Interactive comment on "Leaf Area Index Changes Explain GPP Variation across an Amazon Drought Stress Gradient" *by* Sophie Flack-Prain et al.

Sophie Flack-Prain et al.

s.flack-prain@ed.ac.uk

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We thank the reviewer for their time and effort. We found their comments very helpful and considered all of them in the revised version of our manuscript.

Author responses to reviewer comments are denoted by AR.

General Comments The authors investigate the importance of different drivers (LAI, leaf traits, climate) for GPP at both temporal and spatial scale across a drought stress gradient in the amazonian region using the Soil-Plant-Atmosphere (SPA) ecosystem model. The SPA model is applied at 7 sites, using sites specific parameters and is forced with LAI observed from hemispherical photographs. Simulation experiments and machine learning techniques are used to investigate their scientific questions.

They find that indirect effects via plant traits and ecosystem structural changes, here expressed as LAI, are found to be the main driver of GPP across a spatial drought gradient, but the sensitivity of GPP to changes in these drivers varied with the gradient. On a sub-annual timescale climatic drivers were found to be more important for GPP. The authors discuss how these direct physiological and indirect mechanism affect GPP but fail to explain the added value of forcing their model with observed LAI and to explain in detail how this forced LAI propagates down the modelling structure of SPA. The manuscript is well written and well structured, however, with many repetitions that should be deleted to make space for more details on your methods. As explained in detail in the comments below, I would like the authors to consider my questions and comments, before I recommend the publication of this manuscript.

AR 1. The brief summary of how LAI is forced within the model (lines 232-237) has been expanded to provide a more in-depth description, and instead included in the '2.1 The Soil Plant Atmosphere model (SPA)' subsection (see comments AR 10 and AR 5). In addition, as suggested, we outline the value of using LAI data to force the model. Constraining simulated LAI using field observations was integral to the model experiments conducted. It allowed us to quantify the direct effects of different LAI timeseries on GPP under different plot conditions. If the LAI timeseries were not constrained we would be unable to quantify these effects.

Throughout the manuscripts, your hypothesis/conclusions are repeated (abstract, introduction, discussion, and conclusion). This takes up a lot of space that could otherwise have been used elsewhere in the manuscript. Therefore, I urge you to delete several of these repeated paragraphs. Please see the specific comments below for my suggestions.

AR 2. The repetition of hypotheses and conclusions has been revised as per the specific comments (AR 7, AR 8, AR 13 and AR 17).

The title Leaf Area Index Changes Explain GPP variations across an Amazon Drought

Stress Gradient is not surprising as LAI generally scales well with GPP, and hence you would expect the changes to do so as well. Moreover, as also stated in the manuscript, the changes of LAI are affected by drought stress, and thus it is indirectly the drought stress that is causing the variation in GPP. Lastly, the title does not fully cover all three research questions made by the authors in the manuscript, although it points towards your most interesting finding. However, I would suggest that you reconsider the title.

AR 3. The authors put forward an alternative title 'The importance of physiological, structural and trait responses to drought stress in driving spatial and temporal variation in GPP across Amazon forests'. Or simplified to 'The mechanisms driving spatial and temporal variation in GPP across an Amazon drought stress gradient'.

Several times you state that changes in LAI is an indirect structural effect from changes in soil moisture. From there, it follows that it is LAI which drives the GPP across the MCWD gradient. A strong emphasis is throughout the manuscript put on LAI and LAI as a driver of GPP, while LAI is strongly impacted by drought stress. However, the model is forced with LAI from hemispherical photographs, but the authors do not explain how the forced LAI is linked to and impact the simulated soil moisture content. From Fig. 2 it follows that LAI impacts the foliage carbon pool, and this pool together with carbon pool of fine roots and soil moisture impacts GPP, but the link between the forced LAI and soil moisture is not well explained for your model setup. Please clarify this in the manuscript.

AR 4. In the model, hydraulic transport is coupled across the soil-plant atmosphere continuum. As a result, higher evaporative demand under increased LAI drives increased root water uptake and consequently a depletion in soil moisture. The link between LAI and soil moisture within the model is now described in the '2.1 The Soil Plant Atmosphere model (SPA)' subsection.

Several times you briefly mention the C allocation (line 232 to 241, Fig. 2 and Supplement material). In the text you state that allocation to NPPleaf occurs first. Normally

NPP is considered a flux, and normally you would allocate to a pool. Thus, do you mean that allocation to the foliar stock occurs first? If assimilation does not provide the C need for allocation to support the LAI, you take from the labile/non-structural carbon pool. However, in the supplement material in the last three equations, you state that if the labile pool has been depleted you allocate from the total NPP. Surely this must only be the case when you have enough NPP to sustain the foliar stock as required by the LAI. Please clarify this in the manuscript.

AR 5. The reviewer is correct in their summation of the C allocation scheme. Allocation towards NSC storage is executed in subsequent time steps when the NPPleaf requirement does not exceed total NPP. This is now clarified in the manuscript.

Specific Comments

Line 88 can be read as if you say LAI is a trait. Conventionally, LAI is not considered a trait (you could use max LAI), but rather relates to the ecosystem structure. Thus, for clarification could you please consider rephrasing the sentence to e.g.: Changes to both ecosystem structure and traits, such as LAI, rooting depth and carboxylation capacity, are expected to be more longstanding (Meir et al., 2015a).

AR 6. Corrected as suggested

Line 142-162 As the introduction is already very long, and much of your hypothesis is repeated later in the manuscript, I would highly recommend deleting these paragraphs.

AR 7. See AR 8 comment

Line 175-181 These lines are almost identical to your scientific research questions listed in the introduction. Please consider deleting one or the other.

AR 8. Removed (175-181) as suggested

Line 232-234 You state that the mapping of canopy dynamics is critical, and that changes in canopy dynamics cause disparity between field observations and model

predictions – how well is canopy dynamics simulated by SPA? How is the LAI forced over the canopy layers in SPA? Please elaborate on these aspects in the manuscript and explain how your study improve these shortcomings.

AR 9. The capacity of SPA to accurately simulate canopy dynamics is demonstrated in LópezâĂŘBlanco et al. (2018) Sus et al. (2010). However, simulated canopy dynamics in the presented manuscript are tightly constrained to observations (LAI and leaf litterfall are forced and calibrated using field measurements respectively). The vertical distribution of leaf area is kept constant throughout model experiments, as current field data is insufficient to provide an accurate depiction of how vertical distributions change with canopy density across the MCWD gradient. As suggested by the reviewer, we have expanded on these aspects and considered how this study could prove useful to model development. The presented study directs model development attentions towards the indirect-structural and trait effects of drought stress. The importance of canopy dynamics in driving GPP, suggests C allocation and plant traits including leaf lifespan will prove important to capturing climate change responses. Though the link between traits and canopy dynamics was outside the scope of this manuscript, it is the subject of ongoing research by the authors.

Line 232-237 NPPLeaf was calculated as the difference between the foliar C stock of the previous time step and that which would equate to field measured LAI. The field measured LAI has a monthly resolution. In principle you would have foliar C stock that could change at every model time step. But if the foliar C stock already equates to the field measured LAI, because the resolution of the forced LAI is monthly, NPPLeaf would just be zero.

AR 10. Field measurements of LAI were interpolated to scale from monthly to daily estimates. This is now clarified in the manuscript.

Line 239 This sentence is not clear.

AR 11. Edited to explain additional functions of the NSC pool such as phloem transport

and osmoregulation.

Line 243 How was the SPA model calibration constraint by an upper and lower sample error of LAI? Please add clarification to the text.

AR 12. The model was forced using the observed LAI timeseries plus and minus the sample error for each plot. This is now clarified in the text.

Line 301-302 These lines are repetitions, and not needed. Please consider deleting.

AR 13. Deleted

Line 308 There is something wrong with the structure of this sentence.

AR 14. Reworked. "A positive, but non-significant, correlation existed between model and field estimates of seasonal soil moisture range (R^2=0.35, p=0.21, RMSE=5%)."

Line 320-325 The correlation between GEM estimated and SPA simulation GPP are non-significant and moderate. As GPP is imperative for your analysis, have you considered the impact it might have on you results? Have you investigated how the GEM estimated GPP relates to the LAI form the hemispherical photographs?

AR 15. Discussion on the GEM-SPA GPP comparison and its potential impact is now included in the limitation sections. We recognise that the lack of significant correlation between SPA and GEM GPP estimates could impact the interpretation of our results. However, we highlight the difficulties of having a small sample size (Line 416) and that five of the seven plots were within the error estimates of field measurements. We also note that current GEM GPP estimates are based on sample error and do not account for assumptions used in scaling to derive GPP estimates. In response to the reviewers question, GPP estimates are not significantly correlated with LAI (R^2=0.18, p=0.33), likely due to concurrent shift towards higher photosynthetic capacity at drier sites.

Line 326 Please explain why the GPPSPA variance is calculated under the LAI standard error.

AR 16. LAI upper and lower sample error were used to calculate an estimate of SPA uncertainty based on model input data. With regards to other model inputs, the availability of trait uncertainty estimates was variable and plot dependent, and there were no uncertainty estimates for hourly meteorological data. We were consequently limited to LAI estimates.

Line 401-410 This paragraph sounds like a conclusion, and since you have a Conclusion section, where this is also stated, I would suggest you delete this paragraph.

AR 17. Deleted

Line 437-449 You mention how changes in LAI is a response to precipitations regimes, and even call it a key response mechanism. Then, one could infer that it is just as much changes in precipitation that explains the changes in GPP as it is LAI. You state that changes in LAI is an indirect effect from climate âĂŤ although the impact might be somewhat delayed, but did you investigate lagged correlations and variances between precipitation and GPP?

AR 18. With respect to annual timescales the field data used were across 2 years only, limiting the scope to test for lag effects. However, this could certainly prove an interesting investigation for the future. Across sub-annual timescales we are unable to compare field estimates of GPP (due to the nature of biometric estimates), however model experiment 3 found that the effect of moisture stress was better captured via VPD (line 392).

Line 452 You do not have a forest at steady state, if it is changing and experiencing trends. Please explain what you mean by a steady state forest – is it continuous cover, constant number of trees etc.? Or better yet refrain from using the term.

AR 19. Term omitted

Line 465-468 With the SPA model you are not able to quantify the impact of soil nutrient on the GPP-MCWD interactions because you lack nutrient cycling in the SPA model.

However, according to Table 1 there is a huge P gradient across your sites, therefore please discuss how this could possible affect your results.

AR 20. As the reviewer highlights soil nutrients varies widely across sites. However we note that there is no significant interaction between GPP and soil phosphorous (GEM R^2= 0.1, p=0.48; SPA R^2=0.01, p=0.81) or soil nitrogen (GEM R^2=0.37 , p=0.14; SPA R^2=0.31, p=0.19). We recognise that nutrient limitation likely impacts GPP across the MCWD gradient, effected through both nutrient availability and plants acquisition capacity (which is dependent on moisture-stress). We expect to capture soil nutrient effects in part via the inclusion of site specific leaf nutrient estimates as a model inputs (which influence simulated photosynthetic and metabolic rate). However, our assumption is limited by the divergence in canopy strategies across the gradient which likely impacts how plants use available nutrients. Discussion on nutrient limitation is now included in '4.5 Limitations and Opportunities'.

Line 477 It is unclear which analysis this sentence is referring to. Your analysis or the work by Quesada et al 2012 mentioned in the previous sentence? Please clarify and elaborate on this statement.

AR 21. This statement refers to the presented analysis (Experiment 1). Differences in root depth and biomass can alleviate water constraints to photosynthesis via the direct physiological pathway (i.e stomatal conductance). But in the absence of C cycle feedbacks, changes in root depth and biomass do not drive changes in emergent canopy properties (i.e. LAI) which proved most important in determining GPP. This is now clarified in the text.

Line 515 What do you mean by GPP is demand limited across spatial scale? Is it the atmospheric transpirational demand? And how does this relate to your already conducted analysis of you results? According to your own analysis, LAI is explaining most of the variation across the spatial scale (sec. 3.5.1, sec. 3.5.2, and 4.2). You must elaborate on the statement.

AR 22. This statement referred to the role of ecosystem structure and traits (i.e. demand) in determining spatial variation in GPP, in comparison to the supply limit observed across sub-annual timescales. However we recognise that the statement was unclear and have amended it to the following "Our results indicate that with respect to soil moisture, GPP is constrained via indirect pathways (i.e. ecosystem structure and traits) across spatial scales, but is limited via direct pathways (i.e. physiology) across sub-annual timescales (Figure 1)."

Line 517 In this section, or possible add another section to the discussion, you will also have to address the uncertainties from the intrinsic model behaviour. You recognised already in line 245 that the model uncertainty is underestimated due to the lack of intrinsic model error. However, during your discussion this is not assessed at all. Please assess these uncertainties in particular in relation to the moisture stress and how the plant hydraulics is modelled in SPA and acknowledge its limitations.

AR 23. As suggested, we have added a discussion on model limitations into the '4.5 Limitations and Opportunities' section. As evidenced by Bonan et al. (2014) the representation of plant hydraulics is a particular strength for SPA. However the model is not without its limitations. Notably, SPAs use of community weighted mean traits (and trait distributions) could influence the simulated response to environmental change.

Line 544-546 Something is wrong with this part of sentences. Please rephrase.

AR 24. Rephrased. "acquisition potential (Q2). We identify the potential vulnerability"

Line 549-551 I agree. And to my knowledge, some models already do so. Line 576 According to the manuscript preparation guidelines for authors for Biogeoscience, Journal names are to be abbreviated according to the Journal Title Abbreviations by Caltech Library (see https://www.biogeosciences.net/for_authors/manuscript_preparation.html).

AR 25. Corrected

Line 1010 Table 2, delete 'subsequently allowed to fluctuate'. This is already implied by being initial conditions.

AR 26. Corrected

Line 1095 Figure 1, NPPLeaf does not classify as a trait. Please correct the figure accordingly.

AR 27. Corrected

Supplement Material:

Please use accurate mathematical expression (e.g. then; should be âĞŠ) and make sure the equations are not in italic.

AR 28. Corrected

Please consider numerating your equations If the LAI is forced using monthly time series, then how does the LAI change between the daily time steps in the calculations for NPPLeaf i? Is it because you nudge the LAI, and hence not force it at every time step? Please clarify.

AR 29. Numbering added. See AR 10 for clarification on LAI change at each timestep. As mentioned already, the three latter equations are confusing. If the labile pool is depleted ($NSC_i < NSC_{i-1}$) then you allocate from the total NPP pool to the labile pool. I assume that this is only the case when $NPPLeaf_i$ is met by the daily assimilation? Please clarify and complete your sets of equations for all cases

AR 30. See AR 5.

Technical corrections:

In general, Please reconsider the usage of the word whilst – it reads a little pretentious.

AR 31. Corrected

Line 32 Abbreviate GPP in line 32, not line 34

AR 32. Corrected

Line 88 Abbreviate LAI in line 88, not line 90

AR 33. Corrected

Line 100 Please change p50 to ψ50

AR 34. Corrected

Line 195 Please Abbreviate NPP here

AR 35. Corrected

Line 307 Add a space between the two sentences.

AR 36. Corrected

Line 473-774 Add they to the sentence: . . . so they may be acclimated. . .

AR 37. Corrected

Line 716 Please change CO2 to CO2

AR 38. Corrected to subscript

Line 716 Please change CO 2 to CO2

AR 39. Corrected to subscript

Line 929 Please change CO 2 to CO2

AR 40. Corrected to subscript

Line 981 Please change CO2 to CO2

AR 41. Corrected to subscript

Line 996-999 Table 1: Please include the abbreviation of RAINFOR in the Table 1 text.

AR 42. Added

Should RAINFOR be above the second horizontal line?

AR 43. No, the row name should read 'RAINFOR site code'. This could be resolved by adjusting table dimensions or adding a hyphen.

Is there no site code for Tanguro?

AR 44. No, it is not on the RAINFOR database (though RAINFOR does hold data on other Tanguro plots).

Please use correct degree symbol for the unit of Mean annual air temperature.

AR 45. Corrected

Would it be possible to add species composition or just dominant species at each site to the table?

AR 46. This could be added. However, species richness varies between 65 and 195 across plots, with the most common species typically accounting for less than 20% of stems.

Line 1095 Please delete the single parenthesis in this line.

AR 47. Corrected

Line 1112 Please correct nodule to module.

AR 48. This was supposed to refer to 'nodule' however as this does not read well we have changed it to node.

References

BONAN, G. B., WILLIAMS, M., FISHER, R. A. & OLESON, K. W. 2014. Modeling stomatal conductance in the earth system: linking leaf water-use efficiency and wa-ter transport along the soil–plant–atmosphere continuum. Geoscientific Model Devel-opment, 7, 2193-2222. LÓPEZâĂŘBLANCO, E., LUND, M., CHRISTENSEN, T. R., TAMSTORF, M. P., SMALLMAN, T. L., SLEVIN, D., WESTERGAARDâĂŘNIELSEN,

A., HANSEN, B. U., ABERMANN, J. & WILLIAMS, M. 2018. Plant traits are key determinants in buffering the meteorological sensitivity of net carbon exchanges of Arctic tundra. Journal of Geophysical Research: Biogeosciences, 123, 2675-2694. SUS, O., WILLIAMS, M., BERNHOFER, C., BÉZIAT, P., BUCHMANN, N., CESCHIA, E., DOHERTY, R., EUGSTER, W., GRÜNWALD, T. & KUTSCH, W. 2010. A linked carbon cycle and crop developmental model: Description and evaluation against measurements of carbon fluxes and carbon stocks at several European agricultural sites. Agriculture, ecosystems & environment, 139, 402-418.