Photosynthesis responses to intrinsic water use efficiency depend on atmospheric feedbacks and modify the magnitude of response to elevated CO_2

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Abstract

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Photosynthesis and transpiration affect the Earth system by altering carbon, water, and energy fluxes. Plants have valves on leaves called stomata that regulate gas exchange needed for these processes, thus tightly linking the flux of water and carbon. Water use efficiency represents plant water loss per carbon gain and can vary based on plant type and environmental conditions. It has observational uncertainty but in land models is typically simplified to one value per plant type. Here we examined how perturbations of water use efficiency influence photosynthesis using coupled Earth System model experiments. We found that while low water use efficiency perturbations led to a monotonic reduction in photosynthesis nearly everywhere, high water use efficiency perturbations have a photosynthetic response that is regionally dependent and sensitive to the inclusion of a dynamic atmosphere and leaf area. Notably, photosynthesis in the Amazon and central North America increases with an increase in water use efficiency, while photosynthesis in boreal regions decreases with increasing water use efficiency. The photosynthetic response to an increase in water use efficiency in these regions reversed with the inclusion of a dynamic atmosphere and dynamic leaf area, largely due to sensitivity to temperature and vapor pressure deficit increases. In contrast, low water use efficiency perturbations consistently resulted in a global decline in photosynthesis, with the inclusion of a dynamic atmosphere and leaf area modifying only

the magnitude of the response. We also found that water use efficiency influenced the plant photosynthetic response to elevated atmospheric carbon dioxide (CO_2), with both high and low perturbations modifying the total photosynthetic response on average by 89% and 37%, respectively. Assumptions about water use efficiency in land models and what components of the model we allow to dynamically respond significantly affect the climate outcome. By evaluating different assumptions of water use efficiency, our study contributes to the understanding of uncertainty in plant photosynthesis under future climate projections and how these projections may differ from real-world scenarios.

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GLOSSARY

CESM: NCAR's Community Earth System Model

CLM: Community Land Model used in CESM

CAM: Community Atmosphere Model used in CESM

BGC: Biogeochemistry mode in CLM

PFT: Plant Functional Type

WUE: Plant Water Use Efficiency

IWUE: Plant Intrinsic Water Use Efficiency

G_{1M}: Medlyn slope in the Medlyn model for stomatal conductance

A_N: Photosynthesis

G_S: Stomatal conductance

VPD: Vapor Pressure Deficit

G_0: Medlyn intercept in the Medlyn model for stomatal conductance

C_S: Atmospheric CO_2 concentration

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DEDICATION

with all my heart to *baba* and *mama*

Chapter 1

INTRODUCTION

Terrestrial plants influence Earth's climate through processes like photosynthesis and transpiration and contribute to uncertainties in projections of future climate. Environmental factors such as light, water, and nutrient availability, temperature, and carbon dioxide (CO_2) concentration affect plant processes, and plant processes in turn influence climate [3]. Photosynthesis acts as a carbon sink, removing CO_2 from the atmosphere, converting it into sugars and then plant tissues, storing carbon into their biomass as they grow. A change in photosynthesis can also change leaf area, which would influence total transpiration [7]. Transpiration accounts about 60% of latent heat flux over land [22], so a change in transpiration alters the partitioning of the latent and sensible turbulent heat fluxes, which affects temperature, atmospheric water vapor, cloud, and radiative properties [2, 13]. Thus, understanding plant uncertainty is crucial to our understanding the climate.

The rate of photosynthesis is set by parameters that represent biochemical processes including light acquisition and fixation of CO_2 that depend on environmental variables including light, nutrients, atmospheric CO_2, temperature, atmospheric dryness, and soil water [6]. Resource limitations such as insufficient light, nutrients, atmospheric CO_2,or water stress can constrain photosynthetic biochemical reactions, while temperature change can increase the biochemical reactions up to a thermal optimal determined by plant functional type [12, 24]. Additionally, plants can acclimate to changes in temperature up to 35-40°C though the thermal optimum for biochemical processes typically is less than that [9, 12, 16]. Experimental observations have also shown that the photosynthetic response to increasing temperatures can be modified by water availability, with limited water decreasing photosynthetic capacity at higher temperatures [11].

Plant carbon uptake and water loss are both regulated by valves on leaves called stomata. Stomata regulate these fluxes by opening and closing. The theory for optimal stomatal behavior suggests that plants dynamically adjust their stomatal opening to achieve an optimal balance between the rate of photosynthesis and the water loss from transpiration [4]. Alternatively, empirical formulations for stomatal behavior are based on experimental observations of stomatal behavior under different environmental conditions such as atmospheric dryness and CO_2 concentration [1, 14]. Efforts have been made to integrate the optimal and empirical approaches, aiming to reconcile observations with the theory of stomatal behavior [17]. Both optimal and empirical approaches yield similar results at leaf, canopy, and global scale simulations [8], but, more recently, hydraulics-based stomatal optimization approaches have been shown to perform better when evaluated against leaf-level observations [19].

Regardless of the approach taken to model stomatal behavior, a more open stomata tends to increase transpiration and the uptake of carbon for photosynthesis. As a result, photosynthesis and transpiration are tightly coupled. The relative rate of these processes can be related to water use efficiency (WUE) as follows:

$$WUE = \frac{Photosynthesis}{Transpiration} = \frac{A_n}{g_s \cdot VPD}, \tag{1.1}$$

where stomatal conductance (g_s) is the estimated rate of gas exchange based on stomatal aperture. Closed stomata have no or low g_s and open stomata have high g_s. Transpiration is inherently related to g_s, with transpiration being proportional to g_s multiplied by the gradient of vapor pressure deficit (VPD). A larger WUE means that a plant is more water efficient— less water is lost per carbon gain. WUE is difficult to quantify on a landscape scale because photosynthesis and transpiration are difficult to quantify at scales beyond leaf-level.

Another way to measure water use efficiency is to derive it from the carbon isotope composition of tree-rings and leaves [20]. This quantity, called the intrinsic water use efficiency (iWUE), is similar to WUE but replaces transpiration with stomatal conductance as follows:

$$iWUE = \frac{Photosynthesis}{Stomatal\ \ Conductance} = \frac{A_n}{g_s}. \tag{1.2}$$

WUE and iWUE are similar: both represent the ratio of carbon gain to water loss. Equation 1.2 is focused on the stomatal response to environmental conditions while equation 1.1 is influenced by abiotic evaporative potential due to atmospheric dryness. iWUE directly modulates photosynthesis and indirectly modulates transpiration, so changes in iWUE is related to both carbon and water fluxes and thus to climate.

iWUE has observational uncertainty. Additionally, both components of iWUE, photosynthesis and stomatal conductance, are expected to change with a changing climate. As some regions get hotter and drier, plants are inclined to close their stomata to minimize water loss through transpiration, decreasing stomatal conductance, resulting in a decrease in CO_2 uptake and decreasing photosynthesis. However, the impact of changing climate due to a reduced stomatal conductance on photosynthesis can be offset by increasing CO_2. With a larger CO_2 gradient, plants can take up the same amount of carbon at a smaller stomatal aperture. Generally, under higher atmospheric CO_2, plants will have higher iWUE, closing their stomata and losing less water per carbon they fix for photosynthesis [10]. Plants may also be able to increase photosynthesis under high CO_2, by increasing leaf area, though studies have suggested that the increase does not extend to long-term carbon storage through tree ring growth [18, 21]. Changing leaf area also changes the amount of plant stomata, assuming that stomata density on leaves is constant, which would drive changes in total fluxes of carbon and water.

1.1 Uncertainty in iWUE

iWUE is an emergent property of plants, which is not directly specified within process-based models that explicitly represent photosynthetic rates and stomatal conductance (eg. Farquhar, Ball-Berry, Medlyn). In climate models iWUE is determined by a common parameterization for the photynthesis-stomatal system: the Medlyn model for stomatal conductance [17]. In the Medlyn model, stomatal conductance, g_s, is given by

$$g_s = g_0 + 1.6(1 + \frac{g_{1M}}{\sqrt{VPD}})\frac{A_n}{c_s}, \tag{1.3}$$

where A_n is photosynthesis, c_s is the atmospheric CO_2 concentration, VPD is vapor pressure deficit, and g_0 is the Medlyn intercept (minimum stomatal conductance, when the stomata are completely closed). A_n is linearly proportional to g_s, so an increase in stomatal conductance relates to an increase in photosynthesis if all other variables remain constant. c_s and $\sqrt{\text{VPD}}$ are inversely proportional to g_s. The Medlyn slope, g_{1M}, is an empirically estimated parameter based on field observations.

Relating equation 1.2 and 1.3, iWUE is inversely proportional to and can be modulated by g_{1M}:

$$iWUE \propto \frac{1}{g_{1M}}, \tag{1.4}$$

given that A_n is sufficiently large. There is a large range of variability of the g_{1M} across plant types and within a plant type [15, 23]. Typically, a g_{1M} value is assigned to each plant type in global-scale models. In the National Center for Atmospheric Research (NCAR) Community Land Model (CLM), g_{1M} has a varied spatial distribution since there are fourteen different plant functional types (PFTs), and each PFT has a unique spatial distribution and a different g_{1M}. *Since there is large uncertainty in the value of g_{1M} for each plant type, the spatial distribution of iWUE at the global scale is also uncertain and therefore so too will the regional climate response to increasing CO_2.*

In this study we examine (1) the impact of uncertainty in g_{1M}, and therefore uncertainty in iWUE, on climate, (2) the climate feedbacks that in turn contribute to the change in iWUE, and (3) the uncertainty in iWUE and climate under rising atmospheric CO_2 concentrations. We focused on the response of photosynthesis because it is directly tied to the carbon cycle by taking in carbon and indirectly connected to the water cycle through its close relationship with plant transpiration.

Chapter 2
METHODS

2.1 Model Configurations

We defined two configurations. The "Land-Atmosphere" configuration was run with a dynamic atmosphere and a land model that included a dynamic leaf area, resulting in changes in both atmospheric conditions and leaf area in response to iWUE perturbations. The "Land-Only-fixed leaf" configuration forced the same land model with a prescribed meteorology but the leaf area was held to the climatological leaf area, so there were no changes in both atmospheric conditions and leaf area in response to iWUE perturbations.

We performed global-scale simulations of the Community Earth System Model version 2 (CESM2) at 0.9x1.25° resolution [5]. CESM2 is comprised of the Community Land Model 5 (CLM5), the Community Atmosphere Model 6 (CAM6), and a slab ocean from the CESM2 CMIP6 preindustrial control run. Land-Atmosphere simulations had active biogeochemistry that allowed for leaf area to dynamically respond to climate. Land-Only-fixed leaf simulations had prescribed leaf phenology, including fixed climatological leaf area. The prescribed meteorological forcing of the Land-Only-fixed leaf simulations were from the output of the default iWUE Land-Atmosphere simulation. The prescribed atmospheric conditions were driven by the coupler history files of the Land-Atmosphere simulation, which is saved every 3 hours. The 3-hourly history files are interpolated to 30 minutes when they are used for the Land-Only-fixed leaf simulations. All simulations were run for 120 years, with the first 40 years discarded to account for time for the system to reach equilibrium. We used an idealized CO_2 forcing, with preindustrial CO_2 at 284.7ppm and 2x preindustrial CO_2 at 569.4ppm. All non-CO_2 forcings were at preindustrial levels.

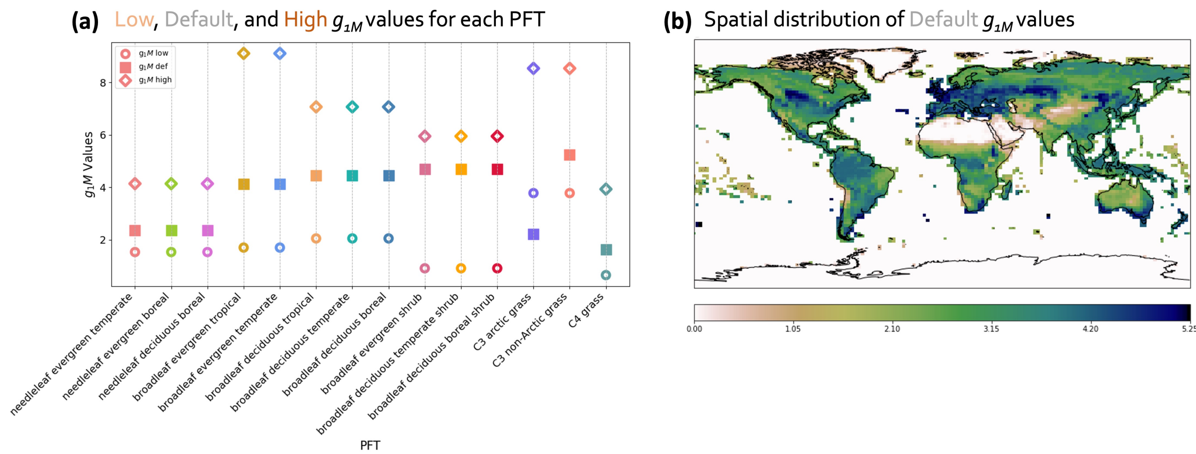

Figure 2.1: (a) Scatterplot of the default and perturbed medlyn slope parameter, g_{1M}, for each vegetation type in the CLM. (b) Spatial plot of default aggregate g_{1M} values used in CLM.

2.2 iWUE Perturbations

We perturbed iWUE by setting g_{1M} to a minimum and maximum for each PFT based on the 5^{th} and 95^{th} percentile from field observations [15]. We compared those perturbed simulations against simulations with the default parameter values used in CLM5 (Figure 2.1a). The spatial distribution of PFTs and their default g_{1M} values result in a spatially varying distribution of aggregate g_{1M} values (Figure 2.1b). Changes in g_{1M} are directly linked to iWUE through the formulation of the Medlyn model, so we describe our results in terms of the change in iWUE to a perturbed g_{1M} (Figure 2.2a).

2.3 Experimental Design

In order to isolate of the effects of multiple processes at different scales that comprise the full climate response to iWUE, we performed nine simulations. Six simulations use the Land-Atmosphere configuration. We set g_{1M} to either default, low, or high values and the atmospheric CO_2 level to preindustrial levels and to 2x preindustrial atmospheric CO_2 levels (Table 2.1). We also performed the three g_{1M} experiments for each iWUE perturbation

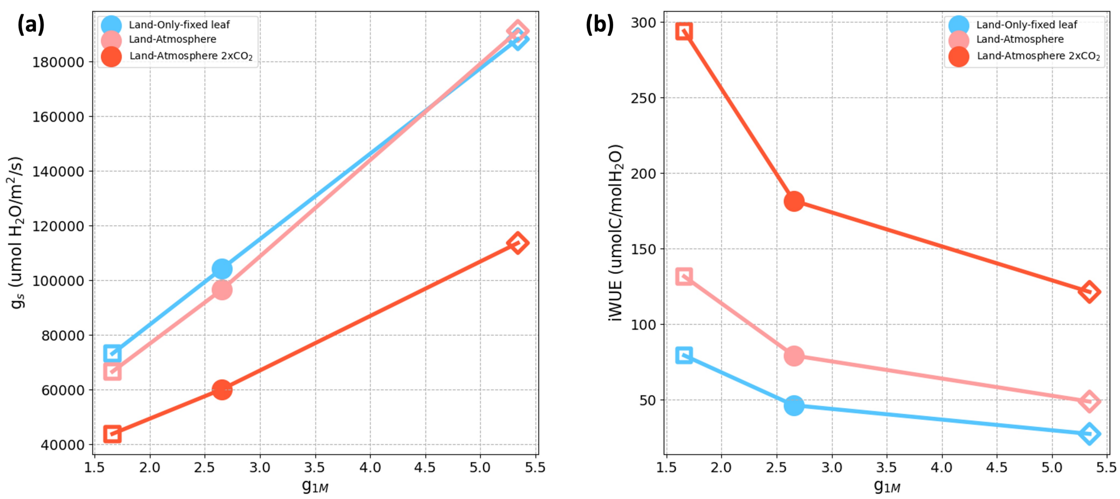

Figure 2.2: Globally averaged Medlyn slope g_{1M} vs *(a)* globally averaged iWUE and *(b)* globally averaged stomatal conductance g_s for the Land-Only-fixed leaf and Land-Atmosphere simulations at 1x and 2xCO_2.

Table 2.1: Summary of simulations.

1x Pre-Industrial atmospheric CO_2	Land-Atmosphere *(Land-Atmosphere)*	Dynamic Leaf Area	Low g_{1M}
			Default g_{1M}
			High g_{1M}
	Land only *(Land-Only-fixed leaf)*	Fixed Leaf Area	Low g_{1M}
			Default g_{1M}
			High g_{1M}
2x Pre-Industrial atmospheric CO_2	Land-Atmosphere *(Land-Atmosphere)*	Dynamic Leaf Area	Low g_{1M}
			Default g_{1M}
			High g_{1M}

with the Land-Only-fixed leaf configuration, setting CO_2 to preindustrial levels and the mean climatology to the that of the default iWUE Land-Atmosphere simulation forced by preindustrial CO_2 as described above. The Land-Only-fixed leaf simulations are used to understand the changes in iWUE, photosynthesis, and climate in the Land-Atmosphere preindustrial CO_2 simulations.

2.3.1 Quantifying impact of a g_{1M} perturbation on iWUE and climate

To quantify a climate response to a change in iWUE, we calculated the response of a variable to an iWUE perturbation by comparing the high and low iWUE against the default iWUE simulation for each configuration. For all analysis we averaged across years to quantify the equilibrium response to an iWUE perturbation as slab ocean simulations represent equilibrium conditions and provide many samples of a climate state over time. We report both the absolute difference and percentage difference for individual variables. Percentage difference was calculated by taking the absolute difference and dividing it by the average value in the default iWUE simulation. Generally, the spatial patterns in photosynthetic response calculated annually were similar to those from the growing season only, and so we report the annual averages here.

2.3.2 Quantifying impact of dynamic atmosphere and dynamic leaf area

To understand how atmospheric and leaf area feedbacks modify the climate impact of iWUE choice, we compared the Land-Only-fixed leaf and Land-Atmosphere configurations by comparing their differences between the high or low iWUE and the default iWUE experiments within a single model configuration. For example, we compared the difference between the high and default iWUE experiment for the Land-Only-fixed leaf configuration with the difference between the high and default iWUE experiment for the Land-Atmosphere configuration. We also compared the change in direction of photosynthetic response between the Land-Atmosphere and Land-Only-fixed leaf configurations for the high iWUE experiments by filtering for (1) statistical significant photosynthetic responses to high iWUE perturbation in the Land-Only-fixed leaf and Land-Atmosphere configurations by two-tailed, independent t-tests and (2) a sign change in photosynthetic response between the two configurations.

2.3.3 Quantifying impact of elevated atmospheric CO_2

We performed two comparisons with the 2xCO_2 simulations. First, we quantified the absolute response to an increase in CO_2 by comparing 2xCO_2 simulations to the parallel 1xCO_2 simulations. Second, we quantified how an iWUE perturbation modifies the absolute response tin an increase in CO_2. We did this using a difference of differences, where, similarly to previous comparisons, we took the difference between the low or high iWUE and the default iWUE experiment at 1xCO_2 and compared it with the same difference at 2xCO_2. The first comparison explains how iWUE and climate work differently at higher CO_2 and the second comparison shows how the iWUE perturbation modifies the photosynthetic response to an increase in CO_2.

2.4 Perturbed Meteorology Simulations

To isolate the effects of temperature and VPD on photosynthesis we used simulations in which a single meteorological variable was modified in each experiment. We used global-scale ”synthetic meteorology” simulations from Zarakas et. al., 2024, which we call here ”perturbed meteorology” simulations. These simulations were also run in a very similar version of the CESM2 climate model as our iWUE experiments with CLM5, active biogeochemistry, CAM6, the slab ocean from the CESM2 CMIP6 preindustrial control run, and idealized preindustrial CO_2 forcing of 284.7ppm. Simulations were branched from the same spinup and run for 20 years each. For each perturbed meteorology simulation, a single meteorological variable in the atmospheric output of the control simulation was perturbed. We used a total of two perturbed meteorology simulations and one control run. The first perturbed meteorology simulation has a 1°C increase at the bottom of the atmosphere for each grid cell. The second perturbed meteorology simulation has a 10% increase in specific humidity at the bottom of the atmosphere for each grid cell.

For each perturbed meteorology simulation, we calculated the expected response of photosynthesis (δGPP) to the change in temperature or VPD due to iWUE perturbation. We calculated the expected response of photosynthesis to a single meteorological perturbation as follows:

$$\begin{aligned}
\Delta GPP_{\text{perturb}} &= GPP_{\text{perturb}} - GPP_{\text{control}} \,, \\
\Delta Var_{\text{perturb}} &= Var_{\text{perturb}} - Var_{\text{control}} \,. \\
\Delta Var_{\text{Land-Atm}} &= Var_{\text{Land-Atm perturb iWUE}} - Var_{\text{Land-Atm Def iWUE}} \,, \\
\delta GPP_{\text{expected}} &= \frac{\Delta GPP_{\text{perturb}}}{\Delta Var_{\text{perturb}}} \times \Delta Var_{\text{Land-Atm}} \,,
\end{aligned} \tag{2.1}$$

where Var is either temperature or VPD. Since the Land-Only-fixed leaf simulations do not have changes in bottom of the atmosphere temperature or VPD, we did not include them in this part of the analysis.

We used the perturbed meteorology simulations to attribute how much photosynthetic response difference between the Land-Only-fixed leaf and Land-Atmosphere configurations was due to changes in temperature and vapor pressure deficit (VPD). The temperature perturbed simulation accounts for both the direct and indirect effects of temperature on photosynthesis, including the effect of VPD. The specific humidity perturbed simulation held temperature constant, isolating the effects of VPD on photosynthesis. VPD was calculated based on the the bottom of the atmosphere temperature, pressure, and specific humidity.

2.5 Statistical Significance

We filtered our reported results for statistical significance using a two-tailed Student's t-test with an assumed 120 degrees of freedom. The t-test was used to determine if responses in the perturbed iWUE simulations differed from those in the default iWUE simulation.

Chapter 3
RESULTS

3.1 iWUE perturbation

3.1.1 low iWUE

In the Land-Atmosphere low iWUE experiment, photosynthesis decreased across the globe (Figure 3.1b). We found larger absolute decreases in photosynthesis near the equator, due to greater plant productivity in the tropics. Photosynthesis decreased with decreasing iWUE since plants were forced to open their stomata and transpire more (Figure 3.4b&c). Greater transpiration rates depleted plant water supply making plants more soil water stressed (Figure 3.4d), leading to a decrease the number of leaves plants support (Figure 3.4g) which decreased total photosynthesis (Figure 3.1b). Although VPD decreased, decreasing atmospheric water stress, the influence of soil water stress on plants was greater and led to the decrease in photosynthesis that we observed.

3.1.2 high iWUE

Photosynthetic response to high iWUE perturbation had a much smaller magnitude than low iWUE perturbation. In the Land-Atmosphere high iWUE experiment, photosynthetic response was regionally sensitive, also with stronger response near the equator (Figure 3.1d). Regions at the same latitude had different photosynthetic response; In the Amazon there were decreases in photosynthesis while in southeast Asia there were increases in photosynthesis. Other notable differences in photosynthetic response were the decreases in Australia, continental United States, east China, and Europe and the increases in Mexico, India, and most of the boreal regions.

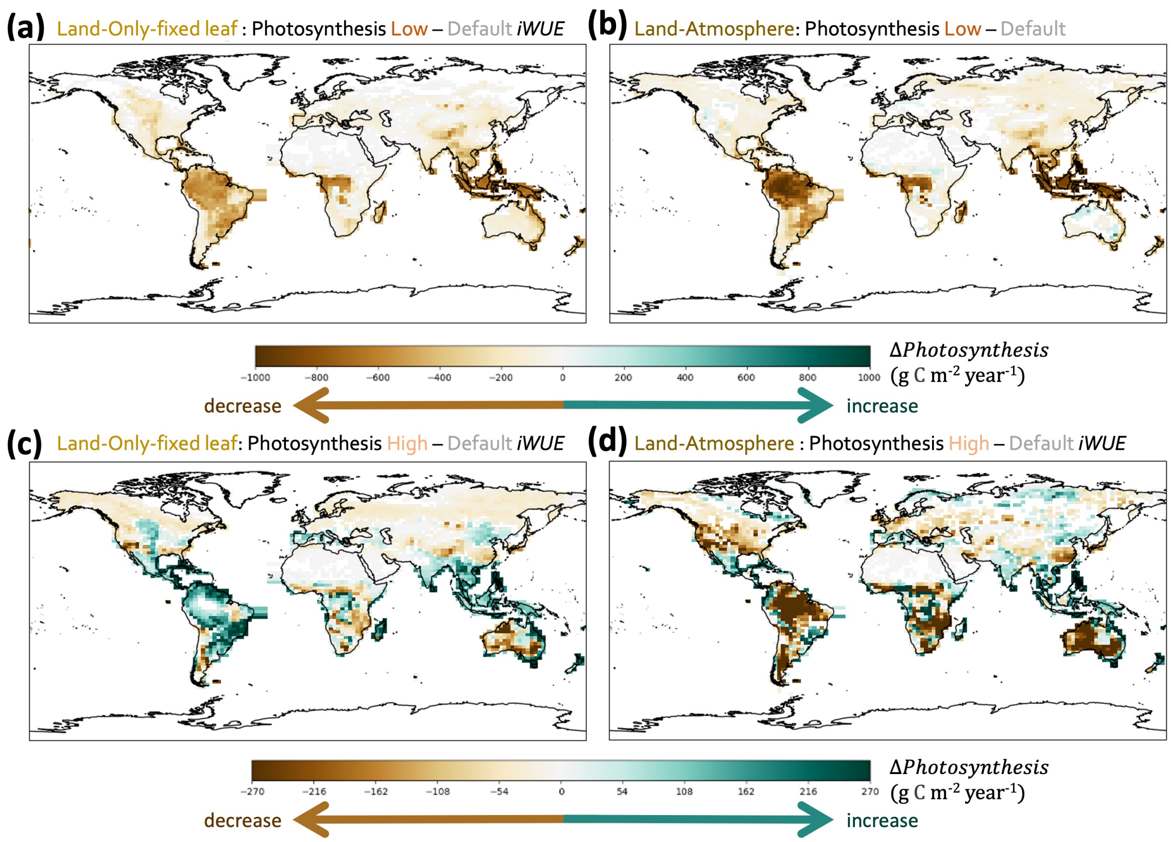

Figure 3.1: Spatial difference plot of photosynthesis for low iWUE at *(a)* Land-Only-fixed leaf and *(b)* Land-Atmosphere configurations and high iWUE at *(c)* Land-Only-fixed leaf and *(d)* Land-Atmosphere configurations.

3.2 Role of a dynamic atmosphere and dynamic leaf area

3.2.1 low iWUE

The photosynthetic response to low iWUE was similar with and without dynamic atmosphere and dynamic leaf area as shown by the comparison between the Land-Only-fixed leaf and Land-Atmosphere low iWUE experiments. Both experiments had decreases across the globe (Figure 3.1a&b) with similar spatial patterns but a different magnitude of change. The larger photosynthesis decreases in Land-Atmosphere low iWUE experiment were largely driven by leaf area decreases (Figure 3.4g) since the Land-Only-fixed leaf low iWUE experiment had no leaf area change. The inclusion of a dynamic atmosphere and leaf area amplified the response to decreased iWUE.

3.2.2 high iWUE

In contrast to the low iWUE experiments, the high iWUE experiments had a different photosynthetic response to perturbation when dynamic leaf area and atmosphere are included. Both the Land-Only-fixed leaf and Land-Atmosphere experiments had a regionally sensitive response but with different spatial patterns (Figure 3.1c&d). There were differences in both the magnitude and sign of photosynthetic response when the atmosphere and leaf area area allowed to respond. In particular, we found a change in the sign of response of photosynthesis to changes in iWUE in the Amazon, central North America (central NA), and boreal regions (Figure 3.2). We discussed each of these three regions in further detail below.

3.2.3 Relationship between g_{1M} and iWUE

We directly perturbed g_{1M}, resulting in varying iWUE perturbations between the Land-Only-fixed leaf and Land-Atmosphere experiment for each region. Generally, we expected photosynthesis to increase with higher iWUE. In the Amazon, the Land-Only-fixed leaf experiment had a less of an increase in iWUE at low g_{1M} (Figure 3.7b), suggesting that the Land-Only-fixed leaf experiment should have had a more moderate increase photosyn-

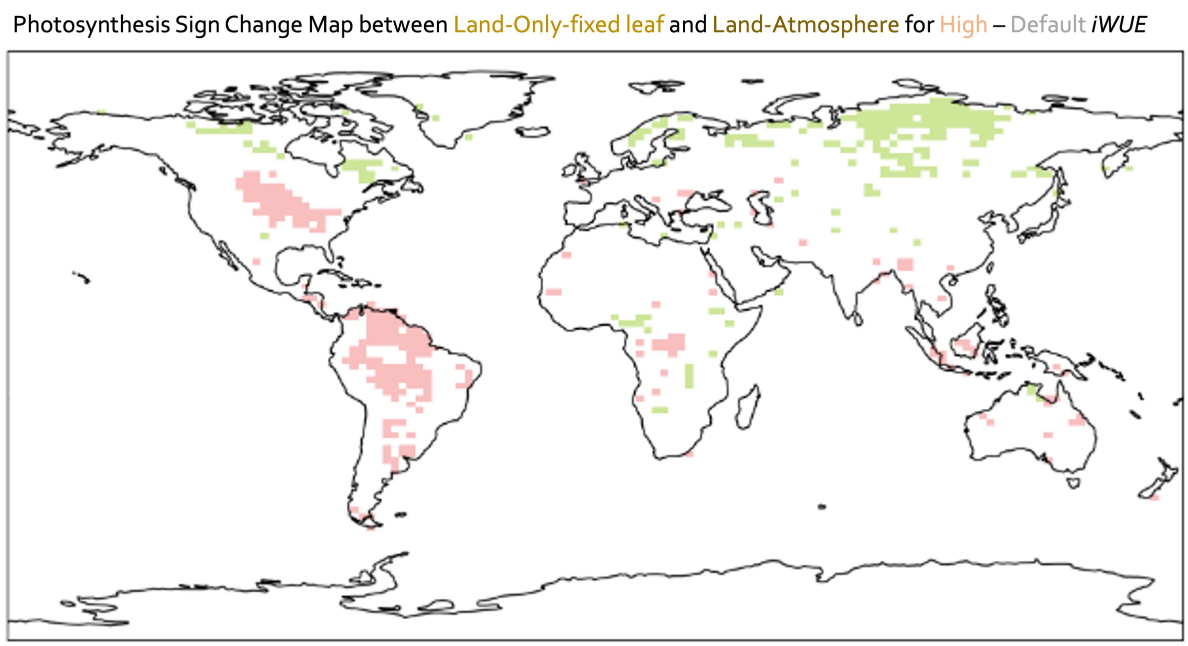

Figure 3.2: A spatial plot that shows the sign change in photosynthetic response between the Land-Only-fixed leaf and Land-Atmosphere experiment. Colors grids have a sign change and the color represents the direction of change.

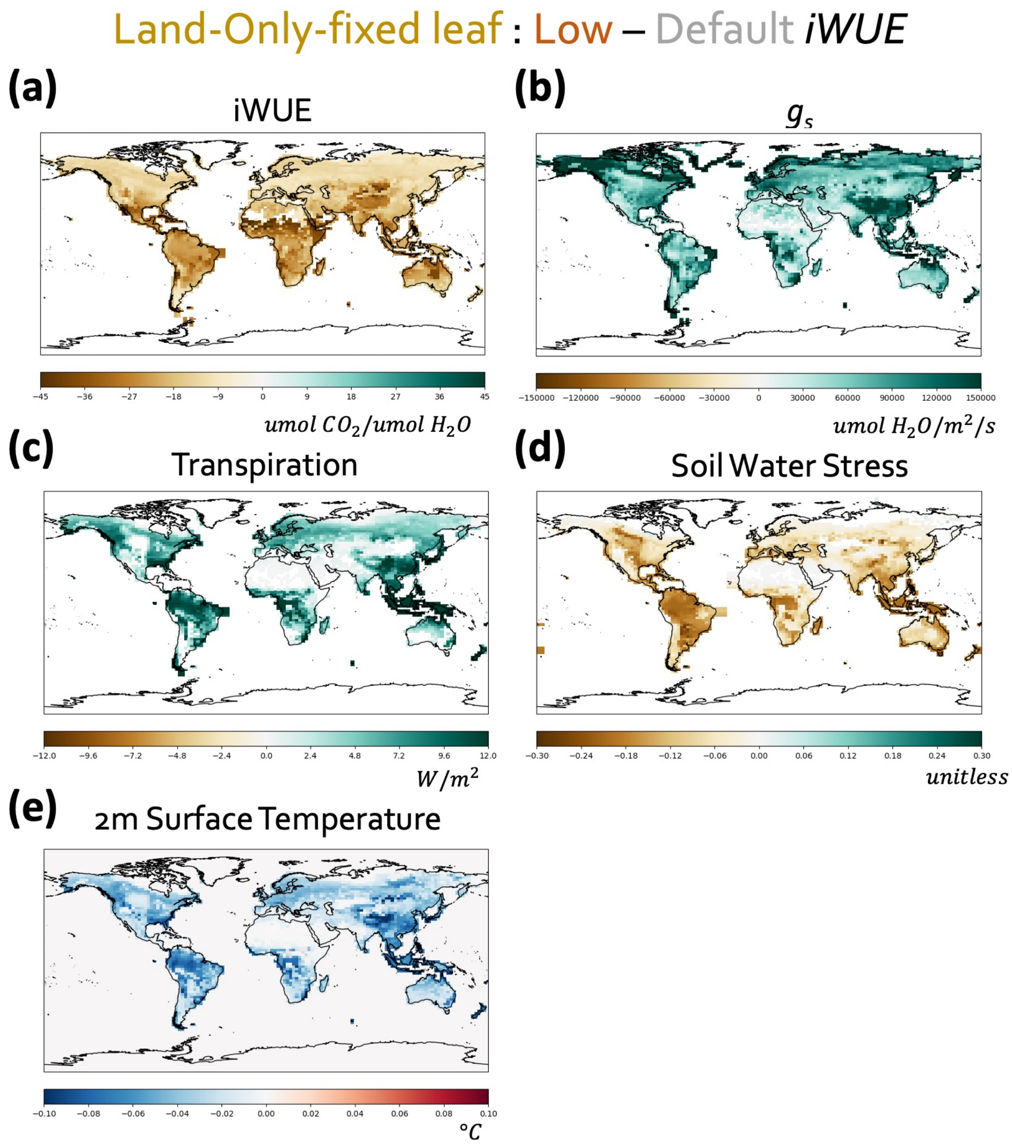

Figure 3.3: Spatial difference plots of *(a)* iWUE, *(b)* stomatal conductance, *(c)* transpiration, *(d)* soil water stress, and *(e)* surface temperature for low iWUE at Land-Only-fixed leaf configuration.

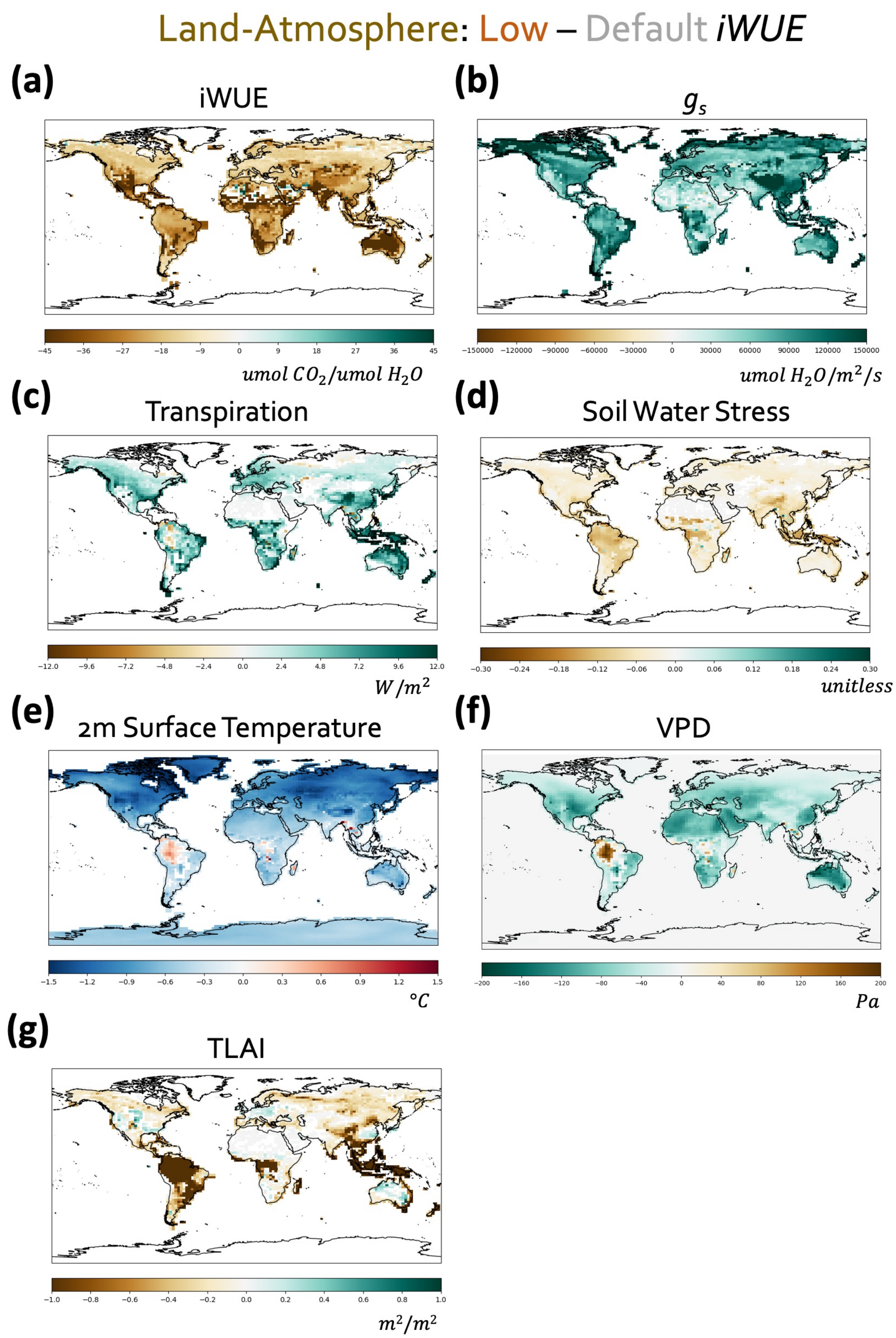

Figure 3.4: Spatial difference plots of *(a)* iWUE, *(b)* stomatal conductance, *(c)* transpiration, *(d)* soil water stress, *(e)* surface temperature, *(f)* vapor pressure deficit, and *(g)* total leaf area for low iWUE at Land-Atmosphere configuration.

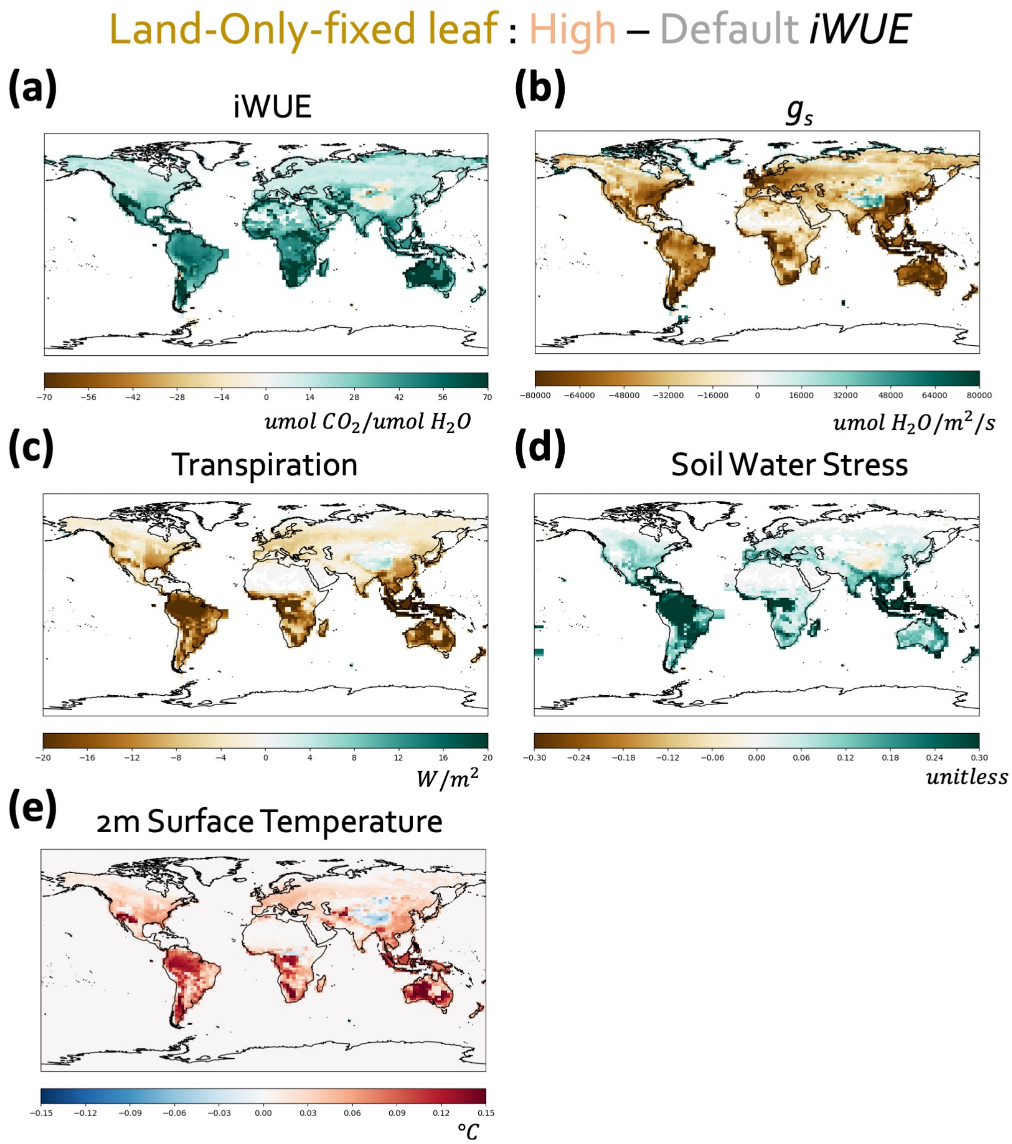

Figure 3.5: Spatial difference plots of (*a*) iWUE, (*b*) stomatal conductance, (*c*) transpiration, (*d*) soil water stress, and (*e*) surface temperature for high iWUE at Land-Only-fixed leaf configuration.

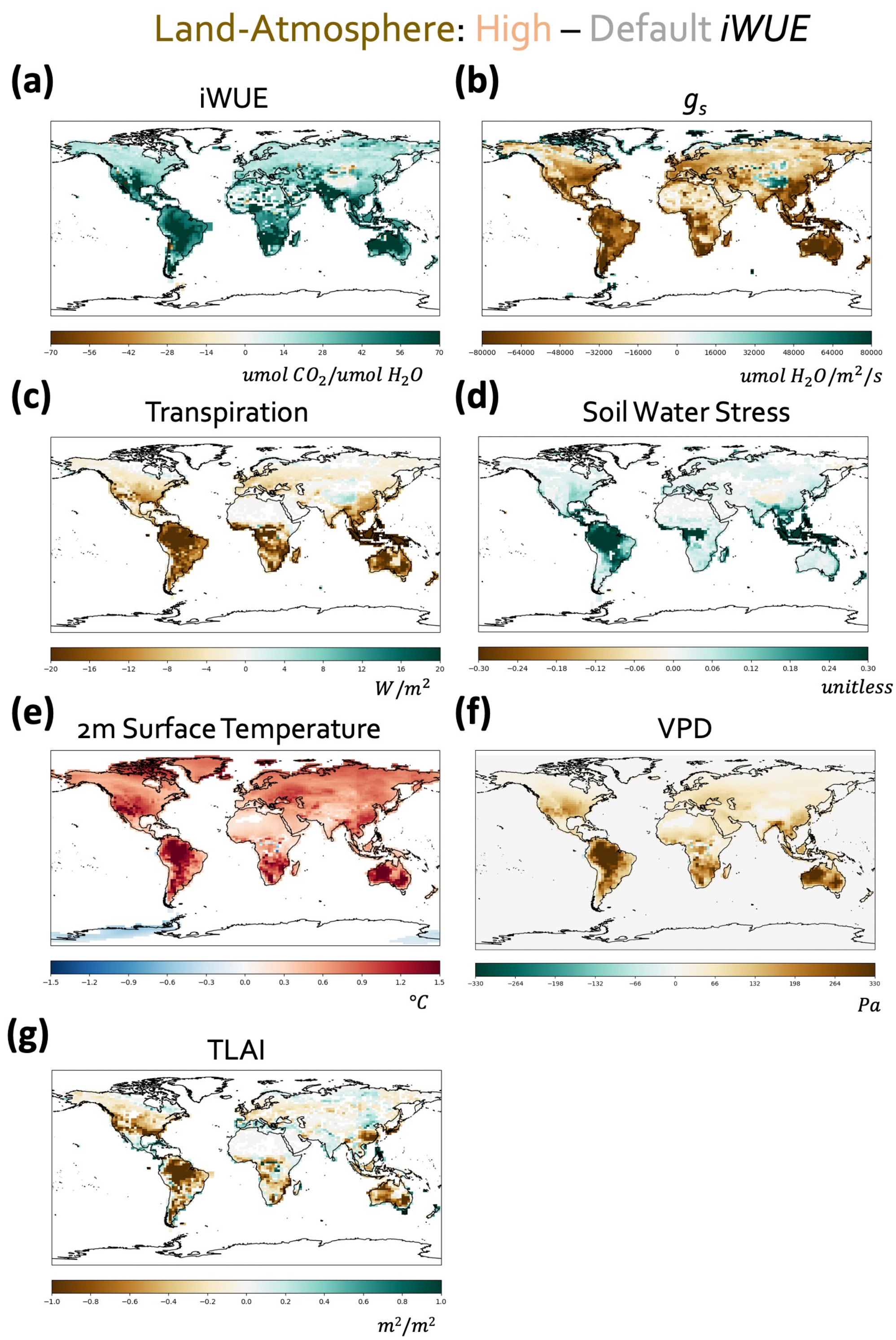

Figure 3.6: Spatial difference plots of (a) iWUE, (b) stomatal conductance, (c) transpiration, (d) soil water stress, (e) surface temperature, (f) vapor pressure deficit, and (g) total leaf area for high iWUE at Land-Atmosphere configuration.

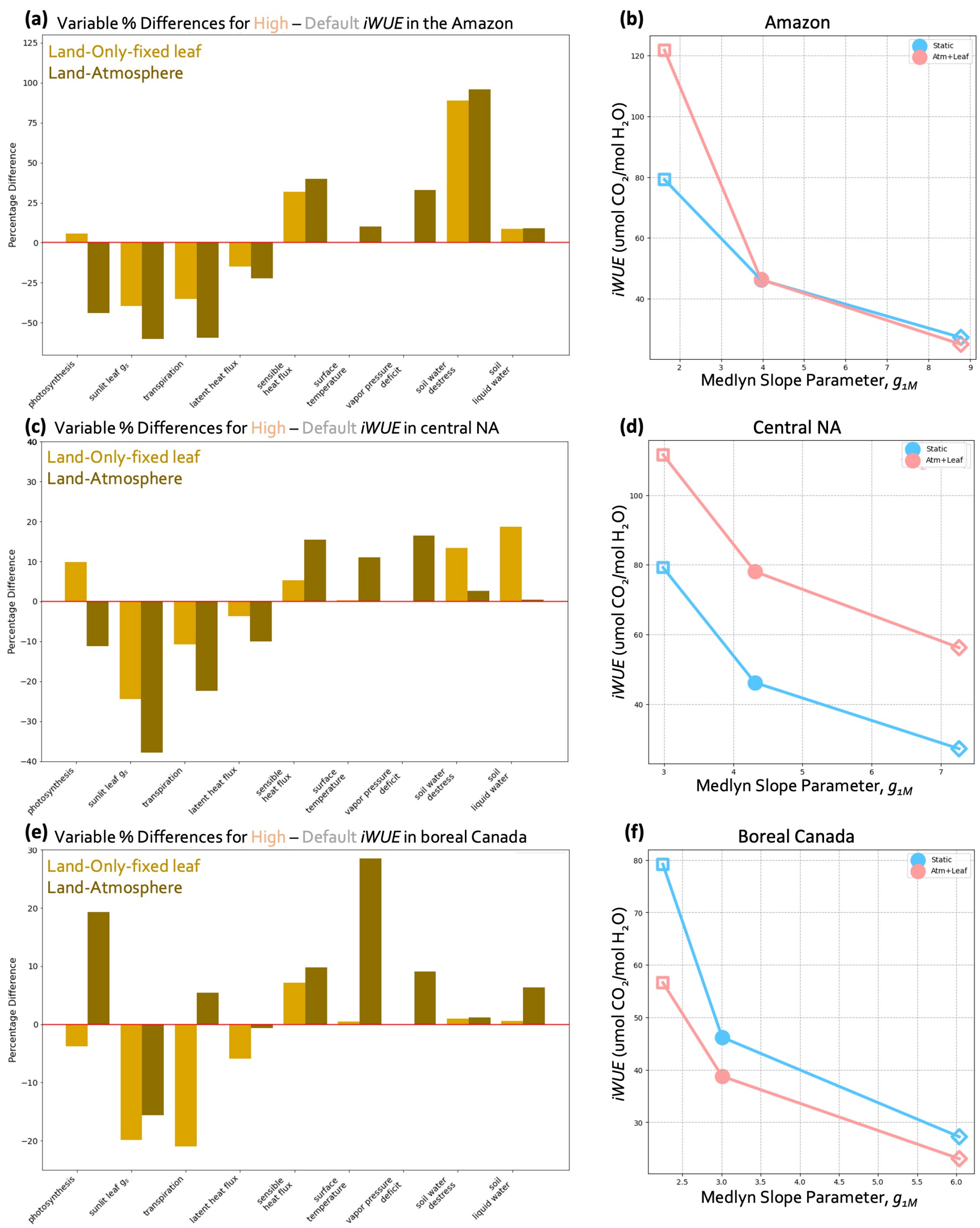

Figure 3.7: Percentage differences of photosynthesis and variables that can influence photosynthesis between the Land-Only-fixed leaf and Land-Atmosphere low iWUE experiments in the *(a)* Amazon, *(c)* central North America, and *(e)* boreal Canada. The relationship between g_{1M} and iWUE is plotted for each region *(b)*, *(d)*, *(f)* .

thesis compared to the Land-Atmosphere experiment. However this was contrary to what we found, as the Land-Atmosphere experiment showed an absolute decrease in photosynthesis. The Land-Atmosphere high iWUE experiment had photosynthesis decreases while the Land-Only-fixed leaf high iWUE experiment had photosynthesis increases (Table 3.1; Figure 3.7a). We also observed unexpected photosynthetic responses in central NA and boreal Canada. The central NA results mirrored those of the Amazon, with the central NA Land-Only-fixed leaf experiment having less of an iWUE increase at low g_{1M} (Figure 3.7d) suggesting a great photosynthesis increase in the Land-Atmosphere experiment. We saw that both the Land-Atmosphere and Land-Only-fixed leaf high iWUE experiments exhibited the same unexpected trends as the Amazon, with absolute decreases in photosynthesis for the Land-Atmosphere and increases in the Land-Only-fixed leaf high iWUE experiment (Table 3.1; Figure 3.7c). In contrast to the Amazon and central NA regions, the boreal Canada Land-Only-fixed leaf experiment had a greater increase in iWUE with low g_{1M} perturbation compared to the Land-Atmosphere experiment (Figure 3.7f), which gave us the expectation that the Land-Only-fixed leaf experiment would have a greater increase in photosynthesis. Again, contrary to what we found, photosynthesis had increases for the Land-Atmosphere and absolute decreases for the Land-Only-fixed leaf high iWUE experiment (Table 3.1; Figure 3.7e). We explored reasons why in Section 4.

3.2.4 Amazon

In the Amazon, we observed decreases in photosynthesis for the Land-Atmosphere high iWUE experiment and increases in photosynthesis for the Land-Only-fixed leaf high iWUE experiment (Table 3.1; Figure 3.7a). Stomatal conductance was largely influenced by high iWUE perturbation and decreased for both experiments (Table 3.1). The two experiments also had the similar changes in transpiration and heat fluxes (Table 3.1). The decrease in transpiration with high iWUE decreased latent heat flux, with sensible heat flux increasing to compensate for the decrease. Since plants were transpiring less, they were pulling less water from the ground to replenish their water stores, so there was increased soil water availability.

The responses of soil water availability variables between the two experiments were also similar, with decreases in soil water stress and relatively smaller increases in soil liquid content (Table 3.1). With the inclusion of a dynamic atmosphere, we were allowing the atmosphere to respond to the changes in plant transpiration by increasing temperature and VPD (Table 3.1) due to feedbacks with the atmosphere. Drier air may have caused the greater stomatal closure in the Land-Atmosphere experiment (Table 3.1). This can explain the higher increase in iWUE at low g_{1M}, as the stomatal conductance response to the inclusion of a dynamic atmosphere resulted in a smaller g_s term in equation 1.2 and a greater increase in iWUE. The dynamic atmosphere also allowed reaction to the transpiration decrease and water vapor by decreasing in low cloud coverage that typically reflect incoming solar radiation, so a reduction in clouds increased incoming radiation (Table 3.1) and increased temperature which would drive further increases in VPD if water vapor remained constant.

3.2.5 Central North America

In central North America, we saw the same photosynthetic response sign change as the Amazon, where photosynthesis decreased in the Land-Atmosphere and increases in the Land-Only-fixed leaf high iWUE experiment (Table 3.1; Figure 3.7c). Relative to the Land-Atmosphere experiment, the Land-Only-fixed leaf experiment had smaller decreases in stomatal conductance, which were accompanied by smaller decreases in transpiration and resulted in smaller changes in turbulent heat fluxes (Table 3.1). The Land-Only-fixed leaf experiment also had smaller decreases in soil water stress and smaller increases in soil liquid water content (Table 3.1). We also observed the Land-Atmosphere experiment having larger increases in temperature and VPD, similarly to what we observed in the Amazon (Table 3.1).

3.2.6 Boreal Canada

In boreal Canada we saw an opposite sign of photosynthetic response between the Land-Atmosphere and Land-Only-fixed leaf experiments when compared to the Amazon and central North America. Photosynthesis increased for the Land-Atmosphere and decreased for the

Land-Only-fixed leaf high iWUE experiment (Table 3.1; Figure 3.7e). Again, high iWUE decreased stomatal conductance, so we observed stomatal closure (Table 3.1). Accompanying that was a decrease in transpiration and changes in turbulent heat fluxes for the Land-Only-fixed leaf experiment. In contrast, we saw a slight increase in transpiration for the Land-Atmosphere experiment instead, but a decrease in latent heat flux and increase in sensible heat flux consistent with the Land-Only-fixed leaf experiment (Table 3.1). The transpiration increases in the Land-Atmosphere experiment despite the decreases in stomatal conductance could be explained by the increases in leaf area. Since it was a measure of total transpiration, the effect of leaf area increases was greater than the effect of stomatal closure. Water availability largely stayed the same, but the Land-Atmosphere experiment had an greater increase in soil liquid content (Table 3.1). Similar to the patterns we saw in the other regions, in the Land-Atmosphere experiment there were much higher increases in surface temperature and in VPD (Table 3.1). The change in VPD to high iWUE perturbation was smaller relative to the Amazon which could have been due to the difference in changes to surface temperature (Figure 3.7). The percentage change for temperature was larger in boreal Canada but the actual magnitude was not as large compared to the Amazon (0.55°C vs 2.72°C). Temperature increases in boreal Canada were likely due to decreases in albedo from increased leaf area [2] rather than changes in turbulent heat flux partitioning.

3.2.7 Perturbed meteorology analysis

We analyzed a separate series of perturbed meteorology CESM simulations, where only one meteorological variable was perturbed with a prescribed atmosphere, to get an expectation of the sensitivity of photosynthesis to a change in temperature or VPD. Using the rate of photosynthesis change per unit temperature or VPD multiplied by the change in temperature or VPD in our perturbed iWUE simulations, we calculated the expected photosynthetic response to a change in temperature or VPD (Equation 2.1; Figure 3.8).

We compared the expected photosynthetic responses to the difference in photosynthetic response between the Land-Only-fixed leaf and Land-Atmosphere experiments to disentangle

Table 3.1: Climate Variable Responses to high iWUE perturbation

Variable	Amazon				Central NA				Boreal Canada			
	Land-Only-fixed leaf		Land-Atmosphere		Land-Only-fixed leaf		Land-Atmosphere		Land-Only-fixed leaf		Land-Atmosphere	
	unit	%	unit	%	unit	%	unit	%	unit	%	unit	%
Photosynthesis ($gC/m^2/yr$)	108.91	5.61	-859.48	-43.86	108.11	9.91	-115.12	-11.11	-21.18	-3.74	98.52	19.28
Sunlit leaf g_s ($gH_2O/m^2/s$)	-0.78	-39.54	-1.12	-60.09	-0.54	-24.46	-0.78	-37.88	-0.35	-19.90	-0.28	-15.60
Transpiration (W/m^2)	-20.72	-35.08	-35.66	-59.48	-3.45	-10.69	-6.58	-22.37	-1.70	-21.01	0.38	5.43
LH flux (W/m^2)	-14.43	-15.07	-21.58	-22.34	-1.78	-3.63	-4.72	-10.02	-1.44	-5.90	-0.15	-0.67
SH flux (W/m^2)	13.21	31.85	16.16	39.79	1.53	5.33	4.41	15.40	1.31	7.15	1.85	9.75
Soil water stress	-0.39	-88.84	-0.49	-123.33	-0.11	-13.34	-0.03	-2.69	-0.01	-0.97	-0.01	-1.22
Soil liquid water (kg)	80.42	8.79	81.92	9.01	123.24	18.72	3.43	0.44	4.16	0.58	45.38	6.38
T_s (°C)	0.09	0.34	2.72	10.21	0.02	0.28	0.95	10.96	0.01	0.46	0.55	28.52
VPD (Pa)	0.00	0.00	671.71	32.95	0.00	0.00	124.52	16.44	0.00	0.00	27.26	9.09
Low Cloud Fraction	0.00	0.00	-0.06	-38.59	0.00	0.00	-0.04	-14.41	0.00	0.00	0.02	-3.64
Total Leaf Area (m^2/m^2)	0.00	0.00	-2.07	-53.28	0.00	0.00	-0.37	-16.38	0.00	0.00	0.15	12.34

how much temperature and VPD affected the photosynthetic response to iWUE perturbation. In the Amazon and central NA we observed that an increase in temperature tended to slightly decrease photosynthesis while an increase in VPD drastically decreased photosynthesis. The magnitude of photosynthetic response that could be attributed to VPD was similar to the observed change in photosynthesis between the Land-Only-fixed leaf and Land-Atmosphere experiments. In boreal Canada we observed the opposite, where an increase in temperature increased photosynthesis, matching the direction of difference in photosynthetic response between the Land-Only-fixed leaf and Land-Atmosphere experiments. However, an increase in VPD still caused a decrease in photosynthesis. The magnitude of photosynthetic change caused by temperature and VPD in boreal Canada were much smaller than the observed change in photosynthesis between the Land-Only-fixed leaf and Land-Atmosphere experiments.

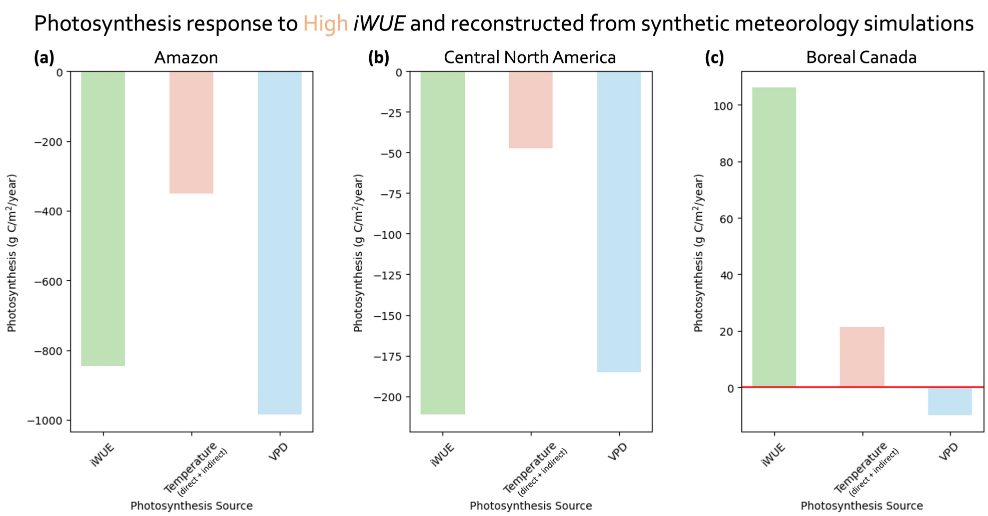

Figure 3.8: Photosynthetic response to changes in the configuration ($\Delta GPP_{Land-Atmosphere} - \Delta GPP_{Land-Only-fixedleaf}$) and expected photosynthetic response from perturbed meteorology for temperature ($\frac{\Delta GPP_T}{\Delta T_T} \cdot \delta T_{Land-Atmosphere}$) and VPD ($\frac{\Delta GPP_{VPD}}{\Delta VPD_{VPD}} \cdot \delta VPD_{Land-Atmosphere}$) in *(a)* the Amazon, *(b)* central NA, and *(c)* boreal Canada.

3.3 Linearity of photosynthetic response

We saw photosynthetic responses to iWUE perturbations in all configurations of CESM that we tested. To assess if photosynthetic response to iWUE perturbations were linear when different components were allowed to be interactive or not, we compared photosynthetic response of the Land-Only-fixed leaf, dynamic atmosphere only, dynamic leaf area only, and Land-Atmosphere simulations. If the response were linear, we would expect the sum of the Land-Only-fixed leaf, dynamic atmosphere only, and dynamic leaf area only simulations photosynthetic response to equal the total photosynthetic response for the Land-Atmosphere simulations. However, we found that they did not linearly combine and that the nonlinearity was not consistent between global and regional scales. Each region had very different photosynthetic responses at each configuration, implying that regional photosynthetic responses were nonlinear in different ways (Figure 3.9).

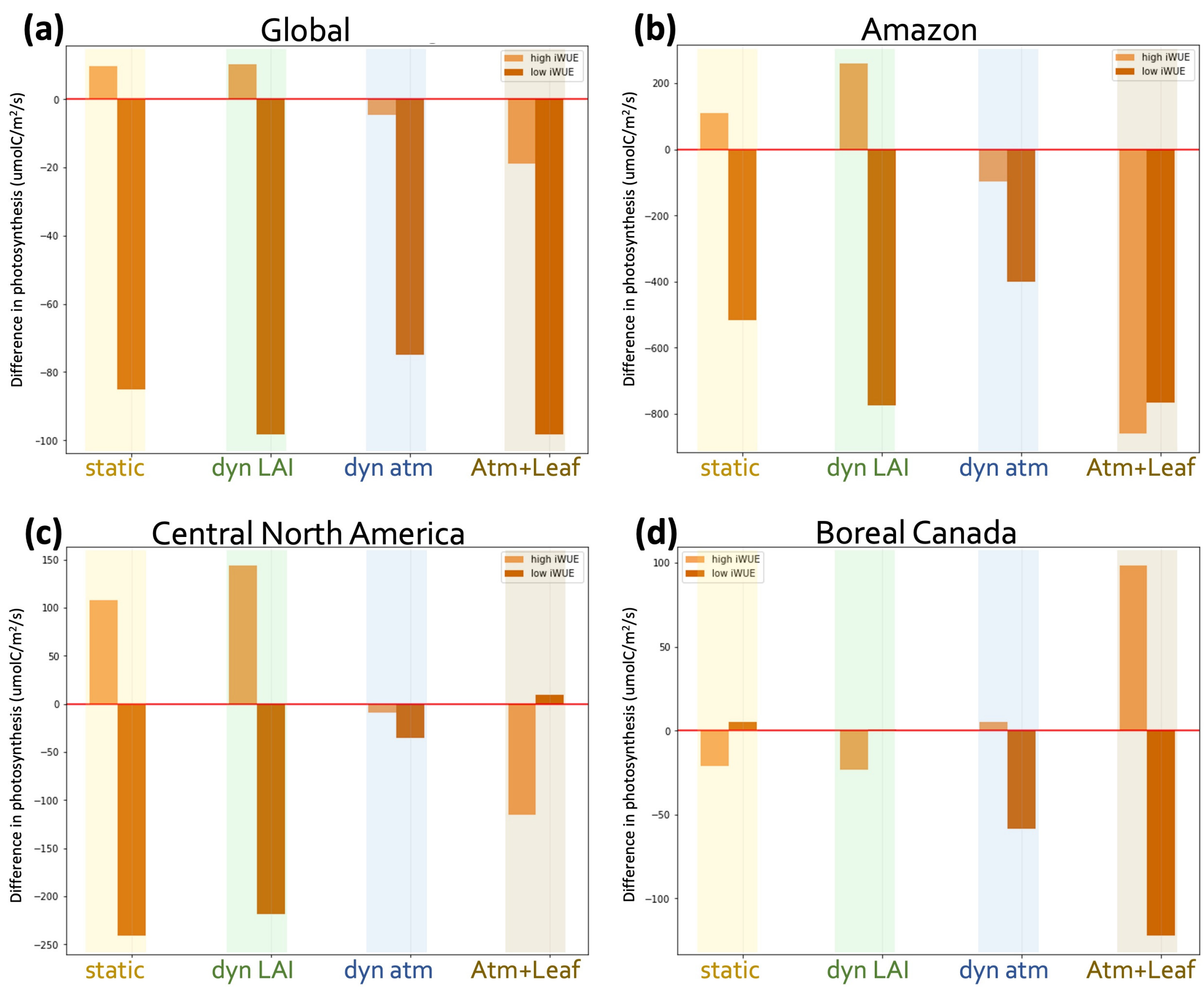

Figure 3.9: Bar plots of the absolute photosynthetic response to iWUE perturbation for the Land-Only-fixed leaf, dynamic LAI only, dynamic atmosphere only, and Land-Atmosphere, averaged over *(a)* the globe, *(b)* the Amazon, *(c)* central North America, and *(d)* boreal Canada

3.3.1 Elevated atmospheric CO_2

Under elevated CO_2, we observed photosynthesis increases across the globe (Figure 3.10), consistent at different iWUE values. The relationship between g_{1M} and iWUE is preserved at 2xCO_2 (Figure 2.2b).

Under 2xCO_2, the photosynthesis changes in low iWUE were smaller in magnitude than

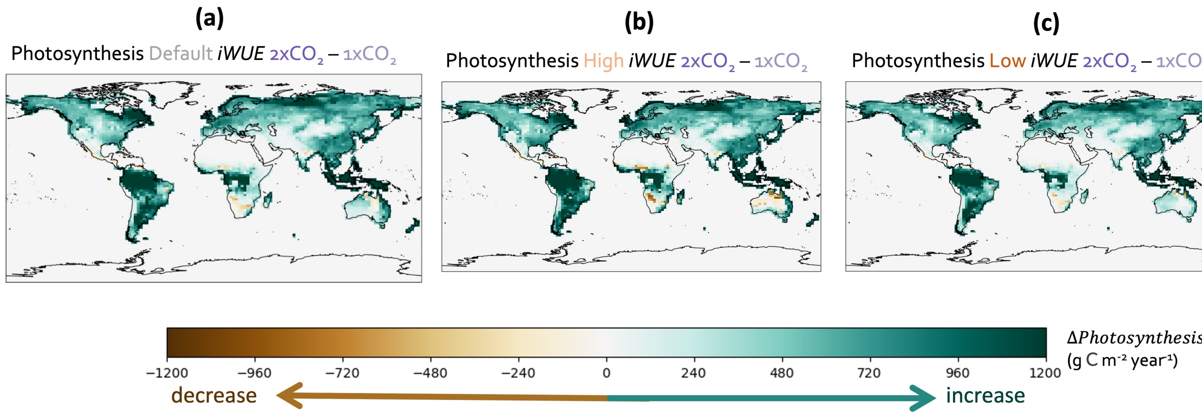

Figure 3.10: Photosynthesis difference spatial plot of default iWUE between $1xCO_2$ and 2x preindustrial atmospheric CO_2 concentrations for *(a)* default, *(b)* high, and *(c)* low iWUE perturbations. iWUE is constant for each comparison.

those for high iWUE, and the opposite was true for the $1xCO_2$ experiments. The additional photosynthetic response that iWUE perturbation caused at $2xCO_2$ accounted on average about 89% and 37%, for high and low iWUE perturbation respectively, of the total photosynthetic response and was regionally sensitive (Figure 3.11). Regions that had smaller total photosynthetic response to elevated CO_2 had larger influences of iWUE perturbation to photosynthetic response relative to the overall response. Though both perturbations had regionally sensitive responses, high iWUE generally had increases in photosynthesis and low iWUE generally had decreases in photosynthesis. Overall, the climate response to elevated CO_2 was overwhelmingly strong, relative to the responses to iWUE perturbations.

3.3.2 Australia

In the elevated CO_2 simulations, Australia emerged as an intriguing region, as we observed a negative photosynthetic response going from $1xCO_2$ to $2xCO_2$ at high iWUE, contrary to the rest of the globe (Figure 3.10b). In Australia, the overall photosynthetic response to elevated CO_2 was weak relative to the rest of the globe, but its responses to both low and high iWUE perturbations were relatively strong (Figure 3.10 and Figure 3.11. When

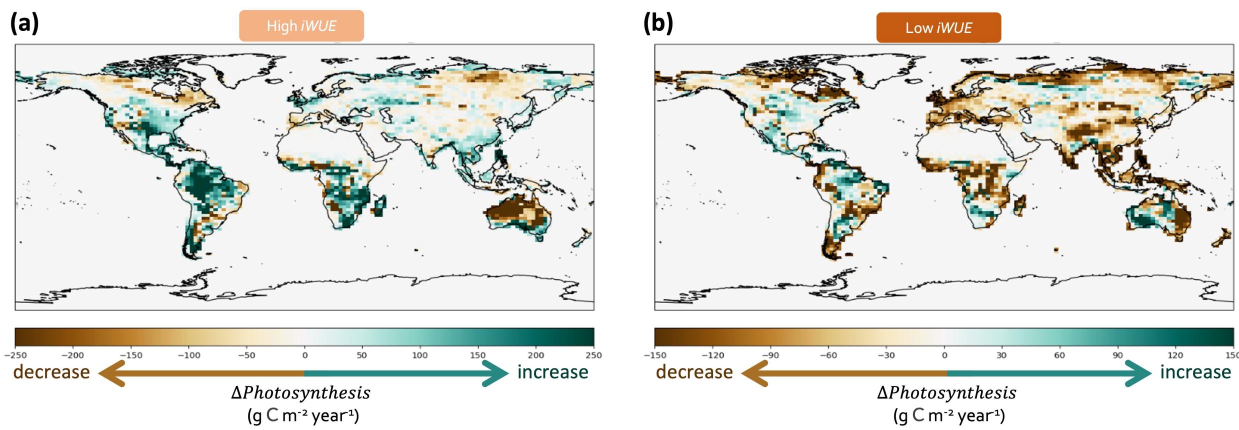

Figure 3.11: Spatial difference plot showing *(a)* high and *b)* low iWUE perturbations modification to photosynthetic response at 2xCO_2.

the total photosynthetic at elevated CO_2 was normalized by total leaf area, Australia and the Amazon had similar magnitudes of response (Figure 3.12a). In response to high iWUE perturbation, leaf area decreased significantly in Australia, with leaf area nearly reaching zero in the west and halving in the east (Figure 3.12c).

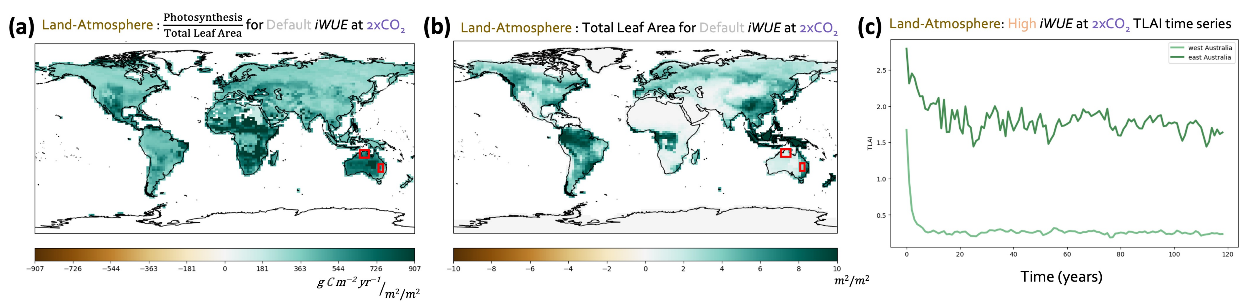

Figure 3.12: *(a)* Global spatial plot of total photosynthesis normalized by leaf area index at each grid for the Land-Atmosphere default iWUE experiment at 2xCO_2. *(b)* Global spatial plot of total leaf area index for the Land-Atmosphere default iWUE experiment at 2xCO_2. *(c)* and *(d)* Time series of total leaf area index (TLAI)for west and east Australia. The time series data was from pulled from the red boxes drawn in *(a)* and *(b)*.

Chapter 4
DISCUSSION

4.1 Implications for iWUE in CESM

One g_{1M} value is currently used to represent each PFT in CLM, which we used as our control, or "default" value, in our simulations. Our iWUE perturbations gave us insight as to how climate models could be over or underestimating photosynthesis if real world plants had a different iWUE than the default value used in models.

With our high g_{1M}, or low iWUE, perturbation, we expected photosynthesis to decrease if we assumed g_s remained constant in equation 1.2. iWUE perturbation technically also modifies g_s, which did not stay constant in our simulations, but we simplified how equation 1.2 would change to have an expectation for photosynthetic response. We observed results that matched our expectation in Section 3.1.1, with photosynthesis decreasing across the globe (Figure 3.1a&b). If the default iWUE in models were higher than the iWUE of real world plants, then we could be grossly overestimating plant photosynthesis, and thus overestimating plant carbon uptake.

For low g_{1M}, or high iWUE, perturbation, we expected the opposite photosynthesis response. Photosynthesis was expected to increase if we made the same assumption that g_s were constant in equation 1.2. However, we saw from Section 3.1.2 and 3.2.2 that photosynthesis had a regionally sensitive response to high iWUE perturbation (Figure 3.1c&d). In other words, depending on the region, if plants in the real world had a higher iWUE than that currently used in models, plant photosynthesis could be over or underestimated. For example, southeast Asia plant photosynthesis would be underestimated and east China plant photosynthesis would be overestimated. The regional sensitivity may have been due to a difference of PFT distribution in each region, with each PFT potentially having a different response to the climate response from high iWUE perturbation.

4.2 Inclusion of a dynamic atmosphere evoked strong temperature and VPD response that affected photosynthesis

As mentioned in Section 4.1, we expected photosynthesis to increase with higher iWUE but instead observed regional sensitivity. Not only was photosynthetic response to high iWUE not consistent across regions, it was also not consistent across configurations, flipping sign in photosynthetic response with the inclusion of a dynamic atmosphere and dynamic leaf area. In addition to that, the direction of the sign change in photosynthetic response was opposite of what we expected (Section 3.2.3). Based on what we know about photosynthesis and its response to environmental factors, we explored four possible hypotheses why photosynthesis was not changing in response to a change in iWUE the way we would expect. First the experiments could have differences in stomatal conductance in response to g_{1M} (h1), second could be response to plant soil water stress (h2), third could be response to change in temperature (h3), and fourth could be response to plant atmospheric water stress (h4). We focused on regions that had a sign change in photosynthetic response between the Land-Atmosphere and Land-Only-fixed leaf high iWUE experiments.

To start, there was g_s decrease in response to high iWUE perturbation in almost all regions for both Land-Atmosphere and Land-Only-fixed leaf experiments (Figure 3.5b and Figure 3.6b), which would have decreased carbon uptake. If we only considered the change in g_s, we would have expected to consistently see a decrease in photosynthesis across the globe. The Tibetan Plateau region did not match the general global g_s response (Figure 3.5b and Figure 3.6b) was because the C3 arctic grass PFT default g_{1M} used in CLM was lower than the low g_{1M} perturbation we got from Lin et. al. 2015 (Figure 2.1a). We did not see a global photosynthesis decrease, so stomatal conductance response (h1) could not fully explain the photosynthetic responses to high iWUE. The changes in soil water stress, temperature, and atmospheric water stress vary more across regions, so we broke down our exploration of them below.

4.2.1 VPD driven photosynthesis decreases in the Amazon and central North America

In the Amazon, soil water availability had increased similarly in percentage for both Land-Atmosphere and Land-Only-fixed leaf experiments, decreasing soil water stress (h2), so we would expect an increase in photosynthesis from this process alone. In the Land-Only-fixed leaf experiment, we observed photosynthetic increase which is most likely driven by soil water stress (h2) because temperature (h3) and VPD (h4) did not change much with fixed atmospheric forcing. Similarly, for the Land-Only-fixed leaf experiment in central NA we observed a large increase in soil water availability, however, the percentage photosynthesis increase in the central NA Land-Only-fixed leaf experiment was greater compared to the Amazon even though the percentage increases in water availability were smaller. This suggests that plants in central NA were more sensitive to increases in water availability and decreases in soil water stress (h2).

For simulations with an dynamic atmosphere and leaf area, the observed photosynthesis decreases in the Land-Atmosphere experiment were not explained by soil water stress (h2) in either the Amazon or central NA. In the Amazon, contrary to our expectations, we observed a decrease in photosynthesis despite the increase in soil water availability. Meanwhile, in central NA, water availability barely increased so its effects on photosynthesis were likely minimal. The main differences between the Land-Atmosphere and Land-Only-fixed leaf experiment were the surface temperature (h3) and VPD (h4) responses. Temperature and VPD are closely linked, as VPD is a function of temperature and can be thought of as an indirect effect of temperature changes. Temperature (h3) increased significantly in both the Amazon and central NA, which could potentially push plants beyond their thermal optimum for photosynthesis [24]. However, CLM represents photosynthetic acclimation to the 10-day temperature average plant temperature up to 35°C [16] which reduces the impact of hot temperatures, with maximum daily temperatures in central NA never exceeding 31°C, and about 20% of maximum daily temperatures in the Amazon exceeding 35°C.

We largely attribute the photosynthetic decreases with a dynamic atmosphere to a response to VPD (h4) as the magnitude of our expected photosynthesis response to increase in VPD alone explains the total signal (Figure 3.8). The percentage and magnitude of photosynthesis decrease due to the inclusion of a dynamic atmosphere was larger in the Amazon compared to central NA, suggesting that plants in the Amazon are more sensitive to an increase in VPD (h4). The expected photosynthesis response from temperature (h3), which includes both direct effects of temperature and indirect effects of temperature's impact on VPD, were much smaller in magnitude than the expected photosynthesis response from VPD alone, supporting VPD (h4) as the main driver. This also implies that the direct effect of a temperature (h3) increase may increase photosynthesis in the Amazon and central NA. However, we expect that the direct and indirect effects do not linearly combine (Zarakas et. al., 2024).

4.2.2 Temperature increased photosynthesis in boreal Canada

In the high iWUE Land-Only-fixed leaf experiment, the decrease in stomatal conductance (h1) in boreal Canada had a greater effect on photosynthetic response than the small increase in soil water availability (h2), with decreased carbon uptake leading to less photosynthesis. In the high iWUE Land-Atmosphere experiment photosynthesis increased in boreal Canada. Soil water availability (h2), temperature (h3), and VPD (h4) all increase. If boreal plants were strongly influenced by VPD (h4) as they were in the Amazon and central NA, we would have expected a decrease in photosynthesis. Yet photosynthesis increased, implying that plants were more sensitive to the direct effects of increases in temperature (h3) than in VPD (h4) and that temperatures remained below thermal optimum. The gap in magnitude of boreal Canada's photosynthesis response between the total signal and the expected response to increase in temperature can be explained by the observed increase in leaf area (Figure 3.6 & Table 3.1).

The expected photosynthesis responses from temperature for all three regions suggest that the total effect of temperature (h3) on photosynthesis is influenced by the background climate. A low baseline temperature region, like boreal Canada, may have positive responses to temperature increases while a high baseline temperature region, like the Amazon and central NA, may have negative responses to temperature increases, through both direct temperature effects and indirect effects of higher VPD.

4.3 iWUE perturbation modifies photosynthetic response to elevated CO_2

A doubling of atmospheric CO_2 concentration from preindustrial to 2x preindustrial changes the c_s term in equation 1.3, and therefore we expected a decrease in stomatal conductance and an increase in iWUE at elevated CO_2 which we found in our results. As expected, we saw high iWUE modify elevated CO_2 photosynthetic response to be higher and low iWUE modify elevated CO_2 photosynthetic response to be lower (Figure 3.11). Similar to preindustrial CO_2 conditions, under the future scenario of elevated atmospheric CO_2, if real world plants had a higher iWUE than the default used in the model, our climate projections would be underestimating plant photosynthesis and plants as a carbon sink. The opposite would be true if real world plants had a lower iWUE than the default used in the model.

One notable exception is Australia, where high iWUE perturbation unexpectedly decreased photosynthetic response to elevated CO_2 (Figure 3.11). The photosynthetic response to high iWUE was so strong that we saw an overall negative response in photosynthesis going from $1xCO_2$ to $2xCO_2$ at high iWUE (Figure 3.10b) when we expected an overall positive response in photosynthesis like the rest of the globe. Australia has less total leaf area than other regions in the the preindustrial state, so the absolute photosynthetic response to doubling of CO_2 would not be as large relative to regions with greater leaf area (Figure 3.12b), and we attribute the large photosynthesis substantially decreases at high iWUE to plants decreasing their leaf area(Figure 3.12c). The leaf area decreases may be due to plants overheating from absence of the transpiration temperature regulation in models, lack of carbon uptake from decreased stomatal conductance, or both.

Chapter 5
CONCLUSIONS

The choice of iWUE used to represent each plant functional type in CLM5 impacted photosynthetic rates. Decreasing iWUE from the default had a large decrease on photosynthesis while increasing iWUE had regionally dependent effects on photosynthetic response. The magnitude of photosynthetic response varied regionally but was greater in the tropics. In particular, the Amazon and central NA regions exhibited decreases in photosynthesis (-43.86% and -11.11% respectively) while boreal regions experienced increases (19.28%).

The inclusion of a dynamic atmosphere enabled the climate to respond differently, primarily with temperature changes in response to changes in surface fluxes and VPD changes in response to changes in temperature and transpiration. The sign of photosynthetic response to these temperature changes for high iWUE perturbation experiments depended on the background climate of the region. In the Amazon (high baseline temperature) photosynthesis decreased with further increase in temperature while in boreal Canada (low baseline temperature) photosynthesis increased with further increase in temperature. The photosynthetic response in the Amazon and central NA, or high baseline temperature regions, was largely driven by increases in VPD (indirect temperature effect). This has implications that the Earth system response to our choice of iWUE depends on which aspects of the Earth system are allowed to dynamically respond.

Both low and high iWUE perturbations changed the photosynthetic response to elevated atmospheric CO_2 on average by about 37% and 89%, respectively. A choice of low iWUE tended to decrease the photosynthetic response, while a choice of high iWUE tended to increase the photosynthetic response. While the photosynthetic responses to iWUE perturbation at elevated CO_2 tended to match expectations based on the conceptual understanding derived from the iWUE equation, there were still regionally sensitive responses to the perturbations that remained unexplained. It would be worth exploring causes of the regional sensitivity at $2xCO_2$ by looking at factors that affect photosynthesis, similarly to our $1xCO_2$ regional analysis.

This research mainly focused on how photosynthesis would be affected by altering plant carbon-water tradeoffs. Overall we found that the answer was more complicated than one might initially guess, but that the large signals could be explained by considering sensitivity to temperature and water. Next steps would be to expand this analysis to understand the implications of how assumptions about iWUE impact the hydrological cycle. We find that that plant transpiration is greatly affected by iWUE perturbations, effects that we expect to cascade to water budget variables like precipitation, evapotranspiration, and runoff. Understanding how the hydrological cycle shifts with our choice of iWUE and changes under future climate has the potential to improve risk assessment of droughts heatwaves, flooding, and water availability that affect the health of our ecosystems and human populations. We show that future climate projections could be significantly different based on what value we use to represent iWUE in Earth system models, in addition to better characterizing the role of biological uncertainty in future climate.

VITA

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