

Response to Reviewer #1

We thank Referee #1 for his/her comments, which are addressed as explained below. The Referee's text is reported in *Italic* and our responses in roman.

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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

10 *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.*

15 We thank the reviewer for the supportive comment on presentation and relevance. We agree that this is a theoretical study that leverages existing models, but it is novel in i) comparing PETA and stomatal optimization approaches, ii) exploring the consequences of changes in leaf area index on gas exchange in the optimization models (an often neglected aspect), and iii) analytically demonstrating that previous stomatal optimization models—once the marginal use efficiency is calculated as a part of the optimization problem—are equivalent and can be reduced to a simple mass balance constraint (stomata adjust to

20 use available water). These are novel methodological aspects, but there is a further, more conceptual novelty angle: iv) the contributions of trends in CO₂, VPD, and dry period durations on gas exchange and water use efficiency (WUE) are disentangled showing when and how much the positive CO₂ effects on net assimilation and WUE are diminished or enhanced by altered VPD and dryness.

Compared to previous work on this topic, our contribution has the advantage of analytical transparency. We agree that the

25 selected models rest on several assumptions (most are common in other modelling studies as well), but we strived to list the assumptions and discussed limitations in result interpretation stemming from these assumptions. In this way, we hope to have achieved a balance between mathematical clarity (which requires more assumptions than in more complex but less transparent models) and realism. Some assumptions have indeed a strong effect on the results, but the analytical framework of both PETA and stomatal optimization models allows us to test scenarios where these assumptions are partly relaxed, as

30 explained in response to the next comment.

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 w_0 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.

The reviewer points to the important issue of resource allocation aboveground (leaf area changes) vs. belowground (changes in root density or depth distribution). If rooting density or depth increases under elevated atmospheric CO₂ concentration, it is possible that the soil water storage capacity will also increase, providing enough water for a canopy with higher leaf area index. We thank the reviewer for also hinting at a way to assess trade-offs between leaf and root allocation. Indeed, the root zone water storage capacity (w_0) depends on rooting depth, as w_0 is the product of soil porosity and rooting depth (Table 2 in the manuscript). Letting this parameter vary with changing leaf area index could then account for different degrees of allocation belowground as atmospheric CO₂ increases.

To proceed in this direction, we need first to prescribe end-member variations in w_0 . In one extreme scenario, allocation to the roots does not change with elevated CO₂ and the associated change in leaf area, because w_0 is fixed. Even with higher allocation belowground, if access to water does not change due, e.g., to the presence of a layer limiting root penetration, w_0 would also be fixed. In these cases, the results in the submitted manuscript are valid. Empirical data on leaf area-rooting depth coordination are not extensive, as most datasets focus on biomass allocation (e.g., Niklas and Enquist, 2002). Nevertheless, there is evidence that in mature trees within a given plant functional group, higher leaf area does not necessarily translate into deeper roots despite proportional increases of root and leaf biomass (Smith-Martin et al., 2020). This evidence suggests that increasing plant size such as under elevated CO₂ could alter both above and belowground biomass (which is expected) but higher leaf area does not imply deeper roots. Elevated CO₂ shifts the fine root distribution to deeper layers (Iversen, 2010), but it is not clear if this shift results also in higher water access.

In a second scenario, w_0 could be coordinated with leaf area index L according to a power law function,

$$w_0 \sim L^\beta, \tag{1}$$

where the exponent β is larger than zero (if $\beta = 0$, Eq. 1 recovers the first scenario) and at most equal to one (isometric scaling). Data in Figure R1 shows that herbaceous annual vegetation exhibits an exponent $\beta < 1$, when considering different time points during plant growth. This suggests that deepening of the root system occurs before substantially increasing leaf

area, but this result is limited to annual species growing over a few months. Any extrapolation to perennial species and trees
65 can be problematic. Nevertheless, the scaling in Figure 3 can be used to define an upper bound for $\beta \approx 0.35$. Most likely,
any type of vegetation would exhibit β values between these two extreme scenarios, i.e., $0 \leq \beta < 0.35$.

Having established end-member scenarios for rooting depth-leaf area coordination, we can now assess the consequences on
predicted gas exchange. Note that in the PETA model there are no parameters related to roots, so the following results are
limited to the stomatal optimization model. The combined effect of w_0 and L on gas exchange emerges from the relation of
70 optimal stomatal conductance and w_0 and L (Eq. (32) in the submitted manuscript; this equation is valid for both OPT2 and
OPT3),

$$\bar{g} = \frac{w_0(x_0 - x_T)}{v_a D L T_d}. \quad (2)$$

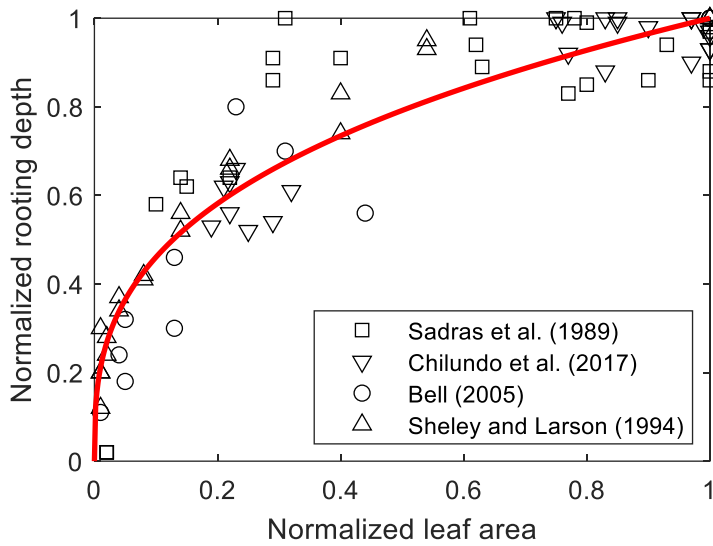
From this equation, it is clear that all else being equal, stomatal conductance is expected to scale as the ratio of w_0 over L .
Accounting for the possible coordination of w_0 and L via Eq. (1), the leaf area effect on stomatal conductance becomes,

$$\bar{g} \sim L^{\beta-1}. \quad (3)$$

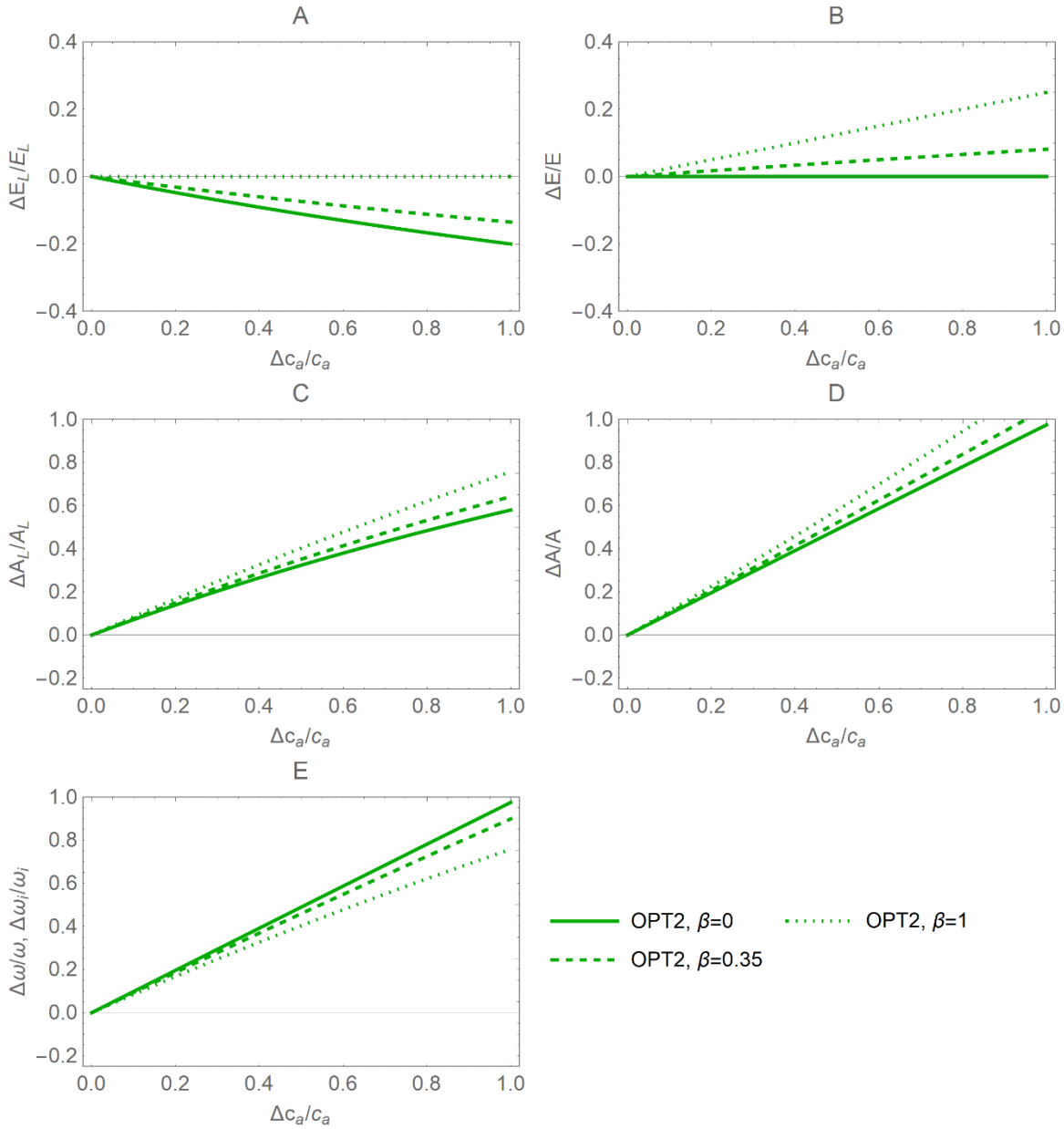
This remains an inverse relation qualitatively similar to the one assumed in the submitted manuscript (where $\beta = 0$), as long
75 as $\beta < 1$, which—as discussed above—is likely the case. However, when β increases, the effect of higher L on stomatal
conductance decreases, which in turn alters the predicted optimal stomatal conductance-atmospheric CO_2 concentration
relations, as illustrated in Fig. R2. Increasing values of β reduce the LAI-mediated negative effect of elevated CO_2 on
stomatal conductance and leaf transpiration (Fig. R2a), creates a positive CO_2 effect on canopy transpiration (which is
insensitive to CO_2 concentration when $\beta = 0$) (Fig. R2b), and enhances the positive CO_2 effect on both leaf and canopy net
80 assimilation (Fig. R2c-d). In contrast, the positive CO_2 effect on water use efficiency is reduced when $\beta > 0$.

If offered the opportunity to revise the manuscript, we will introduce the data analysis in Fig. R1 (including also additional
datasets we might find) and include Fig. R2 either in the Supplementary Information or in the main text depending on
comments from the editors and other reviewers. This analysis will strengthen the discussion points in section 4.4, which will
become less speculative and more supported by a dedicated analysis.

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90 **Fig. R1.** Maximum rooting depth as a function of leaf area during plant growth, as measured across herbaceous wild and cultivated species. Both root depth and leaf area are normalized by the maximum values for each species to allow a visual comparison (data from Sadras et al., 1989; Chilundo et al., 2017; Bell, 2005; Sheley and Larson, 1994). The red curve is the allometric scaling relation obtained through least square fitting of the data: normalized root depth \sim (normalized leaf area)^{0.34} ($R^2=0.89$).



95 **Fig. R2.** Relative changes in leaf-level (A, C) and canopy-level (B, D) gas exchange rates as a function of relative change in atmospheric CO₂ concentration c_a , as predicted by the optimal stomatal control model OPT2 for different values of the root depth-leaf area scaling exponent (β): A) leaf-level transpiration rate (E_L), B) canopy-level transpiration rate (E), C) leaf-level assimilation rate (A_L), D) canopy-level assimilation rate (A), and E) water use efficiency (ω). The solid lines correspond to the limiting case of fixed rooting depth ($\beta = 0$); the dashed lines correspond to the case shown in Fig. R1; the dotted lines represent the extreme (and unrealistic) case of proportional changes in leaf area and rooting depth ($\beta = 1$). Vapor pressure deficit and dry period length are fixed (Table 2); resource availability $\alpha = 0.5$.

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Also related to the biomass growth and leaf area question, I find the α parameter somewhat confusing. It is meant to
105 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.

110 The reviewer's interpretation is correct. In the publication defining the resource availability index α (Donohue et al., 2017), it
is related to leaf area index—if L is large, α is low, indicating that resources are not sufficient to ensure a full canopy. This
definition based on leaf area, however, neglects the possibility that maximum leaf area (suggestive of high resource
availability) can change depending on location. For example, high-radiation environments can sustain a larger leaf area
compared to low-radiation environments. To avoid a this assumed correlation of L and α , we thus decided to let these
115 quantities vary independently. It should be noted that except for the initial analysis in Fig. 5, all our results are obtained for
fixed $\alpha=0.5$, indicating an intermediate canopy state that permits some degree of leaf area adjustment.

*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
120 shape. I think this part of the model formulation needs some further explanation and discussion.*

EucFACE has been characterized as a site of intermediate resource availability, with $\alpha=0.57$ (see Table 2 in Donohue et al.,
2017). This low value of α is due to the relatively low leaf area index at EucFACE, but the reviewer is correct in saying that
low α does not imply high growth potential—in fact, quite the opposite if soil nutrients are limiting. We see the point and
125 share the concern, though for the purpose of our study, we set α to a fixed value in order to study the effect of atmospheric
 CO_2 concentration, VPD and dry period duration on gas exchange. Therefore, a different relation between leaf area index
change and α would not alter our results, but it would slightly alter their interpretation—in the original submission, we
discussed sensitivities to elevated CO_2 in terms of resource availability, while we should instead focus on conditions that
allow plants to adjust their leaf area or not. This change in terminology is feasible, and we propose to re-interpret α by
130 focusing on forest age and in general canopy status with respect to a locally-defined maximum leaf area index. These aspects
are already mentioned in the current manuscript, but we can explain them further in the Theory section, as well as in the
Discussion.

135 **References**

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