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

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Key Points:

- Low water-use efficiency reduces photosynthesis globally while high water-use efficiency impacts on photosynthesis vary by location
- Photosynthesis at high water-use efficiency is altered by interactive surface temperature with opposite sensitivity at high vs low latitudes
- Water-use efficiency modifies the total photosynthetic response to elevated 2xCO_2 by 6.4% for high and -9.6% for low perturbation

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Abstract

Plant stomata mediate the fluxes of both carbon and water between the land and the atmosphere. The ratio between photosynthesis and stomatal conductance (g_s), or intrinsic water-use efficiency (iWUE), can be directly inferred from leaf or tree-ring carbon isotope composition. In many Earth system models, iWUE is inversely proportional and controlled by a parameter (g_{1M}) in the calculation of g_s. Here we examine how iWUE perturbations, setting g_{1M} to the 5th (low) and 95th (high) percentile for each plant type based on observations, influence photosynthesis using coupled Earth System model simulations. We find that while lower iWUE leads to reductions in photosynthesis nearly everywhere, higher iWUE had a photosynthetic response that is surprisingly regionally dependent. Higher iWUE increases photosynthesis in the Amazon and central North America, but decreases photosynthesis in boreal Canada under fixed atmospheric conditions. However, the photosynthetic response to higher iWUE in these regions unexpectedly reverses when the atmosphere dynamically responds due to spatially differing sensitivity to increases in temperature and vapor pressure deficit. iWUE also influences the photosynthetic response to atmospheric CO_2, with higher and lower iWUE modifying the total global response to elevated 2x preindustrial CO_2 by 6.4% and -9.6%, respectively. Our work demonstrates that assumptions about iWUE in Earth system models significantly affect photosynthesis and its response to climate. Further, the response of photosynthesis to iWUE depends on which components of the model are included, therefore studies of iWUE impacts on historical or future photosynthesis can not be generalized across model configurations.

Plain Language Summary

Plants affect the Earth system's carbon, water, and energy fluxes through photosynthesis and transpiration, regulated by stomata on leaves that control the gas exchange needed for these processes. Intrinsic water-use efficiency (iWUE) represents how efficiently a plant uses water by indicating how much the stomata are open per unit of carbon it gains for photosynthesis. Observations show a range of iWUE across and within plant types in varying environments which is not captured in Earth system models. In our study, we explored how changes in iWUE impact photosynthesis using Earth System models. We find that lower iWUE generally decreases photosynthesis everywhere while higher iWUE has mixed effects, increasing photosynthesis in regions like the Amazon and central North America but decreasing it in boreal Canada. These responses change when we allow the atmosphere to respond to changes on land, mainly due to spatially varying sensitivity to warmer temperature and drier air. Additionally, iWUE changes alter the photosynthetic response to higher atmospheric CO_2, with higher and lower iWUE changing total global photosynthesis by 6.4% and -9.6%, respectively. Our study helps clarify uncertainties in how plant photosynthesis might respond to climate change, improving our understanding of potential future scenarios.

1 Introduction

Photosynthesis acts as a carbon sink, removing carbon dioxide (CO_2) from the atmosphere, converting it into sugars used to construct plant tissues and thereby storing carbon as plants grow. Multiple environmental factors such as light, water, nutrient availability, temperature, and atmospheric CO_2 level affect photosynthesis. Photosynthesis is tightly coupled with transpiration, which accounts for about 60% of latent heat flux over land (Wei et al., 2017), as both processes are regulated by gas exchange with the atmosphere through stomata. Thus changes in plant type, plant functioning, or sensitivity of plant functioning to environmental conditions can alter the fluxes of both water and CO_2 with the atmosphere. These plant processes and their responses to rising atmospheric CO_2 in turn influence climate (Field et al., 1995; G. B. Bonan, 2008, 2015;

Laguë et al., 2019). The ratio of these two fluxes, known as water-use efficiency (WUE) describes how efficiently plants photosynthesize relative to their water loss and is an emergent property of plants that can be estimated directly through leaf gas exchange measurements and inferred through eddy flux and tree-ring carbon isotope composition. As both photosynthesis and transpiration are influenced by many factors, each with accompanying uncertainty, the representation of the ratio between them also carries the inherent uncertainties from both component fluxes. Observation-based estimates of this emergent property show a wide range across different plant types and even within a single plant type (Lin et al., 2015). In contrast, Earth System models typically simplify the representation of this ratio by using a single value for each plant type (Lawrence et al., 2019). To evaluate the significance and magnitude of the difference caused by the oversimplification of this representation in existing models, we investigate how different assumptions about plant water-use strategies in Earth system models impact photosynthesis under both historical and future climate conditions.

Plant carbon uptake and water loss are both regulated by the opening and closing of stomata. 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 (Cowan & Farquhar, 1977). Alternatively, empirical formulations for stomatal behavior are based on observations of stomatal behavior under different environmental conditions such as atmospheric dryness and atmospheric CO_2 level (Ball et al., 1987; Leuning, 1995). Efforts have been made to integrate the optimal and empirical approaches, aiming to reconcile observations with the theory of optimal stomatal behavior (Medlyn et al., 2011). Both optimal and empirical approaches yield similar results in leaf, canopy, and global scale simulations (Franks et al., 2017), but, more recently, hydraulics-based stomatal optimization approaches have been shown to perform better when evaluated against leaf level observations (Sabot et al., 2022). Stomatal behavior sensitivity to environmental conditions, such as temperature and water availability, varies by plant type, with those possessing increased hydraulic resistance along the soil-leaf pathway being better at maintaining water transport and leaf area under stress, reducing vulnerability to drought and atmospheric dryness (Trugman et al., 2019).

Regardless of the approach taken to capture stomatal behavior, more open stomata tend to increase both transpiration and the uptake of carbon for photosynthesis, and vice-versa for more closed stomata. As a result, photosynthesis and transpiration are tightly coupled, though they can become decoupled under high temperature conditions (Kauwe et al., 2019). The relative rate of these processes can be related to water-use efficiency (WUE) as follows:

$$WUE = \frac{Photosynthesis}{Transpiration} = \frac{A_n}{g_{total} \cdot VPD}, \tag{1}$$

where g_{total} represents the combined effect of stomatal conductance (g_s), the rate of gas exchange based on stomatal aperture, and boundary layer conductance to water vapor, both of which are added in parallel. 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 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 directly at canopy to landscape scales because photosynthesis and transpiration are difficult to quantify beyond the leaf level.

WUE at the organismal level can, however, be inferred from the carbon isotope composition of tree-rings and leaves (Saurer et al., 2014), which enables the construction of records that span decades to centuries-long time periods. The carbon isotope composition of tree rings tells us about the discrimination against C^{13} isotopes relative to C^{12} isotopes, which is largely dictated by the diffusion of CO_2 through the stomata and CO_2

fixation by Rubisco (Adams et al., 2020). This measurable WUE quantity, called the intrinsic water-use efficiency (iWUE), is similar to WUE but replaces transpiration with stomatal conductance as follows:

$$iWUE = \frac{Photosynthesis}{Stomatal\ \ Conductance} = \frac{A_n}{g_s}. \quad (2)$$

WUE and iWUE are similar: both represent the ratio of carbon gain to water loss. Equation 2 is focused on the stomatal response to environmental conditions while in equation 1 g_s is additionally influenced by abiotic evaporative potential due to atmospheric dryness. We focus here on iWUE, in particular due to the potential to relate our findings to tree-ring based isotopic observations.

Both components of iWUE, photosynthesis and stomatal conductance, are expected to change with a changing climate (Adams et al., 2020; Li et al., 2023). Plants can adapt to hotter temperatures by physiologically adjusting their biochemical process rates to raise their thermal optimum for photosynthesis, but this adaptation is limited by water availability, and beyond a certain temperature threshold, further increases reduce these biochemical reactions (Kattge & Knorr, 2007; Yamori et al., 2014; Lombardozzi et al., 2015; Kumarathunge et al., 2019, 2020). Additionally, under hotter and drier conditions, plants are expected to close their stomata to minimize water loss through transpiration, decreasing stomatal conductance (Oren et al., 1999; Mott & Peak, 2010), resulting in a decrease in CO_2 uptake and a decrease in photosynthesis. The impact on photosynthesis from changing climate driven by reduced stomatal conductance can be offset by increasing atmospheric CO_2. With a larger CO_2 gradient between the atmosphere and plant interior, plants can assimilate the same amount of carbon with 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 (Keenan et al., 2013; Frank et al., 2015). Plants may also be able to increase photosynthesis under higher CO_2, by increasing leaf area, though studies have suggested that the increase does not extend to long-term above ground carbon storage through tree ring growth (Peñuelas et al., 2011; Sleen et al., 2014). Changing leaf area also changes the total number of plant stomata, assuming that stomata density on leaves is constant, which would drive changes in total fluxes of carbon and water (Field et al., 1995). Additional factors at the plant scale (e.g., nutrient and water availability effects on photosynthesis and g_s) could cause iWUE to differ from these theoretical expectations, and one study found slower rates of iWUE increase over recent decades, and no significant changes in iWUE relative to atmospheric CO_2 when comparing decadal averages over the past century (Adams et al., 2020).

1.1 Uncertainty in iWUE

iWUE is an emergent property of plants, resulting from the coupled behavior of photosynthesis and stomatal conductance. In common process-based models that explicitly represent photosynthesis rates and stomatal conductance (e.g. Farquhar, Caemmerer, & Berry, 1980, Ball et al., 1987, Leuning, 1995, Medlyn et al., 2011) iWUE is not directly specified, although it is closely related to one of the empirically fit parameters in many formulations. In the Medlyn et al. (2011) formulation of stomatal conductance, g_s, is given by

$$g_s = g_0 + 1.6(1 + \frac{g_{1M}}{\sqrt{VPD}})\frac{A_n}{c_s}, \quad (3)$$

where A_n is photosynthesis, c_s is the atmospheric CO_2 level, VPD is vapor pressure deficit, and g_0 is the Medlyn intercept (minimum stomatal conductance, when the stomata are completely closed). A_n is coupled to g_s, and an increase in stomatal conductance relates to an increase in photosynthesis. Within land models, A_n and g_s are solved in a coupled system with the Medlyn model and Farquhar photosynthesis model equations. The Medlyn slope, g_{1M}, is an empirically estimated parameter based on field observations.

For intuition of the relationship between iWUE and g_{1M}, we can relate equation 2 and 3, and see that iWUE is inversely proportional to and can be modulated by g_{1M} with:

$$iWUE \propto \frac{1}{g_{1M}}, \tag{4}$$

under constant environmental conditions when A_n is sufficiently different from zero.

Observation-based estimates of g_{1M} show a large variation both across plant types and within a plant type (Lin et al., 2015; Wolz et al., 2017; Y. Liu et al., 2021). In many land surface models, including those within Earth system models, a single g_{1M} value is assigned to each plant type as estimated from observations. In the land surface component of the Community Earth System Model version 2 (CESM2), the average g_{1M} within a grid cell has spatial variation (Fig. 1b) since there are fourteen different plant functional types (PFTs), and each PFT has a unique spatial distribution and a different g_{1M} derived from Lin et al. (2015). Given that there is large uncertainty in the value of g_{1M} for each plant type (e.g., Lin et al., 2015), the actual spatial distribution of average iWUE is also uncertain, which is likely to have impacts on both the mean-state climate and responses to increasing CO_2 due to the impact of iWUE on surface fluxes of water and energy.

In this study we examine: (1) the impact of uncertainty in g_{1M}, and therefore uncertainty in iWUE, on mean-state photosynthesis; (2) the mechanisms and feedbacks through which different assumptions about iWUE impact photosynthesis and how they vary spatially; and (3) the impact of uncertainty in iWUE on the response of photosynthesis to elevated atmospheric CO_2 levels. We focused our analysis on the response of photosynthesis because it integrates the response of both carbon and water cycling to assumptions about iWUE.

2 Methods

2.1 Model Configurations

We used the Community Earth System Model version 2 (CESM2; Danabasoglu et al., 2020), an open-source Earth system model, to estimate the response of photosynthesis to assumptions about iWUE. CESM2 is comprised of the Community Land Model 5 (CLM5; Lawrence et al., 2019), the Community Atmosphere Model 6 (CAM6; Bogenschutz et al., 2018), and a slab ocean based on output from the CESM2 Coupled Model Intercomparison Project Phase 6 (CMIP6) preindustrial control run (Danabasoglu & Gent, 2009). We performed global-scale simulations of CESM2 at 0.9x1.25° spatial resolution.

In order to isolate the impacts of (1) atmospheric response and (2) dynamic leaf area to assumptions about iWUE, we defined two configurations of CESM2. The "Land-Atmosphere" configuration was run with a dynamic atmosphere and a land model that included active biogeochemistry and prognostic leaf area that allowed for leaf area to dynamically respond to climate, resulting in changes in both atmospheric conditions and leaf area in response to iWUE perturbations. The "Land-Only-Fixed-Leaf" configuration is the same land model but with the leaf area phenology specified as a repeating seasonal cycle of climatological leaf area, so there were no changes in both atmospheric conditions and year-to-year leaf area in response to iWUE perturbations. 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.

In order to compare the response of atmospheric feedbacks and prognostic leaf area under equivalent meteorological conditions, we prescribed the meteorological forcing in the Land-Only-Fixed-Leaf simulations using the output of the default iWUE Land-Atmosphere simulation saved at 3 hourly intervals. The 3-hourly saved meteorological data is interpolated to 30 minute time resolution to drive the Land-Only-Fixed-Leaf simulations. We

Table 1. Summary of Simulations.

Simulation Name	CO_2	Atmosphere	Leaf Area	g_{1M}	iWUE
Land-Atmosphere high iWUE	$1xCO_2$	dynamic	prognostic	low	high
Land-Atmosphere default iWUE				default	default
Land-Atmosphere low iWUE				high	low
Land-Only-Fixed-Leaf high iWUE	$1xCO_2$	prescribed	prescribed	low	high
Land-Only-Fixed-Leaf default iWUE				default	default
Land-Only-Fixed-Leaf low iWUE				high	low
Land-Atmosphere $2xCO_2$ high iWUE	$2xCO_2$	dynamic	prognostic	low	high
Land-Atmosphere $2xCO_2$ default iWUE				default	default
Land-Atmosphere $2xCO_2$ low iWUE				high	low

analyzed 80 years of a 120-year simulation, after discarding the first 40 years to allow the system to reach equilibrium.

2.2 iWUE Perturbations

We quantify the response of photosynthesis to assumptions about iWUE by perturbing the stomatal slope parameter, g_{1M}, within equation 3. 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 observations (Lin et al., 2015; Fig. 1a), such that we have one set of simulations with "high iWUE" that use the 5^{th} percentile values for g_{1M} and one set of simulations for "low iWUE" that use 95^{th} percentile values for g_{1M} (since iWUE and g_{1M} are inversely related) We compared the high and low iWUE simulations against simulations with the default g_{1M} parameter values used in CLM5, noting that these default values do not represent the mean or median of the observations we used for perturbation (Fig. 1a). The average g_{1M} for any given location varies due to the spatial distribution of PFTs and the range of default g_{1M} values across PFTs (Fig. 1b). Changes in iWUE mirror changes in g_{1M} due to the formulation of the Medlyn model, however they are not equivalent and iWUE can also be modulated by changes in photosynthesis. We find that iWUE changes in the direction and approximate magnitude we expect associated with a change in g_{1M} (Fig. S1a), and thus we describe our results in terms of the change in iWUE associated with a perturbed g_{1M}. The relationship between g_{1M} and iWUE is inversely proportional (Eq. 4) and further explanation about the relationship can be found in Supplemental Text S1.

2.3 Simulation design

In order to isolate of the effects of multiple processes that comprise the full climate and ecosystem response to iWUE, we performed nine simulations (Table 1). For each simulation we set g_{1M} to either default, low, or high values corresponding to default, high, or low iWUE. We tested two configurations of CESM2, one with atmosphere and prognostic leaf area components working interactively ("Land-Atmosphere"), and one where both meteorological forcing and leaf area phenology are prescribed ("Land-Only-Fixed-Leaf", see further description above). Both configurations were run at preindustrial atmospheric CO_2 levels (284.7 ppm) and the Land-Atmosphere configuration was additionally run with 2x preindustrial atmospheric CO_2 levels (569.4 ppm) in order to assess the iWUE response to elevated CO_2.

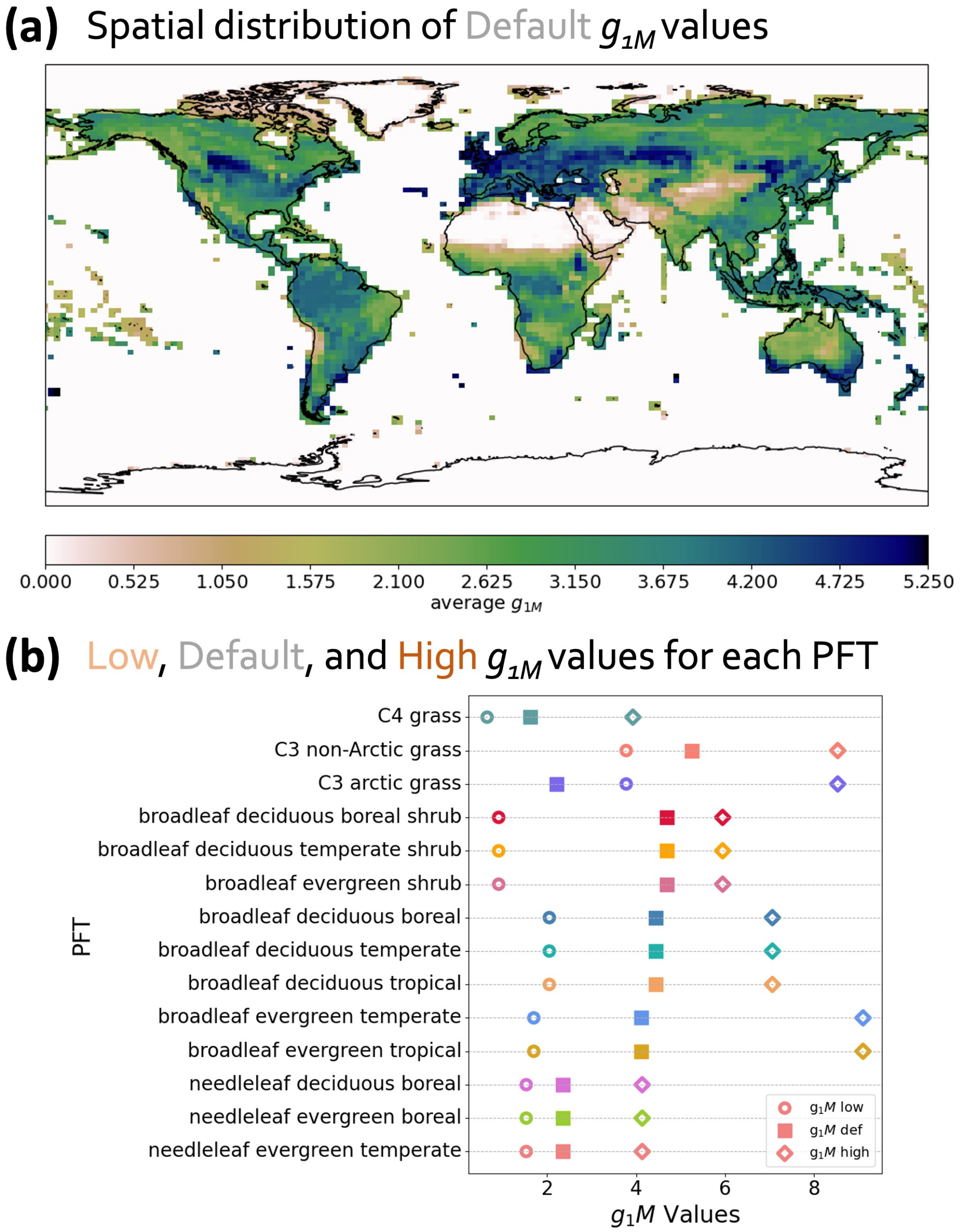

Figure 1. (*a*) Spatial plot of default PFT-area-weighted g_{1M} values used in CLM5. (*b*) Plot of the default and perturbed Medlyn slope parameter, g_{1M}, for each vegetation type in the CLM5.

2.3.1 Quantifying impact of perturbations in iWUE

We implement perturbations to iWUE through changes in the g_{1M} parameter as described above, resulting in simulations with higher or lower iWUE relative to the default in CLM5. To quantify a photosynthesis or climate response to a change in iWUE, we calculated the response of a variable by comparing the simulations with either high or low iWUE against the simulations with default iWUE. We averaged across all 80 post-spinup 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 actual difference between simulations and percentage difference between simulations for individual variables. Unless otherwise noted, percentage difference for a variable was calculated by taking the relative difference of that variable between two simulations and dividing it by the time average in the default iWUE simulation. The focus of our analysis is on photosynthesis and we found that 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 prognostic leaf area

To understand how the combined atmospheric and leaf area feedbacks modify the climate impact of iWUE choice, we compared the response of a variable to an g_{1M} perturbation within the Land-Only-Fixed-Leaf to the same response in the Land-Atmosphere configuration. For example, we compared the difference between the high and default iWUE simulation for the Land-Only-Fixed-Leaf configuration with the difference between the high and default iWUE simulation for the Land-Atmosphere configuration. In addition to calculating the absolute difference we also compared just the change in sign of photosynthetic response between the Land-Atmosphere and Land-Only-Fixed-Leaf configurations for the high iWUE simulations. We filtered for grid cells with a sign change in photosynthetic response to iWUE perturbation between the Land-Only-Fixed-Leaf and Land-Atmosphere 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 of a variable to an increase in CO_2 by comparing 2xCO_2 simulations to their parallel configuration 1xCO_2 simulations (e.g. Land-Atmosphere high iWUE (2xCO_2) - Land-Atmosphere high iWUE (1xCO_2)). Second, we quantified how the response of a variable to elevated CO_2 is modified by changing iWUE. We did this using a difference of differences, e.g. (high iWUE (2xCO_2) - high iWUE (1xCO_2)) - (default iWUE (2xCO_2) - default iWUE (1xCO_2)).

2.3.4 Regional analysis

In addition to global climate response to perturbations in iWUE, we focused on three regions that had a change in sign of photosynthetic response between the Land-Atmosphere and Land-Only-Fixed-Leaf configurations for the high iWUE simulations, with each spanning different background climates: the tropical forest Amazon (13°S to 5°S and 68°W to 57°W), the temperate grassland central North America (central NA; 40°N to 52°N and 103°W to 96°W), and boreal forest Canada (50°N to 57°N and 78°W to 69°W). Regional climate response was averaged spatially across the grid cells in each region.

2.4 Perturbed meteorology simulations

In addition to comparing our different iWUE simulations, we directly isolated the effects of temperature and vapor pressure deficit (VPD) on photosynthesis using additional simulations in which a single meteorological variable was modified in the Land-Atmosphere default iWUE configuration. We used global-scale "synthetic meteorology" simulations from Zarakas, Swann, and Battisti (2024), which we call here "perturbed meteorology" simulations. These simulations were each branched from a control run and run for 20 years using a very similar version of the CESM2 climate model as the version we used for the Land-Atmosphere default iWUE configuration. For each perturbed meteorology simulation, a single meteorological variable in the atmospheric output of the control simulation was perturbed, and the output compared to the control run. We used two perturbed meteorology simulations, first for temperature which had a 1°C increase at the bottom of the atmosphere for each grid cell, and second to calculate the effect of changes in VPD by imposing a 10% increase in specific humidity at the bottom of the atmosphere for each grid cell. 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, thereby isolating the effects of VPD on photosynthesis. VPD was calculated based on the the bottom of the atmosphere temperature, pressure, and specific humidity. Details on how we calculated the expected response of photosynthesis to temperature and VPD changes from iWUE perturbation can be found in Supplemental Text S2.

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 VPD. Specifically, if the "expected photosynthesis change" ($\delta GPP_{expected}$ in Eq. S1d) associated with the change in the meteorological variable (either temperature or VPD) is very similar to the difference in photosynthesis change simulated by the Land-Atmosphere and Land-Only-Fixed-Leaf high vs default iWUE, then we can infer that the difference in photosynthesis between the Land-Atmosphere (high minus default iWUE) and Land-Only-Fixed-Leaf (high minus default iWUE) configurations is mainly mediated through the change in that climate variable.

2.5 Statistical significance

We used a test of statistical significance to determine if responses in the perturbed iWUE simulations differed from those in the default iWUE simulation. We based the tests on the variability of annual average values. We report our results as statistically significant when a two-tailed student's t-test with an assumed 40 degrees of freedom has a p-value that passes the false discovery rate of 0.05. The false discovery rate, or the fraction of false positives, is important in our analysis because we perform a t-test at many grid cells and accounting for it makes our p-values more conservative (Wilks, 2016). Spatial maps show stippled grid cells that pass the statistical test.

3 Results

3.1 Photosynthetic response to iWUE

The total global photosynthesis rate in the Land-Atmosphere simulations varied across our iWUE perturbations, with 120 PgC/yr for the default iWUE, 99 PgC/yr for the low iWUE, and 112 PgC/yr for the high iWUE. Below we describe the causes for changes in photosynthesis in each iWUE perturbation in more detail.

3.1.1 Impacts of Low iWUE (low minus default iWUE)

In the Land-Atmosphere low iWUE simulation, photosynthesis decreased across the globe (Fig. 2b) relative to the default iWUE. There were larger absolute decreases in photosynthesis near the equator, due to greater overall plant productivity in the tropics. Photosynthesis decreased with lower iWUE because plants open their stomata and transpire more (Figs. S3b&c) leading to a cascade of changes to other variables that affect photosynthesis. Greater transpiration rates deplete plant and soil water supply making plants more soil water stressed (Fig. S3d), leading to a decrease in the number of leaves that a plant can support (Fig. S3g) which decreased total photosynthesis (Fig. 2b). VPD decreased along with decreases in surface temperature due to greater transpiration, which decreased atmospheric water stress. One might have expected this to alleviate overall plant water stress, however the increase in soil water stress was greater than the decrease in atmospheric water stress with low iWUE which accounts for the decrease in photosynthesis in our simulations.

The photosynthetic response to low iWUE was similar with and without dynamic atmosphere and prognostic leaf area (cf. Figs. 2a&b). Both configurations showed decreases in photosynthesis across the globe in response to lower iWUE with similar spatial patterns but with a larger magnitude of change in the Land-Atmosphere low iWUE simulation driven largely by leaf area decreases (Fig. S3g) that are precluded in the Land-Only-Fixed-Leaf configuration.

3.1.2 Impacts of High iWUE (high minus default iWUE)

Photosynthetic response to high iWUE perturbations are also generally negative but much smaller in magnitude than for low iWUE perturbations (cf. Figs. 2b&d), with global average photosynthesis (also referred to as gross primary production or GPP) decreases of 138 gC/m^2/year for lower iWUE and only 50 gC/m^2/year for higher iWUE. However, regions at the same latitude had different photosynthetic response to higher iWUE: in the Amazon there were decreases in photosynthesis while in southeast Asia there were increases in photosynthesis (Fig. 2d). The asymmetrical pattern of the photosynthetic response to higher iWUE in the Land-Atmosphere configuration is similar to that of the precipitation response, suggesting a connection between the two (cf. Fig. 2d and Fig. S5h). However, water availability variables such as soil water stress and VPD do not reflect the same asymmetrical response pattern (cf. Fig. 2d and Figs. S5f&g). Interestingly, Land-Atmosphere high minus default iWUE precipitation response pattern is also similar to the precipitation asymmetry pattern in response to higher CO_2 in Kooperman, Chen, et al. (2018), which is consistent since iWUE generally increases with higher CO_2.

In contrast to the low iWUE simulations, the high iWUE simulations had a different photosynthetic response when leaf area and the atmosphere are allowed to dynamically respond. High iWUE simulations in both configurations (Land-Only-Fixed-Leaf and Land-Atmosphere) have geographically varying responses including regions with increases in photosynthesis and regions with decreases in photosynthesis (cf. Figs. 2c&d). In particular, the sign of response of photosynthesis to high iWUE depends in many regions on whether the atmosphere and/or leaf area are allowed to change including in the Amazon, central North America (central NA), and boreal Canada (Fig. 2e). We discuss each of these three regions in further detail below. Regions with the same direction of photosynthetic response between the Land-Only-Fixed-Leaf and Land-Atmosphere high iWUE simulations tend to have a larger response in the Land-Atmosphere simulation. This is because, similarly to the low iWUE simulations, allowing leaf area to change in the Land-Atmosphere simulation amplifies the photosynthetic response—for example, regions with a decrease in photosynthesis experience a larger decrease in the Land-Atmosphere simulation due to decreases in leaf area (cf. Figs. 2c&d and Fig S5g).

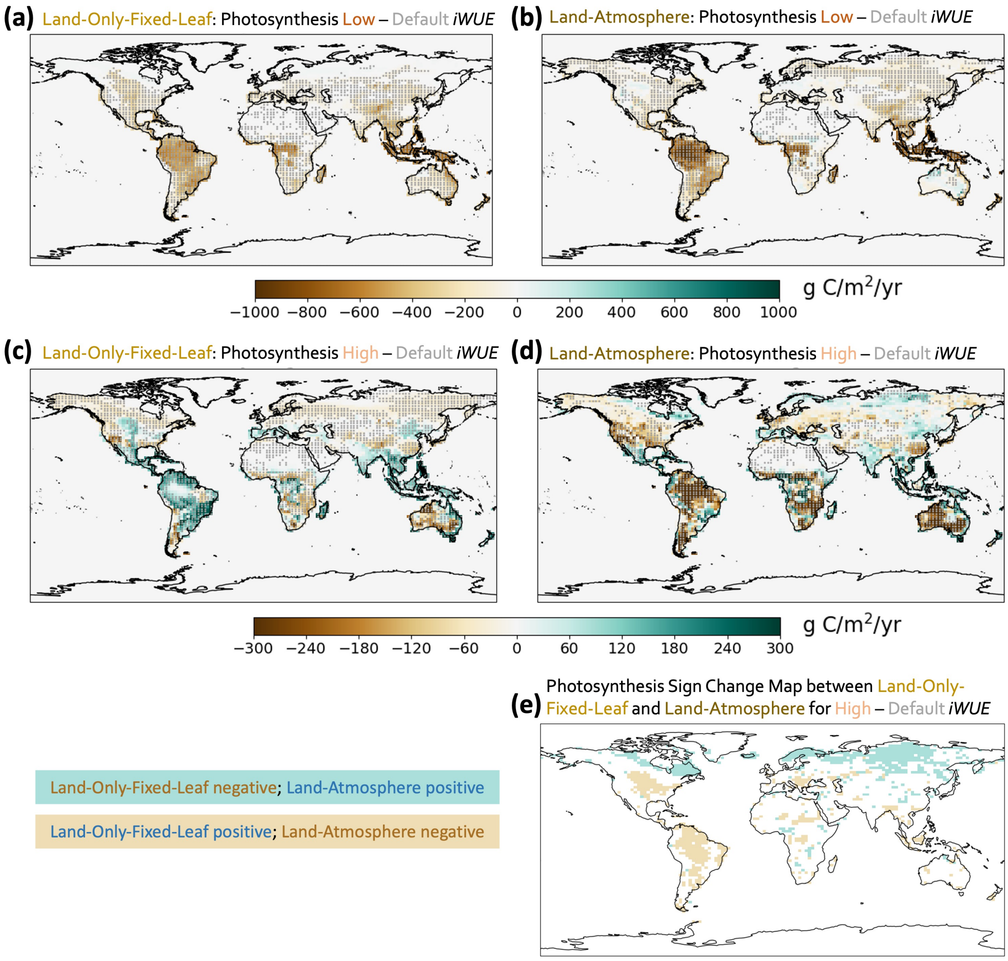

Figure 2. Spatial difference plots of photosynthesis for low minus default iWUE at *(a)* Land-Only-Fixed-Leaf and *(b)* Land-Atmosphere configurations and high minus default iWUE at *(c)* Land-Only-Fixed-Leaf and *(d)* Land-Atmosphere configurations. The response to low and high iWUE are at different scales. Stippled grid cells represent statistically significant differences. *(e)* A spatial plot showing the difference in the sign of the photosynthetic change in the Land-Only-Fixed-Leaf and Land-Atmosphere high minus default iWUE simulations. Colored grids indicate where the sign of the change in the Land-Atmosphere simulation is opposite to that in the Land-Only-Fixed-Leaf simulation and the color represents the direction of change.

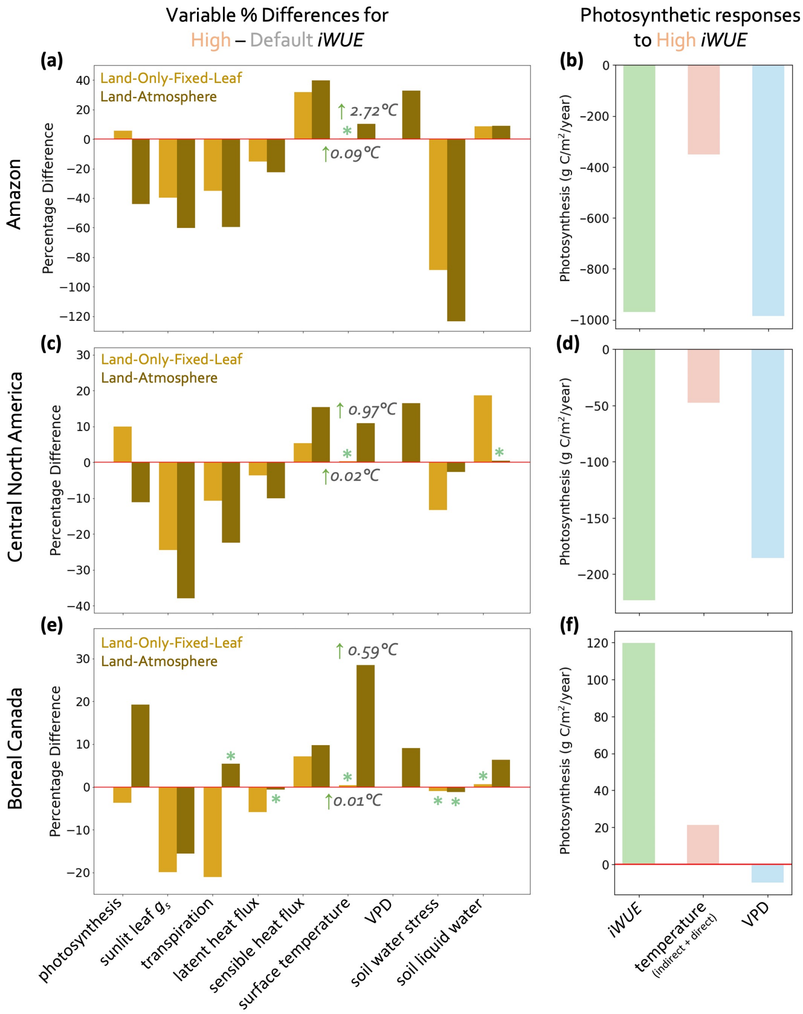

Figure 3. Percentage differences of photosynthesis and variables that can influence photosynthesis between the high and default iWUE simulations using the Land-Only-Fixed-Leaf and Land-Atmosphere configurations in the *(a)* Amazon, *(c)* central North America, and *(e)* boreal Canada. Bars with a green (*) are not statistically different from zero. The expected photosynthetic response estimated from perturbed meteorology for temperature ($\frac{\Delta GPP_T}{\Delta T_T} \cdot \delta T_{Land-Atmosphere}$; red bar) and VPD ($\frac{\Delta GPP_{VPD}}{\Delta VPD_{VPD}} \cdot \delta VPD_{Land-Atmosphere}$; blue bar) in *(b)* the Amazon, *(d)* central NA, and*(f)* boreal Canada. Temperature includes both direct effects of warming and indirect effects of VPD. The absolute difference in photosynthesis due to the change in iWUE (high minus default) between the Land-Atmosphere and Land-Only-Fixed-Leaf configurations are shown in green ($\Delta GPP_{Land-Atmosphere} - \Delta GPP_{Land-Only-Fixed-Leaf}$). Note that the y-axis is unique to each plot.

3.1.3 Regional responses to high iWUE

In the Amazon, there were opposite responses of photosynthesis to high iWUE (high iWUE minus defalt iWUE) between the model configurations with and without a dynamic atmosphere and prognostic leaf area, with decreases in photosynthesis using the Land-Atmosphere configuration, and vice versa using the Land-Only-Fixed-Leaf configuration (cf. Figs. 2c&d; Table 2; Fig. 3a). Transpiration decreased in both the Land-Atmosphere and Land-Only-Fixed-Leaf configurations as plants closed their stomata more in response to high iWUE (low $g_{!M}$), with a larger decrease occurring in the Land-Atmosphere configuration (Table 2). As expected, increases in temperature and VPD were larger for the high minus default iWUE in the Land-Atmosphere configuration compared to the Land-Only-Fixed-Leaf configuration, which used a prescribed atmosphere. The difference in response (dynamic atmosphere vs prescribed atmosphere) can be attributed (1) to larger decreases in latent cooling due to larger transpiration declines and (2) to cloud feedbacks that occur when the atmosphere is allowed to respond: the atmosphere responds to a decrease in transpiration, an increase in temperature, and an increase in VPD by decreasing low cloud coverage. Low clouds reflect incoming solar radiation, so a reduction in clouds further increases temperature and VPD (Table 2). Under decreased evaporation, in this case transpiration, the warming effect of decreased cloud cover is typically larger than decreased latent cooling (Laguë et al., 2023). The temperature impact of larger decreases in latent cooling for the Land-Atmosphere configuration also applies to central NA, while shortwave cloud feedbacks also affect temperatures in both central NA and boreal Canada. The Amazon had the largest magnitude of temperature increases (2.72°C) compared to the central NA (0.97°C) and boreal Canada (0.59°C) despite having the highest baseline temperature.

In central NA, we saw the same difference in photosynthetic response to model configuration as we saw in the Amazon, with decreases in photosynthesis in the Land-Atmosphere configuration and increases in the Land-Only-Fixed-Leaf configuration for the high iWUE simulation compared to the default iWUE simulation (Table 2; Fig. 3c). We attribute the response of photosynthesis to direct effects of temperature and effects of drier air (higher VPD) using perturbed meteorology simulations. We find in both the Amazon and central NA, an increase in temperature alone tended to slightly decrease photosynthesis while an increase in VPD alone drastically decreased photosynthesis. We attribute VPD as the cause of the decrease in photosynthesis in both regions because the magnitude of photosynthetic response to VPD alone was similar to the change in photosynthesis that we found between the Land-Only-Fixed-Leaf and Land-Atmosphere configurations (Figs. 3b&d).

Unlike in the Amazon and Central NA, in boreal Canada the photosynthetic response to high iWUE (high minus default iWUE) in the Land-Atmosphere configuration is opposite to that in the Land-Only-Fixed-Leaf configuration. Over boreal Canada, photosynthesis increased in the Land-Atmosphere configuration and decreased in the Land-Only-Fixed-Leaf configuration for high iWUE simulations compared to the default iWUE simulations (Table 2; Fig. 3e). Similar to the patterns we saw in the other regions, the Land-Atmosphere simulation had much larger increases in surface temperature and in VPD (Table 2) relative to the simulations with prescribed atmospheric conditions. The VPD increase in boreal Canada was smaller than in the Amazon, consistent with a smaller absolute temperature change (cf. Figs. 3a&e).

We find that that the Land-Atmosphere configuration has both higher photosynthesis and higher temperature in boreal Canada relative to the Land-Only-Fixed-Leaf configuration (Fig. 3e). Using perturbed meteorology simulations we find that in boreal Canada photosynthesis increases in response to elevated temperature alone and decreases in response to elevated VPD alone (Fig. 3f). Thus the higher temperatures in the Land-Atmosphere configuration should cause the direction of change in photosynthesis that we saw, although the magnitude attributable to either temperature or VPD from perturbed meteorology simulations is much smaller in boreal Canada relative to the other regions that we analyze.

3.2 Elevated atmospheric CO_2

Under elevated CO_2, we find that photosynthesis increases across the globe for all iWUE simulations (Figs. 4a-c), with an increase in 66 PgC/yr for default iWUE, 70 PgC/yr for high iWUE, and 60 PgC/yr for low iWUE. Additional details of photosynthetic response to elevated CO_2 for globe and the boreal, temperate, and tropical bands can be found in Table S2. The relationship between g_{1M} and iWUE is preserved at elevated CO_2, where decreasing g_{1M} corresponds to increasing iWUE and vice versa (Fig. S1b).

We find that perturbations to iWUE additionally modify the increase in photosynthesis to elevated CO_2 (Figs. 4d&e). Generally we find that high iWUE increases photosynthesis further, and low iWUE perturbation moderates the increase in photosynthesis, although there are regions which do not follow this pattern. However, overall, the additional photosynthetic response to iWUE perturbations are small relative to the photosynthetic response to elevated CO_2. Assumptions about iWUE modify the total global photosynthetic response to a doubling of preindustrial CO_2 by 6.4% for high iWUE and by -9.6% for low iWUE relative to default iWUE. At high iWUE, photosynthesis increases in 58% of grid cells and decreases in 42% of grid cells. In contrast, at lower iWUE, photosynthesis increases in only 27% of grid cells and decreases in 74% of grid cells.

We note that Australia has an absolute decrease in response to elevated CO_2 with high iWUE contrary to the rest of the globe, and a larger relative change response to iWUE (Fig. 4). We find that this can be explained by the substantial reduction in leaf area in response to high iWUE (whether due to perturbations in g_{1M} or elevated CO_2), with leaf area nearly reaching zero in the west and halving in the east with high iWUE (explanation of leaf area decrease in Supplemental Text S3; Fig. S7).

4 Discussion

4.1 Implications for choice of iWUE in Earth system models

In CESM2, one g_{1M} value is currently used to represent each PFT, a practice which is common across similar models (G. Bonan, 2019; Sabot et al., 2022). Our results provide insight as to how Earth system models may be over or underestimating photosynthesis in both the mean-state and in response to elevated CO_2 if real world plants have a different iWUE than the default value used in models.

In response to lower iWUE (and therefore high g_{1M} perturbation) g_s is expected to increase, and thus photosynthesis is also expected to increase due to the coupling between g_s and photosynthesis at the leaf level (Collatz et al., 1991; Medlyn et al., 2011; Franks et al., 2017). In our low minus default iWUE simulations, g_s did increase as expected, but our expectation for photosynthesis did not hold (Section 3.1.1), with photosynthesis decreasing across the globe (Fig. 2a&b). If plants in the real world had a lower iWUE than what is currently used in CESM2, then models would be substantially overestimating plant photosynthesis as well as plant carbon uptake. Our result is consistent with studies that have shown that CESM2 overestimates photosynthesis and leaf area (Hu et al., 2022; Song et al., 2021).

With higher iWUE (and therefore low g_{1M}), g_s is expected to decrease, and thus photosynthesis is also expected to decrease due to the coupling between g_s and photosynthesis at the leaf level (Collatz et al., 1991; Medlyn et al., 2011; Franks et al., 2017). However, we found increases in photosynthesis in some regions and decreases in other regions (Sections 3.1.2 & 3.1.2; Figs. 2c&d). Thus, depending on the region, if plants in

Table 2. Climate Variable Responses to high iWUE (low minus default g_{1M})

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)	**110***	**5.7***	**-858***	**-43.8***	**109***	**9.9***	**-114***	**-11.0***	**-21.4***	**-3.7***	**100***	**19.5***
Sunlit leaf g_s (gH$_2$O/m^2/s)	**-0.77***	**-39.4***	**-1.12***	**-60.2***	**-0.54***	**-24.4***	**-0.78***	**-37.8***	**-0.35***	**-19.9***	**-0.28***	**-15.4***
Transpiration (W/m^2)	**-20.7***	**-35.0***	**-35.6***	**-59.5***	**-3.46***	**-10.7***	**-6.57***	**-22.2***	**-1.71***	**-21.0***	**0.42**	**5.7**
Latent heat flux (W/m^2)	**-14.4***	**-15.1***	**-21.6***	**-22.3***	**-1.79***	**-3.6***	**-4.71***	**-10.0***	**-1.45***	**-5.9***	**-0.09**	**-0.4**
Sensible heat flux (W/m^2)	**13.2***	**31.8***	**16.2***	**39.7***	**1.54***	**5.4***	**4.40***	**15.3***	1.32*	7.2*	1.81*	9.6*
Soil water stress (unitless)	**-0.40***	**-89.1***	**-0.49***	**-123***	**-0.11***	**-13.4***	**-0.03***	**-2.7***	-0.01	-1.0	-0.01	-1.2
Soil liquid water (kg)	80.1*	8.8*	81.6*	9.0*	**123***	**18.7***	**3.19**	**0.4**	**4.17**	**0.6**	**45.9***	**6.4**
Surface temperature (°C)	**0.09**	**0.3**	**2.72***	**10.2***	**0.02**	**0.3**	**0.97***	**11.1***	**0.01**	**0.5**	**0.59***	**31.1***
VPD (Pa)	-	-	**673***	**33.0***	-	-	**125***	**16.5***	-	-	**27.9***	**9.3***
Low cloud cover (fraction)	-	-	**-0.07***	**-38.7***	-	-	**-0.04***	**-14.6***	-	-	**-0.03***	**-3.7***
Incident solar radiation (W/m^2)	-	-	2.00*	0.9*	-	-	**4.19***	**2.4***	-	-	**2.05***	**1.7***
Total leaf area (m^2/m^2)	-	-	**-2.07***	**-53.3***	-	-	**-0.37***	**-16.4***	-	-	**0.16***	**12.5***

We represent the statistical significance of two comparisons, between simulations with different iWUE (*), and between the two model configurations (bold). A star (*) indicates high minus default iWUE responses pass a test for statistical significance, where the null hypothesis is that there is no difference between the high iWUE and default iWUE simulations. **Bolded** values indicate where the differences between the Land-Only-Fixed-Leaf and Land-Atmosphere configurations for high minus default iWUE pass a test for statistical significance, where the null hypothesis tested is that there is no difference between these two sets of differences.

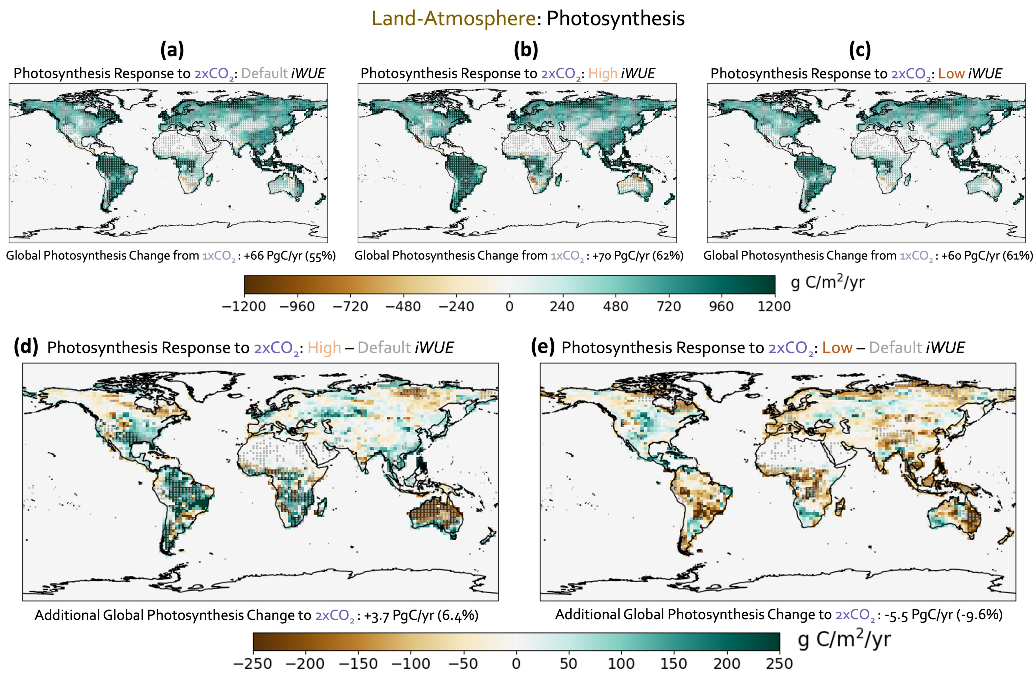

Figure 4. Photosynthesis difference spatial plots of default iWUE between 1xCO_2 and 2x preindustrial atmospheric CO_2 levels for *(a)* default, *(b)* high, and *(c)* low iWUE perturbations, where iWUE is constant for each comparison. Spatial difference plots showing the additional change in photosynthesis in response to a doubling of atmospheric CO_2 in the Land-Atmosphere configuration when the default g_{1M} (default iWUE) is replaced by *(d)* low g_{1M} (high iWUE) and *(e)* high g_{1M} (low iWUE). The additional change in photosynthesis is calculated by taking the difference of the photosynthetic response to iWUE perturbation at 2xCO_2 and 1xCO_2 (e.g. 2xCO2(high – default iWUE) – 1xCO2(high – default iWUE)). Stippled grid cells represent statistically significant differences. Grid cells are statistically significant if the photosynthetic response to iWUE perturbation at 2xCO_2 is different from the photosynthetic response to at 1xCO_2.

the real world had a higher iWUE than that currently used in CESM2, plant photosynthesis could be either over or underestimated.

We find similar implications under the future scenario of elevated atmospheric CO_2– if real world plants had a higher iWUE than the default used in CESM2, future climate projections would be underestimating plant photosynthesis and terrestrial carbon sink. The opposite would be true if real world plants had a lower iWUE than the default iWUE used in the model.

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

As mentioned above (Section 4.1), we expected photosynthesis to decrease with higher iWUE but although we find some regions of decrease we also find regions of increase (Figs. 2c&d). Not only was photosynthetic response to high iWUE not consistent across regions, it was also not consistent across configurations of CESM2, flipping sign between increasing and decreasing photosynthetic response to the same change in iWUE depending on the the inclusion of a dynamic atmosphere and prognostic leaf area (Fig. 2e). The change in the sign of photosynthetic response to iWUE can be largely attributed to the inclusion of a dynamic atmosphere rather than prognostic leaf area (cf. Fig. 2e and Fig. S6). In addition to the differences between model configurations, the direction of the sign change in photosynthetic response was negative over many regions when the atmosphere was allowed to dynamically respond, which was opposite of what we expected (Supplemental Text S1).

To explain why photosynthesis shows a different direction of response to an increase in iWUE when the atmosphere is allowed to dynamically respond (Land-Atmosphere configuration compared to the Land-Only-Fixed-Leaf configuration), we explored four possible conjectures based on what we know about photosynthesis and its response to environmental factors. First, the high iWUE and default iWUE simulations could have differences in g_s in response to g_{1M} (conjecture 1; c1). Second, photosynthesis could be responding to plant soil water stress (conjecture 2; c2). Third, photosynthesis could be responding to a change in temperature which differs between the Land-Atmosphere and Land-Only-Fixed-Leaf configurations (conjecture 3; c3). Fourth, photosynthesis could be responding to atmospheric water stress (conjecture 4; c4). We focused on regions that had a change in the sign of photosynthetic response to iWUE between the Land-Atmosphere and Land-Only-Fixed-Leaf high iWUE simulations (Fig. 2e).

To start, there was a g_s decrease in response to high iWUE perturbation in almost all regions for both Land-Atmosphere and Land-Only-Fixed-Leaf simulations (Fig. S4b and Fig. S5b), which would on its own cause a decrease in photosynthesis, and thus changes in g_s (c1) alone cannot explain the difference in photosynthetic response between the two model configurations. We note that the Tibetan Plateau region did not match the general global g_s response (Fig. S4b and Fig. S5b) because the C3 arctic grass PFT default g_{1M} used in CLM was lower than the low g_{1M} perturbation derived from Lin et al. (2015) (Fig. 1a). The changes in soil water stress, temperature, and atmospheric water stress vary more across regions, so we discuss the response by region below.

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

For simulations with a prescribed atmosphere (Land-Only-Fixed-Leaf configuration), we found a photosynthetic increase in the Amazon and central NA in response to high iWUE which is most likely driven by a reduction in soil water stress (c2) because temperature (c3) and VPD (c4) did not change much with fixed atmospheric forcing (Fig. 3). This occurs in both the Amazon and in central NA although the percentage increase in photosynthesis in central NA was greater compared to the Amazon even though the percentage increases in water availability were smaller. This suggests that photosynthesis in central NA is more sensitive to increases in water availability and decreases in soil water stress (c2).

For simulations with a dynamic atmosphere and prognostic leaf area (Land-Atmosphere configuration), we find that photosynthesis decreases. This can not be explained by soil water stress (c2), which is alleviated with high iWUE in the Amazon and remains neutral central NA. The main differences between the response to high iWUE in Land-Atmosphere and Land-Only-Fixed-Leaf configurations are in the surface temperature (c3) and VPD (c4) responses. Temperature (c3) increased significantly in both the regions, which could potentially push plants beyond their thermal optimum for photosynthesis (Yamori et al., 2014; Figs. S4e & S5e). However, CLM represents photosynthetic acclimation (Lombardozzi et al., 2015) which reduces the negative impact of hot temperatures.

We attribute the photosynthetic decreases with a dynamic atmosphere primarily to a response to VPD (c4) as the magnitude of our expected photosynthetic response to increase in VPD alone explains the total signal (Figs. 3b&d) and is substantially larger than the response to temperature (c3) alone. The photosynthesis decrease is larger in the Amazon compared to central NA, suggesting that plants in the Amazon are more sensitive to an increase in VPD (c4). This is consistent with prior work showing that photosynthesis declines at high temperatures in tropical forests are mostly due to VPD effects rather than direct temperature effects in CLM5 (Zarakas, Swann, Koven, et al., 2024).

4.2.2 Temperature increased photosynthesis in boreal Canada

For boreal Canada we find a decrease in photosynthesis in response to high iWUE in simulations with a prescribed atmosphere (Land-Only-Fixed-Leaf configuration). In the high iWUE Land-Only-Fixed-Leaf simulation, we find support for the first conjecture as the decrease in g_s (c1) in boreal Canada had a greater effect on photosynthetic response than the small increase in soil water availability (c2) (Fig. 3e). When the atmosphere is allowed to respond to high iWUE, photosynthesis increased in boreal Canada. Soil water availability (c2), temperature (c3), and VPD (c4) all increase. If boreal plants were strongly influenced by higher VPD (c4) as they were in the Amazon and central NA, this would cause a decrease in photosynthesis. Yet photosynthesis increased, implying that plants were more sensitive to the direct effects of increases in temperature (c3) than in VPD (c4) and that temperatures remained below thermal optimum (Fig. 3f). Although our direct attribution of the response of photosynthesis to an increase in temperature is smaller than the total increase in photosynthesis that we find, this could be explained by increased leaf area which is not included in our perturbed meteorology simulations (Fig. S5; Table 2).

The expected photosynthetic responses from temperature for all three regions suggest that the total effect of temperature (c3) 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 effects of higher VPD, which are indirectly driven by elevated temperature.

5 Conclusions

The choice of iWUE used to represent each plant functional type in CESM2 impacts photosynthetic rates. Decreasing iWUE from the default had a large decrease on photosynthesis while increasing iWUE had regionally dependent impact on photosynthetic response. In particular, the Amazon and central NA regions exhibited decreases in photosynthesis (-43.8% and -11.0% respectively) while boreal Canada experienced increases (19.5%) when the atmosphere and leaf area are allowed to respond.

The inclusion of a dynamic atmosphere enabled the climate to respond differently to perturbations in iWUE, driven by both temperature and VPD. Changes in temperature resulted from changes in surface energy partitioning and reductions in cloud cover and changes in VPD resulted from changes in temperature and transpiration. The sign of photosynthetic response to these temperature changes for high iWUE perturbation simulations depended on the background climate of the region. In the Amazon and central NA, with a high baseline temperature, photosynthesis decreased with further increase in temperature. In contrast, in boreal Canada, with a low baseline temperature, photosynthesis increased with further increase in temperature. The photosynthetic response in the Amazon and central NA 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.

Currently in CESM2, which uses the Medlyn stomatal conductance formulation (Medlyn et al., 2011), plants tend to decrease g_s under high temperatures and high VPD to reduce water loss through transpiration. However, some plant species have been observed to increase g_s under heat stress, presumably increasing transpiration for evaporative cooling to prevent thermal leaf death or as an unavoidable response to intense heat (Marchin et al., 2022). This plant response to high temperatures is currently not implemented in any Earth System models and decouples A_n and g_s (Marchin et al., 2023). In the context of our results, our simulations could be underestimating plant transpiration under high temperatures and high VPD conditions, particularly for the high iWUE simulations. The greater water fluxes could lead to different atmospheric feedbacks (e.g., dampen the response of increases in temperature and VPD) and consequently affect the photosynthetic response.

Both high and low iWUE perturbations changed the total global photosynthetic response to elevated atmospheric CO_2 by 6.4% and -9.6%, respectively with some regional variation. This has implications for the total land carbon sink under elevated CO_2, with higher iWUE tending to increased gross photosynthesis, which tends to increase land carbon sink, while lower iWUE would do the opposite and tend to decrease the land carbon sink, all else being equal. However, warmer temperatures can counteract increases in the land carbon sink by increasing plant respiration and ecosystem carbon loss.

Our research mainly focused on how photosynthesis would be affected by altering plant carbon-water trade-offs. Overall we found that the answer was more complicated than one might initially guess, but that the response of photosynthesis can be explained by considering sensitivity to temperature and water availability. We find that plant transpiration is greatly affected by iWUE perturbations, with likely implications for water budget variables like precipitation, evapotranspiration, and runoff (Kooperman, Chen, et al., 2018; Kooperman, Fowler, et al., 2018; Fowler et al., 2019; Mankin et al., 2019). We show that, given the response of photosynthesis to iWUE even at elevated CO_2, future climate projections could be significantly different based on how g_{1M} and thus iWUE is parameterized in Earth system models.

Our findings show that changes in iWUE, whether due to plant adaptation to climate change or land-use changes, can have a large impact on photosynthesis. This affects predictions of how photosynthesis will respond to environmental changes. If our assumptions about iWUE are incorrect, we risk poorly modeling not only the mean-state photosynthesis but also its response to global change. This uncertainty underscores the need for the research community to better represent iWUE in models. To do so, we need to collect more measurements of iWUE and its components, photosynthesis and stomatal conductance. Measurements across a diversity of plant types, background climates, and CO_2 environments would enable the community to build models that incorporate spatial variability of plant traits and to more effectively use perturbed parameter ensembles to better quantify uncertainty in photosynthesis.

6 Open Research

The original data for this study are all available. Data used to perturb the Medlyn slope parameter can be found at https://figshare.com/articles/dataset/Optimal_stomatal_behaviour_around_the_world/1304289?file=1886204 (Lin et al., 2015). Model output from the iWUE perturbation simulations are available the Dryad Digital Repository for this paper (DOI: 10.5061/dryad.c59zw3rj0; A. X. Liu et al., 2024). Model output from the perturbed meteorology simulations used in this paper is available in another Dryad Digital Repository (DOI: 10.5061/dryad.h44j0zpw1; Zarakas, Swann, & Battisti, 2024). CESM2 is open source and all code can be found on Github at https://github.com/ESCOMP/CESM.

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Supporting Information for "Photosynthetic responses to intrinsic water-use efficiency depend on atmospheric feedbacks and modify the magnitude of response to elevated CO_2"

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Text S1. Relationship between g_{1M} and iWUE

We directly perturbed g_{1M} in our simulations, resulting in varying iWUE perturbations between the Land-Only-Fixed-Leaf and Land-Atmosphere simulation for each region. Generally, we expected photosynthesis to increase with higher iWUE. In the Amazon, the Land-Only-Fixed-Leaf simulation had less of an increase in iWUE at low g_{1M} (Figure S1c), suggesting that the Land-Only-Fixed-Leaf simulation should have had a more moderate increase photosynthesis compared to the Land-Atmosphere simulation. However this was contrary to what we found, as the Land-Atmosphere simulation showed an absolute decrease in photosynthesis. The Land-Atmosphere high iWUE simulation had photosynthesis decreases while the Land-Only-Fixed-Leaf high iWUE simulation had photosynthesis increases (Table 2; Figure 3a). We also observed unexpected photosynthetic responses in central NA. The central NA results mirrored those of the Amazon, with central NA in the Land-Only-Fixed-Leaf simulation having less of an iWUE increase at low g_{1M} (Figure S1d) suggesting a greater photosynthesis increase in the Land-Atmosphere simulation. We saw that both the Land-Atmosphere and Land-Only-Fixed-Leaf high iWUE simulations 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 simulation (Table 2; Figure 3c). Like the Amazon and central NA regions, boreal Canada in the Land-Atmosphere simulation had a greater increase in iWUE with low g_{1M} perturbation compared to the Land-Only-Fixed-Leaf simulation (Figure S1e), which gave the same expectation that the Land-Atmosphere simulation would have a greater increase in photosynthesis. Contrary to the other regions, in boreal Canada, photosynthesis had increases for the Land-Atmosphere and absolute decreases for the Land-Only-Fixed-Leaf high iWUE simulation (Table 2; Figure 3e), which matched expectations. We explored reasons why in Section 4.

Text S2. Perturbed meteorology simulation calculations

For each perturbed meteorology simulation, we calculated the expected response of photosynthesis ($\delta GPP_{expected}$) 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:

$$\Delta GPP_{\text{met Var}} = GPP_{\text{Land-Only perturb met Var}} - GPP_{\text{Land-Only control met}} \ , \tag{1a}$$

$$\Delta Var_{\text{met Var}} = Var_{\text{perturb met Var}} - Var_{\text{control met}} \ , \tag{1b}$$

$$\Delta Var_{\text{Land-Atm}} = Var_{\text{Land-Atm perturb iWUE}} - Var_{\text{Land-Atm default iWUE}} \ , \tag{1c}$$

$$\delta GPP_{\text{expected}} = \frac{\Delta GPP_{\text{met Var}}}{\Delta Var_{\text{met Var}}} \times \Delta Var_{\text{Land-Atm}} \ , \tag{1d}$$

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. The first two equations (Eq. 1a&b) were calculated using the default values for iWUE and the "perturb met Var" refers to perturbed meteorology simulations.

Text S3. Reasons why leaf area decreases in Australia in response to high iWUE at elevated CO_2

In the main text, we attribute large photosynthesis decrease at high iWUE to plants decreasing their leaf area. We hypothesize two reasons for the the decrease in leaf area below.

The first reason why leaf area decreases could be due to plants overheating. Since we were perturbing a high iWUE, plant stomata were forced to close more, which decreased transpiration. This was followed by a decrease in latent heat flux and water vapor in the air, contributing heat and dryness to an atmosphere already warmed from the increase in CO_2. In the real world plants transpire to regulate temperatures, but in model world that function is not implemented, so our plants in Australia could not cool down and may have decreased leaf area due to overheat. The second reason for leaf area reductions could be carbon starvation from stomatal closure. We already forced stomata close to some degree with our high iWUE perturbation, which could be amplified by an increase in atmospheric water stress due to an increase in VPD from decreased transpiration. If plants closed their stomata too much, they would not be able to diffuse in enough carbon dioxide for photosynthesis to upkeep its leaves and starve, hence the term carbon starvation.

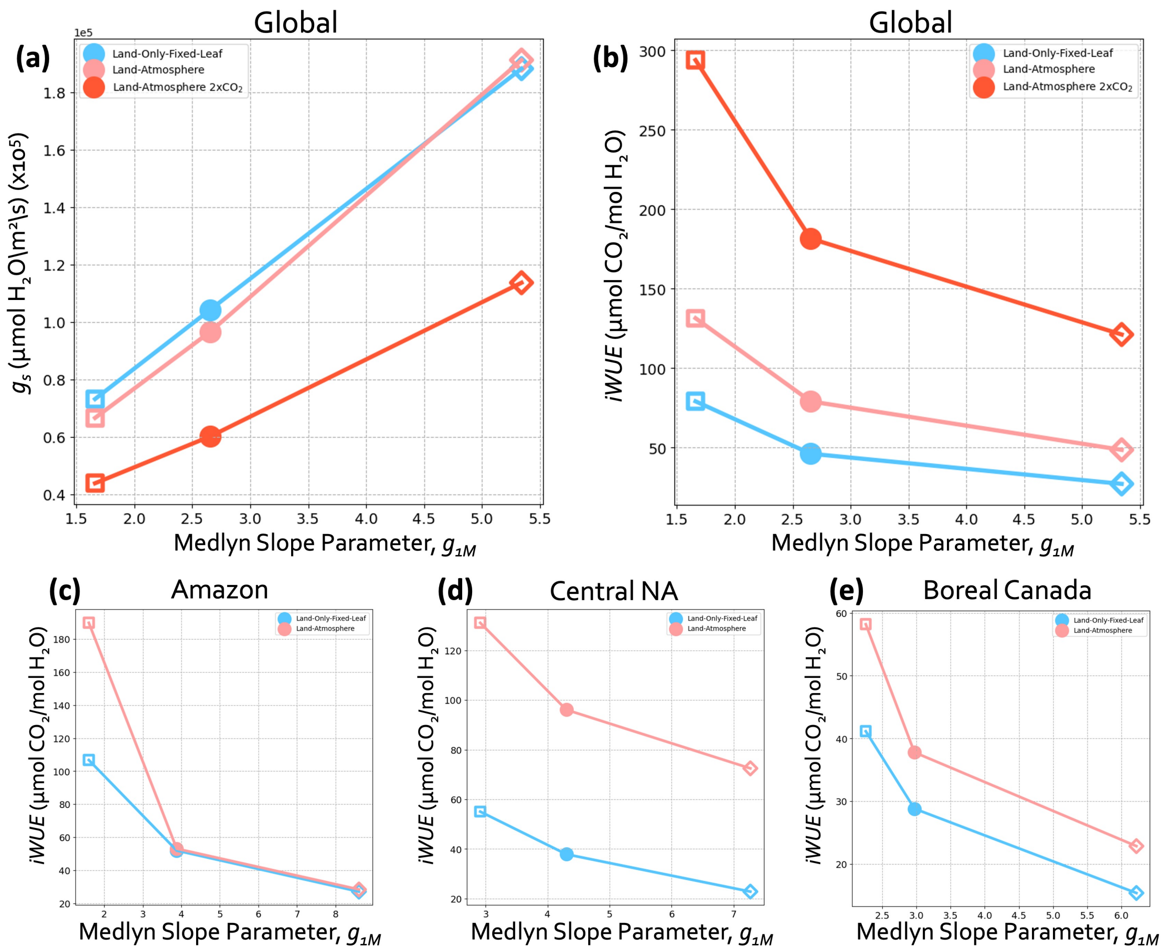

Figure S1. Globally averaged Medlyn slope g_{1M} vs *(a)* globally averaged iWUE and *(b)* globally averaged stomatal conductance g_s for the Land-Only-Fixed-Leaf and Land-Atmosphere simulations at 1x and 2xCO_2. The relationship between g_{1M} and iWUE is plotted regionally for *(c)* the Amazon, *(d)* central NA, and *(e)* boreal Canada.

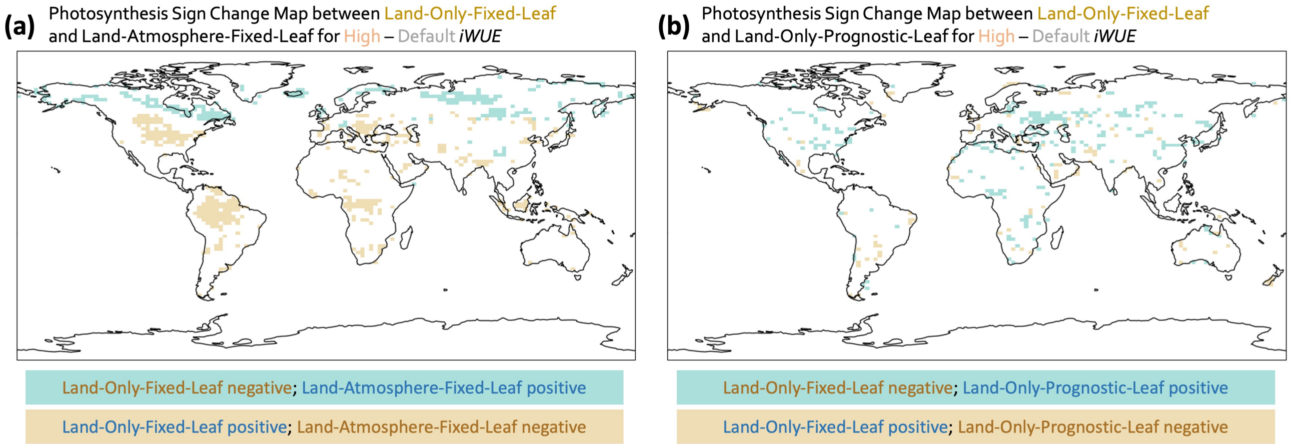

Figure S6. Spatial plots showing the difference in the sign of the photosynthetic change in the Land-Only-Fixed-Leaf high minus default iWUE simulations and high minus default iWUE simulations for configurations that have either *(a)* the inclusion of a dynamic atmosphere (Land-Atmosphere-Fixed-Leaf) or *(b)* a prognostic leaf area (Land-Only-Prognostic-Leaf). Refer to Table S1 for configuration details. Colored grids indicate where the sign of the change in the Land-Atmosphere-Fixed-Leaf or Land-Only-Prognostic-Leaf simulations is opposite to that in the Land-Only-Fixed-Leaf simulation and the color represents the direction of change.

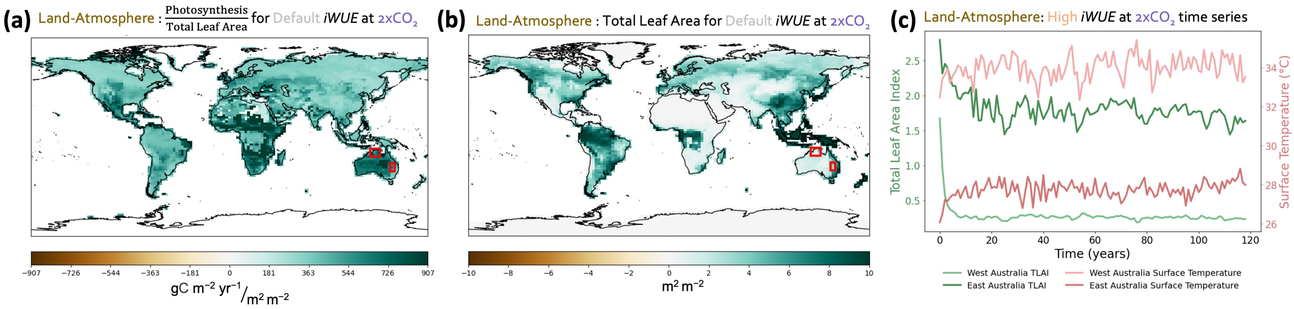

Figure S7. *(a)* Global spatial plot of total photosynthesis normalized by total leaf area index (TLAI) at each grid cell for the Land-Atmosphere default iWUE simulation at $2xCO_2$. *(b)* Global spatial plot of TLAI for the Land-Atmosphere default iWUE simulation at $2xCO_2$. *(c)* Time series of TLAI and surface temperature for west and east Australia. The time series data was from pulled from the red boxes drawn in *(a)* and *(b)*.

Table S1. Summary of Additional Simulations.

Simulation Name	CO_2	Atmosphere	Leaf Area	g_{1M}	iWUE
Land-Atmosphere-Fixed-Leaf high iWUE	$1xCO_2$	dynamic	prescribed	low	high
Land-Atmosphere-Fixed-Leaf default iWUE				default	default
Land-Only-Prognostic-Leaf high iWUE	$1xCO_2$	prescribed	prognostic	low	high
Land-Only-Prognostic-Leaf default iWUE				default	default

[a] Additional simulations used to attribute the change in sign of photosynthetic response between the Land-Atmosphere and Land-Only-Fixed-Leaf configurations to the inclusion of a dynamic atmosphere and a prognostic leaf area (Fig. S6).

Table S2. Photosynthetic (GPP) Response to elevated CO_2 at different iWUE.

Region	Latitude Range	iWUE	Starting GPP (PgC/yr)	Ending GPP (PgC/yr)	% Change
Global	0-90°N and °S	default	119	185	54.6
		high	112	182	61.8
		low	99	159	61.0
Boreal	50-60°N and °S	default	1.7	2.9	75.9
		high	1.6	2.9	77.4
		low	1.5	2.8	79.3
Temperate	23.5-50°N and °S	default	15	22	44.9
	(excludes	high	14	21	50.2
	boundary values)	low	14	20	46.2
Tropical	0-23.5°N and °S	default	18	26	45.3
		high	17	26	55.4
		low	13	21	55.4

[a] Photosynthetic (GPP) response for 2x minus 1x preindustrial CO_2 at default, high, and low iWUE for different latitude belts (Figs. 4a-c). GPP values are rounded to either the nearest whole number or two significant figures, whichever is more precise, and percentage changes are rounded to one decimal place.