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Annual net primary productivity of a cyanobacteria dominated biological soil crust in the Gulf savanna, Queensland, Australia

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Abstract. Biological soil crusts are a common element of the Queensland (Australia) dry savannah ecosystem and are composed of cyanobacteria, algae, lichens, bryophytes, fungi and heterotrophic bacteria. Here we report on the annual net primary productivity of a cyanobacteria dominated biological soil crust form the Boodjamulla National Park in north western Queensland using a semi-automatic cuvette system. The dominating cyanobacteria are the filamentous species *Sypmplocastrum purpurascens* together with *Scytonema* sp. The recording period lasted from July 1st 2010 to June 30th 2011. Metabolic activity was found from November 2010 until mid-April 2011 only, referring to 23.6% of the total time of the year. With the onset of the raining season in November, the first month of activity had a pronounced respiratory loss of CO_2. Also the last month of the raining season had a negative CO_2 balance. Of the metabolic active period, 48.6% were net photosynthesis and 51.4% dark respiration. Net photosynthetic uptake of CO_2 during daylight was reduced at 32.6% of the time by water suprasaturation during. In total, the biological soil crust fixed 229.09 mmol CO_2 m^{-2} yr^{-1}, referring to an annual carbon gain of 2.75 g m^{-2} yr^{-1}. Due to malfunction of the automatic cuvette system, data from September and October 2010, together with days in November and December 2010 could not be analysed for net photosynthesis and respiration. Based on climatic and gas exchange data from November 2010, an estimated loss of 88 mmol CO_2 m^{-2} was found for the two month, resulting in annual rates of 143.08 mmol CO_2 m^{-2} yr^{-1}, equivalent to a carbon gain of 1.72 g m^{-2} yr^{-1}. The bulk net photosynthetic activity occurred above a relative humidity above 42%, indicating a suitable climatic combination of temperature and water availability, and a light intensity well above 200 µmol photons m^{-2} s^{-1} photosynthetic active radiation. The Boodjamulla biocrust showed a highly seasonally varying CO_2 gas exchange pattern divided into metabolically inactive winter month and active summer month. The metabolic active period starts with a period (up to 3 month) of carbon loss, probably due to regrowth before a four month period of carbon gain. This must be taken into consideration for future analyses and modelling of carbon balances in comparable biocrust ecosystems.

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1. Introduction

Biological soil crusts (named "biocrusts" throughout the text) are a consortium of heterotrophic bacteria, cyanobacteria, algae, fungi, lichens and bryophytes in different proportions with photoautotrophic organisms dominating their biomass. They cover dryland soil surfaces and can make up to 70% of a dryland ecosystem's living cover (Belnap 1995; Belnap et al. 2016), but also occur in other climatic regions where competition with vascular plants is low (Büdel, 2001; Büdel et al., 2014). Due to the poikilohydric character of biocrust organisms, biocrusts exhibit a high resilience under extreme conditions and a remarkable adaptation to various combinations of climatic factors (e.g. Karsten et al., 2016; Sancho et al. 2016 and citations herein), thus making them excellent candidates for pioneering hostile environments on our planet. There is good evidence that cyanobacterial dominated biocrusts have inhabited Earths soil surfaces at least 2600 million years ago (Watanabe et al., 2000; for an overview see also Beraldi-Campesi and Retallack, 2016). Lalonde and Konhauser (2015) point to the importance of oxygenic photosynthesis of early biocrusts providing sufficient equivalents for oxidative-weathering reactions in benthic and soil environments. This certainly also points to the role of biocrusts in soil formation and soil fertility. Consequently, there is growing interest in carbon gain of biocrusts (Lange and Belnap, 2016) and their CO_2 exchange rates are considered relevant on local and global scales (e.g. Castillo-Monroy et al. 2011; Wilske et al. 2009; Elbert et al., 2012; Porada et al., 2013, 2014). Process based models as used by Porada et al. (2013; 2014) are still based on a few available datasets covering a small set of BSC types, organisms, geographical regions, and climatic situations (see also summary in Sancho et al., 2016).

Regarding CO_2 gas exchange of biocrusts on a long term basis, a number of studies were published either on the basis of long term measurements or modelled from single or grouped measurements. Two biocrust groups can be distinguished, one group where biocrusts experienced carbon gain and another group where biocrusts experienced carbon loss. Among the first group, a biocrust from the Mojave Desert exposed a net input of 11.7 g C m^{-2} yr^{-1} (Brostoff et al., 2005), a biocrust of the northern Negev Desert, Israel had a net carbon deposition of 0.7-5.1 g m^{-2} yr^{-1} (Wilske et al., 2008, 2009), and a biocrust from a desert region of northwest China showed a carbon sequestration of 3.46 to 6.05 g C m^{-2} yr^{-1} (Feng et al., 2014). On the other hand, where biocrust ecosystems lose carbon, for example, a biocrust of southeast Utah that was found to be a typical net carbon source (Bowling et al., 2011), a biocrust in the Colorado Plateau, USA was losing 62 ± 8 g C m^{-2} yr^{-1} (Darrouzet-Nardi et al., 2015), and a biocrusts from the Gurbantunggut Desert, Northwestern China showed a release from 48.8 ± 5.4 to 50.9 ± 3.8 g C m^{-2} yr^{-1} (Su et al., 2013). So far, it is unclear what is triggering a biocrust as either a sink or a source of C. Another important finding for the design of our study presented here is, that the determination of CO_2 gas exchange of single species removed from the biocrust context, rather than studying the whole BSC system (Colesie et al., 2016; Elbert et al., 2012). This does not necessarily represent the ecological response of an intact biocrust (Weber et al., 2012).

In this study we focus on biological soil crusts occurring in the Gulf Plains bioregion covering 8,868 km^2 and characterized by woodlands and extensive perennial grasslands. Since the late 1800's almost the entire region was grazed by cattle on large leasehold stations (Williams & Büdel 2012). Our investigation site is situated in the Boodjamulla National Park in the Gulf Plains dry savannah region of north-eastern Australia, established in 1985 and since then, cattle grazing ceased. Cyanobacteria dominated biocrusts are important drivers of ecosystem function throughout Queensland's dry savannah and especially in the Boodjamulla National Park (Williams et al., 2014). Annually there is very little rainfall during the winter-dry season. In the summer-wet season build-up early storms precede its onset; days are low in humidity with high ambient (>40◦C) and soil surface temperatures (60-74◦C). In the wet season monsoon rains and tropical storms result in vast flooded plains and ephemeral wetlands, leaving the ground saturated for several weeks (Williams et al. 2014). This led us to the questions how the Boodjamulla biocrusts respond to the pronounced seasonality of water availability and if they are sources or sinks for carbon. Coming from the observation that we could not resurrect the biocrusts photosynthetic activity in the middle of the dry season, even after soaking them in water for more than 24 hours (Williams et al. 2014), we hypothesize that there must be considerable regrowth of the crust-forming cyanobacteria before the biocrust performs positive net photosynthesis.

2. Material and methods

2.1 Investigation site

Boodjamulla National Park (18.39°S, 138.62°E) is situated in the Gulf Savannah of north-eastern Australia covering an area of 2,820 km^2. Mean annual rainfall is 641 mm falling mostly between December and February, although it can be highly variable with up to 1121 mm falling in the wet years (www.bom. gov.au). Boodjamulla is mainly situated on sandstone, limestone, calcium carbonate or tufa formations sustaining Eucalyptus and *Melaleuca* woodlands, floodplains, grasslands and riparian vegetation (Fig. 1). The biological soil crusts of this area are dominated by the cyanobacteria *Symplocastrum purpurascens* (Gomont ex Gomont) Anagnostidis (Fig. 2a, b, d-f), *Scytonema* sp. (Fig. 2a, b), *Symploca* sp., and *Nostoc commune* Vaucher ex Bornet et Flahault as well as other *Nostoc* species. Other organisms occurring regularly in the Boodjamulla biocrust are the hairy liverwort *Riccia crinita* Taylor, the lichens *Peltula patellata* (Bagl.) Swinscow & Krog, *Heppia lutosa* (Ach.) Nyl. and *Placidium squamulosum* (Ach.) Breuss and other small non-fertile lichen species. For a more detailed description of the locality and the biocrust see Williams and Büdel (2012) and Williams et al. (2014). We selected a site next to the camp of the national park rangers station (Fig. 1a) with luxuriant biocrust growth (Fig. 1b), and to guarantee maximum control of the monitoring setup (Figs 1c-e) kindly provided by the national park rangers. The biocrust we used here for the analysis was formed by the two cyanobacteria *S. purpurascens* and *Scytonema* sp. with small amounts of *Nostoc* sp. but did not include bryophytes or lichens, only small amounts of *Nostoc* sp. could be found here and there.

2.2 Sampling and sample treatment

Samples for the determination of light-, temperature- and water content related CO_2 gas exchange (factorial analysis), as well as samples for the one year monitoring were collected in the direct vicinity of the instrumental setup site (Fig. 1a-c). Great care was taken for the homogeneity of all samples. For a proper collection we removed only those top soil parts stabilized by the biocrust and that was a layer between 5 – 8 mm thick using a spatula 8 cm wide. Soil particles from underneath the removed top soil layer not fixed to the crust by any filamentous structures were removed carefully using a soft brush and tweezers.

For the factorial analysis (light-, temperature- and water content related photosynthesis) samples were stored air dried in a 10 cm Petri-dish, sealed and brought to the laboratory, where they were stored frozen (-20°C) until used for the measurements. Prior to the measurements, samples were allowed to defrost at 23°C for 12 h in an air tight box a t low light intensities (<< 50 µmol photons m^{-2} s^{-1}) in order to avoid decondensation. Subsequently samples were dehydrated and kept at 23 °C and natural day-night cycles (~150 µmol photons m^{-2} s^{-1}) for 2 days. All measurements were done with three independent samples (3 treatments with 3 samples = 9 different samples).

As there was only one semi-automatic cuvette system available, we could not replicate the measurements. To partly overcome this problem, we used several samples over the year, making sure that the area related gas exchange was in the same range. For the one year monitoring we used in total 21 different samples (see also Fig. 3), each one collected immediately before being exposed in the cuvette system. Samples were placed in a basket of thermoplastic resin with borings in the bottom to avoid standing water during rain events. The basket had a fixed size and all samples had exactly the same exposed surface of 16.5 cm² (Fig. 1 d). All samples were tested for a comparative large NP and DR rate under the given environmental conditions. From the 21 samples used, 11 were selected for the long-term monitoring (A10, C5, C14, C11B, S1, 2B, BS1, BS2, BS3, BS4, BS7; see Fig. 3).

2.3 CO_2 gas exchange under controlled conditions

CO_2 gas exchange measurements were conducted under controlled laboratory conditions using minicuvette systems (CMS 400 and GFS 3000, Walz Company, Effeltrich, Germany). The response of net photosynthesis (NP) and dark respiration (DR) to water content (WC) was determined for light, temperature and WC. Samples were weighed between measurements and WC was later calculated as mm precipitation equivalent after determination of dry weight following 5 days in a desiccator over silica gel. To obtain the NP response to light, fully hydrated samples (n=3) were exposed to stepwise increasing photosynthetic active radiation (PAR) from 0 to 2500 µmol photons m^{-2} s^{-1} near optimal temperature (32°C) and ambient CO_2 concentration. The light cycle (about 30 min duration) was repeated until the samples were completely dry (after 3–4 h). Light saturation was defined as the PAR at 90% of maximum NP. The temperature related NP and DR were determined at increasing temperatures from 22 – 47°C at 1500 µmol photons m^{-2} s^{-1} and optimal WC (n=3).

The reaction of NP and DR to different biocrust water contents were determined at constant light (1500 µmol photons m^{-2} s^{-1}) and different temperature steps, from 22, 27, 32, 37, 42 to 47°C (n= 3). Samples completely soaked with water were installed in the cuvette and NP and DR were measured in short time intervals (roughly 10 minutes) until the samples were almost dry and did not show any NP nor DR reactions.

In all factorial analyses, the CO_2 exchange of the samples was related to chlorophyll *a* content. For chlorophyll determination, the samples were ground to small pieces and then extracted two times with di-methyl-sulfoxide (DMSO) at 60 °C for 90 minutes. The chlorophyll a + b content was determined and calculated according to (Ronen and Galun, 1984).

2.4 Monitoring of CO_2 gas exchange

Monitoring of the CO_2-gas exchange of the biological soil crust sample in the field was recorded using a semi-automatic cuvette system (ACS) as described in detail by Lange (2002). Full technical details of the ACS (Walz Company, Effeltrich, Germany) are given in Lange et al. (1997). We therefore focus on some major topics of the procedure here. The whole device is composed of two major parts, first the cuvette system itself that is exposed in the natural environment of the biocrust (Fig. 1c) and secondly the controlling and data acquisition unit together with two infrared gas analysers (IRGA) for CO_2 ambient and CO_2 samples (Binos, Rosemount, Hanau, Germay) and a pumping unit regulated by mass flow controllers (Fig. 1e). For safety reasons a data printer and a graphics plotter were added as well.

The soil crust samples were exposed on the lower part of the cuvette (Fig. 1d, arrow). When the upper lid was open (H in Fig. 1d), the sample was fully exposed to the natural environment. Measurements were taken every 30 minutes during which the cuvette was closed for 3 min. We recorded the CO_2 exchange of the sample and absolute ambient CO_2 partial pressure as well as mass flow, air temperature, the sample surface temperature, air humidity, and ambient photosynthetic radiation at the samples level. Net photosynthesis and DR were related to the area covered by the biocrust.

3. Results

The dominating cyanobacteria of the biocrust used for the long term monitoring was the felt- to tuft-like filamentous cyanobacterium *Symplocastrum purpurascens* forming a dark brownish stratum with erect tapering bunches of filaments (Fig. 2a-d) and the felt-like greyish *Scytonema* sp. inside and on top of the substratum (Fig. 2a-b). *S. purpurascens* is characterized by distinctly lamellate, reddish to purple-red sheath (colourless in shade). The filaments (trichome plus sheath; Fig. e, f). After the first rains, new trichomes form at the tips of the cyanobacterial layer.

3.1 CO_2 gas exchange under controlled conditions

When exposed to stepwise increasing PAR intensities, the biocrust did not reach full saturation of NP at optimal water content (31.66 ± 2.61 nmol CO_2 mg^{-1} chlorophyll *a* s^{-1} at a WC of 0.70 ± 0.08 mm and 32°C; n= 3) even at 2500 µmol photons m^{-2} s^{-1}. At a WC below the optimal WC, a decline of NP (21.28 ± 5.69 nmol CO_2 mg^{-1} chlorophyll *a* s^{-1} at a WC of 0.51 ± 0.08 mm was observed, as was also the case for WC well above optimal WC, 20,66 ± 6,24 nmol CO_2 mg^{-1} chlorophyll *a* s^{-1} at a WC of 0.97 ± 0.14 mm or 7,56 ± 3,73 nmol CO_2 mg^{-1} chlorophyll *a* s^{-1} at a WC of 1.32 ± 1.56 mm and 2.26 ± 0.22 nmol CO_2 mg^{-1} chlorophyll *a* s^{-1} at a WC of 1.88 ± 0.13 mm (Fig. 4a).

Increasing air temperature from 22 to 47°C resulted in an increase of NP from 19.8 ± 1.44 nmol CO_2 mg^{-1} chlorophyll *a* s^{-1} to 32.39 ± 4.47 nmol CO_2 mg^{-1} chlorophyll *a* s^{-1} (n = 3) without saturation. The increase of dark respiration was less expressed and ranged from -3.09 nmol CO_2 mg^{-1} chlorophyll *a* s^{-1} at 22°C to -6.33 ± 1.37 nmol CO_2 mg^{-1} chlorophyll *a* s^{-1} at 47°C air temperature (n = 3; Fig. 4b).

For testing the reaction of NP and DR to biocrust WC, completely wet samples (n = 3) were exposed in the cuvette system and measured at 6 different temperatures (22, 27, 32, 37, 42 and 47°C). Their NP and DR were recorded until samples were dry. Regarding CO_2 fixation, the optimal WC of the biocrust was 0.7 ± 0.08 mm WC. At all temperatures the biocrust exposed a clear optimum WC (range of 0.61 to 0.77 mm) where they reached their maximum NP and WC below and above this optimum led to a strong decline or even a complete stop of NP (Fig. 4c). At WC of about 0.2 mm the biocrust starts NP and DR and with increasing WC, NP had a steep incline to the maximum. A further increase of the WC created suprasaturation. NP then strongly decreased to less than a tenth of the maximal NP at optimal WC and could drop down to zero or even become negative at higher temperatures and remained at this level (Fig. 4c).

3.2 Monitoring of CO_2 gas exchange

Monitoring of diurnal CO_2 gas exchange of the Boodjamulla biocrust started on July 1st 2010 and lasted until June 30th 2011. Measurements were taken every 30 minutes day and night. There was no measurable gas exchange from July to end of September 2010 and from mid-April to June 2011. With the onset of the first seasonal rains in November, the biocrust showed mainly CO_2 loss during the days, despite the fact of PAR levels of 2000 - 2500 µmol photons m^{-2} s^{-1} (Fig. 5). CO_2 loss during the day was in the range of up to 1 µmol m^{-2} s^{-1}. Air temperature reached values of up to 46°C and relative air humidity increased up to 100% during the night, dropping down to levels of 20% during the day (Fig. S1). The first positive NP was observed on November 16th (Fig. S1). From December 2010 to March 2011 rain events below 1.5 mm resulted in negative NP whereas higher precipitation initiated positive NP of up to 8 µmol CO_2 m^{-2} s^{-1} (Fig. S2-S5). In April the rainy season ceased and small precipitation events resulted in a CO_2 loss during the day of up to 2 µmol m^{-2} s^{-1} (Fig. S6). The CO_2 content of the ambient air fluctuated between day and night from 370 to 470 ppm during the rainy season. Fluctuation was less expressed in the dry season. During dark cloudy days with or without rain, fluctuation was diminished (Figs. S1-S6). In

September and October 2010, the investigation plot got the first rains. However, although we could record metabolic activity, we were not able to calculate NP and DR due to malfunction of the ACS during these initial two months as well as the following days: November 1st – 2nd, 10th – 14th, 18th -20th, December 1st- 2nd, 12th, 30th – 31st and March 22nd – 23rd. These data were excluded from further analyses (see supplementary figures S1-S6). An estimation on the basis of climatic data from September and October 2010 together with gas exchange data from November 2010 resulted in an estimated CO_2 loss of 88 mmol m^{-2}.

The sensitive interaction of the biocrust and the environmental factors can be observed in the reaction of diurnal CO_2 gas exchange over the months. For example in the night from December 31st 2010 to January 1st 2011, the biocrust was inactive but did show some DR at the end of the night and positive NP was measured from the morning till the afternoon. As we did not record any rain, the biocrust must have been activated by dew fall or probably from some moisture in the soil as the soil was wet the day before. In the afternoon of January 1st, a heavy rainfall occurred resulting in a strong water suprasaturation of the biocrust. Net photosynthesis immediately became negative but recovered in the late afternoon, a pattern that could be observed also on January 2nd and 3rd. On January 3rd PAR was so intensive that the biocrust dried and metabolic activity ceased completely. The biocrust did not dry on the two days before and there was DR during the whole night (Fig. 6). When comparing all positive NP values of the metabolic active period to the referring PAR and temperature values, the light saturation of the biocrust NP was reached at 2200 µmol/m² · s (Fig. 7a), whereas the temperature optimum was found at 37°C (Fig. 7b). The comparison of NP with relative air humidity and PAR showed that almost all of NP was found at a relative air humidity above 42% (Fig. 8).

While November 2010 and April 2011 had a negative CO_2 and carbon balance, December 2010 to March 2011 were positive (Table 1). Net primary productivity of the Boodjamulla biocrust was 229.09 mmol CO_2 m^{-2} yr^{-1}, referring to a carbon fixation rate of 2.75 g m^{-2} yr^{-1} (Table 1; Fig. 5). Applying the September-October estimation, annual values were reduced to 143.08 mmol CO_2 m^{-2} yr^{-1} equivalent to 1.72 g C m^{-2} yr^{-1}. Of the 8760 hours of the one-year measuring period, the biocrust was metabolically active for 2186 hours, representing 25% of the whole period. Of that 48.6% were NP and 51.4% DR (Fig. 9). The biocrust suffered from a reduced CO_2 uptake during NP periods due to water suprasaturation over 29.2% of the photosynthetic active time (Fig. 10).

4. Discussion

We found a clearly seasonal activity pattern of the Boodjamulla biocrust, exposing an inactive winter period with no measurable CO_2 gas exchange from July to mid-September 2010 and mid-April to end of June 2011. Metabolic activity was found in the summer months only, starting with September 23rd 2010 with the first rain events and continued until April 18th 2011. Due to malfunction of the ACS, measurements from September and October and some days of November and December 2010 were not useable to calculate NP and DR. An estimation based on rainfall data from September and October,

together with the referring gas exchange values from November suggests a CO_2 loss of roughly 88 mmol m^{-2}. Net primary productivity was determined as 1.72 g C m^{-2} yr^{-1} (2.75 g C m^{-2} yr^{-1} without Sept.-Oct. correction). Our results state the Boodjamulla biocrust act as a carbon dioxide sink and this result is in line with the findings of several other studies. For example, of a cyanobacteria-dominated biocrust from the Mojave Desert, USA with a C gain of 11.5 g m^{-2} yr^{-1} (Brostoff et al., 2005), a cyanobacteria, algae, lichen and moss biocrust from the Negev Desert, Israel with a C gain of 0.7 to 5.1 g m^{-2} yr^{-1} (Wilske et al., 2008, 2009) or a cyanobacteria, lichen and moss biocrust of the Mu Us Desert in China with a C gain of 3.46 to 6.05 g m^{-2} yr^{-1} (Feng et al., 2014).

However, there are several studies that clearly demonstrate that biological soil crusts can also act as C sources to the atmosphere. When studying a cyanobacteria dominated biocrust of the arid grassland in southeast Utah, USA applying the Eddy covariance method, Bowling et al. (2010) could not decide if this biocrust is a sink or a source as there were some grasses involved in the plot. However, when these author applied a top soil chamber for gas exchange measurements, they found the same biocrust a typical C source (Bowling et al. 2011). A cyanobacteria, lichen dominated biocrust from the Gurbantungut Desert, China was reported as quite a large C source with a loss of -48.8 ± 5.4 to -50.9 ± 3.8 g C m^{-2} yr^{-1} (Su, Y. G. et al., 2012, 2013) and a very similar biocrust type of the arid grassland of the Colorado Plateau, USA exposed surprisingly similar values of -62 ± 8 g C m^{-2} yr^{-1} (Darrouzet-Nardi et al., 2015). How can this astonishing and at first glance contradictory fact be explained? When comparing methodology and how measurements were taken, sheds some light on this phenomenon. All investigations, including our own study, that found biocrusts acting as sinks used CO_2 gas exchange devices with a separate cuvette where the samples had to be removed from the biocrust (Brostoff et al., 2005; Feng et al., 2014) except the study of Wilske et al. (2008, 2009) that used a top soil chamber measuring the biocrust in situ. All other studies used top soil chambers where the biocrust is measured in situ (Bowling et al., 2011; Su et al., 2013; Darrouzet-Nardi et al., 2015). The main difference found was the thickness of the biocrust plus sub-crust (soil) layer used. While those studies revealing the biocrusts as C sources used collars penetrating 20 to 35 cm deep into the soil (Bowling et al., 2011; Su et al., 2013; Darrouzet-Nardi et al., 2015), the studies attributing biocrust to C sinks used either pieces of biocrusts from 1 to 5 cm thickness (this study, Brostoff et al., 2005; Feng et al., 2014), or a collar penetrating only 5.5 cm into the soil (Wilske et al., 2008, 2009). The metabolic activity of heterotrophic organisms from deeper soil levels apparently influence the CO_2 gas exchange measurements accordingly as was already indicated in the investigation of Bowling et al. (2011) on the biocrust underlying soil biotic community. Yet, soils are not a perpetual motion machine in terms of carbon balance, the can only respire as much carbon as is introduced into the system. If carbon does not come from the autotrophic part of the soil system, it must be introduced from outside, either via litter transport, blown dust, animals, or with run-on water from the surrounding environment.

Maximum net CO_2 uptake rates of the Boodjamulla biocrust (8.3 µmol CO_2 m^{-2} s^{-1}) clearly exceed those of a comparable cyanobacteria dominated crusts from the Negev Desert, Israel reaching maximal values of 1.12 µmol CO_2 m^{-2} s^{-1}

(Lange et al., 1992) and from the Colorado Plateau, USA with 1.97 µmol CO_2 m^{-2} s^{-1} (Darrouzet-Nardi et al., 2014). The higher NP rates of the Boodjamulla biocrust are probably related to the felt like structure on the soil surface (Fig. 2a-d), while the Negev Desert biocrust was a thin layer of cyanobacterial filaments slightly beneath the surface. Annual carbon fixation rates of cyanobacteria dominated biocrusts of arid regions are generally lower (this study; Brostoff et al., 2005; Feng et al., 2014; Wilske et al., 2009) when compared with those of other crust types, where lichens and bryophytes are involved (see summarizing table 15.2 in Sancho et al., 2016; Elbert et al., 2012; Porada et al., 2013) or the carbon gain of isolated organisms as for example the green algal lichen *Lecanora muralis* (Schreber) Rabenh. from a rock crust with 21.5 g C m^{-2} yr^{-1} (Lange 2002, 2003a, b).

The Boodjamulla biocrust exposed metabolic activity only 25% of the whole year, made up of 12.3% NP and 12.8% DR (Fig. 9). In 29.2% of the photosynthetic active time CO_2 fixation was considerably lowered water suprasaturation. For comparison, the lichen *L. muralis* from temperate climate was active for 35.5% of year, made up of 16.7% NP and 18.9% DR. Of the time of possible photosynthesis, the lichen was heavily depressed by water suprasaturation at 38.5% (Lange, 2003a). It is obvious that the strict seasonal rainfall pattern is a major reason for the considerably lower metabolic activity of the savannah-type biocrust from Boodjamulla compared to the rock crust lichen *L. muralis* in the temperate climate with rainfall events during the whole year. As characteristic for poikilohydric organisms, both the Boodjamulla biocrust as well as the rock crust lichen suffer considerably from water suprasaturation causing waterlogged gas diffusion channels and thus drastically limiting CO_2 gas exchange (see Green et al., 2011 and references therein). A striking feature certainly is the pronounced seasonality regarding net photosynthetic rates of the biocrust, starting with 3 month of negative CO_2 balances then increasing NP rates from November 2010 to February 2011 followed by a rapid decrease in late March to mid-April 2011 (Fig. 5). This points to the fact, that the developmental stage of a biocrust is an important factor for photosynthetic performance. This view is supported to some extent by the results of a study determining NP rates depending on successional stages rather than the developmental stages. In this study the authors classified biocrusts as early successional (*Microcoleus*) or later successional stages (*Nostoc/Scytonema* or *Placidium/Collema*) and differences in NP, which was on average 1.2-2.8-fold higher in later successional crusts compared to the early successional stages (Housman et al., 2006). Considering the Boodjamulla biocrust as perhaps an early successional stage, where an increase in carbon gain might be expected in the future when lichens and bryophytes estblish to form a later successional soil crust.

All metabolic activity is bound to the presence of water and it is therefore important to know the role of water content on photosynthetic and respiratory CO_2 exchange. The Boodjamulla biocrust achieved maximum NP values at 0.49-0.77 mm and had a lower compensation point for NP at 0.12 mm WC. Comparable values were found for the Negev biocrust studied by Lange et al. (1992) and the rock crust lichen *L. muralis* (Lange, 2002). In the green algal biocrust lichens from Utah, *Diploschistes diacapsis* (Ach.) Lumbsch, *Psora cerebriformis* W. Weber, and *Squamarina lentigera* (Weber) Poelt photosynthetic metabolism is activated by extremely small amounts of moisture. The lower compensation point for NP is

between 0.05 and 0.27 mm WC. Maximal NP occurs between 0.39 and 0.94 mm WC (Lange et al., 1997). The values for the cyanobacterial soil crust lichen *Collema tenax* (Swartz) Ach. however, were considerably higher with the lower NP compensation point at 0.2 mm WC and maximal NP between 0.8 to 1.2 mm WC, but performed NP under much higher temperatures than the above mentioned green algal lichens (Lange et al., 1998).

Almost all gas exchange activity of the Boodjamulla biocrust occurred at air relative humidity above 42% (Fig. 8). This however must be taken with care as it does not mean that the biocrust is active at this value and above. Like all cyanobacteria investigated so far, the cyanobacteria of the Boodjamulla biocrust are also not activated by air humidity alone (unpublished results). The value of 42% relative humidity is merely a good indicator for the right combination of WC (rainfall dependent), temperature and light. A comparable observation has been made by Raggio et al. (2017), who found air relative humidity (<< 50%) and air temperature as the best predictors of metabolic activity duration for four different biocrust types across Western Europe. In a number of cases we found activation of the biocrust without any measurable precipitation (Fig. 6, supplementary figure S3, January 4th-5th). This is likely explained by dew formation, a non-rainfall water source recently found playing in important role in biocrusts (Ouyang and Hu, 2017) and observed at Boodjamulla during wet season. There are a number of studies that found dew formation in biocrust systems, for example the study of Jacobs et al. (2000), where in a desert environment of Israel daily amounts of dew ranged between 0.1 mm/night and 0.3 mm/night. Dew formation determined for an inland dune biocrust community in Germany formation ranged from 0.042 kg/m² and 0.178 kg/m² within 2 days (Fischer et al.; 2012). Even fog was identified as a major source of non-rainfall water driving biocrust productivity in the Atacama Desert of Chile, where approximately 8% to 24% of the fog water flux available to the BSCs at the soil surface (Lehnert et al., submitted).

Applying an experimental air temperature increase of 2–3°C, Maestre et al. (2013) observed a drastic reduction in biocrust cover of ca. 44% in 4 years in a dryland ecosystem in Spain. Soil CO_2 efflux was increased and soil net CO_2 uptake was reduced with the additional warming. As the Boodjamulla biocrust is not very sensitive to temperature itself regarding NP and DR (Fig. 4b), a special effect of warming on carbon gain is only expected indirectly, when warming is related to rainfall amount and regime. We could speculate that less, but heavier rain events could certainly effect the Boodjamulla biocrust by increasing suprasaturation periods resulting in lower carbon gain.

5. Conclusion

The Boodjamulla biocrust showed a highly seasonal photosynthesis related metabolic activity divided into four major periods: 1) the metabolically inactive winter month; 2) the onset of the photosynthetic active period, starting with roughly three month having a negative balance, probably due to regrowth of the biocrust; 3) a four-month period of carbon gain; and 4) about one month with a negative balance until a complete cease of activity. During the four periods, NP varies and his must be taken into consideration for future analyses and modelling of carbon balances in comparable biocrust ecosystems.

Methodological approaches analysing the carbon cycling of biocrusts need to take into consideration, that including or excluding sub-biocrust partitions might influence the status of the biocrust as being either considered as a sink or a source. This clearly shows the urgent need for more long-term measurements in order to understand and construct better and more consistently models of different biological soil crusts of the world.

Acknowledgement

We acknowledge the Waayni people, traditional owners of Boodjamulla National Park and thank the staff of Boodjamulla and Adels Grove. Special thanks to Stephen Williams for all his support and Tres McKenzie for onsite assistance. We also thank AgForce Qld and Century Mine for their financial and in-kind support.

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Legend to the figures

Figure 1: Boodjamulla National Park, measuring site. a) Housing area for the NP-rangers and NP-administration with locality of biological soil crusts and the measuring site (white circle). b) Dark patches of a biological soil crust between grass tussocks (red scale 2.5 cm). c) Klapp cuvette system installed in two water filled basins to avoid small animals occupying the device. d) Measuring head of the clap cuvette system, the lid is open exposing the wire mesh basket with the sample (IR = infrared thermocouple, L = light sensor for PAR, T = tubing for gas exchange, VP = vibration plate ensuring a regular movement of the air when the cuvette is closed, H = light translucent head closing every 30 minutes for 2.5 minutes measurement). e) Hut with the data recording devices and control module.

Figure 2: a) **C**lose-up of the dry Boodjamulla biocrust at the measuring site, grey areas are dominated by the cyanobacterium *Scytonema* sp., dark-brownish areas dominated by *Symplocastrum purpurascens*. b) Same as in a, but after rehydration. c) Cross fraction of the *S. purpurascens* dominated biocrust and its stratification (EPS = extracelluar polysaccharide sheath; LT-SEM). d) In situ top view of the *S. purpurascens* biocrust. e, f) Filament with red sheath from the top of the biocrust and from beneath with a more or less colorless sheath (f).

Figure 3: Scheme of samples used over the whole period of one year. Y-axis = signature of samples, bars indicate period of exposure in the cuvette system.

Figure 4: Response of net photosynthesis and dark respiration to water content, different PAR and temperature of the *S. pupurascens* dominated biocrust; a) response of net photosynthesis to increasing PAR at different water content at 32°C; b) response of net photosynthesis and dark respiration to increasing air temperature at 1500 µmol photons/m² · s, mean values of n = 3, one sample out of three measured shown here; c) response of net photosynthesis and dark respiration to increasing biocrust water content at 1500 µmol photons/m² · s and an air temperature of 47°C, one sample out of three measured shown here.

Figure 5: Annual CO_2 balance on a daily basis of the Boodjamulla biocrust.

Figure 6: Detail of diurnal CO_2 gas-exchange from January 2011, showing rain events resulting in water suprasaturation of the biocrust. Blue bars indicate the approximate duration of rainfall. Green lines indicate gas-exchange during daylight and black lines during the night.

Figure 7: a) Net photosynthesis from all days related to light intensity (PAR). The biocrust shows a saturation at 2200 µmol photon/m² •s and a slight depression at 2400 and more µmol photons/m² • s. b) Net photosynthesis from all days related to air temperature. The optimum temperature is at 35 °C but the biocrust still performs very well at 42 °C.

Figure 8: Net photosynthesis of the Boodjamulla biocrust related to air humidity and light. Colour key: yellow = no activity, orange to red = CO_2 loss during the day (suprasaturation), light green to violet = CO_2 uptake.

Figure 9: Mean diel activity of the Boodjamulla biocrust; black = inactive, light grey = photosynthetically active, dark grey = dark respiration, hatched = metabolic activity but due to technical failure of instrumentation, not clear if NP or DR.

Figure 10: Monthly extent of water suprasaturated periods during the photosynthetic (NP) active time of the Boodjamulla biocrust. Black = periods of suprasaturation, light grey = periods of conducive water supply.

Supplementary figures

Figure S1-S6: Each month with metabolic activity is shown. One month is represented as a set of three graph pairs (except April where metabolic activity ceased by mid-month), each pair composed of an upper graph showing CO2 gas-exchange (green and black curves) and PAR (brown curve) and a lower graph showing ambient CO2 concentration (black curve), air temperature (red curve), and relative air humidity (blue curve).

Figure S1: Diel carbon dioxide gas exchange in November 2010

Figure S2: Diel carbon dioxide gas exchange in December 2010

Figure S3: Diel carbon dioxide gas exchange in January 2011

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Figure S4: Diel carbon dioxide gas exchange in February 2011

Figure S5: Diel carbon dioxide gas exchange in March 2011

Figure S6: Diel carbon dioxide gas exchange in April 2011

Table 1: Monthly net primary productivity of the Boodjamulla biological soil crust (values in brackets are an estimation only, not based on measurements; see text for explanantion).

	NPP (NP-DR)	
Month	**(mmol CO_2 m^{-2} $month^{-1}$)**	**(g C m^{-2} $month^{-1}$)**
July	0	0
August	0	0
September 2010	0 (-2.0)	0 (-0.02)
October 2010	0 (-86.0)	0 (-1.06)
November 2010	-210.26	-2.53
December 2010	110.20	1.32
January 2011	99.58	1.20
February 2011	80.99	0.97
March 2011	174.11	2.09
April 2011	-25.54	-0.31
May 2011	0	0
June 2011	0	0
Annual	**229.09 mmol CO_2 m^{-2} yr^{-1} (143,08 mmol CO_2 m^{-2} yr^{-1})**	**2.75 g C m^{-2} yr^{-1} (1.72 g C m^{-2} yr^{-1})**

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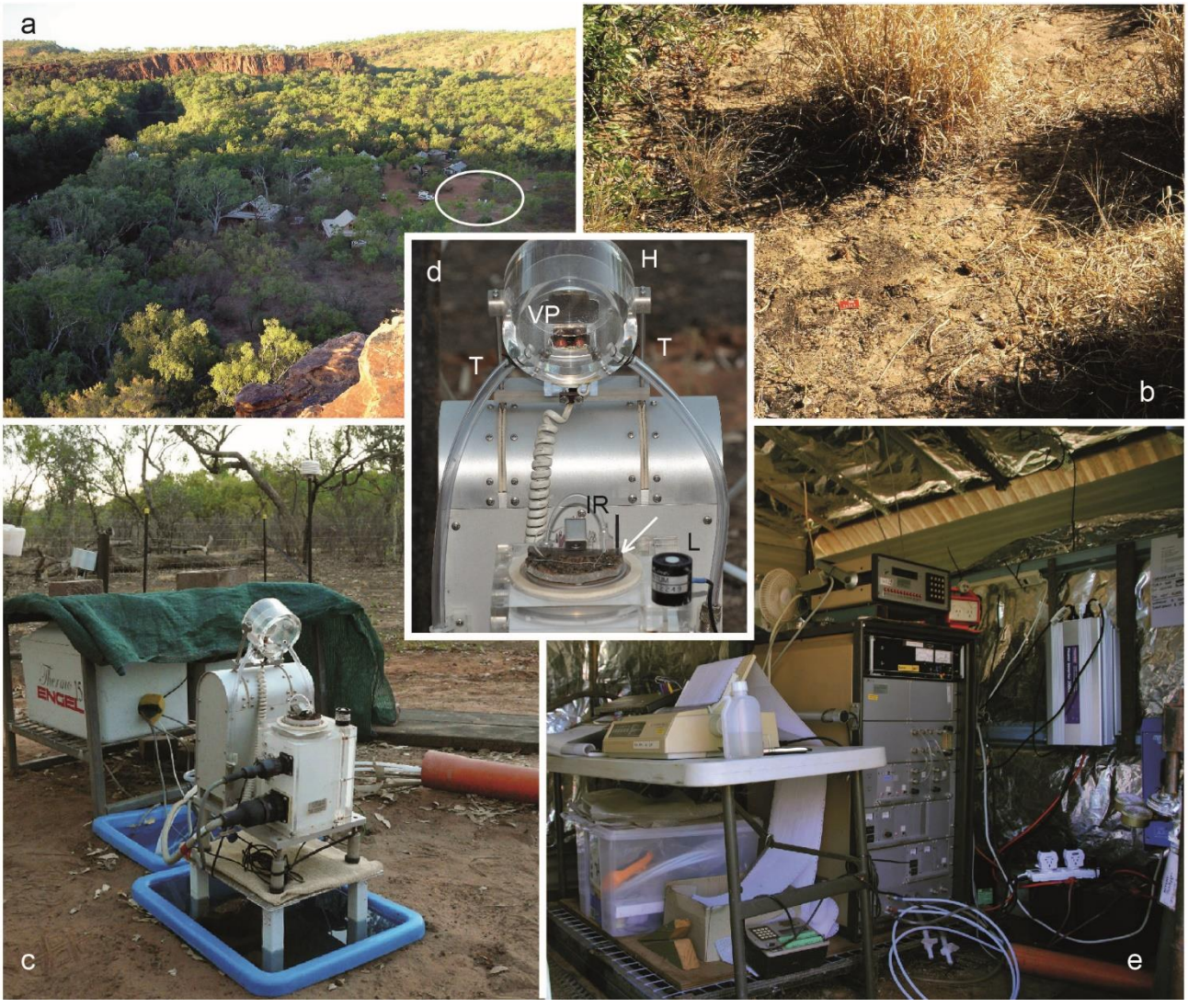

Figure 1

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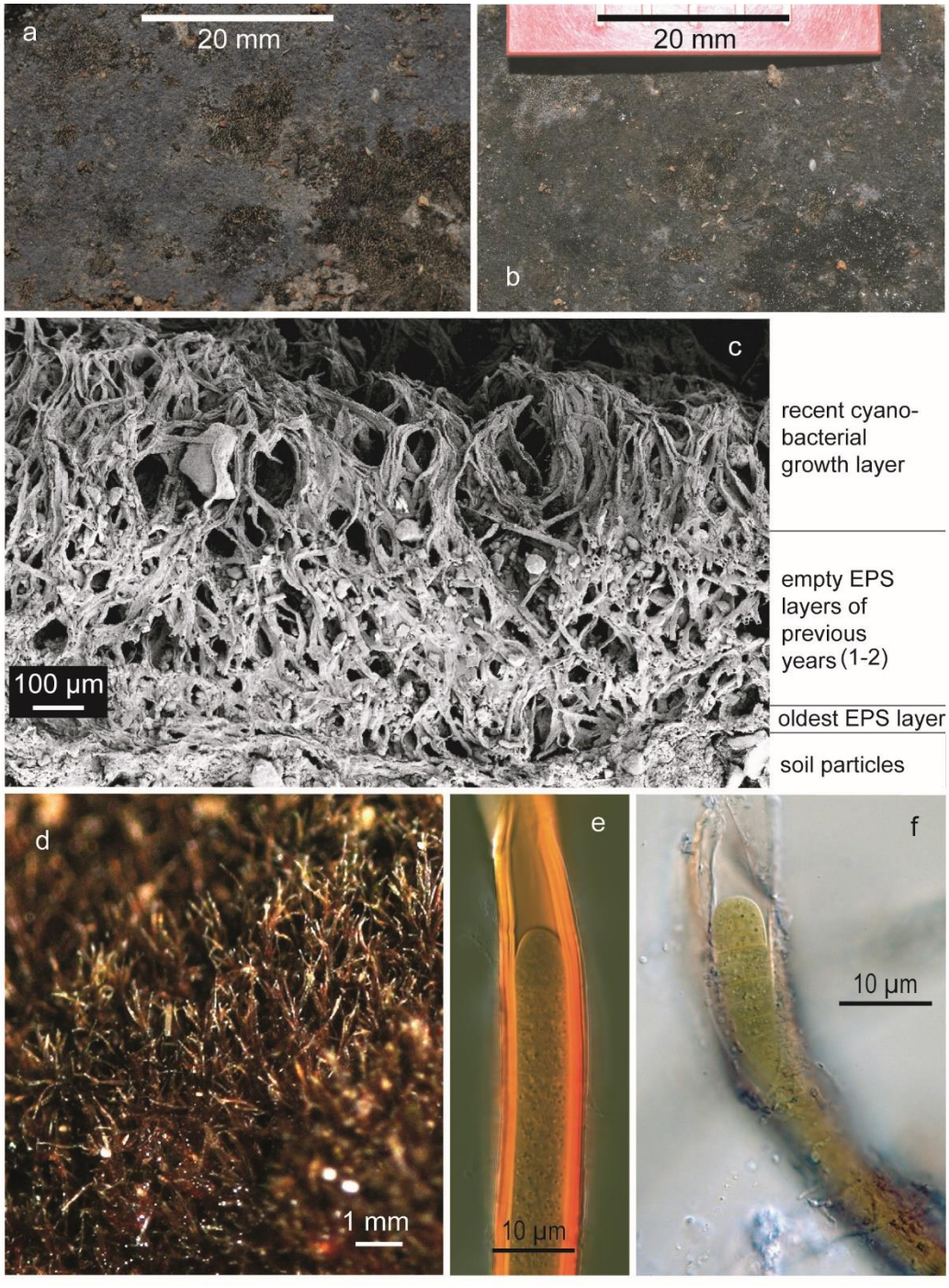

Figure 2

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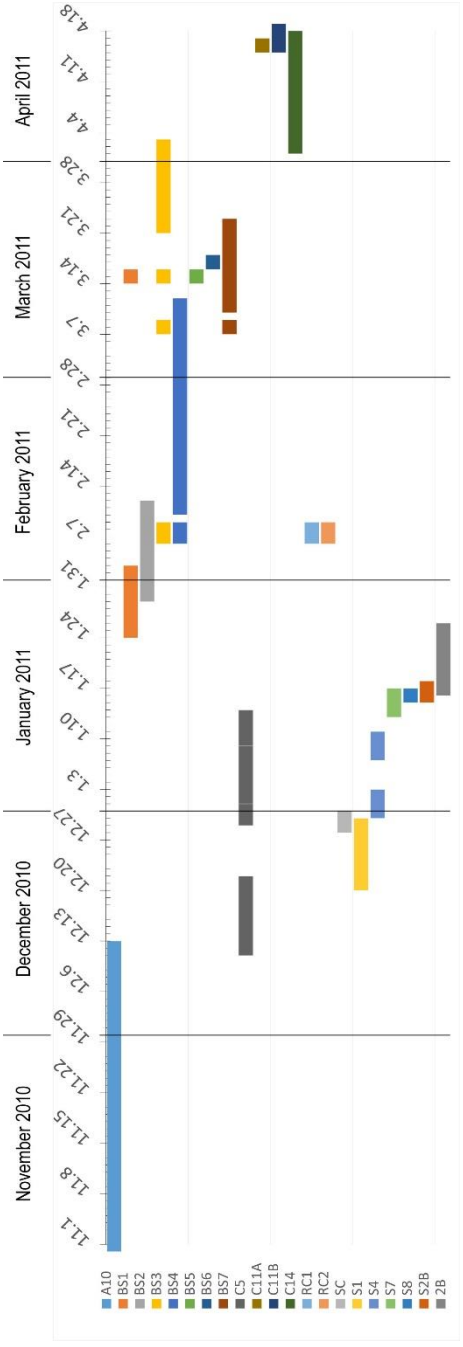

Figure 3

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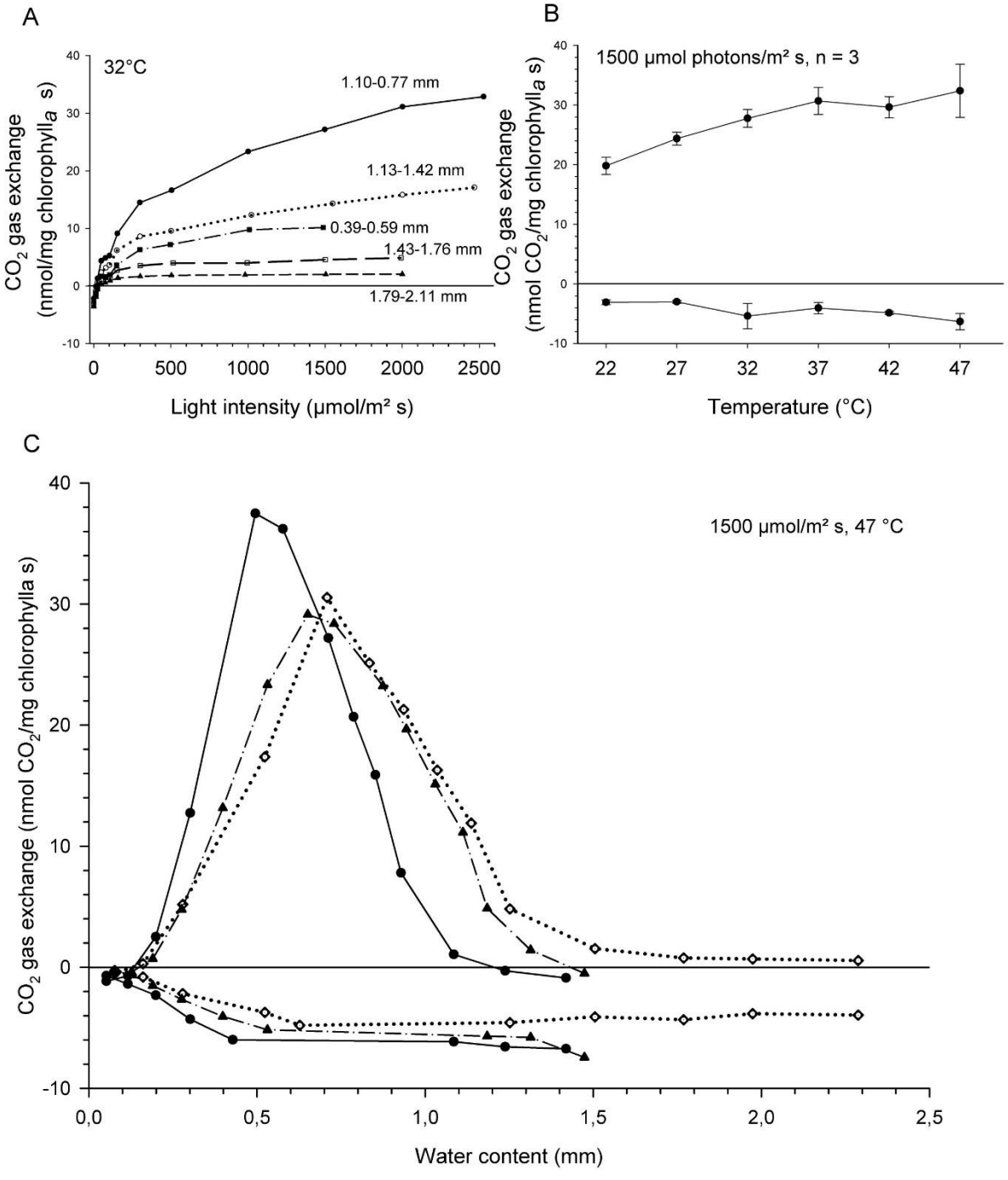

Figure 4

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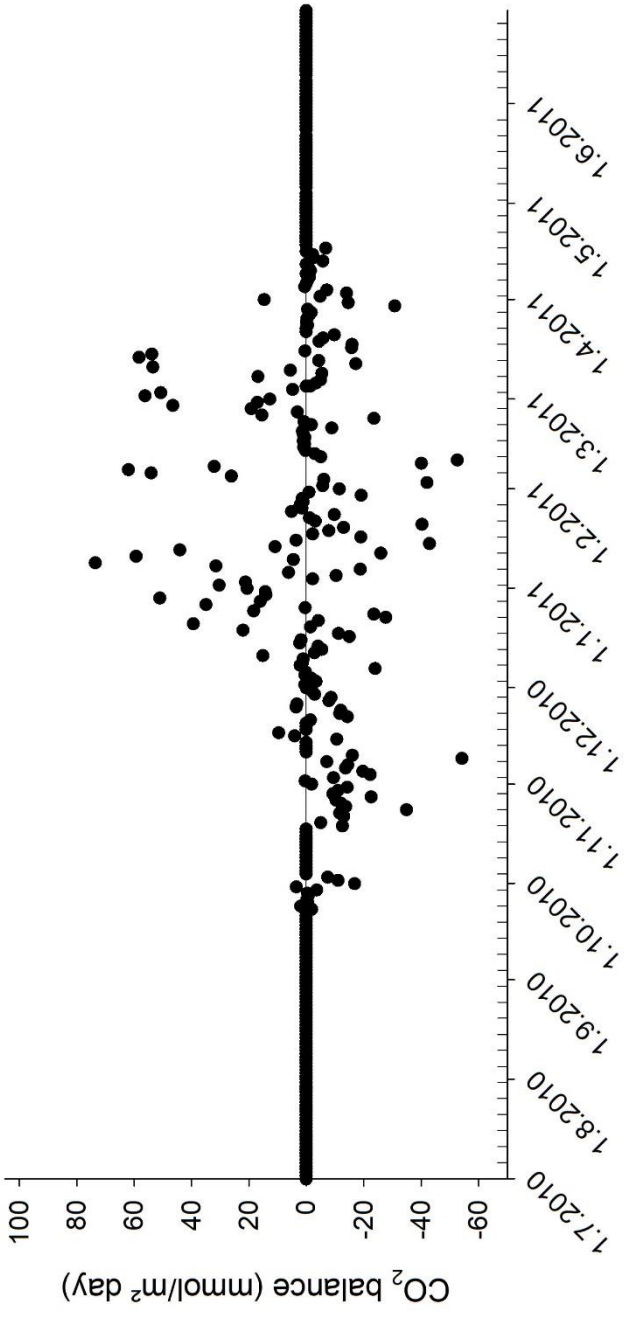

Figure 5

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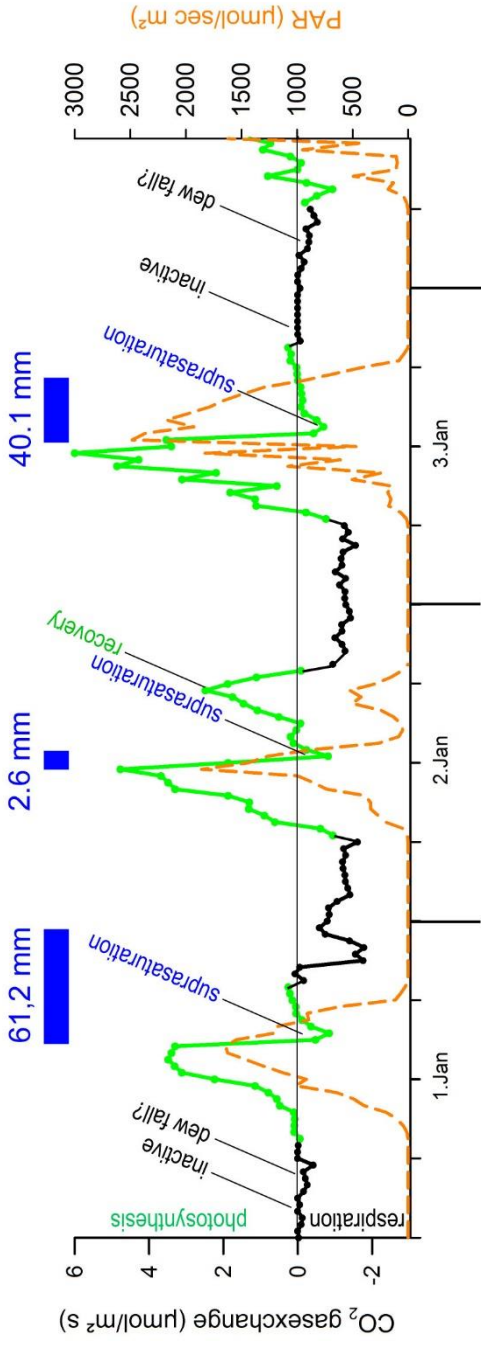

Figure 6

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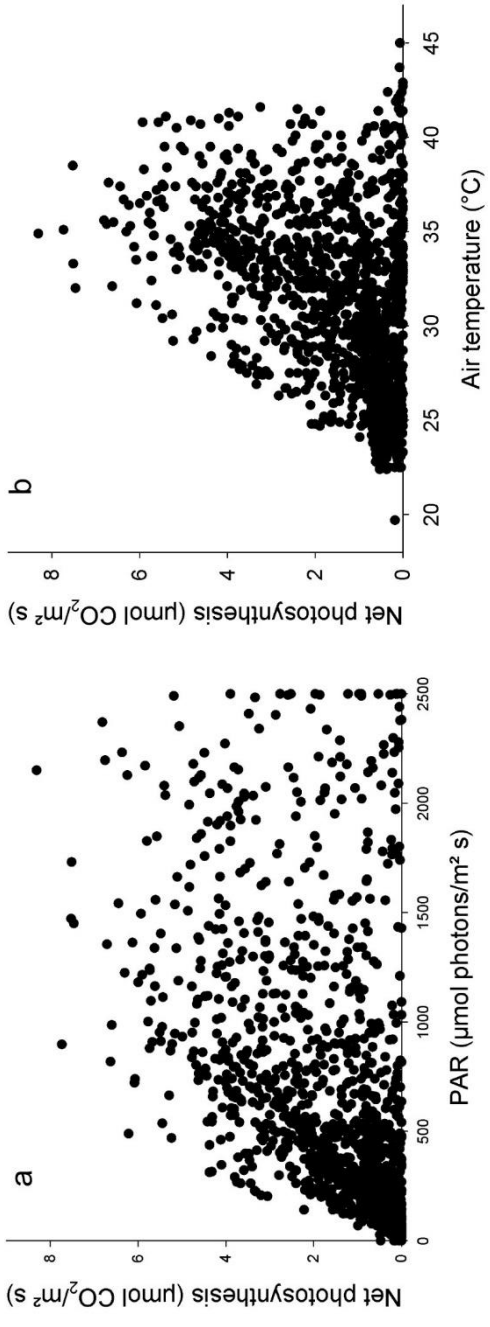

Figure 7

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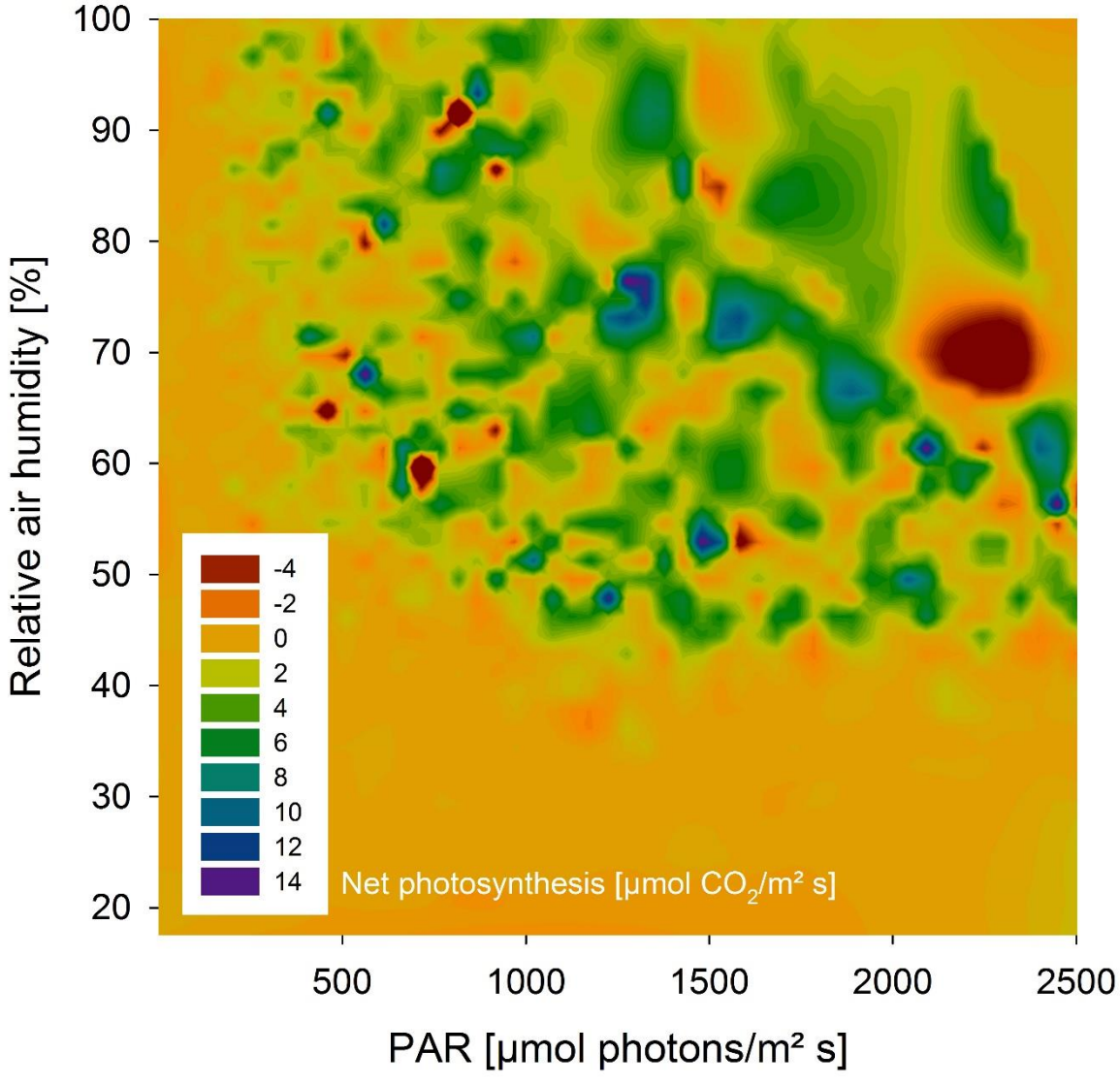

Figure 8

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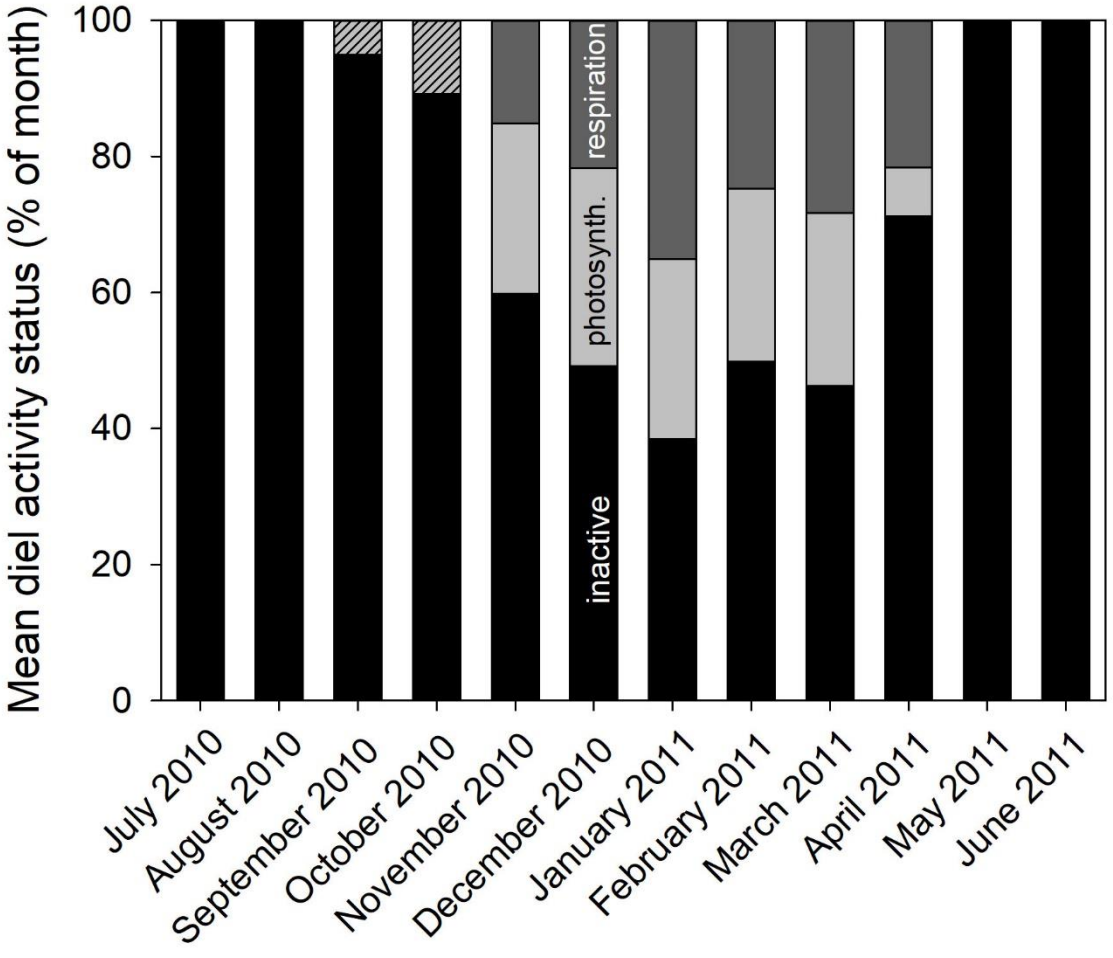

Figure 9

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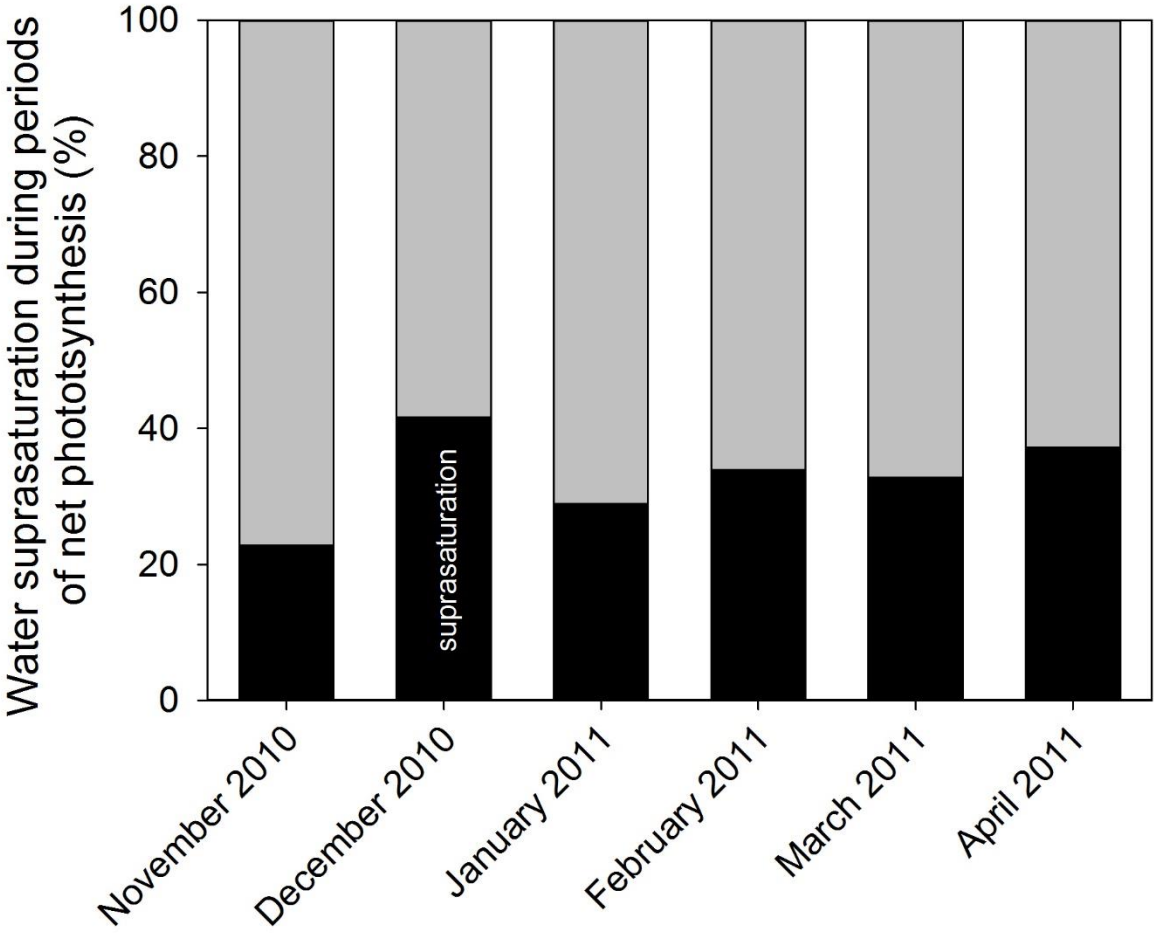

Figure 10