

***Interactive comment on* “Estimating global carbon uptake by lichens and bryophytes with a process-based model” by P. Porada et al.**

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Estimating global carbon uptake by lichens and bryophytes with a process-based model

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Reply to the comments of anonymous referee 1

We would like to thank the referee for the thorough and helpful review of the manuscript. By changing the text according to this response, we hope to improve the manuscript and account for the concerns raised by the referee. The (summarised) reviewer’s comments are in italic text, while our responses are formatted as standard text.

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1. *Given a certain thallus water content, the corresponding maximum photosynthetic activity is only reached after a time delay. This effect is not included in the model and could be represented by an additional strategic parameter.*

For all we know at the moment, the time delay of photosynthetic activity could be implemented as an independent parameter into the model, which means that a random value is assigned to each “strategy”. It seems, however, that the time delay is not independent but it is controlled by several other factors:

- The activation of photosynthesis is probably associated with carbon costs, such as investment into protection mechanisms (Lidén et al., 2010). Since there are various protection mechanisms (Gray et al., 2007), the costs of activation will likely vary, too. It is possible that a short time delay is associated with higher carbon costs than a long time delay, since more resources into protection have to be invested. This would imply that a short time delay mainly pays off in microhabitats with frequently changing moisture conditions, as described by (Jonsson Čabrajčić et al., 2010; Lidén et al., 2010).
- If the time delay is indeed an independent property (maybe because competition is too weak to select for it), lichen species with short as well as long time delays should be found randomly distributed in many different microhabitats, which does not seem to be the case.
- Given a certain species, the time delay is not a fixed property, but it depends on the length of the preceding dry period (Gray et al., 2007; Proctor, 2010; Ried, 1960).

To model the time delay of photosynthetic activity, these open questions would have to be clarified, implying that the metabolic costs associated with the time delay and the relation between length of time delay and length of dry period would have to be determined. This is not possible based on the present knowledge. Thus, we decided not to include the time delay into the model at the moment.

We will discuss the potential importance of delayed activation of photosynthesis for metabolic activity (Jonsson et al., 2008; Jonsson Čabrajić et al., 2010; Lidén et al., 2010) and the open questions concerning the implementation of this property into the model in section B3.4 of our manuscript. We will also change the statement that the exact shape of the relation between metabolic activity and water content is not known. Instead we will refer to (Jonsson Čabrajić et al., 2010) to give an example how photosystem activity is related to water content. Moreover, we will refer to (Lange, 2002, 1980) to give examples of the relation between dark respiration and water content.

2. *The difference in metabolic activation between lichens with a cyanobacterial photobiont versus a green algal one could be represented by an additional strategy parameter.*

The need for liquid water to be activated is a physiological constraint of cyanobacteria and it seems to be a disadvantage for the carbon balance of cyanolichens. This disadvantage, however, could be compensated by some other property of cyanobacteria that is beneficial for the lichens, such as nitrogen fixation, for instance. We cannot account for this property because nutrient limitation is not implemented in the model. Thus, since we cannot consistently represent all distinct properties of cyanobacteria and the associated tradeoffs in our model, we decided not to model cyanolichens explicitly. They may, however, be implicitly simulated by model “strategies” which have physiological properties similar to cyanolichens. We will mention the different requirements of cyanolichens with regard to metabolic activation in section B3.4 of our manuscript and explain why we did not include this trait.

3. *The model has avoided any mentioning of the fungal component of the lichens. The fungus contributes to respiration but not to Rubisco content, therefore the relation of these two variables in the model should account for the fungus.*

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Although we did not mention the fungal component of lichens, it is implicitly represented in the model, since the biomass of a lichen integrates fungal as well as algal/cyanobacterial biomass. The maintenance respiration in the model is assumed to be controlled by the average Rubisco content of the total biomass. Hence, a lichen with a high fraction of algal/cyanobacterial biomass which has a low Rubisco content should have a maintenance respiration similar to a lichen with a low fraction of algal/cyanobacterial biomass which has a high Rubisco content, because the Rubisco content of the whole total biomass would be similar. This assumption is valid as long as fungal and algal/cyanobacterial biomass do not differ much in some component which is not correlated with Rubisco content but which causes respiration. The chlorophyll a content, for instance, has been shown to affect respiration (Palmqvist et al., 2002). It should, however, correlate with Rubisco content since photosynthesis requires both of these components. We will clarify this in our manuscript in sections 2.2 and B5.2.

4. *The model assumes a constant relationship between Rubisco and maintenance respiration across “strategies” (species), even though at least one study has shown that photosynthetic capacity increases more than maintenance respiration with increased nitrogen content across lichens albeit also being dependent on morphology and photobiont taxa.*

We agree that the relation between photosynthetic capacity (which correlates with Rubisco content (Palmqvist et al., 1998)) and specific maintenance respiration exhibits considerable scatter across lichen species (Palmqvist et al., 2002). It is, however, impractical to implement all properties of lichens that may lead to deviations from the constant relationship between Rubisco and maintenance respiration into the model. The best way to account for the scatter in the linear relation c would then be to add a random term S of the form $Respiration = c * [Rubisco] + S$. We do not, however, have enough data to quantify the magnitude of S . Already the estimation of the linear relation itself had to be done by “educated



guess". We will point out in sections 2.2 and B5.2 that the respiration of lichens is a complex process and may also be influenced by other factors than photosynthetic capacity. To our knowledge, however, these factors cannot be quantified to an extent that makes it possible to include them in the model.

5. *The CCM implemented in the model should be discussed more clearly regarding its possible purpose in the symbiosis.*

We will point out in section 2.2 of our manuscript that we assume that the CCM in lichens works similarly than in free living cyanobacteria. Based on this assumption, the CCM implemented in our model represents an advantage for the organisms in case of low internal CO₂ concentrations in a water saturated thallus. We will add these points also to section B3.5. We will then discuss in section 4 that the observed pattern of CCM makes sense regarding how we implemented the CCM. We will point out that the CCM which cyanobacteria and some algae possess is not necessarily the reason why they are part of the symbiosis and that not enough is known about how the CCM works in lichens and bryophytes to make definitive statements.

6. *The Tables and Figures in the B-section should be presented together with their corresponding equations and the references to data for these equations should be presented together with their corresponding equations, tables and figures.*

The format of *Biogeosciences Discussions* requires the present structure of the manuscript. The version published in *Biogeosciences* will not have separate parts for tables and figures. In this version, the figures and tables containing references for the equations will be presented together with the equations in the respective sections of the appendix. Only the overview tables which contain the model parameters with their numerical values and the model variables will be placed at the end of the appendix.

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