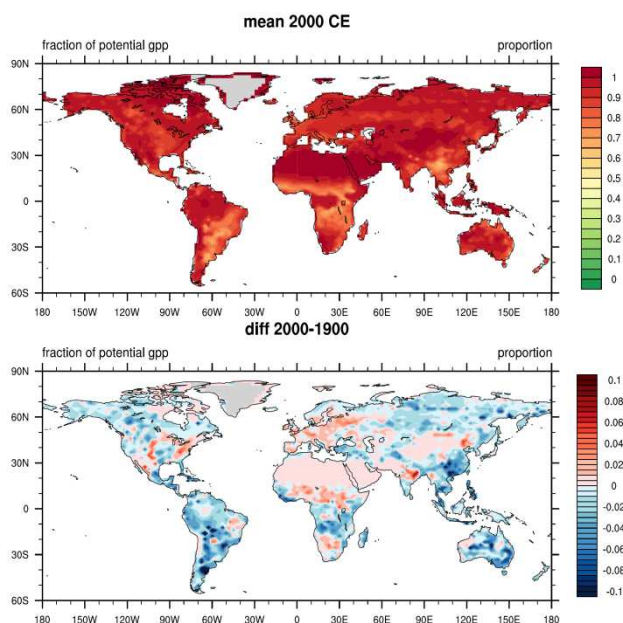


Figure R4: An index for nitrogen limitation, FPG top) and its 20<sup>th</sup> century change (bottom) as simulated by CLM4.5. FPG is indicative of nitrogen limitation and varies between 1 (no nitrogen limitation) and 0.

Nitrogen demand is the amount of nitrogen required to transfer all available carbon from photosynthesis into plant carbon. The fraction FPG describes by how much nitrogen demand to support plant growth is downregulated to match nitrogen availability. A value of 1 corresponds to non-nitrogen limited conditions. As shown in Figure R4, 20<sup>th</sup> century changes in annual and grid-cell mean FPG are relatively small.

The fraction  $f_{dreg}$  used to calculate the intercellular CO<sub>2</sub> partial pressure and thus <sup>13</sup>C discrimination (Eq. 4 and 6 in the submitted manuscript) is closely related to FPG. We therefore also expect that annual mean values in  $f_{dreg}$  changed little over the 20<sup>th</sup> century (Unfortunately, output for  $f_{dreg}$  is not available).

It remains difficult to draw conclusions from annual or monthly values of FPG and  $f_{dreg}$  as these variables are evaluated on the model time step and influence simulated fractionation and iWUE in a non-linear way (see e.g. Eqs. 4, 6, and 9 in the submitted manuscript and Eqs. 4, 6, and 12 in the resubmitted manuscript).

Concerning the second explanation, I don't understand what the key message should be. Is it the general form of the Ball-Berry model and the prescribed relationship between  $g_s$  and  $A_n$ ? In this case it should be mentioned that this model or similar models are used in most land surface models (see e.g. Sato et al. 2015, JGR Biogeosciences). If the reason for the strong iWUE trend is due to an inadequate relationship between  $g_s$  and  $A_n$ , we should see a similar behavior in other land surface models. A comparison with other models is missing here.

The text "Another possibility for the model-data mismatch is that the photosynthesis formulation in CLM4.5 may not adequately represent the relationship between stomatal conductance and assimilation" is changed to read:

"Another possibility for the model-data mismatch is that the photosynthesis formulation in CLM4.5 may not adequately represent the relationship between stomatal conductance and assimilation and related adjustment processes to long-term environmental changes. CLM4.5 employs the experimentally well-verified and widely-used Ball-Berry equation (Eq. 7) applying globally uniform, time invariant slope parameters,  $m$ , for C3 and C4 plants. Thus, any potential adjustment of  $m$  to changes in environmental conditions, including the century-scale increase in atmospheric CO<sub>2</sub> or changes in water stress are not considered. It is currently unclear whether such adjustment processes occur and the current understanding of the underlying physiological mechanisms of stomatal responses is incomplete (e.g. Miner et al., 2017)."

New text was added to describe the results of Sato and co-workers and resulting conclusions for this work:

"(Sato et al., 2015) investigated the influence of the use of vapor pressure deficit (VPD) versus relative humidity (RH) in Ball-Berry-type stomatal conductance formulations. About half of the investigated models apply RH as a driving variable (Eq. 7), despite the fact that VPD is considered the more relevant controlling factor. The global warming simulations reveal an increase in VPD and little change in RH. Their results suggest that the increase in VPD under global warming leads to a stronger downregulation of stomatal conductance ( $g_s$ ) and  $c_i/c_a$  for the VPD formulations compared to the RH formulation. This implies that replacing RH by VPD in the Ball-Berry equation in CLM4.5 may, without further adjustments, even increase the disagreement between modeled and reconstructed changes in discrimination and in iWUE."

It is then argued that the trend may partly be attributed to changes in relative humidity, but no data are shown that would support this statement. What does the CRUNCEP climate forcing dataset suggest? Is there a trend in relative humidity that could explain the strong trend to some extent? Do areas that show a decrease in discrimination also show a decrease in relative humidity? The role of relative humidity (and possibly other climate variables) is an interesting aspect to discuss at this point, but it should be supported by data and discussed in context of the factorial simulations that were made.

This was not our intention. We do not argue that the changes in discrimination are due to long-term changes in relative humidity. We rather suggest “that assimilation is shifted towards times with lower relative humidity (page 18, line 28)”.

This point is rather subtle and follows from Eq. 14 (now Eq. 7 in the resubmitted manuscript). The text from lines 25 to 31 on page 18 of the submitted manuscript is deleted to avoid misunderstanding and for brevity.

It also mentioned that the value of the stomatal slope parameter  $m$  might be too high. It would be good to provide some more information, here or in the method section. What is the value of  $m$ ? Is it constant across PFTs? I agree that  $m$  is probably too high for coniferous forests, but not necessarily for other vegetation types. If the value of  $m$  is to be discussed here, the authors should at least cite Lin et al. 2015, Nature Climate Change, who looked more generally at patterns of  $m$  across PFTs. They used a slightly different model, but that shouldn't affect the patterns of  $m$ , see also Miner et al. 2016 Plant, Cell & Environment.

Done. The value of  $m$  is now mentioned in the methods section. Parameter values are  $m=9$  for C3 plants and for  $m=4$  C4 plants. These parameters are time invariant.

The review of Miner et al. (2016) yields mean values for  $m$  of 9.8, 8.7, and 6.8 for angiosperm evergreen, angiosperm deciduous and for gymnosperm trees, respectively (Their figure 1). Aranibar et al. (2005) also inferred larger values of  $m$  using observed foliar  $^{13}\text{C}$  values in pine.

The following text is now added in the discussion:

“The value of  $m$  is set to nine in CLM4.5 for all C3 plants world-wide. This value is within the observational range, but species differences (e.g., evergreen versus deciduous) are neglected by using a single value. The review of (Miner et al., 2017) yields mean values for  $m$  of 9.8, 8.7, and 6.8 for angiosperm evergreen, angiosperm deciduous and for gymnosperm trees, respectively (Their figure 1). (Aranibar et al., 2006) inferred values of  $m$  around 10 to 12 using observed foliar  $^{13}\text{C}$  values in pine.”

Changing  $m$  would certainly affect the absolute values of  $i\text{WUE}$  and discrimination, but would it make a difference to the simulated percentage trend in  $i\text{WUE}$  as shown in Figure 7? If the value of  $m$  is taken as a reason for the overestimated trend in  $i\text{WUE}$  by CLM4.5 this needs to be shown somehow. In my opinion, a change in  $m$  would primarily change the spatial patterns of the simulated discrimination.

(Duarte et al., 2016) present in their figure A1 results from sensitivity simulations where only the parameter  $m$  was changed in the model setup. The change in leaf  $\delta^{13}\text{C}$  is larger and the change in

discrimination is smaller for the lower value of  $m$  ( $m$  equal 6 instead of 9). The following sentence is added: "In addition, the 20th century change in isotopic discrimination is reduced."

The formulation implemented in the LPX is better able to capture the observed  $iWUE$  trend. But is that really because of the optimization? I would argue that also the Ball-Berry model (Eq. 14) predicts a constant  $c_i/c_a$  and thus a trend in  $iWUE$  that is proportional to  $c_a$ , provided that  $rH$  and  $m$  do not change over time. In my eyes this is indicative of changes in  $rH$ , or more likely, problems with the nitrogen downregulation, as discussed earlier. Why not testing this? The CLM4.5 model could be run with a version that does not include the nitrogen downregulation. The comparison of this alternative version with the version used in this study could be used to answer the question whether the problem lies in the nitrogen downregulation or in the stomatal conductance scheme (Eq. 14). If the alternative model version still shows a stronger  $iWUE$  trend than expected, this would be a stronger indication that an optimization based approach indeed works better. Maybe new global runs are not necessary, and a simple analysis based on Eq. 6 would suffice. However, without testing this, the statement (p.20, l.27f) remains speculative and should not be mentioned in the conclusion of the paper. In general, this part of the discussion needs to be revised according to the comments above.

The following statement is deleted: "and may be interpreted as supportive of a plant strategy towards optimizing assimilation and minimizing water loss under changing environmental conditions" on p20, l27 as requested. The remaining text reads: "The results suggest constant  $c_i/c_a$  over the 20th century. The results suggest that it is desirable to adjust the implementation of photosynthesis and conductance in CLM4.5 towards a better agreement with observation-derived century-scale trends in  $\delta^{13}C$  discrimination and intrinsic water-use efficiency."

Further, we have clarified the discussion on photosynthesis-conductance relationship and optimization. The existing text has been replaced by:

"Alternative conductance-photosynthesis formulations, may be preferable, compared to the Ball-Berry relation as used in CLM4.5. The Ball-Berry relation is viewed as consistent with an optimization (Cowan I. R. and D., 1977) of stomatal conductance towards maintaining a constant water use efficiency by optimizing carbon gain per unit water loss. However, a number of alternative formulations are found in the literature. These differ in potentially important ways. For example, (Medlyn et al., 2011) suggest that the slope parameter increases with increasing temperature; further the inverse of the square root of vapor pressure deficit is used instead of relative humidity in their relationship. (Prentice et al., 2014) and (Wang et al., 2016) rely on an optimality hypothesis considering the costs of maintaining both water flow and photosynthetic capacity. These authors use information on the spatial gradients in  $\delta^{13}C$  from stable isotope measurements on leaf material (Cornwell et al., 2016) to develop their photosynthesis-conductance relation. The slope parameter proposed by (Prentice et al., 2014) depends on a number of variables, e.g., the temperature-dependent Michaelis-Menten coefficient for Rubisco-limited photosynthesis, viscosity of water, or the water potential difference between soil and leaf or foliage height. Hence, the slope parameter varies with environmental conditions in this approach. (Bonan et al., 2014) implemented different photosynthesis-conductance modules within a CLM4.5 model version featuring a multi-layer canopy and compared results with leaf analyses and eddy covariance fluxes at six forest sites. The continuous soil-plant-atmosphere (SPA) module, optimizing carbon gain per unit water loss and considering hydraulic safety, performs similar or better than the Ball-Berry formulations used in CLM4.5. A better performance is particularly achieved under soil moisture stressed conditions."

p. 19: The behavior of  $iWUE$  and  $c_i/c_a$  as reconstructed from the tree-ring measurements and modeled by LPX-Bern is compared to other studies. The nice thing on this paragraph is that it is very comprehensive. But it could be clearer with respect to the method used in the cited studies. Rather than just listing the studies you could sort them by method, i.e. mention other isotope-based studies first, then other methods. At the moment studies using the same methods (e.g. FACE) are mentioned in different parts of this section (Ainsworth & Long, 2005 and De Kauwe et al. 2013) which seems a bit fuzzy. I think this aspect is important as different methods are associated with different uncertainties (which, however, do not have to be discussed here).

Done. The studies are now grouped according to the underlying method.

With respect to the eddy covariance records it may be interesting to mention that a recent study (Knauer et al. 2016, New Phytologist) found that large-scale carbon and water fluxes are not in agreement with a constant  $c_i$ , but rather with a constant  $c_i/c_a$ .

Done. The following text is added after the reference to the studies by Battipaglia et al. and Keenan et al.:

“However, these studies may be affected by local conditions not representative for larger scales and be influenced by temporal sampling biases as the record length of FACE and eddy-covariance measurements is limited. Indeed, the individual tree-ring records shown in Figure 7 show considerable site-to-site variability as well as decadal variability. In addition, factors other than  $c_i/c_a$ , e.g. vapor pressure deficit, may influence trends at eddy covariance sites (Knauer et al., 2017). The suggestion of a constant  $c_i$  under increasing  $CO_2$  is challenged by (Knauer et al., 2017). These authors find that the ecosystem trends reported by (Keenan et al., 2013) and a scenario of a constant  $c_i$  as also suggested by (Battipaglia et al., 2013), are in conflict with observed large-scale trends in continental discharge, evapotranspiration, and the seasonal  $CO_2$  exchange. Rather, the comparison of observational data and model outcome by (Knauer et al., 2017) support the finding of a physiological regulation towards a constant  $c_i/c_a$  under rising atmospheric  $CO_2$ .”

p. 20: The effects of land use change and representation issues between the datasets/model simulations are adequately addressed. It may be helpful for the reader to mention the Figures again where the described aspects can be seen.

Done. Figure 4 is now mentioned at two places in the paragraph on land use.

Figures In some figures (e.g. Fig.2), the color code and the associated numbers are very small and hard to read. It would be ok to have fewer color classes as they are hard to distinguish.

Done. The number of labels is reduced and their size increased in Figures 2 to 4. Units are changed from  $gC\ m^{-2}$  to  $kgC\ m^{-2}$  to reduce the number of digits.

Fig. 2: For the difference maps, please state what is subtracted from what, at least in the legend.

The differences are based on decadal means (1996-2005 minus 1896-1905). The caption is revised: “The estimates are based on decadal means (1996-2005 and 1996-2005 minus 1896-1905, respectively).”

Fig. 5: representing the differences in mean  $\delta^{13}C$  as barplots is not appropriate here. I recommend to remove the bars and show the error bars only, also in Fig. 6.

We prefer to keep the bars for a clear distinction between the difference and the error estimates.

From Fig. 5 onwards: Some of the points on the map are hard to see. It would be helpful if their representation could be changed.

Our choice represents a trade-off between the visibility of individual dots and the visibility of all dots.



## Review 2: A. Ballantyne

Here the authors compare a compilation of tree ring and leaf isotope data from around the world with isotopic simulations from two common land surface models. While several studies have compared isotopic estimates of  $iWUE$  with model simulations of  $iWUE$ , especially at regional scales. This study is novel in that it is one of the few to actually investigate isotopic tracer simulations within models as a critical diagnostic for how accurate models are at simulating the global C cycle. In principle, this approach allows us to evaluate to what extent the terrestrial biosphere is being fertilized by increased atmospheric  $CO_2$ ; however, I think that the authors could further partition the response of  $iWUE$  into its component processes of assimilation and transpiration (at least in the models). This may also help reconcile why the models appear to show differing degrees of  $iWUE$  response.

### General Comments:

I suspect that the two models investigated here differ considerably in how stomatal conductance is simulated and this is having a big impact ultimately on the isotopic tracers. While these models may be responding similarly to increases in atmospheric  $CO_2$  they may be responding to different metrics of atmospheric water vapor. As the authors point out, assimilation in CLM is modeled as a function of RH and  $CO_2$ , while it is my understanding that in LPJ stomatal conductance is modeled as a function of VPD. While RH and VPD may be inversely related in some environments, this is not always the case and their relationship might vary over the 20th century. It would be nice to see how assimilation and transpiration have responded over the 20th century independently in the two models. This may also help explain why LPX and CLM show different responses of  $iWUE$  over the 20th century.

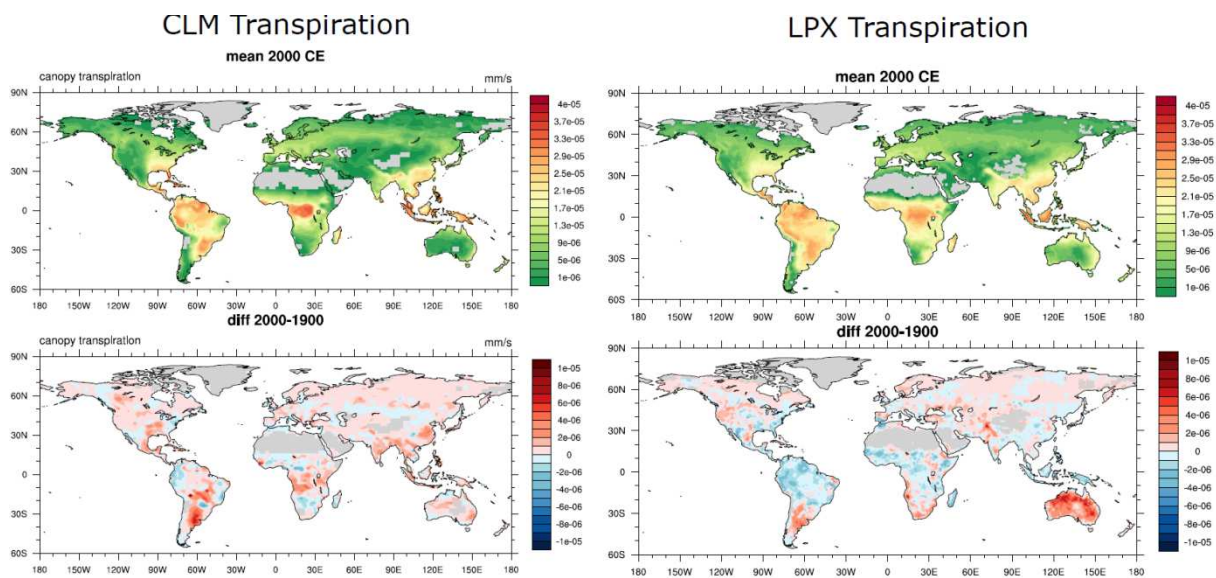


Figure R5: Simulated transpiration (in mm/s) for the decade around year 2000 (top) and 20<sup>th</sup> century changes (bottom; 1996-2005 minus 1896-1905).

The panels shown in Figure R5 are added to figure 2. The following text is added on page 13:

"Simulated evapotranspiration is similar for the two models." and

“Simulated 20<sup>th</sup> century changes in annual-mean transpiration are generally small in both models, except in Australia for LPX and in parts of Latin America for CLM4.5. Generally an increase in transpiration is found in boreal and temperate forest regions in both models. Transpiration is slightly decreasing in LPX and slightly increasing in CLM4.5 in most tropical forest regions. “

**Specific Comments:**

P1L12 ‘water loss by transpiration.’

Done. Text changed as requested.

P2L4 ‘and water transpiration’

Done. Text changed as requested.

P2L22 Graven article is on 14C not 13C as cited. Check reference as they may have also included 13C in their simulations.

Done. Reference removed.

P2L27 conductance can be of CO<sub>2</sub> or H<sub>2</sub>O, could be more specific here and say ‘transpiration’ as the process and H<sub>2</sub>O as the mass.

Stomatal conductance is used here as a general term for H<sub>2</sub>O and CO<sub>2</sub>. Transport of <sup>12</sup>CO<sub>2</sub>, <sup>13</sup>CO<sub>2</sub>, and H<sub>2</sub>O through the stomata are by molecular diffusion. This process depends on molecule mass and leads to the “fractionation” between the <sup>13</sup>CO<sub>2</sub> and <sup>12</sup>CO<sub>2</sub> fluxes. Text is not changed.

P3L7 While the authors mention many 13C tree ring records, they fail to mention the pioneering work by Tans et al. which is found in the references.

Done. Reference added.

P3L22 ‘to complement recent advances in simulating marine carbon isotopes’

Done. Sentence changed to read: “This is a step towards fully coupled isotope-enabled CESM applications and complements recent advances in simulating marine carbon isotopes”.

P4L24 ‘reactant to product’

Done. Text changed as requested.

P5L10 I believe that diffusion is only relevant for fractionation in non vascular plants such as bryophytes as well.

Done. Text clarified by adding reference to Farquhar et al., 1989 at the beginning of the paragraph. Non-vascular plants are not included in the standard setup of CLM4.5

P6L6 more realistically related to the gradient between internal water pressure and atmospheric water pressure (approximated as vapor pressure deficit or VPD).

Done. Text clarified. The description of the relationship between conductance and assimilation in CLM4.5 is clarified and Eq. 14 (submitted MS) is moved here to page 6 (now Eq. 7).

P7L7 del 13C signature of what? Atmosphere? Please clarify

Done. Text clarified to read: “Note that no  $\delta^{13}\text{C}$  observational data, e.g., from tree-rings or atmospheric samples, was used as a constraint in the assimilation.”

Eqn 8 Isn't this the same as Eqn 7? But not quite sure  $c^*$  is specified in Eqn 7.

Done. Model description is revised. Please see reply to reviewer 1 and revised manuscript.

P9L9 del 13 C is estimated as the ‘weighted flux’ of component GPP fluxes from PFTs from within grid cell. Omit ‘GPP is used as a weight’.

Done. Sentence deleted as requested.

Eqn 11. I don't think that this equation is necessary (especially given the number of equations already included) and this can simply be explained.

Done. Equation 11 deleted and text adjusted.

P10L14 While this approximation of 36.16 holds well within 0.1% isotopic ratio differences are per 1000, so is this enough significant figures?

Done. Text clarified. The approximation is for Eq. 12 (in the submitted MS) and not for 36.16. It holds exactly:  $q=1.6(a-b) = 1.6(27-4.4) = 36.16$ . Additionally, four significant digits are enough as units here correspond to “permil units” and are not “per 1000”. Text clarified to read: “The approximation given in Eq. 14 holds well within 0.1%.”

P11L1 Not sure that you need to correct for the offset if you are only focusing on the trends and normalizing them across sites, regardless this should not affect your analysis.

We agree with the reviewer that this correction hardly influences our analyses and does not alter conclusions. Nevertheless, the relative change in iWUE depends weakly on the magnitude of the discrimination ( $\Delta_i(t_1)$ ) as evident from equation 13 (Eq. 15 in resubmission) and as clearly stated in the manuscript.

P12L18 Were the CLM and LPX simulations conducted with or without land use change and does this have any impact on the global isotopic budget.

Yes, anthropogenic land use is considered in the CLM and LPX simulations as stated on p6, line 26 for CLM and on page 8, line 22). Land use maps from Hurtt et al., 2006 are used in both models. Implications for the global isotopic budget are discussed on page 20, line 14 to 21 in the submitted manuscript.

P13L13 ‘changes in the atmospheric del13C source’

Done. Text adjusted as requested.

P13L15 ‘globally-averaged’ what? Soil, atmosphere?

Done. Text clarified to read: “There is a substantial offset between the models for globally-averaged soil and vegetation pools, with CLM4.5 being around 5 per mil more negative.”

P13L34 2.42 and 3.22 per mil these should have units

Done. Per mil units added.

P14L8 Maybe these global mean estimates should be reported first before noting all the regional differences and more nuanced results.

Done. Global mean estimates are now reported before the regional differences.

P14L12 'bias of the models'

Done. Typo corrected.

P14L28 Were any trend statistics (e.g. Mann-Kendall) conducted on the observations or models?

As suggested, we performed a Mann-Kendall analysis on the discrimination time series. The trend in discrimination of C3 trees is most monotonic in CLM-4.5 ( $\tau = -0.9$ ), less monotonic in the average tree-ring record ( $\tau = -0.6$  for annual data and  $-0.7$  for decadal mean data) and almost negligible in the LPX-Bern output ( $\tau = -0.2$ ).

The Mann-Kendall test provides information to which extent a trend is monotonic, but does not provide information on the magnitude of the trend. We do not plan to add the results from this test to the manuscript. It is clear from Figure 7 that the trends in discrimination and iWUE are larger in CLM4.5 than in LPX and the tree-ring data (see also Figure R6 below).

In response to the comment, we added the following text to the caption of figure 7: **Standard deviations calculated over all observations of century-scale changes (1980s minus 1900s) are 0.72 for  $\Delta i$  and 9.76 for iWUE, respectively.**

P15L10 These aren't really 'spatial' correlations

Done. Word spatial deleted.

P15L15to21 This paragraph seems to fit better in the methods

Done. Paragraph moved to method section. This implied a slight rearrangement of the subsections in the method section. Spin-up and transient simulations for both CLM4.5 and LPX are now described in the same subsection.

P16L24 Model simulations with increased CO<sub>2</sub> and constant climate change could be compared at least quantitatively to FACE data.

This is beyond the scope of this study. For a comparison between carbon-nitrogen land models and FACE data we refer to the literature, e.g., (Zaehle et al., 2014).

P16L34 'Recall, however, that ...represent annual or multi-annual averages that have been weighted by C assimilation or allocation'

Done. Text adjusted as proposed.

P17L28 This paragraph is rather short think about combining.

We prefer to keep the paragraph as is to give the same weight to the conclusions drawn at the end of this and the previous paragraph.

Eqn. 14 Would also be interesting to compare how conductance is simulated in LPX. While assimilation in both models is clearly responding to increasing atmospheric CO<sub>2</sub>, I suspect that transpiration may be responding differentially in the models due to different stomatal response to atmospheric water demand.

The methods section is revised and explains how conductance is modelled in LPX. See response to a similar comment by reviewer 1.

P18L27 For the CLM response you should look at the relative changes in CO<sub>2</sub> and relative humidity over time (this should be a prognostic variable in the model). Also see work by Isaac Held on the response of the hydrologic cycle to atmospheric warming. Essentially, at the global scale RH does not change in response to warming; however, this might not be true over land. So it would be interesting to see in CLM how RH has changed at the tree ring sites.

This point is rather subtle and follows from Eq. 14 (Eq. 7 in resubmitted MS). We will delete the text from line 25 to 31 on page 18 of the submitted manuscript to avoid misunderstanding and for brevity. Please see also reply to reviewer 1, concerning this point.

P20L5 Similar work by Penuelas et al (2011) has shown an increase in water use efficiency but not necessarily an increase in annual ring width. However, a true test would be the relationship between WUE and Biomass- not sure if Klein looked at biomass in this study.

Done. The following text was added:

“Similarly, (Peñuelas et al., 2011), analyzing changes in tree ring  $\delta^{13}\text{C}$  and growth at 47 sites worldwide, inferred little change in discrimination,  $c_i/c_a$ , and an increase in iWUE of 20.5% from 1960 to 2000. 18 of the 35 studies with growth data show an increase in growth with time, while the others show no or negative growth changes.”

In addition, we also discuss work by Streit et al.: “(Streit et al., 2014) measured needle gas exchange and analyzed  $\delta^{13}\text{C}$  of needles and tree rings of *Larix decidua* and *Pinus mugo* after nine years of free air CO<sub>2</sub> enrichment. Both species showed an increase in net photosynthesis and, in agreement with (Keel et al., 2006), small or no changes in conductance under elevated CO<sub>2</sub> and a change in iWUE roughly in proportion to the increase in CO<sub>2</sub>. Elevated CO<sub>2</sub> induced increased basal area growth in *L. decidua*, but not in *P. mugo*. Neither nitrogen limitation, nor end-product limitation, and, in agreement with other FACE studies (Bader et al., 2010; Liberloo et al., 2007), no downregulation of maximal photosynthetic rate was found.

P20L9 It seems that both of these FACE studies report a consistent increase in WUE, but of slightly different magnitudes. It is interesting that the responses are so different between European forests and the N. American forests. Unfortunately, most of the FACE studies have been conducted in the Eastern US, where there are no tree ring isotope records.

Thank you. We do not plan to extend the discussion on these FACE studies.

Figure 3. not so sure that the Carvalhais estimates are ‘observations’, maybe ‘derived from’ or ‘constrained by’ observations.

Done. Text modified to read “derived from observations”.

Figures 5 and 6. I am not sure that you need both of these figures as they illustrate the same data. Perhaps move one to supplemental.

We will keep both figures as part of the manuscript. This decision is also in response to the comment of reviewer 1 on the visibility of the tree-ring data dots. Showing only regional maps as in Figure 6 would provide incomplete information of the global picture, whereas showing only the global map as in Figure 5 would affect clarity and visibility of regional results.

Figure 7. Can you include all of the tree ring records as thin grey traces in this figure? Would be nice to see some distribution of the observations to see if all the obs are bound by the model simulations.

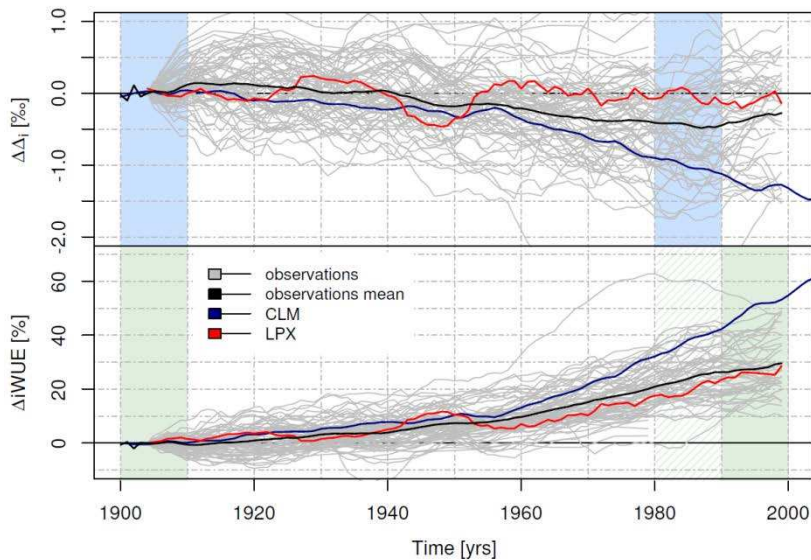


Figure R6: Changes in discrimination and iWUE. Similar as figure 7 in the original manuscript, but with individual tree ring series added (thin gray lines). All model and tree-ring series represent decadal-smoothed values.

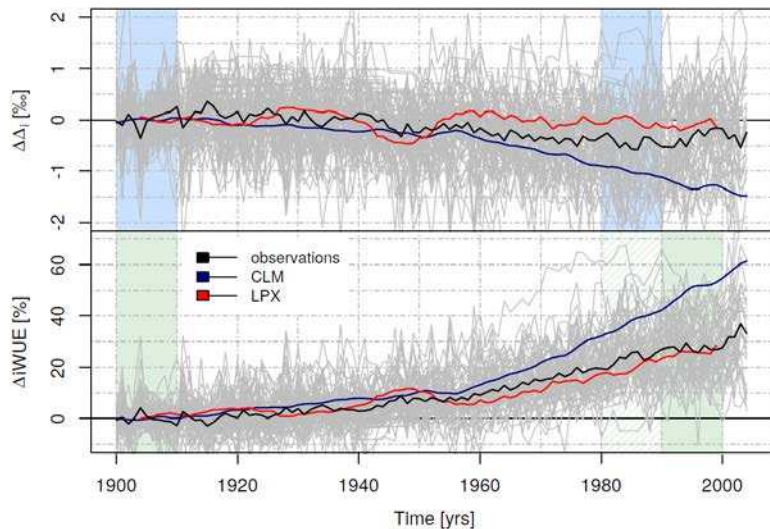


Figure R7: Same as Figure R6, but tree-ring series represent annual values.

We will replace Figure 7 with Figure R6 as requested.

Figure 8. Not sure that you need the discrimination equation, which should be defined in the text.

Done. Equation removed from figure caption. Equation 5, showing this definition, is now mentioned.

Figure 9. The right hand panels where certain variables have been kept constant is not explained in the caption

Done. Explanation added to the caption:

“The bar plots show the regional average change in discrimination of C3 trees as calculated from tree-ring  $\delta^{13}\text{C}$  data (gray) and from results of the standard simulations of CLM4.5 (filled blue) and LPX (filled red) and from factorial runs (pattern). Individual driving factors (climate,  $\text{CO}_2$ , N-deposition, and land use) were kept constant in the factorial runs as explained in the main text and indicated by the legend.”

Figures 11 and 12. Once again these figures are both great but they illustrate redundant information maybe move one to the supplemental information.

We will keep both figures as part of the manuscript for the same reason as discussed above for figures 5 and 6

In summary, with tree ring isotope data we are only able to approximate iWUE and cannot partition this response between assimilation and transpiration. However, in the models you can partition these processes, so it would be interesting to see how transpiration and assimilation are responding in the models, which may help identify processes that can reconcile these model simulations.

Figure on transpiration will be added as requested. See response to main comment above.

## References

Aranibar, J. N., Berry, J. A., Riley, W. J., Pataki, D. E., Law, B. E., and Ehleringer, J. R.: Combining meteorology, eddy fluxes, isotope measurements, and modeling to understand environmental

- controls of carbon isotope discrimination at the canopy scale, *Global Change Biology*, 12, 710-730, 10.1111/j.1365-2486.2006.01121.x, 2006.
- Bader, M. K.-F., Siegwolf, R., and Körner, C.: Sustained enhancement of photosynthesis in mature deciduous forest trees after 8 years of free air CO<sub>2</sub> enrichment, *Planta*, 232, 1115-1125, 10.1007/s00425-010-1240-8, 2010.
- Ball, J. T., Woodrow, I. E., and J.A. Berry, J. A.: A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions., in: *Progress in Photosynthesis Research*. Vol. 4. Proceedings of the 7th International Congress on Photosynthesis, edited by: Biggins, J., Martinus, Nijhoff Publishers, Dordrecht, The Netherlands, 221–224, 1987.
- Battipaglia, G., Saurer, M., Cherubini, P., Calfapietra, C., McCarthy, H. R., Norby, R. J., and Francesca Cotrufo, M.: Elevated CO<sub>2</sub> increases tree-level intrinsic water use efficiency: insights from carbon and oxygen isotope analyses in tree rings across three forest FACE sites, *New Phytologist*, 197, 544-554, 10.1111/nph.12044, 2013.
- Bonan, G. B., Williams, M., Fisher, R. A., and Oleson, K. W.: Modeling stomatal conductance in the earth system: linking leaf water-use efficiency and water transport along the soil–plant–atmosphere continuum, *Geosci. Model Dev.*, 7, 2193-2222, 10.5194/gmd-7-2193-2014, 2014.
- Carvalhais, N., Forkel, M., Khomik, M., Bellarby, J., Jung, M., Migliavacca, M., u, M., Saatchi, S., Santoro, M., Thurner, M., Weber, U., Ahrens, B., Beer, C., Cescatti, A., Randerson, J. T., and Reichstein, M.: Global covariation of carbon turnover times with climate in terrestrial ecosystems, *Nature*, 514, 213-217, 10.1038/nature13731  
<http://www.nature.com/nature/journal/v514/n7521/abs/nature13731.html#supplementary-information>, 2014.
- Collatz, G., Ribas-Carbo, M., and Berry, J. A.: Coupled photosynthesis-stomatal conductance model for leaves of C<sub>4</sub> plants, *Australian Journal of Plant Physiology*, 19, 519-538, 1992.
- Collatz, G. J., Ball, J. T., Grivet, C., and Berry, J. A.: Physiological and environmental regulation of stomatal conductance, photosynthesis, and transpiration: A model that includes a laminar boundary layer, *Agric. For. Meteorol.*, 54, 107-136, 1991.
- Cornwell, W. K., Wright, I., Turner, J., Maire, V., Barbour, M., Cernusak, L., Dawson, T., Ellsworth, D., Farquhar, G., Griffiths, H., Keitel, C., Knohl, A., Reich, P., Williams, D., Bhaskar, R., Cornelissen, J. H. C., Richards, A., Schmidt, S., Valladares, F., Körner, C., Schulze, E. D., Buchmann, N., and Santiago, L.: A global dataset of leaf delta 13C values, *Scientific Data*, in press, doi:10.5061/dryad.3jh61, 2016.
- Cowan I. R., and D., F. G.: Stomatal function in relation to leaf metabolism and environment, in: *Integration of Activity in the Higher Plant*, edited by: Jennings, D. H., Cambridge University Press, Cambridge, 471-505, 1977.
- Duarte, H. F., Raczka, B. M., Ricciuto, D. M., Lin, J. C., Koven, C. D., Thornton, P. E., Bowling, D. R., Lai, C. T., Bible, K. J., and Ehleringer, J. R.: Evaluating the Community Land Model (CLM 4.5) at a Coniferous Forest Site in Northwestern United States Using Flux and Carbon-Isotope Measurements, *Biogeosciences Discuss.*, 2016, 1-35, 10.5194/bg-2016-441, 2016.
- Farquhar, G. D., von Caemmerer, S., and Berry, J. A.: A biochemical model of photosynthetic CO<sub>2</sub> assimilation in leaves of C<sub>3</sub> species, *Planta*, 149, 78-90, 1980.
- Farquhar, G. D., Ehleringer, J. R., and Hubick, K. T.: Carbon Isotope Discrimination and Photosynthesis, *Annual Review of Plant Physiology and Plant Molecular Biology*, 40, 503-537, 10.1146/annurev.pp.40.060189.002443, 1989.
- Haxeltine, A., and Prentice, I. C.: BIOME3: An equilibrium terrestrial biosphere model based on ecophysiological constraints, resource availability, and competition among plant functional types, *Global Biogeochem. Cycles*, 10, 693-709, 1996a.
- Haxeltine, A., and Prentice, I. C.: A general model for the light use efficiency of primary production, *Functional Ecology*, 10, 551-561, 1996b.
- Joos, F., Gerber, S., Prentice, I. C., Otto-Bliesner, B. L., and Valdes, P. J.: Transient simulations of Holocene atmospheric carbon dioxide and terrestrial carbon since the Last Glacial Maximum, *Global Biogeochemical Cycles*, 18, 2004.
- Keel, S. G., Pepin, S., Leuzinger, S., and Körner, C.: Stomatal conductance in mature deciduous forest trees exposed to elevated CO<sub>2</sub>, *Trees*, 21, 151, 10.1007/s00468-006-0106-y, 2006.



- Keel, S. G., Joos, F., Spahni, R., Saurer, M., Weigt, R. B., and Klesse, S.: Simulating oxygen isotope ratios in tree ring cellulose using a dynamic global vegetation model, *Biogeosciences*, 13, 3869-3886, 10.5194/bg-13-3869-2016, 2016.
- Keenan, T. F., Hollinger, D. Y., Bohrer, G., Dragoni, D., Munger, J. W., Schmid, H. P., and Richardson, A. D.: Increase in forest water-use efficiency as atmospheric carbon dioxide concentrations rise, *Nature*, 499, 324-327, 10.1038/nature12291 <http://www.nature.com/nature/journal/v499/n7458/abs/nature12291.html#supplementary-information>, 2013.
- Knauer, J., Zaehle, S., Reichstein, M., Medlyn, B. E., Forkel, M., Hagemann, S., and Werner, C.: The response of ecosystem water-use efficiency to rising atmospheric CO<sub>2</sub> concentrations: sensitivity and large-scale biogeochemical implications, *New Phytologist*, 213, 1654-1666, 10.1111/nph.14288, 2017.
- Leuenberger, M.: To what extent can ice core data contribute to the understanding of plant ecological developments of the past?, in: *Stable Isotopes as Indicators of Ecological Change*, edited by: Dawson, T., and Siegwolf, R., Elsevier, Amsterdam, 211-233, 2007.
- Liberloo, M., Tulva, I., Raim, O., Kull, O., and Ceulemans, R.: Photosynthetic stimulation under long-term CO<sub>2</sub> enrichment and fertilization is sustained across a closed *Populus* canopy profile (EUROFACE), *New Phytologist*, 173, 537-549, 10.1111/j.1469-8137.2006.01926.x, 2007.
- Lloyd, J., and Farquhar, G. D.: <sup>13</sup>C discrimination during CO<sub>2</sub> assimilation by the terrestrial biosphere, *Oecologia*, 99, 201-215, 1994.
- McCarroll, D., and Loader, N. J.: Stable isotopes in tree rings, *Quat. Sci. Rev.*, 23, 771-801, <http://dx.doi.org/10.1016/j.quascirev.2003.06.017>, 2004.
- Medlyn, B. E., Duursma, R. A., Eamus, D., Ellsworth, D. S., Prentice, I. C., Barton, C. V. M., Crous, K. Y., De Angelis, P., Freeman, M., and Wingate, L.: Reconciling the optimal and empirical approaches to modelling stomatal conductance, *Global Change Biology*, 17, 2134-2144, 10.1111/j.1365-2486.2010.02375.x, 2011.
- Miner, G. L., Bauerle, W. L., and Baldocchi, D. D.: Estimating the sensitivity of stomatal conductance to photosynthesis: a review, *Plant, Cell & Environment*, n/a-n/a, 10.1111/pce.12871, 2017.
- Monteith, J. L.: A reinterpretation of stomatal responses to humidity, *Plant, Cell & Environment*, 18, 357-364, 10.1111/j.1365-3040.1995.tb00371.x, 1995.
- Peñuelas, J., Canadell, J. G., and Ogaya, R.: Increased water-use efficiency during the 20th century did not translate into enhanced tree growth, *Global Ecology and Biogeography*, 20, 597-608, 10.1111/j.1466-8238.2010.00608.x, 2011.
- Prentice, I. C., Dong, N., Gleason, S. M., Maire, V., and Wright, I. J.: Balancing the costs of carbon gain and water transport: testing a new theoretical framework for plant functional ecology, *Ecology Letters*, 17, 82-91, 10.1111/ele.12211, 2014.
- Sato, H., Kumagai, T. o., Takahashi, A., and Katul, G. G.: Effects of different representations of stomatal conductance response to humidity across the African continent under warmer CO<sub>2</sub>-enriched climate conditions, *Journal of Geophysical Research: Biogeosciences*, 120, 979-988, 10.1002/2014jg002838, 2015.
- Scholze, M., Kaplan, J. O., Knorr, W., and Heimann, M.: Climate and interannual variability of the atmosphere-biosphere <sup>13</sup>C<sub>2</sub>O flux, *Geophys. Res. Lett.*, 30, 10.1029/2002GL015631, 2003.
- Scholze, M., Ciais, P., and Heimann, M.: Modeling terrestrial <sup>13</sup>C cycling: Climate, land use and fire, *Global Biogeochem. Cycles*, 22, 1-13, 10.1029/2006GB002899, 2008.
- Sitch, S., Smith, B., Prentice, I. C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J. O., Levis, S., Lucht, W., Sykes, M. T., Thonicke, K., and Venevsky, S.: Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model, *Global Change Biology*, 9, 161-185, 2003.
- Streit, K., Siegwolf, R. T. W., Hagedorn, F., Schaub, M., and Buchmann, N.: Lack of photosynthetic or stomatal regulation after 9 years of elevated [CO<sub>2</sub>] and 4 years of soil warming in two conifer species at the alpine treeline, *Plant, Cell & Environment*, 37, 315-326, 10.1111/pce.12197, 2014.
- Wang, H., Prentice, I. C., Cornwell, W., Keenan, T., Davis, T., Wright, I., Evans, B., and Peng, C.: A universal model for carbon dioxide uptake by plants, *bioRxiv*, 2016.

- Zaehle, S., Medlyn, B. E., De Kauwe, M. G., Walker, A. P., Dietze, M. C., Hickler, T., Luo, Y., Wang, Y.-P., El-Masri, B., Thornton, P., Jain, A., Wang, S., Warlind, D., Weng, E., Parton, W., Iversen, C. M., Gallet-Budynek, A., McCarthy, H., Finzi, A., Hanson, P. J., Prentice, I. C., Oren, R., and Norby, R. J.: Evaluation of 11 terrestrial carbon–nitrogen cycle models against observations from two temperate Free-Air CO<sub>2</sub> Enrichment studies, *New Phytologist*, 202, 803-822, 10.1111/nph.12697, 2014.
- Zhu, Q., Iversen, C. M., Riley, W. J., Slette, I. J., and Vander Stel, H. M.: Root traits explain observed tundra vegetation nitrogen uptake patterns: Implications for trait-based land models, *Journal of Geophysical Research: Biogeosciences*, 121, 3101-3112, 10.1002/2016jg003554, 2016a.
- Zhu, Q., Riley, W. J., Tang, J., and Koven, C. D.: Multiple soil nutrient competition between plants, microbes, and mineral surfaces: model development, parameterization, and example applications in several tropical forests, *Biogeosciences*, 13, 341-363, 10.5194/bg-13-341-2016, 2016b.
- Zhu, Q., Riley, W. J., and Tang, J.: A new theory of plant–microbe nutrient competition resolves inconsistencies between observations and model predictions, *Ecological Applications*, 27, 875-886, 10.1002/eap.1490, 2017.

# 20<sup>th</sup>-century changes in carbon isotopes and water-use efficiency: Tree-ring based evaluation of the CLM4.5 and LPX-Bern models

Kathrin M. Keller<sup>1,2</sup>, Sebastian Lienert<sup>1,2</sup>, Anil Bozbiyik<sup>1,2</sup>, Thomas F. Stocker<sup>1,2</sup>, Olga V. Churakova (Sidorova)<sup>3,4</sup>, David C. Frank<sup>2,5,6</sup>, Stefan Klesse<sup>2,5,6</sup>, Charles D. Koven<sup>7</sup>, Markus Leuenberger<sup>1,2</sup>, William J. Riley<sup>7</sup>, Matthias Saurer<sup>5,8</sup>, Rolf Siegwolf<sup>5,8</sup>, Rosemarie B. Weigt<sup>8</sup>, and Fortunat Joos<sup>1,2</sup>

<sup>1</sup>Climate and Environmental Physics, Physics Institute, University of Bern, Switzerland

<sup>2</sup>Oeschger Centre for Climate Change Research, University of Bern, Switzerland

<sup>3</sup>Institute for Environmental Sciences, University of Geneva, Switzerland

<sup>4</sup>Siberian Federal University, Krasnoyarsk, Russia

<sup>5</sup>Swiss Federal Research Institute WSL, Birmensdorf, Switzerland

<sup>6</sup>Laboratory of Tree Ring Research, the University of Arizona, Tucson, USA

<sup>7</sup>Lawrence Berkeley National Lab (LBNL), Berkeley, CA, USA

<sup>8</sup>Paul Scherrer Institute, Villigen, Switzerland

*Correspondence to:* K.M. Keller (keller@climate.unibe.ch)

**Abstract.** Measurements of the stable carbon isotope ratio ( $\delta^{13}\text{C}$ ) on annual tree rings offer new opportunities to evaluate mechanisms of variations in photosynthesis and stomatal conductance under changing  $\text{CO}_2$  and climate, especially in conjunction with process-based biogeochemical model simulations. The isotopic discrimination is indicative of the ratio between the  $\text{CO}_2$  partial pressure in the intercellular cavities and the atmosphere ( $c_i/c_a$ ) and of the ratio of assimilation to stomatal conductance, termed intrinsic water-use efficiency (iWUE). We performed isotope-enabled simulations over the industrial period with the land biosphere module (CLM4.5) of the Community Earth System Model and the LPX-Bern dynamic global vegetation model. Results for C3 tree species show good agreement with a global compilation of  $\delta^{13}\text{C}$  measurements on leaves, though modeled  $^{13}\text{C}$  discrimination by C3 trees is smaller in arid regions than measured. A compilation of seventy-six tree-ring records, mainly from Europe, boreal Asia, and western North America, suggest on average small 20<sup>th</sup>-century changes in isotopic discrimination and in  $c_i/c_a$  and an increase in iWUE of about 27% since 1900. LPX-Bern results match these century-scale reconstructions, supporting the idea that the physiology of stomata has evolved to optimize trade-offs between carbon gain by assimilation and water loss by transpiration. In contrast, CLM4.5 simulates an increase in discrimination and in turn a change in iWUE that is almost twice as large as revealed by the tree-ring data. Factorial simulations show that these changes are mainly in response to rising atmospheric  $\text{CO}_2$ . The results suggest that the down-regulation of  $c_i/c_a$  and of photosynthesis by nitrogen limitation is possibly too strong in the standard setup of CLM4.5 or there may be ~~more fundamental~~ problems associated with the ~~prescribed relationship between conductance and assimilation~~ implementation of conductance, assimilation, and related adjustment processes to long-term environmental changes.

## 1 Introduction

Measurements of the stable isotope  $^{13}\text{C}:^{12}\text{C}$  ratio ( $\delta^{13}\text{C}$ ) on samples from air and natural archives hold information on the carbon cycling in the Earth System. A particularly important area of isotopic research is to clarify mechanisms ~~governing~~ controlling  $\delta^{13}\text{C}$  carbon assimilation and water transpiration by land plants (Farquhar et al., 1989; Saurer et al., 2014; Voelker et al., 2016) and their role for the global terrestrial carbon sink (Ciais et al., 2013). There are numerous other interesting applications of  $\delta^{13}\text{C}$  in the context of Earth System science. The modern decrease in atmospheric  $\delta^{13}\text{C}\text{CO}_2$  is an unequivocal testimony to the input of isotopically-light fossil and terrestrial carbon by human activities (Keeling et al., 1979; Francey et al., 1999).  $\delta^{13}\text{C}$  data representing atmospheric air are used to quantify the global ocean and land carbon sources and sinks (Keeling et al., 1989; Joos and Bruno, 1998; Trudinger et al., 2002; Bauska et al., 2015), ~~to identify~~. Furthermore,  $\delta^{13}\text{C}$  observations allow identification of the imprint of fossil fuel carbon in atmospheric air to quantify regional-to-local-scale land carbon sources and sinks (Torn et al., 2011; Vardag et al., 2016), or to evaluate air-sea transfer velocity parameterizations (Krakauer et al., 2006).  $\delta^{13}\text{C}$  data from the modern ocean are applied to infer the oceanic uptake of anthropogenic carbon (Heimann and Maier-Reimer, 1996; Gruber et al., 1999; Sonnerup and Quay, 2012; Becker et al., 2016), while paleo proxy  $\delta^{13}\text{C}$  data from ocean sediments and ice cores permit ~~us to infer~~ inference of land carbon changes between the last glacial maximum and the current warm period (Shackleton, 1977; Ciais et al., 2012; Peterson et al., 2014), ~~to identify~~. Paleo  $\delta^{13}\text{C}$  data are also used to trace water mass, circulation and biological productivity changes on glacial-interglacial time scales and during past abrupt events (Menviel et al., 2012; Schmittner and Somes, 2016), to disentangle processes of past glacial-interglacial carbon cycle changes (Menviel and Joos, 2012; Schneider et al., 2013; Eggleston et al., 2016), and of ancient climate events (Kennett and Stott, 1991; Korte and Kozur, 2010).

Box models, ocean and land only models, and Earth System Models of Intermediate Complexity (Siegenthaler and Joos, 1992; Aranibar et al., 2006; Lai et al., 2006; Tschumi et al., 2011; Holden et al., 2013; Schmittner et al., 2013) have been traditionally evaluated by  $\delta^{13}\text{C}$  data and used for the interpretation of  $\delta^{13}\text{C}$  observations. Yet, despite such potential,  $^{13}\text{C}$  has only been implemented recently in comprehensive Earth System Models and its subcomponents (~~Tagliabue and Bopp, 2008; Graven et al., 2012~~). Now carbon isotopes have been implemented in the ocean component of the Community Earth System Model (CESM) (Jahn et al., 2015) ~~and in~~. In this manuscript we present the implementation of  $\delta^{13}\text{C}$  in the CESM land module.

Isotopic discrimination of plants following the C3 photosynthesis pathway depends on  $\text{CO}_2$  assimilation and stomatal conductance (Farquhar et al., 1982; Lloyd and Farquhar, 1994) which themselves depend on the availability of nitrogen, water, and light, as well as species-specific leaf traits. Discrimination and variations thereof are thus indicative of the extent to which carbon assimilation by plants, fueling plant growth, is limited by factors such as drought and nitrogen limitation. In other words, quantification of isotopic discrimination changes over time ~~permits one to evaluate and permits the evaluation of~~ responses of stomatal conductance and assimilation to environmental variation and extremes. Environmental changes on the policy-relevant time scale of global warming include increasing atmospheric  $\text{CO}_2$ , climate change and increasing nitrogen deposition. Tree ring  $\delta^{13}\text{C}$  records capture the influence of local climate variability with measured  $\delta^{13}\text{C}$  variations used to reconstruct, for ex-

ample, fluctuations in temperature (Treydte et al., 2009; Sidorova et al., 2013), precipitation (Schubert and Jahren, 2011), or cloud cover (Gagen et al., 2011; Young et al., 2012).

The intrinsic water-use efficiency (iWUE), defined as the ratio between assimilation and stomatal conductance, is closely related to  $^{13}\text{C}$  discrimination. Rising atmospheric  $\text{CO}_2$  concentrations can have a fertilizing effect on plants, which in turn potentially increases iWUE (Keenan et al., 2013; Saurer et al., 2014) – at least as long as plant growth is not limited by other factors such as nitrogen or phosphorus supply (Reich et al., 2014; Yang et al., 2016) or water stress (Walker et al., 2015).

There is a rich literature on changes in  $^{13}\text{C}$  isotopic discrimination and iWUE and on observational evidence from  $\delta^{13}\text{C}$  tree-ring records (McCarroll and Loader, 2004; Fichtler et al., 2010; Leonardi et al., 2012; Churakova (Sidorova) et al., 2014, 2016a; Lévesque et al., 2014), FACE-type experiments (Battipaglia et al., 2013; Klein et al., 2016),  $\delta^{13}\text{C}$  site measurements (Pataki et al., 2003; Bowling et al., 2014) and  $\delta^{13}\text{C}$  paleo data (Voelker et al., 2016). These data generally suggest small to moderate decadal-to-century-scale changes in discrimination that correspond to a 20<sup>th</sup>-century increase in iWUE of order in the order of 20% and physiological control towards a constant ratio of the partial pressure of  $\text{CO}_2$  within the leaf's stomatal cavity to the  $\text{CO}_2$  pressure outside the leaf ( $c_i/c_a$ ; Saurer et al., 2004; Leonardi et al., 2012; Frank et al., 2015) and, more generalized, a pattern of stomatal optimization towards minimizing water loss per unit carbon assimilated (Voelker et al., 2016).

$\delta^{13}\text{C}$  data are used to evaluate global and local models of plant growth, carbon cycling, and of land-atmosphere isotopic fluxes for atmospheric carbon balancing (Scholze et al., 2003, 2008; Suits et al., 2005; Danis et al., 2012; van der Velde et al., 2014).  $\delta^{13}\text{C}$  data from leaf material (Cornwell et al., 2016) are used by Prentice et al. (2014) and Wang et al. (2016) to develop the representation of assimilation in land biosphere models following an optimization principle to balance carbon gain by assimilation and water loss.

The goal of this study is to present the implementation of  $\delta^{13}\text{C}$  in the land component, CLM4.5, of CESM and LPX-Bern and to discuss the model performance for  $\delta^{13}\text{C}$  on the global scale. This is a step towards fully coupled isotope-enabled CESM applications and complementing the effort on complements recent advances in simulating marine carbon isotopes (Jahn et al., 2015). We compare the CLM4.5 and LPX-Bern results to a data set of  $\delta^{13}\text{C}$  measurements on modern leaf material (Cornwell et al., 2016), a comprehensive compilation of century-scale  $\delta^{13}\text{C}$  tree-ring records, as well as to results from the isotope-enabled LPX-Bern dynamic global vegetation model. We discuss spatial and century-scale trends in isotopic discrimination and iWUE of the two models in light of observational evidence, and the models contrasting implementations of stomatal conductance and the balance between carbon assimilation and water loss.

## 2 Methods

### 2.1 CLM4.5

We use the Community Land Model version 4.5 (CLM4.5; Oleson et al., 2013), the land component of the Community Earth System Model version 1.2.0 (CESM1.2; Hurrell et al., 2013). The implementation of  $^{13}\text{C}$  is outlined below (Section 2.1.1). A comprehensive description of the implementation of carbon isotopes in CLM4.5 is given in the Technical Description (Oleson

et al., 2013), further details elsewhere for  $^{13}\text{C}$  (Raczka et al., 2016; Duarte et al., 2016) and  $^{14}\text{C}$  (Koven et al., 2013). In addition to the land, carbon isotopes are also implemented in the ocean model of CESM1.2 (Jahn et al., 2015).

CLM4.5 features fully prognostic terrestrial carbon and nitrogen cycling which comprises all vegetation, litter, and soil organic matter pools (Oleson et al., 2013). Each grid cell is composed of multiple, independently represented land use classes. Each class has its own set of plant functional types (PFTs), snow and soil columns.

Vegetation comprises ~~15~~ fifteen different PFTs, which are classified into three different phenological groups: evergreen, ~~with a fraction of annual leaf growth persisting longer than one year;~~ seasonal-deciduous, ~~with one growing season per year (mainly temperature and length of day-controlled);~~ and stress-deciduous, ~~with potentially multiple growing seasons per year (temperature and soil moisture-controlled).~~ Fourteen of these PFTs follow the C3 photosynthetic pathway (11 tree PFTs: ~~temperate needle-leaved evergreen trees, boreal needle-leaved evergreen trees, boreal needle-leaved deciduous trees, tropical broad-leaved evergreen trees, temperate broad-leaved evergreen trees, tropical broad-leaved deciduous trees, temperate broad-leaved deciduous trees, boreal broad-leaved deciduous trees, temperate broad-leaved evergreen shrubs, temperate broad-leaved deciduous shrubs, boreal broad-leaved deciduous shrubs;~~ 2 grass PFTs: ~~arctic grasses, cool grasses;~~ grasses and crops) and one the C4 path (warm grasses). Altogether, 20 carbon and 19 nitrogen pools per PFT represent carbon (C) and nitrogen (N) in vegetation. C and N are tracked for leaf, live stem, dead stem, live coarse root, dead coarse root, and fine root pools and corresponding storage pools representing, respectively, short-term and long-term storage of non-structural carbohydrates and labile nitrogen.

Decomposition of fresh litter material (including C and N) into progressively more recalcitrant forms of soil organic matter is represented as a cascade of transformations between decomposing coarse woody debris, litter, and soil organic matter pools. Depending on the C:N ratios of involved pools and the amount of carbon lost by respiration, each transformation can generate either a source or a sink of new mineral nitrogen.

Steps that result in an uptake of mineral nitrogen (e.g., immobilization fluxes) are subject to rate limitation, depending on the availability of mineral nitrogen and the sum of nitrogen demands from immobilization, photosynthesis, nitrification, and denitrification. If mineral N is less than the sum of these demands, fluxes are downregulated in order to match N supply. We note that the "Relative Demand" downregulation in CLM4.5 has recently been shown to be inaccurate in several tropical (Zhu et al., 2016b), tundra (Zhu et al., 2016a), and grassland (Zhu et al., 2017) systems. In addition to the cycling of nitrogen within the plant – litter – soil organic matter system, CLM represents external sources, including atmospheric deposition and biological nitrogen fixation. CLM also represents other N sinks not included in this budgeting, including leaching and losses in fire.

Photosynthesis in C3 and C4 plants is based on Farquhar et al. (1980) and Collatz et al. (1992), respectively. The maximum rate of carboxylation at 25°C varies with an assumed static foliage nitrogen concentration and specific leaf area and is a PFT specific parameter. It is assumed that leaf nitrogen and sunlight decrease exponentially with cumulative leaf area index from the canopy top to bottom. Accordingly, the carboxylation rate and other photosynthesis parameter decrease exponentially within the canopy. Leaf level photosynthesis is scaled to the canopy level by integration over the total leaf area. This is done separately for sunlit and shaded leaves and by considering the exponential scaling.

The allocation of carbon and nitrogen is determined in the following steps: First, gross primary productivity (GPP) is calculated under the assumption of unlimited nitrogen supply. Then, from GPP the maintenance respiration demand is subtracted. Following this, the actual nitrogen supply is compared against the nitrogen demand and GPP, if necessary, downregulated. Finally, the available carbon is either utilized for plant growth and growth respiration or stored for growth in the subsequent years. Ghimire et al. (2016) recently presented an improved scheme which avoids ~~instantaneous downregulation of assimilation~~ this instantaneous downregulation by N limitation.

### 2.1.1 Carbon isotope discrimination during photosynthesis in CLM4.5

Isotopic ratios are usually reported as deviation from a standard material:

$$\delta^{13}\text{C} = \left( \frac{R_{\text{sample}}}{R_{\text{std}}} - 1 \right) \cdot 1000 \quad (1)$$

where  $R_{\text{sample}}$  and  $R_{\text{std}}$  denote the  $^{13}\text{C}/^{12}\text{C}$  molar ratios of the sample and the standard material. Isotopic fractionation factors,  $\alpha$ , are here defined as the ratio of the carbon isotope ratios in reactant ~~and to~~ product (Farquhar et al., 1989) (We note that  $\alpha$  is also defined by the ratio of product ratio to reactant ratio in the literature). The fractionation factor for photosynthetic assimilation of  $\text{CO}_2$  from canopy air is then:

$$\alpha_{psn} = R_{\text{air}}/R_{GPP} \quad (2)$$

where  $R_{\text{air}}$  and  $R_{GPP}$  denote the  $^{13}\text{C}/^{12}\text{C}$  molar ratios in the canopy air and in the resulting gross primary productivity flux incorporated in the plant material.  $\alpha$  larger than unity results in a discrimination against the heavier isotope and therefore to a depletion of  $^{13}\text{C}$  in GPP and plant material compared to air. Discrimination is also expressed by  $\Delta_i$ , the deviation of  $\alpha$  from unity and here multiplied by 1000 for conformity with the  $\delta^{13}\text{C}$  notation ( $\Delta_i = (\alpha - 1) \cdot 1000$ ).

Photosynthesis in CLM4.5 and, embedded in this process, photosynthetic discrimination, are implemented in two steps following Farquhar et al. (1989). Step 1), given that no enzymatic fractionation is of relevance, the diffusion of  $\text{CO}_2$  across the leaf boundary layer and into the stomata, is associated with a kinetic isotope effect of  $a=4.4$ . During step 2), enzymatic fixation, the effect on C3 plants is  $b=27$ . These two steps are additive and result in the leaf-level fractionation factor; however, note that in the case of C4 plants only step 1) is of relevance. The CAM photosynthetic pathway is not considered in the model.

The leaf-level fractionation factors ( $\alpha_{psn}$ ) of C3 and C4 plants are defined as:

C4 plants:

$$\alpha_{psn} = 1 + \frac{a}{1000} \quad (3)$$

C3 plants:

$$\alpha_{psn} = 1 + \frac{a + (b - a) \frac{c_i^*}{c_a}}{1000} \quad (4)$$

where  $c_i^*$  and  $c_a$  represent the intercellular and atmospheric ~~partial pressure concentration~~ of CO<sub>2</sub> (~~Pa/mol~~), respectively.

5 This results in an isotopic discrimination between assimilated plant material ( $\delta^{13}C_{\text{plant}}$ ) and atmospheric CO<sub>2</sub> ( $\delta^{13}c_a$ ) expressed in permil units (Farquhar et al., 1989) for C3 plants as:

$$\Delta_i = (\delta^{13}c_a - \delta^{13}C_{\text{plant}})/(1 + \delta^{13}C_{\text{plant}}/1000) \quad (5)$$

and can be approximated by  $\Delta_i = a + (b - a)c_i^*/c_a$  (Farquhar et al., 1989). Fractionation factors for all other land biosphere fluxes are set to unity and, thus, no further discrimination occurs in the land model.

10 The kinetic isotope effect during CO<sub>2</sub> fixation is constrained by  $c_i^*$  which, in turn, depends on the net carbon assimilation during photosynthesis ( $a_n$ ;  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). The asterisk in  $c_i^*$  denotes the consideration of nitrogen down-regulation in the photosynthesis calculation (for details, see Oleson et al., 2013) which is implemented as follows:

$$c_i^* = c_a - a_n(1 - f_{dreg}) \frac{(1.4g_s) + (1.6g_b)}{g_b g_s} \quad (6)$$

15 where  $f_{dreg}$  is the downscaling factor due to nitrogen limitation,  ~~$p$  is atmospheric pressure (Pa)~~,  $g_b$  is leaf boundary layer conductance, and  $g_s$  is leaf stomatal conductance for water ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ).

In CLM4.5, assimilation is calculated before nitrogen limitation is considered. Thus,  $c_i$  in the photosynthesis module is different from  $c_i^*$ .  $c_i$  follows from Eq. 6 with  $f_{dreg} = 0$ . In other words, plants photosynthesize carbon at a potential, nitrogen unlimited rate. Photosynthesis  $a_n$  and, in turn, stomatal conductance  $g_s$  are not directly affected by nitrogen limitation. The flow of water and carbon through the stomata is simulated to occur by molecular diffusion and a ratio of 1.6 applies between the diffusivity of water and CO<sub>2</sub>, while a diffusivity ratio of 1.4 is assumed for the leaf boundary layer (Oleson et al., 2013). Stomatal conductance,  $g_s$ , itself is linearly related to the product of ~~assimilation leaf net photosynthesis~~ ( $a_n$ ) and the relative humidity at the leaf surface,  $R_h$ , and the inverse of the CO<sub>2</sub> ~~mixing ratio concentration at the leaf surface~~,  $c_s$  (Ball et al., 1987; Collatz et al., 1991; Oleson et al., 2013) :

$$g_s = m \cdot \frac{R_h}{c_s} \cdot a_n + b \quad (7)$$



25 where  $b$  is a minimal conductance as a function of soil water availability, and  $m$  a constant parameter, defining the slope between  $a_n$  and  $g_s$ .  $m$  is set to 9 for  $C_3$  plants and to 4 for  $C_4$  plants (Oleson et al., 2013) Both assimilation and stomatal conductance are downregulated by a drought stress factor which depends on soil moisture availability and can vary between 0 and 1. Nitrogen limitation and water stress can therefore result in a downregulation of ~~stomatal conductance and, thereby, of~~  $c_i^*/c_a$  and thus to a reduction in the carbon isotope discrimination of  $C_3$  plants in CLM4.5.

Equation 6 represents the constraint that  $CO_2$  consumption by photosynthesis ( $A = a_n \cdot (1 - f_{dreg})$ ) equals the transport of  $CO_2$  through the leaf boundary layer and the stomata into the stomatal cavity. The latter is the product of the ~~partial pressure~~ gradients-concentration gradient between the atmosphere and the stomatal cavity ( $c_a - c_i^*$ ) and an overall conductance for  $CO_2$  ( ~~$g_{CO_2} = (g_b g_s) / p(1.4g_s + 1.6g_b)$~~   $g_{CO_2} = (g_b g_s) / (1.4g_s + 1.6g_b)$ ) ( $\mu\text{mol m}^{-2} \text{s}^{-1} \text{Pa}^{-1}$ ). Thus, we can also write:

$$A = g_{CO_2} \cdot (c_a - c_i^*) = g_{CO_2} \cdot c_a \cdot (1 - c_i^*/c_a) \quad (8)$$

### 2.1.2 Spin-up and transient simulations and model forcings

10 ~~Starting with empty pools, the model is brought into equilibrium with the following steps: 1) accelerated decomposition of soil organic matter with perpetual 1850 Common Era (CE) forcing (1000 model years), 2) normal decomposition with perpetual 1850 CE forcing (500 model years), 3) transition to 1900 CE conditions (100 model years) and 4) transient simulation over the 20<sup>th</sup> century (1900-2005). During steps 1) and 2), both default model options, atmospheric  $\delta^{13}C$  is held on a constant value of -6‰. The first step, based on the accelerated decomposition technique by Thornton and Rosenbloom (2005), accelerates~~  
 15 ~~the equilibration of the soil carbon pools. During step 3) the model is adjusted to 1900 CE conditions by applying transient atmospheric  $pCO_2$  and  $\delta^{13}C$  forcing (years 1800-1900) together with CRU-NCEP climate forcing data (repeated years 1901-1920; Viovy, 2005). Step 4), the 20<sup>th</sup>-century simulation, is run with both transient atmospheric and climatic forcing data (years 1901-2005; Viovy, 2011). In both steps 3) and 4), the atmospheric forcing of  $CO_2$  is Law Dome (Etheridge et al., 1996; MacFarling Meure et al., 2006),  $\delta^{13}C$  is a combination of Rubino et al. (2013) and, from 1993 on, White et al. (2015) (Fig. 1). Land use area and change is~~  
 20 ~~prescribed following Hurtt et al. (2006)~~ In the following sections, we will, for simplicity and for consistency with the isotopic literature and the LPX description, omit the superscript of  $c_i^*$  and denote  $c_i^*$  also by  $c_i$ .

## 2.2 LPX-Bern 1.3

The Land surface Processes and eXchanges (LPX-Bern 1.3) model (Spahni et al., 2013; Stocker et al., 2013; Saurer et al., 2014; Churakova (Sidorova) et al., 2016b; Ruosch et al., 2016; Keel et al., 2016) is based on the Lund-Potsdam-Jena (LPJ)  
 25 dynamic global vegetation model (Sitch et al., 2003, see also Joos et al. 2001; Gerber et al. 2004; Strassmann et al. 2008). LPX combines process-based, large-scale representations of terrestrial vegetation dynamics, the dynamics of terrestrial carbon and nitrogen stocks and fluxes, and land-atmosphere exchanges of water, carbon dioxide, methane, nitrous oxide, and carbon and water isotopes in a modular framework.

Following the assimilation of multiple experimental constraints, such as net primary productivity (NPP) (Olson et al., 2013) and the seasonal fraction of absorbed photosynthetically active radiation (Gobron et al., 2006), several key model parameters were updated. Note that no ~~explicit constraint for the  $\delta^{13}\text{C}$  signatures was used~~ observational data, e.g., from tree-rings or atmospheric samples, was used as a constraint in the assimilation. A list of the updated parameters and their values can be found in Tab. 1.

Each grid cell in LPX is subdivided into different land use classes (areas with natural mineral soils, peatland, other wetlands, cropland, pasture, urban). LPX simulates the distribution of PFTs based on bioclimatic limits for plant growth and regeneration, and plant-specific parameters that govern plant competition for light, water (Sitch et al., 2003), and nitrogen (Xu-Ri and Prentice, 2008; Xu-Ri et al., 2012). Here, seven generic tree PFTs all following the C3 photosynthetic pathway (~~tropical broad-leaved evergreen trees, tropical broadleaved raingreen trees, temperate needle-leaved evergreen trees, temperate broad-leaved evergreen trees, temperate broad-leaved summer green trees, boreal needle-leaved evergreen trees, boreal broadleaved summer green trees~~) together with C3 grasses/forbs, and C4 grasses are considered on natural non-peatland areas. The two PFTs on cropland and pastures have the same properties as the C3 and C4 grasses on natural land and grow depending upon climatic conditions. ~~Tree PFTs and fires are excluded from the agricultural cell fraction.~~ On peatland, two PFTs (~~food-tolerant~~ C3 graminoids and Sphagnum moss) grow. Seven carbon and nitrogen pools per PFT represent leaves, sapwood, heartwood, fine roots, aboveground leaf litter, aboveground woody litter, and belowground litter. Separate soil organic carbon and nitrogen pools receive input from litter of all PFTs. N input by biological N fixation is implied by maintaining prescribed C to N ratios in litter and soil pools. Inorganic soil nitrogen pools receive input from litter and soil decomposition and through atmospheric N deposition and are subject to plant uptake, leakage, and gaseous losses (Xu-Ri and Prentice, 2008).

~~Daily photosynthesis~~ Photosynthesis and stomatal control in LPX is described by Haxeltine and Prentice (1996b) as summarized elsewhere (Keel et al., 2016; Sitch et al., 2003). The equations for water supply from soil and transpiration, assimilation, and canopy conductance are solved simultaneously by varying the ratio  $c_i/c_a$ , also termed  $\lambda$ , to yield self-consistent values for these properties.

Total day time net photosynthesis,  $A_{dt}$ , is modeled following Collatz et al. (1991, 1992) which is a Farquhar model (Farquhar et al., 1980) generalized for global modeling purposes (for details, see Haxeltine and Prentice, 1996a). ~~An empirical convective boundary layer parameterization (Monteith, 1995) couples the carbon and water cycle. The plant-available water is proportional to the soil-water content in the top 2 m and hydraulic constraints limiting tree height are not explicitly considered. Soils are subdivided in eight soil layers linked by percolation. Soil-water content is fed by precipitation (after interception by vegetation canopy) and snow melt. Beside plant transpiration, water is also removed from the soil by direct soil evaporation, percolation and runoff (Gerten et al., 2004). Transpiration is described as a function of potential evapotranspiration and stomatal conductance ( $g_{\text{H}_2\text{O}}$ ), assuming water-saturated cell walls in the stomata. The  $\text{CO}_2$  flux from the atmosphere to the stomatal cavity is proportional to the  $\text{CO}_2$  difference between the atmosphere and the stomatal cavity ( $c_a - c_i$ ). Stomatal conductance for water,  $g_{\text{H}_2\text{O}}$ , partial pressure and  $\lambda$ .  $A_{dt}$  is computed from a formulation which gives a gradual transition between light-limited and carbon dioxide,  $g_{\text{CO}_2}$ , are linearly related by their molecular diffusivities ( $g_{\text{H}_2\text{O}}/g_{\text{CO}_2} = 1.6$ ). Here it is important to note~~  $A_{dt}$  is a function of incoming radiation, temperature, day length, and atmospheric  $\text{CO}_2$  difference between the atmosphere and the stomatal cavity ( $c_a - c_i$ ).

~~that the stomatal conductance for water explicitly excludes all plant water losses not directly associated with photosynthesis, Rubisco-limited rate of photosynthesis. The amount of photosynthetically active radiation absorbed by the entire canopy increases with the modelled leaf area index following Beer's law and is used to compute the light-limited photosynthesis rate. The N content and Rubisco activity of leaves are assumed to vary seasonally and with canopy position in a way to maximize~~

5  $A_{dt}$ .

~~Canopy conductance,  $g_c$ , is linked to  $A_{dt}$  through~~

$$g_c = g_{min} + \frac{1.6A_{dt}}{c_a(1-\lambda)} \quad (9)$$

~~where  $g_{min}$  is a PFT specific minimum canopy conductance.~~

10 ~~Daily transpiration of water is calculated for each PFT as the minimum of a plant- and soil limited supply function ( $E_{supply}$ ) and the demand for transpiration ( $E_{demand}$ ).  $E_{supply}$  is the product of root-weighted soil moisture availability and a maximum water supply rate that is equal for all PFTs.  $E_{demand}$  is calculated following the empirical relation between evaporation efficiency and surface conductance of Monteith (1995) :~~

$$E_{demand} = E_{eq}\alpha_m \left[ 1 - \exp\left(\frac{-g_c\phi}{g_m}\right) \right] \quad (10)$$

15 ~~where  $E_{eq}$  is the equilibrium evaporation rate, dependent on temperature and radiation,  $g_m$  and  $\alpha_m$  are empirical parameters,  $g_c$  is the canopy conductance, and  $\phi$  the fraction of present foliage area to ground area (i.e. ~~cuticular and lenticular transpiration. Under non-water stressed condition the ratio  $e_i/c_a$  is set~~, projected leaf area). Eq. 10 is solved for  $E_{demand}$  using the non-water-stressed potential canopy conductance which is calculated using Eq. 9 and a fixed ratio  $\lambda$  to compute  $A_{dt}$ .  $\lambda$  is set equal to 0.8. ~~Otherwise, stomatal conductance, and thus  $e_i$ , is varied to optimize assimilation for given environmental conditions, namely irradiance, temperature, water supply from soils and  $CO_2$  concentration. This optimization is performed~~~~

20 ~~with the constraints that the  $CO_2$  assimilation,  $A$  (i.e., total daytime net photosynthesis), equals the  $CO_2$  flux from the atmosphere into the stomatal cavity and that transpiration does not exceed water supply. It holds, similarly as for CLM4.5 following~~

25 ~~Sitch et al. (2003) to approximate non-water-stressed conditions and as a starting value for the iterative computation of carbon assimilation and transpiration under water shortage. In case of water-stressed conditions when  $E_{demand}$  exceeds  $E_{supply}$ , canopy conductance and photosynthesis are down-regulated;  $E_{demand}$  is set to  $E_{supply}$  and Eq. 10 is solved for  $g_c$ . Knowing  $g_c$  and  $c_a$ ,  $\lambda$  is varied in the photosynthesis module until the following relationship is satisfied:~~

$$A = g_{CO_2} \cdot dt(\lambda) = \frac{g_c - g_{min}}{1.6} c_a - c_i(1 - \lambda) \quad (11)$$

NPP ~~, allocated annually to plant pools, is downregulated~~ is downregulated on the daily model time step if N-demand exceeds N-availability from the inorganic soil nitrogen pools, ~~which are subject to leakage and gaseous losses.~~ Daily NPP is integrated over a year and allocated annually to vegetation. Thus, in contrast to CESM there is no immediate feedback of nitrogen limitation on ~~assimilation (and isotopic discrimination)~~ isotopic discrimination on a daily time scale, but there is a long-term feedback by annual changes in vegetation structure and, in turn, photosynthesis and carbon assimilation.

### 2.2.1 Carbon isotope discrimination during photosynthesis in LPX

The isotopic discrimination during assimilation is calculated on a daily time step following Farquhar et al. (1989). Thus, the same discrimination formulations as in CESM (eqEq. 3 and 4) are used in LPX. ~~Note~~ We recall, however, that the intercellular CO<sub>2</sub> ~~pressure is~~ concentration is, unlike in CLM4.5, not downregulated by nitrogen limitation in LPX. For sphagnum mosses, discrimination during assimilation is fixed to -30‰. As in CESM, no further discrimination is assumed in LPX. In earlier LPX applications,  $\delta^{13}\text{C}$  was implemented following Scholze et al. (2003) and discrimination modeled following Lloyd and Farquhar (1994). Here, we adjusted the discrimination formulations and used instead the simpler formulations of Farquhar et al. (1989) for consistency with CLM4.5 and the computation of iWUE as described below. We note that our conclusions do not depend on this choice. LPX yields similar 20<sup>th</sup>-century changes in discrimination and iWUE for both formulations. However, simulated  $\delta^{13}\text{C}$  of carbon assimilated by C3 trees is generally less negative (by about 2‰) when applying the Lloyd and Farquhar (1994) formulation and agreement with leaf  $\delta^{13}\text{C}$  is less favorable.

~~The~~

### 2.3 Spin-up and transient simulations and model forcings

**CLM:** Starting with empty pools, the CLM model is brought into equilibrium with the following steps: 1) accelerated decomposition of soil organic matter with perpetual 1850 Common Era (CE) forcing (1000 model years), 2) normal decomposition with perpetual 1850 CE forcing (500 model years), 3) transition to 1900 CE conditions (100 model years) and 4) transient simulation over the 20<sup>th</sup> century (1900–2005). During steps 1) and 2), both default model options, atmospheric  $\delta^{13}\text{C}$  is held on a constant value of -6‰. The first step, based on the accelerated decomposition technique by Thornton and Rosenbloom (2005), accelerates the equilibration of the soil carbon pools. During step 3) the model is adjusted to 1900 CE conditions by prescribing transient atmospheric pCO<sub>2</sub> and  $\delta^{13}\text{C}$  (years 1800–1900) together with CRU-NCEP climate forcing data (repeated years 1901–1920; Viovy, Step 4), the 20<sup>th</sup>-century simulation, is run with both transient atmospheric pCO<sub>2</sub> and  $\delta^{13}\text{C}$  and climatic forcing data (years 1901–2005; Viovy). In both steps 3) and 4), atmospheric CO<sub>2</sub> is prescribed following Law Dome data (Etheridge et al., 1996; MacFarling Meure et al., 2006) and atmospheric samples; prescribed atmospheric  $\delta^{13}\text{C}$  is a combination of data from Rubino et al. (2013) and, from 1993 on, White et al. (2015) (Fig. 1). Land use area and change is prescribed following Hurtt et al. (2006).

**LPX:** The LPX model is forced with CRU TS3.23 climate data (Harris et al., 2014) and the same atmospheric CO<sub>2</sub> and  $\delta^{13}\text{C}$  forcing is used data is prescribed as in CLM4.5 . Land use maps are prescribed following Hurtt et al. (2006). After the spin-up procedure, the model is adjusted to 1900 CE conditions by applying transient atmospheric pCO<sub>2</sub> and  $\delta^{13}\text{C}$  forcing (years

1765-1900) together with recycled climate data (years 1901-1930). Then, the 20<sup>th</sup> century is simulated with **both-transient**  
30 **atmospheric-transient atmospheric CO<sub>2</sub> and δ<sup>13</sup>C** and climatic forcing data (years 1901-2007).

**Factorial runs** were performed in addition to the standard simulation. Each setup is the same as for the 20<sup>th</sup>-century simulations, however with one driving factor held constant: (i) *cCLIM*, constant climate (repeated years 1901-1920 for CLM4.5 and 1901-1930 for LPX). (ii) *cCO<sub>2</sub>*, constant atmospheric CO<sub>2</sub> concentrations, only done with LPX. (iii) *cNDEP*, constant atmospheric nitrogen deposition, only done with LPX. (iv) *cLU*, constant land use, only done with LPX. The difference between the factorial simulation and standard simulation is attributed to the driving factor that was held constant in the factorial run. An interaction term is computed from the difference between the change simulated in the standard simulations and the sum of all attributed changes.

5 The two models are forced with two slightly different climate data sets as CLM4.5 is run on a sub-hourly time step, while a daily time step is used in LPX. CRU NCEP, used to force CLM4.5, is a combination of the CRU TS3.2 monthly climatology (resolution of 0.5°x0.5°) and the NCEP reanalysis product with a time step of six hours (2.5°x2.5°). The results of the factorial runs, presented later, suggest generally a small influence of this difference in forcings on simulated discrimination and iWUE. We further investigated the potential impact of using two different climate data products. The CRU NCEP data are interpolated  
10 on the 1°x1° LPX grid and integrated to monthly values for use in LPX. LPX is run with the modified CRU NCEP and, as usual, with CRU-TS3.22 in the standard model setup where climate is changing transiently and the factorial setup with “constant climate” (cCLIM). Difference in simulated changes in discrimination and iWUE are small for both cases. In conclusion, the large model differences, presented in the result section, are not caused by differences in climate input data.

## 2.4 Observations

15 Two different observational datasets are used to evaluate the model simulations. The first dataset is a compilation of δ<sup>13</sup>C time series measured on tree rings (for an overview, see Tab. A1). The time series cover at least the years 1900–1985 (if possible 2005) and comprise a wide range of different tree species and locations. Since absolute values are highly variable, depending on factors such as, e.g., species, tree age or location (McCarroll and Loader, 2004), we refrain from a direct comparison of absolute values and focus on the changes over the course of the century.

20 The second dataset is a compilation of δ<sup>13</sup>C measurements on leaves (Cornwell et al., 2016). The dataset comprises data of C3, C4 as well as CAM plants, however, to ensure comparability between models and observations only data of C3 plants are used.

The observational δ<sup>13</sup>C data are compared with ten-year averages of available model output to remove interannual variability from the model data. For CESM, data are compared to the simulated grid-cell average of the δ<sup>13</sup>C signature of the “live stem”  
25 pool. This pool has a very fast turnover time (0.7/year; Oleson et al., 2013) and no post photosynthetic fractionation occurs in the model during the allocation of assimilated carbon. Modeled δ<sup>13</sup>C in the live stem pool represents thus on average the δ<sup>13</sup>C signature of the leaves of C3 trees. For LPX the δ<sup>13</sup>C signature of daily GPP,  $GPP_{(t,PFT)}$ , is averaged for all tree PFTs within a grid cell and the land use class “mineral soil”. **-GPP is used as a weight:**

$$\delta^{13}\text{C}_{av} = \sum_t \sum_{PFT} \frac{GPP_{(t,PFT)} \times \delta^{13}\text{C}_{(t,PFT)}}{\sum_t \sum_{PFT} GPP_{(t,PFT)}} \quad (12)$$

$t$  is time and the sum is over 10 years.  $PFT$  is the index for PFTs and the sum is over all tree PFTs (without including  
5 grasses).

The evolution of  $\delta^{13}\text{C}$  in (C3) trees is a consequence of both the changes in atmospheric  $\delta^{13}\text{C}$  as well as changes in fractionation, related to changes in  $c_i/c_a$  (Eq. 4) and thus to a combination of physiological adjustments of trees and ecosystems to  $\text{CO}_2$ , climate, and other environmental changes. The atmospheric  $\delta^{13}\text{CO}_2$  record shows a century-scale decrease in  $\delta^{13}\text{C}$  caused by  
10 Suess Effect (e.g., Tans et al., 1979), is a precisely known external forcing. To account for this effect, we focus on the isotopic discrimination  $\Delta_i$  between assimilated plant material and atmospheric  $\text{CO}_2$  (Eq. 5).

Changes in discrimination of C3 plants are related to the ratio of photosynthesis to the conductivity of carbon through the stomata, two relevant tree physiological parameters regulating carbon and water fluxes. The ratio of net daytime photosynthesis to stomatal conductance for water vapor ( $A/g_{\text{H}_2\text{O}}$ ) is also known as iWUE and discussed in the literature (e.g., Scheidegger  
15 et al., 2000; Saurer et al., 2004, 2014). Using Eq. 5 and 6 for CLM4.5 and Eq. 11 for LPX, the definition of iWUE, and a ratio of 1.6 between the conductance of water and  $\text{CO}_2$  we obtain:

$$\text{iWUE} = \frac{A(t)}{g_{\text{H}_2\text{O}}(t)} = c_a(t) \frac{b - \left[ \frac{\delta^{13}c_a(t) - \delta^{13}c_{\text{plant}}(t)}{1 + \frac{\delta^{13}c_{\text{plant}}(t)}{1000}} \right]}{1.6(b - a)} \quad (13)$$

~~We use In the following, the symbol  $\Delta$  is used to denote a temporal change (not to be confused with the symbol for discrimination  $\Delta_i$ ). The change in iWUE For example,  $\Delta\text{iWUE}$ , from time  $t_1$  to is the difference between iWUE at time  $t_2$  is:~~

20  $\Delta\text{iWUE} = \text{iWUE}(t_2) - \text{iWUE}(t_1)$

and time  $t_1$ . We approximate  $\Delta\text{iWUE}$  to better understand how  $\Delta\text{iWUE}$  depends on discrimination, changes in discrimination and atmospheric  $\text{CO}_2$ . The  $\text{CO}_2$  concentration  $c_a(t_2)$  is expressed as the sum of  $c_a(t_1)$  and the change in  $\text{CO}_2$ ,  $\Delta c_a$  in  
equations 13 and 14. Similarly for the difference between the atmospheric and plant  $\delta^{13}\text{C}$  ( $d = \delta^{13}c_a - \delta^{13}c_{\text{plant}}$ ), we write  $d$   
( $t_2$ ) =  $d(t_1) + \Delta d$ . The term  $1 + \frac{\delta^{13}c_{\text{plant}}}{1000}$  is denoted as  $k$ . Variations in  $k$  are of order 1‰ and have a small influence on  $\Delta\text{iWUE}$ .

25 Then, it follows for the difference in iWUE,  $\Delta\text{iWUE}$ :

$$\begin{aligned}\Delta iWUE &\cong + \frac{\Delta c_a \cdot b}{q} - \frac{c_a(t_2)}{q} \cdot \frac{\Delta d}{k(t_2)} - \frac{\Delta c_a}{q} \cdot \frac{d(t_1)}{k(t_2)} \\ &\cong 0.7467 \cdot \Delta c_a - \frac{1}{36.16} \cdot [c_a(t_2) \cdot \Delta \Delta_i + \Delta c_a \cdot \Delta_i(t_1)]\end{aligned}\quad (14)$$

$q$  denotes the term  $1.6(b - a)$  and is with  $b=27$  and  $a=4.4$  equal to 36.16. ~~This approximation~~ The approximation given in Eq. 14 holds well within 0.1%.

Equation 14 shows that  $\Delta iWUE$  is linearly related to the isotopic discrimination at time  $t_1$ ,  $\Delta_i(t_1)$  and the change in discrimination between  $t_1$  and  $t_2$ ,  $\Delta \Delta_i$ . In other words, the change in  $iWUE$  depends both on the change in discrimination as well as on the initial magnitude of the discrimination. The sensitivity in  $\Delta iWUE$  is about 7 times larger for a unit change in  $\Delta \Delta_i$  compared to a unit change in  $\Delta_i(t_1)$  when assuming a change in  $CO_2$  from 300 to 350 ppm as reconstructed for the period 1900 to 1980. Under increasing  $CO_2$ , discrimination and thus  $iWUE$  may change. The larger the decrease in discrimination the larger the increase in  $iWUE$  and vice versa.

The relative change in  $iWUE$  may be expressed, again very accurately, as follows:

$$\frac{\Delta iWUE}{iWUE(t_1)} \simeq \frac{\Delta c_a}{c_a(t_1)} - \frac{c_a(t_2)}{c_a(t_1)} \times \frac{\Delta \Delta_i}{(b - \Delta_i(t_1))} \quad (15)$$

The relative change in  $iWUE$  scales in proportion with the relative change in atmospheric  $CO_2$  in the absence of a change in discrimination. It also scales with changes in discrimination. For typical values, a unit change in discrimination changes the relative change in  $iWUE$  by 50 to 100%. Further, the relative change in  $iWUE$  depends on the difference between ~~between-~~  $b$  ( $=27$ ) and the isotopic discrimination  $\Delta_i(t_1)$  ( $\approx 20$ ). This difference is typically 7 and so a unit change in  $\Delta_i(t_1)$  affects the second term in equation 15 by about 14% and the relative change in  $iWUE$  typically between 0 and 10%. We note that equation 15 is non-linear and so the numerical values given here are illustrative.

~~The equations 13 and 14 are~~ Equation 13 is evaluated for LPX and CESM by using the annual-mean  $\delta^{13}C$  signature of C3 plants for CESM (live stem) and LPX (GPP) within each pixel. We note that in CLM4.5 leaf boundary conductance is also explicitly modeled, and  $g_{H_2O}$  in Eq. 13 reflects thus the ratio of photosynthesis to the total conductivity through the leaf boundary layer and the stomata of water, whereas in LPX  $g_{H_2O}$  reflects the resistance by the stomata only. In CLM4.5, the ratio between the conductivity for  $H_2O$  and  $CO_2$  may vary between 1.4 ( $g_s \gg g_b$ ) to 1.6 ( $g_b \gg g_s$ ) (Eq. 6). Here, we have assumed for simplicity a factor of 1.6 for CLM4.5, LPX and observational data. This simplification introduces an uncertainty of up to 11% in computed trends for CLM4.5.

Turning to the tree-ring data, there are isotopic offsets between assimilated material and cellulose. The leaf-level model for fractionation is more representative for the bulk matter rather than a specific chemical compound such as cellulose. We correct for this isotope offset between cellulose and total organic matter ( $\delta^{13}C_{\text{plant-corrected}} = \delta^{13}C_{\text{plant cellulose}} - \text{offset}$ ) following Saurer

et al. (2014) and using an offset of 1.2‰ for all tree species. This correction has a relatively small influence: as discussed above, a change in  $\delta^{13}\text{C}_{\text{plant}}$  by 1‰ affects the relative change in iWUE by about 10%.

In the following, we will present and discuss annual or multi-annual averages of the related variables  $\delta^{13}\text{C}$ ,  $c_i/c_a$ , discrimination  $\Delta_i$ , iWUE, and  $A/g$ . These values represent, similarly to Eq. 12, weighted-averages. The time-varying carbon assimilation rate, or more generally, the assimilation rate multiplied by the fraction of assimilates allocated to the carbon reservoir under consideration (e.g. leaves, tree ring) act as the weighting factors.

### 3 Results

#### 3.1 Primary productivity and carbon pools

We first compare GPP, [evapotranspiration](#), vegetation and soil carbon stocks of the two models (Tab. 2, Fig. 2), as well as model results to observation-based estimates of vegetation carbon (Fig. 3; Carvalhais et al., 2014). Both models show highest GPP per unit land area in the tropics and low GPP in arid regions. Overall, the GPP patterns are similar between the two models.

5 However, the tropical maxima in GPP are about a third larger in CLM4.5 than in LPX. [Simulated evapotranspiration is similar for the two models.](#)

[Estimates of total vegetation carbon, including below and aboveground biomass, were derived by Carvalhais et al. \(2014\) from a collection of estimates for pan-tropical regions and for northern and temperate forests based on radar remote-sensing retrievals.](#) The global carbon inventory of vegetation is overestimated by a factor of two by CLM4.5 and slightly underestimated by LPX compared to the estimate of Carvalhais et al. (2014) (Tab. 2). CLM4.5 simulates too much vegetation [carbon](#) in northern mid-to-high latitudes and overestimates vegetation carbon [stock](#) by more than a factor of two in tropical forests (Fig. 3) (Negrón-Juárez et al., 2015; Koven et al., 2015a). Correspondingly, we expect a negative bias in the global-mean  $\delta^{13}\text{C}$  signature of vegetation in CLM4.5. LPX simulates vegetation carbon stocks in relatively good agreement with observation-based estimates (Fig. 3). Both models underestimate vegetation carbon in parts of southeastern Asia. Overall, the spatial correlation (r) between modeled and observation-based vegetation carbon is 0.83 for CLM4.5 and 0.85 for LPX.

The global carbon inventory in soils of LPX is 1700 GtC, while CLM4.5 simulates a twice larger soil C inventory of 3900 GtC (Tab. 2). This larger inventory mainly stems from the large carbon stocks simulated by CLM4.5 in peatland and permafrost regions (Koven et al., 2013, 2015b) and in northern mid-latitude regions (Fig. 2). CLM4.5 includes formulation for carbon storage in deep soils. The large soil carbon inventory of CLM4.5 is in contrast to that of its predecessor, CLM4 (Oleson et al., 2010), which severely underestimated the global soil carbon reservoir by 50% and more (Todd-Brown et al., 2013; Anav et al., 2013; Tian et al., 2015), especially at the Northern high latitudes (Foereid et al., 2014). LPX, in the version applied here, does not include formulations for carbon storage below 2 m. An evaluation of peat and permafrost carbon stocks simulated by LPX is provided by Spahni et al. (2013). Data on soil carbon have particularly high uncertainties with notable discrepancies between different data sets (e.g.; Carvalhais et al., 2014; Hugelius et al., 2014).

25 Simulated GPP and carbon stocks change over the industrial period in response to increasing atmospheric  $\text{CO}_2$ , land use, climate change and nitrogen deposition. Both models indicate almost everywhere an increase in GPP over the course of the



20<sup>th</sup> century (Fig. 2). Globally-averaged GPP increases from 148 GtC/yr in 1900 to 168 GtC/yr in 2000 for CLM4.5 and from 132 to 149 GtC for LPX. In the case of CLM4.5 the increase is especially pronounced in the tropics, particularly in Indonesia (Fig. 2), whereas LPX simulates a large increase in GPP in Australia.

30 Simulated 20<sup>th</sup> century changes in annual-mean evapotranspiration are generally small in both models, except in Australia for LPX and in parts of Latin America for CLM4.5. Generally an increase in evapotranspiration is found in boreal and temperate forest regions in both models. Evapotranspiration is slightly decreasing in LPX and slightly increasing in CLM4.5 in most tropical forest regions.

For vegetation carbon, both models show large areas with decreasing C storage in the mid latitudes (Europe, North America) and parts of the tropics, especially South-East Asia, in response to deforestation (Fig 2). Areas with a negative vegetation C balance are more widespread in LPX than CLM4.5 in tropical and subtropical Africa and South America. LPX simulates a relatively small increase in the vegetation stocks of remaining "natural" tropical forests, whereas CLM4.5 shows considerable increase in vegetation C in the remaining tropical forests of Africa, America, and Indonesia. This large increase in CLM4.5 is related to the strong stimulation of GPP and the long overturning time scale of vegetation carbon in tropical forests. As a result, the decrease in globally-integrated vegetation C storage is more than two times larger for LPX than for CLM4.5 (-55 GtC to -21 GtC, Tab. 2, Fig. 1b).

For soil C (Fig. 2), CLM4.5 shows a general increase over the 20<sup>th</sup> century which is especially pronounced in the tropics. For LPX the picture is more heterogeneous, with increases (decreases) in South America, Africa, Australia and the high latitudes (parts of the US and Eurasia, India). Globally, the models simulate an increase of 45 (CLM) and 19 (LPX) GtC, respectively (Tab. 2, Fig. 1). Overall, global carbon storage in the land biosphere increases by 34 GtC in CLM4.5 and decreases by 35 GtC in LPX over the 20<sup>th</sup> century. Independent estimates of the difference between anthropogenic emissions and ocean uptake plus ~~atmospheric growth~~ increase in atmospheric CO<sub>2</sub> suggest an increase in land carbon storage by roughly 20 GtC (Le Quéré et al., 2015) over the 20<sup>th</sup> century.

### 15 3.2 Simulated $\delta^{13}\text{C}$ of primary productivity, vegetation and soil carbon: spatial distributions and 20<sup>th</sup>-century trends

Global maps of the  $\delta^{13}\text{C}$  signature of GPP, vegetation and soil carbon in the year 2000 and related 20<sup>th</sup>-century changes are shown in Fig. 4. We note that isotopic fractionation, typically in the order of 20‰ for C3 plants, is only 4.4‰ for C4 plants, growing in high temperature, high light intensity regions. The grid-cell average  $\delta^{13}\text{C}$  signature of GPP therefore reflects to a large extent the occurrence or absence of C4 plants. Vegetation distribution is prescribed in CLM4.5 and simulated in LPX, CAM plants are not represented in both models. Both models show less negative isotopic signatures in arid and semi-arid low-latitude regions. In comparison to CLM4.5, LPX simulates in the year 2000 much larger areas with  $\delta^{13}\text{C}$  larger than -16‰. These areas include central and western parts of the US, Argentina, large parts of Southern Asia and parts of southern Australia. This is related to a larger share of C4 plants in these regions in LPX than in CLM4.5.

25 Atmospheric  $\delta^{13}\text{C}$  decreases by about 1.3‰ over the 20<sup>th</sup> century (Fig. 1a). Thus, without a change in isotopic discrimination, we would expect an equal decrease in the GPP signature. Accordingly, CLM4.5 and LPX show a decrease in  $\delta^{13}\text{C}$  of GPP in most areas (Fig. 4).

In LPX, large 20<sup>th</sup>-century increases in the  $\delta^{13}\text{C}$  signature of GPP of up to 5‰ are simulated in many low and mid latitude areas indicating an expansion of C4 plants under warming and rising CO<sub>2</sub> as well as the influence of land use. Processes such as the conversion of forests into C4 pastures in the tropics can substantially affect the isotopic signature of total terrestrial vegetation at a location (Townsend et al., 2002; Kaplan et al., 2002). In CLM4.5, the influence of the negative atmospheric  $\delta^{13}\text{C}$  trend is offset mainly by changes in discrimination in the eastern US, Europe and East Asia, resulting in slightly positive  $\delta^{13}\text{C}$  changes in these areas (Fig. 4). Note that, in contrast to LPX, crops are treated as C3 plants in CLM4.5 (Oleson et al., 2013). This explains the land use-related, differing trends between models in regions such as North and South America, Africa and South-East Asia. Distribution and 20<sup>th</sup>-century change in  $\delta^{13}\text{C}$  of vegetation and soil are very similar to the distribution of  $\delta^{13}\text{C}$  of GPP. However, temporal trends are generally smaller in the soil carbon pools than for GPP.

The average  $\delta^{13}\text{C}$  signature of the globally-averaged pool of vegetation carbon is more negative than that of soil and leaf carbon (Fig. 1). This reflects the share of organic matter assimilated by the C4 path versus that by the C3 path in these globally-averaged pools. Generally, the share of C4-derived organic matter is much smaller than the contribution by C3-derived matter. Correspondingly the average  $\delta^{13}\text{C}$  signature of globally-averaged C pools is strongly negative and closer to that of C3 plants. The contribution of C4-derived organic matter is very small for the globally-averaged vegetation pool and absent for the stem carbon pool, but noticeable for the leaf and soil carbon pool. Further, the globally-averaged leaf  $\delta^{13}\text{C}$  signature decreases in both models over the 20<sup>th</sup> century, mainly in response to [changes in the atmospheric  \$\delta^{13}\text{C}\$  forcing source](#). Trends are less developed in the other global pools due to their longer [life-residence](#) times.

There is a substantial offset [of globally-averaged values](#) between the models [for globally-averaged soil and vegetation pools](#), with CLM4.5 being around 65‰ more negative ([Table 2](#)). In addition to the already mentioned widespread, comparably less negative  $\delta^{13}\text{C}$  signatures simulated by LPX, this can be attributed to the spatial distribution of carbon pools in CLM4.5. As is evident from Fig. 3, CLM4.5 simulates higher vegetation and soil carbon stocks in the high latitudes and tropical forest regions than LPX. Since these regions are characterized by C3 plant cover and thus comparably negative signatures (see Fig. 4), the result is a shift of the global averages towards more negative  $\delta^{13}\text{C}$  in CLM4.5 compared to LPX.

### 3.3 Modelled versus measured leaf $\delta^{13}\text{C}$

In this section, we evaluate how well modelled  $\delta^{13}\text{C}$ , and thus isotopic discrimination, of C3 tree species compares with a global compilation of  $\delta^{13}\text{C}$  measurements on leaf material from C3 plants (Cornwell et al., 2016) (Figs 5, 6). Unlike the previous analyses, this comparison is not (or hardly) affected by land use as the comparison is for C3 trees only on unmanaged lands. However, a few caveats apply. We compare grid-cell averages (with GPP or mass as weights; see section 2.4) from all simulated C3 plants with site measurements for individual species. Difference in  $\delta^{13}\text{C}$  are reported for different species. In addition, differences within a species, even growing at the same site, can be as large or even larger as those between species (McCarroll and Loader, 2004; Leuenberger, 2007, and references therein). [Differences in the rooting depth, water transport](#)

25 ~~systems, root-to-leaf distance, leaf morphology, or in irradiance (sunlit versus shadow) affect discrimination.~~ In addition,  $\delta^{13}\text{C}$  in the canopy air may deviate from the prescribed atmospheric  $\delta^{13}\text{C}$ , representative of tropospheric background air. Deviations may arise due to varying additions of isotopically-depleted respired carbon and of carbon from fossil sources to local air.

The ~~bar plots in Fig. 5 and 6 indicate the mean  $\delta^{13}\text{C}$  of the leaf data and of modeled grid-cell averages for C3 plants at the measurement locations for observations, CLM4.5, and LPX, respectively. On average,  $\delta^{13}\text{C}$  of all 344 leaf samples is  $-27.54\text{‰}$  compared to a corresponding average of  $-26.29\text{‰}$  for CLM4.5 and  $-26.14\text{‰}$  for LPX. This suggests a discrimination of  $19.5\text{‰}$ ,  $18.3\text{‰}$  and  $18.1\text{‰}$  relative to the atmospheric  $\delta^{13}\text{C}$  signature of approx.  $-8\text{‰}$ , respectively. According to eq. 4, these values correspond to a ratio between internal and atmospheric partial pressure,  $c_i/c_a$ , of 0.67 for the leaf data and of 0.63 and 0.61 for CLM4.5 and LPX, respectively. The bias of the models is particularly large in arid regions and larger for LPX than for CLM4.5, whereas good agreement between models and leaf data is found in the remaining regions, e.g., Europe or Alaska (Fig. 6).~~

The  $\delta^{13}\text{C}$  of C3 plants from CLM4.5 and LPX show similar spatial gradients. Both models reasonably capture the observations, though spatial correlations between data and models are low (CLM:  $r=0.36$ ; LPX:  $r=0.34$ ). Root-mean-square errors (RMSE) between models and data are  $2.42\text{‰}$  (CLM) and  $3.22\text{‰}$  (LPX). Largest discrimination and most negative  $\delta^{13}\text{C}$  is simulated in high northern latitude regions and in tropical moist forests and lowest discrimination in arid regions of inner Asia, southwestern North America, Patagonia, southern Africa, and parts of Australia. Low discrimination and high (less negative)  $\delta^{13}\text{C}$  correspond to low stomatal conductance, low leaf internal  $\text{CO}_2$  partial pressure and therefore reduced assimilation. However, these high  $\delta^{13}\text{C}$  values are not supported by the leaf measurements, when assuming that the leaf samples are regionally representative (Fig. 6). Maxima in  $\delta^{13}\text{C}$  are a few permil higher for LPX than for CLM4.5 in these regions. This suggests a stronger downregulation of stomatal conductance by water stress in LPX than in CLM4.5 in these regions.

~~The bar plots in Fig. 5 and 6 indicate the mean  $\delta^{13}\text{C}$  of the leaf data and of modeled grid-cell averages for C3 plants at the measurement locations for observations, CLM4.5, and LPX, respectively. On average,  $\delta^{13}\text{C}$  of all 344 leaf samples is  $-27.54\text{‰}$  compared to a corresponding average of  $-26.29\text{‰}$  for CLM4.5 and  $-26.14\text{‰}$  for LPX. This suggests a discrimination of  $19.5\text{‰}$ ,  $18.3\text{‰}$  and  $18.1\text{‰}$  relative to the atmospheric  $\delta^{13}\text{C}$  signature of approx.  $-8\text{‰}$ . According to eq. 4, these values correspond to a ratio between internal and atmospheric partial pressure,  $c_i/c_a$ , of 0.67 for the leaf data and of 0.63 and 0.61 for CLM4.5 and LPX, respectively. As discussed above, the bias of the model is particularly large in arid regions and larger for LPX than for CLM4.5, whereas good agreement between models and leaf data is found in the remaining regions, e.g., Europe or Alaska (Fig. 6).~~

In summary,  $\delta^{13}\text{C}$  and, by implication, discrimination of C3 trees is reasonably represented in both models, when considering the caveats discussed at the beginning of this section and the simplicity of the isotopic model approach. However, both models tend to overestimate  $\delta^{13}\text{C}$  in comparison with the leaf data in many arid regions.

### 3.4 $^{13}\text{C}$ – century-scale trend

Next, simulated century-scale trends in the discrimination,  $\Delta_i$  (Eq. 5, see also methods) of C3 tree species are discussed and compared to the corresponding trends derived from 76 tree-ring  $\delta^{13}\text{C}$  records (Fig. 7 to 10 and Tab. A1). Again grid-cell

25 averages for C3 trees are compared to site data. Similar caveats as discussed for the comparison between leaf measurements and modeled  $\delta^{13}\text{C}$  apply for this trend analysis. The term "average" refers again to an average over those grid cells with measurements only. 74 of the 76 sites are located in three regions (Figs Fig. 9), with more than half of the sites (51) in Europe, and with only seven records in Asia and 16 records in western North America. For these two regions, the comparison of regional model and data averages is therefore hampered by the scarcity of site data and the complex topography along the  
30 Rocky Mountains, while the "global" average is biased towards Europe.

On average, discrimination inferred from the tree-ring records varies within a few tens of a permil in the first and second half of the 20<sup>th</sup> century (Fig. 7). There is a transition to less discrimination in the 1940s, with no clear trend before and afterwards. Similar to the measurements, LPX-Bern yields no long-term trend in the discrimination of C3 trees. In contrast, discrimination of C3 trees simulated by CLM4.5 shows a trend towards smaller values over the 20<sup>th</sup> century. The discrepancy between tree-ring data and CLM4.5 results grows towards the present and is larger than one permil after year 2000.

Next, we analyse spatial and regional changes in the discrimination of C3 trees by comparing the differences in  $\Delta_i$  between the 1980s and 1900s decades. CLM4.5 simulates a decreasing trend in the discrimination  $\Delta_i$  of C3 trees almost everywhere where C3 trees grow. In other words, the ratio of internal to atmospheric  $\text{CO}_2$  partial pressure,  $c_i/c_a$ , decreases over the  
5 20<sup>th</sup> century. The simulated decrease in  $\Delta_i$  for CLM4.5 is larger than suggested by the tree-ring data. The average change in discrimination ((1980-1989)-(1900-1909)) is -0.36 in the tree-ring data and -0.94 in CLM4.5. The observations show on average a slight positive change in  $\Delta_i$  (+0.18) in the North America region and a slight negative change (-0.13) in the Asian region and a relatively large decrease in  $\Delta_i$  in Europe (-0.54) (Fig. 9). The three corresponding regional averages for CLM4.5 are between 0.52 and 0.79 more negative. LPX simulates generally small (positive or negative) changes in  $\Delta_i$  of C3 trees over  
10 the last century. Exceptions are areas at the margin of C3 tree covered regions such as the southern limit of the boreal tree belt that show a large positive change (Fig. 8). For grid-cells with measurements, the average change in  $\Delta_i$  for LPX is with +0.06 very small (Fig. 10). For the three selected regions, LPX simulates changes in  $\Delta_i$  that are between 0.45 to 0.54 more positive than suggested by the tree-ring records (Fig. 9). We note that the agreement between tree-ring data and LPX is better for previous and later decades (Fig. 7).

15 The ~~spatial~~ correlations  $r$  between models and observation-derived changes in  $\Delta_i$  are relatively low, with values of 0.40 (CLM) and 0.27 (LPX). Here, possible explanations are the strong spatial heterogeneity of both measurements and model simulations combined with a limited number of observational data and the overall small changes in discrimination of e.g. only -0.36 for the average of tree-ring data or that the models do not properly represent photosynthesis and stomatal conductance. The RMSEs of changes in  $\Delta_i$  are 0.93 (CLM) and 1.07 (LPX).

20 ~~Factorial runs were performed in addition to the standard simulation (Fig. 8 to 10). Each setup is the same as for the 20<sup>th</sup> century simulations, however with one driving factor held constant: (i) *eCLIM*, constant climate (repeated years 1901-1920 for CLM4.5 and 1901-1930 for LPX). (ii) *eCO<sub>2</sub>*, constant atmospheric  $\text{CO}_2$  concentrations, only done with LPX. (iii) *eNDEP*, constant atmospheric nitrogen deposition, only done with LPX. (iv) *eLU*, constant land use, only done with LPX. The difference between the factorial simulation and standard simulation is attributed to the driving factor that was held constant in the factorial~~

25 ~~run. An interaction term is computed from the difference between the change simulated in the standard simulations and the sum of all attributed changes.~~

The factorial simulations with LPX reveal that average changes in  $\Delta_i$  attributable to individual drivers are small. Thus, the relatively small changes in discrimination simulated by LPX are not the result of offsetting influences of different drivers. In detail, a somewhat complex interaction of the driving factors in shaping the change in  $\Delta_i$  and non-negligible interaction  
30 between climate and CO<sub>2</sub> is found. Keeping nitrogen deposition or land use constant has generally a negligible influence on the change in  $\Delta_i$  (Fig. 9.10). On average, a positive change in  $\Delta_i$  is attributed to the CO<sub>2</sub> change for all sites (+0.03), the European (+0.05) and the Asian sites (+0.09), and a negative change for the North American sites (-0.18). Thus, the increase in CO<sub>2</sub> does not cause a general downregulation of  $c_i/c_a$  in LPX. The influence of climate is small on average over all sites (+0.07) and for the European sites (-0.08). At the North American sites and the few Asian sites climate change tends to increase discrimination by about 0.7 and 0.4, respectively.

For CLM4.5, the change in  $\Delta_i$  attributed to climate change is small, except for the North American sites. There, a positive influence (+0.55) similar as found for LPX is inferred. The other drivers together cause on average a change in discrimination  
5 between -0.79 and -1.16 in the three regions. This suggests that the simulated decrease in discrimination and in  $c_i/c_a$  in the CLM4.5 runs is mainly linked to increasing CO<sub>2</sub> and a corresponding downregulation of  $c_i/c_a$  (Eq. 6). The downregulation in CLM4.5 is larger than suggested by the tree-ring records.

Soil moisture and stomatal conductance are coupled and influence each other and discrimination. 20<sup>th</sup> century changes in soil moisture are small in the factorial simulations where climate is kept constant. For the standard model setup, changes in soil moisture simulated by CLM and LPX are also small in large parts of Europe and Asia, where most of our tree-ring data are located. Despite these small changes in soil moisture, large differences in discrimination changes are found between the two models in these simulations and regions (Fig. 9). This suggests that the primary reason for the model-model difference in simulated 20<sup>th</sup> century changes in discrimination is rooted in the different parameterizations of the photosynthesis-conductance coupling.

### 15 3.5 <sup>13</sup>C – century-scale trend in iWUE

Of particular importance are changes in stomatal conductance and photosynthetic carbon assimilation since they are the primary controls of plant-atmosphere water and CO<sub>2</sub> exchange, carbon assimilation and, ultimately, tree growth (Lambers et al., 2008). Changes in the ratio of these two processes, also termed iWUE (see Eq. 13), thus reflect a change in assimilation, in conductance, or both (Scheidegger et al., 2000; Saurer et al., 2004, 2014).

20 Similar as in the previous sections, we compare relative changes in iWUE (Eq. 15) from the tree-ring records with model results (Figs. 10, 11, 12). Changes are evaluated between the 1990 decade and 1900 decade as in Saurer et al. (2014).

As shown by Eq. 15, the relative change in iWUE increases equal to the relative change in atmospheric CO<sub>2</sub> in the absence of changes in discrimination. This is equal to 23% for the change from (1900-1909) to (1990-1999). A negative change in discrimination, as simulated for CLM4.5, contributes to a further increase in iWUE.

25 In the standard setup (see also maps), both models show a substantial increase in iWUE over the century of approx. 52%  
(CLM) and 25% (LPX). The globally averaged observations iWUE derived from  $\delta^{13}\text{C}$  measurements show a value of 28%,  
which concurs with previous studies reporting increases in iWUE of 27.8% and approx. 30% for European forests (Saurer et al.,  
2014; Frank et al., 2015) and 17% for high latitude forests (Trahan and Schubert, 2016). While LPX is in good agreement with  
30 the available observations (both globally and regionally), CLM4.5 appears to overestimate 20<sup>th</sup>-century changes in iWUE by  
about a factor of two in Europe and the Asian region.

The drivers behind modeled changes in iWUE can be investigated based on the sensitivity experiments already discussed in  
the previous section for discrimination. As expected, all simulations show similar changes in iWUE in LPX. The small changes  
in discrimination simulated by LPX do not strongly affect iWUE and the relative change in iWUE of LPX (24.6%) is close  
to the relative change in atmospheric CO<sub>2</sub> (23%). Simulations with and without climate change with CLM4.5 yield similar  
results, pointing again to a downregulation of  $c_i/c_a$  under raising CO<sub>2</sub> by the implemented nitrogen limitation.

## 4 Discussion

5 This study presents the implementation of  $\delta^{13}\text{C}$  in two global land biosphere models, CLM4.5 and LPX-Bern 1.3 and a global  
compilation of 20<sup>th</sup> century tree ring  $\delta^{13}\text{C}$  records. Results from isotope-enabled simulations over the industrial period are  
investigated for regional carbon stocks and carbon isotope signatures (Figs. 1 to 4) and for the global carbon and  $^{13}\text{C}$  budgets  
(Table 2) of the land biosphere. The performance of the two models in terms of modern isotopic discrimination of C3 plants is  
evaluated by comparing model results with a global compilation of  $\delta^{13}\text{C}$  measurements on leaf material (Figs. 5, 6). The main  
10 focus of the study is on the analysis of 20<sup>th</sup> century changes in isotopic discrimination,  $\Delta_i$ , in the ratio of CO<sub>2</sub> concentrations  
between the stomatal cavity and the atmosphere,  $c_i/c_a$ , and in the ratio between assimilation and stomatal conductance,  $A/g_s$ ,  
termed intrinsic water use efficiency iWUE. The comparison of model results with observational estimates from the  $\delta^{13}\text{C}$  tree  
ring records permits us to evaluate the performance of the two models with respect to linkages between photosynthesis and  
stomatal conductance on the leaf level (Figs. 7 to 12).

15 The "minimal" discrimination model of Farquhar et al. (1989) was implemented in CLM4.5 and LPX-Bern. This model  
assumes fixed discrimination for C4 plants and that discrimination by C3 plants is directly proportional to  $c_i/c_a$ . Genetic  
species-specific variations in  $\delta^{13}\text{C}$  are not considered here, though they can be considerable (Marshall et al., 2008; Yang et al., 2015).  
The influence of rooting depth, water transport systems, root-to-leaf distance, leaf morphology, and irradiance (sunlit versus  
shaded) on discrimination is neglected. However, these factors may affect discrimination. Reported isotopic differences within a  
20 species, even growing at the same site, can be as large or even larger as those between species (McCarroll and Loader, 2004; Leuenberger, 2004).  
We also neglect fractionation between different pools within plants and soils (Wingate et al., 2010; Brüggemann et al., 2011).  
Despite these limitations, we provide a comprehensive framework for a model-data comparison and derive new insights into  
patterns of physiological plant adaptation to 20<sup>th</sup> century environmental changes.

### 4.1 Isotopic signatures, pools and fluxes of the global land biosphere

25 A high spatial correlation of simulated vegetation carbon with observational estimates is found for both models. However, CLM4.5 overestimates carbon stocks in vegetation by a factor of two or more in many regions compared to the data of  
Carvalho et al. (2014), while data-model agreement is reasonable for LPX (Fig. 3). Global soil carbon stock is 1700 GtC  
in LPX and much smaller than the 3900 GtC simulated by CLM4.5. Larger soil carbon inventories in CLM4.5 than LPX are  
mainly simulated in northern mid and high-latitudes (Fig. 2). Only the top two meters of soils are considered in LPX, while  
30 CLM4.5 includes deeper soil layers.

Both models feature most negative  $\delta^{13}\text{C}$  in high latitude and in tropical-forest regions (Fig. 4) and isotopically heavier  
signatures in semi-arid and arid regions, where typically C4 plants are abundant. The global average assimilation-weighted  
 $\delta^{13}\text{C}$  signature of GPP is -20.6‰ in LPX and -24.9‰ in CLM4.5 in the year 2000. The associated discrimination is 12.4‰  
in LPX and 16.7‰ in CLM4.5, respectively. The CLM4.5 estimate is within the range (15.7 to 18.1‰) of previous studies  
as summarized in Suits et al. (2005) and Scholze et al. (2008). This may point to a too large abundance of C4 plants in LPX.  
Differences in soil and vegetation carbon and in C3 and C4 plant abundance affect also the global isotopic budgets of the two  
models as the relative importance of C4-derived plant and soil material is less in CLM4.5 than in LPX. On global average, the  
mean  $\delta^{13}\text{C}$  signature of all land biosphere carbon is 4.6‰ more negative in CLM4.5 than in LPX (Table 2).

5 Turning to 20<sup>th</sup> century changes, both models simulate a wide-spread and strong increase in GPP (Fig. 2), mainly in response  
to CO<sub>2</sub> fertilization under increasing atmospheric CO<sub>2</sub>. On the other hand, 20<sup>th</sup> century changes in evapotranspiration are  
generally small in both models (Fig. 2). The two models bracket independent estimates of the net change in global land  
biosphere carbon stocks over the last century (20 GtC), with CLM4.5 showing slightly larger uptake (35 GtC) and LPX-Bern  
1.3 showing a release of carbon (35 GtC) instead of an uptake.

10 Land use is treated differently in the two models. In CLM4.5, C3 and C4 species are replaced by a C3 crop when land is  
converted to cropland. This results in a negative 20<sup>th</sup>-century change in  $\delta^{13}\text{C}$  of GPP of several permil (grid cell average)  
in tropical and subtropical regions affected by land use (Fig. 4). In contrast, in LPX C3 and C4 crops have identical PFT  
parameters as C3 and C4 grasses and grow under competition on pasture and cropland. Thus, conversion of tropical and  
subtropical forests (C3 trees) to cropland or pasture results in an increase of C4 grasses and a decrease of C3 plants. Correspondingly,  
15 a positive 20<sup>th</sup>-century change in  $\delta^{13}\text{C}$  of up to five permil is simulated in regions undergoing land use changes (Fig. 4). The  
implication is that for atmospheric  $\delta^{13}\text{C}$  budget analyses (Keeling et al., 1989; Ciais et al., 1995; Joos and Bruno, 1998; Scholze et al., 2000)  
the correct crop type (C3 vs C4) should be specified in the models.

#### **4.2 $\delta^{13}\text{C}$ in leaves of C3 plants: modern distribution**

The mean and spatial gradients in discrimination of C3 trees simulated by CLM4.5 and LPX are evaluated using the leaf  $\delta^{13}\text{C}$   
20 data of Cornwell et al. (2016). Both models reasonably represent the observation-based distribution in discrimination of C3  
trees, though modeled discrimination is on average too small compared to the measurements, in particular in arid regions (Figs.  
5, 6). The low discrimination in arid regions may be due to a mismatch in scale between local site conditions and grid-cell  
averages. Potentially, trees at sites with relatively good growing conditions were selected for the  $\delta^{13}\text{C}$  analysis, while modeled  
trees experience grid-cell average soil water conditions.

25 In applications with the predecessor of LPX (Joos et al., 2004; Scholze et al., 2008)  $\delta^{13}\text{C}$  was implemented following Scholze et al. (2008) discrimination modeled following Lloyd and Farquhar (1994). Here, we adjusted the discrimination formulations and use instead the simpler formulations of Farquhar et al. (1989) for consistency with CLM4.5 and with the computation of iWUE from tree-ring  $\delta^{13}\text{C}$  measurements. We note that our conclusions do not depend on this choice. LPX yields similar 20<sup>th</sup>-century changes in discrimination and iWUE for both formulations. However, simulated  $\delta^{13}\text{C}$  of carbon assimilated by C3 trees is generally less negative (by about 2‰) when applying the Lloyd and Farquhar (1994) formulation and agreement with leaf  $\delta^{13}\text{C}$  is less favorable.

The difference between the two implementations arises from additional processes considered in the approach of Lloyd and Farquhar (1994) different parameter choice. Here, fractionations associated with the diffusion of  $\text{CO}_2$  from the stomatal cavity to the cell wall, entrance of  $\text{CO}_2$  in solution at the cell wall, and transport within the cell, as well as photorespiration are neglected. The discriminations by the first three processes are set to be constant in the earlier implementation following Scholze et al. (2003), neglecting a minor temperature dependency associated with the carboxylation by PEP-c (Lloyd and Farquhar, 1994). The discrimination associated with respiration varies with atmospheric  $\text{CO}_2$  and the photocompensation point, but is small. In addition,  $b$ , the discrimination during photosynthetic fixation, is set to 27 in this study and to 27.5 in the earlier implementation.

5 Overall, the consideration of the additional processes and the difference in  $b$  result in an approximately constant offset between the two implementations. This highlights that absolute values of discrimination depend on uncertain model parameters. Agreement or disagreement between leaf and model data (or tree ring and model data) concerning absolute levels of  $\delta^{13}\text{C}$  (Figs. 5, 6) may not be interpreted as an indication of the performance of the conductance/photosynthesis module.

### 4.3 20<sup>th</sup> century changes in carbon isotopes and water use efficiency of C3 plants

10 A set of seventy-six 20<sup>th</sup>-century  $\delta^{13}\text{C}$  tree-ring chronologies, mainly from Europe, boreal Asia and western North America was compiled (Table A1). The  $\delta^{13}\text{C}$  tree-ring data show on average no or little change in isotopic discrimination (Fig. 7). It remains unclear whether there is an overall small decrease in discrimination over the 20<sup>th</sup> century, given the still limited number of records and the large variability of the averaged and individual  $\delta^{13}\text{C}$  records. Small or no changes in discrimination of C3 plants imply that the ratio of  $\text{CO}_2$  partial pressure within the leaf stomatal cavity to that of atmospheric air ( $c_i/c_a$ ) remained roughly unchanged over the 20<sup>th</sup> century. It also implies that the ratio between carbon assimilation by photosynthesis and stomatal conductance ( $A/g$ ), termed intrinsic water use efficiency (iWUE), change in iWUE is approximately equal to the relative change in atmospheric  $\text{CO}_2$  (Eq. 15). This change is about 25% over the 20<sup>th</sup> century and 43% since preindustrial. We recall, however, that isotopic signatures and the related variables ( $c_i/c_a$ ,  $\Delta_i$ , iWUE,  $A/g$ ) as considered here represent weighted annual or multi-annual averages with assimilation (or carbon allocation) as weights that have been weighted by C assimilation or allocation.

Discrimination  $\Delta_i$ ,  $c_i/c_a$ , and iWUE ( $A/g$ ) as well as their changes are closely related. These variables hold, in the framework applied in this study (e.g., Eqs. 4, 5, 13, 15), basically the same information. For iWUE this information is transformed by the known atmospheric  $\text{CO}_2$  evolution. As shown by Eq. 15, iWUE increases in proportion with  $\text{CO}_2$  in the absence of a change in discrimination. A substantial increase in discrimination of more than 2 permil would be required to offset this



25 change. It is therefore no surprise that Silva and Horwath (2013) find an increase in iWUE when using randomized  $\delta^{13}\text{C}$  records in a Monte Carlo analysis instead of actual tree-ring data. Their finding does, however, not invalidate the usefulness of iWUE as a physiological meaningful interpretation of  $\delta^{13}\text{C}$  tree-ring records particularly as many studies have shown that non-randomized  $\delta^{13}\text{C}$  measurements contain well-known environmental signals ranging from the Suess effect to inter-annual to centennial changes in climate.

30 ~~The "minimal" discrimination model of Farquhar et al. (1989) was implemented in CLM4.5 and LPX-Bern. This model assumes fixed discrimination for C4 plants and that discrimination by C3 plants is directly proportional to  $c_i/c_a$ . A more complex model is for example proposed by Lloyd and Farquhar (1994). Genetic species-specific variations in  $\delta^{13}\text{C}$  are not considered here, though they can be considerable (Yang et al., 2015). We also neglect fractionation between different pools within plants and soils (Wingate et al., 2010; Brüggemann et al., 2011).~~

35 We applied the tree-ring  $\delta^{13}\text{C}$  data to test whether the current CLM4.5 and LPX-Bern implementation for  $\delta^{13}\text{C}$ , stomatal conductance, photosynthesis and related  $\text{CO}_2$  fertilization, nitrogen limitation, and water-use efficiency mechanisms are consistent with the tree-ring records. Simulated changes by LPX agree on average excellently with the tree-ring data (Fig. 7). LPX shows little change in the discrimination by C3 trees and the evolution of the average change in iWUE closely matches the tree-ring reconstruction. In contrast to the data, CLM4.5 results show a steadily decreasing trend in discrimination by C3 trees,  
5 roughly in parallel with rising  $\text{CO}_2$  concentrations (Figs. 1, 7). The average decrease in discrimination by C3 trees for the grid cells with data amounts to about 1.5‰ by the end of the simulation and the increase in iWUE is about two times the change indicated by the tree-ring data. The decrease in discrimination corresponds to a decrease in  $c_i/c_a$  (Eq. 4). In other words, the leaf internal partial pressure  $c_i$  is downregulated too strongly in CLM4.5 at least in the regions with tree-ring data.

Factorial simulations demonstrate that these overestimated trends are dominated by the response of CLM4.5 to increasing  
10 atmospheric  $\text{CO}_2$ , and not by the response to changes in climate. Factorial and sensitivity simulations also show that differences in trends between CLM4.5 and LPX are not related to trends in soil moisture nor to (small) differences in the applied climate forcing data. The downregulation in  $c_i/c_a$  in CLM4.5 therefore does not reflect a response to drought or worsening climatic conditions for  $\text{CO}_2$  assimilation. These findings suggest that the main reason for the model-model and model-tree ring data difference in the trends of discrimination and iWUE is rooted in the parameterization of the photosynthesis-conductance  
15 coupling.

It is difficult to trace in complex models such as CLM4.5 origins of data-model mismatch. There are two aspects in the current implementation of photosynthesis and conductance in CLM4.5 that may be problematic (Bonan et al., 2014; Ghimire et al., 2016). First, nitrogen downregulation of photosynthesis and conductance occurs on the sub-hourly model time step, although it is not plausible that leaf structures adjust so quickly. Second, the relationship between assimilation of carbon and  
20 transpiration of water ~~is prescribed, while it is proposed that the physiology of stomata has evolved to optimize carbon gain versus water loss~~ (Ball et al., 1987) is prescribed with time-invariant and globally constant parameters.

~~In CLM4.5, photosynthesis~~ Regarding nitrogen limitation, photosynthesis for isotopic discrimination is downregulated immediately, on the subhourly time step of the model, by limited nitrogen availability in CLM4.5 (Eq. 6). This can lead to a depression of assimilation in the isotope calculation during times of high assimilation. As explained in the method

25 section, photosynthesis of carbon and stomatal conductance for water is computed, unlike for discrimination, without nitrogen limitation. Instead, the allocation of gross primary productivity to carbon pools is downregulated under nitrogen limitation. This downregulation is on annual average generally less than 20% in forested regions and 20<sup>th</sup> century changes in downregulation are generally small (within ±2%) in areas with tree ring data.

Raczka et al. (2016) applied a recalibrated version of CLM4.5 at a single site (Niwot Ridge, US) in simulations with and without nitrogen limitation. These authors show that nitrogen downregulation strongly affects the change in average  $c_i/c_a$  over the 20<sup>th</sup> century. At their site, changes in  $c_i/c_a$  and in discrimination were positive over the industrial period and the century-scale change in discrimination was smaller when nitrogen limitation was not active. The observation-estimated seasonal cycle in discrimination at Niwot Ridge is better reproduced without nitrogen limitation than with limitation. Indeed, Raczka et al. (2016) suggest that downregulation of assimilation and  $c_i/c_a$  by nitrogen limitation (Eq. 6) may be too strong in CLM4.5. Ghimire et al. (2016) implemented an alternative formulation for nitrogen limitation in CLM4.5, where nitrogen availability affects the maximum rate of photosynthesis ( $V_{cmax}$ ) on slow time scales through changes in the leaf carbon-to-nitrogen ratio. This reduces the global bias in GPP, leaf area index, and biomass and improved water-use efficiency predictions compared to the original CLM4.5 formulation.

Another possibility for the model-data mismatch is that the photosynthesis formulation in CLM4.5 may not adequately represent the relationship between stomatal conductance and assimilation. ~~Stomatal conductance  $g$  is related to assimilation,  $A$ , by the following equation~~ and related adjustment processes to long-term environmental changes. CLM4.5 employs the experimentally well-verified and widely-used Ball-Berry equation (Eq. 7) applying globally uniform, time invariant slope parameters,  $m$ , for C3 and C4 plants. Thus, any potential adjustment of  $m$  to changes in environmental conditions, including the century-scale increase in atmospheric  $CO_2$  or changes in water stress are not considered. It is currently unclear whether such adjustment processes occur and the current understanding of the underlying physiological mechanisms of stomatal responses is incomplete (e.g. Miner et al., 2017). The value of  $m$  is set to nine in CLM4.5 ~~↔~~

$$g = m \cdot \frac{R_h}{CO_2} \cdot A + b$$

where  $R_h$  is the relative humidity at the leaf surface,  $b$  a minimal conductance as a function of soil water availability, and for all C3 plants world-wide. This value is within the observational range, but species differences (e.g., evergreen versus deciduous) are neglected by using a single value. The review of Miner et al. (2017) yields mean values for  $m$  a constant parameter, defining the slope between  $A$  and  $g$ . Eq. 7 is of 9.8, 8.7, and 6.8 for angiosperm evergreen, angiosperm deciduous and for gymnosperm trees, respectively (their figure 1). Aranibar et al. (2006) inferred values of  $m$  around 10 to 12 using observed foliar  $^{13}C$  values in pine.

Eqs 7 and 6, defining the photosynthesis-conductance coupling are evaluated on the sub-hourly time step of the model and the variables  $A$ ,  $R_h$  and  $\alpha$ ,  $CO_2$ , and  $f_{dreq}$  vary daily and seasonally, while we investigate here decadal-to-century-scale trends. This hampers a simple interpretation of Eq. 7 the two equations, in particular in terms of expected temporal changes in iWUE and

whether expected century-scale changes in discrimination may be positive or negative. As shown in Fig. 8, simulated changes in discrimination are positive in small areas of South America and Southeast Australia, and thus opposite to the world-wide trend simulated by CLM4.5. Equation 7 implies that annual, assimilation-weighted iWUE ( $iWUE = A/(g-b) = 1/m \cdot CO_2/R_h$ ) is large and discrimination small when the assimilation-weighted ratio of  $CO_2/R_h$  is large. For century-scale trends, this suggests that assimilation is shifted toward times with lower relative humidity when discrimination decreases and the relative increase in iWUE is larger than the relative increase in  $CO_2$ . Such a decrease is simulated in most areas by CLM4.5. As shown in Fig. 8, the opposite situation is found in small areas of South America and Southeast Australia where

Sato et al. (2015) investigated the influence of the use of vapor pressure deficit (VPD) versus relative humidity (RH) in Ball-Berry-type stomatal conductance formulations. About half of the investigated models apply RH as a driving variable (Eq. 7), despite the fact that VPD is considered the more relevant controlling factor. The global warming simulations reveal an increase in VPD and little change in RH. Their results suggest that the increase in VPD under global warming leads to a stronger downregulation of stomatal conductance ( $g_s$ ) and  $c_i/c_a$  for the VPD formulations compared to the RH formulation. This implies that replacing RH by VPD in the Ball-Berry equation in CLM4.5 -simulated may, without further adjustments, even increase the disagreement between modeled and reconstructed changes in discrimination are positive and the relative increase in iWUE smaller than in  $CO_2$  and in iWUE.

Duarte et al. (2016) and Raczka et al. (2016) recalibrated CLM4.5 to match site-specific conditions in a conifer forest in the Northwestern US and at Niwot Ridge, Colorado. These studies find a substantial 20<sup>th</sup>-century increase in discrimination for their site-calibrated versions. One does expect from Eq. 7 that a change in the slope parameter  $m$  will result in a proportional change in the absolute magnitude of iWUE and a corresponding change in discrimination. Duarte et al. (2016) reduced  $m$  by a third in their single site version. In turn, simulated discrimination was altered by about 2.5‰ roughly corresponding to the expected 33% change in iWUE. In addition, the 20<sup>th</sup> century change in isotopic discrimination is reduced. In brief, model structure in CLM4.5 permits both positive and negative changes in discrimination under rising  $CO_2$ , the slope parameter  $m$ , potentially affecting trends in discrimination, is set time invariant and globally uniform for all C3 plants, and the relationship between  $A$  and  $g-g_s$  is assumed to be linear for constant  $CO_2$  and relative humidity.

In LPX, the shape of the relationship between  $g$  and  $A$  is not as tightly prescribed as in CLM4.5. Rather,  $A$  and  $c_i/c_a$  are optimized for given environmental conditions as described in the method section. This optimization leads to small 20<sup>th</sup>-century changes in simulated isotopic discrimination in agreement with the observational evidence. The parameterization used in LPX is for the daily model time step and may not be readily transferred to models with a sub-hourly time step.

This suggests that such an optimization procedure—Alternative conductance-photosynthesis formulations, may be preferable, compared to prescribing a fixed slope parameter linking assimilation and conductance as in the Ball-Berry relation as used in CLM4.5. The Ball-Berry relation is viewed as consistent with an optimization (Cowan and Farquhar, 1977) of stomatal conductance towards maintaining a constant water use efficiency by optimizing carbon gain per unit water loss. However, a number of alternative formulations are found in the literature. These differ in potentially important ways. For example, Medlyn et al. (2011) suggest that the slope parameter increases with increasing temperature; further the inverse of the square root of vapor pressure deficit is used instead of relative humidity in their relationship. Prentice et al. (2014) and

Wang et al. (2016) rely on an optimality hypothesis considering the costs of maintaining both water flow and photosynthetic capacity. These authors use information on the spatial gradients in  $\delta^{13}\text{C}$  from stable isotope measurements on leaf material (Cornwell et al., 2016) to develop their photosynthesis-conductance relation. The slope parameter proposed by Prentice et al. (2014) depends on a number of variables, e.g., the temperature-dependent Michaelis-Menten coefficient for Rubisco-limited photosynthesis, viscosity of water, or the water potential difference between soil and leaf or foliage height. Hence, the slope parameter varies with environmental conditions in this approach. Bonan et al. (2014) implemented different photosynthesis-conductance modules within a CLM4.5 model version featuring a multi-layer canopy and compared results with leaf analyses and eddy covariance fluxes at six forest sites. The continuous soil-plant-atmosphere (SPA) module, optimizing carbon gain per unit water loss and considering hydraulic safety, performs similar or better than the Ball-Berry formulations used in CLM4.5. A better performance is particularly achieved under soil moisture stressed conditions. ~~A new photosynthesis model is proposed by Prentice et al. (2014) and Wang et al. (2016). These authors rely on an evolutionary optimality hypothesis and use information on the spatial gradients in  $\delta^{13}\text{C}$  from stable isotope measurements on leaf material (Cornwell et al., 2016) to develop their model.~~

It is a task for the future to explore whether the implementation of such optimizing modules will lead to a more realistic simulation of the spatio-temporal changes in isotopic discrimination. Taken together, agreement between CLM-modeled and observational trends in discrimination may be improved in the future by adjusting model parameters such as the slope parameter  $m$ , replacing formulations for nitrogen limitation, e.g. following Ghimire et al. (2016), and by implementing photosynthesis photosynthesis-conductance routines that adhere to an optimization principle as proposed by Bonan et al. (2014) in the literature (Bonan et al., 2014; Prentice et al., 2014).

#### 4.4 Consistency with previous studies

The small changes in discrimination, an increase in iWUE proportional to the atmospheric  $\text{CO}_2$  increase, and approximately constant  $c_i/c_a$  over the 20<sup>th</sup> century as reconstructed by our tree-ring compilation and simulated by LPX-Bern is consistent with most, but not all studies. As reported by Voelker et al. (2016), studies that are consistent with the notion of constant  $c_i/c_a$  include work by Wong et al. (1979); Saurer et al. (2004); Ward et al. (2005); Bonal et al. (2011); Franks et al. (2013) early work by Wong et al. (1979) measuring  $A$  and  $g$  of leaves in a chamber, and a range of tree ring  $\delta^{13}\text{C}$  studies (Saurer et al., 2004; Ward et al., 2005) as well as a meta-analysis of FACE experiments (Ainsworth and Long, 2005). The European  $\delta^{13}\text{C}$  tree-ring records analyzed by Frank et al. (2015) and Saurer et al. (2014) also point to a moderate control towards a constant  $c_i/c_a$  ratio. Leonardi et al. (2012) conclude that the temporal variation in  $\delta^{13}\text{C}$  in their long-term isotope tree-ring chronologies for 53 sites worldwide supports the hypothesis of an active plant mechanism that maintains a constant ratio between intercellular and ambient  $\text{CO}_2$  concentrations. Lévesque et al. (2014) reported, from their  $\delta^{13}\text{C}$  tree ring data, an increase in iWUE over the last 50 yr in the range of 8 to 29% for xeric and mesic sites in the Alps and Switzerland. At their sites, drought-induced stomatal closure has reduced transpiration at the cost of reduced carbon uptake and growth. Churakova (Sidorova) et al. (2016a) report different iWUE strategies with almost constant  $c_i/c_a$  for European larch since the 1990s and continuously increasing iWUE for mountain pine trees since the 1980s in the Swiss National Park. Liu et al. (2014a) find moderate changes in  $c_i/c_a$  and an increase in iWUE by 36% in

a riparian forest in Northwestern China from 1920 to 2012. Similarly, Peñuelas et al. (2011), analyzing changes in tree ring  $\delta^{13}\text{C}$  and growth at 47 sites worldwide, inferred little change in discrimination,  $c_i/c_a$ , and an increase in iWUE of 20.5% from 1960 to 2000. 18 of the 35 studies with growth data show an increase in growth with time, while the others show no or negative growth changes. Voelker et al. (2016) analyzed studies of  $\delta^{13}\text{C}$  and photosynthetic discrimination in woody angiosperms and  
30 gymnosperms that grew across a range of  $\text{CO}_2$  spanning at least 100 ppm and combining paleo data, tree-ring records, and FACE-type experiments. They conclude that woody plants respond to increasing  $\text{CO}_2$  by regulating leaf gas-exchange along a continuum of  $c_a - c_i$  and  $c_i/c_a$  that minimizes water loss for a given amount of C gain and therefore increasingly minimizes the likelihood of exposure to drought stress. Summarizing five years of results from the Basel FACE experiment, Klein et al. (2016) find that iWUE increased in their experiment by 38% at the needle level, as a result of higher assimilation at constant conduc-  
5 tance. Interestingly, Klein et al. (2016) could not identify an increase in plant carbon stocks corresponding to the increase in assimilation and the fate of the additionally assimilated carbon remains unclear. The 38% increase in iWUE is comparable to the increase from ambient (400 ppm) to elevated (550 ppm) and in line with observations reported by De Kauwe et al. (2013) as well as a meta-analysis of FACE experiments (Ainsworth and Long, 2005). Streit et al. (2014) measured needle gas exchange and analyzed  $\delta^{13}\text{C}$  of needles and tree rings of *Larix decidua* and *Pinus mugo* after nine years of free air  $\text{CO}_2$  enrichment. Both species showed an increase in net photosynthesis and, in agreement with Keel et al. (2006), small or no changes in conductance under elevated  $\text{CO}_2$  and a change in iWUE roughly in proportion to the increase in  $\text{CO}_2$ . Elevated  $\text{CO}_2$  induced increased basal area growth in *L. decidua*, but not in *P. mugo*. Neither nitrogen limitation, nor end-product limitation, and, in  
10 agreement with other FACE studies (Bader et al., 2010; Liberloo et al., 2007), no downregulation of maximal photosynthetic rate was found.

In contrast, Battipaglia et al. (2013) report an increase in iWUE between 50 and 90% for the ORNL, DUKE, and POP-EUROFACE Face sites and that  $c_i$  was likely maintained constant and  $^{13}\text{C}$  discrimination reduced under elevated  $\text{CO}_2$ . A scenario of constant  $c_i$  under increasing  $\text{CO}_2$  concentrations is also suggested by Keenan et al. (2013) who report a strong  
15 increase in water-use efficiency summarizing results from eddy-covariance measurements at about 20 temperate and boreal forest sites in the Northern Hemisphere.

~~The mean and spatial gradients in discrimination of C3 trees simulated by CLM4.5 and LPX are evaluated using the leaf  $\delta^{13}\text{C}$  data of Cornwell et al. (2016). Both models reasonably represent the observation-based distribution in discrimination of C3 trees, though modeled discrimination is on average too small compared to the measurements, in particular in arid regions. The  
20 low discrimination in arid regions may be due to a mismatch in scale between local site conditions and grid-cell averages. Potentially, trees at sites with relatively good growing conditions were selected for the  $\delta^{13}\text{C}$  analysis, while modeled trees experience grid-cell average soil water conditions.~~

~~The global average assimilation-weighted  $\delta^{13}\text{C}$  signature of GPP is  $-20.6\text{‰}$  in LPX and  $-24.9\text{‰}$  in CLM4.5 in the year 2000. The associated discrimination is  $12.4\text{‰}$  in LPX and  $16.7\text{‰}$  in CLM4.5, respectively. However, these studies may be affected by  
25 local conditions not representative for larger scales and be influenced by temporal sampling biases as the record length of FACE and eddy-covariance measurements is limited. Indeed, the individual tree-ring records in Figure 7 show considerable site-to-site variability as well as decadal variability. In addition, factors other than  $c_i/c_a$ , e.g. vapor pressure deficit, may influence trends~~

at eddy covariance sites (Knauer et al., 2017). The CLM4.5 estimate is within the range (15.7 to 18.1‰) of previous studies as summarized in Suits et al. (2005); Scholze et al. (2008). This may point to a too large abundance of C4 plants in LPX.

30 suggestion of a constant  $c_i$  under increasing CO<sub>2</sub> is challenged by Knauer et al. (2017). These authors find that the ecosystem trends reported by Keenan et al. (2013) and a scenario of a constant  $c_i$ , as also suggested by Battipaglia et al. (2013), are in conflict with observed large-scale trends in continental discharge, evapotranspiration, and the seasonal CO<sub>2</sub> exchange. Rather, the comparison of observational data and model outcome by Knauer et al. (2017) support the finding of a physiological regulation towards a constant  $c_i/c_a$  under rising atmospheric CO<sub>2</sub>.

Land use is treated differently in the two models investigated herein. In CLM4.5, C3 and C4 species are replaced by a C3 crop when land is converted to cropland. This results in a negative

## 5 5 Conclusions

We compiled 20<sup>th</sup> -century change in century  $\delta^{13}\text{C}$  of GPP of several permit (grid-cell average) in tropical and subtropical regions affected by land use. In contrast, in LPX C3 and C4 crops have identical PFT parameters as C3 and C4 grasses and grow under competition on pasture and cropland. Thus, conversion of tropical and subtropical forests (C3 trees) to cropland or pasture results in an increase of C4 grasses and a decrease of tree ring records for seventy-three sites (Table 1). The records are used to reconstruct changes in the ratio of CO<sub>2</sub> concentration within the stomatal cavity of C3 plants. Correspondingly, a positive trees and the atmosphere,  $c_i/c_a$ , and to reconstruct changes in the intrinsic water use efficiency, iWUE, denoting the ratio of photosynthesis to conductance (A/g). The implementation of <sup>13</sup>C and isotopic discrimination during photosynthesis in the Community Land Model (CLM4.5) and in the LPX-Bern (version 1.3) is documented. Results from isotope-enabled simulations compared to the tree ring reconstructions as well as to a published compilation of  $\delta^{13}\text{C}$  of leaf material. The tree-ring results suggest, on average, constant  $c_i/c_a$  over the 20<sup>th</sup> -century change in  $\delta^{13}\text{C}$  of up to five permil is simulated in regions undergoing land use changes. The implication is that for atmospheric  $\delta^{13}\text{C}$  budget analyses, the correct crop type (C3 vs C4) should be specified in the models.

century and iWUE to have increased in proportion with atmospheric CO<sub>2</sub>. The simulated changes in discrimination,  $c_i/c_a$ , and iWUE are consistent with the reconstructions for LPX-Bern 1.3, whereas CLM4.5 shows larger trends and overestimates 20<sup>th</sup> century changes in iWUE by almost a factor of two (Fig. 7). This suggest that it is desirable to adjust the implementation of photosynthesis and conductance in CLM4.5 towards a better agreement with observation-derived century-scale trends in <sup>13</sup>C discrimination and intrinsic water-use efficiency. In conclusion, this study demonstrates that existing information on the magnitude and trends of stable carbon isotopes permits the evaluation of global land carbon cycle models. In particular,  $\delta^{13}\text{C}$  data provide insight on the fundamental relationship between carbon assimilation and stomatal conductance controlling the flow of CO<sub>2</sub> and water. Tree ring records are useful as they cover retrospectively decadal-to-century time scales not accessible by laboratory or field experiments and the relevant instrumental records, but a time scale that is directly relevant for the response of plants to the decadal-to-century-scale rise in CO<sub>2</sub> and to global warming. The results suggest constant  $c_i/c_a$  over the 20<sup>th</sup> century and may be interpreted as supportive of a plant strategy towards optimizing assimilation and minimizing water loss

~~under changing environmental conditions. The results suggest that it is desirable to adjust the implementation of photosynthesis and conductance in CLM4.5 towards a better agreement with observation-derived century-scale trends in  $^{13}\text{C}$  discrimination and intrinsic water-use efficiency.~~

*Acknowledgements.* We thank B. Otto-Bliesner and E. Brady for supporting this and the work of the CESM isotope group and for hosting FJ during visits at NCAR. We thank A. Ballantyne and an anonymous reviewer for constructive comments. The research leading to these results was supported through Swiss National Science Foundation (SNF) projects 200020\_147174, 20020\_159563, and CRSII3\_136295 (Sinergia Project iTREE). OVC acknowledges support by Marie Curie IIF (EU-ISOTREC 235122), the Marie Heim-Vögtlin Program (MHV PMPDP2\_145507), and Era.Net RUSplus project ELVECS (SNF project number: IZRPZ0\_164735). WJR and CDK were supported by the Director, Office of Science, Office of Biological and Environmental Research of the US Department of Energy under Contract No. DE-AC02-05CH11231 as part of their Regional and Global Climate Modeling program. Simulations with CLM4.5 were carried out at the Swiss National Supercomputing Centre in Lugano, Switzerland.

## References

- Ainsworth, E. A. and Long, S. P.: What have we learned from 15 years of free-air CO<sub>2</sub> enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO<sub>2</sub>, *New Phytologist*, 165, 351–372, doi:10.1111/j.1469-8137.2004.01224.x, 2005.
- Anav, A., Friedlingstein, P., Kidston, M., Bopp, L., Ciais, P., Cox, P., Jones, C., Jung, M., Myneni, R., and Zhu, Z.: Evaluating the land and ocean components of the global carbon cycle in the CMIP5 Earth System Models, *Journal of Climate*, 26, 6801–6843, 2013.
- Aranibar, J. N., Berry, J. A., Riley, W. J., Pataki, D. E., Law, B. E., and Ehleringer, J. R.: Combining meteorology, eddy fluxes, isotope measurements, and modeling to understand environmental controls of carbon isotope discrimination at the canopy scale, *Global Change Biology*, 12, 710–730, doi:10.1111/j.1365-2486.2006.01121.x, 2006.
- Bader, M. K.-F., Siegwolf, R., and Körner, C.: Sustained enhancement of photosynthesis in mature deciduous forest trees after 8 years of free air CO<sub>2</sub> enrichment, *Planta*, 232, 1115–1125, doi:10.1007/s00425-010-1240-8, <http://dx.doi.org/10.1007/s00425-010-1240-8>, 2010.
- Bale, R. J., Robertson, I., Salzer, M. W., Loader, N. J., Leavitt, S. W., Gagen, M., Harlan, T. P., and McCarroll, D.: An annually resolved bristlecone pine carbon isotope chronology for the last millennium, *Quaternary Research*, 76, 22 – 29, doi:10.1016/j.yqres.2011.05.004, 2011.
- Ball, J. T., Woodrow, I. E., , and Berry, J. A.: A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions, in: *Progress in Photosynthesis Research*. Vol. 4. Proceedings of the 7th International Congress on Photosynthesis, p. 221–224, Nijhoff Publishers, Dordrecht, The Netherlands, 1987.
- Ballantyne, A. P., Baker, P. A., Chambers, J. Q., Villalba, R., and Argollo, J.: Regional differences in South American monsoon precipitation inferred from the growth and isotopic composition of tropical trees, *Earth Interactions*, 15, 1–35, doi:10.1175/2010EI277.1, 2011.
- Battipaglia, G., Saurer, M., Cherubini, P., Calfapietra, C., McCarthy, H. R., Norby, R. J., and Francesca Cotrufo, M.: Elevated CO<sub>2</sub> increases tree-level intrinsic water use efficiency: insights from carbon and oxygen isotope analyses in tree rings across three forest FACE sites, *New Phytologist*, 197, 544–554, doi:10.1111/nph.12044, 2013.
- Bauska, T. K., Joos, F., Mix, A. C., Roth, R., Ahn, J., and Brook, E. J.: Links between atmospheric carbon dioxide, the land carbon reservoir and climate over the past millennium, *Nature Geoscience*, 8, 383–387, 2015.
- Becker, M., Andersen, N., Erlenkeuser, H., Humphreys, M. P., Tanhua, T., and Körtzinger, A.: An internally consistent dataset of  $\delta^{13}\text{C}$ -DIC in the North Atlantic Ocean – NAC13v1, *Earth System Science Data*, 8, 559–570, doi:10.5194/essd-8-559-2016, 2016.
- Bonal, D., Ponton, S., Le Thiec, D., Richard, B., Ningre, N., Hérault, B., Ogée, J., Gonzalez, S., Pignatelli, M., Sabatier, D., and Guehl, J.-M.: Leaf functional response to increasing atmospheric CO<sub>2</sub> concentrations over the last century in two northern Amazonian tree species: a historical  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  approach using herbarium samples, *Plant, Cell & Environment*, 34, 1332–1344, 2011.
- Bonan, G. B., Williams, M., Fisher, R. A., and Oleson, K. W.: Modeling stomatal conductance in the earth system: linking leaf water-use efficiency and water transport along the soil–plant–atmosphere continuum, *Geoscientific Model Development*, 7, 2193–2222, doi:10.5194/gmd-7-2193-2014, 2014.
- Bowling, D. R., Ballantyne, A. P., Miller, J. B., Burns, S. P., Conway, T. J., Menzer, O., Stephens, B. B., and Vaughn, B. H.: Ecological processes dominate the  $^{13}\text{C}$  land disequilibrium in a Rocky Mountain subalpine forest, *Global Biogeochemical Cycles*, 28, 352–370, doi:10.1002/2013GB004686, 2014.
- Brüggemann, N., Gessler, A., Kayler, Z., Keel, S. G., Badeck, F., Barthel, M., Boeckx, P., Buchmann, N., Brugnoli, E., Esperschütz, J., Gavrichkova, O., Ghashghaie, J., Gomez-Casanovas, N., Keitel, C., Knohl, A., Kuptz, D., Palacio, S., Salmon, Y., Uchida, Y., and



- Bahn, M.: Carbon allocation and carbon isotope fluxes in the plant-soil-atmosphere continuum: a review, *Biogeosciences*, 8, 3457–3489, doi:10.5194/bg-8-3457-2011, 2011.
- Carvalhais, N., Forkel, M., Khomik, M., Bellarby, J., Jung, M., Migliavacca, M., Mu, M., Saatchi, S., Santoro, M., Thurner, M., Weber, U., Ahrens, B., Beer, C., Cescatti, A., Randerson, J. T., and Reichstein, M.: Global covariation of carbon turnover times with climate in terrestrial ecosystems, *Nature*, 514, 213–217, doi:10.1038/nature13731, 2014.
- Churakova (Sidorova), O. V., Eugster, W., Zielis, S., Cherubini, P., Etzold, S., Saurer, M., Siegwolf, R., and Buchmann, N.: Increasing relevance of spring temperatures for Norway spruce trees in Davos, Switzerland, after the 1950s, *Trees*, 28, 183–191, doi:10.1007/s00468-013-0941-6, 2014.
- Churakova (Sidorova), O. V., Saurer, M., Bryukhanova, M. V., Siegwolf, R. T., and Bigler, C.: Site-specific water-use strategies of mountain pine and larch to cope with recent climate change, *Tree Physiology*, 36, 942–953, doi:10.1093/treephys/tpw060, 2016a.
- Churakova (Sidorova), O. V., Shashkin, A. V., Siegwolf, R. T., Spahni, R., Launois, T., Saurer, M., Bryukhanova, M. V., Benkova, A. V., Kuptsova, A. V., Peylin, P., Vaganov, E. A., Masson-Delmotte, V., and Roden, J.: Application of eco-physiological models to the climatic interpretation of  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  measured in Siberian larch tree-rings, *Dendrochronologia*, 39, 51–59, 2016b.
- Ciais, P., Tans, P. P., White, J. W. C., Trolier, M., Francey, R. J., Berry, J. A., Randall, D. R., Sellers, P. J., Collatz, J. G., and Schimel, D. S.: Partitioning of ocean and land uptake of  $\text{CO}_2$  as inferred by  $\delta^{13}\text{C}$  measurements from the NOAA Climate Monitoring and Diagnostics Laboratory Global Air Sampling Network, *Journal of Geophysical Research: Atmospheres*, 100, 5051–5070, doi:10.1029/94JD02847, 1995.
- Ciais, P., Tagliabue, A., Cuntz, M., Bopp, L., Scholze, M., Hoffmann, G., Laurantou, A., Harrison, S. P., Prentice, I. C., Kelley, D. I., Koven, C., and Piao, S. L.: Large inert carbon pool in the terrestrial biosphere during the Last Glacial Maximum, *Nature Geoscience*, 5, 74–79, doi:10.1038/ngeo1324, 2012.
- Ciais, P., Sabine, C., Bala, G., Bopp, L., Brovkin, V., Canadell, J., Chhabra, A., DeFries, R., Galloway, J., Heimann, M., Jones, C., Quéré, C. L., Myneni, R., Piao, S., and Thornton, P.: Carbon and other biogeochemical cycles, in: *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Stocker, T.F., Qin, G.-K., Plattner, M., Tignor, S.K., Allen, J., Boschung, A., Nauels, Y., Xia, V., Bex, and P.M. Midgley (eds.)], Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA., 2013.
- Collatz, G., Ball, J., Grivet, C., and Berry, J. A.: Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: a model that includes a laminar boundary layer, *Agricultural and Forest Meteorology*, 54, 107–136, 1991.
- Collatz, G., Ribas-Carbo, M., and Berry, J.: Coupled photosynthesis-stomatal conductance model for leaves of  $\text{C}_4$  plants, *Australian Journal of Plant Physiology*, 19, 519–538, 1992.
- Cornwell, W., Wright, I., Turner, J., Maire, V., Barbour, M., Cernusak, L., Dawson, T., Ellsworth, D., Farquhar, G., Griffiths, H., Keitel, C., Knohl, A., Reich, P., Williams, D., Bhaskar, R., Cornelissen, J., Richards, A., Schmidt, S., Valladares, F., Körner, C., Schulze, E., Buchmann, N., and Santiago, L.: A global dataset of leaf  $\Delta^{13}\text{C}$  values, *Dryad Digital Repository*, doi:10.5061/dryad.3jh61, 2016.
- Cowan, I. R. and Farquhar, G.: Stomatal function in relation to leaf metabolism and environment, in: *Integration of Activity in the Higher Plant*, edited by Jennings, D. H., pp. 471–505, Cambridge University Press, Cambridge, 1977.
- Danis, P.-A., Hatté, L., Misson, L., and Guiot, J.: MAIDENiso: a multiproxy biophysical model of tree-ring width and oxygen and carbon isotopes, *Canadian Journal of Forest Research*, 42, 1697–1713, doi:10.1139/x2012-089, 2012.
- De Kauwe, M. G., Medlyn, B. E., Zaehle, S., Walker, A. P., Dietze, M. C., Hickler, T., Jain, A. K., Luo, Y., Parton, W. J., Prentice, I. C., Smith, B., Thornton, P. E., Wang, S., Wang, Y.-P., Wårlind, D., Weng, E., Crous, K. Y., Ellsworth, D. S., Hanson, P. J., Kim, H.-S., Warren, J. M.,

- Oren, R., and Norby, R. J.: Forest water use and water use efficiency at elevated CO<sub>2</sub>: a model-data intercomparison at two contrasting temperate forest FACE sites, *Global Change Biology*, 19, 1759–1779, doi:10.1111/gcb.12164, 2013.
- Duarte, H. F., Raczka, B. M., Ricciuto, D. M., Lin, J. C., Koven, C. D., Thornton, P. E., Bowling, D. R., Lai, C.-T., Bible, K. J., and Ehleringer, J. R.: Evaluating the Community Land Model (CLM 4.5) at a coniferous forest site in Northwestern United States using flux and carbon-isotope measurements, *Biogeosciences Discussions*, 2016, 1–35, doi:10.5194/bg-2016-441, 2016.
- Edwards, T. W., Birks, S. J., Luckman, B. H., and MacDonald, G. M.: Climatic and hydrologic variability during the past millennium in the eastern Rocky Mountains and northern Great Plains of western Canada, *Quaternary Research*, 70, 188–197, 2008.
- Eggleston, S., Schmitt, J., Bereiter, B., Schneider, R., and Fischer, H.: Evolution of the stable carbon isotope composition of atmospheric CO<sub>2</sub> over the last glacial cycle, *Paleoceanography*, 31, 434–452, doi:10.1002/2015PA002874, 2016.
- Etheridge, D. M., Steele, L. P., Langenfelds, R. L., Francey, R. J., Barnola, J.-M., and Morgan, V. I.: Natural and anthropogenic changes in atmospheric CO<sub>2</sub> over the last 1000 years from air in Antarctic ice and firn, *J. Geophys. Res.*, 101, 4115–4128, doi:10.1029/95JD03410, 1996.
- Farquhar, G., O’Leary, M., and Berry, J.: On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves, *Functional Plant Biology*, 9, 121–137, 1982.
- Farquhar, G. D., von Caemmerer, S., and Berry, J. A.: A biochemical model of photosynthetic CO<sub>2</sub> assimilation in leaves of C<sub>3</sub> species, *Planta*, 149, 78–90, doi:10.1007/BF00386231, 1980.
- Farquhar, G. D., Ehleringer, J. R., and Hubick, K. T.: Carbon isotope discrimination and photosynthesis, *Annual Review of Plant Physiology and Plant Molecular Biology*, 40, 503–537, doi:10.1146/annurev.pp.40.060189.002443, 1989.
- Fichtler, E., Helle, G., and Worbes, M.: Stable-carbon isotope time series from tropical tree rings indicate a precipitation signal, *Tree-Ring Research*, 66, 35–49, doi:10.3959/2008-20.1, 2010.
- Foereid, B., Ward, D. S., Mahowald, N., Paterson, E., and Lehmann, J.: The sensitivity of carbon turnover in the Community Land Model to modified assumptions about soil processes, *Earth System Dynamics*, 5, 211–221, 2014.
- Francey, R. J., Allison, C. E., Etheridge, D. M., Trudinger, C. M., Enting, I. G., Leuenberger, M., Langenfelds, R. L., Michel, E., and Steele, L. P.: A 1000-year high precision record of δ<sup>13</sup>C in atmospheric CO<sub>2</sub>, *Tellus B*, 51, 170–193, doi:10.1034/j.1600-0889.1999.t01-1-00005.x, 1999.
- Frank, D. C., Poulter, B., Saurer, M., Esper, J., Huntingford, C., Helle, G., Treydte, K., Zimmermann, N. E., Schleser, G. H., Ahlstrom, A., Ciais, P., Friedlingstein, P., Levis, S., Lomas, M., Sitch, S., Viovy, N., Andreu-Hayles, L., Bednarz, Z., Berninger, F., Boettger, T., D’Alessandro, C. M., Daux, V., Filot, M., Grabner, M., Gutierrez, E., Haupt, M., Hiltunen, E., Jungner, H., Kalela-Brundin, M., Krapiec, M., Leuenberger, M., Loader, N. J., Marah, H., Masson-Delmotte, V., Pazdur, A., Pawelczyk, S., Pierre, M., Planells, O., Pukiene, R., Reynolds-Henne, C. E., Rinne, K. T., Saracino, A., Sonninen, E., Stievenard, M., Switsur, V. R., Szczepanek, M., Szychowska-Krapiec, E., Todaro, L., Waterhouse, J. S., and Weigl, M.: Water-use efficiency and transpiration across European forests during the Anthropocene, *Nature Climate Change*, 5, 579–583, 2015.
- Franks, P. J., Adams, M. A., Amthor, J. S., Barbour, M. M., Berry, J. A., Ellsworth, D. S., Farquhar, G. D., Ghannoum, O., Lloyd, J., McDowell, N., Norby, R. J., Tissue, D. T., and von Caemmerer, S.: Sensitivity of plants to changing atmospheric CO<sub>2</sub> concentration: from the geological past to the next century, *New Phytologist*, 197, 1077–1094, 2013.
- Gagen, M., Zorita, E., McCarroll, D., Young, G. H. F., Grudd, H., Jalkanen, R., Loader, N. J., Robertson, I., and Kirchhefer, A.: Cloud response to summer temperatures in Fennoscandia over the last thousand years, *Geophysical Research Letters*, 38, doi:10.1029/2010GL046216, 2011.

- Gerber, S., Joos, F., and Prentice, I.: Sensitivity of a dynamic global vegetation model to climate and atmospheric CO<sub>2</sub>, *Global Change Biology*, 10, 1223–1239, 2004.
- Gerten, D., Schaphoff, S., Haberlandt, U., Lucht, W., and Sitch, S.: Terrestrial vegetation and water balance – hydrological evaluation of a dynamic global vegetation model, *Journal of Hydrology*, 286, 249–270, 2004.
- 5 Ghimire, B., Riley, W. J., Koven, C. D., Mu, M., and Randerson, J. T.: Representing leaf and root physiological traits in CLM improves global carbon and nitrogen cycling predictions, *Journal of Advances in Modeling Earth Systems*, 8, 598–613, doi:10.1002/2015MS000538, 2016.
- Gobron, N., Pinty, B., Ausedat, O., Chen, J. M., Cohen, W. B., Fensholt, R., Gond, V., Huemmrich, K. F., Lavergne, T., Méline, F., Privette, J. L., Sandholt, I., Taberner, M., Turner, D. P., Verstraete, M. M., and Widlowski, J.-L.: Evaluation of fraction of absorbed photosynthetically active radiation products for different canopy radiation transfer regimes: Methodology and results using Joint Research Center products derived from SeaWiFS against ground-based estimations, *Journal of Geophysical Research: Atmospheres*, 111, doi:10.1029/2005JD006511, 2006.
- 10 Graven, H. D., Gruber, N., Key, R., Khatiwala, S., and Giraud, X.: Changing controls on oceanic radiocarbon: New insights on shallow-to-deep ocean exchange and anthropogenic CO<sub>2</sub> uptake, *Journal of Geophysical Research: Oceans*, 117, doi:10.1029/2012JC008074, 2012.
- 15 Gruber, N., Keeling, C. D., Bacastow, R. B., Guenther, P. R., Lueker, T. J., Wahlen, M., Meijer, H. A. J., Mook, W. G., and Stocker, T. F.: Spatiotemporal patterns of carbon-13 in the global surface oceans and the oceanic suess effect, *Global Biogeochemical Cycles*, 13, 307–335, doi:10.1029/1999GB900019, 1999.
- Harris, I., Jones, P., Osborn, T., and Lister, D.: Updated high-resolution grids of monthly climatic observations – the CRU TS3.10 Dataset, *International Journal of Climatology*, 34, 623–642, doi:10.1002/joc.3711, 2014.
- 20 Hartl-Meier, C., Zang, C., Büntgen, U., Esper, J., Rothe, A., Göttelein, A., Dirnböck, T., and Treyde, K.: Uniform climate sensitivity in tree-ring stable isotopes across species and sites in a mid-latitude temperate forest, *Tree Physiology*, 35, 4–15, doi:10.1093/treephys/tpu096, 2015.
- Haxeltine, A. and Prentice, I. C.: A general model for the light-use efficiency of primary production, *Functional Ecology*, 10, 551–561, 1996a.
- 25 Haxeltine, A. and Prentice, I. C.: BIOME3: An equilibrium terrestrial biosphere model based on ecophysiological constraints, resource availability, and competition among plant functional types, *Global Biogeochemical Cycles*, 10, 693–709, doi:10.1029/96GB02344, <http://dx.doi.org/10.1029/96GB02344>, 1996b.
- Heimann, M. and Maier-Reimer, E.: On the relations between the oceanic uptake of CO<sub>2</sub> and its carbon isotopes, *Global Biogeochemical Cycles*, 10, 89–110, doi:10.1029/95GB03191, 1996.
- 30 Holden, P. B., Edwards, N. R., Müller, S. A., Oliver, K. I. C., Death, R. M., and Ridgwell, A.: Controls on the spatial distribution of oceanic  $\delta^{13}\text{C}_{DIC}$ , *Biogeosciences*, 10, 1815–1833, doi:10.5194/bg-10-1815-2013, 2013.
- Hugelius, G., Strauss, J., Zubrzycki, S., Harden, J. W., Schuur, E. A. G., Ping, C.-L., Schirmermeister, L., Grosse, G., Michaelson, G. J., Koven, C. D., O'Donnell, J. A., Elberling, B., Mishra, U., Camill, P., Yu, Z., Palmtag, J., and Kuhry, P.: Estimated stocks of circumpolar permafrost carbon with quantified uncertainty ranges and identified data gaps, *Biogeosciences*, 11, 6573–6593, doi:10.5194/bg-11-6573-2014, 2014.
- 35 Hurrell, J. W., Holland, M. M., Gent, P. R., Ghan, S., Kay, J. E., Kushner, P. J., Lamarque, J.-F., Large, W. G., Lawrence, D., Lindsay, K., Lipscomb, W. H., Long, M. C., Mahowald, N., Marsh, D. R., Neale, R. B., Rasch, P., Vavrus, S., Vertenstein, M., Bader, D., Collins, W. D., Hack, J. J., Kiehl, J., and Marshall, S.: The Community Earth System Model: A framework for collaborative research, *Bulletin of the American Meteorological Society*, 94, 1339–1360, 2013.

- Hurt, G. C., Frolking, S., Fearon, M. G., Moore, B., Shevliakova, E., Malyshev, S., Pacala, S. W., and Houghton, R. A.: The underpinnings of land-use history: three centuries of global gridded land-use transitions, wood-harvest activity, and resulting secondary lands, *Global Change Biology*, 12, 1208–1229, 2006.
- Jahn, A., Lindsay, K., Giraud, X., Gruber, N., Otto-Bliesner, B. L., Liu, Z., and Brady, E. C.: Carbon isotopes in the ocean model of the Community Earth System Model (CESM1), *Geoscientific Model Development*, 8, 2419–2434, doi:10.5194/gmd-8-2419-2015, 2015.
- Joos, F. and Bruno, M.: Long-term variability of the terrestrial and oceanic carbon sinks and the budgets of the carbon isotopes  $^{13}\text{C}$  and  $^{14}\text{C}$ , *Global Biogeochemical Cycles*, 12, 277–295, doi:10.1029/98GB00746, 1998.
- Joos, F., Prentice, I., Sitch, S., Meyer, R., Hooss, G., Plattner, G., Gerber, S., and Hasselmann, K.: Global warming feedbacks on terrestrial carbon uptake under the Intergovernmental Panel on Climate Change (IPCC) emission scenarios, *Global Biogeochemical Cycles*, 15, 891–907, 2001.
- Joos, F., Gerber, S., Prentice, I., Otto-Bliesner, B., and Valdes, P.: Transient simulations of Holocene atmospheric carbon dioxide and terrestrial carbon since the Last Glacial Maximum, *Global Biogeochemical Cycles*, 18, 2004.
- Kaplan, J. O., Prentice, I. C., and Buchmann, N.: The stable carbon isotope composition of the terrestrial biosphere: Modeling at scales from the leaf to the globe, *Global Biogeochemical Cycles*, 16, 8–1–8–11, 2002.
- Keel, S. G., Pepin, S., Leuzinger, S., and Körner, C.: Stomatal conductance in mature deciduous forest trees exposed to elevated  $\text{CO}_2$ , *Trees*, 21, 151, doi:10.1007/s00468-006-0106-y, <http://dx.doi.org/10.1007/s00468-006-0106-y>, 2006.
- Keel, S. G., Joos, F., Spahni, R., Saurer, M., Weigt, R. B., and Klesse, S.: Simulating oxygen isotope ratios in tree ring cellulose using a dynamic global vegetation model, *Biogeosciences*, 13, 3869–3886, doi:10.5194/bg-13-3869-2016, 2016.
- Keeling, C. D., Mook, W. G., and Tans, P. P.: Recent trends in the  $^{13}\text{C}/^{12}\text{C}$  ratio of atmospheric carbon dioxide, *Nature*, 277, 121–123, doi:10.1038/277121a0, 1979.
- Keeling, C. D., Bacastow, R. B., Carter, A. F., Piper, S. C., Whorf, T. P., Heimann, M., Mook, W. G., and Roeloffzen, H.: A three dimensional model of atmospheric  $\text{CO}_2$  transport based on observed winds: 1. Analysis of observational data, in: *Aspects of Climate Variability in the Pacific and the Western Americas*, edited by Peterson, D. H., pp. 165–236, American Geophysical Union, 1989.
- Keenan, T. F., Hollinger, D. Y., Bohrer, G., Dragoni, D., Munger, J. W., Schmid, H. P., and Richardson, A. D.: Increase in forest water-use efficiency as atmospheric carbon dioxide concentrations rise, *Nature*, 499, 324–327, doi:10.1038/nature12291, 2013.
- Kennett, J. P. and Stott, L. D.: Abrupt deep-sea warming, palaeoceanographic changes and benthic extinctions at the end of the Palaeocene, *Nature*, 353, 225–229, doi:10.1038/353225a0, 1991.
- Kimak, A. and Leuenberger, M.: Are carbohydrate storage strategies of trees traceable by early–latewood carbon isotope differences?, *Trees*, 29, 859–870, doi:10.1007/s00468-015-1167-6, 2015.
- Klein, T., Bader, M. K.-F., Leuzinger, S., Mildner, M., Schleppei, P., Siegwolf, R. T., and Körner, C.: Growth and carbon relations of mature *Picea abies* trees under 5 years of free-air  $\text{CO}_2$  enrichment, *Journal of Ecology*, 104, 1720–1733, doi:10.1111/1365-2745.12621, 2016.
- Knauer, J., Zaehle, S., Reichstein, M., Medlyn, B. E., Forkel, M., Hagemann, S., and Werner, C.: The response of ecosystem water-use efficiency to rising atmospheric  $\text{CO}_2$  concentrations: sensitivity and large-scale biogeochemical implications, *New Phytologist*, 213, 1654–1666, doi:10.1111/nph.14288, <http://dx.doi.org/10.1111/nph.14288>, 2016–22438, 2017.
- Knorre, A. A., Siegwolf, R. T. W., Saurer, M., Sidorova, O. V., Vaganov, E. A., and Kirilyanov, A. V.: Twentieth century trends in tree ring stable isotopes ( $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$ ) of *Larix sibirica* under dry conditions in the forest steppe in Siberia, *Journal of Geophysical Research: Biogeosciences*, 115, doi:10.1029/2009JG000930, 2010.

- Korte, C. and Kozur, H. W.: Carbon-isotope stratigraphy across the Permian–Triassic boundary: A review, *Journal of Asian Earth Sciences*, 39, 215 – 235, doi:10.1016/j.jseaeas.2010.01.005, 2010.
- 5 Koven, C. D., Riley, W. J., Subin, Z. M., Tang, J. Y., Torn, M. S., Collins, W. D., Bonan, G. B., Lawrence, D. M., and Swenson, S. C.: The effect of vertically resolved soil biogeochemistry and alternate soil C and N models on C dynamics of CLM4, *Biogeosciences*, 10, 7109–7131, 2013.
- Koven, C. D., Chambers, J. Q., Georgiou, K., Knox, R., Negron-Juarez, R., Riley, W. J., Arora, V. K., Brovkin, V., Friedlingstein, P., and Jones, C. D.: Controls on terrestrial carbon feedbacks by productivity versus turnover in the CMIP5 Earth System Models, *Biogeosciences*, 12, 5211–5228, doi:10.5194/bg-12-5211-2015, 2015a.
- 10 Koven, C. D., Lawrence, D. M., and Riley, W. J.: Permafrost carbon-climate feedback is sensitive to deep soil carbon decomposability but not deep soil nitrogen dynamics, *Proceedings of the National Academy of Sciences*, 112, 3752–3757, 2015b.
- Krakauer, N. Y., Randerson, J. T., Primeau, F. W., Gruber, N., and Menemenlis, D.: Carbon isotope evidence for the latitudinal distribution and wind speed dependence of the air-sea gas transfer velocity, *Tellus B*, 58, 390–417, doi:10.1111/j.1600-0889.2006.00223.x, 2006.
- 15 Lai, C.-T., Riley, W., Owensby, C., Ham, J., Schauer, A., and Ehleringer, J. R.: Seasonal and interannual variations of carbon and oxygen isotopes of respired CO<sub>2</sub> in a tallgrass prairie: Measurements and modeling results from 3 years with contrasting water availability, *Journal of Geophysical Research: Atmospheres*, 111, doi:10.1029/2005JD006436, 2006.
- Lambers, H., Chapin, F. S., and Pons, T. L.: *Plant Physiological Ecology*, Springer New York, 2008.
- 20 Le Quéré, C., Moriarty, R., Andrew, R. M., Canadell, J. G., Sitch, S., Korsbakken, J. I., Friedlingstein, P., Peters, G. P., Andres, R. J., Boden, T. A., Houghton, R. A., House, J. I., Keeling, R. F., Tans, P., Arneeth, A., Bakker, D. C. E., Barbero, L., Bopp, L., Chang, J., Chevallier, F., Chini, L. P., Ciais, P., Fader, M., Feely, R. A., Gkritzalis, T., Harris, I., Hauck, J., Ilyina, T., Jain, A. K., Kato, E., Kitidis, V., Klein Goldewijk, K., Koven, C., Landschützer, P., Lauvset, S. K., Lefèvre, N., Lenton, A., Lima, I. D., Metzl, N., Millero, F., Munro, D. R., Murata, A., Nabel, J. E. M. S., Nakaoka, S., Nojiri, Y., O’Brien, K., Olsen, A., Ono, T., Pérez, F. F., Pfeil, B., Pierrot, D., Poulter, B., Rehder, G., Rödenbeck, C., Saito, S., Schuster, U., Schwinger, J., Séférian, R., Steinhoff, T., Stocker, B. D., Sutton, A. J., Takahashi, T., Tilbrook, B., van der Laan-Luijckx, I. T., van der Werf, G. R., van Heuven, S., Vandemark, D., Viovy, N., Wiltshire, A., Zaehle, S., and Zeng, N.: Global Carbon Budget 2015, *Earth System Science Data*, 7, 349–396, doi:10.5194/essd-7-349-2015, 2015.
- 25 Leavitt, S. W., Chase, T. N., Rajagopalan, B., Lee, E., Lawrence, P. J., and Woodhouse, C. A.: Southwestern U.S. drought maps from pinyon tree-ring carbon isotopes, *Eos Trans*, 88, 39–40, doi:10.1029/2007EO040005, 2007.
- 30 Leonardi, S., Gentilella, T., Guerrieri, R., Ripullone, F., Magnani, F., Mencuccini, M., Noije, T. V., and Borghetti, M.: Assessing the effects of nitrogen deposition and climate on carbon isotope discrimination and intrinsic water-use efficiency of angiosperm and conifer trees under rising CO<sub>2</sub> conditions, *Global Change Biology*, 18, 2925–2944, doi:10.1111/j.1365-2486.2012.02757.x, 2012.
- Leuenberger, M.: To what extent can ice core data contribute to the understanding of plant ecological developments of the past?, in: *Stable Isotopes as Indicators of Ecological Change*, edited by Dawson, T. and Siegwolf, R., p. 211–233, Elsevier: Amsterdam, 2007.
- 35 Lévesque, M., Siegwolf, R., Saurer, M., Eilmann, B., and Rigling, A.: Increased water-use efficiency does not lead to enhanced tree growth under xeric and mesic conditions, *New Phytologist*, 203, 94–109, doi:10.1111/nph.12772, 2014.
- Liberloo, M., Tulva, I., Raïm, O., Kull, O., and Ceulemans, R.: Photosynthetic stimulation under long-term CO<sub>2</sub> enrichment and fertilization is sustained across a closed *Populus* canopy profile (EUROFACE), *New Phytologist*, 173, 537–549, doi:10.1111/j.1469-8137.2006.01926.x, <http://dx.doi.org/10.1111/j.1469-8137.2006.01926.x>, 2007.

- Liu, J., Chen, F., Chen, J., Zhang, X., Liu, J., and Bloemendal, J.: Weakening of the East Asian summer monsoon at 1000-1100 A.D. within the Medieval Climate Anomaly: Possible linkage to changes in the Indian Ocean-western Pacific, *Journal of Geophysical Research: Atmospheres*, 119, 2209–2219, 2014a.
- Liu, X., Wang, W., Xu, G., Zeng, X., Wu, G., Zhang, X., and Qin, D.: Tree growth and intrinsic water-use efficiency of inland riparian forests in northwestern China: evaluation via  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  analysis of tree rings, *Tree Physiology*, doi:10.1093/treephys/tpu067, 2014b.
- Lloyd, J. and Farquhar, G.:  $^{13}\text{C}$  discrimination during  $\text{CO}_2$  assimilation by the terrestrial biosphere, *Oecologia*, 99, 201–215, doi:10.1007/BF00627732, 1994.
- 10 Loader, N., Young, G., Grudd, H., and McCarroll, D.: Stable carbon isotopes from Torneträsk, northern Sweden provide a millennial length reconstruction of summer sunshine and its relationship to Arctic circulation, *Quaternary Science Reviews*, 62, 97–113, 2013.
- MacFarling Meure, C., Etheridge, D., Trudinger, C., Steele, P., Langenfelds, R., van Ommen, T., Smith, A., and Elkins, J.: Law Dome  $\text{CO}_2$ ,  $\text{CH}_4$  and  $\text{N}_2\text{O}$  ice core records extended to 2000 years BP, *Geophysical Research Letters*, 33, doi:10.1029/2006GL026152, 2006.
- Marshall, J. D., Brooks, J. R., and Lajtha, K.: Sources of Variation in the Stable Isotopic Composition of Plants, pp. 22–60, Blackwell Publishing Ltd, doi:10.1002/9780470691854.ch2, 2008.
- McCarroll, D. and Loader, N. J.: Stable isotopes in tree rings, *Quaternary Science Reviews*, 23, 771–801, 2004.
- Medlyn, B. E., Duursma, R. A., Eamus, D., Ellsworth, D. S., Colin Prentice, I., Barton, C. V. M., Crous, K. Y., de Angelis, P., Freeman, M., and Wingate, L.: Reconciling the optimal and empirical approaches to modelling stomatal conductance, *Global Change Biology*, 17, 2134–2144, doi:10.1111/j.1365-2486.2010.02375.x, 2011.
- 20 Menviel, L. and Joos, F.: Toward explaining the Holocene carbon dioxide and carbon isotope records: Results from transient ocean carbon cycle-climate simulations, *Paleoceanography*, 27, doi:10.1029/2011PA002224, 2012.
- Menviel, L., Joos, F., and Ritz, S.: Simulating atmospheric  $\text{CO}_2$ ,  $^{13}\text{C}$  and the marine carbon cycle during the Last Glacial–Interglacial cycle: possible role for a deepening of the mean remineralization depth and an increase in the oceanic nutrient inventory, *Quaternary Science Reviews*, 56, 46 – 68, doi:10.1016/j.quascirev.2012.09.012, 2012.
- 25 Miner, G. L., Bauerle, W. L., and Baldocchi, D. D.: Estimating the sensitivity of stomatal conductance to photosynthesis: a review, *Plant, Cell & Environment*, pp. n/a–n/a, doi:10.1111/pce.12871, <http://dx.doi.org/10.1111/pce.12871>, pCE-16-0713.R1, 2017.
- Monteith, J. L.: A reinterpretation of stomatal responses to humidity, *Plant, Cell & Environment*, 18, 357–364, doi:10.1111/j.1365-3040.1995.tb00371.x, 1995.
- Negrón-Juárez, R. I., Koven, C. D., Riley, W. J., Knox, R. G., and Chambers, J. Q.: Observed allocations of productivity and biomass, and turnover times in tropical forests are not accurately represented in CMIP5 Earth system models, *Environmental Research Letters*, 10, doi:10.1088/1748-9326/10/6/064017, 2015.
- Oleson, K. W., Lawrence, D. M., B, G., Flanner, M. G., Kluzek, E., J, P., Levis, S., Swenson, S. C., Thornton, E., Feddema, J., Heald, C. L., francois Lamarque, J., yue Niu, G., Qian, T., Running, S., Sakaguchi, K., Yang, L., Zeng, X., and Zeng, X.: Technical Description of version 4.0 of the Community Land Model (CLM), NCAR/TN-478+STR, Tech. rep., National Center for Atmospheric Research (NCAR), Boulder, USA, 2010.
- 35 Oleson, K. W., Lawrence, D. M., Bonan, G. B., Drewniak, B., Huang, M., Koven, C. D., Levis, S., Li, F., Riley, W. J., Subin, Z. M., Swenson, S. C., Thornton, P. E., Bozbiyik, A., Fisher, R., Kluzek, E., Lamarque, J.-F., Lawrence, P. J., Leung, L. R., Lipscomb, W., Muszala, S., Ricciuto, D. M., Sacks, W., Sun, Y., Tang, J., and Yang, Z.-L.: Technical description of version 4.5 of the Community Land Model (CLM), NCAR/TN-503+STR, Tech. rep., National Center for Atmospheric Research (NCAR), Boulder, USA, 2013.

- Olson, R., Scurlock, J., Prince, S., Zheng, D., and Johnson, K.: NPP multi-biome: NPP and driver data for ecosystem model-data intercomparison, R2, doi:10.3334/ORNLDAAC/615, 2013.
- 5 Pataki, D. E., Ehleringer, J. R., Flanagan, L. B., Yakir, D., Bowling, D. R., Still, C. J., Buchmann, N., Kaplan, J. O., and Berry, J. A.: The application and interpretation of Keeling plots in terrestrial carbon cycle research, *Global Biogeochemical Cycles*, 17, doi:10.1029/2001GB001850, 2003.
- Peterson, C. D., Lisiecki, L. E., and Stern, J. V.: Deglacial whole-ocean  $\delta^{13}\text{C}$  change estimated from 480 benthic foraminiferal records, *Paleoceanography*, 29, 549–563, doi:10.1002/2013PA002552, 2014.
- 10 Peñuelas, J., Canadell, J. G., and Ogaya, R.: Increased water-use efficiency during the 20th century did not translate into enhanced tree growth, *Global Ecology and Biogeography*, 20, 597–608, doi:10.1111/j.1466-8238.2010.00608.x, 2011.
- Prentice, I. C., Dong, N., Gleason, S. M., Maire, V., and Wright, I. J.: Balancing the costs of carbon gain and water transport: testing a new theoretical framework for plant functional ecology, *Ecol Lett*, 17, 82–91, doi:10.1111/ele.12211, 2014.
- Raczka, B., Duarte, H. F., Koven, C. D., Ricciuto, D., Thornton, P. E., Lin, J. C., and Bowling, D. R.: An observational constraint on stomatal function in forests: evaluating coupled carbon and water vapor exchange with carbon isotopes in the Community Land Model (CLM4.5), 15 *Biogeosciences*, 13, 5183–5204, doi:10.5194/bg-13-5183-2016, 2016.
- Reich, P. B., Hobbie, S. E., and Lee, T. D.: Plant growth enhancement by elevated  $\text{CO}_2$  eliminated by joint water and nitrogen limitation, *Nature Geoscience*, 7, 920–924, 2014.
- Robertson, I., Rolfe, J., Switsur, V. R., Carter, A. H. C., Hall, M. A., Barker, A. C., and Waterhouse, J. S.: Signal strength and climate relationships in  $^{13}\text{C}/^{12}\text{C}$  ratios of tree ring cellulose from oak in southwest Finland, *Geophysical Research Letters*, 24, 1487–1490, 20 doi:10.1029/97GL01293, 1997.
- Rubino, M., Etheridge, D. M., Trudinger, C. M., Allison, C. E., Battle, M. O., Langenfelds, R. L., Steele, L. P., Curran, M., Bender, M., White, J. W. C., Jenk, T. M., Blunier, T., and Francey, R. J.: A revised 1000 year atmospheric  $\delta^{13}\text{C}\text{-CO}_2$  record from Law Dome and South Pole, Antarctica, *Journal of Geophysical Research: Atmospheres*, 118, 8482–8499, doi:10.1002/jgrd.50668, 2013.
- Ruosch, M., Spahni, R., Joos, F., Henne, P. D., van der Knaap, W. O., and Tinner, W.: Past and future evolution of *Abies alba* forests 25 in Europe – comparison of a dynamic vegetation model with palaeo data and observations, *Global Change Biology*, 22, 727–740, doi:10.1111/gcb.13075, 2016.
- Sato, H., Kumagai, T., Takahashi, A., and Katul, G. G.: Effects of different representations of stomatal conductance response to humidity across the African continent under warmer  $\text{CO}_2$ -enriched climate conditions, *Journal of Geophysical Research: Biogeosciences*, 120, 979–988, doi:10.1002/2014JG002838, <http://dx.doi.org/10.1002/2014JG002838>, 2014JG002838, 2015.
- 30 Saurer, M., Cherubini, P., and Siegwolf, R.: Oxygen isotopes in tree rings of *Abies alba*: The climatic significance of interdecadal variations, *Journal of Geophysical Research: Atmospheres*, 105, 12461–12470, doi:10.1029/2000JD900160, 2000.
- Saurer, M., Siegwolf, R. T. W., and Schweingruber, F. H.: Carbon isotope discrimination indicates improving water-use efficiency of trees in northern Eurasia over the last 100 years, *Global Change Biology*, 10, 2109–2120, 2004.
- Saurer, M., Kress, A., Leuenberger, M., Rinne, K. T., Treydte, K. S., and Siegwolf, R. T. W.: Influence of atmospheric circulation 35 patterns on the oxygen isotope ratio of tree rings in the Alpine region, *Journal of Geophysical Research: Biogeosciences*, 117, doi:10.1029/2011JD016861, 2012.
- Saurer, M., Spahni, R., Frank, D. C., Joos, F., Leuenberger, M., Loader, N. J., McCarroll, D., Gagen, M., Poulter, B., Siegwolf, R. T., Andreu-Hayles, L., Boettger, T., Dorado Linan, I., Fairchild, I. J., Friedrich, M., Gutierrez, E., Haupt, M., Hiltunen, E., Heinrich, I., Helle, G., Grudd, H., Jalkanen, R., Levanić, T., Linderholm, H. W., Robertson, I., Sonninen, E., Treydte, K., Waterhouse, J. S., Woodley, E. J., Wynn,

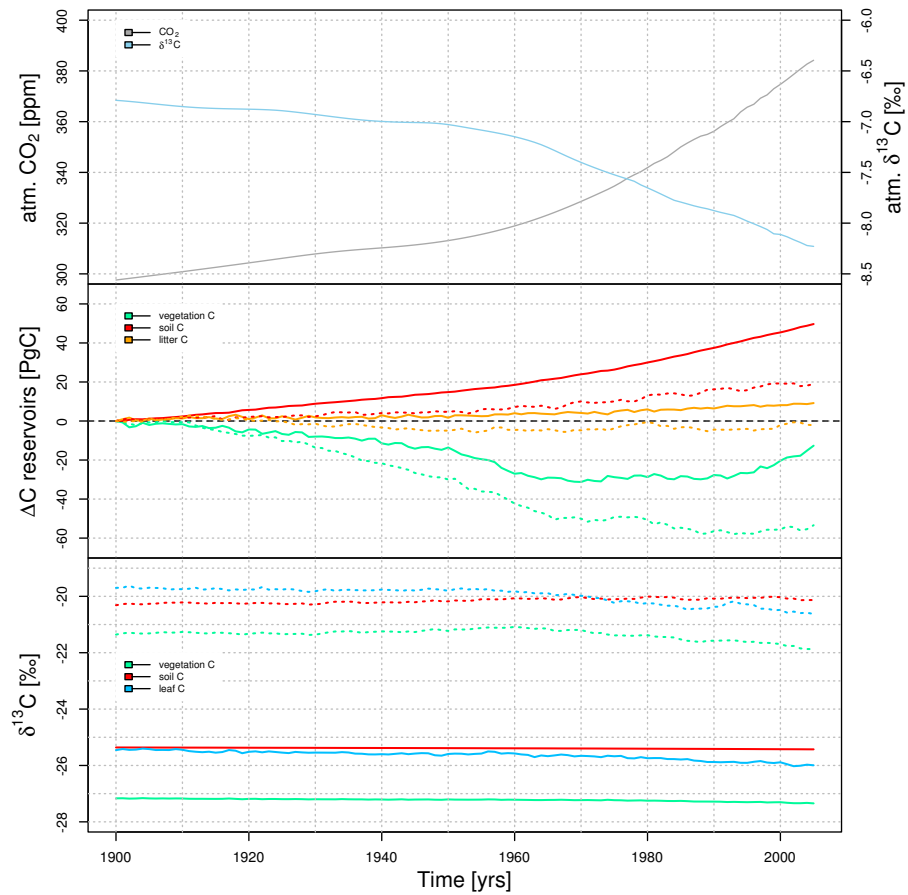
- P. M., and Young, G. H.: Spatial variability and temporal trends in water-use efficiency of European forests, *Global Change Biology*, 20, 3700–3712, 2014.
- Scheidegger, Y., Saurer, M., Bahn, M., and Siegwolf, R.: Linking stable oxygen and carbon isotopes with stomatal conductance and photosynthetic capacity: a conceptual model, *Oecologia*, 125, 350–357, doi:10.1007/s004420000466, 2000.
- Schmittner, A. and Somes, C. J.: Complementary constraints from carbon ( $^{13}\text{C}$ ) and nitrogen ( $^{15}\text{N}$ ) isotopes on the glacial ocean's soft-tissue biological pump, *Paleoceanography*, 31, 669–693, doi:10.1002/2015PA002905, 2016.
- Schmittner, A., Gruber, N., Mix, A. C., Key, R. M., Tagliabue, A., and Westberry, T. K.: Biology and air-sea gas exchange controls on the distribution of carbon isotope ratios ( $\delta^{13}\text{C}$ ) in the ocean, *Biogeosciences*, 10, 5793–5816, doi:10.5194/bg-10-5793-2013, 2013.
- Schneider, R., Schmitt, J., Köhler, P., Joos, F., and Fischer, H.: A reconstruction of atmospheric carbon dioxide and its stable carbon isotopic composition from the penultimate glacial maximum to the last glacial inception, *Climate of the Past*, 9, 2507–2523, doi:10.5194/cp-9-2507-2013, 2013.
- Scholze, M., Kaplan, J. O., Knorr, W., and Heimann, M.: Climate and interannual variability of the atmosphere-biosphere  $^{13}\text{CO}_2$  flux, *Geophysical Research Letters*, 30, doi:10.1029/2002GL015631, 2003.
- Scholze, M., Ciais, P., and Heimann, M.: Modeling terrestrial  $^{13}\text{C}$  cycling: Climate, land use and fire, *Global Biogeochemical Cycles*, 22, doi:10.1029/2006GB002899, 2008.
- Schubert, B. A. and Jahren, A. H.: Quantifying seasonal precipitation using high-resolution carbon isotope analyses in evergreen wood, *Geochimica et Cosmochimica Acta*, 75, 7291–7303, 2011.
- Shackleton, N. J.: Carbon-13 in uvigerina: Tropical rainforest history and the equatorial Pacific carbonate dissolution cycles, in: *The Fate of Fossil Fuel  $\text{CO}_2$  in the Ocean*, edited by Andersen, N. R. and Malahoff, A., pp. 401–428, Plenum, New York, 1977.
- Sidorova, O. V., Siegwolf, R. T. W., Saurer, M., Naurzbaev, M. M., and Vaganov, E. A.: Isotopic composition ( $\delta^{13}\text{C}$ ,  $\delta^{18}\text{O}$ ) in wood and cellulose of Siberian larch trees for early Medieval and recent periods, *Journal of Geophysical Research: Biogeosciences*, 113, n/a–n/a, <http://dx.doi.org/10.1029/2007JG000473>, 2008.
- Sidorova, O. V., Siegwolf, R. T. W., Saurer, M., Shashkin, A. V., Knorre, A. A., Prokushkin, A. S., Vaganov, E. A., and Kirilyanov, A. V.: Do centennial tree-ring and stable isotope trends of *Larix gmelinii* (Rupr.) Rupr. indicate increasing water shortage in the Siberian north?, *Oecologia*, 161, 825–835, doi:10.1007/s00442-009-1411-0, 2009.
- Sidorova, O. V., Siegwolf, R. T. W., Saurer, M., Naurzbaev, M. M., Shashkin, A. V., and Vaganov, E. A.: Spatial patterns of climatic changes in the Eurasian north reflected in Siberian larch tree-ring parameters and stable isotopes, *Global Change Biology*, 16, 1003–1018, doi:10.1111/j.1365-2486.2009.02008.x, 2010.
- Sidorova, O. V., Saurer, M., Myglan, V. S., Eichler, A., Schwikowski, M., Kirilyanov, A. V., Bryukhanova, M. V., Gerasimova, O. V., Kalugin, I. A., Daryin, A. V., and Siegwolf, R. T. W.: A multi-proxy approach for revealing recent climatic changes in the Russian Altai, *Climate Dynamics*, 38, 175–188, doi:10.1007/s00382-010-0989-6, 2012.
- Sidorova, O. V., Siegwolf, R. T. W., Myglan, V. S., Ovchinnikov, D. V., Shishov, V. V., Helle, G., Loader, N. J., and Saurer, M.: The application of tree-rings and stable isotopes for reconstructions of climate conditions in the Russian Altai, *Climatic Change*, 120, 153–167, doi:10.1007/s10584-013-0805-5, 2013.
- Siegenthaler, U. and Joos, F.: Use of a simple model for studying oceanic tracer distributions and the global carbon cycle, *Tellus Series B Chemical and Physical Meteorology B*, pp. 186–207, doi:10.1034/j.1600-0889.1992.t01-2-00003.x, 1992.
- Silva, L. C. R. and Horwath, W. R.: Explaining global increases in water use efficiency: Why have we overestimated responses to rising atmospheric  $\text{CO}_2$  in natural forest ecosystems?, *PLoS ONE*, 8, 1–5, doi:10.1371/journal.pone.0053089, 2013.



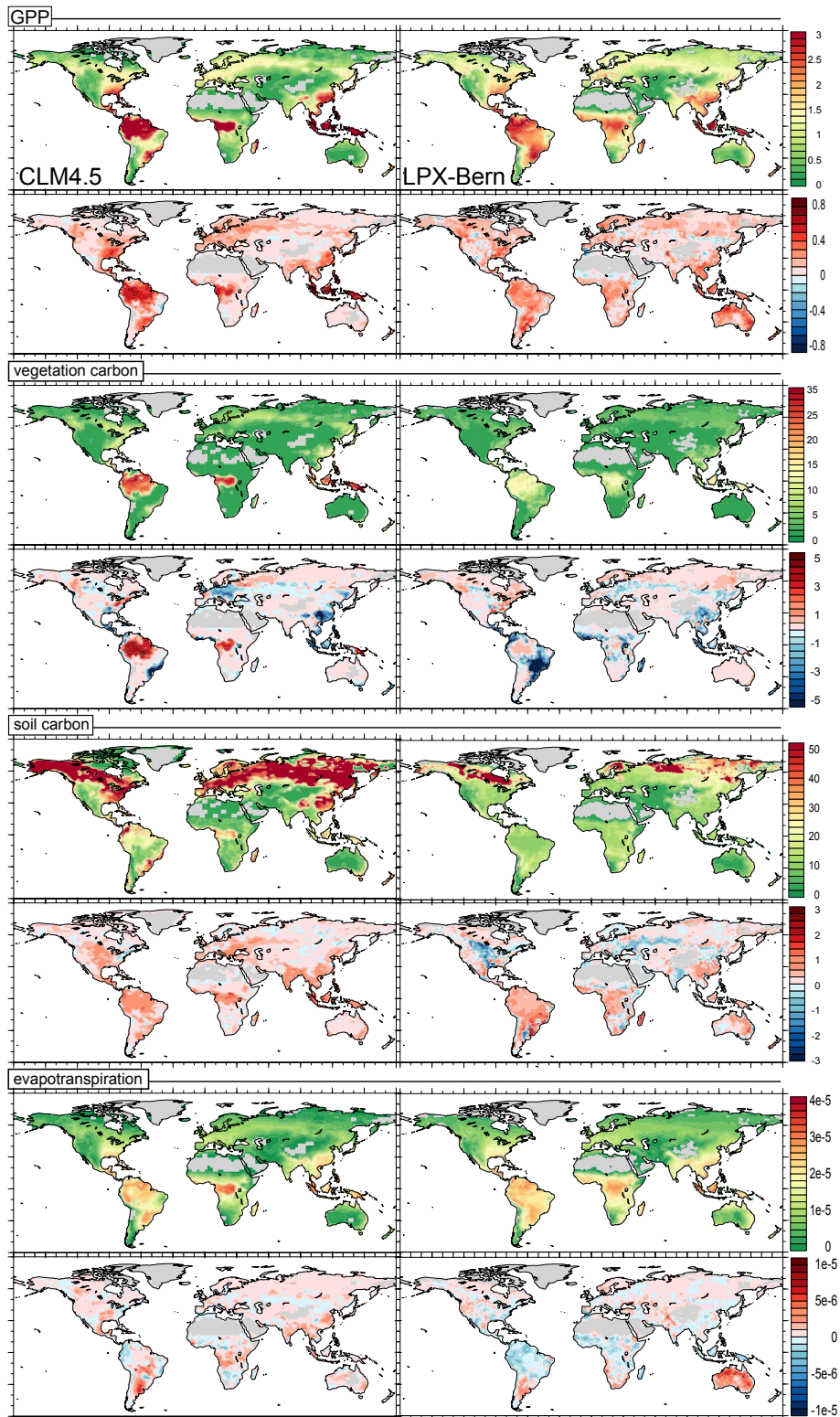
- Sitch, S., Smith, B., Prentice, I., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J., Levis, S., Lucht, W., Sykes, M., Thonicke, K., and Venevsky, S.: Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model, *Global Change Biology*, 9, 161–185, 2003.
- 5 Sonnerup, R. E. and Quay, P. D.:  $^{13}\text{C}$  constraints on ocean carbon cycle models, *Global Biogeochemical Cycles*, 26, doi:10.1029/2010GB003980, 2012.
- Spahni, R., Joos, F., Stocker, B. D., Steinacher, M., and Yu, Z. C.: Transient simulations of the carbon and nitrogen dynamics in northern peatlands: from the Last Glacial Maximum to the 21<sup>st</sup> century, *Climate of the Past*, 9, 1287–1308, doi:10.5194/cp-9-1287-2013, 2013.
- Stocker, B. D., Roth, R., Joos, F., Spahni, R., Steinacher, M., Zaehle, S., Bouwman, L., Xu-Ri, and Prentice, I. C.: Multiple greenhouse-gas  
10 feedbacks from the land biosphere under future climate change scenarios, *Nature Climate Change*, 3, 666–672, 2013.
- Strassmann, K. M., Joos, F., and Fischer, G.: Simulating effects of land use changes on carbon fluxes: past contributions to atmospheric  $\text{CO}_2$  increases and future commitments due to losses of terrestrial sink capacity, *Tellus Series B-Chemical and Physical Meteorology*, 60, 583–603, 2008.
- Streit, K., Siegwolf, R. T. W., Hagedorn, F., Schaub, M., and Buchmann, N.: Lack of photosynthetic or stomatal regulation after 9 years  
15 of elevated  $[\text{CO}_2]$  and 4 years of soil warming in two conifer species at the alpine treeline, *Plant, Cell & Environment*, 37, 315–326, doi:10.1111/pce.12197, <http://dx.doi.org/10.1111/pce.12197>, 2014.
- Suits, N. S., Denning, A. S., Berry, J. A., Still, C. J., Kaduk, J., Miller, J. B., and Baker, I. T.: Simulation of carbon isotope discrimination of the terrestrial biosphere, *Global Biogeochemical Cycles*, 19, doi:10.1029/2003GB002141, 2005.
- Tagliabue, A. and Bopp, L.: Towards understanding global variability in ocean carbon-13, *Global Biogeochemical Cycles*, 22,  
20 doi:10.1029/2007GB003037, 2008.
- Tans, P. P., De Jong, A. F. M., and Mook, W. G.: Natural atmospheric  $^{14}\text{C}$  variation and the Suess effect, *Nature*, 280, 826–828, doi:10.1038/280826a0, 1979.
- Thornton, P. E. and Rosenbloom, N. A.: Ecosystem model spin-up: Estimating steady state conditions in a coupled terrestrial carbon and nitrogen cycle model, *Ecological Modelling*, 189, 25 – 48, doi:10.1016/j.ecolmodel.2005.04.008, 2005.
- 25 Tian, H., Lu, C., Yang, J., Banger, K., Huntzinger, D. N., Schwalm, C. R., Michalak, A. M., Cook, R., Ciais, P., Hayes, D., Huang, M., Ito, A., Jain, A. K., Lei, H., Mao, J., Pan, S., Post, W. M., Peng, S., Poulter, B., Ren, W., Ricciuto, D., Schaefer, K., Shi, X., Tao, B., Wang, W., Wei, Y., Yang, Q., Zhang, B., and Zeng, N.: Global patterns and controls of soil organic carbon dynamics as simulated by multiple terrestrial biosphere models: Current status and future directions, *Global Biogeochemical Cycles*, 29, 775–792, doi:10.1002/2014GB005021, 2015.
- Todd-Brown, K. E. O., Randerson, J. T., Post, W. M., Hoffman, F. M., Tarnocai, C., Schuur, E. A. G., and Allison, S. D.: Causes of variation  
30 in soil carbon simulations from CMIP5 Earth system models and comparison with observations, *Biogeosciences*, 10, 1717–1736, 2013.
- Torn, M. S., Biraud, S. C., Still, C. J., Riley, W. J., and Berry, J. A.: Seasonal and interannual variability in  $^{13}\text{C}$  composition of ecosystem carbon fluxes in the U.S. Southern Great Plains, *Tellus B*, 63, 181–195, doi:10.1111/j.1600-0889.2010.00519.x, 2011.
- Townsend, A. R., Asner, G. P., White, J. W. C., and Tans, P. P.: Land use effects on atmospheric  $^{13}\text{C}$  imply a sizable terrestrial  $\text{CO}_2$  sink in tropical latitudes, *Geophysical Research Letters*, 29, 68–1–68–4, doi:10.1029/2001GL013454, 2002.
- 35 Trahan, M. W. and Schubert, B. A.: Temperature-induced water stress in high-latitude forests in response to natural and anthropogenic warming, *Global Change Biology*, 22, 782–791, doi:10.1111/gcb.13121, 2016.
- Treydte, K., Frank, D., Esper, J., Andreu, L., Bednarz, Z., Berninger, F., Boettger, T., D’Alessandro, C. M., Etien, N., Filot, M., Grabner, M., Guillemain, M. T., Gutierrez, E., Haupt, M., Helle, G., Hiltavuori, E., Jungner, H., Kalela-Brundin, M., Krapiec, M., Leuenberger, M., Loader, N. J., Masson-Delmotte, V., Pazdur, A., Pawelczyk, S., Pierre, M., Planells, O., Pukiene, R., Reynolds-Henne, C. E., Rinne, K. T.,

- Saracino, A., Saurer, M., Sonninen, E., Stievenard, M., Switsur, V. R., Szczepanek, M., Szychowska-Krapiec, E., Todaro, L., Waterhouse, J. S., Weigl, M., and Schleser, G. H.: Signal strength and climate calibration of a European tree-ring isotope network, *Geophysical Research Letters*, 34, L24 302–, doi:10.1029/2007GL031106, 2007.
- 5 Treydte, K. S., Schleser, G. H., Helle, G., Frank, D. C., Winiger, M., Haug, G. H., and Esper, J.: The twentieth century was the wettest period in northern Pakistan over the past millennium, *Nature*, 440, 1179–1182, doi:10.1038/nature04743, 2006.
- Treydte, K. S., Frank, D. C., Saurer, M., Helle, G., Schleser, G. H., and Esper, J.: Impact of climate and CO<sub>2</sub> on a millennium-long tree-ring carbon isotope record, *Geochimica et Cosmochimica Acta*, 73, 4635 – 4647, doi:10.1016/j.gca.2009.05.057, 2009.
- 10 Trudinger, C. M., Enting, I. G., Rayner, P. J., and Francey, R. J.: Kalman filter analysis of ice core data 2. Double deconvolution of CO<sub>2</sub> and  $\delta^{13}\text{C}$  measurements, *Journal of Geophysical Research: Atmospheres*, 107, ACH 5–1–ACH 5–24, doi:10.1029/2001JD001112, 2002.
- Tschumi, T., Joos, F., Gehlen, M., and Heinze, C.: Deep ocean ventilation, carbon isotopes, marine sedimentation and the deglacial CO<sub>2</sub> rise, *Climate of the Past*, 7, 771–800, 2011.
- van der Velde, I. R., Miller, J. B., Schaefer, K., Masarie, K. A., Denning, S., White, J. W. C., Tans, P. P., Krol, M. C., and Peters, W.: Biosphere model simulations of interannual variability in terrestrial 13C/12C exchange, *Global Biogeochemical Cycles*, 27, 637–649, doi:10.1002/gbc.20048, 2013.
- 15 van der Velde, I. R., Miller, J. B., Schaefer, K., van der Werf, G. R., Krol, M. C., and Peters, W.: Terrestrial cycling of <sup>13</sup>C<sub>2</sub> by photosynthesis, respiration, and biomass burning in SiBCASA, *Biogeosciences*, 11, 6553–6571, doi:10.5194/bg-11-6553-2014, 2014.
- Vardag, S. N., Hammer, S., and Levin, I.: Evaluation of 4 years of continuous  $\delta^{13}\text{C}(\text{CO}_2)$  data using a moving Keeling plot method, *Biogeosciences*, 13, 4237–4251, doi:10.5194/bg-13-4237-2016, 2016.
- 20 Viovy, N.: CRU-NCEPv4 dataset. See <http://dods.extra.cea.fr/data/p529viov/cruncep/>, 2011.
- Voelker, S. L., Brooks, J. R., Meinzer, F. C., Anderson, R., Bader, M. K.-F., Battipaglia, G., Becklin, K. M., Beerling, D., Bert, D., Betancourt, J. L., Dawson, T. E., Domec, J.-C., Guyette, R. P., Körner, C., Leavitt, S. W., Linder, S., Marshall, J. D., Mildner, M., Ogée, J., Panyushkina, I., Plumpton, H. J., Pregitzer, K. S., Saurer, M., Smith, A. R., Siegwolf, R. T. W., Stambaugh, M. C., Talhelm, A. F., Tardif, J. C.,
- 1285 Van de Water, P. K., Ward, J. K., and Wingate, L.: A dynamic leaf gas-exchange strategy is conserved in woody plants under changing ambient CO<sub>2</sub>: evidence from carbon isotope discrimination in paleo and CO<sub>2</sub> enrichment studies, *Global Change Biology*, 22, 889–902, doi:10.1111/gcb.13102, 2016.
- Walker, X. J., Mack, M. C., and Johnstone, J. F.: Stable carbon isotope analysis reveals widespread drought stress in boreal black spruce forests, *Global Change Biology*, 21, 3102–3113, doi:10.1111/gcb.12893, 2015.
- 1290 Wang, H., Prentice, I. C., Cornwell, W., Keenan, T., Davis, T., Wright, I., Evans, B., and Peng, C.: A universal model for carbon dioxide uptake by plants, *bioRxiv*, doi:10.1101/040246, 2016.
- Ward, J. K., Harris, J. M., Cerling, T. E., Wiedenhoeft, A., Lott, M. J., Dearing, M.-D., Coltrain, J. B., and Ehleringer, J. R.: Carbon starvation in glacial trees recovered from the La Brea tar pits, southern California, *Proceedings of the National Academy of Sciences*, 102, 690–694, doi:10.1073/pnas.0408315102, 2005.
- 1295 White, J., Vaughn, B., and Michel, S.: Stable isotopic composition of atmospheric carbon dioxide (<sup>13</sup>C and <sup>18</sup>O) from the NOAA ESRL Carbon Cycle Cooperative Global Air Sampling Network, 1990-2014, University of Colorado, Institute of Arctic and Alpine Research (INSTAAR), [ftp://aftp.cmdl.noaa.gov/data/trace\\_gases/CO2\\_2sc13/flask/](ftp://aftp.cmdl.noaa.gov/data/trace_gases/CO2_2sc13/flask/), 2015.
- Wingate, L., Ogée, J., Burlett, R., Bosc, A., Devaux, M., Grace, J., Loustau, D., and Gessler, A.: Photosynthetic carbon isotope discrimination and its relationship to the carbon isotope signals of stem, soil and ecosystem respiration, *New Phytologist*, 188, 576–589, 2010.

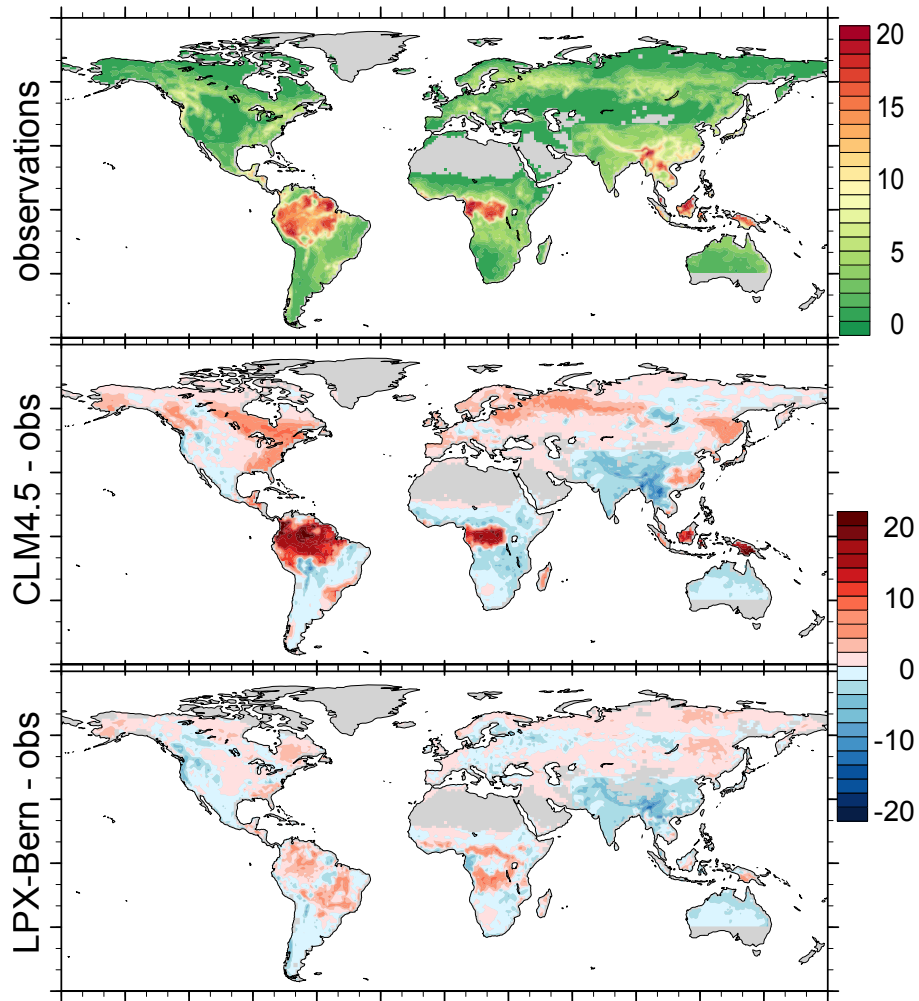
- 1300 Wong, S. C., Cowan, I. R., and Farquhar, G. D.: Stomatal conductance correlates with photosynthetic capacity, *Nature*, 282, 424–426, doi:10.1038/282424a0, 1979.
- Woodborne, S., Hall, G., Robertson, I., Patrut, A., Rouault, M., Loader, N. J., and Hofmeyr, M.: A 1000-year carbon isotope rainfall proxy record from South African baobab trees (*Adansonia digitata* L.), *PLoS ONE*, 10, 1–18, doi:10.1371/journal.pone.0124202, 2015.
- Xu-Ri and Prentice, I.: Terrestrial nitrogen cycle simulation with a dynamic global vegetation model, *Global Change Biology*, 14, 1745–1764, doi:10.1111/j.1365-2486.2008.01625.x, 2008.
- 1305 Xu-Ri, Prentice, I. C., Spahni, R., and Niu, H. S.: Modelling terrestrial nitrous oxide emissions and implications for climate feedback, *New Phytologist*, 196, 472–488, doi:10.1111/j.1469-8137.2012.04269.x, 2012.
- Yang, X., Thornton, P. E., Ricciuto, D. M., and Hoffman, F. M.: Phosphorus feedbacks constraining tropical ecosystem responses to changes in atmospheric CO<sub>2</sub> and climate, *Geophys. Res. Lett.*, 43, 7205–7214, doi:10.1002/2016GL069241, 2016.
- 1310 Yang, Y., Siegwolf, R., and Koerner, C.: Species specific and environment induced variation of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in alpine plants, *Frontiers in Plant Science*, 6, 2015.
- Young, G. H. F., McCarroll, D., Loader, N. J., Gagen, M. H., Kirchhefer, A. J., and Demmler, J. C.: Changes in atmospheric circulation and the Arctic Oscillation preserved within a millennial length reconstruction of summer cloud cover from northern Fennoscandia, *Climate Dynamics*, 39, 495–507, doi:10.1007/s00382-011-1246-3, 2012.
- 1315 Zhu, Q., Iversen, C. M., Riley, W. J., Slette, I. J., and Vander Stel, H. M.: Root traits explain observed tundra vegetation nitrogen uptake patterns: Implications for trait-based land models, *Journal of Geophysical Research: Biogeosciences*, 121, doi:10.1002/2016JG003554, 2016a.
- Zhu, Q., Riley, W. J., Tang, J., and Koven, C. D.: Multiple soil nutrient competition between plants, microbes, and mineral surfaces: model development, parameterization, and example applications in several tropical forests, *Biogeosciences*, 13, 341–363, doi:10.5194/bg-13-1320-2016, 2016b.
- 1320 Zhu, Q., Riley, W. J., and Tang, J.: A new theory of plant–microbe nutrient competition resolves inconsistencies between observations and model predictions, *Ecological Applications*, 27, doi:10.1002/eap.1490, 2017.



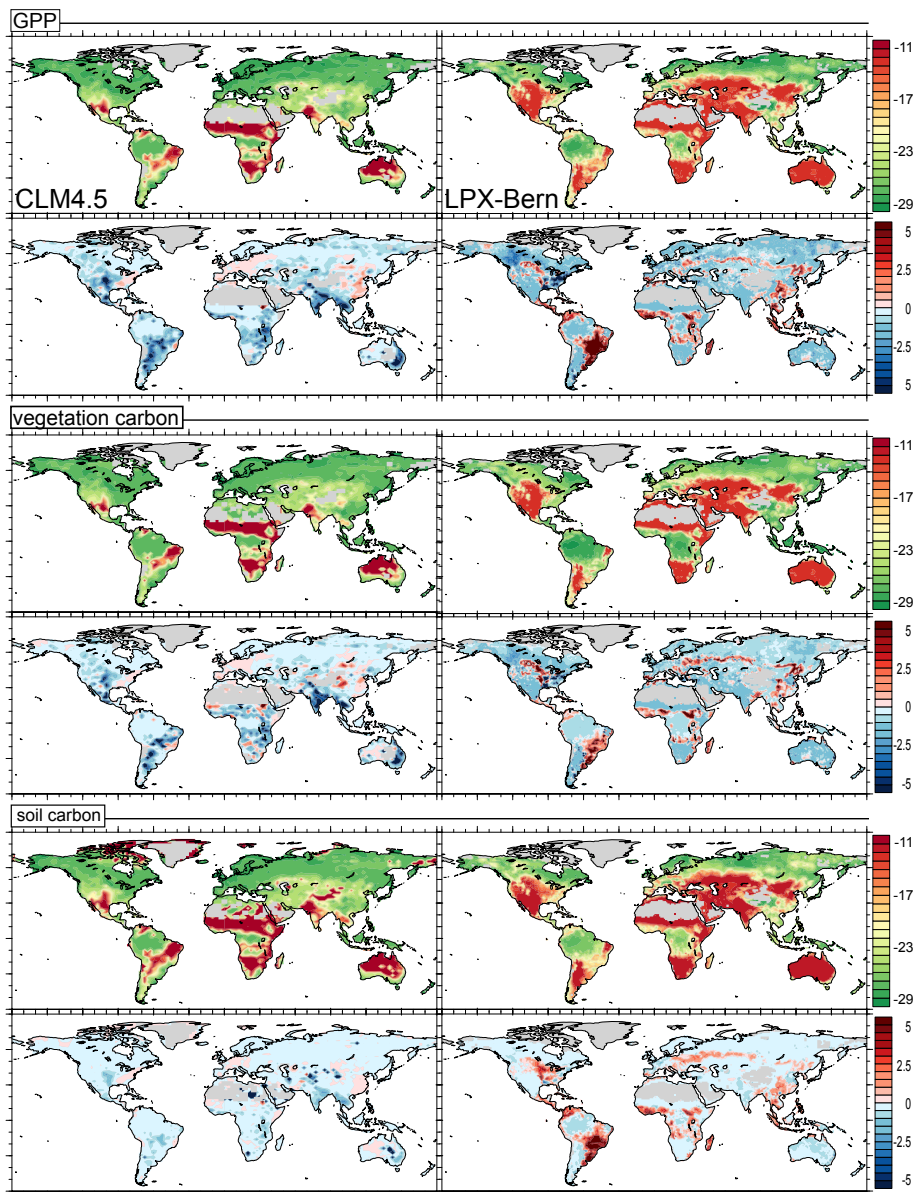
**Figure 1.** a) Prescribed evolution of atmospheric CO<sub>2</sub> and its δ<sup>13</sup>C signature, b) simulated changes in the global inventory of carbon stored in vegetation (green), litter (orange), soils (red), c) Evolution of the global average (mass-weighted) δ<sup>13</sup>C signature of carbon in leaves, vegetation, and soils (CLM4.5: solid, LPX: dotted).



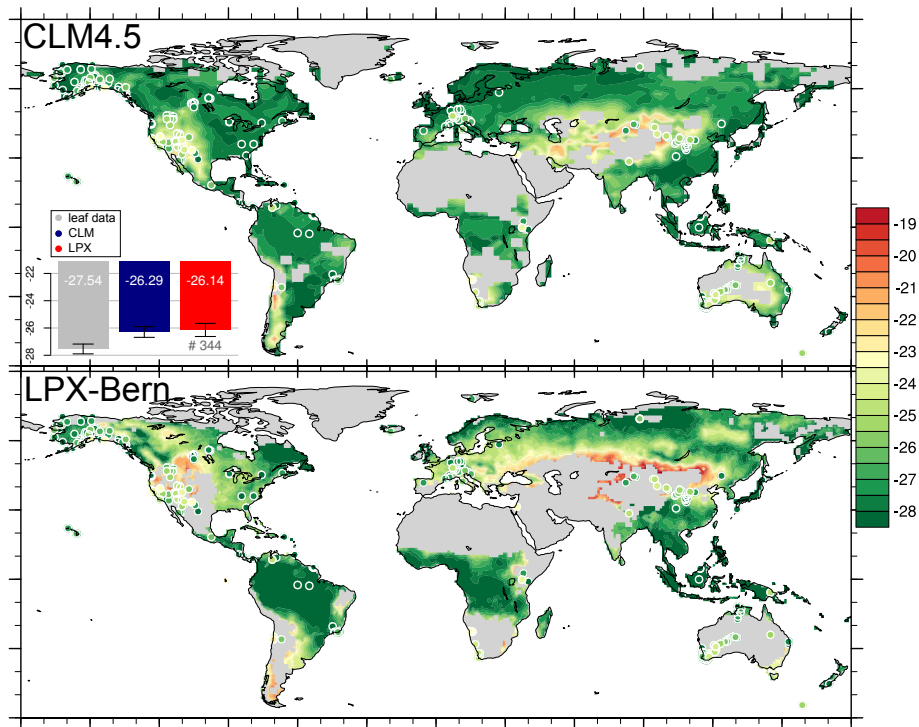
**Figure 2.** GPP ( $\text{gCkgC/m}^2/\text{yr}$ ), vegetation carbon ( $\text{gCkgC/m}^2$ ) and soil carbon ( $\text{gCkgC/m}^2$ ) and evapotranspiration ( $\text{mm/s}$ ) in the year 2000 (top) and the difference between 1900 and 2000 (below). The estimates are based on decadal means ( $1896-1905-1996-2005$  and  $1996-2005$  minus  $1896-1905$ , respectively).



**Figure 3.** Estimated modern distribution of vegetation carbon [derived](#) from observations (Carvalhais et al., 2014) (top) and the differences of model minus observation-derived distributions for CLM4.5 (middle) and LPX (bottom). All results are in  $\text{gC}/\text{m}^2$  and averages for the decade 1996 to 2005 are used for the model distributions.



**Figure 4.**  $\delta^{13}\text{C}$  (‰) of GPP, vegetation carbon and soil carbon in the year 2000 (top) and the change from 1900 to 2000 (below). The estimates are based on decadal means (1896-1905 and 1996-2005, respectively).



**Figure 5.**  $\delta^{13}\text{C}$  as measured on leaves of C3 trees (colored circles; Cornwell et al., 2016) and as simulated by a) CLM4.5 and b) LPX (shading) for the decade 1996 to 2005. Samples for the measurements were taken between 1975 and 2014. The bar plot shows the average over all measurements (gray) and the average signature of C3 trees of the corresponding grid cells for CLM4.5 (blue) and LPX (red). The number below the red bar indicates the number of available measurements.



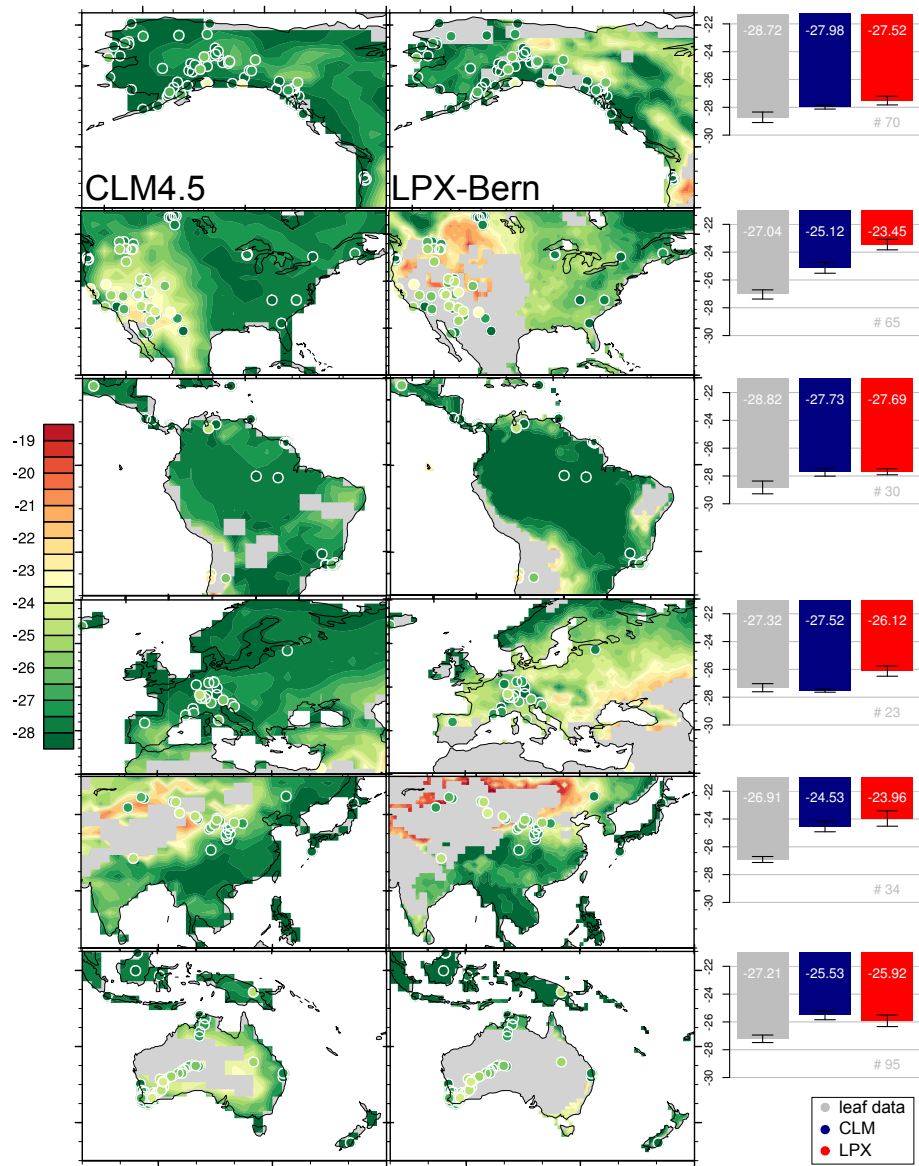
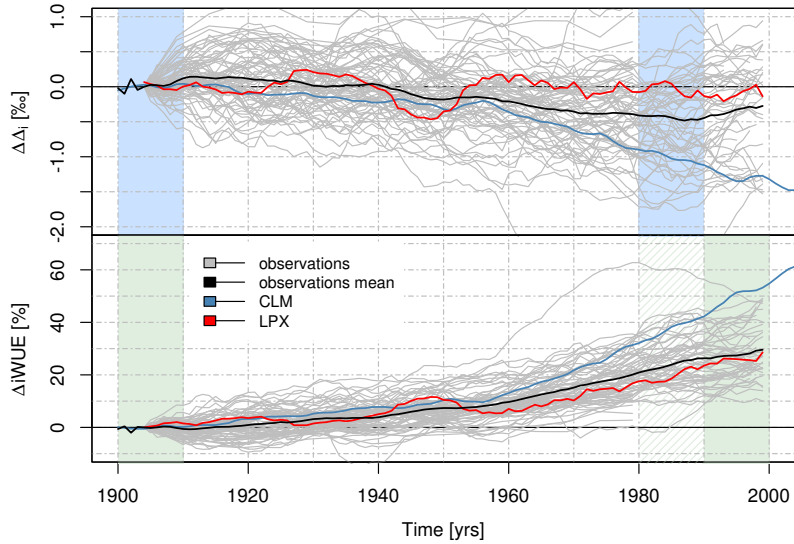
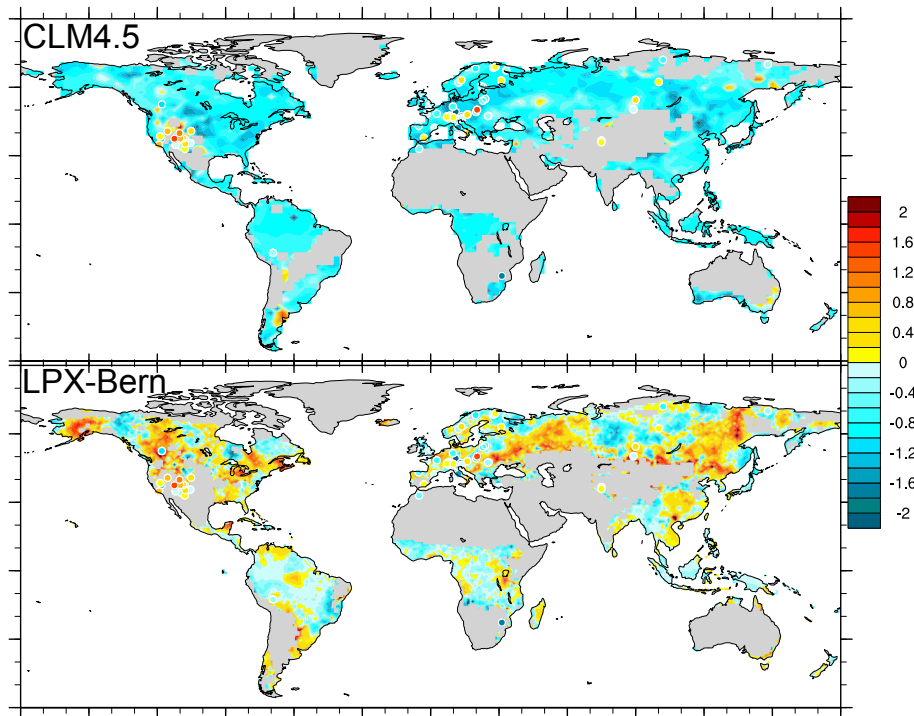


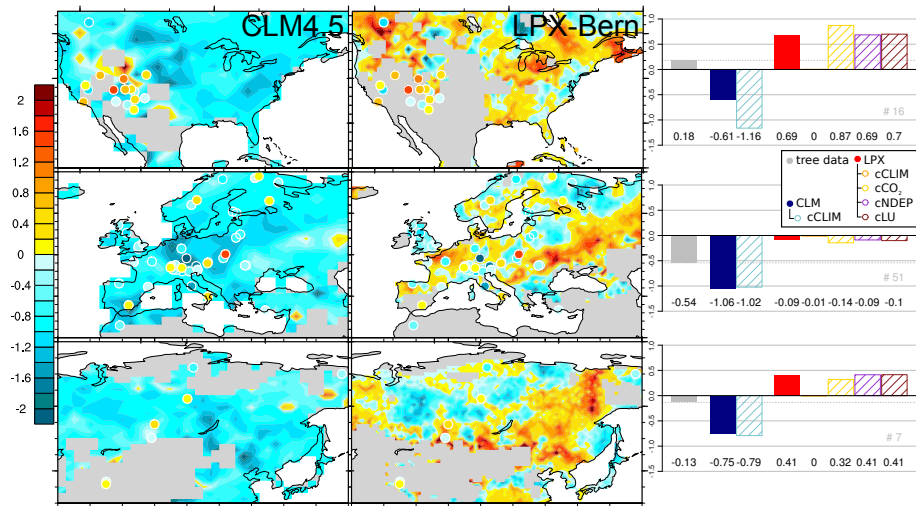
Figure 6. Same as Fig. 5 for selected regions.



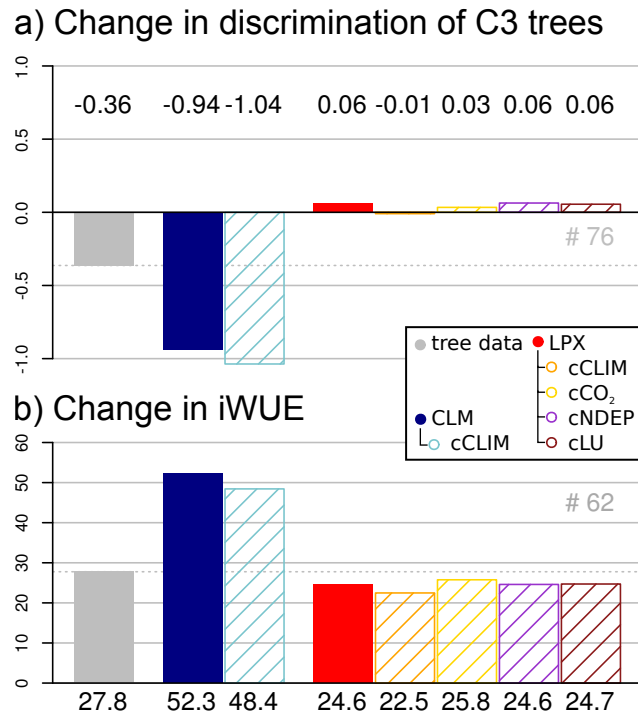
**Figure 7.** 20<sup>th</sup>-century changes in the discrimination  $\Delta_i$  of C3 trees ( $(\delta^{13}C_a - \delta^{13}C_{plant}) / (1 + \frac{\delta^{13}C_{plant}}{1000})$ ) and iWUE (%) as measured on tree rings (black) and modeled by CLM4.5 (blue) and LPX (red). Observations are represented by the average over all measurements (see Tab. A1), models by the average of the mean grid-cell signature of C3 trees and for all model grid cells where measurements are available. Values are given w.r.t. the decade 1900, the background colors indicate the respective decades investigated for changes in discrimination (Figs. 8, 9, 10) and iWUE (Figs. 10, 11, 12.) Absolute values of iWUE for the decade [1900 to 1909](#) [1900-1909](#) are 78 for the observation and LPX-Bern and 50 for CLM4.5. [Standard deviations calculated over all observations of century-scale changes \(1980s minus 1900s\) are 0.72 for  \$\Delta\_i\$  and 9.76 for iWUE, respectively.](#)



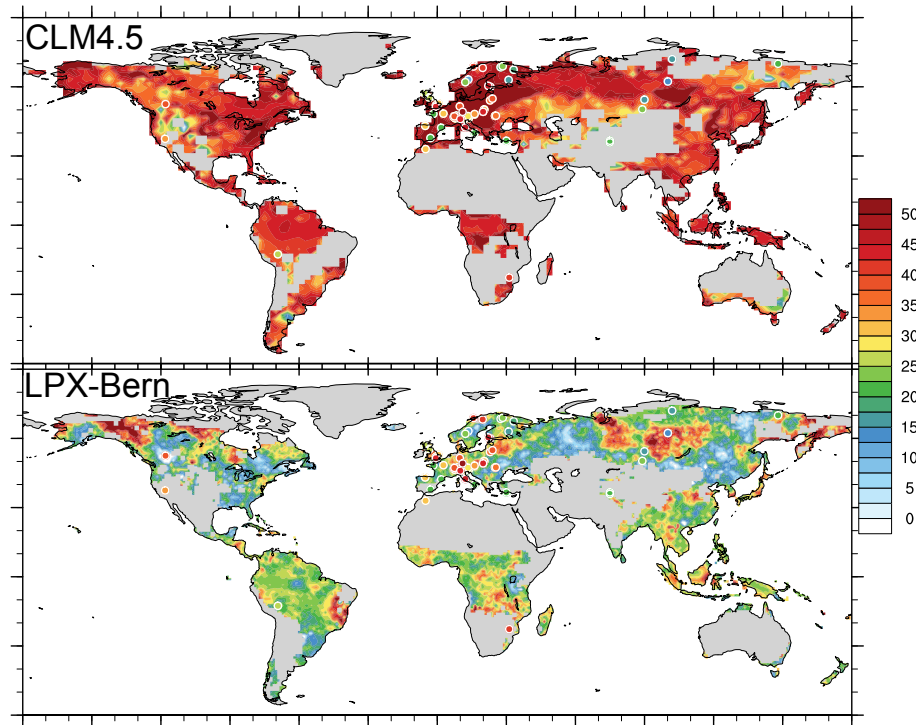
**Figure 8.** Century-scale change in the discrimination  $\Delta_i$  of C3 trees. The discrimination  $(\delta^{13}C_a - \delta^{13}C_{plant}/1 + \frac{\delta^{13}C_{plant}}{1000})$  is calculated from  $\delta^{13}C$  tree-ring data (colored circles) and (a) CLM4.5 and (b) LPX model results [using equation 5](#). The changes are based on decadal means (1980s minus 1900s).



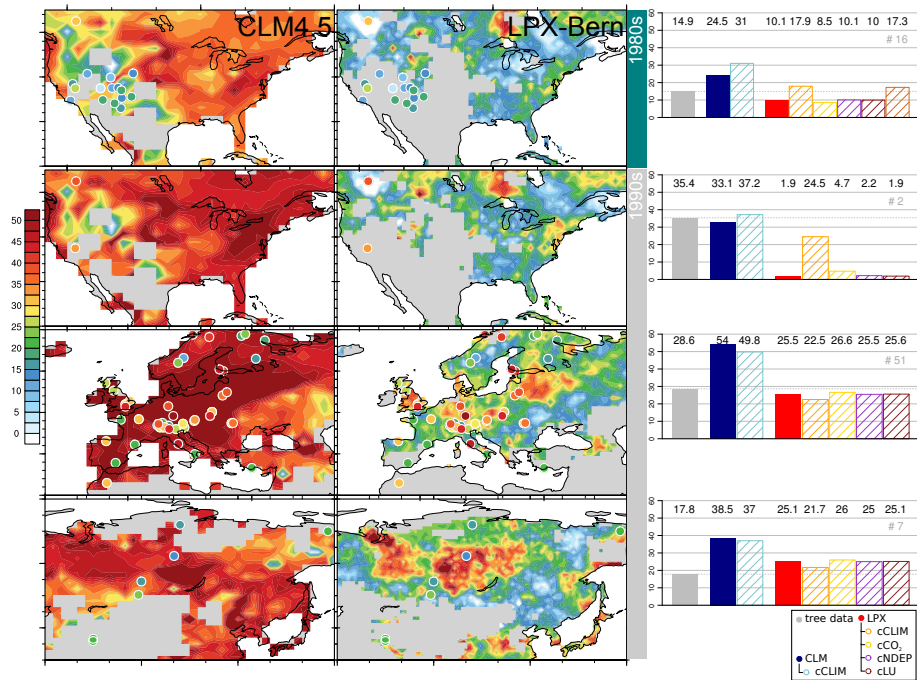
**Figure 9.** Same as Fig. 8 but for three selected regions. The bar plots show the regional average change in discrimination over all of C3 trees as calculated from tree-ring measurements  $\delta^{13}\text{C}$  data (gray) and from results of the average for standard simulations of CLM4.5 (filled blue) and LPX (filled red) of and from factorial runs (pattern). Individual driving factors (climate,  $\text{CO}_2$ , N-deposition, and land use) were kept constant in the factorial runs as explained in the main text and indicated by the legend. Model averages are computed from the mean grid-cell discrimination of C3 trees and for all model grid cells where tree-ring estimates are available. The number of available tree-ring records is indicated.



**Figure 10.** Century-scale changes in a) discrimination  $\Delta_i$  and b) iWUE (%) of C3 trees as calculated from tree-ring  $\delta^{13}\text{C}$  data (gray) and from results of the standard simulations of CLM4.5 (filled blue) and LPX (filled red) and from factorial runs (pattern). Individual driving factors (climate,  $\text{CO}_2$ , N-deposition, and land use) were kept constant in the factorial runs as explained in the main text and indicated by the legend. The number of available records is indicated in each subpanel. All estimates are based on decadal means (a): 1980s minus 1900s; b) 1990s minus 1900s.



**Figure 11.** Century-scale changes in iWUE (%) of C3 trees as calculated from  $\delta^{13}\text{C}$  tree-ring data (colored circles) and (a) CLM4.5 and (b) LPX model results. The changes are based on decadal means (1990s minus 1900s).



**Figure 12.** Same as Fig. 11 but for three selected regions. The bar plots show the regional average change in iWUE (%) over all tree-ring measurements (gray) and the average for CLM4.5 (blue) and LPX (red) of the mean grid-cell iWUE of C3 trees and for all model grid cells where tree-ring estimates are available. Individual driving factors (climate, CO<sub>2</sub>, N-deposition, and land use) were kept constant in the factorial runs (patterns) as explained in the main text and indicated by the legend in the bar plots. The number of available records is indicated in each subplot. All estimates are based on decadal means (a): 1980s minus 1900s; (b), (c), (d): 1990s minus 1900s.

**Table 1.** Parameter values of LPX-Bern that were modified from the previous model version (LPX v1.2) and as used in this study (LPX v1.3). The new values were determined by maximizing agreement with a set of observational data.

<b>Parameter</b>		<b>LPX v1.2</b>	<b>LPX v1.3</b>
$\alpha_a$	Fraction of PAR assimilated at ecosystem level relative to leaf level	0.5	0.620
$\alpha_{C3}$	Intrinsic quantum efficiency of CO <sub>2</sub> uptake in C3 plants	0.07	0.0857
$\theta$	Co-limitation shape parameter	0.7	0.694
$g_m$	Canopy conductance scaling parameter for water demand calculation	3.24	2.95
$\alpha_m$	Priestley-Taylor coefficient in water demand calculation	1.4	1.764
$\tau_{sapwood}$	Sapwood to heartwood turnover [yr]	20	11.1
$k_{la:sa}$	Allometric scaling parameter: leaf area to sapwood area	1.0	1.3
$k_{mort}$	Coefficient of growth efficiency in mortality equation	0.01	0.0118
$E_{0,hr}$	Temperature sensitivity of heterotrophic respiration [K]	308.56	222.0
$f_{atm}$	Fraction of litter entering atmosphere directly	0.6	0.66
$f_{slow}$	Fraction of litter entering slow soil pool	0.015	0.0106
$k_{soil,tune}$	Tuning factor for soil decay	0.7	0.840
$nitr_{max}$	Maximum nitrification rate	0.1	0.0923
$f_{immob,soil}$	Nitrogen immobilization in soil	0.0	0.249
$ox_{past}$	Fraction of direct oxidation of leaf turnover on pastures	0.4	0.298
$ox_{crop}$	Fraction of direct oxidation of leaf turnover on cropland	0.9	0.9094



**Table 2.** Integrals and mean isotopic signatures of global carbon pools: steady state in the year 2000 (mean 1996-2005) and change over the 20<sup>th</sup> century for both models and an observational dataset (Carvalhais et al., 2014).

<b>C reservoir [GtC]</b>	<b>CLM</b>	<b>LPX</b>	<b>Observations</b>
<i>in the year 2000</i>			
GPP	168	149	-
vegetation	874	425	442
soil	3916	1710	2397
litter	82	260	-
leaf	21	24	-
<b>total C</b>	5099	2405	-
<i>change over 20<sup>th</sup> century</i>			
GPP	20	17	-
vegetation	-21	-55	-
soil	45	19	-
litter	8	-3	-
leaf	2	5	-
<b>total C</b>	32	-35	-
<b>C reservoir [<math>\delta^{13}\text{C}</math>; ‰]</b>	<b>CLM</b>	<b>LPX</b>	<b>Observations</b>
<i>in the year 2000</i>			
GPP	-24.9	-20.7	-
total C	-27.6	-23	-
total C [GtC ‰]	-140660	-55227	-
<i>change over 20<sup>th</sup> century</i>			
GPP	-0.74	-0.45	-
total C	-0.00	0.21	-
total C [GtC ‰]	-904	1329	-

Table A1:  $\delta^{13}\text{C}$  tree-ring time series compiled for this study.

#	Site	Country	Period	Lat	Lon	Reference
1	Dachstein	Austria	1900-1996	47.28	13.36	Saurer et al. (2014)
2	Lainzer Tiergarten	Austria	1900-2003	48.18	16.20	Treydte et al. (2007)
3	Poellau	Austria	1900-2002	47.95	16.06	Treydte et al. (2007)
4	Columbia	Canada	1900-1990	52.50	-118.00	Edwards et al. (2008)
5	Bromarv	Finland	1901-2002	60.00	23.08	Treydte et al. (2007)
6	Ilomantsi	Finland	1900-2002	62.98	30.98	Treydte et al. (2007)
7	Kessi/Inari	Finland	1900-2002	68.93	28.42	Treydte et al. (2007)
8	Laanila	Finland	1900-2002	68.50	27.50	Gagen et al. (2011)
9	Turku	Finland	1900-1994	60.41	22.17	Robertson et al. (1997)
10	Fontainebleau	France	1900-2000	48.38	2.67	Treydte et al. (2007)
11	Rennes	France	1900-1999	48.25	-1.70	Treydte et al. (2007)
12	Dransfeld	Germany	1900-2002	51.50	9.78	Treydte et al. (2007)
13	Franconia	Germany	1900-2005	49.15	11.00	Saurer et al. (2014)
14	Monte Cimino	Italy	1900-2005	42.41	12.20	Klesse et al. in prep
15	Serra di Crispo	Italy	1900-2003	39.93	16.20	Treydte et al. (2007)
16	Trento	Italy	1900-2004	45.98	11.66	Saurer et al. (2014)
17	Panemunus Silas	Lithuania	1900-2002	54.88	23.97	Treydte et al. (2007)
18	Col Du Zad	Morocco	1900-2000	32.97	-5.07	Treydte et al. (2007)
19	Forfjorddalen	Norway	1900-2001	68.79	15.72	Young et al. (2012)
20	Gutuli	Norway	1900-2003	62.00	12.18	Treydte et al. (2007)
21	Bagrot	Pakistan	1900-1998	35.90	74.93	Treydte et al. (2006)
22	Boibar	Pakistan	1900-1998	36.62	74.98	Treydte et al. (2006)
23	Ballantyne	Peru	1900-2004	-12.60	-69.20	Ballantyne et al. (2011)
24	Niopolomice Gibiel	Poland	1900-2003	50.12	20.38	Treydte et al. (2007)
25	Niopolomice Gibiel	Poland	1900-2003	50.12	20.38	Treydte et al. (2007)
26	Suwalki	Poland	1900-2003	54.10	22.93	Treydte et al. (2007)
27	Cucuraena	Romania	1900-2005	47.40	25.08	Klesse et al. in prep
28	Giupalau	Romania	1900-2005	47.45	25.45	Klesse et al. in prep
29	Altai	Russia	1900-2005	50.23	89.04	Sidorova et al. (2012)
30	Indigirka	Russia	1900-2004	70.00	148.00	Sidorova et al. (2008)
31	Khakasia	Russia	1900-2005	54.41	89.96	Knorre et al. (2010)
32	Khibiny	Russia	1900-2005	67.41	33.15	Saurer et al. (2014)
33	Taimyr	Russia	1900-2005	72.00	102.00	Sidorova et al. (2010)
34	Tura	Russia	1900-2005	62.32	100.14	Sidorova et al. (2009)
35	Hlinna Dolina1	Slovakia	1900-2005	49.19	19.90	Weigt et al. in prep
36	Hlinna Dolina2	Slovakia	1900-2005	49.19	19.90	Weigt et al. in prep
37	Veza	Slovenia	1907-2005	46.37	13.69	Saurer et al. (2014)
38	Pafari	South Africa	1900-2005	-22.70	31.25	Woodborne et al. (2015)
39	Cazorla	Spain	1900-2005	37.81	-2.96	Treydte et al. (2007)
40	Pinar de Lillo	Spain	1900-2002	43.07	-5.25	Treydte et al. (2007)

Continued on next page

**Table A1 – continued from previous page**

#	Site	Country	Period	Lat	Lon	Reference
41	Pedraforca	Spain	1900-2005	42.24	1.70	Treydte et al. (2007)
42	Furuberget	Sweden	1900-2005	63.16	13.50	Saurer et al. (2014)
43	Torneträsk	Sweden	1900-2005	68.22	19.72	Loader et al. (2013)
44	Bettlachstock	Switzerland	1900-1995	47.22	7.42	Saurer et al. (2000, 2012)
45	Cavergno	Switzerland	1900-2003	46.35	8.60	Treydte et al. (2007)
46	Davos north	Switzerland	1900-2005	46.82	9.86	Klesse et al. in prep
47	Laegern B	Switzerland	1900-2005	47.48	8.36	Klesse et al. in prep
48	Loetschental	Switzerland	1900-2004	46.43	7.80	Saurer et al. (2014)
49	Loetschental N19	Switzerland	1900-2005	46.39	7.77	Klesse et al. in prep
50	Salvenach	Switzerland	1900-2005	46.91	7.15	Kimak and Leuenberger (2015)
51	Swiss National Park	Switzerland	1900-2005	46.00	10.00	Churakova (Sidorova) et al. (2016a)
52	Vigera	Switzerland	1900-2003	46.50	8.77	Treydte et al. (2007)
53	Elmali	Turkey	1900-2005	36.60	30.02	Saurer et al. (2014)
54	Lochwood	UK	1900-2003	55.27	-3.43	Saurer et al. (2014)
55	Sandringham	UK	1900-1994	52.83	0.50	Saurer et al. (2014)
56	Southern Upl.	UK	1907-2005	57.10	-5.43	Saurer et al. (2014)
57	Windsor	UK	1900-2003	51.41	-0.59	Treydte et al. (2007)
58	Woburn	UK	1900-2003	51.98	-0.59	Treydte et al. (2007)
59	Alton	USA	1900-1984	37.44	-112.49	Leavitt et al. (2007)
60	Aztec	USA	1900-1984	37.00	-107.82	Leavitt et al. (2007)
61	Blanco	USA	1900-2005	37.45	-118.17	Bale et al. (2011)
62	Cerro Colorado	USA	1900-1984	35.28	-107.72	Leavitt et al. (2007)
63	Dry Canyon	USA	1900-1984	37.58	-108.55	Leavitt et al. (2007)
64	Gate Canyon	USA	1900-1984	39.88	-110.23	Leavitt et al. (2007)
65	Hawthorne	USA	1900-1984	38.43	-118.75	Leavitt et al. (2007)
66	Kane Springs	USA	1900-1984	37.52	-109.90	Leavitt et al. (2007)
67	Lamoille	USA	1900-1984	40.69	-115.47	Leavitt et al. (2007)
68	Lower Colonias	USA	1900-1984	35.56	-105.55	Leavitt et al. (2007)
69	Mimbres	USA	1900-1984	33.00	-107.93	Leavitt et al. (2007)
70	NE AZ	USA	1900-1984	34.08	-109.35	Leavitt et al. (2007)
71	NC AZ	USA	1900-1984	34.83	-111.98	Leavitt et al. (2007)
72	Owl Canyon	USA	1900-1984	40.79	-105.18	Leavitt et al. (2007)
73	Ozena	USA	1900-1984	34.72	-119.24	Leavitt et al. (2007)