



Modelling climate
change responses in
tropical forests

L. Rowland et al.

Modelling climate change responses in tropical forests: similar productivity estimates across five models, but different mechanisms and responses

L. Rowland¹, A. Harper², B. O. Christoffersen^{1,3}, D. R. Galbraith⁴,
H. M. A. Imbuzeiro⁵, T. L. Powell⁶, C. Doughty⁷, N. M. Levine⁸, Y. Malhi⁷,
S. R. Saleska³, P. R. Moorcroft⁶, P. Meir^{1,9}, and M. Williams¹

¹School of GeoSciences, University of Edinburgh, Edinburgh, UK

²College of Engineering, Mathematics, and Physical Science, University of Exeter, Exeter, UK

³Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona, USA

⁴School of Geography, University of Leeds, Leeds, UK

⁵Grupo de Pesquisas em Interação Atmosfera–Biosfera, Universidade Federal de Viçosa, Minas Geras, Brazil

⁶Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts, USA

⁷Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



⁸Department of Biological Sciences, University of Southern California, Los Angeles, CA, USA

⁹Australian National University, Canberra, ACT 0200, Australia

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Correspondence to: L. Rowland (lucy.rowland@ed.ac.uk)

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Modelling climate change responses in tropical forests

L. Rowland et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Abstract

Accurately predicting the response of Amazonia to climate change is important for predicting changes across the globe. However, changes in multiple climatic factors simultaneously may result in complex non-linear responses, which are difficult to predict using vegetation models. Using leaf and canopy scale observations, this study evaluated the capability of five vegetation models (CLM3.5, ED2, JULES, SiB3, and SPA) to simulate the responses of canopy and leaf scale productivity to changes in temperature and drought in an Amazonian forest. The models did not agree as to whether gross primary productivity (GPP) was more sensitive to changes in temperature or precipitation. There was greater model–data consistency in the response of net ecosystem exchange to changes in temperature, than in the response to temperature of leaf area index (LAI), net photosynthesis (A_n) and stomatal conductance (g_s). Modelled canopy scale fluxes are calculated by scaling leaf scale fluxes to LAI, and therefore in this study similarities in modelled ecosystem scale responses to drought and temperature were the result of inconsistent leaf scale and LAI responses among models.

Across the models, the response of A_n to temperature was more closely linked to stomatal behaviour than biochemical processes. Consequently all the models predicted that GPP would be higher if tropical forests were 5 °C colder, closer to the model optima for g_s . There was however no model consistency in the response of the A_n – g_s relationship when temperature changes and drought were introduced simultaneously. The inconsistencies in the A_n – g_s relationships amongst models were caused by non-linear model responses induced by simultaneous drought and temperature change. To improve the reliability of simulations of the response of Amazonian rainforest to climate change the mechanistic underpinnings of vegetation models need more complete validation to improve accuracy and consistency in the scaling of processes from leaf to canopy.

GMDD

7, 7823–7859, 2014

Modelling climate change responses in tropical forests

L. Rowland et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



1 Introduction

Continuing increases in atmospheric CO₂ are likely to cause increases in temperature and changes in precipitation across Amazonia (Good et al., 2013; Jupp et al., 2010; Malhi et al., 2009; Marengo et al., 2012). However, significant uncertainty remains regarding the response of tropical forests to warming temperatures (Corlett, 2011; Reed et al., 2012; Wood et al., 2012) and altered precipitation (Meir et al., 2008; Meir and Woodward, 2010). Such uncertainties are propagated into models, resulting in substantial variability in modelled responses to changes in temperature and drought (Friedlingstein et al., 2006; Galbraith et al., 2010; Powell et al., 2013; Sitch et al., 2008). These responses need to be rigorously assessed to enable further improvement in our current capability to predict the impacts of climate change.

The ecosystem responses of models to multi-factor changes in climate can be difficult to interpret because of complex nonlinear responses (Zhou et al., 2008), which can vary substantially between vegetation models with different model structures. Previous modelling analyses have shown a greater sensitivity of carbon storage in Amazonian forests to increased temperature than reduced precipitation (Galbraith et al., 2010). However the compound effect of drought on temperature responses when simulating Amazonian forest (Luo et al., 2008), makes evaluating model responses to simultaneous changes in precipitation and temperature complex.

Concurrent changes in temperature and precipitation can cause a complex chain of positive and negative feedbacks (Fig. 1). Increased temperature and reduced precipitation can directly affect stomatal conductance (g_s) through increasing vapour pressure deficit (VPD), or indirectly affect g_s through reducing SWC (Fig. 1). g_s limits photosynthesis (A_n), and therefore gross primary productivity (GPP). However A_n can also be limited by changes in leaf biochemistry (V_{cmax} and J_{max} , Fig. 1). How A_n is limited by temperature increase is important as changes in leaf biochemistry at high temperatures are the result of permanent damage to proteins, whereas changes in g_s are less permanent, but result in changes in water use, and potentially water use efficiency.

GMDD

7, 7823–7859, 2014

Modelling climate change responses in tropical forests

L. Rowland et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Modelling climate change responses in tropical forests

L. Rowland et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Currently there is no consensus on how A_n will respond to temperature, some studies find a direct impact through leaf biochemistry (Doughty, 2011; Doughty and Goulden, 2008), and others an indirect effect initiated by changes in g_s , because of g_s limitation occurring at lower temperatures those required for protein damage (Lloyd and Farquhar, 2008). The lack of data for tropical trees means these responses remain poorly constrained, though drought and warming can be examined using limited field data from drought and warming experiments (da Costa et al., 2014; Nepstad et al., 2002) and from extreme events within the natural range of the climate (Marengo et al., 2012).

The response of vegetation models to temperature change or drought occurs through the aggregated changes in finer scale processes, for example at the leaf level. Correctly simulating the mechanisms at the leaf-scale is therefore important to maintain confidence in canopy-scale predictions. Leaf-scale responses in models are scaled using LAI to simulate the processes at the canopy scale, therefore inaccuracies in both leaf scale fluxes or how they are scaled can produce substantial errors in ecosystem scale fluxes (Bonan et al., 2012). Currently no model–data comparisons exist that allow for the evaluation of combined temperature and precipitation/drought sensitivity of ecosystem fluxes in relation to LAI and leaf scale processes in tropical forests. However if we are to identify accurately how to improve simulated responses of Amazonian forests to future climate change it is vital that model output is evaluated against data from the leaf to the canopy scale.

At the Tapajós national forest in north east Brazil, Doughty and Goulden (2008) collected data on the response of net ecosystem exchange (NEE) to change in atmospheric temperature and the response of A_n and g_s to short-term artificial leaf warming. Doughty and Goulden (2008) found reductions in forest productivity at air temperatures above 28 °C, which corresponds to significant reductions in A_n and g_s at leaf temperatures above 30–33 °C. They suggested that tropical forests may therefore already be close to a temperature threshold, beyond which productivity will decline.

Here we use the data published by Doughty and Goulden (2008) to evaluate the temperature responses within models at both the leaf and canopy scale and investigate how the model formulations might impact predicted responses to multiple climatic factors. This study is part of a wider model inter-comparison project which aims to explore how well vegetation models simulate drought in the eastern Amazon (Powell et al., 2013). In this study we evaluate: (1) how the forest productivity of five vegetation models (CLM3.5, ED2, JULES, SiB3, SPA) responds to changes in temperature, (2) what leaf scale processes drive canopy scale changes in productivity and (3) how both leaf and canopy scale temperature sensitivities are influenced by concurrent changes in precipitation at the Tapajós forest site in eastern Brazil. In all models we simulate first an ambient and then a 50 % reduction in the incoming precipitation during the wet season from 2000–2006 analogous to the imposed drought treatment, linked to a -5 , 0 , $+2$, $+4$, and $+6$ °C change to the ambient air temperature (T_{air}). These simulations cover a range of likely and possible increases in temperature for the Amazon region in the coming century (Christensen et al., 2007; Collins et al., 2013; Malhi et al., 2009) and can be evaluated against existing data from Doughty and Goulden (2008). This study is the first to evaluate, using data, the inter-model variability in the leaf and canopy responses to changes in temperature and precipitation at a tropical forest site.

2 Materials and methods

2.1 Model description

The five models used in this study were the Community Land Model version 3.5 coupled to the Dynamic Global Vegetation model (CLM3.5-DGVM; hereafter CLM3.5), the Ecosystem Demography model version 2 (ED2), the Simple Biosphere model version 3 (SiB3), the Soil–Plant–Atmosphere model (SPA) and the Joint UK Land Environment Simulator version 2.1 (JULES). A brief description of each of the models is given here and in Table 1 (also see Powell et al., 2013). The simplest canopy structure is in SiB3.

GMDD

7, 7823–7859, 2014

Modelling climate change responses in tropical forests

L. Rowland et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

Modelling climate change responses in tropical forests

L. Rowland et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



SiB3 has a fixed LAI and uses a big-leaf model which simulates the response of the top canopy and integrates this response throughout the canopy according to a light and leaf nitrogen (N) extinction coefficient (Baker et al., 2008; Sellers et al., 1992, 1996). CLM3.5 is also a big-leaf model, however it separates the canopy into a sunlit leaf fraction (leaves which receive both direct and diffuse light) and a shaded leaf fraction (leaves which receive only diffuse light), which change dynamically with sun angle and canopy light penetration (Oleson et al., 2004, 2008). The version of JULES used in this study simulates 10 canopy layers with equal leaf area increments. Leaf nitrogen decays exponentially through the canopy and radiation interception is simulated following the two-stream approximation of Sellers (1985). SPA also has a layered canopy model, and here used three canopy layers, with separate sunlit and shaded fractions (Williams, 1996; Williams et al., 2005). ED2 mathematically approximates the properties of an individual-based forest gap model, separately modelling the stems of three types of trees (early, mid and late successional) and grasses on a continuum of leaf light levels from fully shaded to fully sunlit (Kim et al., 2012; Medvigy et al., 2009; Moorcroft et al., 2001). SiB3 and SPA simulate only 1 plant functional type (PFT), set to tropical evergreen broadleaf; JULES and CLM3.5 simulate 5 PFT's, but this site simulated a fractional cover > 95 % evergreen broadleaf trees. ED2 simulates 3 successional stages (pioneer, mid-successional and late-successional) of a single PFT, tropical evergreen broadleaf trees.

All of the models use enzyme-kinetic A_n equations, derived from Farquhar et al. (1980), Farquhar and Sharkey (1982), Kirschbaum and Farquhar (1984) and Collatz et al. (1991). In all models temperature can affect A_n directly through temperature response functions on the maximum rate of carboxylation of RuBP (V_{cmax}), the CO_2 compensation point, and the Michaelis–Menten constants (K_c and K_o), and in SPA the maximum rate of electron transport (J_{max}). Temperature can also indirectly change A_n through changing the VPD at the leaf surface, which alters g_s . CLM3.5, ED2 and SiB3 use the Ball–Berry stomatal conductance model (Collatz et al., 1991). JULES calculates g_s by relating the ratio of internal to external CO_2 to the humidity deficit (Cox

et al., 1998). SPA is unique in that it models stomatal conductance by simulating an aqueous continuum between the soil and leaf water: g_s and photosynthesis are maximised using an isohydric assumption that at each time-step leaf water potential does not drop below a critical level (-2.5 MPa; see Williams et al., 1996; Fisher et al., 2007).

5 CLM3.5, ED2, SiB3 and JULES alter g_s using a water stress factor (β ; a value ranging 0–1 where 1 indicates no soil water stress and 0 indicates complete soil water limitation). A detailed description of the effect of soil water stress on g_s and A_n in these models is given by Powell et al. (2013).

2.2 Site

10 The throughfall exclusion in the Tapajós National Forest (TNF, 2.897° S, 54.952° W) is located on an Oxisol soil, and has a mean annual precipitation of approximately 2 m year^{-1} ; the site is described in detail by Nepstad et al. (2002). This plot was selected for this experiment because on the temperature response of canopy level net ecosystem exchange (NEE) was collected at a nearby site (km83; Doughty and Goul-
15 den, 2008). The canopy NEE measurements were from an eddy covariance tower from July 2000 to July 2001, when light levels were above $1000\ \mu\text{mol m}^{-2}\text{ s}^{-1}$ (Doughty and Goul-
den, 2008). Leaf level responses of stomata conductance and photosynthesis to increases in leaf temperature in fully sunlit canopy leaves were from 3 species in
20 2004 (see Doughty and Goul-
den, 2008; Goul-
den et al., 2004).

2.3 Meteorological data and soil properties

The model simulations were driven using hourly meteorological data (precipitation, T_{air} , specific humidity, short and long-wave radiation and air pressure) measured above the canopy at the site from 1 January 2002–31 December 2004. The short-wave radiation was split into 68 % direct and 32 % diffuse, and then this was split into 43 % visible and 57 % near-infrared for direct, and 52 % visible and 48 % near-infrared for diffuse
25 (Goudriaan, 1977).

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



The soil properties were standardised across all models to create a similar soil physical environment, thereby testing only for differences in vegetation functioning (see Powell et al., 2013). Only biological properties such as rooting depth, root biomass, as well as the total number of soil layers were left as model specific soil properties.

2.4 Experimental design

All of the models went through a standard spin-up procedure prior to simulations (see Powell et al., 2013). Following the spin-up period, a series of five model simulations, with varying T_{air} , were performed for an eight-year period (which was intended to simulate 1999–2006, see Powell et al., 2013) for ambient precipitation (control simulations) and for simulations with a 50% reduction in wet season rainfall (drought simulations). The 2002–2004 meteorological data were recycled over the eight year simulation period. To explore the effects of changes in T_{air} on the models we performed five model simulations which consisted of simulations with the hourly 2000–2006 ambient T_{air} adjusted by $-5, 0$ (ambient T_{air}), $+2, +4$ and $+6^{\circ}\text{C}$. 1999 was the baseline year for which no changes from ambient temperature and precipitation were implemented. Our analysis was focused on increases in temperature; however we included a simulation with temperatures 5°C lower than ambient temperatures, on the basis that some models may have processes optimised for temperate regions where average T_{air} is lower. VPD was adjusted according to the changes in air temperature.

2.5 Model output and evaluation

All the data in this study was processed to match the collection methods and processing done by Doughty and Goulden (2008; hereafter referred to as DG), as closely as possible. Therefore, to compare the models' predictions NEE with the flux data, we extract canopy level fluxes when photosynthetic photon flux density (PPFD) was $> 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$, the conditions used by DG. PPFD was not available for the whole period; therefore we use the measured shortwave radiation to estimate PPFD.

Modelling climate change responses in tropical forests

L. Rowland et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Modelling climate change responses in tropical forests

L. Rowland et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



A conversion factor of 2 is used to convert from shortwave radiation (W m^{-2}) to PPFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$) based on an empirical relationship calculated from the flux tower at the study site (Doughty, unpublished data). The results on hourly time-steps from each model for the period of (2000–2006) for the five ambient temperature simulations (with offset of -5 , $+0$, $+2$, $+4$ and $+6$ °C) were pooled. Model output was then placed into 1 °C bins of T_{air} for the canopy-scale analysis (GPP, NEE, ecosystem respiration (R_{eco})) or leaf temperature (T_{leaf}), for leaf scale analysis, as done in the DG study. Accounting for non-gaussian distributions in model output the median and the 15.9th and 84.1th quantiles of the binned model output are plotted to represent the mean and 1 SD of the temperature response curve of any model variable. The data from the drought and control simulations are considered separately.

To explore the relative sensitivity of models to changes in temperature and drought a linear relationship between the temperature increase per control simulation (-5 , 0 , 2 , 4 , 6 °C) and final year (2006) GPP was used to calculate the change in GPP per 1 °C increase T_{air} for each model (Table 2). This value was used to calculate the increase in temperature necessary to produce the same loss of GPP as the ambient T_{air} drought simulation, where there is a 50 % reduction in wet season rainfall (Table 2).

DG published data for the temperature response of A_n and g_s of sunlit leaves during the dry season when PPFD is $> 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$. CLM3.5 and SPA are the only models which have separate output for sunlit and shaded leaves. Consequently data from the sunlit leaves of these models from periods of high PPFD ($> 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) during the dry season (July–December) were used for comparison. The effect of increasing T_{air} reducing modelled soil water content (via increased VPD and consequent leaf transpiration) had to be removed from the model outputs to make it comparable to the DG data, where individual leaves were artificially warmed. Therefore we only selected model outputs from the temperature simulations if the soil water content in the rooting zone was in the top quartile of the values from the ambient control simulation, this corresponded to β values of > 0.9 in CLM3.5. For consistency with the sunlit leaf

analysis, the analysis of canopy average leaf data from all models was done using dry season data with PPFD > 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

The relative sensitivity of the five models to changes in temperature and precipitation is assessed by comparing the interactive and non-interactive effects of the 50 % reduction in wet season precipitation (drought simulation) with the -5 , 0 , and $+6$ $^{\circ}\text{C}$ change in T_{air} on ecosystem fluxes at the end of the 8 year simulation (2006).

3 Results

3.1 Canopy scale responses

The models have similar responses of NEE and GPP to increasing T_{air} . DG observed a reduction in carbon uptake as NEE went from -17.4 ± 0.3 to -7.9 ± 1.1 $\mu\text{mol m}^{-2} \text{s}^{-1}$, corresponding to an increase in T_{air} from 28 – 32 $^{\circ}\text{C}$ (Fig. 2a). The modelled NEE begins to increase at a lower T_{air} (22 – 25 $^{\circ}\text{C}$). The modelled increase in NEE from 28 – 32 $^{\circ}\text{C}$, in all models except SPA (2.47 – 3.87 $\mu\text{mol m}^{-2} \text{s}^{-1}$), is substantially less than observed by DG; model increases in NEE in SPA from 28 – 32 $^{\circ}\text{C}$ are closer to those observed by DG (-15.8 to -7.0 $\mu\text{mol m}^{-2} \text{s}^{-1}$; Fig. 2a). The increase in modelled NEE at high temperatures is caused by a decline in GPP across all models (Fig. 2b). As T_{air} increases from 16 to 38 $^{\circ}\text{C}$ the average decline in GPP from all models is 20.9 ± 3.2 $\mu\text{mol m}^{-2} \text{s}^{-1}$. In contrast the mean model decline in R_{eco} over the same modelled T_{air} range was 4.2 ± 1.8 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 2c). The decline in modelled ecosystem respiration is low because in all models a decline in autotrophic respiration with increasing temperature (linked in the models with reduced GPP) is opposed by an increase in heterotrophic respiration (data not shown).

Declines in GPP corresponded to declines in LAI. Between 25 to 38 $^{\circ}\text{C}$ the decline in GPP in CLM3.5 (89 ± 38 %), and SPA (82 ± 26 %) was greater than the other models (Fig. 2b) and was matched by greater declines in LAI over the same temperature range (4.2 ± 1.0 $\text{m}^2 \text{m}^{-2}$, CLM3.5 and 4.4 ± 0.9 $\text{m}^2 \text{m}^{-2}$ in SPA, relative to only 0.6 ± 0.3 $\text{m}^2 \text{m}^{-2}$

Modelling climate change responses in tropical forests

L. Rowland et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



in ED2 and $0.4 \pm 0.1 \text{ m}^2 \text{ m}^{-2}$ in JULES; Fig. 2d). The inter-model variability in LAI is large; at 25°C the median LAI value in ED2 ($3.6 \pm 0.3 \text{ m}^2 \text{ m}^{-2}$) is 3 times smaller than the median values in CLM3.5 ($10.7 \pm 1.0 \text{ m}^2 \text{ m}^{-2}$). Observed mean LAI at the TNF under non-drought conditions ranged from $5.5\text{--}6.3 \text{ m}^2 \text{ m}^{-2}$ from 2000 to 2005 (Brando et al., 2008) and therefore the modelled values span a range $\sim 70\%$ above and below the measured LAI (Fig. 2d).

Combined drought and warming had compound effects on GPP, R_{eco} , and LAI. In Fig. 3 the change in GPP, R_{eco} , and LAI for the $T_{\text{air}} -5^\circ\text{C}$ and $T_{\text{air}} +6^\circ\text{C}$ simulations relative to the control simulation in the last year (2006) of the drought simulation is shown as a fraction of the year of the control simulation. The effect of temperature and drought was strongest in CLM3.5 where GPP is the same in the drought and control simulation at $T_{\text{air}} -5^\circ\text{C}$, but where a complete forest dieback to grassland was observed when drought was combined with a $+6^\circ\text{C}$ temperature increase (GPP values for grassland are not shown, Fig. 3a). In JULES, SiB3 and SPA the GPP was also the same in the control and the drought simulation at $T_{\text{air}} -5^\circ\text{C}$; however GPP is 61, 58 and 44 % lower respectively than the control when a $+6^\circ\text{C}$ increase in T_{air} occurs simultaneously with drought (Fig. 3a). The combined effect of temperature and drought on GPP and R_{eco} is lowest in ED2, because it was the only model to have a strong drought effect on GPP, R_{eco} and LAI in the $T_{\text{air}} -5^\circ\text{C}$ simulation (Fig. 3). In CLM3.5 and SPA, GPP and LAI have the same fractional reductions with drought, at higher temperatures (Fig. 3a and c), indicating a tight coupling between the LAI and canopy productivity. JULES, had the smallest GPP-LAI feedback, contrasting ED2 which had greater fractional reduction in LAI than GPP (Fig. 3c), despite low absolute values of LAI (Fig. 2). Reductions in LAI in ED2 are strongly related to drought at all temperatures, caused by greater mortality and leaf shedding in the drought simulations (see Fig. 6 in Powell et al., 2013).

We find a continuum of temperature vs. drought sensitivity amongst the models. If temperature vs. drought sensitivity is expressed as the equivalent temperature increase necessary to produce the same GPP loss as in the ambient T_{air} drought simulation (50 % reduction in wet season rainfall; Table 2), a low equivalent temperature would

Modelling climate change responses in tropical forests

L. Rowland et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



represent a greater GPP sensitivity to temperature increase and/or a lower GPP sensitivity to drought. Likewise a higher equivalent temperature represents a lower GPP sensitivity to temperature increase and/or a higher GPP sensitivity to drought. The equivalent temperature increase to reproduce the GPP loss with drought was lowest in SPA (4.92 °C), moderate in JULES and CLM3.5 (8.61 and 8.83 °C, respectively), and highest in SiB3 and ED2 (15.70 and 17.50 °C, respectively; Table 2). However across all the models a 5 °C reduction in ambient T_{air} resulted in an increase in forest productivity as GPP rose between 3.3–8.7 MgC ha⁻¹ yr⁻¹ in all models (Table 2).

3.2 Leaf scale responses

Leaf scale A_n and g_s oppose LAI responses; the model with the smallest change in LAI (ED2) has the highest A_n and the model with the largest change in LAI (CLM3.5) has the lowest A_n (Figs. 2 and 4). Similarly the models with no or limited responses of LAI to temperature change (SiB3 and ED2; Fig. 2), showed the strongest responses of A_n to temperature change (Fig. 4). Such trade-offs result in high model variation in the shape and magnitude of the temperature responses of A_n , g_s , transpiration (ET) and V_{cmax} (Figs. 4 and 5). As T_{leaf} increases from 25 to 40 °C the inter-model range of A_n values increases 1.9 times from 1.65 to 3.16 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 4a), indicating greater uncertainty of A_n at higher temperatures. The optimum A_n in SPA, SiB3, JULES, CLM3.5 and ED2 occurs at T_{leaf} values of 25, 26, 27, 30 and 30 °C respectively (Fig. 4a) and significantly before the optimum point on V_{cmax} (Fig. 5). In all models the A_n optimum is linked to g_s and the decline in canopy average A_n occurs at, or within, 1 °C of the T_{leaf} at which g_s starts to decline (Fig. 4a and b). At $T_{\text{leaf}} > 25$ °C the variability between the model responses of V_{cmax} increases (Fig. 5). In CLM3.5, ED2, JULES, SiB3 and SPA the V_{cmax} optima was set to 35, 40, 32, 36 and 30 °C respectively (10 °C of variation). Between the models there is a large variation in how quickly V_{cmax} declined following the optima; in CLM3.5 V_{cmax} declined 50 % at 9 °C over the optimum, contrasting with the same decline only after 17 °C over the optimum in SPA (Fig. 5).

Modelling climate change responses in tropical forests

L. Rowland et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Modelling climate change responses in tropical forests

L. Rowland et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



There was high variability in the magnitude and temperature response of g_s across the models. The maximum canopy average g_s values in SiB3 ($486 \text{ mmol m}^{-2} \text{ s}^{-1}$ at 25°C) and ED2 ($384 \text{ mmol m}^{-2} \text{ s}^{-1}$ at 23°C) are substantially higher than CLM3.5 ($49 \text{ mmol m}^{-2} \text{ s}^{-1}$ at 20°C), JULES ($70 \text{ mmol m}^{-2} \text{ s}^{-1}$ at 25°C) and SPA ($200 \text{ mmol m}^{-2} \text{ s}^{-1}$ at 24°C ; Fig. 4b). Declining g_s causes the steepest decline in ET in CLM3.5 and SPA after 35 and 30°C respectively (Fig. 4c). In CLM3.5 a strong constriction in ET is caused by the strong influence of β on g_s (Fig. 4d). β is reduced by $85 \pm 31\%$ in CLM3.5 as T_{leaf} increase from 30 – 40°C . The decline in β over the same T_{leaf} range was only $14 \pm 1\%$ in ED2, $38 \pm 5\%$ in JULES and $7.9 \pm 1\%$ in SiB3 (Fig. 4d).

For each model there are apparent, but variable, relationships between g_s and A_n (Fig. 6), but no obvious relationships between A_n and V_{cmax} (Fig. 7). The slope of A_n against g_s indicates intrinsic water use efficiency (IWUE); if a linear fit is forced through the g_s and A_n data for each model temperature simulation, it is apparent that all models simulate increasing IWUE with increasing leaf temperature. The increase in IWUE from the lowest to the highest temperature simulation is higher in the drought than control simulations in all models; however there is high variability in the g_s and A_n slope when drought and control simulations of the same temperature are directly compared. Some models have lower IWUE in the drought simulations at all temperatures (CLM3.5, SPA), others have higher IWUE in the drought simulations at all temperatures (SiB3) and others (ED2 and JULES) start off with higher IWUE in the control simulations at the lower temperature simulations but switch to higher IWUE in the drought simulations at high temperature simulations (Table 3; Fig. 6).

When the effect of soil water stress is removed and sunlit leaf level values are compared to the DG data for the models which could output sunlit leaf only values of g_s and A_n (SPA and CLM3.5; Fig. 8), the peak A_n of sunlit leaves in SPA at 25°C ($8.72 \pm 0.24 \mu\text{mol m}^{-2} \text{ s}^{-1}$) is similar to the peak in the DG leaf scale data at 30.5°C ($8.44 \pm 0.17 \mu\text{mol m}^{-2} \text{ s}^{-1}$; Fig. 8a). In CLM3.5 the peak A_n at 29°C is considerably higher ($13.48 \pm 0.20 \mu\text{mol m}^{-2} \text{ s}^{-1}$), although it occurs at a similar temperature to the observed peak, but both CLM3.5 and SPA show a decline of A_n with temperature

similar to the data. Modelled g_s , however, shows a poor match to the observations (Fig. 8b). Peak g_s values occur at substantially lower T_{leaf} values in CLM3.5 (27 °C) and SPA (25 °C) than observed (33.5 °C; Fig. 5b). The peak sunlit g_s in SPA are also significantly higher ($434 \pm 88 \text{ mmol m}^{-2} \text{ s}^{-1}$) than the observations ($123 \pm 4 \text{ mmol m}^{-2} \text{ s}^{-1}$) and show a very sharp decline not observed in the data (Fig. 8b).

4 Discussion

4.1 Canopy and leaf-scale feedbacks

The response of NEE and GPP to short-term changes in temperature was demonstrated substantially greater consistency across models than that of LAI (Fig. 2). Within the models which had dynamic LAI the change in LAI ranged from $4.5 \text{ m}^2 \text{ m}^{-2}$ in SPA to $1.0 \text{ m}^2 \text{ m}^{-2}$ in ED2. Interestingly, ED2, JULES and SiB3 all showed very little change in absolute LAI values with changes in temperature, despite the fact that ED2 and JULES are dynamic vegetation models and SiB3 does not have dynamic LAI. This is contrasted with a sharp decrease in LAI in response to changes in temperature in CLM3.5 and SPA (Fig. 2d). The inter-range in LAI values across the 5 models (maximum range $7.5 \text{ m}^2 \text{ m}^{-2}$) was however greater than any decline in LAI with T_{air} . If leaf scale fluxes are scaled using an inaccurate LAI, the simulation of both accurate leaf and canopy scale fluxes is not possible (Bonan et al., 2012; Lloyd et al., 2010; Mercado et al., 2006, 2009). Given the large variability in LAI responses across the models, it would be expected that there should be a greater variability in GPP than was observed. Models have to compensate variability in canopy structural parameters, such as LAI, through adjustment in other leaf scale parameters if consistency in ecosystem-scale responses is to be maintained (Bonan et al., 2012). We therefore suggest that the variability in LAI responses is compensated for by variations in parameterisation at the leaf-scale, which in turn drive similarly high variation in the leaf-scale fluxes.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Modelling climate change responses in tropical forests

L. Rowland et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



We found substantial variation in the magnitude and temperature responses of leaf scale parameters: peak V_{cmax} had a 10°C T_{leaf} range across the models (Fig. 5), g_{s} values varied by over an order of magnitude (Fig. 4b), β and ET values showing increasingly large disparities with increasing T_{leaf} (Fig. 4c and d), and the inter-modal A_{n} range had a two fold increase between T_{leaf} values of $25\text{--}40^{\circ}\text{C}$ (Fig. 4a). Such variability across the models suggests that any similarities in responses of NEE to temperature between models are caused by different processes having differing feedbacks at the leaf-scale. Without more data to evaluate which models are producing both the correct V_{cmax} and g_{s} , responses to temperature, it is hard to have confidence in predictions of climate change in Amazonian simulated by either one or multiple models.

The models did agree that reductions in g_{s} with increasing temperature were the main cause of reductions in forest productivity (Lloyd and Farquhar, 2008). A_{n} decline was related to g_{s} decline (Table 3; Fig. 6), but not V_{cmax} decline (Fig. 7) and the decline in A_{n} with increasing T_{leaf} occurred prior to the T_{leaf} peak in V_{cmax} (Figs. 4b and 5). The slope of $A_{\text{n}}\text{--}g_{\text{s}}$ reflects IWUE and our study demonstrates that all the models predict an increase in IWUE with rising leaf temperatures and an accentuation of this change under drought conditions (Table 3; Fig. 6). Very steep $A_{\text{n}}\text{--}g_{\text{s}}$ slopes at higher leaf temperatures suggests that as the ecosystem warms A_{n} becomes more sensitive to reductions in g_{s} , and therefore that stomatal controls are likely to have greater influence at higher temperatures; this suggests that even at high temperatures (up to 6°C above ambient) reductions in A_{n} are caused mainly by stomatal, rather than a biochemical responses. These results reflect patterns found in leaf warming data from the Tapajos forest which show that reductions in A_{n} start to occur at $4\text{--}5^{\circ}\text{C}$ before the optimum point for V_{cmax} and J_{max} in sunlit leaves (Tribuzy, 2005), but not the responses of other longer term leaf warming experiments at the same site which experienced changes in leaf biochemistry with increasing leaf temperatures (Doughty, 2011). Substantially more data is therefore required to effectively test such results.

IWUE was highly variable across the models, particularly with the introduction of precipitation change (Table 3; Fig. 6). Variability in the $A_{\text{n}}\text{--}g_{\text{s}}$ relationships are related to

differences in how β is calculated by models (Powell et al., 2013; Zhou et al., 2013), as β alters g_s (Fig. S1) and A_n . β is altered by changes in SWC which can be caused by changes in temperature (via increased VPD altering SWC), as well as changes in precipitation. The decrease in β with temperature increase was highly variable between models (Fig. 4d). Consequently, the direct influence of soil water stress on g_s , A_n and ET, vs. the indirect effect of VPD, as temperature and precipitation changed was inconsistent between models. Resolving these inconsistencies is important, as water stress functions impact the ratio of modelled latent to sensible heat fluxes and so when coupled to global climate models they alter climate and vegetation feedbacks (Harper et al., 2014). Improving how water stress is simulated in models is therefore essential to improving temperature and drought responses in tropical forests.

When considering SPA, a model that uses a more mechanistic water stress response (and focusing only on periods of high soil water content to remove the water stress response of A_n), g_s still varied substantially from the response and magnitude of the DG data (Fig. 8). Given the DG data was averaged from only three top canopy species, compared to deriving from all sunlit leaves in CLM3.5 and SPA, some degree of variations between the model and the data is expected. However, the variability between the peak data and peak model g_s is > 4 times (Fig. 8b) and the modelled temperature optima for g_s (25–27 °C) was substantial lower than observed by DG (33.5 °C). Had the modelled temperature optima for g_s been closer to the observed temperature optima (33.5 °C), V_{cmax} , may have had a greater limitation on A_n , as at the observed g_s temperature optima (33.5 °C) some models are past the V_{cmax} temperature optimum (Fig. 5). Consequently in this study the dominance of the effect of g_s on photosynthesis may be derived from low g_s optima in the models.

Given that CLM3.5 and SPA are in the lower range of the total model variability for the g_s and A_n of an average canopy leaf (aggregated sunlit and shaded leaf; Fig. 4a and b), the variation from the data is likely to be substantially larger if sunlit leaf data could be extracted from all models. Considering the importance of g_s in controlling leaf productivity, the suitability of the empirical models of g_s used in these models

Modelling climate change responses in tropical forests

L. Rowland et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



requires further testing (Bonan et al., 2014). The use of optimised rather than empirical models may provide an opportunity to improve the capability to simulate g_s responses to temperature and water stress in greater detail (Heroult et al., 2013; Medlyn et al., 2013, 2011; Zhou et al., 2013).

4.2 Combined drought and temperature sensitivities

The responses of modelled forest production to combined changes in precipitation and temperature was highly variable. Rising T_{air} in CLM3.5 and SPA caused very strong compound effects of temperature on drought induced reductions in GPP, R_{eco} and LAI (Fig. 3). In ED2, the drought effect on GPP was stronger than the other models (Fig. 3) because of a strong drought-mortality effect at this site (Powell et al., 2013). Considerable model disparity in the response of A_n and LAI to drought and temperature (Figs. 2, 4 and 6) resulted in substantial variation in relative sensitivity of models to temperature and drought. Previous modelling studies have shown that there is high variability in how sensitive models are to temperature and drought (Friedlingstein et al., 2006; Galbraith et al., 2010; Luo et al., 2008; Sitch et al., 2008), but that vegetation models have greater sensitivity to rises in temperature than drought (Galbraith et al., 2010). This study demonstrates that there is actually a continuum in model responses from models that require a low increase in ambient T_{air} to cause the same GPP loss as a 50 % reduction in wet season rainfall (SPA, 4.9 °C), to models that have a very strong drought response and therefore require a substantial increase in ambient T_{air} to replicate the same GPP loss as a 50 % reduction in wet season rainfall (ED2, 17.5 °C; Table 2). As a 6 °C rise in temperature and a 50 % reduction in rainfall are changes which may occur in Amazonia during the 21st century (Christensen et al., 2007; Collins et al., 2013), we suggest that there is currently no consensus between vegetation models as to whether there will be a stronger drought or temperature response to future climate change within tropical forests. Across the models, the dominance of stomatal control on productivity resulted in GPP increasing when ambient T_{air} was reduced by 5 °C and the temperature was closer to the modelled g_s optimum. This result suggests models are

Modelling climate change responses in tropical forests

L. Rowland et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



currently predicting that Amazonian forests are operating beyond a temperature and VPD optimum. Given that the models underestimate the point at which NEE declines with T_{air} by 3–6 °C and the point at which g_s declines with T_{leaf} by 7.5–9.5 °C (Figs. 2 and 4), it is likely that the models in this study may be biased towards temperature calibrations for temperate ecosystems. Consequently, as well as moving towards implementing more mechanistic responses to improve models, more research to test and adjust their temperature responses in tropical ecosystem is necessary.

5 Conclusion

This is the first study in which canopy and leaf temperature responses from multiple vegetation models are analysed and compared to existing data on leaf and canopy temperature responses from a tropical forest site. This study finds models lie along a continuum of those which have a greater sensitivity of GPP to changes in temperature relative to drought and those which have a greater sensitivity to drought relative to a change in temperature. Any consistency in model responses to temperature and drought were however, the result of inconsistent leaf-scale responses, which were compensating for substantial variation in the magnitude and response of LAI to drought and temperature.

All the models in this study predict that reductions in A_n are dominated by stomatal rather than biochemical responses and that tropical forest productivity will become more sensitive to reductions in g_s as temperatures rise. The dominance of the effect of g_s rather than V_{cmax} on A_n results in all the models predicting greater forest productivity when temperatures are 5 °C below ambient and closer the temperature of the g_s optimum. Despite consistent prediction of increasing IWUE with temperature rise, there was however no consistency between models in how IWUE will respond to combined changes in temperature and drought. It seems therefore that the consistency of model responses is reduced as changes in multiple climate variables are introduced simultaneously. To effectively simulate the response of the Amazon forest to changes

Modelling climate change responses in tropical forests

L. Rowland et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



in multiple climatic factors substantial improvements are needed in how leaf scale processes and leaf to canopy scaling are simulated. Further measurement campaigns are also required to generate consistent leaf and canopy scale data for independent model evaluation.

5 **The Supplement related to this article is available online at doi:10.5194/gmdd-7-7823-2014-supplement.**

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10
15
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Modelling climate change responses in tropical forests

L. Rowland et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Modelling climate change responses in tropical forests

L. Rowland et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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Modelling climate change responses in tropical forests

L. Rowland et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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Modelling climate change responses in tropical forests

L. Rowland et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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Modelling climate change responses in tropical forests

L. Rowland et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Lloyd, J., Patiño, S., Paiva, R. Q., Nardoto, G. B., Quesada, C. A., Santos, A. J. B., Baker, T. R., Brand, W. A., Hilke, I., Gielmann, H., Raessler, M., Luizão, F. J., Martinelli, L. A., and Mercado, L. M.: Optimisation of photosynthetic carbon gain and within-canopy gradients of associated foliar traits for Amazon forest trees, *Biogeosciences*, 7, 1833–1859, doi:10.5194/bg-7-1833-2010, 2010.

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Modelling climate change responses in tropical forests

L. Rowland et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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Modelling climate change responses in tropical forests

L. Rowland et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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Modelling climate change responses in tropical forests

L. Rowland et al.

Table 1. Summary of the characteristics of each of the four vegetation models (CLM3.5, ED2, SiB3, SPA).

	CLM3.5	ED2	SiB3	SPA	JULES
No. of plant function types	5	4	1	1	10
Canopy structure	Big-leaf	Gap model	Big-leaf	Layered canopy	Layered Canopy
Leaf Area index	Dynamic	Dynamic	Fixed	Dynamic	Dynamic
Division of sunlit and shaded leaf	Y (discrete division)	N	N	Y (discrete division)	N
Simulation of water stress on A_n and g_s .	Water stress factor	Water stress factor	Water stress factor	Linked soil–leaf water potential/resistance model to g_s model.	Water stress factor
Origin of photosynthesis model	Farquhar et al. (1980); Farquhar and Sharkey (1982); Collatz et al. (1991)	Farquhar et al. (1980); Farquhar and Sharkey (1982); Collatz et al. (1991)	Farquhar et al. (1980); Farquhar and Sharkey (1982); Collatz et al. (1991)	Farquhar et al. (1980); Kirschbaum and Farquhar (1984); McMurtrie et al. (1992)	Farquhar et al. (1980); Farquhar and Sharkey (1982); Collatz et al. (1991)
Key model references	Bonan et al. (2003); Levis et al. (2004); Oleson et al. (2008)	Medvigy et al. (2009); Kim et al. (2012)	Sellers et al. (1992); Sellers et al. (1996); Baker et al. (2008)	Williams (1996); Williams et al. (2005); Fisher et al. (2006)	Best et al. (2011); Clark et al. (2011)

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Modelling climate change responses in tropical forests

L. Rowland et al.

Table 2. Model values for GPP ($\text{MgC ha}^{-1} \text{yr}^{-1}$) for the last year (2006) of the ambient air temperature control plot simulation ($T_{\text{air}} +0^\circ\text{C}$), the control plot simulation -5°C ($T_{\text{air}} -5^\circ\text{C}$), the control plot simulation $+6^\circ\text{C}$ ($T_{\text{air}} +6^\circ\text{C}$) and the ambient air temperature drought plot simulation ($T_{\text{air}} +0^\circ\text{C}$). The equivalent temperature is the elevation in the control plot simulation temperature needed to replicate the same magnitude reduction in GPP as the drought simulation, for the year 2006 and at ambient temperatures. The equivalent temperature is derived from a linear relationship between GPP values in 2006 and the air temperatures in the 5 temperature simulations per model.

	CLM3.5	ED2	SiB3	SPA	JULES
Control GPP $T_{\text{air}} -5^\circ\text{C}$	40.74	31.74	35.27	38.23	36.73
Control GPP $T_{\text{air}} +0^\circ\text{C}$	36.68	28.31	31.95	29.55	31.16
Control GPP $T_{\text{air}} +6^\circ\text{C}$	28.03	20.70	27.50	15.89	20.08
Drought GPP $T_{\text{air}} +0^\circ\text{C}$	26.47	10.79	20.86	19.55	18.13
Equivalent T_{air}	8.83	17.50	15.70	4.92	8.61

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)


Modelling climate change responses in tropical forests

L. Rowland et al.

Table 3. The slope of the relationships of A_n with g_s (intrinsic water use efficiency; IWUE), shown in Fig. 6 for each temperature run (ambient air temperature T_{air} -5 , $+0$, $+2$, $+4$, and $+6$ °C) in the control and drought simulations (Fig. 6f–j), for each model. (Note: NA in CLM3.5 drought simulations indicates the model changes to a grassland.)

	Control Simulations					Drought Simulations				
	CLM3.5	ED2	SiB3	SPA	JULES	CLM3.5	ED2	SiB3	SPA	JULES
$T_{\text{air}} -5$ °C	0.84	0.42	0.09	0.49	0.50	0.73	0.29	0.10	0.27	0.50
$T_{\text{air}} +0$ °C	0.93	0.56	0.49	0.68	0.83	0.93	0.40	0.93	0.24	0.60
$T_{\text{air}} +2$ °C	1.01	0.67	0.58	0.73	1.01	1.08	0.53	1.11	0.41	0.97
$T_{\text{air}} +4$ °C	1.05	0.79	0.65	1.00	1.18	NA	0.78	1.20	0.74	1.37
$T_{\text{air}} +6$ °C	1.11	0.95	0.69	1.50	1.32	NA	1.10	1.22	1.15	1.73

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)

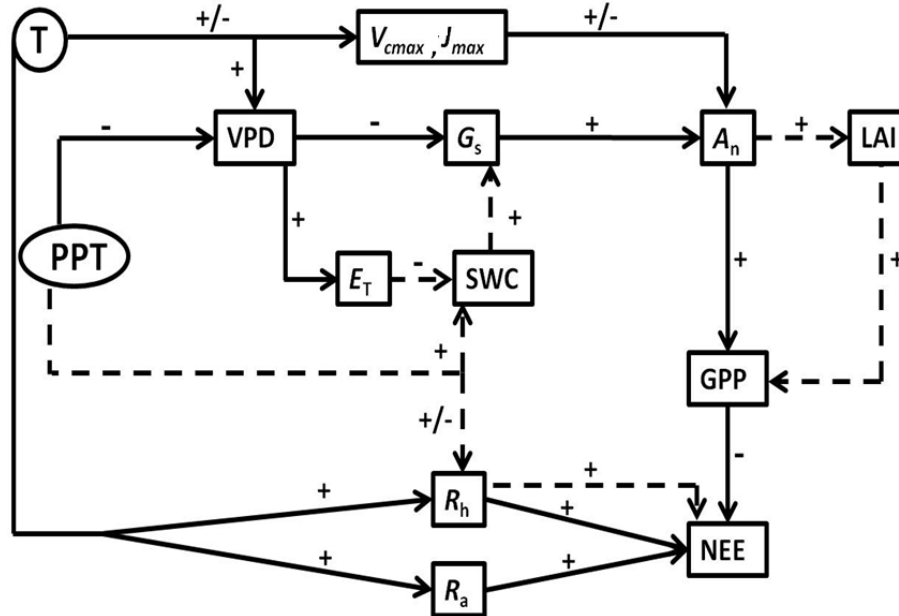



Figure 1. Schematic diagram showing how droughts, via the combined effects of increased air temperature (T) and reductions in precipitation (PPT), affect the carbon cycle of a tropical forest, including the effects on: vapour pressure deficit (VPD), evapo-transpiration (E_T), stomatal conductance (g_s), soil water content (SWC), net photosynthesis (A_n), leaf area index (LAI), the maximum rates of RuBP carboxylation and electron transport (V_{cmax} and J_{max} respectively), autotrophic respiration (R_a) heterotrophic respiration (R_h), gross primary productivity (GPP), and net ecosystem exchange (NEE). + signs indicate a positive effect, – signs indicate a negative effect, and \pm indicate the possibility of both a positive and negative effect. Solid arrows represent responses which occur over short timescales of minutes to hours, whereas dashes arrows represent responses which can occur over longer timescales from days to months.

Modelling climate change responses in tropical forests

L. Rowland et al.

Title Page

Abstract Introduction

Conclusions References

Tables Figures

◀ ▶

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Modelling climate change responses in tropical forests

L. Rowland et al.

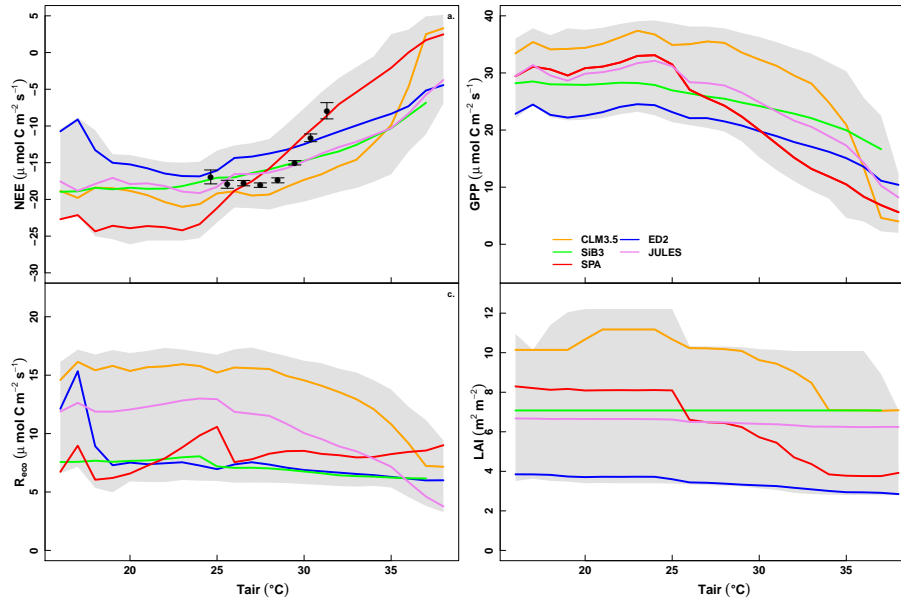


Figure 2. Comparison of the air temperature (T_{air} , $^{\circ}\text{C}$) response of **(a)** daytime net ecosystem exchange (NEE, $\mu\text{mol m}^{-2} \text{s}^{-1}$; note that negative values of NEE indicate carbon sequestration), **(b)** gross primary productivity (GPP, $\mu\text{mol m}^{-2} \text{s}^{-1}$), **(c)** ecosystem respiration (R_{eco} , $\mu\text{mol m}^{-2} \text{s}^{-1}$), **(d)** leaf area index (LAI, $\text{m}^2 \text{m}^{-2}$). The lines show the median model responses from the five control temperature runs per model pooled and divided into 1°C temperature bins. The grey shaded area shows the combined 15.9th and 84.1th quantiles for all models. The black points and error bars in panel **(a)** show the eddy-flux inferred NEE (cf. Fig. 4 in Doughty and Goulden, 2008).

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[⏪](#)
[⏩](#)
[◀](#)
[▶](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)


Modelling climate change responses in tropical forests

L. Rowland et al.

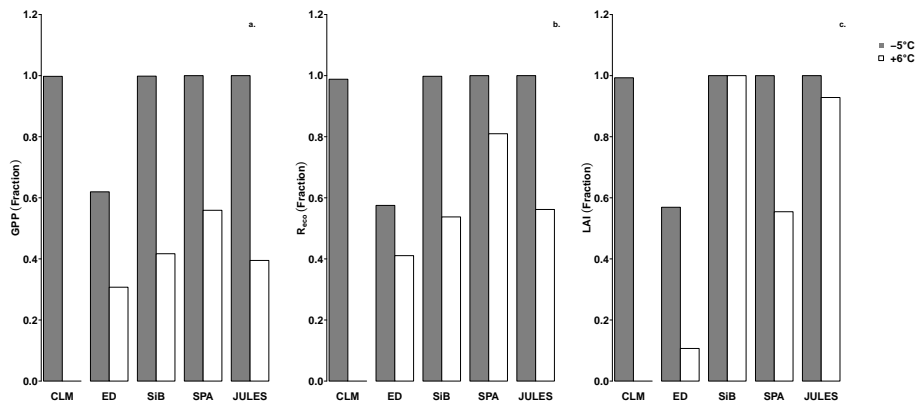


Figure 3. Modelled effect of short-term changes in temperature and drought. Fractional change in: **(a)** gross primary productivity (GPP) **(b)** ecosystem respiration (R_{eco}) and **(c)** leaf area index (LAI) on the final year (2006) in the drought run relative to the control run are shown for the $T_{\text{air}} -5^{\circ}\text{C}$ (grey bars) and $T_{\text{air}} +6^{\circ}\text{C}$ (white bars).

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Modelling climate change responses in tropical forests

L. Rowland et al.

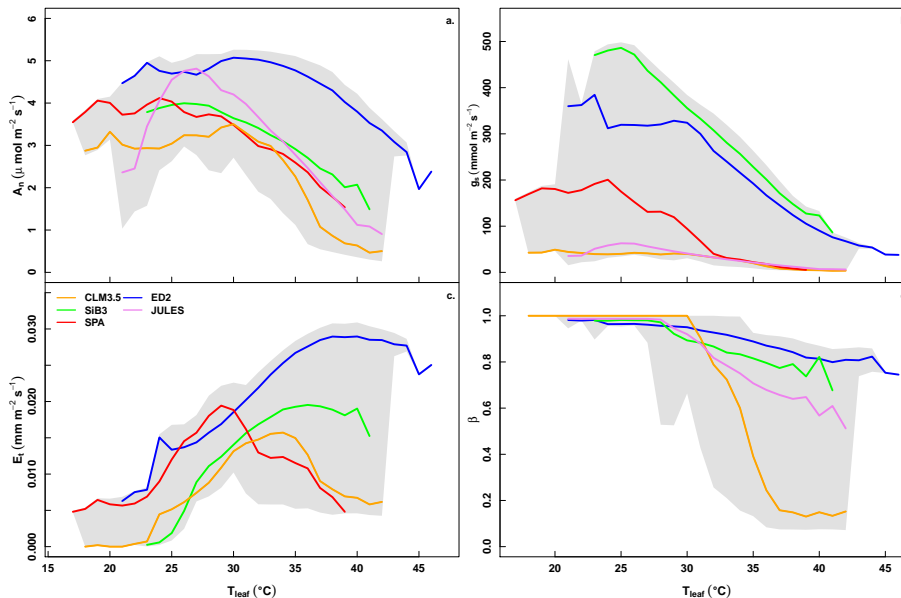


Figure 4. Comparison of the dry season mean (sunlit + shaded leaves, weighted by their respective LAIs) leaf-level response to temperature (T_{leaf} ; °C) of **(a)** net photosynthesis (A_n , $\mu\text{mol m}^{-2} \text{s}^{-1}$), **(b)** stomatal conductance (g_s , $\text{mmol m}^{-2} \text{s}^{-1}$), **(c)** leaf transpiration (E_t , $\text{mm m}^{-2} \text{s}^{-1}$), and **(d)** the soil water stress factor (β) for average canopy leaves (note: SPA does not simulate β). The lines show the median model responses from the control plot for the five temperature simulations pooled and divided into 1 °C temperature bins for each model. The grey shaded area shows the combined 15.9th and 84.1th quantiles for all models. (Note: JULES E_t data is missing from these runs.)

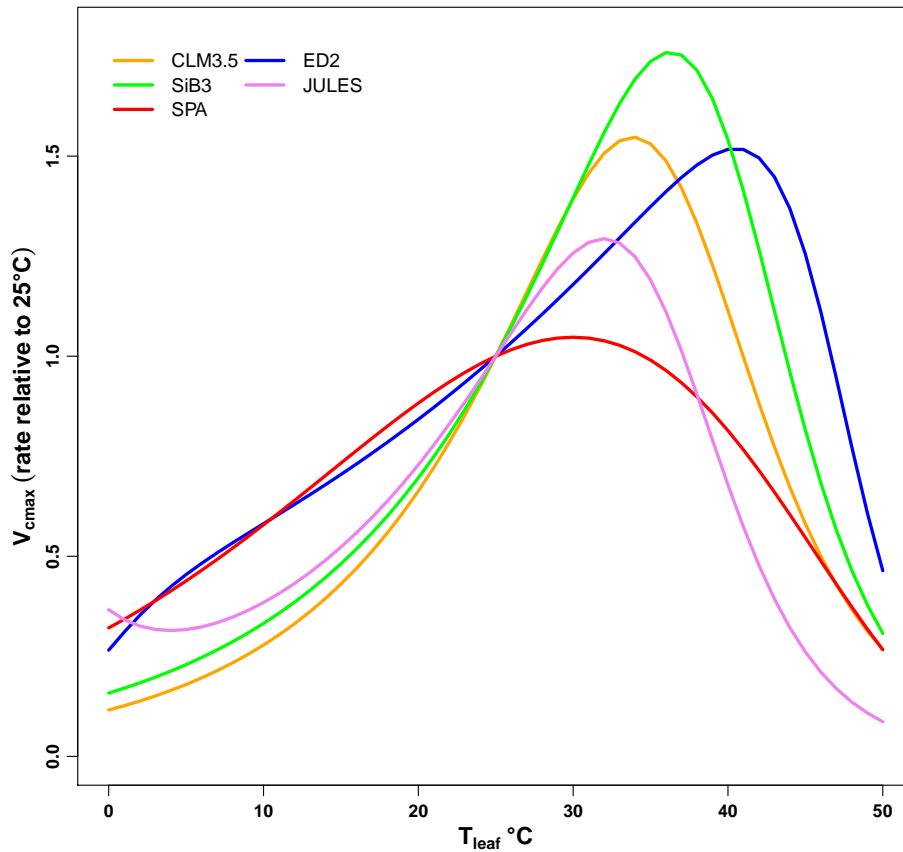


Figure 5. The temperature response of V_{cmax} for each model show relative to the V_{cmax} at 25 °C per model.

Modelling climate change responses in tropical forests

L. Rowland et al.

Title Page

Abstract Introduction

Conclusions References

Tables Figures

◀ ▶

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Modelling climate change responses in tropical forests

L. Rowland et al.

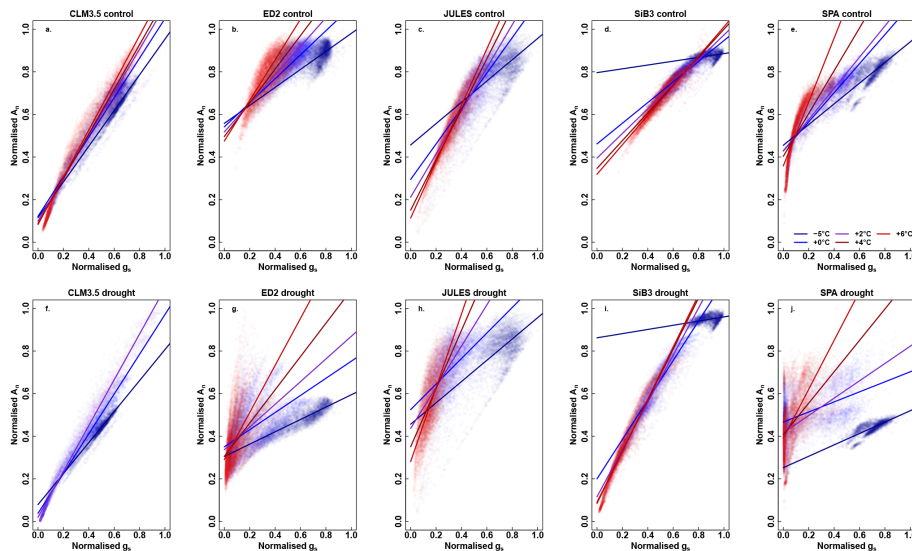


Figure 6. The relationship between dry season stomatal conductance (g_s) and photosynthesis (A_n) normalised by their respective maximum values when PPFD > 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Values are shown for each temperature run (ambient air temperature -5 , $+0$, $+2$, $+4$, and $+6^\circ\text{C}$) in the control (**a–e**) and drought simulations (**f–j**), for each model. Values are from sunlit and shaded leaves, weighted by their respective LAIs. A linear line is forced through the A_n , g_s data for each temperature run to indicate the steepness of the slope, which represents intrinsic water use efficiency. Data and linear lines are coloured from deep blue to deep red to differentiate the additions to ambient air temperature (see legend).

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Modelling climate change responses in tropical forests

L. Rowland et al.

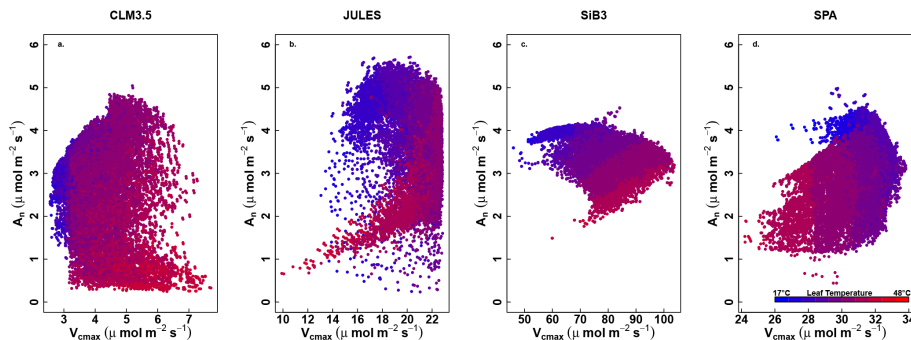


Figure 7. The relationship between V_{cmax} ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and photosynthesis (A_n , $\text{mmol m}^{-2} \text{s}^{-1}$) for each model in the dry season of the control runs, with PPFD > $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$. Values are from sunlit and shaded leaves, weighted by their respective LAIs. Results are shown across all leaf temperatures explored in this study (colour change from blue to red indicated increasing leaf temperature).

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)

[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)

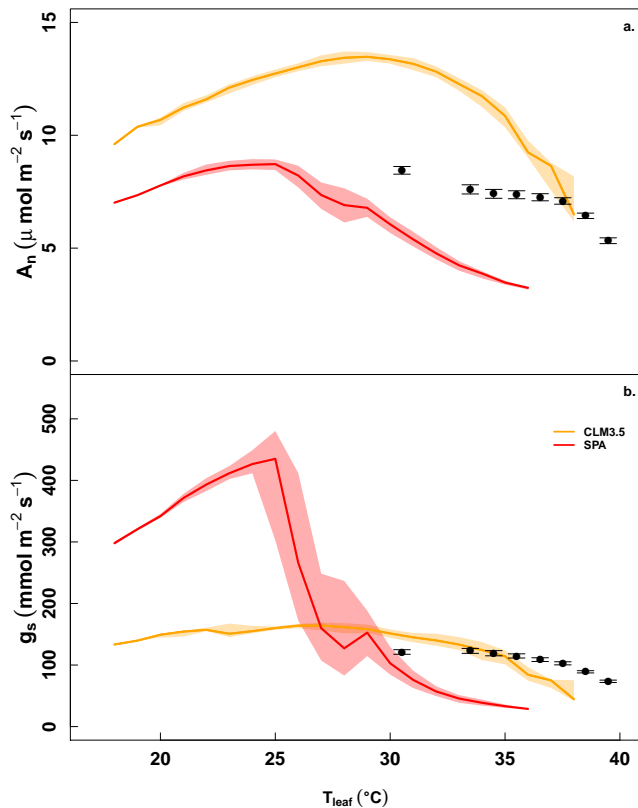



Figure 8. The sunlit leaf-level response of dry season **(a)** net photosynthesis (A_n , $\mu\text{mol m}^{-2} \text{s}^{-1}$) and **(b)** stomatal conductance (g_s , $\mu\text{mol m}^{-2} \text{s}^{-1}$) to leaf temperature (T_{leaf} ; $^{\circ}\text{C}$) for CLM3.5 (orange) and SPA (red). The lines show the median model responses from the control plot for the five temperature simulations pooled and divided into 1°C temperature bins for each model. The shaded areas around each line show the 15.9th and 84.1th quantiles for each model. Data from Doughty and Goulden is shown as black points; error bars show the standard error.