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Geoscientific Model Development
Discussions

Implementation and evaluation of the unified stomatal optimization approach in the Functionally Assembled Terrestrial Ecosystem Simulator (FATES)

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Abstract. Stomata play a central role in regulating the exchange of carbon and water vapor between ecosystems and the atmosphere. Their function is represented by land surface models (LSMs) by conductance models. The Functionally Assembled Terrestrial Ecosystem Simulator (FATES) is a dynamic vegetation demography model that can simulate both detailed plant demographic and ecophysiological dynamics. To evaluate the effect of stomatal conductance model representation on forest water and carbon fluxes in FATES, we implemented an optimality-based stomatal conductance model—the Medlyn (MED) model, that simulates the relationship between photosynthesis (A) and stomatal conductance to water vapor (g_{sw}) as an alternative to the FATES default Ball-Woodrow-Berry (BWB) model. To evaluate how the behavior of FATES is affected by stomatal model choice, we conducted a model sensitivity analysis to explore the response of g_{sw} to synthetic climate forcing variables including atmospheric CO_2 concentration, air temperature, radiation, and vapor pressure deficit (VPD). We found that modeled g_{sw} values varied greatly between the BWB and MED formulations due to the different default stomatal slope parameters (g_1). After harmonizing g_1 and holding the same stomatal intercept parameter (g_0) for both model formulations, we found that the divergence in modeled g_{sw} was limited to conditions when the VPD exceeded 1.5 kPa. We then evaluated model simulation results against measurements from a wet evergreen forest in Panama. Results showed that both the MED and BWB model formulations were able to capture the magnitude and diurnal change of measured g_{sw} and A but underestimated both by about 30 % when the soil was predicted to be very dry. Our study suggests that the parameterization of stomatal conductance models and current model response to drought are the critical areas for improving model simulation of CO_2 and water fluxes in tropical forests.

Keywords: FATES, stomatal conductance, photosynthesis, optimization theory, soil moisture, tropical forests

1 Introduction

Global climate change has resulted in significant modifications to Earth's ecosystems through changing weather patterns, an increased frequency and severity of extreme drought, floods, and heatwaves, which has resulted in increased risk for terrestrial vegetation (Pachauri et al., 2014; Reichstein et al., 2013; Gatti et al., 2021). The exchange of water vapor and carbon dioxide between plants and the atmosphere is dominated by transport through stomata (Hetherington and Woodward, 2003; Kala et al., 2016). The mechanisms regulating stomatal opening involve complex biochemical and biophysical processes that are currently not represented in land surface models (LSMs) (Lawson et al., 2014; Buckley and Mott, 2013; Blatt, 2000; Davies et al., 2002). However, a range of much simpler, largely empirical, formulations that describe the responses of stomata to their environment have been successfully used by LSMs for many years. Most of them require only two parameters i.e. the intercept parameter (g_0), which is the conductance when photosynthesis (A) is zero, and slope parameter (g_1) that describe the relationship between stomatal conductance to water vapor (g_{sw}) and a regressor term that includes A and environmental variables (Damour et al., 2010; Berry et al., 2010). The most widely used g_{sw} representation, and the default formulation used in the Functionally Assembled Terrestrial Ecosystem Simulator (FATES), is the Ball-Woodrow-Berry model (BWB, Ball et al., 1987), where g_{sw} is based on an empirical relationship with A, atmospheric carbon dioxide concentration at the leaf surface (C_a), and atmospheric relative humidity (H) as Eq. (1):

$$g_{\mathrm{sw}} = g_0 + g_1 \frac{A}{C_\mathrm{a}} H, \tag{1}$$

The optimality-based unified stomatal conductance model (Medlyn model, MED, Medlyn et al., 2011), based on the assumption that plants will attempt to maximize carbon gain while minimizing water loss (Cowan and Farquhar, 1977), has been proposed as an alternative, but still simple to implement, representation of g_{sw} in LSMs (De Kauwe et al., 2015; Lawrence et al., 2019). The basic functional form of the MED model is shown in Eq. (2):

$$g_{\mathrm{sw}} = g_0 + 1.6\left(1 + \frac{g_1}{\sqrt{\mathrm{VPD}}}\right)\frac{A}{C_\mathrm{a}}, \tag{2}$$

Although the functional form of the MED model is similar to the BWB model, g_1 is based on underlying optimization theory and has a strong theoretical link to plant water use efficiency. The MED model is also favored by many plant physiologists given that g_{sw} responds to VPD rather than H (Rogers et al., 2017). Importantly, the g_1 parameter has also been found to vary significantly across a wide range of different plant functional types (PFTs) and climate regions (Lin et al., 2015). Better representation of g_{sw} in LSMs requires efforts in improving the fidelity of g_1 parametrization by PFT, typically obtained through field measurement campaigns (Lin et al., 2015; Wu et al., 2020) or model inversion (Bonan et al., 2011; Fer et al., 2018). For example, De Kauwe et al. (2015) derived PFT-specific g_1 parameter from Lin et al. (2015) for the CABLE model and found a significant reduction in annual fluxes of transpiration using MED compared with the original model formulation (Leuning, 1995). Despite considerable analysis supporting the adoption of the MED model in LSMs (De Kauwe et al., 2014; Lawrence et al., 2019), the formulation has not been widely adopted by LSMs and is not common in dynamic vegetation models (Fisher et al., 2018).

Exploring plants' physiological responses to key environmental variables is emerging as a promising way to understand model representation and evaluate model behaviors (Rogers et al., 2017; Bonan et al., 2011). Stomatal conductance in the MED and BWB models responds to direct environmental drivers including atmospheric CO_2 concentration and VPD or H at the leaf surface, and indirect drivers like radiation and leaf surface temperature through the influence from photosynthesis (see Eq. (1) & Eq. (2) in Franks et al., 2017). Evaluating the BWB and MED

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formulations to changing climate in a complete LSM, where atmospheric, ecological, and hydrologic processes are highly coupled, is urgently needed to understand model responses within a larger domain.

Improved projection of the response of ecosystems to global climate change hinges upon understanding model representations of plants' responses to a hotter and drier future (Sullivan et al., 2020). To mimic the drought effects on ecosystems, some models have included a soil water stress factor (often denoted as β) which is used to reduce the "base rate" of g_0 and g_1 in stomatal conductance module. In some cases, it is also used to lower the maximum carboxylation rate of Rubisco (V_{cmax}), or the maximum rate of electron transport (J_{max}) which reduces A in Eq. (1) and Eq. (2) and therefore can reduce g_{sw} in relation to soil water stress as well (De Kauwe et al., 2013; Rogers et al., 2017). However, the application of a β factor on different physiological parameters has not been evaluated against measurements for g_{sw} models. Therefore, evaluating different g_{sw} schemes and parameterization with data collected under normal and stressed conditions may help reveal areas for model improvement.

In this study, we explored the impact of stomatal behavior under simulated and realistic environmental conditions in the Functionally Assembled Terrestrial Ecosystem Simulator (FATES) model (Koven et al., 2020). We implemented the MED model as an alternative approach to the default BWB method for simulating leaf-scale g_{sw} based on optimization theory. The FATES model is a dynamic vegetation demography model that simulates leaf to ecosystem-scale carbon, water, and energy fluxes, as well as cohort-level plant growth, competition, and mortality processes, enabling FATES to predict the distribution, structure, and composition of vegetation (Fisher et al., 2015; Koven et al., 2020). FATES itself is not a standalone model, but instead is used in conjunction with a host land model, and is currently coupled with the Community Land Model (CLM, Lawrence et al., 2019) and the Energy Exascale Earth System Model (E3SM) Land Model (ELM, Holm et al., 2020). Using FATES and the MED and BWB representations we addressed two main questions: (1) How do projected leaf-level and canopy-level CO_2 and water vapor fluxes differ between the BWB and MED formulations in response to key meteorological forcing variables? (2) How do the two model outputs of stomatal conductance and photosynthesis compare to leaf-level gas exchange data collected through a dry season in a tropical forest?

2 Methods

2.1 Implementation of the Medlyn model into FATES

We implemented the MED stomatal conductance model as an alternative way to the BWB model in the calculation of g_{sw} in FATES. A detailed description of numerical calculation can be found in online documentation (FATES Development Team, 2020b). It should be noted that the intercept parameter (g_0) and maximum carboxylation rate of Rubisco (V_{cmax}) (in calculating A) in Eq. (1) and Eq. (2) are multiplied by an empirical soil moisture stress factor (β) by default in the FATES model. β factor ranges from one when the soil is wet to zero when the soil is dry. β factor depends on the soil water potential of each soil layer, the root distribution of the PFT, and a plant-dependent response to soil water stress as shown in Eq. (3):

$$\beta = \sum_{j=1}^{nj} w_j r_j, \tag{3}$$

where w_j is a plant wilting factor for layer j and r_j is the fraction of roots in layer j. For more details on the calculation of the plant wilting factor and the fraction of roots, see the CLM version 4.5 (CLM4.5) technical note (Oleson et al., 2013).

2.2 The San Lorenzo, Panama Model Testbed Site

Our model simulations were made on a single tropical forest located in the San Lorenzo Protected Area, Panama (9°16′51.71″ N, 79°58′28.27″ W, elevation 25 m). The Smithsonian Tropical Research Institute maintains a canopy-access crane that provides access to the forest canopy and allowed us to compare our simulations with previous measurements (Wu et al., 2020). The site is characterized as a moist tropical forest, with mean annual temperature of 26 °C, with only small seasonal variation. The mean annual precipitation is 3300 mm, 90 % of this precipitation falls during the wet season (May-December). More details about the site can be found in Wright et al. (2003).

For our study, we conducted all model simulations using the FATES model coupled with the CLM version 5.0.34 (CLM5). For all simulations, we initialized the FATES model using real-world forest inventory data (Condit et al., 2009) to better facilitate a comparison with field measurements (see Sect. 2.4) by matching the internal cohort structure (similar height and functional types) with that observed in inventory data. Inventory data from the most recent census in the year of 1999 were used as the initial state for the simulations.

2.3 Sensitivity simulations of FATES with synthetic forcing

The MED and BWB stomatal conductance models differ in the representation of atmospheric dryness as well as the stomatal slope parameter (g_1). To isolate the influence of structural and parametric differences on FATES simulations using the MED and BWB stomatal models, we employed three model ensemble simulations, BWB, MED-default and MED-B, and parameterization associated with a broad-leaved evergreen tropical tree (BET) PFT.

For the BWB configuration we used the BWB model with a default g_1 value of 8 (unitless) for the BET PFT in FATES. In our MED-default setup, the MED model was parameterized with g_1 set to 4.1 kPa$^{0.5}$ to match the best estimate from Lin et al. (2015). To constrain the model difference to structural difference we also ran FATES with the MED model with a g_1 value that was harmonized with the BWB model in FATES, which was abbreviated as MED-B. Here, we assumed g_1 for BWB (g_{1b}) = 8, air temperature = 25 ℃ and H = 0.8 as in Franks et al. (2017) in Eq. (4) to obtain a BWB-equivalent g_1 = 2.39 kPa$^{0.5}$ in the MED-B simulation (g_{1m}). For all simulations, the intercept parameter (g_0) was fixed at 1000 μmol m^{-2} s^{-1}.

$$g_{1b} = \frac{1.6}{H}\left(1 + \frac{g_{1m}}{\sqrt{D_s}}\right), \tag{4}$$

Following model initialization, the model was run with synthetic climate forcing data. Our synthetic climate forcing, "VPD", "T_{air}", "Radiation", and "CO_2", represented the scenarios of a linear increase in hourly air vapor pressure deficit (VPD_{air}), air temperature, photosynthetically active radiation (PAR), and atmospheric CO_2 concentration, respectively, while other climate forcing data were kept as constant. The details for these scenarios were listed in Table 2. In addition, we set the precipitation to 1.47×10^{-5} mm/s, surface pressure to 99626 Pa, wind speed to 4.8 m/s, and longwave radiation to 407.4 W/m^2 for all these scenarios, which represent annual average conditions at our field site. To keep the temperature changing whilst other variables remained constant in the T_{air} scenario, given the physical dependence of saturated water vapor on air temperature (Ficklin and Novick, 2017), we had to adjust the specific humidity, which is a model input variable, together with air temperature to keep the VPD fixed at 1 kPa for the Medlyn-type simulations (MED-default and MED-B). For the T_{air} scenario in the BWB model, the relative humidity (H) was kept as 80 % as H rather than VPD was used in the BWB model (Franks et al., 2017). We then studied the responses of g_{sw}, net photosynthesis (A_{net}), gross primary productivity (GPP), evapotranspiration (ET), and number of plants per hectare (nplant) to these drivers for the top layer (averaged across sunlit and shaded leaves) of the canopy.

Table 2. Scenario setting for the sensitivity simulations

Scenario	VPD_{air} (kPa)	Air temperature (°C)	PAR (μmol m^{-2}s^{-1})	CO_2 (ppm)
VPD	0-2.5	25	1500	400
T_{air}	1	5-50	1500	400
Radiation	1	25	0-2000	400
CO_2	1	25	1500	100-1000

2.4 Evaluation of FATES against in situ measurements

We compared the modeled diurnal g_{sw} and A_{net} of upper canopy layers with measured values (Wu et al., 2020). The data were collected at the San Lorenzo field site at monthly intervals across the dry season and the beginning of the wet season during a strong ENSO year 2016. The g_{sw} and A_{net} of top of canopy leaves of eight species were measured across four months starting in February 2016 and ending in May 2016. Measurements of g_{sw} and A_{net} were performed with a LICOR 6400 where the conditions of light, humidity, CO_2 concentration, and temperature surrounding the leaves were fixed to the ambient conditions. Using this dataset, the g_1 values of the BWB and MED models were estimated for each species (see Table 2 in Wu et al., 2020). We used those estimations to parametrize the g_{sw} model in FATES and we used their g_{sw} and A_{net} measurements to compare with FATES simulation results. It should be noted that the g_1 values we used were varied between 4.43 to 8.3 for the BWB model, and between 1.14 kPa$^{0.5}$ and 2.85 kPa$^{0.5}$ for the MED model, both values were lower than the defaults for evergreen tropical trees in both of the models, as discussed in Wu et al. (2020). An ensemble of simulations with varying measured species-specific g_1 values were carried out to evaluate the impact of stomatal slope parameterization on FATES simulated g_{sw} and A_{net}. In addition, V_{cmax} at 25 °C was set to 63 μmol m^{-2} s^{-1} based on the *A-Ci* curves measured at the same time during the campaigns. Other parameters such as J_{max} and leaf dark respiration rate (R_{dark}) at 25 °C were directly calculated by FATES based on their relationship with V_{cmax} or leaf nitrogen content.

For our simulations, we used the observed hourly weather data including precipitation, air temperature, and humidity from the PA-SLZ meteorological station (Faybishenko et al., 2019) as the atmospheric forcing data to drive the FATES simulations. Atmospheric CO_2 concentration was set to a background level of 403.3 ppm based on data from the NOAA's Mauna Loa observatory, which is also very close to the chamber CO_2 concentration.

2.5 Drought effects on physiological parameters

In FATES, a soil water stress factor (β) is used to adjust g_0 and V_{cmax} in the original form of the BWB model (Bonan et al., 2011). For the MED approach we implemented, we also applied the β factor in the same manner as the default setting (Sect. 2.1). However, to the best of our knowledge, this relevance of β factor has not been rigorously tested for tropical ecosystems, in comparison with measured g_{sw} and A_{net}. We therefore explored whether this formulation of β factor accurately represents observed physiological responses to soil water stress, and whether the stress factor should also be applied to the stomatal slope parameter (g_1) for both the BWB and MED models. To test this, we designed model simulations (Table 3) to assess how the inclusion of the β factor modifies modeled g_{sw} and A_{net} and the comparison with the measurements. In these simulations, g_1 and V_{cmax} were set as the averages across all the species measured for the BET PFT.

Table 3. Model simulations for studying soil water stress effects on physiological parameters in FATES

Experiment	g_0	g_1	V_{cmax}
Default	on	off	on
Exp 1	on	off	off
Exp 2	on	on	on
Exp 3	on	on	off
Exp 4	off	off	off

on = soil water stress effect is turned on, off = soil water stress effect is turned off in the simulation.

3 Results

3.1 Model responses to climatic drivers

The responses of g_{sw} and A_{net} to synthetic climatic drivers as modeled by the BWB (BWB model with default g_1) and MED-default (MED model with default g_1) simulations had similar shapes (Fig. 1&2, blue and black lines). The MED-default yielded markedly higher g_{sw} than BWB for all climatic drivers considered with an average difference of 75 % (Fig. 1). The MED-default simulation also resulted in higher estimations of A_{net} but the increase over the BWB simulation was much smaller (around 15 % on average) than the increase in g_{sw} (Fig. 2). When the VPD increased above 1.5 kPa, the two models showed a strong additional divergence. At a VPD of 2.0 kPa projected g_{sw} and A_{net} from the BWB simulation was 316 % and 86 % lower than projections from the MED-default simulation (Fig. 1c&2c).

The particularly large divergence between the BWB and the MED-default simulations can be explained by a combination of parametric and structural differences. Comparison of the MED-B (where we used a parameterization equivalent to that of BWB in the MED model) with the BWB limited potential model deviation to structural difference between the two approaches. Both simulations yielded similar responses of g_{sw} and A_{net} to radiation, temperature, and CO_2 (Figs.1a,1b,1d, 2a, 2b&2d, blue and red lines), demonstrating that the differences between the BWB and MED-default settings were attributable to the difference in parameterization associated with g_1. With harmonized parameterization of g_1 the divergence between the two models above a VPD of 1.5 kPa was still readily apparent (Fig. 1c&2c, blue and red lines). The MED-B simulation showed a slight decrease of g_{sw} with high VPD while g_{sw} modeled with the BWB simulation decreased more markedly when VPD was beyond 1.5 kPa. At 2.0 kPa the BWB simulation projected g_{sw} and A_{net} that were 126 % and 53 % lower than the MED-B simulation. For the temperature response of g_{sw}, BWB and MED-B were very similar although BWB had slightly higher g_{sw} values than MED-B (Fig. 1d, blue and red lines).

In contrast to the g_{sw} response, the differences between BWB and MED-default were smaller for A_{net}, except when VPD was above 1.5 kPa (Fig. 2, blue and black lines). The use of measured g_1 for the MED model (MED-default) did not markedly change the magnitude of A_{net} compared with MED-B (Fig. 2, red and black lines), suggesting that A_{net} is not as sensitive as g_{sw} to the different parameterization of g_1 for these two models. When we explored the ecosystem-scale responses (Fig. 3&4), we found that the patterns of ET and GPP mirrored the leaf-level responses described above when using our synthetic climatic drivers. The difference between BWB and MED-B was also apparent when VPD was above 1.5 kPa (Fig. 3c&4c, blue and red lines).

To rule out that these differences were related to changes in underlying plant community structure, we looked for any significant changes in cohort density (number of plants per hectare). Our results showed that there was no significant change (Fig. S1) thus these ecosystem-scale responses were primarily related to changes in underlying leaf-level physiology.

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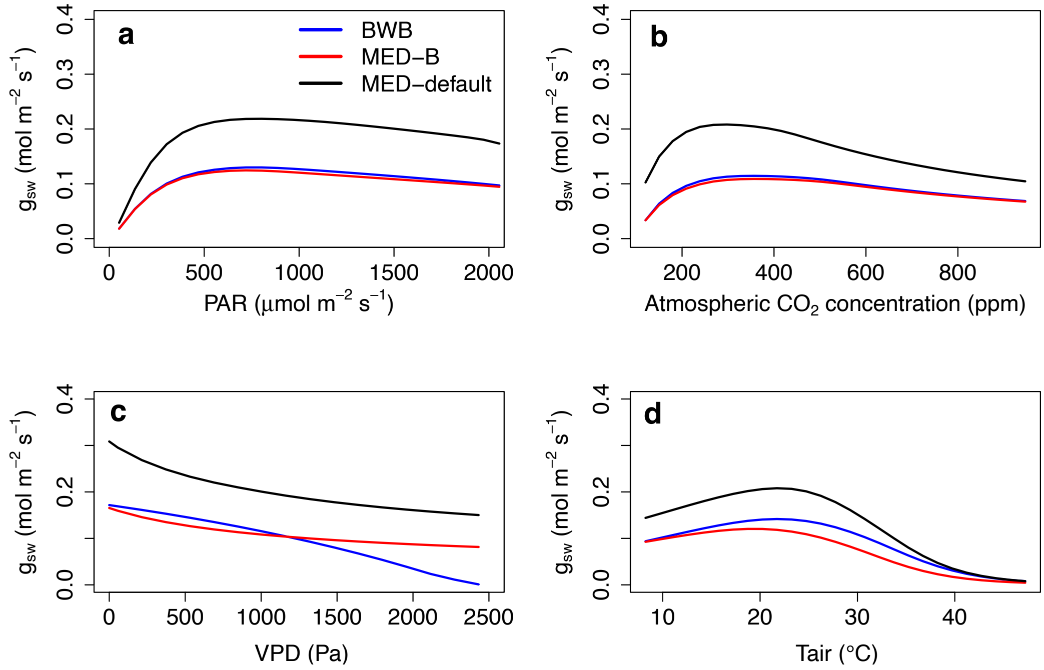

220 **Fig. 1. The responses of stomatal conductance (g_{sw}) to scenarios (a) Radiation, (b) CO_2, (c) VPD, and (d) T_{air} for the three model setups: BWB (blue), MED-B (red), and MED-default (black).**

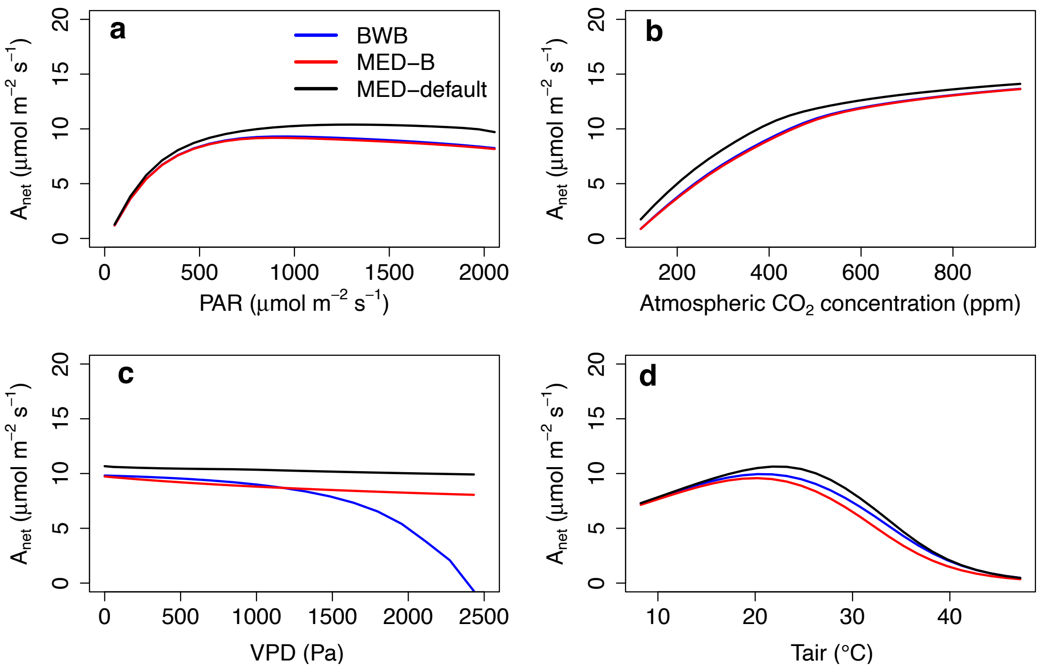

Fig. 2. The responses of net photosynthesis (A_{net}) to scenarios (a) Radiation, (b) CO$_2$, (c) VPD, and (d) T$_{air}$ for the three model setups: BWB (blue), MED-B (red), and MED-default (black).

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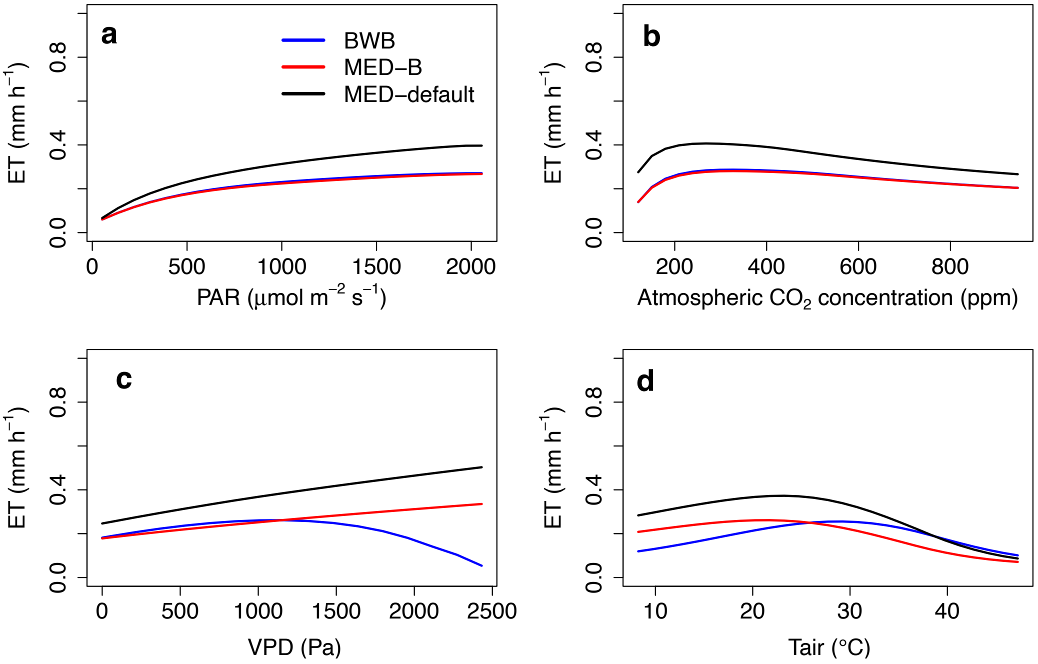

Fig. 3. The responses of evapotranspiration (ET) to scenarios (a) Radiation, (b) CO_2, (c) VPD, and (d) T_{air} for the three model setups: BWB (blue), MED-B (red), and MED-default (black).

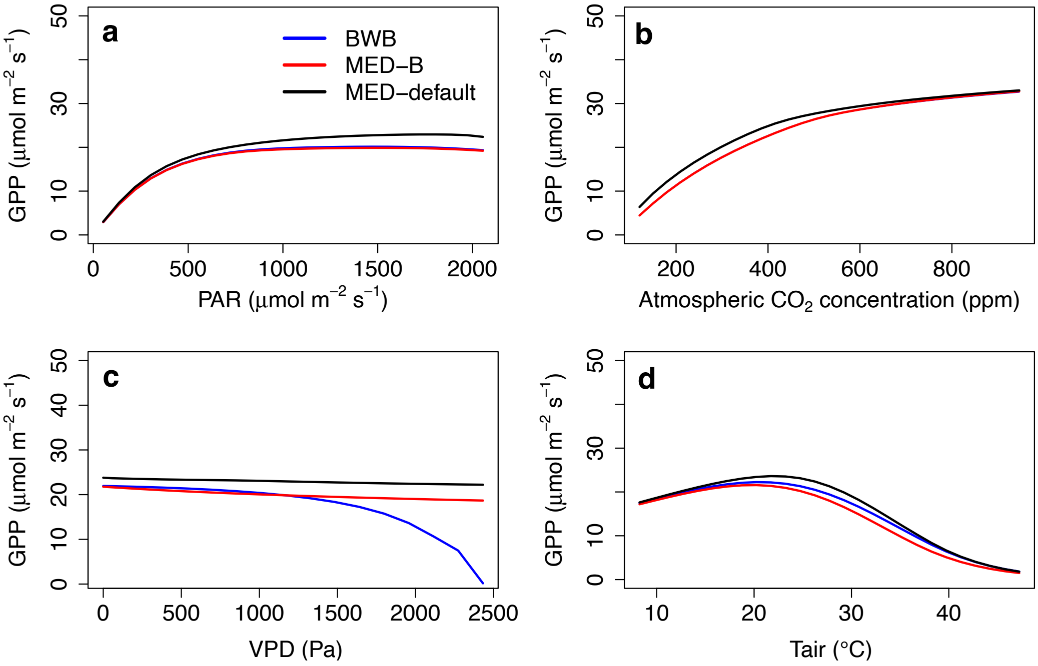

Fig. 4. The responses of gross primary productivity (GPP) to scenarios (a) Radiation, (b) CO₂, (c) VPD, and (d) T_{air} for the three model setups: BWB (blue), MED-B (red), and MED-default (black).

3.2 Model evaluation against field measurements

Before comparing the results of the BWB and MED model representations within FATES against field measurements, we first evaluated the consistency of the FATES climate forcing data with those correspondingly measured by our gas exchange instruments during the measurement campaigns. Given that the climate forcing data used in FATES were derived from the site meteorological measurements, we anticipated that the two conditions would be comparable. We found that for photosynthetically active radiation, relative humidity, and CO_2 concentration, the atmospheric and leaf chamber conditions at time of measurements were in reasonably close agreement, while the in situ measured air temperature and VPD were higher than climate data in all months (Fig. 5a, 6a, 7a &8a).

To account for measurement and natural variability of g_1 across different species, we set up and ran a series of FATES simulations driven by meteorological forcing data with different g_1 values. These experiments showed that FATES g_{sw} was sensitive to different g_1 values for both model formulations (Fig. 5-8). The MED model ensemble results of A_{net} and g_{sw} with different g_1 values, represented as the envelopes in Fig. 5b and Fig. 5c, generally overlapped with those from the BWB model, with comparable averages. However, we also found that the MED model showed more abrupt changes in g_{sw} than BWB model under certain conditions in February and May. These abrupt changes

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corresponded with periods of very low VPD (0.1 kPa). Compared with field measurements, both models captured the diurnal patterns well (Fig. S2) but tended to underestimate A_{net} and g_{sw} significantly in the month of April by about 30 %, at the peak of the dry season (Fig. 7).

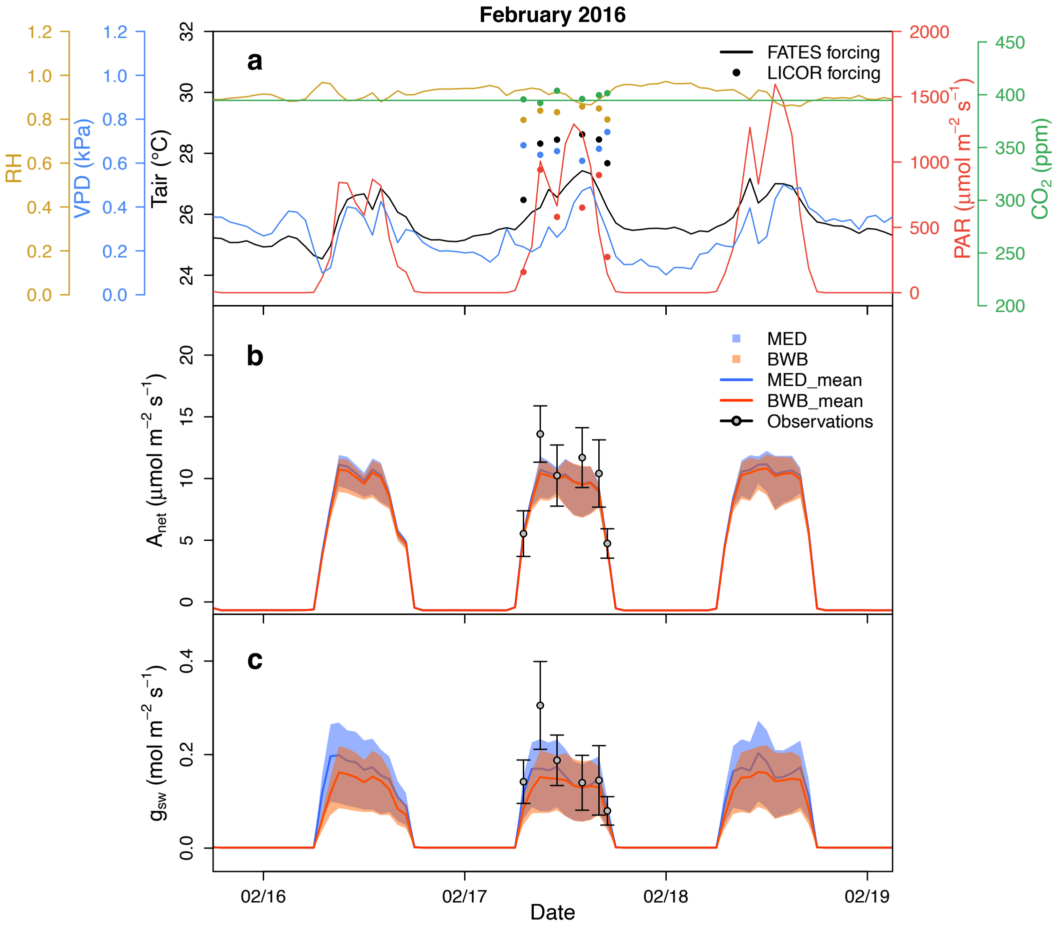

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Fig. 5. (a) Diurnal change in climate factors during measurement periods in February, (b) model-data comparison of net photosynthesis rate (A_{net}) in February, (c) model-data comparison of stomatal conductance (g_{sw}) in February. In panel (a), lines and filled points represent climate data used in FATES and in situ measurements, respectively. Different colors are for different types, black for temperature, red for PAR, blue for VPD, green for atmospheric CO_2 concentration, and gold for relative humidity. In panel (b) and panel (c), shading represents range of FATES model ensemble results with different measured g_1 values for different species, while lines represent the averages of the ensemble results. Blue shading and lines are for results from the MED model, and red for the BWB model. Gray filled circles for the measured data represent averages across species. Black error bars for the measured data represent the 95 % CI across species. 265

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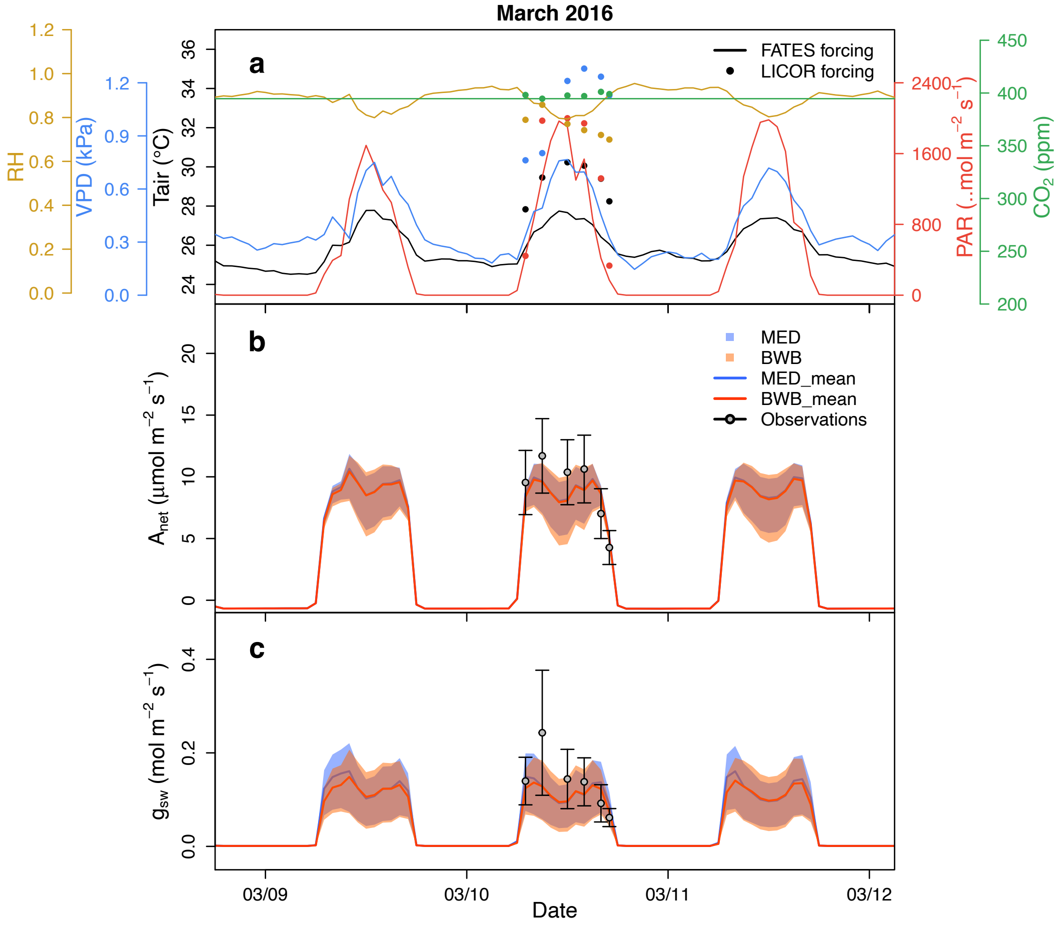

Fig. 6. Similar to Fig. 5, but for March.

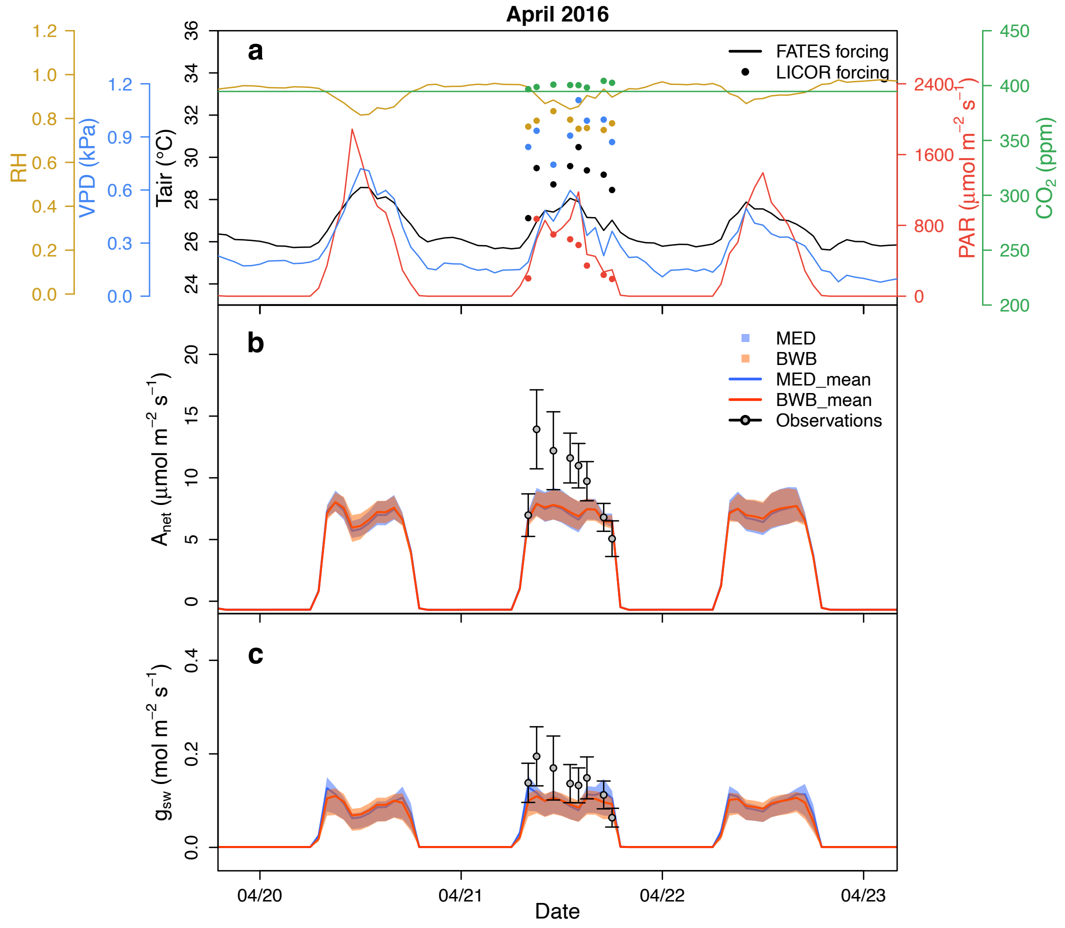

Fig. 7. Similar to Fig. 5, but for April.

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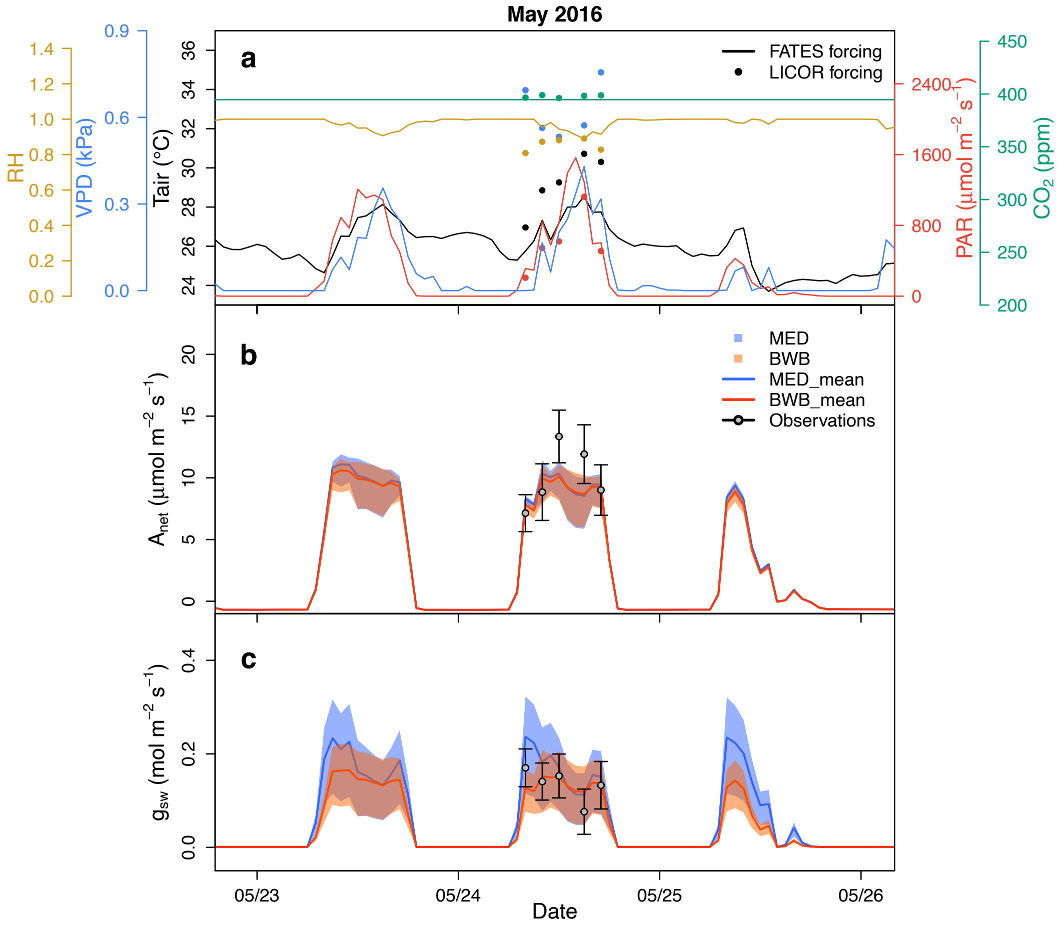

Fig. 8. Similar to Fig. 5, but for May.

3.3 Water stress factor on physiological parameters

By April 2016 soil moisture content (averaged over all the soil layers) predicted by FATES reached an annual minimum (0.7) (Fig. S3). FATES also underestimated g_{sw} and A_{net} by the largest margin in April, when compared to our field measurements (Fig. 7). To explore this further, we conducted additional experiments focused to evaluate the use of the β factor to modify g_0, g_1, and V_{cmax}. For the month of April in 2016, we compared a range of different model simulation experiments where the β factor was applied in different combinations to g_0, g_1, and V_{cmax} (Table 3, Fig. 9). The results from Exp. 1 and Exp. 4 showed high overlap, indicating that considering the β effect on g_0 does not influence modeled carbon and water fluxes. However, when applied to V_{cmax} the β factor reduced g_{sw} and A_{net} by 15 %-20 % (Exp. 2 vs. Exp. 3, Fig. 9). Applying the β factor to g_1 also reduced g_{sw} and A_{net} by 10 %-50 % (Exp. 1 vs. Exp. 3, Fig. 9). Unsurprisingly, comparing model results with β applied to all or no parameters showed the largest differences (30 %-80 %) (Exp. 2 vs. Exp. 4, Fig. 9). Default simulations with the β factor on g_0 and V_{cmax} underestimated A_{net} by 29 %, and g_{sw} by 26 % for the MED model. However, the results from simulations with no β

effects or with β only applied on g_0 (Exp. 1&4) corresponded best to the observations, in which A_{net} was only underestimated by 15 %, and g_{sw} by 9 % for the MED model (Fig. 9a&9b). There was also a significant improvement of performance when the β effects were removed from equations in the BWB model (Fig. 9c&9d).

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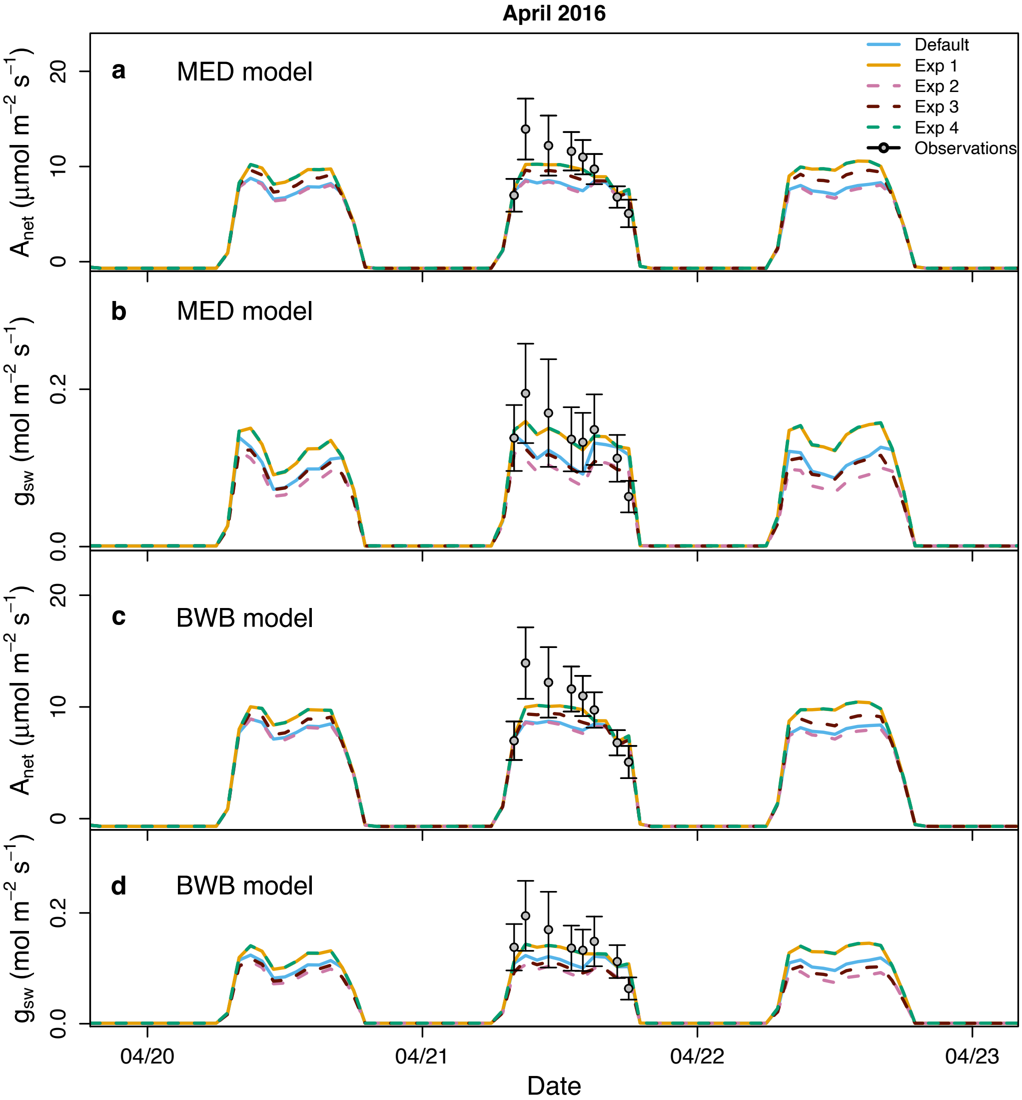

Fig. 9. Comparison of the diurnal changes of net photosynthesis (A_{net}) and stomatal conductance (g_{sw}) measurements in April for the (a&b) MED model and the (c&d) BWB model with different soil water stress effects on parameters in FATES against measurements (Exp. 1-4).

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4 Discussion

4.1 Advances in understanding of model difference

We implemented the MED stomatal model in FATES and compared model projections of CO_2 and water vapor exchange to the existing BWB formulation. The two models diverged considerably in the responses of both leaf-level (g_{sw} and A_{net}, Fig. 1&2) and canopy-level (GPP and ET, Fig. 3&4) fluxes to a wide range of light, air temperature, VPD, and CO_2 concentration with default stomatal slope parameter (g_1). When parameterization of g_1 was harmonized between the MED and BWB formulations, the difference was much lower in responses to varying light, temperature and CO_2 conditions but were markedly apparent at VPD above 1.5 kPa.

Our analysis of the general model responses against synthetic climate forcing presents some advantages over previous evaluations. First, some studies found different stomatal conductance models varied considerably in water-limited regions (Knauer et al., 2015; Morales et al., 2005), but were unable to attribute the difference to specific climate drivers as all factors, such as temperature and humidity are closely related (Galbraith et al., 2010; Rowland et al., 2015). In their recent experimental study of a tropical forest, Smith et al. (2020) found that stomatal response to VPD, rather than to temperature, is the primary mechanism for high-temperature photosynthetic declines in tropical forests by separating the temperature effect and VPD effect. This along with our findings highlighted the need to improve the representation of stomatal conductance responses to VPD in models. Second, most previous modeling studies relied on evaluating model performance against benchmarks such as eddy-covariance data and remote-sensing products (De Kauwe et al., 2015), which are limited to the current climate conditions and ecoregions. Therefore, it is not possible to test model behaviors under all possible climate change scenarios. Our studies solved the above issue by including simulations driven by a wide range of climate forcing. Third, the realism of leaf-level model responses within the whole CTSM-FATES model after we implemented a new module is easily detected and assessed. The response curves of modeled A_{net} are directly comparable to the leaf-level gas exchange measurements, such as light and CO_2 response curves and are therefore powerful diagnostic tools (Rogers et al., 2017). The g_{sw} response curves produced by the sensitivity simulations could also been assessed. The model results also gave some insights into how the leaf-level responses scale up to the ecosystem-level responses, which is more relevant to the ultimate fates of carbon and water in ecosystems. Fourth, by using the calibrated and default parameters to run the models, we were able to separate effects of model structure and parameterization on model differences.

As highlighted previously by Franks et al. (2017), the influence of parameterization dominates potential differences due to model choice, further emphasizing the need to develop robust approaches to estimate g_1 and understand covariance with environmental drivers, such as soil moisture availability, and other leaf traits that may facilitate the use of trait-trait or trait-environment relationships to enable model parameterization (De Kauwe et al., 2015; Héroult et al., 2013; Lin et al., 2015; Wu et al., 2020). The structural differences are attributable to the different representation of humidity in the BWB and MED models (i.e., H vs. VPD) and are consistent with the previous studies (Rogers et al., 2017; Knauer et al., 2015; Franks et al., 2017). This suggests that when implemented in a dynamic vegetation

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demography model (FATES) the choice of stomatal model only has a small effect on projections of leaf and canopy level CO_2 and water vapor fluxes under conditions of VPD below 1.5 kPa. Under higher VPD, higher g_{sw} values were simulated using the MED model compared with the BWB model and led to higher net photosynthesis, ET, and GPP. This suggests that the MED formulation would predict tropical evergreen broadleaf forests to be more resistant to extreme atmospheric drought than with the BWB formulation. As the global surface temperature is projected to increase, the VPD is also expected to increase (Ficklin and Novick, 2017; Yuan et al., 2019; Kolby Smith et al., 2016). Therefore, the difference between the two models under high VPD conditions will project radically different ecosystem carbon and water dynamics under future climate change scenarios.

4.2 Model responses under simulated water stress

Our field campaign, which occurred during the 2016 ENSO event, enables us to evaluate model performance under various climate conditions, including extreme drought. Overall, simulations made with FATES with both g_{sw} models captured the dynamics of measured upper canopy leaf-level fluxes well in moist days, which proves the utility of the current stomatal conductance models in LSMs for non-stress conditions.

However, at the peak of the dry season this underestimation was notable and resulted in part from application of a soil water stress (β) factor used to modify leaf physiology in response to reduced soil moisture content. In FATES, the β factor affects g_0 and V_{cmax} through an empirical modification. Experimental evidence about how physiological parameters change in response to soil water conditions is diverse. Some previous studies found g_1 was relatively stable under water stress (Gimeno et al., 2016; De La Motte et al., 2020; Xu and Baldocchi, 2003). Other studies found a range of responses of g_1 to drought across different plant species (Miner and Bauerle, 2017; Zhou et al., 2013). For g_0, it was reported to decrease under water stress (Miner and Bauerle, 2017; Misson et al., 2004), but also to show no response to drought (Barnard and Bauerle, 2013). Drought nearly universally lowered V_{cmax} in plants (Zhou et al., 2013). However, some argued that effects of mild and moderate droughts on apparent V_{cmax} were negligible (Aranda et al., 2012; Bota et al., 2004; Cano et al., 2013), others showed a range of responses resulting in a 10 %-25 % reduction in V_{cmax} (Galmés et al., 2007; Grassi and Magnani, 2005; Keenan et al., 2010; Limousin et al., 2010; Misson et al., 2010; Wilson et al., 2000; Zait and Schwartz, 2018). Despite these extensive experimental studies of β effects on plants' physiological parameters, understanding of the sensitivity and reality of β effects in models is still inadequate. In this study, we have conducted several model simulations to test the impacts of the β factor applied on g_0, g_1 or V_{cmax} on water and CO_2 fluxes in FATES. Our results showed that FATES was more sensitive to soil water stress with the β factor applied to either g_1 or V_{cmax}, but less sensitive when the β factor was applied to g_0 (Fig. 9). Overall, we found that the predictions of g_{sw} and A_{net} were closer to the measurements when the β factor was totally excluded from the model formulation. Two causes could explain this result: the β calculation is not accurate in this forest, or the modeled decrease in g_0, g_1 or V_{cmax} by the β factor is not representative of the plant's response to drought in this forest. A previous study by Bonan et al. (2014) also showed a strong underestimation of GPP under significant drought when using the same β effect in CLM4.5. To this end, recent efforts emerge including hydraulic approach and chemical signaling through abscisic acid (ABA) to enable a more mechanistic understanding of the plants' response to drought in LSMs (Verhoef and Egea, 2014; Rogers et al., 2017; Sperry and Love, 2015).

4.3 Implications for evaluating model performance

Our FATES sensitivity analysis simulations utilized synthetic meteorological conditions meant to allow us to isolate the impacts of individual abiotic drivers on model behavior. These included the main environmental drivers of air temperature (T_{air}), atmospheric CO_2 concentration, radiation, and humidity. Our method in keeping VPD in the air constant when studying model response to varying T_{air} by adjusting specific humidity concurrently is inspiring for other modelers. Our simulations also give some insights into the influence of leaf surface temperature (T_{leaf}). In most LSMs, T_{leaf} is the balance of environmental drivers and leaf biophysical activities, and it is one of the most important variables regulating leaf biochemical responses such as photosynthesis and respiration (Kumarathunge et al., 2019; Leuning, 2002). But as T_{leaf} is an emergent variable in FATES we could only control T_{air} rather than T_{leaf} in our sensitivity analysis simulations. In scenarios with changing radiation, although we have fixed T_{air}, T_{leaf} was also increasing (Fig. S4), which resulted in slight decreasing trends of g_{sw} and A_{net} in response to radiation as T_{leaf} exceeded the temperature optimum of g_{sw} and A_{net} (Fig. 1d& Fig. 2d). But the influence of T_{leaf} change was limited for other response curves (Fig. S4). As LSMs are developing with more and more new theories, testing the basic physiological responses, and identifying the major gaps compared with existing modules should be the first steps. We advocate that the sensitivity simulations with synthetic climate forcing represented in this study could be a routine test in the future model development efforts.

For the model evaluation against site-level measurements, we found it is necessary to check the consistency of climate forcing used in models and that measured by the instruments (Héroult et al., 2013). In our study, the in situ measured T_{air} and VPD were higher than those recorded by a nearby meteorological station (Fig. 5a, Fig. 6a, Fig. 7a & Fig. 8a). The mismatch is partially related to the challenge of matching leaf chamber conditions with atmospheric conditions, avoiding condensation in the leaf chamber, or the use of a pump to move air across the leaf surface during gas exchange measurements. The slight deviation of modeled g_{sw} and A_{net} against measurements when soil was relatively wet (measured in February, March, and May) can be partly attributed to the mismatch of T_{air} and VPD used in the model compared with the same in situ measurements. In this study we evaluated the inclusion of the MED model in FATES in a tropical forest, however future efforts could include evaluation at sites of different ecosystem types, and at regional and global scales for carbon and water cycles.

5 Conclusions

Implementing new plant physiological theories such as the optimal stomatal conductance model, into dynamic vegetation models is crucial to keep the models up to date and to enable the exploration of new behaviors and capacities to track ecosystem responses under continued global change. In this study, we added the optimality-based Medlyn model into the state-of-the-art dynamic vegetation model FATES as an alternative to the default Ball-Woodrow-Berry model and then tested model behaviors in response to key independent climate drivers. Our model evaluation demonstrated that the major difference between the two models was caused by the parameterization of the critical stomatal slope parameter (g_1). When parameters were harmonized, the potential for markedly different projections of water vapor and CO_2 fluxes between stomatal conductance models only occurred as VPD rose above 1.5 kPa. We also compared model performance with some measurements in an evergreen tropical forest. Modeled CO_2 and water vapor fluxes in the dry season of a drought year were similar between models and closely matched observations, except at the peak of the dry season when a soil moisture correction factor was used to adjust physiological parameters. After removing this adjustment, projections for both models improved. Our study shows that the parameterization of g_1 and the application of the correction factor associated with decreasing soil moisture content are the key targets for improving model representation of CO_2 and water fluxes in tropical forests. In addition, observational datasets collected at high VPD (>1.5 kPa) are needed to evaluate model projections of gas exchange in tropical forests under global change scenarios that include increasing VPD.

Code availability

The FATES model is available at https://github.com/NGEET/fates (https://doi.org/10.5281/zenodo.3825474, FATES Development Team, 2020b). The specific FATES version used in this study is the one that merged the Medlyn model with git commit "9a4627a" and the version corresponds to tag "sci.1.37.0_api.11.2.0" (https://doi.org/10.5281/zenodo.5851984, FATES Development Team, 2020a). FATES was run here within CLM5. The latest release version of CLM5 is available at https://github.com/ESCOMP/ctsm (https://doi.org/10.5281/zenodo.3779821, CTSM Development Team, 2020), which is also the version used in this study. Scripts to run all the model experiments, create synthetic climate forcing and analyze model outputs are available at https://github.com/Qianyuxuan/Scripts_for_papers/tree/main/Medlyn_model (https://doi.org/10.5281/zenodo.5854740, Li and Serbin, 2022).

Author contributions

QL, AR, and SS designed the simulations and QL carried them out. QL, AR, SS, and JL analyzed the results. QL prepared the manuscript with contributions from all co-authors.

Competing interests

The authors declare that they have no conflict of interest.

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