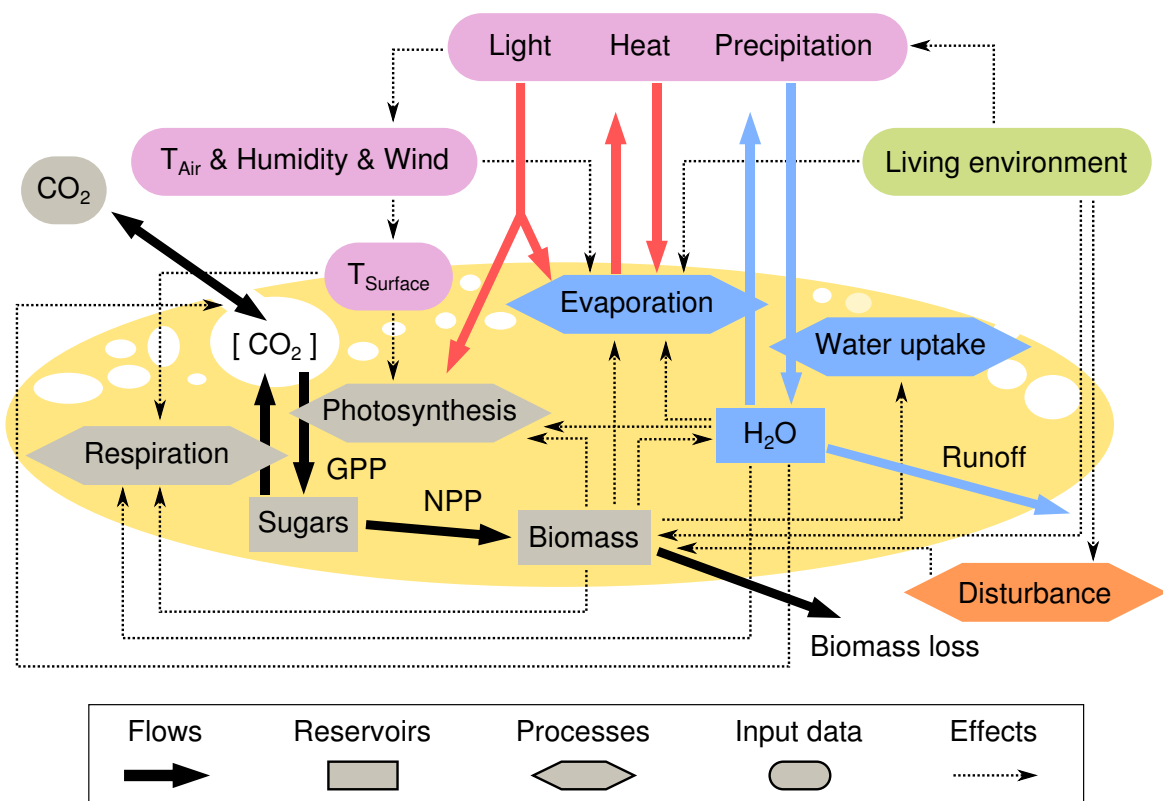


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Process-based Modelling of Lichens and Bryophytes and their Role in Global Biogeochemical Cycles

by
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Process-based Modelling of Lichens and Bryophytes and their Role in Global Biogeochemical Cycles

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1. Introduction

Lichens and bryophytes are a highly adaptive and functionally diverse group of organisms. They are known for their ability to survive in extreme environments and for their large variety of shapes and colours. But what role do they play in the earth system? More precisely, to what extent do these organisms influence global biogeochemical cycles, such as the carbon cycle? Although they have been suggested to have significant impacts on terrestrial biogeochemistry, few studies provide numbers to substantiate these claims at the global scale. This thesis presents methods to quantify the biogeochemical impacts of lichens and bryophytes for large regions. Thereby, it allows for an assessment of the role these organisms play in global biogeochemical cycles.

1.1. Distinctive properties of lichens and bryophytes

Lichens and bryophytes show characteristic physiological properties which distinguish these organisms from vascular plants.

Lichens, for a start, are no real plants, but a symbiosis of a fungus and at least one green alga or cyanobacterium. The fungal partner of the symbiosis is called *mycobiont* and the algal/cyanobacterial partner is called *photobiont* due to its ability for photosynthesis. The body of a lichen is called *thallus* and it consists of fungal hyphae which enclose the symbiotic algae or cyanobacteria (see Fig. 1.1). The shape of the thallus varies largely between species, it can be flat, leafy, branched like a little shrub or hair-like (see Fig. 1.2). It can even assume a gelatinous or powdery form. The maximum size of the thallus is also species-specific. It ranges from less than a mm² to a length of over 2 m (Nash III, 1996, p. 4). Furthermore, lichen species differ considerably in growth rate, with maximum rates of several mm yr⁻¹, and some species can reach an age of over 1000 years (Nash III, 1996, p. 4). The mycobiont is able to produce many different pigments, which contributes to a large variety of thallus colours observed in lichens, ranging from white, yellow or orange to green, brown, gray or black (see Fig. 1.2).

The lichen symbiosis may result in advantages for both partners. The mycobiont may protect the photobiont from excessive light, it may act as a water reservoir and it may enlarge the surface area for acquisition of water and nutrients. The photobiont, in turn, provides products of photosynthesis. If the photobiont is a cyanobacterium, it can also contribute to the nutrient supply by fixation of atmospheric nitrogen. It is not entirely clear, however, if the lichen symbiosis is truly mutualistic. The mycobiont may benefit more, as indicated by the slower growth of symbiotic algae compared to their free living relatives (Ahmadjian, 1993). Nevertheless, the symbiosis allows both partners to expand into habitats where they could not survive on their own, such as dry areas in case of algae or areas without carbon sources in case of fungi.

Bryophytes are a category of non-vascular plants which comprises mosses, liverworts and hornworts. These plants are called non-vascular because they lack true vascular tissue containing lignin. Some species, however, possess cells specialised for the transport of water and nutrients. Instead of roots, bryophytes have rhizoids which serve mainly for attachment (see Fig. 1.1). Bryophytes are usually small, not larger than 10 cm. Some species, however, may reach a height of 1 m (Bell and Hemsley, 2011, p. 102).

An alternative way to differentiate between bryophytes and vascular plants is by means of their life cycle: Land plants show an alternation of generations, which means that a diploid sporophyte produces haploid spores by meiosis. These spores then develop into haploid gametophytes by mitosis. The fully developed gametophytes then produce haploid gametes, meaning sperm and eggs, which combine into the next generation of diploid sporophytes. In vascular plants, usually the sporophyte is the dominant part of the life cycle, such as a tree, for instance, while the gametophyte is small and short-lived such as a pollen grain. In bryophytes, however, the gametophyte is dominant while the sporophyte is small, attached to the gametophyte and dependent on nutrient supply from the gametophyte.

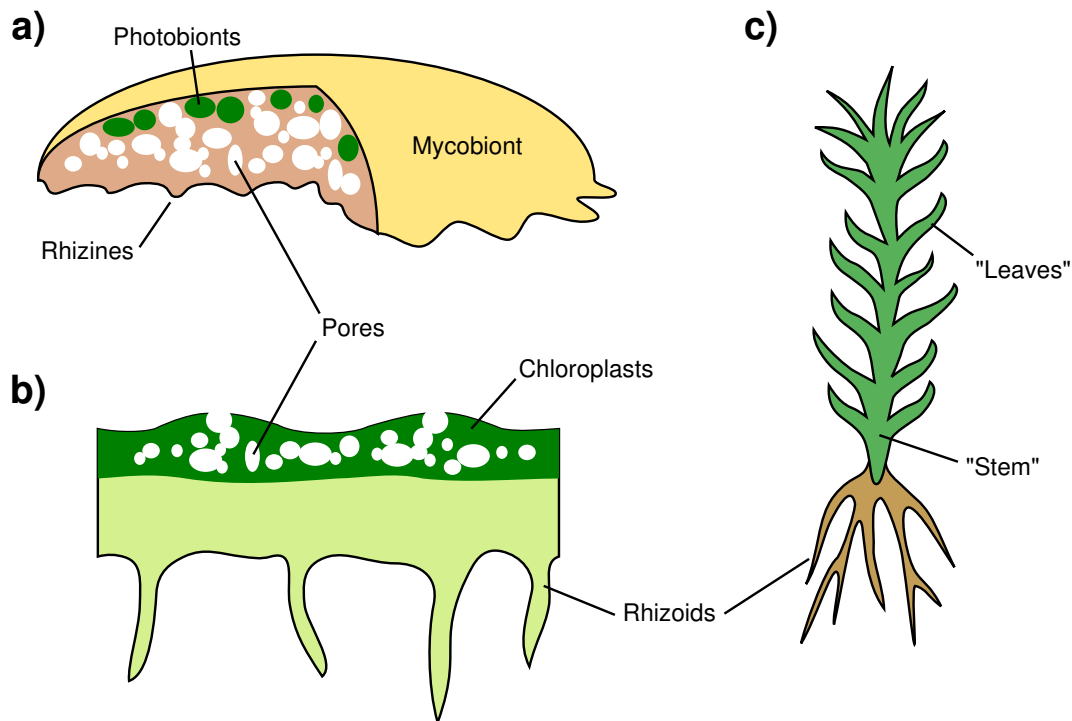


Figure 1.1.: Overview of the structures of lichens and bryophytes: a) example of a cross section of a leafy lichen. In the upper part of the thallus the photobionts are located, the middle layer contains air-filled pores and at the bottom of the thallus rhizines for attachment can be found b) cross section of a liverwort. Similar to a leafy lichen, the upper part of the thallus is rich in chloroplasts and the bottom bears rhizoids c) profile of a typical moss, showing non-vascular "leaves" arranged around a non-vascular "stem" and rhizoids at the bottom.

Mosses, liverworts and hornworts can be distinguished by several morphological features: Mosses always have a stem covered with leaves (see Fig. 1.1). Both stem and leaves are not particularly differentiated compared to vascular plants (see Fig. 1.2). Moreover, the rhizoids of mosses are multicellular. Liverworts, in contrast, always have single-celled rhizoids and most of them also have cells containing oil bodies, which most of the other bryophytes lack. Liverworts are mostly flat and compact or leafy with lobed and segmented leaves and flattened stems (see Fig. 1.2). Hornworts have a horn-shaped sporophyte and the cells of most species contain pyrenoids, which are assemblages of a chloroplast and other organelles.

Lichens and bryophytes populate various habitats around the world. They live on rock surfaces and some lichens even live in the rock interior in the upper zone where light is still available. Lichens and bryophytes also grow on soil surfaces such as desert sand, for instance, and they form carpets on the forest floor at high latitudes. Under wet conditions, the growth of mosses can lead to the formation of extensive peatlands. As epiphytes, lichens and bryophytes cover branches and leaves of plants. Lichens can be tightly attached to their substrate like a crust or they can be loosely attached, hanging like curtains from the branches of trees, for example. Since lichens and bryophytes have no real roots but only rhizines/rhizoids for attachment, they have to acquire water and nutrients from the atmosphere or directly from the substrate.

Both lichens and bryophytes 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 comparable to those of vascular plants. Consequently, the thallus is frequently in a dry state. Most species, however, are able to tolerate this state of desiccation by inactivating their metabolism. They can reactivate as soon as the thallus is moistened again. For many lichens and bryophytes even dew or fog are sufficient for activation, they are not dependent on liquid water from rain or snowmelt. The length of the dry period a lichen or bryophyte can tolerate without damage is species-specific and it is usually related to the climatic conditions of the habitat. Hence, the high adaptability of these organisms results from avoiding extreme environmental conditions rather than coping with them. This allows them to populate a large range of habitats.

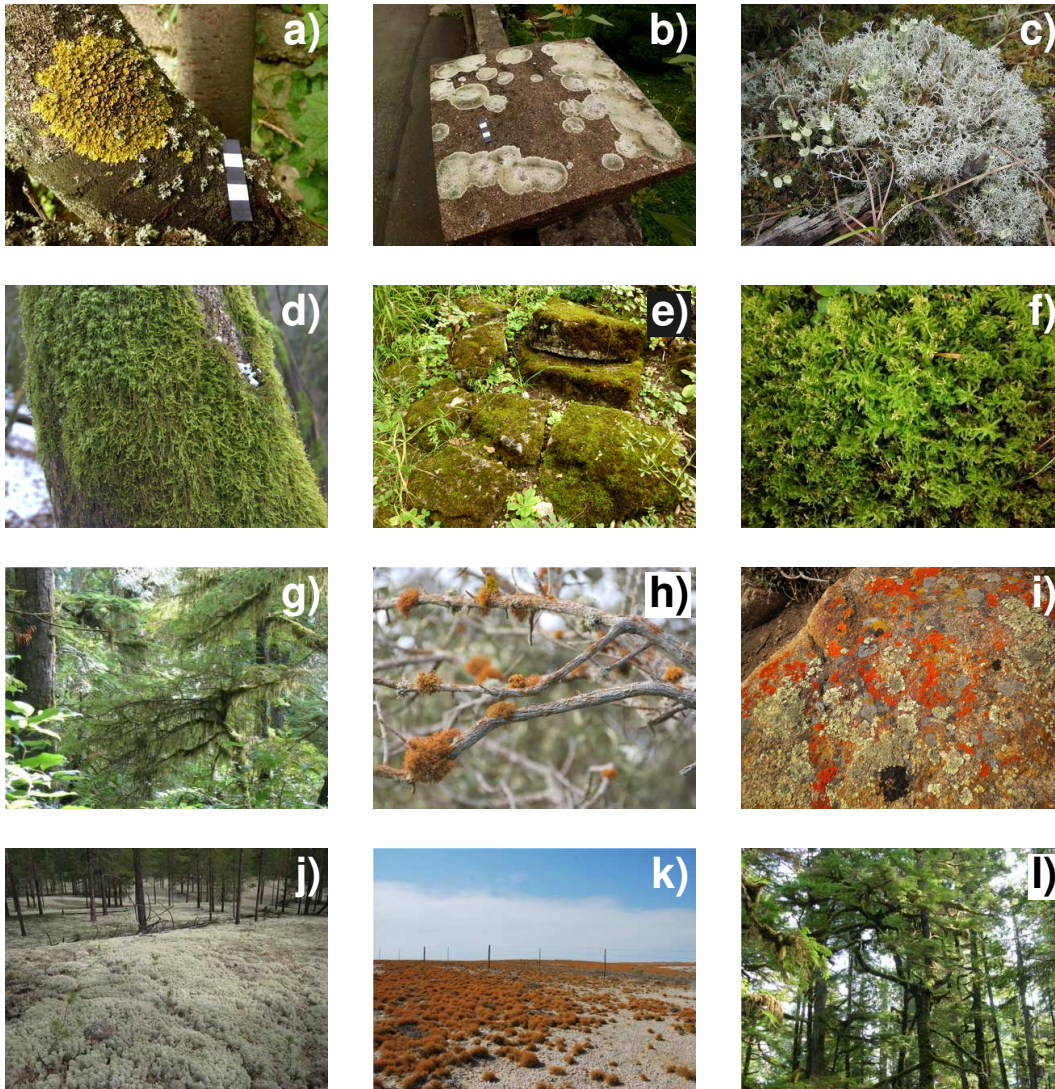


Figure 1.2.: Pictures of lichens and bryophytes: a) lichen *Xanthoria parietina* on a tree branch in Germany b) lichen *Lecanora* sp. on a stone wall in Germany. The scale bar on the pictures a) and b) has a length of 5 cm c) close-up of the lichen *Cladonia rangiferina* in Siberia d) moss on the trunk of a tree in a forest in Luxembourg e) moss on boulders in a park in Germany. The size of the boulders is approximately 30 cm f) close-up of the moss *Plagiomnium undulatum* in a park in Germany. The field of view has a width of approximately 5 cm g) epiphytic beard lichens in a forest on Vancouver Island, Canada h) epiphytically growing lichen *Teloschistes capensis*, at Cape Point, South Africa i) lichens of various colours on a granite rock in the Alps j) mats of the lichen *Cladonia stellaris* on the floor of a Siberian forest j) lichen fields in the Namib desert at Alexanderbay, South Africa l) trees covered with lichens and mosses on Vancouver Island, Canada (Pictures by courtesy of Susanne Arens (i), Axel Kleidon (c,j), Maik Renner (d), Hartmut Thiel (g,l) and Bettina Weber (h,k)).

1.2. Global biogeochemical impacts of lichens and bryophytes

Lichens and bryophytes have been suggested to play a major role in global biogeochemical cycles, at present day as well as throughout Earth's history.

One example for this is the exchange of carbon with the atmosphere due to photosynthesis and respiration. According to Elbert et al. (2012), the global net carbon uptake by lichens and bryophytes amounts to 7% of terrestrial net primary productivity (NPP). This value is comparable to the annual release of carbon by burning of biomass or by combustion of fossil fuels, respectively.

A more significant impact of lichens and bryophytes on global biogeochemical cycles may result from biological nitrogen fixation (BNF), which is carried out by cyanobacteria. These organisms are not only free-living, e.g. in biological soil crusts, but they also participate as photobionts in the lichen symbiosis or live on the surface of bryophytes (Cornelissen et al., 2007). According to Elbert et al. (2012), they are responsible for roughly 50% of terrestrial nitrogen fixation by vegetation (Galloway et al., 2004). The relative importance of lichens and bryophytes for BNF varies between ecosystems. Regarding northern European boreal forests, for instance, DeLuca et al. (2002) find that the symbiosis between cyanobacteria and feather moss is a main source of biologically fixed nitrogen.

Another example for the influence of lichens and bryophytes on global biogeochemistry is biotic enhancement of surface weathering rates. The organisms affect both physical as well as chemical weathering processes. Enhancement of chemical weathering results from the release of oxalic acid and other lichen compounds, alkalinolysis, and respiratory CO₂ (Berthelin, 1988; Chen et al., 2000; Büdel et al., 2004; Weber et al., 2011). Lenton et al. (2012) implemented the enhancement of weathering by early non-vascular plants into a biogeochemical model of the Phanerozoic. In this way, they were able to simulate a significant drawdown of atmospheric CO₂ during the Ordovician via silicate weathering. A further decrease in atmospheric CO₂ levels was attributed to enhanced marine productivity due to the release of phosphorus from weathered rocks into the oceans. This also implies an impact of early non-vascular plants on the phosphorus cycle. The decrease in simulated global surface temperature resulting from the marine CO₂ sink explained Ordovician glaciations. The importance of biologically enhanced weathering for the regulation of the surface temperature of the Earth is also illustrated by the work of Schwartzman and Volk (1989). They show that the maintenance of planetary habitability during evolution depended on the cooling effect of biotic weathering. Another possible relation between enhanced weathering and planetary evolution is suggested by Kennedy et al. (2006). They propose that the increased degree of weathering of soil material caused by primitive biota promoted the burial of organic carbon towards the end of the Proterozoic. This may have caused a rise in atmospheric O₂ which is a possible explanation for the evolution of multicellular life.

To summarise, there are many indications for considerable impacts of lichens and bryophytes on biogeochemical cycles, today and in the geological past.

1.3. Goal of this thesis

So far, attempts to quantify the role of lichens and bryophytes in global biogeochemical cycles have been based on empirical upscaling from measurements. Elbert et al. (2012), for instance, use a large amount of data from field experiments or laboratory measurements to estimate characteristic median values of net carbon uptake as well as biological 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 the uptake of carbon and the fixation of nitrogen.

The goal of this thesis is to develop an alternative, process-based modelling approach to quantify impacts of lichens and bryophytes on biogeochemistry at the global scale. This modelling approach does not depend on extrapolation from measurements. Instead, it is based on the fact that climate and other environmental factors control the potential of lichens and bryophytes to influence biogeochemical cycles, e.g. via the supply of light or water. Consequently, the model relates climate and environmental factors to biogeochemical functions of lichens and bryophytes. Thereby, the focus is on biogeochemical cycles of carbon, nitrogen and phosphorus and on chemical weathering.

The approach consists of the following steps:

- A process-based numerical model is designed which captures the relevant relations between carbon uptake by lichens and bryophytes and climate and other environmental factors.
- The model is used to estimate carbon uptake by lichens and bryophytes at the global scale. The estimates are then compared to observational data to assess the assumptions behind the model.
- The estimated carbon uptake by lichens and bryophytes is related to their requirements for nitrogen and phosphorus via the nutrient content of biomass. In this way, potential nitrogen and phosphorus uptake by lichens and bryophytes are derived. To estimate potential chemical weathering by the organisms, their phosphorus requirements are translated into weathered rock by assuming that they obtain phosphorus from surface rocks. Also these estimates are compared to observational data for evaluation.

The estimates presented here allow for an assessment of the significance of lichens and bryophytes for global biogeochemical cycles of carbon, nitrogen and phosphorus and for chemical weathering. Moreover, this process-based approach could add credibility to the existing, empirically derived estimates of global biogeochemical impacts of lichens and bryophytes.

Developing a model of global carbon uptake by lichens and bryophytes, however, is not straightforward, although the influences of climate factors on carbon uptake by these organisms have been analysed by numerous studies at the regional scale and in laboratory experiments (e.g. Brostoff et al. (2005); Cowan et al. (1992); Green et al. (1998); Lange (2002); Palmqvist and Sundberg (2000); Sundberg et al. (1997)). The

difficulties in translating climate relations from the regional or laboratory scale to a global model are mainly due to spatio-temporal variation of climate factors and large functional variation of lichen and bryophyte species.

The uptake of carbon by lichens and bryophytes, for example, is strongly dependent on their water content, which is controlled by the supply of water by rainfall, fog or dew and the loss of water by evaporation. These factors are temporally variable. In deserts, for instance, water uptake can be limited to a short period of dewfall before dawn. Consequently, to predict carbon uptake as a function of water content, climate factors controlling water supply and loss have to be provided in form of a time series with high resolution and also the water status of the organism has to be tracked. This applies in a similar way also to other factors which influence carbon uptake, such as light and temperature. Furthermore, the considerable spatial variation of the climate factors at the global scale has to be explicitly represented in the model, since it may lead to large differences in carbon uptake between regions. At high latitudes, for example, carbon uptake by lichens and bryophytes on the ground can reach high values, while it is usually much lower on the floor of the tropical rainforest. This can be explained by differences in the light and temperature conditions of the two locations (Nash III, 1996, p. 176).

Not only the climate factors have to be represented in a sufficient temporal and spatial resolution in the model, also further properties of the environment have to be considered. Lichens and bryophytes which grow as epiphytes in the canopy, for instance, experience climatic conditions different from those on the ground. Hence, the model should distinguish between these two locations of growth. Disturbance, such as fire or herbivory, is another factor that may significantly affect carbon uptake by lichens and bryophytes and that should therefore be represented in the model.

Even if climate and other environmental conditions are well known, it is not trivial to relate these factors to carbon uptake by lichens and bryophytes at the global scale. This is due to the high functional variation of lichen and bryophyte species. Since the organisms vary strongly in their physiological properties, it is impractical to use globally uniform relations between environmental or climate factors and carbon uptake. Photosynthesis, for example, usually shows a temperature optimum. If a globally uniform value of optimum temperature was used, carbon uptake by the organisms would show a latitudinal pattern, with a maximum value where the surface temperature equals the optimum temperature of photosynthesis. In reality, however, lichen and bryophyte species differ in their optimum temperature of photosynthesis. Thus, neglecting this interspecific variation would lead to biases in the estimate of carbon uptake. Therefore, the relations between climate and carbon uptake should also take into account the functional variation of lichens and bryophytes. This is also true for the relations between carbon uptake and requirements for nitrogen and phosphorus.

The derivation of nitrogen fixation and phosphorus uptake from rocks by lichens and bryophytes based on their carbon uptake is associated with further challenges. Quantifying the requirement of the organisms for nutrients does not automatically determine their actual rates of nitrogen fixation and phosphorus extraction, since alternative sources for these nutrients may exist. Both nitrogen and phosphorus could be obtained through de-

position on the thallus from the atmosphere or they could be taken up directly from the substrate. Therefore it should be tested to what extent the potential rates approximate the actual rates of nitrogen fixation and phosphorus uptake from surface rocks.

1.4. Outline of the thesis

In the following two chapters, detailed methods are presented to quantify the impacts of lichens and bryophytes on global biogeochemical cycles. Both chapters have been submitted in similar form to scientific journals¹.

Chapter 2 focuses on modelling carbon uptake by lichens and bryophytes at the global scale. The model is described and the estimates predicted by the model are compared to observational data of carbon uptake. The limitations of the model are discussed in detail. This chapter has been submitted to *Biogeosciences*².

Chapter 3 describes how estimates of carbon uptake by lichens and bryophytes obtained from the model are utilised to predict potential nitrogen and phosphorus uptake and chemical weathering by these organisms. The estimates are compared to observations and their plausibility is discussed. This chapter has been submitted to *Global Biogeochemical Cycles*.³

Chapter 4 contains a summary of the findings presented in this thesis. They are partitioned into *General outcomes* of the approach, its *limitations* and the associated *implications*. The chapter concludes with several suggestions for future applications of the methods presented here.

In the appendix, a detailed description can be found of the model of carbon uptake by lichens and bryophytes. It includes all model equations, parameters and variables and short descriptions of all processes implemented in the model. Moreover, the appendix contains additional model output which complements the estimates presented in Chapter 2.

¹The contributions of the four co-authors to the two submitted journal articles were in the form of scientific comments to the text and provision of literature references.

²Porada P, Weber B, Elbert W, Pöschl U, Kleidon A, Estimating global carbon uptake by lichens and bryophytes with a process-based model. *Biogeosciences*, *in press*

³Porada P, Weber B, Elbert W, Pöschl U, Kleidon A, Estimating impacts of lichens and bryophytes on global biogeochemical cycles of nitrogen and phosphorus and on chemical weathering *Global Biogeochemical Cycles*, *accepted*

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

In this chapter, a process-based modelling approach is presented which aims at estimating global net carbon uptake by lichens and bryophytes as a function of environmental conditions, such as climate¹. To explain the structure of the model, it is described how lichens and bryophytes are represented as components of an ecosystem, how the uptake of carbon depends on climate, environmental factors and the physiological status of the organisms themselves, and how the relations between carbon uptake and environmental conditions are parameterised. Thereby, a special emphasis is laid on the representation of the functional variation of lichens and bryophytes in the model. By running the model with climate forcing data and additional information about the environment, estimates of global net carbon uptake by lichens and bryophytes are obtained. These estimates are presented as global maps of carbon uptake and they are evaluated by comparing the simulated values to observational data. To further assess the model, a sensitivity analysis is performed. The results of the simulation are extensively discussed at the end of the chapter.

This is the first process-based model which quantifies net carbon uptake by lichens and bryophytes at the global scale. Most previous modelling studies which include lichens and bryophytes focus on net primary productivity (NPP) of moss in boreal and arctic regions, especially in peatlands (see e.g. Wania et al. (2009); Frolking et al. (2002); Yurova et al. (2007)). Others focus on ecosystem responses to climate change (Bond-Lamberty and Gower, 2007; Euskirchen et al., 2009; Zhuang et al., 2006; Turetsky et al., 2012), simulating peat accumulation (Frolking et al., 2010) or peatland microtopography (Nungesser, 2003). The model presented here aims at a more general representation of lichens and bryophytes that makes it possible to estimate the productivity of these organisms under a broad range of environmental conditions around the globe.

The model is similar to many global vegetation models (see Fig. 2.1). 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

¹Note that the term “net carbon uptake” is used throughout the thesis, instead of “Net Primary Productivity” (NPP). While NPP is a standard term for vascular vegetation which is frequently used in the modelling community, “net carbon uptake” is more general and descriptive. In the context of this thesis, it corresponds to NPP. Furthermore, “Carbon” is abbreviated with a capital “C” and it is placed next to the corresponding unit symbol throughout the thesis. This is done in order to avoid confusion with biomass or CO₂. To distinguish “C” from another unit symbol, “C” and the associated unit symbol are put in brackets. In the appendix, further abbreviations are used to clarify the units of model parameters and variables where necessary. These are CO₂, O₂, “Rubisco”, e⁻ (electrons) and H₂O.

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, the lichen and bryophyte model describes the organisms 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. The lichen and bryophyte 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.

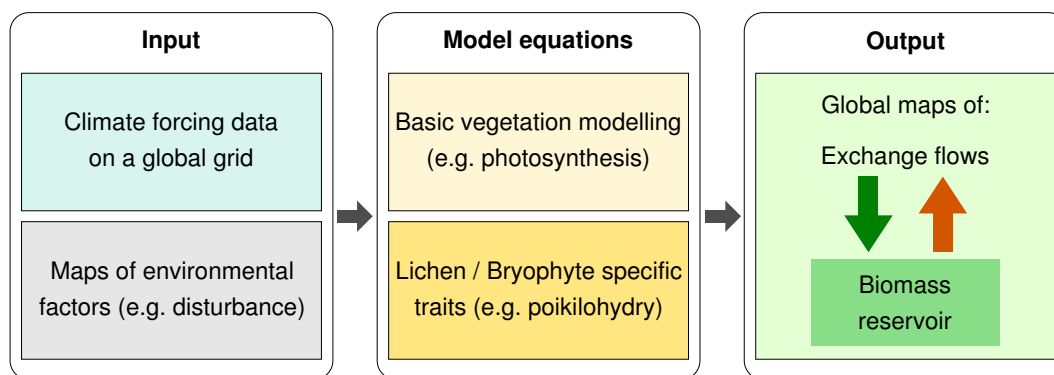


Figure 2.1.: Overview of the functioning of the model. Input data are translated via model equations into exchange flows of carbon, which are used to calculate changes in the biomass reservoir.

The chapter is structured in the following way: Sect. 2.1 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. 2.2 together with an evaluation of the model performance. Furthermore, the uncertainty regarding the values of model parameters is assessed through a sensitivity analysis. In Sect. 2.3 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.

2.1. 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. Regarding lichens, the biomass of the fungal and the algal/cyanobacterial partner are simulated in an aggregated form as one pool of biomass with average properties.

Changes in the size of the 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 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.

2.1.1. Model processes

In the following, the physiological processes implemented in the model are described. First, the effects of the living environment on lichens and bryophytes are named. Then, it is explained how water content and climatic factors relate to physiological properties of the organism. Finally, the exchange flows between the organism and its environment are described

For simplicity, equations are omitted in the text. Instead, 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 B.7 to B.13 in the appendix.

Living environment

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. 2.2). 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 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. 2.2). 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 by the available area.

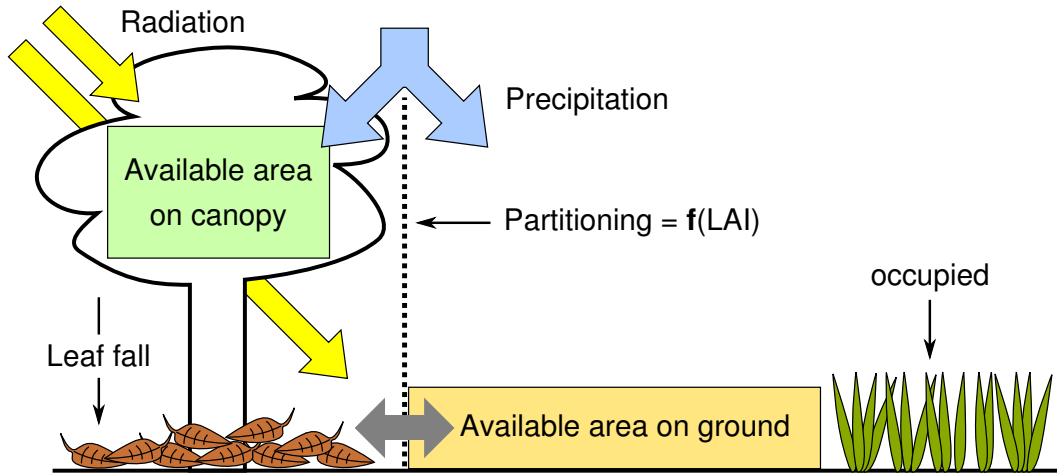


Figure 2.2.: Effect of the Leaf Area Index (LAI) on area for growth and climate forcing. Available area on ground is a linearly decreasing function of LAI. The same function is used to partition precipitation between canopy and soil. The vertical distribution of light is calculated according to Beer's law as a function of LAI.

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.

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 saturation, 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 saturation to a maximum value of 0 at a certain threshold saturation. If the water saturation 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 determines both the relative strength of photosynthesis as well as that of respiration as a function of water saturation (Lange, 1980, 2002; Lidén et al., 2010; Williams and Flanagan, 1998). The metabolic activity is assumed to increase linearly from 0 at zero water saturation to 1 at the threshold saturation. It remains 1 if the water saturation 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.

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.

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

Exchange flows

A schematic of the exchange flows of carbon and water between lichens and bryophytes and their environment is shown in Fig. 2.3 together with relations to climate forcing and reservoirs inside the thallus.

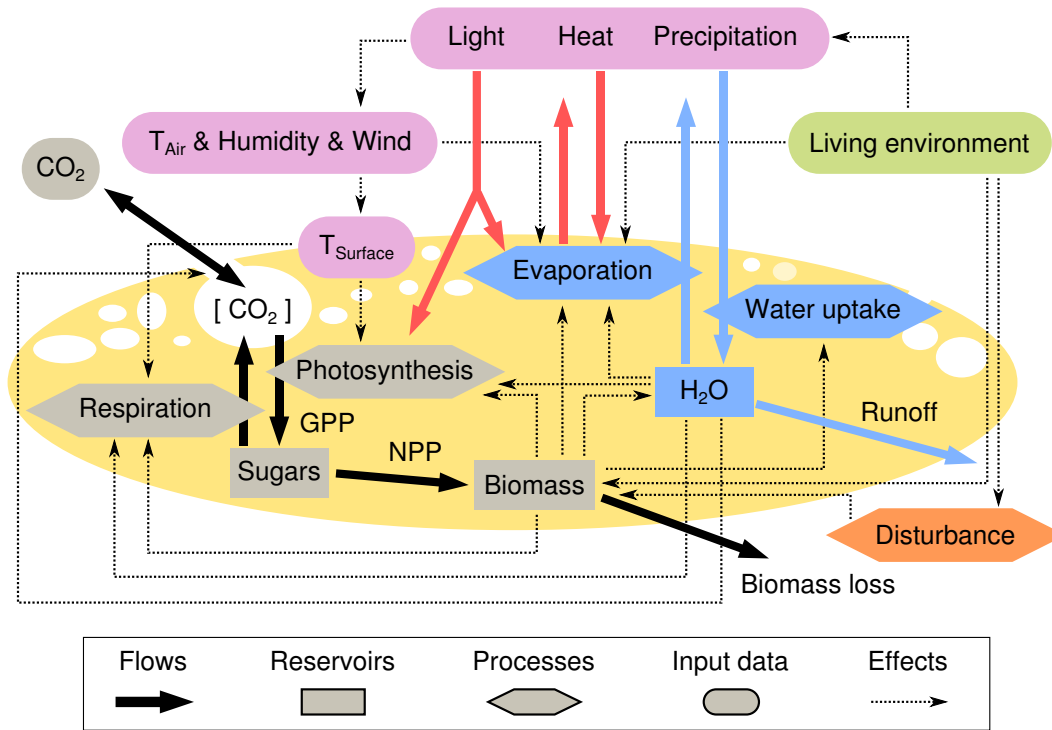


Figure 2.3.: Schematic of the carbon and water relations of a lichen or bryophyte simulated by the model. Dotted arrows illustrate effects of climate forcing, living environment and state variables on physiological processes of a lichen or bryophyte. These processes are associated with exchange flows (solid arrows) of carbon (black), water (blue) and energy (red).

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 Q₁₀ 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 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.

2.1.2. 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. Here, these parameterisations are called “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. 2.4).

The studies of Bloom et al. (1985); 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 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 B.9 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

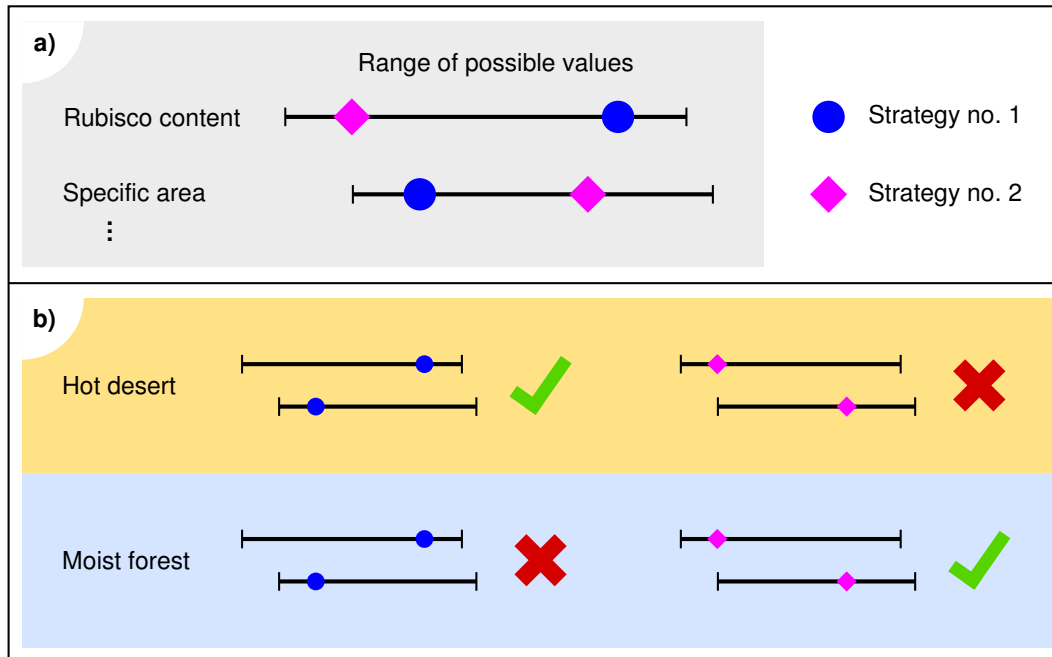


Figure 2.4.: Generation of physiological strategies and their survival. a) Many random parameter combinations (strategies) are sampled from ranges of possible values. The strategies are then run in each grid cell of the model. b) Example: In a hot desert, strategy 1 survives, because a small specific 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.

(CCM) or not. For the model, it is assumed that the CCM in lichens works similarly than in free living cyanobacteria. Based on this assumption, the CCM implemented in the model represents an advantage for the organisms in case of low internal CO_2 concentrations in a water saturated thallus. 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. Note that in lichens, fungal as well as algal/cyanobacterial biomass contribute to respiration while only the algal/cyanobacterial biomass contains Rubisco. In the model, however,

lichen respiration is assumed to be controlled by the Rubisco content averaged over the total biomass.

The relationships between parameters are called tradeoffs and they are assumed to have constant values. This means that although the value of one parameter (e.g. Rubisco content) may vary across species, the tradeoff-function which relates this parameter to another one (e.g. respiration) should be more or less the same for many different species.

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 CO_2 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 ($V_{\text{C,max}}$). Since both rates represent costs for the 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 CO_2 , but to increase the CO_2 concentration in the photobionts. If the organism is limited by low CO_2 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 B.10.

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 B.11.

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 B.8.

2.1.3. 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 hours 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 B.3). 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 it is assumed 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 a weight of one is assumed 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 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 for several biomes. Hence, for each biome the spatial average of simulated net carbon uptake is compared to a “characteristic”, observation-based value of net carbon uptake on an order-of-magnitude basis. This rough method of model-data comparison results from the difference in scale between model estimates and observations: The observational data are spatially and temporally discrete point-scale measurements which show a high variation, e.g. 8-1450 (g biomass) m⁻² yr⁻¹ for *Sphagnum* (Gunnarsson, 2005). It is very problematic to extrapolate from these variable point measurements to large regions, such as a model grid cell, which is about 50000 km² at 45°N. In order to quantify net carbon uptake at the large scale of a model grid cell, the point-scale values would have to be weighted by area coverage. High-resolution data that relate coverage to net carbon uptake, however, are not available at large scales. Therefore, a “characteristic” value of net carbon uptake for a large region is estimated instead. This region should not be a grid cell of the model, since the grid is an artificial segmentation of the landscape. Instead, the biome classification is used as a basis for the model-data comparison. Biomes are homogeneous regarding climate and ecology at the large-scale. Hence, they allow for the estimation of a “characteristic”, observation-based value of net carbon uptake.

To obtain a “characteristic” value of net carbon uptake for each biome, the median of all measurements is computed which are listed in the studies associated with this biome. The median is used instead of the mean of all values, because computing the mean implicitly assumes equal weights for all values. As discussed above, these weights are not known.

The studies selected for the model-data comparison are limited to those which report estimates of average, long-term net carbon uptake based on surface coverage of lichens or bryophytes. Studies which estimate only maximum rates of carbon uptake or carbon uptake per area lichen/bryophyte or per gram biomass cannot be used. To include such studies, assumptions would have to be made about the active time of lichens and bryophytes throughout the year, about their ground coverage etc. Hence, the modelled estimates would not be compared to data but to another, empirical model. These criteria lead to the exclusion of many studies which measure productivity of lichens and bryophytes. Consequently, only 4 out of 14 biomes are represented in the field studies: Tundra, boreal forest, desert and tropical rainforest.

For a list of studies used in the model-data comparison see Table 2.1. The list does not comprise all existing studies which provide observational data on net carbon uptake of lichens and bryophytes. It should be sufficient, however, to illustrate the order of magnitude of net carbon uptake.

The model is run for 2000 years with an initial number of 3000 strategies. The simulation length of 2000 years 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 years of the simulation, since this period corresponds to the longest disturbance interval in the model. The simulation described above takes 7 days on 48 processors of a parallel computer. The source code (written in Fortran 95) is available on request (pporad@bgc-jena.mpg.de).

Table 2.1.: Overview of the studies used to evaluate the model. The value in brackets in the column “Net carbon uptake” corresponds to the number of observations contained in the respective study. A ‡-symbol denotes studies which provide one or more ranges instead of single values. In these cases, the mean value is calculated of the upper and lower bound of each range and the range of these calculated mean values is shown in the table. If net carbon uptake is reported in units of gram biomass, a factor of 0.4 (relative weight of carbon in CH₂O) is used as a conversion factor for carbon.

Study	Biome	Net carbon uptake [(g C) m ⁻² yr ⁻¹]
(Billings, 1987)	Tundra	10
(Lange et al., 1998b)	Tundra	4.7 - 20.4 (4)
(Oechel and Collins, 1976)	Tundra	38.5 - 171 (2)
(Schuur et al., 2007)	Tundra	12 - 60 (3)
(Shaver and Chapin III, 1991)	Tundra	2 - 68 (4)
(Uchida et al., 2006)	Tundra	1.9
(Uchida et al., 2002)	Tundra	6.5
(Billings, 1987)	Boreal forest	9.7 - 78 (2)
(Bisbee et al., 2001)	Boreal forest	25
(Camill et al., 2001)	Boreal forest	9.2 - 75.9 (8)
(Gower et al., 1997)	Boreal forest	12
(Grigal, 1985)	Boreal forest	128 - 152 (2)
(Harden et al., 1997)	Boreal forest	60 - 280 (3) ‡
(Bond-Lamberty et al., 2004)	Boreal forest	0 - 297.1 (14)
(Mack et al., 2008)	Boreal forest	0.4 - 16.2 (7)
(Oechel and Van Cleve, 1986)	Boreal forest	40 - 44 (2)
(Reader and Stewart, 1972)	Boreal forest	14.4
(Ruess et al., 2003)	Boreal forest	29.2 - 31.2 (2)
(Swanson and Flanagan, 2001)	Boreal forest	104
(Szumigalski and Bayley, 1996)	Boreal forest	15.2 - 81.2 (10)
(Thormann, 1995)	Boreal forest	23.2 - 73.2 (3)
(Vogel et al., 2008)	Boreal forest	12 - 32 (9)
(Wieder and Lang, 1983)	Boreal forest	216 - 316 (3)
(Brostoff et al., 2005)	Desert	11.7
(Garcia-Pichel and Belnap, 1996)	Desert	0.54
(Jeffries et al., 1993)	Desert	0.07 - 1.5 (3) ‡
(Klopatek, 1992)	Desert	5.3 - 29 (4) ‡
(Clark et al., 1998)	Tropical forest	37 - 64 (2)

2.2. 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 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. To estimate the effect of uncertain model parameter values on the predictions of the model, a sensitivity analysis is performed.

2.2.1. Modelled net carbon uptake

The global estimate of net carbon uptake by lichens and bryophytes amounts to 0.34 (Gt C) yr⁻¹ for the “average” weighting method and 3.3 (Gt C) yr⁻¹ for the “maximum” weighting method (for a description of the weighting methods see Sect. 2.1.3). The global biomass is 4.0 (Gt C) (average) and 46 (Gt C) (maximum), respectively.

Maps are shown 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. 2.1.3. The maps are based on the “average” weighting method. The “maximum” weighting shows very similar patterns and the corresponding maps are shown in Fig. A.1 a) to d).

The net carbon uptake by lichens and bryophytes is shown in Fig. 2.5 a). In some areas, such as Greenland and the driest parts of deserts, none of the simulated lichen and bryophyte “strategies” (see Sect. 2.1.2) is able to survive and net carbon uptake is equal to zero there. The biomes differ largely with respect to carbon uptake. While deserts are characterised by the lowest productivity, the highest values are reached in the boreal zone and in the moist tropics. In the tropical rainforest the high productivity is mainly due to the high carbon uptake by epiphytic lichens and bryophytes (see Fig. 2.5 c)). In the boreal zone, lichens and bryophytes in the canopy as well as on the ground contribute significantly to carbon uptake (see Fig. 2.5 d)). Biomass (Fig. 2.5 b)) 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.

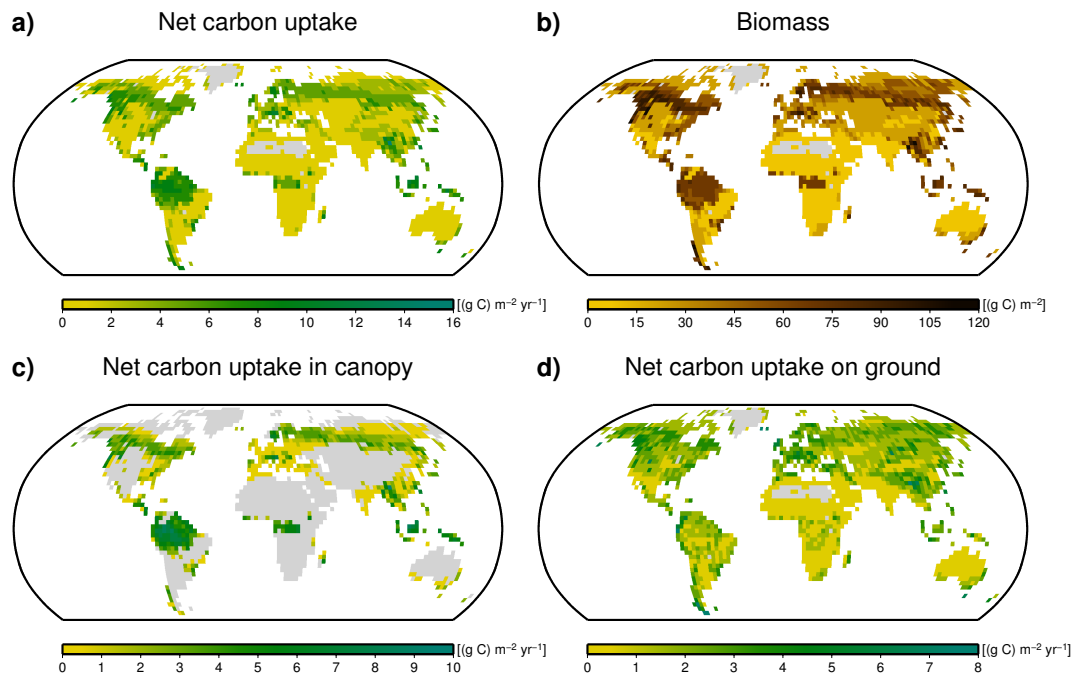


Figure 2.5.: Global maps of model estimates. a) Net carbon uptake by lichens and bryophytes. b) Biomass of lichens and bryophytes. c) Net carbon uptake by lichens and bryophytes living in the canopy. d) Net carbon uptake by lichens and bryophytes living on the ground. The estimates are based on time averages of the last 100 yr of a 2000-yr run with 3000 initial strategies. They correspond to the “average” weighting method (see Sect. 2.1.3). Areas where no strategy has been able to survive are shaded in grey.

Figure 2.6 a) 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. A.2. Figure 2.6 b) 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.

Figures 2.6 c) and 2.6 d) show the global patterns of two characteristic lichen and bryophyte parameters. As described in Sect. 2.1.2 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 2.6 c) 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. 2.6 d) 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 temperature and CCM fraction similar to those living on the ground. The corresponding maps are shown in Fig. A.2.

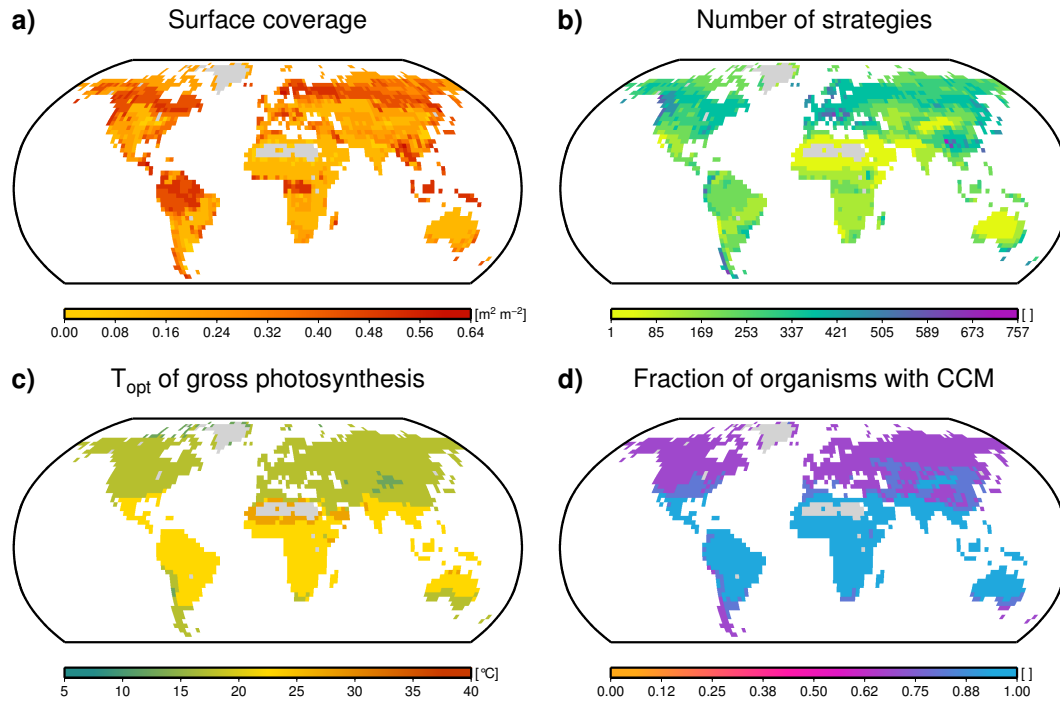


Figure 2.6.: Global maps of model estimates. a) Area covered by lichens and bryophytes per m^2 ground. b) Number of surviving strategies at the end of a model run. c) Optimum temperature of gross photosynthesis of lichens and bryophytes on the ground. d) Fraction of lichens and bryophytes on the ground 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. 2.1.3). Areas where no strategy has been able to survive are shaded in grey.

2.2.2. Evaluation

Figure 2.7 shows a comparison between model estimates and observational data with regard to net carbon uptake for four biomes. As discussed in Sect. 2.1.3, the observational data are point-scale measurements which show high variation. Therefore, the median of the observed values from a biome is used as a “characteristic” value of net carbon uptake. This median value is compared to the upper and lower bound of simulated net carbon uptake averaged over the biome (see Sect. 2.1.3 for a description how the bounds are derived). Also the variation of carbon uptake between the most and the least productive grid cell in a biome is shown for both bounds of the model estimates. Figure 2.7 illustrates that the model estimates are characterised by high variation. The range between the upper and lower bound of net carbon uptake is around one order of magnitude. The range of productivity of the grid cells in a biome is up to four orders of magnitude.

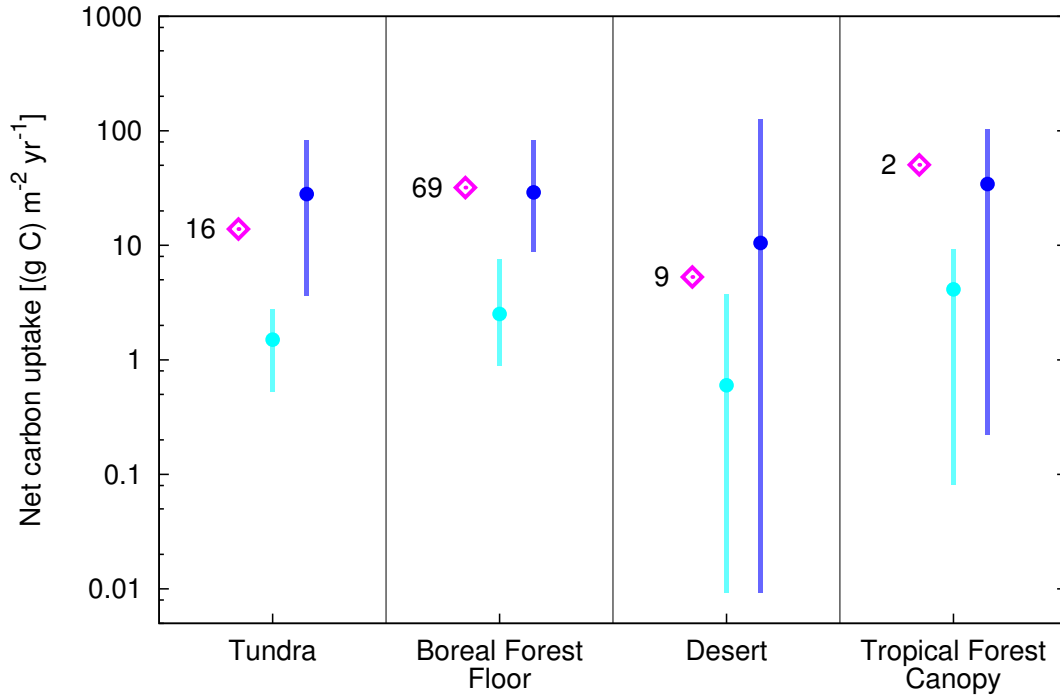


Figure 2.7.: Comparison of net carbon uptake estimated by the model to observational data. A magenta diamond corresponds to the median of the observed values in the respective biome. The number left to the diamond is the number of observed values. See Table 2.1 for an overview of the studies on which the observations are based. The light blue colour corresponds to the lower bound of the model estimate and the dark blue colour to the upper bound. The vertical bars represent the range between the most and least productive grid cell in a certain biome, while the dots show the mean productivity of all grid cells in this biome. To be consistent with the measurements from the field studies, only the simulated carbon uptake in the canopy is considered for the biome “Tropical Forest” while for the other biomes only carbon uptake on the ground is considered. The model results are derived from a 2000-yr run with 3000 initial strategies.

Considering the upper and lower bounds of simulated net carbon uptake in each biome,

the model estimates agree relatively well with the “characteristic” values of net carbon uptake derived from observational data. For the boreal zone and the tropical rainforest, the “characteristic” values are closer to the upper bound of net carbon uptake. In the boreal zone, the data-based value matches the simulated upper bound, in the tropical rainforest it exceeds the upper bound. Possible reasons for these patterns are discussed in Sect. 2.3.

2.2.3. Sensitivity analysis

As described in Sect. 2.1.2 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 exceeds the capacities of this work. Therefore, the parameter values are 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 a sensitivity analysis is performed (see Table 2.2). 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 B.8 and B.10.

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. 2.3. For reasons of computation time a different simulation setup (400 years, 300 strategies) is used for the sensitivity analysis. Therefore, the net carbon uptake values for the control run (Table 2.2) 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. A.2). It is thus assumed that the sensitivity of the model does not change significantly with increased simulation time and number of initial strategies.

Table 2.2.: Influence of uncertain model parameters on simulated net carbon uptake. “Average” and “Maximum” correspond to two different weighting methods for the results (see Sect. 2.1.3). 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
	-	+	-	+	
Change in parameter value					
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		

2.3. Discussion

In this chapter global net carbon uptake by lichens and bryophytes is estimated using a process-based model. In the following, the plausibility of the model estimates is discussed with respect to the patterns and the absolute values. Furthermore, an overview is given of the limits of the approach with a focus on the different sources of uncertainty in the model and possible improvements.

2.3.1. Global patterns of net carbon uptake

The model predicts plausible patterns of productivity and biomass (see Fig. 2.5) as well as cover, number of surviving strategies and characteristic parameters (see Fig. 2.6). The productivity of lichens and bryophytes in deserts seems to be generally limited by low water supply while the boreal zone and the moist tropics and subtropics are characterised by high values of productivity. 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 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, p.178). 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 high productivity of lichens and bryophytes near the ground. The description of topographic and climatic conditions used in the model, however, is not specific enough to account for 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 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 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 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. The form of the CCM implemented in the model is useful in situations where CO₂ is limited, either due to low supply from the atmosphere or due to the negative effect of high temperatures on cellular CO₂ concentration. 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 CO₂. Additionally, the high temperatures in the tropics result in low cellular solubility of CO₂ compared to O₂, further reducing CO₂ available for photosynthesis. 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. 2.2.3, the parameters describing the costs of the CCM are not very well known. Moreover, this parameterisation is based on free living cyanobacteria. The CCM in lichens and bryophytes could work differently. Furthermore, it has to be pointed out that the CCM which cyanobacteria and some algae possess is not necessarily the reason why they are part of the symbiosis. Not enough is known about how the CCM works in lichens and bryophytes to make definitive statements. Thus, although the global patterns of optimum temperature and CCM cannot be evaluated on a quantitative basis, these patterns help to assess qualitatively the plausibility of the model results given the assumptions made in the model.

2.3.2. Comparison of model estimates to data

The observational data used to evaluate the model show high variation. As explained in Sect. 2.1.3 it is therefore problematic to extrapolate from these point-scale measurements of carbon uptake to a value for a large region, such as a model grid cell. The “characteristic”, observation-based values of net carbon uptake should therefore be interpreted as order-of-magnitude estimates.

In the boreal zone and in the moist tropics, the “characteristic” values are closer to the upper bound of simulated net carbon uptake than to the lower one (see Fig. 2.7). This indicates that the more productive model strategies may represent a better approximation of the net carbon uptake by real lichens and bryophytes in these regions. A possible explanation for this result is that the lichen and bryophyte species occurring in these ecosystems are influenced by competition and are consequently driven towards high productivity. Another explanation would be that the model underestimates productivity in these regions.

For the tropics, it is difficult to make definitive statements due to the low number of observations available. In the study of Elbert et al. (2012), net carbon uptake in the tropical rainforest canopy is estimated to be only 15.2 (g C) m⁻² yr⁻¹. This value compares well to the modelled range. As discussed in Sect. 2.1.3, however, the estimates from Elbert et al. (2012) are based on assumptions about active time and coverage of lichens and bryophytes.

In the boreal zone, the “characteristic” value is more robust due to the large number of observations. The fact, that it matches the upper bound of the spatial average model

estimate may be explained by the lack of an explicit simulation of the peat in the model. The peat layer may represent an additional water storage for bryophytes that is not associated with respiration costs. This is not reflected in the model, where the strategies have to “pay” for the water storage in biomass via the respiration cost of biomass. Hence, the model may underestimate the water supply in regions where peat occurs. This effect is probably most pronounced in peatlands which are not explicitly simulated in the model but included in the boreal forest biome. Given the limitations of the model regarding simulating peat water storage, the model estimates for the boreal zone averaged over the whole boreal landscape seem to be reasonable.

2.3.3. Sensitivity analysis

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 2.2). 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 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. 2.1.2), they should be determined as accurately as possible.

2.3.4. Limitations and possible improvements

The modelling approach presented here has several limitations which lead to uncertainty regarding the estimate of net carbon uptake. Different aspects of these limitations of the model are discussed, namely spatial resolution, interactions of strategies, parameter uncertainty and simplifying assumptions. Possible improvements in this respect are mentioned.

Spatial resolution

The spatial resolution of the model grid is too coarse to represent microclimatic or microtopographic features. It has been shown, however, that variation of environmental conditions at the small scale can have an effect on carbon uptake of lichens and bryophytes (e.g. Nungesser (2003); Lange et al. (1998b)). This leads to the question, if these differences in carbon uptake cancel out for large regions or not. The differences in productivity would probably not cancel out if the relations between climate and carbon uptake were strongly nonlinear. Then, the value of carbon uptake derived from the mean climate of a large region would differ from the mean of the values of net carbon uptake based on all the microclimates within that region. In this case, neglecting sub-grid scale variation would lead to systematic biases in the model estimates.

To assess the effect of variation in environmental conditions on the model estimates a sensitivity analysis is performed (see Table 2.2). The model does not seem to show strong nonlinear behaviour. Compared to the effect of the parameters which describe tradeoffs, the model estimates are rather insensitive to changes in environmental/climatic conditions. Of course, it cannot be ruled out that small-scale variation has some effect on the model estimates, but the lack of microclimatic and microtopographic data at the global scale makes it impossible to quantify this effect.

Interactions of strategies

As shown in Fig. 2.7, the unknown relative abundance of the strategies (see Sect. 2.1.3) leads to large differences between the “average” and the “maximum” estimates of net carbon uptake. Hence, a significant reduction in the uncertainty of the model estimates could be achieved by quantifying the relative abundance of the strategies. This could be done, for instance, by implementing a scheme that simulates competition between lichen or bryophyte strategies. Such a scheme would be a promising perspective for extending the model. At the moment, however, not enough quantitative data are available about competition and other ecological interactions between different lichen and bryophyte species to integrate these processes into the model.

Parameter uncertainty

The model has been shown to be sensitive to the parameters which describe tradeoffs (see Sect. 2.2.3). For some of these tradeoff parameters, 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 only one study could be found that quantified the diffusivity for CO_2 as a function of water saturation. The latter, however, is much more useful for modelling CO_2 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 $V_{\text{C},\max}$. 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 $V_{\text{C},\max}$ 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.

Even if relations between two parameters can be derived from data in a quantitative way, they are usually characterised by some scatter. This is due to additional factors which influence the relation but which are not considered in the model. Differences in specific respiration across strategies, for example, are assumed to result only from differences in the Rubisco content of the strategies or properties that correlate with Rubisco content, such as photosynthetic capacity (Palmqvist et al., 1998). This simple tradeoff is an approximation, as illustrated by the scatter in the relation between Rubisco content and respiration across lichen species (Palmqvist et al., 2002). There seem to be some factors that contribute to respiration in lichens which are not correlated with Rubisco content but which differ across species. It is, however, impractical to implement all these factors into the model, since already the simple tradeoff-relation between Rubisco content and respiration had to be established by “educated guess”.

Simplifying assumptions

To focus on the goal of modelling lichen and bryophyte productivity at the global scale, several simplifying assumptions are made in the model. In the following some of these assumptions are discussed which concern the representation of the organisms in the model as well as the implementation of environmental conditions.

In the model, it is assumed that lichen respiration only depends on the Rubisco content averaged over the total biomass of the organism. Hence, a lichen with a high fraction of algal/cyanobacterial biomass which has a low Rubisco content should have a respiration similar to a lichen with a low fraction of algal/cyanobacterial biomass which has a high Rubisco content, because the Rubisco content of the whole total biomass would be similar. This assumption is valid as long as those components of fungal and

algal/cyanobacterial biomass which are not related to Rubisco content exhibit similar specific respiration. This might not be the case for all lichen species. Some of the observed variation in the relation between Rubisco content and specific respiration rate (Palmqvist et al., 2002) might be explained by different respiration rates of some components of fungal and algal/cyanobacterial tissue which are not correlated with Rubisco content. It is difficult, however, to separately quantify all components of lichen and bryophyte biomass that contribute to respiration.

Another important aspect of lichen and bryophyte physiology is the relation between water content and metabolic activity. Not all facets of this relation are included in the model. Lichens with cyanobacterial photobionts, for instance, need liquid water to activate their metabolism. This physiological constraint seems to be a disadvantage for the cyanolichens since it shortens the time available for carbon uptake. The disadvantage, however, could be compensated by some other property of cyanobacteria that is beneficial for the lichens, such as nitrogen fixation, for instance. This property cannot be accounted for because nutrient limitation is not implemented in the model. Thus, since not all distinct properties of cyanobacteria and the associated tradeoffs can be consistently represented in the model, cyanolichens are not explicitly modelled. They may, however, be implicitly simulated by model strategies which have physiological properties similar to cyanolichens.

A further property of the relation between water content and metabolic activity is that in some species, the metabolic activity corresponding to a certain water content is only reached after a time delay (Jonsson et al., 2008; Jonsson Čabrajić et al., 2010; Lidén et al., 2010). The delay is not only species-specific, but it also depends on the length of the preceding dry period (Ried, 1960; Gray et al., 2007; Proctor, 2010). Possible reasons for the delay of photosynthetic activation are the removal of protection mechanisms against drying or the repair of damage resulting from dry conditions (Lidén et al., 2010). These mechanisms are probably associated with carbon costs for the organism, which means that the duration of the delay may be dependent on the amount of carbon invested in repair or protection. Hence, there may be a tradeoff between the benefit of a short delay of activation and the cost of investment into different mechanisms which facilitate a short delay. Therefore, implementing the delay of activation into the model is problematic since the carbon costs of the various protection or repair mechanisms are not known.

As discussed in Sect. 2.3.2 the model does not explicitly simulate a peat layer. The difficulty with including peat into the model lies in the additional information on environmental conditions that is necessary to predict peat formation. The ability to form an additional water storage which is not accompanied by respiration costs could be assigned to the strategies in the model. If this ability for water storage was set to be independent of environmental conditions, however, the strategies which have the ability of increased water storage would grow everywhere. Since peat formation depends on anoxic conditions, however, it cannot take place everywhere. Thus, productivity would be largely overestimated. Consequently, a model that simulates the hydrological conditions at the global land surface would be needed to determine which regions are suitable for peat formation (see e.g. Wania et al. (2009)). This would add another level of complexity to

the model and it would shift the focus from simulating net carbon uptake of lichens and bryophytes towards land surface modelling.

2.4. Conclusions

In this chapter, estimates of global net carbon uptake by lichens and bryophytes are presented which are derived by a process-based model. The simulated patterns of carbon uptake and other properties of lichens and bryophytes are plausible, also the order of magnitude of the estimated global net carbon uptake of 0.34 to 3.3 (Gt C) yr⁻¹ agrees with other studies, e.g. the one by Elbert et al. (2012). Given the uncertainties regarding the evaluation of the model, the estimates are in good agreement with observational data. The sensitivity analysis shows that the model is quite robust concerning environmental factors. It is sensitive, however, to changes in some physiological properties of lichens and bryophytes. Limitations of the model are mainly due to the uncertainty associated with some physiological parameters and the simplifications regarding the representation of several physiological processes and environmental conditions.

The uncertainties in the evaluation and parameterisation of the model follow from the large-scale nature of the approach presented here. Within these constraints, the model is a useful tool to quantify the productivity of lichen and bryophytes at the global scale. The model estimates confirm the suggestion by Elbert et al. (2012) that the role of lichens and bryophytes in the global carbon cycle should not be neglected.

3. Estimating impacts of lichens and bryophytes on global biogeochemical cycles of nitrogen and phosphorus and on chemical weathering

In this chapter, estimates are presented on the impacts of lichens and bryophytes on global biogeochemical cycles of nitrogen, phosphorus and weathering. These estimates complement the values of global net carbon uptake by the organisms which are presented in the previous chapter. In this way, a comprehensive overview can be provided of the role of lichens and bryophytes for global biogeochemistry.

While the previous chapter focuses on the description of the model of carbon uptake and the assessment of the model predictions, this chapter lays more emphasis on the application of the model estimates. This means that the contributions of lichens and bryophytes to biogeochemical cycles of nitrogen, phosphorus and weathering which are quantified in this chapter are not directly simulated by a model. Instead, potential rates of nitrogen fixation, phosphorus uptake and chemical weathering are derived from model-based estimates of carbon uptake. This is done in several steps: By combining the net carbon uptake estimates with nitrogen and phosphorus content of lichens and bryophytes, the requirements of the organisms for these nutrients and thus their potential uptake are quantified. Since phosphorus is mainly derived from rocks, the potential for chemical weathering is then calculated as a function of phosphorus requirements of lichens and bryophytes growing on rock surfaces, combined with the phosphorus content of surface rocks. The estimates of potential nitrogen fixation, phosphorus uptake and chemical weathering are presented in form of global maps and they are evaluated by comparison to observational data where possible. The potential contribution of lichens and bryophytes to global biogeochemical cycles is discussed regarding the estimates established here.

The chapter is structured in the following way: Sect. 3.1 describes how potential rates of nitrogen fixation, phosphorus uptake and chemical weathering by lichens and bryophytes are estimated based on the carbon uptake of the organisms. The results of the calculation are presented in Sect. 3.2 together with an evaluation that shows different sources of uncertainty in the approach. In Sect. 3.3 the plausibility of the derived potential rates is assessed and limitations as well as possible improvements of the approach presented here are discussed.

3.1. Methods

3.1.1. The net carbon uptake model

Global estimates of net carbon uptake by lichens and bryophytes are used to derive their potential rates of nitrogen fixation, phosphorus uptake and chemical weathering. The carbon uptake is quantified by a process-based model which is described in detail in the previous chapter. Therefore, only a short overview of the model is given here: Lichens and bryophytes are simulated as reservoirs of biomass on a global rectangular grid with a resolution of 2.8125 degrees, similar to many global vegetation models. The dynamics of these reservoirs are controlled by exchange flows of carbon, such as photosynthesis or respiration which are driven by gridded climate input data, taken from the WATCH data set (Weedon et al., 2011). The model includes lichen and bryophyte-specific traits such as poikilohydry or the dependence of CO₂ diffusivity on water content. Furthermore, it separately simulates lichens and bryophytes living on the ground and in the canopy since the two locations differ in many aspects such as light and precipitation regime. In contrast to many other vegetation models, the model also accounts for the functional variation of the organisms. This means that many random lichen and bryophyte “strategies” are generated for each grid cell of the model. These “strategies” differ in certain characteristic parameters, such as photosynthetic capacity or optimum temperature and, consequently, also in their carbon uptake. “Strategies” without a sufficient carbon gain do not “survive” in the model and are therefore not considered in the calculation of the results. To obtain mean carbon uptake for a certain grid cell, the surviving “strategies” have to be weighted. Since their abundance is unknown, the model predicts net carbon uptake in form of a range of possible values. The lower bound corresponds to equal weights for all “strategies” in a grid cell while the upper bound corresponds to a weight of one for the most productive “strategy” and zero for all others.

As described in the previous chapter, the net carbon uptake model is run with repeating climate forcing and many initial “strategies” until a steady state is reached regarding the fluxes and reservoirs of carbon as well as the number of surviving “strategies”. Estimates of global net carbon uptake of lichens and bryophytes are then calculated by time averages over the last part of the model run. They are shown in Fig. 3.1 (see also Fig. 2.5 and A.1 for details). In this chapter, these estimates are used to derive nutrient requirements and chemical weathering. Note that the carbon uptake model itself does not contain any representation of nutrients for simplicity. Hence, nutrient limitation of carbon uptake is not included.

3.1.2. Nutrient content of lichens and bryophytes, resorption and leaching

The synthesis of biomass requires both the uptake of carbon and nutrients, such as nitrogen and phosphorus. Hence, knowing the nutrient content of biomass, the nutrient requirement associated with a certain value of net carbon uptake can be estimated. Histograms of nitrogen and phosphorus content of lichens and bryophytes based on values from the literature are shown in Fig. 3.2. The nutrient requirement for each grid cell of the model is then calculated by multiplying the range of simulated net carbon

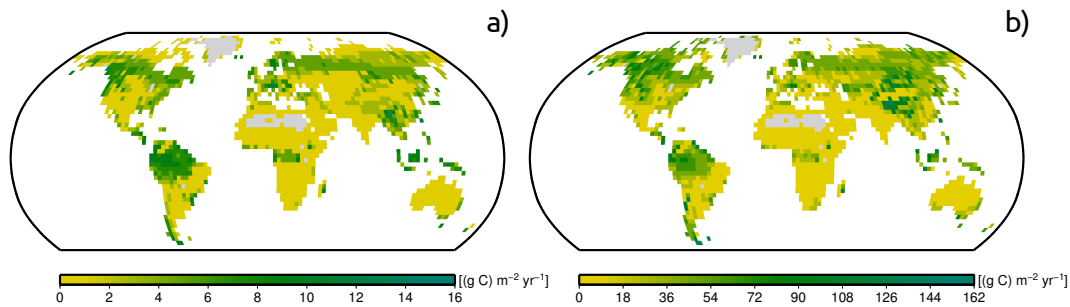


Figure 3.1.: Simulated net carbon uptake by lichens and bryophytes from chapter 2. a) Lower bound of the model estimates, obtained by equal weights for all surviving “strategies” in each grid cell. b) Upper bound, corresponding to the net carbon uptake of the most productive “strategy” in each grid cell.

uptake by the median of the possible values of nutrient content. Moreover, an upper bound of nutrient requirement is estimated by multiplying the carbon uptake of the most productive “strategy” in a grid cell by the maximum nutrient content from the literature. A lower bound is then calculated by multiplying the carbon uptake corresponding to equal weights for all “strategies” in a grid cell by the minimum nutrient content from the literature.

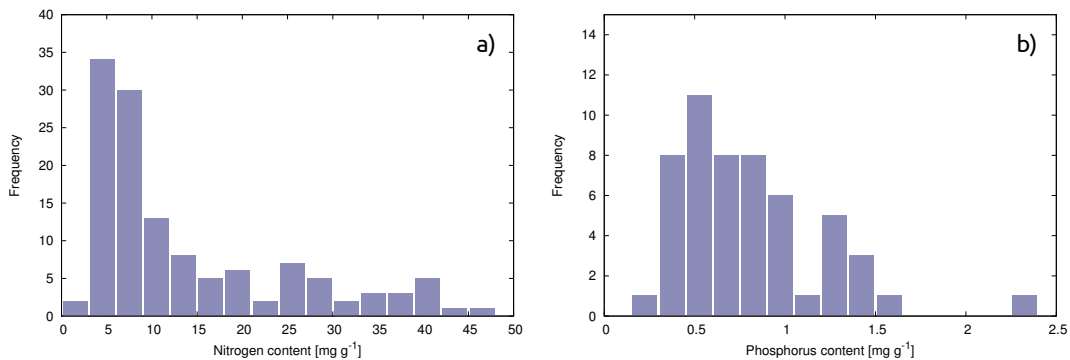


Figure 3.2.: a) Nitrogen and b) Phosphorus content of lichens and bryophytes in mg nutrient per g biomass. The values are taken from Aerts et al. (1999); Chapin III et al. (1980); Chapin III and Shaver (1988); Chapin III (1989); Hogan et al. (2010a,b); Johansson et al. (2011); Lang et al. (1980); Shaver and Chapin III (1991); Tomassen et al. (2004); Waite and Sack (2011); Palmqvist et al. (2002).

The nutrient content of biomass alone, however, is not sufficient to quantify the true nutrient requirements of biomass synthesis. Also resorption of nutrients from senescent tissue (Eckstein et al., 1999) and leaching of acquired nutrients prior to their integration into biomass (Belnap, 2002) have to be considered. Only a few studies, however, provide concrete estimates for nutrient resorption and leaching regarding lichens and bryophytes. Therefore, three scenarios are used to account for the uncertainty associated with resorption and leaching: a) a “high requirement” scenario where resorption is set to zero and leaching to the maximum value found in the literature, 70 % (Belnap, 2002) b) a

“medium requirement” scenario where resorption for nitrogen is set to 66 % and for phosphorus to 50 %. These values are based on data of a single species (Eckstein, 2000; Chapin III and Shaver, 1989) and the general observation that lichens and bryophytes are relatively efficient regarding nutrient resorption. Leaching is set to 35 % which is the middle of the range of possible values from the literature (Belnap, 2002; Pike, 1978) c) a “low requirement” scenario where resorption is set to the highest value observed, 80 % (Eckstein et al., 1999) and leaching is set to zero. An overview of the different scenarios of nutrient content, resorption and leaching is shown in Table 3.1.

Table 3.1.: Minimum, maximum and medium/median values of nutrient content, given in mg nutrient per g biomass, and resorption and leaching, given in fractions. The first value for medium resorption corresponds to nitrogen and the second to phosphorus. Regarding the other values of resorption and leaching, no distinction between nitrogen and phosphorus is made due to lack of specific data. See text for references for the values.

Factor	Nitrogen content	Phosphorus content	Resorption	Leaching
Minimum	2	0.26	0.0	0.05
Median	8	0.7	-	-
Medium value	-	-	0.66 / 0.5	0.35
Maximum	45.5	2.37	0.8	0.7

3.1.3. Validation of nitrogen requirement

Fixation of atmospheric nitrogen is not the only way for lichens and bryophytes to acquire this nutrient. They can also extract organic nitrogen from wet and dry deposition, for instance. Hence, the estimated nitrogen requirement is compared to observational data of nitrogen fixation from the literature to assess whether requirement is a good approximation to realised fixation by the organisms.

The comparison is done on a biome basis, which means that for each biome, the spatial average of nitrogen requirement is compared to a “characteristic”, observation-based value of nitrogen fixation on an order-of-magnitude basis. This method of comparison is chosen due to the difference in scale between estimates and observations. The estimates of nitrogen requirement are based on large regions which correspond to the grid cells of the carbon uptake model. The observations of nitrogen fixation, however, are temporary point-scale measurements which show high variation (see Table 3.2). It is problematic to extrapolate from these measurements to large regions and long time periods (see e.g. Liengen (1999) and Nash III (1996, p. 229)). Hence a “characteristic” value is used for these regions instead. For this purpose the median is computed of all measurements contained in the studies associated with the respective region. The biome classification is used as a basis for the comparison because biomes are relatively homogeneous regarding climate and ecology at large scales. The biomes are defined by the map of Olson et al.

(2001) which is also used for the net carbon uptake model in chapter 2. Nine out of 14 biomes from this map, however, cannot be represented in the comparison because not enough suitable studies could be found.

Due to the factors carbon uptake, nitrogen content, resorption and leaching (see Sect. 3.1) the estimates of nitrogen requirement exhibit some uncertainty. To assess this uncertainty, the minimum and maximum values of carbon uptake, nitrogen content, resorption and leaching (see Table 3.1) are stepwise multiplied. This means that the uncertainty resulting from the range of net carbon uptake, for instance, is represented by multiplying the lower and upper bound of carbon uptake by median nitrogen content and medium values of resorption and leaching. The combined uncertainty due to the ranges of carbon uptake and nitrogen content then corresponds to the upper bound of carbon uptake multiplied by maximum observed nitrogen content and the lower bound multiplied by minimum nitrogen content. These values are still multiplied by medium resorption and leaching. The uncertainty resulting from resorption and leaching is then obtained analogously. To illustrate the components of uncertainty, the corresponding ranges are included in the comparison of the estimates of nitrogen requirement to observational data.

Table 3.2.: Overview of the field studies used to compare nitrogen fixation by lichens and bryophytes with their nitrogen requirements. Biomes are abbreviated as follows: TU = Tundra, BO-F = Boreal forest floor, TE-C = Temperate evergreen canopy, DE = Desert, TR-F = Tropical rainforest floor and TR-C = Tropical rainforest canopy. Some studies provide more than one observed value (e.g. due to different habitats). The number of observations is put in brackets in the column “Nitrogen fixation”. A ‡ symbol denotes studies which provide one or more ranges instead of single values. In these cases, the mean value is calculated of the upper and lower bound of each range and the range of these calculated mean values is shown in the table.

Study	Biome	Nitrogen fixation [$\text{g m}^{-2} \text{yr}^{-1}$]
(Alexander and Schell, 1973)	TU	0.015
(Basilier et al., 1978)	TU	1.0 - 6.4 (4)
(Crittenden, 1975)	TU	0.0062 - 0.17
(Forman and Dowden, 1977)	TU	0.022 - 0.18 (3) ‡
(Granhall and Selander, 1973)	TU	0.16 - 9.4 (2)
(Gunther, 1989)	TU	0.0025 - 0.01 (3)
(Henry and Svoboda, 1986)	TU	0.085 - 0.1 (2)
(Kallio, 1975)	TU	0.15 - 0.38 (3)
(DeLuca et al., 2002)	BO-F	0.17
(Gunther, 1989)	BO-F	0.005 - 0.045 (2)
(Huss-Danell, 1977)	BO-F	0.1
(Lagerström et al., 2007)	BO-F	0.05 - 0.2 (3)
(Zackrisson et al., 2004)	BO-F	0.025 - 0.15 (3) ‡
(Zackrisson et al., 2009)	BO-F	0.16
(Antoine, 2004)	TE-C	0.15 - 1.65 (5)
(Brown and Dalton, 2002)	TE-C	0.2
(Denison, 1973)	TE-C	0.59 ‡
(Denison, 1979)	TE-C	0.4
(Granhall and Lindberg, 1978)	TE-C	0.035
(Green et al., 1980)	TE-C	0.5 ‡
(Pike, 1978)	TE-C	0.45
(Sucoff, 1979)	TE-C	0.006 - 0.24 (4)
(Belnap, 2002)	DE	1.3
(Coxson and Kershaw, 1983)	DE	1.4
(Holst et al., 2009)	DE	0.003 - 0.008 (2)
(Jeffries et al., 1992)	DE	0.01 - 0.22 (3) ‡
(Klopatek, 1992)	DE	0.83 - 5.75 (4) ‡
(Malam Issa et al., 2001)	DE	0.35
(Russow et al., 2008)	DE	1.3
(Rychert and Skujiņš, 1974)	DE	5.5
(Skarpe and Henriksson, 1987)	DE	0.2
(Thiet et al., 2005)	DE	0.41 ‡
(Veluci et al., 2006)	DE	0.13
(Zhao et al., 2010)	DE	0.4
(Crews et al., 2001)	TR-F	0.1 - 0.2 (3)
(Cusack et al., 2009)	TR-F	0.38
(Kurina and Vitousek, 2001)	TR-F	0.02 - 0.045 (3)
(Matzek and Vitousek, 2003)	TR-F	0.008 - 0.06 (6)
(Forman, 1975)	TR-C	0.48
(Freiberg, 1998)	TR-C	0.35 ‡
(Matzek and Vitousek, 2003)	TR-C	0.004 - 0.04 (6)

3.1.4. Chemical weathering

The phosphorus requirements of lichens and bryophytes can be used to derive potential rates of chemical weathering at rock surfaces. This implies that the organisms release weathering agents in order to extract phosphorus from rocks. Although this has not been proven yet, it is a realistic scenario for the following reasons: Releasing weathering agents to extract nutrients is a common strategy among plants, as illustrated by the widespread mycorrhiza (Landeweert et al., 2001; Lambers et al., 2008). Furthermore, it has been shown that plants with mycorrhiza release more weathering agents when they are limited by phosphorus (Smits et al., 2012). All lichens have a fungal component and according to Taylor et al. (2009) also some bryophytes form symbiosis with fungi. Read et al. (2000) show that some of these fungi also participate in mycorrhiza. Moreover, there are examples for the solubilization of phosphorus from rock substrates by lichens and bryophytes and free-living fungi (Seneviratne and Indrasena, 2006; Lenton et al., 2012; Banfield et al., 1999; Sharma, 2011). Thus, given that the organisms are able to derive phosphorus from rock material, it seems likely that they use it to meet their phosphorus demands.

Calculating potential chemical weathering from phosphorus demand is done in several steps. First, the net carbon uptake calculated by the model is constrained to that fraction which is due to lichens and bryophytes growing on rock surfaces. This is done by multiplying carbon uptake in each grid cell of the model by the fraction of rock surfaces in this grid cell. As described in Sect. 3.1.2 the phosphorus content of biomass is used to translate carbon uptake on rock surfaces into phosphorus requirements. The phosphorus requirements on rock surfaces are then divided by the phosphorus content of surface rocks (see Fig. 3.3). This yields an estimate of chemically weathered rock material. The phosphorus content of rocks is obtained by assigning the values of phosphorus content shown in Table 3.3 to the classes of a lithology map (Amiotte Suchet et al., 2003).

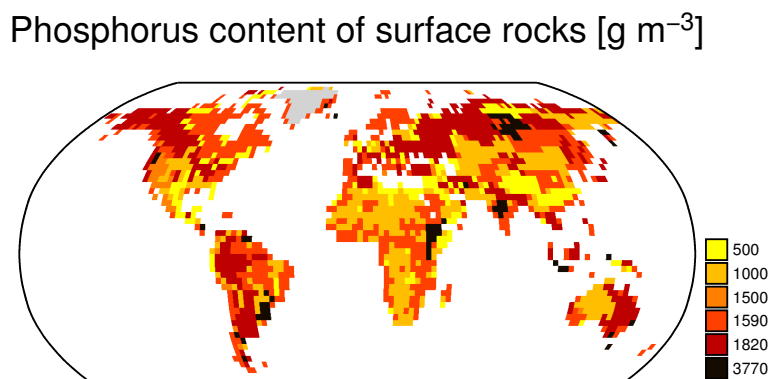


Figure 3.3.: Phosphorus content of surface rocks for the six lithological classes listed in Table 3.3.

Table 3.3.: Lithological classes, rock density and phosphorus content (in g phosphorus per kg rock). The classes are derived from Amiotte Suchet et al. (2003) and rock density is taken from Yang et al. (2013) and references therein. The phosphorus content of surface rocks is taken from Newman (1995). Phosphorus content of igneous rocks is only given in form of a range of values in Newman (1995). Thus, the lower end of this range is assigned to Rhyolite and Granite and the upper end to Basalt.

Lithological class	Rock density [kg m ⁻³]	Phosphorus content [g kg ⁻¹]
sandstone	2500	0.4
limestone	2500	0.2
shale	2600	0.7
granite	2650	0.6
rhyolite	2500	0.6
basalt	2900	1.3

3.2. Results

Potential rates of nitrogen fixation, phosphorus uptake and chemical weathering by lichens and bryophytes are presented in form of global maps in Fig. 3.4 a) to d). The maps are based on the lower bound of net carbon uptake predicted by the model, multiplied by the median of the nutrient content and by “medium requirement” values of resorption and leaching (see Sect. 3.1).

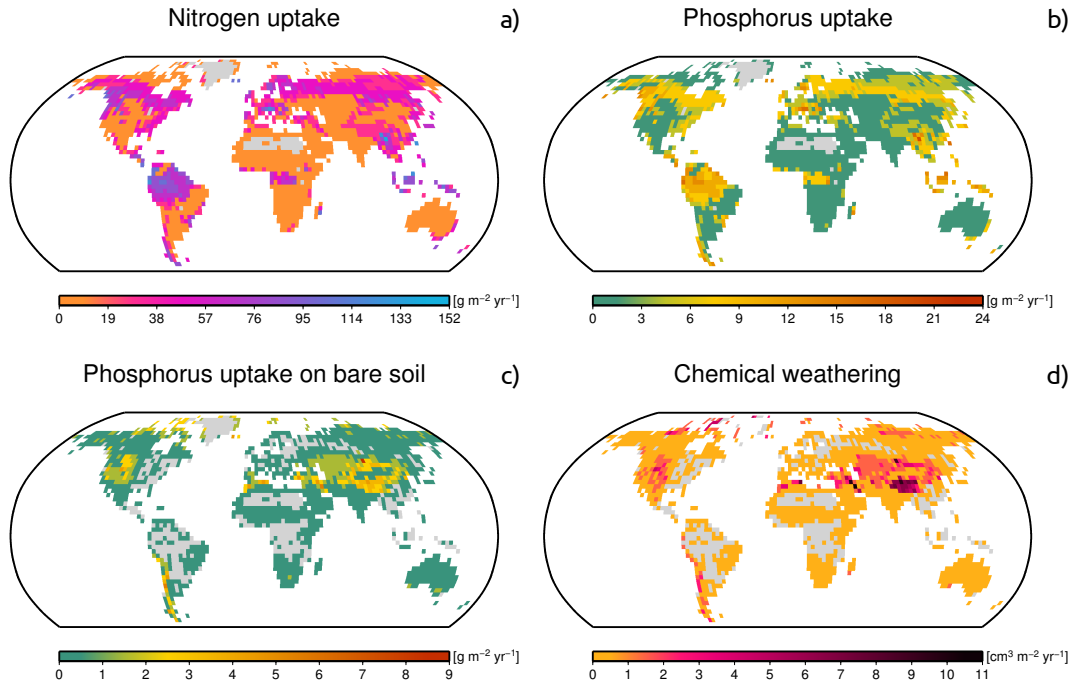


Figure 3.4.: a) Nitrogen and b) phosphorus requirement of lichens and bryophytes. c) Phosphorus requirement of lichens and bryophytes growing on rock surfaces. d) Chemical weathering of rock surfaces by lichens and bryophytes (cm^3 of rock). The maps correspond to the lower bound of simulated net carbon uptake, multiplied by the median of the nutrient content and by “medium requirement” values of resorption and leaching.

The nitrogen requirement of lichens and bryophytes is shown in Fig. 3.4 a). Since the factors *nutrient content*, *resorption* and *leaching* are globally uniform and temporally constant, the pattern of nitrogen requirement corresponds to that of average net carbon uptake (see chapter 2). The same is true for the pattern of phosphorus requirement which is shown in Fig. 3.4 b). Net carbon uptake is mainly controlled by water availability, with maximum values in forested regions and minimum values in deserts. The phosphorus requirement of lichens and bryophytes growing on rock surfaces is shown in Fig. 3.4 c). This pattern differs markedly from the one of total net carbon uptake, with maximum values in regions with a high fraction of rock surface area, such as mountain ranges and deserts. Furthermore, productivity is higher in cool arid and semi-arid regions than in hot regions. The pattern of potential chemical weathering associated with the uptake of phosphorus, shown in Fig. 3.4 d), is similar to the one of phosphorus requirement on rock surfaces. The phosphorus content of surface rocks (Fig. 3.3) does not seem to have

a significant impact on the pattern.

Global total values of nitrogen and phosphorus requirements and chemical weathering are derived by multiplying the values in each grid cell by the area of that cell and then adding them up. They are shown in Table 3.4 for different combinations of net carbon uptake, nutrient content, resorption and leaching.

Table 3.4.: Global total values of nitrogen and phosphorus requirements and chemical weathering. Different combinations of three factors are shown which contribute to uncertainty in the estimates: The lower and upper bound of net carbon uptake ($C_{\text{low}}/C_{\text{up}}$), minimum, median and maximum nutrient content ($N_{\text{min}}/N_{\text{med}}/N_{\text{max}}$) and the low, medium and high scenario of resorption and leaching ($S_{\text{low}}/S_{\text{med}}/S_{\text{high}}$). The factors are described in Sect. 3.1. The unit for nutrient requirement is [Tg yr^{-1}] and for weathering it is [$\text{km}^3 \text{yr}^{-1}$] of rock. For comparison, estimates of nitrogen fixation by cryptogamic covers from Elbert et al. (2012) are shown as well as a range of global chemical weathering rates from Newman (1995) and Gaillardet et al. (1999). Global estimates for chemical weathering or phosphorus uptake by lichens and bryophytes could not be found.

Factors	C_{low}	C_{up}	C_{low}	C_{up}	Observations
	N_{med}	N_{med}	N_{min}	N_{max}	
	S_{med}	S_{med}	S_{low}	S_{high}	
Nitrogen requirement	3.5	34	0.35	1207	49
Phosphorus requirement	0.46	4.6	0.046	65	-
Chemical weathering	0.058	1.1	0.0057	16	0.26 - 2.6

The nitrogen requirements of lichens and bryophytes based on net carbon uptake are compared to median values of observed nitrogen fixation on a biome basis (see Fig. 3.5). In this way, it can be tested whether nitrogen requirement is a reasonable approximation to fixation from the atmosphere (see Sect. 3.1.3 for details).

Since the model separately simulates lichens and bryophytes living on the ground and in the canopy, model estimates and observations are compared individually for ground and canopy in the tropical forest biome. For the evergreen temperate forest biome, the comparison is done only for the canopy since no suitable measurements for the ground are available.

The uncertainty in the predicted rates of nitrogen requirement is illustrated by vertical bars in Fig. 3.5. It results from three different factors (see Sect. 3.1): a) The range of net carbon uptake predicted by the model, denoted by circles. b) The range of possible nitrogen content of lichens and bryophytes, represented by rectangles. c) The uncertain values of nitrogen resorption and leaching, illustrated by diamonds. These factors explain the broad range of uncertainty regarding the estimates of nitrogen requirement of lichens and bryophytes, which is up to four orders of magnitude.

The triangles in Fig. 3.5 illustrate the range of nitrogen requirement associated with

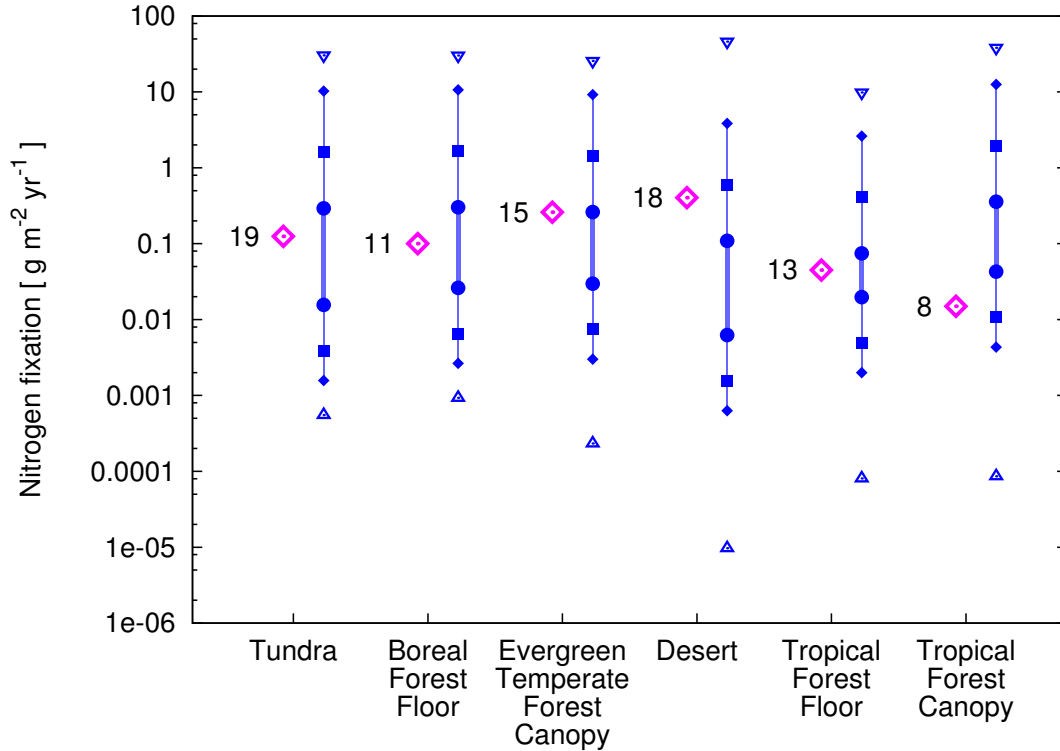


Figure 3.5.: Comparison of nitrogen requirement estimated by the model to observational data of nitrogen fixation. A magenta open diamond corresponds to the median of the observed values in the respective biome. The number left to the diamond is the number of observed values. See Table 3.2 for an overview of the studies on which the observations are based. The blue vertical bars represent the uncertainty in the estimates of nitrogen requirement. The blue symbols denote several factors contributing to the uncertainty, namely net carbon uptake (circles), nitrogen content (rectangles), resorption and leaching (diamonds). The triangles illustrate the influence of climatic variation within a biome on the estimate of nitrogen requirement. See text for more details.

climatic variability between the grid cells of a biome. They are calculated in the same way as the diamonds, but instead of using net carbon uptake averaged over all grid cells of a biome as a basis for the calculation, only the grid cells are used which have the highest or lowest values of net carbon uptake in a biome, respectively.

The uncertainty in estimated nitrogen requirement is roughly equally partitioned between the three factors net carbon uptake, nitrogen content and resorption/leaching. Each factor contributes around an order of magnitude, leading to a total uncertainty of three to four orders of magnitude. The climatic variability differs between biomes, being highest in deserts, intermediate in tropical forests and lowest in boreal forest and tundra.

The median values of observed nitrogen fixation lie within the uncertainty range of the estimates of nitrogen requirement. In deserts, however, the observations are located towards the upper end of the uncertainty range while they are at the lower end in the tropical forest canopy. Possible reasons for these patterns are discussed in Sect. 3.3.

3.3. Discussion

In this chapter net carbon uptake by lichens and bryophytes combined with their nutrient content is used as a basis to estimate potential rates of nitrogen fixation, phosphorus uptake and chemical weathering by these organisms.

3.3.1. Potential nitrogen fixation

The medium estimates of nitrogen requirement ranging from 3.5 to 34 Tgyr⁻¹ (see Table 3.4) are similar to the estimate of Elbert et al. (2012). This inspires further confidence regarding the magnitude of global nitrogen fixation by lichens and bryophytes, particularly because Elbert et al. (2012) use an approach different from ours. The estimates suggest that the organisms play an important role in global biological nitrogen fixation. A possible explanation for the estimates being lower than those of Elbert et al. (2012) is the missing implementation of free-living cyanobacteria in the net carbon uptake model. The fact that the carbon uptake estimated by the model is also lower than that suggested by Elbert et al. (2012) supports this explanation.

As discussed in Sect. 3.1.3 the observed values of nitrogen fixation are short-term, point-scale measurements which show a large variation. Since it is difficult to extrapolate from these observations to annual values of nitrogen fixation for large regions, the median values shown in Fig. 3.5 should be seen as “characteristic” order-of-magnitude estimates.

In general, the comparison of estimated nitrogen requirement and observed rates of nitrogen fixation on a biome basis shows a reasonable agreement (see Fig. 3.5). All observed “characteristic” values lie within the uncertainty range of the estimates.

With the exception of the tropical rainforest canopy, the “characteristic” values seem to be slightly above the middle of the estimated ranges of nitrogen requirement, especially in deserts. There are several possible explanations for this pattern:

First, only a small fraction of lichens and bryophytes host cyanobacteria, for example. The net carbon uptake model, however, is not able to determine which of the simulated “strategies” correspond to nitrogen-fixing lichens and bryophytes. Instead, it calculates a weighted average of the carbon uptake of all “strategies”. Thus, if the carbon uptake of the nitrogen-fixing lichens and bryophytes differed significantly from the carbon uptake of the non-fixing species, estimates of nitrogen fixation based on nitrogen requirement would be biased. The pattern in Fig. 3.5 would therefore suggest that nitrogen-fixing lichens and bryophytes have a higher productivity than non-fixing species, except for the tropical forest canopy, where the pattern is reversed.

Second, nitrogen-fixing lichens have a higher nitrogen concentration than green algal lichens (Nash III, 1996, p. 231). Applying a higher nitrogen concentration to the method of estimating nitrogen requirement would result in increased values of requirement which may better match the “characteristic” values of nitrogen fixation. As stated above, however, the net carbon uptake model cannot separately compute the carbon uptake of nitrogen-fixing lichens and bryophytes and therefore their nitrogen requirement cannot be determined.

Third, the medium estimates of resorption and leaching may not be appropriate for

every biome. In deserts, for example, high values of observed fixation relative to requirement could result from high losses by leaching, which often occur after rewetting of the thallus.

Fourth, the “characteristic” values may not be representative for the associated biome. The largest part of the observations for the tropical forest canopy, for instance, are made on Hawaii (see Table 3.2). Hence, nitrogen fixation by Hawaiian epiphytic lichens and bryophytes might be lower than the average fixation in the whole tropical rainforest canopy.

In spite of the uncertainties in the estimates as well as in the observational data, the model of nitrogen requirement seems to be a reasonable predictor of biotic nitrogen fixation by lichens and bryophytes.

3.3.2. Potential phosphorus uptake and chemical weathering

No global estimates of phosphorus uptake and chemical weathering by lichens and bryophytes were found except from the results presented here. Regarding chemical weathering, the studies of Jackson and Keller (1970) and Stretch and Viles (2002) provide some regional estimates ranging from 1.1 to 2.9 $\text{cm}^3 \text{m}^{-2} \text{yr}^{-1}$ of rock. These values are comparable to the estimates shown in Fig. 3.4 d). At the global scale, estimates of total chemical weathering are available, which integrate all biotic and abiotic processes contributing to chemical weathering. Newman (1995) give a value of 0.26 to 2.6 $\text{km}^3 \text{yr}^{-1}$ of rock and Gaillardet et al. (1999) state 0.85 $\text{km}^3 \text{yr}^{-1}$. The estimate of 0.06 to 1.1 $\text{km}^3 \text{yr}^{-1}$ is on the same order of magnitude as these values, which seems reasonable. Weathering by lichens and bryophytes should be lower than the total global value, since also vascular plants and abiotic processes contribute to weathering at the surface. Nevertheless, the estimated potential for chemical weathering by lichens and bryophytes suggests that these organisms may contribute significantly to the biotic enhancement of global chemical weathering.

3.3.3. Limitations and possible improvements

There are several possibilities to improve and extend the approach presented here. Improvements could be made regarding the considerable amount of uncertainty in the estimates (see Table 3.4). The uncertainty results from several factors: The first one is the range of average net carbon uptake predicted by the model, which results from the unknown abundances of the different “strategies” in each grid cell (see Sect. 3.1.1 and 2.1.3). Consequently, the range could be reduced by determining the relative abundance of each “strategy” in a grid cell. This could be done, for example, by implementing ecological interactions of the “strategies” in the model. There are, however, not enough quantitative data available about competition and other interactions between different lichen and bryophyte species to integrate these processes into the model. The second factor contributing to the uncertainty of the estimates is the relatively large spread of nutrient content of biomass (see Fig. 3.2). A possible way to reduce this uncertainty would be to correlate nutrient content with some other property of lichens and bryophytes in

the model. Then, the nutrient content of each “strategy” would be determined. One candidate for such a property is the Rubisco content of the model “strategies”. Palmqvist et al. (1998) showed that Rubisco content is correlated with chlorophyll *a*, which is in turn correlated with nitrogen content (Palmqvist et al., 2002). Phosphorus content could then be derived from nitrogen content via the N:P ratio of biomass. The relation between chlorophyll *a* and nitrogen content, however, exhibits a large scatter. One possible explanation for this is the fact that the fraction of nitrogen allocated to tissues which are not related to chlorophyll *a* content, such as fungal cell walls, is not constant, as shown by Palmqvist et al. (1998). Due to these problems possible correlations between nutrient content and Rubisco content of lichens and bryophytes are not taken into account. The third factor that causes uncertainty in the estimates is nutrient resorption and leaching. As discussed by Eckstein et al. (1999) and Belnap (2002), both processes can be significant. According to Cornelissen et al. (2007); Ellis et al. (2005); Hyvärinen and Crittenden (2000), lichens and bryophytes resorb nitrogen as well as phosphorus from senescent tissue. Moreover, they seem to be relatively efficient at resorbing nutrients, with typical values around 50% (Cornelissen et al., 2007; Eckstein, 2000). The whole observed range of resorption from 0 to 80%, however, is included since only one species (*Hylocomium splendens*) was found in the literature for which both resorption as well as nutrient content are specified (Eckstein, 2000; Chapin III and Shaver, 1989). Also the whole range of possible values of leaching found in the literature, from 0 to 70%, is included, because the factors that control the strength of leaching could not be quantified. Therefore, more knowledge about the controlling factors of resorption and leaching is needed to reduce the uncertainty associated with these processes.

3.4. Conclusions

In this chapter, potential rates of nitrogen fixation, phosphorus uptake and chemical weathering by lichens and bryophytes are derived from global values of net carbon uptake by these organisms. The estimated potential nitrogen fixation by lichens and bryophytes of 3.5 to 34 Tg yr⁻¹ seems plausible and agrees both with the results of Elbert et al. (2012) and with observational data. Also estimated potential phosphorus uptake (0.46 to 4.6 Tg yr⁻¹) and chemical weathering (0.058 to 1.1 km³ yr⁻¹ of rock) have realistic orders of magnitude. The estimates are associated with relatively large uncertainties, but the available data about nutrient dynamics in lichens and bryophytes do not allow for a significant reduction of this uncertainty at the moment.

The calculated values of potential nitrogen fixation, phosphorus uptake and chemical weathering suggest that the approach presented here is appropriate to derive upper limits for the impacts of lichens and bryophytes on global biogeochemistry. Regarding the order of magnitude of the estimates, lichens and bryophytes may play a significant role for global biogeochemical cycles.

4. Summary and conclusions

This thesis presents estimates of net carbon uptake and potential rates of nitrogen fixation, phosphorus uptake and chemical weathering by lichens and bryophytes at the global scale. This is achieved by developing a global-scale process-based model of lichen and bryophyte productivity, which quantifies exchange flows of carbon between organisms and environment as a function of climate and other environmental factors. The modelled estimates of carbon uptake are then used as a basis to derive the nutrient demand of lichens and bryophytes and, consequently, their potential for nitrogen fixation, phosphorus uptake and for chemical weathering at the surface. Where possible, the estimates are evaluated by comparison to observational data and limitations as well as potential improvements of the approach presented here are discussed.

4.1. General outcomes

As described in the introduction, the goal of this thesis is to quantify impacts of lichens and bryophytes on global biogeochemical cycles by using a modelling approach. Referring to the three steps listed in Sect. 1.3, the following general outcomes can be reported:

- The process-based numerical model described in Chapter 2 comprises the physiological relationships necessary to predict net carbon uptake by lichens and bryophytes as a function of climate and other environmental factors.
- The predicted global net carbon uptake of 0.34 to 3.3 (Gt C) yr⁻¹ has a realistic order of magnitude compared to empirical studies (Elbert et al., 2012). The simulated patterns of carbon uptake are plausible and a comparison of model estimates to observational data on a biome basis shows good agreement. Also patterns of lichen and bryophyte properties other than carbon uptake seem to be represented by the model in a realistic way, such as biomass, area cover, physiological properties and relative number of strategies.
- The medium estimates of nitrogen requirement which range from 3.5 to 34 Tg yr⁻¹ compare well on an order of magnitude basis to the result of Elbert et al. (2012). Comparing nitrogen requirement to observational data of nitrogen fixation for several biomes also results in good agreement in general. This suggests that nitrogen requirement is a reasonable approximation of nitrogen fixation by lichens and bryophytes. The presented estimates of carbon uptake and nitrogen fixation are somewhat lower than those of Elbert et al. (2012). Their study, however, also includes free-living algae and cyanobacteria which is a possible reason for their higher estimates. An assessment of the estimated potential rates of phosphorus

uptake by lichens and bryophytes is impractical since no observational data or other global estimates in this respect could be found. Also the estimated numbers of potential chemical weathering by the organisms cannot be compared to other estimates for the same reason. They seem, however, to have a realistic order of magnitude compared to regional as well as global estimates of total chemical weathering of surface rocks.

4.2. Limitations of the approach

The estimates presented here are associated with relatively large ranges of uncertainty which result from several different factors: Regarding the model of carbon uptake, the spatial and temporal resolution of the input data may lead to biases in the estimates in case of strongly nonlinear model behaviour (see Sect. 2.3.4). Another important factor that causes uncertainty in the estimate of net carbon uptake is the unknown abundance of strategies. The uncertainty associated with this factor can at least be quantified by the “average” and “maximum” scenarios of carbon uptake. Probably the most important source of uncertainty in the model results from little-known values of parameters which describe environmental factors or physiological processes of lichens, such as carbon uptake and nutrient dynamics (see Sect. 2.3.4). In most cases, the uncertainty associated with a certain parameter can be quantified and is included in the model, e.g. via randomly sampling ranges of possible parameter values (Sect. 2.1.2) or by scenarios of nutrient resorption and leaching (Sect. 3.1.2). Several parameters, however, have to be determined by “educated guess”. This concerns mainly parameters that describe tradeoffs (Sect. 2.1.2). At the moment, the only way to reduce this parameter uncertainty is by more experimental work on the physiological properties of lichens and bryophytes.

Like all models, the approach presented here makes several simplifying assumptions. This concerns mainly the representation of the environment, since the focus of the model is on the physiological processes of lichens and bryophytes that control their carbon uptake. Consequently, some specific environments which contain lichens and bryophytes, such as cloud forests and peatlands are not explicitly simulated. These small-scale ecosystems are approximated in the model by large-scale environmental conditions. Also the physiological processes of the lichens and bryophytes are modelled in a simplified way. Only those processes which are supposed to be essential for carbon uptake are considered in the model.

There are good reasons to simplify the model as much as possible given its purpose. Introducing a new physiological process or a more complex representation of the environment usually results in additional model parameters. Hence, the model estimates can only be improved if the values of the new parameters are well known. Otherwise the uncertainty due to a simplified representation of a process or an environmental factor is merely replaced by the uncertainty due to additional unknown parameter values.

The lack of known parameter values is the reason why nitrogen fixation, phosphorus uptake and chemical weathering by lichens and bryophytes are derived as potential

rates, based on their carbon uptake. A direct estimate would require a large amount of information about the environment, such as nutrient deposition rates, a phosphorus budget of the soil solution or the kinetics of weathering reactions at the surface. Since this information is not available at the global scale, the calculation of potential rates represents a functional alternative to the direct approach.

Another aspect is the difference in scale between the observations used to evaluate the model and the spatial resolution of the model. As discussed in Sect. 2.1.3 and 3.1.3 it is problematic to obtain observation-based values for large regions such as a model grid cell, since the measurements are sparse and highly variable. From a model development perspective, however, observational data are crucial to understand which processes are not correctly simulated by the model and need further refinement. Without sufficiently exact observations, many different model parameterisations may agree with measured data. Thus, to avoid this problem of “equifinality” it may be more useful to extend the possibilities to evaluate the model than to implement more processes in the model and to add more parameters.

4.3. Implications

In spite of the uncertainty in the estimates, the outcomes of this thesis suggest that lichens and bryophytes contribute considerably to global biogeochemical cycles. The global estimate of their net carbon uptake corresponds to approximately 1 to 6 % of the global terrestrial Net Primary Productivity (NPP) (Ito, 2011) while the medium estimate of potential nitrogen fixation amounts to 4 to 32 % of terrestrial biological nitrogen fixation (Galloway et al., 2004). Hence, lichens and bryophytes can be a significant part of the carbon and nitrogen cycles of ecosystems. This is especially true for regions with low productivity of vascular plants or low supply of nutrients. In nitrogen-limited ecosystems, the input of nitrogen into the system by lichens and bryophytes may represent an important nutrient source for vascular plants. Furthermore, lichens and bryophytes may significantly enhance surface weathering rates, since their potential for chemical weathering estimated here has the same order of magnitude as total global weathering rates at the surface (Newman, 1995; Gaillardet et al., 1999). This confirms suggestions by Lenton et al. (2012) regarding the considerable influence of early non-vascular plants on global climate in the geological past via the silicate weathering feedback.

4.4. Outlook

The approach presented here could be extended in several possible directions. The model of carbon uptake by lichens and bryophytes, for instance, could be run at a much smaller spatial scale, such as a small catchment or even a hillslope. This would not require substantial changes to the model, since it resolves the physiological processes of the organisms at a fundamental level. This means, that most of the model parameters that describe physiological processes of lichens and bryophytes can be measured in the laboratory and are therefore independent of the scale at which the model is applied. Only

model parameters that describe the environment would have to be adapted to the regional scale since they usually integrate many scale-dependent environmental processes. Applying the model to small spatial scales has the following potential benefits: First, the effect of microclimatic variation on the predicted carbon uptake could be quantified by running the model with two sets of input data, one with coarse resolution and one with fine resolution, and comparing the estimates to measurements from the same area. Second, the availability of more accurate and diverse observational data of carbon uptake at the regional scale could be used to assess particular processes implemented in the model, such as dew formation and uptake or the activation of photosynthesis and respiration as a function of water content. Third, it may be possible to obtain quantitative data about ecological interactions between different lichen and bryophyte species at a small spatial scale. Then, the abundance of the strategies in the model could be determined by simulating competition, for example. In this way the uncertainty in carbon uptake which results from the unknown abundance of model strategies could be significantly reduced. Fourth, also nitrogen and phosphorus balances might be available at small spatial scales. This would allow for a better assessment of the estimated potential rates of nitrogen fixation, phosphorus uptake and chemical weathering by lichens and bryophytes.

An important aspect of these potential benefits is their consistency. This means that climate forcing data with a high spatio-temporal resolution, for instance, should be accompanied by measurements of carbon uptake which also have a high spatio-temporal resolution and which originate from the same area. Only then is it possible to compare the high-resolution model estimates directly to observational data, which is necessary for an assessment of the model that goes beyond the one performed in this thesis. Ideally, also the physiological properties of those lichen and bryophyte species would be measured which are abundant in the region covered by the model simulation. In this way, the ranges of possible parameter values could be further narrowed and more exact model results could be obtained.

Also at the global scale, different applications of the model are possible. The method of deriving chemical weathering from simulated net carbon uptake can also be applied to the geological past. For this purpose, the sensitivity of modelled net carbon uptake by lichens and bryophytes to atmospheric CO_2 -concentration could be quantified. This CO_2 -sensitivity of carbon uptake could then be translated directly into a sensitivity of chemical weathering by lichens and bryophytes to atmospheric CO_2 . The sensitivity of carbon uptake to factors other than CO_2 , such as temperature, for instance, could be approximated by simple relationships between these factors and atmospheric CO_2 . The history of atmospheric CO_2 -concentration is relatively well known throughout the geological past (e.g. Berner (1998)). Consequently, the contribution of early lichens and bryophytes to global weathering rates in the course of Earth's history could be quantified. Since weathering also affects atmospheric CO_2 -concentration through silicate weathering at long time scales, the role of lichens and bryophytes in the feedback between weathering and atmospheric CO_2 could be examined by this approach.

Impacts of climate change on the productivity of lichens and bryophytes represent another potential application of the model at the global scale. The largest relative

increase in surface temperature associated with global warming is expected to take place at high latitudes. Thus, also the impacts of rising temperatures on ecosystems might be most pronounced in these regions. At high latitudes, lichens and bryophytes can be important contributors to carbon uptake, (e.g. Street et al. (2012); Turetsky et al. (2010)). Consequently, it is important to quantify the effects of warming on the productivity of these organisms. To achieve this, a process-based model is necessary since it calculates productivity as a function of climate factors. In contrast, estimates derived by empirical approaches, such as upscaling, for example, may not be valid anymore under changed climatic conditions. Lichens and bryophytes are seldom considered explicitly in modelling studies of climate change (Turetsky et al., 2012). Hence, the approach presented here may allow for a quantitative assessment of the impacts of climate change on the global biogeochemical functions of lichens and bryophytes.

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A. Additional model output

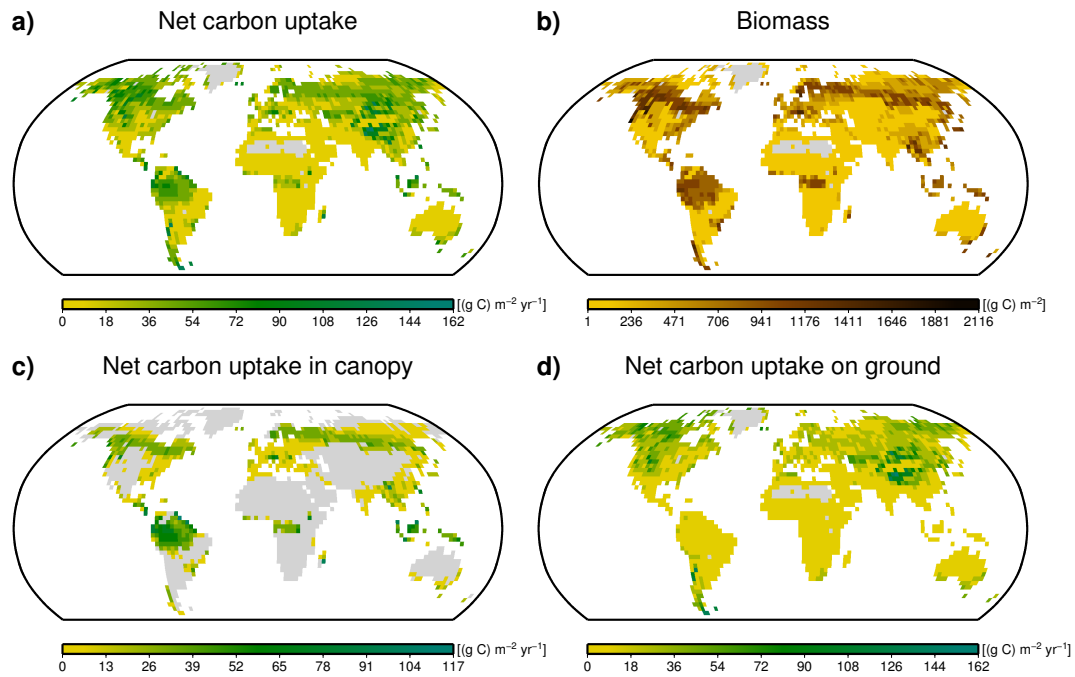


Figure A.1.: Global maps of model estimates based on time averages of the last 100 yr of a 2000-yr run with 3000 initial strategies. The estimates shown in a) to d) are based on the “maximum” weighting method while the ones shown in Fig. 2.5 are based on the “average” weighting method. Areas where no strategy has been able to survive are shaded in grey.

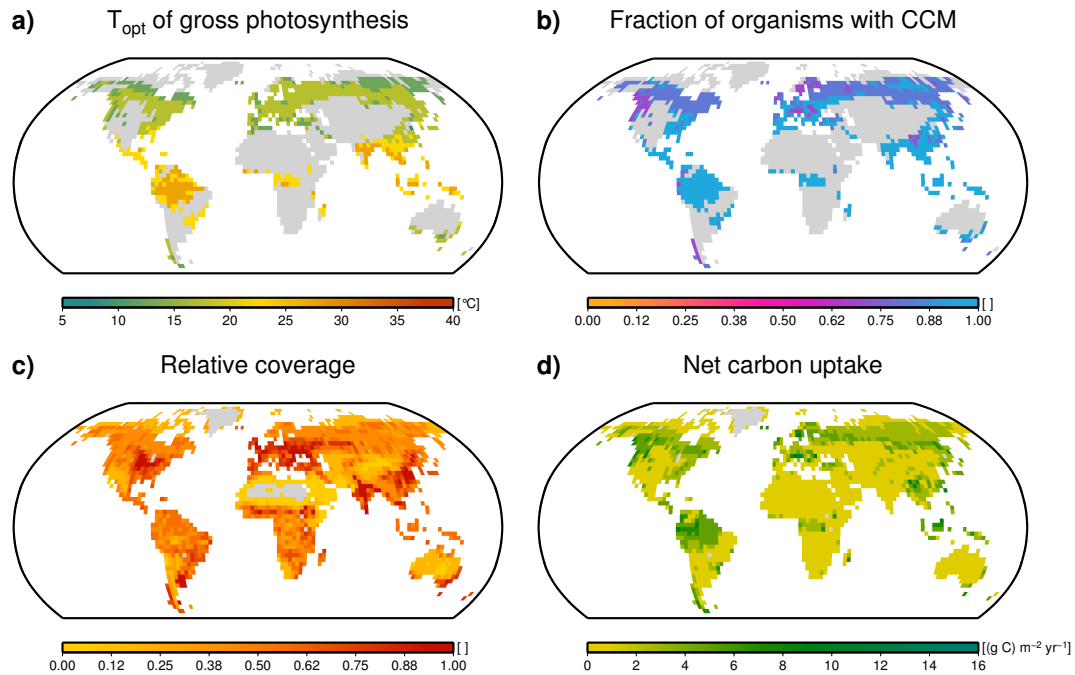


Figure A.2.: a) to c) are global maps of model estimates derived by time averages of the last 100 yr of a 2000-yr run with 3000 initial strategies and they are based on the “average” weighting method. a) and b) show optimum temperature and CCM fraction of lichens and bryophytes living in the canopy, which adds to Fig. 2.6, 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.

B. Model details

In the following sections, the technical details of the model are explained. Section B.1 describes how strategies are generated from parameter ranges. Moreover, references are provided for these parameter ranges. Sections B.2 to B.7 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. 2.1. The values and the units of the parameters and variables used in the model equations are tabulated in Sects. B.8 and B.9. 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 B.1.

Table B.1.: Overview of the nomenclature of parameters and variables in the model.

Prefix	Parameter or variable	Table(s)
<i>c</i>	Natural constant	B.7
<i>p</i>	Parameter	B.8 (Environment) B.11 (Lichens and Bryophytes)
<i>x</i>	Strategy parameter	B.9
<i>w</i>	Tradeoff parameter	B.10
<i>s</i>	State variable	B.14
<i>f</i>	Flow variable	B.15
none	Other variable	B.12 (Boundary conditions) B.13 (Environment) B.16 (Lichens and Bryophytes)

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

B.1. 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. 2.1.2). To create the strategies, these 15 characteristic parameters are assigned through randomly sampling ranges of possible values. The parameters and the corresponding ranges are listed in Table B.9. 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:

$$x = N(x_{\max} - x_{\min}) + x_{\min} \quad (\text{B.1})$$

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:

$$x = x_{\min} e^{N \log\left(\frac{x_{\max}}{x_{\min}}\right)} \quad (\text{B.2})$$

where the symbols have the same meaning as in Eq. B.1. The exponential function is used to represent each order of magnitude of the range equally. If the limits of the range were 1 and 10000, for instance, using Eq. B.1 would result in 90 % of the values lying between 1000 and 10000. Hence, values from the range 1 to 1000 would be strongly underrepresented. By using Eq. B.2 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. B.1: 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.

B.1.1. 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 there should be no reason to assume a priori that a certain value of the albedo is more frequent than the others.

B.1.2. 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 (B.1). An exponential mapping is used for the range of possible values.

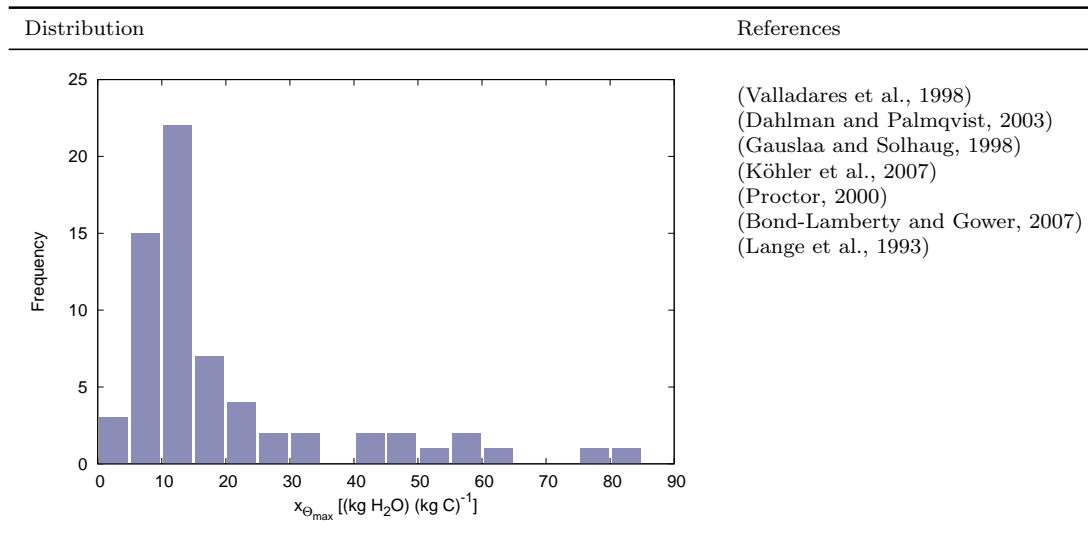


Figure B.1.: Overview of the distribution of specific water storage capacity $x_{\Theta_{\max}}$.

B.1.3. 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 (B.2). An exponential mapping is used for the range of possible values.

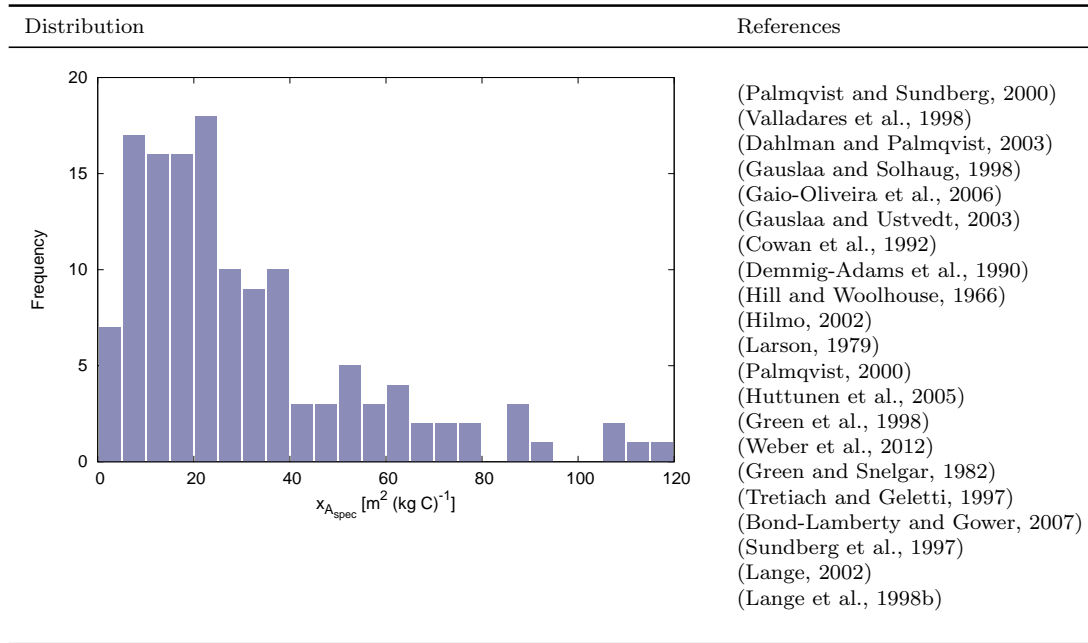


Figure B.2.: Overview of the distribution of specific projected area $x_{A_{\text{spec}}}$.

B.1.4. 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 %.

B.1.5. Threshold saturation and shape of water potential curve

As described in Sect. 2.1.1 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. B.3.1. $\Psi_{\text{H}_2\text{O}}$ has a value of $-\infty$ at zero water content and reaches a maximum value of 0 at a certain threshold saturation (see Fig. B.3). 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. B.3 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. B.3.3.

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. B.3.5.

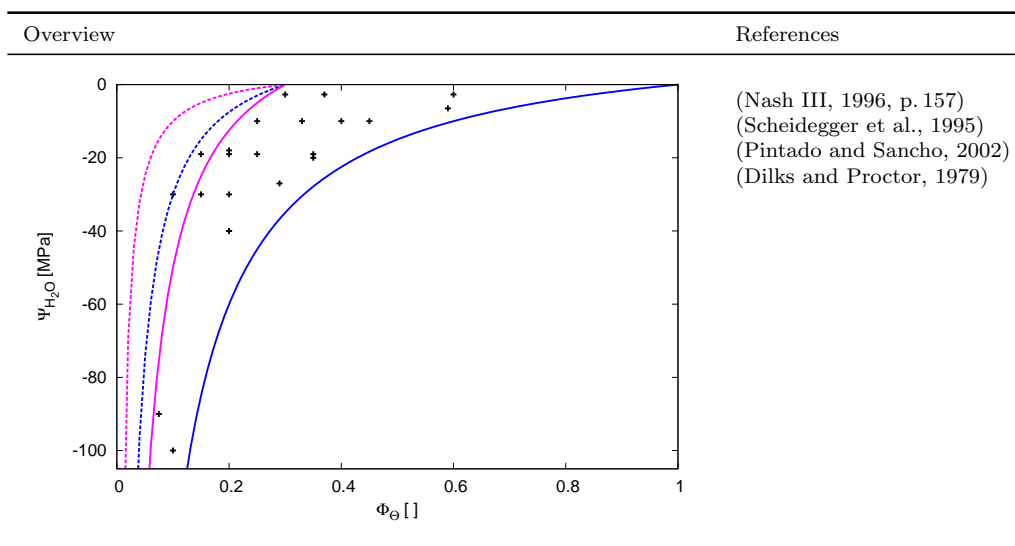


Figure B.3.: Water potential $\Psi_{\text{H}_2\text{O}}$ as a function of water saturation Φ_{Θ} . Four example curves are shown. The two blue curves correspond to a value of $x_{\Psi_{\text{H}_2\text{O}}} = 15.0$ which represents the middle of the range of possible values. The dashed blue curve corresponds 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.

B.1.6. Molar carboxylation rate of Rubisco

The molar carboxylation rate of Rubisco $x_{V_{C,\max}}$ represents the maximum carboxylation velocity of a Rubisco molecule (B.4). 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.

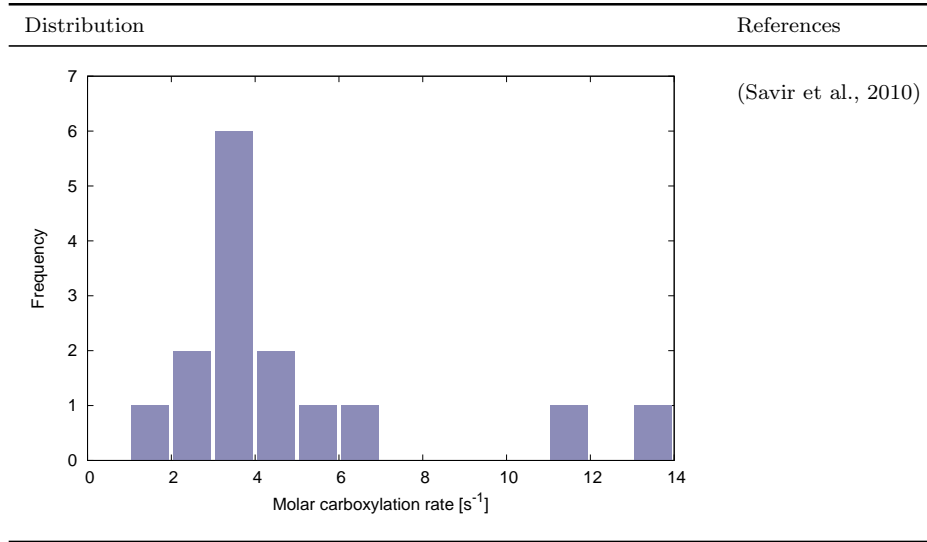


Figure B.4.: Overview of the distribution of the molar carboxylation rate of Rubisco.

B.1.7. Molar oxygenation rate of Rubisco

The molar oxygenation rate of Rubisco $x_{V_{O,\max}}$ represents the maximum oxygenation velocity of a Rubisco molecule (B.5). 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.

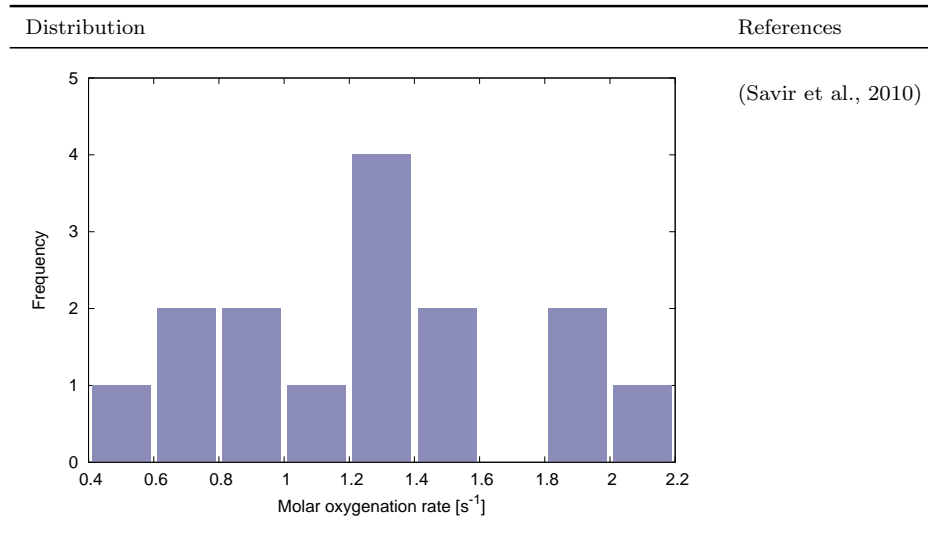


Figure B.5.: Overview of the distribution of the molar oxygenation rate of Rubisco.

B.1.8. 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. B.6 and B.7. 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. B.1, since the resulting range would be physiologically unrealistic. Instead, the values are rounded to the nearest integer. The influences of the two parameters on respiration rate are shown in Fig. B.8.

Moreover, the respiration rate is related to Rubisco content and turnover rate of the thallus, as described in Sect. 2.1.2. The details of these relationships are explained below in section B.5.2 and B.5.6.

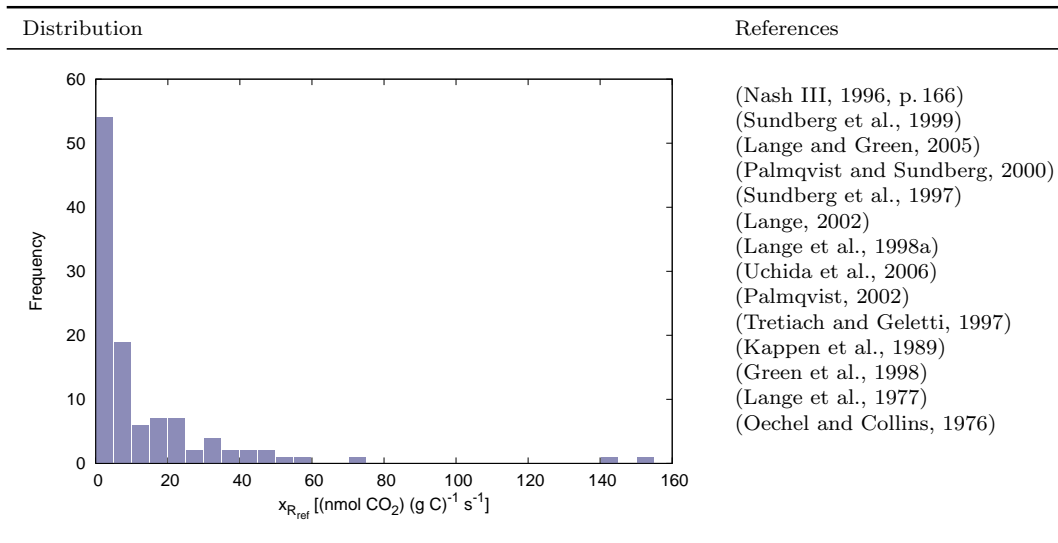


Figure B.6.: Overview of the distribution of the reference maintenance respiration rate at 10 °C, $x_{R_{\text{ref}}}$.

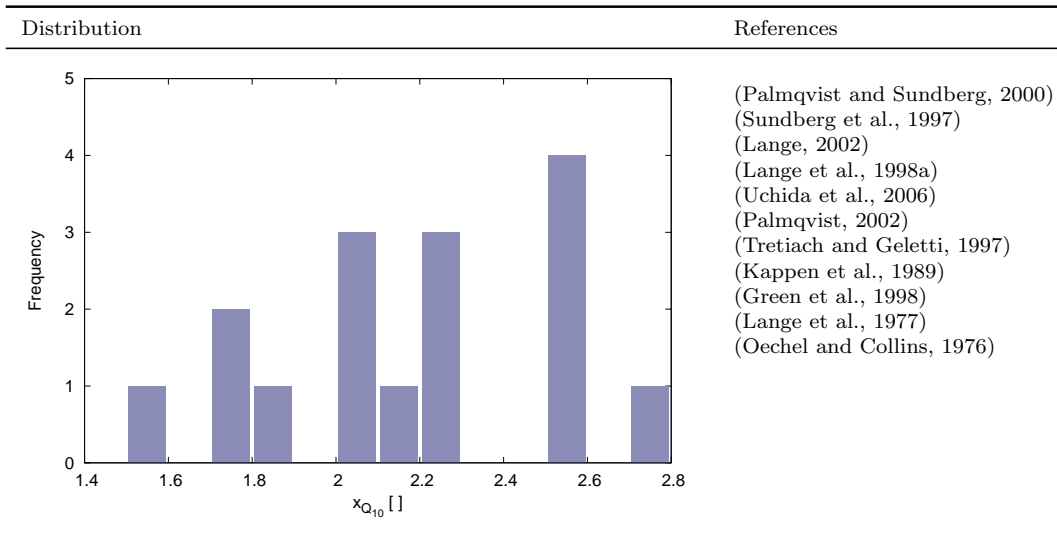


Figure B.7.: Overview of the distribution of the Q_{10} value of respiration $x_{Q_{10}}$.

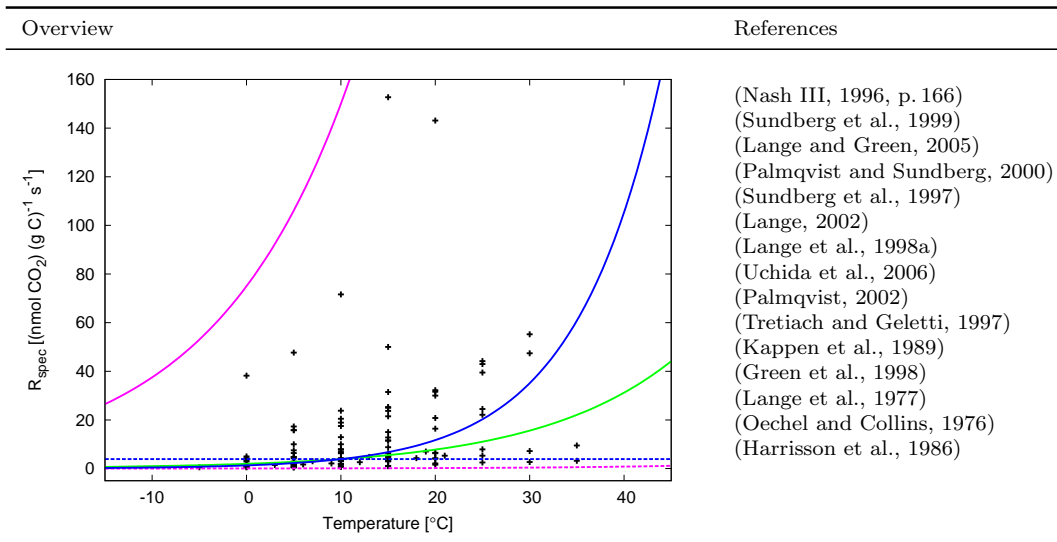


Figure B.8.: Influence of reference maintenance respiration $x_{R_{ref}}$ and Q_{10} value of respiration $x_{Q_{10}}$ on specific respiration rate R_{spec} . The green line shows the response of respiration to temperature for values of $x_{R_{ref}}$ and $x_{Q_{10}}$ which are both in the middle of their 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.

B.1.9. Optimum temperature of photosynthesis

The optimum temperature of photosynthesis $x_{T_{\text{opt,PS}}}$ represents the temperature at which gross photosynthesis shows a maximum (B.9). A linear mapping is used for the range of possible values. The range is not calculated by the method described for Eq. B.1 since the resulting values would be physiologically unrealistic. Instead, the limits derived from the data are extended by 10 and 5 Kelvin, respectively.

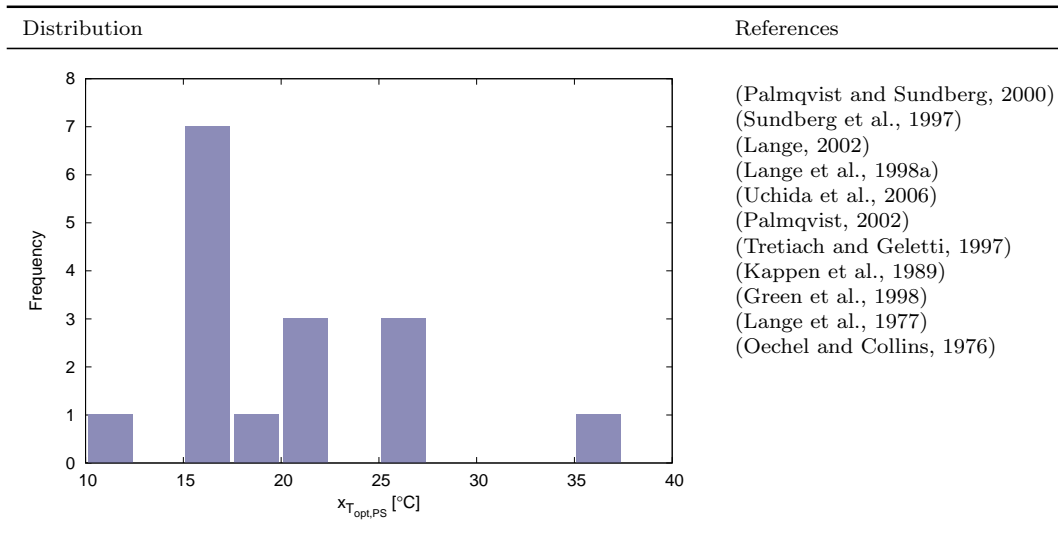


Figure B.9.: Overview of the distribution of the optimum temperature of photosynthesis $x_{T_{\text{opt,PS}}}$.

B.1.10. 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 B.2) are not sufficient to estimate the shapes of the ranges of x_{E_a, K_C} and x_{E_a, K_O} . It is assumed 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. B.1.

Table B.2.: 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	
79430	36380	(Medlyn et al., 2002)
59536	35948	"
109700	14500	"
80500	-	"

B.1.11. 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 CO₂, but to increase the CO₂ 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 %.

B.1.12. 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 no reason could be found 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.

B.2. 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. B.2.1 and B.2.2. 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. B.2.3 to B.2.5.

B.2.1. 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_{radS} and longwave radiation ϕ_{radL} are calculated by:

$$\phi_{\text{radS}} = \begin{cases} (1.0 - x_\alpha) (1.0 - e^{-p_{\lambda_s}(A_{\text{LAI}}+A_{\text{SAI}})}) & \text{if organism in canopy} \\ (1.0 - x_\alpha)e^{-p_{\lambda_s}(A_{\text{LAI}}+A_{\text{SAI}})} & \text{if organism on ground} \end{cases} \quad (\text{B.3})$$

and

$$\phi_{\text{radL}} = \begin{cases} p_\epsilon (1.0 - e^{-p_{\lambda_l}(A_{\text{LAI}}+A_{\text{SAI}})}) & \text{if organism in canopy} \\ p_\epsilon e^{-p_{\lambda_l}(A_{\text{LAI}}+A_{\text{SAI}})} & \text{if organism on ground} \end{cases} \quad (\text{B.4})$$

where x_α is the albedo of a lichen or bryophyte for shortwave radiation and p_ϵ is the emissivity of an organism for longwave radiation. p_{λ_s} and p_{λ_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:

$$\phi_{\text{prec}} = \begin{cases} p_{\eta_{\text{rain}}} \frac{A_{\text{LAI}}}{p_{\text{LAI}_{\text{max}}}} & \text{if organism in canopy} \\ 1.0 - \frac{A_{\text{LAI}}}{p_{\text{LAI}_{\text{max}}}} & \text{if organism on ground} \end{cases} \quad (\text{B.5})$$

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

B.2.2. Available area

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

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:

$$A_{\text{ground,max}} = \min \left(A_{\text{baresoil}}, 1.0 - \frac{A_{\text{LAI}}}{p_{\text{LAI,max}}} \right) \quad (\text{B.6})$$

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 $p_{\text{LAI,max}}$ 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. B.2.3 for details). Thus the available area for growth is written as:

$$A_{\text{canopy,max}} = A_{\text{LAI}} + A_{\text{SAI}} \quad (\text{B.7})$$

where A_{SAI} is SAI.

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

$$A_{\text{thallus}} = \begin{cases} \min(x_{\text{Aspec}} s_{\text{B}}, A_{\text{canopy,max}}) & \text{if organism in canopy} \\ \min(x_{\text{Aspec}} s_{\text{B}}, A_{\text{ground,max}}) & \text{if organism on ground} \end{cases} \quad (\text{B.8})$$

where x_{Aspec} 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:

$$\Phi_{\text{area}} = \begin{cases} \frac{A_{\text{thallus}}}{\max(A_{\text{canopy,max}}, 1.0)} & \text{if organism in canopy} \\ A_{\text{thallus}} & \text{if organism on ground} \end{cases} \quad (\text{B.9})$$

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. B.9 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 $0.6 / 0.8$.

B.2.3. Disturbance interval

The disturbance interval τ_{veg} is assigned according to biome and location of growth (see Table B.3). Disturbance leads to an instantaneous loss of biomass. The following processes are represented in the model:

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. B.2.2, 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.

Table B.3.: Overview of the disturbance intervals τ_{veg} of different biomes. The \star 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 B.4 and B.5 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 B.4 and B.5).

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

Table B.4.: References for the disturbance intervals τ_{veg} [years] 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	(Chandrashekar 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)	-	-

Table B.5.: References for the disturbance intervals τ_{veg} [years] 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 is estimated by “best guess” due to lack of data.

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

B.2.4. 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):

$$r_H = \frac{\log\left(\frac{p_{\Delta_u} - \Delta_d}{z_0}\right) \log\left(\frac{p_{\Delta_u} - \Delta_d}{z_{0,h}}\right)}{p_\kappa^2 u} \quad (\text{B.10})$$

where p_κ is the von Karman constant, u is near surface wind speed, p_{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. B.10 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):

$$z_0 = \begin{cases} p_{z_0, \text{canopy}}, & \text{if organism in canopy} \\ p_{z_0, \text{floor}}, & \text{if organism on forest floor} \\ p_{z_0, \text{GDT}}, & \text{if organism on ground outside forest} \end{cases} \quad (\text{B.11})$$

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:

$$z_{0,h} = p_{z_0, \text{mh}} z_0 \quad (\text{B.12})$$

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

The displacement height is related to roughness length via:

$$\Delta_d = p_{z_0, d} z_0 \quad (\text{B.13})$$

where $p_{z_0, d}$ is the ratio between displacement height and roughness length. The value of $p_{z_0, d}$ 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.

B.2.5. 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 :

$$\chi_G = \begin{cases} 0 & \text{if organism in canopy} \\ 1 & \text{if organism on ground} \end{cases} \quad (\text{B.14})$$

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:

$$C_{\text{soil}} = \begin{cases} p_{C_{\text{soil,D}}}, & \text{if organism in desert} \\ p_{C_{\text{soil,F}}}, & \text{if organism not in desert} \end{cases} \quad (\text{B.15})$$

$$k_{\text{soil}} = \begin{cases} p_{k_{\text{soil,D}}}, & \text{if organism in desert} \\ p_{k_{\text{soil,F}}}, & \text{if organism not in desert} \end{cases} \quad (\text{B.16})$$

B.3. Water relations

The water saturation of a lichen or bryophyte is defined in Sect. B.3.1. It controls three physiological properties: Diffusivity for CO₂ (Sect. B.3.2), water potential (Sect. B.3.3) and metabolic activity (Sect. B.3.4).

B.3.1. 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:

$$\Theta_{\max} = \frac{x_{\Theta_{\max}} s_B}{c_{\rho_{\text{H}_2\text{O}}}} \quad (\text{B.17})$$

where $x_{\Theta_{\max}}$ 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:

$$\Phi_{\Theta} = \frac{s_{\Theta}}{\Theta_{\max}} \quad (\text{B.18})$$

B.3.2. 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. B.10) and it is calculated according to:

$$D_{\text{CO}_2} = (w_{D_{\text{CO}_2,\max}} - w_{D_{\text{CO}_2,\min}})(1.0 - \Phi_{\Theta})^{w_{D_{\text{CO}_2}}} + w_{D_{\text{CO}_2,\min}} \quad (\text{B.19})$$

where $w_{D_{\text{CO}_2,\min}}$ is the minimum value of CO₂ diffusivity, $w_{D_{\text{CO}_2,\max}}$ is the maximum value of CO₂ 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. B.10, while $w_{D_{\text{CO}_2,\min}}$ and $w_{D_{\text{CO}_2,\max}}$ 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 CO₂ diffusivity and metabolic activity. This is explained below in Sect. B.3.5.

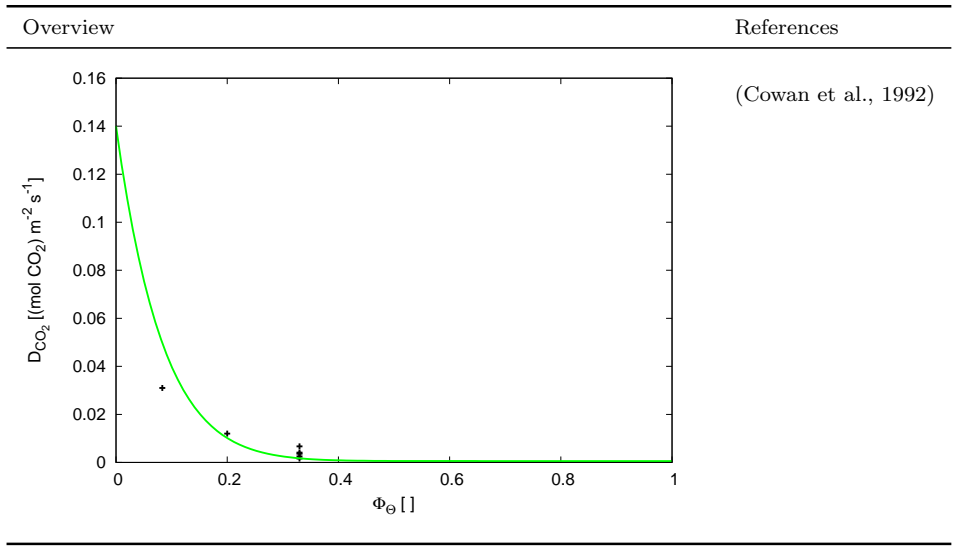


Figure B.10.: Diffusivity for CO_2 , D_{CO_2} , as a function of water saturation Φ_Θ . The black data points are derived from the studies listed in the right column.

B.3.3. Water potential

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

$$\Psi_{\text{H}_2\text{O}} = \min \left(0.0, x_{\Psi_{\text{H}_2\text{O}}} \left(1.0 - \frac{x_{\Phi_{\Theta, \text{sat}}}}{\Phi_{\Theta}} \right) \right) \quad (\text{B.20})$$

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. B.1.5 and the curve is shown in Fig. B.3. 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. B.3.5.

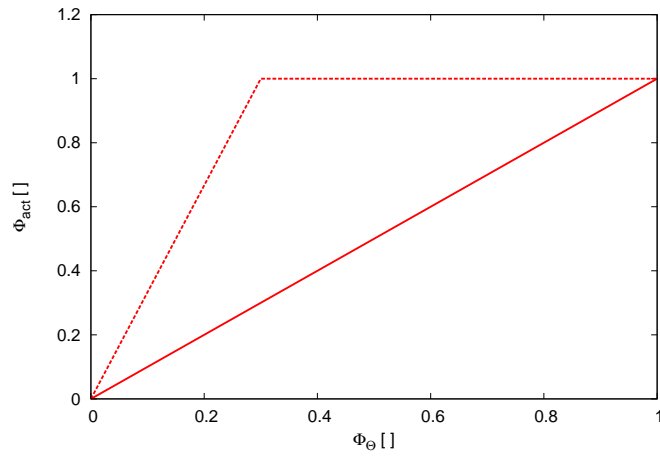
B.3.4. Metabolic activity

The metabolic activity of a lichen or bryophyte is represented by the variable Φ_{act} and it relates the processes *photosynthesis* and *respiration* to the water content of the organism (Nash III, 1996, p. 157). The papers of Lange (1980, 2002), for instance, show how dark respiration increases with water content at constant temperature while the studies by Jonsson Čabrajčić et al. (2010); Williams and Flanagan (1998) show an increase of photosynthetic activity/capacity with water content. A common feature of these experiments with different species is that dark respiration as well as photosynthetic activity saturate and assume a constant value above a species-specific threshold water content. The shape of the activity curve from zero water content to this threshold water content is nonlinear and it shows species-specific variation. The extent of the nonlinearity, however, is relatively small and can be approximated by a linear relationship where the strategy parameter *threshold saturation*, $x_{\Phi_{\Theta, \text{sat}}}$, captures some variation. Hence, the metabolic activity is assumed to increase linearly from 0 at zero water content to 1 at the threshold saturation (Fig. B.11). Φ_{act} is then written as:

$$\Phi_{\text{act}} = \min \left(1.0, \frac{\Phi_{\Theta}}{x_{\Phi_{\Theta, \text{sat}}}} \right) \quad (\text{B.21})$$

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. B.3.5.



(Nash III, 1996, p. 157)
(Lange, 1980)
(Lange, 2002)
(Jonsson Čabrajić et al., 2010)
(Williams and Flanagan, 1998)

Figure B.11.: Metabolic activity Φ_{act} as a function of water saturation Φ_{Θ} . The dashed line corresponds to $x_{\Phi_{\Theta}, \text{sat}} = 0.3$ and the solid line corresponds to $x_{\Phi_{\Theta}, \text{sat}} = 1.0$

B.3.5. Tradeoff between CO₂ diffusivity and metabolic activity

The CO₂ diffusivity of the thallus, D_{CO_2} , decreases with increasing water saturation Φ_Θ (see Sect. B.3.2). The metabolic activity of a lichen or bryophyte Φ_{act} , however, increases with Φ_Θ (see Sect. B.3.4). This leads to a tradeoff: At low Φ_Θ the potential inflow of CO₂ 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. 2.1.2).

The tradeoff is illustrated in Fig. B.12: 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} .

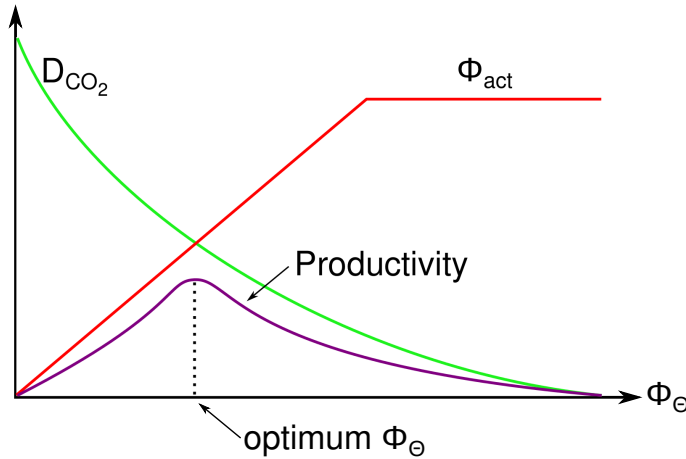


Figure B.12.: Effect of water saturation Φ_Θ on CO₂ diffusivity D_{CO_2} , metabolic activity Φ_{act} and on the associated productivity. The productivity has a maximum at an optimum Φ_Θ .

B.4. 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. 2.3). Furthermore, it determines potential evaporation and surface temperature. In the following sections the relations between potential evaporation (Sect. B.4.3), surface temperature (Sect. B.4.4) and climate forcing are described. The factors necessary for the calculation of these relations are:

1. Net radiation (see Sect. B.4.1)
2. Saturation vapour pressure (see Sect. B.4.2)
3. Aerodynamic resistance to heat transfer (see Sect. B.2.4)
4. Relative humidity

Also snow affects physiological processes of lichens and bryophytes. The dynamics of the snow layer are explained in Sect. B.4.5 while the effects of the snow layer on physiological processes are described in the sections related to these processes.

B.4.1. 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 $f_{\text{radLW}\uparrow}$ is calculated as a function of surface temperature and air temperature:

$$f_{\text{radLW}\uparrow} = (4.0c_{\sigma}T_{\text{air}}^3T_{\text{surf}} - 3.0c_{\sigma}T_{\text{air}}^4) \Phi_{\text{area}} \quad (\text{B.22})$$

where T_{air} is air temperature, T_{surf} is surface temperature and c_{σ} is the Stefan-Boltzmann constant. Equation B.22 is a linearisation of the standard equation for 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. B.9). This factor thus converts $f_{\text{radLW}\uparrow}$ to Watts per m² ground.

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

$$f_{\text{Qsoil}} = k_{\text{soil}} \frac{T_{\text{surf}} - s_{\text{Tsoil}}}{p_{\Delta_z}} \Phi_{\text{area}} \chi_{\text{G}} \quad (\text{B.23})$$

where k_{soil} is the thermal conductivity of the soil (see Eq. B.16), T_{surf} is the surface temperature of the thallus, s_{Tsoil} is soil temperature and p_{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_{Qsoil} to zero if a lichen or bryophyte is living in the canopy (see Eq. B.14).

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

$$s_{T_{\text{soil}}} = s_{T_{\text{soil}}} + \frac{f_{Q_{\text{soil}}}}{C_{\text{soil}}\Phi_{\text{area}}p_{\Delta_z}}p_{\Delta_t} \quad (\text{B.24})$$

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, p_{Δ_z} is the damping depth of the soil for a diurnal cycle and p_{Δ_t} is the time step of the model.

Net radiation f_{H} is written as:

$$f_{\text{H}} = \phi_{\text{rad}_S}f_{\text{rad}_{\text{SW}\downarrow}}\Phi_{\text{area}} + \phi_{\text{rad}_L}f_{\text{rad}_{\text{LW}\downarrow}}\Phi_{\text{area}} - \phi_{\text{rad}_L}f_{\text{rad}_{\text{LW}\uparrow}} - f_{Q_{\text{soil}}} \quad (\text{B.25})$$

where ϕ_{rad_S} is a conversion factor for shortwave radiation (see Eq. B.3) and ϕ_{rad_L} is a conversion factor for longwave radiation (see Eq. B.4). $f_{\text{rad}_{\text{SW}\downarrow}}$ and $f_{\text{rad}_{\text{LW}\downarrow}}$ 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. B.9). $f_{\text{rad}_{\text{LW}\uparrow}}$ is already multiplied by Φ_{area} in Eq. B.22, the same applies for $f_{Q_{\text{soil}}}$ in Eq. B.23.

B.4.2. 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):

$$e_{\text{sat},0} = p_{e_{s,3}}e^{\frac{p_{e_{s,1}}T_{\text{air},C}}{p_{e_{s,2}}+T_{\text{air},C}}} \quad (\text{B.26})$$

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 $x_{\Phi_{\Theta,\text{sat}}}$ (see Sects. B.1.5 and B.3.3), 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):

$$\phi_{e_{\text{sat}}} = \frac{1.0\text{E}6\Psi_{\text{H}_2\text{O}}c_{\text{M}_{\text{H}_2\text{O}}}}{c_{\text{R}_{\text{gas}}}T_{\text{air},C}c_{\rho_{\text{H}_2\text{O}}}} \quad (\text{B.27})$$

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, $c_{\text{R}_{\text{gas}}}$ 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.

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

$$e_{\text{sat}} = e^{\phi_{e_{\text{sat}}}}e_{\text{sat},0} \quad (\text{B.28})$$

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

$$d_{e_{\text{sat}}} = e^{\left(\frac{p_{e_{s,1}} T_{\text{air,C}}}{p_{e_{s,2}} + T_{\text{air,C}}} + \phi_{e_{\text{sat}}}\right)} \left(\frac{p_{e_{s,1}} p_{e_{s,2}} p_{e_{s,3}}}{(p_{e_{s,2}} + T_{\text{air,C}})^2} - \frac{\phi_{e_{\text{sat}}}}{T_{\text{air}}} \right) \quad (\text{B.29})$$

B.4.3. 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):

$$E_{\text{pot}} = \frac{f_{\text{H}} d_{e_{\text{sat}}} + c_{C_{\text{air}}} \frac{e_{\text{sat}} - \Phi_{\text{RH}} e_{\text{sat}}}{r_{\text{H}}} \Phi_{\text{area}}}{(d_{e_{\text{sat}}} + c_{\gamma}) c_{\Delta H_{\text{vap,H}_2\text{O}}} c_{\rho_{\text{H}_2\text{O}}}} \quad (\text{B.30})$$

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_{γ} is the psychrometric constant, $c_{\Delta H_{\text{vap,H}_2\text{O}}}$ 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. B.25.

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.

B.4.4. Surface temperature

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

$$T_{\text{surf}} = \frac{T_{\text{air}} - \frac{e_{\text{sat}} - \Phi_{\text{RH}} e_{\text{sat}}}{d_{e_{\text{sat}}} + c_{\gamma}} + \frac{\left(\phi_{\text{radS}} f_{\text{radSW}\downarrow} + \phi_{\text{radL}} (f_{\text{radLW}\downarrow} + 3.0 c_{\sigma} T_{\text{air}}^4) + \frac{k_{\text{soil}}}{p_{\Delta z}} s_{T_{\text{soil}}} \chi_{\text{G}}\right) c_{\gamma} r_{\text{H}}}{c_{C_{\text{air}}} (d_{e_{\text{sat}}} + c_{\gamma})}}{1.0 + \frac{\left(\phi_{\text{radL}} 4.0 c_{\sigma} T_{\text{air}}^3 + \frac{k_{\text{soil}}}{p_{\Delta z}} \chi_{\text{G}}\right) c_{\gamma} r_{\text{H}}}{c_{C_{\text{air}}} (d_{e_{\text{sat}}} + c_{\gamma})}} \quad (\text{B.31})$$

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, $f_{\text{radSW}\downarrow}$ and $f_{\text{radLW}\downarrow}$ 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, $p_{\Delta z}$ 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.

B.4.5. Snow layer

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 $p_{\Delta_{\text{snow}}}$ (Pannewitz 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):

$$f_{\text{snowmelt}} = \min \left(3.22 \frac{\max(0.0, T_{\text{air}} - c_{T_{\text{melt}, \text{H}_2\text{O}}})}{86400 \cdot 1000}, \frac{s_{\text{snow}}}{p_{\Delta_t}} + f_{\text{snow,atm}} \right) \quad (\text{B.32})$$

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 , p_{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:

$$s_{\text{snow}} = \max(0.0, s_{\text{snow}} + (f_{\text{snow,atm}} - f_{\text{snowmelt}} - s_{\text{snow}} p_{\tau_{\text{ice}}}) p_{\Delta_t}) \quad (\text{B.33})$$

where the last term describes lateral movement of the snow pack. The parameter $p_{\tau_{\text{ice}}}$ 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):

$$\Delta_{\text{snow}} = s_{\text{snow}} \frac{c_{\rho_{\text{H}_2\text{O}}}}{p_{\rho_{\text{snow}}}} \quad (\text{B.34})$$

In case a lichen or bryophyte is covered by a snow layer that exceeds the critical thickness $p_{\Delta_{\text{snow}}}$, a different method than Eq. B.31 is used to compute the surface temperature T_{surf} of the thallus:

$$T_{\text{surf}} = \begin{cases} T_{\text{air}}, & \text{if organism in canopy} \\ \frac{\frac{p_{\text{ksnow}}}{\Delta_{\text{snow}}} T_{\text{air}} + \frac{k_{\text{soil}}}{p_{\Delta_z}} s_{T_{\text{soil}}}}{\frac{p_{\text{ksnow}}}{\Delta_{\text{snow}}} + \frac{k_{\text{soil}}}{p_{\Delta_z}}} & \text{if organism on ground} \end{cases} \quad (\text{B.35})$$

where p_{ksnow} 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, p_{Δ_z} is the damping depth of the soil for a diurnal cycle and $s_{T_{\text{soil}}}$ is soil temperature. Note that Eq. B.35 does not have any effects on the metabolism of lichens or bryophytes, since they are assumed to be inactive under snow. Eq. B.35 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 B.35 results from assuming a steady state of the surface.

B.5. Carbon exchange flows

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

1. Inflow of CO₂ from the atmosphere into the pore space of the thallus (see Sect. B.5.1)
2. Uptake of CO₂ from the pore space (Gross Primary Productivity, GPP) and storage as sugars (see Sect. B.5.2)
3. Maintenance and growth respiration (see Sect. B.5.4)
4. Growth, which is the transformation of the stored sugars into biomass (see Sect. B.5.4)
5. Biomass loss (see Sect. B.5.6)

The relations of these flows to the balances of the carbon reservoirs of a lichen or bryophyte are described in Sect. B.5.7.

B.5.1. Inflow of CO₂ into the thallus

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:

$$f_{\text{CO}_2,\text{in}} = D_{\text{CO}_2} \frac{CO_{2,\text{atm}} - CO_{2,\text{thallus}}}{1.0\text{E}6} \Phi_{\text{area}} \quad (\text{B.36})$$

where D_{CO_2} is the diffusivity of the thallus for CO₂, $CO_{2,\text{atm}}$ is the atmospheric CO₂ concentration, $CO_{2,\text{thallus}}$ 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 CO₂ flows out of the thallus.

B.5.2. 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 $V_{\text{C,max}}$.

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

$$V_{C,\max} = x_{V_{C,\max}} \Xi_{\text{Rub}} e^{-\left(\frac{T_{\text{surf}} - x_{T_{\text{opt,PS}}}}{p_{\Omega}}\right)^2} \quad (\text{B.37})$$

where $x_{V_{C,\max}}$ is the molar carboxylation rate of Rubisco (see Sect. B.1.6) 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. B.1.9) and the shape of the temperature response curve is determined by the parameter p_{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. 2.1.2). The exact shape of this relation could not be determined, since not enough studies could be found where both Ξ_{Rub} and $x_{R_{\text{ref}}}$ are measured. Thus, a simple linear function is assumed:

$$\Xi_{\text{Rub}} = w_{\text{Rub,R}} x_{R_{\text{ref}}} \quad (\text{B.38})$$

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. B.2 with $N = 0.5$. The limits of the range of possible values of $x_{R_{\text{ref}}}$ can be found in Table B.9. To compute $\overline{\Xi_{\text{Rub}}}$ also Eq. B.2 is used with $N = 0.5$, although the range of possible values of Ξ_{Rub} (see Table B.6) 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. B.38, however, implies that both the range of $x_{R_{\text{ref}}}$ and the range of Ξ_{Rub} have the same shape. Hence, using Eq. B.2 to estimate $\overline{\Xi_{\text{Rub}}}$ is a consistent approach. Note that using the median of the values from Table B.6 to compute $\overline{\Xi_{\text{Rub}}}$ instead of using Eq. B.2 does not significantly change the value of $w_{\text{Rub,R}}$.

Table B.6.: 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	"

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

$$J_{\max} = \phi_{\text{JV}} V_{C,\max} \quad (\text{B.39})$$

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

$$\phi_{JV} = \max \left(0.0, w_{JV,1} \left(T_{\text{surf}} - c_{T_{\text{melt},\text{H}_2\text{O}}} \right) + w_{JV,2} \right) \quad (\text{B.40})$$

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. B.13. ϕ_{JV} is limited to non-negative values since a negative J_{max} would make no sense from a physiological viewpoint.

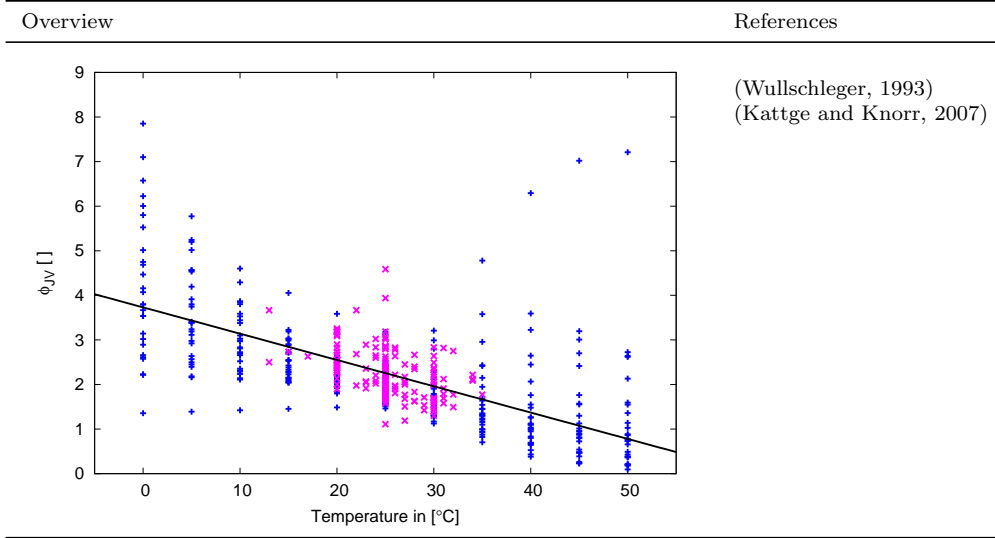


Figure B.13.: Ratio of J_{max} to $V_{C,\text{max}}$, ϕ_{JV} , (black line) as a function of temperature. The magenta data points are taken from the study of Wullschlegel (1993) while the blue points are derived by the equations used in Kattge and Knorr (2007).

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. 2.1.2) 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:

$$J = \min \left(f_{\text{rad}_{\text{SW}\downarrow}} \phi_{\text{rad}_s} p_{\text{PAR}} p_{\text{quant}} w_{\text{CCM},e} \Phi_{\text{area}}, J_{\text{max}} s_B \right) \quad (\text{B.41})$$

where $f_{\text{rad}_{\text{SW}\downarrow}}$ is the flow of shortwave radiation, ϕ_{rad_s} is a conversion factor that includes albedo and LAI (see Sect. B.2.1), p_{PAR} is a factor that converts shortwave radiation into photosynthetically active radiation and p_{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. B.5.3 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 $V_{C,\max}$ 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:

$$K_C = 0.001 w_{K_{C,1}} x_{V_{C,\max}}^{w_{K_{C,2}}} e^{\frac{(T_{\text{surf}} - p_{T_{\text{ref,PS}}}) x_{E_{a,K_C}}}{p_{T_{\text{ref,PS}}} c_{R_{\text{gas}}} T_{\text{surf}}}} \quad (\text{B.42})$$

and

$$K_O = 0.001 \frac{x_{V_{O,\max}}}{w_{K_{O,1}} \left(\frac{x_{V_{C,\max}}}{w_{K_{C,1}} x_{V_{C,\max}}} \right)^{w_{K_{O,2}}}} e^{\frac{(T_{\text{surf}} - p_{T_{\text{ref,PS}}}) x_{E_{a,K_O}}}{p_{T_{\text{ref,PS}}} c_{R_{\text{gas}}} T_{\text{surf}}}} \quad (\text{B.43})$$

where $x_{V_{C,\max}}$ is the molar carboxylation rate of Rubisco (see Sect. B.1.6) and $x_{V_{O,\max}}$ is the molar oxygenation rate of Rubisco (see Sect. B.1.7). The factor 0.001 is used to convert K_C and K_O into mol per m^3 . The exponentials in Eqs. B.42 and B.43 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. B.1.10).

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 $x_{V_{C,\max}}$ and $x_{V_{O,\max}}$. 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 as:

$$\Gamma_* = 0.5 O_{2,\text{cell}} \frac{x_{V_{O,\max}} K_C}{x_{V_{C,\max}} K_O} \quad (\text{B.44})$$

where $O_{2,\text{cell}}$ is the concentration of O_2 in the chloroplast of a lichen or bryophyte, $x_{V_{C,\max}}$ and $x_{V_{O,\max}}$ 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:

$$O_{2,\text{cell}} = \frac{1000.0}{p_{\text{SO}_2}} O_{2,\text{atm}} \quad (\text{B.45})$$

where $O_{2,\text{atm}}$ is the atmospheric O_2 concentration and p_{SO_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 $C_{\text{CO}_2,\text{cell}}$ 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:

$$CO_{2,\text{cell}} = \frac{1000.0}{p_{S_{CO_2}}} CO_{2,\text{thallus}} \quad (\text{B.46})$$

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

Knowing $CO_{2,\text{cell}}$, $O_{2,\text{cell}}$, J , K_C , K_O , $x_{V_{C,\text{max}}}$ and $x_{V_{O,\text{max}}}$, 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:

$$f_{\text{GPP,L}} = J \frac{CO_{2,\text{cell}} - \Gamma_*}{4.0CO_{2,\text{cell}} + 8.0\Gamma_*} \Phi_{\text{act}} \quad (\text{B.47})$$

and

$$f_{\text{GPP,W}} = x_{V_{C,\text{max}}} s_B \frac{CO_{2,\text{cell}} - \Gamma_*}{CO_{2,\text{cell}} + K_C \frac{1.0 + O_{2,\text{cell}}}{K_O}} \Phi_{\text{act}} \quad (\text{B.48})$$

where $CO_{2,\text{cell}}$ 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 $O_{2,\text{cell}}$ is the O_2 concentration in the chloroplast. Φ_{act} is the metabolic activity of a lichen or bryophyte (see Sect. B.3.4). 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 $f_{\text{GPP,W}}$:

$$f_{\text{GPP}} = \min(f_{\text{GPP,L}}, f_{\text{GPP,W}}) \quad (\text{B.49})$$

B.5.3. Carbon Concentration Mechanism

Some lichens and bryophytes possess a Carbon Concentration Mechanism (CCM, see Sects. 2.1.2 and B.1.11). 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. It is assumed here that the CCM in lichens works similarly than in free living cyanobacteria. The increased CO_2 concentration in the chloroplasts can then be calculated as a function of pore space CO_2 concentration:

$$CO_{2,\text{cell}} = \min(w_{\text{CCM},1} CO_{2,\text{thallus}}, w_{\text{CCM},2} CO_{2,\text{thallus}} + w_{\text{CCM},3}) \quad (\text{B.50})$$

where $CO_{2,\text{cell}}$ and $CO_{2,\text{thallus}}$ 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. B.14.

The form of the CCM implemented in the model represents a tradeoff for a lichen or bryophyte: The increased CO_2 concentration in the chloroplasts which depends on

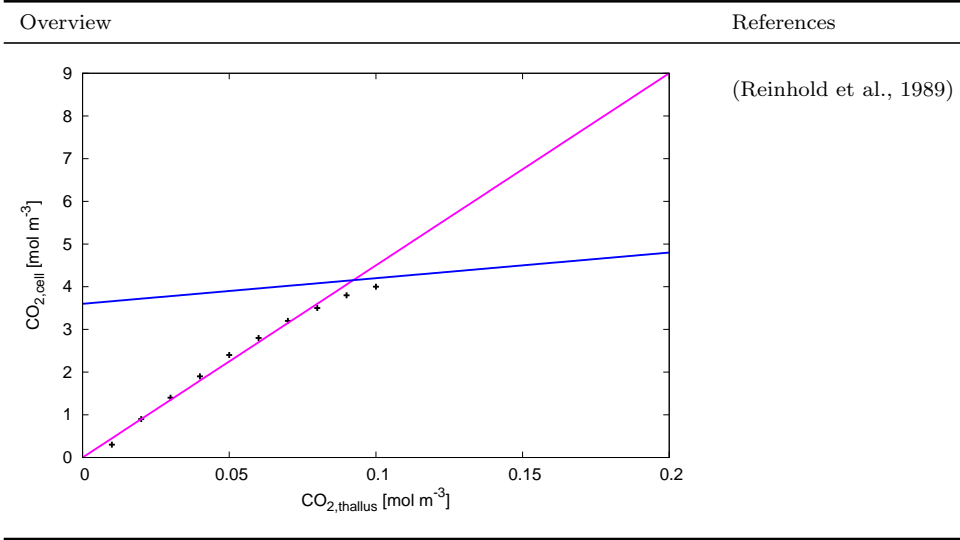


Figure B.14.: CO_2 concentration in the chloroplasts, $CO_{2,cell}$, as a function of pore space CO_2 concentration $CO_{2,thallus}$. The black data points are taken from the study of Reinhold et al. (1989). The minimum of the magenta and blue lines is used to fit the data.

$w_{CCM,1}$, $w_{CCM,2}$ and $w_{CCM,3}$ 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 $w_{CCM,e}$ (see Eq. B.41). 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.

B.5.4. 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. B.8 in Sect. B.1.8 and it is written as:

$$R_{spec} = x_{R_{ref}} x_{Q_{10}}^{\frac{T_{surf} - p_{T_{ref,R}}}{p_{T_{ref,R}} - c_{T_{melt,H_2O}}}} \quad (B.51)$$

where $x_{R_{ref}}$ 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, $p_{T_{ref,R}}$ is the reference temperature and $c_{T_{melt,H_2O}}$ is the melting temperature of water.

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

$$f_{R_{main}} = \min \left(\frac{s_C}{c_{M_C} p_{\Delta t}}, R_{spec} s_B \Phi_{act} \right) \quad (B.52)$$

where s_C is the sugar reserve of a lichen or bryophyte, c_{M_C} is the molar mass of carbon, $p_{\Delta t}$ 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. B.52 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:

$$f_{\text{growth}} = \min \left(\frac{s_C}{c_{\text{MC}} p_{\Delta t}} - f_{\text{R}_{\text{main}}}, x_{\text{alloc}} \frac{s_C}{c_{\text{MC}} 86400} \Phi_{\text{act}} \right) p_{\eta_{\text{growth}}} \quad (\text{B.53})$$

where s_C is the sugar reserve of a lichen or bryophyte, c_{MC} is the molar mass of carbon, $p_{\Delta t}$ is the time step of the model and $f_{\text{R}_{\text{main}}}$ is maintenance respiration. x_{alloc} is the fraction of the sugar reservoir allocated to growth per day, 86400 is the number of seconds per day, Φ_{act} is metabolic activity, and $p_{\eta_{\text{growth}}}$ is the efficiency of the transformation of sugars to biomass.

The respiration associated with growth, $f_{\text{R}_{\text{growth}}}$ is then written as a function of growth efficiency $p_{\eta_{\text{growth}}}$ and growth f_{growth} :

$$f_{\text{R}_{\text{growth}}} = \left(\frac{1.0}{p_{\eta_{\text{growth}}}} - 1.0 \right) f_{\text{growth}} \quad (\text{B.54})$$

B.5.5. Steady State of internal CO_2

Two carbon exchange flows depend on the internal CO_2 concentration of the thallus $\text{CO}_{2,\text{thallus}}$, namely the inflow of CO_2 from the atmosphere into the pore space, $f_{\text{CO}_{2,\text{in}}}$ (Eq. B.36), and the uptake of CO_2 from the pore space by GPP, f_{GPP} (Eq. B.49). The model, however, does not simulate explicitly the pore space of the thallus. Hence, it is not possible to determine the absolute amount of CO_2 in the thallus. Instead, a steady-state approach is used to calculate $\text{CO}_{2,\text{thallus}}$. It is assumed that the exchange flow of CO_2 between pore space and atmosphere, $f_{\text{CO}_{2,\text{in}}}$, balances the net CO_2 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 CO_2 into the pore space, consisting of maintenance respiration $f_{\text{R}_{\text{main}}}$ and growth respiration $f_{\text{R}_{\text{growth}}}$ (Eqs. B.52 and B.54). The equation for the steady state of pore space CO_2 is thus written as:

$$f_{\text{CO}_{2,\text{in}}} = f_{\text{R}_{\text{main}}} + f_{\text{R}_{\text{growth}}} - f_{\text{GPP}} \quad (\text{B.55})$$

Equation B.55 is then solved for $\text{CO}_{2,\text{thallus}}$ to determine the values for $f_{\text{CO}_{2,\text{in}}}$ and f_{GPP} .

B.5.6. Biomass loss

The turnover rate of the biomass of lichens or bryophytes, τ_{B} , is calculated similarly to the Rubisco content (see Sect. B.5.2) as a function of the reference respiration rate at 10 °C, $x_{\text{R}_{\text{ref}}}$. The relation between τ_{B} and $x_{\text{R}_{\text{ref}}}$ represents a tradeoff and results from a physiological constraint, namely metabolic stability of enzymes (see Sect. 2.1.2). The

exact shape of this relation could not be determined, since not enough studies could be found where both τ_B and $x_{R_{ref}}$ are measured. Thus, a simple linear function is assumed:

$$\tau_B = w_{loss,R} x_{R_{ref}} \quad (\text{B.56})$$

where the tradeoff-parameter $w_{loss,R}$, which represents the slope of the line, is determined by two points: the origin (0,0) and the point $(\overline{\tau_B}, \overline{x_{R_{ref}}})$, where $\overline{x_{R_{ref}}}$ is the average reference respiration rate and $\overline{\tau_B}$ is the average turnover rate. $\overline{x_{R_{ref}}}$ is calculated by Eq. B.2 with $N = 0.5$. The limits of the range of possible values of $x_{R_{ref}}$ can be found in Table B.9. To compute $\overline{\tau_B}$ also Eq. B.2 is used with $N = 0.5$ (see Fig. B.15). The range of possible values of τ_B is set to 0.03 - 1.5 (see Sect. B.1).

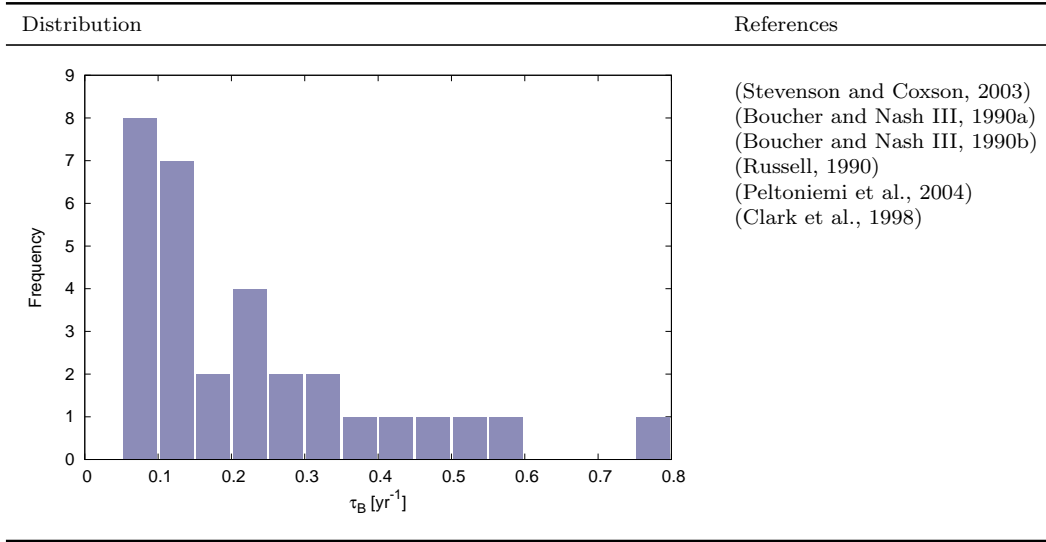


Figure B.15.: Overview of the distribution of turnover rate τ_B .

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

$$f_{loss} = \tau_B \frac{s_B}{c_{MC} 3.1536E7} \quad (\text{B.57})$$

where τ_B is the turnover rate, s_B is the biomass of a lichen or bryophyte and c_{MC} 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.

B.5.7. 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:

$$s_C = \max(0.0, s_C + (f_{GPP} - f_{R_{main}} - f_{R_{growth}} - f_{growth}) c_{MC} p_{\Delta t}) \quad (\text{B.58})$$

where f_{GPP} is GPP, $f_{\text{R}_{\text{main}}}$ is maintenance respiration, $f_{\text{R}_{\text{growth}}}$ is growth respiration, f_{growth} is growth c_{M_C} is the molar mass of carbon and p_{Δ_t} is the time step of the model. The balance of the biomass reservoir s_{B} is written as:

$$s_{\text{B}} = \max(0.0, s_{\text{B}} + (f_{\text{growth}} - f_{\text{loss}}) c_{\text{M}_\text{C}} p_{\Delta_t}) \quad (\text{B.59})$$

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

B.6. 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:

$$f_{\text{water,up}} = (f_{\text{rain,atm}} + f_{\text{snowmelt}}) \phi_{\text{prec}} \Phi_{\text{area}} \quad (\text{B.60})$$

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.

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

$$f_{\text{evap}} = \min\left(\frac{s_{\Theta}}{p_{\Delta_t}}, E_{\text{pot}}\right) \quad (\text{B.61})$$

where s_{Θ} is the water content of a lichen or bryophyte, p_{Δ_t} is the time step of the model and E_{pot} is potential evaporation (see Eq. B.30).

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

$$f_{\text{runoff}} = \frac{\max(0.0, s_{\Theta} + \max(0.0, f_{\text{water,up}} - f_{\text{evap}}) p_{\Delta_t} - \Theta_{\text{max}})}{p_{\Delta_t}} \quad (\text{B.62})$$

where s_{Θ} is the water content of a lichen or bryophyte, $f_{\text{water,up}}$ is water uptake, f_{evap} is evaporation, p_{Δ_t} is the time step of the model and Θ_{max} is the water storage capacity of the thallus (see Eq. B.17).

The water balance is then written as:

$$s_{\Theta} = \max(0.0, s_{\Theta} + (f_{\text{water,up}} - f_{\text{evap}} - f_{\text{runoff}}) p_{\Delta_t}) \quad (\text{B.63})$$

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 p_{Δ_t} is the time step of the model.

B.7. Exchange flows of energy

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

$$f_{Q_{\text{atm,L}}} = f_{\text{evap}} c_{\Delta H_{\text{vap,H}_2\text{O}}} c_{\rho_{\text{H}_2\text{O}}} \quad (\text{B.64})$$

where f_{evap} is evaporation, $c_{\Delta H_{\text{vap,H}_2\text{O}}}$ is the enthalpy of vaporisation and $c_{\rho_{\text{H}_2\text{O}}}$ is the density of liquid water. The flow of sensible heat, $f_{Q_{\text{atm,S}}}$, is written as:

$$f_{Q_{\text{atm,S}}} = \frac{(T_{\text{surf}} - T_{\text{air}}) c_{C_{\text{air}}}}{r_{\text{H}}} \Phi_{\text{area}} + (E_{\text{pot}} - f_{\text{evap}}) c_{\Delta H_{\text{vap,H}_2\text{O}}} c_{\rho_{\text{H}_2\text{O}}} \quad (\text{B.65})$$

where T_{surf} is surface temperature, T_{air} is air temperature, $c_{C_{\text{air}}}$ 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, $c_{\Delta H_{\text{vap,H}_2\text{O}}}$ is the enthalpy of vaporisation and $c_{\rho_{\text{H}_2\text{O}}}$ is the density of liquid water. Note that $f_{Q_{\text{atm,S}}}$ 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. B.64). 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:

$$f_{\text{H}} = f_{Q_{\text{atm,L}}} + f_{Q_{\text{atm,S}}} \quad (\text{B.66})$$

where f_{H} is net radiation (see Eq. B.25), $f_{Q_{\text{atm,L}}}$, is the flow of latent heat and $f_{Q_{\text{atm,S}}}$ is the flow of sensible heat.

B.8. Model parameters

Table B.7.: 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. B.22, B.31
$c\Delta H_{\text{vap,H}_2\text{O}}$	Enthalpy of vaporisation	2.45E6	J kg^{-1}	Eqs. B.30, B.64, B.65
cC_{air}	Heat capacity of air	1297.0	$\text{J m}^{-3} \text{K}^{-1}$	Eqs. B.30, B.31, B.65
$c\rho_{\text{H}_2\text{O}}$	Density of liquid water	1000.0	kg m^{-3}	Eqs. B.17, B.27, B.30, B.34, B.64
c_γ	Psychrometric constant	65.0	Pa K^{-1}	Eqs. B.30, B.31
$cM_{\text{H}_2\text{O}}$	Molar mass of water	0.018	kg mol^{-1}	Eq. B.27
cM_{C}	Molar mass of carbon	0.012	kg mol^{-1}	Eqs. B.52, B.53, B.57, B.58, B.59
cR_{gas}	Universal gas constant	8.3145	$\text{J mol}^{-1} \text{K}^{-1}$	Eqs. B.27, B.42, B.43
$cT_{\text{melt,H}_2\text{O}}$	Melting temperature of water	273.0	K	Eqs. B.32, B.40, B.51

Table B.8.: Overview of model parameters describing environmental conditions. Parameters marked by the ***** symbol are included in a sensitivity analysis (see Table 2.2) because their values are not known very accurately.

Parameter	Description	Value	Unit	Reference
p_{SCO_2}	Solubility of CO ₂ in water	0.0334	mmol m ⁻³	Eq. B.46
p_{SO_2}	Solubility of O ₂ in water	0.00126	mmol m ⁻³	Eq. B.45
p_ϵ	Emissivity of organism (long-wave radiation)	0.97	[]	Eq. B.4
p_{λ_s}	Extinction coefficient (short-wave radiation)	* 0.5	[]	Eq. B.3
p_{λ_1}	Extinction coefficient (long-wave radiation)	0.95	[]	Eq. B.4
$p_{e_{s,1}}$	Parameter for saturation vapour pressure	17.27	[]	Eqs. B.26, B.29
$p_{e_{s,2}}$	Parameter for saturation vapour pressure	237.3	°C	Eqs. B.26, B.29
$p_{e_{s,3}}$	Parameter for saturation vapour pressure	610.8	Pa	Eqs. B.26, B.29
p_κ	von Karman constant	0.41	[]	Eq. B.10
p_{Δ_u}	Measurement height for wind speed	10.0	m	Eq. B.10
$p_{z_0, \text{canopy}}$	Roughness length of forest	* 0.1	m	Eq. B.11
$p_{z_0, \text{floor}}$	Roughness length of forest floor	* 0.01	m	Eq. B.11
$p_{z_0, \text{GDT}}$	Roughness length of grassland, desert & tundra	* 0.05	m	Eq. B.11
$p_{z_0, \text{mh}}$	Ratio between z_0 of momentum and humidity	0.1	[]	Eq. B.12
$p_{z_0, \text{d}}$	Ratio between displacement height and z_0	5.42	[]	Eq. B.13
p_{Δ_z}	Damping depth of the soil for a diurnal cycle	0.15	m	Eqs. B.23, B.24, B.31, B.35
$p_{C_{\text{soil}, \text{D}}}$	Heat capacity of desert soil	* 1.1E6	J m ⁻³ K ⁻¹	Eq. B.15
$p_{C_{\text{soil}, \text{F}}}$	Heat capacity of non-desert soil	* 2.2E6	J m ⁻³ K ⁻¹	Eq. B.15
$p_{k_{\text{soil}, \text{D}}}$	Thermal conductivity of desert soil	* 0.3	W m ⁻¹ K ⁻¹	Eq. B.16
$p_{k_{\text{soil}, \text{F}}}$	Thermal conductivity of non-desert soil	* 1.5	W m ⁻¹ K ⁻¹	Eq. B.16
$p_{k_{\text{snow}}}$	Thermal conductivity of snow	* 0.15	W m ⁻¹ K ⁻¹	Eq. B.35
$p_{\rho_{\text{snow}}}$	Density of snow	250.0	kg m ⁻³	Eq. B.34
$p_{\Delta_{\text{snow}}}$	Critical snow depth for activity	* 0.1	m	Sect. B.4.5
$p_{\tau_{\text{ice}}}$	Turnover rate of ice sheets	* 0.01	yr ⁻¹	Eq. B.33
$p_{\text{LAI}_{\text{max}}}$	Maximum Leaf Area Index in data set	5.7	[]	Eqs. B.5, B.6
$p_{\eta_{\text{rain}}}$	Interception efficiency of canopy	* 0.15	[]	Eq. B.5
p_{Δ_t}	Time step of the model	3600	s	Eqs. B.32, B.33, B.24, B.52, B.53, B.58, B.59, B.61, B.62, B.63
$p_{T_{\text{ref}, \text{R}}}$	Reference temperature of respiration	283	K	Eq. B.51
$p_{T_{\text{ref}, \text{PS}}}$	Reference temperature of photosynthesis	298	K	Eqs. B.42, B.43

Table B.9.: Overview of lichen or bryophyte random parameters used in the model.

Parameter	Description	Range	Unit	Reference
x_α	Albedo	0 - 1	[]	Sect. B.1.1, Eq. B.3
$x_{\Theta_{\max}}$	Specific water storage capacity	1 - 160	$(\text{kg H}_2\text{O}) (\text{kg C})^{-1}$	Fig. B.1, Eqs. B.17, B.62
$x_{A_{\text{spec}}}$	Specific projected area	0.3 - 240	$\text{m}^2 (\text{kg C})^{-1}$	Fig. B.2, Eq. B.8
x_{loc}	Location of growth	Canopy or ground	[]	Sect. B.1.4
$x_{\Phi_{\Theta, \text{sat}}}$	Threshold saturation for water potential	0.3 - 1	[]	Fig. B.3, Eqs. B.20, B.21
$x_{\Psi_{\text{H}_2\text{O}}}$	Shape parameter for water potential curve	5 - 25	[]	Fig. B.3, Eqs. B.20, B.27
$x_{V_{\text{C}, \max}}$	Molar carboxylation rate of Rubisco	0.6 - 26.8	s^{-1}	Fig. B.4, Eqs. B.37, B.42, B.43, B.44, B.48
$x_{V_{\text{O}, \max}}$	Molar oxygenation rate of Rubisco	0.1 - 2.5	s^{-1}	Fig. B.5, Eqs. B.43, B.44
$x_{R_{\text{ref}}}$	Reference maintenance respiration	1E-7 - 1.5E-4	$(\text{mol CO}_2) (\text{kg C})^{-1} \text{s}^{-1}$	Fig. B.6, Eqs. B.38, B.51, B.56
$x_{Q_{10}}$	Q ₁₀ value of respiration	1 - 3	[]	Fig. B.7, Eq. B.51
$x_{T_{\text{opt}, \text{PS}}}$	Optimum temperature of photosynthesis	278 - 313	K	Fig. B.9, Eq. B.37
$x_{E_{\text{a}, \text{K}_\text{C}}}$	Enzyme activation energy of K_{C}	3E4 - 1.3E5	J mol^{-1}	Table B.2, Eq. B.42
$x_{E_{\text{a}, \text{K}_\text{O}}}$	Enzyme activation energy of K_{O}	5E3 - 5.5E4	J mol^{-1}	Table B.2, Eq. B.43
x_{CCM}	Carbon Concentration Mechanism (CCM)	CCM present or not	[]	Sect. B.1.11
x_{alloc}	Fraction of carbon allocated to growth	0 - 1	[]	Sect. B.1.12, Eq. B.53

Table B.10.: Overview of model parameters associated with lichen or bryophyte tradeoffs. Parameters marked by the ***** symbol are included in a sensitivity analysis (see Table 2.2) 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 CO₂ 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 CO₂ levels.

Parameter	Description		Value	Unit	Reference
$w_{D_{CO_2,max}}$	Maximum thallus diffusivity for CO ₂	*	0.14	(mol CO ₂) m ⁻² s ⁻¹	Eq. B.19
$w_{D_{CO_2,min}}$	Minimum thallus diffusivity for CO ₂	*	5.7E-4	(mol CO ₂) m ⁻² s ⁻¹	Eq. B.19
$w_{D_{CO_2}}$	Factor for water CO ₂ diffusivity curve		12	[]	Fig. B.10, Eq. B.19
$w_{Rub,R}$	Rubisco per respiration	*	3.6	(mol Rubisco) (mol CO ₂) ⁻¹ s	Eq. B.38
$w_{loss,R}$	Turnover per respiration	*	54771	(kg C) s (mol CO ₂) ⁻¹ yr ⁻¹	Eq. B.56
$w_{JV,1}$	Slope of ϕ_{JV}	*	-0.06	[]	Eq. B.40
$w_{JV,2}$	Intercept of ϕ_{JV}	*	3.7	[]	Eq. B.40
$w_{K_C,1}$	Parameter for K _C		1.32	[]	Eqs. B.42, B.43
$w_{K_C,2}$	Parameter for K _C		2.03	[]	Eqs. B.42, B.43
$w_{K_O,1}$	Parameter for K _O		5.7E-3	[]	Eq. B.43
$w_{K_O,2}$	Parameter for K _O		0.51	[]	Eq. B.43
$w_{CCM,e}$	Cost parameter for CCM		0.67	[]	Eq. B.41
$w_{CCM,1}$	Parameter for CCM	*	45	[]	Eq. B.50
$w_{CCM,2}$	Parameter for CCM		3.6	[]	Eq. B.50
$w_{CCM,3}$	Parameter for CCM		6	[]	Eq. B.50

Table B.11.: Constant model parameters associated with lichen or bryophyte properties.

Parameter	Description	Value	Unit	Reference
p_{PAR}	Conversion factor for photosynthetically active radiation	2.0699E-6	mol J ⁻¹	Eq. B.41
p_{quant}	Conversion of quanta light into electrons	0.5	[]	Eq. B.41
p_{Ω}	Shape parameter for T response of photosynthesis	18	K	Eq. B.37
$p_{\eta_{growth}}$	Efficiency of sugar to biomass conversion	0.75	[]	Eqs. B.53, B.54

B.9. Model variables

Table B.12.: Boundary conditions for the model.

Variable	Description	Unit	Reference
$CO_{2,atm}$	Atmospheric CO ₂ concentration	ppm	Eq. B.36
$O_{2,atm}$	Atmospheric O ₂ concentration	ppm	Eq. B.45
T_{air}	Air temperature	K	Eqs. B.22, B.26, B.27, B.29, B.31, B.32, B.35, B.65
$f_{radSW\downarrow}$	Ingoing shortwave radiation	$W m^{-2}$	Eqs. B.25, B.31, B.41
$f_{radLW\downarrow}$	Ingoing longwave radiation	$W m^{-2}$	Eqs. B.25, B.31
$f_{rain,atm}$	Rainfall	$m^3 m^{-2} s^{-1}$	Eq. B.60
$f_{snow,atm}$	Snowfall	$m^3 m^{-2} s^{-1}$	Eqs. B.32, B.33
Φ_{RH}	Relative humidity	[]	Eqs. B.30, B.31
u	Near surface wind speed	$m s^{-1}$	Eq. B.10
$A_{baresoil}$	Area fraction of unoccupied soil	$m^2 m^{-2}$	Eq. B.6
A_{LAI}	Leaf Area Index (monthly resolution)	$m^2 m^{-2}$	Eqs. B.3, B.4, B.5, B.6, B.7
A_{SAI}	Stem Area Index (monthly resolution)	$m^2 m^{-2}$	Eqs. B.3, B.4, B.7

Table B.13.: Variables associated with the environment.

Variable	Description	Unit	Reference
z_0	Roughness length of surface for momentum	m	Eqs. B.10, B.11, B.12, B.13
$z_{0,h}$	Roughness length of surface for humidity	m	Eqs. B.10, B.12
r_H	Aerodynamic resistance to heat transfer	$s m^{-1}$	Eqs. B.10, B.30, B.31, B.65
Δ_d	Displacement height for wind speed	m	Eqs. B.10, B.13
τ_{veg}	Disturbance interval	years	Table B.3
C_{soil}	Soil heat capacity	$J m^{-3} K^{-1}$	Eqs. B.15, B.24
k_{soil}	Soil thermal conductivity	$W m^{-1} K^{-1}$	Eqs. B.16, B.25, B.31, B.35
$f_{snowmelt}$	Snowmelt	$m^3 m^{-2} s^{-1}$	Eqs. B.32, B.33, B.60
s_{snow}	Snow reservoir	$m^3 m^{-2}$	Eqs. B.32, B.33, B.34
Δ_{snow}	Thickness of Snow cover	m	Eqs. B.34, B.35
$A_{ground,max}$	Available area for growth on ground	$m^2 m^{-2}$	Eqs. B.6, B.8
$A_{canopy,max}$	Available area for growth in canopy	$m^2 m^{-2}$	Eqs. B.7, B.8, B.9
$s_{T_{soil}}$	Soil temperature	K	Eqs. B.23, B.24, B.31, B.35
e_{sat}	Saturation vapour pressure	Pa	Eqs. B.28, B.30, B.31
$e_{sat,0}$	Saturation vapour pressure (open water)	Pa	Eqs. B.26, B.28
$\phi_{e_{sat}}$	Reduction factor for saturation vapour pressure	[]	Eqs. B.27, B.28, B.29
$d_{e_{sat}}$	Slope of saturation vapour pressure curve	[]	Eqs. B.29, B.30, B.31
E_{pot}	Potential evaporation	$m^3 m^{-2} s^{-1}$	Eqs. B.30, B.61, B.65

Table B.14.: State variables of lichens or bryophytes.

Variable	Description	Unit	Reference
s_B	Biomass of lichen or bryophyte	$(\text{kg C}) \text{ m}^{-2}$	Eqs. B.8, B.17, B.41, B.48, B.52, B.57, B.59
s_C	Sugar reservoir of lichen or bryophyte	$(\text{kg C}) \text{ m}^{-2}$	Eqs. B.52, B.53, B.58
s_Θ	Thallus water content	$\text{m}^3 \text{ m}^{-2}$	Eqs. B.18, B.61, B.62, B.63

Table B.15.: Variables describing flows between lichens or bryophytes and their environment.

Variable	Description	Unit	Reference
$f_{\text{rad}_{LW}\uparrow}$	Outgoing longwave radiation	W m^{-2}	Eqs. B.22, B.25
$f_{Q_{\text{soil}}}$	Ground heat flux	W m^{-2}	Eqs. B.23, B.24, B.25
f_H	Net radiation	W m^{-2}	Eqs. B.25, B.30
$f_{Q_{\text{atm},L}}$	Latent heat flow	W m^{-2}	Eqs. B.64, B.66
$f_{Q_{\text{atm},S}}$	Sensible heat flow	W m^{-2}	Eqs. B.65, B.66
$f_{\text{water,up}}$	Water uptake	$\text{m}^3 \text{ m}^{-2} \text{ s}^{-1}$	Eqs. B.60, B.62, B.63
f_{evap}	Evaporation from thallus surface	$\text{m}^3 \text{ m}^{-2} \text{ s}^{-1}$	Eqs. B.61, B.62, B.63, B.64, B.65
f_{runoff}	Runoff	$\text{m}^3 \text{ m}^{-2} \text{ s}^{-1}$	Eqs. B.62, B.63
$f_{\text{CO}_2,\text{in}}$	Inflow of CO_2 into the thallus	$(\text{mol CO}_2) \text{ m}^{-2} \text{ s}^{-1}$	Eqs. B.36, B.55
$f_{\text{GPP},L}$	Light-limited rate of photosynthesis	$(\text{mol CO}_2) \text{ m}^{-2} \text{ s}^{-1}$	Eqs. B.47, B.49
$f_{\text{GPP},W}$	CO_2 -limited rate of photosynthesis	$(\text{mol CO}_2) \text{ m}^{-2} \text{ s}^{-1}$	Eqs. B.48, B.49
f_{GPP}	Gross Primary Productivity (GPP)	$(\text{mol CO}_2) \text{ m}^{-2} \text{ s}^{-1}$	Eqs. B.49, B.55, B.58
$f_{R_{\text{main}}}$	Maintenance respiration	$(\text{mol CO}_2) \text{ m}^{-2} \text{ s}^{-1}$	Eqs. B.52, B.53, B.55, B.58
$f_{R_{\text{growth}}}$	Growth respiration	$(\text{mol CO}_2) \text{ m}^{-2} \text{ s}^{-1}$	Eqs. B.54, B.55, B.58
f_{growth}	Growth	$(\text{mol C}) \text{ m}^{-2} \text{ s}^{-1}$	Eqs. B.53, B.54, B.58, B.59
f_{loss}	Biomass loss	$(\text{mol C}) \text{ m}^{-2} \text{ s}^{-1}$	Eqs. B.57, B.59

Table B.16.: Variables associated with lichens or bryophytes.

Variable	Description	Unit	Reference
$\Psi_{\text{H}_2\text{O}}$	Water potential	MPa	Fig. B.3, Eq. B.20
R_{spec}	Specific maintenance respiration rate	$(\text{mol CO}_2) (\text{kg C})^{-1} \text{s}^{-1}$	Eqs. B.51, B.52
ϕ_{radS}	Conversion factor for shortwave radiation	[]	Eqs. B.3, B.25, B.31, B.41
ϕ_{radL}	Conversion factor for longwave radiation	[]	Eqs. B.4, B.25, B.31
ϕ_{prec}	Conversion factor for precipitation	[]	Eqs. B.5, B.60
Φ_{area}	Fraction of available area covered by organism	[]	Eqs. B.9, B.22, B.23, B.24, B.25, B.30, B.36, B.41, B.60, B.65
A_{thallus}	Thallus area per m^2 ground	$\text{m}^2 \text{m}^{-2}$	Eqs. B.8, B.9
χ_{G}	Switch for ground heat flux	[]	Eqs. B.14, B.23, B.31
Θ_{max}	Water storage capacity	m	Eqs. B.17, B.18
Φ_{Θ}	Water saturation	[]	Eqs. B.18, B.19, B.20, B.21
D_{CO_2}	Diffusivity for CO_2	$(\text{mol CO}_2) \text{m}^{-2} \text{s}^{-1}$	Eqs. B.19, B.36
Φ_{act}	Metabolic activity	[]	Eqs. B.21, B.47, B.48, B.52, B.53
T_{surf}	Surface temperature	K	Eqs. B.22, B.23, B.31, B.35, B.37, B.40, B.42, B.43, B.51, B.65
$\text{CO}_{2,\text{thallus}}$	CO_2 concentration in thallus pore space	ppm	Eqs. B.36, B.46, B.50
$\text{CO}_{2,\text{cell}}$	CO_2 concentration in chloroplast	mol m^{-3}	Eqs. B.46, B.47, B.48, B.50
$V_{\text{C},\text{max}}$	Maximum carboxylation rate	$(\text{mol CO}_2) (\text{kg C})^{-1} \text{s}^{-1}$	Eqs. B.37, B.39
J_{max}	Maximum electron transport rate	$(\text{mole}^-) (\text{kg C})^{-1} \text{s}^{-1}$	Eqs. B.39, B.41
Ξ_{Rub}	Specific Rubisco content	$(\text{mol Rubisco}) (\text{kg C})^{-1}$	Eqs. B.37, B.38
ϕ_{JV}	Ratio of J_{max} to $V_{\text{C},\text{max}}$	[]	Eqs. B.39, B.40
K_{C}	Michaelis-Menten constant of carboxylation	$(\text{mol CO}_2) \text{m}^{-3}$	Eqs. B.42, B.44, B.48
K_{O}	Michaelis-Menten constant of oxygenation	$(\text{mol O}_2) \text{m}^{-3}$	Eqs. B.42, B.44, B.48
$\text{O}_{2,\text{cell}}$	O_2 concentration in chloroplast	mol m^{-3}	Eqs. B.44, B.45, B.48
Γ_*	CO_2 compensation point	$(\text{mol CO}_2) \text{m}^{-3}$	Eqs. B.44, B.47, B.48
J	Actual electron transport rate	$(\text{mole}^-) \text{m}^{-2} \text{s}^{-1}$	Eqs. B.41,
τ_{B}	Turnover rate of biomass	yr^{-1}	Fig. B.15, Eq. B.56, B.57

C. Short summary of the thesis

This thesis presents a process-based modelling approach to quantify carbon uptake by lichens and bryophytes at the global scale. Based on the modelled carbon uptake, potential global rates of nitrogen fixation, phosphorus uptake and chemical weathering by the organisms are estimated. In this way, the significance of lichens and bryophytes for global biogeochemical cycles can be assessed.

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 uptake of 0.34 to 3.3 Gt yr⁻¹ of carbon and global patterns of productivity are in accordance with empirically-derived estimates.

Based on the simulated estimates of net carbon uptake, further impacts of lichens and bryophytes on biogeochemical cycles are quantified at the global scale. Thereby the focus is on three processes, namely nitrogen fixation, phosphorus uptake and chemical weathering. The presented estimates have the form of potential rates, which means that the amount of nitrogen and phosphorus is quantified which is needed by the organisms to build up biomass, also accounting for resorption and leaching of nutrients. Subsequently, the potential phosphorus uptake on bare ground is used to estimate chemical weathering by the organisms, assuming that they release weathering agents to obtain phosphorus. The predicted requirement for nitrogen ranges from 3.5 to 34 Tg yr⁻¹ and for phosphorus it ranges from 0.46 to 4.6 Tg yr⁻¹. Estimates of chemical weathering are between 0.058 and 1.1 km³ yr⁻¹ of rock. These values seem to have a realistic order of magnitude and they support the notion that lichens and bryophytes have the potential to play an important role for global biogeochemical cycles.

Curriculum Vitae

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Born: June 24th 1984 in Bochum
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Basic Education

1990 – 1994 Bodieckschule (Primary School) in Dortmund
1994 – 1998 Gymnasium an der Schweizer Allee (Secondary School) in Dortmund
1998 – 2003 Graf-Münster-Gymnasium (Secondary School) in Bayreuth
2003 Graduation (Abitur, 1.5)

Military Service

2003 – 2004 II./Luftwaffenausbildungsregiment 3, Bayreuth

University Education

2004 – 2009 Studies in Geoecology, University of Potsdam
2009 Diploma (M.Sc.) in Geoecology (1.0)
Thesis: “Entropy Budget of the Soil Hydrological Cycle”
Institution: Institute for Geoecology at the University of Potsdam (Prof. W. Lucht), Max-Planck-Institute for Biogeochemistry (Dr. A. Kleidon)

Doctoral Studies

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Topic: “Process-based Modelling of lichens and bryophytes and their impacts on global biogeochemical cycles”

Institution: Institute for Geosciences at the University of Mainz (Prof. U. Pöschl), Max-Planck-Institute for Biogeochemistry (Dr. A. Kleidon)

Publications

Peer-reviewed

Porada P, Weber B, Elbert W, Pöschl U, Kleidon A, Estimating Impacts of Lichens and Bryophytes on Global Biogeochemical Cycles of Nitrogen and Phosphorus and on Chemical Weathering *Global Biogeochemical Cycles*, *accepted*

Porada P, Weber B, Elbert W, Pöschl U, Kleidon A, Estimating global carbon uptake by Lichens and Bryophytes with a process-based model. *Biogeosciences* **10** 6989-7033, 2013, doi:10.5194/bg-10-6989-2013

Porada P, Kleidon A, Schymanski S J, Entropy production of soil hydrological processes and its maximisation. *Earth Syst. Dynam.* **2** 179-190, 2011, doi:10.5194/esd-2-179-2011

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Buendia C, Arens S, Hickler T, Higgins S, Porada P, Kleidon A, On the potential vegetation feedbacks that enhance phosphorus availability—insights from a process-based model linking geological and ecological time scales *Biogeosciences Discuss.* **10** 19347-19407, 2013, doi:10.5194/bgd-10-19347-2013

Other

Porada P, Arens S, Buendia C, Gans F, Schymanski S J, Kleidon A, A simple global land surface model for biogeochemical studies, *Technical Reports—Max-Planck-Institute for Biogeochemistry* **18**, 2010.

Scientific activities

Conferences

Porada P, Weber B, Elbert W, Pöschl U, Kleidon A: Process-based modelling of lichen and bryophyte productivity at the global scale (Invited talk). *Workshop on Vegetation-Soil Interactions in High Latitudes*, Stockholm, 2013

Porada P, Weber B, Elbert W, Pöschl U, Kleidon A: Estimating Impacts of Lichens and Mosses on Global Biogeochemical Cycles (Poster). *ICYESS conference*, Hamburg, 2013

Porada P, Weber B, Elbert W, Pöschl U, Kleidon A: Global Productivity of Lichens, Mosses and Crusts (Poster & Talk). *EGU General Assembly*, Vienna, 2012

Porada P, Kleidon A: A Process-based Model of Global Lichen Productivity (Poster, 3rd place in poster competition). *iLeaps conference*, Garmisch-Partenkirchen, 2011

Porada P, Kleidon A, Schymanski S J: Soil hydrological processes—A thermodynamic perspective (Poster). *EGU General Assembly*, Vienna, 2010

Porada P, Kleidon A, Schymanski S J: The Soil hydrological cycle: A Thermodynamic Perspective (Poster). *Terrabites Symposium*, Hamburg, 2010

Porada P, Kleidon A, Schymanski S J: Does MEP help to predict the partitioning of soil hydrological flows? (Poster). *Workshop on Maximum Entropy Production in the Earth System*, Jena, 2009

Porada P, Kleidon A, Schymanski S J: Entropy Production of Soil Hydrological Processes (Talk). *Workshop on Maximum Entropy Production in the Earth System*, Jena, 2008

Additional Qualifications

Programming	Fortran 95, C, Matlab, R, scripting (Bash, Gnuplot, CDO, GMT), basic GIS, Inkscape, Latex, Unix
Languages	German (native), English (fluent), French (advanced)
Reviews	Hydrology and Earth System Sciences, Biological Reviews, Materials Science Forum
Organisation	Tutor for beginning students of Geoecology Co-organisation of the Workshop on Maximum Entropy Production in the Earth System in Jena Presenting simulations of the hydrological cycle and limits to wind energy at the “Long Night of Sciences” in Jena Presentation on thermodynamics of the atmosphere at the “Forsche Schüler Tag” in Jena
Personal interests	Classical and electric guitar, Judo, philosophy, history, hobby-cartoonist

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