Eco-physiological characterization of early successional biological soil crusts in heavily human impacted areas

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Abstract. Eco-physiological characterizations of photoautotrophic communities are not only necessary to identify the response of carbon fixation related to different climatic factors, but also to evaluate risks connected to changing environments. In biological soil crusts (BSCs), the description of eco-physiological features is difficult, due to the high variability in taxonomic

10 composition and variable methodologies applied. Especially for BSCs in early successional stages, the available datasets are rare or focused on individual constituents, although these crusts may represent the only photoautotrophic component in many heavily disturbed ruderal areas, like parking lots or building areas with increasing surface area worldwide. We analyzed the response of photosynthesis and respiration to changing BSC water contents, temperature and light in two early successional BSCs. We investigated if the response of these parameters was different between intact BSC and the isolated dominating

15 components. BSC dominated by the cyanobacterium *Nostoc commune* and dominated by the green alga *Zygogonium ericetorum* were examined. A major divergence between the two BSCs was their absolute carbon fixation rate on a chlorophyll basis, which was significantly higher for the cyanobacterial crust. Nevertheless, independent of species composition, both crust types and their isolated organisms had convergent features like high light acclimatization and a minor and very late occurring depression in carbon uptake at water suprasaturation. This particular setup of eco-physiological features may enable these

20 communities to cope with a high variety of climatic stresses, and may therefore be a reason for their success in heavily disturbed areas with ongoing human impact. However, the shape of the response was different for intact BSC compared to separated organisms, especially in absolute net photosynthesis rates. This emphasizes the importance of measuring intact BSCs under natural conditions for collecting reliable data for meaningful analysis of BSC ecosystem services.

1 Introduction

25 In drylands, the eco-physiological characterization of biological soil crusts (BSCs) is a useful instrument for the evaluation and prediction of ecosystem functioning under recent climate change scenarios (Maestre et al., 2011). Biological soil crusts are small scale communities, composed of bryophytes, lichens, cyanobacteria, green algae, heterotrophic bacteria and microfungi, within or on top of the uppermost millimeters of soil surfaces (Belnap et al., 2016), that are often used as model systems to characterize the biodiversity–ecosystem function relationship in soils (Bowker et al., 2010). While there is sound

documentation regarding eco-physiological characterizations for BSC organisms from hot and cold deserts as well drylands (Hawes et al., 1992; Lange et al., 1992; Housman, 2006; Novis et al., 2007), studies from temperature regions are rare. In temperate regions, BSCs are not a typical 'steady state' vegetation type. They are either restricted to continuously disturbed habitats, are an initial stage of succession after heavy disturbances or present in areas held in arrested succession. In such early

5 successional stages, BSCs are mainly composed of cyanobacteria and/or green algae (Fischer et al., 2010). Although the physiological capacity of these organisms may be negligible in relation to lichen and bryophyte dominated BSCs (Belnap et al., 2001), they are crucial study organisms for understanding BSC function in temperate regions.

In temperate regions anthropogenic disturbances like forestry, traffic lanes or trampling (Webb and Wilshire, 1983) create new land surfaces (Walker and Willig, 1999) where microclimatic conditions can favor BSC development. This is due to the

10 fact that BSCs in general are initial colonizers of open surfaces (Fischer et al., 2010; Veste et al., 2011) where cyanobacteria and green algae appear as pioneers (Belnap, 2006). Ongoing disturbance prevents proceeding recovery; thus, the species richness remains at a low level, a phenomenon also referred to as arrested succession (Webb and Wilshire, 2012). In the natural BSC succession, lichens and bryophytes would broaden the initial colonization (Belnap and Eldrigde, 2001; Belnap, 2006), however, in areas of arrested succession cyanobacteria and green algae are more resistant to the disturbance and thus remain

15 the dominant BSC organisms (Kuske et al., 2011). Areas where vegetation remains in a state of arrested succession are appearing more frequently due to a growing need for space by humans (Housman, 2006) and new habitats derived from accelerating human activities are fairly understudied (Rindi, 2007). Aside from ongoing human disturbance, areas affected negatively by climate change might experience shifts in species composition towards cyanobacteria and green algae as the dominant BSC contributors, due to warming and a lower water availability (Zelikova et al., 2012; Reed et al., 2012; Escolar

20 et al., 2012). These areas will increase in space until the end of the 21st century (Solomon et al., 2007), which strengthens the need for eco-physiological investigations on cyanobacteria and green algae in the BSC context. Nonetheless, climax communities with mosses or lichens being present exist also in dry areas with high temperatures (e.g. Zedda et al., 2011 or Weber et al., 2012), so it is not possible to generalize this pattern.

Organisms of ruderal habitats often possess specific physiological adaptations, for example high physiological plasticity

25 (Grime & Pierce, 2012). Cyanobacteria and green algae are key constituents and only the primary producers during a) early succession, b) regeneration processes of habitats under constant anthropogenic pressure, and c) in BSCs of demanding habitats, e.g. hot (Büdel, 1999) and cold deserts (Büdel et al., 2016; Karsten et al., 2010a). Typical taxa of green algae and cyanobacteria found in early successional BSCs of the temperate zone are, for example: *Zygogonium ericetorum* (Pluis, 1994; Büdel, 2001a), *Klebsormidium* spp. (Pluis, 1994), *Microcoleus* spp. (Belnap et al., 2001) and *Nostoc* spp. (Pandey et al., 2005).

30 Comparing eco-physiological literature of cyanobacteria and green algae reveals that cyanobacteria are in general a well-studied group of organisms. In the absence of other photoautotrophic organisms in BSCs, they provide the most important ecosystem services (Makhalanyane et al., 2015 and sources therein). Terrestrial cyanobacteria are important in many ecosystems, due to their ability to fix atmospheric nitrogen and sequester carbon (Dojani et al., 2011; Büdel et al., 2016) and play important roles in global biogeochemical cycles (Raven, 2012). Most studies on the ecophysiology of single cyanobacteria

species or cyanobacterial dominated BSCs were carried out in desert or polar environments (Hawes et al., 1991; Lange et al., 1992; Housman, 2006; Novis et al., 2007). In contrast to cyanobacteria, reliable records of eukaryotic algal groups appear to be restricted to studies in soils of temperate and alpine regions (Karsten et al., 2010b). Although green algal dominated BSCs occur rarely in temperate regions, where they do, they have high soil surface coverage (Büdel et al., 2016). Green algae serve

5 as key organisms in BSC formation in all ecosystems, especially in temperate, arctic and high alpine regions (Büdel et al., 2016). A lack of information on green algae in general and especially on temperate, ruderal areas seems surprising because green algae occur in virtually all terrestrial habitats and on manmade surfaces (Gaylarde and Morton, 1999; Tomaselli et al., 2000; Büdel, 2011). The ecosystem services provided by green algae include stabilization of soil surfaces, improvement of soil structure, soil fertility and the influencing of hydrological processes (Bailey et al., 1973; Hu et al., 2002; Reisser, 2007).

10 The current status of eco-physiology of terrestrial green algae has been described as being based on assumptions and deductions rather than on experimental data (Reisser, 2007). Additionally, most green algal focused studies have investigated organisms after a prolonged period of cultivation (e.g. Karsten et al., 2010a, b), which could have changed their eco-physiological responses over time, as these organisms are well known to have a high acclimatization potential to differing environmental factors (Colesie et al., 2012; Belnap et al., 2016).

15 One application for detailed eco-physiological descriptions is modelling on a global scale. Post millennial interest in carbon gain of BSCs has increased (Lange and Belnap, 2016) and their CO_2 exchange rates are now considered relevant even on a global scale (Elbert et al., 2012; Porada et al., 2013, 2014). Unfortunately, modern process based models as used by Porada et al. (2013; 2014) are still based on few available datasets, that cover few different BSC types, organisms, geographical regions, and climatic situations which even exclude cyanobacteria and green algal dominated BSCs. Problematic is also the focus on

20 isolated organisms rather than studying the whole BSC system (see Colesie et al., 2016 or sources in Elbert et al., 2012). One organism studied out of several BSC organisms does not represent the ecological response of a complete BSC (Weber et al., 2012).

The goal of this study is to present a detailed description of the eco-physiological performance of a cyanobacterial and a green algal dominated BSC regarding their photosynthetic response to different water, light and temperature conditions of temperate

25 habitats. This will allow an overview of in situ gas exchange rates correlated to local climate and therefore produce a suitable database for potential global scale models. The study also provides an eco-physiological dataset for BSCs in habitats with ongoing human disturbance. Additionally, it demonstrates the value of measuring BSCs as a system instead of as single components.

Two major research questions were raised: 1) What is the eco-physiological performance of an intact cyanobacterial or green

30 algal BSC? A higher physiological flexibility is predicted for cyanobacteria and green algae compared to bryophytes and lichens. This would enable the groups to cope with a wide range of abiotic stresses.

2) To what extent can the photosynthetic rate of the BSC be delineated from single organism measurements? We expect differences between measurements of complete BSCs (with attached soil and soil organisms), of the isolated organisms, and

bare soil alone. In theory, a mathematical addition of "separated organisms" plus "bare soil" should equal the complete system reading.

2 Material and methods

2.1 Study site and organisms

Two anthropogenically impacted sites with constant disturbance were selected. Both sites were located in south western Germany (Fig. 1a) and were dominated by either green algae or cyanobacteria. The sites were 50 km from each other, which excludes any macroclimatic differences. Mean annual air temperature is 9.9 °C and mean annual precipitation 741.3 mm (Weather station of the Agrarmeteorologie Rhineland–Palatinate Morlautern).

Site 1 – Mehlinger heath. The Mehlinger heathland (MH, Fig. 1b) is a former military training ground (Ruby 1979) close to the city of Kaiserslautern (49°48' N, 7°83' E). Once the military use was abandoned, a BSC dominated by green algae developed between dense heather stands, which formed as a part of the natural successional process. With 150 ha, the site is the largest heathland system of southern Germany. It is situated 320 to 340 m a.s.l. and soils are acidic (pH = 5.28, Felde, personal communication), mostly due to their origin from red sandstone of the early Triassic (Landesamt für Geologie und Bergbau, Rhineland–Palatinate), with a loamy soil texture, very low organic carbon content (<1%) and a water holding capacity of 40%. Since 2001 it has been a natural reserve with an ongoing human management regime to preserve the heathland system. Vascular plant vegetation is dominated by *Calluna vulgaris*. In general, the cryptogamic diversity concerning cyanobacteria and green algae in this habitat is poor (Stanula, 2011), with only five and one species described, respectively. The sampling site is close to a look-out point, where trampling is unpreventable. The dominant organism in the occurring BSC is the green algae *Zygogonium ericetorum* (Fig. 1c).

Site 2 – Parking lot. Cyanobacteria dominated BSC samples were collected from a parking lot (PL) at an equestrian farm (Fig. 1d) near the city of Zweibrücken (49°19' N, 7°25' E), 369 m a.s.l. The bedrock is composed of base rich (pH = 6.81; Felde, personal communication) limestone that originates from early Triassic with a coarse gravel overlay, with a loamy sand soil texture, 6% organic carbon and a water holding capacity of 30%. Daily use by cars and trampling prevent the development of higher vegetation. Some bryophyte species occur: *Hypnum cupressiforme* and *Tortula muralis*. The cyanobacterium *Nostoc commune* Vaucher ex Bornet & Falhault (Fig. 1e) is the dominant organism in these BSCs and is clearly visible with the naked eye. Sampling depth at both sides was between 0.8 to 1 cm.

2.2 Sample collection

Sample collection was conducted in spring 2016 at both study sites. Samples were selected according to the dominant occurrence of *N. commune* or *Z. ericetorum*. A green algal or cyanobacterial dominated BSC was defined as covering at least 50% of the soil surface in a 20 cm diameter petri dish. Once collected, the samples were first allowed to dry at room temperature

and then were kept frozen at -20 °C until measurements. Frozen storage is described as being suitable for long term storage of BSC components for experimental studies (Tamaru et al., 2005; Seckbach, 2007).

2.3 CO₂ exchange

CO_2 exchange measurements were completed according to Colesie et al. (2014). Before measurements, the intact BSC samples underwent a reactivation process which consisted of two days exposure to 4 °C in the dark. Afterwards they were fixed in the gas exchange cuvette and sprayed with sterile, filtered water to activate their metabolism 24 hours prior to measurement. Ahead of the measurements, full water saturation was achieved by submerging the samples in water for ten minutes. Excessive water and droplets were carefully shaken from the sample before measurements.

Within each crust type (cyanobacterial and green algal) three separate series of measurements were conducted. First the intact crust (named $BSC_{all;}$ defined as the entire non-manipulated BSC including attached soil with an unknown amount of heterotrophic organisms), was used for the measurements. Once these were completed we separated the dominant organisms from the crust and measured the separated organism (named BSC_{dom}; the dominant organism of the crust, isolated from the soil, washed and dissected thoroughly) and the underlying soil (named BSC_{soil}; the underlying soil and all other microscopic organisms, except for the dominant one) separately. The following terminology will henceforth be used for the cyanocrust: C-BSC_{all}; C-BSC_{dom} and C-BSC_{soil}; for the green algal crust: G-BSC_{all}; G-BSC_{dom} and G-BSC_{soil}.

The CO_2 gas exchange measurements were conducted under controlled laboratory conditions using a minicuvette system (GFS 3000, Walz Company, Effeltrich, Germany). To obtain full eco-physiological response to changing light conditions and water contents fully hydrated samples (n=3 each sampling site) were exposed to stepwise increasing light from 0 to 2000 µmol photons m^{-2} s^{-1} (0, 25, 50, 100, 300, 500, 1000, 1500, 1750, 2000 photons m^{-2} s^{-1}) at two temperatures (17 °C and 25 °C) and ambient CO_2 concentrations to test for light levels required to saturate the photosynthesis and the operation temperature for this experiment. The lack of difference between the light saturation points at these two temperatures (grouped t-test; C-BSC_{all}: t-value=-0,971, FG=3, p=0.403; G-BSC_{all}: t-value=-1,271, FG=4, p=0.273) demonstrated that light saturation does not vary with temperature and could therefore be held stable during the following experiments. The light cycles (about 40 min duration) were repeated until the samples were completely dry (after 6 – 7 h) and samples were weighted after each light cycle in order to determine the water content. WC was calculated as mm precipitation equivalent. Sample dry weight was determined after 3 days in a drying oven (Heraeus Instruments T6P, Thermo Fischer Scientific Inc.) at 60 °C. The CO_2 exchange of the samples was related to soil crust surface and chlorophyll content, the latter determined after Ronen and Galun, (1984). The curves for the 25 °C measurements were fitted with the Smith function (e.g. Lange et al., 1998) and light saturation was defined as the photosynthetic photon flux density at 90% of maximum NP according to the fitted curve. Light compensation was the intersection of the curve with the x-axis, calculated from the last negative and first positive point of the fitted curve, which was completed for each sample separately.

Additionally, the response of net photosynthesis (NP) and dark respiration (DR) to water content (WC) at different temperatures was determined from complete desiccation cycles (the water saturated phase to the air-dried status) at saturating

light conditions (the operational light was set to 985 µmol photons m^{-2} s^{-1} for C-BSC and 1260 µmol photons m^{-2} s^{-1} for G-BSC, which represent the results from the 25 °C light cycle measurement), ambient CO_2 and a set of different temperatures (7, 12, 17, 25 °C) for n=6 C-BSC and n=4 G-BSC. The chosen temperatures are in accordance with other eco-physiological studies on BSCs (e.g. Weber et al., 2012; Lange et al., 1997; Lange, 1980) and represent the average temperature range of temperate Europe/ Germany (see e.g. site Homburg in Raggio et al., 2017). Optimum water content was calculated as the amount of water in mm precipitation equivalent where NP was above 90% of maximal NP, whereas a minor depression because of suprasaturation was defined as NP being constantly below 75% of maximum NP of the sample.

To determine a possible effect of abiotic CO_2 release from BSC attached soil, the soil was measured before and after being autoclaved (see supplemental material Table S6).

2.4 Species identification

N. commune and *Z. ericetorum* were studied using a light microscope (Axiokop, Zeiss, Germany) and identified using Geitler, (1932) and Ettl & Gärtner, (1995). Additionally, other photoautotrophic cells from one gram of soil material were identified and counted, to get an overview of the photosynthetic active organisms that were present in the soil after the most abundant organism of the BSC had been removed.

2.5 Data analysis

Light compensation points and light saturation levels of the two types of BSC were compared with a grouped t-test. To test for differences between mean values of cardinal points for photosynthesis (maximum NP and DR at the same temperatures, optimal water content range and water compensation points) for BSC$_{all}$, BSC$_{soil}$ and BSC$_{dom,}$ a multifactorial analysis of variance (Statistica 10, Stat soft), with a Tukey post-hoc test was applied. Prior to the analysis, all data were checked for Gaussian distribution and homogeneity of variance and successfully log transformed if they did not fit these criteria. BSC$_{all}$, BSC$_{dom,}$ BSC$_{soil}$ (referred to as "organization level" from here on) and temperature were always the explanatory variables, while optimum water content, water compensation point, maximum net photosynthesis and maximum dark respiration were dependent variables. Paired t-tests were applied to detect differences in total NP rates of BSC$_{all}$ and NP rates of BSC$_{dom}$ and BSC$_{soil}$ taken together. The optimum water content range was compared by statistically testing if the upper and lower limits between the BSC$_{dom}$, BSC$_{soil}$ or BSC$_{all}$ differed. A multifactorial ANOVA was applied where organization level and temperature were the explanatory variables while either (a) the upper or (b) the lower limit of the optimum water content range was the dependent variable.

3 Results

3.1 Gas exchange

3.1.1 Light dependent photosynthetic response

Maximum photosynthetic rates per area were reached at 2000 µmol photons m^{-2} s^{-1} for both, C-BSC$_{all}$ and G-BSC$_{all}$ (Fig. 2a
5 and 2b), as it was impossible to increase PAR above this value with the GFS 3000 due to instrument limitations. Neither
organism showed photoinhibition even at the highest light intensities applied (2000 µmol photons m^{-2} s^{-1}).

The light compensation point of photosynthesis was higher for G-BSC$_{all}$ (254 ± 53 µmol photons m^{-2} s^{-1}) compared to C-BSC$_{all}$
(151 ± 25 µmol photons m^{-2} s^{-1}). However, there was no statistical support for the difference between the BSCs (grouped t-
test: t-value=2.58; df=4; p=0.06), mostly owing to the high standard deviations caused by high sample variation.

10 Light saturation of NP (90% of maximal) was significantly different for both types and reached 985 ± 31 µmol photons m^{-2} s^{-1} for C-BSC$_{all}$ and 1260 ± 53 µmol photons m^{-2} s^{-1} for G-BSC$_{all}$ (grouped t-test: t-value=7.75; df=4; p=0.002).

3.1.2 Net photosynthesis

For the *N. commune* dominated BSC (Fig. 3a) the organization level had a significant effect on the NP performance (F=38.06;
15 p=0.000). NP was up to 4.3 times higher in C-BSC$_{dom}$ than in C-BSC$_{all}$ (Tukey post-hoc test: p= 0.000), whereas there was no
difference between C-BSC$_{all}$ and C-BSC$_{soil}$. NP at 25 °C was significantly higher than at 7 °C and 12 °C for all, C-BSC$_{all}$, C-
BSC$_{dom}$ and C-BSC$_{soil}$ (F=9.41; p=0.000; Tukey post-hoc test: p 7 °C=0.000; p 12 °C=0.000).

In the *Z. ericetorum* dominated BSC (Fig. 3b) NP also changed with organization level (F=53.61; p=0.000). There was a
significant difference between G-BSC$_{soil}$ and G-BSC$_{all}$ (Tukey post-hoc test: p=0.03), and G-BSC$_{dom}$ NP differed from both
20 (Tukey post-hoc test: p G-BSC$_{all}$=0.000; p G-BSC$_{soil}$=0.000). NP of G-BSC$_{dom}$ was 5.5 times higher than in G-BSC$_{all}$. There
was no temperature dependency of NP visible for either the G-BSC$_{all}$, G-BSC$_{dom}$ or G-BSC$_{soil}$.

The effects of organization level and temperature on DR can be seen in Fig. S1 and Tables S7-S9.

3.1.3 Water dependent photosynthetic response

25 The response to changing water contents in both BSCs and their separate components are shown in two exemplifying graphs
(*N. commune* Fig. 4a and *Z. ericetorum* Fig. 4b). Neither the water-response curve of G-BSC$_{dom}$, nor C-BSC$_{dom}$, resembled the
response of BSC$_{all}$. The NP in C-BSC$_{dom}$ was three times higher compared to C-BSC$_{all}$, and doubled in G-BSC$_{dom}$ (for statistical
analyses see Table S1-3). Respiration in C-BSC$_{soil}$ was strikingly small in a *N. commune* dominated system and did not
resemble the respiratory response in C-BSC$_{all}$ or the C-BSC$_{dom}$, whereas respiration was pronounced in a *Z. ericetorum*
30 dominated G-BSC$_{all}$. Respiration of G-BSC$_{soil}$, G-BSC$_{all}$ and G-BSC$_{dom}$ all seemed to follow the same pattern, although the

values differed slightly between all three, with highest rates in G-BSC$_{soil}$. A general observable pattern was that NP of BSC$_{soil}$ and BSC$_{dom}$ combined never equalled NP of BSC$_{all}$ in both BSC types (paired t-test; results for *N. commune*-crust: t-value=-6.43; df=23; p=0.000; *Z. ericetorum*-crust: t-value=-5.05; df=15; p=0.000).

C-BSC$_{dom}$ showed a minor depression in net photosynthesis at high water contents (Table 1). An even smaller depression was visible in the C-BSC$_{all}$. Due to the cross sensitivity of the GFS 3000 analyzer for CO_2 and H_2O molecules, it was impossible to measure such high water contents for the C-BSC$_{dom}$, as the amount of water brought into the measuring system was too high to produce reliable measurement values. Also in G-BSC$_{dom}$ and in G-BSC$_{all}$ a minor depression was expressed between 63–71% normalized water content.

The optimum water content had a smaller range for C-BSC$_{all}$ (1.21 to 1.39 mm) compared to C-BSC$_{dom}$ (0.56 to 0.83 mm); for G-BSC$_{all}$ it was between 1.44 and 1.57 mm and for G-BSC$_{dom}$ between 0.58 and 0.79 mm. The values for optimum water content between both BSC$_{all}$ types were close, as well as between both BSC$_{dom}$ which show similar values, independent of species. The maximum water holding capacity was 3.29 ± 0.89 mm for C-BSC$_{all}$ and 4.66 ± 1.38 mm for G-BSC$_{all}$. In percent dry weight C-BSC$_{dom}$ could hold up to 4562%, while sustaining 88% of its maximum NP rate, but G-BSC$_{dom}$ could only take up 435% with 18% of its maximum NP rate (see Fig. 4).

Both BSC$_{all}$ optimum water content ranges were significantly higher than the corresponding BSC$_{dom}$ optimum water content ranges (multifactorial ANOVA *N. commune*: df=2; F=15.24; p=0.000; multifactorial ANOVA *Z. ericetorum*: df=2; F=30.08; p=0.000). The optimal water content differed heavily with organization level and was broadest in BSC$_{dom}$ for both BSC-types (Fig. 5; *N. commune*: F=43.20; p=0.000; *Z. ericetorum*: F=66.28; p=0.000). This pattern is expected, as extracellular polymeric substances have a different water holding capacity than soil. Nonetheless, both BSC$_{all}$ and their respective BSC$_{dom}$ samples, showed a broad optimum water content range (Fig. 5), compared to soil alone. Both limits of BSC$_{dom}$ in both types, were not statistically different, which was also the case for BSC$_{all}$ (for statistical results see Table S4 & S5)

3.2 Net photosynthesis per area vs. net photosynthesis per chlorophyll content

A significant difference between NP calculated per area and NP per chlorophyll content became obvious after comparing the results: NP/chlorophyll was up to two magnitudes higher in C-BSC than in G-BSC, although G-BSC had an up to 181 times higher chlorophyll content per area (Table S9), which would theoretically enable the G-BSC to assimilate more CO_2 than the C-BSC. To investigate whether the higher NP rate in C-BSC was due to actual eco-physiological differences (like a carbon concentrating mechanism, CCM) or because of the reference value used, we calculated the effect the reference value had on the NP rates between both investigated organisms.

First, NP per area was calculated for C-BSC$_{dom}$ and G-BSC$_{dom}$ at each temperature. Then the ratio of C-BSC$_{dom}$ to G-BSC$_{dom}$ was calculated for NP/area rates. The same ratio of NP/area rates was calculated between C-BSC$_{all}$ and G-BSC$_{all}$.

Afterwards, NP was calculated on chlorophyll basis for the same samples and each temperature. The ratio of NP/chlorophyll between C-BSC$_{dom}$ and G-BSC$_{dom}$ and then between C-BSC$_{all}$ and G-BSC$_{all}$ was calculated. If both ratios, NP/area and

NP/chlorophyll, were of equal size, it would be possible to conclude that only eco-physiological reasons, like a CCM, were responsible for the much higher NP rates in the cyanobacterial dominated crust. However, the NP/chlorophyll ratio was always higher than NP/area ratio (grouped t-test: t-value=-2.167; df=14; p=0.05; Fig. 6) e.g. BSC_{all} at 25 °C: NP/area 6 times higher in C-BSC_{all}; NP/chlorophyll 42 times higher in C-BSC_{all}.

3.3 Photosynthetic active and heterotrophic organisms in soil

The number of cells of photosynthetic active organisms in soil samples was similar for both study sites (26 ± 3 cells per gram soil for MH and 19 ± 2 for PL). The abiotic gas release, measured after autoclaving the soil, was about 20 % of the gas exchange before autoclaving (Table S6).

4 Discussion

In this study, we received profound evidence that early successional BSCs expose a considerable physiological flexibility which in turn might be responsible for their pronounced stress tolerance and their success in heavily disturbed habitats. As light is one of the major drivers for photosynthetic rates in BSCs, the cardinal points in response to light were examined. For BSCs photosynthetic organisms the light level compensating respiration normally lies between 60 to 100 photons m-2 s^{-1} (Green & Proctor, 2016), which indicates comparability to classical "sun plant" features. Our results support these findings and the variation within our measurements, indicated by high standard deviations, reflects a very high sampling site internal variation. This may be a result of spatially small-scale shading of, e.g. *Calluna vulgaris* in the Mehlinger heathland, or higher plants at the border of Parking Lot. As high light adapted organisms, light saturation points of BSC organisms are almost always at, or above, 700 µmol photons m^{-2} s^{-1} (Green & Proctor, 2016). This is well supported by our data with LSP consistently being over 900 µmol photons m^{-2} s^{-1} for both, C-BSC_{all} and G-BSC_{all}.

The second major driver for photosynthetic responses in BSCs is water, thus the photosynthetic cardinal points in response to water content were examined. The lack of differences in the optimal water content between C-BSC_{dom} and G-BSC_{dom}, and between the G-BSC_{all} and C-BSC_{all}, indicates that both organism groups share the same functional role in the BSC consortium and can operate at near optimal conditions over a variety of different water contents, as it would be expected for highly stress tolerant crust pioneer species. Explaining the variability in eco-physiological response to water content are the relatively high standard deviations and broad range of optimal water contents for the dominant organisms, compared to other species (e.g. $0.25 – 0.35$ mm in *Fulgensia fulgens* (Lange et al., 1998)). Optimal water content of a BSC in a temperate habitat (Homburg; 3.32 mm; Europe, Germany; Colesie et al., 2014) is 2 mm higher than in our study ($1.21 – 1.57$mm), probably due to the low biomass in the investigated early successional habitats in this study. Colesie et al., (2014) proposed that biomass is the driving factor shaping the optimal water content within a system, with low biomass needing less water to achieve maximum net photosynthesis. A general difference between BSC_{all} and BSC_{dom} concerning optimal water content is likely due to the different water holding capacities of the soil. Even at high water contents, C-BSC_{dom} only showed a slight depression of NP (Fig. 4).

Depression in G-BSC$_{dom}$ occurred relatively late (Table 1). Considering that these crusts live in a temperate climate, where precipitation is high enough to support forest vegetation, a depression of NP at high water contents might be a disadvantage, although a depression is common in other BSC organisms (e.g. several lichens; Lange et al., 1997). Additionally, *N. commune* can gain up to 20–30 times its dry weight in water (Satho et al., 2002; Shaw et al., 2003), which is stored mostly in exopolymeric substances (EPS) (Tomaselli & Giovannetti, 1993; Kovacic, 2000). *Z. ericetorum* only shows a slight difference in morphology when dried (Fritsch, 1916; Holzinger et al., 2010), and therefore cannot store as much water as *N. commune*. In addition, *Z. ericetorum* is rarely exposed to high water contents around the cell, and therefore, may show an earlier depression of net photosynthesis at high water contents. Furthermore, a carbon concentrating mechanism (CCM) was detected in *N. commune* (see Fig. S2), but not in *Z. ericetorum*. Through this mechanism, the internal CO_2 partial pressure around the carboxylating enzymes is increased, which improves photosynthetic efficiency. Simultaneously, CCMs decrease the CO_2 concentration around the photosynthesizing cells. Through this increasing diffusion gradient for CO_2 transport the adverse effects of suprasaturation with water can be overcome (Lange, 2001).

The third major driver of photosynthesis in BSCs is temperature. Temperature showed different effects on net photosynthesis rates in both organism groups. In C-BSC$_{all}$ NP was only higher at 17 °C and 25 °C compared to lower temperatures (7 °C and 12 °C), whereas in G-BSC$_{all}$ no difference was observable at any temperature. This indicates a high temperature tolerance, which was also noticed by Borstoff et al. (2005), who could not pinpoint an exact temperature optimum for a BSC during field studies in western Mojave Desert. BSC components are not necessarily adapted to high temperatures. Although soil surfaces at which BSCs live can reach up to 50 °C on a normal summer day (Hoppert et al., 2004), the organisms are already dry and inactive when these temperatures are reached (Raggio et al. 2017). Presumably this is the case for G-BSC$_{all}$, but not likely for the C-BSC$_{all}$ in this study. Due to the high water holding capacities of *Nostoc* thalli, activity periods during daytime are prolonged. This may coincide with a temperature increase, as has been reported for gelatinous, slow drying lichens (e.g. *Collema tenax*; Lange, 2001). In Antarctica, where Novis et al., (2007) conducted a study on the importance of *N. commune* in Antarctic habitats, it was observed that this organism tends to have its highest NP rates at unusually high temperatures (20.5 °C). However, the results of Novis et al., (2007) should be treated with caution, because it is very likely that organisms corresponding to the description of *N. commune* from polar and temperate regions may be genetically distinct (Novis & Smissen, 2006) and therefore should not be compared so readily. Nevertheless, in general cyanobacteria are better adapted to high temperatures than green algae (Castenholz & Waterbury, 1989; Lange et al., 1998).

In summary, both crust types were largely unaffected by changes in water content and had high light compensation and exceptionally high light saturation points. Net photosynthesis of G-BSC$_{all}$ was unaffected by increasing temperatures, while C-BSC$_{all}$ only had increased NP rates with higher temperatures. Both fit well within known eco-physiological patterns of different BSC components (see Lange & Belnap, 2001), and show a lower net photosynthesis compared to BSC components of advanced successional stages (see e.g. Lange, 2001). The high physiological variability in photosynthetic cardinal points places *N. commune* and *Z. ericetorum* crusts as similar to other BSC contributors, such as lichens and bryophytes. This characterizes these organisms as stress tolerators within the typical patterns of Grimes CSR-model (Grime & Pierce, 2012).

Life history traits of stress tolerators include slow growth rates, high rates of nutrient retention, low phenotypic plasticity and a response to environmental stresses through physiological variability (Grime & Pierce, 2012).

To aid in future investigations on BSCs methodological procedures will now be discussed. First, an unavoidable complication in gas exchange measurements of BSCs is to take abiotic release of CO_2 into account (Inglima et al., 2009; Weber et al., 2012), aside from the biotic respiration of BSC, phototrophic and heterotrophic organisms. The CO_2 release of alkaline and saline substrates can even exceed those of organic activity (Shanhun et al., 2012; Sancho et al., 2016). The abiotic release in this study accounted for only 20 % and 26 % (MH and PL, respectively) of total soil respiration rate, which is close to what Weber et al., (2012) measured in the Succulent Karoo and Shanhun et al., (2013) with 25% in Antarctica.

Secondly, besides an obvious effect of organization level on NP and DR rates (see Fig. 3, and Fig. S1), the water response curves of BSC_{all} and BSC_{dom} alone differed. Although the courses of their curves were similar, net photosynthesis rates were never equally high for BSC_{all} and BSC_{dom} (Fig. 4a and b). Adding NP rates of BSC_{soil} to BSC_{dom} did not equal the values and NP was always higher in BSC_{dom} compared to BSC_{all} in both crust types. This fact confirms the view of BSCs being communities or systems rather than random accumulations of organisms and strengthens the need for long term field monitoring studies of an intact BSC. Causes that might have led to the unexpected NP rate could be self-shading or water logging. An organism lying on top of an intact BSC has a species specific structure (e.g. lobes of *N. commune* over one another or the spherical structure of *Z. ericetorum* algal mats) that will be changed and rearranged while being washed and placed separately in a cuvette. Through this thallus manipulation and subsequent exposure, the internal diffusion resistance is decreased and the self-shading protective mechanisms in those organisms damaged. Aeroterrestrial filamentous green algae, such as *Klebsormidium crenulatum* form multilayers mat like structures on top of or interwoven with the upper millimeters of soil (Karsten et al., 2010b), contributing to self-shading of individual filaments inside a population. The same is visible in *Z. ericetorum*. While rearranging the organisms the protective layer of dead or highly melanosed cells on top of the crust is either removed or shifted, resulting in unprotected but highly active cells being subjected to high light intensities. So, although the high light intensities will cause damage, through reactive oxygen species production for example, the NP response itself is higher than before. Overlapping lobes in *N. commune* may also cause reduced NP rates in an intact BSC system. Bowker et al., (2002) hypothesized that sunscreen pigments produced by *Nostoc* protect other, less pigmented taxa, which includes a self-shading protective mechanism for lower lobes of the same species. Recent data suggests that shading effects due to such three dimensional spatial arrangements may be more important than previously assumed (Karsten & Rindi, 2010). Another possibility that could lead to decreased NP in a complete BSC system is water logging between filaments of the organisms (Garcia-Pichel & Belnap, 2001). The diffusion resistance of CO_2 in water is higher than in air (Cowan et al., 1992), and will reduce NP rates. A water suprasaturated system, as it can be found in the closely growing mats of *Z. ericetorum* or *N. commune*, could have a disadvantage against a widely spread organism surface in the cuvette, that is aerated all around.

Thirdly, we propose a methodological consideration concerning reference values of photosynthesis in gas exchange measurements in general. To compare cardinal points of photosynthesis between organisms or samples of the same species it is necessary to base the photosynthetic values on either dry weight, area or chlorophyll content, which are the most common

reference values in literature. In Fig. 6 it becomes apparent that the ratio of NP per area and NP per chlorophyll content in C-BSC_{dom} and G-BSC_{dom} differ substantially, although the ratio should be similar if both reference values were equally suited for gas exchange measurements in those organisms. This difference is most probably due to the different composition of photoactive pigments in the two organism groups. Terrestrial green algae possess chlorophyll a and b, whereas cyanobacteria only possess chlorophyll a, which is considered in the calculation of chlorophyll content. But cyanobacteria also possess phycobilisomes and super antennae allowing capture of photosynthetically active radiation from low photon flux densities and the green part of the spectrum (Lüttge, 2011), which are not considered in calculations of this reference value. A much more suitable value than chlorophyll content is therefore area, which has been used in this study. Nonetheless, this value is not perfect as there are probably many dead cells still bound to the EPS of living cells that distort area measurements, and of course it is not useful if fruticose lichens are investigated. Additionally, the arrangement of the BSC does have an influence on the photosynthetic signal, considering that *N. commune* is almost flat while *Z. ericetorum* has a more spherical structure as the BSC gets older. It is therefore of immense importance to decide which reference value should be used when comparing the eco-physiological response of BSC systems.

5 Conclusion

In this study, we present the first detailed eco-physiological dataset describing photosynthetic performance of early successional BSCs. A relative temperature independence of NP, as well as late or no water depression and an adaptation to high light intensities was demonstrated for both early successional BSCs and their separated dominant organisms. This broad physiological amplitude indicates strong stress tolerance in both organism groups and may be the reason for their success in heavily disturbed areas. The results can be incorporated into global scale carbon cycle models. Additionally, this study emphasizes the importance of measuring a complete BSC rather than their single components, as not only taxonomic composition but also spatial arrangement seems to be an important factor shaping photosynthetic response in BSC systems. Lastly, the methodological approach demonstrated that a comparison of photosynthetic values in cyanobacteria and green algae should be based on area rather than chlorophyll content.

Acknowledgements

We would like to thank Andreas Klein and the Untere Naturschutzbehörde of Kaiserslautern for providing us access to the Mehlinger heath. Also, we would like to thank Dr. Vincent Felde and his students at the Justus-Liebig-University of Gießen for providing us information about soil data of the both investigated systems. Additionally, we would like to thank Dr. Emilio Rodriguez-Caballero for the opportunity to be part of this special issue on biological soil crusts. Finally, we want to thank the three referees for their expert opinions on this manuscript, which helped to improve it.

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Tables

Table 1: Water content at which net photosynthesis is below 75% of maximum net photosynthesis including standard deviations.

	Normalized water content [%]
C-BSC$_{all}$ [a]	**84.3 ± 15.9**
C-BSC$_{dom}$ [a,b]	**71.7 ± 16.5**
G-BSC$_{all}$ [a,b]	**70.9 ± 15.1**
G-BSC$_{dom}$ [b]	**62.8 ± 18.5**

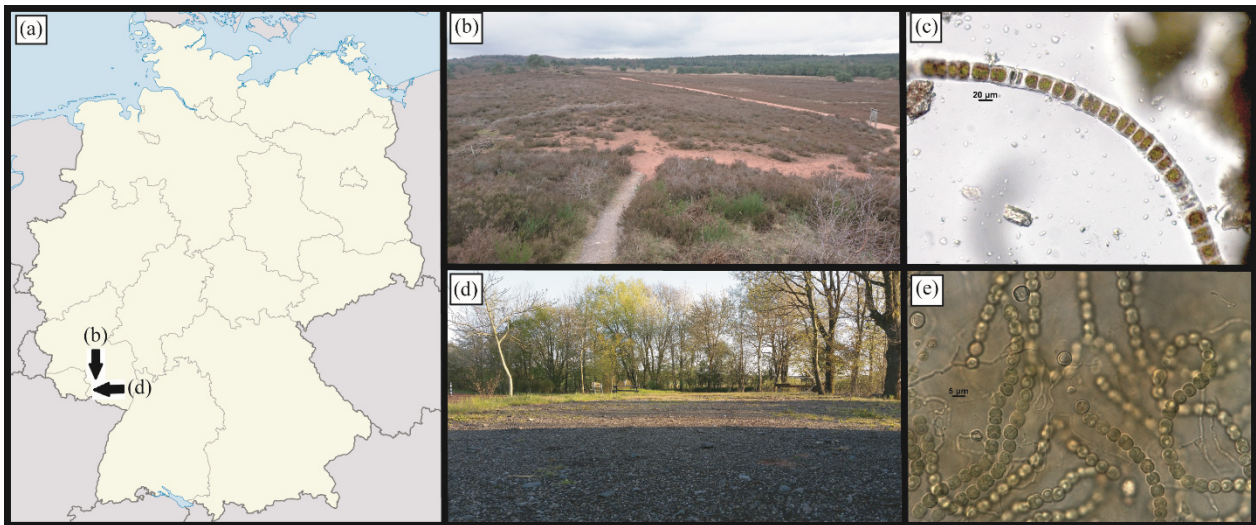
Superscripted letters represent statistical differences.

Figures

Figure 1: Organisms and map of the study site in Germany, Rhineland–Palatinate (a): Top pictures are from study site 1, Mehlinger Heath viewed from the look-out (b) and microscopic images of the crust dominating organism *Zygogonium ericetorum* (c); bottom
10   **depicts study site 2, a parking lot at an equestrian farm near Zweibrücken (d) and microscopic images of the crust dominating organism *Nostoc commune* (e).**

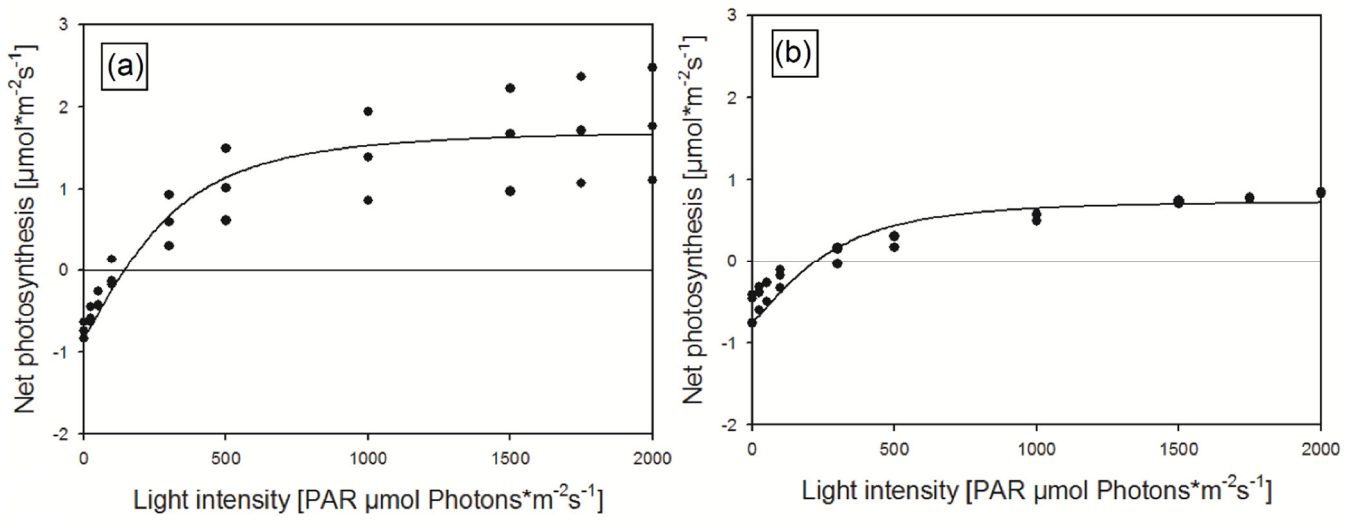



Figure 2: Light dependent photosynthetic response curves of intact BSC with (a) C-BSC$_{all}$ and (b) G-BSC$_{all}$. n=3.

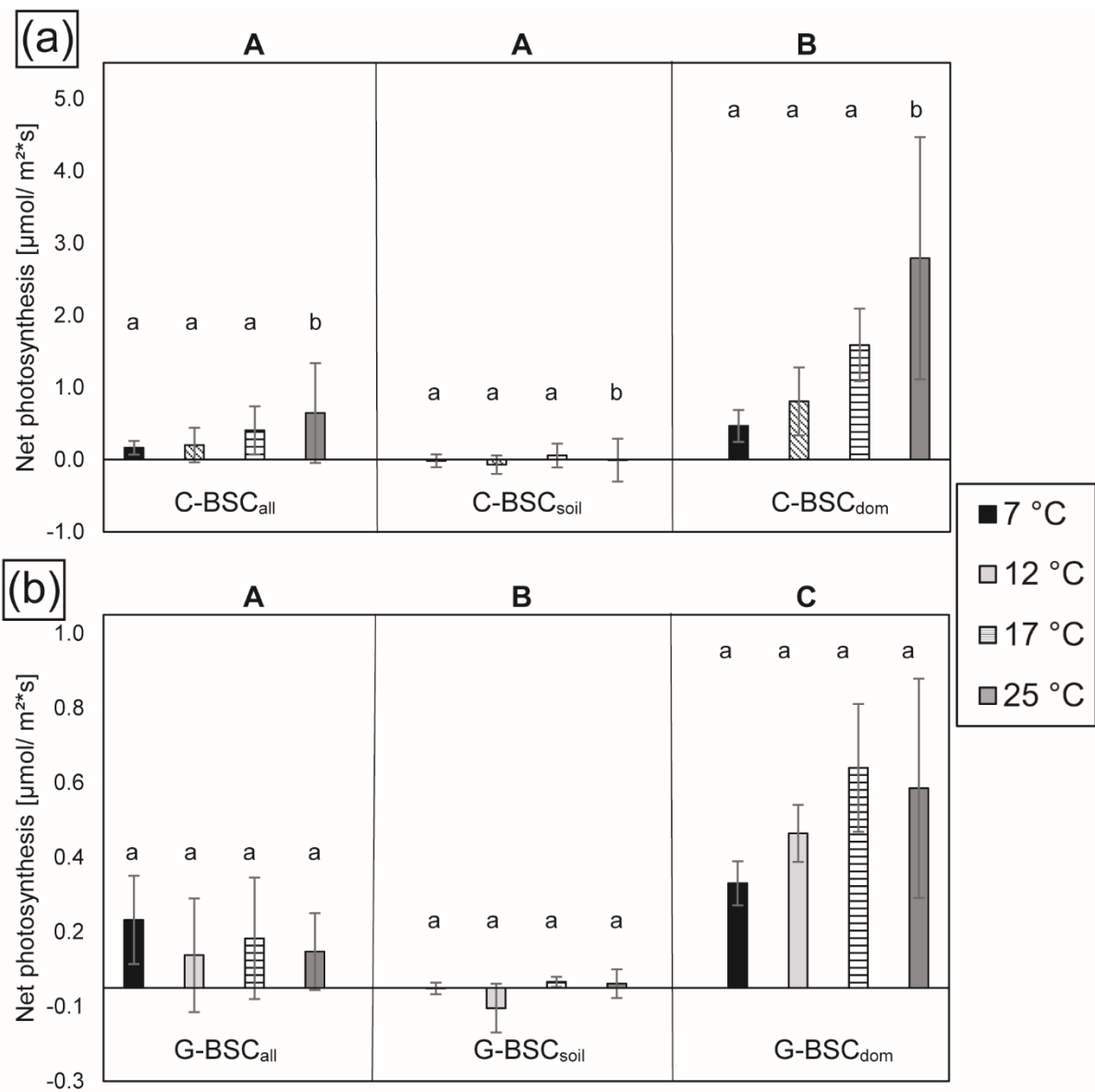



Figure 3: Temperature dependent net photosynthesis per area in (a) *N. commune* **and (b)** *Z. ericetorum* **dominated BSCs, separated dominant organism and separate soil. Capital letters indicate significant differences in organization level between BSC, organism and soil; lower case letters compare temperature differences of one of the organization groups only. Sample size was n=6 for** *N. commune***; n=4 for** *Z. ericetorum***.**

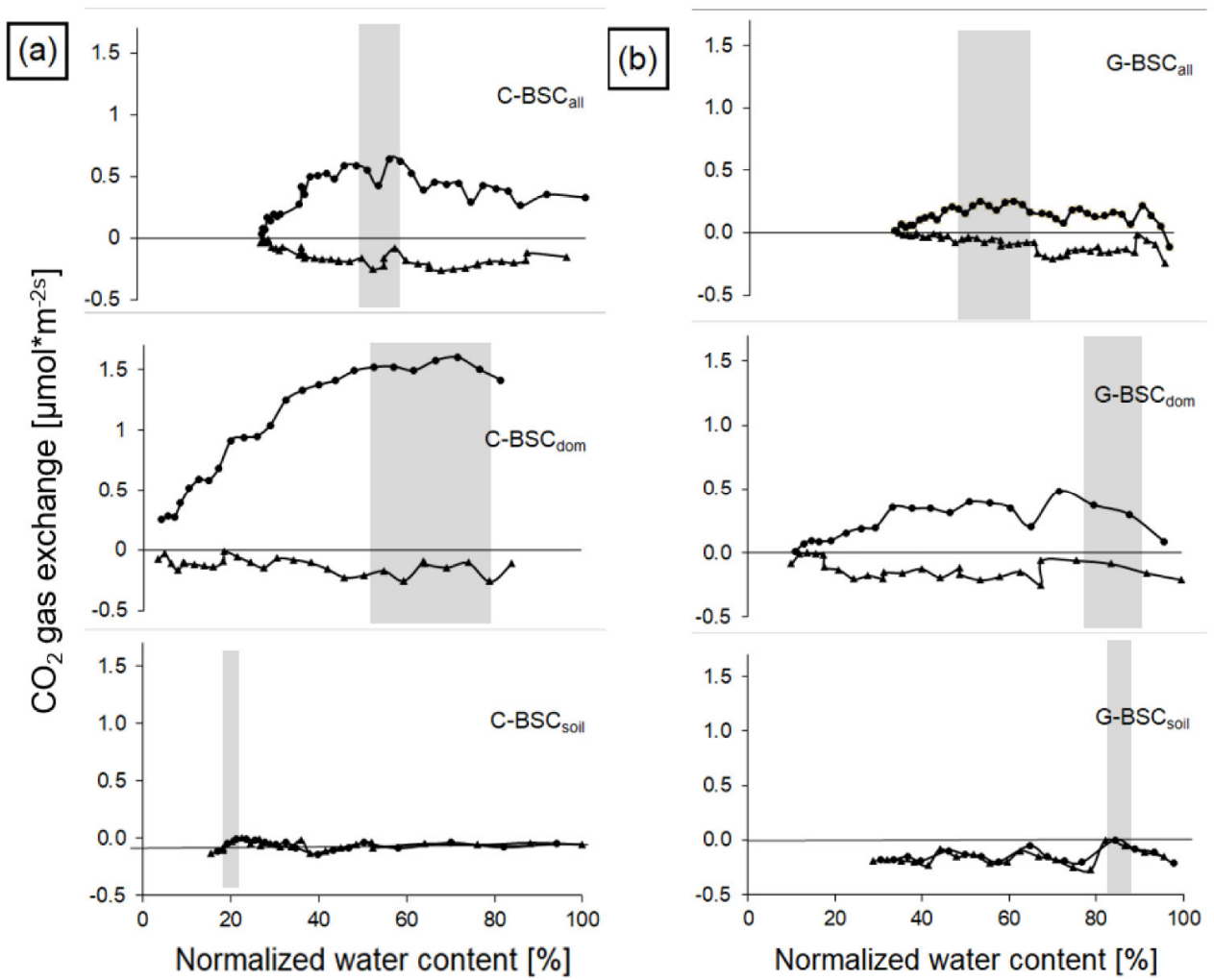



Figure 4: Responses of net photosynthesis (dots) and dark respiration (triangles) to normalized water content for intact BSC, the isolated dominant organisms and in soil at 12°C. Measurements were taken at saturating light and a temperature of 12°C. (a) C-BSC (985 µmol photons m^{-2} s^{-1}) and (b) G-BSC (1260 µmol photons m^{-2} s^{-1}). Grey bars indicate optimum water content.

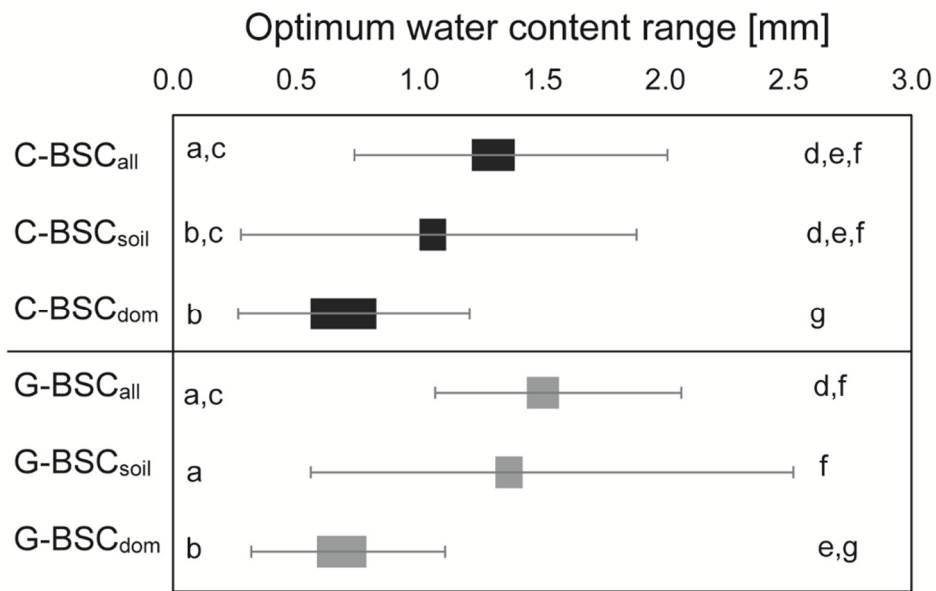



Figure 5: Optimum water content range, in mm precipitation, of a cyanobacteria dominated BSC (upper three; black bars) and a green algal dominated BSC (lower three; grey bars) and their respective separated components. Sample size is n=24 for all C-BSC and 16 for all G-BSC.

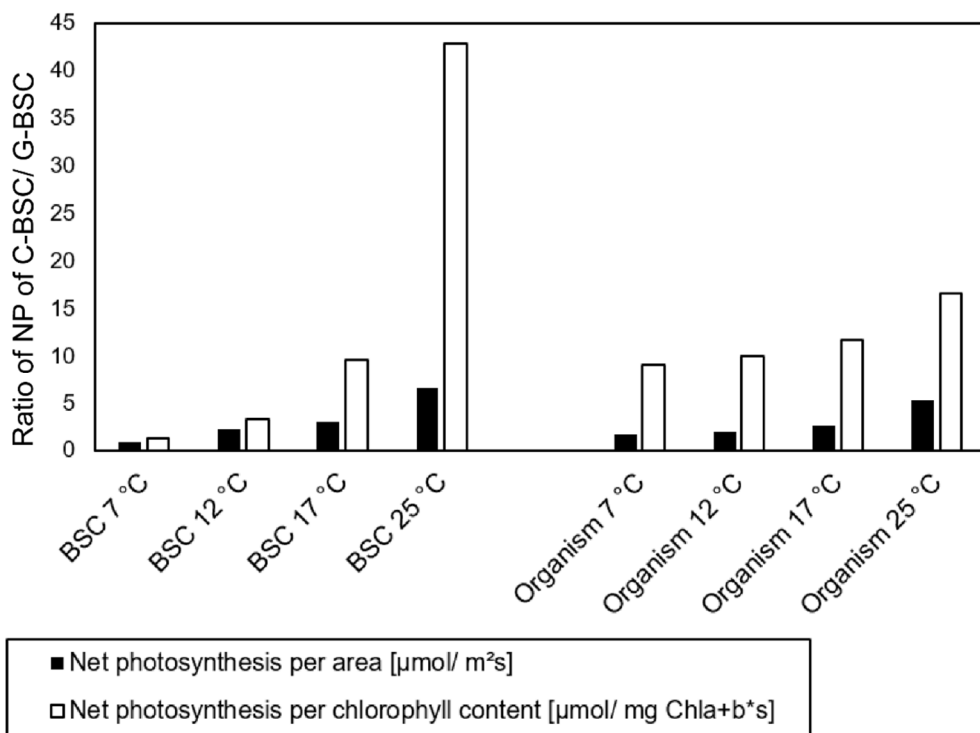



Figure 6: Difference in the ratio of net photosynthesis based on either area or chlorophyll content between C-BSC$_{dom}$ and G-BSC$_{dom}$ (organism) and also between C-BSC$_{all}$ and G-BSC$_{all}$, (BSC) measured at different temperatures.