

# Responses to RC1

Dear referee,

Thank you very much for your reading. We really appreciate your contribution to helping us to improve our manuscript with helpful suggestions and comments. Here below, your comments are highlighted in black and italicised and our replies are highlighted in blue. We sincerely hope that you are satisfied with our replies and our proposed changes.

Sincerely yours,

Julia Bres and co-authors.

## ***General Comments:***

*I found this paper to be very interesting and a good first step in estimating the impact of the evolution of angiosperms. Though there are limitations to this study, I think that they were very nicely and plainly listed and acknowledged as such. This study will an important contribution to the continuing attempts to better represent paleo vegetation in climate modeling.*

*I think the paper could use some work with the grammar. There are a lot of sentences that are missing needed commas or need be rearranged for clarity. I have attempted to point these out when possible.*

*I think this paper fits well within the scope of Biogeosciences and would recommend its publication pending minor to moderate revisions.*

Thank you for these comments. In the following, we provide detailed replies and corrections for RC1 concerns. We also rephrased several sentences following the referee suggestions to improve the grammar.

## ***Specific Comments:***

*Abstract:*

*Line 14 and 15: “Stage”? Maybe “state” would be better.*

We modified the text accordingly.

*Line 15: Irrigated? That sounds off. Maybe say that the leaves are kept more flush with water?*

We rephrased to “more densely veinated”.

*Introduction:*

*Line 54: Not sure if this falls into “specific” or “technical”, but surely there is a better phrase than “a lot”? Maybe “Even if other functional traits evolved during the angiosperm radiation, . . .” is better ?*

We agree and we rephrased accordingly.

*Methods:*

*Lines 98-104: This sentence is very hard to comprehend. Way too much information in one sentence. I recommend splitting it up. Also, should “a day respiration” be “daily respiration”?*

We agree. We rephrased accordingly. Now, you can read : ”Within the model used in ORCHIDEE (Yin and Struik 2009), leaf operational stomatal conductance to H<sub>2</sub>O ( $g_s$  in mol m<sup>-2</sup>[leaf] s<sup>-1</sup>) depends on the net carbon assimilation (A in molCO<sub>2</sub> m<sup>-2</sup>[leaf] s<sup>-1</sup>), the daily respiration ( $R_d$  in molCO<sub>2</sub> m<sup>-2</sup>[leaf] s<sup>-1</sup>), the intercellular CO<sub>2</sub> partial pressure ( $C_i$  in bar), the  $C_i$ -based CO<sub>2</sub> compensation point in the absence of  $R_d$  ( $C_i^*$  in bar) and the residual stomatal conductance to H<sub>2</sub>O ( $g_0$  in mol m<sup>-2</sup>[leaf] s<sup>-1</sup>), to account for a non-zero conductance when the carbon assimilation is zero (Farquhar, Caemmerer, and Berry 1980; Ball, Woodrow, and Berry 1987; Yin and Struik 2009). Finally, the leaf operational stomatal conductance to H<sub>2</sub>O is modulated by a factor  $f_{cpl}$ , describing the strength of the coupling between A and  $g_s$ , which is function of the leaf-to-air vapor pressure deficit (kPa) and that we will further name “leaf hydraulic capacity” ...”

*Lines 106-108: Again, this sentence is hard to comprehend. Suggest changing “leaves morphologic and physiologic traits” to “the morphologic and physiologic traits of leaves” for clarity. Otherwise, this sentence should be split for clarity.*

The sentence is now rephrased as : ”The semi-empirical formalism of  $g_s$  allows to account for both the structural conductance, linked to the morphologic and physiologic traits of leaves (e.g.  $D_v$ ,  $D_s$  and S) developed on the long-term plant evolution history, and the dynamical conductance, related to the short-term stomatal opening and closing depending on the environment.”

*Lines 118-132: This section is much more clear and should be a model for sentences listed above.*

Thank you for this remark, we have now used this section as a model.

*Line 171: This sentence is awkward and should be changed to “A lower value for  $y$  indicates a lower stomata-to-vein distance and a higher. . . .” Or something similar.*

It now reads “A lower value for  $y$  indicates a lower stomata-to-vein distance and a higher  $g_{\text{anat}}^{\text{max}}$ .”

*Line 187: Why was solar radiation set at 99%? For instance, in the Late Paleozoic, solar radiation is thought to be 3% lower based on the modeling of Crowley and Baum 1992. Is there similar modeling evidence for the Cretaceous. If so, it should be cited. If not, it should be justified.*

From Gough formulation (1981), the solar constant rose from 98.76 to 99.4 % of its present-day value between 144 Ma and 65 Ma (the lower and upper bounds of the Cretaceous). We actually underestimated it by setting it at 1345 W.m<sup>-2</sup>, which is 98.53 % of its present-day value. Based on the values depicted in Laugié et al. (2020) with the IPSL model, we estimate that this 0.5 % underestimation should translate to a homogeneous cooling of no more than 0.8°C and should not alter our results.

*Line 201: I’m not sure I agree with the 5-fold lower photosynthetic and hydraulic capabilities of pre-angiosperms because it is based on the notion that vein density trumps all other physiological attributes, but for the purpose of a sensitivity analysis and your paper, it is appropriate and important. Carry on.*

Yes, it is a strong assumption that we make. We clarify that point in the introduction: “Paleobotanical data show that several traits from the soil-plant-atmosphere continuum have evolved during the Cretaceous. Specifically, root thickness and wood structure have evolved towards greater hydraulic efficiency (Brundrett 2002; Wheeler and Baas 2019]. In this paper, we focus on the upper part of this continuum, considering changes in leaf stomatal conductance and leaf photosynthetic capacity.”

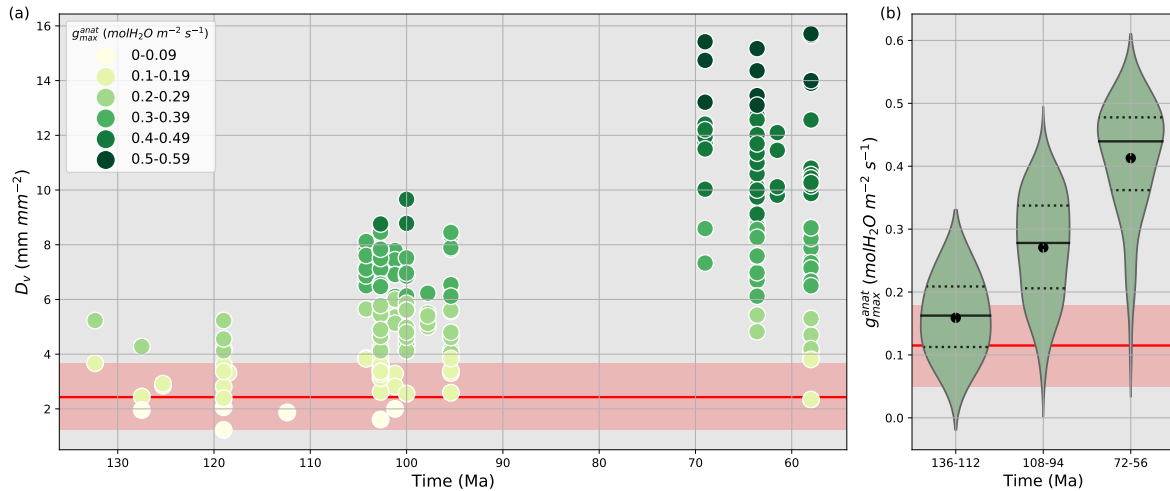
*Results:*

*Line 219: “3-fold” instead of “3-time”.*

Corrected.

*Line 223-224: The fact that gymnosperm function was not accessed is a problem for me. Yes, without a doubt, angiosperms have displaced gymnosperms as the dominant plant through time, but they still, to this day, occupy vast and important parts of the Earth’s surface. Understanding their response in terms of a global climate model is important for the whole story of the increase in angiosperm dominance across the earth surface. Ultimately, judging the effect of angiosperms in the face of no change in gymnosperms seems to be missing a large part of the story. However, given your stated purpose, and the fact that needleleaf gymnosperms are not widespread in your paleovegetation distribution map, it is appropriate.*

Indeed, explaining the gymnosperm response to pCO<sub>2</sub> variations, as well as explaining the long-term persistence of gymnosperms, is out of the scope of our study. Here, not addressing the case of the long-term physiological evolution of gymnosperms is justified by the fossil data that shows their vein density remains constant over the Cretaceous (Feild et al. 2011). To make it clearer for the reader, we have added the mean value (one standard deviation) for gymnosperm vein density and maximal anatomic stomatal conductance to H<sub>2</sub>O on figure 2.



(a) Time evolution of fossil vein densities ( $\text{mm mm}^{-2}$ , y-axis) adapted from Feild et al. 2011 and the corresponding maximal stomatal conductance to  $\text{H}_2\text{O}$  ( $\text{mol m}^{-2} \text{s}^{-1}$ , filled circles) calculated by the anatomic relationship developed by Brodrribb et al., 2007 and Brodrribb et al., (2010). (b) Subdivision of maximal stomatal conductance to  $\text{H}_2\text{O}$  ( $\text{mol m}^{-2} \text{s}^{-1}$ ) by time periods. The solid line is the median, the dotted lines are the first and third quartiles, and the point is the mean value for each time period.

Line 255-257: Doesn't this show the importance of highlighting the modeled change in angiosperms vs. gymnosperms? Gymnosperms are showing the resilience of coming to dominance during the low  $\text{CO}_2$  of the Late Paleozoic Ice Age.

We agree. Although the resilience of gymnosperms is out of the scope of our study, future studies could focus on traits linked to fire resistance, as they have been shown to be crucial to explain the long-term persistence of some gymnosperm clades - namely the Pinus clade (Singh et al. 2018).

Line 263-264: Soil water is always the limiting factor, especially in the tropics.

We show more in the text that this is what we were expecting.

Line 271-276: Indeed. Leaves do not function in a vacuum. Without accessing the whole canopy, we cannot truly trust the implications.

Indeed, it is one of the strengths of our modelling approach.

Discussion:

Line 478: I do not understand this sentence. Are you saying vein density is stomatal size and density? Or are you saying that vein density and stomatal size and density need to be accounted for? Clarify

Here, we mean that the  $\alpha$  factor applied in Eq. (1) to the coupling factor (fcpl) does not fully represent the change in the maximal anatomic stomatal conductance inferred from the morphological leaf traits, such as  $D_v$  (but another approach could consider  $D_s$  and S). Indeed, we have seen that  $g_s$  is 3-fold lower for

the perturbed experiments compared to the reference ones, while we explicitly account for a 5-fold decrease in  $fcpl$  and  $V_{cmax}$ , to mimic maximal anatomic stomatal conductance variation. One way to improve our parameterization of proto-angiosperm vegetation in land surface models is to explicitly model both structural and dynamic conductance, and apply the 5-fold decrease to the structural conductance, as it represents leaf traits evolution. We acknowledge that the sentence was not clear and we rephrased it : “ The  $\alpha$  factor applied in Eq. (1) to the coupling factor ( $fcpl$ ) does not fully represent the change in the maximal anatomic stomatal conductance as it should be considering changes inferred from vein density. We have seen that reducing the hydraulic or photosynthetic capacity by a factor of 5 (or a combination of both), leads to a 3-fold decrease in leaf stomatal conductance. It emphasizes the need, in the future, to improve the parameterization of stomatal conductance in global models by explicitly modelling both structural and dynamic conductance.”

***Technical corrections:***

*Introduction:*

*Line 34: Should there be a space between “95” and “%”? I was under the impression that there should not.*

We will check with the copy-setting board. According to Biogeosciences guidelines, “Spaces must be included between number and unit (e.g. 1 %, 1 m)” for figure content guidelines but nothing is mentioned for manuscript composition.

*Line 35: Change “at the expanse” to “at the expense”.*

Corrected.

*Line 42: This sentence would be clearer with “i.e., stomata” was parenthetical.*

We agree, we have added the parentheses.

*Line 61: “of H<sub>2</sub>O”, not “to H<sub>2</sub>O”.*

Stomatal conductance to H<sub>2</sub>O or to CO<sub>2</sub> is widely used, for instance in Franks et Beerling (2009), White et al. (2020) or Lammertsma et al. (2011). We would prefer keep “to H<sub>2</sub>O”.

*Line 63: seems as though “simulation design” would be better than “choices made”?*

We agree, it is now rephrased.

*Lines 98-104: In line with my earlier comment on this sentence: To improve this sentence, or sentences after editing, I suggest placing the abbreviation for parameters inside the parentheses with the units.*

Indeed, it is clearer with parentheses.

*Line 182: Need comma after “both”.*

Corrected.

*Figure 3 caption: Should this read “fixed through time”?*

Yes, it is now changed.

## References

- Ball, J Timothy, Ian E Woodrow, and Joseph A Berry (1987). “A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions”. In: *Progress in photosynthesis research*. Springer, pp. 221–224. DOI: [https://doi.org/10.1007/978-94-017-0519-6\\_48](https://doi.org/10.1007/978-94-017-0519-6_48).
- Brodribb, Tim J and Taylor S Feild (2010). “Leaf hydraulic evolution led a surge in leaf photosynthetic capacity during early angiosperm diversification”. In: *Ecol. Lett.* 13.2, pp. 175–183. DOI: <https://doi.org/10.1111/j.1461-0248.2009.01410.x>.
- Brodribb, Tim J, Taylor S Feild, and Gregory J Jordan (2007). “Leaf maximum photosynthetic rate and venation are linked by hydraulics”. In: *Plant Physiol.* 144.4, pp. 1890–1898. DOI: <https://doi.org/10.1104/pp.107.101352>.
- Brundrett, Mark C (2002). “Coevolution of roots and mycorrhizas of land plants”. In: *New Phytol.* 154.2, pp. 275–304. DOI: <https://doi.org/10.1046/j.1469-8137.2002.00397.x>.
- Farquhar, Graham D, S von von Caemmerer, and Joseph A Berry (1980). “A biochemical model of photosynthetic CO<sub>2</sub> assimilation in leaves of C<sub>3</sub> species”. In: *Planta* 149.1, pp. 78–90. DOI: <https://doi.org/10.1007/BF00386231>.
- Feild, Taylor S et al. (2011). “Fossil evidence for Cretaceous escalation in angiosperm leaf vein evolution”. In: *P. Natl. Acad. Sci. USA* 108.20, pp. 8363–8366. DOI: <https://doi.org/10.1073/pnas.1014456108>.
- Franks, PJ and DJ Beerling (2009). “CO<sub>2</sub>-forced evolution of plant gas exchange capacity and water-use efficiency over the Phanerozoic”. In: *Geobiology* 7.2, pp. 227–236. DOI: <https://doi.org/10.1111/j.1472-4669.2009.00193.x>.
- Gough, DO (1981). “Solar interior structure and luminosity variations”. In: *Physics of solar variations*. Springer, pp. 21–34. DOI: [https://doi.org/10.1007/978-94-010-9633-1\\_4](https://doi.org/10.1007/978-94-010-9633-1_4).
- Lammertsma, Emmy I et al. (2011). “Global CO<sub>2</sub> rise leads to reduced maximum stomatal conductance in Florida vegetation”. In: *Proceedings of the National Academy of Sciences* 108.10, pp. 4035–4040. DOI: <https://doi.org/10.1073/pnas.1100371108>.
- Laugié, Marie et al. (2020). “Stripping back the modern to reveal the Cenomanian–Turonian climate and temperature gradient underneath”. In: *Climate of the Past* 16.3, pp. 953–971. DOI: <https://doi.org/10.5194/cp-16-953-2020>.
- Singh, Surendra P et al. (2018). “Insights on the persistence of pines (*Pinus* species) in the Late Cretaceous and their increasing dominance in the Anthropocene”. In: *Ecology and evolution* 8.20, <https://doi.org/10345-10359>. DOI: <https://doi-org.insu.bib.cnrs.fr/10.1002/ece3.4499>.
- Wheeler, Elisabeth A and Pieter Baas (2019). “Wood evolution: Baileyan trends and functional traits in the fossil record”. In: *IAWA journal* 40.3, pp. 488–529. DOI: <https://doi.org/10.1163/22941932-40190230>.
- White, Joseph D et al. (2020). “A process-based ecosystem model (Paleo-BGC) to simulate the dynamic response of Late Carboniferous plants to elevated O<sub>2</sub> and aridification”. In: *Am. J. Sci.* 320.7, pp. 547–598. DOI: <https://doi.org/10.2475/09.2020.01>.
- Yin, X and PC Struik (2009). “C<sub>3</sub> and C<sub>4</sub> photosynthesis models: An overview from the perspective of crop modelling”. In: *NJAS-Wagen. J. Life Sc.* 57.1, pp. 27–38. DOI: <https://doi.org/10.1016/j.njas.2009.07.001>.