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## Comment on bg-2022-36

Benjamin Stocker (Referee)

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Referee comment on "Consistent responses of vegetation gas exchange to elevated atmospheric CO<sub>2</sub> emerge from heuristic and optimization models" by Stefano Manzoni et al., *Biogeosciences Discuss.*, <https://doi.org/10.5194/bg-2022-36-RC2>, 2022

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This paper contrasts predictions of contrasting models of ecosystem transpiration and assimilation during rain-free periods ("dry-down events") under different levels of elevated atmospheric CO<sub>2</sub> (eCO<sub>2</sub>), modulated also by simultaneous changes in temperature and relative humidity of the ambient air. The models are formulated in a simplified form to find analytical solutions, while maintaining some essential feedbacks and resolving principles that are founded on observations and understanding of ecosystem mechanisms. This is a different approach compared to the approach taken in global vegetation models and the land components of Earth System Models. The advantage of reduced-form approaches as presented here is that emerging ecosystem behaviour can be linked directly to assumptions and mathematical properties of the model, and thus offer insights into "what matters most".

In my understanding, the most important result of the present study is that, irrespective of the chosen model, eCO<sub>2</sub>-driven acclimation of leaf-level physiology and ecosystem-level structure (morphology) interact in such a way that a reduction of leaf-level transpiration is compensated by increased ecosystem foliage area (L) to fully exploit a constrained (limiting) resource - here water (Abstract l. 29 and Conclusions l., 736).

This is a useful insight for understanding observed vegetation greening and streamflow trends in water-limited regions of the Earth and it is interesting that this is a consistent prediction that appears not to be subject to model formulation. I think the paper by Manzoni et al. could be a useful contribution to the literature if the authors manage to convincingly address a few major issues that I would like to raise in the following.

I should disclaim that I did not verify the (extensive) algebra presented in the manuscript. Please excuse me for the limited time I can invest in this review.

## MAJOR

(1) While the interaction of physiological and structural adjustments are presented as a key conclusion, it is unclear to what extent this is a model prediction or an assumption. Apparently, changes in  $L$  are prescribed to increase under  $eCO_2$ . This seems to imply that this interaction is not founded on first principles but is a direct reflection of an assumption that is built into all models (although admittedly an assumption with demonstrated empirical support, Fig. 3). Similarly, the conclusion that vegetation physiology and structure adjusts in such a way as to fully exploit the limiting resource, seems to be an assumption, rather than a prediction. The Cowan & Farquhar (1977) approach to predicting physiological responses subject to  $A-\lambda E$  maximisation starts with the presumption of a constrained amount of plant-accessible water and therefore has to predict that this amount of water be transpired over the course of a dry-down ("imposing the condition that all available water is used by the end of the dry period", l. 670). Similarly for the PETA model (as I understand Donohue et al., 2013 - please clarify if not the same principles are applied in Donohue et al., 2017): Foliage area changes are predicted subject to "known" changes in leaf-level water use efficiency and a constrained amount of available water (corresponding to precipitation). In other words, all available water is assumed to be consumed. (But then, I must be misunderstanding something here, given that  $L$  changes are prescribed also in the PETA model here.) A clarification of these points would help to better understand the relevance of assumptions and the purely predictive ability of the model (and therefore what can defensibly be presented as a conclusion from the present study).

(2) Another potentially useful insight of the present study is that realistic stomatal responses to  $eCO_2$  can be predicted only with stomatal optimality models with a "dynamic feedback" (OPT2 and OPT3), but not with an "instantaneous optimality" model (OPT1). In the models investigated here, this "instantaneous optimality"-based prediction follows from a constant  $\lambda$ , and given a constrained amount of transpirable water. This result is then used to argue that OPT1 (representing in general an "instantaneous optimality" model) is not realistic. This could be misunderstood as a demonstration of a general uselessness of similar "instantaneous optimality"-based models (e.g., Prentice et al., 2014; Sperry et al., 2016; Wolf et al., 2016). However, not all "instantaneous optimality" models are based on optimising C assimilation for a constrained amount of transpiration, and stomatal conductance is (in line with observations) predicted by several "instantaneous optimality" models to decline with rising  $CO_2$  (Stocker et al., 2020, see their Eq. C1; Joshi et al., 2021 Fig. 2). Hence, the presentation of instantaneous vs. dynamic feedback optimality models runs the danger of creating a straw-man argument. A clarification and intuitive explanation of why stomatal conductance is predicted to increase by OPT1 but not in other "instantaneous optimality"-based models, seems needed.

(3) The discussion of the investigated models in the context of the extensive literature on other modelling approaches to simulating physiology in response to soil moisture dry-downs is relatively slim. The single statement referring to such alternatives on l. 680 ("While these approaches are more physiologically accurate and their predictions compare well with observed trends, they do not guarantee that the water use is optimal over the whole optimization period.") does not do it justice in my view. I want to avoid a more fundamental debate over the "constrained water" assumption of Cowan & Farquhar (1977)

(How can a plant know in advance how long the current dry-down will last? How can it know how to optimally make use of available water from now until the [future] end of the dry-down? Why wouldn't it be advantageous for a competitor to consume water immediately rather than save it for the future?), but the justification of not discussing alternative modelling approaches by stating that "they do not guarantee that the water use is optimal over the whole optimization period" seems unfair - particularly in view of the argument that I want to avoid getting into ;-).

(4) The present manuscript is heavy on algebra. I understand that this is central to the reasoning of the presented analysis, but I recommend that all efforts be made that this manuscript can be read and its reasoning intuitively understood without deciphering the algebra. In general, reasonable efforts should be made to reduce the algebra, possibly relegating parts to the Appendix, while still maintaining the essential descriptions. Sorry that my point here is not more specific, but I recommend that the presentation of the science be presented to appeal to the widest possible audience.

#### MINOR

The specific scientific question and scope of the manuscript and the model investigation is not immediately clear. The last sentence of the abstract points to the essence being the coordination of physiology and morphology in their response to eCO<sub>2</sub>. Then, the question is stated more precisely as "... but it is not clear if and under which conditions these two effects balance out." (l. 44 ). Is this the central question? Does the paper answer this question? If so, could an answer to that question be given more clearly in the Conclusion section? The introduction shifts attention to other questions (l. 65, l. 105-107) and answers to these make up much of the Conclusions section instead. This comes at the cost of a not so well-defined scope overall.

The different model variants could be better linked with specific hypotheses about controls and mechanisms determining stomatal responses to eCO<sub>2</sub>. Are there specific questions to be answered by comparing predictions from the different models?

l. 39 "stimulates plant growth and thus increases leaf area": Is increased leaf area a consequence of stimulated growth?

l. 41 "open canopies": A dependence of the eCO<sub>2</sub> effect on leaf area subject to initial leaf area (open canopy) is mentioned throughout the manuscript. In view of canopies being open due to water limitation, nutrient limitations, low temperatures, or simply due to young age, is often not specified, but may be relevant for responses and certainly for underlying mechanisms. Could references to "open canopies" be made more specific throughout?

l. 73-74: "The model is based ..." Add: ... and the assumption that vegetation in water-limited regions makes full use of a constrained flux of water ( $\sim$ precipitation).

l. 83: "Stomatal optimization" models are referred to as models relying on the "Lagrange multiplier"  $\lambda$ . This seems to be a too narrow definition of "stomatal optimization". In my understanding, models that predict stomatal responses to changes along the soil-plant-atmosphere continuum may be considered here too (e.g., Sperry et al., 2016; Wolf et al., 2016).

Table 1: Confusing use of 'T' in  $T_a$  and  $T_d$ , while the two 'T' are different variables with different units.  $E_{SR}$  not explained.

l. 147: Spell out that  $c_i:c_a$  is assumed to remain constant under  $eCO_2$ .

l. 150: " $A_L$  is a linear function of  $c_i$  but with a declining slope at high  $CO_2$  concentration". This seems to be a contradiction in itself. Either it's linear or has a varying slope.

## REFERENCES

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