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Observed nighttime conductance alters modeled global hydrology and carbon budgets

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The terrestrial biosphere regulates climate through carbon, water, and energy exchanges with the atmosphere. Land surface models estimate plant transpiration, which is actively regulated by stomatal pores, and provide projections essential for understanding Earth's carbon and water resources. Empirical evidence from 204 species suggests that significant amounts of water are lost through leaves at night, though land surface models typically reduce stomatal conductance to nearly zero at night. Here, we apply observed nighttime stomatal conductance values to a global land surface model, to better constrain carbon and water budgets. We find that our modifications increase transpiration up to 5 % globally, reduce modeled available soil moisture by up to 50 % in semi-arid regions, and increase the importance of the land surface on modulating energy fluxes. Carbon gain declines up to ~ 4 % globally and > 25 % in semi-arid regions. We advocate for realistic constraints of minimum stomatal conductance in future climate simulations, and widespread field observations to improve parameterizations.

1 Introduction

Terrestrial plants must balance their need to obtain CO_2 with the risk of desiccation if transpiration continues unchecked. Higher plants evolved stomatal pores to control the exchange of water and carbon between the leaf interior and the atmosphere (Hetherington and Woodward, 2003). Stomatal function, thus, is the dominant control over terrestrial fluxes of water and carbon. Most large-scale land-surface models use an empirical representation of stomatal conductance (g_s), similar to the Ball–Woodrow–Berry (BWB) model (Ball, 1988; Ball et al., 1987; Collatz et al., 1991; Leuning, 1995; Medlyn et al., 2011; Sellers et al., 1996), to calculate plant gas exchange. The BWB model is linear, with two constants, the intercept (g_o) and slope (g_1), and estimates g_s from the rate of CO_2 assimilation (A), atmospheric humidity (h_r), and internal leaf CO_2 concentration. The original BWB model parameters were fitted to observations of leaf

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gas exchange for ten plant species, with different g_o values for each species, ranging from -310 to $130 \text{ mmol m}^{-2} \text{ s}^{-1}$ (Ball, 1988). Many land surface models, however, use only two g_o values, (10 and $40 \text{ mmol m}^{-2} \text{ s}^{-1}$ for C_3 plants and C_4 plants, respectively; Collatz et al., 1991; Oleson et al., 2013; Sellers et al., 1996). Conductance during the night (and whenever A is 0) is thus represented using g_o . Recent advances in our ability to observe nighttime stomatal conductance (Caird et al., 2007; Phillips et al., 2010), $g_{s,n}$, illustrate that values are often larger in the field than the BWB predicts.

A comprehensive database (see Table S1 in the Supplement) of 204 observed $g_{s,n}$ values illustrates that the minimum BWB g_s values (equivalent to g_o) used in most land-surface models starkly differ with observed mean and median $g_{s,n}$ values. The available data for $g_{s,n}$ range from 0 – $450 \text{ mmol m}^{-2} \text{ s}^{-1}$ with an overall mean of $78 \text{ mmol m}^{-2} \text{ s}^{-1}$ (excluding hemi-parasites and CAM plants, which were omitted from model testing). Observations of $g_{s,n}$ are, on average, ten times higher in broadleaf tropical deciduous species (Table 1; $129 \text{ mmol m}^{-2} \text{ s}^{-1}$) and seven times higher in temperate broadleaf deciduous trees ($73 \text{ mmol m}^{-2} \text{ s}^{-1}$) compared to the $10 \text{ mmol m}^{-2} \text{ s}^{-1}$ used in many land-surface models. Potential benefits of a high $g_{s,n}$ might include the transport of nutrients (Dios et al., 2013; Scholz et al., 2007; Zeppel et al., 2014) or processes related to embolism repair, but these ideas remain untested. Nonetheless, the discrepancy between parameterized g_o and observed $g_{s,n}$ serves as motivation to investigate the response of the land surface to more realistic minimum g_s values.

Field measurements of $g_{s,n}$ have never before been incorporated into a global land surface model, despite the possible impacts on surface hydrology, ecosystem carbon gain, and land–atmosphere feedbacks. We use a global land-surface model, the Community Land Model (CLM) version 4.5, forced with a data atmosphere and driven with observed leaf area indices (CLM4.5SP), to test the sensitivity of the land surface to using realistic minimum g_s from observed $g_{s,n}$, averaged by plant functional type (PFT; Table 1). Since the BWB approach is primarily intended to predict daytime stomatal behavior, application of $g_{s,n}$ in a global model is unclear. We therefore test three methodologies for implementing observed $g_{s,n}$: (1) modifying the BWB intercept (g_o), (2) set-

ting a nighttime threshold value, and (3) setting a minimum threshold value. We anticipate that implementing observed $g_{s,n}$ values will increase plant transpiration, altering carbon and water budgets on regional and global scales.

2 Methods

2.1 Modeling

This study used the Community Land Model version 4.5 with prescribed leaf area indices (CLM4.5SP; originally described by Lawrence et al., 2011, technical details updated by Oleson et al., 2013) to test the impact of changing the minimum stomatal conductance on simulated global water and carbon cycles. The CLM4.5SP simulations were run with CRU-NCEP climate forcing data (combines Climate Research Unit (CRU) TS 3.2 monthly climatology with National Oceanic and Atmospheric Administration National Center for Environmental Prediction (NCEP) and NCAR 2.5° × 2.5° 6 hourly reanalysis; downloaded at: <http://dods.ipsl.jussieu.fr/igcmg/IGCM/BC/OOL/OL/CRU-NCEP/>), a historical atmospheric dataset that includes observed precipitation, temperature, downward solar radiation, surface wind speed, specific humidity, and air pressure from 1901 through 2010, and did not include the influences of nitrogen deposition, land use change, or changing CO₂ concentrations.

The CLM4.5SP uses the coupled Farquhar photosynthesis and BWB g_s models to simulate plant physiology (Bonan et al., 2011; Oleson et al., 2013). The BWB g_s is calculated based on the equation:

$$g_s = g_o + g_1(Ah_r/C_a) \quad (1)$$

where g_o and g_1 are empirical fitting parameters of the minimum g_s and the slope of the conductance–photosynthesis relationship, respectively; A is net assimilation rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$); h_r is the fractional humidity at the leaf surface (dimensionless), and C_a is the CO₂ concentration at the leaf surface ($\mu\text{mol mol}^{-1}$). When implemented in the

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unmodified CLM4.5SP, g_o is $10 \text{ mmol m}^{-2} \text{ s}^{-1}$ for all C_3 plants and $40 \text{ mmol m}^{-2} \text{ s}^{-1}$ for all C_4 plants, and is adjusted by a soil wetness factor every time-step.

Values of $g_{s,n}$ based on literature data (Table S1) are typically larger than the g_o values used in current implementations of the BWB model. The $g_{s,n}$ data, grouped and then averaged by PFT, were used to modify simulated minimum g_s using three methodologies. First, the Δg_o method replaced the BWB minimum conductance, g_o , value for each simulated PFT with the observed $g_{s,n}$ (Table 1), resulting in a uniform increase to g_s during both day and night (referred to as the Δg_o simulation; tested previously by Barnard and Bauerle, 2013). Second, the Δg_{night} method implemented the BWB model in its standard form (Eq. 1; the g_o and g_1 values are the same as the control), but included a minimum threshold that was applied at night, based on observed $g_{s,n}$ for each PFT, below which g_s could not fall. Third, the Δg_{min} method extended the observation-based threshold used in the Δg_{night} simulation to all times during the day or night, so that g_s never fell below the minimum threshold value found in Table 1. These three modified simulations were compared to a control simulation using the unmodified BWB formulation. Similar to the unmodified simulation that adjusts the g_o parameter based on a soil wetness scalar, the Δg_{night} and Δg_{min} modifications also adjusted the minimum g_s threshold by a soil wetness scalar that ranges from zero to one, at every time-step. Each simulation was run for 25 years with monthly output to determine the long-term impact of changing minimum conductance, and for one year with half-hourly output to determine the changes in diel patterns.

2.2 Data collection

Values of $g_{s,n}$ were obtained from field and glasshouse studies, using Scopus (www.scopus.com), with data for 204 records across 150 species and cultivars (Table S1). Records available were predominately for temperate plants (93 records) and crops (34), with more data available for broad-leaf plant types (89) than needle-leaf plants (16; Zeppel et al., 2014).

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3 Results and discussion

3.1 Implementation of $g_{s,n}$

Incorporating observed minimum constraints on g_s in all modified simulations increased g_s and transpiration compared to the control simulation, illustrated in Fig. 1 for a highly impacted semi-arid location in Ethiopia (see Fig. S1 in the Supplement for other regions). The large variability in the observational dataset causes substantial uncertainty in the simulations, masking the differences among parameterizations and highlighting the impact of $g_{s,n}$ on transpiration (Fig. S2 in the Supplement). The sensitivity of g_s and transpiration to the altered g_o parameter in the Δg_o simulation is large (Barnard and Bauerle, 2013; Bowden and Bauerle, 2008). Since the higher g_o is added to g_s in the BWB calculation at every model time step (see Eq. 1), altering g_o increases transpiration throughout the entire diel cycle, and produces changes in the daytime evaporative flux that are irrelevant to observations of $g_{s,n}$. We consider that uniformly adjusting the g_o parameter does not represent the correct implementation of observed $g_{s,n}$ values.

If g_o cannot be equated to plant minimum g_s , this raises the possibility of whether g_o has a theoretical interpretation beyond an empirical fitting parameter. It is possible that g_o is equivalent to cuticular conductance (g_{cut}), or conductance that is not regulated by the stomatal guard cells (Caird et al., 2007), occurring during the day and night. Niyogi and Raman (1997) describe g_o as cuticular conductance, though there is no record of g_o being tested or described as g_{cut} previously. Studies that have quantified g_{cut} found that g_{cut} was a low proportion, $< 10\%$, of total g_s and less than measured $g_{s,n}$ (Caird et al., 2007; Zeppel et al., 2014). The values of g_o used in current implementations of the Ball–Berry model for C_3 plants ($10 \text{ mmol m}^{-2} \text{ s}^{-1}$) fall within the range of measured g_{cut} values (4 to $20 \text{ mmol m}^{-2} \text{ s}^{-1}$; Caird et al., 2007). Assuming g_o does have a theoretical function of representing g_{cut} , rather than $g_{s,n}$, incorporating an observed threshold of minimum g_s is necessary. Whether g_o functions theoretically as g_{cut} in the

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BWB model needs further evaluation, as adjusting simulated g_o has large impacts on canopy conductance and transpiration (Fig. 1; Barnard and Bauerle, 2013). Regardless, observed $g_{s,n}$ is larger than modeled g_o and functions differently, and therefore should be considered independently in model parameterizations.

The Δg_{\min} and Δg_{night} simulations represent the intended change in minimum g_s with greater fidelity, by limiting the minimum value without increasing g_s at every model time step. Interestingly, in restricting only nighttime conductance, the Δg_{night} simulation allows daytime g_s to decrease below the nighttime threshold during the dry season in semi-arid ecosystems (Fig. 1a). This occurs when A_n nears zero in shade or low humidity, causing g_s to fall to the default g_o . In contrast, the Δg_{\min} simulation restricts minimum g_s at all times, and therefore daytime values are never less than the water-adjusted $g_{s,n}$. This increases canopy-averaged daytime g_s compared to the unmodified simulation whenever daytime g_s values fall below the minimum threshold (Fig. 1a and c).

The data in Table S1 is a compilation of all available published $g_{s,n}$ data, and reports $g_{s,n}$ values for 204 distinct plants. Of these, only four plants exhibit higher daytime g_s than $g_{s,n}$, and two of those are Crassulacean acid metabolism (CAM) plants, which by definition open their stomata at night to gain carbon dioxide and close their stomata during the day, and were not used in our parameterization. These data suggest that $g_{s,n}$ is typically less than daytime g_s . Most data presented in Table S1 are average daytime and nighttime values under non-drought stressed conditions, and are likely only reported for leaves in sunlit canopy layers. Thus, these data do not elucidate whether, at any given time, daytime values might drop below the nighttime threshold, but only suggest that, on average, they do not.

In the context of the model simulations, low daytime g_s occurs any time that Ah_r/C is low. Thus, operationally, these are conditions which are poorly illuminated (in shade or at dawn/dusk and night), or when humidity is low. The CLM4.5SP contains a representation of the shaded canopy, which has lower g_s and often reaches the minimum daytime threshold (g_o in the unmodified, Δg_o , and Δg_{night} simulations; and $g_{s,n}$ in the

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Δg_{\min} simulation). The central issue in determining whether the Δg_{\min} or Δg_{night} simulation is a better representation of minimum g_s is whether, under the same conditions in the real world, daytime g_s might be lower than $g_{s,n}$. For example, if observational data support that daytime g_s is less than $g_{s,n}$ in shaded canopy layers, then the Δg_{night} simulation is a better parameterization. However, if observational data suggest that daytime g_s is consistently higher than $g_{s,n}$, then the Δg_{\min} simulation is a better parameterization. While observational data are not available to specifically answer this question, the available data (presented in Table S1) imply that daytime g_s is on average higher than $g_{s,n}$, supporting the Δg_{\min} parameterization.

The possible existence of a higher $g_{s,n}$ compared to daytime g_s raises an interesting question about the potential selective advantage for leaves with a high $g_{s,n}$. The scientific community does not fully understand the physiology of this plant function at present. It is hypothesized that high $g_{s,n}$ may provide a beneficial function to the plant, such as embolism repair or nutrient transport. Critically, it is not clear whether these potential functions are only relevant at night (and daytime g_s can be lower than $g_{s,n}$), or whether high $g_{s,n}$ is representative of a general strategy of higher overall minimum g_s . We are not aware of data that exist to support either possibility, and advocate for observations that will help determine the functional significance of $g_{s,n}$.

From a model or theoretical perspective, it is important to note that the reason that simulated g_s values are reduced to as low as $10 \text{ mmol m}^{-2} \text{ s}^{-1}$ (or lower, if down-regulated for water stress) is a function of the universal parameterization of all C_3 plants with that value of g_o . Given that it is unlikely that this value is universal for all plants, we consider that the large difference between the Δg_{\min} or Δg_{night} simulations is an artifact of the poorly constrained parameterization of the daytime BWB model.

It should be noted that all the minimum thresholds implemented in our simulations (Δg_o , Δg_{night} , and Δg_{\min}) are adjusted by a soil water scalar (β_{soil}). Therefore, the nighttime (Δg_{night}) and the minimum (Δg_{\min}) thresholds are altered according to the degree of soil moisture stress. When the daytime g_s value is lower than the g_{night} threshold in the Δg_{night} simulation (Fig. 1c), the g_{night} threshold is already down-regulated for water

stress. In this scenario, the daytime minimum g_s is less than the nighttime g_s when water stress is equivalent. Physiological theory suggests that this will only happen if the benefits of $g_{s,n}$ allow for higher nighttime than daytime water loss, though data are unavailable to elucidate this hypothesis.

Responses to dry soil conditions are mediated both through the minimum g_s values, and through the impact of soil moisture on photosynthetic capacity and leaf maintenance respiration, which are also multiplied by β_{soil} . Many of the impacts of our simulations result from feedbacks between higher transpiration rates resulting in faster depletion of soil moisture store, and therefore greater constraint on photosynthesis. These results are all emergent features of the model and should not be interpreted as direct results of the altered parameterization.

3.2 Global water and carbon

When averaged over 25 years, incorporating observed rates of $g_{s,n}$ increased transpiration losses up to 30 % in the Amazon, and > 30 % in some arid regions, in part due to the small absolute magnitude of available soil water (Fig. 2a–c). Semi-arid regions are primarily broad-leaf shrub and C_3 grass PFTs that have particularly high values of observed $g_{s,n}$ (Table 1), and have high nighttime vapor pressure deficits that interact with higher minimum g_s values, causing large nighttime transpiration rates. Using median rather than mean values caused only small (< 1.5 %) differences in transpiration (Figs. S3 and S4 in the Supplement). Though the magnitude of response is different depending on parameterization used, the increases in transpiration imply that current model estimates of plant water loss are underestimated in many regions.

Simulated higher transpiration resulting from higher minimum g_s also has ecosystem-scale ramifications for hydrology (McLaughlin et al., 2007). For example, the increased transpiration resulted in drier soils compared to the control simulation (Fig. 2g–i), with Δg_{min} causing > 40 % soil moisture decreases in semi-arid ecosystems like the Southwestern United States and much of Australia (> 10 % in Δg_{night}). Additionally, the Δg_{min} estimated changes to surface runoff are large in some regions,

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such as the 10–25 % decreases in the tropics (5–10 % in Δg_{night} ; Fig. 2d–f), suggesting that current runoff estimates may be too large. Hydrologic changes in soil moisture and runoff in response to increased g_s have previously been documented in catchments in southeastern United States (McLaughlin et al., 2007), and our results suggest that changes to stomatal conductance have similar consequences in CLM4.5SP simulations. Additionally, increasing minimum g_s caused gross primary productivity (GPP) to decrease (Fig. 3) by 10 to > 25 % in many semi-arid regions. These are regions where water availability already restricts GPP, and the decreases in soil moisture caused by higher transpiration likely impart even more drought-induced stomatal closure.

To more directly evaluate the potential influence of minimum g_s on the climate system, we calculate the change in terrestrial coupling to the atmosphere. The terrestrial coupling index (Dirmeyer, 2011) estimates the degree to which changes in soil moisture control surface energy fluxes to the atmosphere. This study uses root-zone soil moisture rather than soil moisture over spatially constant soil depth to highlight the direct impact of vegetation and minimum g_s on surface fluxes. Here we calculate the terrestrial coupling index during boreal summer months when warmer temperatures allow for the highest g_s rates. We find that the terrestrial coupling strength increases when using the Δg_{min} implementation, but is generally unchanged for Δg_{night} (Fig. 4), meaning root-zone soil moisture exerts a greater control on surface flux variability for Δg_{min} . This increased terrestrial coupling to the atmosphere largely mirrors the reductions in GPP and soil moisture in semi-arid ecosystems, and may reinforce climate extremes such as droughts or heat waves (Hirschi et al., 2011; Miralles et al., 2014).

3.3 Evaluating $g_{s,n}$

Evaluating the performance of the new $g_{s,n}$ parameterizations is challenging for numerous reasons. First, our model scales from leaf-level g_s and $g_{s,n}$ estimates to canopy transpiration. The best way of evaluating the model is to compare simulated and observed canopy transpiration because the model captures the average of an entire canopy, which is comprised of multiple plant functional types, rather than individual

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plant functional types. Incorporating realistic minimum g_s increases global evapotranspiration and decreases global runoff compared to globally-scaled observations, while estimates of GPP from all simulations fall within the range of global GPP estimates from observations (Table 2; Bonan et al., 2011, 2012; Li et al., 2011). However, these comparisons should be used with caution, since eddy covariance data used in estimating the GPP and evapotranspiration observations are susceptible to errors at night (Fisher et al., 2007; van Gorsel et al., 2008; Kirschbaum et al., 2007; Medlyn et al., 2005) due to a lack of sufficient canopy turbulence that precludes detection of nighttime transpiration using this measurement methodology, and are not useful for evaluating the changes in water fluxes tested in this study. Other data for evaluating model responses to minimum g_s on large spatial scales are not yet available.

A comparison of simulated canopy transpiration to transpiration calculated from sap flux data in Australia (Fig. 5) illustrates that a minimum g_s threshold improves transpiration estimates during the early part of the night, though simulated nighttime rates are still low. Sap flow is measured at the base of the tree, so there is typically a lag between when sap flow is measured and when the canopy transpires, and this lag is also notable in comparing observed sap flow with simulated estimates of transpiration. Estimating nighttime transpiration using this methodology is convoluted with the refilling of aboveground water stores depleted during the day, and thus is not directly comparable to our simulations. It should also be noted that the model does not have a semi-arid plant functional type, so semi-arid plants are typically represented in the model as deciduous plant functional types.

Given that our study focused only on one aspect of the g_s formulation within a land surface model, evaluating daytime g_s and other aspects of the BWB model function (i.e., photosynthetic drivers of daytime g_s , feedbacks to water availability, etc.) are all subject to pre-existing deficiencies in the representation of a host of other model processes. For example, there are only two values of the g_1 (slope) parameter in the BWB model, one for C_3 and one for C_4 plants (Sellers et al., 1996), and this parameter has not been modified or comprehensively evaluated within the context of the CLM4.5SP.

Indeed, the use of the BWB model at all is currently the subject of some debate (Bonan et al., 2014; De Kauwe et al., 2015). Further, daytime g_s is also dependent on the photosynthetic capacity, and observations of V_{cmax} and J_{max} (Bonan et al., 2011; Kattge and Knorr, 2007) indicate very wide ranges of plant functional type variation in these properties, also limiting our confidence that the globally averaged parameters used in the default model will lead to accurate g_s and transpiration at most locations. We choose not to focus on these and other parameters that effect daytime g_s , as it does not directly impact the representation of $g_{s,n}$, and is therefore beyond the scope of this paper.

4 Conclusion

The rate of minimum g_s estimated from the BWB model used in many global land surface models is typically smaller than observed $g_{s,n}$ (Barnard and Bauerle, 2013), as demonstrated in a review of 204 species (Zeppel et al., 2014). Including a minimum g_s threshold based on observations results in large simulated hydrologic changes, such as decreased soil moisture and runoff (Fig. 2), particularly in semi-arid regions where water availability already restricts growth. In addition to potentially increasing drought stress in sensitive regions, this has the impact of reducing plant growth (Fig. 3) and changing the modeled terrestrial coupling to the atmosphere (Fig. 4). While the balance of our arguments favors the Δg_{min} implementation of $g_{s,n}$, this study primarily illustrates the potential sensitivity of global simulations to minimum g_s considerations, and serves as motivation for additional field experiments, particularly in semi-arid areas, to discern better representations of low g_s conditions. To better understand the future of these sensitive ecosystems, widespread field observations, quantification of minimum daytime g_s , and a better understanding of the physiological causes and consequences of nighttime transpiration are necessary so that land surface models can robustly incorporate observations and theory.

Author contributions. D. L. Lombardozzi, M. J. B. Zeppel, and R. A. Fisher conceived the project. M. J. B. Zeppel assembled the $g_{s,n}$ datasets; D. L. Lombardozzi ran model simulations; and D. L. Lombardozzi and A. Tawfik analyzed model simulations, with guidance from R. A. Fisher. All authors contributed to writing the paper.

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Table 1. Old and new minimum stomatal conductance values used in CLM4.5SP. Units are $\text{mmol m}^{-2} \text{s}^{-1}$.

Plant Functional Type	Old Value	Mean New Value	Median New Value	Standard Deviation	<i>n</i>
temperate needle-leaf evergreen tree	10	16.896	10	20.80332642	12
boreal needle-leaf evergreen tree	10	8	8	NA	1
needle-leaf deciduous tree	10	35.367	35	6.457811807	3
tropical broadleaf evergreen tree	10	90.488	75.5	67.85015923	8
temperate broadleaf evergreen tree	10	34.017	27	28.2627804	25
tropical broadleaf deciduous tree	10	129	129	41.01219331	2
temperate broadleaf deciduous tree	10	72.637	41.66	83.52495039	22
boreal broadleaf deciduous tree	10	50	50	NA	1
broadleaf evergreen shrub	10	65.353	29	116.0616668	16
broadleaf deciduous shrub	10	129.644	60	145.5387501	9
c3 grass	10	157.988	161	67.31744598	24
C4 grass	40	93.933	48.5	125.5325881	6
crop	10	60.629	36.7	60.74543722	21
					150

New Value, Standard Deviation and *n* are based on data pooled from the literature.

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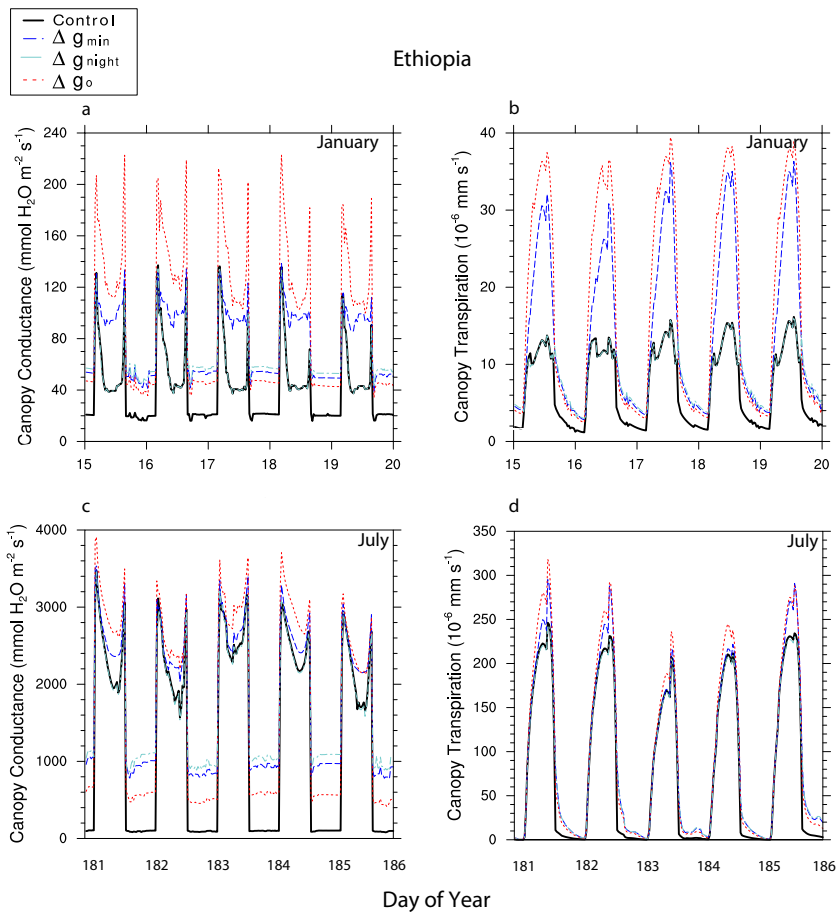
Table 2. Global values from CLM simulations and observations*.

Simulation	$g_{s,n}$ data used	GPP (PgCyr ⁻¹)	ET (10 ³ km ³ yr ⁻¹)	Runoff (10 ³ km ³ yr ⁻¹)
Control	n/a	157.83	65.6148	30.462
g_o	Mean	152.56	72.6555	24.2141
g_{night}	Mean	156.068	66.0926	30.0724
g_{min}	Mean	151.252	68.6843	27.8161
g_o	Median	153.641	71.5441	25.1739
g_{night}	Median	156.346	66.031	30.119
g_{min}	Median	152.385	67.8881	28.51
Observation		119–175	65.13	37.7521

* Global gross primary productivity (GPP), evapotranspiration (ET) and runoff values. Observed values presented in Bonan et al. (2011), Welp et al. (2011), and Lawrence et al. (2011).

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Figure 1. Diurnal time-series of canopy conductance (**a, c**) and transpiration (**b, d**) for Ethiopia over five days in mid-January (**a, b**) and mid-July (**c, d**). The control simulation (solid black line) had lower conductance and transpiration than the Δg_o simulation (dotted red line) and the Δg_{\min} simulation (dashed blue line). The Δg_{night} simulation (dot-dashed teal line) had higher nighttime conductance and transpiration than the control simulation, but similar daytime conductance and transpiration, allowing for daytime conductance to fall below the nighttime threshold. The Δg_o simulation added the observed $g_{s,n}$ values to the conductance calculation at every time, day or night, which is not theoretically aligned with the function of including observed $g_{s,n}$. As a result, the Δg_o simulation was eliminated from further analyses. Note that all minimum thresholds (g_o , g_{night} , and g_{\min}) were adjusted using a soil moisture scalar.

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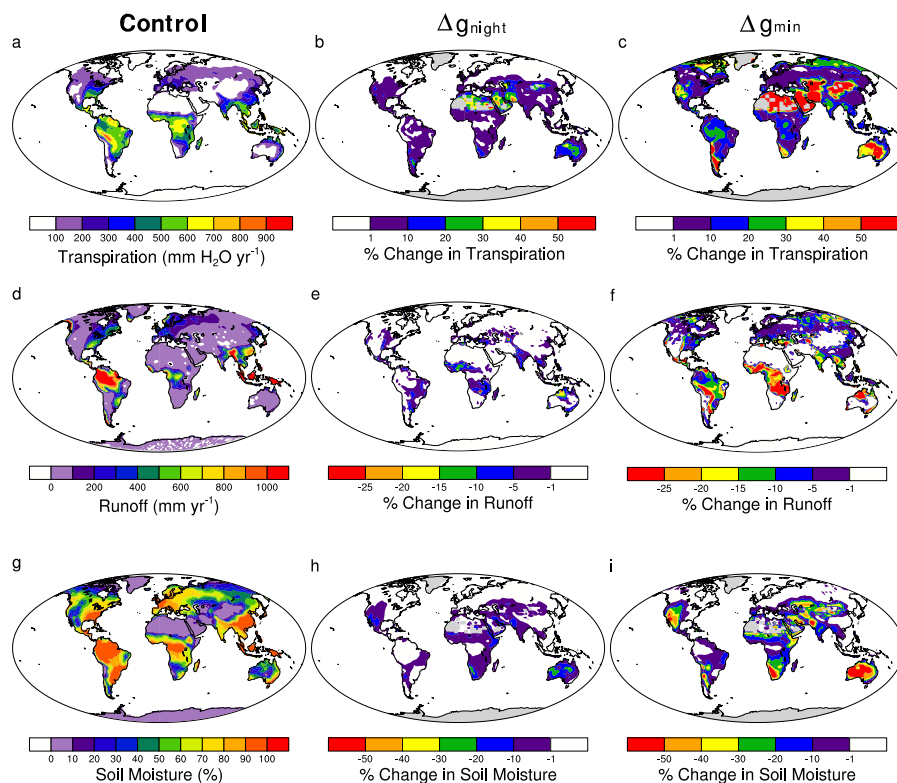


Figure 2. Simulated average transpiration (a), runoff (d), and soil moisture (g) for a control simulation; and percent change from control in transpiration (b, c), runoff (e, f), and soil moisture (h, i) after including a nighttime threshold (Δg_{night} ; b, e, h) or a minimum g_s threshold (Δg_{min} ; c, f, i) based on observational data. Note that both nighttime and minimum thresholds were adjusted based on a soil moisture scalar.

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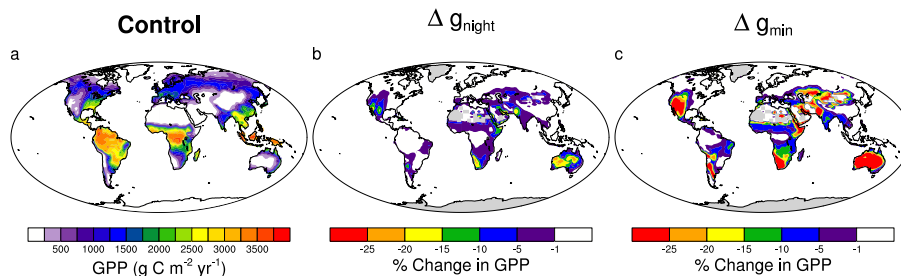


Figure 3. Average gross primary productivity (GPP) for a control simulation (**a**), and percent change from control (**b**, **c**) after including a nighttime threshold (Δg_{night} ; **b**) or a minimum g_s threshold (Δg_{min} ; **c**) based on observational data. Note that both nighttime and minimum thresholds were adjusted based on a soil moisture scalar.

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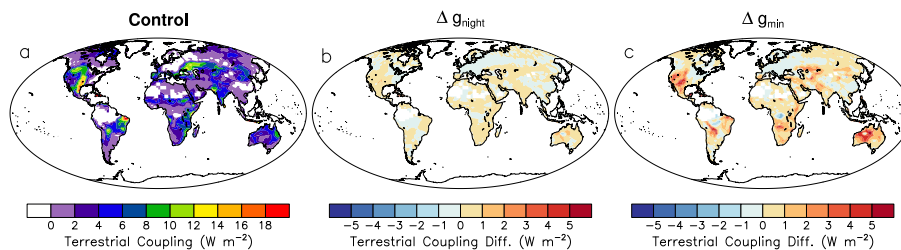


Figure 4. Terrestrial coupling for June–July–August for a control simulation (**a**), and the difference from control (**b**, **c**) after including a nighttime threshold (Δg_{night} ; **b**) or a minimum g_s threshold value (Δg_{min} ; **c**) based on observational data. Note that both nighttime and minimum thresholds were adjusted based on a soil moisture scalar.

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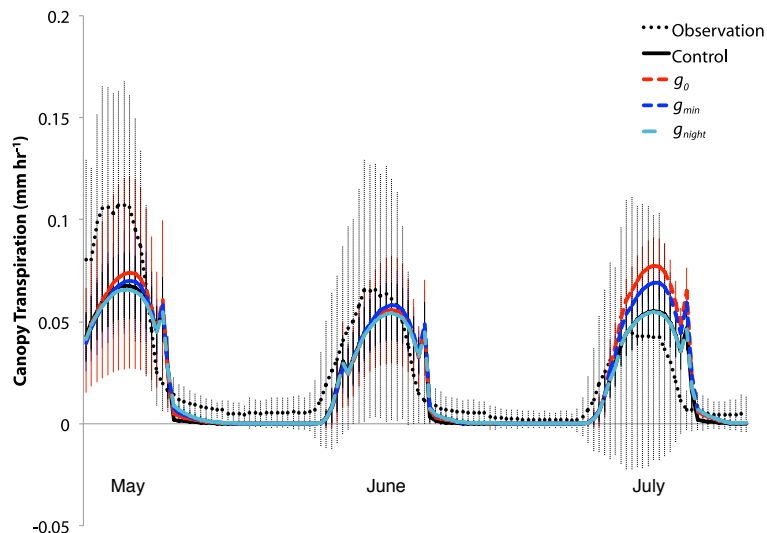


Figure 5. Average diel canopy transpiration for the months of May, June, and July in Castlereagh, Australia (observation, dotted black line), estimated from sap flux measurements of Red Gum and Iron Bark, the dominant tree species in the canopy. Average simulated canopy transpiration for the grid cell corresponding to Castlereagh, Australia for the control (unmodified; solid black line), Δg_o (Ball–Berry g_o parameter adjusted; red line), Δg_{night} (minimum nighttime threshold added; teal line), and Δg_{min} (minimum conductance threshold added; blue line) simulations. Error bars corresponding to the observations (dashed) and each simulation (solid) are colored accordingly, and are calculated as \pm one standard deviation from the mean. Note that the simulations use meteorological forcings from an atmospheric dataset (see Methods), not the local meteorology from when the measurements were collected (some meteorological data was collected at the site, but not all variables required by the model). The simulated grid cell covers a much larger area than the observational data collection site.

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