

Interactive comment on “The Impact of a Simple Representation of Non-Structural Carbohydrates on the Simulated Response of Tropical Forests to Drought” by Simon Jones et al.

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1. I felt the details on how the model was parametrised could be improved. I strongly felt the paper needs a table with parameters used, which would make this paper repeatable.

This is a good suggestion, and we agree that the description of model parametrisation, in general, is not sufficiently clear. We have added the following table to show all the parameters in SUGAR, their ranges, and values used in the Caxiuanã simulations. We have also updated the derivation of the parameter evaluation process which we also include below. This includes details on how to parametrise SUGAR for single site runs, where initialisation data from the site is available (i.e. as in the Caxiuanã simulations) and how SUGAR might be parametrised for more general or global simulations. We have also outlined the distinction between running SUGAR offline and coupling it to a land surface model (LSM), which is not really clear in the current manuscript. Hopefully this will make it clearer how we have evaluated the parameters in these simulations and how to apply SUGAR to other experiments.

To address the point regarding parameter evaluation we outline below the complete process, including a discussion of what data can be used depending on the nature of the simulation being conducted. We will happily add this section to the main body of the paper between the model description and methods section. We will also update the methods section to more clearly outline how this process is applied to both experiments in the paper. Note, for the purposes of this response we include below the definitions of symbols, however, in the updated manuscript we would omit these since they are defined in the model description section.

Parameter evaluation - derivation

First we address parameters that have standard or commonly used values within the land surface modelling literature, and parameters that can be directly estimated from empirical data. These are q_{10} and Y_g , and f_{NSC} respectively.

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q_{10}

The Q10 function is commonly used to describe the temperature dependence of plant respiration and growth in LSMs. Growth and respiration both depend on temperature via a Q10 function with the standard q_{10} parameter value of 2.0 (Ryan 1991).

Y_g

The Y_g parameter is derived in Thornley and Johnson (1990), and estimated to equal 0.75. Y_g or similar parameters are used in LSMs (e.g Clark et al. 2011), often with an equivalent value of 0.75.

f_{NSC}

The f_{NSC} parameter represents the equilibrium NSC pool size as a fraction of total structural carbon. This can be set directly using empirical data e.g. for tropical forests using Wurth et al. (2005). Note that studies such as Wurth et al. (2005) present NSC stocks as a fraction of total dry mass and so data should be adjusted to account for non-carbon mass.

a_{K_m}

It is not possible to directly evaluate a_{K_m} from empirical data. It is given the default value of 0.5, since this gives numerically stable results on the commonly used time-step of 1 hour, and the dependence of respiration and growth on NSC begins to saturate at reasonable NSC mass fractions.

The remaining parameters, ϕ and α , cannot be evaluated directly using empirical data so below we outline how the model equations can be manipulated to find ϕ

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and α in terms of quantities that can be estimated using observations.

We start by finding the rate of change of NSC mass fraction, W_{NSC} , where $W_{NSC} = C_{NSC}C_v$, in terms of C_{NSC} and C_v :

$$dW_{NSC}dt = 1C_vdC_{NSC}dt - W_{NSC}1C_vdC_vdt \quad (1)$$

We then consider the case where the NSC mass fraction is constant and the left hand side of equation (1) is zero. In reality the NSC mass fraction of forest will not be exactly constant and variations in environmental variables will cause changes in NSC stocks. However, for a non-stressed forest it is a good assumption that over a prolonged period, τ_{stable} , the NSC mass fraction will be roughly constant. For example, we can assume that over the course of one year, a non-stressed forest will use as much carbon as it assimilates and consequently will end the year with roughly the same NSC stock with which it started. This means that we can integrate equation (1) over this period and set the left hand side equal to zero:

$$0 = \int_{\tau_{stable}} (1C_vdC_{NSC}dt - W_{NSC}1C_vdC_vdt) dt \quad (2)$$

We then consider two cases:

1. Uncoupled simulations

When SUGAR is run offline, i.e. it is not coupled to a LSM, the dC_vdt term must be neglected and we assume C_v is constant. Hence:

$$dW_{NSC}dt = 1C_vdC_{NSC}dt \quad (3)$$

We then use the equation (1 in the original manuscript) for the rate of change of NSC:

$$0 = \int_{\tau_{stable}} (\Pi_G C_v - RC_v - GC_v) dt \quad (4)$$

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To evaluate ϕ we use the equation for total carbohydrate utilisation and rearrange:

$$\phi \int_{\tau_{stable}} F_Q(T) W_{NSC} W_{NSC} + K_m dt = \int_{\tau_{stable}} \Pi_G C_v dt \quad (5)$$

We divide both sides by τ_{stable} and assume that this can be approximated as:

$$\phi F_Q^*(T) W_{NSC}^* W_{NSC}^* + K_m = (\Pi_G C_v)^* \quad (6)$$

Where the asterisk denotes a temporal average over the period τ_{stable} . i.e for variable X :

$$X^* = \frac{1}{\tau_{stable}} \int_{\tau_{stable}} X dt \quad (7)$$

Rearranging, we find the expression for ϕ

$$\phi = W_{NSC}^* + K_m F_Q^*(T) W_{NSC}^* (\Pi_G C_v)^* \quad (8)$$

By definition, the average NSC mass fraction is equal to f_{NSC} . Using this and equation (6 in the original manuscript), this becomes

$$\phi = 1 + a_{K_m} F_Q^*(T) (\Pi_G C_v)^* \quad (9)$$

This means that to evaluate ϕ , we require an estimate of average specific GPP over some stable period, and the average temperature during that period. If SUGAR is used at a single site these can be evaluated directly using GPP, biomass and temperature data if these are available. If these data are not available then the specific GPP can be approximated as the steady state carbon residency time, τ (e.g. in Carvalhais et al. 2004) and the temperature can found using global climatology data over the same period.

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To evaluate α , we re-write equation (4) as:

$$0 = \int (\Pi_N C_v - G C_v) dt \quad (10)$$

Again we divide by the integration period, τ_{stable} , and assume this can be written as:

$$0 = \Pi_N^* C_v^* - G C_v^* \quad (11)$$

hence:

$$\Pi_N^* = G^* \quad (12)$$

Similarly using equation (4), we find

$$\Pi_G^* = U^* \quad (13)$$

Dividing equation (12) by equation (13) gives:

$$\alpha = CUE^* \quad (14)$$

where $CUE^* = \frac{\Pi_N^* \Pi_G^*}{G^* U^*}$, is the time averaged carbon use efficiency of the non-stressed forest over the period τ_{stable} .

Again this can be evaluated using data from a single site if available, or using more general estimates of CUE (e.g. Chambers et al. 2004, Gifford et al. 1995, Dewar 1998) if not.

2. Coupled simulations

When SUGAR is coupled to a LSM, the rate of change of structural biomass cannot be neglected, and we must consider the following equation.

$$dC_v dt = G - \Lambda \quad (15)$$

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where Λ represents all losses of structural carbon (i.e mortality + litter-fall) and its form depends on which LSM is being used.

We make the further assumption that NSC is lost at a rate proportional to the loss of structural carbon. Equation (1 in the original manuscript) then becomes:

$$dC_{NSC}dt = \Pi_G - G - R_p - W_{NSC}\Lambda \quad (16)$$

Substituting equations (15 and 16) into equation (1) gives

$$dW_{NSC}dt = \Pi_G C_v - (1 + W_{NSC}) G C_v - R_p C_v \quad (17)$$

To evaluate ϕ and α we then follow the same procedure as described above for uncoupled simulations. Doing so we find,

$$\phi = 1 + a_{K_m} F_Q^*(T)(1 + \alpha f_{NSC}) (\Pi_G C_v)^* \quad (18)$$

and

$$\alpha = CUE^*(1 + f_{NSC})(1 - f_{NSC}CUE^*) \quad (19)$$

Again, these can be evaluated using GPP, NPP, biomass and temperature data from a single site, if available or using observed carbon residency time and carbon use efficiency at larger scales if not.

2. I felt a number of the plots were a little redundant. In fact, if you run their code, I'd say the time-series of NSC, perhaps with the addition of changing water availability, would be more insightful as to how the model works.

We appreciate your comment and note that the second reviewer also requested we include time-series of NSC. We attach a new figure of predicted NSC mass fraction in each plot from SUGAR (fig. 1). We also attach new figures that compare

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time-series of predicted plant respiration (fig. 2) and PCE (fig. 3) from JULES and SUGAR. The reason for their initial omission was that besides the annual means of respiration and PCE presented in fig 6, there are no data for respiration, PCE or NSC to evaluate against the models against. We felt that since we could not evaluate any of these time-series against empirical data, it would not be worth including them in the manuscript. However, we accept your point that in terms of showing how the model works, these figures are much more useful than the figures provided.

3. I was a little bothered about how different the implementation of NSC actually was from LSMs that assume excess GPP goes into a labile pool, which is then used for growth/respiration? If I'm doing the authors a disservice here then I apologise, but perhaps a few more words outlining this distinction are required. I guess the bigger point I'm making here is that I was anticipating clear hypotheses about *how* and *when* such a labile pool would be used. I do not see these. For example, does the plant aim to maintain a minimum labile pool? What sets this? How big a pool does it accumulate? How would these things vary between PFTs? In the same way, what about the timing of utilisation? The authors spend the introduction sets up a clear link to water stress and this model as a plausible buffering mechanism. But the treatment of water stress in the manuscript is insufficient. It occurs to me that the authors are assuming that a plant will regulate GPP in the same way with and without a NSC pool (this is implied by the offline implementation). But does this make sense? The details are not given, but presumably in JULES water stress reduced the assimilation rate via reducing V_{cmax} . But if you have a NSC pool, would that imply a plant might be a little riskier? If it has some stockpile, why be quite so sensitive to water availability? I have nothing to support this line of thinking, but it seems pretty testable and logical (if only to me!).

In SUGAR, both respiration and growth depend on NSC pool size, meaning that only NSC is available to support respiration. This is supported by the recent work by Collalti

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et al. 2019, that shows that respiration is neither strongly correlated with photosynthesis or total biomass but controlled more by labile carbon reserves. This is an important distinction between SUGAR and other representations of NSCs or labile carbon in other LSMs. As far as we are aware, many representations of NSC used in LSMs calculate respiration before considering the NSC pool meaning that when respiration demand exceeds total assimilate and reserve carbon, it is possible for either or both the growth flux or NSC pool to enter a negative state. This essentially means that the entire biomass pool is available to support respiration, which we know is not possible in plants

In this paper, we have focused on the original development of SUGAR and its first-order impact on fluxes (respiration and growth). Follow-up research, which will comprise the second and third chapter of my PhD, is ongoing to determine plant strategies for maintaining a minimum NSC pool size. We do not plan on including these further results in the paper but have responded to the reviewer questions below and will include some of this in the discussion section of our revised manuscript.

How and when is the pool used?

The pool is updated every model time step (which can range from half-hourly to daily timescales), so it is essentially always in use. Photosynthesis is only used to replenish the pool, while respiration and growth are always supported by the pool. The pool therefore represents both old NSC storage and more recent instantaneous assimilates. We will amend the current manuscript to make this clearer.

How does the plant maintain NSC?

The plants in SUGAR do not actively aim to maintain NSC. The NSC content is currently controlled purely by asynchrony between GPP and PCE. Forests are able to maintain NSC levels if specific photosynthetic rate ($\pi_G = \Pi_G C_v$) remains constant. Specific photosynthesis is of course not constant and varies in response to changing climatic conditions which induces changes in the NSC pool. However, if

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the perturbations in specific respiration cancel out over the period of, for example 1 year, then the NSC pool will be maintained over that year. If these perturbations do not cancel out, as is the case in the TFE simulation at Caxiuanã, then the NSC pool is depleted. In these simulations we are looking at the first order effect that this variation in NSC has on carbon fluxes and are neglecting further coupled effects that this may have on either vegetation dynamics or photosynthesis, which we felt were beyond the current scope of this current manuscript. Nonetheless, as pointed out by the reviewer, these are important processes that may significantly change the behaviour of plants within SUGAR, and hence are the focus of current ongoing research. Again we do not plan on including further results on this in this paper but below is a short discussion on these processes that we will include in our discussion section in a revised manuscript.

Coupling the NSC pool to vegetation dynamics:

1. Litterfall and mortality driven by NSC depletion:

If the specific photosynthesis declines then this will cause a decrease in NSC mass fraction. We have explored the effect that this has on predictions of respiration and growth in this paper, but in theory this should also have an effect on vegetation dynamics. If NSC reserves remain depleted, and maintenance respiration is down-regulated as a result (as predicted by SUGAR) for a prolonged period, then we would expect this to be accompanied by a loss of biomass through either mortality or increased litter-fall, depending on how mortality is represented in the LSM being used. Representing this process is clearly a challenge given the scarcity of data directly showing carbon starvation induced mortality/biomass loss. SUGAR, however, can be used as a tool to test possible representations of these processes and drive and direct data collection.

2. Active storage:

We are exploring the possibility of allowing the parameter ϕ to vary in time in response to either NSC content or specific photosynthetic rate, so that the plants

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are able to actively regulate how NSC is used for respiration and growth depending on how much NSC or photosynthate is available. This may be necessary if specific photosynthesis declines significantly in models as forests grow (something we have found in JULES). Allowing ϕ to vary in time would also help to prevent the NSC pool from accumulating to unrealistic levels, although this is not a problem we have encountered too often and so we do include such a detailed discussion on this.

Water stress and coupling the NSC pool to photosynthesis

The only interaction with water availability comes through the already existing interaction with GPP in JULES. Coupling the NSC pool to GPP is again an important process but one we thought beyond the current scope of the model. Given recent developments in modelling stomatal closure and hydraulic damage (Eller 2019) this is something we hope to explore.

4. As I said above, the results are pretty convincing, but they are also indirect. There is nothing to support the model results being for the right mechanistic reasons. We have nothing that shows us the NSC timeseries (not shown) is supported experimentally from the through-fall experiment. We have nothing to say the respiration from this pool is supported experimentally. In both cases, I suspect a reader will anticipate such plots, I certainly did. Do such data exist? I have no idea if they do or not.

We regret that scaled-up NSC and plant respiration time-series do not exist from the throughfall experiment. This is in part, because scaling NSC measurements up to a whole plant and whole plot scale is difficult and has extremely large associated errors (Quentin 2015). Consequently, time-series of whole forest NSC stocks cannot be generated to a useful level of accuracy. This is similarly true for respiration data which is usually collected at an organ level. We have attached new figures of both NSC and

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respiration time-series since as you rightly mentioned before they give a better idea of how the model works, however, unfortunately we are unable to include observations in these figures. In follow-up research we hope to evaluate SUGAR further at other Amazonian sites, where respiration data may be available through other measurement methods, i.e. via eddy-flux measurements.

5. Finally, the authors put forward an argument that the NSC model results at the throughfall experiment are limited by the poor representation of water stress on GPP in JULES. This is testable. All the authors have to do is make the GPP reduction less sensitive to water stress and plug these GPP values into their model. My suspicion is that the agreement with the obs may not improve, but I might be wrong. It would be worth testing this rather than speculating.

This is a very good suggestion and we attach two figures (figs. 4 & 5) which are the same as figures 5 and 6 in the original manuscript but with JULES simulations where the soil moisture stress has been reduced. The soil moisture stress in JULES is represented by multiplying photosynthesis by a piece-wise linear function of soil moisture, the so called ' β function'. Beta can be between 0 and 1, where 0 is complete soil moisture stress and 1 is no soil moisture stress. We have reduced the sensitivity of photosynthesis to soil moisture by simply defining a new beta function, $\beta' = \min(\beta * 1.5, 1.0)$. This is clearly not a scientifically justifiable method, but for a quick and easy first look at how this would affect our results we think that it is acceptable. First looking at the control panel in both figures, you can see that this has not had a large effect on the model predictions, which is to be expected since there is already little soil moisture stress in the control simulations. With respect to the TFE plot, looking first at the bar graph of carbon fluxes, you can see that the reduction in soil moisture stress has improved predictions of PCE in both models, particularly in the start of the experiment. SUGAR in particular now accurately captures PCE in the first 4-5 years of the experiment where JULES does not. However, looking at predictions of NPP and respiration, as well as the accumulated NPP figure, you can see that while

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SUGAR more accurately captures PCE, it is not capturing the allocation between NPP and respiration correctly. JULES interestingly now captures NPP accumulation in the TFE plot quite well. This is perhaps not too surprising since the assumptions made in SUGAR are relatively simple. In particular, this highlights that the assumption that growth and respiration have the same dependence on NSC may not hold for the TFE plot and that the forest is in some way prioritising respiration over growth. This in itself is an interesting result and we would be happy to include the above analysis and discussion in the revised manuscript.

Introduction

To be honest, I found the whole first paragraph completely unrelated to the focus of the paper. I think the paper would really benefit from a more relevant opening paragraph, entirely up to the authors what they do here, just a suggestion.

The first paragraph was written to provide a brief overview of the wider context of general land surface modelling. However, we agree that it is perhaps a step too far away from the focus of the paper and so in our revised manuscript we will remove the first paragraph and use what is currently the second paragraph which has a closer focus to the paper topic.

Pg 2, In 24: "and so plants rely heavily on their NSC reserves". Are there any numbers to support this statement? How heavily? For how long?

There is unfortunately little data on an ecosystem scale that directly quantifies how much NSC is used during periods of drought, because, as stated above, coming up with whole plant estimations is still extremely complex and suffers from huge levels of uncertainty. The evidence of large discrepancy between utilisation and assimilation (Metcalfe et al. 2010, Doughty 2015 a,b) is given to imply that NSC must be relied upon during these periods, but we aren't aware of any ecosystem level measurements

C13

that directly show NSC dependence. We will reword this to reflect the uncertainty, e.g.: "and so plants rely heavily on their NSC reserves" → "which implies that plants rely heavily on NSC reserves"

Pg 2, In 41: what is the evidence for carbon starvation leading to mortality? My understanding is that it is essentially non-existent outside of a few potted experiments? See for example, Adams et al. A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. I think this could be more carefully phrased.

This is a good point and it is true that there is not a large amount evidence that shows plants dying directly from carbon starvation. However, the point that we were trying to make here is that it is actually still not clear what the main driver of plant mortality is during drought. The theory tells us that both carbon starvation and hydraulic failure have the capacity to kill plants, but directly observing either process is extremely challenging. Nonetheless, what the literature actually shows is that plants are unlikely to die exclusively of carbon starvation or hydraulic failure and although one may trigger the path towards mortality, both carbon starvation and hydraulic failure are likely to be part of the mortality process (Sevanto et al. 2013). It is also likely that the two processes are not independent of each other since both carbon assimilation and water loss are controlled by stomatal conductance (Rowland et al. 2015). Consequently, capturing drought induced mortality will likely require representations of both hydraulics and carbohydrate storage. The other point to make is that most droughts do not actually lead to mortality and plants are resistant to most natural declines in water availability. The most important things to understand, therefore, are how plants are able to withstand drought and how they recover from them afterwards. We would argue that to understand these two processes requires an understanding of the theoretical threats that face plants during drought, and that while there is sparse evidence to show that carbon starvation is a significant killer during drought does not mean we should neglect it as a threat. Modelling NSC storage in LSMs may present

C14

an opportunity to test the relationship between carbon starvation and hydraulic failure, in particular in conjunction with recent developments of stomatal modelling (Eller et al. 2018). It is probably fair to say that this is not really clear in our current manuscript and we have not really discussed the relationship between the two processes. We would be happy to include the above discussion in our revised manuscript to make our position clearer on this.

Pg 3, Second paragraph "Despite...". Obviously biased, and feel free to ignore...but I will draw your attention to "Mahmud et al. Inferring the effects of sink strength on plant carbon balance processes from experimental measurements. Biogeosciences.", which I think is a nice attempt to exploit experimental data to help mechanistically unpick the role of sink control. I highlight this paper because the focus was specifically to aid model development - "This can largely be attributed to a scarcity of ecosystem level data (NSC content and distribution) that can be used to parametrise and evaluate models for a range of species and climates that covers all plant functional types (PFTs) C3 BGD Interactive comment Printer-friendly version Discussion paper used in LSMs".

This is definitely a useful piece of work and thank you for bringing it to our attention. The revised manuscript will include this as an example of available NSC data for use in modelling efforts. It may also be useful in current and future work and developments of SUGAR where specific utilisation rates may vary depending on NSC build up or depletion as briefly discussed above.

Methods $\hat{\text{A}}\hat{\text{T}}\hat{\text{A}}\hat{\text{T}}$ * Is there any supporting evidence for the assumptions in SUGAR? It's fine if there isn't but it might be nice to cite some relevant literature if there is. For example, section 2.2...

This is a good suggestion and we note that the second reviewer also commented on the lack of discussion on some of the assumptions made in SUGAR. Below is a

C15

discussion of the key assumptions in SUGAR and some justification behind them, which we will include in the model description to go alongside the model equations. The main assumptions in SUGAR are:

1. GPP is all collected by a single pool of carbohydrate (sugars and starches are not distinguished) which is entirely readily available for respiration (R) and growth (G).

The is a simplification that we believe is necessary to represent NSC dynamics in large-scale land surface models like JULES, and it is a necessary assumption to keep the model simple and parameter sparse. There is obviously no evidence to support a single NSC pool that is readily available for use. In theory we could apply SUGAR to multiple organ tissues (eg. In Rastetter et al 1991), however, this would require representation of transport between the pools, which are difficult to represent and parametrise. Also many LSMs do not represent distinct wood tissues such as heartwood. Many LSMs, including JULES, split biomass allometrically between carbon pools and splitting the NSC pool in this way would not add any new dynamics to the model.

2. G and R vary with temperature as a Q_{10} functional with a q_{10} value of 2.0.

The Q_{10} function is a commonly used representation of the response of plant respiration and growth to temperature and a q_{10} value of 2.0 is also a standard value (Ryan 1991). Changing the temperature dependence in SUGAR would be a relatively easy procedure and so this could be explored in future work, however, for the purposes of this work we felt that using this more simple representation would be sufficient.

3. G and R depend on NSC via a Michaelis-Menten function.

The Michaelis-Menten equation is a widely used description of enzyme kinetic which can be applied to both plant respiration and growth Thornley (1971).

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4. R and G have the same NSC dependence

The assumption that maintenance respiration and growth share the same NSC dependence essentially reduces maintenance and growth respiration to one variable. Combining equations (4), (7) and (8), total plant respiration can be written as:

$$R_p = (R_{m0} + 1 - Y_g Y_g G_0) F_Q(T) C_v C_{NSC} C_{NSC} + K_m C_v$$

which, using that $\phi = R_{m0} + G_0 Y_g$ and equation (14), can be written as:

$$R_p = (1 - \alpha\alpha) G$$

It can therefore be interpreted that all respiration is associated with the growth of new structural material. This is explored in Thornley (2011). Using this assumption, Thornley is able to replicate the same results that are achieved using the more classical maintenance-growth respiration paradigm. For SUGAR this assumption is an important one that drastically simplifies the parameter estimation process, which was one of the main aims of developing the model. While we recognise that it is indeed a simplification of reality, we felt that the work in Thornley (2011), was sufficient justification given the benefit that using it provides.

In 2.5, it would be useful for the parameter ranges to be given to the reader? The section is titled parameter estimation but I've got no idea after reading it what values were used. I think a table with assumed parameters and/or ranges would be very useful for a reader who wished to repeat any of this. Currently, the only defined terms are the Q10 and Yg. For example, in the results: "All other parameters (Yg, aKm , q10) are kept constant at their default values (see model description)." Where was the value of aKm given?

We have updated this section to make the parameter evaluation process clearer.

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We have also included parameter ranges where appropriate in the new parameter table above. With regards to a_{K_m} , we acknowledge that this not a well evaluated parameter, in the sense that it is not evaluated using empirical data. The default value of 0.5 was chosen since it gives numerically stable results (smaller values of a_{K_m} can cause numerical instability with the commonly used minimum time-step of 1 hour). Larger values of a_{K_m} also mean that the saturation effect that is provided by using michaelis-menten kinetics do not come into effect within a reasonable range of NSC concentrations. We accept that this is not a scientifically rigorous justification and so attach amended plots (figs. 6 & 7) from the Caxiuanã simulations with an in-built sensitivity study for a_{K_m} . The range of a_{K_m} values tested is 0.1-2.0. These figures will replace figures 5 and 6 in the original manuscript.

I think the methods would benefit from a few sentences/paragraph explaining how the model works beyond the equations. Most of the introduction set up an interpretation of the use of NSC during periods of water stress but this theme is not returned to once in the methods. How does water stress interact here? It clearly isn't directly, but just comes about due to growth demand? What about the timescales of utilisation or storage increase? My reading of the model is that there is no specific hypothesis being tested here about increases in NSC. It is simply the difference between C uptake and utilisation. I don't really see that this goes beyond what many LSMs currently assume with respect to a excess carbon storage pool. I was expected a hypothesis about how plants might aim to maintain a storage pool, which I do not see. Equally, something about how they might prioritise a draw-down of this pool.

We refer back to the above discussion on NSC maintenance in point 3 of this response and to the discussion of model assumptions in the first point under methods—. We will include these discussions in the revised manuscript to give a clearer description of how the model works outside of the equations and the distinction we see from previous work.

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Pg 6: "optimised so that annual GPP and NPP in the control forest agree with observations." What specifically was optimised here?

We used a previous configuration of JULES that had been parametrised using data from Caxiuanã but found that GPP was being underestimated relative to the control data from Metcalfe et al. 2010 and Da Costa et al. 2014) so we increased leaf nitrogen content, which increased predicted GPP.

Specifically we changed parameters:

vint from 7.21 to 12.0

vsl from 19.22 to 25.0

We also changed fdr from 0.01 to 0.0075 to correct carbon use efficiency in the control plot. The same parametrisation was then used in the TFE simulation.

Surely the SUGAR model was simple enough to just embed in JULES. Some further explanation is warranted here as to why this wasn't just done...

We are currently working on coupling SUGAR into JULES. The reason we did not do this in this paper is that it introduced some unexpected questions about how NSC interacts with processes including competition, mortality and land use change which are all modelled in the vegetation dynamics module in JULES (TRIFFID). There are also issues that relate to long term growth in JULES in which as the forest grows, specific photosynthesis declines and the forest is unable to maintain NSC concentration. We are looking at solving this by introducing an implicit active storage component to SUGAR by allowing ϕ to vary in time in response to either carbohydrate content or specific photosynthesis rate.

We recognise and accept that these are potentially very impactful processes

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that may change the assumptions in SUGAR, however, ongoing work on this is suggesting that on the time-scales of the simulations in this paper, there will not be a significant change in the behaviour of SUGAR, and therefore the results of this work, beyond the realm of standard differences between coupled and uncoupled model simulations. Our main aim here was really to explore how SUGAR affects predictions of carbon fluxes (i.e respiration and growth) and we are aiming to look at vegetation dynamics (by coupling to TRIFFID) in future work.

Results

As a general statement, I found it odd to start with the spatial interpretation rather than a site-level analysis. Doing it this way round is harder to see how the model is really working and to me (at least), it would make more sense to reverse the presentation of the results. Or alternatively, it would be useful to see a time-series extracted from Fig 2. For example, "This decline in seasonal variation is caused by an increase in dry season carbon expenditure and a decrease in the wet season carbon expenditure.". It would be nice to see this...

The aim of the spatial experiment was to demonstrate that modelling NSC has a significant impact on large scale ecosystem modelling, which is really the main purpose of SUGAR. The Caxiuanã experiments were then conducted to provide a more detailed evaluation, at a scale where data could be easily compared to the model output. Our main aim is to demonstrate that modelling NSC does not have a negligible effect on predictions of ecosystem carbon fluxes, rather than to improve simulations of the Caxiuanã drought experiment, which is why we have presented the simulations in this order. However, we accept that the spatial experiment does not clearly demonstrate how the model works so we attach a time-series of basin averaged simulated PCE along with the basin average driving GPP, that shows more clearly what SUGAR is doing to predictions of PCE (fig. 8).

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I understand Fig 2 is a sensitivity experiment, but how are we meant to interpret whether the SUGAR model is improving / degrading growth predictions? I can see that increasing the f_{NSC} dampens the variation, but is this dampening supported in any way? I wonder if Fig 3 is strictly necessary? It seems to be implied by Fig 2, I feel like you need one or the other. Perhaps it is a supplementary figure. I'd much rather a few time-series plots!

Unfortunately data that is sufficiently resolved to see this buffering effect at a basin scale doesn't exist, as far as we are aware. For this reason we originally only looked at the general effect that SUGAR has using statistical metrics rather than presenting time-series.

The implication of Fig 4 is that the respiration assumption in the model becomes more important as f_{NSC} increases. How sensible is the assumed respiration eqn...this seems quite important.

The respiration equation is certainly not as detailed as many models but we feel that it captures the essential elements (i.e temperature and carbon availability). Please see the discussion on the key assumptions of SUGAR, above in point 1 of Methods in this response.

In the first paragraph of 4.2, it would be good to explain why JULES NPP and SUGAR NPP differ at all? If there is no water stress where does this difference come from? Do the models have different respiration assumptions? A shift in time-scale of growth?

SUGAR, at least in part, buffers any change in GPP (see new Caxiuanã PCE time-series plot). In the control simulations there is natural seasonal variation in GPP that is buffered by the NSC pool, which changes both respiration and growth relative to

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JULES. This change is relatively small since the variation in GPP is small compared to the TFE simulation, but is sufficient to cause changes in the predictions of NPP.

Following the sensitivity experiment in Fig 2 onwards, my interpretation was that it was therefore not obvious how to parameterise the model. As such, I was expecting to see some form of uncertainty envelope around the SUGAR model line in Fig 5? How was SUGAR parametrised in this set of runs? I found this very unclear in my head at this point of the manuscript.

In the Caxiuanã simulations, SUGAR was parametrised using the first year of output data from JULES (i.e the year before the panels were put in), together with empirical data as described in the parameter table above. Parameters, f_{NSC} , q_{10} and Y_g were parameterised using empirical data or commonly used values as described above. Parameters α and ϕ were parametrised using the first year of JULES output. For example, α was found by taking the average CUE over this year. For a_{K_m} we have since conducted a sensitivity study, since this was the least constrained parameter and our updated plots now show an uncertainty envelope based on allowing a_{K_m} to vary between 0.1 and 2.0. Hopefully this process has been clarified by our discussion above, which we will include in the Methods section of the revised manuscript.

With Fig 5, arguably you don't need panel b, you could perhaps then include a respiration comparison between JULES and SUGAR? No idea what that looks like...

We will include both a comparison of respiration and PCE between SUGAR and JULES as well as the NSC time-series from SUGAR for each plot in the revised manuscript (see attached).

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Parameter	Units	Value (Cax)	Range	Description	Justification
f_{NSC}	kgkg ⁻¹	0.16	0.1-0.4	Equilibrium NSC mass fraction	(Wurth et al 2005)
q_{10}		2.0		Factor by which respiration and growth increase given a 10 degree warming	(Ryan 1991)
Y_g		0.75		Growth conversion efficiency	(Thornley and Johnson
a_{K_m}		0.1-2.0	0.1-2.0	Relates the half saturation NSC mass fraction (K_m) with the equilibrium pool size (f_{NSC})	Sensitivity study carried out
CUE^*		0.32	0.3-0.5	Steady state carbon use efficiency	Used to evaluate α Coupled run: $CUE^*1 + f_{NSC}(1 - CUE^*)$ CUE^* is usually between 0.3 and 0.5 for a tropical forest (Wurth et al 2004, Gifford et al 1998) see parameter evaluation
τ	yr	5.15	1.18 - 6.49	Steady state vegetation carbon residency time	Used to evaluate ϕ . run: $\phi = 1 + a_{K_m} \tau F_Q^*(T)$ Coupled run: $1 + a_{K_m} \tau F_Q^*(T)(1 + CUE^*)$ e.g. (Carvalhais 2004). see parameter evaluation for derivation

f_{NSC} is the fraction of NSC relative to total structural carbon and so estimates of NSC as a fraction of total dry mass should be adjusted to account for non-carbon biomass.

Table 1. Parameters in SUGAR