Temperature acclimation of photosynthesis and respiration: A key uncertainty in the carbon cycle-climate feedback

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Abstract Earth System Models typically use static responses to temperature to calculate photosynthesis and respiration, but experimental evidence suggests that many plants acclimate to prevailing temperatures. We incorporated representations of photosynthetic and leaf respiratory temperature acclimation into the Community Land Model, the terrestrial component of the Community Earth System Model. These processes increased terrestrial carbon pools by 20 Pg C (22%) at the end of the 21st century under a business-as-usual (Representative Concentration Pathway 8.5) climate scenario. Including the less certain estimates of stem and root respiration acclimation increased terrestrial carbon pools by an additional 17 Pg C (~40% overall increase). High latitudes gained the most carbon with acclimation, and tropical carbon pools increased least. However, results from both of these regions remain uncertain; few relevant data exist for tropical and boreal plants or for extreme temperatures. Constraining these uncertainties will produce more realistic estimates of land carbon feedbacks throughout the 21st century.

1. Introduction

The world's vegetation regulates climate in part by controlling carbon fluxes between the biosphere and the atmosphere [*Bonan*, 2008]. Photosynthesis and ecosystem respiration are the largest terrestrial carbon fluxes, and the net balance of these processes determines carbon-based ecosystem services like food and timber production [*Beer et al.*, 2010] and can buffer Earth's climate from anthropogenic CO_2 emissions. To understand how these ecosystem services will change in the future, the current generation of Earth System Models (ESMs) incorporates terrestrial responses to increasing CO_2 concentrations and climate change, though different ESMs represent these processes in diverse ways, resulting in considerable variability in carbon storage estimates among models. Many ESMs project that terrestrial carbon pools (combined plant and soil carbon pools) will increase by the end of the 21st century under a business-as-usual forcing scenario (Representative Concentration Pathway, RCP8.5) while a few project a loss (model range = −150 to 750 Pg C) [*Friedlingstein et al.*, 2014]. The magnitude of the net carbon gain or loss is dependent on the balance of a climate-driven decrease and a CO_2-driven increase in terrestrial carbon accumulation. Under a scenario where CO_2 increases by 1% per year, the climate-driven decrease ranged across models from −50 to −500 Pg C, while the CO_2-driven increase ranged from +300 to +1200 Pg C [*Arora et al.*, 2013].

The simulated climate-carbon feedbacks in ESMs assume an invariant, instantaneous response of plant physiological processes to changes in temperature. However, empirical evidence suggests that these instantaneous responses often vary with prevailing temperature, implying that plants "acclimate" to changes in recently experienced temperature [*Atkin et al.*, 2005, *Atkin and Tjoelker*, 2003, *Berry and Björkman*, 1980; *Sage and Kubien*, 2007; *Smith and Dukes*, 2013; *Way and Yamori*, 2014; *Yamori et al.*, 2014]. As such, representing physiological acclimation to prevailing temperatures could meaningfully influence simulations of carbon cycling in ESMs [*Ziehn et al.*, 2011; *Booth et al.*, 2012; *King et al.*, 2006; *Friend*, 2010; *Galbraith et al.*, 2010] and is thought to be a primary uncertainty in carbon cycle simulations [*Bernacchi et al.*, 2009; *Arneth et al.*, 2012; *Booth et al.*, 2012; *Ziehn et al.*, 2011].

Projections of combined plant and soil carbon pools over the 21st century are uncertain [*Friedlingstein et al.*, 2014], in part due to the simulated magnitude of response to CO_2 [*Arora et al.*, 2013], as well as to the unforced model variability (i.e., without the influence of climate or CO_2 forcing) [*Lombardozzi et al.*, 2014]

and inaccurate representation of processes such as land use and land cover change, nitrogen availability, and soil carbon turnover, which regulate rates of ecosystem carbon gain and loss. Though ESMs estimate that CO_2 fertilization is a stronger driver of terrestrial carbon gain than climate change [*Arora et al.*, 2013; *Friedlingstein et al.*, 2006], modifications to the climate response, such as the inclusion of temperature acclimation, will affect the magnitude of the carbon cycle response to future climate forcings.

Model parameterizations to account for the acclimation of C_3 photosynthesis and leaf respiration were proposed by *Kattge and Knorr* [2007] and *Atkin et al.* [2008], respectively [also see *June et al.*, 2004; *King et al.*, 2006; *Wythers et al.*, 2013, 2005; *Ziehn et al.*, 2011]. In this study, we tested the sensitivity of terrestrial carbon pools to parameterization of C_3 photosynthetic and plant respiratory temperature acclimation using the Community Land Model, version 4.5, with active carbon and nitrogen biogeochemical cycling CLM4.5 (BGC) in simulations from 1850 to 2100 using a business-as-usual future climate forcing scenario (RCP8.5) from 2005 to 2100. Note that we focus on plant temperature acclimation and do not include representations of heterotrophic respiration acclimation, despite its importance in soil carbon pools [*Frey et al.*, 2013]. We tested four versions of the model to determine the importance of plant temperature acclimation to terrestrial carbon storage: (1) without acclimation, (2) including photosynthetic acclimation (C_3 plants only), (3) including photosynthetic and leaf respiratory acclimation, and (4) including photosynthetic and whole plant respiratory (leaf, stem, and root) acclimation. We expected that including temperature acclimation would increase terrestrial carbon pools throughout the 21st century, particularly in tropical and arctic latitudes where high and low temperatures likely limit the physiological processes governing terrestrial carbon gain. The impacts of changes in individual processes (i.e., photosynthetic or respiratory acclimation) on simulated land carbon uptake have been investigated in some global models [*Arneth et al.*, 2012; *King et al.*, 2006; *Atkin et al.*, 2008], though this is the first time that the combined impacts of photosynthetic and respiratory temperature acclimation have been evaluated.

2. Methods

The CLM4.5(BGC) [*Oleson et al.*, 2013] is an updated version of CLM4 [*Lawrence et al.*, 2011]. Key model improvements pertinent to the carbon cycle are revisions to the leaf photosynthesis and canopy integration [*Bonan et al.*, 2011, 2012], vertically resolved soil carbon and nitrogen biogeochemistry [*Koven et al.*, 2013], and permafrost hydrology [*Swenson et al.*, 2012]. Whereas the CLM4 carbon-nitrogen biogeochemical parameterization—CLM4(CN)—loses carbon over the twentieth century, CLM4.5(BGC) gains carbon and is in better agreement with observations [*Koven et al.*, 2013].

The revised C_3 photosynthesis parameterization uses the temperature kinetics of Rubisco derived from experimental studies [*Bernacchi et al.*, 2001, 2003], modified to include high-temperature stress [*Leuning*, 2002], as described by *Bonan et al.* [2011, 2012]. In this formulation, the temperature response of the parameters V_{cmax} (maximum rate of carboxylation), J_{max} (maximum potential rate of electron transport), R_d (dark respiration), Γ_* (CO_2 compensation point), and K_c and K_o (Michaelis-Menten constants) vary with leaf temperature using the Arrhenius function:

$$f(T_v) = \exp\left[\frac{\Delta H_a}{298.15\Re}\left(1 - \frac{298.15}{T_v}\right)\right] \tag{1}$$

where T_v is leaf temperature (K), $\Re$ is the gas constant ($8.314\,\mathrm{J\,K^{-1}\,mol^{-1}}$), and ΔH_a is the activation energy ($\mathrm{J\,mol^{-1}}$). Thermal breakdown of metabolic processes is included by further multiplying V_{cmax}, J_{max}, and R_d by a high-temperature stress function [*Leuning*, 2002]:

$$f_H(T_v) = \frac{1 + \exp\left(\frac{298.15\Delta S - \Delta H_d}{298.15\Re}\right)}{1 + \exp\left(\frac{\Delta S T_v - \Delta H_d}{\Re T_v}\right)} \tag{2}$$

where ΔH_d is the deactivation energy ($\mathrm{J\,mol^{-1}}$) and ΔS is entropy ($\mathrm{J\,K^{-1}\,mol^{-1}}$). Equations (1) and (2) together form the peaked Arrhenius function, with a maximum rate at a specified temperature [*Johnson et al.*, 1942]. Three parameters (ΔH_a, ΔH_d, and ΔS) determine the shape of the temperature response and the temperature optimum (Table 1). Values of ΔH_a are from *Bernacchi et al.* [2001], with the ΔH_a value for J_{max} from *Bernacchi et al.* [2003]. *Leuning* [2002] gives ΔH_d and ΔS for V_{cmax} and J_{max}. The ΔS value for R_d is taken here as the average of those for V_{cmax} and J_{max}. In the implementation without temperature acclimation, these

Table 1. Temperature Dependence Parameters for C_3 Photosynthesis[a]

Parameter	ΔH_a (J mol^{-1})	ΔH_d (J mol^{-1})	ΔS (J mol^{-1} K^{-1})
V_{cmax}	65,330	149,250	485
J_{max}	43,540	152,040	495
R_d	46,390	150,650	490
Γ_*	37,830	–	–
K_c	79,430	–	–
K_o	36,380	–	–

[a]The parameters in this table do not allow for temperature acclimation of photosynthesis; acclimation is implemented using equations (3) and (4).

parameters are constant and are the same for all plant functional types. The resulting temperature optimum is 33.3°C for V_{cmax} and 29.4°C for J_{max}. The relationship of J_{max} to V_{cmax} at 25°C is $J_{max25} = 1.97V_{cmax25}$.

We implemented the representation of photosynthetic temperature acclimation that was proposed by *Kattge and Knorr* [2007] for C_3 plants, which was previously implemented in the JULES model [*Arneth et al.*, 2012], and allows the form of the peaked Arrhenius functions to shift with growth temperature. Specifically, the photosynthetic acclimation to growth temperature is achieved by allowing ΔS to vary with growth temperature (defined as the running 10 day mean temperature, T_{10} in K, calculated within the model based on air temperature from the forcing data) using an empirical relationship fitted to the temperature responses of 36 species grown at different temperatures, as

$$\Delta S = 668.39 - 1.07(T_{10} - T_f) \qquad \text{for} \quad V_{cmax}$$
$$\Delta S = 659.70 - 0.75(T_{10} - T_f) \qquad \text{for} \quad J_{max} \qquad (3)$$

where T_f is the freezing point of water. The temperature dependence of ΔS causes the temperature optimum of V_{cmax} and J_{max} to vary with growth temperature and increase with warmer temperature. The acclimation parameterization used new values from *Kattge and Knorr* [2007], where $\Delta H_d = 200,000$, $\Delta H_a = 72,000$ for V_{cmax}, and $\Delta H_a = 50,000$ for J_{max}, with the same values used for all C_3 plant functional types. Additionally, the ratio J_{max25}/V_{cmax25} varies with growth temperature, also from *Kattge and Knorr* [2007]:

$$J_{max\,25}/V_{c\,max\,25} = 2.59 - 0.035(T_{10} - T_f) \qquad (4)$$

The growth temperatures considered by *Kattge and Knorr* [2007] range from 11 to 35°C. Outside of this range, we do not allow further acclimation to very high or low temperatures. This likely limits the effect of acclimation in arctic and tropical latitudes and during the spring and fall. In our simulations, the 10 day running mean temperature, calculated based on the historical and future (RCP8.5) forcing scenarios, was used to represent the growth temperature in the acclimation terms. This is the same as the 10 day running mean used by *Atkin et al.* [2008] for respiratory acclimation but different from the 30 day mean temperature used by *Kattge and Knorr* [2007] for photosynthetic acclimation. We choose to use a 10 day running mean for long-term photosynthetic and respiratory acclimation to be consistent between the photosynthetic and respiratory acclimation terms. *Dietze* [2014] found that the timescale of acclimation is likely inconsequential over a time span of 3–45 days, so we assume that the sensitivity to a 10 day versus 30 day running mean is negligible.

To test the effects of plant temperature acclimation, we ran four CLM4.5(BGC) simulations. Each simulation ran from 1850 to 2100 with land use change using atmospheric forcing data archived from previous Community Earth System Model simulations using historical forcings through 2005 and the Representative Concentration Pathway 8.5 forcing (RCP8.5) [*Meehl et al.*, 2012] through 2100. Each simulation was spun up using 1850 forcings until carbon pools stabilized. A 100 year time series of the spun-up 1850 control simulation provided estimates of internal model variability (i.e., the unforced variability without the influence of climate or CO_2 forcing).

We compared two simulations to assess the importance of photosynthetic acclimation. The first simulation, termed "no photosynthetic acclimation," did not use the *Kattge and Knorr* [2007] parameterization, meaning that ΔS and the ratio J_{max25}/V_{cmax25} were held constant (values in Table 1; equations (3) and (4) not used) rather than varying with growth temperature. The second simulation included photosynthetic temperature acclimation for C_3 plants as described above and was termed "photosynthetic acclimation."
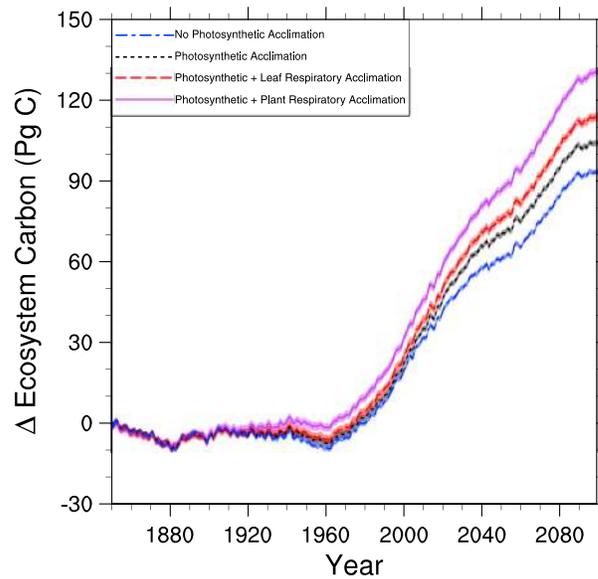
Figure 1. The change in global values of total ecosystem carbon pools relative to 1850 in Community Land Model (CLM) simulations that alter temperature acclimation (photosynthesis and respiration). Shading represents ±1 standard deviation of internal model variability.

We used two additional simulations, both of which featured the photosynthetic temperature acclimation described above, to assess the effects of respiratory acclimation. The first of these, termed "photosynthetic and leaf respiratory acclimation," further included a representation of leaf respiration temperature acclimation. The parameterization was derived using experimental data from 19 species grown at four different growth temperatures [*Campbell et al.*, 2007] and adjusts the basal rate of leaf respiration, rather than the temperature response [*Atkin et al.*, 2008]. The acclimated simulated leaf basal respiration rate, R_A, is modified based on the 10 day running mean temperature, T_{10}, relative to a reference temperature, T_{ref} (298.15 K in the model). The temperature deviation is multiplied by a correction factor, C ($-0.00794\,K^{-1}$), fitted to the empirical data of *Campbell et al.* [2007] by *Atkin et al.* [2008]:

$$R_A = R_T \times 10^{C \times (T_{10} - T_{ref})} \tag{5}$$

The nonacclimated leaf respiration rate, R_T, is calculated using the peaked Arrhenius function with parameter values in Table 1. The last simulation, termed "photosynthetic and plant respiratory acclimation," extended the respiration acclimation function above to additionally encompass both stem and root respiratory acclimation, similar to previous testing in the MOSES-TRIFFID model framework by *Atkin et al.* [2008]. The root and stem parameter estimates were based on data collected for leaf respiration acclimation, however, so there was large uncertainty associated with this simulation, and it was not a key focus of this analysis. In contrast with photosynthetic acclimation, which was only applied to C$_3$ plants, respiration acclimation was used for all plant functional types.

3. Results and Discussion

Including photosynthetic and leaf respiratory temperature acclimation amplified the gain in the global terrestrial carbon pools by up to 22% (40% if including stem and root respiration acclimation), relative to a simulation without temperature acclimation, by the end of the 21st century (Figure 1). Relative to 1850, photosynthetic acclimation increased total global carbon gained in the terrestrial carbon pool by 10.7 ± 1.1 Pg C at 2100 (the ± terms here and below are standard deviations of internal model variability) compared to the simulation with no temperature acclimation (Figure 1). Including leaf respiration acclimation and photosynthetic acclimation increased the global terrestrial carbon pool by a total of 20.3 ± 1.6 Pg C at 2100, and including plant respiration (leaf, stem, and root) and photosynthetic acclimation increased the global terrestrial carbon pool by a total of 37.4 ± 1.6 Pg C at 2100 compared to the simulation with no acclimation (Figure 1).

Models used in the Coupled Model Intercomparison Project Phase 5 (CMIP5) simulations lose carbon as planetary temperature increases [*Friedlingstein et al.*, 2006; *Arora et al.*, 2013; *Ciais et al.*, 2013]. Our results suggest that the net global carbon loss with warming is reduced when photosynthesis and respiration acclimation is considered (Figure S1 in the supporting information), with analogous trends anticipated in other land surface models. For example, photosynthetic acclimation increased global gross primary productivity in JULES by 25% at 2100 compared to not including photosynthetic acclimation [*Arneth et al.*, 2012], and including respiration acclimation increased global plant and soil carbon pools in 2100 by approximately 75 Pg C in GTEC 2.0 [*King et al.*, 2006] and increased net primary productivity by 9% at 2100 in temperate
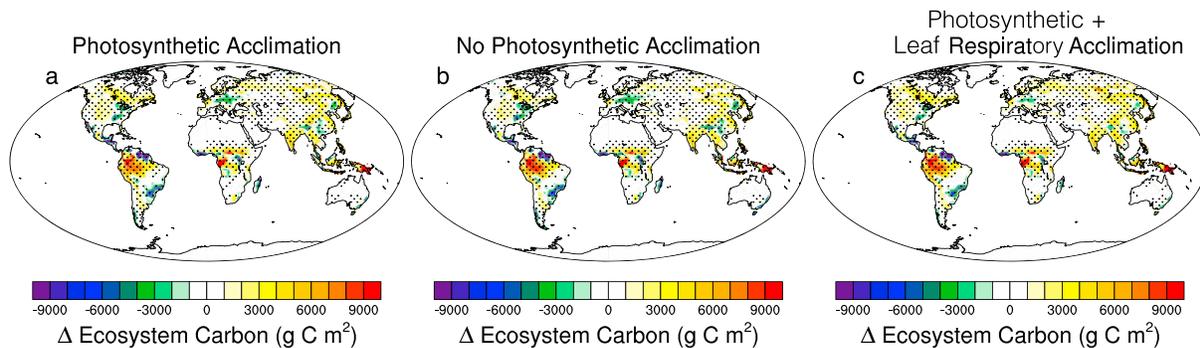
Figure 2. The spatial distribution of changes in ecosystem carbon pools relative to 1850 (ΔC = 2100–1850) in simulations that (a) include photosynthetic temperature acclimation, (b) do not include temperature acclimation, and (c) include photosynthetic and leaf respiratory temperature acclimation. Stippling indicates a significant change relative to 1850, defined as larger than ±2 standard deviations (calculated from internal variability).

boreal sites using PnET-CN [*Wythers et al.*, 2013]. In our simulations, the CLM4.5(BGC) without temperature acclimation gained ~93 Pg C at 2100 (Figure 1) due to the forcing scenario, placing the global terrestrial carbon gain on the low end of the range simulated by the other models that gain carbon (total range: −150 to 750 Pg C) [*Friedlingstein et al.*, 2014]. The additional ~10–20 Pg C caused by including temperature acclimation, or more (37 Pg C) if stem and root respiration acclimate in the same manner as leaf respiration, is large relative to CLM4.5(BGC) carbon gain (93 Pg C without acclimation), likely due to the low CO_2 fertilization response caused by the representation of nitrogen limitation in the model's carbon-nitrogen biogeochemistry, which is not included in most other land surface models [*Bonan and Levis*, 2010; *Arora et al.*, 2013; *Ciais et al.*, 2013; *Smith and Dukes*, 2013]. However, this carbon gain is small relative to the range of carbon gain across CMIP5 models.

Spatial patterns of terrestrial carbon illustrate that in most locations, carbon pools were substantially larger in 2100 compared to 1850 in simulations with and without temperature acclimation (Figure 2), likely due to CO_2 fertilization [*Arora et al.*, 2013; *Williams et al.*, 2014]. The largest carbon increases were in tropical regions, with more than 6000 g C m^{-2} gained in the Amazon and Congo regions (Figure 2). We compared the carbon changes in the temperature acclimation simulations over the period 1850 to 2100 relative to the changes in the simulation without temperature acclimation to gain a clearer depiction of the differences between simulations (Figure 3). Compared to the simulation without temperature acclimation, including temperature acclimation resulted in greater carbon gains in the Arctic, primarily due to photosynthetic temperature acclimation (Figures 3 and S2b). There was a large net carbon gain (>6000 g C m^{-2}) in the tropics by the end of the 21st century in all simulations (Figure 2); however, the net carbon gain in the tropics was smaller in simulations that included temperature acclimation (Figure 3). Including respiratory acclimation allowed for somewhat larger increases in tropical carbon pools than including photosynthetic acclimation alone (Figure 2), though the increase was still less than the simulation without temperature acclimation (Figure 3). *Atkin et al.* [2008] similarly found that including plant respiratory acclimation reduced respiration rates in tropical regions by up to 20% (i.e., causing carbon gain). Since the parameter estimates for stem and root respiratory acclimation are based on leaf respiratory acclimation measurements and therefore highly uncertain, we focus analysis on simulations including leaf, not plant (as in *Atkin et al.* [2008]), respiratory acclimation.

Temperature acclimation led to a smaller net carbon gain by 2100 in the tropics, in part because simulations including temperature acclimation had more carbon in the tropics in 1850 than simulations without acclimation (Figure S3). Exploring this for the Amazon Basin (northwest bound: 0°N, 70°W; southeast bound: 10°S, 50°W), the absolute magnitude of ecosystem carbon was highest at all times in the simulation that included photosynthetic temperature acclimation, though the total carbon increase from 1850 to 2100 was less than the carbon increase over the same time period without temperature acclimation (Figure S2a). In the acclimation simulations, the Amazonian carbon gain plateaued at 2.80 Pg C yr^{-1} by the end of the 21st century, suggesting a possible limitation by another ecosystem driver. Other studies have shown that nutrients [*Cleveland et al.*, 2011; *Norby et al.*, 2010] and drought [*Zhao and Running*, 2010] limit tropical net primary productivity (NPP). However, soil wetness was similar for all simulations throughout the 21st century, and leaf
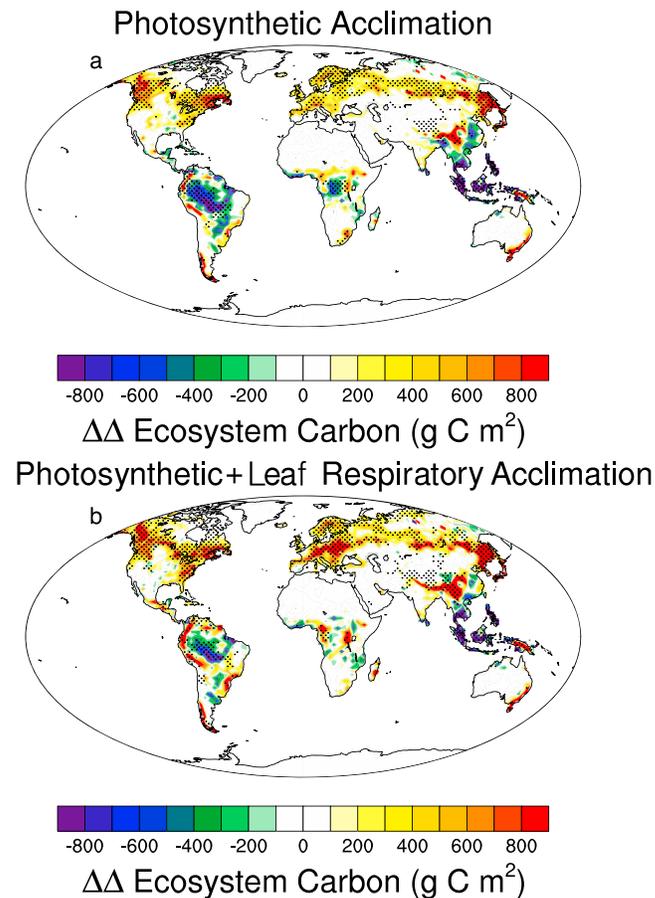
Figure 3. Difference in the change in ecosystem carbon over the simulation (ΔC, Figure 2) relative to the simulation without temperature acclimation for simulations that include (a) photosynthetic temperature acclimation (difference between Figures 2a and 2b) and (b) photosynthetic and leaf respiration temperature acclimation (difference between Figures 2c and 2b). "ΔΔ" denotes the temporal change from 1850 and the departure between two experiments. Stippling indicates a significant change, defined as larger than ±2 standard deviations (calculated from internal variability).

area index and nitrogen limitation of photosynthesis were more limiting in simulations not including temperature acclimation (Figure S4). It is possible that the nitrogen cycle was stimulated by including acclimation (N fixation is a function of NPP in CLM, so higher productivity might result in less N limitation), resulting in faster rates of soil decomposition that reduced the amount of carbon stored in Amazonian soils, leading to a lower rate of terrestrial carbon gain during the 1850–2100 time period.

In addition to allowing plants to adjust to changes in temperature, incorporating temperature acclimation allows for geographic variability in plant responses to temperature [*Leuning*, 2002], as noted in the changes in 1850 ecosystem carbon pools in simulations including acclimation (Figure S3). While tropical carbon pools increased in 1850 in response to temperature acclimation, carbon pools were smaller in many other locations, with large decreases in high latitudes when leaf respiration acclimation was included, akin to the high-latitude respiratory increases (i.e., carbon loss) in response to leaf respiration acclimation found by *Atkin et al.* [2008]. This pattern emerges from the formulation of leaf respiratory acclimation, which allows respiration to acclimate to cooler temperatures as well as warmer temperatures, increasing respiratory carbon

losses in cooler regions and decreasing respiration in warmer regions. Unlike the changes in geographic variability, including temperature acclimation did not alter the seasonal variability of gross primary product (Figure S5), which resembled the seasonal variability seen in FLUXNET-MTE data [*Bonan et al.*, 2011].

Though the functions used to simulate temperature acclimation are among the best approximations currently available for large-scale modeling (but see *Atkin et al.* [2015]), there remain large uncertainties associated with the parameterizations. For example, acclimation can change the basal rates and temperature responses of photosynthesis and respiration and might also differentially affect the photosynthetic processes of electron transport and carboxylation. Additionally, whether or not the J_{max25}/V_{cmax25} ratio (equation (4)) acclimates to temperature changes is uncertain. However, it is still unclear from available data whether acclimation of one or all of these processes should be incorporated into models. Also noteworthy is the fact that the acclimation functions were developed based on data from primarily temperate plants (photosynthesis) [*Kattge and Knorr*, 2007] and subtropical plants (respiration) [*Atkin et al.*, 2008], though other plant functional types might respond differently [*Atkin et al.*, 2005, 2015; *Smith and Dukes*, 2013; *Slot and Kitajima*, 2015]. In fact, recent evidence highlights that tropical trees may not acclimate to changes in future temperatures [*Vårhammar et al.*, 2015] (but see *Slot et al.* [2015]). This is particularly important since our results show that acclimation impacts tropical and arctic latitudes most strongly, and data for these plant types had little influence on the development of the acclimation formulations we used. Also, the temperature range over which

acclimation is restricted (11–35°C, as in *Kattge and Knorr* [2007]) will largely impact these same regions, as well as spring and fall times of the growing season.

Additionally, the photosynthetic acclimation functions were primarily developed from a variety of different plants that were grown under different temperature regimes. Fewer than half of the species were grown under multiple temperatures. Therefore, the acclimation functions contained an implicit assumption of high plasticity in temperature response, in contrast to the default model, which assumed no acclimation or plasticity at all. It is not clear whether this parameterization represents acclimation to changing temperature over time or simply differences in instantaneous responses of species over space. In reality, some intermediate case is likely to be realized, but our parameterization assumes that temperature changes through time, representing acclimation. Analysis of respiration acclimation shows that temporal acclimation can also improve estimates of leaf respiration across space [*Vanderwel et al.*, 2015]. There is additional uncertainty associated with choosing a 10 day acclimation temperature, though *Dietze* [2014] and *Atkin et al.* [2008] find the uncertainty associated with length of acclimation time period to be small. Last, the parameterizations do not account for interactions with other environmental factors, such as drought and nutrient availability, which might alter the acclimation response. These uncertainties require further investigation.

4. Conclusion

Processes like temperature acclimation can contribute to the land carbon sink but are currently overlooked in future ESM projections, despite the increase in terrestrial carbon gain that results from including temperature acclimation in models. We focus our analysis on one model to isolate the impact of changing a single parameterization on future terrestrial carbon projections, which serves to highlight the range of parameterization uncertainty. We expect that including temperature acclimation in other models will cause an increase in the multimodel mean carbon uptake (e.g., photosynthetic acclimation also increases carbon in JULES) [*Arneth et al.*, 2012]. However, we acknowledge that intermodel differences, as well as uncertainty in natural variability, are important for determining changes in carbon cycle projections. In addition to understanding the model response uncertainty, future research should prioritize understanding the biochemical mechanisms controlling acclimation to improve model parameterizations. Indeed, determining whether field observations truly capture acclimation is essential to future modeling efforts. It is also necessary to understand how photosynthetic and respiration acclimation behave in concert and whether representing acclimation of each process independently, as we have done here, is representative of observed behaviors. Addressing these and associated uncertainties will improve the representation of photosynthesis and respiration in ESMs and change projections of terrestrial carbon pools.

References

Arneth, A., L. Mercado, J. Kattge, and B. B. B. Booth (2012), Future challenges of representing land-processes in studies on land-atmosphere interactions, *Biogeosciences*, 9, 3587–99.

Arora, V. K., et al. (2013), Carbon–concentration and carbon–climate feedbacks in CMIP5 Earth System Models, *J. Clim.*, 26, 5289–5314.

Atkin, O. K., and M. G. Tjoelker (2003), Thermal acclimation and the dynamic response of plant respiration to temperature, *Trends Plant Sci.*, 8, 343–351.

Atkin, O. K., D. Bruhn, V. M. Hurry, and M. G. Tjoelker (2005), The hot and the cold: Unravelling the variable response of plant respiration to temperature, *Funct. Plant Biol.*, 32, 87–105.

Atkin, O. K., L. J. Atkinson, R. A. Fisher, C. D. Campbell, J. Zaragoza-Castells, J. W. Pitchford, F. I. Woodward, and V. Hurry (2008), Using temperature-dependent changes in leaf scaling relationships to quantitatively account for thermal acclimation of respiration in a coupled global climate vegetation model, *Global Change Biol.*, 14, 2709–2726.

Atkin, O. K., et al. (2015), Global variability in leaf respiration in relation to climate, plant functional types and leaf traits, *New Phytol.*, 206, 614–636.

Beer, C., et al. (2010), Terrestrial gross carbon dioxide uptake: Global distribution and covariation with climate, *Science*, 329, 834–838.

Bernacchi, C. J., E. L. Singsaas, C. Pimentel, A. R. Portis Jr., and S. P. Long (2001), Improved temperature response functions for models of Rubisco-limited photosynthesis, *Plant Cell Environ.*, 24, 253–259.

Bernacchi, C. J., C. Pimentel, and S. P. Long (2003), In vivo temperature response functions of parameters required to model RuBP-limited photosynthesis, *Plant Cell Environ.*, 26, 1419–1430.

Bernacchi, C. J., D. M. Rosenthal, C. Pimentel, S. P. Long, and G. D. Farquhar (2009), Modeling the temperature dependence of C_3 photosynthesis, in *Photosynthesis in Silico: Understanding Complexity From Molecules to Ecosystems*, edited by A. Laisk, L. Nedbal, and Govindjee, pp. 231–246, Springer Science + Business Media B.V., Netherlands.

Berry, J., and O. Björkman (1980), Photosynthetic response and adaptation to temperature in higher plants, *Annu. Rev. Plant Physiol. Plant Mol. Biol*, 31, 491–543.

Bonan, G. B. (2008), Forests and climate change: Forcings, feedbacks, and the climate benefits of forests, *Science*, 320, 1444–1449.

Bonan, G. B., and S. Levis (2010), Quantifying carbon-nitrogen feedbacks in the Community Land Model (CLM4), *Geophys. Res. Lett.*, 37, L07401, doi:10.1029/2010GL042430.

Bonan, G. B., P. J. Lawrence, K. W. Oleson, S. Levis, M. Jung, M. Reichstein, D. M. Lawrence, and S. C. Swenson (2011), Improving canopy processes in the Community Land Model version 4 (CLM4) using global flux fields empirically inferred from FLUXNET data, *J. Geophys. Res.*, *116*, G02014, doi:10.1029/2010JG001593.

Bonan, G. B., K. W. Oleson, R. A. Fisher, G. Lasslop, and M. Reichstein (2012), Reconciling leaf physiological traits and canopy flux data: Use of the TRY and FLUXNET databases in the Community Land Model version 4, *J. Geophys. Res.*, *117*, G02026, doi:10.1029/2011JG001913.

Booth, B. B. B., C. D. Jones, M. Collins, I. J. Totterdell, P. M. Cox, S. Sitch, C. Huntingford, R. A. Betts, G. R. Harris, and J. Lloyd (2012), High sensitivity of future global warming to land carbon cycle processes, *Environ. Res. Lett.*, *7*, doi:10.1088/1748-9326/7/2/024002.

Campbell, C. D., L. J. Atkinson, J. Zaragoza-Castells, M. Lundmark, O. K. Atkin, and V. Hurry (2007), Acclimation of photosynthesis and respiration is asynchronous in response to changes in temperature regardless of plant functional type, *New Phytol.*, *176*, 375–389.

Ciais, P., et al. (2013), Carbon and Other Biogeochemical Cycles, in *Climate Change 2013: The Physical Science Basis. Contribution of Working Group 1 to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by T. F. Stocker et al., pp. 1–106, Cambridge Univ. Press, U. K., and New York.

Cleveland, C. C., et al. (2011), Relationships among net primary productivity, nutrients and climate in tropical rain forest: A pan-tropical analysis, *Ecol. Lett.*, *14*, 939–47.

Dietze, M. C. (2014), Gaps in knowledge and data driving uncertainty in models of photosynthesis, *Photosynth. Res.*, *119*, 3–14.

Frey, S. D., J. Lee, J. M. Melillo, and J. Six (2013), The temperature response of soil microbial efficiency and its feedback to climate, *Nat. Clim. Change*, *3*, 395–398.

Friedlingstein, P., et al. (2006), Climate-carbon cycle feedback analysis: Results from the C4MIP model intercomparison, *J. Clim.*, *19*, 3337–3353.

Friedlingstein, P., M. Meinshausen, V. K. Arora, C. D. Jones, A. Anav, S. K. Liddicoat, and R. Knutti (2014), Uncertainties in CMIP5 climate projections due to carbon cycle feedbacks, *J. Clim.*, *27*, 511–526.

Friend, A. D. (2010), Terrestrial plant production and climate change, *J. Exp. Bot.*, *61*, 1293–1309.

Galbraith, D., P. E. Levy, S. Sitch, C. Huntingford, P. Cox, M. Williams, and P. Meir (2010), Multiple mechanisms of Amazonian forest biomass losses in three dynamic global vegetation models under climate change, *New Phytol.*, *187*, 647–665.

Johnson, F., H. Eyring, and R. Williams (1942), The nature of enzyme inhibitions in bacterial luminescence: Sulphanilamide, urethane, temperature, pressure, *J Cell Comp. Physiol.*, *20*, 247–248.

June, T., J. R. Evans, and G. D. Farquhar (2004), A simple new equation for the reversible temperature dependence of photosynthetic electron transport: A study on soybean leaf, *Funct. Plant Biol.*, *31*, 275–283.

Kattge, J., and W. Knorr (2007), Temperature acclimation in a biochemical model of photosynthesis: A reanalysis of data from 36 species, *Plant Cell Environ.*, *30*, 1176–1190.

King, A. W., C. A. Gunderson, W. M. Post, D. J. Weston, and S. D. Wullschleger (2006), Plant respiration in a warmer world, *Science*, *312*, 536–537.

Koven, C. D., W. J. Riley, Z. M. Subin, J. Y. Tang, M. S. Torn, W. D. Collins, G. B. Bonan, D. M. Lawrence, and S. C. Swenson (2013), The effect of vertically resolved soil biogeochemistry and alternate soil C and N models on C dynamics of CLM4, *Biogeosciences*, *10*, 7109–7131.

Lawrence, D. M., et al. (2011), Parameterization improvements and functional and structural advances in version 4 of the Community Land Model, *J. Adv. Model. Earth Syst.*, *3*, M03001, doi:10.1029/2011MS00045.

Leuning, R. (2002), Temperature dependence of two parameters in a photosynthesis model, *Plant Cell Environ.*, 1205–1210.

Lombardozzi, D., G. B. Bonan, and D. W. Nychka (2014), The emerging anthropogenic signal in land–atmosphere carbon-cycle coupling, *Nat. Clim. Change*, *4*, 796–800.

Meehl, G. A., et al. (2012), Climate system response to external forcings and climate change projections in CCSM4, *J. Clim.*, *25*, 3661–3683.

Norby, R. J., J. M. Warren, C. M. Iversen, B. E. Medlyn, and R. E. McMurtrie (2010), CO_2 enhancement of forest productivity constrained by limited nitrogen availability P, *Natl. Acad. Sci. U.S.A.*, *107*, 19,368–19,373.

Oleson, K., et al. (2013), Technical description of version 4.5 of the Community Land Model (CLM) NCAR Tech. Note, 434 pp.

Sage, R. F., and D. S. Kubien (2007), The temperature response of C_3 and C_4 photosynthesis, *Plant Cell Environ.*, *30*, 1086–1106.

Slot, M., and K. Kitajima (2015), General patterns of acclimation of leaf respiration to elevated temperatures across biomes and plant types, *Oecologia*, *177*, 885–900.

Slot, M., C. Rey-Sánchez, S. Gerber, J. W. Lichstein, K. Winter, and K. Kitajima (2015), Thermal acclimation of leaf respiration of tropical trees and lianas: Response to experimental canopy warming, and consequences for tropical forest carbon balance, *Global Change Biol.*, *20*, 2915–2926.

Smith, N. G., and J. S. Dukes (2013), Plant respiration and photosynthesis in global-scale models: Incorporating acclimation to temperature and CO_2, *Global Change Biol.*, *19*, 45–63.

Swenson, S. C., D. M. Lawrence, and H. Lee (2012), Improved simulation of the terrestrial hydrological cycle in permafrost regions by the Community Land Model, *J. Adv. Model. Earth Syst.*, *4*, M08002, doi:10.1029/2012MS000165.

Vanderwel, M. C., M. Slot, J. W. Lichstein, P. B. Reich, J. Kattge, O. K. Atkin, K. J. Bloomfield, M. G. Tjoelker, and K. Kitajima (2015), Global convergence in leaf respiration from estimates of thermal acclimation across time and space, *New Phytol.*, *207*, 1026–1037.

Vårhammar, A., G. Wallin, C. M. McLean, M. E. Dusenge, B. E. Medlyn, T. B. Hasper, D. Nsabimana, and J. Uddling (2015), Photosynthetic temperature responses of tree species in Rwanda: Evidence of pronounced negative effects of high temperature in montane rainforest climax species, *New Phytol.*, *206*, 1000–1012.

Way, D. A., and W. Yamori (2014), Thermal acclimation of photosynthesis: On the importance of adjusting our definitions and accounting for thermal acclimation of respiration, *Photosynth. Res.*, *119*, 89–100.

Williams, I. N., M. S. Torn, W. J. Riley, and M. F. Wehner (2014), Impacts of climate extremes on gross primary production under global warming, *Environ. Res. Lett.*, *9*, doi:10.1088/1748-9326/9/9/094011.

Wythers, K. R., P. B. Reich, M. G. Tjoelker, and P. B. Bolstad (2005), Foliar respiration acclimation to temperature and temperature variable Q_{10} alter ecosystem carbon balance, *Global Change Biol.*, *11*, 435–449.

Wythers, K. R., P. B. Reich, and J. B. Bradford (2013), Incorporating temperature-sensitive Q_{10} and foliar respiration acclimation algorithms modifies modeled ecosystem responses to global change, *J. Geophys Res. Biogeosci.*, *118*, 77–90, doi:10.1029/2011JG001897.

Yamori, W., K. Hikosaka, and D. Way (2014), Temperature response of photosynthesis in C_3, C_4 and CAM plants: Temperature acclimation and temperature adaptation, *Photosynth. Res.*, *119*, 101–117.

Zhao, M., and S. W. Running (2010), Drought-induced reduction in global terrestrial net primary production from 2000 through 2009, *Science*, *329*, 940–943.

Ziehn, T., J. Kattge, W. Knorr, and M. Scholze (2011), Improving the predictability of global CO_2 assimilation rates under climate change, *Geophys. Res. Lett.*, *38*, L10404, doi:10.1029/2011GL047182.