Response to the Editor

We thank Dr. Solly for encouraging us to submit a revised manuscript. We have already detailed how we planned to revise our manuscript in the responses to the reviewers' comments posted in the public discussion forum. In this letter, we only describe how the planned changes have been implemented in the revised manuscript, and leave our arguments in support to those changes in the open discussion to avoid unnecessary repetitions. All comments by the Reviewers are reported in *Italic* and our responses are in roman. Please note that the attached track-change version is not accurate as it had to be prepared *a posteriori* and the 'compare' function in Word marked as modified some text (especially in the Introduction) that in fact had not been altered.

Response to Reviewer #1

This study is a theoretical analysis of the effects of elevated CO2 on carbon and water fluxes at the leaf and canopy level. The authors use four different models describing carbon water relations, one heuristic (PETA) and three optimality based, and run these under different CO2, soil moisture and VPD conditions. Results show that all models predict relatively constant canopy scale transpiration and implicitly an increase in water use efficiency. The paper is well written and the models clearly explained. The question of how plants will respond to future increased atmospheric CO2 and dryer conditions remains one of the critical questions in plant ecophysiology, so in principle this study is highly timely and relevant. However, in practice, it is in my opinion a purely theoretical exercise that largely uses pre-existing models and knowledge and has some pretty big assumptions.

No change was made in response to this initial supportive comment. We acknowledge that this is a theoretical study whose assumptions are stated as clearly as possible (see additional explanations in the response to the reviewer).

I find that the assumption that most affects the results is that related to the increase in leaf area with increased CO2. The logic behind this assumption is that as photosynthesis increases, there is more carbon available for growth and therefore the leaf area increases in turn. However, from observations and elevated CO2 experiments we know that often there is a shift in allocation and while overall growth goes up, leaf area might not, as resources get allocated belowground to deal with other resource limitations. This has implications not only for the ΔL quantity in the model, but also for soil moisture limitations, in particular in the OPT3 formulation. The authors themselves acknowledge this limitation in the discussion and state that optimizing both carbon-water relations and allocation would lead to a too complex model. But surely there are some intermediary options between no belowground allocation and fully optimal allocation. For example, the parameter w0 could be varied as it is a function of rooting depth and it could be a trade off between rooting depth and ΔL. Although I am sure the authors know their models better than I do and come up with the best way of doing this.

We fully agree with the reviewer and introduced a new analysis to address their comment. We collected empirical evidence of the relation between rooting depth and leaf area index and in herbaceous vegetation and trees, focusing on changes in these plant characteristics during growth rather than along spatial gradients. This dataset, together with analytical derivations based on allometric theory, allowed defining a power law relation between rooting depth and leaf area index that generalized our original results to cases in which rooting depth increases with leaf area. This new analysis is included in Appendix C, which also contains a figure illustrating the data and the scaling relations, as well as a variant of main text Fig. 5 where the effect of deeper roots under elevated CO_2 concentrations is shown. We conclude from this analysis that for reasonable values of the power law exponent in the rooting depth-leaf area index relation, the effects on the CO_2 responses of gas exchange rates are minor and would not alter the main results originally presented. These results are discussed in Section 4.4.

Also related to the biomass growth and leaf area question, I find the α parameter somewhat confusing. It is meant to represent resource availability. What this appears to mean in the model, if I understand correctly, is that for a low resource availability (α close to zero), there is a strong increase in leaf area. This is because at high resource availability the canopy would be already almost closed and there is no room to grow while conversely at a low availability the canopy is open and the plants can grow more. But if the resource in question is for example nutrients, at low availability we would in reality see no growth response whatsoever, as we do at, for example, the EucFACE experiment. This would make the ΔL dependency on α more like a bell shape. I think this part of the model formulation needs some further explanation and discussion.

To address the reviewer's concern (shared with Reviewer #2), we re-interpreted α by focusing on forest age and in general canopy status with respect to a locally-defined maximum leaf area index. The updated definition reads "This index represents how far vegetation is from the maximum L expected for that location. High α indicates an old stand or in general a stand with L close to the maximum, where additional leaf area increases are not possible" (Section 2.2). The most important results of our work (Fig. 6-8) are obtained for a fixed value of α, or in other words for a given canopy status. Therefore, different interpretations on the meaning of α should not alter our conclusions. We do agree with the reviewer that applying the PETA model in a prognostic way across sites would require a consistent estimation approach for α (but that is outside our scope).

Response to Reviewer #2

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 CO2 (eCO2), 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 funded 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, eCO2-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.*

No change was made in response to this initial supportive comment.

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 eCO2. This seems to imply that this interaction is not funded 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-λE 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).

We agree that the models do not predict changes in leaf area, but changes in gas exchange after accounting for prescribed variations in leaf area. This assumption sets only a boundary for the optimization problem, but does not offer clues on the trajectory of stomatal conductance during the dry period—that is the actual solution of the optimization problem. We used the PETA model formulation from Donohue et al. (2017), in which leaf area is expressed as an empirical function of α without a specific constraint on canopy transpiration (Eq. (7) in the main text); therefore, also in our contribution canopy transpiration is not assumed to be fixed—the finding that transpiration is almost insensitive to elevated atmospheric CO_2 concentration is a result of the model. To clarify, we re-phrased the second key assumption stated at the beginning of Section 2: "[plants] have acclimated to the atmospheric conditions by varying their growing season LAI (which is prescribed in both models) and stomatal conductance". This assumption is also re-stated in Sections 2.4: "… the same LAI changes are included in both PETA and optimization models by combining Eq. **Error! Reference source not found.** and **Error! Reference source not found.** to determine $\Delta L/L$" and 2.5: "In both the PETA and optimization models, LAI varies with atmospheric CO_2 concentration and VPD in the same manner (Fig. 1)."

We agree with the reviewer that the differences between model assumptions vs. predictions were not presented clearly and revised the manuscript in the following ways:

- In the revised Fig. 1, we presented more clearly the distinction between assumptions and results of each model.
- We clarified in Section 2.2 where describing the PETA model: "Equation (8) also shows that canopy transpiration can vary unless both leaf-level transpiration and leaf area index are constant. This result of the PETA model differs from a key assumption of the stomatal optimization model (Sections 2.3.2 and 2.3.3)." and in Section 2.3.2 where describing the solution of the stomatal optimization problem: "It is important to emphasize that this specific stomatal conductance trajectory is not a result of our assumption that all available water is used. Rather, it is the solution that best balances the water consumption rate over time to maximize net assimilation."

(2) Another potentially useful insight of the present study is that realistic stomatal responses to eCO2 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 λ, 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 CO2 (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.

We totally agree, and now explained in the Introduction that we focus on stomatal conductance models based on optimal control; we also provided a more balanced and accurate comparison with other approaches in the Discussion, including acknowledgement of their value:

- Introduction, added citation of Buckley and Schymanski (2014): "This approach is equivalent to performing an 'instantaneous' optimization without considering the soil water dynamics or changes in leaf area that can feedback to leaf-gas exchange, albeit at longer time scales compared to the opening and closure of stomata in response to environmental stimuli (Buckley and Schymanski, 2014)"
- Introduction: "Among the numerous models available (Mencuccini et al., 2019; Wang et al., 2020, and references therein), we focus here on those formulated as an optimal control problem in which stomatal conductance is solved through time."
- Section 4.4: "Interestingly, also optimizing c_i/c_a to maximize carbon gains minus water transport costs per unit of net CO_2 assimilation (Prentice et al., 2014) results in increasing stomatal conductance with c_a at pre-industrial c_a values (Fig. S2 in Joshi et al., 2022)."
- Later in Section 4.4: "Other models based on instantaneous maximization of C gains for given costs offer alternative frameworks to predict responses to atmospheric CO_2 concentrations and other environmental changes (Sperry et al., 2017; Mencuccini et al., 2019; Huang et al., 2018; Bassiouni and Vico, 2021; Prentice et al., 2014; Joshi et al., 2022). For example, the model based on Prentice et al. (2014) correctly predicts the observed short-term decrease in stomatal conductance under elevated (but not pre-industrial) atmospheric CO_2 (Eq. (C1) in Stocker et al., 2020) without invoking leaf area adjustments."

Regarding an intuitive explanation of the counterintuitive optimal response of stomatal to elevated CO_2 concentration with the OPT1 formulation, we now explained (Discussion Section 4.4): "In the stomatal optimization models, these erroneous responses arise because at low CO_2 concentration a small increase in stomatal conductance results in large net CO_2 assimilation gains compared to the higher water losses, resulting in the counterintuitive opening of stomata as atmospheric CO_2 concentration is increased."

(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 ;-).

We have expanded Section 4.4 in the Discussion as detailed in our reply to comment (2), and elaborated on the 'philosophical' difference between the instantaneous maximization *vs.* optimal control approaches, also in Section 4.4: "While these approaches are physiologically accurate in the way they balance instantaneous C gains and losses and their predictions compare well with observed trends, they do not guarantee that the water use is optimal over a given time interval. In other words, instantaneous maximization models rest on the assumption that future C gains are so uncertain that maximizing short-term gains is more convenient (in an evolutionary sense). In contrast, models based on optimal control theory rest on the assumption that future gains are expected because climatic conditions are to some degree predictable (rain on average occurs every td days), or that plant responses have been adapted to 'anticipate' these long-term, probabilistic conditions. These approaches can be seen as end-member cases along a continuum of possible optimization strategies."

(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.

We moved most of the material from Section 2.3 "Optimal stomatal control models" to Appendix B, leaving a streamlined text presenting the results in an intuitive way. We left Sections 2.1 and 2.2 as they are, since they provide basic equations or final analytical results (not derivations). Other minor re-arrangements were done to improve clarity and flow (e.g., the soil moisture balance is now described in the section on optimization models, as it is most relevant there).

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 eCO2. 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.

We re-phrased the research questions as follows, including a statement of our further methodological aim to compare model predictions and discuss the limitations of the PETA and optimization models:

“1. How do physiological (stomatal conductance) and morphological (leaf area) adjustments coordinate to determine leaf and canopy gas exchange rates under atmospheric CO_2 concentrations?

2. How do these physiological and morphological adjustments vary under combined changes in CO_2 concentration and atmospheric or soil drought?

By comparing the predictions of the PETA and optimization models, a theoretical perspective on these questions is offered, while identifying advantages and limitations in these different modelling approaches.”

In the conclusions, we more clearly answer these questions: “Both models predict low sensitivity of canopy transpiration rates to a changing climate, indicating that morphological adjustments (leaf area increase) compensate physiological adjustments (stomatal closure).” The very last sentence in the Conclusions re-states the same message: “Overall, these results imply that physiological and morphological traits acclimate to changing environmental conditions in a coordinated manner to ensure that limiting resources such as water are used efficiently.”

The different model variants could be better linked with specific hypotheses about controls and mechanisms determining stomatal responses to eCO2. Are there specific questions to be answered by comparing predictions from the different models?

The differences between the stomatal optimization model variants are presented in Fig. 3 and commented upon in the Discussion. Because the optimization approach surrogates detailed physiological processes by assuming an ecological ‘goal’ function, it is difficult to link these model variants to specific mechanistic hypotheses. Therefore, identifying controlling mechanisms might be quite speculative and we would prefer to avoid that.

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

Higher net assimilation provides resources for faster growth, and hence also higher leaf area (assuming resources are invested both above and belowground). No changes were made in response to this comment.

l. 41 “open canopies”: A dependence of the eCO2 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?*

Clarifications to this regard have been added in Section 2.2 (also in response to a comment by Reviewer #1): "This index represents how far vegetation is from the maximum L expected for that location. High α indicates an old stand or in general a stand with L close to the maximum, where additional leaf area increases are not possible."

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 (~precipitation).

Only the 2013 formulation of the PETA hypothesis relies on this assumption, and we use the 2017 version, so it might be confusing to include this assumption here. No changes were made in response to this comment.

l. 83: "Stomatal optimization" models are referred to as models relying on the "Lagrange multiplier" λ. 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).

We added in the Introduction: "Among the numerous optimization-based models available (Mencuccini et al., 2019; Wang et al., 2020, and references therein), we focus here on those formulated as an optimal control problem in which stomatal conductance is solved through time." (See also response to comment (2).)

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.

The symbol used for the dry period duration was changed to t_d; the symbol E_{SR} was changed to E_W.

l. 147: Spell out that ci:ca is assumed to remain constant under eCO2.

l. 150: "A_L is a linear function of ci but with a declining slope at high CO2 concentration". This seems to be a contradiction in itself. Either it's linear or has a varying slope.

A clarification was added to address both comments: "As a result, A_L is a linear function of c_i, but the slope of the relation decreases with increasing atmospheric CO_2 concentration; moreover, this approximation allows retaining variations in c_i/c_a with c_a (Katul et al., 2010)."

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