

BGD

10, 3735–3846, 2013

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

This discussion paper is/has been under review for the journal Biogeosciences (BG).
Please refer to the corresponding final paper in BG if available.

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

P. Porada¹, B. Weber², W. Elbert³, U. Pöschl³, and A. Kleidon¹

¹Max Planck Institute for Biogeochemistry, P.O. Box 10 01 64, 07701 Jena, Germany

²University of Kaiserslautern, P.O. Box 3049, 67653 Kaiserslautern, Germany

³Max Planck Institute for Chemistry, P.O. Box 3060, 55020 Mainz, Germany

Received: 14 January 2013 – Accepted: 4 February 2013 – Published: 28 February 2013

Correspondence to: P. Porada (pporad@bgc-jena.mpg.de)

Published by Copernicus Publications on behalf of the European Geosciences Union.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

Abstract

Lichens and bryophytes are abundant globally and they may even form the dominant autotrophs in (sub)polar ecosystems, in deserts and at high altitudes. Moreover, they can be found in large amounts as epiphytes in old-growth forests. Here, we present the first process-based model which estimates the net carbon uptake by these organisms at the global scale, thus assessing their significance for biogeochemical cycles. The model uses gridded climate data and key properties of the habitat (e.g. disturbance intervals) to predict processes which control net carbon uptake, namely photosynthesis, respiration, water uptake and evaporation. It relies on equations used in many dynamical vegetation models, which are combined with concepts specific to lichens and bryophytes, such as poikilohydry or the effect of water content on CO₂ diffusivity. To incorporate the great functional variation of lichens and bryophytes at the global scale, the model parameters are characterised by broad ranges of possible values instead of a single, globally uniform value. The predicted terrestrial net carbon uptake of 0.34 to 3.3 (Gt C) yr⁻¹ and global patterns of productivity are in accordance with empirically-derived estimates. Considering that the assimilated carbon can be invested in processes such as weathering or nitrogen fixation, lichens and bryophytes may play a significant role in biogeochemical cycles.

1 Introduction

Lichens and bryophytes are different from vascular plants: Lichens are no real plants, but a symbiosis of a fungus and at least one green alga or cyanobacterium, whereas bryophytes, such as mosses or liverworts, are plants which have no specialised tissue such as roots or stems. Both groups are poikilohydrous, which means that they cannot actively control their water content because they do not have an effective epidermal tissue, a cuticle or stomata. Mainly due to their ability to tolerate desiccation, combined with large functional variation, they are extremely adaptive organisms that can cope

BGD

10, 3735–3846, 2013

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

⏮

⏭

◀

▶

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



with a great range of climatic conditions (Nash III, 1996). They grow as epiphytes on the bark or even on the leaves of trees, they cover rock outcrops and they form carpets on the forest floor at high latitudes. As a part of biological soil crusts, they also populate the surface of desert soils (Belnap and Lange, 2003).

In spite of their global abundance, however, the effect of lichens and bryophytes on global biogeochemical cycles has been examined only by a few studies. The work of Elbert et al. (2012), for instance, suggests a significant contribution of cryptogamic covers, which largely consist of lichens and bryophytes, to global cycles of carbon and nitrogen. They use a large amount of data from field experiments or lab measurements to estimate characteristic mean values of net carbon uptake and nitrogen fixation for each of the world's biomes. By multiplying these mean values with the area of the respective biome they arrive at global numbers for uptake of carbon and nitrogen. While their estimate for global net carbon uptake amounts to 7% of terrestrial net primary productivity (NPP), the derived value of nitrogen fixation corresponds to around 50% of the terrestrial uptake, representing a large impact on the global nitrogen cycle.

Lichens and bryophytes may have also played an important role with respect to biogeochemical cycles in the geological past. From the early Paleozoic on, the predecessors of today's lichens and bryophytes have likely contributed to the enhancement of surface weathering rates (Lenton et al., 2012). The organisms accelerate chemical weathering reactions of the substrate by releasing organic acids, complexing agents, hydroxide ions or respiratory CO_2 (Jackson and Keller, 1970; Berthelin, 1988; Chen et al., 2000; Büdel et al., 2004; Weber et al., 2011). On long time scales, weathering rates of silicates control atmospheric CO_2 concentration and thus have a large influence on global climate. The work of Schwartzmann and Volk (1989) shows, for example, that without biotic enhancement of weathering in the course of evolution, atmospheric CO_2 would have remained at a high level. The surface temperature associated with this CO_2 level would probably have been too high for complex life to evolve. Lenton et al. (2012) focus on the effect of the predecessors of modern bryophytes on atmospheric CO_2 concentration during the Ordovician. According to their experiments,

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)



[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



these early non-vascular plants could have caused a considerable drawdown in atmospheric CO₂ levels via the silicate weathering feedback and, consequently, a decrease in global surface temperature. Furthermore, the release of phosphorus from the weathered rocks into the oceans could have led to a rise in marine productivity and therefore to further cooling. According to Lenton et al. (2012) this could explain two temporary glaciations at the end of the Ordovician period.

Here, we present a process-based modelling approach to estimate the global net carbon uptake of lichens and bryophytes. In this way, we are able to assess the role of these organisms regarding global biogeochemical cycles.

The model is called “LiBSi” (Lichen and Bryophyte Simulator). It is similar to many global vegetation models (see Fig. 1). These models describe plants in a simplified way instead of simulating them with all their detailed structures. Vegetation is usually represented by a reservoir of biomass, which changes as a function of exchange flows of carbon. These exchange flows depend on processes such as photosynthesis and respiration, which are represented by a set of equations. The equations use environmental factors such as radiation or water supply as input values which are either prescribed or derived from climate forcing data. In spite of their simplicity, global vegetation models are capable of predicting NPP to a reasonable accuracy (Randerson et al., 2009).

Similar to these models, our model describes lichens and bryophytes as reservoirs of biomass located either on the soil or in the canopy and it is based on equations to represent photosynthesis and other physiological processes. These concepts are combined with properties and processes specific to lichens and bryophytes, such as the decrease of diffusivity for CO₂ with increasing water content or the proportional relationship between metabolic activity and water saturation. The model differs from most other vegetation models with respect to the parameters contained in the model equations. Most models use parameter values that describe an “average” organism, such as a typical rain forest tree, for example. Our model uses ranges of possible parameter values which are derived from the literature. This approach is similar to the one used in the JeDi-DGVM (Jena Diversity-Dynamic Global Vegetation Model), which

predicts global biogeochemical flows as well as biodiversity patterns (Pavlick et al., 2012). In this way, the model accounts for the large functional variation of lichens or bryophytes at the global scale concerning properties such as photosynthetic capacity or specific area.

The paper is structured in the following way: Sect. 2 contains a description of the model, including an overview of the reservoirs and exchange flows as well as the environmental factors that control these flows. In addition, the method for simulating functional variation of lichens and bryophytes by parameter ranges is explained. Estimates of net carbon uptake are presented in Sect. 3 together with an evaluation of the model performance. The model is evaluated by comparing simulated productivity of lichens and bryophytes with observational data. Furthermore, the uncertainty regarding the values of model parameters is assessed through a sensitivity analysis. In Sect. 4 the plausibility of the simulated patterns of productivity is discussed. Also the limitations of the approach presented here are analysed considering the outcomes of model evaluation and sensitivity analysis. Several potential improvements of the model and its applicability to further research are discussed.

2 Model description

Lichens and bryophytes are described in the model by a reservoir approach, which means that they are represented by pools of chemical substances. These are biomass, sugar reserves, water and internal CO₂ concentration.

Changes in the size of these pools are due to input and output flows of carbon or water. Carbon is assimilated by photosynthesis from the atmosphere and temporarily stored as sugars. The sugars are then respired for maintenance or transformed into biomass. Water is taken up and evaporates via the thallus surface. The water content of the thallus influences several physiological processes, such as CO₂ diffusion.

The processes which determine the carbon and water flows are driven by climate. In addition to the climate forcing, also properties of the living environment affect lichens

BGD

10, 3735–3846, 2013

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

and bryophytes in the model. These properties depend on the location of growth, which is either the canopy or the ground, as well as the surrounding vegetation, which is described by a biome classification.

2.1 Model processes

5 In the following, we describe the physiological processes implemented in the model. First, we name the effects of the living environment on lichens and bryophytes. Then, we explain how water content and climatic factors relate to physiological properties of the organism. Finally, we describe the exchange flows between the organism and its environment.

10 For simplicity, we will not present any equations. All equations used in the model can be found in Appendix B and are explained there. The parameters associated with the equations are listed in Tables B7 to B13 in the Appendix.

2.1.1 Living environment

15 In the model, lichens and bryophytes can be located either in the canopy or on the ground. The location of growth is important for the radiation and precipitation regime the organism is exposed to (see Fig. 2). Lichens and bryophytes living in the upper part of the canopy, for example, may receive more shortwave radiation than those living beneath the canopy. Additionally, the location of growth determines the available area for growth. The available area in the canopy is assumed to be the sum of Leaf Area Index (LAI) and Stem Area Index (SAI). The available area on the ground depends on
20 (a) the amount of soil not occupied by other vegetation and (b) LAI, since the litter layer resulting from leaf fall impedes the growth of lichens and bryophytes (see Fig. 2). Once a lichen or bryophyte covers the available area completely it cannot grow anymore. Since the biomass of an organism is related to its surface area, also biomass is limited
25 by the available area.

BGD

10, 3735–3846, 2013

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Another factor that shapes the living environment of lichens and bryophytes is the biome where the organisms are located. In the model, the biome controls the frequencies of disturbance events, such as fire or treefall, for instance. Furthermore, both location of growth and biome determine the aerodynamic roughness of the surface where lichens or bryophytes grow. A forest, for example, has a higher roughness than a flat desert. Together with wind speed, surface roughness has a large impact on the aerodynamic resistance to heat transfer between the surface and the atmosphere (Allen et al., 1998). Lichens and bryophytes in the canopy of an open forest, for instance, exchange heat faster than those on the flat surface of a desert.

2.1.2 Water relations

The water saturation of a lichen or bryophyte is the ratio of actual water content to water storage capacity of the thallus, where the latter is proportional to biomass. The water saturation controls three important physiological properties:

1. The diffusivity of the thallus for CO_2 which is inversely related to water content, since water leads to a swelling of cells and thus to a narrowing of the diffusion pathways (Cowan et al., 1992).
2. The water potential which increases from $-\infty$ at zero water content to a maximum value of 0 at a certain threshold saturation. If the water content is above this threshold, all cells in the thallus are fully turgid and extracellular water may exist inside the thallus or on its surface.
3. The metabolic activity of a lichen or bryophyte which is assumed to increase linearly from 0 at zero water content to 1 at the threshold saturation. It remains 1 if the water content exceeds the threshold saturation. This relation accounts for the fact, that water is needed in the cells of the organism to activate enzymes and to enable chemical reactions. At constant temperature, the relation of metabolic

BGD

10, 3735–3846, 2013

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

activity and water content is proportional to the one of dark respiration and water content.

Note that the water relations implemented in the model allow to represent the species-specific dependency of photosynthesis on water content. At low water content, photosynthesis is limited by metabolic activity while at higher water content it is limited by the diffusivity of the thallus for CO₂. Depending on the relative strength of these limitations, different shapes of the relation between photosynthesis and water content can be simulated.

2.1.3 Climate relations

The climate forcing consists of air temperature, wind speed, relative humidity, precipitation and downwelling short- and longwave radiation. These climatic factors influence exchange flows of carbon and water between lichens and bryophytes and their environment. Furthermore, the climatic factors directly control two physiological properties of lichens and bryophytes, namely potential evaporation and surface temperature.

Both potential evaporation and surface temperature are calculated according to Monteith (1981) as a function of four factors:

1. Net radiation, which is the sum of downwelling short- and longwave radiation, upwelling longwave radiation and the ground heat flux.
2. Saturation vapour pressure, which is calculated as a function of air temperature (Allen et al., 1998). It is also influenced by the water potential of a lichen or bryophyte (Nikolov et al., 1995).
3. Aerodynamic resistance to heat transfer.
4. Relative humidity.

Additionally to the climate forcing, physiological processes of lichens and bryophytes are affected by the presence of snow. If the snow layer exceeds a certain thickness, it

BGD

10, 3735–3846, 2013

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



is assumed that the metabolism of the organisms is reduced due to lack of light and low temperature.

2.1.4 Exchange flows

A schematic of the exchange flows of carbon and water between lichens and bryophytes and their environment is shown in Fig. 3 together with relations to climate forcing and reservoirs inside the thallus.

The inflow of CO₂ into the pore space of the lichen or bryophyte depends on the gradient between the partial pressure of CO₂ in the atmosphere and in the pore space as well as the diffusivity of the thallus for CO₂.

The uptake of CO₂ from the pore space (Gross Primary Productivity, GPP) is computed as a minimum of a light-limited rate, which depends on intercepted shortwave radiation, and a CO₂-limited rate, which is a function of pore space CO₂ (Farquhar and von Caemmerer, 1982). Both rates also depend on the surface temperature of the organism (Medlyn et al., 2002) and its metabolic activity status. Photosynthesis is assumed to peak around an optimum surface temperature (June et al., 2004).

Respiration is modelled by a Q_{10} relationship as function of biomass and temperature (Kruse et al., 2011). Same as GPP it also depends on metabolic activity. The respired CO₂ is released into the pore space.

Hence, the CO₂ balance of the lichen or bryophyte pore space is controlled by inflow, GPP and respiration. GPP is added to the sugar reservoir, while respiration is subtracted. Then, a certain fraction of the sugar reservoir is transformed into biomass with a certain efficiency. This constitutes the Net Primary Productivity (NPP). The balance of the biomass reservoir is then determined by NPP and biomass loss, which includes regular processes such as tissue turnover or leaching of carbohydrates (Melick and Seppelt, 1992). Additionally, disturbance events which occur at characteristic time intervals lead to a reduction of biomass.

Evaporation from the lichen or bryophyte thallus is computed as a minimum of water content and potential evaporation. Since lichens and bryophytes cannot actively

BGD

10, 3735–3846, 2013

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



control water loss, evaporation is not affected by the activity status of the organism. Water uptake takes place via the thallus surface. Where water input exceeds maximum storage capacity, surplus water is redirected to runoff. The water balance of the lichen or bryophyte is thus determined by evaporation and water uptake.

2.2 Model parameters

The equations that describe physiological processes in the model are parameterised and the parameters can be subdivided into two categories: properties of lichens and bryophytes and characteristics of the environment of the organisms. Since lichens and bryophytes have a large functional variation, the parameters that represent their properties, such as specific area or photosynthetic capacity, are characterised by large ranges of possible values. To incorporate the functional variation of lichens and bryophytes into the model, many physiological strategies are generated by randomly sampling the ranges of possible parameter values. We call these parameterisations “strategies” and not “species”, because they do not correspond exactly to any species that can be found in nature. Nevertheless, these strategies are assumed to represent the physiological properties of real lichen and bryophyte species in a realistic way. Hence, the functional variation of the organisms can be simulated without knowing the exact details of each species.

The model is then run with all strategies, but not every strategy is able to maintain a positive biomass in each grid cell, which is necessary to survive. The results are computed by averaging only over the surviving strategies of each grid cell. Thus, climate is used as a filter to narrow the ranges of possible parameter values in each grid cell and therefore to make the results more accurate (see Fig. 4).

The studies of Bloom et al. (1985) and Hall et al. (1992) analyse from a theoretical perspective the relations between the “strategy” of an organism and the success of this organism regarding natural selection in a certain environment. Follows and Dutkiewicz (2011) apply this approach to marine ecosystems while Kleidon and Mooney (2000) use it to predict biodiversity patterns of terrestrial vegetation. The applicability of this

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



method to modelling biogeochemical fluxes of terrestrial vegetation has been successfully demonstrated by the JeDi-DGVM (Pavlick et al., 2012).

The 15 model parameters which are included in the random sampling method are listed in Table B9 in the appendix. They represent structural properties of the thallus of a lichen or bryophyte, such as specific area or water storage capacity. They also describe implications of the thallus structure, such as the relation between water content and water potential. Furthermore characteristics of the metabolism are considered, such as optimum temperature. Also parameters which have categorical values are used: a lichen or bryophyte can either live in the canopy or at the soil surface (see Sect. 2.1.1). Another categorical parameter determines if the organism has a carbon concentration mechanism (CCM) or not. Although regulation of the CCM has been observed (Miura et al., 2002), the model contains a fixed representation of the CCM for simplicity.

Some of the 15 parameters mentioned above are related to further lichen or bryophyte parameters. The respiration rate at a certain temperature, for instance, is assumed to be related to Rubisco content and turnover rate. Hence, the parameters “Rubisco content” and “turnover rate” are not sampled from ranges of possible values, but determined by the value of the parameter “respiration rate”. The reason for this relationship is an underlying physiological constraint, in this case, maintenance costs of enzymes. A lichen or bryophyte with a high concentration of Rubisco, for example, has to maintain these enzymes and therefore also shows a high respiration rate and a high turnover rate. These relationships are called tradeoffs. The parameters which describe the tradeoffs are assumed to have constant values.

Six tradeoffs are implemented in the model. The first tradeoff describes the relation between Rubisco content, respiration rate and turnover rate explained above. The second tradeoff relates the diffusivity for CO₂ to the metabolic activity of the lichen or bryophyte via its water content. This means that a high diffusivity is associated with a low water content which results in a low activity. The third tradeoff describes the positive correlation between the maximum electron transport rate of the photosystems (J_{\max}) and the maximum carboxylation rate ($V_{C,\max}$). Since both rates represent costs for the

BGD

10, 3735–3846, 2013

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Estimating global carbon uptake by lichens and bryophytesP. Porada et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

organism and photosynthesis is the minimum of the two, it would be inefficient if they were independent from each other. The fourth tradeoff is associated with the carbon concentration mechanism (CCM). In case a lichen or bryophyte possesses a CCM, a part of the energy acquired by the photosystems is not used to fix CO₂, but to increase the CO₂ concentration in the photobionts. If the organism is limited by low CO₂ or high photorespiration but enough light is available, a CCM can lead to higher productivity. The fifth and sixth tradeoffs concern the Michaelis-Menten constants of the carboxylation and oxygenation reactions of Rubisco. They relate these constants to the molar carboxylation and oxygenation rates of Rubisco. One tradeoff is usually associated with more than one parameter. The model parameters that describe tradeoffs are listed in Table B10.

The model contains several additional lichen or bryophyte parameters which are not directly associated with tradeoffs, but which represent physiological or physical constraints. Therefore, they are assumed to have constant values. They can be found in Table B11.

In addition to the parameters that describe properties of the lichens and bryophytes, the model contains parameters that represent environmental conditions. They describe the extinction of light as a function of LAI, the interception efficiency for precipitation of the canopy, characteristics of the snow cover, thermal properties of the upper soil layer, roughness of the surface regarding wind and the time intervals for disturbance in the different biomes. For the sake of simplicity, no ranges are specified for these parameters, only average values of the corresponding variables are used. The density of snow, for instance, varies typically from 100 to 500 kg m⁻³ (Domine et al., 2011) depending on many factors, such as age, for example, which are not considered in the model. Hence, snow density is set to a constant global average value. For a list of parameters related to environmental conditions, see Table B8.

2.3 Simulation setup

The model runs on a global rectangular grid with a resolution of 2.8125 degrees (T42), hence all input data are remapped to this resolution. The land mask and the climate forcing are taken from the WATCH data set (Weedon et al., 2011). This data set comprises shortwave radiation, downwelling longwave radiation, rainfall, snowfall, air temperature at 2 m height, wind speed at 10 m height, surface pressure and specific humidity. The latter two variables are used to compute relative humidity. The temporal resolution of the data is 3 h and the years 1958 to 2001 are used. Since the model runs on an hourly time step, the data is interpolated. In addition to the climate forcing, the model uses maps of LAI and SAI in a monthly resolution and a temporally constant map of bare soil area, which are taken from the Community Land Model (Bonan et al., 2002). They are used to provide estimates for the available area for growth and the light environment. A biome map which is taken from Olson et al. (2001) is used to represent disturbance by assigning characteristic disturbance intervals to each biome (see Table B3). Furthermore, surface roughness is determined as a function of the biome.

The model provides output for each surviving strategy in a grid cell independently. Hence, to obtain an average output value for a certain grid cell the different strategies have to be weighted. Since ecological interactions between species are not considered in the model, it is not possible to determine the relative abundance and thus the weight of each strategy. Therefore, the uncertainty due to the unknown weights of the strategies has to be included into the results. As lower bound for net carbon uptake in a certain grid cell we assume that all strategies are equally abundant and the estimate thus corresponds to equal weights for all surviving strategies. This weighting method is called “average”. Since strategies that do not grow much are probably not as abundant as strongly growing strategies, the true net carbon uptake is probably underestimated by this method. As an upper bound we assume a weight of one for the strategy with the highest growth and zero for all other strategies. This weighting method is called “maximum” and it is probably an overestimate of the true value, since competition between

BGD

10, 3735–3846, 2013

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



species would have to be very strong to reduce diversity to such an extent. The upper and lower bounds derived from the two weighting methods are then used for the evaluation of the model.

The model is evaluated by comparing model estimates to observational data on a biome basis. Hence, data from several field study sites located in a certain biome are compared to the simulated net carbon uptake averaged over all grid cells of this biome. Only studies which report estimates of net carbon uptake based on surface coverage of lichens or bryophytes are used for evaluating the model. This facilitates a direct comparison of model estimates and observations. The estimates from these studies show a large variability, even for the same site they differ by more than an order of magnitude. Moreover, the number of studies is quite limited. Only 4 out of 14 biomes are represented in the field studies: Tundra, boreal forest, desert and tropical rainforest. For both forest biomes only one study site is available, respectively, making reliable estimates of net carbon uptake difficult. Nevertheless, we think that the data from the field studies is suitable to give a rough idea of the mean net carbon uptake in a certain biome.

The model is run for 2000 yr with an initial number of 3000 strategies. The simulation length of 2000 yr is sufficient to reach a dynamic steady state regarding the carbon balance of every strategy, which also implies that the number of surviving strategies has reached a constant value. Furthermore, the initial strategy number of 3000 is high enough to achieve a representative sampling of the ranges of possible parameter values. This means running the model with 3000 different strategies leads to a very similar result. The model output is averaged over the last 100 yr of the simulation, since this period corresponds to the longest disturbance interval in the model.

3 Results

The model presented here is designed to predict global net carbon uptake by lichens and bryophytes. The predicted values are shown in form of maps as well as global

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



average numbers. Additionally, further properties of lichens and bryophytes estimated by the model are presented to illustrate the large range of possible predictions. To assess the quality of the predictions, the model estimates are compared to observational data. Since this study is the first process-based approach to quantify the productivity of lichens and bryophytes at the global scale, comparison of the results with other models is not possible. To estimate the effect of uncertain model parameter values on the predictions of the model, a sensitivity analysis is performed.

3.1 Modelled net carbon uptake

The global estimate of net carbon uptake by lichens and bryophytes amounts to 0.34 (GtC) yr⁻¹ for the “average” weighting method and 3.3 (GtC) yr⁻¹ for the “maximum” weighting method (for a description of the weighting methods see Sect. 2.3). The global biomass is 4.0 (Gt C) (average) and 46 (Gt C) (maximum), respectively. Note that we use a capital “C” to abbreviate carbon throughout the manuscript. To avoid confusion with unit symbols, we put C and the associated unit in brackets.

We show maps of the global net carbon uptake by lichens and bryophytes, biomass, surface coverage, number of surviving strategies and two characteristic parameters, the optimum temperature of gross photosynthesis and the fraction of organisms with a Carbon Concentration Mechanism (CCM). These maps are created from time averages over the last 100 yr of the simulation described in Sect. 2.3. The maps are based on the “average” weighting method. The “maximum” weighting shows very similar patterns and the corresponding maps are shown in Fig. A1a to d.

The net carbon uptake by lichens and bryophytes is shown in Fig. 5a. In some areas, such as Greenland and the driest parts of deserts, no strategy is able to survive and net carbon uptake is equal to zero there. The biomes differ largely with respect to carbon uptake. While dry areas are characterised by the lowest productivity, the highest values are reached in forested areas. In the tropical rainforest the high productivity is mainly due to the high carbon uptake by epiphytic lichens and bryophytes (see Fig. 5c). In the boreal zone, lichens and bryophytes in the canopy as well as on the ground contribute

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



significantly to carbon uptake (see Fig. 5d). Biomass (Fig. 5b) exhibits a global pattern similar to carbon uptake. At high latitudes, however, the ratio of biomass to carbon uptake seems to be slightly higher than in the tropics.

Figure 6a shows the global absolute cover of lichens and bryophytes in m^2 projected surface area of the organisms per m^2 ground. Since the available area can be higher than one in the canopy, high values of absolute cover do not necessarily mean high fractional cover. On the contrary, the fractional cover is highest in regions with low absolute cover, especially grasslands and agricultural areas, since the available area in these regions is very small. A map of fractional cover is shown in Fig. A2. Figure 6b shows the number of surviving strategies at the end of the simulation. The global pattern is slightly different from the pattern of carbon uptake. Although forested regions show the highest number of strategies, the high latitudes are richer in strategies than the tropics.

Figure 6c and 6d shows the global patterns of two characteristic lichen and bryophyte parameters. As described in Sect. 2.2 these parameters are sampled randomly from ranges of possible values to create many artificial strategies. Thus, at the start of a simulation possible values from the range of a certain parameter are present in equal measure in each grid cell. During the simulation, however, parameter values from certain parts of the range might turn out to be disadvantageous in a certain climate and the corresponding strategies might die out. This leads to a narrowing of the range and consequently to global patterns of characteristic parameters. These patterns reflect the influence of climate on properties of surviving strategies. Figure 6c shows the optimum temperature of gross photosynthesis of lichens and bryophytes living on the ground. The optimum temperature shows a latitudinal pattern, with high values in the tropics and low values towards the poles or at high altitudes. In Fig. 6d the fraction of organisms on the ground is shown which have a Carbon Concentration Mechanism (CCM). Also this parameter is characterised by a latitudinal pattern. The fraction of organisms with a CCM is almost one in the tropics, while it is approximately 0.5 in polar regions. Lichens and bryophytes living in the canopy exhibit global patterns of optimum

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

temperature and CCM fraction similar to those living on the ground. The corresponding maps are shown in Fig. A2.

3.2 Evaluation

Figure 7 shows a comparison between model estimates and observational data with regard to net carbon uptake for 4 biomes. Considering the order of magnitude and the large scale patterns of net carbon uptake, the model results agree well with the observations. There are, however, large uncertainties due to variability in the data, the difference between “average” and “maximum” estimate and the climatic differences between the grid cells of a certain biome. Furthermore, there are too few data points to make any definitive statements. More detailed comparisons between modelled and observed carbon uptake, however, are beyond the scope of this study (as discussed in Sect. 4). The field studies corresponding to the data points in Fig. 7 are listed in Table 1.

3.3 Sensitivity analysis

As described in Sect. 2.2 model parameters that describe tradeoffs, physiological constraints or environmental properties are assumed to have constant values. Some of these parameter values have already been estimated in other studies and thus they can be taken directly from the literature. Others, however, have yet to be determined. A reliable estimate of these unknown parameter values would require a considerable amount of experimental data, which is beyond the scope of this study. Therefore, the parameter values were derived by “educated guess” using the available information from the literature (see Appendix B). To assess the impact of these parameter values on the model result we perform a sensitivity analysis (see Table 2). Note that some of the parameters tested in the sensitivity analysis are aggregated into a single process. For a detailed overview of the parameters see Tables B8 and B10.

BGD

10, 3735–3846, 2013

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)



[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



In general, the model is not very sensitive to the parameter values which applies both for the “average” and “maximum” weighting methods. Regarding the environmental parameters a change by 50 % leads to a 10 % or less change in the modelled net carbon uptake in most cases. Only disturbance interval and rain interception efficiency have a slightly larger influence. The parameters that describe tradeoffs have a larger impact. Changing the relation of water content to diffusivity for CO₂ by 50 %, for instance, leads to a change in “average” net carbon uptake by almost 50 %. The effect of the respiratory costs associated with Rubisco content is similarly strong. The climate forcing has only a moderate influence on the simulated net carbon uptake. Note that the variation in climate forcing is only 20 % compared to 50 % for the parameters. This is done to avoid generating unrealistic climatic regimes.

The turnover parameter affects “maximum” and “average” net carbon uptake in opposite ways. Moreover, the effects of the parameters $J_{\max}/V_{C,\max}$, light extinction and surface roughness on carbon uptake are not straightforward to explain. These points are discussed in Sect. 4. For reasons of computation time we used a different simulation setup (400 yr, 300 strategies) for the sensitivity analysis. Therefore, the net carbon uptake values for the control run (Table 2) differ from the ones presented above. The pattern of productivity, however, is very similar to those of the longer run with more strategies (see Fig. A2). We thus assume that the sensitivity of the model does not change significantly with increased simulation time and number of initial strategies.

4 Discussion

In this study we estimate global net carbon uptake by lichens and bryophytes using a process-based model. In the following, we discuss the plausibility of the model estimates with respect to the patterns and the absolute values. Furthermore, we give an overview of the limits regarding the accuracy of the predictions as well as the certainty of parameter values.

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



The model predicts plausible patterns of productivity and biomass (see Fig. 5) as well as cover, number of surviving strategies and characteristic parameters (see Fig. 6). The productivity of lichens and bryophytes in deserts seems to be generally limited by low water supply while forested areas are characterised by high values of productivity.

5 The vertical pattern of productivity in tropical forests is different from the one in boreal forests and it probably can be attributed to forest structure and temperature: The boreal forests have a relatively open canopy with large, sunlit areas in between that allow for lichen or bryophyte growth. Since this is not the case in the dense tropical lowland forests carbon uptake on the ground is lower than in the boreal zone. Furthermore, in

10 the moist lowland forest, high temperatures at night together with high humidity near the soil surface cause high respiratory losses for lichens and bryophytes and therefore constrain their growth (Nash III, 1996). This is also reflected in the ratio of biomass to carbon uptake, which is slightly lower in the tropics than at high latitudes. Tropical cloud forests, however, which also exist in the lowland (Gradstein, 2006), may facilitate

15 high productivity of lichens and bryophytes near the ground. The spatial resolution of the climate data and the biome map, however, is not high enough to represent these ecosystems. Hence, at a large spatial scale, the climate of the high latitudes seems to be more favourable for a large range of lichen and bryophyte growth strategies than the tropical climate, which is also illustrated by the higher number of strategies of the boreal

20 forest zone compared to the tropical one. Nevertheless, the potential for productivity seems to be highest in the moist tropics, although survival in this region is more difficult.

The surface coverage shows a plausible range of values. In deserts, it is in the order of 10% or lower and in (sub)polar regions, it is around 30%, which seems realistic. In forested regions, it ranges from 40 to 65%, which is plausible since the available area

25 is larger than 1 m² per m² ground for lichens and bryophytes living in the canopy.

The latitudinal pattern of the optimum temperature of gross photosynthesis is realistic, since the mean climate in the tropics is warmer than in polar regions or at high altitudes. The fact that the edges of the parameter range are not represented in the map can be explained as follows: extreme climatic conditions, which could be associated

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

with extreme values of the optimum temperature of gross photosynthesis, often do not persist for long time periods. Lichens and bryophytes are usually inactive during these periods and are therefore not affected by them. Extreme temperatures that last for longer periods of time are probably only present at the microclimatic scale and are therefore absent from the grid cell climate. Same as optimum temperature, also the latitudinal pattern of the fraction of organisms with a CCM makes sense. A CCM is useful in situations where CO_2 is limited, either due to low supply from the atmosphere or due to high photorespiration. These conditions are met in the tropics. The moist climate in the rainforest generally leads to high water content of the thallus, which results in a low diffusivity for CO_2 . Additionally, the high temperatures in the tropics result in high photorespiration, further reducing the available CO_2 in the pore space. Although the global pattern is plausible, the fraction of lichens and bryophytes with a CCM seems to be generally too high. The reason for this could be that the metabolic costs of a CCM are underestimated in the model. As mentioned in Sect. 3.3, the parameters describing the costs of the CCM are not very well known. Although the global patterns of optimum temperature and CCM probably cannot be evaluated on a quantitative basis, these patterns help to assess qualitatively the plausibility of the model results.

The model results are in good agreement with observational data (see Fig. 7). There are, however, relatively large uncertainties associated with this comparison, mainly due to the large variability in the observational data. One reason for this variability in productivity might be differences in microclimate at the study sites. These differences can be considerable, although the sites belong to the same large-scale mean climate. Another reason for the variability in the observations might be the effect of biodiversity on net carbon uptake. While one site might be dominated by a species that is very well adapted to the local climate and thus exhibits a high productivity, another site might be populated by less productive species. This would lead to differing estimates of net carbon uptake. The model results suggest that both mechanisms play a role (Fig. 7): due to physiological variation between the strategies, the estimates for the “average” and “maximum” weighting methods differ largely. Also, the difference in

productivity between the grid cells with the most and the least favourable climate of a certain biome is substantial.

Another source of uncertainty is the spatial resolution of the model. Even if the number of field studies was high enough to reliably estimate a mean productivity for each biome, comparing the study sites to the model grid cells is not straightforward. Due to the much larger spatial scale, the climate of a grid cell represents a mean state of the local climates that can be found in the cell. Hence, the climatic variability derived from the grid cells belonging to a certain biome might be smaller than the corresponding microclimatic variability in this biome. Depending on the degree of nonlinearity in the relation between climate and net carbon uptake, an estimate of mean net carbon uptake based on the climate of grid cells might be biased compared to the mean of the observed values. Since the relation between climate and net carbon uptake is a complex function of many variables, quantifying its nonlinearity is difficult. Reducing the spatial resolution of the model down to the microclimatic scale, however, is virtually impossible. While the limited amount of observational data and the coarse spatial resolution of the model are issues that cannot be resolved easily, a significant improvement in the accuracy of the model predictions could be achieved by quantifying the abundance of the strategies as described in Sect. 2.3. By implementing a scheme that simulates competition between lichen or bryophyte strategies, the large difference between the “average” and the “maximum” estimate (Fig. 7) could be reduced. Such a scheme would be a promising perspective for extending the model.

Considering the sensitivity analysis, the general behaviour of the model is plausible. Increasing the Rubisco content per base respiration rate, for example, leads to an increase in net carbon uptake and vice versa (see Table 2). Some effects, however, require further explanation:

1. The turnover parameter affects net carbon uptake based on “maximum” and “average” weighting in opposite ways. The “maximum” estimate is as expected: a higher turnover rate leads to lower biomass and therefore lower productivity. The “average” estimate could be explained by a statistical effect: a higher turnover

BGD

10, 3735–3846, 2013

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)



[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



rate causes the death of many less productive strategies, thereby increasing the average value of productivity compared to lower turnover rates.

2. The ratio $J_{\max}/V_{C,\max}$ is positively correlated with productivity, which is not self-evident. The correlation is due to the fact that in the model, J_{\max} is derived from a given $V_{C,\max}$ via the ratio of the two. Hence, changing this ratio only affects J_{\max} .
3. The light extinction parameter is negatively correlated with total productivity of lichens and bryophytes. Since the parameter partitions the light input between canopy and soil surface, the ground receives less light if the canopy absorbs more and vice versa. Hence, the impact of this parameter on productivity can be explained by assuming that the decrease in carbon uptake on the ground overcompensates the increase in the canopy.
4. Surface roughness and wind speed are both negatively correlated with the aerodynamic resistance to heat transfer. They consequently have a positive effect on potential evaporation. Therefore the lichens and bryophytes are more frequently desiccated and their productivity decreases.

The overall outcome of the sensitivity analysis of the model is satisfactory. Parameters that describe environmental conditions do not have a large impact on simulated net carbon uptake. This means that it is not absolutely necessary to specify ranges for the environmental parameters in order to obtain a good estimate of the uncertainty of the model results. The model is, however, quite sensitive to parameters that describe tradeoffs. Since these parameters are assumed to have constant values (Sect. 2.2), they should be determined as accurately as possible. Unfortunately, the data available in the literature currently only allow “educated guesses”. Determining accurate values for these parameters, however, is not per se difficult. Only one study, for instance, has measured both Rubisco content and base respiration rate simultaneously, but in many studies one of them has been determined. Considering the diffusivity of the thallus for CO_2 , a large body of studies describes the relation between productivity and water

content, but we found only one study that quantified the diffusivity for CO₂ as a function of water content. The latter, however, is much more useful for modelling CO₂ diffusion through the thallus on a process basis. Hence, accumulating more empirical data that is suitable to determine the values of the parameters that describe tradeoffs with higher accuracy would be a very efficient way to improve the model. One example of a such a study is the work of Wullschleger (1993) which analyses the ratio between J_{\max} and $V_{C,\max}$. For a large number of vascular plants this ratio is approximately 2. The reason for this constant ratio is the fact, that a high J_{\max} is not useful if the $V_{C,\max}$ is low and vice versa, since productivity is the minimum of the two rates. As both rates are associated with metabolic costs, a tradeoff emerges.

To summarise, the model is able to produce realistic global patterns of net carbon uptake by lichens and bryophytes. The uncertainty concerning the absolute value of carbon uptake is relatively high, but the observational data available to evaluate the model also show large variability. Given that this study is supposed to be a first order estimate of global lichen and bryophyte productivity, the outcomes are satisfying. Regarding possible improvements of the model it would be useful to implement competition between the strategies. In this way, the uncertainty due to the unknown abundance of the strategies could be eliminated. Furthermore, it would be beneficial if values of model parameters that describe tradeoffs could be determined more accurately.

5 Conclusions and outlook

In this paper, we present the first process-based model of global net carbon uptake by lichens and bryophytes. The model explicitly simulates processes such as photosynthesis and respiration to quantify exchange flows of carbon between organisms and environment. The predicted global net carbon uptake of 0.34 to 3.3 (GtC) yr⁻¹ has a realistic order of magnitude compared to empirical studies (Elbert et al., 2012). The values of productivity correspond to approximately 1 to 6 % of the global terrestrial Net Primary Productivity (NPP) (Ito, 2011). Furthermore, the model represents the large

BGD

10, 3735–3846, 2013

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)



[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



functional variation of lichens and bryophytes by simulating many different physiological strategies. The performance of these strategies under different climatic regimes is used to narrow the range of possible values of productivity. This method is an efficient way to incorporate the effects of biodiversity on productivity into a vegetation model (Pavlick et al., 2012). The predicted global patterns of surviving strategies are plausible from a qualitative perspective. To further reduce the number of possible values for productivity, competition between the different strategies could be implemented. This would also make the representation of functional variation of lichens and bryophytes in the model more realistic.

The uptake of carbon is only one of many global biogeochemical processes where lichens and bryophytes are involved. They probably also play an important role in the global nitrogen cycle due to the ability of some lichens to fix nitrogen (around 50 % of terrestrial uptake) (Elbert et al., 2012). The fixation of nitrogen, however, is relatively expensive from a metabolic viewpoint. It would be interesting to quantify the costs of this process at the global scale and its relation to nutrient limitation.

While nitrogen can be acquired from the atmosphere, phosphorus usually has to be released from rocks by weathering. Thus, lichens and bryophytes might increase their access to phosphorus or other important nutrients by enhancing weathering rates at the surface through exudation of organic acids and complexing agents. Since weathering rates control atmospheric CO₂ concentration on geological time scales, lichens and bryophytes might have influenced global climate considerably throughout the history of the earth (Lenton et al., 2012).

Lichens and bryophytes have to invest carbon in order to fuel nitrogen fixing enzymes or produce organic acids necessary for weathering. Hence, these investments could be implemented as a cost function into the model, making it possible to quantify the associated processes at the global scale. Quantifying the carbon budget of lichens and bryophytes can thus be seen as a first step towards estimating the impact of these organisms on other biogeochemical cycles.

Appendix A

See Figs. A1–A2.

Appendix B

Model details

5 In the following sections, the technical details of the model are explained. Section B1 describes how strategies are generated from parameter ranges. Moreover, references are provided for these parameter ranges. Sections B2 to B7 contain all model equations that are associated with physiological processes of lichens and bryophytes. Furthermore, references are given for the theoretical background and the parameterisation of the equations. The equations are ordered according to the structure of Sect. 2. The values and the units of the parameters and variables used in the model equations are tabulated in Sects. “Model parameters” and “Model variables” (see Tables B6 to B15). The tables contain references to the respective equations. To make the equations more easily readable, characteristic prefixes are added to the model parameters and the associated tables are structured accordingly. The prefixes, the type of parameter and the associated table(s) can be found in Table B1.

15 For further details on the implementation of parameters and equations in the model we refer to the source code of the model which is available on request (pporad@bgc-jena.mpg.de).

20 B1 Generation of strategies

To account for the large functional variability of lichens and bryophytes, many strategies are generated in the model which differ from each other in 15 characteristic parameters (see Sect. 2.2). To create the strategies, these 15 characteristic parameters are assigned through randomly sampling ranges of possible values. The parameters and

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



the corresponding ranges are listed in Table B9. Assignment of parameter values is performed in two steps: (a) for each strategy, a set of 15 random numbers uniformly distributed between 0 and 1 is sampled. The random numbers are generated by a Latin Hypercube algorithm (McKay et al., 1979). This facilitates an even sampling of the 15-dimensional space of random numbers, since the space is partitioned into equal subvolumes from which the random numbers are then sampled. (b) The 15 random numbers are mapped to values from the ranges of the parameters. Since the purpose of the sampling is to represent the whole range of a parameter as evenly as possible, two different mapping methods are used, a linear one for parameters that have only a small range of possible values, and an exponential one for parameters that span more than one order of magnitude.

If the possible values of a parameter x span a relatively small range, a random number between 0 and 1 is linearly mapped to this range according to:

$$x = N(x_{\max} - x_{\min}) + x_{\min} \quad (\text{B1})$$

where N is a random number between 0 and 1. x_{\max} and x_{\min} are the maximum and the minimum value from the range of possible values for the parameter x . To ensure that the ranges are sufficiently broad, more extreme values than those found in the literature are used as limits. For this purpose, the mean of the literature based parameter values is computed. x_{\min} is then calculated by subtracting the distance between the mean and the lowest value found in the literature from this lowest value. x_{\max} is calculated by adding the distance between mean and highest value found in the literature to this highest value. A precondition for this procedure is that the parameter values span a relatively small range, as mentioned above. Otherwise, subtracting the above mentioned distance from the mean would result in negative values.

If the possible values of a parameter span a large range, the mapping from a random number between 0 and 1 to this range is exponential and written as:

$$x = x_{\min} e^{N \log\left(\frac{x_{\max}}{x_{\min}}\right)} \quad (\text{B2})$$

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

where the symbols have the same meaning as in Eq. (B1). The exponential function is used to represent each order of magnitude of the range equally. If the limits of the range were 1 and 10 000, for instance, using Eq. (B1) would result in 90 % of the values lying between 1000 and 10 000. Hence, values from the range 1 to 1000 would be strongly underrepresented. By using Eq. (B2) this problem is avoided, which is particularly important if the model is run with low numbers of strategies. In this case, the underrepresentation of strategies with parameter values from the lower end of the range could lead to unrealistic model results. To be consistent with the exponential mapping, the limits of the range are also calculated differently than for Eq. (B1): x_{\min} is assumed to be half the lowest value found in the literature, while x_{\max} is set to the double of the highest value found in the literature.

Additionally random numbers can be transformed into categorical values. This is done by assigning a lichen or bryophyte to a certain category if the corresponding random number is below a threshold, and otherwise to another category. The threshold is a number between 0 and 1.

In the following, each of the 15 strategy parameters is shortly described together with references for the range of possible values.

B1.1 Albedo

The albedo x_{α} of a lichen or bryophyte is assumed to vary from 0 to 1. The reason for this assumption is that lichens and bryophytes show a large variety of colors and therefore a large range of possible values for the albedo (Kershaw, 1975). For simplicity, each strategy has a fixed value of x_{α} . In reality, species can adapt their albedo to different environmental conditions. This can be represented in the model by strategies differing only in the value of x_{α} .

A linear mapping is used for the parameter range since we found no reason to assume a priori that a certain value of the albedo is more frequent than the others.

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

B1.2 Specific water storage capacity

The specific water storage capacity $x_{\Theta_{\max}}$ represents the maximum amount of water per gram carbon a lichen or bryophyte can store (Fig. B1). An exponential mapping is used for the range of possible values.

B1.3 Specific projected area

The specific projected area $x_{A_{\text{spec}}}$ represents the surface area per gram carbon of a lichen or bryophyte projected onto a plane (Fig. B2). An exponential mapping is used for the range of possible values.

B1.4 Location of growth

The location of growth x_{loc} of a lichen or bryophyte is a categorical variable. Two categories are possible: canopy and ground. Since no data could be found about the relative abundance of lichens and bryophytes living in the canopy and the ones living on the ground, the probability for each location of growth is 50 %.

B1.5 Threshold saturation and shape of water potential curve

As described in Sect. 2.1.2 the water potential $\Psi_{\text{H}_2\text{O}}$ is an increasing function of the water saturation of the thallus, Φ_{Θ} , which is described below in Sect. B3.1. $\Psi_{\text{H}_2\text{O}}$ has a value of $-\infty$ at zero water content and reaches a maximum value of 0 at a certain threshold saturation (see Fig. B3). This threshold saturation represents the partitioning between water stored in the cells of the thallus and extracellular water. It is described by the parameter $x_{\Phi_{\Theta, \text{sat}}}$. The theoretical limits of $x_{\Phi_{\Theta, \text{sat}}}$ are 0 and 1, where 0 would mean that the lichen or bryophyte stores all its water extracellularly and 1 would mean that no extracellular storage capacity exists. A lower limit of 0 is physiologically unrealistic. Some mosses have, however, a relatively large capacity to store water extracellularly (Proctor, 2000). Hence, the lower limit of $x_{\Phi_{\Theta, \text{sat}}}$ is set to 0.3. An upper limit of 1.0 seems

realistic, since significant amounts of extracellular water do not seem to occur in many lichens under natural conditions (Nash III, 1996, p. 161). Due to the small range of possible values for $x_{\Phi_{\Theta, \text{sat}}}$ a linear mapping is used for this parameter.

A second parameter, $x_{\Psi_{\text{H}_2\text{O}}}$, determines the shape of the water potential curve from zero water content to the threshold saturation. Given a certain value of $x_{\Phi_{\Theta, \text{sat}}}$, the parameter $x_{\Psi_{\text{H}_2\text{O}}}$ controls the water content of the thallus in equilibrium with a certain atmospheric vapour pressure deficit. Since the range of possible values of $x_{\Psi_{\text{H}_2\text{O}}}$ is quite limited a linear mapping is used. The limits for this range are estimated using the data points in Fig. B3 and are set to 5.0 and 25.0, respectively. The calculation of the water potential $\Psi_{\text{H}_2\text{O}}$ is given below in Sect. B3.3.

Furthermore, the relation between water content and water potential influences the tradeoff between CO_2 diffusivity and metabolic activity. This is explained in detail below in Sect. B3.5.

B1.6 Molar carboxylation rate of Rubisco

The molar carboxylation rate of Rubisco $x_{V_{C, \text{max}}}$ represents the maximum carboxylation velocity of a Rubisco molecule (Fig. B4). The data are taken from a study that analyses a broad range of photoautotrophs. An exponential mapping is used for the range of possible values.

B1.7 Molar oxygenation rate of Rubisco

The molar oxygenation rate of Rubisco $x_{V_{O, \text{max}}}$ represents the maximum oxygenation velocity of a Rubisco molecule (Fig. B5). The data are taken from a study that analyses a broad range of photoautotrophs. A linear mapping is used for the range of possible values.

BGD

10, 3735–3846, 2013

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

B1.8 Reference maintenance respiration rate and Q_{10} value of respiration

The specific respiration rate of lichens and bryophytes, R_{SPEC} , is controlled by two parameters: the reference respiration rate at 10°C , $x_{R_{\text{ref}}}$, and the Q_{10} value of respiration, $x_{Q_{10}}$. The distributions of these parameters are shown in Figs. B6 and B7. For $x_{R_{\text{ref}}}$ an exponential mapping is used while for $x_{Q_{10}}$ a linear mapping is used. The limits of $x_{Q_{10}}$ are not calculated by the method described for Eq. (B1), since the resulting range would be physiologically unrealistic. Instead, the values were rounded to the nearest integer. The influences of the two parameters on respiration rate are shown in Fig. B8.

Moreover, the respiration rate is related to Rubisco content and turnover rate of the thallus, as described in Sect. 2.2. The details of these relationships are explained below in Sects. B5.2 and B5.6.

B1.9 Optimum temperature of photosynthesis

The optimum temperature of photosynthesis $x_{T_{\text{opt,PS}}}$ represents the temperature at which gross photosynthesis shows a maximum (Fig. B9). A linear mapping is used for the range of possible values. The range is not calculated by the method described for Eq. (B1) since the resulting values would be physiologically unrealistic. Instead, the limits derived from the data were extended by 10 and 5 Kelvin, respectively.

B1.10 Enzyme activation energy of K_C and K_O

K_C and K_O are the Michaelis-Menten constants of the carboxylation and oxygenation reactions of Rubisco. The enzyme activation energies x_{E_a, K_C} and x_{E_a, K_O} control the temperature response of K_C and K_O . The available data (see Table B2) are not sufficient to estimate the shapes of the ranges of x_{E_a, K_C} and x_{E_a, K_O} . We assume that the parameters do not span several orders of magnitude and hence apply a linear mapping. The limits of the parameter ranges are calculated according to the method described for Eq. (B1).

BGD

10, 3735–3846, 2013

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

B1.11 Carbon Concentration Mechanism (CCM)

The parameter x_{CCM} is a categorical variable. It controls if a lichen or bryophyte possesses a Carbon Concentration Mechanism (CCM) or not. If a CCM is present, a part of the energy acquired by the photosystems is not used to fix CO_2 , but to increase the CO_2 concentration in the photobionts. Since no data could be found about the relative abundance of lichens and bryophytes with and without a CCM, the probability to possess a CCM is set to 50 %.

B1.12 Fraction of carbon allocated to growth

The parameter x_{alloc} represents the fraction of the sugar reservoir that is allocated to growth each day. x_{alloc} therefore describes the partitioning of assimilated carbon between storage pools and biomass. Since we found no reason for a fixed value of x_{alloc} for all strategies, the possible values are assumed to range from 0 to 1 and a linear mapping is used.

B2 Living environment

The location of growth of a lichen or bryophyte strongly influences its radiation and precipitation regime and the available area for growth (Sect. 2.1.1). The equations describing these influences are listed and explained below in Sects. B2.1 and B2.2. Further environmental effects on lichens and bryophytes depend not only on the location of growth but also on the biome. These are disturbance frequency, aerodynamic resistance to heat transfer and soil thermal properties as well as ground heat flux. The equations related to these effects can be found below in Sects. B2.3 to B2.5.

B2.1 Radiation and precipitation regime

Radiation and precipitation flows are partitioned between the canopy and the ground. This partitioning is described by factors which represent the fraction of the flow that

reaches the surface of a lichen or bryophyte. For the partitioning of radiation, Beer's law is used (Bonan, 2008, p. 254) and the associated factors for shortwave radiation ϕ_{rad_S} and longwave radiation ϕ_{rad_L} are calculated by:

$$\phi_{\text{rad}_S} = \begin{cases} (1.0 - x_\alpha) \left(1.0 - e^{-\rho_{\lambda,s}(A_{\text{LAI}} + A_{\text{SAI}})}\right) & \text{if organism in canopy} \\ (1.0 - x_\alpha) e^{-\rho_{\lambda,s}(A_{\text{LAI}} + A_{\text{SAI}})} & \text{if organism on ground} \end{cases} \quad (\text{B3})$$

5 and

$$\phi_{\text{rad}_L} = \begin{cases} p_e \left(1.0 - e^{-\rho_{\lambda,l}(A_{\text{LAI}} + A_{\text{SAI}})}\right) & \text{if organism in canopy} \\ p_e e^{-\rho_{\lambda,l}(A_{\text{LAI}} + A_{\text{SAI}})} & \text{if organism on ground} \end{cases} \quad (\text{B4})$$

10 where x_α is the albedo of a lichen or bryophyte for shortwave radiation and p_e is the emissivity of an organism for longwave radiation. $\rho_{\lambda,s}$ and $\rho_{\lambda,l}$ are extinction coefficients for short-wave radiation (Bonan, 2008, p. 254) and longwave radiation (Kustas and Norman, 2000), respectively. A_{LAI} and A_{SAI} are Leaf Area Index (LAI) and Stem Area Index (SAI).

The partitioning of precipitation is assumed to be a linearly decreasing function of LAI and the fraction of precipitation that reaches a lichen or bryophyte is:

$$\phi_{\text{prec}} = \begin{cases} p_{\eta_{\text{rain}}} \frac{A_{\text{LAI}}}{\rho_{\text{LAI,max}}} & \text{if organism in canopy} \\ 1.0 - \frac{A_{\text{LAI}}}{\rho_{\text{LAI,max}}} & \text{if organism on ground} \end{cases} \quad (\text{B5})$$

15 where $p_{\eta_{\text{rain}}}$ is the interception efficiency of the canopy for precipitation, A_{LAI} is Leaf Area Index and $\rho_{\text{LAI,max}}$ is the maximum LAI in the data set, both derived from Bonan et al. (2002).

B2.2 Available area

20 The available area for growth of a lichen or bryophyte per m^2 ground depends on its location of growth, which is either the ground or the canopy (see Sect. 2.1.1). The

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



available area on the ground, $A_{\text{ground,max}}$, is determined by two factors: (a) the amount of bare soil, which means soil surface that is not occupied by herbaceous vegetation, such as grasses or crops. Bare soil area is highest in non-vegetated areas such as deserts or mountain tops, but also in forested areas, since the ground is not per se occupied there. For simplicity, the area occupied by tree trunks is neglected. (b) Leaf Area Index (LAI), which affects the available area on ground through leaf fall by trees: under dense canopies (high LAI), a constantly renewed litter layer impedes the growth of lichens and bryophytes. Under open canopies (low LAI), a certain fraction of the soil surface is not affected by leaf fall, thus providing area for growth.

The available area on the ground is calculated according to:

$$A_{\text{ground,max}} = \min \left(A_{\text{baresoil}}, 1.0 - \frac{A_{\text{LAI}}}{\rho_{\text{LAI,max}}} \right) \quad (\text{B6})$$

where A_{baresoil} is the area of soil not occupied by herbaceous vegetation derived from Bonan et al. (2002). A_{LAI} is Leaf Area Index and $\rho_{\text{LAI,max}}$ is the maximum LAI in the data set.

The available area in the canopy, $A_{\text{canopy,max}}$ is assumed to be the sum of LAI and Stem Area Index (SAI). This means that the strategies are assumed to grow on all parts of the canopy, which means stems (i.e. trunks and twigs) and leaves. Growth on leaves, however, is assumed to be possible only for evergreen vegetation (see Sect. B2.3 for details). Thus the available area for growth is written as:

$$A_{\text{canopy,max}} = A_{\text{LAI}} + A_{\text{SAI}} \quad (\text{B7})$$

where A_{SAI} is SAI.

The surface area of a lichen or bryophyte per m^2 ground, A_{thallus} , is calculated according to:

$$A_{\text{thallus}} = \begin{cases} \min(x_{A_{\text{spec}}} S_{\text{B}}, A_{\text{canopy,max}}) & \text{if organism in canopy} \\ \min(x_{A_{\text{spec}}} S_{\text{B}}, A_{\text{ground,max}}) & \text{if organism on ground} \end{cases} \quad (\text{B8})$$

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

where $x_{A_{\text{spec}}}$ is the specific area of a lichen or bryophyte, s_B is the biomass per m^2 ground and $A_{\text{canopy,max}}$ and $A_{\text{ground,max}}$ are the available area in the canopy and on the ground, respectively. This means that A_{thallus} is limited by the available area. Since biomass is related to surface area via the specific area, also biomass is limited by available area.

The fraction of available area that is covered by a lichen or bryophyte is described by the variable Φ_{area} . This variable is necessary to obtain flows per m^2 ground instead of m^2 lichen or bryophyte. If the respiration flow per m^2 thallus is known, for instance, multiplication by Φ_{area} gives the respiration flow per m^2 ground. This is important because the purpose of the model is to predict global flows of carbon and water per m^2 ground. Φ_{area} is calculated according to:

$$\Phi_{\text{area}} = \begin{cases} \frac{A_{\text{thallus}}}{\max(A_{\text{canopy,max}}, 1.0)} & \text{if organism in canopy} \\ A_{\text{thallus}} & \text{if organism on ground} \end{cases} \quad (\text{B9})$$

where A_{thallus} is the surface area of a lichen or bryophyte and $A_{\text{canopy,max}}$ is the available area in the canopy. The maximum function is used in Eq. (B9) to ensure that the reference for the exchange flows is a m^2 ground, not a m^2 of lichen or bryophyte. If, for example, the available area in the canopy was 0.8 m^2 per m^2 ground and the thallus area was 0.6 m^2 per m^2 ground, the exchange flows per m^2 ground should be multiplied by a Φ_{area} of 0.6, and not by $0.6/0.8$.

B2.3 Disturbance interval

The disturbance interval τ_{veg} is assigned according to biome and location of growth (see Table B3). Disturbance leads to an instantaneous loss of biomass. The following processes are represented in the model:

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)



[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

1. Fire or treefall. In this case the biomass of a strategy is set back to the initial value each time a disturbance takes place. Fire and treefall are assumed to affect both strategies living on the ground as well as those living in the canopy.
2. Leaf fall, which affects only strategies living in the canopy. As described in Sect. B2.2, strategies in the canopy are assumed to live on trunks and twigs as well as on leaves. If leaf fall takes place, the biomass of a strategy is reduced to the fraction that is sustained by stem area, while the fraction that was growing on the leaf area is set to zero. Growth on leaves from deciduous forests is precluded, since the leaves are all shed at the same time of year. Although leaf fall is not a disturbance, its effect on biomass is represented similarly to a disturbance event in the model. Hence, leaf fall is listed here.
3. Herbivory, which is restricted in the model to large-scale grazing by herds of animals. It is thus assumed to affect only strategies living on the ground of savanna, grassland, desert or tundra. Other types of herbivory, which take place on smaller scales and also more frequently, are included in the biomass loss term (e.g. epiphytic herbivory by snails).

The implementation of disturbance used here leads to an oscillation of biomass over time, with a slow build-up between disturbance events and an instantaneous reduction during the event. Such an oscillation is unrealistic on the scale of a grid cell where the ecosystem is usually in a “shifting mosaic steady state”. This means, fires, treefall and leaf fall do not affect the whole grid cell, but only a small fraction of it. The purpose of the model, however, is to predict mean biomass. It does not matter if this mean value is derived by averaging over many individuals in a grid cell which are in different states of a disturbance cycle or if the mean is derived by the time average over a whole cycle for just one individual. Hence, if the averaging period is at least as long as one disturbance interval, the mean value is correct.

B2.4 Aerodynamic resistance to heat transfer

The aerodynamic resistance to heat transfer, r_H , controls exchange flows of heat between the surface of lichens or bryophytes and the atmosphere. It is calculated according to Allen et al. (1998):

$$r_H = \frac{\log\left(\frac{\rho_{\Delta_u} - \Delta_d}{z_0}\right) \log\left(\frac{\rho_{\Delta_u} - \Delta_d}{z_{0,h}}\right)}{\rho_k^2 u} \quad (\text{B10})$$

where ρ_k is the von Karman constant, u is near surface wind speed, ρ_{Δ_u} is the measurement height for wind speed, Δ_d is the displacement height for wind speed and z_0 and $z_{0,h}$ are the roughness length of momentum and humidity, respectively. The stability corrections which are used in some cases to make Eq. (B10) more accurate (Liu et al., 2007) are neglected here for simplicity.

The roughness length z_0 describes the impact of the surface on the flow of air above it. z_0 is parameterised as one of three possible values (Stull, 1988, p. 380):

$$z_0 = \begin{cases} \rho_{z_0, \text{canopy}}, & \text{if organism in canopy} \\ \rho_{z_0, \text{floor}}, & \text{if organism on forest floor} \\ \rho_{z_0, \text{GDT}}, & \text{if organism on ground outside forest} \end{cases} \quad (\text{B11})$$

Note that this parameterisation implies that large-scale structures such as forests dominate the aerodynamic properties of the surface. The shape of lichens or bryophytes growing on that surface is assumed to have only a small impact on the roughness length and is consequently neglected in the model. z_0 is related to $z_{0,h}$ according to:

$$z_{0,h} = \rho_{z_0, \text{mh}} z_0 \quad (\text{B12})$$

where $\rho_{z_0, \text{mh}}$ is the ratio between the roughness length of humidity and momentum (Allen et al., 1998).

BGD

10, 3735–3846, 2013

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



The displacement height is related to roughness length via:

$$\Delta_d = \rho_{z_0,d} z_0 \quad (\text{B13})$$

where $\rho_{z_0,d}$ is the ratio between displacement height and roughness length. The value of $\rho_{z_0,d}$ is derived from the relations $\Delta_d = 2/3$ vegetation height and $z_0 = 0.123$ vegetation height. These relations are adapted from (Allen et al., 1998) and represent rough approximations. Determining average values for displacement height for the each biome, however, would be beyond the scope of this study.

B2.5 Soil thermal properties

The ground heat flux f_G affects the energy balance of a lichen or bryophyte if the organism is living on the ground. Typically, the soil temperature is lower than the surface temperature during the day and higher during the night, leading to heat exchange between thallus and soil. If a lichen or bryophyte is living in the canopy, heat exchange with the soil is neglected, since it is assumed that thallus of the organism is in a thermal equilibrium with the canopy layers below. The effect of location of growth on f_G is represented by the variable χ_G :

$$\chi_G = \begin{cases} 1 & \text{if organism in canopy} \\ 0 & \text{if organism on ground} \end{cases} \quad (\text{B14})$$

The ground heat flux is not only affected by the temperature gradient between thallus and soil, but also by soil properties. These are the soil heat capacity C_{soil} and the thermal conductivity of the soil k_{soil} (Lawrence and Slater, 2008; Anisimov et al., 1997; Peters-Lidard et al., 1998). Since they depend on the average water content of the soil, desert soils are parameterised differently from non-desert soils in the model:

$$C_{\text{soil}} = \begin{cases} \rho_{C_{\text{soil}},D}, & \text{if organism in desert} \\ \rho_{C_{\text{soil}},F}, & \text{if organism not in desert} \end{cases} \quad (\text{B15})$$

$$k_{\text{soil}} = \begin{cases} \rho_{k_{\text{soil},D}}, & \text{if organism in desert} \\ \rho_{k_{\text{soil},F}}, & \text{if organism not in desert} \end{cases} \quad (\text{B16})$$

B3 Water relations

The water saturation of a lichen or bryophyte is defined in Sect. B3.1. It controls three physiological properties: diffusivity for CO₂ (Sect. B3.2), water potential (Sect. B3.3) and metabolic activity (Sect. B3.4).

B3.1 Water saturation

The water storage capacity Θ_{max} describes how much water a lichen or bryophyte can store per m² ground. Θ_{max} is assumed to be proportional to biomass per m² ground:

$$\Theta_{\text{max}} = \frac{x_{\Theta_{\text{max}}} s_B}{c_{\rho_{\text{H}_2\text{O}}}} \quad (\text{B17})$$

where $x_{\Theta_{\text{max}}}$ is the specific water storage capacity, s_B is the biomass of a lichen or bryophyte and $c_{\rho_{\text{H}_2\text{O}}}$ is the density of liquid water. The water saturation Φ_{Θ} is then calculated as the ratio of the actual water content s_{Θ} and the water storage capacity:

$$\Phi_{\Theta} = \frac{s_{\Theta}}{\Theta_{\text{max}}} \quad (\text{B18})$$

B3.2 Diffusivity for CO₂

The diffusivity of the thallus for CO₂ is represented by the variable D_{CO_2} . It decreases from a maximum value to a minimum value with increasing water saturation (see Fig. B10) and it is calculated according to:

$$D_{\text{CO}_2} = (w_{D_{\text{CO}_2,\text{max}}} - w_{D_{\text{CO}_2,\text{min}}})(1.0 - \Phi_{\Theta})^{w_{D_{\text{CO}_2}}} + w_{D_{\text{CO}_2,\text{min}}} \quad (\text{B19})$$

3772

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

where $w_{D_{\text{CO}_2,\text{min}}}$ is the minimum value of CO_2 diffusivity, $w_{D_{\text{CO}_2,\text{max}}}$ is the maximum value of CO_2 diffusivity, Φ_{Θ} is the water saturation of the thallus and $w_{D_{\text{CO}_2}}$ is a parameter that determines the shape of the diffusivity curve. $w_{D_{\text{CO}_2}}$ is estimated using the data points in Fig. B10, while $w_{D_{\text{CO}_2,\text{min}}}$ and $w_{D_{\text{CO}_2,\text{max}}}$ are taken from the literature (Cowan et al., 1992).

The relation between D_{CO_2} and Φ_{Θ} is an important component of the tradeoff between CO_2 diffusivity and metabolic activity. This is explained below in Sect. B3.5.

B3.3 Water potential

The water potential $\Psi_{\text{H}_2\text{O}}$ is an increasing function of water saturation and it is calculated according to:

$$\Psi_{\text{H}_2\text{O}} = \min \left(0.0, x_{\Psi_{\text{H}_2\text{O}}} \left(1.0 - \frac{x_{\Phi_{\Theta,\text{sat}}}}{\Phi_{\Theta}} \right) \right) \quad (\text{B20})$$

where Φ_{Θ} is the water saturation. The parameter $x_{\Phi_{\Theta,\text{sat}}}$ is the threshold saturation. If Φ_{Θ} is above this threshold, all cells in the thallus are fully turgid. Additional water is assumed to be stored extracellularly. $x_{\Psi_{\text{H}_2\text{O}}}$ is a parameter that determines the shape of the water potential curve. The parameters of the water potential curve are discussed in further detail in Sect. B1.5 and the curve is shown in Fig. B3. The influence of the relation between water saturation and water potential on the tradeoff between CO_2 diffusivity and metabolic activity is explained below in Sect. B3.5.

B3.4 Metabolic activity

The metabolic activity of a lichen or bryophyte is represented by the variable Φ_{act} . It is assumed to increase linearly from 0 at zero water content to 1 at the threshold saturation (Fig. B11). This assumption is based on the fact, that metabolic activity of lichens and bryophytes increases with their water content (Nash III, 1996, p. 157). The exact

shape of this relation is not known, but it should be proportional to the relation between dark respiration and water content at constant temperature. We thus approximate this relation by a linear one. Φ_{act} is written as:

$$\Phi_{\text{act}} = \min \left(1.0, \frac{\Phi_{\Theta}}{x_{\Phi_{\Theta}, \text{sat}}} \right) \quad (\text{B21})$$

5 where Φ_{Θ} is the water saturation of the thallus and $x_{\Phi_{\Theta}, \text{sat}}$ is the threshold saturation. The relation between Φ_{act} and Φ_{Θ} is an important component of the tradeoff between CO_2 diffusivity and metabolic activity. This is explained below in Sect. B3.5.

B3.5 Tradeoff between CO_2 diffusivity and metabolic activity

10 The CO_2 diffusivity of the thallus, D_{CO_2} , decreases with increasing water saturation Φ_{Θ} (see Sect. B3.2). The metabolic activity of a lichen or bryophyte Φ_{act} , however, increases with Φ_{Θ} (see Sect. B3.4). This leads to a tradeoff: at low Φ_{Θ} the potential inflow of CO_2 in the thallus and thus potential productivity are high, but the low Φ_{act} limits the actual productivity. At high Φ_{Θ} productivity is limited by low D_{CO_2} , although the lichen or bryophyte is active. Since both the relation between D_{CO_2} and Φ_{Θ} and the relation between Φ_{act} and Φ_{Θ} are controlled by underlying physiological constraints, the associated parameters, such as $w_{D_{\text{CO}_2}}$, are assumed to have constant values (see Sect. 2.2).

20 The tradeoff is illustrated in Fig. B12: to maximise productivity, a lichen or bryophyte should try to spend most of the time near the optimum water saturation. It can achieve this goal through appropriate values of the characteristic parameters which control water content. These are mainly $x_{\Phi_{\Theta}, \text{sat}}$, $x_{\Psi_{\text{H}_2\text{O}}}$ and $x_{\Theta_{\text{max}}}$, but also parameters that indirectly influence water content of the thallus, such as x_{α} , $x_{A_{\text{spec}}}$ and x_{loc} .

B4 Climate relations

The climate forcing (air temperature, wind speed, relative humidity, precipitation and downwelling short- and longwave radiation) influences almost all physiological processes of lichens and bryophytes (see Fig. 3). Furthermore, it determines potential evaporation and surface temperature. In the following sections the relations between potential evaporation (Sect. B4.3), surface temperature (Sect. B4.4) and climate forcing are described. The factors necessary for the calculation of these relations are:

1. Net radiation (see Sect. B4.1).
2. Saturation vapour pressure (see Sect. B4.2).
3. Aerodynamic resistance to heat transfer (see Sect. B2.4).
4. Relative humidity.

Also snow affects physiological processes of lichens and bryophytes. The dynamics of the snow layer are explained in Sect. B4.5 while the effects of the snow layer on physiological processes are described in the sections related to these processes.

B4.1 Net radiation

Net radiation is the sum of downwelling short- and longwave radiation, upwelling longwave radiation and the ground heat flux. Ingoing short- and longwave radiation are derived from the climate forcing data.

Outgoing longwave radiation $f_{\text{rad}_{\text{LW}_1}}$ is calculated as a function of surface temperature and air temperature:

$$f_{\text{rad}_{\text{LW}_1}} = \left(4.0c_{\sigma}T_{\text{air}}^3T_{\text{surf}} - 3.0c_{\sigma}T_{\text{air}}^4 \right) \Phi_{\text{area}} \quad (\text{B22})$$

where T_{air} is air temperature, T_{surf} is surface temperature and c_{σ} is the Stefan-Boltzmann constant. Equation (B22) is a linearisation of the standard equation for

BGD

10, 3735–3846, 2013

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



power emitted by the surface of a black body (Stefan-Boltzmann law). It is taken from Monteith (1981). The factor Φ_{area} is the fraction of available area that is covered by the thallus (see Eq. B9). This factor thus converts $f_{\text{rad}_{\text{LWf}}}$ to Watts per m^2 ground.

The ground heat flux $f_{Q_{\text{soil}}}$ is written as a function of the temperature difference between the thallus of a lichen or bryophyte and the soil:

$$f_{Q_{\text{soil}}} = k_{\text{soil}} \frac{T_{\text{surf}} - s_{T_{\text{soil}}}}{\rho_{\Delta_z}} \Phi_{\text{area}} \chi_G \quad (\text{B23})$$

where k_{soil} is the thermal conductivity of the soil (see Eq. B16), T_{surf} is the surface temperature of the thallus, $s_{T_{\text{soil}}}$ is soil temperature and ρ_{Δ_z} is the damping depth of the soil for a diurnal cycle (Bonan, 2008, p. 134). Φ_{area} is the fraction of available area that is covered by the thallus. χ_G is a switch to set $f_{Q_{\text{soil}}}$ to zero if a lichen or bryophyte is living in the canopy (see Eq. B14).

To compute soil temperature $s_{T_{\text{soil}}}$, the balance for the soil heat reservoir is used:

$$s_{T_{\text{soil}}} = s_{T_{\text{soil}}} + \frac{f_{Q_{\text{soil}}}}{C_{\text{soil}} \Phi_{\text{area}} \rho_{\Delta_z}} \rho_{\Delta_t} \quad (\text{B24})$$

where $f_{Q_{\text{soil}}}$ is the ground heat flux, C_{soil} is soil heat capacity, Φ_{area} is the fraction of available area covered by a lichen or bryophyte, ρ_{Δ_z} is the damping depth of the soil for a diurnal cycle and ρ_{Δ_t} is the time step of the model.

Net radiation f_H is written as:

$$f_H = \phi_{\text{rad}_S} f_{\text{rad}_{\text{SWf}}} \Phi_{\text{area}} + \phi_{\text{rad}_L} f_{\text{rad}_{\text{LWf}}} \Phi_{\text{area}} - \phi_{\text{rad}_L} f_{\text{rad}_{\text{LWf}}} - f_{Q_{\text{soil}}} \quad (\text{B25})$$

where ϕ_{rad_S} is a conversion factor for shortwave radiation (see Eq. B3) and ϕ_{rad_L} is a conversion factor for longwave radiation (see Eq. B4). $f_{\text{rad}_{\text{SWf}}}$ and $f_{\text{rad}_{\text{LWf}}}$ are the downwelling shortwave and longwave radiation flows derived from the climate forcing data. Φ_{area} is a factor to reduce the radiation flows to the fraction per m^2 ground that reaches the thallus of a lichen or bryophyte (see Eq. B9). $f_{\text{rad}_{\text{LWf}}}$ is already multiplied by Φ_{area} in Eq. (B22), the same applies for $f_{Q_{\text{soil}}}$ in Eq. (B23).

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



B4.2 Saturation vapour pressure

The saturation vapour pressure above an open water surface $e_{\text{sat},0}$ is calculated as a function of air temperature according to Allen et al. (1998):

$$e_{\text{sat},0} = p_{e_{s,3}} e^{\frac{p_{e_{s,1}} T_{\text{air},C}}{p_{e_{s,2}} + T_{\text{air},C}}} \quad (\text{B26})$$

5 where $p_{e_{s,1}}$, $p_{e_{s,2}}$ and $p_{e_{s,3}}$ are empirical parameters and $T_{\text{air},C}$ is the air temperature in degree Celsius, calculated as $T_{\text{air},C} = T_{\text{air}} - c_{T_{\text{melt},\text{H}_2\text{O}}}$.

If the water saturation of a lichen or bryophyte is below the threshold saturation $x_{\Phi_{\text{O},\text{sat}}}$ (see Sects. B1.5 and B3.3), the water potential at the surface of the thallus becomes negative. Hence the saturation vapour pressure is reduced by the factor $\phi_{e_{\text{sat}}}$ which is calculated according to Nikolov et al. (1995):

$$\phi_{e_{\text{sat}}} = \frac{1.0\text{E}6 \Psi_{\text{H}_2\text{O}} c_{\text{M}_{\text{H}_2\text{O}}}}{c_{R_{\text{gas}}} T_{\text{air},C} c_{\rho_{\text{H}_2\text{O}}}} \quad (\text{B27})$$

where $\Psi_{\text{H}_2\text{O}}$ is the water potential of the thallus, $c_{\text{M}_{\text{H}_2\text{O}}}$ is the molar mass of water, $c_{R_{\text{gas}}}$ is the universal gas constant, $T_{\text{air},C}$ is the air temperature, $c_{\rho_{\text{H}_2\text{O}}}$ is the density of liquid water and the factor 1.0E6 is used to convert from MPa to Pa.

15 Hence the saturation vapour pressure above the thallus of a lichen or bryophyte, e_{sat} , is written as (Nikolov et al., 1995):

$$e_{\text{sat}} = e^{\phi_{e_{\text{sat}}}} e_{\text{sat},0} \quad (\text{B28})$$

The slope of the saturation vapour pressure curve, $d_{e_{\text{sat}}}$, is calculated by differentiating e_{sat} after $T_{\text{air},C}$:

$$20 \quad d_{e_{\text{sat}}} = e^{\left(\frac{p_{e_{s,1}} T_{\text{air},C}}{p_{e_{s,2}} + T_{\text{air},C}} + \phi_{e_{\text{sat}}}\right)} \left(\frac{p_{e_{s,1}} p_{e_{s,2}} p_{e_{s,3}}}{(p_{e_{s,2}} + T_{\text{air},C})^2} - \frac{\phi_{e_{\text{sat}}}}{T_{\text{air}}} \right) \quad (\text{B29})$$

B4.3 Potential evaporation

The potential evaporation E_{pot} above the thallus of a lichen or bryophyte is written as the sum of two independent potential flows: One driven by net radiation and another one driven by the vapour pressure deficit of the atmosphere (Monteith, 1981):

$$E_{\text{pot}} = \frac{f_H d_{e_{\text{sat}}} + c_{C_{\text{air}}} \frac{e_{\text{sat}} - \Phi_{\text{RH}} e_{\text{sat}}}{r_H} \Phi_{\text{area}}}{(d_{e_{\text{sat}}} + c_Y) c_{\Delta H_{\text{vap}, \text{H}_2\text{O}}} c_{\rho_{\text{H}_2\text{O}}}} \quad (\text{B30})$$

where f_H is net radiation, $d_{e_{\text{sat}}}$ is the slope of the saturation vapour pressure curve, e_{sat} is saturation vapour pressure and Φ_{RH} is relative humidity. $c_{C_{\text{air}}}$ is the heat capacity of air, r_H is the aerodynamic resistance to heat transfer, c_Y is the psychrometric constant, $c_{\Delta H_{\text{vap}, \text{H}_2\text{O}}}$ is the enthalpy of vaporisation and $c_{\rho_{\text{H}_2\text{O}}}$ is the density of liquid water. The factor Φ_{area} reduces the part of E_{pot} related to vapour pressure deficit to the fraction per m^2 ground covered by the thallus of a lichen or bryophyte. The part of E_{pot} driven by net radiation is already corrected for surface coverage in Eq. (B25).

Note that both parts of E_{pot} can be negative. If net radiation is negative, the thallus emits more energy to the ground or the atmosphere than it receives. Consequently, dew forms on the thallus surface. This process can be an important source of moisture for lichens or bryophytes, especially in deserts (Nash III, 1996, p. 6). If relative humidity is larger than one and therefore the vapour pressure deficit is negative, fog forms above the thallus surface. Also this process can contribute to the water supply of a lichen or bryophyte.

BGD

10, 3735–3846, 2013

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

B4.4 Surface temperature

Lichen surface temperature T_{surf} is derived from the same factors as potential evaporation. It is written according to Monteith (1981) as:

$$T_{\text{surf}} = \frac{T_{\text{air}} - \frac{e_{\text{sat}} - \Phi_{\text{RH}} e_{\text{sat}}}{d_{e_{\text{sat}}} + c_{\gamma}} + \frac{(\phi_{\text{radS}} f_{\text{radSWL}} + \phi_{\text{radL}} (f_{\text{radLWL}} + 3.0 c_{\sigma} T_{\text{air}}^4) + \frac{k_{\text{soil}}}{\rho_{\Delta z}} s_{T_{\text{soil}}} \chi_{\text{G}}) c_{\gamma} r_{\text{H}}}{c_{C_{\text{air}}} (d_{e_{\text{sat}}} + c_{\gamma})}}{1.0 + \frac{(\phi_{\text{radL}} 4.0 c_{\sigma} T_{\text{air}}^3 + \frac{k_{\text{soil}}}{\rho_{\Delta z}} \chi_{\text{G}}) c_{\gamma} r_{\text{H}}}{c_{C_{\text{air}}} (d_{e_{\text{sat}}} + c_{\gamma})}}} \quad (\text{B31})$$

5 where T_{air} is air temperature, e_{sat} is saturation vapour pressure, Φ_{RH} is relative humidity, $d_{e_{\text{sat}}}$ is the slope of the saturation vapour pressure curve and c_{γ} is the psychrometric constant. ϕ_{radS} and ϕ_{radL} are conversion factors for shortwave and longwave radiation, f_{radSWL} and f_{radLWL} are the downwelling shortwave and longwave radiation flows and c_{σ} is the Stefan-Boltzmann constant. k_{soil} is the thermal conductivity of the soil, $\rho_{\Delta z}$ is the damping depth of the soil for a diurnal cycle, $s_{T_{\text{soil}}}$ is soil temperature and χ_{G} is a switch to set $f_{Q_{\text{soil}}}$ to zero if a lichen or bryophyte is living in the canopy. $c_{C_{\text{air}}}$ is the heat capacity of air and r_{H} is the aerodynamic resistance to heat transfer.

B4.5 Snow layer

15 The snow cover leads to a reduction of light input for lichens and bryophytes. Furthermore, it changes the dynamics of the water supply and the temperature regime compared to a situation without snow cover. It is assumed in the model that lichens and bryophytes are not able to photosynthesise if the snow cover above them exceeds a certain critical thickness $p_{\Delta_{\text{snow}}}$ (Pannowitz et al., 2003). Since it is impractical to simulate the water content of the organisms under snow, also dark respiration is assumed to be negligible in this situation. This means that no metabolic activity takes place except for turnover of biomass.

To calculate the thickness of the snow cover a mass balance is used. It consists of input by snowfall and output by snowmelt and slow, lateral movement of the snow pack due to gravity. The latter term has only a negligible effect on a seasonal snow cover. The snow balance for Greenland, however, would be always positive without ice moving laterally towards the ocean in form of glaciers.

Snowmelt f_{snowmelt} is calculated as a function of air temperature (Bergström, 1992):

$$f_{\text{snowmelt}} = \min \left(3.22 \frac{\max(0.0, T_{\text{air}} - c_{T_{\text{melt}, \text{H}_2\text{O}}})}{86400 \cdot 1000}, \frac{s_{\text{snow}}}{\rho_{\Delta_t}} + f_{\text{snow, atm}} \right) \quad (\text{B32})$$

where T_{air} is air temperature and $c_{T_{\text{melt}, \text{H}_2\text{O}}}$ is the melting temperature of water, the factor 86400 is the number of seconds per day, the factor 1000 converts from mm to m and the factor 3.22 is a dimensionless empirical parameter. s_{snow} is the snow reservoir on the surface, measured in m^3 liquid water equivalents per m^2 , ρ_{Δ_t} is the time step of the model and $f_{\text{snow, atm}}$ is the input flow of snow from the atmosphere.

The balance of the snow reservoir s_{snow} is written as:

$$s_{\text{snow}} = \max \left(0.0, s_{\text{snow}} + (f_{\text{snow, atm}} - f_{\text{snowmelt}} - s_{\text{snow}} \rho_{\tau_{\text{ice}}}) \rho_{\Delta_t} \right) \quad (\text{B33})$$

where the last term describes lateral movement of the snow pack. The parameter $\rho_{\tau_{\text{ice}}}$ represents the turnover of ice shields and it is set by “best guess” to 1 % per year.

To convert the snow reservoir s_{snow} from water equivalents to thickness of snow cover Δ_{snow} in meters, s_{snow} is multiplied by the fraction of density of water and density of snow (Domine et al., 2011):

$$\Delta_{\text{snow}} = s_{\text{snow}} \frac{c_{\rho_{\text{H}_2\text{O}}}}{\rho_{\rho_{\text{snow}}}} \quad (\text{B34})$$

In case a lichen or bryophyte is covered by a snow layer that exceeds the critical thickness $\rho_{\Delta_{\text{snow}}}$, a different method than Eq. (B31) is used to compute the surface

temperature T_{surf} of the thallus:

$$T_{\text{surf}} = \begin{cases} T_{\text{air}}, & \text{if organism in canopy} \\ \frac{\frac{\rho k_{\text{snow}}}{\Delta_{\text{snow}}} T_{\text{air}} + \frac{k_{\text{soil}}}{\rho \Delta_z} s_{T_{\text{soil}}}}{\frac{\rho k_{\text{snow}}}{\Delta_{\text{snow}}} + \frac{k_{\text{soil}}}{\rho \Delta_z}} & \text{if organism on ground} \end{cases} \quad (\text{B35})$$

where ρk_{snow} is the thermal conductivity of snow (Domine et al., 2011), Δ_{snow} is the thickness of the snow layer, T_{air} is air temperature, k_{soil} is the thermal conductivity of the soil, $\rho \Delta_z$ is the damping depth of the soil for a diurnal cycle and $s_{T_{\text{soil}}}$ is soil temperature. Note that Eq. (B35) does not have any effects on the metabolism of lichens or bryophytes, since they are assumed to be inactive under snow. Equation (B35) is only implemented in the model to compute approximate values for the surface temperature under snow. In a snow-covered canopy, the surface temperature is assumed to be equal to air temperature, for simplicity. On the snow-covered ground, the surface temperature is assumed to be controlled only by heat conduction from atmosphere to surface and from surface to soil. Equation (B35) results from assuming a steady state of the surface.

B5 Carbon exchange flows

The model simulates the following flows of carbon related to lichens and bryophytes:

1. Inflow of CO_2 from the atmosphere into the pore space of the thallus (see Sect. B5.1).
2. Uptake of CO_2 from the pore space (Gross Primary Productivity, GPP) and storage as sugars (see Sect. B5.2).
3. Maintenance and growth respiration (see Sect. B5.4).
4. Growth, which is the transformation of the stored sugars into biomass (see Sect. B5.4).

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



5. Biomass loss (see Sect. B5.6).

The relations of these flows to the balances of the carbon reservoirs of a lichen or bryophyte are described in Sect. B5.7.

B5.1 Inflow of CO₂ into the thallus

- 5 The inflow of CO₂ from the atmosphere into the pore space of the thallus, $f_{\text{CO}_2, \text{in}}$, is proportional to the gradient between the partial pressures of CO₂ in the atmosphere and in the pore space. It is written as:

$$f_{\text{CO}_2, \text{in}} = D_{\text{CO}_2} \frac{\text{CO}_{2, \text{atm}} - \text{CO}_{2, \text{thallus}}}{1.0\text{E}6} \Phi_{\text{area}} \quad (\text{B36})$$

- 10 where D_{CO_2} is the diffusivity of the thallus for CO₂, $\text{CO}_{2, \text{atm}}$ is the atmospheric CO₂ concentration, $\text{CO}_{2, \text{thallus}}$ is the CO₂ concentration in the pore space of the thallus and the factor 1.0E6 is used to convert the gradient from ppm to a fraction between 0 and 1. The variable Φ_{area} converts $f_{\text{CO}_2, \text{in}}$ from a flow per m² lichen or bryophyte into a flow per m² ground. Note that $f_{\text{CO}_2, \text{in}}$ can also be negative, which means that the CO₂ concentration inside the thallus is higher than in the atmosphere and consequently
- 15 CO₂ flows out of the thallus.

B5.2 GPP

- The uptake of CO₂ from the pore space (Gross Primary Productivity, GPP) is computed according to Farquhar and von Caemmerer (1982) as a minimum of a light-limited rate and a CO₂-limited rate. The light-limited rate is an increasing function of the absorption of light by a lichen or bryophyte. The organism, however, cannot absorb light to an arbitrary extent. Hence, the light-limited rate is constrained to a maximum rate J_{max} . The CO₂-limited rate is an increasing function of the CO₂ concentration in the chloroplasts of a lichen or bryophyte. It saturates, however, at very high values of CO₂ concentration. The maximum rate at saturation is $V_{\text{C}, \text{max}}$.
- 20

The maximum carboxylation rate $V_{C,\max}$ of a lichen or bryophyte is calculated as:

$$V_{C,\max} = x_{V_{C,\max}} \Xi_{\text{Rub}} e^{-\left(\frac{T_{\text{surf}} - x_{T_{\text{opt,PS}}}}{\rho_{\Omega}}\right)^2} \quad (\text{B37})$$

where $x_{V_{C,\max}}$ is the molar carboxylation rate of Rubisco (see Sect. B1.6) and Ξ_{Rub} is the specific Rubisco content of a lichen or bryophyte. The exponential describes the influence of surface temperature T_{surf} on $V_{C,\max}$ (Medlyn et al., 2002). $V_{C,\max}$ is assumed to peak around an optimum surface temperature $x_{T_{\text{opt,PS}}}$ (see Sect. B1.9) and the shape of the temperature response curve is determined by the parameter ρ_{Ω} (June et al., 2004).

The Rubisco content Ξ_{Rub} is a function of the reference respiration rate at 10°C, $x_{R_{\text{ref}}}$. This relationship represents a tradeoff and results from a physiological constraint, namely maintenance costs of enzymes (see Sect. 2.2). The exact shape of this relation could not be determined, since we could not find enough studies where both Ξ_{Rub} and $x_{R_{\text{ref}}}$ are measured. Thus, we assume a simple linear function:

$$\Xi_{\text{Rub}} = w_{\text{Rub},R} x_{R_{\text{ref}}} \quad (\text{B38})$$

where the tradeoff-parameter $w_{\text{Rub},R}$, which represents the slope of the line, is determined by two points: the origin (0,0) and the point $(\overline{\Xi_{\text{Rub}}}, \overline{x_{R_{\text{ref}}}})$, where $\overline{x_{R_{\text{ref}}}}$ is the average reference respiration rate and $\overline{\Xi_{\text{Rub}}}$ is the average Rubisco content. $\overline{x_{R_{\text{ref}}}}$ is calculated by Eq. (B2) with $N = 0.5$. The limits of the range of possible values of $x_{R_{\text{ref}}}$ can be found in Table B9. To compute $\overline{\Xi_{\text{Rub}}}$ we also use Eq. (B2) with $N = 0.5$, although the range of possible values of Ξ_{Rub} (see Table B6) does not span several orders of magnitude. This small range of values is probably due to the small sample size (3 data points). The assumption of a linear relationship for Eq. (B38), however, implies that both the range of $x_{R_{\text{ref}}}$ and the range of Ξ_{Rub} have the same shape. Hence, using Eq. (B2) to estimate $\overline{\Xi_{\text{Rub}}}$ is a consistent approach. Note that using the median of the values from

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Table B6 to compute $\overline{\Xi_{\text{Rub}}}$ instead of using Eq. (B2) does not significantly change the value of $w_{\text{Rub},R}$.

The maximum electron transport rate J_{max} of a lichen or bryophyte is calculated as:

$$J_{\text{max}} = \phi_{JV} V_{C,\text{max}} \quad (\text{B39})$$

5 where $V_{C,\text{max}}$ is the maximum carboxylation rate and ϕ_{JV} is the ratio of J_{max} to $V_{C,\text{max}}$. ϕ_{JV} depends on the surface temperature of a lichen or bryophyte and is written as:

$$\phi_{JV} = \max \left(0.0, w_{JV,1} \left(T_{\text{surf}} - c_{T_{\text{melt},\text{H}_2\text{O}}} \right) + w_{JV,2} \right) \quad (\text{B40})$$

10 where T_{surf} is surface temperature and $c_{T_{\text{melt},\text{H}_2\text{O}}}$ is the melting temperature of water. The two parameters $w_{JV,1}$ and $w_{JV,2}$ are derived by the data shown in Fig. B13. ϕ_{JV} is limited to non-negative values since a negative J_{max} would make no sense from a physiological viewpoint.

15 The fact that $V_{C,\text{max}}$ and J_{max} are positively correlated implies a tradeoff between these two variables. This tradeoff results from physiological constraints (see Sect. 2.2) in form of metabolic costs of $V_{C,\text{max}}$ and J_{max} . Since both the maximum of the light-dependent rate and the maximum of the CO_2 -dependent rate are associated with costs for the organism, but GPP is computed as a minimum of the two rates it would be inefficient if $V_{C,\text{max}}$ and J_{max} were independent from each other.

The actual rate of electron transport J is calculated as the minimum of the maximum rate of the photosystems J_{max} and the supply by shortwave radiation:

$$20 \quad J = \min \left(f_{\text{rad}_{\text{swl}}} \phi_{\text{rad}_s} \rho_{\text{PAR}} \rho_{\text{quant}} w_{\text{CCM},e} \Phi_{\text{area}}, J_{\text{max}} s_B \right) \quad (\text{B41})$$

where $f_{\text{rad}_{\text{swl}}}$ is the flow of shortwave radiation, ϕ_{rad_s} is a conversion factor that includes albedo and LAI (see Sect. B2.1), ρ_{PAR} is a factor that converts shortwave radiation into photosynthetically active radiation and ρ_{quant} converts quanta of light into electrons. $w_{\text{CCM},e}$ is a factor that represents the investment of electrons in a Carbon Concentration

Mechanism if present (see Sect. B5.3 below). Φ_{area} reduces the electron flow to the area covered by a lichen or bryophyte and s_B is the biomass of the organism.

Besides $V_{C,\text{max}}$ and J_{max} , the Michaelis-Menten constants of the carboxylation and oxygenation reactions of Rubisco, K_C and K_O , affect the shape of the light-dependent rate and the CO_2 -dependent rate of GPP. They are calculated as:

$$K_C = 0.001 w_{K_{C,1}} x_{V_{C,\text{max}}}^{w_{K_{C,2}}} e^{\frac{(T_{\text{surf}} - p_{T_{\text{ref,PS}}}) x_{E_a, K_C}}{p_{T_{\text{ref,PS}}} c_{R_{\text{gas}}} T_{\text{surf}}}} \quad (\text{B42})$$

and

$$K_O = 0.001 \frac{x_{V_{O,\text{max}}}}{w_{K_{O,1}} \left(\frac{x_{V_{C,\text{max}}}}{w_{K_{C,1}} x_{V_{C,\text{max}}}} \right)^{w_{K_{O,2}}}} e^{\frac{(T_{\text{surf}} - p_{T_{\text{ref,PS}}}) x_{E_a, K_O}}{p_{T_{\text{ref,PS}}} c_{R_{\text{gas}}} T_{\text{surf}}}} \quad (\text{B43})$$

where $x_{V_{C,\text{max}}}$ is the molar carboxylation rate of Rubisco (see Sect. B1.6) and $x_{V_{O,\text{max}}}$ is the molar oxygenation rate of Rubisco (see Sect. B1.7). The factor 0.001 is used to convert K_C and K_O into mol per m^3 . The exponentials in Eqs. (B42) and (B43) describe the influence of surface temperature T_{surf} on K_C and K_O . $p_{T_{\text{ref,PS}}}$ is the reference temperature of photosynthesis and $c_{R_{\text{gas}}}$ is the universal gas constant. x_{E_a, K_C} and x_{E_a, K_O} are the enzyme activation energies of the carboxylation and oxygenation reactions, respectively (see Sect. B1.10).

The parameters $w_{K_{C,1}}$, $w_{K_{C,2}}$, $w_{K_{O,1}}$ and $w_{K_{O,2}}$ relate K_C and K_O to $x_{V_{C,\text{max}}}$ and $x_{V_{O,\text{max}}}$. According to Savir et al. (2010), these relations result from a tradeoff between the carboxylation velocity and the CO_2 affinity of the Rubisco enzyme.

The variable Γ_* represents the CO_2 compensation point of photosynthesis in the absence of respiration as described in Farquhar and von Caemmerer (1982). It is written

BGD

10, 3735–3846, 2013

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

as:

$$\Gamma_* = 0.5 O_{2,\text{cell}} \frac{x_{V_{O_2,\text{max}}} K_C}{x_{V_{C,\text{max}}} K_O} \quad (\text{B44})$$

where $O_{2,\text{cell}}$ is the concentration of O_2 in the chloroplast of a lichen or bryophyte, $x_{V_{C,\text{max}}}$ and $x_{V_{O_2,\text{max}}}$ are the maximum velocities and K_C and K_O are the Michaelis-Menten constants of the carboxylation and oxygenation reactions, respectively.

The O_2 concentration in the chloroplast $O_{2,\text{cell}}$ is calculated as a function of the O_2 concentration in the pore space of the thallus, which is assumed to be equal to the atmospheric one:

$$O_{2,\text{cell}} = \frac{1000.0}{p_{S_{O_2}}} O_{2,\text{atm}} \quad (\text{B45})$$

where $O_{2,\text{atm}}$ is the atmospheric O_2 concentration and $p_{S_{O_2}}$ is the solubility of O_2 (von Caemmerer, 2000, p. 9). The factor 1000 is used to write $O_{2,\text{cell}}$ in mol per m^3 .

Accordingly, the CO_2 concentration in the chloroplast $\text{CO}_{2,\text{cell}}$ is calculated as a function of the CO_2 concentration in the pore space of the thallus, which depends on the exchange flows of carbon between the organism and the atmosphere:

$$\text{CO}_{2,\text{cell}} = \frac{1000.0}{p_{S_{\text{CO}_2}}} \text{CO}_{2,\text{thallus}} \quad (\text{B46})$$

where $\text{CO}_{2,\text{thallus}}$ is the pore space CO_2 concentration and $p_{S_{\text{CO}_2}}$ is the solubility of CO_2 (von Caemmerer, 2000, p. 9). The factor 1000 is used to write $\text{CO}_{2,\text{cell}}$ in mol per m^3 .

Knowing $\text{CO}_{2,\text{cell}}$, $O_{2,\text{cell}}$, J , K_C , K_O , $x_{V_{C,\text{max}}}$ and $x_{V_{O_2,\text{max}}}$, the light-limited rate and the CO_2 -limited rate of photosynthesis can be calculated. They are written according to Farquhar and von Caemmerer (1982) as:

$$f_{\text{GPP,L}} = J \frac{\text{CO}_{2,\text{cell}} - \Gamma_*}{4.0 \text{CO}_{2,\text{cell}} + 8.0 \Gamma_*} \Phi_{\text{act}} \quad (\text{B47})$$

and

$$f_{\text{GPP},W} = x_{V_C,\text{max}} s_B \frac{\text{CO}_{2,\text{cell}} - \Gamma_*}{\text{CO}_{2,\text{cell}} + K_C \frac{1.0 + \text{O}_{2,\text{cell}}}{K_O}} \Phi_{\text{act}} \quad (\text{B48})$$

where $\text{CO}_{2,\text{cell}}$ is the concentration of CO_2 in the chloroplast, Γ_* is the CO_2 compensation point, K_C and K_O are the Michaelis-Menten constants of the carboxylation and oxygenation reactions, respectively, and $\text{O}_{2,\text{cell}}$ is the O_2 concentration in the chloroplast. Φ_{act} is the metabolic activity of a lichen or bryophyte (see Sect. B3.4). It accounts for the effect of poikilohydry on photosynthesis and it represents an extension to the original equations of Farquhar and von Caemmerer (1982). $x_{V_C,\text{max}}$ is the maximum specific carboxylation rate and s_B is the biomass of a lichen or bryophyte.

The GPP of a lichen or bryophyte is then calculated as the minimum of $f_{\text{GPP},L}$ and $f_{\text{GPP},W}$:

$$f_{\text{GPP}} = \min(f_{\text{GPP},L}, f_{\text{GPP},W}) \quad (\text{B49})$$

B5.3 Carbon Concentration Mechanism

Some lichens and bryophytes possess a Carbon Concentration Mechanism (CCM, see Sects. 2.2 and B1.11). If a CCM is active, a fraction of the electrons generated by the photosystems is invested in increasing the CO_2 concentration in the chloroplasts instead of being used in the Calvin cycle.

This increased CO_2 concentration in the chloroplasts can be calculated as a function of pore space CO_2 concentration:

$$\text{CO}_{2,\text{cell}} = \min(w_{\text{CCM},1} \text{CO}_{2,\text{thallus}}, w_{\text{CCM},2} \text{CO}_{2,\text{thallus}} + w_{\text{CCM},3}) \quad (\text{B50})$$

where $\text{CO}_{2,\text{cell}}$ and $\text{CO}_{2,\text{thallus}}$ are the CO_2 concentrations in the chloroplast and the pore space, respectively. $w_{\text{CCM},1}$, $w_{\text{CCM},2}$ and $w_{\text{CCM},3}$ are parameters derived from the data of Reinhold et al. (1989) which is shown in Fig. B14.

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

The CCM represents a tradeoff for a lichen or bryophyte: The increased CO_2 concentration in the chloroplasts which depends on $w_{\text{CCM},1}$, $w_{\text{CCM},2}$ and $w_{\text{CCM},3}$ directly leads to higher productivity, but the maintenance of the high concentration requires energy which is taken from the electron transport chain in the thylakoid membranes. These costs are represented by the parameter $w_{\text{CCM},e}$ (see Eq. B41). The relation between pore space CO_2 and CO_2 in the chloroplasts as well as the costs of establishing this relation constitute the physiological constraints of the CCM.

B5.4 Respiration & growth

Respiration consists of two parts: Maintenance respiration and growth respiration. The specific maintenance respiration rate R_{spec} is modelled by a Q_{10} relationship (Kruse et al., 2011). It is illustrated in Fig. B8 in Sect. B1.8 and it is written as:

$$R_{\text{spec}} = X_{R_{\text{ref}}} X_{Q_{10}} \frac{T_{\text{surf}} - p_{T_{\text{ref},R}}}{p_{T_{\text{ref},R}} - c_{T_{\text{melt},\text{H}_2\text{O}}}} \quad (\text{B51})$$

where $X_{R_{\text{ref}}}$ is the reference respiration rate at 10°C , $X_{Q_{10}}$ is the Q_{10} value of respiration, T_{surf} is the surface temperature of the organism, $p_{T_{\text{ref},R}}$ is the reference temperature and $c_{T_{\text{melt},\text{H}_2\text{O}}}$ is the melting temperature of water.

The maintenance respiration of a lichen or bryophyte, $f_{R_{\text{main}}}$, is then calculated as a function of R_{spec} and the biomass of the organism:

$$f_{R_{\text{main}}} = \min \left(\frac{s_C}{c_{M_C} \rho_{\Delta_t}}, R_{\text{spec}} s_B \Phi_{\text{act}} \right) \quad (\text{B52})$$

where s_C is the sugar reserve of a lichen or bryophyte, c_{M_C} is the molar mass of carbon, ρ_{Δ_t} is the time step of the model, R_{spec} is the specific maintenance respiration rate, s_B is the biomass of the organism and Φ_{act} is its metabolic activity.

The minimum in Eq. (B52) is used because a lichen or bryophyte cannot respire more carbon per time step than is stored in the sugar reservoir. The respired CO_2 is released into the pore space.

The growth of a lichen or bryophyte is computed as the minimum of the available amount of sugar per time step and a potential flow, which is a function of the sugar reservoir:

$$f_{\text{growth}} = \min \left(\frac{s_C}{c_{M_C} \rho_{\Delta_t}} - f_{R_{\text{main}}}, x_{\text{alloc}} \frac{s_C}{c_{M_C} 86400} \Phi_{\text{act}} \right) \rho_{\eta_{\text{growth}}} \quad (\text{B53})$$

5 where s_C is the sugar reserve of a lichen or bryophyte, c_{M_C} is the molar mass of carbon, ρ_{Δ_t} is the time step of the model and $f_{R_{\text{main}}}$ is maintenance respiration. x_{alloc} is the fraction of the sugar reservoir allocated to growth per day, 86 400 is the number of seconds per day, Φ_{act} is metabolic activity, and $\rho_{\eta_{\text{growth}}}$ is the efficiency of the transformation of sugars to biomass.

10 The respiration associated with growth, $f_{R_{\text{growth}}}$ is then written as a function of growth efficiency $\rho_{\eta_{\text{growth}}}$ and growth f_{growth} :

$$f_{R_{\text{growth}}} = \left(\frac{1.0}{\rho_{\eta_{\text{growth}}}} - 1.0 \right) f_{\text{growth}} \quad (\text{B54})$$

B5.5 Steady State of internal CO₂

Two carbon exchange flows depend on the internal CO₂ concentration of the thallus
 15 CO_{2,thallus}, namely the inflow of CO₂ from the atmosphere into the pore space, $f_{\text{CO}_2,\text{in}}$ (Eq. B36), and the uptake of CO₂ from the pore space by GPP, f_{GPP} (Eq. B49). The model, however, does not simulate explicitly the pore space of the thallus. Hence, it is not possible to determine the absolute amount of CO₂ in the thallus. Instead, a steady-state approach is used to calculate CO_{2,thallus}. It is assumed that the exchange flow
 20 of CO₂ between pore space and atmosphere, $f_{\text{CO}_2,\text{in}}$, balances the net CO₂ exchange flow between pore space and the cells of the organism. This net exchange flow is equal to the sum of uptake from the pore space f_{GPP} and release of CO₂ into the pore space,

consisting of maintenance respiration $f_{R_{\text{main}}}$ and growth respiration $f_{R_{\text{growth}}}$ (Eqs. B52 and B54). The equation for the steady state of pore space CO_2 is thus written as:

$$f_{\text{CO}_2, \text{in}} = f_{R_{\text{main}}} + f_{R_{\text{growth}}} - f_{\text{GPP}} \quad (\text{B55})$$

Equation (B55) is then solved for $\text{CO}_{2, \text{thallus}}$ to determine the values for $f_{\text{CO}_2, \text{in}}$ and f_{GPP} .

B5.6 Biomass loss

The turnover rate of the biomass of lichens or bryophytes, τ_B , is calculated similarly to the Rubisco content (see Sect. B5.2) as a function of the reference respiration rate at 10°C , $x_{R_{\text{ref}}}$. The relation between τ_B and $x_{R_{\text{ref}}}$ represents a tradeoff and results from a physiological constraint, namely metabolic stability of enzymes (see Sect. 2.2). The exact shape of this relation could not be determined, since we could not find enough studies where both τ_B and $x_{R_{\text{ref}}}$ are measured. Thus, we assume a simple linear function:

$$\tau_B = w_{\text{loss}, R} x_{R_{\text{ref}}} \quad (\text{B56})$$

where the tradeoff-parameter $w_{\text{loss}, R}$, which represents the slope of the line, is determined by two points: the origin (0,0) and the point $(\overline{\tau_B}, \overline{x_{R_{\text{ref}}}})$, where $\overline{x_{R_{\text{ref}}}}$ is the average reference respiration rate and $\overline{\tau_B}$ is the average turnover rate. $\overline{x_{R_{\text{ref}}}}$ is calculated by Eq. (B2) with $N = 0.5$. The limits of the range of possible values of $x_{R_{\text{ref}}}$ can be found in Table B9. To compute $\overline{\tau_B}$ we also use Eq. (B2) with $N = 0.5$ (see Fig. B15). The range of possible values of τ_B is set to 0.03–1.5 (see Sect. B1).

The flow of biomass loss f_{loss} , is then calculated as a function of τ_B and the biomass of the organism:

$$f_{\text{loss}} = \tau_B \frac{s_B}{c_{\text{MC}} 3.1536 \text{E}7} \quad (\text{B57})$$

where τ_B is the turnover rate, s_B is the biomass of a lichen or bryophyte and c_{M_C} is the molar mass of carbon. The factor of 3.1536E7 is used to convert τ_B from yr^{-1} to s^{-1} . Note that f_{loss} also includes leaching of carbohydrates and small-scale regular herbivory.

5 B5.7 Carbon balance

Two carbon reservoirs of lichens and bryophytes are simulated in the model: Biomass and sugar reserves. The balance of the sugar reservoir s_C is written as:

$$s_C = \max\left(0.0, s_C + \left(f_{\text{GPP}} - f_{R_{\text{main}}} - f_{R_{\text{growth}}} - f_{\text{growth}}\right) c_{M_C} \rho_{\Delta_t}\right) \quad (\text{B58})$$

where f_{GPP} is GPP, $f_{R_{\text{main}}}$ is maintenance respiration, $f_{R_{\text{growth}}}$ is growth respiration, f_{growth} is growth c_{M_C} is the molar mass of carbon and ρ_{Δ_t} is the time step of the model.

The balance of the biomass reservoir s_B is written as:

$$s_B = \max\left(0.0, s_B + \left(f_{\text{growth}} - f_{\text{loss}}\right) c_{M_C} \rho_{\Delta_t}\right) \quad (\text{B59})$$

where f_{growth} is growth, f_{loss} is biomass loss, c_{M_C} is the molar mass of carbon and ρ_{Δ_t} is the time step of the model.

15 B6 Water exchange flows

The water exchange between a lichen or bryophyte and its environment is represented by three flows: water uptake via rainfall or snowmelt, evaporation from the surface of the thallus and runoff.

Water uptake $f_{\text{water,up}}$ is calculated as:

$$f_{\text{water,up}} = \left(f_{\text{rain,atm}} + f_{\text{snowmelt}}\right) \phi_{\text{prec}} \Phi_{\text{area}} \quad (\text{B60})$$

where $f_{\text{rain,atm}}$ is rainfall, f_{snowmelt} is snowmelt, ϕ_{prec} is the fraction of precipitation that reaches the thallus surface and Φ_{area} reduces water uptake to the area covered by a lichen or bryophyte.

5 Evaporation f_{evap} is calculated as a minimum of demand by potential evaporation and supply by the water reservoir of a lichen or bryophyte:

$$f_{\text{evap}} = \min \left(\frac{s_{\Theta}}{\rho_{\Delta_t}}, E_{\text{pot}} \right) \quad (\text{B61})$$

where s_{Θ} is the water content of a lichen or bryophyte, ρ_{Δ_t} is the time step of the model and E_{pot} is potential evaporation (see Eq. B30).

10 Runoff f_{runoff} is generated when net water uptake exceeds the water storage capacity of the thallus:

$$f_{\text{runoff}} = \frac{\max \left(0.0, s_{\Theta} + \max \left(0.0, f_{\text{water,up}} - f_{\text{evap}} \right) \rho_{\Delta_t} - \Theta_{\text{max}} \right)}{\rho_{\Delta_t}} \quad (\text{B62})$$

where s_{Θ} is the water content of a lichen or bryophyte, $f_{\text{water,up}}$ is water uptake, f_{evap} is evaporation, ρ_{Δ_t} is the time step of the model and Θ_{max} is the water storage capacity of the thallus (see Eq. B17).

15 The water balance is then written as:

$$s_{\Theta} = \max \left(0.0, s_{\Theta} + (f_{\text{water,up}} - f_{\text{evap}} - f_{\text{runoff}}) \rho_{\Delta_t} \right) \quad (\text{B63})$$

where s_{Θ} is the water content of a lichen or bryophyte, $f_{\text{water,up}}$ is water uptake, f_{evap} is evaporation, f_{runoff} is runoff and ρ_{Δ_t} is the time step of the model.

B7 Exchange flows of energy

20 Additionally to exchange flows of carbon and water, the model computes the exchange of energy between lichens and bryophytes and the atmosphere. The flow of latent heat,

$f_{Q_{atm,L}}$, is calculated from evaporation as:

$$f_{Q_{atm,L}} = f_{evap} c_{\Delta H_{vap,H_2O}} c_{\rho_{H_2O}} \quad (B64)$$

where f_{evap} is evaporation, $c_{\Delta H_{vap,H_2O}}$ is the enthalpy of vaporisation and $c_{\rho_{H_2O}}$ is the density of liquid water. The flow of sensible heat, $f_{Q_{atm,S}}$, is written as:

$$f_{Q_{atm,S}} = \frac{(T_{surf} - T_{air}) c_{C_{air}}}{r_H} \Phi_{area} + (E_{pot} - f_{evap}) c_{\Delta H_{vap,H_2O}} c_{\rho_{H_2O}} \quad (B65)$$

where T_{surf} is surface temperature, T_{air} is air temperature, $c_{C_{air}}$ is the heat capacity of air, r_H is the aerodynamic resistance to heat transfer and Φ_{area} is the fraction of available area covered by a lichen or bryophyte. E_{pot} is potential evaporation, f_{evap} is actual evaporation, $c_{\Delta H_{vap,H_2O}}$ is the enthalpy of vaporisation and $c_{\rho_{H_2O}}$ is the density of liquid water. Note that $f_{Q_{atm,S}}$ consists of two parts. The first part depends on the gradient between surface temperature of the organism and air temperature. The second part is the difference between the potential flow of latent heat and the actual one (see Eq. B64). This means, that the ratio of latent heat to sensible heat decreases if the supply of water is not sufficient to support potential evaporation.

The energy balance of the thallus surface, which can be either on the ground or in the canopy, is then calculated as:

$$f_H = f_{Q_{atm,L}} + f_{Q_{atm,S}} \quad (B66)$$

where f_H is net radiation (see Eq. B25), $f_{Q_{atm,L}}$ is the flow of latent heat and $f_{Q_{atm,S}}$ is the flow of sensible heat.

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Acknowledgements. The authors are thankful to Ryan Pavlick, Fabian Gans, Nathaniel Virgo, Stan Schymanski and Jens Kattge for useful discussions about the topic. We thank Steffen Richter and Ulrich Weber for technical support and we give thanks to the Helmholtz Alliance “Planetary Evolution and Life” for funding.

The service charges for this open access publication have been covered by the Max Planck Society.

References

- Allen, R. G., Pereira, L. S., Raes, D., and Smith, M.: Crop evapotranspiration – guidelines for computing crop water requirements, FAO – Food and Agriculture Organization of the United Nations, Rome, Italy, 56, 1998. 3741, 3742, 3770, 3771, 3777
- Angelstam, P. K.: Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes, *J. Veg. Sci.*, 9, 593–602, doi:10.2307/3237275, 1998. 3810
- Anisimov, O. A., Shiklomanov, N. I., and Nelson, F. E.: Global warming and active-layer thickness: results from transient general circulation models, *Global Planet. Change*, 15, 61–77, doi:10.1016/S0921-8181(97)00009-X, 1997. 3771
- Balaguer, L., Manrique, E., de los Rios, A., Ascaso, C., Palmqvist, K., Fordham, M., and Barnes, J. D.: Long-term responses of the green-algal lichen *Parmelia caperata* to natural CO₂ enrichment, *Oecologia*, 119, 166–174, doi:10.1007/s004420050773, 1999. 3812
- Belnap, J. and Lange, O. L. (Eds.): *Biological Soil Crusts: Structure, Function, and Management*, 2nd Edn., Springer, Berlin, 2003. 3737
- Bergström, S.: *The HBV model: Its structure and applications*, Swedish Meteorological and Hydrological Institute, 1992. 3780
- Berthelin, J.: Microbial weathering processes in natural environments, *Physical and Chemical Weathering in Geochemical Cycles*, 33–59, doi:10.1007/978-94-009-3071-1_3, 1988. 3737
- Billings, W. D.: Carbon balance of Alaskan tundra and taiga ecosystems: Past, present and future, *Quaternary Sci. Rev.*, 6, 165–177, doi:10.1016/0277-3791(87)90032-1, 1987. 3805

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



- 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, doi:10.1007/s004420100719, 2001. 3805
- Bloom, A. J., Chapin III, F. S., and Mooney, H. A.: Resource limitation in plants-an economic analogy, *Annu. Rev. Ecol. Syst.*, 16, 363–392, doi:10.1146/annurev.es.16.110185.002051, 1985. 3744
- Bonan, G. (Ed.): *Ecological Climatology*, 2nd Edn., Cambridge University Press, New York, 2008. 3766, 3776
- Bonan, G. B., Oleson, K. W., Vertenstein, M., Levis, S., Zeng, X., Dai, Y., Dickinson, R. E., and Yang, Z.-L.: The land surface climatology of the Community Land Model coupled to the NCAR Community Climate Model, *J. Climate*, 15, 3123–3149, doi:10.1175/1520-0442(2002)015<3123:TLSCOT>2.0.CO;2, 2002. 3747, 3766, 3767
- Bond-Lamberty, B. and Gower, S. T.: Estimation of stand-level leaf area for boreal bryophytes, *Oecologia*, 151, 584–592, doi:10.1007/s00442-006-0619-5, 2007. 3832, 3833
- Bongers, E., Popma, J., Meave del Castillo, J., and Carabias, J.: Structure and floristic composition of the lowland rain forest of Los Tuxtlas, Mexico, *Vegetatio*, 74, 55–80, doi:10.1007/BF00045614, 1988. 3810
- Boucher, V. L. and Nash III, T. H.: Growth patterns in *Ramalina menziesii* in California: Coastal vs. inland populations, *The Bryologist*, 93, 295–302, doi:10.2307/3243516, 1990a. 3846
- Boucher, V. L. and Nash III, T. H.: The role of the fruticose lichen *Ramalina menziesii* in the annual turnover of biomass and macronutrients in a blue oak woodland, *Bot. Gaz.*, 151, 114–118, doi:10.1086/337810, 1990b. 3846
- 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, doi:10.1016/j.flora.2005.06.008, 2005. 3805
- Büdel, B., Weber, B., Kühl, M., Pfanz, H., Sültemeyer, D., and Wessel, D.: Reshaping of sandstone surfaces by cryptoendolithic cyanobacteria: Bioalkalization causes chemical weathering in arid landscapes, *Geobiology*, 2, 261–268, doi:10.1111/j.1472-4677.2004.00040.x, 2004. 3737
- Chandrashekhara, U. M. and Ramakrishnan, P. S.: Vegetation and gap dynamics of a tropical wet evergreen forest in the Western Ghats of Kerala, India, *J. Trop. Ecol.*, 10, 337–354, doi:10.1017/S0266467400008014, 1994. 3810

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

- Chen, J., Blume, H.-P., and Beyer, L.: Weathering of rocks induced by lichen colonization – a review, *Catena*, 39, 121–146, doi:10.1016/S0341-8162(99)00085-5, 2000. 3737
- 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, 12–23, doi:10.1111/j.1744-7429.1998.tb00365.x, 1998. 3805, 3846
- 5 Condit, R., Hubbell, S. P., and Foster, R. B.: Assessing the response of plant functional types to climatic change in tropical forests, *J. Veg. Sci.*, 7, 405–416, doi:10.2307/3236284, 1996. 3811
- Cowan, I. R., Lange, O. L., and Green, T. G. A.: Carbon-dioxide exchange in lichens: Determination of transport and carboxylation characteristics, *Planta*, 187, 282–294, doi:10.1007/BF00201952, 1992. 3741, 3773, 3833, 3841
- 10 Dahlman, L. and Palmqvist, K.: Growth in two foliose tripartite lichens, *Nephroma arcticum* and *Peltigera aphthosa*: Empirical modelling of external vs. internal factors, *Funct. Ecol.*, 17, 821–831, doi:10.1046/j.0269-8463.2003.00804.x, 2003. 3832, 3833
- Demmig-Adams, B., Maguas, C., Adams III, W. W., Meyer, A., Kilian, E., and Lange, O. L.: Effect of high light on the efficiency of photochemical energy conversion in a variety of lichen species with green and blue-green phycobionts, *Planta*, 180, 400–409, doi:10.1007/BF01160396, 1990. 3833
- 15 Dilks, T. J. K. and Proctor, M. C. F.: Photosynthesis, respiration and water content in bryophytes, *New Phytol.*, 82, 97–114, doi:10.1111/j.1469-8137.1979.tb07564.x, 1979. 3834
- 20 Domine, F., Bock, J., Morin, S., and Giraud, G.: Linking the effective thermal conductivity of snow to its shear strength and density, *J. Geophys. Res.*, 116, F04027, doi:10.1029/2011JF002000, 2011. 3746, 3780, 3781
- 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, *Nat. Geosci.*, 5, 459–462, doi:10.1038/ngeo1486, 2012. 3737, 3757, 3758
- 25 Escudero, A. and Mediavilla, S.: Decline in photosynthetic nitrogen use efficiency with leaf age and nitrogen resorption as determinants of leaf life span, *J. Ecol.*, 91, 880–889, doi:10.1046/j.1365-2745.2003.00818.x, 2003. 3811
- 30 Farquhar, G. D. and von Caemmerer, S.: Modelling of photosynthetic response to environmental conditions, in: *Encyclopedia of Plant Physiology*, edited by: Lange, O. L., Nobel, P. S., Osmond, C. B., and Ziegler, H., 12B, Springer, Heidelberg, 1982. 3743, 3782, 3785, 3786, 3787

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

- Ferreira de Lima, R. A., Martini, A. M. Z., Gandolfi, S., and Rodrigues, R. R.: Repeated disturbances and canopy disturbance regime in a tropical semi-deciduous forest, *J. Trop. Ecol.*, 24, 85–93, doi:10.1017/S0266467407004658, 2008. 3810
- Follows, M. J. and Dutkiewicz, S.: Modeling diverse communities of marine microbes, *Annu. Rev. Mar. Sci.*, 3, 427–451, doi:10.1146/annurev-marine-120709-142848, 2011. 3744
- Foster, J. R. and Reiners, W. A.: Size distribution and expansion of canopy gaps in a northern Appalachian spruce-fir forest, *Vegetatio*, 68, 109–114, 1986. 3810
- Gaio-Oliveira, G., Moen, J., Danell, Ö., and Palmqvist, K.: Effect of simulated reindeer grazing on the re-growth capacity of mat-forming lichens, *Basic Appl. Ecol.*, 7, 109–121, 2 doi:10.1016/j.baae.2005.05.007, 2006. 3833
- Gauslaa, Y. and Solhaug, K. A.: The significance of thallus size for the water economy of the cyanobacterial old-forest lichen *Degelia plumbea*, *Oecologia*, 116, 76–84, doi:10.1007/s004420050565, 1998. 3832, 3833
- Gauslaa, Y. and Ustvedt, E. M.: Is parietin a UV-B or a blue-light screening pigment in the lichen *Xanthoria parietina*?, *Photochem. Photobiol. Sci.*, 2, 424–432, 2003. doi:10.1039/b212532c. 3833
- 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, *J. Geophys. Res.*, 102, 29029–29041, doi:10.1029/97JD02317, 1997. 3805
- Gradstein, S. R.: The lowland cloud forest of French Guiana: a liverwort hotspot, *Cryptogam. Bryol.*, 27, 141–152, 2006. 3753
- Green, T. G. A. and Snelgar, W. P.: A comparison of photosynthesis in two thalloid liverworts, *Oecologia*, 54, 275–280, doi:10.1007/BF00378404, 1982. 3833
- Green, T. G. A., Schroeter, B., Kappen, L., Seppelt, R. D., and Maseyk, K.: An assessment of the relationship between chlorophyll a fluorescence and CO₂ gas exchange from field measurements on a moss and lichen, *Planta*, 206, 611–618, doi:10.1007/s004250050439, 1998. 3833, 3837, 3838, 3839, 3840
- Hall, C., Stanford, J., and Hauer, F.: The distribution and abundance of organisms as a consequence of energy balances along multiple environmental gradients, *Oikos*, 65, 377–390, doi:10.2307/3545553, 1992. 3744

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



- Harrisson, P. M., Walton, D. W. H., and Rothery, P.: The effects of temperature and moisture on dark respiration in the foliose lichen *Umbilicaria antarctica*, *New Phytol.*, 103, 443–455, doi:10.1111/j.1469-8137.1986.tb02882.x, 1986. 3839
- Harvey, B. D., Leduc, A., Gauthier, S., and Bergeron, Y.: Stand-landscape integration in natural disturbance-based management of the southern boreal forest, *Forest Ecol. Manag.*, 155, 369–385, doi:10.1016/S0378-1127(01)00573-4, 2002. 3810
- 5 Hill, D. J. and Woolhouse, H. W.: Aspects of the autecology of *Xanthoria parietina* agg., *The Lichenologist*, 3, 207–214, doi:10.1017/S0024282966000227, 1966. 3833
- Hilmo, O.: Growth and morphological response of old-forest lichens transplanted into a young and an old *Picea abies* forest, *Ecography*, 25, 329–335, doi:10.1034/j.1600-0587.2002.250309.x, 2002. 3833
- 10 Huttunen, S., Lappalainen, N. M., and Turunen, J.: UV-absorbing compounds in subarctic herbarium bryophytes, *Environ. Pollut.*, 133, 303–314, doi:10.1016/j.envpol.2004.05.041, 2005. 3833
- Ito, A.: A historical meta-analysis of global terrestrial net primary productivity: are estimates converging?, *Global Change Biol.*, 17, 3161–3175, doi:10.1111/j.1365-2486.2011.02450.x, 2011. 3757
- 15 Jackson, T. A. and Keller, W. D.: A comparative study of the role of lichens and “inorganic” processes in the chemical weathering of recent Hawaiian lava flows, *Am. J. Sci.*, 269, 446–466, doi:10.2475/ajs.269.5.446, 1970. 3737
- Jans, L., Poorter, L., van Rompaey, R. S. A. R., and Bongers, F.: Gaps and forest zones in tropical moist forest in Ivory Coast. *Biotropica*, 25, 258–269, 1 doi:10.2307/2388784, 1993. 3810
- 20 Jeffries, D. L., Link, S. O., and Klopatek, J. M.: CO₂ fluxes of cryptogamic crusts I. Response to resaturation, *New Phytol.*, 125, 163–173, doi:10.1111/j.1469-8137.1993.tb03874.x, 1993. 3805
- 25 June, T., Evans, J. R., and Farquhar, G. D.: A simple new equation for the reversible temperature dependence of photosynthetic electron transport: A study on soybean leaf, *Funct. Plant Biology*, 31, 275–283, doi:10.1071/FP03250, 2004. 3743, 3783
- Kappen, L., Lewis Smith, R. I., and Meyer, M.: Carbon dioxide exchange of two ecodemes of *Schistidium antarctici* in continental Antarctica, *Polar Biol.*, 9, 415–422, doi:10.1007/BF00443227, 1989. 3837, 3838, 3839, 3840
- 30

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

- Kattge, J. and Knorr, W.: Temperature acclimation in a biochemical model of photosynthesis: a reanalysis of data from 36 species, *Plant Cell Environ.*, 30, 1176–1190, 2007. doi:10.1111/j.1365-3040.2007.01690.x. 3844
- Kershaw, K. A.: Studies on lichen-dominated systems, XII, The ecological significance of thallus color, *Can. J. Botany*, 53, 660–667, doi:10.1139/b75-081, 1975. 3761
- Kleidon, A. and Mooney, H.: A global distribution of biodiversity inferred from climatic constraints: results from a process-based modelling study, *Global Change Biol.*, 6, 507–523, doi:10.1046/j.1365-2486.2000.00332.x, 2000. 3744
- Köhler, L., Tobon, C., Frumau, K. F. A., and Bruijnzeel, L. A. S.: Biomass and water storage dynamics of epiphytes in old-growth and secondary montane cloud forest stands in Costa Rica, *Plant Ecol.*, 193, 171–184, doi:10.1007/s11258-006-9256-7, 2007. 3832
- Kruse, J., Rennenberg, H., and Adams, M. A.: Steps towards a mechanistic understanding of respiratory temperature responses, *New Phytol.*, 189, 659–677, doi:10.1111/j.1469-8137.2010.03576.x, 2011. 3743, 3788
- Kustas, W. P. and Norman, J. M.: A two-source energy balance approach using directional radiometric temperature observations for sparse canopy covered surfaces. *Agron. J.*, 92, 847–854, doi:10.2134/agronj2000.925847x, 2000. 3766
- Lange, O. L.: Photosynthetic productivity of the epilithic lichen *Lecanora muralis*: Long-term field monitoring of CO₂ exchange and its physiological interpretation I, Dependence of photosynthesis on water content, light, temperature, and CO₂ concentration from laboratory measurements, *Flora*, 197, 233–249, doi:10.1078/0367-2530-00038, 2002. 3833, 3837, 3838, 3839, 3840
- Lange, O. L. and Green, T. G. A.: Lichens show that fungi can acclimate their respiration to seasonal changes in temperature, *Oecologia*, 142, 11–19, doi:10.1007/s00442-004-1697-x, 2005. 3837, 3839
- Lange, O. L., Geiger, I. L., and Schulze, E.-D.: Ecophysiological investigations on lichens of the Negev Desert V. A model to simulate net photosynthesis and respiration of *Ramalina maciformis*, *Oecologia*, 28, 247–259, 1977. 3837, 3838, 3839, 3840
- Lange, O. L., Büdel, B., Heber, U., Meyer, A., Zellner, H., and Green, T. G. A.: Temperate rain-forest lichens in New Zealand: High thallus water content can severely limit photosynthetic CO₂ exchange, *Oecologia*, 95:303–313, doi:10.1007/BF00320981, 1993. 3832
- 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 CO₂ uptake and net carbon

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

gain, *Arctic Alpine Res.*, 30, 252–261, doi:10.2307/1551972, 1998. 3805, 3833, 3837, 3838, 3839, 3840

Larson, D. W.: Lichen water relations under drying conditions. *New Phytol.*, 82, 713–731, doi:10.1111/j.1469-8137.1979.tb01666.x, 1979. 3833

Lawrence, D. M. and Slater, A. G.: Incorporating organic soil into a global climate model, *Clim. Dynam.*, 30, 145–160, doi:10.1007/s00382-007-0278-1, 2008. 3771

5 Lawton, R. O. and Putz, F. E.: Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest, *Ecology*, 63, 764–777, doi:10.2307/1941025, 1988. 3810

Lenton, T. M., Crouch, M., Johnson, M., Pires, N., and Dolan, L.: First plants cooled the Ordovician, *Nat. Geosci.*, 5, 86–89, doi:10.1038/ngeo1390, 2012. 3737, 3738, 3758

10 Liu, Shaomin, Lu, L., Mao, D., and Jia, L.: Evaluating parameterizations of aerodynamic resistance to heat transfer using field measurements, *Hydrol. Earth Syst. Sci.*, 11, 769–783, doi:10.5194/hess-11-769-2007, 2007. 3770

Martin, P. H. and Fahey, T. J.: Fire history along environmental gradients in the subtropical pine forests of the Cordillera Central, Dominican Republic, *J. Trop. Ecol.*, 22, 289–302, doi:10.1017/S0266467406003178, 2006. 3810

15 Martinez-Ramos, M., Alvarez-Buylla, E., Sarukhan, J., and Pinero, D.: Treefall age determination and gap dynamics in a tropical forest, *J. Ecol.*, 76, 700–716, doi:10.2307/2260568, 1988. 3810

20 McKay, M., Conover, W., and Bechman, R.: A comparison of three methods for selecting values of input variables in the analysis of output from a computer code, *Technometrics*, 21, 239–245, doi:10.2307/1268522, 1979. 3760

Medlyn, B. E., Dreyer, E., Ellsworth, D., Forstreuters, M., Harley, P. C., Kirschbaum, M. U. F., Le Roux, X., Montpied, P., Strassmeyer, J., Walcroft, A., Wang, K., and Loustau, D.: Temperature response of parameters of a biochemically based model of photosynthesis. II. A review of experimental data, *Plant Cell Environ.*, 25, 1167–1179, doi:10.1046/j.1365-3040.2002.00891.x, 2002. 3743, 3783, 3808

25 Melick, D. R. and Seppelt, R. D.: Loss of soluble carbohydrates and changes in freezing point of Antarctic bryophytes after leaching and repeated freeze-thaw cycles. *Antarct. Sci.*, 4, 399–404, doi:10.1017/S0954102092000592, 1992. 3743

30 Miura, K., Kohinata, T., Yoshioka, S., Ohyama, K., and Fukuzawa, H.: Regulation of a carbon concentrating mechanism through CCM1 in *Chlamydomonas reinhardtii*, *Funct. Plant Biol.*, 29, 211–219, 2002. 3745

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

- Monteith, J. L.: Evaporation and surface temperature, *Quart. J. R. Met. Soc.*, 107, 1–27, doi:10.1002/qj.49710745102, 1981. 3742, 3776, 3778, 3779
- Mouillot, F. and Field, C. B.: Fire history and the global carbon budget: a 1° × 1° fire history reconstruction for the 20th century, *Global Change Biol.*, 11, 398–420, doi:10.1111/j.1365-2486.2005.00920.x, 2005. 3810
- 5 Nash III, T. H. (Ed.): *Lichen Biology*, 2nd Edn., Cambridge University Press, New York, 1996. 3737, 3753, 3763, 3773, 3778, 3834, 3837, 3839, 3842
- Navas, M.-L., Ducout, B., Roumet, C., Richarte, J., Garnier, J., and Garnier, E.: Leaf life span, dynamics and construction cost of species from Mediterranean old-fields differing in successional status, *New Phytol.*, 159, 213–228, doi:10.1046/j.1469-8137.2003.00790.x, 2003. 3811
- 10 Nikolov, N. T., Massman, W. J., and Schoettle, A. W.: Coupling biochemical and biophysical processes at the leaf level: An equilibrium photosynthesis model for leaves of C₃ plants, *Ecol. Model.*, 80, 205–235, doi:10.1016/0304-3800(94)00072-P, 1995. 3742, 3777
- Oechel, W. C. and Collins, N. J.: Comparative CO₂ exchange patterns in mosses from two tundra habitats at Barrow, Alaska, *Can. J. Botany*, 54, 1355–1369, doi:10.1139/b76-148, 1976. 3805, 3837, 3838, 3839, 3840
- 15 Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'Amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P., and Kassem, K. R.: Terrestrial ecoregions of the world: A new map of life on earth, *BioScience*, 51, 933–938, doi:10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2, 2001. 3747
- 20 Palmqvist, K.: Tansley review no. 117. Carbon economy in lichens, *New Phytol.*, 148, 11–36, doi:10.1046/j.1469-8137.2000.00732.x, 2000. 3833
- Palmqvist, K.: Cyanolichens: Carbon Metabolism, in: *Cyanobacteria in Symbiosis*, edited by: Rai, A. N., Bergman, B., and Rasmussen, U., Kluwer, Dordrecht, doi:10.1007/0-306-48005-0_5, 2002. 3837, 3838, 3839, 3840
- 25 Palmqvist, K. and Sundberg, B.: Light use efficiency of dry matter gain in five macrolichens: Relative impact of microclimate conditions and species-specific traits, *Plant Cell Environ.*, 23, 1–14, doi:10.1046/j.1365-3040.2000.00529.x, 2000. 3833, 3837, 3838, 3839, 3840
- 30 Pannewitz, S., Schlenzog, M., Green, T. G. A., Sancho, L. G., and Schroeter, B.: Are lichens active under snow in continental Antarctica?, *Oecologia*, 135, 30–38, 2003. 3779

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

- Pavlick, R., Drewry, D. T., Bohn, K., Reu, B., and Kleidon, A.: The Jena Diversity-Dynamic Global Vegetation Model (JeDi-DGVM): a diverse approach to representing terrestrial biogeography and biogeochemistry based on plant functional trade-offs, *Biogeosciences Discuss.*, 9, 4627–4726, doi:10.5194/bgd-9-4627-2012, 2012. 3739, 3745, 3758
- 5 Payette, S., Filion, L., and Delwaide, A.: Disturbance regime of a cold temperate forest as deduced from tree-ring patterns: the Tantare Ecological Reserve, Quebec, Can. J. Forest Res., 20, 1228–1241, doi:10.1139/x90-162, 1990. 3810
- Peltoniemi, M., Mäkipää, R., Liski, J., and Tamminen, P.: Changes in soil carbon with stand age – an evaluation of a modelling method with empirical data. *Global Change Biol.*, 10:2078–
- 10 2091, doi:10.1111/j.1365-2486.2004.00881.x, 2004. 3846
- Peters-Lidard, C. D., Blackburn, E., Liang, X., and Wood, E. F.: The effect of soil thermal conductivity parameterization on surface energy fluxes and temperatures. *J. Atmos. Sci.*, 55, 1210–1224, doi:10.1175/1520-0469(1998)055<1209:TEOSTC>2.0.CO;2, 1998. 3771
- Pintado, A. and Sancho, L. G.: Ecological significance of net photosynthesis activation by water vapour uptake in *Ramalina capitata* from rain-protected habitats in central Spain, *Lichenologist*, 34, 403–413, doi:10.1006/lich.2002.0414, 2002. 3834
- 15 Proctor, M. C. F.: The bryophyte paradox: tolerance of desiccation, evasion of drought, *Plant Ecol.*, 151, 41–49, 2000. 3762, 3832
- Randerson, J. T., Hoffman, F. M., Thornton, P. E., Mahowald, N. M., Lindsay, K., Lee, Y.-H., Nevison, C. D., Doney, S.C., Bonan, G., Stöckli, R., Covey, C., Running, S. W., and Fung, I. Y.: Systematic assessment of terrestrial biogeochemistry in coupled climate–carbon models, *Global Change Biol.*, 15, 2462–2484, doi:10.1111/j.1365-2486.2009.01912.x, 2009. 3738
- 20 Reich, P. B., Walters, M. B., Ellsworth, D.S., Vose, J.M., Volin, J.C., Gresham, C., and Bowman, W. D.: Relationships of leaf dark respiration to leaf nitrogen, specific leaf area and leaf life-span: a test across biomes and functional groups, *Oecologia*, 114, 471–482, doi:10.1007/s004420050471, 1998. 3811
- 25 Reinhold, L., Zvirman, M., and Kaplan, A.: A quantitative model for inorganic carbon fluxes and photosynthesis in cyanobacteria, *Plant Physiol. Bioch.*, 27, 945–954, 1989. 3787, 3845
- Russell, S.: Bryophyte production and decomposition in tundra ecosystems, *Bot. J. Linn. Soc.*, doi:10.1111/j.1095-8339.1990.tb02208.x, 104, 3–22, 1990. 3846
- 30 Savir, Y., Noor, E., Milo, R., and Tlustý, T.: Cross-species analysis traces adaptation of Rubisco toward optimality in a low-dimensional landscape, *P. Natl. Acad. Sci. USA*, 107, 3475–3480, doi:10.1073/pnas.0911663107, 2010. 3785, 3835, 3836

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

- Scheidegger, C., Schroeter, B., and Frey, B.: Structural and functional processes during water vapour uptake and desiccation in selected lichens with green algal photobionts, *Planta*, 197, 399–409, doi:10.1007/BF00202663, 1995. 3834
- 5 Schwartzmann, D. W. and Volk, T.: Biotic enhancement of weathering and the habitability of Earth. *Nature*, 340, 457–460, doi:10.1038/340457a0, 1989. 3737
- Stevenson, S. K. and Coxson, D. S.: Litterfall, growth, and turnover of arboreal lichens after partial cutting in an Engelmann spruce-subalpine fir forest in north-central British Columbia, *Can. J. Forest Res.*, 33, 2306–2320, doi:10.1139/x03-161, 2003. 3846
- 10 Stull, R. B. (Ed.): *An Introduction to Boundary Layer Meteorology*, Kluwer, Dordrecht, 1988. 3770
- Sundberg, B., Palmqvist, K., Esseen, P.-A., and Renhorn, K.-E.: Growth and vitality of epiphytic lichens II, Modelling of carbon gain using field and laboratory data, *Oecologia*, 109, 10–18, doi:10.1007/s004420050052, 1997. 3833, 3837, 3838, 3839, 3840
- 15 Sundberg, B., Ekblad, A., Näsholm, T., and Palmqvist, K.: Lichen respiration in relation to active time, temperature, nitrogen and ergosterol concentrations, *Funct. Ecol.*, 13, 119–125, doi:10.1046/j.1365-2435.1999.00295.x, 1999. 3837, 3839
- Sundberg, B., Näsholm, T., and Palmqvist, K.: The effect of nitrogen on growth and key thallus components in the two tripartite lichens, *Nephroma arcticum* and *Peltigera aphthosa*, *Plant Cell Environ.*, 24, 517–527, doi:10.1046/j.1365-3040.2001.00701.x, 2001. 3812
- 20 Swanson, R. V. and Flanagan, L. B.: Environmental regulation of carbon dioxide exchange at the forest floor in a boreal black spruce ecosystem, *Agr. Forest Meteorol.*, 108, 165–181, doi:10.1016/S0168-1923(01)00243-X, 2001. 3805
- Tanaka, H. and Nakashizuka, T.: Fifteen years of canopy dynamics analyzed by aerial photographs in a temperate deciduous forest, Japan, *Ecology*, 78, 612–620, doi:10.2307/2266034, 1997. 3810
- 25 Thonicke, K., Venevsky, S., Sitch, S., and Cramer, W. The role of fire disturbance for global vegetation dynamics: coupling fire into a dynamic global vegetation model, *Global Ecol. Biogeogr.*, 10, 661–677, 2001. doi:10.1046/j.1466-822X.2001.00175.x. 3810
- 30 Tretiach, M. and Geletti, A.: CO₂ exchange of the endolithic lichen *Verrucaria baldensis* from karst habitats in northern Italy, *Oecologia*, 111, 515–522, doi:10.1007/s004420050265, 1997. 3833, 3837, 3838, 3839, 3840

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

- Turner, M. G., Romme, W. H., Gardner, R. H., O'Neill, R. V., and Kratzi, T. K.: A revised concept of landscape equilibrium: Disturbance and stability on scaled landscapes, *Land. Ecol.*, 8, 213–227, doi:10.1007/BF00125352, 1993. 3810
- 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, *Arct. Antarct. Alp. Res.*, 34, 287–292, doi:10.2307/1552486, 2002. 3805
- 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. 3805, 3837, 3838, 3839, 3840
- Valladares, F., Sancho, L. G., and Ascaso, C.: Water storage in the lichen family *Umbilicariaceae*, *Bot. Acta*, 111, 99–107, 1998. 3832, 3833
- von Caemmerer, S.: *Biochemical Models of Leaf Photosynthesis*, CSIRO Publishing, Collingwood, Australia, 2000. 3786
- Walters, M. B. and Reich, P. B.: Low-light carbon balance and shade tolerance in the seedlings of woody plants: do winter deciduous and broad-leaved evergreen species differ?, *New Phytol.*, 143, 143–154, doi:10.1046/j.1469-8137.1999.00425.x, 1999. 3811
- Weber, B., Scherr, C., Bicker, F., Friedl, T., and Büdel, B.: Respiration-induced weathering patterns of two endolithically growing lichens, *Geobiology*, 9, 34–43, doi:10.1111/j.1472-4669.2010.00256.x, 2011. 3737
- Weber, B., Graf, T., and Bass, M.: Ecophysiological analysis of moss-dominated biological soil crusts and their separate components from the Succulent Karoo, South Africa, *Planta*, 236, 129–139, doi:10.1007/s00425-012-1595-0, 2012. 3833
- Weedon, G. P., Gomes, S., Viterbo, P., Shuttleworth, W. J., Blyth, E., Österle, H., Adam, J. C., Belloin, N., Boucher, O., and Best, M.: Creation of the WATCH forcing data and its use to assess global and regional reference crop evaporation over land during the twentieth century, *J. Hydrometeorol.*, 12, 823–848, doi:10.1175/2011JHM1369.1, 2011. 3747
- Withington, J. M., Reich, P. B., Oleksyn, J., and Eissenstat, D. M.: Comparisons of structure and life span in roots and leaves among temperate trees, *Ecol. Monogr.*, 76, 381–397, doi:10.1890/0012-9615(2006)076[0381:COSALS]2.0.CO;2, 2006. 3811

Wullschleger, S. D.: Biochemical limitations to carbon assimilation in C3 plants - a retrospective analysis of the A/C_i-curves from 109 species. J. Exp. Bot., 44, 907–920, doi:10.1093/jxb/44.5.907, 1993. 3757, 3844

BGD

10, 3735–3846, 2013

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

Table 1. Overview of the studies used to evaluate the model. The symbols refer to the data points shown in Fig. 7.

Study site	Symbol	Net carbon uptake [(g C) m ⁻² yr ⁻¹]	References
Barrow, Alaska	✕	38.5, 171.0 10.0	Oechel and Collins (1976) Billings (1987)
Brooks range, Alaska	+	4.7, 9.6, 15.7, 20.4	Lange et al. (1998)
Svalbard	◆	1.9 6.5	Uchida et al. (2006) Uchida et al. (2002)
Saskatchewan, Canada	▲	12 25 104	Gower et al. (1997) Bisbee et al. (2001) Swanson and Flanagan (2001)
Kaiparowits basin, USA	■	0.6, 2.3	Jeffries et al. (1993)
Mojave desert, USA	◻	11.7	Brostoff et al. (2005)
Costa Rica	▼	37, 64	Clark et al. (1998)

Table 2. Influence of uncertain model parameters on simulated net carbon uptake. “Average” and “Maximum” correspond to two different weighting methods for the results (see Sect. 2.3). The “+” sign denotes an increase in the value of a parameter and “-” signs denotes a decrease. The rightmost column shows the type of increase or decrease.

Net carbon uptake [(g C) m ⁻² yr ⁻¹]	Average		Maximum		Type
	-	+	-	+	
Lichen or bryophyte parameters					
CCM response	0.20	0.28	0.9	1.3	50 %
Ratio $J_{\max}/V_{C,\max}$	0.19	0.27	0.8	1.3	50 %
Diffusivity for CO ₂	0.15	0.35	0.6	1.7	50 %
Turnover per respiration	0.19	0.29	1.3	1.0	50 %
Rubisco per respiration	0.16	0.32	0.6	1.6	50 %
Environmental parameters					
Disturbance interval	0.21	0.27	0.9	1.3	50 %
Light extinction in canopy	0.25	0.24	1.2	1.1	50 %
Rain interception efficiency	0.23	0.27	1.0	1.3	50 %
Max. snow depth for activity	0.25	0.25	1.2	1.2	50 %
Heat conductivity of snow	0.25	0.25	1.2	1.2	50 %
Turnover of ice sheets	0.25	0.25	1.2	1.2	50 %
Soil heat conductivity	0.25	0.25	1.2	1.2	50 %
Soil heat capacity	0.25	0.25	1.2	1.2	50 %
Surface roughness	0.26	0.25	1.2	1.1	50 %
Climate forcing					
Shortwave radiation	0.25	0.25	1.1	1.2	20 %
Air temperature	0.26	0.25	1.2	1.2	2 K
Rainfall/Snowfall	0.25	0.25	1.2	1.2	20 %
Surface windspeed	0.26	0.25	1.2	1.1	20 %
Control run	0.25		1.2		

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#) [Introduction](#)

[Conclusions](#) [References](#)

[Tables](#) [Figures](#)

[⏪](#) [⏩](#)

[◀](#) [▶](#)

[Back](#) [Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

Table B1. Overview of the nomenclature of parameters and variables in the model.

Prefix	Parameter or variable	Table(s)
c	Natural constant	B7
ρ	Parameter	B8 (Environment) B11 (Lichens and Bryophytes)
x	Strategy parameter	B9
w	Tradeoff parameter	B10
s	State variable	B14
f	Flow variable	B15
none	Other variable	B12 (Boundary conditions) B13 (Environment) B16 (Lichens and Bryophytes)

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

⏪

⏩

◀

▶

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



Table B2. Overview of the enzyme activation energies E_a of the Michaelis-Menten constants K_C and K_O .

E_a [J mol ⁻¹]		Reference
K_C	K_O	
79 430	36 380	Medlyn et al. (2002)
59 536	35 948	Medlyn et al. (2002)
109 700	14 500	Medlyn et al. (2002)
80 500	–	Medlyn et al. (2002)

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Table B3. Overview of the disturbance intervals τ_{veg} of different biomes. The ★ symbol means that values from other biomes are used, since no original references could be found. A “–” in the column “Leaves” means that lichens and bryophytes cannot grow on the leaves of the respective vegetation type. The values are derived by calculating the median of a set of values from the literature. These are shown in Tables B4 and B5 below. Disturbance intervals for stems & ground are calculated as the minimum of the median of fire intervals, the median of treefall intervals and the herbivory interval, if present (see Tables B4 and B5).

Biome	τ_{veg} [yr]	
	Stems & ground	Leaves
Tropical rainforest	100	1.4
Tropical dry forest	32	–
Tropical needleleaf forest	100 ★	6.0 ★
Temperate broadleaf forest	100	–
Temperate evergreen forest	100 ★	1.4 ★
Boreal forest	100	6.0
Savanna	5	–
Grassland, desert & tundra	15	–
Mediterranean vegetation	50	2.3

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)

Table B4. References for the disturbance intervals τ_{veg} [yr] of different biomes regarding fire and treefall. A “–” means that the corresponding type of disturbance probably does not play a significant role for lichens and bryophytes living in the biome.

Biome	Fire		Treefall	
	τ_{veg}	Reference	τ_{veg}	Reference
Tropical rainforest	> 100	Mouillot and Field (2005)	~ 100	Lawton and Putz (1988)
	> 800	Thonicke et al. (2001)	~ 50	Martinez-Ramos et al. (1988)
			138	Bongers et al. (1988)
			83	Chandrashekara and Ramakrishnan (1994)
		~ 240	Jans et al. (1993)	
Tropical dry forest	32	Martin and Fahey (2006)	98	Ferreira de Lima et al. (2008)
Temperate broad-leaf forest	> 100	Mouillot and Field (2005)	~ 100	Turner et al. (1993)
	> 200	Thonicke et al. (2001)	~ 45	Payette et al. (1990)
			~ 145	Tanaka and Nakashizuka (1997)
Boreal forest	~ 100	Angelstam (1998)	303	Foster and Reiners (1986)
	140	Harvey et al. (2002)		
	> 100	Mouillot and Field (2005)		
	~ 100	Thonicke et al. (2001)		
Savanna	~ 5	Mouillot and Field (2005)	–	–
	~ 5	Thonicke et al. (2001)		
Grassland, desert & tundra	–	–	–	–
Mediterranean vegetation	~ 50	Thonicke et al. (2001)	–	–

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

Table B5. References for the disturbance intervals τ_{veg} [yr] of different biomes regarding leaf fall and herbivory. A “–” means that the corresponding type of disturbance probably does not play a significant role for lichens and bryophytes living in the biome. The value for herbivory was estimated by “best guess” due to lack of data.

Biome	Leaf fall		Herbivory
	τ_{veg}	Reference	
Tropical rainforest	1.4	Condit et al. (1996)	–
	1.4	Reich et al. (1998)	
	2.0	Walters and Reich (1999)	
Tropical dry forest	–	–	–
Temperate broadleaf forest	–	–	–
Boreal forest	5.8	Withington et al. (2006)	–
	6.2	Reich et al. (1998)	
Savanna	–	–	15
Grassland, desert & tundra	–	–	15
Mediterranean vegetation	1.6	Navas et al. (2003)	–
	2.9	Escudero and Mediavilla (2003)	

BGD

10, 3735–3846, 2013

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)




[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)

Table B6. Overview of the Rubisco content Ξ_{Rub} of lichens and bryophyte.

Ξ_{Rub} [(mol Rubisco) (kg C) ⁻¹]	Reference
1.4 E-5	Balaguer et al. (1999)
2.1 E-5	Sundberg et al. (2001)
9.0 E-6	Sundberg et al. (2001)

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Model parameters

Table B7. Overview of natural constants used in the model.

Parameter	Description	Value	Unit	Reference
c_{σ}	Stefan-Boltzmann constant	5.67E-8	$\text{W m}^{-2} \text{K}^{-4}$	Eqs. B22, B31
$c_{\Delta H_{\text{vap}, \text{H}_2\text{O}}}$	Enthalpy of vaporisation	2.45E6	J kg^{-1}	Eqs. B30, B64, B65
$c_{C_{\text{air}}}$	Heat capacity of air	1297.0	$\text{J m}^{-3} \text{K}^{-1}$	Eqs. B30, B31, B65
$c_{\rho_{\text{H}_2\text{O}}}$	Density of liquid water	1000.0	kg m^{-3}	Eqs. B17, B27, B30, B34, B64
c_{γ}	Psychrometric constant	65.0	Pa K^{-1}	Eqs. B30, B31
$c_{M_{\text{H}_2\text{O}}}$	Molar mass of water	0.018	kg mol^{-1}	Eq. B27
$c_{M_{\text{C}}}$	Molar mass of carbon	0.012	kg mol^{-1}	Eqs. B52, B53, B57, B58, B59
$c_{R_{\text{gas}}}$	Universal gas constant	8.3145	$\text{J mol}^{-1} \text{K}^{-1}$	Eqs. B27, B42, B43
$c_{T_{\text{melt}, \text{H}_2\text{O}}}$	Melting temperature of water	273.0	K	Eqs. B32, B40, B51

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)

Table B8. Overview of model parameters describing environmental conditions. Parameters marked by the ★ symbol are included in a sensitivity analysis (see Table 2) because their values are not known very accurately.

Parameter	Description	Value	Unit	Reference
ρ_{SCO_2}	Solubility of CO ₂ in water	0.0334	mmol m ⁻³	Eq. B46
ρ_{SO_2}	Solubility of O ₂ in water	0.00126	mmol m ⁻³	Eq. B45
ρ_e	Emissivity of organism (long-wave radiation)	0.97	[]	Eq. B4
$\rho_{\lambda,s}$	Extinction coefficient (short-wave radiation)	★ 0.5	[]	Eq. B3
$\rho_{\lambda,l}$	Extinction coefficient (long-wave radiation)	0.95	[]	Eq. B4
$\rho_{e_{s,1}}$	Parameter for saturation vapour pressure	17.27	[]	Eqs. B26, B29
$\rho_{e_{s,2}}$	Parameter for saturation vapour pressure	237.3	°C	Eqs. B26, B29
$\rho_{e_{s,3}}$	Parameter for saturation vapour pressure	610.8	Pa	Eqs. B26, B29
ρ_k	von Karman constant	0.41	[]	Eq. B10
ρ_{Δ_u}	Measurement height for wind speed	10.0	m	Eq. B10
$\rho_{z_0,\text{canopy}}$	Roughness length of forest	★ 0.1	m	Eq. B11
$\rho_{z_0,\text{floor}}$	Roughness length of forest floor	★ 0.01	m	Eq. B11
$\rho_{z_0,\text{GDT}}$	Roughness length of grassland, desert & tundra	★ 0.05	m	Eq. B11
$\rho_{z_0,\text{mh}}$	Ratio between z_0 of momentum and humidity	0.1	[]	Eq. B12
$\rho_{z_0,d}$	Ratio between displacement height and z_0	5.42	[]	Eq. B13
ρ_{Δ_z}	Damping depth of the soil for a diurnal cycle	0.15	m	Eqs. B23, B24, B31, B35
$\rho_{C_{\text{soil},D}}$	Heat capacity of desert soil	★ 1.1E6	J m ⁻³ K ⁻¹	Eq. B15
$\rho_{C_{\text{soil},F}}$	Heat capacity of non-desert soil	★ 2.2E6	J m ⁻³ K ⁻¹	Eq. B15
$\rho_{k_{\text{soil},D}}$	Thermal conductivity of desert soil	★ 0.3	W m ⁻¹ K ⁻¹	Eq. B16
$\rho_{k_{\text{soil},F}}$	Thermal conductivity of non-desert soil	★ 1.5	W m ⁻¹ K ⁻¹	Eq. B16
$\rho_{k_{\text{snow}}}$	Thermal conductivity of snow	★ 0.15	W m ⁻¹ K ⁻¹	Eq. B35
$\rho_{\rho_{\text{snow}}}$	Density of snow	250.0	kg m ⁻³	Eq. B34
$\rho_{\Delta_{\text{snow}}}$	Critical snow depth for activity	★ 0.1	m	Sect. B4.5
$\rho_{\tau_{\text{ice}}}$	Turnover rate of ice sheets	★ 0.01	yr ⁻¹	Eq. B33
$\rho_{\text{LAI}_{\text{max}}}$	Maximum Leaf Area Index in data set	5.7	[]	Eqs. B5, B6
$\rho_{\eta_{\text{rain}}}$	Interception efficiency of canopy	★ 0.15	[]	Eq. B5
ρ_{Δ_t}	Time step of the model	3600	s	Eqs. B32, B33, B24, B52, B53, B58, B59, B61, B62, B63
$\rho_{T_{\text{ref},R}}$	Reference temperature of respiration	283	K	Eq. B51
$\rho_{T_{\text{ref},PS}}$	Reference temperature of photosynthesis	298	K	Eqs. B42, B43

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Table B9. Overview of lichen or bryophyte random parameters used in the model.

Parameter	Description	Range	Unit	Reference
X_α	Albedo	0–1	[]	Sect. B1.1, Eq. B3
$X_{\Theta_{\max}}$	Specific water storage capacity	1–160	(kg H ₂ O) (kg C) ⁻¹	Fig. B1, Eqs. B17, B62
$X_{A_{\text{spec}}}$	Specific projected area	0.3–240	m ² (kg C) ⁻¹	Fig. B2, Eq. B8
X_{loc}	Location of growth	Canopy or ground	[]	Sect. B1.4
$X_{\Phi_{\Theta, \text{sat}}}$	Threshold saturation for water potential	0.3–1	[]	Fig. B3, Eqs. B20, B21
$X_{\Psi_{\text{H}_2\text{O}}}$	Shape parameter for water potential curve	5–25	[]	Fig. B3, Eqs. B20, B27
$X_{V_{\text{C}, \text{max}}}$	Molar carboxylation rate of Rubisco	0.6–26.8	s ⁻¹	Fig. B4, Eqs. B37, B42, B43, B44, B48
$X_{V_{\text{O}, \text{max}}}$	Molar oxygenation rate of Rubisco	0.1–2.5	s ⁻¹	Fig. B5, Eqs. B43, B44
$X_{R_{\text{ref}}}$	Reference maintenance respiration	1E-7–1.5E-4	(mol CO ₂) (kg C) ⁻¹ s ⁻¹	Fig. B6, Eqs. B38, B51, B56
$X_{Q_{10}}$	Q ₁₀ value of respiration	1–3	[]	Fig. B7, Eq. B51
$X_{T_{\text{opt}, \text{PS}}}$	Optimum temperature of photosynthesis	278–313	K	Fig. B9, Eq. B37
$X_{E_{\text{a}, K_{\text{C}}}}$	Enzyme activation energy of K _C	3E4–1.3E5	J mol ⁻¹	Table B2, Eq. B42
$X_{E_{\text{a}, K_{\text{O}}}}$	Enzyme activation energy of K _O	5E3–5.5E4	J mol ⁻¹	Table B2, Eq. B43
X_{CCM}	Carbon Concentration Mechanism (CCM)	CCM present or not	[]	Sect. B1.11
X_{alloc}	Fraction of carbon allocated to growth	0–1	[]	Sect. B1.12, Eq. B53

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Table B10. Overview of model parameters associated with lichen or bryophyte tradeoffs. Parameters marked by the ★ symbol are included in a sensitivity analysis (see Table 2) because their values are not known very accurately. Note that in some cases several parameters are changed simultaneously to test model sensitivity towards a certain property, e.g. both $w_{D_{CO_2,max}}$ and $w_{D_{CO_2,min}}$ for CO_2 diffusivity. Only one of the CCM parameters is included in the sensitivity analysis: changing $w_{CCM,e}$ would be redundant since decreasing the costs of the CCM is analogous to increasing its positive effect. $w_{CCM,2}$ and $w_{CCM,3}$ are only relevant at a transient state of very high pore space CO_2 levels.

Parameter	Description		Value	Unit	Reference
$w_{D_{CO_2,max}}$	Maximum thallus diffusivity for CO_2	★	0.14	$(\text{mol } CO_2) \text{ m}^{-2} \text{ s}^{-1}$	Eq. B19
$w_{D_{CO_2,min}}$	Minimum thallus diffusivity for CO_2	★	5.7E-4	$(\text{mol } CO_2) \text{ m}^{-2} \text{ s}^{-1}$	Eq. B19
$w_{D_{CO_2}}$	Factor for water CO_2 diffusivity curve		12	[]	Fig. B10, Eq. B19
$w_{Rub,R}$	Rubisco per respiration	★	3.6	$(\text{mol Rubisco}) (\text{mol } CO_2)^{-1} \text{ s}$	Eq. B38
$w_{loss,R}$	Turnover per respiration	★	54771	$(\text{kg C}) \text{ s} (\text{mol } CO_2)^{-1} \text{ yr}^{-1}$	Eq. B56
$w_{JV,1}$	Slope of ϕ_{JV}	★	-0.06	[]	Eq. B40
$w_{JV,2}$	Intercept of ϕ_{JV}	★	3.7	[]	Eq. B40
$w_{K_C,1}$	Parameter for K_C		1.32	[]	Eqs. B42, B43
$w_{K_C,2}$	Parameter for K_C		2.03	[]	Eqs. B42, B43
$w_{K_O,1}$	Parameter for K_O		5.7E-3	[]	Eq. B43
$w_{K_O,2}$	Parameter for K_O		0.51	[]	Eq. B43
$w_{CCM,e}$	Cost parameter for CCM		0.67	[]	Eq. B41
$w_{CCM,1}$	Parameter for CCM	★	45	[]	Eq. B50
$w_{CCM,2}$	Parameter for CCM		3.6	[]	Eq. B50
$w_{CCM,3}$	Parameter for CCM		6	[]	Eq. B50

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

Table B11. Constant model parameters associated with lichen or bryophyte properties.

Parameter	Description	Value	Unit	Reference
ρ_{PAR}	Conversion factor for photosynthetically active radiation	2.0699E-6	mol J^{-1}	Eq. B41
ρ_{quant}	Conversion of quanta light into electrons	0.5	[]	Eq. B41
ρ_{Ω}	Shape parameter for T response of photosynthesis	18	K	Eq. B37
$\rho_{\eta_{\text{growth}}}$	Efficiency of sugar to biomass conversion	0.75	[]	Eqs. B53, B54

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Model variables

Table B12. Boundary conditions for the model.

Variable	Description	Unit	Reference
$\text{CO}_{2,\text{atm}}$	Atmospheric CO_2 concentration	ppm	Eq. B36
$\text{O}_{2,\text{atm}}$	Atmospheric O_2 concentration	ppm	Eq. B45
T_{air}	Air temperature	K	Eqs. B22, B26, B27, B29, B31, B32, B35, B65
$f_{\text{rad,swi}}$	Ingoing shortwave radiation	W m^{-2}	Eqs. B25, B31, B41
$f_{\text{rad,lwi}}$	Ingoing longwave radiation	W m^{-2}	Eqs. B25, B31
$f_{\text{rain,atm}}$	Rainfall	$\text{m}^3 \text{m}^{-2} \text{s}^{-1}$	Eq. B60
$f_{\text{snow,atm}}$	Snowfall	$\text{m}^3 \text{m}^{-2} \text{s}^{-1}$	Eqs. B32, B33
Φ_{RH}	Relative humidity	[]	Eqs. B30, B31
u	Near surface wind speed	m s^{-1}	Eq. B10
A_{baresoil}	Area fraction of unoccupied soil	$\text{m}^2 \text{m}^{-2}$	Eq. B6
A_{LAI}	Leaf Area Index (monthly resolution)	$\text{m}^2 \text{m}^{-2}$	Eqs. B3, B4, B5, B6, B7
A_{SAI}	Stem Area Index (monthly resolution)	$\text{m}^2 \text{m}^{-2}$	Eqs. B3, B4, B7

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

Table B13. Variables associated with the environment.

Variable	Description	Unit	Reference
Z_0	Roughness length of surface for momentum	m	Eqs. B10, B11, B12, B13
$Z_{0,h}$	Roughness length of surface for humidity	m	Eqs. B10, B12
r_H	Aerodynamic resistance to heat transfer	m^{-1}	Eqs. B10, B30, B31, B65
Δ_d	Displacement height for wind speed	m	Eqs. B10, B13
τ_{veg}	Disturbance interval	yr	Table B13
C_{soil}	Soil heat capacity	$\text{J m}^{-3} \text{K}^{-1}$	Eqs. B15, B24
k_{soil}	Soil thermal conductivity	$\text{W m}^{-1} \text{K}^{-1}$	Eqs. B16, B25, B31, B35
f_{snowmelt}	Snowmelt	$\text{m}^3 \text{m}^{-2} \text{s}^{-1}$	Eqs. B32, B33, B60
s_{snow}	Snow reservoir	$\text{m}^3 \text{m}^{-2}$	Eqs. B32, B33, B34
Δ_{snow}	Thickness of Snow cover	m	Eqs. B34, B35
$A_{\text{ground,max}}$	Available area for growth on ground	$\text{m}^2 \text{m}^{-2}$	Eqs. B6, B8
$A_{\text{canopy,max}}$	Available area for growth in canopy	$\text{m}^2 \text{m}^{-2}$	Eqs. B7, B8, B9
s_{Tsoil}	Soil temperature	K	Eqs. B23, B24, B31, B35
e_{sat}	Saturation vapour pressure	Pa	Eqs. B28, B30, B31
$e_{\text{sat},0}$	Saturation vapour pressure (open water)	Pa	Eqs. B26, B28
$\phi_{e_{\text{sat}}}$	Reduction factor for saturation vapour pressure	[]	Eqs. B27, B28, B29
$d_{e_{\text{sat}}}$	Slope of saturation vapour pressure curve	[]	Eqs. B29, B30, B31
E_{pot}	Potential evaporation	$\text{m}^3 \text{m}^{-2} \text{s}^{-1}$	Eqs. B30, B61, B65

BGD

10, 3735–3846, 2013

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)**Table B14.** State variables of lichens or bryophytes.

Variable	Description	Unit	Reference
s_B	Biomass of lichen or bryophyte	(kg C) m ⁻²	Eqs. B8, B17, B41, B48, B52, B57, B59
s_C	Sugar reservoir of lichen or bryophyte	(kg C) m ⁻²	Eqs. B52, B53, B58
s_Θ	Thallus water content	m ³ m ⁻²	Eqs. B18, B61, B62, B63

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

Table B15. Variables describing flows between lichens or bryophytes and their environment.

Variable	Description	Unit	Reference
$f_{\text{rad,LWf}}$	Outgoing longwave radiation	W m^{-2}	Eqs. B22, B25
$f_{Q_{\text{soil}}}$	Ground heat flux	W m^{-2}	Eqs. B23, B24, B25
f_H	Net radiation	W m^{-2}	Eqs. B25, B30
$f_{Q_{\text{atm,L}}}$	Latent heat flow	W m^{-2}	Eqs. B64, B66
$f_{Q_{\text{atm,S}}}$	Sensible heat flow	W m^{-2}	Eqs. B65, B66
$f_{\text{water,up}}$	Water uptake	$\text{m}^3 \text{m}^{-2} \text{s}^{-1}$	Eqs. B60, B62, B63
f_{evap}	Evaporation from thallus surface	$\text{m}^3 \text{m}^{-2} \text{s}^{-1}$	Eqs. B61, B62, B63, B64, B65
f_{runoff}	Runoff	$\text{m}^3 \text{m}^{-2} \text{s}^{-1}$	Eqs. B62, B63
$f_{\text{CO}_2,\text{in}}$	Inflow of CO_2 into the thallus	$(\text{mol CO}_2) \text{m}^{-2} \text{s}^{-1}$	Eqs. B36, B55
$f_{\text{GPP,L}}$	Light-limited rate of photosynthesis	$(\text{mol CO}_2) \text{m}^{-2} \text{s}^{-1}$	Eqs. B47, B49
$f_{\text{GPP,W}}$	CO_2 -limited rate of photosynthesis	$(\text{mol CO}_2) \text{m}^{-2} \text{s}^{-1}$	Eqs. B48, B49
f_{GPP}	Gross Primary Productivity (GPP)	$(\text{mol CO}_2) \text{m}^{-2} \text{s}^{-1}$	Eqs. B49, B55, B58
$f_{R_{\text{main}}}$	Maintenance respiration	$(\text{mol CO}_2) \text{m}^{-2} \text{s}^{-1}$	Eqs. B52, B53, B55, B58
$f_{R_{\text{growth}}}$	Growth respiration	$(\text{mol CO}_2) \text{m}^{-2} \text{s}^{-1}$	Eqs. B54, B55, B58
f_{growth}	Growth	$(\text{mol C}) \text{m}^{-2} \text{s}^{-1}$	Eqs. B53, B54, B58, B59
f_{loss}	Biomass loss	$(\text{mol C}) \text{m}^{-2} \text{s}^{-1}$	Eqs. B57, B59

Table B16. Variables associated with lichens or bryophytes.

Variable	Description	Unit	Reference
$\Psi_{\text{H}_2\text{O}}$	Water potential	MPa	Fig. B3, Eq. B20
R_{spec}	Specific maintenance respiration rate	$(\text{mol CO}_2) (\text{kg C})^{-1} \text{s}^{-1}$	Eqs. B51, B52
ϕ_{rad_s}	Conversion factor for shortwave radiation	[]	Eqs. B3, B25, B31, B41
ϕ_{rad_L}	Conversion factor for longwave radiation	[]	Eqs. B4, B25, B31
ϕ_{prec}	Conversion factor for precipitation	[]	Eqs. B5, B60
Φ_{area}	Fraction of available area covered by organism	[]	Eqs. B9, B22, B23, B24, B25, B30, B36, B41, B60, B65
A_{thallus}	Thallus area per m^2 ground	$\text{m}^2 \text{m}^{-2}$	Eqs. B8, B9
χ_{G}	Switch for ground heat flux	[]	Eqs. B14, B23, B31
Θ_{max}	Water storage capacity	m	Eqs. B17, B18
Φ_{Θ}	Water saturation	[]	Eqs. B18, B19, B20, B21
D_{CO_2}	Diffusivity for CO_2	$(\text{mol CO}_2) \text{m}^{-2} \text{s}^{-1}$	Eqs. B19, B36
Φ_{act}	Metabolic activity	[]	Eqs. B21, B47, B48, B52, B53
T_{surf}	Surface temperature	K	Eqs. B22, B23, B31, B35, B37, B40, B42, B43, B51, B65
$\text{CO}_{2,\text{thallus}}$	CO_2 concentration in thallus pore space	ppm	Eqs. B36, B46, B50
$\text{CO}_{2,\text{cell}}$	CO_2 concentration in chloroplast	$(\text{mol CO}_2) \text{m}^{-3}$	Eqs. B46, B47, B48, B50
$V_{\text{C,max}}$	Maximum carboxylation rate	$(\text{mol CO}_2) (\text{kg C})^{-1} \text{s}^{-1}$	Eqs. B37, B39
J_{max}	Maximum electron transport rate	$(\text{mol e}^-) (\text{kg C})^{-1} \text{s}^{-1}$	Eqs. B39, B41
\bar{z}_{Rub}	Specific Rubisco content	$(\text{mol Rubisco}) (\text{kg C})^{-1}$	Eqs. B37, B38
ϕ_{JV}	Ratio of J_{max} to $V_{\text{C,max}}$	[]	Eqs. B39, B40
K_{C}	Michaelis-Menten constant of carboxylation	$(\text{mol CO}_2) \text{m}^{-3}$	Eqs. B42, B44, B48
K_{O}	Michaelis-Menten constant of oxygenation	$(\text{mol O}_2) \text{m}^{-3}$	Eqs. B42, B44, B48
$\text{O}_{2,\text{cell}}$	O_2 concentration in chloroplast	$(\text{mol O}_2) \text{m}^{-3}$	Eqs. B44, B45, B48
Γ_*	CO_2 compensation point	$(\text{mol CO}_2) \text{m}^{-3}$	Eqs. B44, B47, B48
J	Actual electron transport rate	$(\text{mol e}^-) \text{m}^{-2} \text{s}^{-1}$	Eqs. B41,
τ_{B}	Turnover rate of biomass	yr^{-1}	Fig. B15, Eq. B56, B57

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

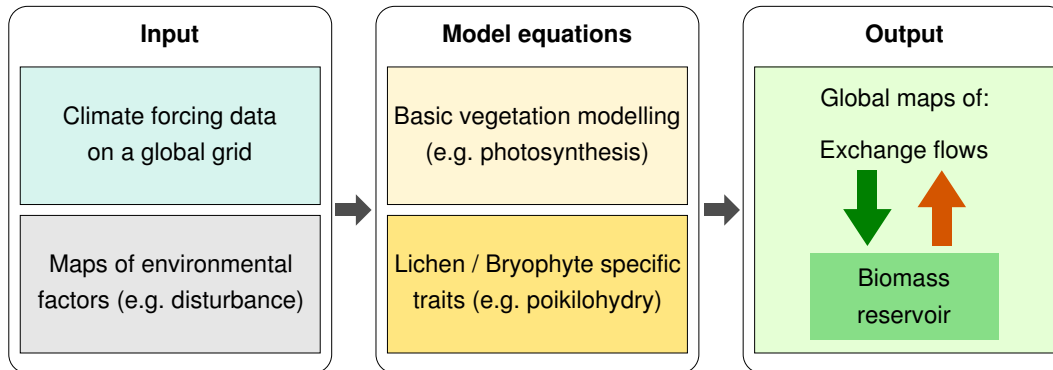


Fig. 1. Overview of the functioning of the model. Input data are translated via model equations into exchange flows of carbon, which are used to calculate changes in the biomass reservoir.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[⏪](#)[⏩](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

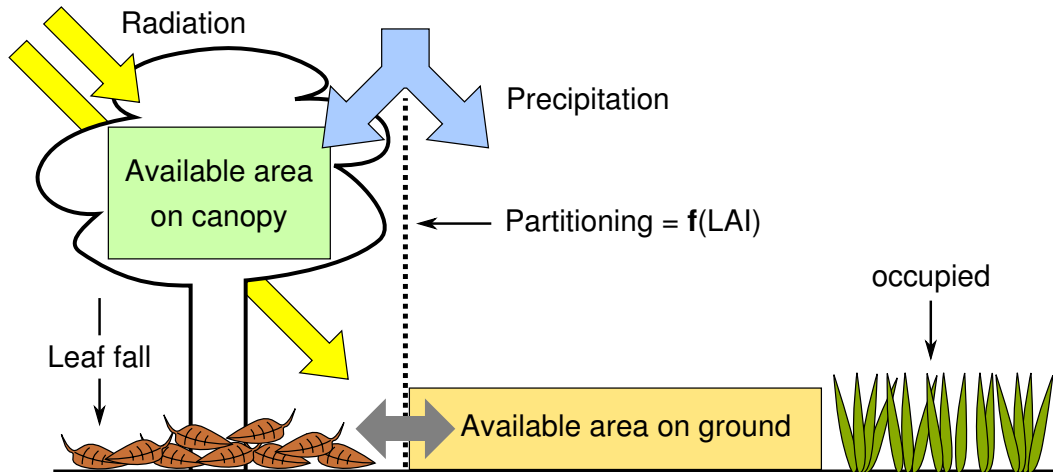


Fig. 2. Effect of the Leaf Area Index (LAI) on area for growth and climate forcing. Available area on ground is a linearly decreasing function of LAI. The same function is used to partition precipitation between canopy and soil. The vertical distribution of light is calculated according to Beer's law as a function of LAI.

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

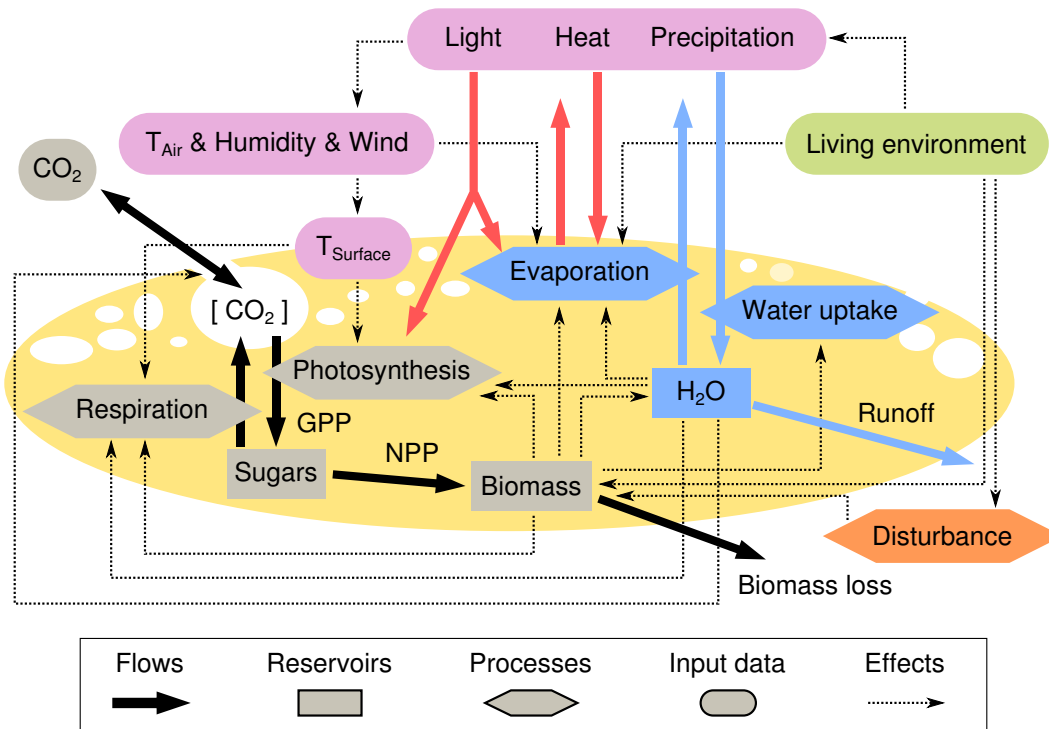


Fig. 3. Schematic of the carbon and water relations of a lichen or bryophyte simulated by the model. Dotted arrows illustrate effects of climate forcing, living environment and state variables on physiological processes of a lichen or bryophyte. These processes are associated with exchange flows (solid arrows) of carbon (black), water (blue) and energy (red).

Title Page	
Abstract	Introduction
Conclusions	References
Tables	Figures
◀	▶
◀	▶
Back	Close
Full Screen / Esc	
Printer-friendly Version	
Interactive Discussion	

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

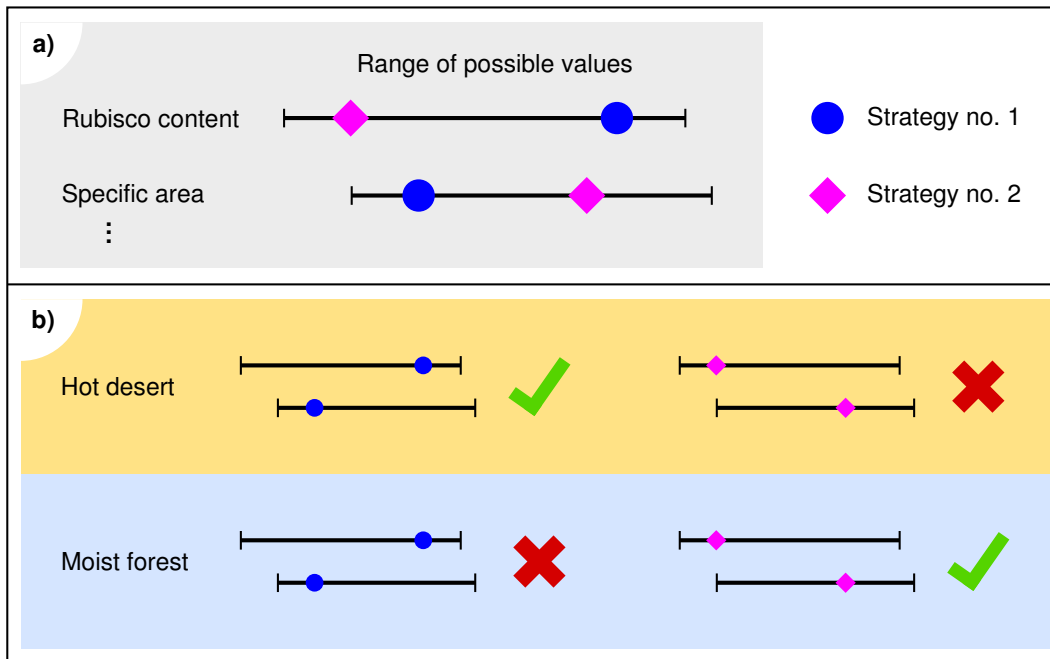


Fig. 4. Generation of physiological strategies and their survival. **(a)** Many random parameter combinations (strategies) are sampled from ranges of possible values. The strategies are then run in each grid cell of the model. **(b)** Example: in a hot desert, strategy 1 survives, because a small specific area reduces water loss by evaporation and a high Rubisco content is adequate to high light intensities. Strategy 2, however, dies out since too much water evaporates due to a large specific area. In a moist forest, strategy 1 dies out because a high Rubisco content is associated with high respiration costs which cannot be covered by low light conditions under a canopy. Strategy 2 can survive since it does not have high respiration costs. Note that these examples are not generally applicable. High specific area, for instance, could also be useful in a desert to collect dew.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

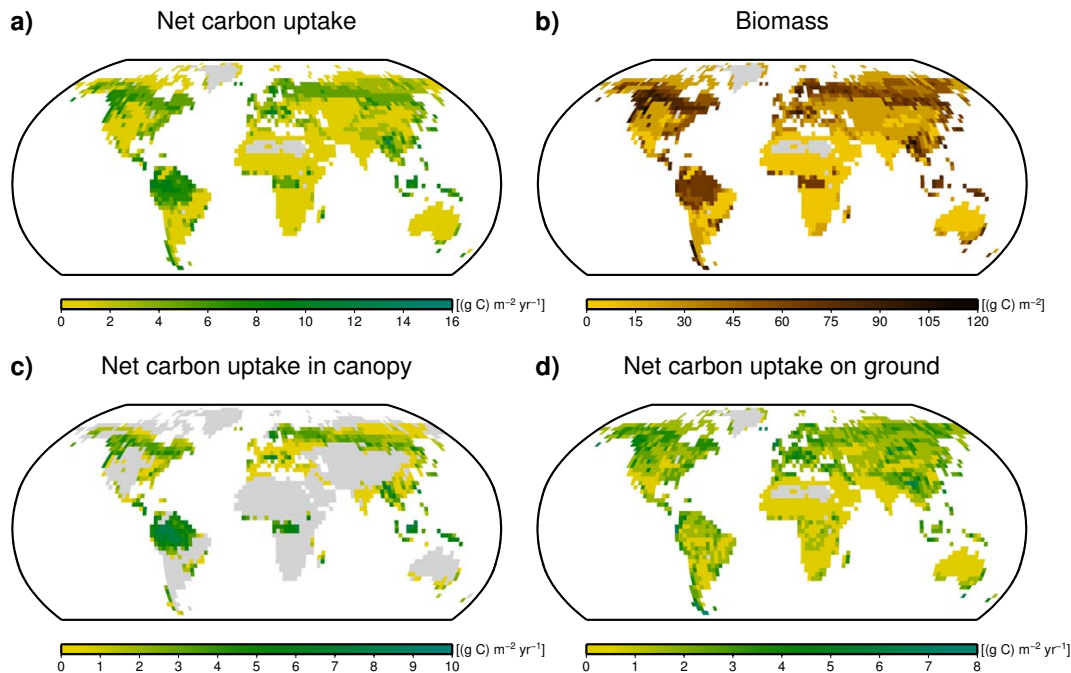


Fig. 5. Global maps of model estimates. **(a)** Net carbon uptake by lichens and bryophytes. **(b)** Biomass of lichens and bryophytes. **(c)** Net carbon uptake by lichens and bryophytes living in the canopy. **(d)** Net carbon uptake by lichens and bryophytes living on the ground. The estimates are based on time averages of the last 100 yr of a 2000-yr run with 3000 initial strategies. They correspond to the “average” weighting method (see Sect. 2.3). Areas where no strategy has been able to survive are shaded in grey.

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[⏪](#)
[⏩](#)
[◀](#)
[▶](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

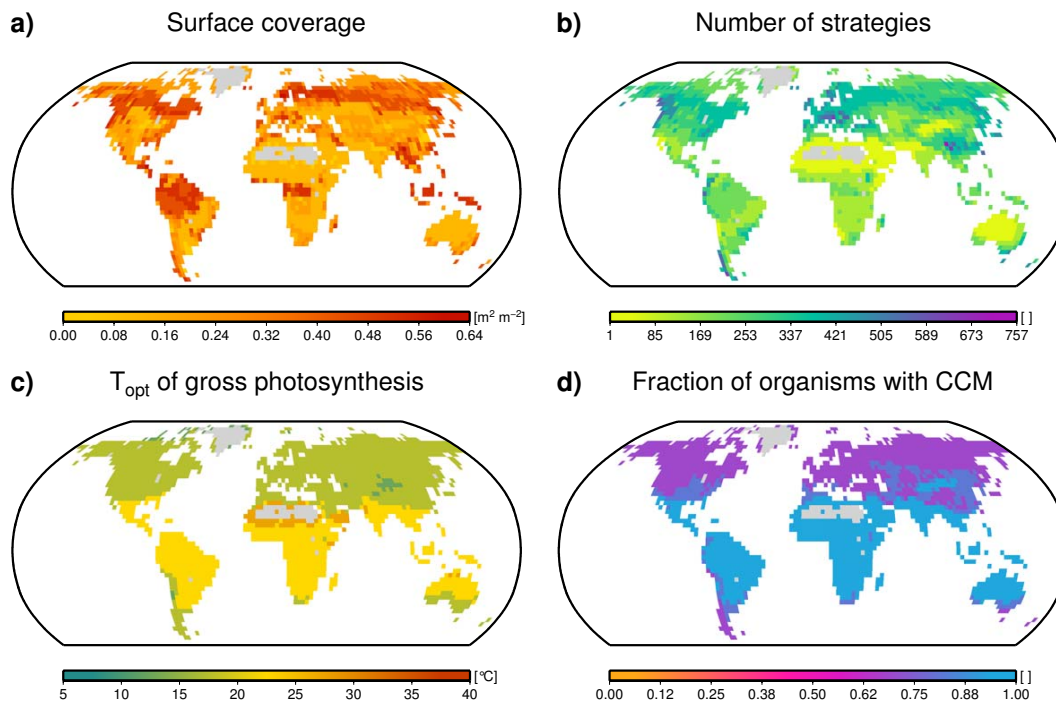


Fig. 6. Global maps of model estimates. **(a)** Area covered by lichens and bryophytes per m^2 ground. **(b)** Number of surviving strategies at the end of a model run. **(c)** Optimum temperature of gross photosynthesis of lichens and bryophytes on the ground. **(d)** Fraction of lichens and bryophytes on the ground with a Carbon Concentration Mechanism (CCM). The estimates are based on time averages of the last 100 yr of a 2000-yr run with 3000 initial strategies. They correspond to the “average” weighting method (see Sect. 2.3). Areas where no strategy has been able to survive are shaded in grey.

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

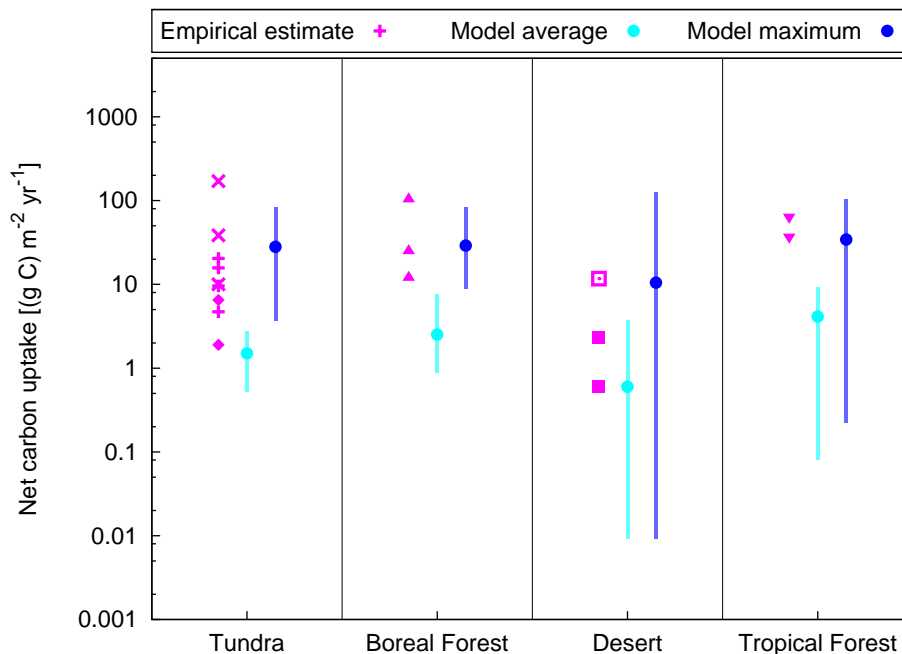


Fig. 7. Comparison of net carbon uptake estimated by the model to observational data. Each symbol corresponds to a different field study site. Model estimates based on “average” as well as “maximum” weighting are shown (see Sect. 2.3). The vertical bars represent the range between the most and least 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.

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[⏪](#)
[⏩](#)
[◀](#)
[▶](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

Additional model output

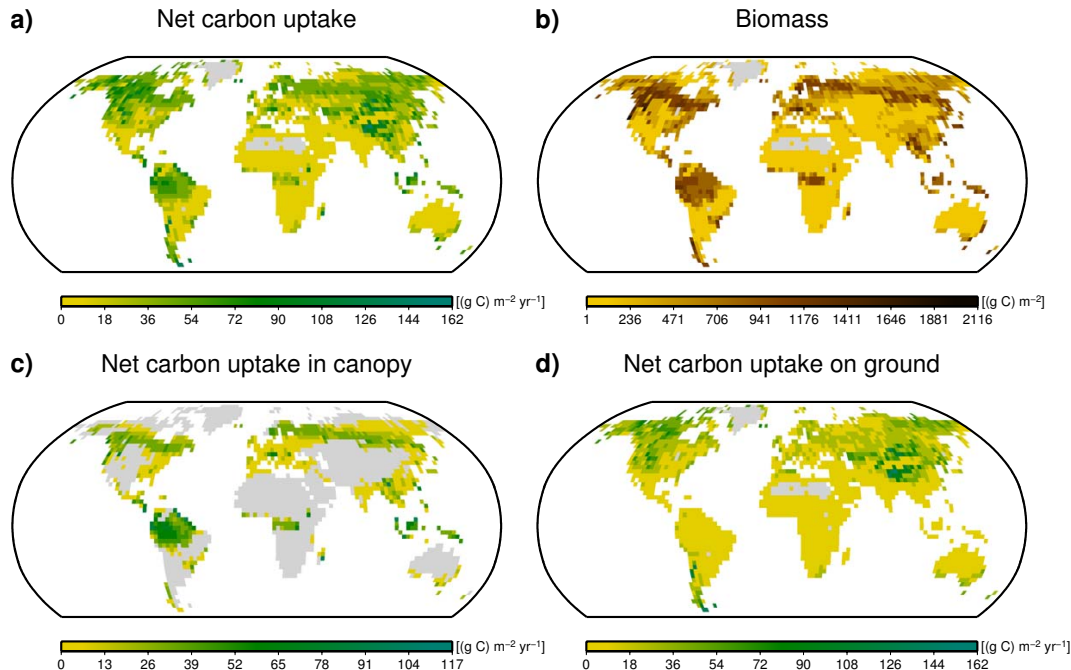


Fig. A1. Global maps of model estimates based on time averages of the last 100 yr of a 2000-yr run with 3000 initial strategies. The estimates shown in (a) to (d) are based on the “maximum” weighting method while the ones shown in Fig. 5 are based on the “average” weighting method. Areas where no strategy has been able to survive are shaded in grey.

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

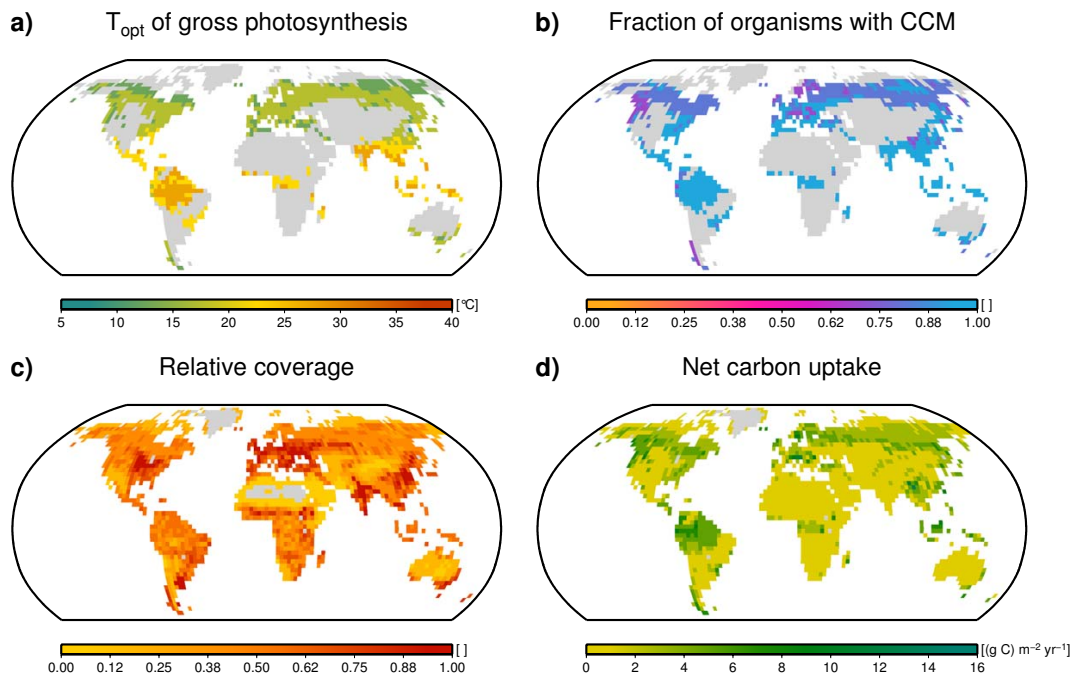


Fig. A2. (a) to (c) are global maps of model estimates derived by time averages of the last 100 yr of a 2000-yr run with 3000 initial strategies and they are based on the “average” weighting method. (a) and (b) show optimum temperature and CCM fraction of lichens and bryophytes living in the canopy, which adds to Fig. 6, where the corresponding estimates for the ground are shown. In (c) the fraction of available area covered by lichens and bryophytes is shown, which is highest in regions where available area on ground is limited due to agriculture. In (d) carbon uptake by lichens and bryophytes is shown for a 400-run with 300 initial strategies. This run is used for the sensitivity analysis. The estimate is based on the “average” weighting method. Areas where no strategy has been able to survive are shaded in grey.

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

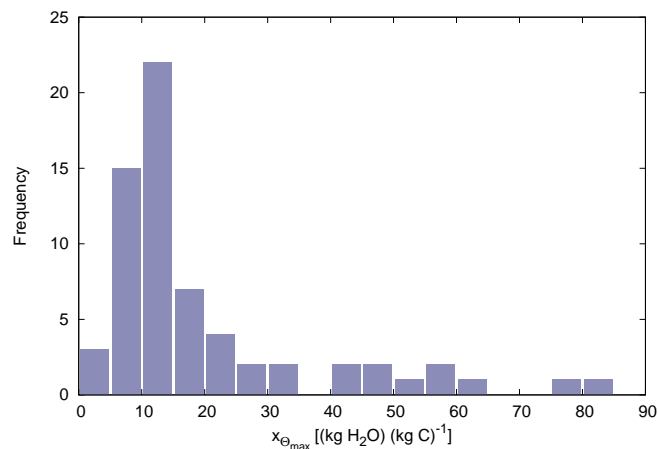
[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

Distribution



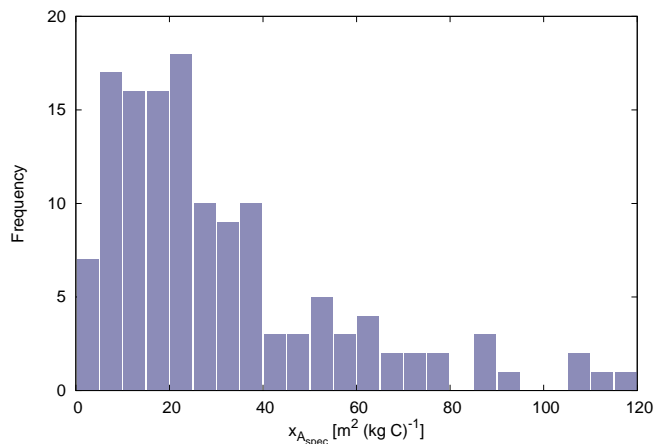
References

Valladares et al. (1998)
 Dahlman and Palmqvist (2003)
 Gauslaa and Solhaug (1998)
 Köhler et al. (2007)
 Proctor (2000)
 Bond-Lamberty and Gower (2007)
 Lange et al. (1993)

Fig. B1. Overview of the distribution of specific water storage capacity $x_{\Theta_{max}}$.

Distribution

References



- Palmqvist and Sundberg (2000)
 Valladares et al. (1998)
 Dahlman and Palmqvist (2003)
 Gauslaa and Solhaug (1998)
 Gaio-Oliveira et al. (2006)
 Gauslaa and Ustvedt (2003)
 Cowan et al. (1992)
 Demmig-Adams et al. (1990)
 Hill and Woolhouse (1966)
 Hilmo (2002)
 Larson (1979)
 Palmqvist (2000)
 Huttunen et al. (2005)
 Green et al. (1998)
 Weber et al. (2012)
 Green and Snelgar (1982)
 Tretiach and Geletti (1997)
 Bond-Lamberty and Gower (2007)
 Sundberg et al. (1997)
 Lange (2002)
 Lange et al. (1998)

Fig. B2. Overview of the distribution of specific projected area $x_{A_{spec}}$.

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

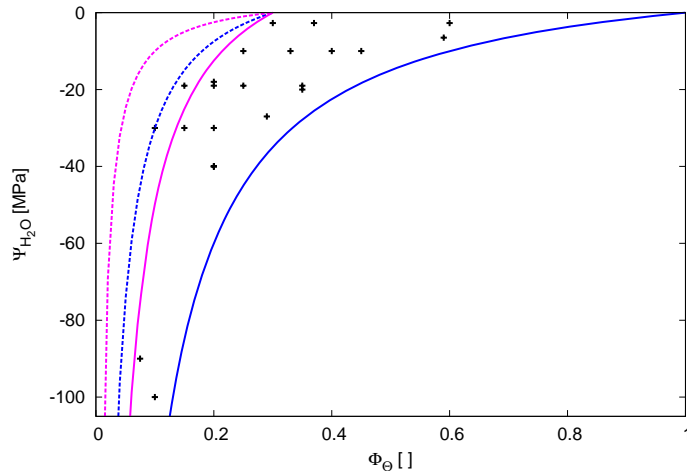
[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



Nash III (1996, p. 157)
 Scheidegger et al. (1995)
 Pintado and Sancho (2002)
 Dilks and Proctor (1979)

Fig. B3. Water potential $\Psi_{\text{H}_2\text{O}}$ as a function of water saturation Φ_{Θ} . Four example curves are shown. The two blue curves correspond to a value of $x_{\Psi_{\text{H}_2\text{O}}} = 15.0$ which represents the middle of the range of possible values. The dashed blue curve corresponds to $x_{\Phi_{\Theta,\text{sat}}} = 0.3$ and the solid blue curve to $x_{\Phi_{\Theta,\text{sat}}} = 1.0$. The two magenta curves correspond to a value of $x_{\Phi_{\Theta,\text{sat}}} = 0.3$. The dashed magenta curve corresponds to $x_{\Psi_{\text{H}_2\text{O}}} = 5.0$ and the solid magenta curve to $x_{\Psi_{\text{H}_2\text{O}}} = 25.0$. The black data points are derived from the studies listed in the right column.

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

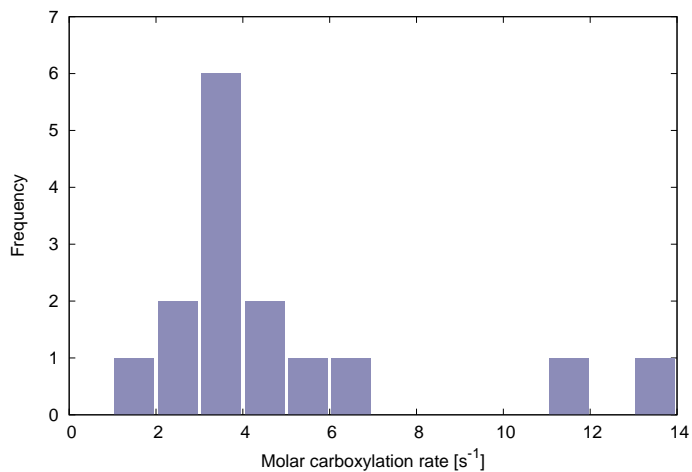
Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

Distribution

References



Savir et al. (2010)

Fig. B4. Overview of the distribution of the molar carboxylation rate of Rubisco.

Estimating global carbon uptake by lichens and bryophytes

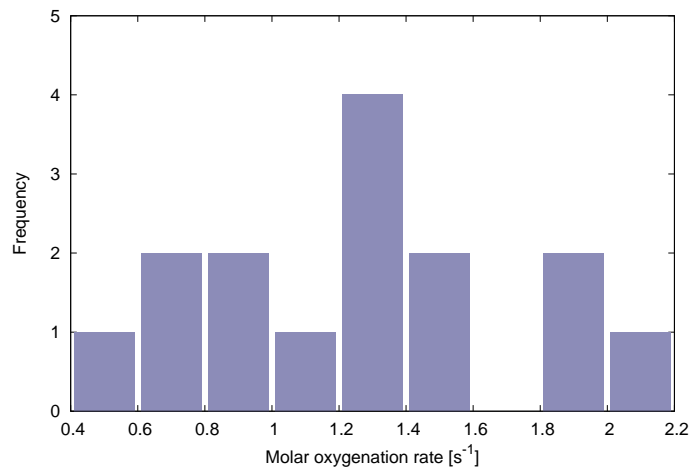
P. Porada et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

Distribution

References

Savir et al. (2010)

**Fig. B5.** Overview of the distribution of the molar oxygenation rate of Rubisco.

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

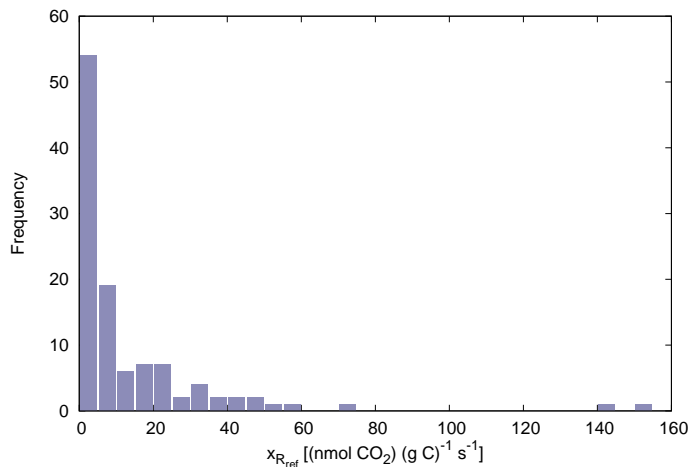
[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

Distribution

References



Nash III (1996)
 Sundberg et al. (1999)
 Lange and Green (2005)
 Palmqvist and Sundberg (2000)
 Sundberg et al. (1997)
 Lange (2002)
 Lange et al. (1998)
 Uchida et al. (2006)
 Palmqvist (2002)
 Tretiach and Geletti (1997)
 Kappen et al. (1989)
 Green et al. (1998)
 Lange et al. (1977)
 Oechel and Collins (1976)

Fig. B6. Overview of the distribution of the reference maintenance respiration rate at 10 °C, $X_{R_{ref}}$.

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

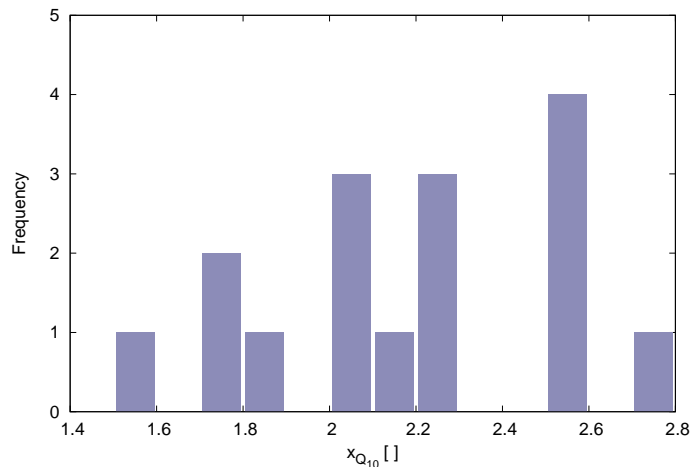
[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

Distribution



References

- Palmqvist and Sundberg (2000)
 Sundberg et al. (1997)
 Lange (2002)
 Lange et al. (1998)
 Uchida et al. (2006)
 Palmqvist (2002)
 Tretiach and Geletti (1997)
 Kappen et al. (1989)
 Green et al. (1998)
 Lange et al. (1977)
 Oechel and Collins (1976)

Fig. B7. Overview of the distribution of the Q_{10} value of respiration $x_{Q_{10}}$.

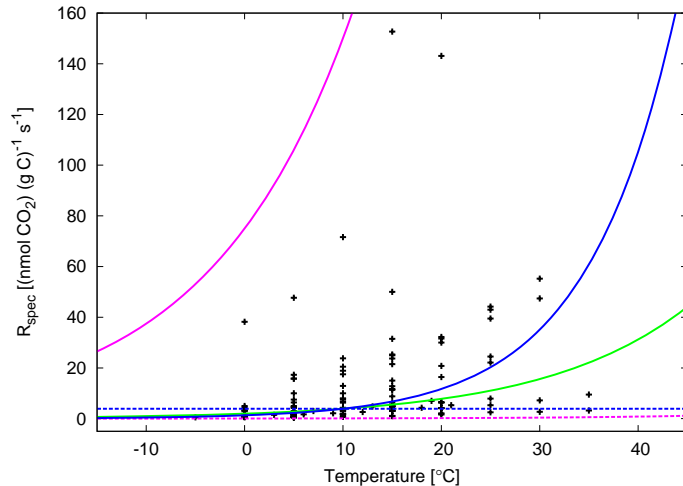


Fig. B8. Influence of reference maintenance respiration $x_{R_{ref}}$ and Q_{10} value of respiration $x_{Q_{10}}$ on specific respiration rate R_{spec} . The green line shows the response of respiration to temperature for values of $x_{R_{ref}}$ and $x_{Q_{10}}$ which are both in the middle of their respective ranges. The blue lines show the effect of the Q_{10} value $x_{Q_{10}}$: The dashed blue line corresponds to $x_{Q_{10}} = 1$ while the solid blue line corresponds to $x_{Q_{10}} = 3$. The magenta lines illustrate the effect of reference respiration rate $x_{R_{ref}}$ at 10°C: the dashed magenta line corresponds to $x_{R_{ref}} = 1E-7$ (mol CO₂) (kg C)⁻¹ s⁻¹ while the solid magenta line corresponds to $x_{R_{ref}} = 1.5E-4$ (mol CO₂) (kg C)⁻¹ s⁻¹. The black data points are derived from the studies listed in the right column.

Nash III (1996)
 Sundberg et al. (1999)
 Lange and Green (2005)
 Palmqvist and Sundberg (2000)
 Sundberg et al. (1997)
 Lange (2002)
 Lange et al. (1998)
 Uchida et al. (2006)
 Palmqvist (2002)
 Tretiach and Geletti (1997)
 Kappen et al. (1989)
 Green et al. (1998)
 Lange et al. (1977)
 Oechel and Collins (1976)
 Harrison et al. (1986)

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

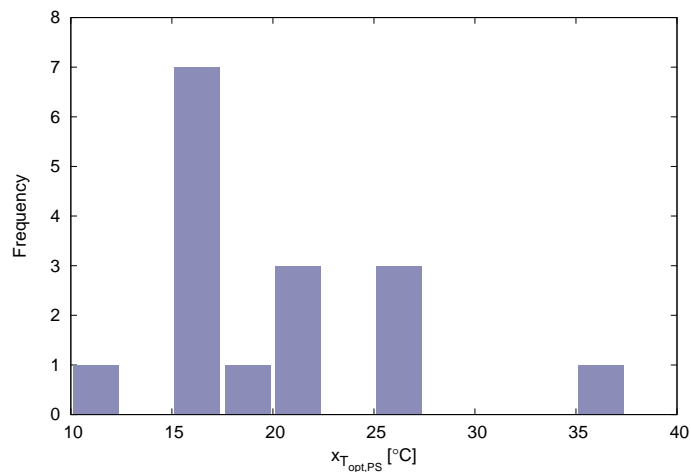
[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



Distribution



References

- Palmqvist and Sundberg (2000)
 Sundberg et al. (1997)
 Lange (2002)
 Lange et al. (1998)
 Uchida et al. (2006)
 Palmqvist (2002)
 Tretiach and Geletti (1997)
 Kappen et al. (1989)
 Green et al. (1998)
 Lange et al. (1977)
 Oechel and Collins (1976)

Fig. B9. Overview of the distribution of the optimum temperature of photosynthesis $x_{T_{opt,PS}}$.

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Overview

References

Cowan et al. (1992)

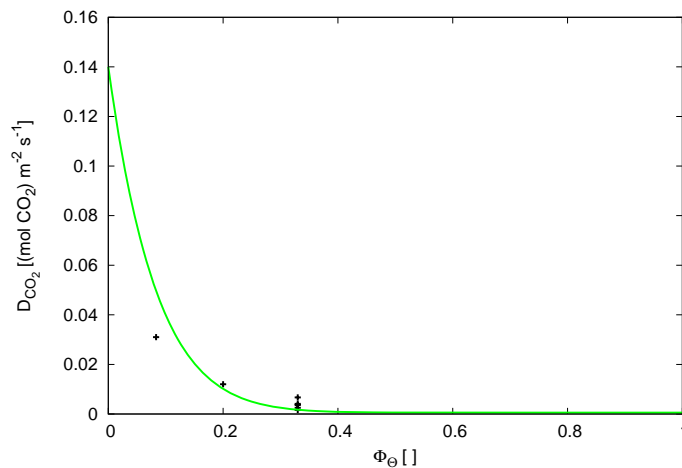


Fig. B10. Diffusivity for CO₂, D_{CO_2} , as a function of water saturation Φ_{θ} . The black data points are derived from the studies listed in the right column.

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Overview

References

Nash III (1996, p. 157)

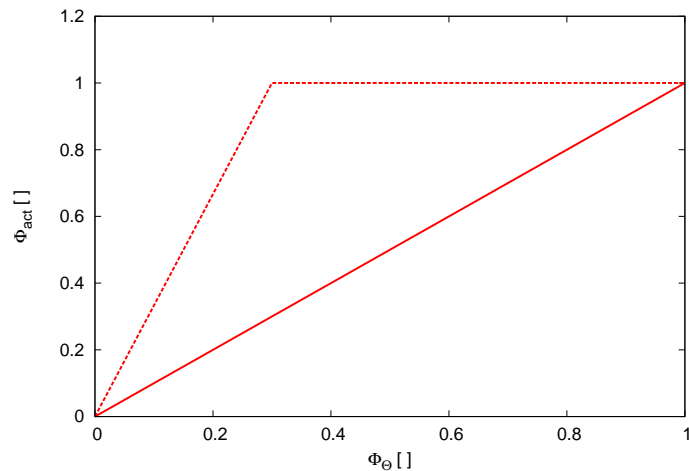


Fig. B11. Metabolic activity Φ_{act} as a function of water saturation Φ_{θ} . The dashed line corresponds to $x_{\Phi_{\theta,sat}} = 0.3$ and the solid line corresponds to $x_{\Phi_{\theta,sat}} = 1.0$.

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

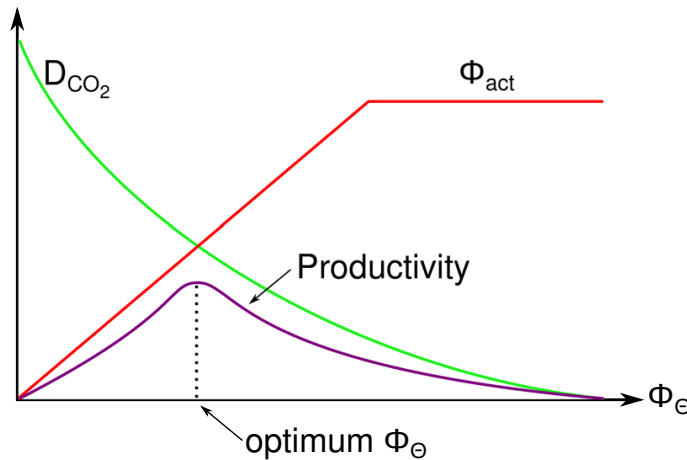


Fig. B12. Effect of water saturation Φ_{Θ} on CO_2 diffusivity D_{CO_2} , metabolic activity Φ_{act} and on the associated productivity. The productivity has a maximum at an optimum Φ_{Θ} .

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[◀](#)[▶](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

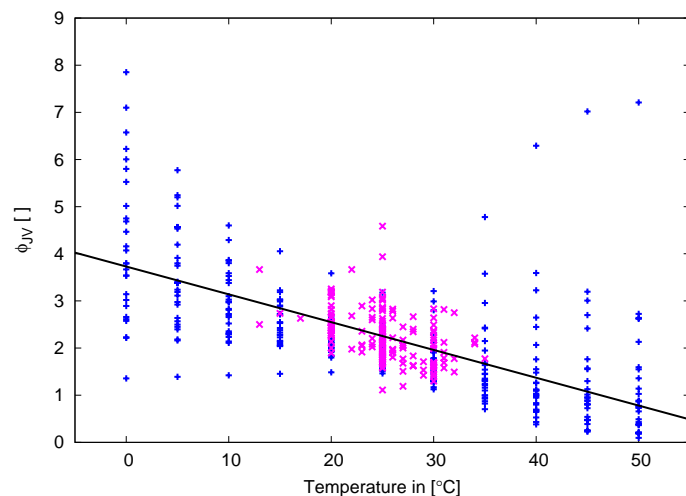
Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Overview

References



Wullschlegler (1993)

Kattge and Knorr (2007)

Fig. B13. Ratio of J_{\max} to $V_{C,\max}$, ϕ_{JV} , (black line) as a function of temperature. The magenta data points are taken from the study of Wullschlegler (1993) while the blue points are derived by the equations used in Kattge and Knorr (2007).

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Overview

References

Reinhold et al. (1989)

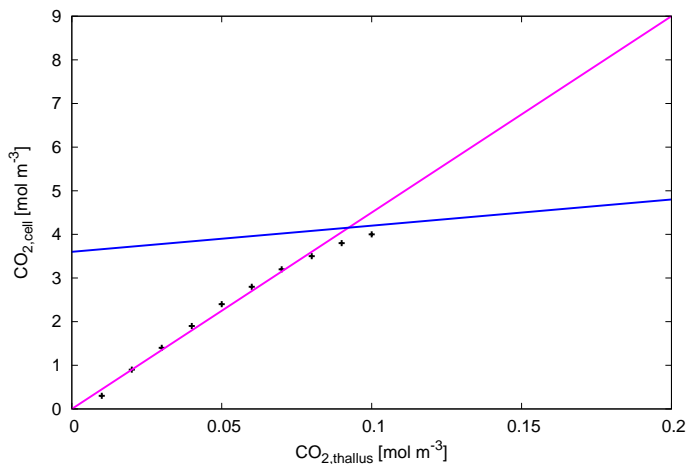


Fig. B14. CO₂ concentration in the chloroplasts, CO_{2,cell}, as a function of pore space CO₂ concentration CO_{2,thallus}. The black data points are taken from the study of Reinhold et al. (1989). The minimum of the magenta and blue lines is used to fit the data.

Estimating global carbon uptake by lichens and bryophytes

P. Porada et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

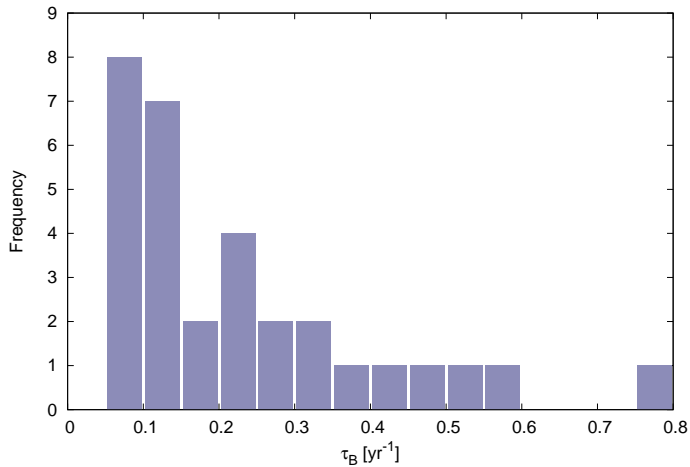
[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

Distribution



References

Stevenson and Coxson (2003)
 Boucher and Nash III (1990a)
 Boucher and Nash III (1990b)
 Russell (1990)
 Peltoniemi et al. (2004)
 Clark et al. (1998)

Fig. B15. Overview of the distribution of turnover rate τ_B .