

Authors Response to Editor (CEC1)

Dear Dr. Astrid Kerckweg,

Here is a point-by-point response to the comments and concerns.

Comment 1: The main paper must give the model name and version number (or other unique identifier) in the title

Response: In order to meet the standardized protocol of the Journal we plan on modifying the title of the article to "A dynamic local scale vegetation model for lycopsids (LYCOM v1.0)". Thank you for pointing this out.

Comment 2: Code must be published on a persistent public archive with a unique identifier for the exact model version described in the paper or uploaded to the supplement, unless this is impossible for reasons beyond the control of authors. All papers must include a section, at the end of the paper, entitled "Code availability". Here, either instructions for obtaining the code, or the reasons why the code is not available should be clearly stated. It is preferred for the code to be uploaded as a supplement or to be made available at a data repository with an associated DOI (digital object identifier) for the exact model version described in the paper. Alternatively, for established models, there may be an existing means of accessing the code through a particular system. In this case, there must exist a means of permanently accessing the precise model version described in the paper. In some cases, authors may prefer to put models on their own website, or to act as a point of contact for obtaining the code. Given the impermanence of websites and email addresses, this is not encouraged, and authors should consider improving the availability with a more permanent arrangement. Making code available through personal websites or via email contact to the authors is not sufficient. After the paper is accepted the model archive should be updated to include a link to the GMD paper.

Response: We would like to include a section on "code availability" specifying the DOI link to the data repository of the model code. As of now, the code has been made available to the reviewers in Zenodo repository and has been specified in the Model code and software section during the submission process.

(Line 593: Latest article)

Code availability: The Model code (LYCOM v1.0) for the discussed article is archived at [10.5281/zenodo.4960947](https://zenodo.org/doi/10.5281/zenodo.4960947)

We look forward to hearing from you in due time regarding our submission and to respond to any further questions and comments you may have.

Yours Sincerely,
Suman Halder

Authors Response Referee1 (RC1)

(Line number latest article/ Line number diff file)

Dear Dr. Christopher Cleal,

We would like to thank you for reviewing our manuscript. We value the comments and will make amends in the upcoming version of the article. The suggestions are highly appreciated and a revised version addressing the comments will enhance the understanding of the readers and put to rest any confusion concerning the study.

Here we have addressed the comments and concerns:

Comment 1: This paper is an attempt to develop a local dynamic vegetation model to show that lycopsids may have had a significant impact on weathering rates and atmospheric CO₂ during Silurian times. I cannot comment on the validity of the model itself, as this is outside my area of competence; I assume that someone more familiar with such models will also be looking at this manuscript. The following comments are mainly restricted to the general context (mainly palaeobotanical) of the results.

Throughout: "Lycophytes" implies a plant division (or phylum), which is debatable and open to confusion. Better to call these plants lycopsids (i.e., class Lycopsidea), which I think few would dispute.

(Changed throughout the article)

Response: In the article, we aim at representing a broad class of vascular plants, hence 'Lycophytes' has been used to represent the phylum Lycophyta. The limited availability of observable data on physiological characteristics mandates us to use data from the broader range of the plant phylum for laying the boundary condition of the model. Using 'Lycopsids' will put to rest some confusion, and help in being more specific. We will include it wherever we can in the revised version. Besides, we need to include 'Lycopodiosida' and 'Lycophytina' as well if we want to replace 'lycophytes' with 'lycopsids' since Zosterophylloids and Protolepidodendrales also thrived in the period of our concern. LYCOM inherits few boundary conditions from them and hence accommodates such species as well.

Comment 2: Lycopsids never really evolved into woody plants as such. The late Palaeozoic arborescent lycopsids had some secondary wood in their trunk, but the majority of its thickness consisted of periderm. The term woody plants is usually used for those gymnosperms and angiosperms whose trunks and stems consisted almost entirely of secondary wood.

Line: (3 / 3)

Response: In the revised version we will refrain from using 'Woody'. In this context, we will state instead: 'Lycopodiales (club mosses) represent a distinct lineage of vascular plants with a long evolutionary history including numerous extant and extinct species which started as tiny herbaceous plants and later went onto growing into forests with tree-like structure.'

Comment 3: Why is Thomas & Watson (1976) being recorded here? This is a record of a large lycopsid trunk found in much younger strata, in the late Bashkirian. If you are talking about the earliest lycopsids, surely reference to late Silurian Baragwanathia would be more relevant.

Line (35 / 40)

Response: Citing Silurian Baragwanathia is apt here and will be included in the revised version in place of Thomas & Watson (1976).

Comment 4 & 5: Neither Rubinstein et al. (2010) nor Steemans et al. (2009) are reporting lycopsids from the Ordovician. They are reporting cryptospore-bearing Eoembryophyta. The lycopsids probably had their origins in the eoembryophytes, but there is no way you could really call these eoembryophytes lycopsids. The earliest lycopsid remains (and lycophyte remains, namely the Zosterophylloids) remain late Silurian in age. It is here that Thomas & Watson (1976) should be mentioned as documenting these arborescent lycopsids, rather than the Gensel & Berry paper.

Line(38 / 45)

Response: The earliest Lycopsid remains from the Silurian will be used for accurate emphasis as follows:

‘This ancient group of vascular plants (Qiu et al., 2006; Wickett et al., 2014) dates back to the Silurian (Garratt et al., 1984), and later evolved tree stature in the Mid-Devonian (Stein et al., 2012) before surpassing a height of 50 meters during the Carboniferous period (Thomas and Watson, 1976; Taylor et al., 2009)’.

Comment 6: I might be mis-interpreting this, but why is it thought that transpiration during the Silurian was into saturated air?

Response: The purpose of the statement was not to imply that Silurian air was always saturated but to point out that our way of simulating stomatal conductance is suitable for a broad range of environmental conditions, including saturated air.

Vapor pressure deficit (VPD) is the most common regulator of stomatal conductance in dynamic global vegetation models for calculating photosynthesis. The use of VPD, however, fails to capture the fact that a plant’s stomata may also react to water loss due to transpiration into saturated air, which is warmed up by radiation and thus may take up water while staying close to saturation during this process. Furthermore, the role of soil moisture for transpiration under dry conditions is addressed by our approach.

Comment 7: I don’t think these Silurian lycopsids had much in the way of underground roots.

Response: The idea of the article is to represent lycopsids in the model and is not restricted to one period in history but a general representation of the potential climate impacts of these evolving plants. We try to explore and capture the consequence of root evolution and scale their impacts throughout history starting from Silurian. With a model like LYCOM a foundation can be laid for further research to scale such interactions with better precision.

The presence of complex root systems has been reported in the Devonian by Matsunaga and Tomescu, 2016 and the article by Hao et al., 2010 confirms evidence of rootlike structure in the Zosterophyllum plants during the Lower Devonian which are precursors of lycopsids. These plants coexisted with lycopsids around the period of our interest which is specifically a transition between the Late Silurian and Early Devonian when the initiation of diversification of vascular plants began. Even though the early lycopsids featured shallow roots, this was a change from the pre-existing non-vascular vegetation with regard to carbon input into soil. Furthermore, infiltration of the topsoil by roots was a significant phenomenon as it altered the water cycle and the structure of the soil. We will refer to the Early Devonian period as the time when lycopsids with roots first appeared from here on.

Comment 8: Bryophytes were not the immediate precursors of the lycopsids – these were the Zosterophylloids (a sister group to the lycopsids) and the various eotracheophytic / eoembryophytic “rhyniophytoid” groups. Lichens are of course fungi (albeit with algal symbionts) and it is difficult to see how they would have contributed significantly to early Palaeozoic levels of photosynthesis. Moreover, most lichens favour hardground-typesubstrates, whereas the model seems to be dealing with plants on soft substrates, and so it is difficult to see the relevance of comparing the effect of lichens against that of lycopsids.

Response: Porada et al., 2016 suggested Lichen and Bryophyte Net Primary Productivity of 14.4 Gigatons per year globally during the Ordovician and influenced the weathering. Besides, their productivity is significant for the ecosystem Net Primary Productivity especially in the Tundra and the Boreal forest where they boast of a net carbon uptake of 1.9-297 g C m⁻² yr⁻¹ (Uchida et al., 2006; Bond-Lamberty et al., 2004) . Porada et al., 2016 suggested an influence of lichens and bryophytes on weathering rates during the Ordovician. The model LYCOM described in this article is suggestive of a greater weathering potential by Lycopsids. Neither bryophytes nor lichens are an immediate precursor to lycopsids, it is just to put in perspective the importance of Lycopsids and uncover their potentials. Since lichens and bryophytes existed before the Lycopsids, the change in weathering potential emphasizes the impacts of lycopsids and their corresponding effects on the biogeochemical cycle.

Comment 9: The evidence does seem to suggest that lycopsids had the potential to increase local levels of photosynthesis and maybe substrate stability. But aerial cover of lycopsids during the Silurian is likely to have been very limited – probably mainly restricted to areas of wet substrates. With such a limited aerial spread, what global impact are they likely to have had in Silurian times on atmospheric composition? On the other hand, it has been suggested that the early eotracheophytes were already influencing atmospheric CO₂ and weathering rates by the Ordovician (e.g., Servais et al. 2019. Palaeogeography, Palaeoclimatology, Palaeoecology, 534: 109280) so it is maybe to be expected that the much larger lycopsids could have been having a larger effect in the late Silurian.

Response: As rightly pointed out, the evidence does suggest that lycopsids had the potential to increase local levels of photosynthesis and modulated water recycling. We want to emphasize the fact that our model is not restricted to any particular period of history, we want to explore the extent of the influence of these plants on the climate of the past. We aim to capture the effects of Lycopsids when they were restricted spatially as well as for the period when they thrived abundantly. We look forward to hearing from you in due time regarding our submission and to respond to any further questions and comments you may have.

Yours Sincerely,
Suman Halder

Bond-Lamberty, B., Wang, C., and Gower, S.: Net primary production and net ecosystem production of a boreal black spruce wildfire chronosequence, *Global Change Biology*, 10, 473–487, doi:10.1111/j.1529-8817.2003.0742.x, 2004.

Hao, S., Xue, J., Guo, D., & Wang, D. (2010). Earliest rooting system and root: shoot ratio from a new Zosterophyllum plant. *New Phytologist*, 185(1), 217-225.

Matsunaga KK, Tomescu AM. Root evolution at the base of the lycophyte clade: insights from an Early Devonian lycophyte. *Ann Bot.* 2016 Apr;117(4):585-98. doi: 10.1093/aob/mcw006. Epub 2016 Feb 26. PMID: 26921730; PMCID: PMC4817433. Porada, P., Lenton, T. M., Pohl, A., Weber, B., Mander, L., Donnadieu, Y., ... & Kleidon, A. (2016).

High potential for weathering and climate effects of non-vascular vegetation in the Late Ordovician.

Nature Communications, 7(1), 1-13.

Uchida, M., Nakatsubo, T., Kanda, H., and Koizumi, H.: Estimation of the annual primary production of the lichen *Cetrariella delisei* in a glacier foreland in the High Arctic, Ny-Ålesund, Svalbard, *Polar Res.*, 25, 39–49, doi:10.3402/polar.v25i1.6237, 2006.

Authors Response Referee2 (RC2)

(Line number latest article/ Line number diff file)

Dear Respected Referee,

We would like to thank you for reviewing our manuscript. We value the suggestions and will try to address the comments to the best of our ability. A revised version of the article will be uploaded soon.

Here we have addressed the comments and concerns:

Comment 1: I preface this review in that I only have expertise on the fossil plant and geological timescaled environmental, climate and weathering implications of the research; I cannot comment in detail on the methods used to develop the model but these seem appropriate and well thought through. The parameters relating to geological factors such as weathering and soil carbon dioxide match my understanding of the subject. it would be important to get feedback from a climate modeller on the paper.

This is an interesting paper that develops a model for the weathering of lycophytes in modern and ancient environments to interpret their environmental and potentially climatic significance. The approach is novel and appropriate, generating what appear to be important implications. Overall, I like this and think the underlying research is solid, but conclude the paper needs to be revised before it is suitable for publication to address a number of points. The absence of up to date and correct information on the early evolution of Lycophyta in the Paleozoic is a problem that leads to incorrect statements being made in various places in the paper. My feeling is that the paper would benefit dramatically from being revised by a palaeobotanist with knowledge of Paleozoic plant in order to correct that aspect of the work as it underpins the rationale for the research. As it is, if the introduction was re-done as outlined below it would be better. It would also benefit from further editing of the language to improve the readability.

Response: The article aims to address the research gap in understanding the effects of Lycopsids for today's climate. Several citations and information will be updated in the upcoming version in order to avoid providing misleading information. We have considered the suggestions in order to provide accurate palaeobotanical evidence.

Comment 2: The principles of the model seem appropriate and these are easy to follow, but some further clarification on specific parameters would be helpful. The results are great as are the conclusions, but both sections could make greater comparisons to the rock record to compare to past conditions. As it is, the paper aims to design a model suitable for the geological past and present, but the results and conclusions only really deal with the present so there is scope to expand this. In the Devonian, Lycophyta were key components in terrestrialization and biogeochemical cycles, as well as being geo-engineers. There is ample scope to introduce these concepts to enhance the impact and implications of the research.

Response: It is true that the current article focuses on simulating today's potential effects of Lycopsids on weathering. This is necessary precondition, in our opinion, to provide estimates for

the geological past. The application of the model to the past, namely the Devonian, however, requires further comprehensive work and is thus beyond the scope of the paper. We plan to carry out these simulations in a follow-up study.

aims to provide a motivation for the study but delves into effects of the Lycopoids for the present. There will be a following article encompassing their effects for the past namely, Devonian.

Comment 3: Specific points:

Lines 11-14. Poor grammar, please revise.

Lines (11-14/ 11-14)

Response: In the revised version, we will state instead:

‘Hence, as a first step, a process-based model is developed to estimate net carbon uptake by these organisms at the local scale. The model includes key features such as distribution of biomass above and below ground, along with a plausible root distribution in the soil affecting water uptake by plants. The stomatal regulation of water loss and its immediate implications for photosynthesis are considered. Moreover, root respiration plays a crucial role in the model by affecting soil carbon dioxide and weathering rates.’

Comment 4: Line 31. The citation to Foster et al. (2017) is disingenuous to the pioneering works on this topic by R. A. Berner, that should be cited here as this is still widely accepted as correct.

Lines (34 / 37)

Response: The works of R.A. Berner will be cited in the revised version of the article.

Comment 5: Lines 35-41. Lycophytes are one of the earliest forms of vascular plants and not THE oldest form. Also, there is no macro-fossil evidence for lycophytes dating back as far as you report; the papers by Steemans et al. and Rubinstein et al. are inappropriately synthesized and mis-quoted, with both showing no pre-Devonian evidence of lycophytes. The present authors confuse Embroyphyta or Tracheophyta which have pre-Devonian evidence, with Lycophyta. This section needs fundamentally revising and appropriate references using – see for example Gensel (2017) Fern Gaz. 20(6): 217-242 and Servais et al. 2019 I Palaeogeog., Palaeoclimatol., Palaeogeog., 534: 109280. The conclusions of Qiu et al. and Wicketts et al. presented are based on clade dating approaches that have no substance in the fossil record – these plants do not go back that far in time.

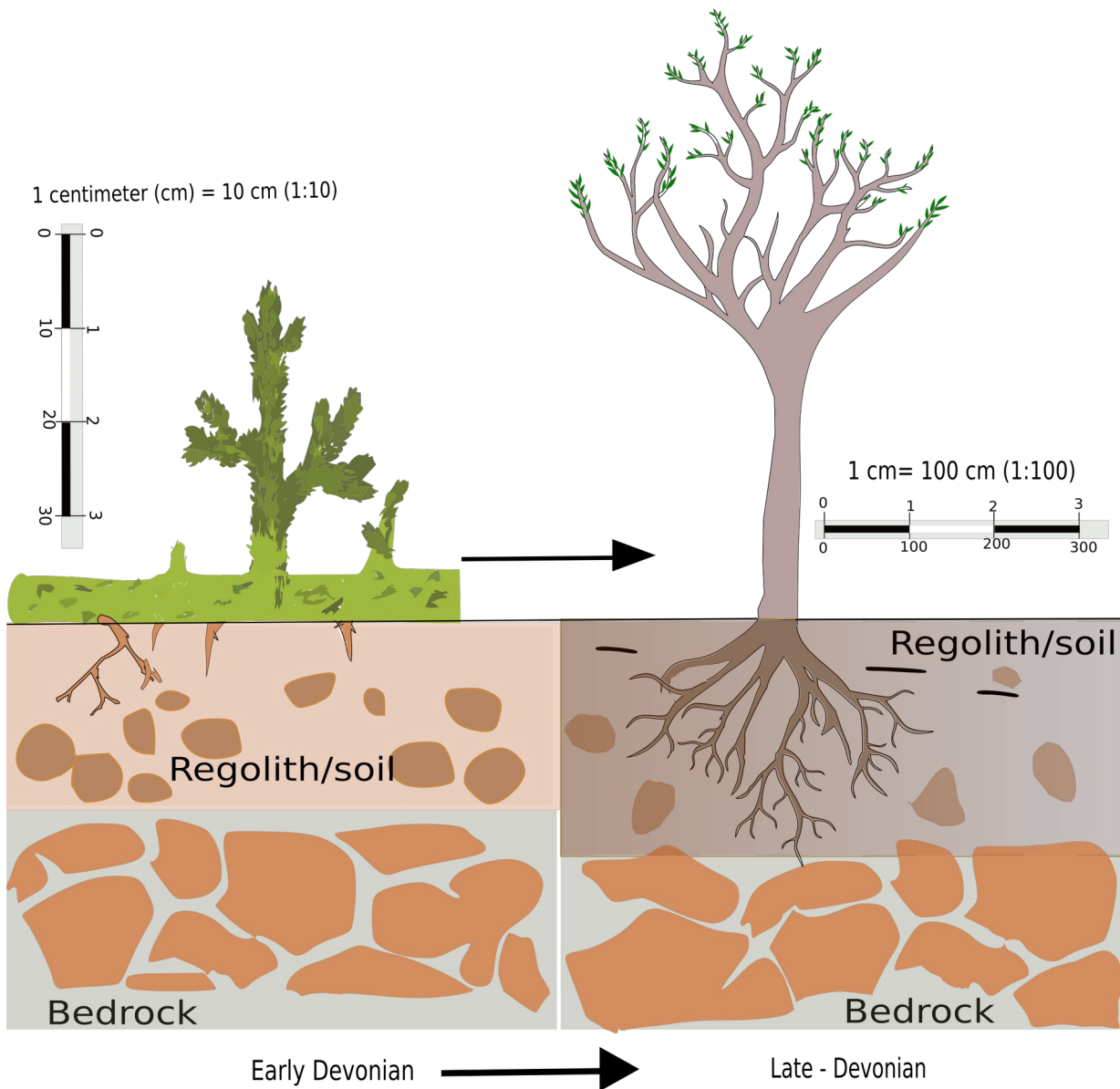
Lines (37-41 /43- 49)

Response : This point has been noted and modified already according the previous posted referee comment. Our primary aim is to provide a broad underlying reasoning for the choice of our parameters in the model. The parameterization of the model uses broad range of plants including Zosterophylloids which is considered to be a sister-group to lycopoids. In the model, we look to incorporate a broad range of species that existed around 410 million years ago. This is done to incorporate bio-diversity and include closely-related species. It is with the same reasoning *Embroyphyta* was initially included but have been excluded. This will be looked into in details to avoid any misinformation.

Comment 6: Figure 1 – please put a scale bar that is easy to comprehend with mm and cm clearly shown. This is very confusing. Also in figure 1, what about regolith/soils? Bedrock looks broken up – why not have solid bedrock rather than round lumps floating in nothing?

Compare with the rooting model of Algeo and Scheckler (1998) for added context and content.

Response: A revised version of the figure 1 with better scaling system and regolith has been generated. An updated version of the representative figure below will be used for the purpose. Since the detailed root structures are beyond the scope of modelling work, we would like to stress on the fact that these diagrams are representative and are for illustrative purposes only. This illustrative figure is inspired from the works of Algeo and Scheckler (2012)



Comment 7: Lines 52-76. This is good but lacks reference and inclusion of key information from Algeo and Scheckler (1988) and Elick et al. (1998) that should be included.

Lines (57-84 / 64- 92)

Response: In the latest version the works of Algeo and Scheckler (1988) and Elick et al. (1998) have been incorporated. The close association of weathering by early vascular plants has been well explored in the studies and we would like to thank you for mentioning them.

Comment 8: Lines 65-71 – needs citations to primary sources of information.

Lines (72-80 / 80- 88)

Response: The upcoming version will substantiate the information with proper citations making the article robust and reliable.

‘Roots were not the only suite of innovations from these kinds of plants, they further developed stomatal control (Kenrick and Strullu-Derrien, 2014; Brodribb and McAdam, 2011) of water loss to be able to photosynthesize under adverse climatic conditions which might have given lycophytes yet another advantage over their contemporaries. The evolution of stomata followed the innovation of roots closely, around 400 million years before the present (Chater et al., 2011; Ruszala et al., 2011). Water loss and NPP are regulated by the opening and closing of stomata (McAdam and Brodribb, 2013). By changing the aperture of the stomata, plants inhibit water loss to prevent desiccation, at the cost of reduced photosynthetic productivity. The combination of adjustable stomata with an internal water transport system i.e. vascularity, was a turning point in plant evolution that might have enabled vascular plants to invade most terrestrial environments, tolerating water stress and exploiting favorable conditions (Raven, 2002).’

Comment 9: Line 101 – lycophytes were not abundant in the Silurian – see comment above.

Line (110 /118)

Response: Although the lycophytes were not abundant in the Silurian, it is certain that their origin can be traced in the Silurian. The above statement has been revised and rewritten asserting Late abundance of lycophytes in the Late Devonian period.

This has been duly noted the change in timeline has been implemented.

Comment 10: Line 104 – all Paleozoic lycophyte genera and species are now extinct.

Line (113 / 123)

Response: It is without doubt that the extant lycophyte species are different from those which existed in the Paleozoic. It is therefore hard to gather information and this poses a unique challenge to our research. Nevertheless, the impacts of existing lycophytes on biogeochemistry can, in our opinion, be used to approximate the potential impacts of their predecessors on the Devonian climate.

Comment 11: Lines 126 – VPD vs. soil water content and potential evaporation; many lycophytes lived in saturated soils so had abundant aerenchyma in their roots – does this affect your model?

Response: The current article focuses on extant lycophytes under various environmental conditions and hence does not incorporate the special case of the effects of aerenchyma tissue. Our current scheme accounts for stomatal control depending on the average climatic condition and atmospheric water demand of the immediate surrounding. This is done for the extant lycopsids under current atmospheric conditions.

The aerenchyma plant tissue is primarily a feature of plants in stress under hypoxic condition. The implication of such tissue is hard to incorporate in our model since these tissues are primarily responsible for Oxygen transport to the root. This hardly affects the potential evaporation or photosynthesis which is our main focus here and hence does not affect the current model. Oxygen limitation of roots may be incorporated in later versions of the model.

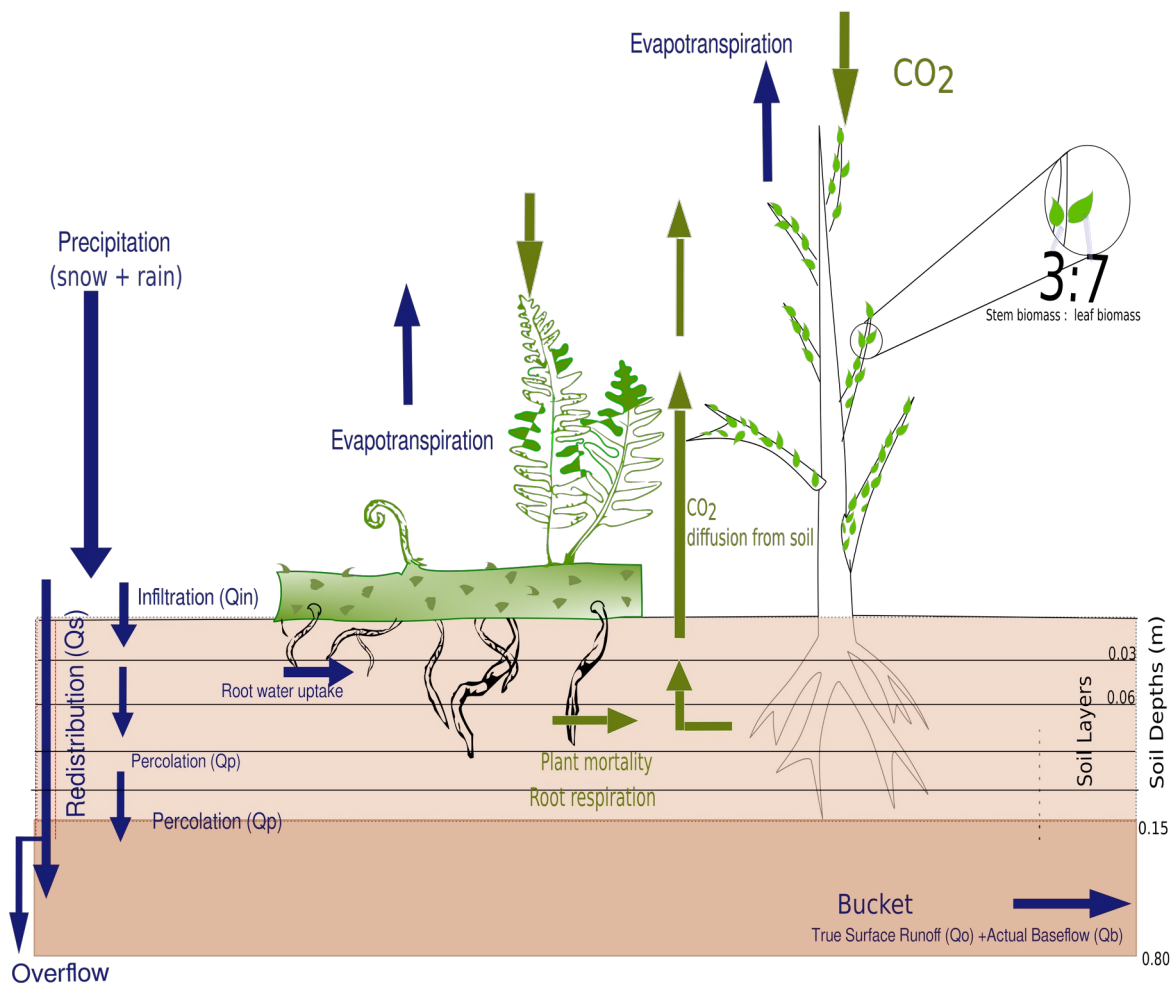
On the other hand, the presence of such tissue would mean a easier release of CO₂ from the soil, which we can incorporate by increasing carbon dioxide diffusion from soil to the atmosphere. The feature will be taken into consideration while simulating for the Devonian and hence a simple scheme of faster diffusion should be enough to capture the implication of such tissues.

Comment 12: Line 128 – there were no lycophytes in the Silurian, so this aim is misguided – no point in reconstructing what wasn't there. Work on the Devonian.

Line (119 /129)

Response: This article primarily lays the foundation for a global version of the model with a motivation to extend it for the past. It is important to focus on the period when the Lycophytes thrived in abundance and hence we shall focus on the time-period around 410 million years ago (Early Devonian).

Comment 13: Figure 2 – nice – but really needs to be two parted showing the horizontal form as in figure 1 as well.



Response : The purpose of the figure is to provide a synopsis of the primary processes devised in the model. The Figure 2 is for pure explanatory purpose. The model does not currently distinguish between an upright or horizontal lycophytes. The updated figure will hopefully provide clarity and help in a better understanding of the model.

Comment 14: Lines 130-135 – the LYCOM model depicts lycophytes as comprising organographically distinct stems and leaves. See recent paper by Hetherington et al. (2021) that shows the basal lycopsid Asteroxylon had three kinds of axes in the body plan; leafy shoot axes, root-bearing axes, and rooting axes. This information is key to understanding the actual plant and needs to be incorporated into the present manuscript. How do your two organs compare or map onto the three of Hetherington et al?

Response: A model as simple as LYCOM provides us with a limited opportunity to incorporate a detailed structural representation of plants in real life. The most important aspect of the Dynamic Vegetation Model (DGVM) is to try and include the processes impacting the Carbon balance and its products. The current state of the model distinguishes between below and above ground biomass, with further division of above ground biomass into leaves and stem. The allocation of the carbon is subject to limitations in water, CO₂ as well as light. The root allocation with soil depth is in agreement with most terrestrial biomes. The earlier works of Dr. Alexander John Hetherington contributed to the understanding of the rooting structure and key features while implementing it in our LYCOM. The works of Hetherington et al. (2020) is impressive and makes our model assumptions robust, but at the same time does not compromise the model performance or outcome.

Comment 15: Lines 348-353 – readjust to the Devonian period. There were NO lycophytes in the Ordovician.

Lines (365-370 / 379- 384)

Response: This point has been noted and will be reflected in the latest version of the manuscript.

Comment 16: Table 1 – please show where individual range values come from for each parameter. This is key to the model, but the sources of data are not explicit for those not referred to an Eq. in the paper e.g. fracTransm, VCm, Vom, EactKc, EactKo, EactKm, EactKj.

(Table 1 updated)

Response: The sources of the data will be mentioned in the upcoming version of the manuscript with explicit references.

Comment 17: Results – nice – but figure 4 is missing in the version I reviewed. However, I would like to see comparisons to values for weathering rates in geological time – how do your results correlate to similar conditions in the Palaeozoic, returning to your aim to understand the impact of early lycophytes on climate and environment.

Response: Since the current focus is today we have drawn comparison from the articles exploring the present weathering scenario. The comparison with the Palaeozoic weathering will only be fair when we run the model for Devonian. The model is under constant development and will be extended for a global paleo-simulation soon.

Comment 18: Conclusions – no mention of relevance or implications to the fossil record. Great for the model, but otherwise disappointing.

Lines (565-572 /581-586)

Response: The LYCOM model draws in information from fossil records as it helps in setting the physiological limitations of the extinct species. Modern lycophytes, such as terrestrial lineages of the Lycopodiaceae, maintain some degrees of functional and morphological conservatism with respect to Early Devonian herbaceous lycopsids and their fore-runners. On this basis, modern lycophytes can be used as a suitable analog system for widespread elements of Early Devonian plant communities. This model therefore can be applied toward investigations targeting weathering

dynamics in early terrestrial ecosystems. This implication of the model to the fossil record is imminent and we therefore try to explore the past using information from such records.

Comment 19: Missing key references

Algeo, T. J., Scheckler, S. E., 1998. *Terrestrial-Marine Teleconnections in the Devonian: Links between the Evolution of Land Plants, Weathering Processes, and Marine Anoxic Events*. *Royal Society of London Philosophical Transactions (B): Biological Sciences*, 353: 113–130

Algeo and Scheckler (2012) *Land plant evolution and weathering rate changes in the Devonian*. *Journal of Earth Science* 21, 75-78.

Elick et al., 1998. *Very Large Plant and Root Traces from the Early to Middle Devonian: Implications for Early Terrestrial Ecosystems and Atmospheric P(CO₂)*. *Geology* 26: 143-146.

Hetherington and Dolan (2017) *The evolution of lycopsid rooting structures: conservatism and disparity*. *New Phytologist* 215: 538-544.

Hetherington et al. (2020) *An evidence-based 3D reconstruction of Asteroxylon mackiei the most complex plant preserved from the Rhynie Chert*. 2021;10:e69447 DOI: 10.7554/eLife.69447

Lines (599- 779)

Response: These key citations have been compiled in the latest version.

We look forward to hearing from you in due time regarding our submission and to respond to any further questions and comments you may have.

Yours Sincerely,
Suman Halder