

Dear Dr. Katrin Fleischer,

Thank you for the constructive comments. We copied your comments below in blue font; our labeled responses are in ordinary black font. We have labeled our responses for ease in cross-referencing. Responses to your comments are labelled “CC1” and responses to Reviewer 1 are labeled “RC1”. We have not yet received responses from a second reviewer. We welcome further discussion during the discussion period.

The premise of the study:

The authors confront a dynamic vegetation model with experimental data from a nutrient fertilization experiment in Costa Rica and assess the validity and consequences of alternative root allocation parameterization. The overarching question the authors address is how root allocation responds to changes in nutrient availability, which is a very valid question to pursue. Evaluating models and their underlying assumptions with direct field observations and experiments is necessary to advance our understanding and gain confidence in model predictions. I appreciate the effort the authors have undertaken with the demographic model ED2, and their joint effort with experimental findings and expertise to advance root dynamics and their interactions with nutrient availability. However, I currently cannot recommend publishing the manuscript due to some concerns.

(Response CC1-1) Thank you for these positive comments, and for the many great suggestions that follow. In a revision, we think that we would revise how we state our overarching questions in order to better align them with our results and discussion. Specifically, we are trying to answer: (a) What model assumptions enable or prevent the model from being consistent with the observations? (b) How can we use the model to generate hypotheses on the longer-term consequences of allocation assumptions?

Main concern:

1. The ecological underpinnings of the chosen parameter sets in regard to fine root allocation are not sufficiently clear. This includes the ecological theory to justify choosing the parameter sets, the discussion of the consequences of these parameter sets, and placing the chosen parameter set and findings within the literature and previous modeling efforts.

(Response CC1-2) Thank you for this comment. Reviewer 1 brought up similar concerns. Please see our responses RC1-2, RC1-3, and RC1-7.

2. The study covers short-term and long-term process effects of the different parameterizations, whereby we can expect different outcomes. The experiment finds that fine root production increases with fertilization.

(Response CC1-3) We agree with this comment.

That does not necessarily mean that higher fertile sites will be characterized by higher fine root production.

(Response CC1-4) For clarification, the 3-year experiment showed that P fertilization did increase fine root production (Waring et al. 2019). Whether this response will persist in the longer term is currently unknown, but we hope to eventually have the experimental data to test this point (lines 365-366 in the original manuscript).

In addition, we are open to the idea that allocation responses to P fertilization on a three-year time scale might differ from correlation analysis (e.g., correlation of soil P with fine root productivity across a strong fertility gradient). Individuals growing on naturally high-P sites, for example, may have had sufficient time to acclimate to their local environment. Also, on decadal to multidecadal time scales, forest demand for P may change as a function of forest age or as species turn over, and such changes can affect relative allocation. We can discuss the distinction between fertilization experiments and correlation analysis in a revision.

The others touch on these aspects of timing in the discussion, and the significance of this difference is crucial for the study, however insufficient emphasis is placed on this in working out the premise of the study and discussing the findings.

(Response CC1-5) We are not sure that we fully understood this comment. Which “others” are being referred to here? We are very open to the idea that short term (3-year) and long term (30-year) responses might be different (lines 77-83), and that is indeed part of the reason why we carried out 30-year simulations.

We note that in our 30-year model simulations, successional changes in forest structure, composition, and function are allowed to occur. But the allocation rule remains fixed (no acclimation). We think it is interesting that the parameterizations that matched the 3-year observations most closely simulated the least AGB accumulation on 30-year time scales with P fertilization. This model result does beg the hypothesis that some acclimation would occur on 30 year time scales. This idea can mathematically be incorporated into the model by having relative fine root allocation be a saturating function of soil P rather than a linear function. Such a rule would help to prevent over-allocation to fine roots under the very high soil P concentrations associated with P fertilization. We hope that these remarks speak to your concern and we would be happy to summarize them in our revision.

Associated with this, the experiment takes place in a young forest stand, the implications of this deserve more discussion.

(Response CC1-6) We agree that forest age could be an important variable related to relative allocation to fine roots. Forests of different ages would be expected to have different composition, structure, and demographic rates. It is interesting that the pattern seen in the relatively young forest of our analysis was similar to the pattern seen in the old growth forests studied by Cunha et al. (2022). In a revision, we are happy to comment on this point.

3. Direct nutrient acquisition via fine roots is only one of several possible mechanisms of how plants can acquire nutrients. The authors mention that the trees are associated with arbuscular mycorrhizae but the implications of this in regard to the outcome of the experiment, and how this might have affected the model performance are not addressed.

(Response CC1-7) Please see our response RC1-7. Waring et al. (2019) found root colonization by mycorrhizal fungi did not vary among nutrient treatments. In the manuscript (Line 386-389)

we discussed the possibility of increased root production but reduced allocation to mycorrhizae, which together might show overall decreased belowground allocation.

#### Additional comments methodology:

The chosen parameter sets reflect negative, constant, and positive relationships between fine root production and soil P. The negative one would reflect the resource-dependent parameterization, however not via internal plant demand and supply (as commonly done) but depending on external P supply, in a linear fashion. This is quite different from any of the previous model approaches, and the parameterizations are all based on a linear relationship between soluble soil P and root allocation. A discussion of the ecological underpinning of this model and the parameterization approach would be helpful. The authors touch upon the ecological theory they are addressing only in the discussion part.

(Response CC1-8) Please see our response CC1-2.

Parameters a and b are coordinated to yield a similar 0.3 root-to-shoot ratio in control plots, but to different settings in fertilized plots. The reason for not testing different parameterization settings in the control plot was not clear to me, it would be helpful if the authors could elaborate on this.

(Response CC1-9) Thank you for this particularly helpful comment. We carried out more simulations so that we more densely sampled parameter space. Some of the main results are presented in our responses RC1-5 (30-year time scale) and RC1-9 (3-year validation).

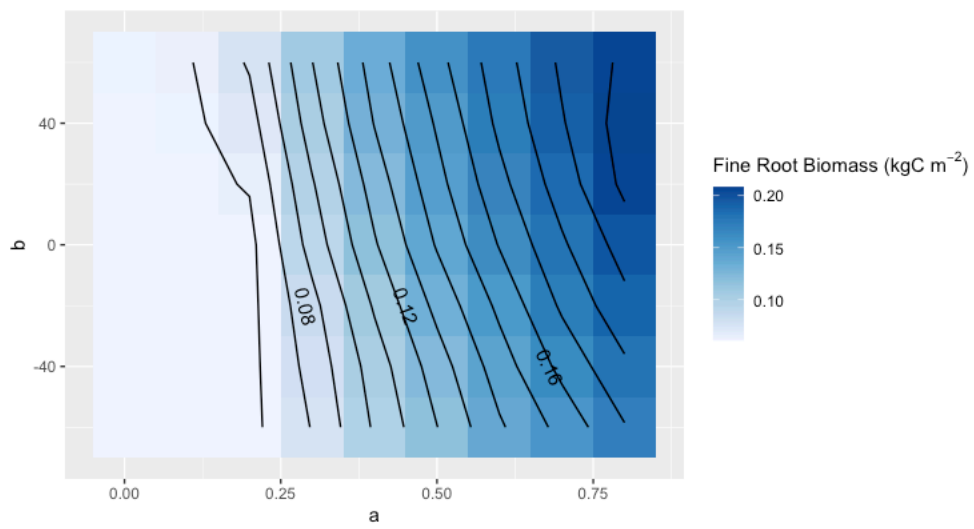
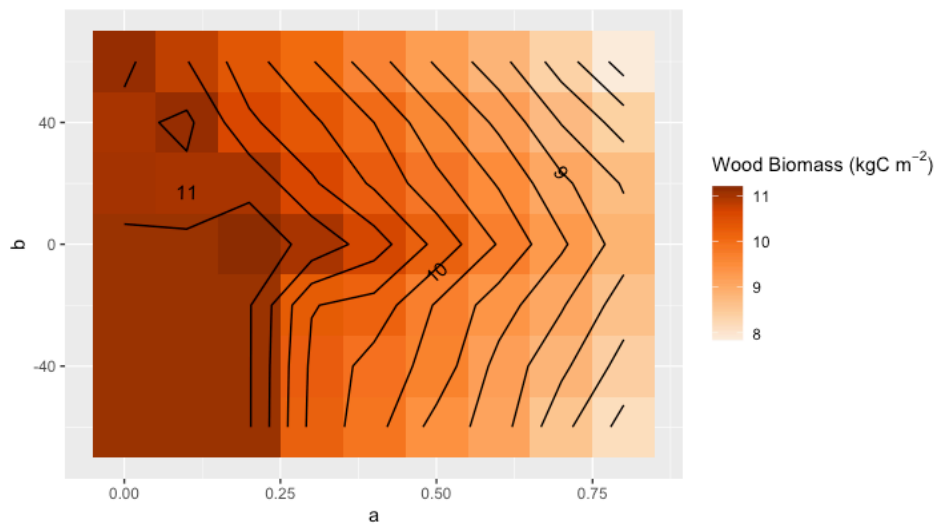
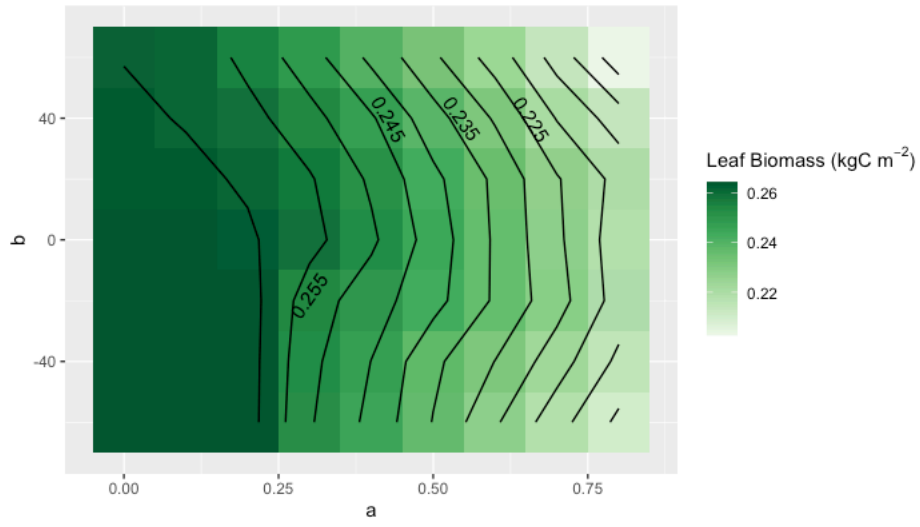
The allocation process as a whole in ED2 is not sufficiently explained. The calculation of the daily leaf and root allocation, and the allometric equations to determine maximum leaf and root allocation, need to be described and included in the discussion. Similarly, the PFTs that are modeled and their parameterizations are not described.

(Response CC1-10) We originally did not present this information because it can be found in other publications (Longo et al. 2019a, Medvigy et al. 2019). However, we would be happy to also provide this information in a revised version of this manuscript. See also response RC1-8.

#### Additional comments results:

One positive parameterization was the only one that agreed well with experimental observations over the 3-year period. Positive parameterizations led to the highest AGB over 30 years, however, not due to alleviation of nutrient limitation but water stress. It would be helpful if the reader would understand how that occurred process-wise. What was the actual allocation to fine roots? And why did that not alleviate nutrient stress?

(Response CC1-11) For a process-level explanation, see response RC1-5. The actual allocation to fine roots is shown on the next page, together with other biomass pools.



Similarly, with P fertilization, positive parameterizations led to too many fine roots over the 30-year time scale. As is described in the abstract as the main finding. Does that not indicate that the chosen parameterization works well for the short term but, importantly, not well in the long term? Is such an assumption about root allocation advisable then? It would be helpful if the authors go beyond “experiments need to measure leaf, root and wood production” in their main take-away for the paper, and rather elaborate on recommendations for model development.

(Response CC1-12) We think that the parameterization works well in the short term in the sense that it yields simulation results that are consistent with observations. We do not know how well the parameterization would work in the long term because we do not have long-term observations to compare the simulations to. Thus, we see a strong need for longer-term experiments exactly in order to make such assessments. We did not mean to imply that the positive parameterization is a “chosen” parameterization, and all of our results displayed multiple parameterizations. We can try to be more clear about this point in a revision.

We offer several additional thoughts spurred by this comment, which we can work into our Discussion: (1) It could be that a saturating response of relative fine root allocation to soil P (rather than a linear response) would maintain the model’s capability of simulating the 3-year observations and also maximize AGB under fertilized and unfertilized conditions. But this would be a more complicated parameterization than the one we employed, and so we did not favor it. (2) It could be that P fertilization over 30 years would expose trees to soil P concentrations that are well outside the natural range. In such a novel environment, the response may well be maladaptive. (3) Under “normal” unfertilized conditions, there does not appear to be any problem with positive parameterizations (Fig. 7a in the original manuscript). As noted in response RC1-5, a scheme that employed a target nonstructural C:P might yield a similar result (but again, such a scheme is unlikely able to simulate the increase in fine root production observed to occur with P fertilization).

We think that model development and experimental work should be coupled. Given our modeling results, we think that the natural next step should be more experiments. Additionally, testing of different parameterizations should be done across a gradient as in the Amazon where data are available.

Given that the experiment took place in a tropical dry forest, the anticipated interactions between soil fertility and water stress are intriguing and it would be helpful if the authors elaborate on the alleviation of water stress in the 30-year simulation that has been touched upon.

(Response CC1-13) Please see our response RC1-5.

Maybe the agreement at the 3-year time scale is not sufficient to evaluate.

(Response CC1-14) We are not exactly sure what is meant here. A three-year time scale is not uncommon in ecosystem experiments. Further, the model represents processes on time scales ranging from seconds to centuries. Ideally, we would constrain the model over a range of time scales (for example, see Trugman et al. 2016; Longo et al. 2019b). Because the Waring et al. (2019)’s fertilization occurs within the range of time scales that the model simulates, we do think

it is appropriate to validate the model on a three year time scale. Note that the model has been validated on somewhat longer time scales at nearby unfertilized plots (Medvigy et al. 2019).

Can the control plots not also be used to evaluate the parameterization, representing rather long-term dynamics? Should the parametrizations not be tested on the control and experimental plots, equally?

(Response CC1-15) We agree that this would be helpful. Please see our response RC1-9. These new results can be included in the revision.

The authors state that ED2 has been validated before. Did the constant parameterization work well before? Did ED2 employ a resource-dependent allocation scheme before? It would be helpful to outline which allocation approaches agreed well with observations and which did not in previous studies with ED2.

(Response CC1-16) ED2 has been validated at a range of ecosystems and for a range of quantities (Medvigy et al. 2009; Medvigy and Moorcroft 2012; Trugman et al. 2016; Xu et al. 2016; Levy-Varon et al. 2019; Longo et al. 2019b; Medvigy et al. 2019). The “constant parameterization” is the one built in to the basic model code, and has never been contrasted with a resource-dependent allocation scheme before. Generally speaking, the model has only been validated for aboveground quantities like AGB production, leaf production, and eddy fluxes. We show here that many parameterizations lead to reasonable wood and leaf production (as the model has been previously validated for), but few lead to reasonable fine root production (as the model has rarely or never been validated before).

The resource limitation theory postulates plant allocation is adjusted to acquire the most limiting resource. Many ecosystem models to date, adopt a resource-dependent allocation scheme, so they would predict that more roots would be produced if soil nutrients were limited, irrespective of the return. The authors find that the experimental results contradict this hypothesis. I believe this apparent contradiction might be a time issue, so that roots grow to acquire the soluble P, while root allocation would decrease once P limitation is alleviated. It might also have to do with mycorrhizal interactions, previous outsourcing of phosphorus acquisition to mycorrhizae now becomes less beneficial with increased nutrient supply and plants switch to “do-it-yourself”. Even if we cannot be certain about any of these hypotheses, a discussion thereof would be helpful.

(Response CC1-17) Thank you for these points. We think that they have largely been addressed in our author comments (different ecosystem models were mentioned in RC1-7, timing issues in response CC1-5 and CC1-12, and mycorrhizal colonizations in CC1-7). We would be happy to revise our manuscript to include discussion of these points.

Line comments:

1. 336 please specify: allocation parameterization sensitive to external nutrient availability.

(Response CC1-18) Thanks for pointing this out. We'll make it clear in revision.

2. 383- 341 what is the implication of that finding?

(Response CC1-19) Is there a typo in the line numbers specified here? We were not sure which lines the reviewer referred to.

3. 344 the model is microbial-explicit. That is an important aspect of the model. It would be helpful if this is included in the manuscript and discussed.

(Response CC1-20) As suggested by the last comment on methodology, we can include model details about microbial mechanisms of soil organic matter decomposition in a revision.

4. 365 For future efforts, the authors can consider evaluating the model and different parameter sets at different locations in the tropical biome, and including an evaluation along a soil fertility gradient, as well as experimental changes. The combination of both would be helpful to discern short-term and long-term effects.

(Response CC1-21) Thanks for the suggestion and please see also our response CC1-4. We can add this to the discussion.

5. 369 The experiment near Manaus found increased primary productivity in response to fertilization, indicating that production was limited by phosphorus. To my understanding, this finding is still consistent with the resource limitation hypothesis, since plants allocated carbon to roots to acquire the nutrients that they were in demand of.

(Response CC1-22) Of concern to us is that relative – and not just absolute – allocation to fine root increased in Cunha et al. (2022) in response to P fertilization.

6. 375 As the authors note, roots are there for acquiring multiple resources at once. A discussion of these interactions would be helpful. The analogy to rain roots is interesting, the authors could elaborate here. The root production after fertilization could potentially be a similar short-term effect to acquire the limiting resource.

(Response CC1-23) We could briefly elaborate on these points in a revision. Regarding time scales, please see our responses CC1-4, CC1-5, and CC1-12.

7. 379 The paragraph on field observation is helpful, however, root stock and root production seem to be mixed up. Since the model evaluation deals with root production, the authors could elaborate on those aspects of the measurements.

(Response CC1-24) We could not find the text where we mixed up root stock and root production.

8. 387 It would be helpful if the authors elaborate on the interactions with mycorrhizae, here, and the implications for this study.

(Response CC1-25) We can comment on this in a revision. Please see response CC1-7.

9. 389 The “supply-limited” hypothesis, which is the basis of this study, should be introduced earlier and placed in context with the alternative hypotheses.

(Response CC1-26) Thanks for the suggestion. We can introduce this concept earlier when setting the premises of this study in a revision.



10. 390 This section could benefit if it discussed what has been learned from this and the previous approaches.

(Response CC1-27) We agree that more can be said here. Some important points include: (1) the sensitivity on one time scale (3 years) can be different from the sensitivity on another time scale (30 years). (2) Different measures of productivity differ in their sensitivity. Just because one measure of productivity is sensitive to a particular parameter does not mean that the model is generally sensitive to that parameter. (3) For some measures of productivity, model sensitivity strongly depends on the nutrient context (that is, whether or not P fertilization is applied).

11. 398 Similarly, in this section, it would be helpful if the authors go beyond the summary of the results here and discuss the implications of these findings. See the main comments above.

(Response CC1-28) Thanks for the suggestion. We disagree with the characterization of this text as a “summary of results”; rather, the text is more of an “interpretation” of results, and so it should be appropriate for a discussion section. The text discusses implications in other places, especially in Section 5, but also to a certain extent in Section 4.4 and other locations.

12. 424 Here it is crucial to discuss that resource-dependent model approaches are not exactly comparable to the negative parameterization applied in this study. See the main comments above.

(Response CC1-29) We appreciate this suggestion and can follow through in a revision.

## **References**

Cunha, H.F.V., Andersen, K.M., Lugli, L.F., Santana, F.D., Aleixo, I.F., Moraes, A.M., Garcia, S., Di Ponzio, R., Mendoza, E.O., Brum, B. and Rosa, J.S., 2022. Direct evidence for phosphorus limitation on Amazon forest productivity. *Nature*, 608(7923), pp.558-562.

Levy-Varon, J.H., Batterman, S.A., Medvigy, D., Xu, X., Hall, J.S., van Breugel, M. and Hedin, L.O., 2019. Tropical carbon sink accelerated by symbiotic dinitrogen fixation. *Nature communications*, 10(1), p.5637.

Longo, M., Knox, R.G., Medvigy, D.M., Levine, N.M., Dietze, M.C., Kim, Y., Swann, A.L., Zhang, K., Rollinson, C.R., Bras, R.L., Wofsy, S.C. and P.R. Moorcroft 2019a. The biophysics, ecology, and biogeochemistry of functionally diverse, vertically and horizontally heterogeneous ecosystems: The Ecosystem Demography model, version 2.2–Part 1: Model description. *Geoscientific Model Development*, 12(10), pp.4309-4346.

Longo, M., Knox, R.G., Levine, N.M., Swann, A.L., Medvigy, D.M., Dietze, M.C., Kim, Y., Zhang, K., Bonal, D., Burban, B., Camargo, P.B., Hayek, M.N., Saleska, S.R., da Silva, R., Rollinson, Bras, R.L., Wofsy, S.C. and P.R. Moorcroft, 2019b. The biophysics, ecology, and biogeochemistry of functionally diverse, vertically and horizontally heterogeneous ecosystems: The Ecosystem Demography model, version 2.2–Part 2: Model evaluation for tropical South America. *Geoscientific Model Development*, 12(10), pp.4347-4374.



Medvigy, D. and Moorcroft, P.R., 2012. Predicting ecosystem dynamics at regional scales: an evaluation of a terrestrial biosphere model for the forests of northeastern North America. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1586), pp.222-235.

Medvigy, D., Wofsy, S.C., Munger, J.W., Hollinger, D.Y. and Moorcroft, P.R., 2009. Mechanistic scaling of ecosystem function and dynamics in space and time: Ecosystem Demography model version 2. *Journal of Geophysical Research: Biogeosciences*, 114, G01002.

Medvigy, D., Wang, G., Zhu, Q., Riley, W.J., Trierweiler, A.M., Waring, B.G., Xu, X. and Powers, J.S., 2019. Observed variation in soil properties can drive large variation in modelled forest functioning and composition during tropical forest secondary succession. *New Phytologist*, 223(4), pp.1820-1833.

Trugman, A.T., Fenton, N.J., Bergeron, Y., Xu, X., Welp, L.R. and Medvigy, D., 2016. Climate, soil organic layer, and nitrogen jointly drive forest development after fire in the North American boreal zone. *Journal of Advances in Modeling Earth Systems*, 8(3), pp.1180-1209.

Waring, B.G., Pérez-Aviles, D., Murray, J.G. and Powers, J.S., 2019. Plant community responses to stand-level nutrient fertilization in a secondary tropical dry forest. *Ecology*, 100(6), p.e02691.

Xu, X., Medvigy, D., Powers, J.S., Becknell, J.M. and Guan, K., 2016. Diversity in plant hydraulic traits explains seasonal and inter-annual variations of vegetation dynamics in seasonally dry tropical forests. *New Phytologist*, 212(1), pp.80-95.