Chapter 15
Carbon Budgets of Biological Soil Crusts at Micro-, Meso-, and Global Scales

Leopoldo G. Sancho, Jayne Belnap, Claudia Colesie, Jose Raggio, and Bettina Weber

15.1 Introduction

Biological soil crusts (biocrusts) inhabit extensive parts of different terrestrial ecosystems and are especially abundant under conditions where vascular plants encounter natural limits of growth (Belnap and Lange 2003). Due to their poikilo-hydric character, biocrusts show resilience under extreme conditions, as well as a remarkable adaptation to the various combinations of different climatic factors found throughout all latitudes from the tropics to the poles (Grote et al. 2010; Colesie et al. 2014). Because biocrusts can fix carbon (C) through photosynthetic activity, they are important in local scale C cycles. In addition, due to their broad distribution, they can also be relevant on ecosystem and global scales (Elbert et al. 2012; Porada et al. 2013, 2014).

In this chapter, several different terms are used when considering CO_2 balance. Net photosynthesis (NP) and dark respiration (DR), respectively, refer to the uptake and release of CO_2 measured with CO_2 gas exchange systems. CO_2 gas exchange

L.G. Sancho (✉) • J. Raggio
Facultad de Farmacia, Departamento de Biologıa Vegetal II, Universidad Complutense, 28040 Madrid, Spain
e-mail: sancholg@ucm.es

J. Belnap
US Geological Survey, Southwest Biological Science Center, Canyonlands Research Station, 2290 S West Resource Blvd, Moab, UT 84532, USA

C. Colesie
Faculty of Biology, Plant Ecology and Systematics, University of Kaiserslautern, Erwin-Schrödinger-Str. 13, 67663 Kaiserslautern, Germany

B. Weber
Multiphase Chemistry Department, Max Planck Institute for Chemistry, Hahn-Meitner-Weg 1, 55128, Mainz, Germany

measurements under controlled conditions allow the identification of cardinal points for photosynthesis (e.g., temperature optimum, light saturation, optimum water content). In long-term observations, an important value is the net primary production (NPP), which is the difference between the gross primary production (GPP) and the autotrophic respiration (AR; Chapin et al. 2006). A further highly relevant variable is net ecosystem production (NEP), which is the difference between gross primary production (GPP) and ecosystem respiration (ER; Randerson et al. 2002). Similar values, net ecosystem carbon balance (NECB) and net ecosystem exchange (NEE), are the net rate of carbon accumulation in (or loss from) ecosystems. NECB can be determined by measuring changes in carbon stocks in vegetation and soil. NECB and NEE differ from NEP if inorganic carbon enters or leaves the system in dissolved form or if fluxes other than C fixation and respiration occur. In addition, we use the term net soil exchange (NSE) for chambers that include only bare or biocrusted soil surfaces and exclude vascular plants.

It must also be remembered that in arid soils, biological activity is not the only driver of CO_2 exchange. It has been recently reported that inorganic CO_2 fluxes in alkaline and saline substrates can exceed those caused by organic activity (Xie et al 2009; Shanhun et al. 2012; Ma et al. 2013). Before producing an accurate approach to the CO_2 balance in arid lands, it is therefore necessary to determine whether inorganic activity in calcareous soils needs to be considered as a sink or a source of carbon, and the abiotic conditions need to be specified. On the other hand, in the most extreme habitats, photosynthetic activity in the soil is mainly restricted to the especially protected microhabitat that occurs under semitransparent pebbles, the so-called hypolithic communities, which are extensively considered in Chap. 11 by Pointing.

In the following sections, we use a multiscale approach to discuss the usefulness of available measuring techniques and methods calculating the CO_2 balance of biocrust communities. In the first section, we focus on the microscale, that is, the individual organism such as a single lichen or bryophyte thallus or a well-defined cyanobacteria colony. We then address CO_2 exchange of a complete ecosystem or at the community level (mesoscale). Finally, we will look at recent approaches to assess the contribution of biocrusts on a global scale.

15.2 The Microscale: Individual Organism Performance

15.2.1 Proposed Methodologies on the Microscale

Direct Measurement of CO_2 Exchange Quantitative measurements of CO_2 fluxes in biocrust organisms are feasible using CO_2 gas exchange systems. The major advantage of CO_2 exchange measurements is that they can provide both accurate response curves of NP to environmental factors, as well as actual exchange rates in the field under quasi-natural conditions. On the other hand, a major disadvantage is

that data are not provided for CO_2 uptake nor do they discriminate between abiotic and biotic CO_2 production.

Lange et al. (1997a) developed an automatically operating cuvette with which they measured quantitative CO_2 exchange in lichens. A major limitation to the use of these systems is that they are expensive, only quasi-automatic (i.e., they need regular, often daily checking), and usually only a small number of samples (often only one) can be measured. Many other studies on quantitative CO_2 exchange measurements are available, but mainly cover only short time periods. Nevertheless, these are often used for calculations and modeling of biocrust C cycling. Lange (2003a) intensively discusses the differences between different extrapolation methods and also the difficulties in upscaling fixation rates to yearly averages. Bader et al. (2010) use the same dataset to show that lower sampling frequencies both within the day and on less than 365 days of the year cause deviations in modeling results and propose supporting extrapolation approaches.

Indirect Measurements Based on Activity Detection Fluorometers, which detect fluorescence of chlorophyll *a*, provide a method to record the activity time of poikilohydric photosynthetic organisms (Schroeter et al. 1992; Schlensog and Schroeter 2001). Recent innovations allow the establishment of long-term chlorophyll fluorescence monitoring systems, which are online and report via telephone or satellites (Büdel et al. 2014; Raggio et al. 2014). The systems not only provide an excellent background on activity periods of the organisms in situ but often also allow determination of the mode of activation (humid air, dew, or rain) to be identified. Such data are necessary for any calculations of productivity over time (Fig. 15.1). Recently, a biocrust wetness sensor was developed, which allows determination of the activity status and water content of biocrusts by means of electrical conductivity measurements (Weber et al. 2016). As these sensors are inexpensive, robust, and easy to use, they can be employed for long-term measurements. Installation of multiple sensors in the field allows assessment of spatiotemporal variability in biocrust C exchange under field conditions. However, these methods do not provide quantitative data on CO_2 uptake or loss. Therefore, in order to obtain measures such as NPP, these methods must be combined with CO_2 gas exchange measurements under varying environmental conditions that can account for the relationship between chlorophyll fluorescence or water content and CO_2 exchange in lichens, algae, and bryophytes. Nevertheless, both techniques have an unquestionable advantage of allowing for unattended long-term noninvasive monitoring of metabolic activity.

Direct Measurement of Mass Gain A relatively easy way to relate microscale CO_2 measurements to the productivity of lichen- or moss-dominated systems (i.e., the NECB) is to use lichenometric data as a baseline to calculate mass gain over a selected time interval. Lichenometry has been widely used to date surfaces, mainly in studies on glacier retreat in both hemispheres (Innes 1988; Winchester and Harrison 2000; Roberts et al. 2010), or to calculate the growth rate of a thallus by direct measurements at time intervals (Armstrong and Bradwell 2010; Sancho and Pintado 2004; Sancho et al. 2011). Annual thallus enlargement measured in
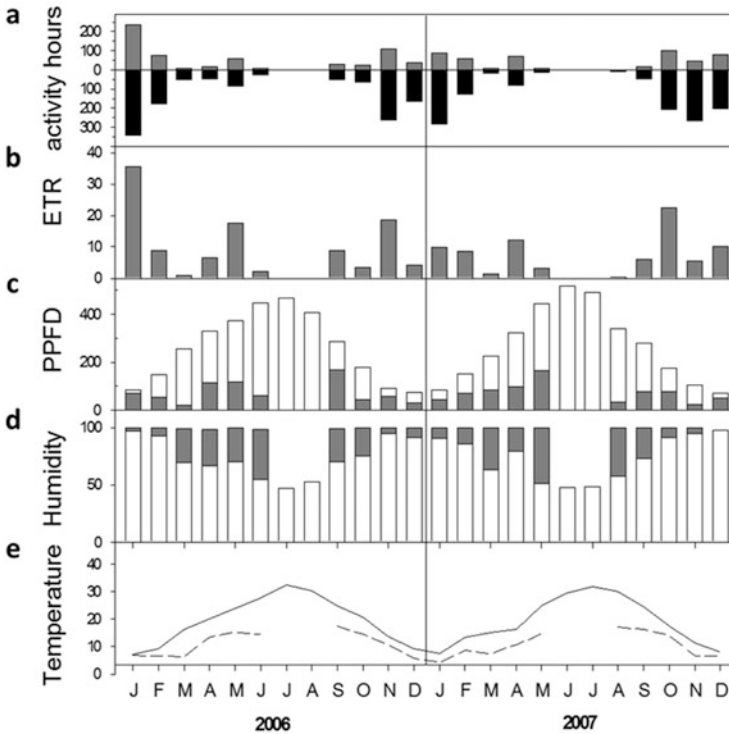
Fig. 15.1 Summary of the activity detected as fluorescence of chlorophyll a and microclimate measured for *Diploschistes diacapsis* assessed in continuous measurements over a period of 2 years, 2006 and 2007, in Almeria (Spain). (**a**) Lichen activity in number of hours active per month: *gray upper part* of bar indicates fluorescence activity under photosynthetic active radiation and *black lower part* indicates fluorescence activity in the dark. (**b**) Sum of electrons transported per month (mol electrons m^{-2} $month^{-1}$). (**c**) Mean PPFD (μmol photons m^{-2} s^{-1}) for each month: *white bars* indicate mean value of the complete month and *gray bars* indicate the mean value for times when the lichen was active. (**d**) Mean relative humidity next to the lichen at the soil surface in each month (%): *white bars* indicate the mean RH for the entire month; the total bar is the mean value of times when the lichen was active. (**e**) Mean lichen temperature of all measurements in each month (*solid line*) and for the periods when the lichens were active (*dashed line*, missing data indicates no activity in those months)

lichenometric studies can be transformed to thallus weight gain after determining the thallus weight per unit area (Raggio et al. 2012). The obtained annual C gains are fully comparable across different ecosystems in the world and improve our understanding of the contribution by lichens, especially epilithic communities, to the global C balance (Table 15.1). Theoretically, a combination of high quality digital photographs, appropriate image analysis programs, and an accurate determination of thallus weight on a surface basis could allow long-term productivity monitoring of crustose lichens without using any expensive and complicated systems.

Table 15.1 Net carbon uptake of different lichen species calculated as (a) dry weight accumulation (g m^{-2}) and (b) carbon assimilation (g m^{-2}). The carbon content in lichens typically ranges between 30 and 40 %, thus values in (b) need to be multiplied by values between 2.5 and 3.3 in order to estimate dry weight accumulation

Lichen species	Growth form	Habitat	Annual growth	References
Buellia frigida	Crustose	Continental Antarctica	0.1 g m^{-2} (a)	Sancho, unpublished
Rhizocarpon geographicum	Crustose	Bipolar	2–5 g m^{-2} (a)	Sancho, unpublished
Buellia latemarginata	Crustose	Maritime Antarctica	7–10 g m^{-2} (a)	Sancho, unpublished
Caloplaca sublobulata	Crustose	Maritime Antarctica	8–11 g m^{-2} (a)	Sancho, unpublished
Placopsis perrugosa	Crustose	Tierra del Fuego, Chile	50–80 g m^{-2} (a)	Sancho, unpublished
Lichen tundra	Mainly fruticose	Boreal Woodland, Canada	100 g m^{-2} (b)	Coxson and Marsh (2001)
Lecanora muralis	Crustose	Temperate Region, Germany	65.0 g m^{-2} (a)	Lange (2003a, b)
Cetrariella delisei	Fruticose	High Arctic	5.1 g m^{-2} (b)	Uchida et al. (2006)
Biocrust	Mainly crustose	Mojave Desert, USA	11.7 g m^{-2} (b)	Brostoff et al. (2005)
Biocrust	Mainly crustose	Chinese Desert	3.46–6.05 g m^{-2} (b)	Feng et al. (2014)

Modeling Methods Modeling is used to estimate annual C budgets. Continuous cuvette measurements, providing data over more than a year, as conducted by Lange (2000, 2003a, b), are an exception. Most commonly, a series of field measurements of CO_2 gas exchange is connected with the concurrent environmental factors. Different types of algorithms or models are then used to link field and laboratory measurements with long-term records of those same environmental factors. The methodological approach is to combine CO_2 gas exchange rates assessed during typical activity days (see Lange and Green 2004) with records of long-term chlorophyll *a* fluorescence and microclimate data (at least one continuous year). These measurements are conducted for the most abundant biocrust types of each area. This approach minimizes theoretical assumptions and extrapolations in the modeling. Several important ecophysiological phenomena in biocrusts have been shown to influence these modeled estimates of CO_2 gas exchange, including depression of photosynthesis at high water contents (Lange et al. 1995; Fig. 15.2) and more frequent than expected biocrust activity at suboptimal light and temperature conditions in the field (Lange and Green 2004). As these phenomena are relevant for productivity calculations, they also need to be analyzed in detail by means of constructing gas exchange estimates at different light and water values in the laboratory. Other factors that have to be taken into account during modeling are
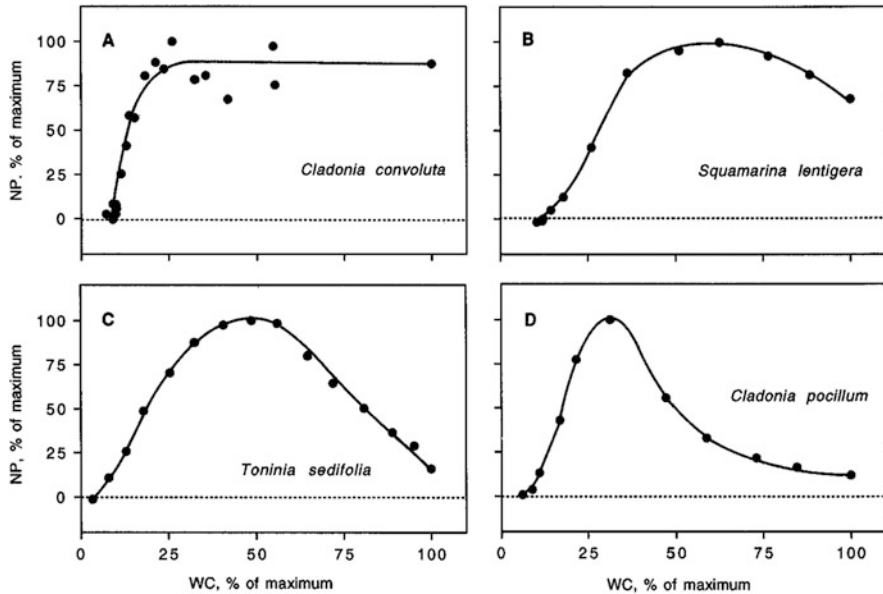
Fig. 15.2 Dependence of net photosynthesis (NP, % of maximum) and thallus water content (WC, % of maximum) in different soil crust lichen species collected in the same locality. Different responses of NP are observed at maximum WC (100 %), from high depression of NP at high WC (**c**, **d**) to low (**b**) or nonexisting depression (**a**). Modified from Lange et al. (1995)

the biotic and abiotic CO_2 fluxes from the soil (Ma et al. 2013; Rey et al. 2014; Weber et al. 2012). These are potentially a major problem in modeling biocrust-derived C fluxes. The large differences between modeled respiration (see Castillo-Monroy et al. 2011) and NPP for desert biocrusts shows that the calculated NPP will be very sensitive to non-biocrust-derived C. However, the literature indicates that abiotic fluxes from soil carbonates, the obvious potential source of C flux from soils, can be very low (Serna-Perez et al. 2006; although see Rey 2015). A combination of the datasets accumulated in the SCIN project (Büdel et al. 2014) with the current knowledge regarding CO_2 fluxes in biocrusts from arid and semiarid environments will allow modeling the behavior of these communities in a global change scenario (Fig. 15.3).

Some other approaches do not produce models for final C balance, but provide useful datasets for future modeling because they contain empirical measurements of gas exchange at the microscale (field and/or laboratory datasets). Lange (2003a) showed that the annual C balance of the lichen approximates its annual increase in biomass, stating that the potential annual primary production of lichen-dominated systems reaches around 8 % of the global mean for terrestrial productivity. Weber et al. (2012) published relevant CO_2 fluxes in mosses from a semidesert in South Africa, underlining in their results the physiological importance of measuring complete biocrusts against measuring isolated components of them (see also Sommerkorn et al. 1999). Finally, some works link CO_2 fluxes at the biocrust
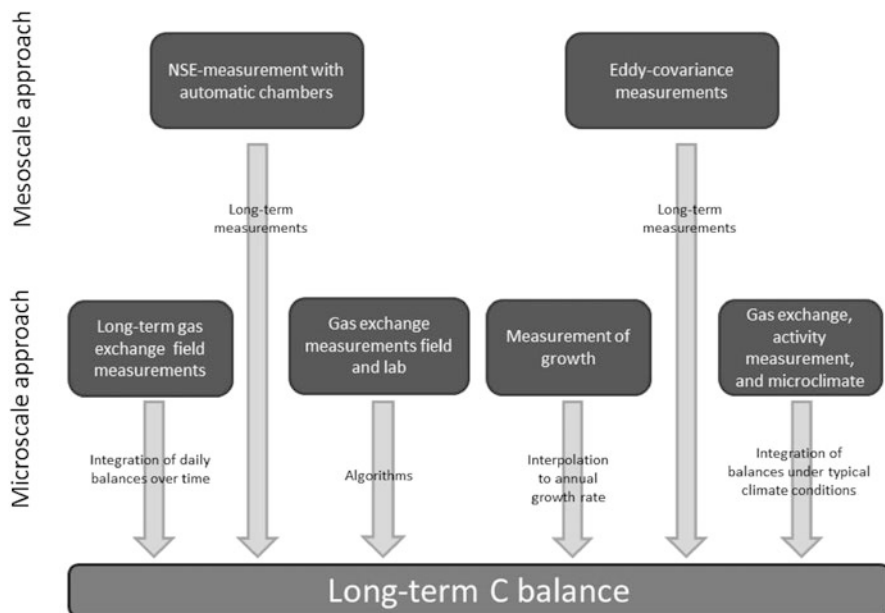
Fig. 15.3 Conceptual model showing how to integrate measuring methods at meso- and micro-scale to calculate long-term C balance in biocrust systems

microscale level with future climate change scenarios (Grote et al. 2010; Maestre et al. 2010, 2013). These works provide large datasets that will help to understand possible consequences of environmental change for C balances in arid or semiarid environments where biocrusts are abundant.

15.2.2   Available Datasets on the Microscale

Tundra   In tundra habitats, poikilohydric organisms form a major part of the overall vegetation. Here, annual C budgets have been estimated. Maximum photosynthesis rates for lichen species in tundra vegetation range from 0.8 nmol g^{-1} s^{-1} for *Sphaerophorus globosus* to 8.0 nmol g^{-1} s^{-1} for *Dactylina arctica* (Tenhunen et al. 1992; Table 15.2). Lichens dominate biocrust communities in well-drained evergreen shrub vegetation as well as in rocky fell-fields and contribute up to 400 g of photosynthetically active biomass m^{-2} (Tenhunen et al. 1992). Along a gradient of increasing water availability, there is a transition from lichen-dominated biocrusts to those dominated by mosses. The NP rates of typical tundra mosses are about three times higher than those of lichens [e.g., maximum NP for *Pogonatum alpinum* is 27.8 nmol g^{-1} s^{-1} (Oechel and Collins 1976) and *Sphagnum squarrosum* is 18.9 nmol g^{-1} s^{-1} (Murray et al. 1989)]. The relatively high NP rates and the generally moist conditions lead to substantial estimates for annual C fixation rates

Table 15.2 Net carbon uptake (g C m^{-2} year^{-1}) of different crust types from the tundra and desert biome

Net carbon uptake (g/m^{-2} year^{-1})	Biome	Organism	References
38.5–171	Tundra	Moss	Oechel and Collins (1976)
10	Tundra	Moss	Billings (1987)
2–68	Tundra	Lichens and mosses	Shaver and Chapin (1991)
4.7–20.4	Tundra	Lichens	Lange et al. (1998)
24.80	Tundra	Moss	Bisbee et al. (2001)
6.5	Tundra	Moss	Uchida et al. (2002)
12–60	Tundra	Moss	Schuur et al. (2007)
5.3–29	Desert	Lichen	Klopatek (1992)
4–11.3	Desert	Lichen	Lange et al. (1992)
0.07–1.5	Desert	Cyanobacteria	Jeffries et al (1993)
16	Desert	Lichen	Lange et al. (1994)
0.54	Desert	Cyanobacteria	García-Pichel and Belnap (1996)
25.8	Steppe	Lichen	Evans and Lange (2003)
11.7	Desert	Cyanobacteria	Brostoff et al. (2005)

in tundra areas, where particularly bryophytes are important in C and N cycling (Turetsky 2003). For example, estimated NPP of feather mosses in the boreal forests reach about 24.80 g C m^{-2} year^{-1} (Bisbee et al. 2001), and in wet areas *Sphagnum* species are also very productive with up to 19 g biomass m^{-2} year^{-1}. Fenton (1980) estimated that mean productivity of Antarctic *Polytrichum alpestre* ranges from 213 to 350 g m^{-2} year^{-1}, while productivity of *Chorisodontium aciphyllum* averages 162 g m^{-2} year^{-1}.

Temperate Habitats In temperate regions, there has only been one study addressing annual C budgets for individual biocrust lichens. Lange (2002, 2003a) measured *Lecanora muralis* using the Klapp cuvette for 15 months and determined its annual C fixation rate to be 21.494 g C m^{-2} year^{-1} (Lange 2002, 2003a). Lange (2000) also used this system on the gelatinous lichen *Collema cristatum* to show very good agreement between NP responses measured in the laboratory and field.

Deserts In deserts, due to restricted water availability, organisms are only sporadically active (Lange et al. 2006; Sponseller 2007; Pintado et al. 2010), causing NPP to be generally much lower than in temperate or polar regions, but as higher plants are sparse, biocrust cover can be very high and thus still play an important role in overall C cycles. However, as biocrust organisms are only metabolically active when wet and precipitation in deserts is highly variable, estimates for NPP of biocrust components are highly variable as well, ranging between 0 and 29 g m^{-2} year^{-1} (Table 15.2). In general, biocrusts in temperate deserts are more easily damaged, and their carbon fixation reduced, by compressional disturbances than those in tundra habitats. In addition, as temperatures are higher in deserts, moisture evaporates more quickly than in tundra, and thus their overall photosynthetic gain is less. However, biocrusts

can access a range of water sources, many of them not being available to higher plants. Some desert lichens (e.g., *Acarospora* cf. *schleicheri*, *Caloplaca volkii*, and *Lecidella crystallina*) can mainly use fog to reactivate their photosynthesis (Lange et al. 1994) and reach an estimated photosynthetic carbon gain of 16 g C m^{-2} year^{-1}. Not only scarcity of water affects C cycles in biocrusts but also surplus water with contents above 60 % generally results in a decline in GP in many biocrust species, probably caused by water-filled pores restricting gas diffusion (Grote et al. 2010; Lange et al. 1997b; Green et al. 1994).

The type of biocrust organism also plays an important role in C fixation at a site. On the Colorado Plateau and in the Chihuahuan Desert, Housman et al. (2006) showed that later successional biocrusts dominated by the cyanobacteria *Nostoc* and *Scytonema* and the lichens *Placidium* and *Collema* typically had a 1.2–1.3-fold higher daily C fixation than early cyanobacterial crusts dominated by the cyanobacterial genus *Microcoleus*. Biocrusts dominated by *Microcoleus vaginatus* growing on dunes are estimated to fix 11.7 g C m^{-2} year^{-1} (Brostoff et al. 2005). Early successional biocrusts from highly disturbed areas, dominated by algae or cyanobacteria, show lower carbon fixation values than those from undisturbed sites where lichens and mosses occur (Table 15.2; Zaady et al. 2000), being in agreement with the photosynthetic capacities found for the individual biocrust components.

15.2.3 Modeling on the Microscale

Castillo-Monroy et al. (2011) proposed that biocrusts in a semiarid ecosystem in Spain were responsible for the greatest proportion of the total soil respiration. Their model was based on the assumption that 85 % of soil respiration could be explained by soil temperature and moisture and predicted a C release between 240.4 and 322.6 g C m^{-2} year^{-1}. Wilske et al. (2009) used a model based on vascular plant studies but adapted that to work only when there is water available in the ecosystem. The model is sustained by (a) the link between biocrust CO_2 fluxes and an indicator of annual metabolic activity and (b) a more simplistic precipitation-driven alternative. The final results showed a large interannual variation in C uptake for biocrust NEE ranging between 0.7 and 5.1 g m^{-2} year^{-1}. An alternative approach is the algorithm proposed by Brostoff et al. (2005), where the NPP is calculated as the difference between maximum NP and maximum DR measured in the field multiplied by the percentage of cover and meteorological indicators of possible biocrust metabolic activity. Using this method, the NPP of biocrusts in the Mojave Desert was 11.7 g C m^{-2} year^{-1} and between 3.46 and 6.05 g C m^{-2} year^{-1} for different biocrust types in a Chinese Desert (Feng et al. 2014). Finally, Uchida et al. (2006) developed a model for the dominant terricolous lichen *Cetrariella delisei* in deglaciated areas of the high Arctic. In their productivity model, they obtained a mean NPP value of 5.1 g dw m^{-2} year^{-1} (about 2295 mg C m^{-2}) per snow free season (Table 15.1). They based their model on the interaction between abiotic factors and CO_2 exchange, always assuming in their algorithms that NP and DR are firstly dependent on water availability and secondly on temperature and radiation.

Water is often available under a suboptimal combination of environmental factors, typically low radiation and low temperature, which usually limits biocrust NP in the field (Lange and Green 2004; Raggio et al. 2014). This is considered to be a reliable approach to model NPP of cryptogams (Lange 2003a, b).

15.3 The Mesoscale: Net Ecosystem Exchange in Biocrusted Soils

15.3.1 Available Datasets on the Mesoscale

Continuous long-term measurements of net ecosystem C exchange (NEE) in biocrust-dominated soils are only available for two desert regions.

Colorado Plateau, USA The first study region is the Colorado Plateau Desert, USA, where there have been three studies on two different soil types. These studies, despite using different measurement techniques and on different soils, obtained very similar results. The first study used large auto-chambers with an internal diameter of 0.36 m^2 and contain dark, late-successional biocrusts consisting of ~10 % moss (mostly *Syntrichia caninervis*), ~5 % lichen (*Collema tenax* and *Collema coccophorum*), and 85 % cyanobacteria (dominated by *Microcoleus vaginatus*) (Darrouzet-Nardi et al. 2015). Measurements were made hourly for 21 months (from winter 2006 through summer 2007). Except following large rain events (ideal conditions for photosynthesis), the soil surface acted as a small C source to the atmosphere. The highest C losses were observed in spring (327 mg C m^{-2} day^{-1}) and the lowest in winter (65 mg C m^{-2} day^{-1}). Of the 627 measurement days, only 6.4 % showed a positive NSE. These data indicated that only larger or extended events kept soils wet long enough for the biocrust activity to result in uptake outweighing losses, whereas smaller events resulted in net C loss.

The second study on the Colorado Plateau occurred on fine sandy loam soils at a site 120 km from the first site, using the same auto-chamber design as above (Fig. 15.4; Bowling et al. 2011). Measurements were done over the course of 300 days (Julian 0–299), although gaps occurred during that time due to equipment malfunction. Soils were covered with a biocrust dominated by the cyanobacterium *Microcoleus vaginatus* with some *Bryum argenteum* moss present as well. Results were very similar to the first study. During the measurement time, only large or almost contiguous smaller rain events resulted in small C uptake (414.7 mg C m^{-2} day^{-1}) by the biocrusted soils (Fig 15.4). As these events were rare, the soil surfaces were mostly a small C source (up to 985.0 mg C m^{-2} day^{-1}) over the course of the experiment.

The third study was at the same site as the second study, but measurements were done using eddy covariance (Bowling et al. 2010). This study further corroborated the results obtained in the first two studies: Biocrust soil surfaces at these sites were
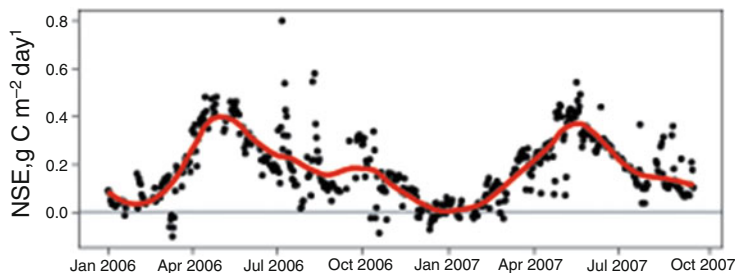
Fig. 15.4 Daily average net soil exchange (NSE) of CO_2-C in control plots from the daily sums dataset over the 21-month measurement period of the study. Positive values indicate net loss of C from soils. *Red curve* is a local regression (loss) with span $= 0.2$

mostly small sources of C (up to 518 mg C m^{-2} day^{-1}), with large rain events resulting in small C uptake (up to 933 mg C m^{-2} day^{-1}). However, there was a sparse cover of vascular plants at this site, and thus these measurements also reflect their influence on C fluxes.

Gurbantunggut Desert The third desert is the Gurbantunggut Desert in northwestern China. Su et al. (2012, 2013) measured C fluxes of different soils dominated by various types of biocrusts (moss, lichen, and cyanobacteria). As in the Colorado Plateau studies, the results show small C losses from the soil during most of the time, with only short intervals of small C uptake. The similarity in magnitude of the losses and uptake compared to the Colorado Plateau data is striking [−2281 to 1244 mg C m^{-2} day^{-1} for the Gurbantunggut Desert (all biocrust and soil types) and −623 to 1660 mg C m^{-2} day^{-1} for the Colorado Plateau Desert].

It is unfortunate that we have so few continuous measurements of NEE for biocrusts, as these few studies strongly suggest that spot measures, whether in the laboratory or field, are not sufficient when trying to understand the role of biocrusts in ecosystem C dynamics. Interpretation of the data from any of these studies is complicated by the fact that it is currently not feasible to separate out the role of biocrusts from that of underlying soil factors, such as respiration from roots, deeper biota, and abiotic losses, as well as effects from the somewhat artificial environment created by our measurement techniques. Despite this complication, the similarity of the values obtained from the two studies at geographically distinct sites indicates that the overall photosynthetic contribution of biocrusts in temperate deserts can mostly offset soil abiotic and biotic losses.

15.4 The Macroscale: Global Carbon Budgets

Two different studies have investigated the contributions of cryptogams to carbon budgets on a global scale (Elbert et al. 2012; Porada et al. 2013). In the first study, Elbert et al. (2012) compiled the available data from more than 200 studies on the

carbon fixation rates of cryptogamic organisms occurring on soil, rocks, and leaves of plants. In most cases, short-time measurements with net photosynthesis rates under optimum conditions had been conducted. These values were scaled to annual NPP rates and assigned to major ecosystems (desert, extratropical forest, steppe, tropical forest, and tundra) to obtain mean NPP values, which were then extrapolated to a global scale. Considering only biocrusts occurring under more arid conditions, comparably high flux rates were obtained for steppe ecosystems (16.0 g C m^{-2} $year^{-1}$) compared to deserts (5.2 g C m^{-2} $year^{-1}$).

Based on their calculations, Elbert et al. (2012) estimated C uptake in these cryptogamic covers to be ~3.9 Pg C $year^{-1}$, corresponding to ~7 % of the net primary production of terrestrial vegetation. When only cryptogamic ground covers are considered, annual C uptake was estimated at ~2.4 Pg C $year^{-1}$ (Fig. 15.5). When restricted to biocrusts, uptake values of ~0.6 Pg C $year^{-1}$ were obtained. This value is ~1 % of the NPP of terrestrial vegetation (~56 Pg $year^{-1}$, Zhao et al. 2005), but in the desert ecosystem, biocrusts account for about 9 % of the total NPP (~0.07 Pg $year^{-1}$ compared to a total NPP of ~0.8 Pg $year^{-1}$; Zhao et al. 2005; Elbert et al. 2012). As mostly measurements of single cryptogamic organisms were used for these calculations with only few data available on complete communities (e.g., biocrusts), these results may be higher than balances of complete biocrusts with fungi, bacteria, and archaea involved.

In this first upscaling approach, several assumptions were made to facilitate an upscaling from short-term measurements to a long-term global scale. In order to come up with long-term data of higher accuracy, the natural cycles of hydration and dehydration and the resulting productivity have to be followed ideally over several years. This knowledge can greatly improve the understanding of seasonal and interannual variability of CO_2 fluxes and allow the development of strong predictive models to assess the behavior of biocrusts in a global change scenario.

In a second approach, Porada et al. (2013) used a process-based model to estimate the global C uptake by lichens and bryophytes across all habitats. In this "Lichen and Bryophyte Simulator," the organisms are described by a reservoir approach that consists of pools of biomass, sugar reserves, water, and internal CO_2 concentration. These pools are changed by input and output flows of C and/or water that are driven by climatic factors and the biotic environment (e.g., location relative to the surrounding vegetation). Utilizing this model, the authors predict a global terrestrial NPP ranging between 0.34 (average method) and 3.3 Gt C $year^{-1}$ (maximum weighing method) by lichens and bryophytes. This is the first approach analyzing the NPP of cryptogams based on a photosynthesis model. Thus, it still contains uncertainties, as for some physiological parameters, little data are available for lichens and mosses. Also, C losses have not been considered and thus NEE/NSE may be very small.

The global patterns of the ground-based NPP rates calculated by Porada et al. (2013) generally agree with those of Elbert et al. (2012), with the highest NPP values in both studies being reached in extratropical forests and the lowest (zero) in the Sahara Desert, due to the lack of water (Fig. 15.5). The overall values, however, are smaller in the study of Porada et al. (2013) compared to Elbert et al. (2012). This is
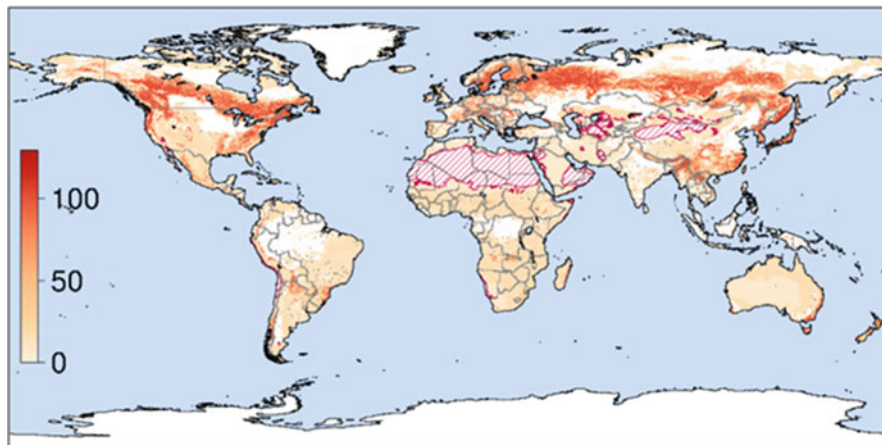
Fig. 15.5 Geographic distribution of atmospheric carbon dioxide fixation by cryptogamic ground covers. The *color coding* indicates the flux intensity in g m^{-2} year^{-1}. *White areas* indicate ecosystems for which no data are available; *hashed areas* were excluded from global budget calculations (annual mean precipitation < 75 mm year^{-1}, and desert areas designated as dune sand/shifting sands and rock outcrops)

possibly, in part, because cyanobacteria and algae were not taken into account in the study, despite their extensive global cover. Nevertheless, this approach allows completely new insights into the global relevance of cryptogamic organisms in C cycles. In addition, Porada et al. (2014) also used this model to calculate the potential N fixation, phosphorus uptake, and chemical weathering by lichens and bryophytes. Investigating global estimates, one has to keep in mind that biocrusts may also indirectly enhance CO_2 uptake by plants through cyanobacterial nitrogen enrichment of the soil (Belnap 2002; Elbert et al. 2012).

15.5 General Future Research Needs and Directions

Despite the potential importance of biocrusts in C cycles at all scales, we have little quantitative data by which to understand their role. Using common protocols, we need to better document how biological (e.g., species composition, organism condition) and physical factors (e.g., activity rates and times as determined by climatic factors, soils) influence C fixation and loss. Across all scales, we need to better understand observed NPP/NSE rates: that is, what portion of the measured NSE is due to biocrust photosynthesis and respiration, and what portion of C losses is due to other sources, such as bacteria, fungi, and soil carbonates? At the microscale, we need more studies on how biological and environmental factors interact to determine photosynthesis and respiration. At the mesoscale level, only eddy covariance and flux towers provide real estimation of CO_2 fluxes of whole

ecosystems. However, these studies are still very rare in biocrust communities, thus seriously limiting our understanding of the role of biocrusts in landscape or larger-scale CO_2 balances and budgets. For this reason, we suggest more such installations, with care paid to standardize protocols and measurements. In addition, because eddy covariance offers direct measurements of C fluxes, these studies could be linked to the modeled outputs at the microscale, giving an opportunity for cross-validation. A validated model could allow predicting the influence of environmental change on C cycling across all scales.

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