Overview

The paper by Mahmud et al. presents a data assimilation exercise where data from a manipulative experiment on small trees had been 'assimilated' by a carbon balance model (CBM). The manipulation aimed to reduce root sink strength by constraining growth space of the root systems with varying pot sizes (5 – 30 L, in 5 L steps, 35L, and a 'free' treatment where trees were grown without limitation). On these trees biomass pools (structural biomass of leaves, wood and roots, non-structural carbohydrates, NSC, in leaves) were measured with different frequencies and used to constrain the CBM which simulated GPP based on parameters derived from punctual measurements of assimilation and respiration. Model runs with different structures (with/without a NSC 'storage' pool) were performed to test how important such a carbon buffer is for CBM simulations. The set of parameters of a best suited model (parametrized with three sink strength classes) was discussed with respect to plant carbon (allocation) dynamics in response to sink limitation. In addition, an attribution analysis was performed which aimed to provide information of the underlying mechanisms responsible for changes in biomass from sink limitation.

The authors highlight the need for including a 'storage' component in vegetation models and the usefulness of their approach for further investigations to 'develop appropriate representations of sink-limited growth in terrestrial biosphere models'.

General comments

This is a very nice project as it combines experimental manipulations with a data assimilation procedure. During the last years I have been running several experiments to manipulate the plant carbon balance. I have been thinking repeatedly about such a data assimilation approach to learn more about plant carbon dynamics and the underlying mechanisms. This study here does exactly this and I applaud the authors for making this progress.

That being said, I think that the interpretation of the data and the general presentation of the manuscript can be improved to increase its impact. For example, one of the main findings of the study, i.e. the importance of a storage component for (more) realistic simulations of plant functioning, is a strawman. Plants do have a storage component and of course models that specifically include carbon storage will be more realistic, in particular in situation where NSC may accumulate due to sink limitations.

In my opinion, the merits of the study are not the particular findings but rather the documentation of the potential of the data assimilation approach. The findings have to be taken with caution as the constraints from measurements are simply not sufficient to allow deeper insights into plant functioning. For example, measurements of assimilation and respiration have been done twice only and the photosynthetic parameters derived from these two measurements were used to estimate GPP over the whole season. How robust are these parameters for that purpose? Similarly, leaves were sampled every second week for NSC measurements and the structural biomass of stem and roots was determined only for the fourth months or at the end of the experiment, respectively. Given these limitations, how relevant are your inferences, for example, that sink limitation has led to reductions in photosynthetic rates or enhanced respiratory losses?

Additionally, NSC were measured in leaves only and their distribution among plant organs estimated with fixed parameters. For a study that specifically aims to highlight the role of NSC storage in plant functional processes, this is a critical shortcoming. Within the experimental period, there may have been substantial shifts in the NSC distribution across organs and this could have a substantial impact on the simulated carbon dynamics.

That being said, I think you should rather discuss the approach, its potential but also its limitations. One aspect, for example, is how well a study on seedlings can 'develop appropriate representations of sink-limited growth in terrestrial biosphere models'. Such models usually simulate mature trees, not seedlings. We have recently published a paper addressing this particular topic: how to make use of seedling studies for inferences on mature trees and modeling of vegetation dynamics (see reference from EEB below). Instead of too many inferences I would like to see a critical evaluation of your method, including an assessment of what data are needed to get better constraints for the model. I have done experiments with small trees in growth chambers where GPP and several components of the carbon balance have been assessed continuously or at high temporal resolution. Applying sink limitation (I used source limitation but also drought, which is also a form of sink limitation) in such an experimental setting would allow making much more robust inferences that with the data set used here. Hence, my suggestion is to move away from the current focus of interpreting plant functional responses and instead concentrate on presenting the approach as a promising avenue for how to gain insights into plant functioning.

I hope my comments can help increasing the paper's impact.

Henrik Hartmann

Specific comments:

Abstract: Please add what species you have been working with.

L 20: processes affected by growth? That doesn't make sense.

L 21: What do you mean by 'component processes'?

L27-29: Not much content in this sentence.

Introduction in general: The structure of several paragraphs is not ideal and reduces the logical flow. For example, on L 55 you start a paragraph by asking how to include source and sink limitations in models but then you move to NSC storage in models. I understand that storage allows buffering discrepancies in source and sink activity but this is not strictly related to the limitations.

A more logical flow would be to say that there is ongoing discussion about realistic implementations of NSC in vegetation models and that, because of their multiple roles in plant functioning, such an implementation also provides a buffer against discrepancies in source and sink activity.

L74-76: Quantify growth by manipulating rooting volume? That also does not make sense.

L 88: Very good point!

L90-97: See also paper by Klein T, Hoch G. 2015. Tree carbon allocation dynamics determined using a carbon mass balance approach. New Phytologist 205, 147-159.

L 105-123: The presentation of the hypothesis is very awkward. Could you present this please in a more accessible and appealing way? This is not a funding proposal but a text intended for keeping readers keen on reading on. Please rephrase and restructure to make this a flowing text.

L137-141: Relocate further up to L 129 (after Australia).

L 142: I suggest presenting the data first, then the model.

Table 1: Why is there no hypothesis for simulation set C?

Results: The results are presented in a very uncommon form. The text repeats the hypotheses (not useful) and reads more like a discussion than a presentation of results. I suggest adapting a more formal style so the reader knows to differentiate between results and interpretation of results.

L 329: You mean Fig. 2. Please correct figure numbering for the following figures also.

Figure 1 (actually Fig. 2): Add title to each panel (leaf, wood, root, NSC).

L 352: Shouldn't this section be presented before the modeling outcome? Parameters first, then the modeled pools?

L 413: Is this a sensitivity analysis?

L 418: This belongs into the methods section.

L 422: And this should go into the figure caption.

Table 4: Most of this information has been reported in Fig. 4 already.

L 460-465: The emphasis here is on inferences on processes that are poorly constrained. See my general comments.

L 466-467 (and at beginning of other paragraphs): Please avoid restating the hypotheses.

Discussion in general:

I'd relocate the focus to discuss the potential of the approach and move away from interpreting the model outcome with respect to plant functioning.

The discussion is somewhat lengthy and verbose. Please be more concise and to the point.

A few suggestions from my own work which are based on whole-plant assessments of the C balance:

Hartmann H, Adams HD, Hammond WM, Hoch G, Landhäusser SM, Wiley E, Zaehle S. 2018. Identifying differences in carbohydrate dynamics of seedlings and mature trees to improve carbon allocation in models for trees and forests. Environmental and Experimental Botany.

Hartmann H, McDowell NG, Trumbore S. 2015. Allocation to carbon storage pools in Norway spruce saplings under drought and low CO_2. Tree Physiology **35**, 243-252.

Hartmann H, Trumbore S. 2016. Understanding the roles of nonstructural carbohydrates in forest trees – from what we can measure to what we want to know. New Phytologist **211**, 386-403.

Huang J, Hammerbacher A, Forkelova L, Hartmann H. 2017. Release of resource constraints allows greater carbon allocation to secondary metabolites and storage in winter wheat. Plant Cell Environ **40**, 672-685.