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

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Response to Thomas Pugh

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.

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

$$R_p = \left(R_{m_0} + 1 - Y_g Y_g G_0\right) F_Q(T) C_v C_{NSC} C_{NSC} + K_m C_v$$

which, using that $\phi = R_{m_0} + G_0 Y_g$ and equation (14), can be written as:

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

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

indeed a simplification of reality, we felt that the work in Thornley (2011), was sufficient justification given the benefit that using it provides. We will include this discussion in a revised manuscript along with a further discussion of the other assumptions in SUGAR (requested by other reviewer), specifically:

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

2. **G and R vary with temperature as a $Q_{10}$ functional with a q10 value of 2.0.**
   The Q10 function is a commonly used representation of the response of plant respiration and growth to temperature and a q10 value of 2.0 is also a standard value (Ryan 1991). Changing the temperature dependence in SUGAR would be a relatively easy procedure and so this could be explored in future work, however, for the purposes of this work we felt that using this more simple representation would be sufficient.

3. **G and R depend on NSC via a Michaelis-Menten function**
   The Michaelis-Menten equation is a widely used description of enzyme kinetic re-
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actions that can be applied to both plant growth and respiration Thornley (1971).

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 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.

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 aKm and q10 are assigned default values with no justification given for the choice. In particular, aKm 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 fNSC 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!

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$f_{NSC}$: 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, attached is are updated plots (figs. 1, 2 & 3) with $f_{NSC} = 0.16$, chosen as double the original maximum tested value.

$q_{10}$ = 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.

$a_{K_m}$ 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). Larger values of $a_{K_m}$ also mean that the saturation effect that is provided by using michaelis-menten kinetics do not come into effect within a reasonable range of NSC concentrations. We accept that this is not a scientifically rigorous justification and so attach amended plots from the Caxiuanã (figs. 4 & 5) simulations with an in-built sensitivity study for $a_{K_m}$. The range of $a_{K_m}$ values tested is 0.1-2.0. These figures will replace figures 5 and 6 in the original manuscript.

<span style="color:red">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)?</span>

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 ($C_{NSC}C_v$) 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 ($\phi$). 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. Below is a further discussion on some of our ongoing work.

We will change the description here to make this clearer. We also include a more detailed discussion on this assumption below which we will include in the derivation of parameter evaluation section in the supplementary materials.

Further discussion:
The NSC pool varies in response to both changes in temperature (via Q10 function $F_Q$) and changes in GPP ($\Pi_G$). More usefully, the NSC mass fraction ($C_{NSC}C_v$) varies in response to changes in temperature and specific photosynthesis ($\pi_G = \Pi_G C_v$). If we write specific photosynthesis as the sum of its average value and variations caused by changes in environment: $\pi_G = \bar{\pi}_G + \pi'_G$, and similarly $F_Q = \bar{F}_Q + F'_Q$ then the NSC mass fraction will deviate from it's equilibrium value if $\pi'_G$ or $F'_Q$ are non zero. This of course happens all the time since GPP and temperature vary on a sub-daily time-scale. However, if over some longer time period these perturbations average to zero then the NSC mass fraction will remain constant over that period. We assume that this is the case in forests under non-stressed conditions that are generally

observed to have relatively stable NSC pools. We then set $f_{NSC}$ equal to observed NSC mass fractions in such forests.

Coupling NSC pool to vegetation dynamics
The two processes we are looking at are:

1. **Litterfall and mortality driven by NSC depletion:**
   If the specific photosynthesis declines then this will cause a decrease in NSC mass fraction. This should then be accompanied by a loss of structural biomass through either a litter-fall or mortality term, that restores NSC mass fraction to its equilibrium value. We felt that this interaction was beyond the scope of this paper where we were looking just at carbon fluxes (R and G) but are exploring it as part of current research.

2. **Active storage:**
   We are exploring the possibility of allowing the parameter $\phi$ to vary in time in response to either NSC content or specific photosynthetic rate, so that the plants are able to actively regulate how NSC is used for respiration and growth depending on how much NSC or photosynthate is available. This may be necessary if specific photosynthesis declines significantly in models as forests grow (something we have found in JULES). Allowing $\phi$ to vary in time would also help to prevent the NSC pool from accumulating to unrealistic levels, although this is not a problem we have encountered too often and so we do include such a detailed discussion on this.

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?

The observations here 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 the attached figures (fig. 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 will update our results section in the revised manuscript with the corrected numbers.

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.

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 Pg. 10, line 10. 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.

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 attached plot of monthly PCE in SUGAR and JULES (fig. 6) which we will include the revised manuscript. 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.

This is a fair comment and we will include this in our discussion. 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 will shift the discussion of our results from NPP and respiration to the prediction of total PCE and also include more of a discussion on allocation of C between G and R. This will link to the discussion above on the validity of the assumption that R and G

have the same NSC dependence.

We agree that these figures would be useful and note that this was also requested by the first reviewer. 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. However, as you say they still provide useful information about how the model works relative to JULES so please see the attached figures (7 & 8) which we will include in our revised manuscript.

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