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

by P. Porada, B. Weber, W. Elbert, U. Pöschl, and A. Kleidon

Reply to the comments of anonymous referee 2

We thank the referee for the review of the manuscript.

- To address the main concern raised by the referee we included more observational data in our comparison of empirical and modelled estimates. For this purpose we added 16 empirical studies to the database (see Table 1) and we also updated Fig. 7 of the manuscript (see Fig. 1 below) showing an order-of-magnitude comparison between model estimates and observations by biome.

- There is a valid reason for our rough method of model-data comparison: The observational data are spatially and temporally discrete point-scale measurements which show a high variation, e.g. $8\text{-}1450 \, \mathrm{g\,m^{-2}\,yr^{-1}}$ for *Sphagnum* (Gunnarsson, 2005). It is very problematic to extrapolate from these varying point measurements to large regions, such as a model grid cell, which is about $50000 \, \mathrm{km^2}$ at 45°N. Thus, we try to derive a "characteristic" value of NPP for large regions instead. We use a biome aggregation due to its climatic and ecological large-scale homogeneity. See point 1 below for a detailed discussion.

  The (summarised) referee's comments are in italic text.

- *The results are unrealistic since net carbon uptake peaks at 18 $gC\,m^{-2}\,yr^{-1}$.* It is not clear how the referee arrives at this number. Our Fig. 7 clearly shows maximum values of carbon uptake exceeding $80 \, \mathrm{gC\,m^{-2}\,yr^{-1}}$ in all biomes. The upper bound of our estimates, shown in Fig. A1, peaks at $162 \, \mathrm{gC\,m^{-2}\,yr^{-1}}$ while the lower bound, shown in Fig. 5, is $16 \, \mathrm{gC\,m^{-2}\,yr^{-1}}$. We think our estimates are realistic. See point 2 for a detailed discussion.

- *There is no comparison to other bryophyte models (see e.g. Turetsky et al. (2012)).* The goal of our study is a global simulation of carbon uptake by lichens as well as bryophytes. The models mentioned by the reviewer, however, focus on growth of moss in boreal and arctic regions, especially in peatlands. We agree with the reviewer that it is useful to give an overview of other modelling studies related to lichens and bryophytes in general. Therefore, we will add a corresponding paragraph to the section "Introduction" (see point 3).

- *The current manuscript is heavily weighed down in equations* The actual paper does not contain any equations. It is written in a way that should not require the reader to read the appendix to understand the model. We added an appendix with the model equations for completeness, better readability and also for reasons of scientific reproducibility.

- *Small-scale variation (e.g. microtopography) is ignored, which sheds doubt on the accuracy of the model.* We think that the influence of small-scale variation on our model estimates is minor, since the impacts of excursions from mean environmental conditions on NPP cancel out at large scales. See point 4 for a more detailed argument.

Detailed comments

1. *How were the studies selected ?*

   The studies were selected to obtain a "characteristic" observation-based value of NPP for large regions.

   To obtain a truly quantitative value of lichen and bryophyte NPP at the large scale of a model grid cell, the point-scale values would have to be weighted by area coverage. High-resolution data that relate coverage to NPP, however, are not available at large scales. Therefore, we try to estimate a value of NPP that is "characteristic" for a certain large region. This region should not be a grid cell of the model, since the grid is an artificial segmentation of the landscape. Instead, we use the biome classification as a basis for our model-data comparison. Biomes are homogeneous regarding climate and ecology at the large-scale. Hence, they allow for the estimation of a "characteristic", observation-based value of NPP. Moreover, the point-scale variation of environmental conditions within a biome should be comparable to that within a grid cell, since both correspond to large areas.

   As described on page 3748, line 7, only studies were used for the model-data comparison which report estimates of average, long-term net carbon uptake based on surface coverage of lichens or bryophytes. Studies which estimate only maximum rates of NPP or NPP per area lichen/bryophyte or per gram biomass cannot be used. To include such studies, we would have to make assumptions about the active time of lichens and bryophytes throughout the year, about their ground coverage etc. Hence, we would not compare our modelled estimates to data but to another, empirical model.

   We used Elbert et al. (2012) as a basis for the selection of studies (see the supplementary material for their study). We had, however, to exclude 31 out of 40 studies due to the criterion of long-term, area-based values mentioned above. This left only one study for the boreal and tropical zone and two studies for deserts. We therefore extended our search but we could not find more studies for deserts and tropical forest. For the boreal zone, we found two additional studies. We did not, however, look explicitly for *Sphagnum* productivity.

   For the revised manuscript, we tried to further increase the number of studies containing observational data of lichen and bryophyte NPP. We also used the references provided by the reviewer. Many of the studies are taken from Turetsky et al. (2010). If NPP was given as gram biomass, we used a factor of 0.4 (weight of

carbon in CH2O) as a conversion factor for carbon. Table 1 shows a list of studies analysed for this response.

This updated list does not contain all existing studies that provide observational data of lichen and bryophyte NPP in the boreal zone. In our opinion, however, it is sufficient to illustrate the order of magnitude of NPP. We did not include the many studies cited in Gunnarsson (2005); Nungesser (2003) because they focus on the productivity of *Sphagnum* in peatlands. This would shift the focus of the comparison strongly towards peatlands. In the revised manuscript we will explain the selection of observational data for comparison in more detail in the section "Simulation setup" and show the updated Table 1 there.

For the revised manuscript we also changed the way of aggregating the observational data. Now we show only one value for each biome, namely the median of all measurements listed in the studies for the respective biome. These median values are shown in the new version of Fig. 7 (see 1). The number next to the median corresponds to the number of observations used for the computation of the median. We use the median instead of the mean of all values, because computing the mean implicitly assumes equal weights for all values. As discussed above, these weights are not known. We do not show the range of measured values from the studies, either, because a study site should not be compared to a grid cell. Instead, we will discuss the high variation of NPP values more extensively in the text in the section "Simulation setup".

We will also extend and clarify the sections "Evaluation" and "Discussion" in our manuscript along the lines of our argument above.

Table 1: Overview of the studies analysed for the revised manuscript. In the boreal zone, a "P" stands for peatland and an "F" for a forested region. The value in brackets in the "NPP" column corresponds to the number of observations in the respective study. A * denotes studies which give ranges instead of single values. In these cases, we used the mean value of the upper and lower bound of each range.

| Study	Biome	NPP($\mathrm{gC\,m^{-2}\,yr^{-1}}$)	Included	Comment
Additional studies				
(Billings, 1987)	boreal(P)	9.7 - 78 (2)	yes	
(Camill et al., 2001)	boreal(F)	9.2 - 75.9 (8)	yes	
(Grigal, 1985)	boreal(P)	128 - 152 (2)	yes	
(Harden et al., 1997)	boreal(F)	60 - 280 (3)*	yes	
(Hobbie and Chapin III, 1996)	boreal(F)	-	no	no number for NPP
(Bond-Lamberty et al., 2004)	boreal(F)	0 - 297.1 (14)	yes	
(Mack et al., 2008)	boreal(F)	0.4 - 16.2 (7)	yes	
(Oechel and Van Cleve, 1986)	boreal(F)	40 - 44 (2)	yes	
(Reader and Stewart, 1972)	boreal(P)	14.4	yes	
(Ruess et al., 2003)	boreal(F)	29.2 - 31.2 (2)	yes	
(Strack, 2008)	boreal(P)	-	no	no number for NPP
(Strack and Price, 2009)	boreal(P)	-	no	no number for NPP
(Szumigalski and Bayley, 1996)	boreal(P)	15.2 - 81.2 (10)	yes	
(Thormann, 1995)	boreal(P)	23.2 - 73.2 (3)	yes	
(Vogel et al., 2008)	boreal(F)	12 - 32 (9)	yes	
(Wieder and Lang, 1983)	boreal(P)	216 - 316 (3)	yes	
(Schuur et al., 2007)	tundra	12 - 60 (3)	yes	
(Shaver and Chapin III, 1991)	tundra	2 - 68 (4)	yes	
(Shaver et al., 1996)	tundra	-	no	NPP not measured
(Garcia-Pichel and Belnap, 1996)	desert	0.54	yes	
(Klopatek, 1992)	desert	5.3 - 29 (4)*	yes	
(Lange et al., 1994)	desert	-	no	no coverage
(Lange et al., 2006)	desert	-	no	no coverage
(Schuur and Matson, 2001)	tropical	-	no	no separate moss NPP
Studies already included in the BGD manuscript				
(Billings, 1987)	tundra	10	yes	
(Lange et al., 1998)	tundra	4.7 - 20.4 (4)	yes	
(Oechel and Collins, 1976)	tundra	38.5 - 171 (2)	yes	
(Uchida et al., 2006)	tundra	1.9	yes	
(Uchida et al., 2002)	tundra	6.5	yes	
(Bisbee et al., 2001)	boreal(F)	25	yes	
(Gower et al., 1997)	boreal(F)	12	yes	
(Swanson and Flanagan, 2001)	boreal(F)	104	yes	
(Brostoff et al., 2005)	desert	11.7	yes	
(Jeffries et al., 1993)	desert	0.07 - 1.5 (3)*	yes	
(Clark et al., 1998)	tropical	37 - 64 (2)	yes	
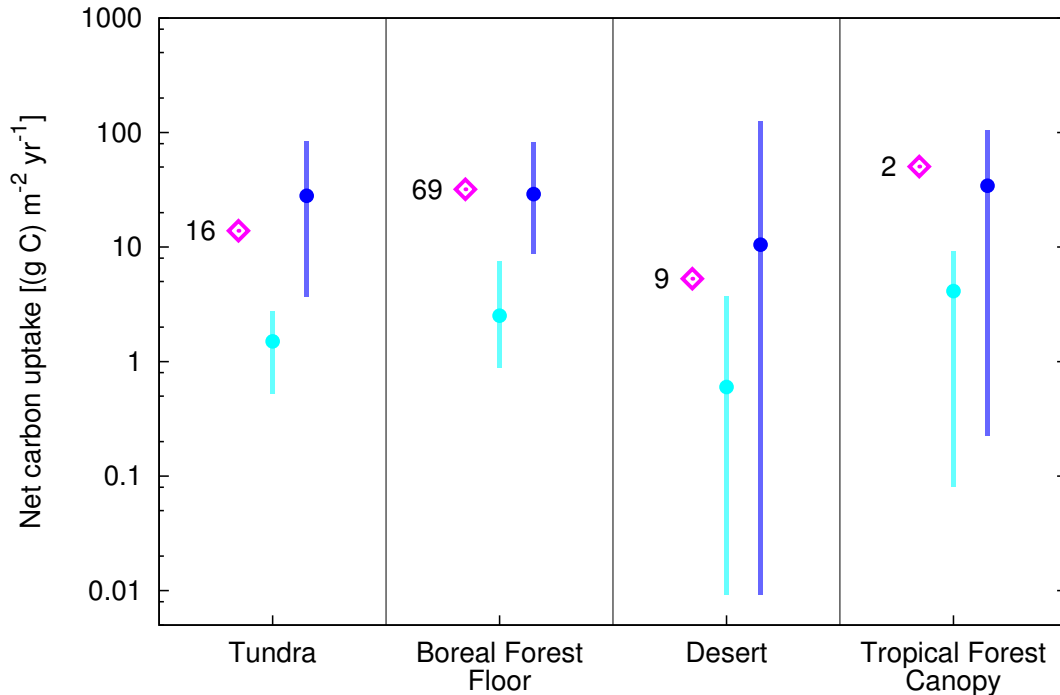
Figure 1: Updated version of Fig. 7. A magenta diamond corresponds to the median of the observed values in the respective biome. The number left to the diamond is the number of observed values. See Table 1 for an overview of the studies on which the observations are based. The light blue colour corresponds to the lower bound of the model estimate and the dark blue colour to the upper bound. The vertical bars represent the range between the most and least productive grid cell in a certain biome, while the dots show the mean productivity of all grid cells in this biome. To be consistent with the measurements from the field studies, only the simulated carbon uptake in the canopy was considered for the biome "Tropical Forest" while for the other biomes only carbon uptake on the ground was considered. The model results are derived from a 2000-yr run with 3000 initial strategies.

2. *The results are unrealistic*

The reviewer seems to have the impression that the model is not suitable to represent the productivity of bryophytes in peatlands in the northern hemisphere. The model does indeed not include a watertable, which means that the "strategies" have to rely on their specific water storage capacity. This may lead to an underestimation of the water supply in peatlands and therefore to an underestimation of NPP. We will add this point to the section "Discussion".

Although the model does not represent the high productivity of some peatlands, the simulated productivity averaged over the whole boreal landscape seems to be

realistic. Our estimate of NPP on ground averaged over the boreal zone is 2.5 - 29 $gC\,m^{-2}\,yr^{-1}$, the range of the grid cells is 0.9 - 83 $gC\,m^{-2}\,yr^{-1}$ (see Fig. 7 in our manuscript).

Modelled estimates of bryophyte NPP are 29.2 $gC\,m^{-2}\,yr^{-1}$ for forested regions (Bond-Lamberty and Gower, 2007). For peatlands (bogs, fens, etc), models predict 58 $gC\,m^{-2}\,yr^{-1}$ (Frolking et al., 1996), 162 - 244 $gC\,m^{-2}\,yr^{-1}$ (Yurova et al., 2007) and 159 $gC\,m^{-2}\,yr^{-1}$ (Wania et al., 2009). The median NPP from several empirical estimates of NPP amounts to 25 $gC\,m^{-2}\,yr^{-1}$ in forested regions and 68 $gC\,m^{-2}\,yr^{-1}$ in peatlands. These values are derived from the studies cited in our revised manuscript (see Table 1 above for details). Regarding peatlands, the studies of Gunnarsson (2005); Nungesser (2003) contain a great number of observational data on *Sphagnum* NPP. Assuming a conversion factor of 0.4 from biomass to carbon (C in CH2O) gives a mean value of 106.4 $gC\,m^{-2}\,yr^{-1}$ for the studies listed in Nungesser (2003) and 103.6 $gC\,m^{-2}\,yr^{-1}$ for Gunnarsson (2005).

As we explained above we think it is problematic to assign a certain value of NPP to the boreal zone based on observations. Nevertheless, the empirical studies and the models cited above suggest a value of bryophyte NPP of around 30 $gC\,m^{-2}\,yr^{-1}$ for forested areas and 100 $gC\,m^{-2}\,yr^{-1}$ for peatlands. These values correspond roughly to our average upper bound for the boreal zone and to the value of the most productive grid cells, respectively. Given the limitations of the model regarding simulating peatlands, we think the model estimates for the boreal zone are reasonable.

- *highest NPP values in forested areas in boreal zone is problematic, since NPP is highest in open peatlands.*

  We will point out in the revised manuscript that peatlands are not explicitly simulated, as explained above. Therefore, the "forested areas"also include peatlands in the model. We will change the term "forested areas" to "boreal zone".

- *Figure 7 does not seem to show good agreement of model estimates and observations. Presenting some statistics or other quantitative information is really necessary here.*

  As we discussed above, it is problematic to compute an R^2-value for the model-data comparison because we cannot compare grid cells to study sites. On an order-of-magnitude basis, we still think the results are realistic. For the boreal zone, the observational data are at the upper bound of the model estimates. We will discuss possible reasons for this (see above) in the revised manuscript.

- *Figure 7: the log scale makes it very difficult to compare points. How about a modeled:observed plot with 1:1 line?*

  The log scale is necessary because the lower bound of our model estimates and the associated range of grid cell values would be unreadable on a linear

scale. A "classical" modeled:observed plot is also problematic. As we have no model estimates at the locations of the study sites, we would have to compare the range of model estimates with points from the empirical studies, and we would still have to use a log scale.

3. *There is no comparison to other bryophyte models (see e.g. Turetsky et al. (2012)).*

   The bryophytes models mentioned by the reviewer are in general specific to growth of moss (*Sphagnum* and, in some cases, feather moss) in boreal and arctic regions, especially in peatlands. The models of Wania et al. (2009); Frolking et al. (2002); Yurova et al. (2007), for instance, are designed to predict NPP of moss in peatlands, while others focus on ecosystem responses to climate change (Bond-Lamberty and Gower, 2007; Euskirchen et al., 2009; Zhuang et al., 2006), simulating peat accumulation (Frolking et al., 2010) or peatland microtopography (Nungesser, 2003). These models are parameterised to represent a specific process, namely moss NPP, in a specific habitat. The purpose of our model, however, is to estimate productivity of bryophytes as well as lichens under a broad range of environmental conditions around the globe. Moreover, we account explicitly for the physiological variation of lichens and bryophytes and for different locations of growth (canopy vs ground). For these reasons, it is not possible to parameterise our model in a way similar to the bryophyte models cited here. Although we could probably implement a "strategy" similar to *Sphagnum*, the physiological and microclimatic data for many other bryophyte and lichen species are not available. As described on page 3744, line 16, the motivation to use random "strategies" in the model is to represent the functional variation of the organisms without knowing the physiological details of each species.

   We will add a paragraph to the section "Introduction" where we will summarise the studies mentioned above and explain the methodological differences to ours.

   - *Not even Clymo's classic work is cited*

     The paper of Clymo (1984) is a basis for many models of peat accumulation. Our focus, however, is global simulation of NPP by lichens as well as bryophytes. Hence, the paper does not fit our purpose since it focuses more on the dynamics of the peat layers than on the NPP of bryophytes.

4. *Model description*

   - *The reader has no idea of the model's timestep*

     The timestep of the model is mentioned on page 3747, line 9 (Sect. 2.3 "Simulation setup"): "...the model runs on an hourly time step ..." and it is also listed in Table B8 in the appendix. Moreover, we refer to this table in the appendix at the beginning of the section "Model description", page 3740, line 11 and also at the beginning of Appendix B ("Model details"), page 3759, line 10.

- *What language is model written in? How long does it take to run? Whats the timestep (yes, I see equation B32 but thats no help)? Is it open source and freely available, if so from where?*

  The language of the model is Fortran 95 and the simulation described in the manuscript (2000 years, 3000 "strategies", 2.8° resolution) takes 7 days on 48 processors of a parallel computer. We will add these points to the section "Simulation setup". For the timestep, see the previous point. Regarding the source code of the model, we write at the beginning of Appendix B ("Model details"): "...the source code of the model which is available on request (pporad@bgc-jena.mpg.de) ..." We will repeat this information also in the section "Simulation setup".

5. *Small-scale variation (e.g. microtopography) is ignored, which sheds doubt on the accuracy of the model.*

   Every model has to make simplifying assumptions, also small-scale models are not an exact replication of natural systems and are therefore not "accurate". The question is rather, if neglecting sub-grid scale variation leads to large errors and systematic biases in the model estimates, meaning the value of global net carbon uptake. This would be the case if the relations between climate and carbon uptake were strongly nonlinear. Then, the value of carbon uptake derived from the mean climate in a grid cell would differ from the mean of the values of net carbon uptake based on all the microclimates within a grid cell. To assess the effect of variation in environmental conditions on the model estimates we performed a sensitivity analysis (see Table 2 in our manuscript). The model does not seem to show strong nonlinear behaviour. Compared to the effect of the physiological parameters, the model estimates are rather insensitive to changes in environmental/climatic conditions. Of course, we cannot rule out that small-scale variation has some effect on the model estimates, but the lack of microclimatic (or microtopographic) data at the global scale makes it impossible to quantify this effect. This issue is discussed already in the section "Discussion" of the manuscript on page 3755, line 3 to 21, but we will extend this section for further clarification.

6. *What kind of bias might be introduced by assuming that the metabolic activity of a lichen or bryophyte is a linear function of water content? (see Williams and Flanagan (1998))*

   Comparing our equation to describe metabolic activity (Eq. B21, pictured in Fig. B11 in the appendix) to the curves in Fig. 2 c) and d) in Williams and Flanagan (1998), it seems that the linear approximation is reasonable. Both the curves in Williams and Flanagan (1998) and our function for metabolic activity show a constant value of full activity above a certain threshold water content. The increase from 0 to full activity in Williams and Flanagan (1998) is nonlinear. Since the threshold water content in our equation of metabolic activity is flexible, however, the bias due to nonlinearity should be small (see orange lines drawn in Fig. 2).

We will add to Sect. B3.4 that the metabolic activity has been shown to increase nonlinearly and that the linear function is an approximation.
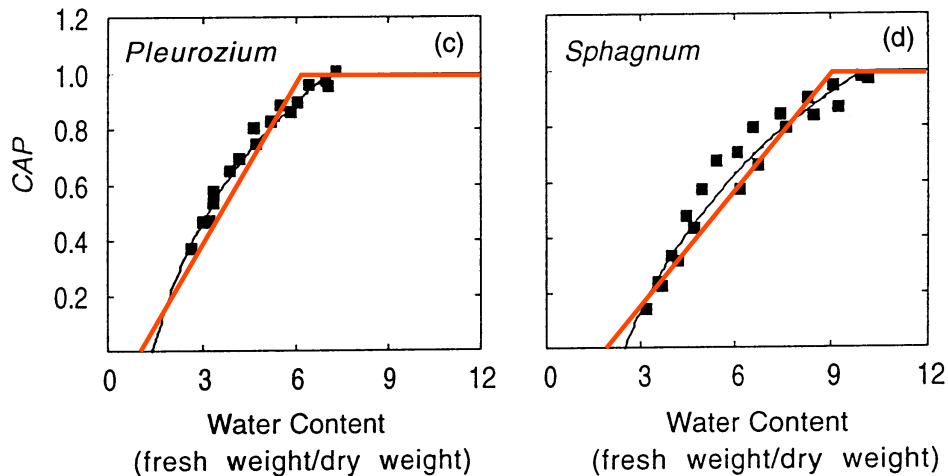

Figure 2: Metabolic activity as a function of water content from Williams and Flanagan (1998). The orange lines are examples for our Eq. B21 with a flexible threshold water content.

7. *by net carbon uptake do you mean NPP? Use a standard term, here and throughout.*

   NPP is a standard term for vascular vegetation and it is frequently used in the modelling community. It is less known in the community of lichenologists and bryologists. Since this paper also addresses this community, we use a general, more descriptive term. We will add to the revised manuscript that net carbon uptake corresponds to NPP.

References

Billings, W.D. Carbon balance of Alaskan tundra and taiga ecosystems: Past, present and future. *Quaternary Science Reviews*, 6:165–177, 1987. doi: 10.1016/0277-3791(87)90032-1.

Bisbee, K.E., Gower, S.T., Norman, J.M., and Nordheim, E.V. Environmental controls on ground cover species composition and productivity in a boreal black spruce forest. *Oecologia*, 129:261–270, 2001. doi: 10.1007/s004420100719.

Bond-Lamberty, B. and Gower, S.T. Estimation of stand-level leaf area for boreal bryophytes. *Oecologia*, 151:584–592, 2007. doi: 10.1007/s00442-006-0619-5.

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

Brostoff, W.M., Sharifi, M.R., and Rundel, P.W. Photosynthesis of cryptobiotic soil crusts in a seasonally inundated system of pans and dunes in the western Mojave Desert, CA: Field studies. *Flora*, 200:592–600, 2005. doi: 10.1016/j.flora.2005.06.008.

Camill, P., Lynch, J.A., Clark, J.S., Adams, J.B., and Jordan, B. Changes in biomass, aboveground net primary production, and peat accumulation following permafrost thaw in the boreal peatlands of Manitoba, Canada. *Ecosystems*, 4:461–478, 2001. doi: 10.1007/s10021-001-0022-3.

Clark, K.L., Nadkarni, N.M., and Gholz, H.L. Growth, net production, litter decomposition, and net nitrogen accumulation by epiphytic bryophytes in a tropical montane forest. *Biotropica*, 30(1):12–23, 1998. doi: 10.1111/j.1744-7429.1998.tb00365.x.

Clymo, R.S. The limits to peat bog growth. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, 303(1117):605–654, 1984. doi: 10.1098/rstb.1984.0002.

Elbert, W., Weber, B., Burrows, S., Steinkamp, J., Büdel, B., Andreae, M.O., and Pöschl, U. Contribution of cryptogamic covers to the global cycles of carbon and nitrogen. *Nature Geoscience*, 5:459–462, 2012. doi: 10.1038/ngeo1486.

Euskirchen, E.S., McGuire, A.D., Chapin III, F.S., Yi, S., and Thompson, C.C. Changes in vegetation in northern Alaska under scenarios of climate change, 2003-2100: Implications for climate feedbacks. *Ecological Applications*, 19(4):1022–1043, 2009.

Frolking, S., Goulden, M.L., Wofsy, S.C., Fan, S.-M., Sutton, D.J., Munger, J.W., Bazzaz, A.M., Daube, B.C., Crill, P.M., Aber, J.D., Band, L.E., X., Wang, Savage, K., Moore, T., and Harriss, R.C. Modelling temporal variability in the carbon balance of a spruce/moss boreal forest. *Global Change Biology*, 2(4):343–366, 1996.

Frolking, S., Roulet, N.T., Moore, T.R., Lafleur, P.M., Bubier, J.L., and Crill, P.M. Modeling seasonal to annual carbon balance of Mer Bleue Bog, Ontario, Canada. *Global Biogeochemical Cycles*, 16(3), 2002.

Frolking, S., Roulet, N.T., Tuittila, E., Bubier, J.L., Quillet, A., Talbot, J., and Richard, P.J.H. A new model of Holocene peatland net primary production, decomposition, water balance, and peat accumulation. *Earth Syst. Dynam.*, 1(1):1–21, 2010. doi: 10.5194/esd-1-1-2010.

Garcia-Pichel, F. and Belnap, J. Microenvironments and microscale productivity of cyanobacterial desert crusts. *Journal of Phycology*, 32:774–782, 1996.

Gower, S.T., Vogel, J.G., Norman, J.M., Kucharik, C.J., Steele, S.J., and Stow, T.K. Carbon distribution and aboveground net primary production in aspen, jack pine and black spruce stands in Saskatchewan and Manitoba, Canada. *Journal of Geophysical Research*, 102(D24):29029–29041, 1997. doi: 10.1029/97JD02317.

Grigal, D.F. *Sphagnum* production in forested bogs of northern Minnesota. *Canadian Journal of Botany*, 63(7):1204–1207, 1985.

Gunnarsson, U. Global patterns of *Sphagnum* productivity. *Journal of Bryology*, 27(3): 269–279, 2005.

Harden, J.W., O'Neill, K.P., Trumbore, S.E., Veldhuis, H., and Stocks, B.J. Moss and soil contributions to the annual net carbon flux of a maturing boreal forest. *Journal of Geophysical Research: Atmospheres (1984–2012)*, 102(D24):28805–28816, 1997.

Hobbie, S.E. and Chapin III, F.S. Winter regulation of tundra litter carbon and nitrogen dynamics. *Biogeochemistry*, 35(2):327–338, 1996.

Jeffries, D.L., Link, S.O., and Klopatek, J.M. CO_2 fluxes of cryptogamic crusts I. Response to resaturation. *New Phytol.*, 125:163–173, 1993. doi: 10.1111/j.1469-8137.1993.tb03874.x.

Klopatek, J.M. Cryptogamic crusts as potential indicators of disturbance in semi-arid landscapes. In *Ecological indicators*, pages 773–786. Springer, 1992.

Lange, O.L., Meyer, A., Zellner, H., and Heber, U. Photosynthesis and water relations of lichen soil crusts: field measurements in the coastal fog zone of the Namib Desert. *Functional Ecology*, pages 253–264, 1994.

Lange, O.L., Hahn, S.C., Meyer, A., and Tenhunen, J.D. Upland tundra in the foothills of the Brooks Range, Alaska, U.S.A.: Lichen long-term photosynthetic CO_2 uptake and net carbon gain. *Arctic and Alpine Research*, 30(3):252–261, 1998. doi: 10.2307/1551972.

Lange, O.L., Green, T.G.A., Melzer, B., Meyer, A., and Zellner, H. Water relations and CO_2 exchange of the terrestrial lichen *Teloschistes capensis* in the Namib fog desert: Measurements during two seasons in the field and under controlled conditions. *Flora*, 201(4):268–280, 2006. doi: 10.1016/j.flora.2005.08.003.

Mack, M.C., Treseder, K.K., Manies, K.L., Harden, J.W., Schuur, E.A.G., Vogel, J.G., Randerson, J.T., and Chapin III, F.S. Recovery of aboveground plant biomass and productivity after fire in mesic and dry black spruce forests of interior Alaska. *Ecosystems*, 11(2):209–225, 2008. doi: 10.1007/s10021-007-9117-9.

Nungesser, M.K. Modelling microtopography in boreal peatlands: hummocks and hollows. *Ecological Modelling*, 165:175–207, 2003. doi: 10.1016/S0304-3800(03)00067-X.

Oechel, W.C. and Collins, N.J. Comparative CO_2 exchange patterns in mosses from two tundra habitats at Barrow, Alaska. *Can. J. Bot.*, 54:1355–1369, 1976. doi: 10.1139/b76-148.

Oechel, W.C. and Van Cleve, K. The role of bryophytes in nutrient cycling in the taiga. In Van Cleve, K., Chapin III, F.S., Flanagan, P.W., Vierect, L.A., and Dyrness, C.T., editors, *Forest ecosystems in the Alaskan taiga. A synthesis of structure and function.*, pages 122–137. Springer, New York, 1986.

Reader, R.J. and Stewart, J.M. The relationship between net primary production and accumulation for a peatland in southeastern Manitoba. *Ecology*, pages 1024–1037, 1972.

Ruess, R.W., Hendrick, R.L., Burton, A.J., Pregitzer, K.S., Sveinbjornsson, B., Allen, M.F., and Maurer, G.E. Coupling fine root dynamics with ecosystem carbon cycling in black spruce forests of interior Alaska. *Ecol. Monogr.*, 73(4):643–662, 2003. doi: 10.1890/02-4032.

Schuur, E.A.G. and Matson, P.A. Net primary productivity and nutrient cycling across a mesic to wet precipitation gradient in Hawaiian montane forest. *Oecologia*, 128: 431–442, 2001. doi: 10.1007/s004420100671.

Schuur, E.A.G., Crummer, K.G., Vogel, J.G., and Mack, M.C. Plant species composition and productivity following permafrost thaw and thermokarst in Alaskan tundra. *Ecosystems*, 10:280–292, 2007. doi: 10.1007/s10021-007-9024-0.

Shaver, G.R. and Chapin III, F.S. Production: Biomass relationships and element cycling in contrasting arctic vegetation types. *Ecological Monographs*, 61(1):1–31, 1991. doi: 10.2307/1942997.

Shaver, G.R., Laundre, J.A., Giblin, A.E., and Nadelhoffer, K.J. Changes in live plant biomass, primary production, and species composition along a riverside toposequence in Arctic Alaska, U.S.A. *Arct. Alp. Res.*, 28(3):363–379, 1996. doi: 10.2307/1552116.

Strack, M. *Peatlands and climate change.* IPS, International Peat Society, 2008.

Strack, M. and Price, J.S. Moisture controls on carbon dioxide dynamics of peat-*Sphagnum* monoliths. *Ecohydrol.*, 2:34–41, 2009. doi: 10.1002/eco.36.

Swanson, R.V. and Flanagan, L.B. Environmental regulation of carbon dioxide exchange at the forest floor in a boreal black spruce ecosystem. *Agricultural and Forest Meteorology*, 108:165–181, 2001. doi: 10.1016/S0168-1923(01)00243-X.

Szumigalski, A.R. and Bayley, S.E. Net above-ground primary production along a bog-rich fen gradient in central Alberta, Canada. *Wetlands*, 16(4):467–476, 1996.

Thormann, M.N. *Primary production and decomposition in fens and marshes in the boreal region of Alberta, Canada.* PhD thesis, University of Alberta, Edmonton, Alta., 1995.

Turetsky, M.R., Mack, M.C., Hollingsworth, T.N., and Harden, J.W. The role of mosses in ecosystem succession and function in Alaskas boreal forest. *Can. J. For. Res.*, 40: 1237–1264, 2010. doi: 10.1139/X10-072.

Turetsky, M.R., Bond-Lamberty, B., Euskirchen, E., Talbot, J., Frolking, S., McGuire, A.D., and Tuittila, E.-S. The resilience and functional role of moss in boreal and arctic ecosystems. *New Phytologist*, 196(1):49–67, 2012. doi: 10.1111/j.1469-8137.2012.04254.x.

Uchida, M., Muraoka, H., Nakatsubo, T., Bekku, Y., Ueno, T., Kanda, H., and Koizumi, H. Net photosynthesis, respiration, and production of the moss *Sanionia uncinata* on a glacier foreland in the high arctic, Ny-Ålesund, Svalbard. *Arctic, Antarctic, and Alpine Research*, 34(3):287–292, 2002. doi: 10.2307/1552486.

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 Research*, 25(1):39–49, 2006. doi: 10.3402/polar.v25i1.6237.

Vogel, J.G., Bond-Lamberty, B.P., Schuur, E.A.G., Gower, S.T., Mack, M.C., O'Connell, K.E.B., Valentine, D.W., and Ruess, R.W. Carbon allocation in boreal black spruce forests across regions varying in soil temperature and precipitation. *Global Change Biology*, 14:1503–1516, 2008. doi: 10.1111/j.1365-2486.2008.01600.x.

Wania, R., Ross, I., and Prentice, I.C. Integrating peatlands and permafrost into a dynamic global vegetation model: 2. Evaluation and sensitivity of vegetation and carbon cycle processes. *Global Biogeochemical Cycles*, 23(3), 2009. doi: 10.1029/2008GB003413.

Wieder, R.K. and Lang, G.E. Net primary production of the dominant bryophytes in a *Sphagnum*-dominated wetland in West Virginia. *Bryologist*, pages 280–286, 1983.

Williams, T.G. and Flanagan, L.B. Measuring and modelling environmental influences on photosynthetic gas exchange in *Sphagnum* and *Pleurozium*. *Plant, Cell & Environment*, 21(6):555–564, 1998.

Yurova, A., Wolf, A., Sagerfors, J., and Nilsson, M. Variations in net ecosystem exchange of carbon dioxide in a boreal mire: Modeling mechanisms linked to water table position. *Journal of Geophysical Research: Biogeosciences (2005–2012)*, 112 (G2), 2007.

Zhuang, Q., Melillo, J.M., Sarofim, M.C., Kicklighter, D.W., McGuire, A.D., Felzer, B.S., Sokolov, A., Prinn, R.G., Steudler, P.A., and Hu, S. CO_2 and CH_4 exchanges between land ecosystems and the atmosphere in northern high latitudes over the 21st century. *Geophysical Research Letters*, 33(17), 2006.