

We would like to thank both reviewers for their detailed and constructive comments and feedback. We present here the amendments that have been made in our revised manuscript along with the relevant discussion from our first response.

Response to reviewer 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 a table (Table 3, page 37) to show all the parameters in SUGAR, their ranges, and values used in the Caxiuanã simulations where applicable. We have also updated the parameter evaluation section (starting page 5 line 26) so that it more clearly outlines how each parameter should be evaluated. We have added a derivation of the expressions given for ϕ and α to the Appendix (starting page 13 line 3).

Finally we have also updated the methods section to more clearly outline how the parameters are evaluated in both experiments in the paper (Page 7 Line 22 and Page 8 Line 20). 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 have included a new figure of predicted NSC mass fraction at Caxiuanã in each plot from SUGAR (Figure 7, Page 28). We have also added new figures that compare time-series of predicted plant respiration and PCE from JULES and SUGAR (Figures A3 & A4, Pages 31 & 32). 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 may be useful. Since we are unable to evaluate these model outputs and to limit the number of main paper figures we have added these as appendix figures.

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 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 updated the model description section to give a stronger description of the model outside of the equations (Page 4 Lines 2-14).

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.

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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 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.

15 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 good suggestion and we have added two figures (Figures A6 & A5, Pages 33 & 34) 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 by 50%. 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. We have included a short sentence of discussion on this on page 12 lines 10-12.

25 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.

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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. We have removed the first paragraph and reworked the second paragraph to create a more relevant first paragraph (Page 1 lines 32-33 and Page 2 lines 1-13).

35 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 (Metcalf 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 that directly show NSC dependence. We have reworded this to reflect the uncertainty (Page 2 Line 35)).

45 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

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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 have added some short discussion on this to the introduction (Page 2 lines 38-42).

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 now includes this as an example of available NSC data for use in modelling efforts (Page 3 Line 27).

Methods — * 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. We have included some discussion on this in the methods section (Page 4 lines 2-14), the new parameter evaluation section (Page 5 line 26 - Page 7 line 13) and in the discussion section (Page 11 lines 43-55) where briefly discuss some of the caveats of some of these assumptions.

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 agree and as partially described above have updated the parameter evaluation section (Page 5 line 26) and included parameter ranges where appropriate in the new parameter table (Page 36). With regards to a_{K_m} , we acknowledge that this is 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) and sensible NSC mass fractions. We accept that this is not a scientifically rigorous justification and so have amended the Caxiuanã simulations and conducted a sensitivity study for a_{K_m} . The range of a_{K_m} values tested is 0.1-2.0. These figures (Figs. 5 & 6) have replaced the original figures from Caxiuanã (Figs. 5 & 6 of 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 point 3 of this response and to the updated paragraph at the start of the model description (Page 4 lines 2-14).

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 effective 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. We have attached these details in a separate word document as supplementary information.

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 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. We have added a new figure (Figure 2 Page 23) which shows a time-series of basin averaged simulated PCE along with the basin average driving GPP. To restrict the number of main paper figures, we have also moved Figure 2 from the original manuscript to the appendix (Figure A1 page 29).

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 fNSC 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 fNSC 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 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. 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 is 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.

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 have include both a comparison of respiration (Page 32) and PCE (Page 31) between SUGAR and JULES as well as the NSC time-series (Page 28) from SUGAR for each plot in the revised manuscript.

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Response to reviewer 2

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1. Reflecting the lack of observations of NSC stocks and dynamics, the model is designed to be parametrised based on more commonly-available measurements such as biomass and GPP. This is an elegant idea, however some fairly substantial assumptions are made to achieve it, and those assumptions are not well explored here. One key assumption, made in Eq. 8, is that the NSC dependence of maintenance respiration is the same as that for plant growth. The implicit hypothesis is that respiration and growth are equally prioritised under resource limitation. As far as I am aware, there is no clear evidence to support this and it is just as likely that the plant should down regulate growth to maintain respiration-related functions. No reasoning or citations are presented to support this key choice. In my opinion a thorough discussion is necessary.
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We thank the reviewer for this comment and note that the first reviewer also commented on this lack of discussion. We agree that insufficient discussion on the assumptions made in the model is given. We have updated the manuscript to include both discussion on these assumptions and a written description of how the model works outside the equations. Specifically we have updated the first paragraph of the model description so that it is clearer what assumptions are being made and how these determine how the model works (Page 4 lines 2-14). We have update the parameter estimation section (Page 5 line 26) which now includes some references to literature that describes some of these assumptions. Finally we have also included some further discussion on some of the caveats of the assumptions made in the model in the discussion section (Page 11 lines 43-55). Hopefully these amendments have made it clearer a. how the model works in terms of the assumptions made and b. where these assumptions are derived from and their validity. 2. I am also a bit curious about the assumption implied in Eq. 3 that NSC in the heartwood is available to trees to use. Is it posited that there are mechanisms that trees can use to extract this NSC from dead wood, in which case citations are needed, or is this simply an assumption to enable use of the widely available

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total biomass information? The latter would seem perfectly reasonable to me, but then does seem to warrant a short discussion about the fraction of total NSC that is typically found in heartwood (e.g. <15%, Richardson et al., 2015).

The limitation here is that most LSMs like JULES do not represent heartwood versus sapwood. Consequently we are forced to assume that the entire pool is readily available to the forest/plant. 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. We accept that this is again a simplification of a reality, however it is a necessary assumption to keep the model simple and parameter sparse. 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 evaluate. The updated model description now references this (Page 4 line 3).

3. Similarly, there has been clear effort to minimise the number of parameters, but choices of parameter values are not well justified in the text. Parameters a_{Km} and q_{10} are assigned default values with no justification given for the choice. In particular, a_{Km} appears to be central to the results. If clear, strong, justification for the choices cannot be given, then the sensitivity of the results to these parameters should be included in the tests. The parameter f_{NSC} is appropriately treated as a range, although I would have been inclined to set upper limit of the range a bit above that actually observed in a tropical forest to explore the parameter space a bit, but fair enough!

f_{NSC} : It is a good suggestion to extend the range of tested f_{NSC} values. This was not done originally as there didn't seem to be a clear or scientific way to pick a higher value. Additionally the buffering effect of the model seems to saturate at larger values of f_{NSC} and we felt that the transition from no NSC to 'some' NSC was captured fairly well with the given range. Nonetheless, we have extended the range in the simulations and updated the figures (Figures 3 & 4). We have updated the results section 5.1 accordingly (Page 8 line 40 - page 9 line 4).

$q_{10} = 2.0$: This is a relatively standard value for Q10 temperature relationships (Ryan 1991) and is commonly used in DGVMs. 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 a standard value of 2.0 would be acceptable. We have included this discussion in the updated parameter estimation section (Page 6 line 1).

a_{K_m} is admittedly a not 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) and gives sensible NSC mass fractions. We accept that this is not a scientifically rigorous justification and so have amended the Caxiuanã simulations and conducted a sensitivity study for a_{K_m} . The range of a_{K_m} values tested is 0.1-2.0. These figures (Figs. 5 & 6) have replaced the original figures from Caxiuanã (Figs. 5 & 6 of original manuscript).

Pg. 4, lines 11-12. So this means that SUGAR assumes that trees actively allocate to storage to maintain a certain store size. Perhaps acknowledge this decision explicitly here, given the active debate on this (which was introduced in the introduction)?

This section may not be worded particularly well. Currently SUGAR assumes no active storage and NSC content is regulated passively by the asynchrony between GPP and U. The assumption that we are making here is that during non-stressed conditions plants do not rely significantly on their NSC reserves so that over the course of a period of one year, the mass fraction of NSC $\left(\frac{C_{NSC}}{C_v}\right)$ remains constant. We then define the parameter f_{NSC} to equal this constant value, which we evaluate using observed NSC mass fractions (Wurth et al 2005). This is then used to determine NSC turnover rate (ϕ). If over a long period of time these perturbations do not average to zero, as in the TFE simulations at Caxiuanã then the NSC pool will either accumulate or deplete. In this study we look primarily at the first-order effect that this has on ecosystem carbon fluxes (respiration and growth) and have neglected the effects on vegetation dynamics. This is clearly an important process that is the focus of ongoing and future work, but we felt was beyond the scope of this paper. We have updated the model description to make this clearer (Page 4 lines 3-5). Pg. 7, line 8. Is this above-ground NPP or total NPP? If the former, how is the output from SUGAR being adjusted to compensate for this in the evaluation?

Thank you for this comment, it is a good observation as we made a mistake in the original manuscript here. The observations show total NPP except for the root increment component, as this data was not available from the site. The model outputs from SUGAR and JULES are both total NPP and so we have made a correction in Figure 5. For the JULES simulation we

have subtracted simulated root increment ($drootC$) from simulated NPP. Since SUGAR does not distinguish between root, stem, leaf etc we take the fraction $\frac{drootC}{NPP_{total}}$ from JULES and multiply by total simulated NPP in SUGAR. This is then taken from the simulated NPP in SUGAR. Simulated root C increment in JULES is negligible relative to total simulated NPP and so this correction does not qualitatively change our results (see updated figure), but we have updated our results section with the corrected numbers (Page 9 line 56). We have also updated the methods section 4.2.3 (Page 8 lines 29-33) to describe this correction.

Pg. 7, line 16. How is the CV calculated? Annual mean of daily (or monthly) values, followed by taking the mean across the simulated years? Or directly over the whole dataset? I'm trying to understand if this is showing intra- or interannual variability.

CV is calculated as standard deviation/mean so for each gridbox, the standard deviation and mean of simulated PCE are calculated over the entire simulation period which is outputted on a monthly time-step. The mean CV quoted is then the spatial mean across the basin. It is a metric of how variable PCE is over the entire period. Both inter and intra annual variability should be captured by this. To reduce the number of figures in the main text, Figure 2 of the original manuscript has been moved to the appendix and is now Figure A1 (Page 29).

Pg. 8, line 31. Doesn't this imply that the NSC store has been underestimated? Perhaps worth exploring how much storage would be required to maintain respiration and growth and how this is affected by parameters like aKm? This could provide a useful hypothesis for future investigation.

This is essentially what we have tried to explore in the discussion paragraph starting Page 12 line 7 (Pg. 10, line 10. of the original manuscript). Rather than explicitly using SUGAR though, we make an inversion using the observed PCE and predicted GPP by JULES to determine the deficit of carbon required to support growth and respiration.

Pg. 9, lines 42-44. Maybe a bit of over interpretation of small differences here? Overall JULES and SUGAR seem equally good for the control plots in Figs. 5 and 6.

It is true that the models do perform very similarly on the control plot, which is really the main positive result of the control simulations, since JULES is already able to capture control fluxes quite accurately. However, the models do perform differently on shorter time-scales, which we think is still an important result that follows on from the basin level simulation results in section 4.1. Admittedly the original figures (5&6) don't really show this very well. The differences are better illustrated by the new plot of monthly PCE in SUGAR and JULES (Figure A3, Page 31). This figure shows how PCE is buffered against the natural seasonal variation in GPP that the control forest experiences in JULES. The annual averages of PCE within JULES and SUGAR are very similar on the control plot, but as can be seen in this figure, the seasonal variation is different.

Pg. 9, line 51. Whilst the down-regulation of respiration in response to depleting NSC may help buffer NPP, it clearly doesn't improve the simulation of respiration, which is more strongly underestimated in SUGAR than in JULES from 2005 onwards. I think this discussion needs to reflect that whilst SUGAR provides a very useful representation of a process we are confident is important, including this process does not by itself radically improve the overall carbon flux simulation for the drought experiment investigated.

This is a fair comment and we have now include this in our updated discussion section (Page 11 line 43). While SUGAR doesn't improve respiration predictions, it does improve predictions of total PCE for the first 5-6 years of the experiment. The reason that the prediction of respiration is not improved relative to JULES is related to the allocation to growth and respiration in SUGAR. We have shifted the discussion of our results from NPP and respiration to the prediction of total PCE and also included more of a discussion on allocation of C between growth and respiration during drought.

Fig. 5. It would be helpful to also see time-series of respiration and NSC storage to allow a full and balanced interpretation.

We note that this was also requested by the other reviewer and so we have included time-series of predicted NSC in the control and TFE plot at Caxiuanã (Figure. 7, Page 28). We have also included new figures comparing both predicted PCE and respiration from JULES and SUGAR (Figures A3 & A4). The reason for their initial omission was that besides the annual respiration presented in Fig 6., there are no data for R and NSC to evaluate these plots. We agree that to allow a full understanding of how the model is working, it is necessary to have these time-series. However, since we are unable to evaluate these model outputs against observations, and in order to reduce the number of figures in the main text, we have only included the time series of NSC as a main figure and put the PCE and respiration time-series in the appendix.

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The Impact of a Simple Representation of Non-Structural Carbohydrates on the Simulated Response of Tropical Forests to Drought

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Abstract. Accurately representing the response of ecosystems to environmental change in land surface models (LSM) is crucial to making accurate predictions of future climate. Many LSMs do not correctly capture plant respiration and growth fluxes, particularly in response to extreme climatic events. This is in part due to the unrealistic assumption that total plant carbon expenditure (PCE) is always equal to gross carbon accumulation by photosynthesis. We present and evaluate a simple 35

model of labile carbon storage and utilisation (SUGAR), designed to be integrated into an LSM, that allows simulated plant respiration and growth to vary independently of photosynthesis. SUGAR buffers simulated PCE against seasonal variation in photosynthesis, producing more constant (less variable) predictions of plant growth and respiration relative to an LSM that does not represent labile carbon storage. This allows the model to more accurately capture observed carbon fluxes at a large-scale drought experiment in a tropical moist forest in the Amazon, relative to the Joint UK Land Environment Simulator LSM (JULES). SUGAR is designed to improve the representation of carbon storage in LSMs and provides a simple framework that allows new processes to be integrated as the empirical understanding of carbon storage in plants improves. The study highlights the need for future research into carbon storage and allocation in plants, particularly in response to extreme climate events such as drought.

10 *Copyright statement.* TEXT

1 Introduction

Correctly representing the balance between plant photosynthesis, growth and autotrophic respiration in the land surface model (LSM) component of Earth System Models (ESMs), is crucial to making accurate projections of global climate in the future. Forests cover nearly 4000 Mha (UN Food and Agriculture Organization Rome, 2015) of the world's land surface and ~~store roughly 850 Pg (861±66) of carbon (Pan et al., 2011).~~ They represent a significant sink of carbon from the atmosphere, sequestering $2.4 \pm 0.4 \text{ PgCyr}^{-1}$, roughly 25% of total annual anthropogenic carbon emissions (IPCC, 2014). ~~The extent to which carbon uptake by forests will continue under future climate change is uncertain, as global climate models (GCM) disagree not only on the magnitude of future terrestrial carbon uptake, but also the sign (Cox et al., 2000; Sitch et al., 2008; Hewitt et al., 2016; Arora et al., 2013). Some models predict large increases in terrestrial carbon stocks by the end of the century, while others predict significant losses, with an uncertainty in projections of more than 160PgC by the year 2100 (Lovenduski and Bonan, 2017). Much of this uncertainty stems from deficiencies in the structure of the land surface model (LSM) component of GCMs and is exacerbated by positive feedback loops between the land and atmosphere (Lovenduski and Bonan, 2017; Huntingford et al., 2009, 2013; Friedlingstein et al., 2001) Significant improvements in LSMs are required to constrain model outputs and reduce uncertainty in future climate projections. The carbon balance of forested ecosystems is dictated by the relative magnitudes of photosynthesis, plant growth and autotrophic respiration.~~ Most LSMs simulate growth and respiration as equal to instantaneous photosynthesis (Fatichi et al., 2014). Consequently at any given time, the total rate of carbon utilisation by respiration and growth, referred to as plant carbon expenditure (PCE), is equal to the rate of carbon accumulation by photosynthesis, commonly referred to as gross primary productivity (GPP). However, in reality growth and respiration are not so strictly coupled to photosynthesis and plants regularly experience periods when the supply of carbon from photosynthesis does not equal the demands of growth and respiration (Körner, 2003; Muller et al., 2011). This asynchrony between supply and demand is facilitated by reserve pools of labile carbon known collectively as non-structural carbohydrates (NSCs). The NSC pool within a plant accumulates when photosynthesis exceeds carbon demand and is drawn upon to sustain growth and respiration when they are not supported by instantaneous photosynthetic assimilation (Hartmann and Trumbore, 2016; Dietze et al., 2014). NSCs therefore act as a buffer, allowing key functional processes to be maintained, even when photosynthetic accumulation is low. This buffering is particularly important during periods of environmental stress, which can lead to reduced productivity over seasonal to multi-annual time-scales. During prolonged periods of stress, carbon utilisation rates can diverge significantly from photosynthesis (Metcalf et al., 2010; Doughty et al., 2015b, a) and so implying that plants rely heavily on their NSC reserves during these periods. Without simulating NSC storage LSMs remain unable to capture this asynchrony between GPP and PCE and so fail to correctly simulate forest level respiration and growth fluxes.

The ability to sustain respiration and growth during periods of reduced productivity is an important process that can allow plants to survive, and recover from extreme short-term climate events, such as drought (Doughty et al., 2015b). ~~Consequently, NSC dynamics are also inextricably linked to plant mortality.~~ Under low water availability the transport of water from roots to other organs can be compromised by the cavitation of xylem tissue in the plant (Martínez-Vilalta et al., 2014; Sperry and Love, 2015; Tyree and Sperry, 1989). Xylem damage can lead to a drop in hydraulic conductance, resulting in damage to plant tissue and increased risk of mortality (Rowland et al., 2015; Anderegg and Anderegg, 2013; McDowell et al., 2008). Plants combat this threat through control over the aperture of their stomata. Closing the stomata reduces water loss through transpiration and lowers the risk of xylem damage and hydraulic failure. The trade-off to this strategy is a

reduction in productivity. The ability of a plant to employ this strategy is therefore reliant on its ability to store and utilise NSC. If carbon demand exceeds supply over long periods of drought, NSC reserves. Carbon starvation and hydraulic failure are tightly linked processes (Mitchell et al., 2013; Adams et al., 2017), not only because of their shared dependence on stomatal conductance, but also due to the role that carbohydrates have in processes such as osmoregulation and potentially in refilling of embolised xylem (Sevanto et al., 2014). Carbon starvation may accelerate the effects of hydraulic failure and in some cases, itself lead directly to mortality (Galiano et al., 2011; Adams et al., 2013). Recent developments in modelling plant hydraulics (Mencuccini et al., 2019; Eller et al., 2018; Sperry et al., 2017; Baker et al., 2008) provide more accurate predictions of stomatal behaviour during drought, however, these developments must also be accompanied by models of carbon storage in order to effectively simulate the trade-off between hydraulic damage and productivity loss. ~~If carbon demand exceeds supply over long periods of drought, NSC reserves will become exhausted, causing essential elements of plant function to fail, a process termed ‘carbon starvation’.~~ ~~Carbon starvation can also lead to increased mortality rates (Galiano et al., 2011; Adams et al., 2013) and so there is a complex balance between stomatal closure and NSC storage (Mitchell et al., 2013; Adams et al., 2017) that must be captured by LSMs in order to accurately capture climate driven mortality~~ Until such developments are made, predictions of plant mortality and recovery in response to climate extremes such as drought will remain uncertain.

Accurately simulating forest mortality is vital to accurate predictions of climate. This is particularly true in tropical regions where terrestrial carbon storage is large (Pan et al., 2011) and forests are frequently subjected to intense periods of environmental stress. Intense dry periods can reduce vegetation productivity and increase plant mortality in the tropics, over both short-term (Phillips et al., 2009; Bastos et al., 2018; Luo et al., 2018; Gloor et al., 2018) and multi-annual time-scales (Rowland et al., 2015; Meir et al., 2018; Metcalfe et al., 2010; Fisher et al., 2007; da Costa et al., 2010). When combined with the effects of fire and land-use change, drought can cause regions such as the Amazon basin to shift from a net sink to a net source of carbon to the atmosphere (Gatti et al., 2014; Liu et al., 2017; Phillips et al., 2009). Loss of terrestrial carbon in the Amazon represents a significant feedback loop in the climate system (Cox et al., 2000) and large losses of biomass could cause drastic and irreversible changes to the climate. However, the nature of this ‘tipping point’ is uncertain, and without accurate representation of forest resilience, including the balance between hydraulic failure and carbon starvation, predictions of large-scale forest die-back will remain unreliable. Drought is predicted to increase in both frequency and severity across the tropical rainforest biome in response to climate change (Marengo et al., 2018; IPCC, 2014). Accurately simulating drought responses is, therefore, a priority for the global modelling community (Corlett, 2016; Fatichi et al., 2016), although many efforts to date have focused on simulating plant hydraulic properties and have largely ignored the development of a NSC pool in models.

Despite their clear role in forest function, our current understanding of how NSCs are produced, stored and used remains poor (Hartmann and Trumbore, 2016). Absolute pool sizes are difficult to quantify (Quentin et al., 2015) and it is not clear how NSC reserves are distributed and transported between different plant organs under stress (Martínez-Vilalta et al., 2016; Sevanto et al., 2014). It is also not clear whether NSC storage is the passive result of asynchrony between supply demand as described above, or whether plants also have the capacity to actively regulate NSC stores at the expense of growth and respiration (Körner, 2003; Palacio et al., 2014; Wiley and Helliker, 2012). This may go some way to explaining the apparent absence of substrate-based modelling approaches within many LSMs. Some optimised modelling studies have been conducted that explore models of NSC storage and the substrate limitation of respiration and growth (Thornley, 1970, 1971, 1972a, b, 1977, 1991, 1997, 2011; Thornley and Cannell, 2000; Dewar et al., 1999). These provide a theoretical framework to develop mechanistic models of NSC storage and utilisation (Hemming et al., 2001; Fritts et al., 2000; Salomón et al., 2019) that allow detailed simulations of plant function. However, there have been few attempts to develop such models in a manner that would be compatible with large scale LSMs (De Kauwe et al., 2014). 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) used in LSMs (Fatichi et al., 2019). Given Site level studies that explore how the components of plant carbon expenditure respond to environmental change (e.g. Mahmud et al., 2018; Metcalfe et al., 2010), provide useful insights into the role of NSCs within a plant and can guide model development. Nonetheless, given our current knowledge and data-availability it is necessary to develop a simplistic-parameter sparse model that can be easily-parametrised off-calibrated against data sources that can be more effectively collected (e.g. growth and respiration data), yet capture the essential characteristics of representing a NSC pool (e.g. de-coupling photosynthesis from growth and respiration). Such an effort will not only constrain future climate projections, but may also be used to stimulate further research that improves our empirical understanding of NSC storage and use.

In this study we present ‘Substrate Utilisation by Growth and Autotrophic Respiration’ (SUGAR), a simplified model of substrate utilisation, designed to work within an LSM. The aim of the model is to allow the decoupling of PCE and GPP in

order to provide a more accurate representation of respiration and growth fluxes, in particular in response to environmental stress. To demonstrate its behaviour and applicability to large scale ecosystem modelling, we use SUGAR to simulate PCE fluxes over the Amazon basin, using GPP data from an ensemble of LSMs, constrained by global fluorescence measurements from the Greenhouse Gases Observing SATellite (GOSAT) (Parazoo et al., 2014) as driving data. We assess the sensitivity of the model to initialised NSC content, within a reasonable range of possible pool sizes and assess the changes the model makes to predictions of ecosystem carbon expenditure. We also test the model under stressed and non-stressed conditions by simulating the world's longest running tropical rainforest through-fall exclusion (TFE) experiment and corresponding control forest in the Caxiuanã National forest, Brazil, over a 16-year period. Previous simulations of the TFE experiment by multiple LSMs has highlighted their inefficiency at capturing the effects of the artificial drought on forest function (Powell et al., 2013). It remains unclear to what extent the lack of NSC dynamics is responsible for the discrepancies between model predictions and observations in these previous studies. We examine the role NSC dynamics has on model predictions during the drought by post processing the output of one of these LSMs, namely the Joint UK Land Environment Simulator (JULES). We compare the results from JULES and the new predictions from SUGAR to observations (Metcalfe et al., 2010; da Costa et al., 2014) as well as a time-series of net primary productivity (NPP) derived from data collected in Rowland et al. (2015).

2 Model description

Our 'Substrate Utilisation by Growth and Autotrophic Respiration (SUGAR)' model simulates a single pool of carbohydrate at a gridbox scale, for each vegetation tile, ~~and is~~ (Fig. 1). ~~Sugars and starches are not distinguished meaning that all carbohydrate is readily available to support respiration and growth. Representing just a single pool in this way keeps the model simple and parameter sparse making integration into an LSM much easier. SUGAR is designed to sit below the photosynthesis component of a LSM (Fig. 1).~~ Assimilated carbon from photosynthesis (GPP) is collected by the NSC pool and the total carbon allocated to respiration and growth is then calculated and taken directly from the NSC pool. ~~The respired carbon is released into the atmosphere and the carbon allocated to growth is given to the demography component of the LSM to be allocated to structural pools.~~ ~~pool is therefore always active and is constantly depleted by growth and respiration, and replenished by photosynthesis.~~ Both growth and respiration ~~depend on temperature and the amount of carbohydrate in the NSC pool relative to the total structural biomass~~ are assumed to be single substrate enzyme reactions and depend on NSC content via the Michaelis-Menten equation. Respiration and growth both depend on temperature via the standard Q_{10} function (Ryan, 1991). Carbohydrate content is not actively regulated by the plants in SUGAR meaning that variations in NSC stores are the passive result of asynchrony between photosynthesis and PCE caused by variations in climate.

2.1 Non-structural carbohydrate pool

The rate of change of NSC content (C_{NSC}) is described by:

$$\frac{dC_{NSC}}{dt} = \Pi_G - R_p - G \quad (1)$$

where Π_G is canopy GPP, R_p is total plant respiration, and G is plant growth.

Using the definition of net primary productivity (Π_N):

$$\Pi_N = \Pi_G - R_p$$

equation (1) is written as:

$$\frac{dC_{NSC}}{dt} = \Pi_N - G \quad (2)$$

To quantify the size of the NSC pool we consider ~~the model under steady state. Under steady state conditions we assume that the NSC mass fraction, defined as the ratio of NSC to structural carbon, is invariant. We denote the steady state mass fraction an unstressed forest at steady state. We define the average or equilibrium NSC pool size at steady state as a fraction of total structural carbon biomass and denote it by f_{NSC} (Eq. (3)), which we also use. This is then used to initialise the model NSC pool.~~

$$f_{NSC} = \left(\frac{C_{NSC}}{C_v} \right)^* \quad (3)$$

where C_v is structural carbon biomass and the asterisk indicates steady state.

2.2 Growth

Plant growth depends on temperature and NSC availability. The temperature dependence is assumed to follow a Q_{10} exponential relationship and the NSC dependence follows Michaelis-Menten reaction kinetics: 10

$$G = G_0 F_Q(T) C_v \frac{C_{NSC}}{C_{NSC} + K_m C_v} \quad (4)$$

where G_0 (yr^{-1}) is the maximum specific growth rate at the reference temperature 25°C , T ($^\circ\text{C}$) is temperature, C_v (kg C m^{-2}) is total structural carbon biomass, K_m is a half saturation constant equal to the NSC mass fraction at which growth rate is half of its maximum value at the reference temperature and related to the steady state NSC mass fraction by Eq. (6), and $F_Q(T)$ is the Q_{10} temperature dependence given by: 15

$$F_Q(T) = q_{10}^{0.1(T-25)} = \exp\left(\ln(q_{10}) \frac{(T-25)}{10}\right) \quad (5)$$

where q_{10} , which is a constant taken to be 2.0 by default.

The half saturation constant K_m is expressed as a fraction (a_{K_m}) of f_{NSC} .

$$K_m = a_{K_m} f_{NSC} \quad (6) \quad 20$$

and where a_{K_m} is a constant with the default value of 0.5

2.3 Respiration

Plant respiration is split into maintenance and growth components. Growth respiration is calculated as a constant fraction of plant growth:

$$R_g = \frac{1 - Y_g}{Y_g} G \quad (7) \quad 25$$

where Y_g is the growth conversion efficiency, or yield, with a default value of 0.75 (Thornley and Johnson, 1990).

Maintenance respiration has the same temperature and NSC dependence as plant growth:

$$R_m = R_{m_0} F_Q(T) C_v \frac{C_{NSC}}{C_{NSC} + K_m C_v} \quad (8)$$

where R_{m_0} (yr^{-1}) is the maximum specific rate of maintenance respiration at the reference temperature 25°C . 30

2.4 Total carbohydrate utilisation

The total rate of NSC utilisation, U , is defined as the sum of plant respiration and growth:

$$U = R_p + G \quad (9)$$

U here is exactly equivalent to PCE and is only denoted differently for convenience and ease of reading. Using this definition, Eq. (1) can be written as:

$$\frac{dC_{NSC}}{dt} = \Pi_G - U \quad (10)$$

Since both respiration and growth have the same NSC and temperature dependence, U is given by:

$$U = \phi F_Q(T) C_v \frac{C_{NSC}}{C_{NSC} + K_m C_v} \quad (11)$$

where $\phi = R_{m_0} + \frac{G_0}{Y_g}$ is the maximum specific rate of utilisation of carbohydrate at the reference temperature 25°C .

2.5 Parameter estimation

Values of ϕ , R_{m_0} and G_0 may be found in terms of commonly measurable variables. °C.

3 Parameter estimation

Detailed time-series data of forest level NSC stocks are extremely difficult to collect and are therefore scarce. This makes parameter evaluation difficult. Here we discuss the evaluation process for each parameter in SUGAR. Some of these parameters, for example the q_{10} parameter, have standard or commonly used values within the LSM literature, and the validity of their given values is beyond the scope of this paper. In these cases we present only a very brief justification. For the remaining parameters, we outline how with a few assumptions we can use the simplicity of SUGAR to evaluate these parameters without the need for detailed NSC data, and instead use more commonly and readily measured variables. An overview of all parameters, their default values and the values used in this study is given in table (2).

First, ϕ is related to the steady state structural carbon turnover time τ , by the parameter a_{K_m} and the steady state Q

– q_{10}

The q_{10} parameter represents the factor by which respiration and growth increase with every 10°C of warming. The exponential Q_{10} function ($F_Q^*(T)$): function is commonly used to describe the temperature dependence of plant metabolism in LSMs with the standard q_{10} value of 2.0 (Ryan, 1991).

– Y_g

The Y_g parameter represents the conversion efficiency of plant growth (Thornley and Johnson, 1990). By default, we assume a value of 0.75, consistent with previous estimates (Thornley and Johnson, 1990), and the parameters assumed in other LSMs (e.g. Clark et al., 2011) It is derived in Thornley and Johnson (1990) and estimated to equal 0.75. Similar parameters are used in other LSMs (e.g. Clark et al., 2011).

– f_{NSC}

The f_{NSC} parameter represents the non-stressed, 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 Würth et al. (2005)). Note that studies such as Würth 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.

– ϕ

The ϕ parameter represents the maximum specific rate of carbohydrate utilisation by plant respiration and growth at the reference temperature of 25°C. To estimate ϕ we consider an unstressed forest at steady-state with an NSC fraction of f_{NSC} . Under these circumstances the forest is neither significantly drawing upon nor adding to the NSC stores and the turnover rate of NSC must equal to the carbon assimilated by photosynthesis. This allows the following expression for ϕ to be found in terms of GPP and forest biomass which are more easily measured at an ecosystem scale than total NSC stocks:

$$\phi = \frac{1 + a_{K_m}}{F_Q^*(T)} \left(\frac{\Pi_G}{C_v} \right)^* \quad (12)$$

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

$$\phi X^* = \frac{1}{\tau_{obs}} \int_{\tau_{obs}} X dt \quad (13)$$

where τ is defined as :-

$$\tau = \frac{C_v}{\Pi_G}$$

To evaluate ϕ , we require an estimate of average specific GPP and average temperature over the period of observation. If SUGAR is used at a single site these can be evaluated directly using GPP, biomass and temperature data where 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. Carvalhais et al., 2014) and the temperature can be found using global climatology data over the same period. 10

– G_0 and R_{m0}

These parameters represent the maximum specific rate of plant growth and maintenance respiration respectively, at the reference temperature of 25°C. To evaluate these parameters we define the parameter α as defined as the ratio of G_0 to ϕ :

$$\alpha = \frac{G_0}{\phi} \quad (14) \quad 15$$

We can then evaluate α again considering a non-stressed forest in steady state, when it is equal to the steady-state average carbon use efficiency (CUE) of the ecosystem over the period of observation:

$$\alpha = CUE^* \quad (15)$$

Again this can be evaluated using data from a single site where available, or using more general estimates of CUE (e.g. Chambers et al., 2004; Gifford, 1995) if not. 20

We then can find G_0 and R_{m0} are then given by: as:

$$G_0 = \alpha\phi \quad (16)$$

and

$$R_{m0} = \left(1 - \frac{\alpha}{Y_g}\right)\phi \quad (17) \quad 25$$

– a_{K_m}

Equations (??) and (??) have been derived by considering the model under steady state conditions (see appendix). Finally, f_{NSC} is set equal to an estimate of ecosystem scale NSC concentration, given as a fraction between 0 and 1. The a_{K_m} parameter relates the half saturation constant (K_m) to the equilibrium NSC pool size (f_{NSC}). It is currently not possible to evaluate a_{K_m} from empirical data. We give this parameter a value of 0.5, as this gives realistic NSC mass fractions. The sensitivity of the SUGAR model to this parameter is examined in this study within the range $a_{K_m} \in [0.1, 2.0]$. 30

4 Methods

4.1 Sensitivity study over the Amazon-Basin

To demonstrate how SUGAR influences predictions of PCE, we conduct a series of simulations over a six and a half year period from June 2009 to December 2015, across the whole Amazon, where f_{NSC} is varied from 0.0005–0.08–0.16. As f_{NSC} 35 represents the initial fraction of the biomass pool that is NSC, a value of 0.0005 is effectively representing a model without NSC. The upper bound of 0.08–0.16 is an estimate of the ecosystem NSC content in a tropical forest in Panama (Würth et al., 2005). The model is driven with monthly GPP data from an ensemble of LSMs constrained by global fluorescence measurements from the Greenhouse Gases Observing SATellite (GOSAT) (Parazoo et al., 2014), and temperature data from CRU-JRA (Harris, 2019). An estimate for τ in each grid-box is found. SUGAR is parametrised as described above with 40 parameters Y_g , a_{K_m} and q_{I0} kept at their default values. A value for ϕ is found for each grid-box using biomass estimates across the Amazon (Avitabile et al., 2016) and the first year of GOSAT GPP. All other parameters (Y_g , a_{K_m} , q_{I0}) are kept constant at their default values (see model description):

To assess the effect that the SUGAR model has on the seasonality predictions of PCE, the coefficient of variation of simulated PCE in each grid-cell is calculated and presented on a colour-mesh map a basin wide average PCE flux is compared 5 to the basin average GPP for each value of f_{NSC} . The Pearson correlation coefficient of simulated PCE and driving GPP, and PCE and the Q_{10} function in each grid cell is also calculated for each value of f_{NSC} and presented on maps.

4.2 Methods - Simulating responses to drought

To evaluate the effectiveness of SUGAR at simulating responses to drought, we tested it at the world's longest tropical drought experiment.

4.2.1 Site Description

The TFE experiment is located in Caxiuanã National Forest, Pará State, Brazil ($1^{\circ}43'3.5''\text{S}$, $51^{\circ}27'36''\text{W}$), where measurements of meteorology and plant physiology of two 1ha plots began in 2001. In January 2002, panels were introduced into one of the plots, excluding c. 50% of rainfall from the soils and subjecting the plot to an artificial drought. Measurements of meteorology and forest physiology continue to the present day (this study looks only up to 2016-12-09). During this period mean annual rainfall was between 1772.6 and 2967.1 mm. Daily incident radiation varied from 419.8 Wm^{-2} to 731.1 Wm^{-2} . A full summary of experimental set up and the most recent collection of results from the site is available in Meir et al. (2018).

At the start of the experiment, total estimated above-ground biomass was $213.9 \pm 14.2 \text{ Mgha}^{-1}$ in the control forest, and $200.6 \pm 13.2 \text{ Mgha}^{-1}$ in the TFE plot. After 13 years of the drought treatment, biomass loss to mortality in the TFE plot had increased by $41.0 \pm 2.7\%$ relative to 2001 values (Rowland et al., 2015). Observations and modelling studies at the site suggest that while GPP declined in response to the artificial drought, PCE was maintained at close to pre-drought levels during at least the first 3-4 years of the experiment (Metcalf et al., 2010; Fisher et al., 2007). NSC reserves are thought to have sustained PCE during this time and it is estimated that the forest had access to c. 20 MgCha^{-1} of available NSC (c. 8% of live biomass) during the drought (Metcalf et al., 2010). It is not possible for LSMs to accurately predict both growth and respiration in the TFE forest without simulating some kind of NSC storage, and makes the experiment an ideal opportunity to test SUGAR.

4.2.2 Simulation descriptions

The TFE experiment and corresponding control plot are simulated over the period 2001-01-01 to 2016-12-09. The first set of simulations are conducted using the Joint UK Land Environment Simulator (JULES) (Best et al., 2011; Clark et al., 2011), driven with the meteorological data collected at Caxiuanã. JULES version 5.2 is used with a pre-existing parametrisation of the site and then optimised so that annual GPP and NPP in the control forest agree with observations. The same configuration is then used to simulate the TFE forest. Both control and TFE plot were initialised and spun up for 176 years using a repeated loop of the control meteorological data. To simulate the effect of the drought experiment, precipitation is halved in the TFE simulation from January 1, 2002, in line with estimates of average exclusion rate.

Gridbox GPP (gpp_gb) and grid-box temperature at 1.5 m above canopy height (t1p5m_gb) outputs from JULES are then used to drive the SUGAR model off-line in each plot. In order to examine how SUGAR compares relative to JULES, it is initialised-parametrised using the first year of output data from JULES (i.e. the year before panels are put in the TFE plot) rather than observations from Caxiuanã (with the exception of an estimate of NSC pool size (f_{NSC}), which is necessary given JULES does not model NSC). The average GPP and biomass of the simulated forest is used to find average specific GPP which is used to evaluate ϕ . The parameter α is evaluated by finding the average CUE of the simulated forest over this year which is then used to evaluate R_{wo} and G_0 . Since the SUGAR simulations are off-line (i.e. not coupled to a Dynamic Global Vegetation Model (DGVM)) we assume that biomass (C_v) remains constant throughout the experiment. This is a necessary assumption that allows the simulations to be performed off-line and the effect of the NSC pool to be examined in isolation. Finally, to test the sensitivity of SUGAR to the parameter a_{K_m} , it is varied from 0.1 to 2.0.

4.2.3 Model Evaluation

Snapshot fluxes (NPP, R_p , PCE) from JULES and SUGAR are evaluated against observations from (Metcalf et al., 2010) and (da Costa et al., 2014) for the periods 2005 and 2009-2011. Model growth output is evaluated against an observed time-series of NPP from both plots. Observed NPP is calculated as the sum of observed biomass increment change does not include root increment due to the difficulty in measuring total root growth at the plot level scale. It is therefore calculated using the above-ground biomass (AGB) increment and total local litterfall (Rowland et al., 2018). litter-fall (Rowland et al., 2018). Both model outputs are altered by removing simulated root increment. In SUGAR this is carried-out using the allometric scaling within JULES. Biomass increment is calculated using tree trunk diameter at breast height (DBH) data and a number of allometric equations (Table 3. The DBH data were collected every 1-3 years for each tree in each plot using dendrometers between July 2000 and December 2014. 2014 (Rowland et al., 2015). The error bars presented are the sum of measurement error from the litterfall data and the 95% confidence intervals of the ensemble of allometric equations. Scaling NSC measurements to a whole plant and whole plot scale is difficult and has large associated errors (Quentin et al., 2015). We therefore evaluate SUGAR primarily against integrated flux and biomass increment data.

5 Results

5.1 Sensitivity study over the Amazon-Basin

In simulations of PCE across the Amazon Basin, the SUGAR model dampens the seasonal variations in both respiration and growth, relative to GPP, maintaining a less variable rate of PCE (Fig. A1). ~~The mean-2). We present the~~ coefficient of variation (CV) of the ~~GPP data across the Amazon is 17.6%~~ (basin averaged GPP and simulated PCE for each value of f_{NSC}). ~~We also present the grid-box bounds of CV which is the coefficient of variation of the least and most variable grid-boxes for each simulation. The CV of the basin average GPP data is 9.51% (grid-box bounds: 7.47 – 40.9%, Fig. A1).~~ When the SUGAR model is initialised with $f_{NSC} = 0.0005$, effectively representing a model with no NSC, the ~~mean CV of PCE across the Amazon is 16.5% (CV of the basin averaged PCE is 9.12% (grid-box bounds: 6.57 – 37.4%, Fig. A1).~~ As f_{NSC} increases the coefficient of variation decreases sharply across all grid boxes. At $f_{NSC} = 0.04$, ~~the CV of variation across the Amazon is 3.73% (grid-box bounds: 3.59 - 29.8%, Fig. A1).~~ The dampening effect starts to saturate at larger values of f_{NSC} and the CV of simulated PCE decreases more slowly with increasing f_{NSC} from this point. At $f_{NSC} = 0.08$, the ~~mean CV value CV of PCE across the Amazon is 8.963.54% (bounds: 3.78 – 25.1%, Fig. A1).~~ Finally at $f_{NSC} = 0.16$ the CV of simulated basin PCE is 3.63% (grid-box bounds: 3.74 - 22.9%, Fig. A1). Increasing the effective size of the NSC pool also reduces the spatial variation in PCE seasonality across Amazonia. Relative to the wetter northern Amazon, the more seasonally dry southern Amazon experiences far greater seasonal variation in GPP. This pattern is mirrored in the seasonal variation of simulated PCE, however, with more NSC in the model the difference between PCE seasonality in the north and south declines, due to a larger decrease in seasonal variation of growth and respiration in the southern regions. This decline in seasonal variation is caused by an increase in dry season carbon expenditure and a decrease in the wet season carbon expenditure. The buffering effect is a consequence of the de-coupling of respiration and growth from GPP, reflected in the decline in the mean correlation coefficient between GPP and PCE from 0.980 (bounds: 0.939 – 1.00) to 0.181 (bounds -0.501 – 0.997) from simulations with the 0 to 8% mass fraction of NSC (Fig. 3). With this decoupling effect there is also a shift in the primary driver of simulated PCE, from GPP (in the 0% NSC mass fraction simulation) to the Q_{10} function (in the 8% NSC mass fraction simulation). This is reflected in the increase in the mean correlation coefficient between simulated PCE and the Q_{10} function (Eq. (5)) in SUGAR from -0.0485 (bounds: -0.651 to 0.517) to 0.637 (bounds: -0.456 to 0.956) in the 0 to 8% NSC mass fraction simulations (Fig. 4).

5.2 Simulations in a tropical moist forest

In the simulations of the control plot, in which the forest was not subject to any artificial drought stress, JULES and SUGAR produce similar results of long term NPP accumulation (Fig. 5), that are both consistent with observations. By the end of the NPP observation period (2014-12-17), JULES predicts a total accumulated NPP of 155.6 MgCha⁻¹ and SUGAR 154.7 MgCha⁻¹. Both results are consistent with observations (Fig. 5, 161.5±22.0 MgCha⁻¹) from the site.

There are some larger differences between JULES and SUGAR on annual time-scales, but in general the models predict comparable annual mean values of control plot PCE, Ra and NPP (Fig. 6). During the first three years of the experiment (2002, 2003, 2004), JULES predicts an annual mean PCE of 35.13 MgCha⁻¹yr⁻¹, and SUGAR predicts 34.79±0.17 MgCha⁻¹yr⁻¹. Both these results lie within the confidence intervals of the observations from the site (Fig. 6, 33.0±2.9 MgCha⁻¹yr⁻¹). The two models differ most in the natural drought years of 2005, 2010 and 2015 in which predicted annual GPP is at its lowest. In 2005 JULES predicts a decrease (relative to the 2002-2004 period) in annual mean PCE to 33.32 MgCha⁻¹yr⁻¹ (-5.15%) whereas SUGAR predicts an increase to 36.18-36.13±0.27 MgCha⁻¹yr⁻¹ (+4.003.85%). The decrease in JULES PCE is caused by a decrease in predicted GPP in 2005. In SUGAR this decrease in GPP is buffered by NSC storage (Fig. 7), and increase in the annual mean temperature drives the increase in predicted PCE. Both results are close to the observed value although the SUGAR result is outside the observed confidence intervals by 0.7800.64%. In 2010 average annual rainfall was 1772.6 mm_{yr}⁻¹, the lowest in the 16 year period (c. 25% decrease on the 16-year mean 2324.2 mm_{yr}⁻¹). This causes a decline in predicted GPP on the control plot from 35.92 MgCha⁻¹yr⁻¹ in 2008 to 32.94 MgCha⁻¹yr⁻¹ in 2010. Consequently, JULES predicts a mean PCE of 33.60 MgCha⁻¹yr⁻¹ over the period 2009-2011 which lies below observed values. SUGAR is able to buffer the forest against the 2010 decline in GPP and allows elevated PCE in 2010 (36.52 36.36±0.36 MgCha⁻¹yr⁻¹) relative to 2008 (34.53-34.52±0.52 MgCha⁻¹yr⁻¹). This allows SUGAR to maintain a mean PCE value over the 2009-2011 period of 36.07-36.00±0.54 MgCha⁻¹yr⁻¹ which is close to observations (Fig. 6).

5.3 Simulating responses to drought

In the TFE plot simulations, SUGAR and JULES diverge significantly in their predictions of NPP, PCE and Ra, with SUGAR more accurately capturing observations than JULES (Figs. 5&6). JULES is able to capture NPP accumulation for approximately 1 year after the start of the drought treatment, however, from 2003 onwards, predicted NPP accumulation drops significantly below the confidence intervals of the observations (Fig. 5). This is driven predominantly by a sharp decline in GPP in response to the declining water availability. SUGAR is able to capture NPP accumulation for much longer and predictions remain within the confidence intervals of the observations until the start of 2009 (Fig. 5). By the end of the observation period JULES predicts a total of 60.6 MgCha⁻¹ of accumulated and SUGAR ~~105.8~~ 105.22 MgCha⁻¹. Neither result lies within observed confidence intervals of the observations (Fig. 5, 126.8±16.9 MgCha⁻¹) although the SUGAR result represents a significant improvement relative to JULES.

During the first 3 years of the experiment, SUGAR is able to buffer a significant decline in predicted GPP on the TFE plot, which drops from 34.90 MgCha⁻¹yr⁻¹ in 2001, to a minimum of 19.61 MgCha⁻¹yr⁻¹ in 2003 (-43.8%). Since JULES does not contain an NSC storage component and PCE is equal to GPP, PCE in JULES also drops by 43.8%, from 34.90 MgCha⁻¹yr⁻¹ in 2001 to 19.61 MgCha⁻¹yr⁻¹ in 2003. As a result JULES predicts a mean PCE value of 24.84 MgCha⁻¹yr⁻¹ over the first three years of drought treatment (2002, 2003, 2004). These values are outside the confidence intervals of the observations and 26.7% below the mean PCE value observed in the TFE plot (33.9±3.6 MgCha⁻¹yr⁻¹, Fig. 6). The SUGAR model is able to maintain PCE at a higher level than JULES during these first three years by drawing upon a mean ~~5.53~~ 5.60±1.01 MgCha⁻¹ of NSC each year to support growth and respiration (Fig. 7). This results in a mean PCE of ~~30.37~~ 30.44±1.01 MgCha⁻¹yr⁻¹ over the period 2002-2004, which lies within the observed confidence interval (Fig. 6). The NSC buffering effect in SUGAR continues in 2005 with SUGAR expending ~~5.80~~ 5.59±0.76 MgCha⁻¹ more carbon than JULES during that year. This means that the predicted annual mean PCE in SUGAR is ~~23.03~~ 22.82±0.76 MgCha⁻¹yr⁻¹ compared to 17.23 MgCha⁻¹yr⁻¹ in JULES. Both results lie below the lower bound of the observed confidence intervals (33.9±3.6 MgCha⁻¹yr⁻¹, Fig. 6), however, the SUGAR result represents a significant improvement relative to JULES. In the latter years of the drought simulations (2009 onwards), the NSC pool becomes significantly depleted (Fig. 7) and the buffering effect in SUGAR (described above) diminishes. Consequently, on annual time-scales, the mean PCE in JULES and SUGAR during the 2009-2011 period are similar (20.76 and ~~21.21~~ 21.20±0.87 MgCha⁻¹yr⁻¹ respectively), although the allocation of carbon to respiration and growth is different, with SUGAR expending more (~~6.70~~ 6.70±0.28 MgCha⁻¹yr⁻¹) carbon on growth than JULES (3.06 MgCha⁻¹yr⁻¹). This difference in allocation allows SUGAR to predict the observed NPP with more skill than JULES, however it means that respiration predictions are reduced relative to JULES and the observations.

6 Discussion

SUGAR alters the relationship between photosynthesis and carbon expenditure. This has implications for simulations of both extreme and more gradual changes in climatic and meteorological conditions. By decoupling PCE from GPP, SUGAR creates a buffering effect that decreases the seasonal variation of carbon expenditure, even in ecosystems where the variation of GPP is already low. As we increase the levels of stored substrate within our simulations, the variability in PCE declines, due to an increased ability to maintain respiration and growth when GPP is low, and replenishment of the NSC pool when GPP is high. This effect is most pronounced in the semi-arid regions of the southern Amazon where there is a strong seasonal cycle in GPP (Fig. A2), corresponding to a strong seasonal pattern of precipitation. Semi-arid regions provide the largest contribution to the global carbon sink anomaly, in part due to this high variability in GPP (Poulter et al., 2014; Ahlström et al., 2015). To represent this contribution, land surface models must capture the response of vegetation to the climate variability experienced in these regions now and in the future. SUGAR provides a mechanistic approach to achieve this by simulating respiration and NPP-growth as a separate function to GPP. Given the strong evidence from observations that NPP and respiration do not have the same seasonal and climatic responses as GPP (Liu et al., 2017; Girardin et al., 2016; Doughty et al., 2015a), accurately predicting future variability in atmospheric CO₂ concentrations (Cox et al., 2013) will be reliant on a sub-model such as SUGAR which can allow this de-coupling to occur. Research demonstrating the importance of highly seasonal arid regions highlights the necessity of substrate-based approaches in large scale ecosystem models and should motivate the community to focus on improving our understanding of NSCs and how to model them.

The sensitivity of the biosphere to climate change has large impacts on the future climate. For example, large losses of tropical forest carbon may represent a tipping point in the climate system that could have highly adverse and irreversible consequences for the global climate (Cox et al., 2000). However, both the nature and likelihood of such a tipping point is

uncertain. Feedbacks between the climate and the carbon cycle mean that small perturbations in the state of the biosphere can make significant changes to the future state of the climate (Friedlingstein et al., 2001). Small changes in the sensitivity of a tropical forest to climate change, may be the difference between the continued absorption of CO₂ by ecosystems such as the Amazon, and the severe die-back scenarios predicted by some models (Huntingford et al., 2013; Phillips et al., 2009). Therefore the difference between a forest that is able to buffer the effects of even a short drought or reduction in productivity, and a forest that is not, may be significant at a global context in the future, even if it appears small in the present day. Non-conservative propagation of perturbations in the state of vegetated ecosystems contributes to large uncertainty in climate models (Huntingford et al., 2009), which greatly reduces our ability to constrain future climate possibilities and tipping points within the carbon-cycle. Accurately representing the response of forest biomass, particularly in the tropics, to changes in climate is crucial to reducing this uncertainty and is a major goal of the climate and land surface modelling community. The buffering effect demonstrated in SUGAR may have an indirect yet large impact on the predictions of future climate by LSMs and provide a more realistic representation of forest sensitivity to climate.

As well as a buffering of carbon expenditure, SUGAR also enables a transition of the primary driver of growth and respiration. With little or no carbohydrate, carbon expenditure in SUGAR is driven predominantly by the rate of photosynthesis (Fig 4). Carbon is used by the ecosystem as soon as it is assimilated, meaning that the rate of expenditure is highly correlated with the rate of photosynthesis. This is often described as ‘source driven carbon dynamics’ meaning that photosynthesis is the key driving flux in determining the carbon balance of the ecosystem. ‘Source driven carbon dynamics’ are at the centre of many LSMs including JULES. As more carbohydrate is added to the ecosystem in SUGAR, temperature becomes the predominant driver of PCE via the Q₁₀ function (Eq. (5), Fig. 4). As more carbon is stored, growth and respiration become less carbon limited and more controlled by the Q₁₀ function within SUGAR. This shift can be seen as a transition towards ‘sink driven carbon dynamics’. Under the theory of sink driven carbon dynamics, environmental variables such as temperature and water-availability exert a direct control over carbon expenditure that can be larger than that of photosynthesis (Körner, 2003; Wiley and Helliker, 2012; Palacio et al., 2014; Fatichi et al., 2014). Processes such as end-product inhibition (Stitt, 1991), in which photosynthesis is inhibited by an excess of assimilate in the leaves, mean that growth and respiration may even exert indirect control over the rate of photosynthesis. The result is that ‘sink’ fluxes (i.e respiration and growth), driven by environmental variables, are the predominant determinants of ecosystem carbon balance. Since the NSC pool in SUGAR does not exert any control over photosynthesis (e.g. via end-product inhibition) the behaviour of SUGAR here cannot be described as truly sink driven. However, SUGAR provides a framework that allows processes such as end-product inhibition to be implemented, and so provides the opportunity to represent both sink and source driven dynamics in LSMs. This allows a greater representation of how the limiting factors of growth and respiration interact with, and respond to a changing climate.

Using the Caxiuanã control simulations we demonstrate that SUGAR and JULES predict very similar long-term NPP accumulation in the natural climate conditions of a tropical moist forest. However, there are larger differences between SUGAR and JULES on an annual time-scale, due to the buffering of the natural variability in GPP by SUGAR. These results further highlight the importance of substrate-based modelling to better capture the responses to natural variation, even under current climate conditions and without extreme events (Doughty et al., 2015a). In the TFE plot, SUGAR makes significant improvements to the prediction of ecosystem carbon fluxes, particularly for accumulated NPP. This improvement is caused by a combination of two processes that occur in SUGAR and that are not present in JULES. The first process is the utilisation of the NSC pool during the early stages of the experiment. SUGAR expends a mean 5.53 Mgha⁻¹ more carbon than is assimilated through photosynthesis in the first three years of drought (2002-2004) and a further 5.80 Mgha⁻¹ in 2005. This allows an increase in both NPP and respiration relative to JULES and is consistent with the analysis in Metcalfe et al. (2010), which suggests the TFE plot was expending 7±4.5 MgCha⁻¹yr⁻¹ more than it was accumulating in 2005, implying that NSC stores were being depleted in response to the drought. The second process is the down regulation of respiration in response to the depleting NSC pool. In the JULES simulations, photosynthesis declines much faster than respiration and, since growth is equal to GPP – Ra in JULES, this means that NPP drops significantly as GPP declines in response to the drought. The result of this effect is that in two years (2005 and 2007), the predicted annual mean NPP by JULES, is negative. Negative NPP is generally considered to be unrealistic, particularly over the time-scale of a year (Roxburgh et al., 2005), and since JULES does not contain a labile carbon pool to support the deficit, missing carbon is taken from the structural pool. The physical interpretation of this is that trees in JULES respire away their structural carbon and shrink. While there is some evidence of recycling and remobilisation of structural compounds, the magnitude of structural carbon being allocated to respiration (via the resulting negative NPP) in these JULES simulations is not realistic. In SUGAR, respiration declines due to the depletion of the NSC pool. This down-regulation of Ra means that a larger proportion of instantaneous GPP is available for NPP, resulting in larger predictions of NPP in SUGAR than JULES, despite similar estimates of total PCE. While ~~NPP (GPP-Ra) may be negative in SUGAR when respiration exceeds photosynthesis, the growth flux that is sent to the structural pools (Eq. (4)) has~~

~~a lower bound of zero. This eliminates the possibility of unrealistic negative growth rates and the respiration of structural carbon~~ this latter process aids the prediction of NPP in SUGAR, it should be noted that observations from Caxiuanã actually indicate an increase in TFE plot respiration between 2005 and 2011 (Metcalf et al., 2010; da Costa et al., 2014). SUGAR is currently unable to capture this increase and this is likely due to the simplicity of the assumptions made within the model. For example, we have assumed that plant growth is directly dependent on carbohydrate availability and temperature only. Water stress may reduce plant growth in SUGAR, but only indirectly by inhibiting photosynthesis and causing a decrease in available carbon. However, in reality plant growth can be affected directly by decreasing water availability through the inhibition of cambial expansion (Balducci et al., 2013; Hsiao, 1973; Boyer, 1970). This decline in growth may even occur before declines in photosynthesis which can cause a build up of NSC and eventually result in an increase in respiration (Fatichi et al., 2014). We are not suggesting that this specific process explains the observed increases in respiration on the drought plot at Caxiuanã, but such interactions between NSC utilisation and the environment are likely to have been important during the TFE experiment. Neither SUGAR nor JULES are able to capture these processes currently. However, by implementing SUGAR within JULES we create a basis upon which we can start to represent these interactions and continue to improve predictions of forest responses to drought.

The ability of SUGAR to accurately capture PCE responses to drought ~~is in these simulations is also~~ somewhat limited by the GPP used to run it. Photosynthesis in JULES has a high sensitivity to reductions in soil moisture (eg., Harper et al., 2016; Williams et al., 2018). In the Caxiuanã simulations JULES predicts an average decline in annual GPP of 4.42 $\text{MgC}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ from 2001 to 2005 in the TFE plot. Combining the observed PCE rates in the TFE plot with the predicted GPP by JULES would imply that the forest is using an average of 10.96 $\text{MgC}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ carbon more than it is assimilating in the first four years. This would then imply that the forest has access to at least 43.86 MgC/ha of NSC, c. 22% of estimated forest biomass. Such a high NSC content is unlikely for tropical forests, which are more likely to have reserves close to 10% (Würth et al., 2005). The other, and more likely explanation is that JULES is overestimating the decline in photosynthesis in response to the drought. To test this, we artificially reduced drought stress in JULES by 50% and repeated the Caxiuanã simulations (Figs. A5 & A6). This improved predictions of PCE in both models, supporting the hypothesis that JULES overestimates the sensitivity of photosynthesis to drought at this site. The recent work to improve stomatal responses to drought stress (Mencuccini et al., 2019; Eller et al., 2018; Sperry et al., 2017) has the potential to significantly improve GPP predictions in LSMs such as JULES. However, there is a clear link between hydraulics and labile carbon storage, given stomatal closure comes at the cost of a reduction in carbon assimilation. The ability of a plant to store and use labile carbon is crucial to its ability to survive, and recover from, drought-induced stomatal closure (Sala and Mencuccini, 2014; O'Brien et al., 2014; Trugman et al., 2018). Without including at least simple representations of NSC storage, the potential of this recent work to improve the representation of stomatal behaviour in response to drought in LSMs, is unlikely to be realised.

SUGAR is a purposefully simple model of NSC storage and is missing some key processes known to be important in defining the complexities of NSC storage and use within a plant. A more complex NSC model might, for example, distinguish between starch and sugar pools, or represent multiple pools for each plant organ, and actively control the input or output of NSC into pools (Martínez-Vilalta et al., 2016; Hartmann and Trumbore, 2016). However, such models would likely require representation of substrate transport between pools and the scaling of NSC ~~values data~~ to the level of trees and forests. Recent advancements in measurement protocols may allow these datasets to be reliably collected (Landhäusser et al., 2018), however, previously the level of uncertainty on such figures has been up to 400% (Quentin et al., 2015). As a result, comprehensive NSC data-sets, measured through time in response to climatic variations and across enough biomes to allow all model PFTs to be evaluated are currently not available. Therefore, this is not a currently viable way to constrain model output. ~~Instead~~ SUGAR is designed to break the direct link between PCE and GPP found in many LSMs and to provide more mechanistic predictions of growth and respiration. It can be parametrised, initialised and evaluated with data that is commonly collected across the globe – Biomass, GPP and temperature (~~to calculate carbon residency time~~); CUE (to find α); and respiration and NPP (for evaluation). It also requires an input of initialised NSC fraction (f_{NSC}) which is not easily measured for an ecosystem, although values of f_{NSC} can be constrained within sensible bounds (Würth et al., 2005). It may also be possible to use SUGAR as a tool to further constrain observed values of NSC content by conducting sensitivity studies of f_{NSC} . Given the existing level of knowledge, it is more robust and realistic to use a simple model such as SUGAR which can be evaluated against more easily available observations such as Ra, PCE, NPP and GPP. As the accuracy and spatial extent of NSC data grows models such as SUGAR can act as a simple skeleton that allows new processes to be implemented into LSMs, to more accurately represent the complexity of plant carbon storage and use.

7 Conclusions

We have developed a simple model of NSC storage, designed to be integrated into an LSM. The model makes significant changes to the variability of growth and respiration predictions in both extreme and more stable climatic conditions. This has large implications for simulations of future climate given the importance of predicting the variability of atmospheric CO₂ concentrations. The model also allows a more mechanistic representation of the limiting factors of carbon expenditure which may become increasingly important as the climate changes in the future. Due to the simplicity of the model it is easily parametrised using pre-existing data and does not require complex datasets of NSC storage which are currently unavailable. This makes the model attractive since it can be easily integrated into LSMs without introducing unreasonable uncertainty in parameter values. The magnitude of the change demonstrates the importance of representing carbon storage in LSMs and we hope will motivate both the modelling and empirical communities to further develop our understanding and model representation of NSC dynamics.

Code availability. A model example of SUGAR for a single site and set up to run at Caxiuanã using output from JULES is available at <http://doi.org/10.5281/zenodo.3547613> For further information or code please contact sj326@exeter.ac.uk

Appendix A: Derivation of model parameters

A1 Derivation of ϕ

~~The NSC model is parametrised using steady state data~~ We start by finding the rate of change of NSC mass fraction,

$W_{NSC} = \frac{C_{NSC}}{C_v}$, in terms of C_{NSC} and C_v :

$$\frac{dW_{NSC}}{dt} = \frac{1}{C_v} \frac{dC_{NSC}}{dt} - W_{NSC} \frac{1}{C_v} \frac{dC_v}{dt} \quad (A1)$$

We consider the case where the NSC pool can be assumed to be in equilibrium. Equation (10) is integrated over the data period, P .

$$\frac{1}{P} \int_t^{t+P} \frac{dC_{NSC}}{dt} dt = \frac{1}{P} \int_t^{t+P} \Pi_G - U dt$$

Using the assumption that the non-structural carbohydrate pools are approximately invariant mass fraction is constant and the left hand side of equation (A1) 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_{obs} , 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 (A1) over this period, it follows that: and set the left hand side equal to zero:

$$0 = \int_{\tau_{obs}} \left(\frac{1}{C_v} \frac{dC_{NSC}}{dt} - W_{NSC} \frac{1}{C_v} \frac{dC_v}{dt} \right) dt \quad (A2)$$

Since we are considering a forest in steady-state, we can neglect the rate of change of structural biomass, $\frac{dC_v}{dt}$

$$\frac{dW_{NSC}}{dt} = \frac{1}{C_v} \frac{dC_{NSC}}{dt} \quad (A3)$$

We then use the equation 1 for the rate of change of NSC:

$$*0 = \int_{\tau_{obs}} \left(\frac{\Pi_G}{C_v} - \frac{R_p}{C_v} - \frac{G}{C_v} \right) dt \quad (A4)$$

and

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

$$20 \quad \underline{U^* \approx \phi F_Q^*(T) C_v^* \phi \int_{\tau_{obs}} F_Q(T) \frac{W_{NSC}}{W_{NSC} + K_m} dt = \int_{\tau_{obs}} \frac{\Pi_G}{C_v} dt} \quad (A5)$$

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

$$\underline{\phi F_Q^*(T) \frac{W_{NSC}^*}{W_{NSC}^* + K_m} = \left(\frac{\Pi_G}{C_v} \right)^*} \quad (A6)$$

Where the asterisk denotes ~~temporal averaging~~ a temporal average over the period τ_{obs} . i.e for variable $X(t)$:

$$\underline{X^* = \frac{1}{P} \int_t^{t+P} X(t) dt}$$

25 X :

$$X^* = \frac{1}{\tau_{obs}} \int X dt \quad (A7)$$

Substituting Eq. (??) and Eq. (??) into Eq. (??) and rearranging using Eq. (3), results in the expression: Rearranging, we find the expression for ϕ

$$\phi = \underline{(f_{NSC} + K_m) \frac{W_{NSC}^* + K_m}{F_Q^*(T) W_{NSC}^*} \left(\frac{\Pi_G}{C_v} \right)^*} \quad (A8)$$

Using Eq. (6), this is further simplified to:

$$\underline{\phi = \frac{\Pi_G^*}{C_{NSC}^* F_Q^*} (1 + a_{K_m}) f_{NSC}}$$

and using Eq. (3) By definition, the average NSC mass fraction is equal to f_{NSC} . Using this and equation (6), this becomes 5

$$\phi = \underline{(1 + a_{K_m}) \frac{1 + a_{K_m}}{F_Q^*(T)} \left(\frac{\Pi_G}{C_v} \right)^*} \quad (A9)$$

Using

$$\underline{\tau = \frac{C_v}{\Pi_G}}$$

~~where τ is the turnover time of structural carbon of the ecosystem, which under steady state conditions is equal to structural~~
This means that to evaluate ϕ , we require an estimate of average specific GPP and average temperature over some reasonable 10
stable unstressed period. If SUGAR is used at a single site these can be evaluated directly using GPP, biomass and temperature
data where available. If these data are not available then the specific GPP can be approximated as the steady state carbon
residency time, ϕ is given by:

$$\underline{\phi = \frac{1 + a_{K_m}}{\tau F_Q^*(T)}}$$

τ (e.g. Carvalhais et al., 2014) and the temperature can found using global climatology data over the same period. 15

A2 Derivation of α

Using Eq.(4) & Eq.(11), the ratio of growth to PCE is: We re-write equation (A4) as:

$$0 = \int \left(\frac{\Pi_N}{C_v} - \frac{G}{C_v} \right) dt \quad (\text{A10})$$

which is, by definition, equal to α . Under steady state conditions growth is equal to NPP and PCE is equal to GPP (from Eq. (2) and Eq. (10)). Hence it follows that: Again we divide by the integration period, τ_{obs} , and assume this can be written as:

$$0 = \frac{\Pi_N^*}{C_v^*} - \frac{G^*}{C_v^*} \quad (\text{A11})$$

hence:

$$\Pi_N^* = G^* \quad (\text{A12})$$

Similarly using equation (A4), we find

$$\Pi_G^* = U^* \quad (\text{A13})$$

Dividing equation (A12) by equation (A13) gives:

$$\alpha = CUE^* \quad (\text{A14})$$

i.e α is equal to the steady state, or mean where $CUE^* = \frac{\Pi_N^*}{\Pi_G^*}$ is the time averaged carbon use efficiency of the ecosystem during the parametrisation period - non-stressed forest over the period τ_{obs} .

Author contributions. SJ, LR, PC, DH and AH developed the SUGAR model code and SJ carried out the simulations. JULES simulations were conducted by SJ with contributions from AH and KW. GPP data from GOSAT were provided by NP. Data from the through-fall exclusion experiment in Caxianã were provided by AdC, PM and LR. SJ prepared the manuscript with contributions from all co-authors. 35

Competing interests. The authors declare that they have no conflict of interest

Acknowledgements. This work has been funded by the Natural Environmental Research Council NE/L002434/1. LR was supported by the UK NERC independent fellowship grant NE/N014022/1. KW was supported by the Newton Fund through the Met Office Climate Science for Service Partnership Brazil (CSSP Brazil). PM was supported by NERC NE/N006852/1 and ARC DP170104091. MM was supported by the Spanish Ministry of Economy and Competitiveness (MINECO) via competitive grants CGL2013-46808-R and CGL2017-89149-C2-1-R. AH acknowledges funding from EPSRC Fellowship EP/N030141/1. 40

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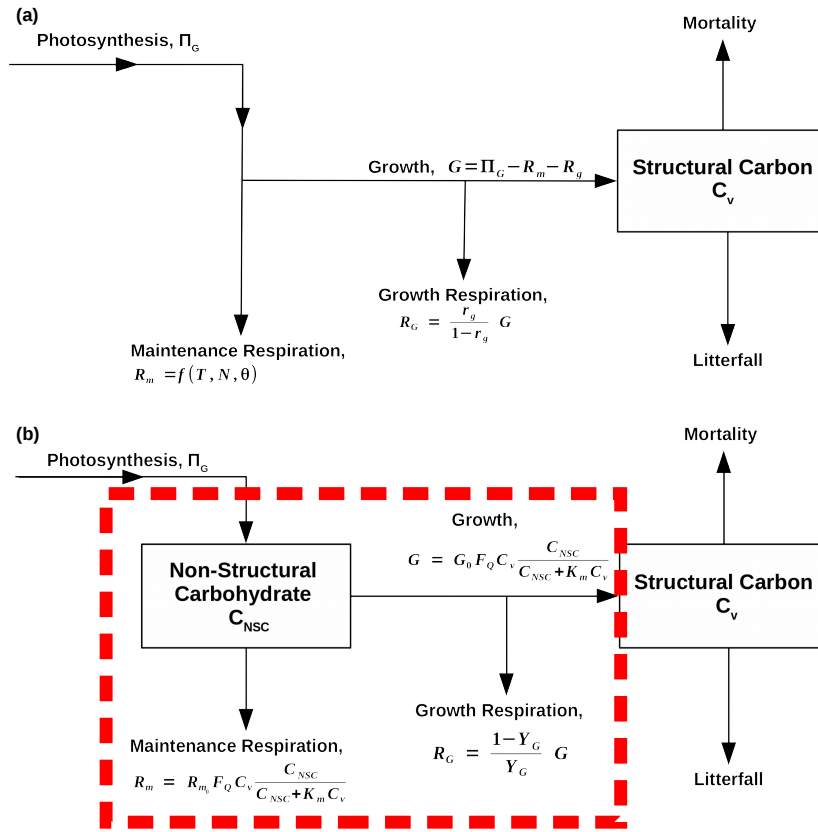


Figure 1. Flow diagrams that demonstrate how SUGAR is designed to change the model structure of carbon allocation within the Joint UK Land Environment Simulator (JULES) (Best et al., 2011; Clark et al., 2011)). Arrows represent fluxes of carbon and black boxes represent carbon pools. **(a)** A representation of the current structure of carbon allocation in JULES. Maintenance respiration (R_m) depends on temperature (T), leaf nitrogen (N) and optionally, water availability (θ). Growth respiration (R_G) is equal to a constant fraction of growth (G) which is equal to photosynthesis (Π_G) less total plant respiration ($R_G + R_m$). Total utilisation of carbon ($R_m + R_G + G$) is always exactly equal to carbon assimilation by photosynthesis (Π_G). **(b)** A representation of how SUGAR would sit within JULES. The red dashed box represents the model boundary of SUGAR. Both maintenance respiration and growth depend on temperature via a Q_{10} function (F_Q), structural biomass (C_v) and non-structural carbohydrate content (C_{NSC}). Growth respiration is a constant fraction of growth.

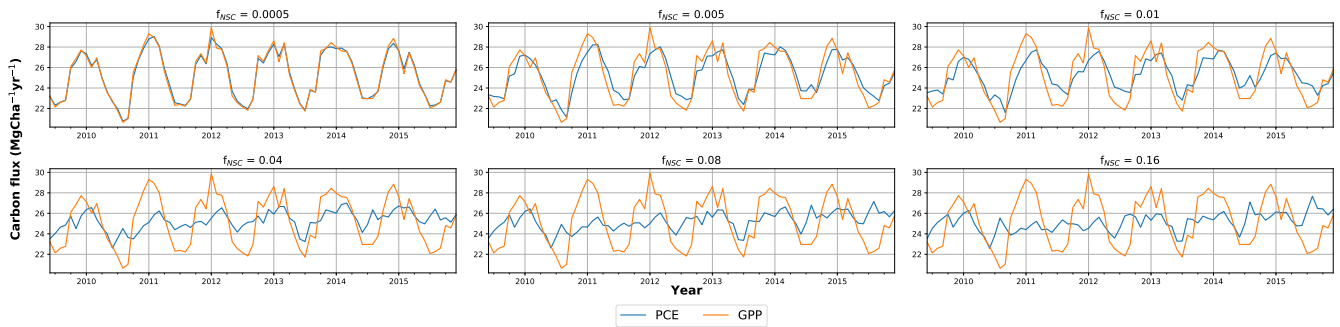


Figure 2. The coefficient of variation of (a) GPP (Parazoo et al., 2014) and (b-f) simulated Plant Carbon Expenditure (PCE) from SUGAR against gross primary productivity (GPP) (Parazoo et al., 2014) for different initialised carbohydrate content as a fraction of grid-box Biomass (f_{NSC}) of grid-box biomass (Avitabile et al., 2016).

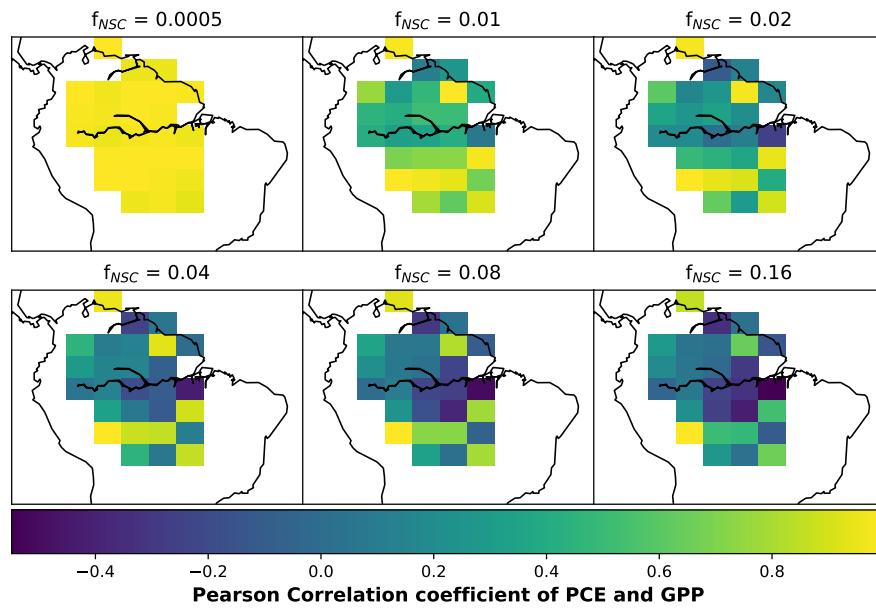


Figure 3. The Pearson correlation coefficient of simulated plant carbon expenditure (PCE) and driving gross primary productivity (GPP) for different initialised carbohydrate contents as a fraction (f_{NSC}) of grid-box biomass. This gives an indication of how important a driver GPP is for PCE in each grid-box.

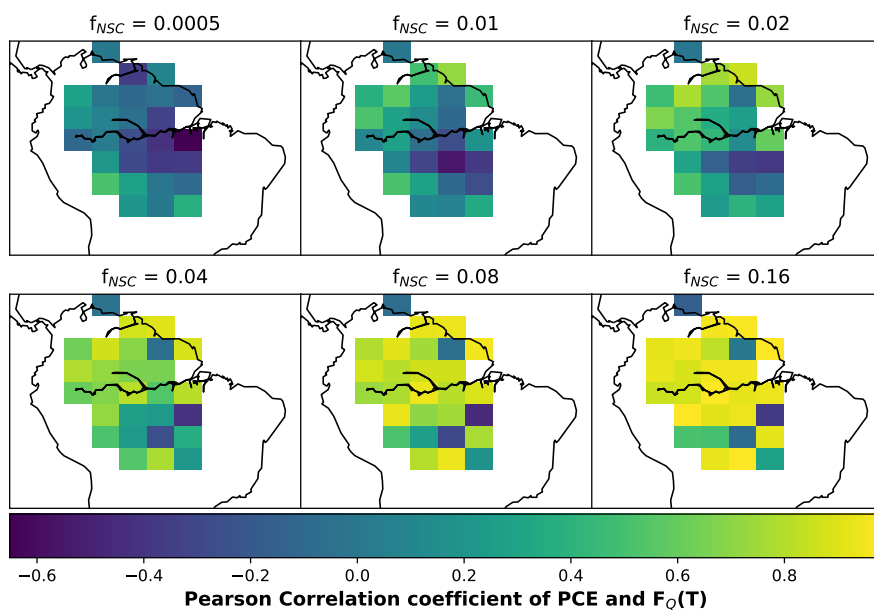


Figure 4. The Pearson correlation coefficient of simulated plant carbon expenditure (PCE) and driving Q_{10} (F_Q) for different initialised carbohydrate contents as a fraction (f_{NSC}) of grid-box biomass. This gives an indication of how important a driver the Q_{10} function is for PCE in each grid-box.

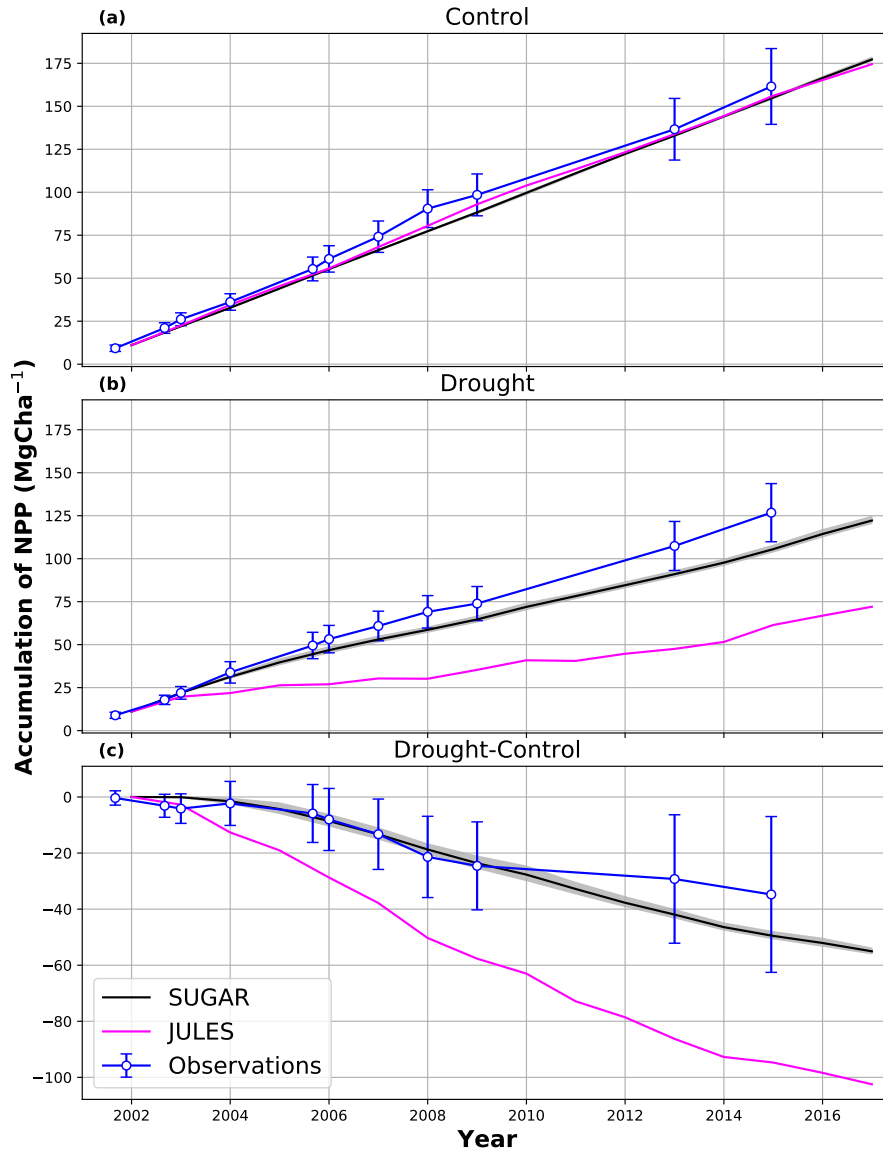


Figure 5. Accumulated Net Primary Productivity at Caxiuanã in (a) Control plot, (b) TFE plot and (c) The difference between the drought and control forest (TFE-control). Observations are calculated as the accumulated sum of [above-ground](#) biomass increment change and [total](#) local litter-fall (Rowland et al., 2018). The presented confidence intervals are the sum of the litterfall measurement error and the 95% confidence intervals of biomass increment calculated from 8 allometric equations using trunk diameter at breast height (DBH) data from Caxiuanã. [The uncertainty envelope on SUGAR represents the maximum and minimum of an ensemble of simulations in which parameter \$a_{K-w}\$ was varied between 0.1 and 2.0.](#)

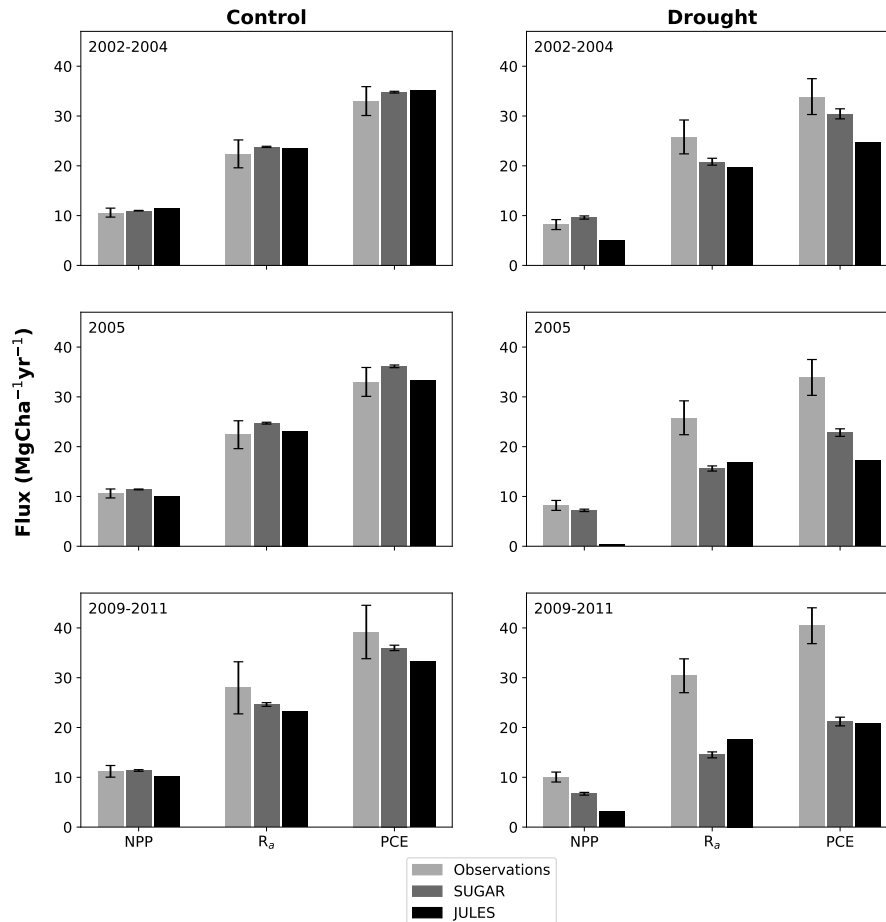


Figure 6. Net primary productivity (NPP), Autotrophic respiration (R_p) and Plant Carbon Expenditure ($PCE = NPP + R_p$); for the periods 2002-2004, 2005 and 2009-2011. The left column is from the control plot and the right is from the through-fall exclusion (TFE) plot. Model predictions from JULES and SUGAR are calculated by taking the mean of each flux over each period. Observations for 2005 are from Metcalfe et al. (2010) and observations from 2009-2011 are from da Costa et al. (2014). Simulated photosynthesis in JULES responded almost instantly to the introduction of the panels on the TFE plot which meant that NPP, R_p and PCE changed significantly in both models between 2002 and 2005. To demonstrate this change we show predicted fluxes during the 2002-2004 period as well as from 2005. Observations for this period are not available to such a comprehensive degree as they are for 2005 and the 2009-2011 period. For this reason we compare the model predictions for 2002-2004 to the 2005 observations. This is reasonable in the control plot where it is plausible that the forest was in steady state (Metcalfe et al., 2010) and so fluxes from 2005 will be similar to those during the 2002-2004 period. In the TFE plot while there were some significant changes in observed carbon fluxes during the first 3 years of the experiment, (for example the production of leaves, flowers and fruits, and fine wood (Rowland et al., 2018; Meir et al., 2018)), the forest largely resisted the effects of the drought during this period (significant increases in mortality were not seen until 2005 (Rowland et al., 2015; Meir et al., 2018)) and so we can similarly expect fluxes from 2002-2004 to be comparable to those from 2005. Nonetheless, care should be taken with these comparisons in both plots. [The error bars on SUGAR represent the maximum and minimum of an ensemble of simulations in which parameter \$a_{K_v}\$ was varied between 0.1 and 2.0.](#)

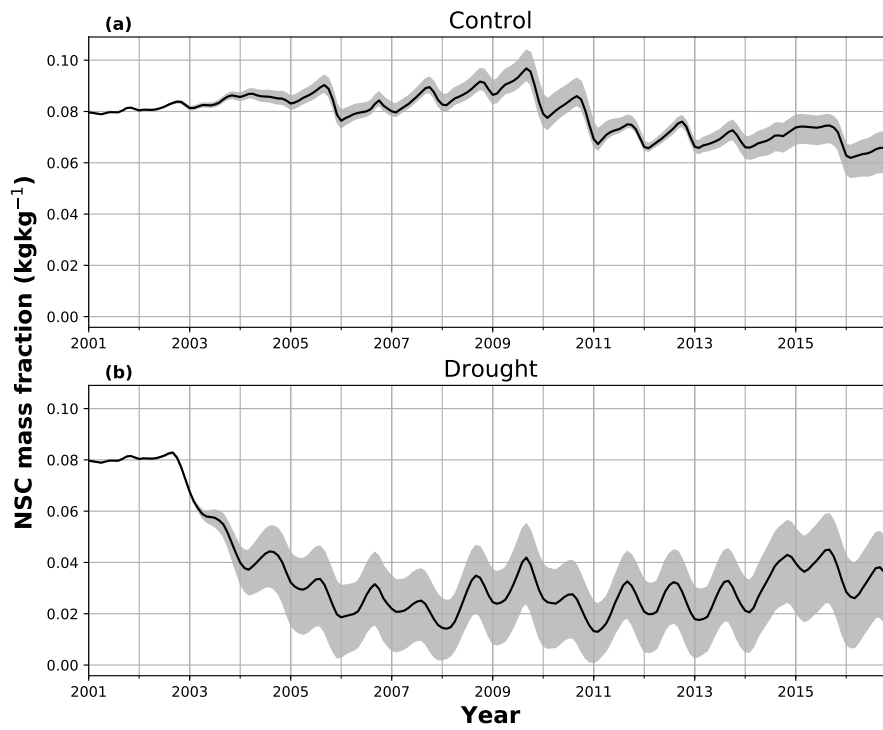


Figure 7. The effect of the parameter $a_{K_{ps}}$ in SUGAR on simulated non-structural carbohydrate (NSC) as a fraction of total carbon biomass, in (a) the control plot and (b) the TFE plot. The mean, maximum and minimum from an ensemble of simulations where $a_{K_{ps}}$ is varied between 0.1 and 2.0 are presented.

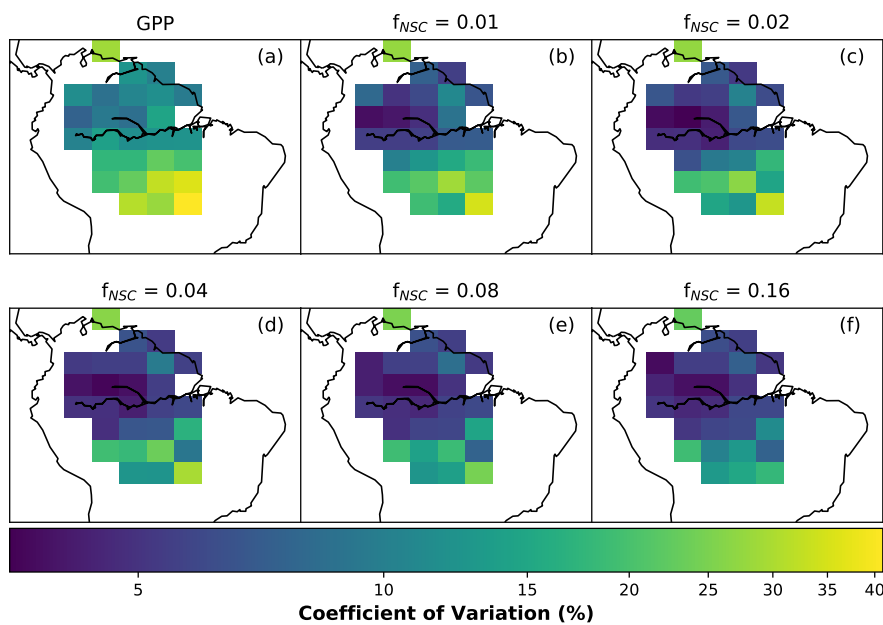


Figure A1. The coefficient of variation of (a) GPP (Parazoo et al., 2014) and (b-f) simulated Plant Carbon Expenditure (PCE) for different initialised carbohydrate content as a fraction of grid-box Biomass (f_{NSC}).

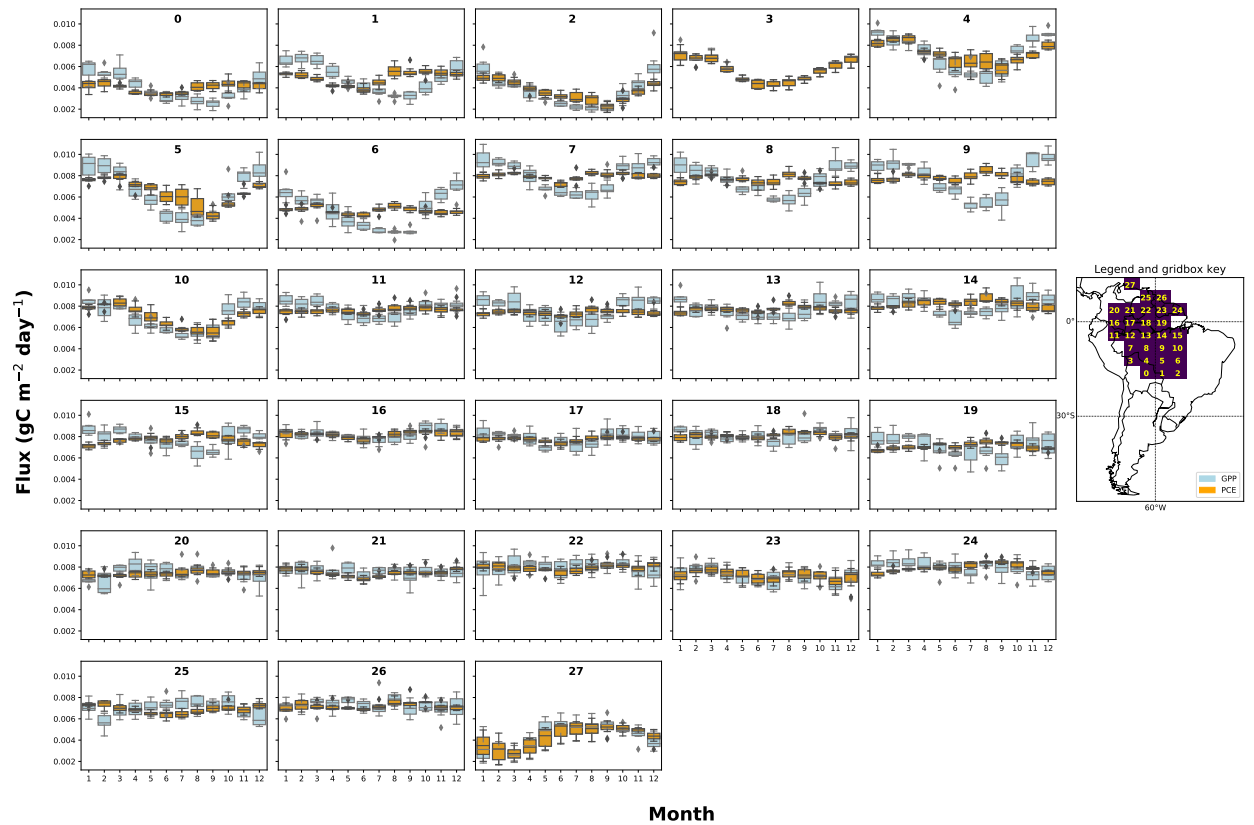


Figure A2. The mean seasonal trend of simulated plant carbon expenditure (PCE) and forcing gross primary productivity (GPP) (Parazoo et al., 2014) for each gridbox in the $f_{NSC}=0.08$ SUGAR simulations. The map key shows which plot corresponds to which grid-box.

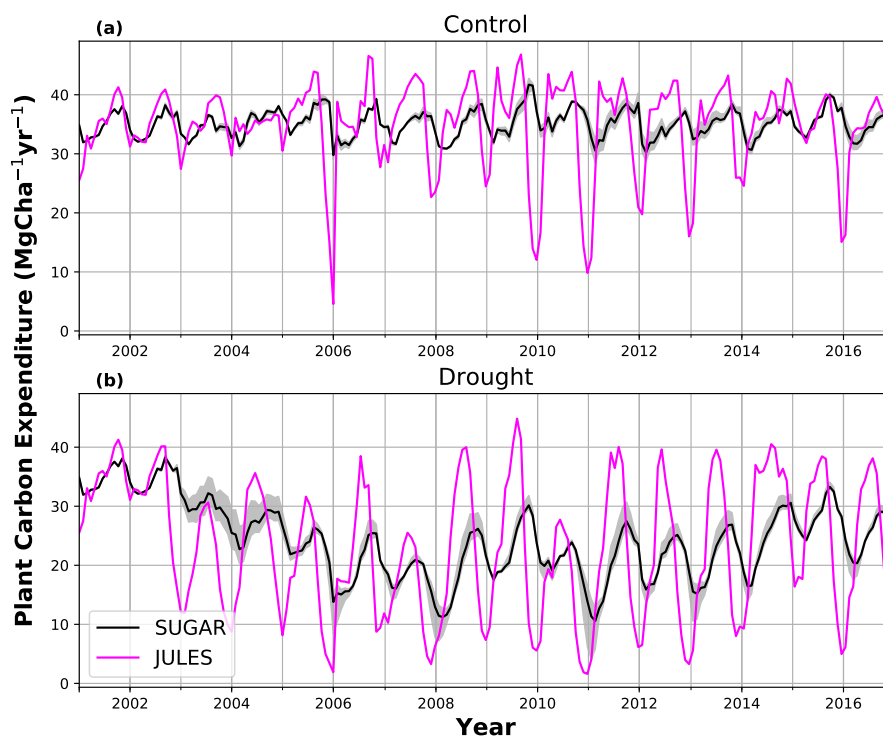


Figure A3. Simulated plant carbon expenditure (PCE) from JULES and SUGAR for (a) the control and (b) the through-fall exclusion (TFE) plots at Caxiuana. A sensitivity study on the parameter $a_{F_{\text{max}}}$ in SUGAR was carried out and the maximum, minimum and ensemble mean PCE are presented. Time-series observations of PCE from the site were not available.

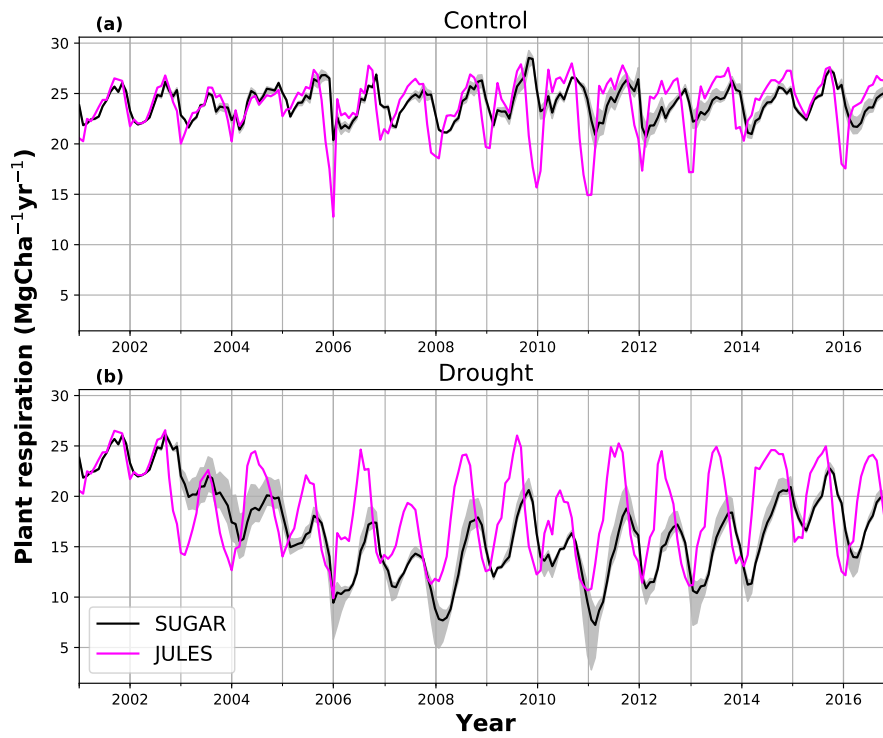


Figure A4. Simulated plant respiration (R) from JULES and SUGAR for (a) the control and (b) the through-fall exclusion (TFE) plots at Caxiuana. A sensitivity study on the parameter $a_{K_{25}}$ in SUGAR was carried out and the maximum, minimum and ensemble mean R are presented. Time-series observations of R from the site were not available.

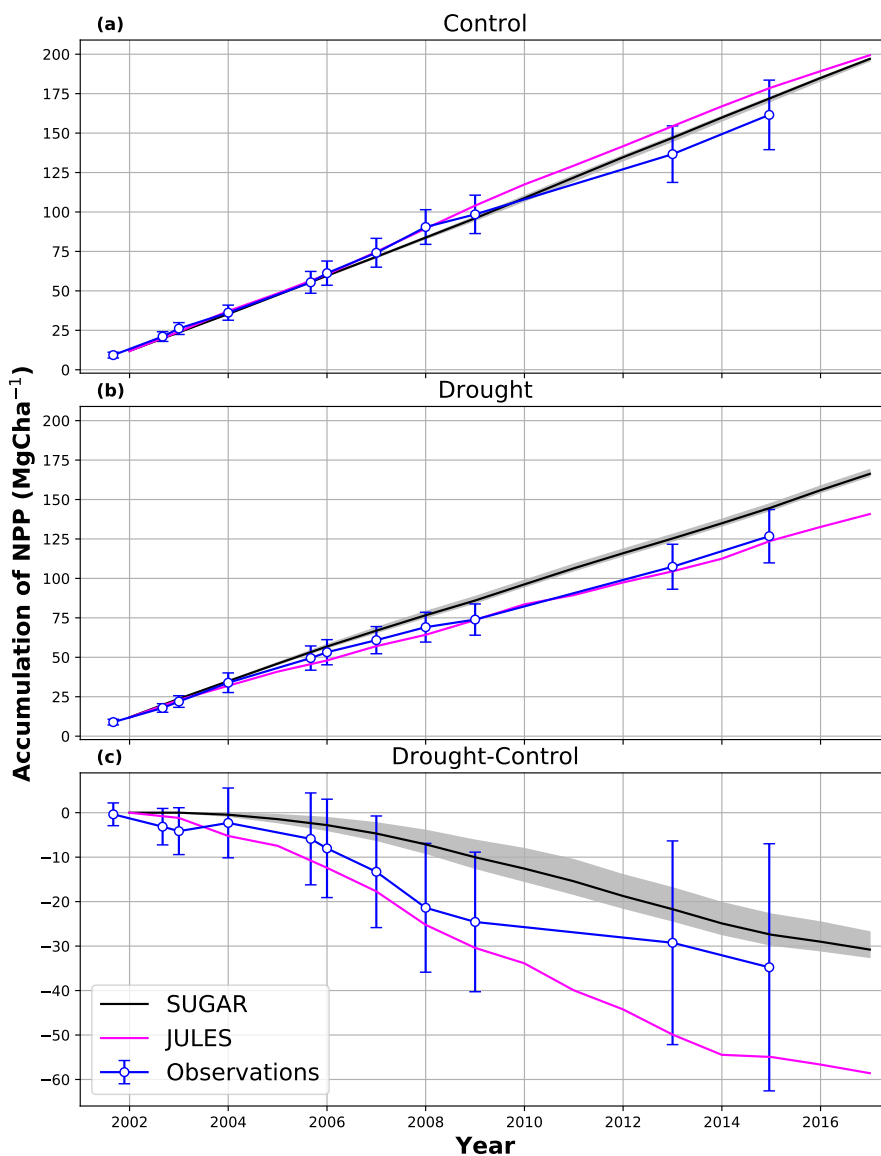


Figure A5. Accumulated Net Primary Productivity at Caxiuanã in (a) Control plot, (b) TFE plot and (c) The difference between the drought and control forest (TFE-control). Soil moisture stress has been artificially reduced in JULES by 50% and the resulting GPP has been used to drive SUGAR. Observations are calculated as the accumulated sum of biomass increment change and local litter-fall (Rowland et al., 2018). The presented confidence intervals are the sum of the litterfall measurement error and the 95% confidence intervals of biomass increment calculated from 8 allometric equations using trunk diameter at breast height (DBH) data from Caxiuanã.

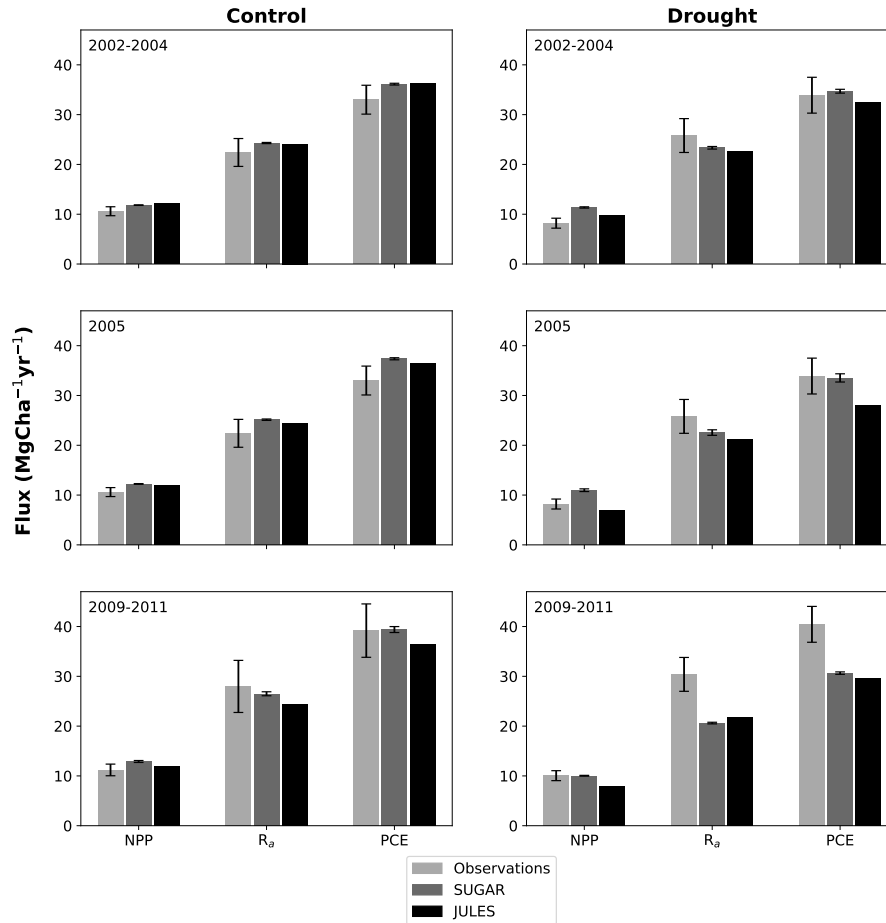


Figure A6. Net primary productivity (NPP), Autotrophic respiration (R_p) and Plant Carbon Expenditure ($PCE = NPP + R_p$); for the periods 2002-2004, 2005 and 2009-2011. The left column is from the control plot and the right is from the through-fall exclusion (TFE) plot. Soil moisture stress has been artificially reduced in JULES by 50% and the resulting GPP has been used to drive SUGAR. Model predictions from JULES and SUGAR are calculated by taking the mean of each flux over each period. Observations for 2005 are from Metcalfe et al. (2010) and observations from 2009-2011 are from da Costa et al. (2014). Simulated photosynthesis in JULES responded almost instantly to the introduction of the panels on the TFE plot which meant that NPP, R_p and PCE changed significantly in both models between 2002 and 2005. To demonstrate this change we show predicted fluxes during the 2002-2004 period as well as from 2005. Observations for this period are not available to such a comprehensive degree as they are for 2005 and the 2009-2011 period. For this reason we compare the model predictions for 2002-2004 to the 2005 observations. This is reasonable in the control plot where it is plausible that the forest was in steady state (Metcalfe et al., 2010) and so fluxes from 2005 will be similar to those during the 2002-2004 period. In the TFE plot while there were some significant changes in observed carbon fluxes during the first 3 years of the experiment, (for example the production of leaves, flowers and fruits, and fine wood (Rowland et al., 2018; Meir et al., 2018)), the forest largely resisted the effects of the drought during this period (significant increases in mortality were not seen until 2005 (Rowland et al., 2015; Meir et al., 2018)) and so we can similarly expect fluxes from 2002-2004 to be comparable to those from 2005. Nonetheless, care should be taken with these comparisons in both plots.

Symbol	Units	Definition
a_{K_m}		Saturation parameter
C_{NSC}	kg C m^{-2}	NSC content
C_v	kg C m^{-2}	Structural carbon content
f_{NSC}		Equilibrium NSC mass fraction
F_Q		Q_{10} function for growth and respiration
G	$\text{kg C m}^{-2} \text{ s}^{-1}$	Plant growth
G_0	s^{-1}	Specific growth rate
q_{10}		Q_{10} value for plant respiration and growth
R_g	$\text{kg C m}^{-2} \text{ s}^{-1}$	Growth respiration
R_m	$\text{kg C m}^{-2} \text{ s}^{-1}$	Maintenance respiration
R_{m_0}	s^{-1}	Specific rate of maintenance respiration
R_p	$\text{kg C m}^{-2} \text{ s}^{-1}$	Total plant respiration
T	$^{\circ}\text{C}$	Temperature
U	$\text{kg C m}^{-2} \text{ s}^{-1}$	Plant carbon expenditure
Y_g		Growth yield coefficient
α		Ratio of plant growth to PCE
Π	$\text{kg C m}^{-2} \text{ s}^{-1}$	Net primary productivity
Π_G	$\text{kg C m}^{-2} \text{ s}^{-1}$	Gross primary productivity
τ	s	Ecosystem carbon residency time
ϕ	s^{-1}	Specific rate of carbohydrate utilisation

Table 1. Definitions of Symbols

Parameter	Units	Value (Cax)	Range	Description	Justification
f_{NSC}	kg kg^{-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_a		0.75		Growth conversion efficiency	(Thornley and Johnson 1990)
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 in this study
α		0.32	0.3-0.5	Ratio of plant growth to total carbohydrate utilisation	Evaluated by setting equal to steady state carbon use efficiency (CUE*). Between 0.3-0.5 for a tropical forest (Chambers et al., 2004; Gifford, 1995)
ϕ	yr	$5.15(1+a_{K_m})$		Maximum specific rate of NSC utilisation at 25°C	Evaluated in terms of a_{K_m} using average specific photosynthesis $\left(\frac{\Pi_G}{C_s^*}\right)$ and temperature (T) of a forest in steady state. $\phi = \frac{1+a_{K_m}}{F_0^*(T)} \left(\frac{\Pi_G}{C_s^*}\right)^*$ Can also be evaluated in terms of vegetation carbon residency time τ (e.g. Carvalhais et al. 2014): $\phi = \frac{1+a_{K_m}}{F_0^*(T)\tau}$

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 2. Parameters in SUGAR

Author	Equation	a	b	c	d	E
Brown-97a-Brown (1997)a	$a + bD + cD^2$	42.69	-12.8	1.242		
Brown-97b-Brown (1997)b	$\exp(a + b\log_e(D))$	-2.134	2.53			
Carvalho-98-Carvalho Jr. et al. (1998)	$1000a\exp(b + c\log_e(D/100))$	0.6	3.323	2.546		
Araujo-99-Araújo et al. (1999)	abD^c	0.6	4.06	1.76		
Chambers-01-Chambers et al. (2001)	$\exp(a + b\log_e(D) + c\log_e(D)^2 + d\log(D)^3)$	-0.37	0.333	0.933	-0.122	
Baker-04-Baker et al. (2004)	$\exp(a + b\log_e(D) + c\log_e(D)^2 + d\log(D)^3)(\rho/0.67)$	-0.37	0.333	0.933	-0.122	
Chave-05-Chave et al. (2005)	$\exp(a + b\log_e(D) + c\log_e(D)^2 + d\log(D)^3)(\rho)$	-1.499	2.148	0.207	-0.0281	
Chave-14-Chave et al. (2014)	$\exp(a - 0.976E + b\log_e(D) + c\log_e(D)^2 + d\log(\rho))$	-1.803	2.673	-0.0299	0.976	-0.051030

D = Diameter at breast height (dbh); ρ = Wood density; a, b, c, d, E are constants.

Table 3. Allometric equations used to calculate above-ground biomass, C_v (kg)