Plant Physiology Increases the Magnitude and Spread of the Transient Climate Response in CMIP6 Earth System Models

Claire M. Zarakas1*, Abigail L. Swann1,2, Marysa M. Laguë1,3, Kyle C. Armour1,4, and James T. Randerson5

1 Department of Atmospheric Sciences, University of Washington
2 Department of Biology, University of Washington
3 Department of Earth and Planetary Sciences, University of California, Berkeley
4 School of Oceanography, University of Washington
5 Department of Earth System Science, University of California, Irvine

*Corresponding author email: czarakas@uw.edu

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Abstract:

Increasing concentrations of CO$_2$ in the atmosphere not only influence climate through CO$_2$’s effect as a greenhouse gas but also through its impact on plants. Plants respond to atmospheric CO$_2$ concentrations in several ways that can alter surface energy and water fluxes and thus surface climate, including changes in stomatal conductance, water use, and canopy leaf area. These plant physiological responses are already embedded in Earth system models, and a robust literature demonstrates that they can affect global-scale temperature. However, the physiological contribution to transient warming has yet to be assessed systematically in Earth system models. Here this gap is addressed using carbon cycle simulations from the 5th and 6th phases of the Coupled Model Intercomparison Project (CMIP) to isolate the radiative and physiological contributions to the transient climate response (TCR). In CMIP6 models, the physiological effect contributes 0.11°C (standard deviation: 0.10°C; range: 0.02 - 0.29°C) of warming to the TCR, corresponding to 5.2% of the full TCR (standard deviation: 4.1%; range: 1.4 - 13.9%). Moreover, variation in the physiological contribution to the TCR across models contributes disproportionately more to the inter-model spread of TCR estimates than it does to the mean. The largest contribution of plant physiology to CO$_2$-forced warming – and the inter-model spread in warming – occurs over land, especially in forested regions.

1. Introduction

Increasing concentrations of atmospheric CO$_2$ alter global temperature through both CO$_2$’s role as a greenhouse gas within the atmosphere (radiative effect) and through plants’ response to CO$_2$ at the land surface (physiological effect). Plants respond to atmospheric CO$_2$ concentrations by regulating their stomata (pores on the leaves which modulate the exchange of CO$_2$ and water vapor between the leaf and the
atmosphere), changing water use, adjusting canopy leaf area, and ultimately, changing species composition and vegetation cover. These plant physiological responses to higher CO\textsubscript{2} can influence land surface temperature by altering land evapotranspiration, surface albedo, and surface roughness, which are important controls over the fluxes of water and energy between the land surface and the atmosphere. Here we use the term “physiological effect” to encompass the net effect of all plant responses to increasing CO\textsubscript{2}, but note that in some past work the term refers solely to the effect of changes in stomatal conductance (e.g. Skinner et al. 2018).

Plant responses to CO\textsubscript{2} modulate land evapotranspiration through two opposing mechanisms. Higher concentrations of CO\textsubscript{2} in the atmosphere provide a larger gradient over which CO\textsubscript{2} diffuses into the interior airspace of leaves. As a result, most plant types close their stomata in response to increasing CO\textsubscript{2} (the stomatal response), thereby decreasing transpiration per leaf area (Field et al. 1995). In contrast, photosynthetic rates in some cases are limited by access to CO\textsubscript{2}, and in those cases more CO\textsubscript{2} can lead to higher rates of photosynthesis, dubbed CO\textsubscript{2} fertilization. This directly impacts photosynthetic rates, with higher photosynthesis (and thus higher stomatal conductance) expected as CO\textsubscript{2} concentrations increase. CO\textsubscript{2} fertilization tends to either have no influence on canopy leaf area or to increase canopy leaf area (Norby and Zak 2011; Donohue et al. 2013), which increases transpiration. The physiological effect’s net influence on land evapotranspiration therefore depends on the relative magnitude of these two changes (the stomatal response and the leaf area response), as well as the extent to which vegetation influences land-atmosphere interactions in a given region (Lian et al. 2018). Most Earth system models (ESMs; Swann et al. 2016; Lemordant et al. 2018) and field experiments (Hungate et al. 2002; Leakey et al. 2009) suggest that the stomatal response term dominates in areas with moderate to high leaf area, leading to a net decrease in land evapotranspiration. However, future projections of

Physiologically-driven reductions in evapotranspiration can warm local land temperatures directly by decreasing evaporative cooling, as well as indirectly through influences on low level humidity, cloud cover, and precipitation. Recent modeling studies have demonstrated that physiologically-driven decreases in land evapotranspiration can reduce cloud cover by decreasing low level relative humidity (Doutriaux-Boucher et al. 2009; Andrews et al. 2011, 2012; Arellano et al. 2012; Lemordant et al. 2018), which amplifies regional physiologically-driven warming. If the leaf area response were to dominate over stomatal responses, the resulting increase in evapotranspiration could decrease land temperatures through these same mechanisms. Kooperman et al. (2018) and Langenbrunner et al. (2019) have also found that physiologically-forced drying of the boundary layer can reduce deep convection and allow for greater advective moisture transport out of lowland forest areas in the lower troposphere, demonstrating that the physiological response not only modulates local surface energy fluxes, but also impacts large scale atmospheric dynamics.

In addition to influencing land surface temperature by altering evapotranspiration, the plant physiological response to CO₂ can also influence land surface temperature by altering land surface albedo. CO₂ fertilization generally decreases albedo (thereby increasing temperature) by increasing leaf area and, within dynamic vegetation models, by shifting plant functional types from grasses to trees (Bala et al. 2006; Andrews et al. 2019). Expansion of forests in boreal and Arctic regions can result in especially large albedo decreases (Betts 2000; Bala et al. 2006; O’ishi et al. 2009; Andrews et al. 2019) because increases in foliage mask bright snow.
The global-scale temperature implications of plants’ physiological responses to CO₂ have been long acknowledged. Sellers et al. (1996) were the first to quantify physiologically-driven warming by coupling a biosphere model to an atmosphere model, finding that under a doubling of CO₂ the physiological effect increased global land temperature by about 0.3°C and mean global temperature by about 0.1°C. Since then, multiple modeling studies have demonstrated that the plant physiological response tends to increase land temperatures in most modern ESMs on annual timescales (Betts et al. 2007; Andrews et al. 2011; Arora et al. 2013; Swann et al. 2016; Lemordant et al. 2016, 2018; Arora et al. 2019) and during heatwaves (Lemordant et al. 2016; Skinner et al. 2018; Lemordant and Gentine 2019).

Because the physiological effect influences surface temperatures, it is therefore relevant to global-scale metrics of climate sensitivity, such as the equilibrium climate sensitivity (ECS) and transient climate response (TCR). From the perspective of the classical radiative forcing-feedback framework (Gregory et al. 2004; Bony et al. 2006; Roe 2009; Boucher et al. 2013), plants’ physiological response to increasing CO₂ can be considered to be a forcing – rather than a feedback – on the climate system because by definition plants are responding to changes in CO₂ rather than to the relatively slow changes in global temperature. However, the timescale over which plants respond to increasing CO₂ ranges from on order seconds to decades. The stomatal response is fast; at the leaf level, stomata respond to changing environmental conditions in less than an hour (Vico et al. 2011), and the timescale of the atmospheric adjustment to the stomatal response occurs on the timescale of a few months (Doutriaux-Boucher et al. 2009; Andrews et al. 2011). Doutriaux-Boucher et al. (2009) have demonstrated that this fast stomatal response rapidly reduces low cloud cover and thereby the cloud radiative effect, which has been shown to be an important contributor to global warming and its uncertainty (Geoffroy et al. 2012). The leaf area and plant distribution responses are
slower, occurring on timescales of years to decades (Fisher et al. 2019). Thus, whether
the physiological effect will be included in the calculation of radiative forcing depends on
the definition used: it would be excluded from the *instantaneous* radiative forcing, which
accounts only for the instantaneous impact of CO$_2$ on the top-of-atmosphere radiation
budget; but it would be included in the *effective* radiative forcing, which allows for
adjustments to the troposphere, stratosphere, and land surface properties (Sherwood et
al. 2015). We will discuss this ambiguity in more detail later, but we focus our analysis
on the influence of the physiological effect on the TCR, which is independent of the
forcing definition used.

Although plants’ physiological responses to CO$_2$ are already embedded in the
ESMs used to estimate the TCR, the physiological effect’s contribution to this metric
has received limited recognition by the climate dynamics community. While studies
focusing on carbon cycle feedbacks have quantified physiologically-driven warming
across models as part of disentangling carbon-concentration and carbon-climate
feedbacks (e.g. Arora et al. 2013, 2019), studies of the physiological contribution to CO$_2$-
forced warming within a climate dynamics framework have been limited to ESMs from a
few individual modeling centers (summarized in Table S1 in the online supplement;
Sellers et al. 1996; Betts et al. 1997; Cox et al. 1999; Douville et al. 2000; Levis et al.
2000; Bala et al. 2006; Betts et al. 2007; Doutriaux-Boucher et al. 2009; Boucher et al.
2009; Cao et al. 2009; O’ishi et al. 2009; Cao et al. 2010; Andrews et al. 2011; Pu and
Dickinson 2012). Physiology’s contribution to the TCR has not been systematically
assessed across models and Coupled Model Intercomparison Project (CMIP) phases.

Additionally, past studies have not specifically quantified the physiological
contribution to the TCR using the same experimental methodology from which the full
TCR is calculated. For example, baseline levels of CO$_2$ have ranged from 280 to 400
ppm across experiments (Table S1 in online supplemental material) and the
physiological effect’s influence on temperature has been analyzed from both abrupt (e.g. Doutriaux-Boucher et al. 2009; Cao et al. 2010; Andrews et al. 2011) and transient (Bala et al. 2006; Boucher et al. 2009) CO₂ perturbations. Modeling studies have also differed in whether they include both the stomatal and leaf area components of the physiological effect or only the stomatal component. While these different experimental designs have provided insights into the mechanisms and timescales of the physiological effect’s influence on climate, they do not provide systematic estimates of the full physiological contribution to the TCR across ESMs.

The lack of systematic inter-model comparison of the physiological contribution to the TCR is a problematic gap in the existing literature because past work suggests that physiologically-driven transient warming may differ across models. Models disagree both on how plants respond to increasing CO₂ (Friedlingstein et al. 2006; Anav et al. 2013; Piao et al. 2013; Smith et al. 2016; Lian et al. 2018) and on how the atmosphere responds to perturbations to the land surface energy budget (Andrews et al. 2009; Devaraju et al. 2018). This suggests that inter-model disagreement about the magnitude of physiologically-driven warming may be an unrecognized contributor to inter-model spread in CO₂-forced warming. Additionally, poor model agreement on the magnitude of physiologically-driven warming would mean that an estimate derived from a single model may not capture the true multi-model mean. To address this gap, we use standardized carbon cycle model simulations from the CMIP phase 5 and 6 archives to quantify (1) the magnitude of the physiological effect’s influence on temperature across models, (2) whether trends in the physiological effect contribute to the increase in the TCR noted for many recent models (Andrews et al. 2019; Gettelman et al. 2019; Golaz et al. 2019; Flynn and Mauritsen 2020), (3) the spatial pattern of physiologically-driven temperature changes, (4) how physiological processes contribute to variability in multi-
model estimates of the TCR, and (5) the mechanism through which the physiological
effect influences temperature.

2. Methods

2.1. CMIP Experiments

As part of CMIP5 and CMIP6, modeling groups performed three concentration-
driven experiments (summarized in Table 1) in which CO₂ concentrations increase by 1
percent per year from pre-industrial levels (284.3 ppm) to a quadrupling of CO₂ (1144.9
ppm), while all other forcings remain at pre-industrial levels. The spatial pattern of
vegetation in these simulations comes from the pre-industrial era; this spatial pattern
remains constant throughout the simulation except for in land models with dynamic
vegetation (see Tables S2 and S3 in online supplemental material), where the
distribution of plant functional types changes based on climate and resource availability.
In one set of simulations, referred to here as ‘FULL’ (CMIP6 experiment ‘1pctCO2’),
both the atmosphere and carbon cycle (on land and in the oceans) experience increasing
CO₂ concentrations. Additional experiments conducted as part of the Coupled Climate–
Carbon Cycle Model Intercomparison Project (C4MIP; Friedlingstein et al. 2006; Jones
et al. 2016) enable us to isolate how much the physiological and radiative effects of CO₂
each contribute to surface warming. In one set of C4MIP simulations, referred to here as
‘RAD’ (CMIP6 experiment ‘1pctCO2-rad’), only the atmosphere experiences increasing
CO₂ concentrations, while the terrestrial and oceanic carbon cycles experience constant
pre-industrial CO₂ concentrations. In another set of C4MIP simulations, referred to here
as ‘PHYS’ (CMIP6 experiment ‘1pctCO2-bgc’), the radiative transfer submodels in the
atmosphere experience constant pre-industrial CO₂ concentrations, while the land
surface and ocean carbon cycle submodels experience the increasing CO₂ concentrations.
We use the concentration-driven pre-industrial control experiment (referred to here as ‘PI’, CMIP6 experiment ‘piControl’) as the baseline from which anomalies are taken.

2.2. Models

We analyze output from all ESMs that had uploaded near-surface air temperature monthly data for the FULL, PI, and PHYS and/or RAD experiment to the Earth System Grid by January 29, 2020. This consisted of 8 CMIP5 models and 9 CMIP6 models (Table 2). These models all include interactive representations of the carbon cycle; plants in these models respond to increasing CO$_2$ by changing leaf area, stomatal conductance, and, in some models, the location and distribution of plant functional types (Tables S2 and S3 in online supplemental material). Ocean responses to increasing CO$_2$ include changes in inorganic and biological carbon cycling, which have negligible direct influences on modeled ocean surface temperature. The only potential direct influences of ocean carbon cycle responses on ocean surface temperatures in the PHYS experiments are through changes in plankton community structure which can alter (1) ocean biogeophysical properties and (2) the emission of gases and particles which influence aerosol formation (Hense et al. 2017). These effects are not represented in most models. When multi-model mean maps are reported, they are calculated after smoothly re-gridding model output to a consistent grid.

2.3. Calculation of the TCR

We calculate the TCR as the change in globally averaged near-surface air temperature during the 20-year window centered on the time of CO$_2$ doubling (years 61-80 of the simulation where CO$_2$ concentration increases by 1% per year) relative to pre-industrial CO$_2$ concentrations. When using the PI experiment as a control, we account for model drift by subtracting the linear trend of PI years 1-140 following Gregory and Forster (2008), where year 1 corresponds to the year at which FULL, RAD, and PHYS
were branched from PI. We refer to the physiological and radiative contributions to the full TCR as TCR\textsubscript{PHYS} and TCR\textsubscript{RAD}, respectively.

We assess whether our estimates of physiologically-driven warming are robust relative to variability in the Earth system by comparing TCR\textsubscript{PHYS} to the distribution of 20-year running mean global temperatures in the full PI control experiments (Figure S1 in the online supplemental material). In two of the CMIP6 models evaluated here (BCC-CSM2-MR and CNRM-ESM2-1), large, multidecadal (greater than 20 year) oscillations exist in the PI control (Figure S1 in the online supplemental material; noted in Parsons et al. (In Revision)). The magnitude of these oscillations greatly exceeds the magnitude of the TCR\textsubscript{PHYS} signal, and thus we cannot confidently quantify the TCR\textsubscript{PHYS} for these two models. These models’ large multidecadal PI oscillations also have implications for TCR\textsubscript{FULL}, as they suggest that model TCR\textsubscript{FULL} estimates may be strongly influenced by variability rather than representing the CO\textsubscript{2}-forced warming signal, since for these models smoothing out variability would require an averaging period of greater than 20 years.

### 2.4. Isolating Physiology’s Influence on Temperature

We quantify the influence of the physiological effect in two ways: as the difference between the FULL and RAD simulations (FULL-RAD) and as the difference between the PHYS and PI simulations (PHYS-PI). Both represent physiology’s influence on the TCR, but FULL-RAD includes any nonlinear interactions between the radiative and physiological effects of increasing CO\textsubscript{2}, while PHYS-PI does not. For example, FULL-RAD would include the interaction between CO\textsubscript{2} fertilization and changes in leaf area (quantified as the leaf area index, LAI) induced by RAD-driven warming. We focus on the FULL-RAD methodology in the main text because it emphasizes how much the physiological effect changes climate relative to what models would otherwise show from radiative forcing alone. Because FULL and RAD branch
from the same point of the PI simulation, FULL-RAD also avoids issues related to drift in the PI control. There is some nonlinearity between the radiative and physiological effects of CO$_2$, but there is poor model agreement on the sign and spatial pattern of the interaction term (Figures S2 and S3 in the online supplemental material).

### 2.5. Partitioning Physiological Influences on Evapotranspiration

We partition the total physiologically-driven change in land evapotranspiration into its component physiological drivers according to Equation 1, where the four terms on the right-hand side indicate the land evapotranspiration change due to (1) changes in leaf area, (2) changes in stomatal conductance (approximated as changes in transpiration per leaf area), (3) interactions between changes in stomatal conductance and changes in leaf area, and (4) changes in land evaporation. The derivation of Equation 1 is included in the online supplemental material.

$$\Delta ET = \left(\frac{T}{L}\right)_{RAD} (\Delta L) + L_{RAD} \left(\Delta \frac{T}{L}\right) + \left(\Delta \frac{T}{L}\right) (\Delta L) + \Delta E$$

where ET = evapotranspiration (mm/day); T = transpiration (mm/day); L = leaf area index (unitless); and E = evaporation (mm/day). The RAD subscript indicates the value from the RAD experiment, and $\Delta$ indicates the physiologically-driven change, as calculated from FULL-RAD.

### 3. Results and Discussion

#### 3.1. Physiology’s Contribution to the TCR

The radiative effect of CO$_2$ is, unsurprisingly, the dominant contributor to the TCR. However, we also find that the physiological response to increased CO$_2$ has a non-negligible secondary contribution to the TCR in many CMIP5 and CMIP6 models. In CMIP6 models, the physiological effect contributes about 0.11°C (standard deviation:
0.10°C; range: 0.02 - 0.29°C) to the TCR, corresponding to 5.2% of the full TCR (standard deviation: 4.1%; range: 1.4 - 13.9%) (Figure 1a). For a few CMIP6 models (especially UKESM1-0-LL and CESM2), the physiological contribution to warming is quite large, accounting for over 10% of the total TCR. In CMIP5 models (note that a different subset of modeling centers have the necessary CMIP5 model simulations; see Table 2), the physiological effect contributes 0.14°C (standard deviation: 0.16°C; range: 0.00 - 0.51°C) to the TCR, corresponding to 6.6% of the full TCR (standard deviation: 6.3%; range: 0.1 - 20.1%).

When comparing the same subset of six models for which we have model output from both CMIP phases, physiologically-driven warming is comparable in CMIP5 and CMIP6. From CMIP5 to CMIP6, the mean TCR\textsubscript{PHYS} across these models remained roughly constant (Table 2). TCR\textsubscript{PHYS} increased for 4 of 6 models (Table 2; Figure 1b), but notably decreased for the model with the highest TCR\textsubscript{PHYS} in CMIP5 (the Met Office Hadley Centre model, which is HadGEM2-ES in CMIP5 and UKESM1-0-LL in CMIP6). This suggests that the increases in TCR\textsubscript{FULL} from CMIP5 to CMIP6 noted for many recent models (Andrews et al. 2019; Gettelman et al. 2019; Golaz et al. 2019; Flynn and Mauritsen 2020) were driven primarily by increases in TCR\textsubscript{RAD} rather than TCR\textsubscript{PHYS}. Physiology’s relative contribution to the TCR decreased in most models (Figure 1a, Table 2), due to many CMIP6 models’ increased values of TCR\textsubscript{RAD}.

The multi-model mean TCR\textsubscript{PHYS} values reported here are within the range of estimates from other studies (summarized in Table S1 in online supplemental material), but on the low side of this range for two reasons. Firstly, this may relate to publication bias: of the eleven modeling centers included in this analysis, the only two modeling centers that had previously published CMIP5 estimates of physiologically-driven warming at 2xCO\textsubscript{2} have above average TCR\textsubscript{PHYS}. Our study is the first to compare TCR\textsubscript{PHYS} across models, and the fact that the existing literature did not capture the full
spread in TCR\textsubscript{PHYS} across models underscores the importance of a multi-model approach. A second reason that our multi-model estimate of TCR\textsubscript{PHYS} is on the low side of previous estimates results from the fact that many previous studies isolated the effect of the stomatal response on near-surface temperatures rather than the net effect of both the stomatal and leaf area response (Table S1 in online supplemental material); we expect a larger temperature increase from the stomatal response alone than from the combined stomatal and leaf area responses because the leaf area response counteracts the stomatal response’s influence on evapotranspiration.

The global mean TCR\textsubscript{PHYS} signal is small in comparison to TCR\textsubscript{FULL}, and it is statistically significant relative to the pre-industrial control for only 4 of 9 CMIP6 and 5 of 8 CMIP5 models at 2xCO\textsubscript{2} (Table S4 in online supplemental material). However, the physiologically-driven warming signal increases with increasing CO\textsubscript{2} concentration, reaching a mean of 0.20°C (standard deviation: 0.12°C; range: 0.03 - 0.45°C) by 4xCO\textsubscript{2} and emerging from the noise (Figure 1b). By 4xCO\textsubscript{2}, physiologically-driven warming is statistically significant for 6 of 9 CMIP6 and 7 of 8 CMIP5 models (Table S4 in online supplemental material). The three CMIP6 models that are not statistically significant by 4xCO\textsubscript{2} (CNRM-ESM2-1, BCC-CSM2-MR, and IPSL-CM6A-LR) are the three models with the most variability in the PI control of all the CMIP5 and CMIP6 models we analyze. The significant physiologically-driven warming at higher CO\textsubscript{2} concentrations, inter-model agreement in the sign of TCR\textsubscript{PHYS}, and consistent spatial pattern of warming (detailed in section 3.2) gives us confidence that we are detecting a real physiologically-driven signal and not just picking up internal variability. However, internal variability is a large source of uncertainty in quantifying TCR\textsubscript{PHYS} (Figure 1b), and this uncertainty is intrinsically included in estimates of TCR\textsubscript{FULL}. Integration of a large-ensembles approach into the next C4MIP is necessary to address this issue and to
reduce uncertainties in the TCR in future work. This could be done through integrating a requirement for a minimum number of initial condition ensembles in the experiment.

3.2. Spatial Pattern of Physiologically-Driven Warming

The physiological effect only directly influences land surface properties, and thus the largest warming driven by the physiological effect occurs over land. In CMIP6 models, the physiological effect results in a land mean warming of 0.21°C at 2xCO$_2$ and 0.41°C at 4xCO$_2$, relative to a corresponding mean ocean warming of 0.07°C and 0.13°C respectively (Figure 2a). Physiologically-driven warming over land is also statistically significant for more ESMs by 2xCO$_2$ than it is for the global mean (Table S4 in online supplemental material). Because most models do not have any mechanism for the physiological effect of CO$_2$ to directly warm the oceans, the modelled physiologically-driven warming over oceans must be the result of remote, land driven warming. The spatial pattern of physiologically-driven warming that we find is consistent with other studies, which also show the greatest warming over land and modest ocean warming (Table S1 in online supplemental material).

The greatest mean physiologically-driven warming occurs over boreal forests and non-glaciated high-latitude land, followed by temperate and tropical forested regions. The agreement across models is reasonably high - at least 6 of 9 CMIP6 models agree that the physiological effect results in warming in these three biomes at 2xCO$_2$, and 8 of 9 CMIP6 models show warming in these biomes at 4xCO$_2$ (Figures S4 and S5). Relative to radiatively-driven warming, physiology also contributes more to land warming than ocean warming, with physiological forcing constituting a mean 7.3% of total CO$_2$-forced land warming at 2xCO$_2$ compared to 4.2% of ocean warming (Figure 2b). The physiological effect therefore amplifies the land/ocean warming contrast: while land warms a mean 1.57 times more than ocean in RAD for CMIP6, the mean land/ocean warming contrast in FULL is 1.62, due to the addition of the physiological effect (Figure
3). This physiologically-driven enhancement of the land/ocean warming contrast was previously demonstrated for Met Office Hadley Centre models (Joshi et al. 2008; Dong et al. 2009), and we show here that this warming contrast is robust across most CMIP models (Figure 3).

The larger absolute and relative physiologically-driven warming over non-glaciated land is consistent with the physiological effect directly influencing land surface properties in regions with plant cover, while influencing glaciated land and oceans only indirectly through changes in heat transport, clouds, and other aspects of climate dynamics. Though the remote influence of physiological forcing on oceans and glaciated land is relatively modest, most models (8 of 9) agree that the physiological effect results in mean warming of near-surface oceanic air and ocean surface layers. The regions of the most robust physiologically-driven oceanic warming across models are the western North Atlantic, equatorial Pacific, equatorial Indian Ocean, and high latitude Pacific.

Byrne and O’Gorman (2018) suggest that increases in the near surface land-ocean temperature contrast are causally driven by temperature change over the ocean. However, the physiologically-driven enhanced land-ocean contrast, where the only initial difference is over the land surface, shows that land surface processes can also initiate the feedback loop of decreasing relative humidity over land leading to a larger increase in temperature over land relative to over ocean. The potential to initiate this loop through land processes is noted by Byrne and O’Gorman (2016), and we further emphasize that point here. It is important to acknowledge the physiological effect’s greater relative contribution to land warming because land warming (rather than global mean warming) is the relevant metric for many societal climate impacts.
3.3. Physiology’s Contribution to Uncertainty in CO₂-Forced Warming

The magnitude of global physiologically-driven warming varies significantly across models (Figures 1 and 4) and this uncertainty contributes to the inter-model spread of TCR estimates. In the CMIP6 models analyzed here, the radiative effect alone explains about 89% of the standard deviation and 91% of the inter-model range in the TCR (Figure 5), with the physiological effect contributing the remaining 11% and 9%, respectively. The physiological effect contributes more to uncertainty in CO₂-forced warming over land. Averaged across all non-glaciated land, the physiological effect explains about 16% of the standard deviation and 18% of the inter-model range mean land warming at 2xCO₂ in CMIP6 (Figure 5). In some highly forested land regions (tropical Africa, southeastern South America, and the southeastern United States), inter-model disagreement in local warming at 2xCO₂ is driven by approximately equal contributions of uncertainty from physiologically- and radiatively-forced warming (Figure 6). These results suggest that the physiological effect is a non-negligible contributor to inter-model spread in the TCR and regional CO₂-forced warming.

However, some of these pre-industrial forested regions, especially southeastern South America, are largely deforested in the present day, which means that in scenario-based future projections the physiological effect may contribute less to uncertainty in these regions than Figure 6 implies.

A limitation of this study is that the C4MIP model output necessary to disentangle physiologically- and radiatively-forced warming is only available for about a quarter of the models for which we can estimate the full TCR (9 of 34 for CMIP6 and 8 of 30 for CMIP5). We therefore cannot quantify TCR_{PHYS}, or the physiological contribution to uncertainty in the TCR, for the remaining CMIP models. Future work could further leverage C4MIP model output to assess whether signatures of...
physiologically-driven warming (such as seasonal variations in the CO2-forced change of
the diurnal temperature range; Bounoua et al. 1999; Collatz et al. 2000; Leeuwen et al.
2011) could be used to estimate the physiological contributions to mean warming from
the FULL experiments alone.

3.4. Mechanism of Physiologically-Driven Warming

3.4.1. Land Mechanism

The physiological effect increases near-surface air temperatures over land by
modifying surface properties which modulate terrestrial energy fluxes (Laguë et al.
2019). This occurs through (1) changes in the partitioning between surface turbulent
fluxes resulting from physiological influences on evapotranspiration, (2) radiative
changes due to physiologically-driven changes in albedo, cloud cover, and column water
vapor, and (3) changes in surface roughness resulting from changes in leaf area and
vegetation distribution.

In most models, plants’ response to CO$_2$ causes a net decrease in mean land
evapotranspiration, especially in the tropics (Figure 7), indicating that stomatal closure
decreases evapotranspiration by enough to offset increases in evapotranspiration from
increased leaf area, though the magnitude and sign of evapotranspiration change does
vary spatially across models. In the CMIP6 multi-model mean at 2xCO$_2$, changes in
stomatal conductance (approximated by the change in transpiration per leaf area)
decreases global land evapotranspiration by 0.14 mm/day (standard deviation: 0.08
mm/day; range: 0.02-0.27 mm/day), global leaf area changes increase evapotranspiration
by 0.19 mm/day (standard deviation: 0.15 mm/day; range: 0.00-0.52 mm/day), and the
interaction between changes in stomatal conductance and leaf area decreases
evapotranspiration by an additional 0.07 mm/day (standard deviation: 0.08 mm/day;
range: 0.00-0.29 mm/day; Figure 8). Land evaporation changes minimally (0.00
mm/day; standard deviation: 0.03 mm/day; range: -0.06 - +0.05 mm/day; Figure 8). In
the multi-model mean, the net effect of these physiological responses is a decrease in evapotranspiration, with the largest and most robust decrease in the tropics (Figures 7, 8, and 9). This physiologically-driven decrease in evapotranspiration due to increased CO₂ has previously been documented for CMIP5 models (Swann et al. 2016; Lemordant et al. 2018), and holds for the new CMIP6 models analyzed here. Under constant net radiation at the surface, this physiologically-driven decrease in evapotranspiration results in more energy leaving the land surface through sensible heating (Figure 9), thereby increasing near-surface air temperatures.

The physiological effect also increases surface and near-surface temperatures by increasing the net radiation reaching the surface. Net shortwave radiation on land increases primarily through albedo decreases and changes in cloud cover (Figure 9). Albedo decreases primarily in high latitudes (Figure 7), due to both increases in leaf area and decreases in snow cover due to increased temperatures. Consistent with previous studies (Doutriaux-Boucher et al. 2009; Andrews et al. 2011, 2012; Arellano et al. 2012; Lemordant et al. 2018), downwelling shortwave radiation (SW_{down}) reaching the surface also increases as a consequence of decreases in cloud cover (especially in Northern Hemisphere mid- and high-latitudes and over the northeastern Amazon; Figure 9), which are driven both by decreases in relative humidity from physiologically-forced reductions in evapotranspiration and by increases in air temperatures. Most models show negligible mean changes in clear-sky SW_{down} (which could be modified by changes in water vapor and aerosols), with the exception of UKESM1-0-LL and CanESM5, which show slight decreases in SW_{down}. This result differs from CMIP5, in which the Hadley Centre model was the only model to show physiologically-driven changes in clear-sky SW_{down}, which increased due to vegetation’s influence on dust optical depth (Andrews et al. 2012).
The physiological effect also influences surface net longwave radiation (Figure 9) through changes in surface and boundary layer temperatures, cloud cover, atmospheric column water vapor, and the partitioning of surface energy fluxes. Outgoing longwave radiation from the land surface \( \text{LW}_{\text{up}} \) increases with increasing surface temperature through the Planck feedback. Warming of the boundary layer (driven by both increased sensible heating and by longwave radiation associated with surface warming) increases downward longwave radiation at the land surface \( \text{LW}_{\text{down}} \), partially offsetting the increase in \( \text{LW}_{\text{up}} \) (Vargas Zeppetello et al. 2019). Physiologically-driven decreases in atmospheric water vapor (which is a strong greenhouse gas) decrease \( \text{LW}_{\text{down}} \), as do cloud changes resulting from reduced land evapotranspiration. The net effect of all of these processes generally results in a decrease of net longwave radiation over most vegetated land.

**3.4.2. Ocean Mechanism**

Because most models do not have any mechanism for the physiological effect of \( \text{CO}_2 \) to directly warm the oceans, the modelled physiologically-driven oceanic warming must be the result of remote, land-driven warming. The physiological effect on land can alter ocean temperatures through (1) advection of continental air that has been directly influenced by changes in land surface properties (e.g. changes in air temperature or moisture content) and (2) changes in atmospheric or oceanic circulation. The fact that the most robust oceanic warming regions are downwind of warming land regions suggests that advection of warm continental air is contributing to oceanic warming. Cloud cover over oceans also decreases in some regions that are downwind of land, particularly in the North Atlantic, increasing ocean temperatures by increasing net radiation (Figure 9).

Teleconnections likely also contribute to ocean warming, based on past work indicating that changes in large-scale atmospheric circulation can be induced by
physiological forcing (Kooperman et al. 2018; Langenbrunner et al. 2019) or other changes in land surface properties (Swann et al. 2012, 2014; Devaraju et al. 2015; Laguë and Swann 2016; Devaraju et al. 2018). Additionally, the physiological effect has the potential to induce changes in ocean circulation (e.g. Diffenbaugh et al. 2004). In particular, the pattern of physiologically-driven oceanic warming in the North Atlantic is consistent with a weakening of the Atlantic Meridional Overturning Circulation (AMOC; e.g. Marshall et al. 2015; Caesar et al. 2018). A potential mechanism is that warming of the air advected off the North American continent would reduce the flux of heat from the ocean to the atmosphere in the subpolar North Atlantic, decreasing deep convection.

While the C4MIP experimental design does not enable us to directly quantify the relative contributions of advection and circulation changes to oceanic warming, exploration of the links between land surface perturbations and ocean temperatures merits further research. Recognizing the oceanic component of physiologically-driven warming is important because it constitutes about half of TCR<sub>PHYS</sub> – even though the magnitude of physiologically-driven oceanic warming is much smaller than land warming on a per area basis, the TCR is a global-scale metric and ocean constitutes about 70% of the Earth’s surface area.

4. Conclusions and Implications

4.1. Magnitude of TCR<sub>PHYS</sub>

The biological and ecological processes governing canopy leaf area and stomatal conductance are often considered to exist squarely in the domain of carbon cycle feedbacks (i.e. they impact the climate system through their influence on CO<sub>2</sub> concentrations themselves). Our analysis demonstrates that these terrestrial carbon
cycle processes are also embedded in global climate sensitivity metrics like the TCR through plants’ impact on land surface properties and surface energy fluxes.

We quantified the plant physiological effect’s small but significant influence on CO$_2$-forced temperature changes, finding that at 2xCO$_2$ the physiological effect contributes about 0.11°C (5.2%) to the TCR and leads to about 0.21°C of warming over non-glaciated land. To put our results into context, the physiological contribution to the TCR is the same order of magnitude as the surface albedo feedback’s contribution to equilibrium warming (8% of the ECS as quantified for CMIP5 models by Vial et al. 2013). Recognizing this physiological component of CO$_2$ forcing is necessary for understanding forcing differences across greenhouse gases (e.g. CH$_4$ does not have added warming from physiology). While the contribution of the physiological effect can be up to 20% of the total TCR in some CMIP5 models, changes in the representation of plant physiology do not appear to be a major driver of the increase in the TCR observed from CMIP5 to CMIP6.

4.2. Physiology’s Role in Forcing, Feedbacks, and ECS

The effective radiative forcing is commonly expressed as a change in net top-of-atmosphere (TOA) radiation following CO$_2$-driven adjustments in tropospheric and stratospheric temperatures, water vapor, clouds, and surface properties, prior to any global-mean surface temperature change (e.g. Boucher et al. 2013; Sherwood et al. 2015). In practice, it is often calculated using simulations in which CO$_2$ is increased while sea-surface temperatures (SSTs) are prescribed to be fixed at pre-industrial values, with some studies estimating and removing the TOA radiative response to land warming when calculating the forcing value (Hansen et al. 2005; Vial et al. 2013; Tang et al. 2019). Meanwhile, radiative feedbacks are traditionally defined by the change in net TOA radiation for a given change in global-mean surface temperature (Bony et al. 2006; Roe 2009).
The physiological response of plants to increasing CO$_2$ poses a challenge to this radiative forcing–feedback paradigm. On the one hand, plants respond directly to the atmospheric CO$_2$ concentration, suggesting that the physiological effect should be classified as part of the forcing. However, because this direct physiological response of plants to CO$_2$ induces changes in surface temperature (even in the absence of the radiative effects of CO$_2$ changes), the TOA radiative response to these changes could also be classified as part of the feedback. Meanwhile, temperature-driven changes in vegetation distribution and leaf area that influence land surface albedo and evapotranspiration should clearly be classified as feedbacks. While it is unclear to us how best to interpret the physiological effect in terms of the forcing–feedback paradigm, the distinction does not impact the results presented here because of our results’ focus on the TCR instead of forcing or feedbacks separately.

However, understanding of the role of the physiological effect in TCR and ECS uncertainty would benefit from greater clarity on whether it should be treated as a forcing or feedback. Indeed, recent work suggests that the TCR may be more sensitive to uncertainty in CO$_2$ radiative forcing than to uncertainty in radiative feedbacks (Lutsko and Popp 2019), but that the ECS is more sensitive to uncertainty in radiative feedbacks (Geoffroy et al. 2012). Thus, while the results here suggest that the physiological effect will act to increase the ECS and its uncertainty – as it has for the TCR – we cannot currently quantify the magnitude of the effect on the ECS in the CMIP5 or CMIP6 ensembles. Additional RAD and PHYS simulations for abrupt CO$_2$ quadrupling, using both fixed SSTs$^1$ to be able to quantify the effective radiative forcing

$^1$ For example, the CMIP6 Cloud Feedback Model Intercomparison Project (CFMIP; Webb et al. 2017) tier 2 experiment piSST-4xCO2-rad, in which SSTs are fixed at pre-industrial levels and only the radiation scheme (and not the vegetation scheme) experience an abrupt quadrupling of CO$_2$. 
and coupled model simulations to be able to estimate ECS, would be valuable in this regard.

4.3. Broad Implications of Carbon Cycle Uncertainty

While we report physiology's mean contribution to warming, we especially emphasize our finding that uncertainty in terrestrial carbon cycle processes contributes to uncertainty in CO₂-forced warming. The spread in the magnitude of physiologically-driven warming across CMIP6 models represents real scientific uncertainty, as there are limited observational constraints to suggest that either the high or low extremes of modeled physiological responses of stomatal conductance, leaf area, and resulting evapotranspiration are within expectations (Medlyn et al. 2011; De Kauwe et al. 2013; Schimel et al. 2015).

It is also possible that ESMs do not probe the full scientific uncertainty surrounding plants' responses to CO₂, as models may contain systematic biases. For example, many models represent stomatal conductance using the same key parameters (e.g. the same slope constant in the Ball-Berry (1987) stomatal conductance model or the g1 fitted parameter in the Medlyn (2011) model) to govern how stomatal conductance responds to increasing CO₂, despite the wide variation in these parameters across and within plant functional types (Lin et al. 2015; Wolz et al. 2017). Similarly, some studies suggest (e.g. Smith et al. 2016) that ESMs systematically overestimate the leaf area increases resulting from CO₂ fertilization, which would mean that models overestimate physiologically-driven albedo decreases and underestimate physiologically-driven evapotranspiration decreases. We would expect this to result in a true physiologically-forced temperature change that is smaller than models suggest at high latitudes (where albedo matters more) and larger than models suggest at low latitudes (where ET matters more). Furthermore, Green et al. (2017) suggest that ESMs may
systematically underestimate some feedbacks between land biosphere changes and the atmosphere.

On the one hand, acknowledging the physiological contribution to uncertainty in modeled CO₂-forced warming suggests that models agree more on the magnitude of radiatively forced warming than the prevailing narrative implies. For atmospheric dynamicists most interested in purely radiatively-driven processes, these findings therefore motivate more deliberate consideration of plant functioning in experimental designs; RAD simulations may be more appropriate than FULL simulations for some climate dynamics questions. On the other hand, acknowledging the physiological contribution means that reducing uncertainty in the true, full TCR requires reducing uncertainty in land surface processes which are especially difficult to constrain. From this perspective, these findings provide a new motivation for further experimental studies to reduce uncertainty in terrestrial carbon cycle processes. For example, we identify that plants’ responses to CO₂ are a major driver of uncertainty in transient warming in tropical Africa, and no free-air CO₂ enrichment (FACE) experiments exist in tropical forests to constrain uncertainty in how those ecosystems will respond to increasing CO₂. Carbon cycle uncertainty is not limited to the carbon cycle, and reducing uncertainty in plants’ response to CO₂ will improve our understanding of physiological warming, thereby reducing overall uncertainty in the total TCR.

5. Data and Code Availability

The majority of model output data used in this study are available in the publicly accessible Earth System Grid Federation (ESGF) repository at https://esgf-node.llnl.gov/projects/esgf-llnl/. Model output from the CESM2 RAD experiment is not yet available on the ESGF repository and is stored on data servers at the National
Center for Atmospheric Research. The code used for this study is available from the corresponding author upon request.

6. Acknowledgements

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7. References


Ball, J. T., I. E. Woodrow, and J. A. Berry, 1987: A Model Predicting Stomatal Conductance and its Contribution to the Control of Photosynthesis under...


——, and Coauthors, 2013: Clouds and aerosols. *Climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.*


Langenbrunner, B., M. S. Pritchard, G. J. Kooperman, and J. T. Randerson, 2019: Why Does Amazon Precipitation Decrease When Tropical Forests Respond to


Parsons, L. A., K. Brennan, R. Junglin Wills, and C. Proistosescu, In Revision:


### TABLE 1. Summary of CMIP experiments used.

<table>
<thead>
<tr>
<th>Experiment</th>
<th>CMIP5 Experiment Name</th>
<th>CMIP6 Experiment Name</th>
<th>Influence of CO$_2$ Concentration on:</th>
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<tr>
<td></td>
<td></td>
<td></td>
<td>Land</td>
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<tr>
<td>FULL</td>
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<td>1pctCO2</td>
<td>1% per year</td>
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<td>1pctCO2-bgc</td>
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<td>Pre-industrial</td>
</tr>
<tr>
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<td>piControl</td>
<td>piControl</td>
<td>Pre-industrial</td>
</tr>
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<td>Model Name</td>
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<td>CMIP6 Model TCR</td>
</tr>
<tr>
<td>-----------------</td>
<td>------------</td>
<td>----------------</td>
<td>----------------</td>
</tr>
<tr>
<td>Beijing Climate Center (BCC)</td>
<td>bcc-csm1-1</td>
<td>1.73 1.67 96.5% 0.05 2.8% 0.06 3.5%</td>
<td>1.73 1.66 95.8% 0.54 31.4% 0.07 4.2%</td>
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<tr>
<td>Canadian Centre for Climate Modelling and Analysis (CCCma)</td>
<td>CanESM2</td>
<td>2.34 2.16 92.0% 0.15 6.5% 0.18 8.0%</td>
<td>2.74 2.64 96.2% 0.04 1.5% 0.10 3.8%</td>
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<td>National Center for Atmospheric Research (NCAR)</td>
<td>CESM1-BGC</td>
<td>1.68 1.56 93.2% 0.11 6.6% 0.12 6.8%</td>
<td>2.06 1.78 86.1% 0.11 5.2% 0.29 13.9%</td>
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<td>NOAA Geophysical Fluid Dynamics Laboratory (NOAA-GFDL)</td>
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<td>1.35 1.35 99.9% 0.05 3.4% 0.00 0.1%</td>
<td>1.61 1.58 98.6% 0.17 10.7% 0.02 1.4%</td>
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<tr>
<td>Met Office Hadley Centre (MOHC)</td>
<td>HadGEM2-ES</td>
<td>2.52 2.01 79.9% 0.37 14.6% 0.51 20.1%</td>
<td>2.79 2.51 90.0% 0.17 6.0% 0.28 10.0%</td>
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<tr>
<td>Institut Pierre Simon Laplace (IPSL)</td>
<td>IPSL-CM5A-LR</td>
<td>2.00 1.97 98.3% 0.11 5.6% 0.03 1.7%</td>
<td>2.31 2.23 96.4% 0.17 7.3% 0.08 3.6%</td>
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<tr>
<td>Norwegian Climate Centre (NCC)</td>
<td>NorESM1-ME</td>
<td>1.56 1.42 90.8% 0.08 5.3% 0.14 9.2%</td>
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<tr>
<td>Max Planck Institute for Meteorology (MPI-M)</td>
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<td>2.02 1.95 96.4% 0.20 9.9% 0.07 3.6%</td>
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<td>NASA Goddard Institute for Space Studies (NASA-GISS)</td>
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<td>Japan Agency for Marine-Earth Science and Technology (JAMSTEC)</td>
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<td>MIROC-ES2L</td>
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<td><strong>Mean</strong></td>
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<tr>
<td><strong>Standard Deviation</strong></td>
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<td>1.94 1.79 93.3% 0.14 6.6% 0.15 6.7%</td>
<td>Consistent Model Subset</td>
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<tr>
<td>All Models</td>
<td>0.40 0.30 6.3% 0.11 3.8% 0.16 6.3%</td>
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<td>0.46 0.41 4.1% 0.18 10.5% 0.10 4.1%</td>
</tr>
<tr>
<td>Consistent Model Subset</td>
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<td>Consistent Model Subset</td>
<td>0.50 0.45 4.8% 0.18 10.7% 0.11 4.8%</td>
</tr>
</tbody>
</table>
TABLE 2. TCR_{FULL}, TCR_{RAD}, and TCR_{PHYS} by model, where TCR_{PHYS} is calculated by both PHYS-PI and TOT-RAD.

The consistent model subset refers to the six models for which the necessary model output is available for both CMIP5 and CMIP6. For the summary statistics in the last four rows, the percentages refer to the mean and standard deviations of the percent contributions across models.
9. Figures

**FIGURE 1.** Physiological contribution to global mean warming. (a) The relationship between the relative contribution of TCR$_{PHYS}$ to the full TCR (i.e. TCR$_{PHYS}$/TCR$_{FULL}$) and the absolute magnitude of TCR$_{PHYS}$, as calculated by FULL-RAD. Marker types indicate CMIP phase (CMIP5: circles; CMIP6: triangles) and colors indicate modeling center. Lines demarcate the multi-model mean for CMIP5 (dashed) and CMIP6 (solid). Note that the set of models included in the average differs between CMIP5 and CMIP6. (b) Global mean physiologically-driven temperature change as a function of CO$_2$ concentration, calculated from FULL-RAD and smoothed with a 20-year boxcar. The dark gray vertical line marks the time of CO$_2$ doubling, and the light gray bar indicates the 20-year period surrounding the time of CO$_2$ doubling. Colors indicate modeling center as in (a), and line types indicate CMIP phase (CMIP5: dashed; CMIP6: solid).
FIGURE 2. Spatial pattern of (a) absolute physiologically-driven warming and (b) physiological percent contribution to total warming at 2xCO$_2$, where physiologically-driven warming is calculated by FULL-RAD. Multi-model means include the 9 CMIP6 models.
**FIGURE 3.** The relationship between the land/ocean warming contrast (the ratio of the change in non-glaciated land temperature to the change in ocean temperature) from RAD (RAD-PI) and FULL (FULL-PI). The gray 1:1 line is where we would expect all models to be if the warming contrast were entirely caused by the radiative effects of CO₂. Physiology’s addition to the warming contrast is the vertical distance between the gray 1:1 line and each point. Marker types indicate CMIP phase (CMIP5: circles; CMIP6: triangles) and colors indicate modeling center as in Figure 1. Lines demarcate the multi-model average for CMIP5 (dashed) and CMIP6 (solid). Note that the set of models included in the average differs between CMIP5 and CMIP6.
FIGURE 4. The relationship between TCR$_{\text{RAD}}$ (RAD-PI) and TCR$_{\text{FULL}}$ (FULL-PI). The gray 1:1 line is where we would expect all models to be if the TCR were entirely caused by the radiative effects of CO$_2$. The added warming from the physiological effect is the vertical distance between the gray 1:1 line and each point. Marker types indicate CMIP phase (CMIP5: circles; CMIP6: triangles) and colors indicate modeling center as in Figure 1.
**FIGURE 5.** Physiology’s contribution to inter-model spread in global mean warming. Inter-model spread in global (black and grey) and land only (green) warming in FULL (FULL-PI) and RAD (RAD-PI), as quantified by the full inter-model range and the standard deviation. The 1:1 line is where we would expect all models to be if inter-model spread in warming were entirely caused by the radiative effects of CO₂. The added inter-model spread from the physiological effect is the vertical distance between the gray 1:1 line and each point. Marker types indicate CMIP phase (CMIP5: circles; CMIP6: triangles).
FIGURE 6. Spatial pattern of physiology’s relative contribution to inter-model spread in CO₂-forced warming. The ratio of the standard deviation (SD; at each grid cell, across models) of physiologically forced warming (calculated from FULL-RAD) to the SD of radiatively forced warming (calculated from RAD-PI) at 2xCO₂ for CMIP6 models. A value of 1 means that the physiological and radiative effects of CO₂ contribute equally to the total uncertainty in local warming at 2xCO₂ across models.
FIGURE 7. Land zonal means of physiologically-driven changes in (a) evapotranspiration and (b) albedo at 2xCO$_2$ for CMIP6 models, as calculated by FULL-RAD.
FIGURE 8. Zonal means of how much physiologically-driven changes in different land processes (stomatal conductance, LAI, and evaporation) contribute to the total multi-model mean physiologically-driven change in land evapotranspiration. Multi-model means in this figure are averaged across all CMIP6 models for which model output is available, which consists of up to 9 models. Transpiration and LAI data necessary for this partitioning were not available for GFDL-ESM4, so this model is only included in the multi-model mean for the total evapotranspiration change. The total evapotranspiration change (black line) is the same as the multi-model mean change in evapotranspiration shown in Figure 7a.
FIGURE 9. Spatial pattern of multi-model mean physiologically-driven changes in surface energy fluxes as calculated by FULL-RAD at the point of CO$_2$ doubling (averaged over years 61-80) for (a) clear-sky downwelling shortwave radiation, (b) cloudy downwelling shortwave radiation, (c) upwelling shortwave radiation, (d) clear-sky downwelling longwave radiation, (e) cloudy downwelling longwave radiation, (f) upwelling longwave radiation, (g) latent heat, and (h) sensible heat. Multi-model means include all CMIP6 models for which model output is available; this consists of up to 9 models. Data for some surface energy fluxes were not available for the following models: GFDL-ESM4 (panels a, b, d, and e), GISS-E2-1-G, 3 (panels c and h) and CNRM-ESM2-1 (panels d and e).