

Interactive comment on “Modelling the habitat preference of two key *Sphagnum* species in a poor fen as controlled by capitulum water retention” by Jinnan Gong et al.

Anonymous Referee #1

Received and published: 8 December 2019

1. Does the paper address relevant scientific questions within the scope of BG? YES
2. Does the paper present novel concepts, ideas, tools, or data? YES
3. Are substantial conclusions reached? YES
4. Are the scientific methods and assumptions valid and clearly outlined? MOSTLY YES
5. Are the results sufficient to support the interpretations and conclusions? ALMOST
6. Is the description of experiments and calculations sufficiently complete and precise to allow their reproduction by fellow scientists (traceability of results)? YES

C1

7. Do the authors give proper credit to related work and clearly indicate their own new/original contribution? NO
8. Does the title clearly reflect the contents of the paper? YES
9. Does the abstract provide a concise and complete summary? YES
10. Is the overall presentation well structured and clear? YES
11. Is the language fluent and precise? YES
12. Are mathematical formulae, symbols, abbreviations, and units correctly defined and used? YES
13. Should any parts of the paper (text, formulae, figures, tables) be clarified, reduced, combined, or eliminated? YES
14. Are the number and quality of references appropriate? NO
15. Is the amount and quality of supplementary material appropriate? YES

Dear authors,

Your paper presents an interesting, physiology-based model of competition between two *Sphagnum* species, attempting a high level of realism in the (large-scale) hydrological regimes and the water-related ecophysiology of the two species studied, *S. fallax* (lawn species) and *S. magellanicum* (hummock species). I generally liked the approach, though I have some remarks and questions that I think are worth addressing before publication of the final version.

General comments

1. Please provide a list of abbreviations! It was hard work trying to follow the methods and results without one.
2. A discussion of some literature very relevant to this study, exploring the same ideas though without using a formal model, is missing:

C2

(Titus, et al. 1983, Titus and Wagner 1984). One of the interesting results of these studies is that there is a seasonal dynamic in the water-content response of photosynthesis. This may be very relevant to your model, if the model is sensitive to these 'water-stress' responses.

(Rydin 1986, 1993a, b, 1997, Rydin and Barber 2001) And more: check the publications by Hakan Rydin, he has been working on competition between Sphagna for a long time.

Another important source, which, however, has not yet been fully published (but a relevant summary with numbers to compare yours against is available in the thesis summary: <http://www.diva-portal.org/smash/get/diva2:1282760/FULLTEXT01.pdf>), is the recent PhD thesis by Fia Bengtsson (Uppsala), in particular chapters 4 and 5.

This paper (Hájek 2014) is also very relevant, among other things for some methodological issues.

3. Model structure: The abstract promises a very wide scope ('dynamic feedback between plant community structure and the environment'), but there is no feedback from the species composition (Modules 1 and 2) on the hydrology (module 3) in the model. Therefore: how does this model really address the feedback you mention? In the discussion, you could also be more explicit about the implications of the species composition on biogeochemical processes, see e.g. (Bengtsson, et al. 2016, Cornelissen, et al. 2007). Alternatively, do not suggest this focus on feedbacks in the abstract and introduction.

The vertical water transport is implemented in detail, but in the detailed modules 1 and 2 there does not seem to be horizontal water exchange between neighbours, although this may play an important role in maintaining Sf in hummocks, supported by the water held in Sm (Rydin 1985 ; Rydin and McDonald 1985 ; Robroek et al. 2007a). In your experiments, basing the drying speed on single capitula, the capitulum density, i.e. facilitation between neighbours in retaining water, could not affect the drying speed,

C3

thereby possibly missing part of the difference between the lawn and the hummock species (i.e. under-estimating the difference).

4. Model parameters / results L487 & L520-522 Please also explain why Sf has an advantage over Sm in the lawns. Why does Sf have faster growth? This is not clear to me at all. According to your photosynthesis measurements, Sf has a lower A_{max} (which seems strange, usually indeed lawn species have higher rates) and the same respiration rate as Sm. Therefore, at high water content and high light, Sm and not Sf should have a benefit in terms of NSC production. As the conversion from NSC to biomass is the same for both species, the only way to explain the higher length growth of Sf in the lawn environment is the higher H_{spc} (higher height growth per unit biomass). Correct?

5. Ecophysiological measurements / model parameters: L1017 You state here that A tended to increase with time and that it peaked at water contents below the maximum, as indeed shown by the theoretical figure 1B, but not by the measured curves in Fig 2C. Indeed I would have expected such a peak. Can you explain the absence of diffusion limitation in your experiment? Good ventilation..? Is it realistic to measure one capitulum in isolation? Lots of air all around it compared to a capitulum immersed in a (wet) Sphagnum mat. . . Consequently, also, how homogeneously will the capitula have dried out in the GFS compared to in a Sphagnum mat?

It has been shown that the speed of drying during gas exchange measurements can strongly affect the conclusions about optimum water content and water compensation point (Hájek 2014). Under quick drying, as in your experiments, it seems typical to get the type of curves you present. However, under slower drying, as would be typical in the field, the optimum WC would be lower and the depression at high WC stronger. In particular the high compensation point you found, at water contents of up to 600%, seems to be a typical artefact of such fast drying, related to the inhomogeneous drying within the capitula.

C4

Also, a field water content of 1470 and 809% water per dry mass seems extremely low for Sphagnum in general and for these species. For *S. magellanicum* I have seen max WC values reported between 2000 and 3000%, and for *S. fallax* of about 1500% (or 1100%, equivalent to 12 gFM/gDM (Titus, et al. 1983)). You even state yourself (Line 270) that 'it is known that W_{max} is around 25-30 g g⁻¹. So I do not understand why you started your experiment at 14,7 and 8,09 g g⁻¹ or where you use these values, as opposed to the values in L277.

If the light curves took up to 120 minutes to complete (why? That is a very long time especially if you only measured at 4 light levels, which seems very little to determine a reliable curve. . .), and drying down to the compensation point took 120-180 minutes, this implies that during the light response measurements you measured a combination of reduced light and reduced water content, so that the curves probably do not reflect only the light response. For determining the A_{max} this should be no problem, as you started at the highest light level, i.e. at A_{max} . Are you sure there was no photoinhibition at these high light levels? This may be a problem when starting light response measurements at the high end, as it would affect the rest of the measurements.

6. Model tests: As an important difference between your and previous models lies in the coupling to environmental fluctuations and stochasticity (L97-98), it would make sense to present a test of the importance of these processes to the model output. Would a simpler model provide similarly good results?

I would also be interested in seeing the effects of the water retention and photosynthetic water-response parameters separately. Especially since the parameters for the latter may suffer from some measurement artefacts.

7. Presentation: L279-352 are all about module 3, which seems a bit unbalanced, seeing that modules 1 and 2 seem more important for the competition results. Model 3 is not tested in this paper. . .

Specific comments

C5

L20 In the introduction it could be explained more clearly why a mechanistic model is needed to predict species compositions under changing water levels. Is a prediction based on known habitat preferences not good enough?

L60-61 how does the species composition affect these processes? In particular (for discussion), how do your species / ecological types affect these processes?

L381 it would be interesting to see the effects of water retention and 'water stress' separately

L471 to me it does not look like photosynthesis of *S. fallax* is more sensitive to changes in the water content, as A_{max} lies at lower water contents than for *S. magellanicum*, suggesting that it can handle dry conditions better.

L552 how exactly may it serve?

L561 Similarly, how could it be used in DVM development? If you can, please try to be more explicit here.

Table 1: R_{s20} was not significantly different between the species, then why use different values here? How large is the effect on the results?

Technical corrections:

L24 employs

L50 why 'during decadal timeframe'?

L57 have

L66 remove 'community'

L69 I do not think that this modelling can be considered a 'space-for-time' approach. The processes are different in space than in time.

L90 . . .that is covered. . . .As competition occurs. . .

C6

L100 within the peatland moss layer
L102 whose competitiveness?
L106 positions a long a
L113 modelled is located
L119 with a sparse cover of vascular plants
L125 The Peatland...
L126 explain 'water-energy conditions'
L128 consisting
L132 are driven
L142-143 A is not directly controlled by CWR, please rephrase
L145 These were not really random variables, but variables randomly selected from a distribution
Eq5: what are the rules for the timing of growth? Any relation to WC?
L191 explain where Kimm is based on
L204 ii) biomass, or NSC?
L212 This order of sentences suggests that an exhaustion of NSC storage would be due to lateral growth, which would not make sense, as lateral growth should not take place if NSC supplies are not enough to sustain both new capitula
L217 why suddenly 'moss parameters' - better use the same terms all the time
L227 how does shoot density vary in the model, if you model one capitulum per grid cell?
L235 where is the centre of the moss layer?

C7

L239 what is the 'capacity of water'?
L264 'where W_{opt} is the optimal water...'
L270-278 It is not clear to me why this equation was needed.
L277 Is the same W_{max} used for both species..? An how about the values in Table B1
L294 are listed
L295-313 Why are snow dynamics important for the model?
L318 What are 'periodic lateral boundary conditions'?
L323 of the model
L346-347 WTs is the multi-year mean of weekly water table?
L474 insert return
L487 This would be a good place to explain why S_f overgrows S_m in the lawns.
L495 in other hydraulic
L513 Explain the 'this could be because', this is not obvious
L520 As A_{max} was lower in S_f , and R_{s20} was the same, it seems that only H_{spec} would explain the result. You could repeat the test adjusting only H_{spec} to test this.
L527 dominated
L544 This would be a good place to explain how these impacts work and what your model thus implies (or could imply when tested under climate-change conditions) for peatland stability and functioning
Table 1: I would recommend adding the units inside the table
Table 1 & Table B1: A in bryophytes is usually expressed in $nmol\ g^{-1}\ s^{-1}$, to avoid to many 0 before significant digits start.

C8

Table 2 and 3: please explain abbreviations

Appendix L 150 at one hertz?

L209 The software is R, R Studio is just an interface

Fig B2: it is impossible to distinguish the models from the data especially in C. See comments above about the curves in C.

Cited references:

Bengtsson, F., Granath, G. and Rydin, H. 2016. Photosynthesis, growth, and decay traits in Sphagnum - a multispecies comparison. - *Ecology and evolution* 6: 3325-41.

Cornelissen, J. H. C., Lang, S. I., Soudzilovskaia, N. A. and During, H. J. 2007. Comparative cryptogam ecology: A review of bryophyte and lichen traits that drive biogeochemistry. - *Annals of Botany* 99: 987-1001.

Hájek, T. 2014. Physiological ecology of peatland bryophytes. - In: Hanson, D. T. and Rice, S. K. (eds), *Photosynthesis in early land plants*. Springer, pp. 233–252.

Rydin, H. 1986. Competition and niche separation in Sphagnum. - *Can J Bot* 64: 1817-1824.

Rydin, H. 1993a. Interspecific competition between Sphagnum mosses on a raised bog. - *Oikos* 66: 413-423.

Rydin, H. 1993b. Mechanisms of interactions among Sphagnum species along water level gradients. - *Advances in Bryology* 5: 153-185.

Rydin, H. 1997. Competition among bryophytes. - *Advances in Bryology* 6: 135-268.

Rydin, H. and Barber, K. E. 2001. Long-term and fine-scale coexistence of closely related species. - *Folia Geobot* 36: 53-61.

Titus, J. E., Wagner, D. J. and Stephens, M. D. 1983. Contrasting Water Relations of Photosynthesis for 2 Sphagnum Mosses. - *Ecology* 64: 1109-1115.

C9

Titus, J. E. and Wagner, D. J. 1984. Carbon Balance for 2 Sphagnum Mosses - Water-Balance Resolves a Physiological Paradox. - *Ecology* 65: 1765-1774.

Interactive comment on Biogeosciences Discuss., <https://doi.org/10.5194/bg-2019-366>, 2019.