Microclimatic conditions and water content fluctuations experienced by epiphytic bryophytes in an Amazonian rain forest

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To be submitted in journal *Biogeosciences, ATTO special issue*

Abstract. In the Amazonian rain forest, major parts of trees and shrubs are covered by epiphytic cryptogams of great taxonomic variety, but their relevance in biosphere-atmosphere exchange, climate processes, and nutrient cycling are largely unknown. As cryptogams are poikilohydric organisms, they are physiologically active only under moist conditions. Thus, information on their water content, as well as temperature and light conditions experienced by them are essential to analyze their impact on local, regional, and even global biogeochemical processes. In this study, we present data on the microclimatic conditions, including water content, temperature, and light conditions experienced by epiphytic bryophytes along a vertical gradient and combine these with above-canopy climate data collected at the *Amazon Tall Tower Observatory* (*ATTO*) in the Amazonian rain forest between October 2014 and December 2016. While the monthly average of above-canopy light intensities revealed only minor fluctuation over the course of the year, the light intensities experienced by the bryophytes varied depending on the location within the canopy, probably caused by individual shading by vegetation. In the understory (1.5 m), monthly average light intensities were similar throughout the year and individual values were extremely low, remaining below 3 µmol m^{-2} s^{-1} photosynthetic photon flux density during more than 84 % of the time. Temperatures showed only minor variations throughout the year with higher values and larger height-dependent differences during the dry season. The indirectly assessed water contents of bryophytes varied depending on precipitation, air humidity, and bryophyte type. Whereas bryophytes at the canopy were affected by diel fluctuations of the relative humidity, those close to the forest floor mainly responded to rainfall patterns. In general, bryophytes growing close to the forest floor were limited by light availability, while those growing in the canopy had to withstand larger variations in microclimatic conditions, especially during the dry season. For further research in this field, these data may be combined with CO_2 gas exchange measurements, to investigate the role of bryophytes in various biosphere-atmosphere exchange processes, and could be a tool to understand the functioning of the epiphytic community in greater detail.

1 Introduction

Cryptogamic communities comprise photosynthesizing organisms, i.e. cyanobacteria, algae, lichens, and bryophytes, which grow together with heterotrophic fungi, other bacteria, and archaea. They can colonize different substrates, such as soil, rock, and plant surfaces in almost all habitats throughout the world (Büdel, 2002; Elbert et al., 2012; Freiberg, 1999). In the tropics, epiphytic bryophyte communities widely cover the stems and branches of trees (Campos et al., 2015). Within that habitat, they may play a prominent role in environmental nutrient cycling (Coxson et al., 1992) and also influence the microclimate within the forest (Porada et al., 2019), thus contributing to the overall fitness of the host plants and the surrounding vegetation (Zartman, 2003). However, they are also affected by deforestation and increasing forest fragmentation (Zartman, 2003; Zotz et al., 1997).

Physiologically, cryptogamic organisms are characterized by their poikilohydric nature, as they do not actively regulate their water status but passively follow the water conditions of their surrounding environment (Walter and Stadelmann, 1968). In a dry state, many of them can outlast extreme weather conditions, being reactivated by water (Oliver et al., 2005; Proctor, 2000; Proctor et al., 2007; Seel et al., 1992), and for several species even fog and dew can serve as a source of water (Lancaster et al., 1984; Lange et al., 2006; Lange and Kilian, 1985; Reiter et al., 2008). In contrast, high water contents (WC) may cause suprasaturation, when gas diffusion is restrained, causing reduced CO_2 gas exchange rates (Cowan et al., 1992; Lange and Tenhunen, 1981; Snelgar et al., 1981) and even ethanolic fermentation, as shown for lichens (Wilske et al., 2001). Accordingly, their physiological activity is primarily regulated by the presence of water and only secondarily by light and temperature (Lange et al., 1996, 1998, 2000; Rodriguez-Iturbe et al., 1999).

In the Amazonian rain forest, cryptogamic communities mainly occur epiphytically on the stems, branches, and even leaves of trees, and in open forest fractions they may also occur on the soil (Richards, 1954). By 2013, 800 species of mosses and liverworts, 250 lichen species, and 1,800 fungal species have been reported for the Amazon region (Campos et al., 2015; Gradstein et al., 2001; Komposch and Hafellner, 2000; Normann et al., 2010; Piepenbring, 2007). Tropical rain forests are characterized by humid conditions, high temperatures with minor annual fluctuations, and an immense species diversity of flora and fauna. Currently, between 16,000 and 25,000 tree species have been estimated for the Amazonian rain forest (Hubbell et al., 2008; ter Steege et al., 2013). The Amazonian rain forest has been described to play important roles in the water cycle, as well as in carbon, nitrogen, and phosphorus fluxes on regional and global scales (Andreae et al., 2015). However, it is also hard to predict to which extent the ongoing and envisioned environmental changes will still ensure its ecological services as the "green lung" and carbon sink of planet Earth (Soepadmo, 1993).

Studies in temperate zones address the importance of cryptogamic communities for the ecosystem (Gimeno et al., 2017; Rastogi et al., 2018), but for the tropical area, only few reports can be found in the literature. There is a lack of information regarding the microclimatic conditions of the habitats colonized by cryptogamic communities in the tropics. Thus, with the long-term continuous measurements presented here, we aim to provide data on seasonality patterns and the vertical profile of the microclimate within the canopy. In the current study, we present the microclimatic conditions, comprising the temperature, light, and WC of epiphytic bryophyte communities along a vertical gradient and an estimation of their activity patterns in response to seasonal variations in climatic conditions.

2 Material and Methods

2.1 Study site

The study site is located within a *terra firme* (plateau) forest area in the Amazonian rain forest, approx. 150 km northeast of Manaus, Brazil. The average annual rainfall is 2,540 mm a^{-1} (de Ribeiro, 1984), reaching its monthly maximum of ~ 335 mm in the wet (February to May) and its minimum of ~ 47 mm in the dry season (August to November) (Andreae et al., 2015). These main seasons are linked by transitional periods covering June and July after the wet and December and January after the dry season (Andreae et al., 2015; Martin et al., 2010; Pöhlker et al., 2016). The *terra firme* forest has an average growth height of ~ 21 meters, a tree density of ~ 598 trees ha^{-1}, and harbors around 4,590 tree species on an area of ~ 3,784,000 km^2, thus comprising a very high species richness compared to other forest types (McWilliam et al., 1993; ter Steege et al., 2013). Measurements were conducted at the research site *ATTO* (*Amazon Tall Tower Observatory*; S 02° 08.602', W 59° 00.033', 130 m a. s. l.), which has been fully described by Andreae and co-authors (2015). It comprises one walk-up tower and one mast of 80 m each, being operational since 2012, and a 325 m tower, which has been erected in 2015. The ATTO research platform has been established to investigate the functioning of tropical forests within the Earth system. It is operated to conduct basic research on greenhouse gas as well as reactive gas exchange between forests and the atmosphere and contributes to our understanding of climate interactions driven by carbon exchange, atmospheric chemistry, aerosol production, and cloud condensation.

2.2 Microclimatic conditions within epiphytic habitat

The parameters temperature and light within/on top of the bryophytes and their WC were measured with a microclimate station installed in September 2014 (Fig. S1). The sensors were placed along a vertical gradient at ~ 1.5, 8, 18, and 23 m above the ground, corresponding to the zones 1 to 4 (i.e., at the base, the lower trunk, the upper trunk, and at the base of the crown) used by Mota de Oliveira and ter Steege (2015), to investigate the variation within the story structure of the forest. At each height level, six WC, two temperature, and two light sensors (except for 1.5 m with only one light sensor) were installed in/on top of different bryophyte communities located on an approximately 26 m high tree (Fig. S2, Table S1). It needs to be mentioned, that not only one single species was measured by one sensor, but usually several bryophyte species and also other cryptogams, such as lichenized and non-lichenized fungi and algae, as well as heterotrophic fungi, bacteria and archaea, which grow together forming a cryptogamic community. Thus, the organisms mentioned throughout this paper were the dominating but not solitarily living species. The restriction of the measurements to one individual tree needs to be considered, as a complete independence of the replicate sensors could not be assured. However, due to the large effort of such an installation within the rain forest, it was not possible to equip more trees with additional instruments. Thus, the data obtained from the measurements on this individual tree should be considered as exemplary. The WC sensors were placed in four different bryophyte communities being heterogeneously distributed along the four height levels. At 1.5 m height, the WC sensors were installed in communities dominated by *Sematophyllum subsimplex* (5 sensors) and *Leucobryum martianum* (1 sensor), at 8 m in *Octoblepharum cocuiense* (3 sensors) and *Symbiezidium barbiflorum* (3 sensors), and at 18 and 23 m in *Symbiezidium barbiflorum* (6 sensors at each height level; Fig. S2, Fig. S3). The temperature sensors were installed in the same communities at each height, and the light sensors were installed adjacent to them on ~ 5 cm long sticks (Fig. S1). As the morphology of the different species affects their overall WC, different maximum WC and patterns of the drying process were observed (Tab. S1, S2). The sensors were installed with the following orientations: at 1.5 and 8 m vertically along the trunk, at 18 m at the upper side of a slightly sloped branch, and at 23 m at the upper side of a horizontal branch. Thus, also the orientation at the stem may influence the WC of the bryophyte communities, not only the species and the height above ground. Furthermore, sample properties as their thickness and density might play a relevant role for their WC, as samples at 1.5 m height tended to be more loose and thinner as compared to the ones at the upper height levels (Fig. S4). Since the installation, automatic measurements at 5-minute intervals were taken with a data logger (CR1000; Campbell Scientific, Logan, Utah, USA) equipped with a relay multiplexer (AM16/32; Campbell Scientific, Bremen, Germany) and two interfaces.

The WC sensors, initially developed for biological soil crust research (Tucker et al., 2017; Weber et al., 2016), were optimized for measurements in epiphytic bryophyte communities by a straight-lined construction and with outer pins of 25 mm length, serving as an effective holdfast. However, during stormy episodes and/or physical friction, some WC and temperature sensors fell out of the moss samples and required a reinstallation. Accordingly, the WC sensor no. 6 (1.5 m) was repositioned in January 2015, WC sensor no. 1 (1.5 m) in November 2015, WC sensor no. 1, no. 6 to no. 24 and all temperature sensors in November 2016. The periods when the sensors were not installed in the bryophyte samples were excluded from the data set.

The WC values were oscillating, causing an inaccuracy corresponding to approximately 15 % dry weight (DW). Besides the specific position in the substrate, the WC also depends on the texture of the sample material, its ion concentration, and the temperature. Because of all these factors influencing the sensor readings, the provided values of the WC should be considered as the best possible estimates and not as exact values. For the temperature measurements, thermocouples (Conatex, St. Wendel, Germany) with a tip length of 80 mm and a measurement accuracy of ± 0.5 °C were used. For the light sensors, GaAsP-photodiodes (G1118, Hamamatsu Photonics Deutschland GmbH, Herrsching, Germany) were placed in a housing covered by a convex translucent polytetrafluoroethylene (PTFE) cap and calibrated against a PAR (photosynthetically active radiation) quantum sensor (SKP215; Skye Instruments, Llandrindod Wells, Powys, UK).

The average daily PAR values were calculated from the data collected during daytime, i.e., 6:00 to 18:00, while PAR_{max} represents the daily maximum value. The values obtained from the light sensors fluctuated by approximately ± 10 µmol m^{-2} s^{-1} photosynthetic photon flux density (PPFD), thus an averaging of 30-minute intervals allowed a smoothening of the data (Fig. S5). The smoothened data were used for detailed illustrations of seasonal variability (Fig. 2 and S6), whereas the 5-minute data were used for calculations in order to also consider short light fleck events. During measurements, the light sensors were regularly checked for algal growth and cleaned accordingly.

2.3 Calculation of the water content (WC)

The WC sensors measure the electrical conductivity in the field (EC_t), which is influenced by temperature; consequently, a temperature correction was performed according to Eq. (1), analogous to Weber et al. (2016):

$$EC_{25} = f_T * EC_t, \qquad (1)$$

with EC_{25} as EC at 25 °C, T as bryophyte temperature [°C] and the temperature conversion factor f_T:

$$f_T = 0.447 + 1.4034\, e^{-T/26.815}. \qquad (2)$$

The WC sensor has a fixed distance between the sensor pins, which ensures that in all sensors the resistance is equal. This guarantees that the electric voltage, being the inverse resistance, is proportional to the electrical conductivity. The values of the sensors were recorded as electrical voltage in mV and by calibration transformed into the WC of the samples, which is given as dry weight percentage (% DW).

A calibration was conducted for all the communities dominated by different bryophyte species. For this, samples of them were collected in the forest area surrounding the ATTO site. They were removed from the stem with a pocket knife and stored in paper bags in an air conditioned lab container until calibration (few hours after collection). Prior to the calibration, the samples were cleaned from adhering material using forceps. The weight of the bryophytes was determined when they were moistened until saturation (temperature 30° C, RH 100 %) and again after drying in a dryer overnight (temperature 40° C, RH 30 %) to simulate the natural range of the WC under controlled temperature and RH conditions. The dry weight (DW) was determined after drying at 60° C until weight consistency was reached (Caesar et al., 2018). The WC of the sample was calculated according to the formula in Weber et al. (2016):

$$WC\ [\%\ DW] = \frac{(FW - DW)}{DW} * 100\ \%, \qquad (3)$$

with FW as sample fresh weight [g] and DW as sample dry weight [g].

In a previous approach, calibration curves were established under controlled conditions, logging the electrical conductivity values and the corresponding weight/water content of samples of the different bryophyte species during drying, analogous to (Weber et al., 2016). However, the variability of electrical conductivity values between samples and even at different spots within one sample turned out to be too large and thus this was not a feasible approach to calibrate the sensors. On the other hand, the electrical conductivity values decreased in a linear way with decreasing sample weight, demonstrating that a linear relationship between both factors could be assumed (except for water contents close to saturation).

In the current approach, the calibration of the water content was performed, based on the maximum and minimum values of electrical conductivity reached in the field and the amplitude of the WCs reached during the laboratory measurements. We assumed, that the maximum electrical conductivity achieved in the field corresponds to the maximum WC achieved in the laboratory, due to water saturation of the samples during the laboratory measurement. The minimum electrical conductivity corresponds to water contents after overnight drying, as we are confident that this happened at least a few times during the dry season of the year.

As we got the impression that electrical conductivity values may contain some outliers in the upper data range, we reduced the electrical conductivity data by the uppermost and lowermost 0.1% of the data points (Tab. S3, Fig. S7). Accordingly, the water content (WC) was calculated as follows:

$$WC\ [\%\ DW] = \frac{(EC_i - EC_{perc\ 0.1})}{(EC_{perc\ 99.9} - EC_{\mathrm{perc}\ 0.1})} * (WC_{max} - WC_{min}), \quad (4)$$

with EC_i as electrical conductivity, $EC_{\mathrm{perc}\ 0.1}$ as the minimum electrical conductivity after subtraction of the lower 0.1% of the values, and $EC_{\mathrm{perc}\ 99.9}$ as the maximum electrical conductivity after subtraction of the upper 0.1% of the values measured in the field. WC_{max} corresponds to the maximum WC and WC_{min} to the minimum WC (after overnight drying at 40°C and 30% air humidity) measured in the laboratory.

The measured electrical conductivity values showed short-time oscillations, which could be removed with a 30-minute smoothing algorithm (Fig. S5). Thus, for all calculations the 30-minute averages were considered, except for the estimates of physiological activity. The smoothened data were used for figures and calculations as stated in section 2.2. The electrical conductivity data of replicate samples at the same height and of the same division (moss versus liverwort) were combined to obtain average values for each height.

2.4 Meteorology

For the purpose of long-term monitoring, a set of meteorological parameters is being measured within the ATTO project since 2012. In our study we used rainfall data measured at 81 m [mm min^{-1}] (Rain gauge TB4, Hydrological Services Pty. Ltd., Australia), relative humidity (RH) measured at 26 m [%], air temperature measured at 26 m [°C] (Termohygrometer CS215, Rotronic Measurement Solutions,UK), and photosynthetically active radiation (PAR) measured at 75 m height above the ground [µmol $\mathrm{m}^{-2}\,\mathrm{s}^{-1}$ PPFD] (Quantum sensor PAR LITE, Kipp & Zonen, Netherlands). All data were recorded at 1-minute intervals with data loggers (CR3000 and CR1000, Campbell Scientific, Logan, Utah, USA) on the walk-up tower (Andreae et al., 2015).

For calculation of the average light intensities per month, season or year ($\mathrm{PAR}_{\mathrm{avg}}$ month, $\mathrm{PAR}_{\mathrm{avg}}$ season, $\mathrm{PAR}_{\mathrm{avg}}$ year) only values during daytime (6:00 – 18:00 local time) were considered. Rainfall data are presented as accumulated values in millimeters per month, season, or year, which were calculated by an integration of 5-minute intervals. As there were gaps in the data record of the rain detection, additional information from the WC sensors were used to calculate the number of days with rain events. The sensors at 1.5 m height were found to react reliably to rain events. Thus, the gaps in the rain detection were corrected with the information received from these sensors. Furthermore, the amount of rain within each month was corrected by assuming that during the missing days there were the same amounts as during the rest of the month. Overall, a malfunction of the rain detection was observed on only 6 % of the days (Table S4).

The information on fog events was provided by visibility measurements using an optical fog sensor installed at 50 m height (OFS, Eigenbrodt GmbH, Königsmoor, Germany). Fog was defined to occur at visibility values below 2,000 m.

Time readings are always presented as UTC (universal coordinated time) values, except for diurnal cycles, where local time (LT, i.e., UTC-4) is shown, as labeled in the figures.

2.5 Potential physiological activity of bryophytes

The physiological activity of bryophytes – and of cryptogams in general – is primarily controlled by water and light, whereas temperature plays a secondary role, at least in the environment of the central Amazon (Lösch et al., 1994; Wagner et al., 2013). While the availability of water determines the overall time of physiological activity, the light intensity regulates whether net photosynthesis (NP) or dark respiration (DR) dominates the overall metabolic balance. Furthermore, high nighttime temperatures cause increased carbon losses due to high respiration rates, as previously shown for lichens (Lange et al., 1998, 2000). For tropical bryophytes along an altitudinal gradient in Panama, however, it has been shown that respiration loss during the night might not play the determining role for an overall positive net carbon balance, as species acclimatized to elevated temperatures, but that the restricted time for photosynthesis was a decisive factor (Wagner et al., 2013).

To assess the potential physiological activity of bryophyte communities, the water and light conditions as major drivers of the metabolism were investigated in somewhat greater detail. The lower water compensation point (WCP) presents the minimum WC that allows positive net photosynthesis. For the tropical liverwort *Symbiezidium* spp., occurring in the lowlands near sea level in Panama, WCP values in the range between ~ 30 and ~ 80 % have been determined (Wagner et al., 2013) (Table S5).

The lower light compensation point (LCP_l) represents the minimum light intensity that allows a positive primary production; it ranges between ~ 3 and ~ 12 µmol m^{-2} s^{-1} for bryophytes (based on measurements of *Ectropothecicum* cf. *perrotii, Frullania* spec, *Neckera* spec., *Plagiochila divergens, Plagiochila squamulosa, Porothamnium stipiatum, Porotrichum molliculum, Racopilum tomentosum, Radula boryana, Rhizogonium spiniforme*) occurring in African tropical lowland rain forests (Lösch et al., 1994). The epiphytic bryophytes grew in an upper lowland rain forest in the Kahuzi-Biega National Park (Zaire) at about 800 m a. s. l.. Microclimatic conditions inside the forest were similar to the conditions at the ATTO site, as RH ranged around 60-70 % during sunny days and temperatures remained above 20 °C during night and day. At light intensities below the LCP_l and WCs below the WCP, respiration rates are higher than NP rates, causing overall net respiration to occur.

With regard to temperature, a range for optimum NP (T_{opt}) and an upper compensation point, where NP equals DR (TCP) can be defined. For tropical bryophytes (i. e., the species *Octoblepharum pulvinatum, Orthostichopsis tetragona*, *Plagiochila* sp. 1, *Stictolejeunea squamata*, *Symbiezidium* spp., *Zelometeorium patulum*), T_{opt} ranges between 24 and 27 °C and the TCP ranges between 30 and 36 °C, as described by Wagner and coauthors (Wagner et al., 2013). For long-term survival and growth, the bryophytes need to be predominantly exposed to temperatures below the upper compensation point, at least under humid conditions. The measurements performed by Wagner et al. (2013) were conducted at a study site (BT) in a lowland rainforest in Western Panama on the Bocas del Toro archipelago, located approximately at sea level. The mean temperature was 25 °C (26 °C during day, 24 °C during night), thus slightly warmer than the temperatures measured at ATTO. With 3,300 mm a^{-1} of rain, BT is in a similar range as the ATTO site (2,540 mm a^{-1}). Unfortunately, literature data on the compensation points are rare, facilitating only a first approximate assessment of the physiological processes (Lösch et al., 1994; Wagner et al., 2013). A WC above the compensation point allows NP if both light intensity and temperature are above the lower compensation point. If WCs are above the compensation point but light intensities are too low, or if temperatures are above the upper compensation point, net DR occurs. There is also a narrow span of low WCs, when samples are activated already but despite sufficient light intensities only net respiration can be measured. As this span of WCs is narrow and respiration rates are low, it has been neglected in the current calculations. The compensation points for the different parameters are also to some extent interrelated, e.g., the water compensation point of lichens has been shown to slightly increase with increasing temperature (Lange, 1980), but this can be neglected in such a first qualitative approach. Finally, also inter- and intraspecific variation of compensation points could not be considered in the current study.

2.6 Data analysis

All data processing steps and analyses were performed with the software IGOR Pro (Igor Pro 6.37, WaveMetrics. Inc, Lake Oswego, Oregon, USA). For the average values obtained at the different height levels, the data of the individual sensors were pooled.

3 Results

3.1 Microclimatic conditions

3.1.1 Annual fluctuation of monthly mean values

Over the course of the two years of measurements, the monthly mean values of the WC, temperature, and light conditions experienced by the epiphytic bryophyte communities, as well as the above-canopy meteorological conditions, varied between seasons and years. Comparing the two consecutive years, the effect of an El Niño event was clearly detectable, as rainfall amounts were 35 % lower (525 mm versus 805 mm) and relative air humidity 11 % lower (81 % versus 92 %) between October 2015 and February 2016 as compared to the same time-span in the previous year (Fig. 1, Table S4).

The monthly mean values of above-canopy PAR (PAR_{avg}) were rather stable throughout the years and did not differ between the years 2015 and 2016, ranging between 635 and 1150 µmol m^{-2} s^{-1} during the daytime (Fig. 1, Table 1a). The PAR_{avg} values in the understory at 1.5 m also showed only minor seasonal variation, whereas those at higher levels revealed larger variations (Fig. 2, Fig. S6). However, the light conditions observed at one individual tree are strongly influenced by its canopy structure and foliation and thus could not be considered as data representative for the canopy in general.

Over the course of the years, the monthly mean temperatures at all heights as well as above-canopy temperatures showed a parallel behavior (Fig. 1). The temperatures decreased in a stepwise manner from the canopy to the understory, and temperatures within bryophytes at 23 m height were frequently higher than the temperatures measured above the canopy (Fig. 1, Table 1a, Fig. S8). Overall, temperatures at all height levels were lower and more similar during the wet than the dry seasons.

Over the course of the years, the monthly WCs of epiphytic bryophytes showed similar patterns corresponding to the increasing and decreasing values of rain and RH. During the dry season 2015, it rained on 25 % of the days, while in the previous and subsequent years rain occurred at a higher frequency (58 % and 31 % of the days, respectively; Fig. 1, Table S4). Monthly rain amounts varied from 9 mm during the dry to 341 mm during the wet season. In 2016, the rain increased from January to March and decreased from March to August, while in 2015 the monthly rain amounts were more variable but still lower throughout the year. The lowest monthly average of the RH was observed during the dry season 2015 with 74 ± 15 %. The WC values of epiphytic bryophyte communities were the highest at 23 m, followed by those at 18 m. During the dry seasons, the WCs of mosses at 1.5 m and liverworts at 8 m tended to be the lowest, whereas during the wet seasons the liverworts at 8 m height had the lowest values (Fig. 1, Tab. 2). For most of the height zones the highest monthly averages of the WC values were reached from January to May 2015 and from February to April 2016, whereas the lowest contents were measured from September 2015 to January 2016. The mosses at 8 m height showed rather high WCs during dry season 2015, and these samples showed only a slight alternation between the seasons. Furthermore, the liverworts at 8, 18, and 23 m height showed particularly high conductivity values in November and December 2016, which might be caused by a previously required reinstallation. Consequently, the calculated WC values of the reinstalled sensors need to be considered with special care, as they cannot be directly compared to the values prior to reinstallation.

3.1.2 Seasonal changes between wet and dry season

The wet seasons were characterized by a high frequency of precipitation events, large amounts of rain per event, the frequent appearance of fog, and high RH values, ranging mostly above 70 %. In contrast, during the dry season the precipitation events were much rarer and smaller, there was hardly any occurrence of fog, and the RH regularly had values below 60 % (Fig. 2, Fig. 3, Fig. S6). Comparing environmental conditions of the seasons, the diel amplitudes of ambient light, temperature, and RH were larger in the dry compared to the wet season. While the microclimatic temperature and light conditions within and on top of the epiphytic bryophyte communities followed the above-canopy conditions, modified by canopy shading, the WC of bryophytes did not present a clear pattern (Fig. 3).

The above-canopy light intensity (PAR_{avg} daytime) tended to be higher and to show stronger fluctuations in the dry season than in the wet season (970 ± 650 µmol m^{-2} s^{-1} vs. 740 ± 570 µmol m^{-2} s^{-1}) (Table 2). During both main seasons the average light intensity (PAR_{avg} daytime) decreased from the canopy towards the understory. During the dry season this happened in a regular stepwise manner, whereas in the wet season there were some irregularities, probably caused by the local canopy structure (Fig. 2, 3 Table 2).

The temperatures showed a decreasing gradient from the canopy (wet season: 25.3 ± 2.0 °C, dry season: 27.2± 3.5 °C) towards the understory (wet season: 24.9 ± 1.0 °C, dry season: 25.5± 1.7 °C) and the differences among heights and diel amplitudes were more pronounced during the dry season (Fig. 2, 3, Table 2). At 23 m height, temperatures within the bryophyte communities were frequently higher than the above-canopy values, and during the dry season even the seasonal average temperature was 0.5°C higher, probably due to surface heating (Table 2).

During the wet seasons of 2015 and 2016, rain occurred on average on 84 % of the days and in the dry season on 28 % of the days. During the wet season, an average RH of 95 ± 9 % and frequently even full saturation was reached, while during the dry season the RH reached an average value of 87 ± 14 % (Table 2). Fog was recorded on 60 % of the days during the wet seasons and on 20 % of the days during the dry seasons, respectively (Fig. 2). According to our observations, fog observed above the canopy normally also occurred (at least to some extent) within the forest.

The WC of the mosses at 1.5 and 8 m and the liverworts at 18 m height responded consistently to rain events, while for the liverworts at 8 and 23 m height not in all cases an immediate response was observed. During the wet season, the mosses at 1.5 m height indicated an increased WC over several days after a rain event, while in the dry season they had lower WC values. Overall, the liverworts showed a regular and pronounced nightly increase of the WC, especially during the dry season (Fig. 2, Fig. S6). The WC of the liverworts at 18 m showed a large variation during the dry season in 2016, which was most probably caused by the repositioning in November 2016. Nightly fog might serve as an additional source of water, as in some cases the WC of the bryophyte communities increased upon fog events (Fig. S9).

3.2 Potential physiological activity of bryophytes

Whereas overall light intensities at the upper three height levels were rather similar, with values below 108, 138, and 147 µmol m^{-2} s^{-1} (at 8, 18, and 23 m height) in 90 % of the time, the values at 1.5 m height remained below 10 µmol m^{-2} s^{-1} during the same time fraction. In contrast to that, maximum light intensities were relatively similar high, reaching 1,550 (1.5 m), 1,500 (8 m), 1,040 (18 m), and 950 µmol m^{-2} s^{-1} (23 m) (Fig. 4). In the understory (1.5 m), the lower light compensation point (LCP$_l$), ranging between 3 and 12 µmol m^{-2} s^{-1} (Lösch et al., 1994), was exceeded in 2-19 % of the time during the wet season and in 4-16 % of the time during the dry season, whereas at the two uppermost height levels the bryophytes exceeded these values in 34-47 % of the time during both seasons (Table 3).

The temperatures inside the moss stands mainly ranged between 23.0 °C and 33.0 °C at different height levels within the canopy (Fig. 4). In tropical lowland regions, the optimum temperatures for bryophytes (T$_{opt}$) range between 24.0 °C and 27.0 °C (Wagner et al., 2013). In our studies, temperatures in the understory remained within this range in 2-77 % of the time during the wet season and in 9-60 % of the time during the dry season. In the canopy, temperatures remained in this range in 4-54 % of the time during the wet and in 6-34 % of the time during the dry season (Table 3). In the understory, the upper temperature compensation point (TCP) of 30.0 °C – 36.0 °C (Wagner et al., 2013), above which respiration exceeds photosynthesis, was never surpassed during the wet season and only in 0 – 3 % of the time during the dry season. Similarly, at the uppermost canopy level the upper TCP was surpassed in 0-3 % of the time during the wet and in 3-26 % of the time during the dry season. Overall, the highest temperatures were reached when the bryophytes were relatively dry and most probably inactive (Fig. S10).

The WC of bryophytes differed along the vertical profile, with higher values reached in the canopy (18 and 23 m) than in the understory (1.5 and 8 m). The lower water compensation point (WCP), ranging between 30 and 80 % according to the literature (Wagner et al., 2013), was surpassed by the mosses (1.5 and 8 m) in 53 - 100 % of the time during the wet and in 4-98 % of the time during the dry season. The liverworts at 8 m height exceeded this value in 18-98 % of the time during the wet and in 5-86 % of the time during the dry season. At the uppermost two height levels, the liverworts showed no difference of this rate for both seasons, surpassing the WCP in 93-100 % of the time (Fig. 4; Table 3).

4 Discussion

4.1 Microclimatic conditions

In the current study we measured the microclimatic conditions experienced by epiphytic bryophyte communities at different height levels over the course of more than two years. In previous studies, such data have been assessed only over short time-spans of hours or days (Chazdon and Fetcher, 1984; Lösch et al., 1994; Romero et al., 2006; Wagner et al., 2013; Zotz et al., 1997).

The microclimatic conditions experienced by epiphytic bryophyte communities along a height gradient at the ATTO site followed the meteorological parameters to some extent, but they also revealed microsite-specific properties regarding annual, seasonal, and diel microclimate patterns. Whereas the water content and the temperature mostly followed the patterns of the meteorological parameters precipitation and temperature, the light intensities were clearly altered, particularly in the understory, due to the local canopy structure.

Over the course of two years, the monthly averages of above-canopy light conditions (PAR_{avg}) were rather stable (Table S4). Within the canopy, the monthly PAR_{avg} values at 23 m height tended to be higher during the dry seasons, whereas patterns were less clear at 18 and 8 m height and there was hardly any seasonal variation at 1.5 m height. This was most probably an effect of the canopy structure, cushion orientation, and shading. The sensors at 1.5 and 8 m were installed vertically along the trunk, at 18 m height they were placed on the upper side of a slightly sloped branch, and at 23 m they were positioned on the upper side of a horizontal branch. As the light sensors at 23 m height were located within the canopy, newly growing leaves may have periodically shaded the organisms, which may explain the lower monthly PAR_{avg} values at this height level compared to the values at the lower levels, where sunbeams could come through the canopy of neighboring trees and open space.

The diel patterns of PAR_{avg} are expected to show a decreasing gradient from the canopy to the understory, as the canopy receives most solar radiation, while the understory vegetation is expected to be shaded by foliage and branches. During the dry season this general pattern was indeed observed, whereas during the wet season mean light intensities were often higher at 8 than at 18 and 23 m, probably also caused by canopy shading effects at the upper two height levels. High light intensities above 1000 µmol s^{-2} s^{-1} occurred in the understory only as small light spots of short duration and thus were only observed in 0.008 % of the time. For the understory of a rain forest in Costa Rica, light intensities were reported to range from 10 to 1000 µmol m^{-2} s^{-1}, and more than in 50 % of the total amount of light resulted from sun flecks (Chazdon and Fetcher, 1984). Bryophyte and lichen taxa in the understory are known to be adapted to these low light conditions and are able to make efficient use of the rather short periods of high light intensities (Lakatos et al., 2006; Lange et al., 2000; Wagner et al., 2014).

The temperatures measured inside the bryophyte communities followed the above-canopy temperature at all height levels, with a mostly increasing gradient from the understory towards the canopy, probably caused by a reduced shading effect towards the canopy (Tab. 1, Tab. 2). At the uppermost height level, mean temperatures inside the bryophyte communities often were even higher than the mean above-canopy temperatures. During the wet season, the overall temperature conditions were more buffered due to reduced incoming radiation caused by clouds and a frequent mixing of the air masses during rain events (von Arx et al., 2012; Gaudio et al., 2017; Thompson and Pinker, 1975).

The microclimatic mean temperature differences measured inside the bryophyte stands between the understory (1.5 m) and the canopy (23 m) were 1.5 °C in the dry and only 0.5 °C in the wet season. Compared to these results, a temperature difference of 4.0 °C was determined during the dry season in a tropical evergreen forest in Thailand, while in the wet season it was below 1.0 °C, thus corresponding quite well to our results (Thompson and Pinker, 1975) (Table 2). The daily amplitude of the temperature was about twice as large in the canopy as compared to the understory (Fig. 3.) This could be caused by the exposure to strong solar radiation and higher wind velocity in the canopy compared to the sheltered understory (Kruijt et al., 2000).

Rainfall amounts and relative air humidity values differed between the seasons and also between the years, as they were considerably higher between October 2014 and February 2015 as compared to the following year. This was most probably to an El Niño event, which caused air humidity and WC of bryophytes to be substantially lower compared to the previous dry season (Fig. 1, Table 1). Generally, the moisture conditions, including rain, fog, and RH, differed between seasons, resulting in different WC patterns of bryophytes. A higher frequency of rain during the wet season particularly affected the moss communities at the lower levels (1.5 and 8 m; Fig. S6a, Table 2). At the same time the higher RH and the more frequent occurrence of fog tended to result somewhat higher WC values of the bryophytes during the wet season as compared to the dry season (Fig. 2, Table 2).

The data also suggest that the angle of the stem or branch colonized by the investigated bryophytes played a crucial role for rainwater absorption and the subsequent drying process. The bryophytes at 1.5 and 8 m height were oriented vertically, those at 18 m were placed on the upper side of a slightly sloping branch, and those at 23 m were located on the upper side of a nearly horizontally oriented branch. Long-term climate data have shown that the winds during the wet season predominantly originated from north and north-eastern directions, while during the dry season south- and south-easterly winds prevailed (Pöhlker et al., 2019). At 8 m height, the investigated bryophytes were exposed to the west, and thus were only sometimes directly influenced by precipitation. Also at 23 m height the bryophytes did not always show a clear response to precipitation events, although they were oriented horizontally on a branch (Fig. 2, Fig. S6). Here, also the tree foliation and epiphytic vascular plants might have shielded the sensors from direct precipitation during the wet season.

During the dry season, the drying of the samples located in the canopy occurred quite rapidly after the rain. Most rain events in the Central Amazon occur in the early afternoon (12:00–14:00 LT) and more than 75 % of them are weak events of less than 10 mm (Cuartas et al., 2007), which often cause no complete water saturation of the bryophytes. Consequently, the organisms tend to dry much quicker than after a strong rain event that causes full saturation of the community. Besides the solar radiation, probably also the higher wind velocities accelerated the desiccation of the epiphytic cryptogams in the canopy (Oliver, 1971). During the dry season, the diel above-canopy RH amplitudes were larger and reached lower values, thus also promoting quicker drying of bryophyte samples.

In a rain forest environment, condensation and stemflow water need to be considered as potential additional sources of water for epiphytic covers as well as for near-stem vegetation at the forest floor (Lakatos et al., 2012; van Stan and Gordon, 2018). It has been estimated that in tropical forests the stemflow water could provide up to 4 % of the annual rainfall amount (Lloyd and Marques F, 1988; Marin et al., 2000; van Stan and Gordon, 2018), corresponding to maximum values of 68 and 75 mm in the years 2015 and 2016 at the ATTO site. The WC of bryophytes in the understory responded clearly to rain events during the wet season (Fig. 3a), and subsequently water was lost gradually indicating that large amounts of water were taken up during prolonged rain events, which were subsequently lost again rather gradually, with bryophytes staying wet and active over prolonged time spans (Fig. 2, Fig. S6). The high WC of the bryophyte samples in the canopy can be explained by the higher water holding capacity of the liverwort *Symbiezidium*, which dominated in the canopy, and by its growth on inclined or vertical stems, where water drainage is less effective as compared to the vertical stem at the lower two levels. The relevance of the water holding capacity for the water content of different bryophyte species has already been described in several other studies (Lakatos et al., 2006; Romero et al., 2006; Williams and Flanagan, 1996).

The WC measurements for liverworts at 8, 18, and 23 m height were unexpectedly high in the end of 2016. This can be explained by a reinstallation of some sensors, which previously had fallen out of the moss cushions. Sensor displacement or complete removal from the bryophyte samples might have been caused by mechanical disturbance, like heavy rain events, movement of branches, growth of epiphytic vascular plants, or animal activity. A necessary reinstallation of the sensors unfortunately affected the measured values, as electrical conductivity values vary depending on the bryophyte sample properties. This variability of data, depending on the exact placement of the sensors, illustrates that calculated WCs could only be considered as approximate values. Furthermore, also the density and thickness of the investigated bryophyte sample is of high relevance. These are features, which are closely linked to the species, but also influenced by abiotic habitat conditions (Fig. S4).

4.2 Potential physiological activity of bryophytes

The microenvironmental conditions influence the WC of epiphytic bryophyte communities, but the ability to deal with these conditions differs among species (interspecific variability), being determined by morphological and physiological features. Apart from the interspecific variability, the performance of a single species under differing microenvironmental conditions can also be modulated by short-term acclimation and long-term adaption processes, with the latter being driven by environmental exposure, genetic variation among populations, and plasticity, as, e.g., shown for bryophytes and lichens (Cornelissen et al., 2007; Marks et al., 2019; Pardow et al., 2010). These aspects help to understand the occurrence of bryophytes under widely varying microclimatic conditions within the canopy. During our study, we measured the microenvironmental conditions of epiphytic bryophytes and observed bryophyte taxa to vary depending on these. Additionally, we estimated the potential ranges of physiological activity based on the compensation points for light, temperature, and WC, which have been reported from other studies in tropical forests (Lösch et al., 1994; Wagner et al., 2013). Whereas at the stem bases close to the ground the moss species *Sematophyllum subsimplex*, *Octoblepharum cocuiense*, and *Leucobryum martianum* were dominating, the liverwort *Symbiezidium barbiflorum* was the main species occurring at higher levels along the tree stem. These species have also been reported as being frequent at other tropical rain forest sites (Campos et al., 2015; Dislich et al., 2018; Gradstein and Salazar Allen, 1992; Mota de Oliveira et al., 2009; Pinheiro da Costa, 1999).

In the canopy it is essential for the cryptogams to be adapted to high light conditions and UV radiation in order to avoid cell damage by radiation (Green et al., 2005; Pardow and Lakatos, 2013; Sinha and Häder, 2008; Westberg and Kärnefelt, 1998). As high light conditions mainly occur as short light flecks in the understory, the organisms need to react rapidly and efficiently to changing light conditions to reach overall positive net photosynthesis rates. Furthermore, understory mosses and lichens show higher rates of net photosynthesis at low light conditions as compared to canopy species (Kangas et al., 2014; Lakatos et al., 2006; Wagner et al., 2013). Epiphytic organisms growing under low-light conditions in the understory are also known to have lower LCP_l values compared to the ones in the canopy, as documented for epiphytic lichens in French Guiana (Lakatos et al., 2006).

The temperature regulates the overall velocity of metabolic processes. While it has a strong impact on the respiration, the photosynthetic light reaction is by far less affected by it (Elbert et al., 2012; Green and Proctor, 2016; Lange et al., 1998). As the measured net photosynthesis rates are the sum of simultaneously occurring photosynthesis and respiration processes, positive net photosynthesis may still be reached at higher temperatures, if the photosynthetic capacity is high enough, whereas during the night, high temperatures could cause a major loss of carbon due to high respiration rates (Lange et al., 2000). In the course of our study, the lowest temperatures predominantly occurred during the night, contributing to lower respiration rates, and values were mostly below the upper TCP. Thus, the temperature did not seem to be a limiting factor for the physiological activity of epiphytic bryophytes in this environment (Fig. S10). Similarly, Wagner and coauthors (Wagner et al., 2013) stated that the temperature likely was not a limiting factor for the overall carbon balance of the bryophytes investigated in a low- and highland rainforest in Panama. Unexpectedly, the WC of bryophytes has been shown to be higher in the canopy than in the understory. In the understory, the WCP was surpassed in 4-54 % of the time during the dry season and in 53-95 % of the time during the wet season, whereas at 18 and 23 m it was exceeded in 93 – 100 % of the time, without a clear difference between the seasons. In the understory, the WC of cryptogams seemed to be predominantly regulated by rain events, whereas in the canopy, the samples stayed relatively homogeneously wet over long time spans (Fig. 2). This was unexpected at first sight, as one would expect them to dry quickly at the higher canopy levels. However, as the samples at the two upper canopy levels grew “sitting on top” of nearly horizontal branches, they presumably could store the water over longer time spans as compared to the bryophytes at the lower trunk section, which grew on the vertical stem. Additionally, the liverwort community in the canopy seemed to form thicker and denser cushions, which could store water more effectively as compared to the mosses in the understory, which occurred in thin and rather loose cushions (Fig. S4).

It is difficult to distinguish between the effect of fog and high RH, as fog occurs when high RH values persist already. However, some events indicate that the WC of bryophytes could increase upon fog (Fig. S9), which has also been shown in some other studies (León-Vargas et al., 2006). Also condensation needs to be considered as a water source for cryptogams, as demonstrated for epiphytic lichens (Lakatos et al., 2012). In their study on corticolous epiphytic lichens in a tropical lowland cloud forest, Lakatos and coauthors showed that lichens benefit from dew formation on the thallus surface during noon, and we can assume similar processes to occur quite regularly on epiphytic cryptogams (Lakatos et al., 2012). Unfortunately, this factor could not be evaluated in this study, because some relevant parameters for its calculation were not monitored.

Utilizing the compensation points of water, light, and temperature, one can make rough estimates of the physiological activity patterns of the bryophytes at the different height levels (Table 3). Whereas the lower end of the WCP range (30 % DW) was exceeded during 100 % of the time by the liverworts at the two uppermost height levels, the liverworts at 8 m exceeded this value only in 86 % of the time during the dry season and in 98 % of the time during the wet season. The mosses at 1.5 m height exceeded this value in 54 % of the time during the dry season and in 95 % of the time during the wet season. Considering a WCP of 80 %, the mosses in the understory only exceed this value in 4 % and in 53 % of the time during the dry and the wet season, respectively. Thus, for mosses in the understory, the level of the WCP is highly relevant, whereas for the liverworts in the canopy the complete range of values allows long durations of physiological activity. For the LCP_l (ranging between 3 and 12 µmol m^{-2} s^{-1}) an even more critical pattern was observed, as the communities at the ground level surpassed it only in 4-16 % and in 2-19 % of the time during the dry and the wet season, respectively. In contrast to this, bryophytes at the higher levels (18, 23 m) surpassed these CPs in 38-47 % and in 34-46 % of the time during the dry and the wet season, respectively. Contrastingly, the temperature only rarely was limiting NP and there were no major differences between the height levels or the seasons. At all height levels T_{opt} was reached in 5-60 % of the time during the dry season and in 2-77 % of the time during the wet season.

Combining the ranges of compensation points allows, a rough estimation of the time fractions when NP and DR occur. Our data suggest that at the upper two height levels NP occurred in 27-43 % and DR in 56-66 % of the time during the wet season and in 21-43 % (NP) and in 51-59 % (DR) of the time during the dry season, respectively. At the understory, however, the durations of physiological activity was relatively short and the results for the lowest level suggested that NP and DR occurred only in 1-15 % (NP) and in 53-79 % (DR) of the time during the wet season and in 0-10 % (NP) and in 16-52 % (DR) of the time during the dry season. The large discrepancy between the time ranges for NP and DR calculated for the bryophytes in the canopy and the understory gives reason to expect the LCP_l and the WCP to be at the lower end of the range (3 µmol m^{-2} s^{-1}, 30 %) for the bryophytes at the lowest height level and to be at the upper end of the range (12 µmol m^{-2} s^{-1}, 80 %) for the bryophytes at the two uppermost height levels. For other habitats, LCP_ls as low as 1 µmol m^{-2} s^{-1} have been defined for lichens (Green et al., 1991), and thus it could be possible that the bryophyte communities in the understory exhibit similarly low LCP_l values. However, one also has to keep in mind that the uncertainty inherent in the microclimatic data directly impacts the calculated physiological patterns.

In the environment being studied, the acclimation of the organisms to the environmental conditions is also crucial for their survival. Thus, the time ranges of metabolic activity are only rough estimates, depending on the actual compensation points, which are influenced by inter- and intraspecific variation. There are also some differences between groups, as, e.g., lichens tend to perform photosynthesis at lower WCs than bryophytes, and chlorolichens (with green algae as photobionts) may utilize high air humidity, whereas cyanolichens (cyanobacteria as photobiont) need liquid water (Green et al., 2011; Lange and Kilian, 1985; Raggio et al., 2017). Furthermore, there are also differences between the bryophyte divisions of mosses and liverworts, and also within one division the interspecific variability can also be large.

5 Conclusions

The microclimatic conditions experienced by bryophytes are being assessed in long-term measurements at the ATTO site since October 2014. These measurements provide a unique data set of the micrometeorological conditions within the understory and the inner canopy of tropical rain forests and facilitate a rough estimation of the physiological activity patterns of epiphytic bryophytes along a vertical gradient. Within this tropical rain forest habitat, the WC has turned out to be the key parameter controlling the overall physiological activity of the organisms with major differences between organisms of the canopy and the understory. In the understory the WC of the bryophytes was mostly relatively low and only stayed high for a few days after an intense rain event. In contrast to that, the WC of the bryophytes at higher levels remains high over most of the time, probably caused by the bryophyte morphology and also their growth habitat on top of inclined or horizontal branches. In the canopy, the dominating liverworts responded to the nightly increase of the RH, which was not observed for the mosses in the understory. Thus, the relevant water source for bryophytes in the understory might be rain, while for the bryophytes in the canopy the nightly increase of the RH might be relevant for an activation of the physiological processes. The light intensity during periods of physiological activity mainly determines whether NP dominates or carbon is lost by dominating respiration. As the temperature shows only minor spatial, diel, and seasonal variation relative to the physiological tolerance of the bryophytes, it seems to be of minor physiological relevance within the given habitat. Data on the potential physiological activity of bryophytes and cryptogamic organisms in general are not only relevant for their potential role in carbon cycling, but may also provide new insights into their relevance as sources of bioaerosols and different trace gases. Thus, these data may form a baseline for studies investigating the overall relevance of cryptogams in the context of biogeochemical cycling in tropical habitats. However, the wide ranges of potential activity and the scarcity of literature data illustrate the necessity of CO_2 gas exchange measurements to assess the actual diel and seasonal physiological activity and productivity of rain forest cryptogams under varying environmental conditions.

Data availability

All data are deposited in a data portal, which is accessible via the homepage of the ATTO project (https://www.attoproject.org/) upon request.

Supplement link

Author contribution

BW, CP, and NL designed the measurement setup. NL, CGGB, SB, and APPF conducted the practical measurements. NL, DW, GRC, MS, AA, LRO, FD, and SMO compiled the data and conducted the analyses. All authors discussed the results. NL and BW prepared the manuscript with contributions from all co-authors.

Disclaimer

The authors declare that they have no conflict of interest.

Special issue statement

Acknowledgement

This work has been supported by the Max Planck Society (MPG). We would like to acknowledge the German Federal Ministry of Education and Research (BMBF contracts 01LB1001A and 01LK1602B), supporting this project as well as the construction and operation of the ATTO site. We also acknowledge the support of the Brazilian Ministério da Ciência, Tecnologia e Inovação (MCTI/FINEP contract 01.11.01248.00) as well as the Amazon State University (UEA), FAPEAM, LBA/INPA and SDS/CEUC/RDS-Uatumã for their support during construction and operation of the ATTO site. Furthermore, we would like to thank Ulrich Pöschl for provision of the scientific infrastructure and the possibility to work in the labs. We would like to thank Reiner Ditz, Susan Trumbore, Alberto Quesada, Thomas Disper, Andrew Crozier, Hermes Braga Xavier, Feliciano de Souza Coelho, Josué Ferreira de Souza, Roberta Pereira de Souza, Holger Ritter, Henno Heintz, and Henning Braß for technical, logistical, and scientific support within the ATTO project. NL would like to thank the Max Planck Graduate Center (MPGC) for its support. DW, CGGB, SB, RA, FD, DMZ, APPF, SW, JK, CP and BW appreciate the support by the Max Planck Society. GRC would like to thank for the support of the Instituto Nacional de Pesquisas da Amazônia (INPA) provided by the Programa de Pós-graduação em Botânica. MS and LRO appreciate the support of INPA. AA would like to thank the Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA), RHMG expresses his thanks to the

Federal University of Parana, SMO would like to thank Stichting Het Kronendak, and MOA appreciates the support of the Max Planck Society and the University of San Diego. We would like to thank Maaike Bader and two unknown referees, whose comments helped to considerably improve the manuscript. This paper contains results of research conducted under the Technical/Scientific Cooperation Agreement between the National Institute for Amazonian Research, the State University of Amazonas, and the Max Planck Society. The opinions expressed are the entire responsibility of the authors and not of the participating institutions.

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Tables

Table 1: Annual mean values and standard deviations (± SD) of mean daytime photosynthetically active radiation (PAR_{avg}), daily maxima of photosynthetically active radiation (PAR_{max}), temperature, and water contents (WC) of bryophytes at the four height levels and above the canopy (a). Annual sum of rain and fog days as well as the annual sum of rain (b). Mean values were calculated from 5-minute intervals, whereas for PAR_{max} the daily maximum values were considered. Due to data gaps in the measured rain (shown in brackets), missing values were also extrapolated from existing data as described in methods section (values behind the brackets).

(a)

Height	**2015**		**2016**	
[m]	**Mean**	**± SD**	**Mean**	**± SD**
PAR_{avg} daytime[µmol m^{-2} s^{-1}]				
above-canopy, 75	911	678	841	653
23	34	1	58	8
18	45	15	34	11
8	35	19	17	10
1.5	5	35	4	20
PAR_{max} [µmol m^{-2} s^{-1}]				
above-canopy, 75	2043	579	2153	433
23	320	24	497	51
18	310	38	331	26
8	322	236	116	86
1.5	172	0	99	140
Temperature [°C]				
above-canopy, 26	26.6	3.4	26.4	3.1
23	25.9	1.0	26.5	0.5
18	26.2	0.0	26.3	0.0
8	25.8	0.2	25.8	0.2
1.5	25.4	0.0	25.5	0.1
Water content [%]				
23, Liverwort	282	117	280	438
18, Liverwort	181	50	308	309
8, Liverwort	52	14	140	288
8, Moss	182	93	167	256
1.5 Moss	86	37	69	415

(b)

Parameter	**2015**	**2016**
	Sum	**Sum**
Rain (days)	(199) 202	(197) 215
(mm)	(1680) 1693	(1702) 1863
Fog (days)	21*	28*

*: Gaps in the data record due to malfunction of fog sensor during time window of 31.05. – 20.10.2015, 30.04. – 06.07.2016, and 01.09. – 31.12.2016.

Table 2 Seasonal mean values and standard deviations (± SD) of the mean photosynthetically active radiation (PAR_{avg}), the daily maximum of photosynthetically active radiation (PAR_{max}), the temperature, and the above-canopy relative humidity (RH) or water content (WC) of bryophytes determined at different height levels and above the canopy. Mean values for the respective seasons were calculated from 5-minute intervals of the years 2015 and 2016, except for PARmax, where the daily maximum values were considered.

Height [m]	**PAR_{avg} daytime [µmol m^{-2} s^{-1}]** Mean	± SD	**PAR_{max} [µmol m^{-2} s^{-1}]** Mean	± SD	**Temperature [°C]** Mean	±	**RH (above-canopy) [%], WC [%]** Mean	± SD
Wet season								
above-canopy	738	566	2086	515	25.6	2.5	95	9
23 Liverwort	30	3	248	194	25.3	2.0	283	83
18 Liverwort	39	12	282	175	25.2	1.9	197	66
8 Liverwort	31	26	144		24.9	1.1	66	22
8 Moss							182	63
1.5 Moss	4	15	114	224	24.9	1.0	121	91
Transitional season Wet-Dry								
above-canopy	861	649	2227	182	25.8	3.0	91	11
23 Liverwort	41	72	414	252	25.7	2.8	308	109
18 Liverwort	44	54	351	123	25.4	2.3	200	34
8 Liverwort	66	88	165	218	24.9	1.4	53	10
8 Moss							161	56
1.5 Moss	2	12	61	102	24.6	1.1	55	28
Dry season								
above-canopy	973	647	2100	609	26.7	3.4	87	14
23 Liverwort	55	9	503	231	27.2	3.5	273	125
18 Liverwort	41	13	412	190	26.5	2.9	188	89
8 Liverwort	23	16	295	268	26.0	2.1	63	45
8 Moss							166	70
1.5 Moss	6	25	209	299	25.5	1.7	53	37
Transitional season Dry-Wet								
above-canopy	785	617	1988	509	26.5	3.3	85	15
23 Liverwort	55	91	530	297	27.2	3.7	289	113
18 Liverwort	37	28	185	109	26.6	3.0	227	121
8 Liverwort	21	47	269	178	26.3	2.5	112	84
8 Moss							180	67
1.5 Moss	4	20	107	113	26.0	2.1	74	60

Table 3: The potential time fractions [%], during which the epiphytic bryophytes at the different height levels exceeded the lower compensation points of light (LCP$_l$), the upper compensation points for temperature (TCP), the lower compensation points for water (WCP), and reached the optimal temperature for net photosynthesis (T$_{opt}$). The results are shown separately for a) the wet season (February–May) and b) the dry season (August–November). Values are given for the different height levels (1.5, 8, 18, 23 m) and bryophyte divisions (M=moss, L=liverwort). For the net photosynthesis (NP) it is required that WC > WCP, PAR > LCP$_l$ and T > TCP, for the dark respiration (DR) it is necessary that WC > WCP and PAR < LCP$_l$ or WC > WCP and T > TCP. Five-minute averages of measurements during the entire measurement period from October 2014 to December 2016 were considered. The ranges of the compensation points (CP) and the optimum temperature (opt) were reported in Lösch (1994) and Wagner et al. (2013) (see Table S4).

a) Wet season

Height	**Division**	**LCP$_l$**	**T$_{opt}$**	**TCP**	**WCP**	**NP**	**DR**
		$\geq$ 3-12	24.0-27.0	$\geq$ 30.0-36.0	$\geq$ 30-80		
		µmol m^{-2} s^{-1}	° C	° C	% DW		
[m]	**L/M**	**Time fraction when cardinal points are reached/exceeded [% of time]**					
23	L	34-43	4-54	0-3	98-100	27-38	62-66
18	L	40-46	4-55	0-2	96-100	32-43	56-57
8	L	25-31	2-74	0	18-98	5-40	11-56
8	M				88-100	26-36	54-63
1.5	M	2-19	2-77	0	53-95	1-15	53-79

b) Dry season

Height	**Division**	**LCP$_l$**	**T$_{opt}$**	**TCP**	**WCP**	**NP**	**DR**
		$\geq$ 3-12	24.0-27.0	$\geq$ 30.0-36.0	$\geq$ 30-80		
		µmol m^{-2} s^{-1}	° C	° C	% DW		
[m]	**L/M**	**Time fraction when cardinal points are reached/exceeded [% of time]**					
23	L	42-47	6-34	3-26	96-100	18-41	57-59
18	L	38-46	5-40	0-23	93-100	21-43	51-54
8	L	19-36	8-52	0-10	5-86	3-34	15-55
8	M				84-98	14-39	52-56
1.5	M	4-16	9-60	0-3	4-54	0-10	16-52

Figures

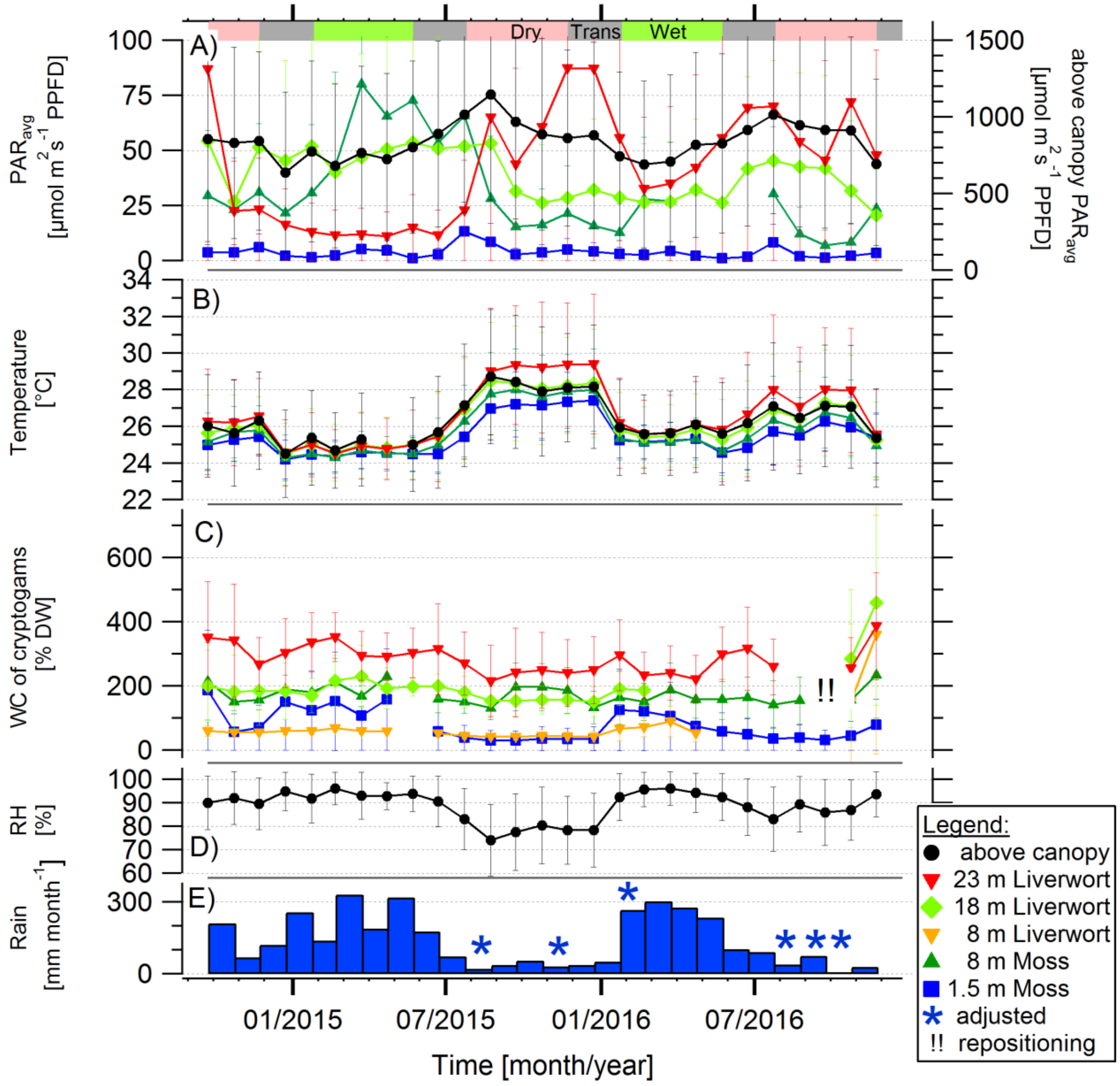
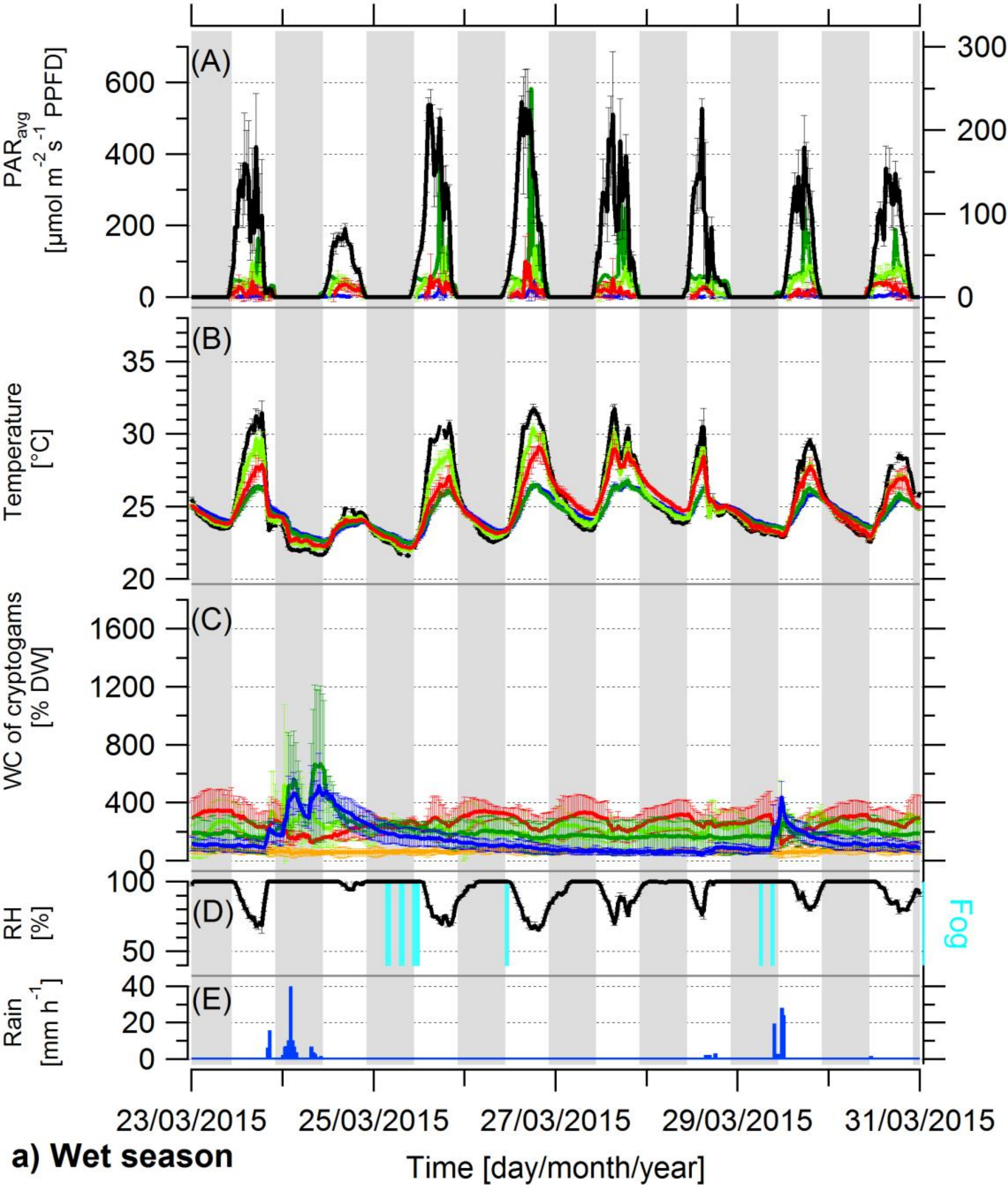


Figure 1: Mean light condition (PAR_{avg}), temperatures, and water content (WC) experienced by bryophyte communities, and above-canopy meteorological conditions in the Amazonian rain forest. The micrometeorological parameters on top/within epiphytic cryptogamic communities represent monthly mean values ± SD of (A) daily average (06:00 – 18:00 LT) of photosynthetically active radiation (PAR_{avg}) on top, (B) temperature within, and (C) WC of cryptogamic communities. The above-canopy meteorological parameters comprise the (A) monthly mean

value of the daily average (06:00 – 18:00 LT) of above-canopy photosynthetically active radiation (PAR_{avg} at 75 m), (B) monthly mean value of above-canopy temperature (at 26 m), (D) monthly mean value of relative air humidity (RH at 26 m height), and (E) monthly amount of rain. Data of replicate sensors installed within communities at the same height level were pooled, while above-canopy parameters were measured with one sensor each. Colored horizontal bars in the upper part of the figure indicate the seasons. Exact values and additional data are presented in Tables S4 and S6.


(A)
PAR$_{avg}$ [µmol m^{-2} s^{-1} PPFD]
0
200
400
600
above canopy PAR$_{avg}$ [µmol m^{-2} s^{-1} PPFD]
0
1000
2000
3000
(B)
Temperature [°C]
20
25
30
35
(C)
WC of cryptogams [% DW]
0
400
800
1200
1600
(D)
RH [%]
50
100
Fog
(E)
Rain [mm h^{-1}]
0
20
40
23/03/2015
25/03/2015
27/03/2015
29/03/2015
31/03/2015
Time [day/month/year]
a) Wet season

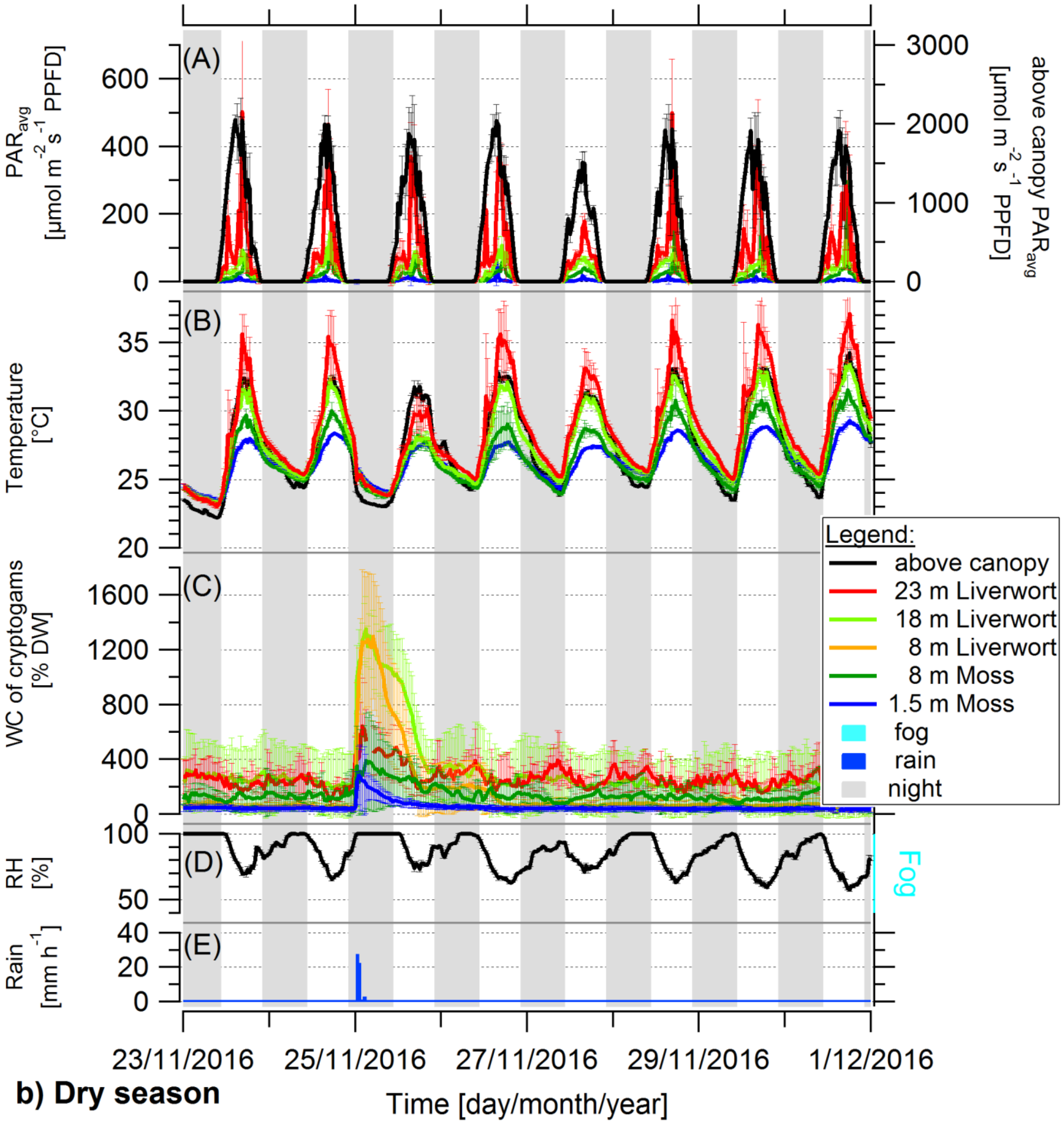


Figure 2: Representative periods during the wet and dry season under average conditions, showing light condition (PAR$_{avg}$), temperature, and water content (WC) of bryophytes, and above-canopy meteorological conditions in the

Amazonian rain forest. Shown are 8-day periods during (a) the wet season 2015 and (b) the dry season 2016. The micrometeorological parameters on top/within epiphytic cryptogamic communities represent (A) the photosynthetically active radiation ($\mathrm{PAR}_{\mathrm{avg}}$) on top, (B) the temperature within, and (C) the WC of cryptogamic communities. The above-canopy meteorological parameters comprise (A) above-canopy photosynthetically active radiation ($\mathrm{PAR}_{\mathrm{avg}}$ at 75 m), (B) above-canopy temperature (at 26 m), (D) relative air humidity (RH at 26 m height), presence of fog events, and (E) rain amount. The data show 30-minute averages ± SD except for rain, which shows hourly sums. Data of replicate sensors installed within communities at the same height level were pooled, while above-canopy parameters were measured with one sensor each. The nighttime is shaded in grey (06:00 – 18:00 LT).

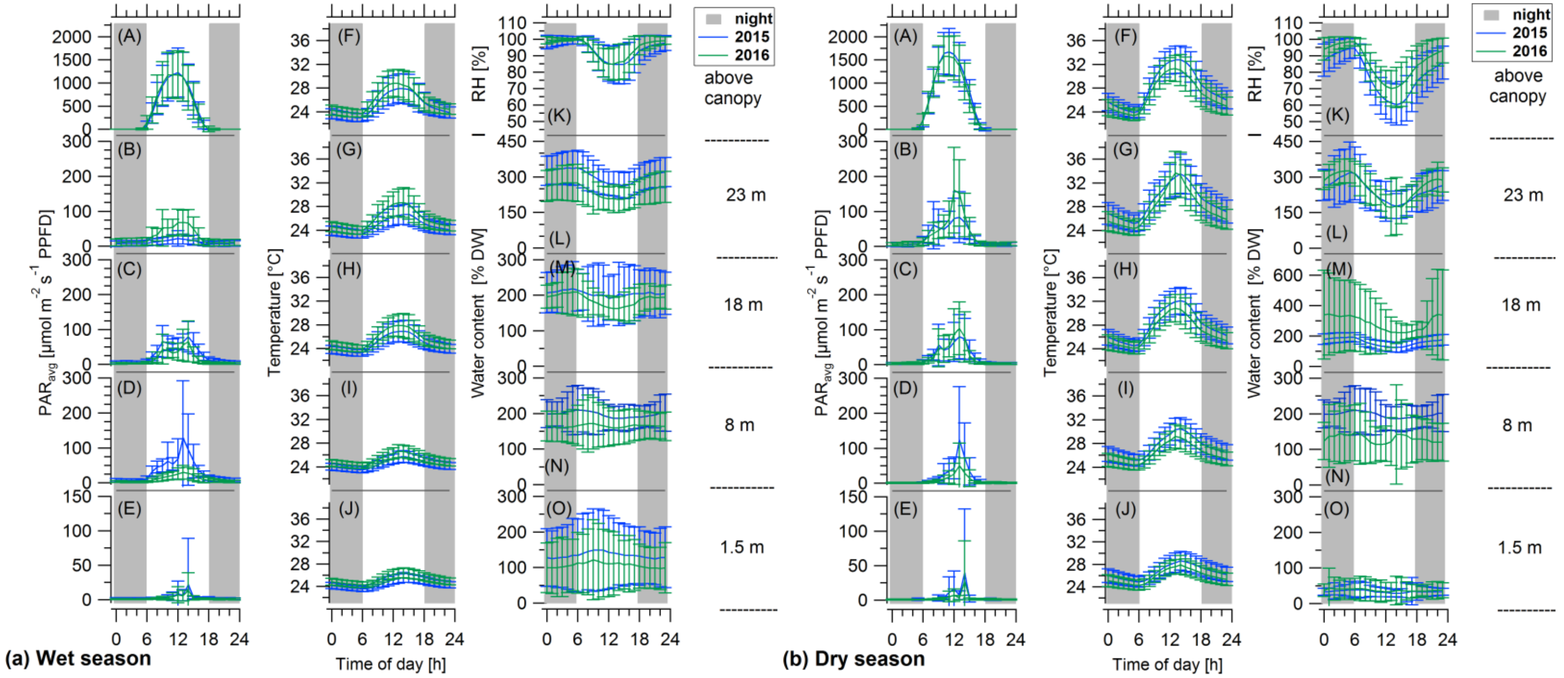
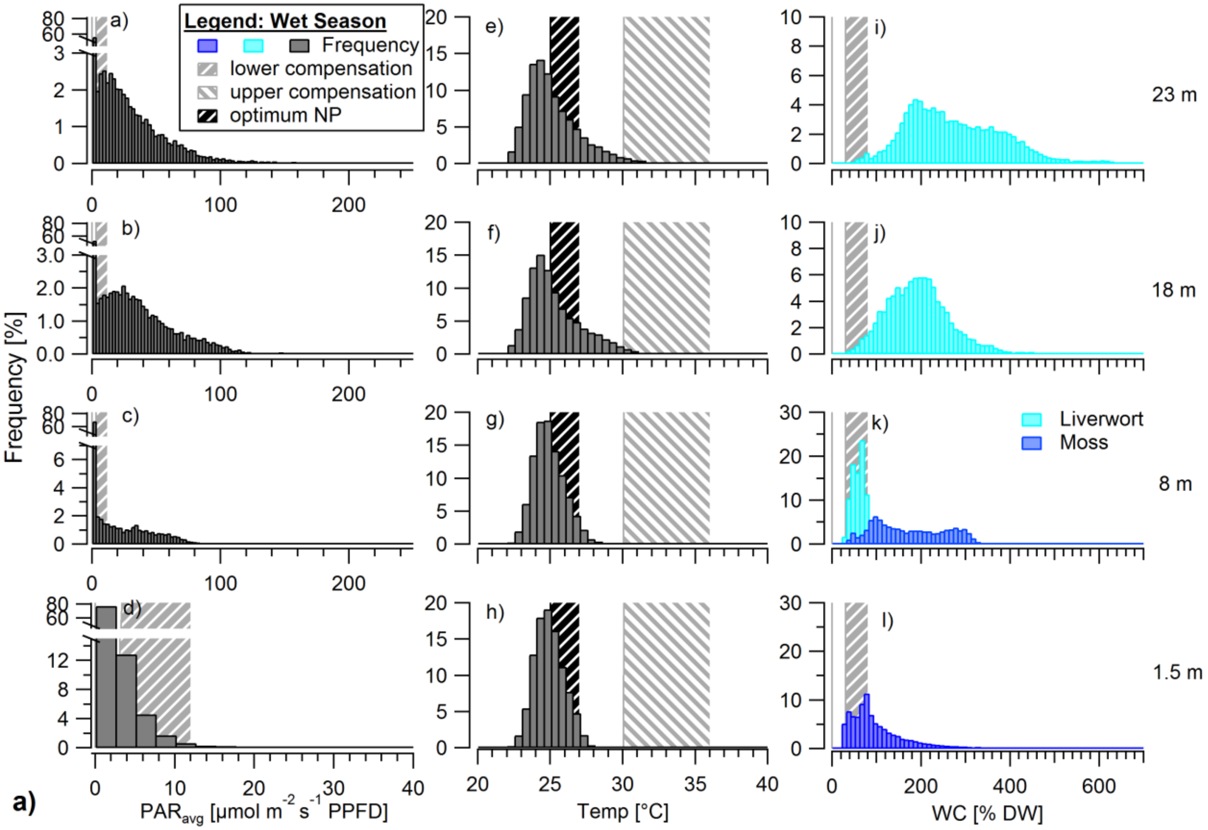


Figure 3: Mean diurnal cycles of light conditions (PAR$_{avg}$), temperature, and water content (WC) of bryophytes, and above-canopy meteorological parameters during (a) wet season and (b) dry season of the years 2015 (blue lines) and 2016 (green lines). The above-canopy meteorological parameters comprise (A) the photosynthetically active radiation (PAR$_{avg}$ at 75 m), (F) the temperature (at 26 m), and (K) the relative air humidity (RH at 26 m height). The micrometeorological parameters measured on top/within epiphytic cryptogamic communities comprise (B – E) the photosynthetically active radiation (PAR) on top, (G – J) the temperature within, and (L – O) the WC of cryptogamic communities at different height levels. Diel cycles were calculated from 30-minute intervals of the whole seasons and show hourly mean values ± SD. Data of the sensors installed at the same height level were pooled, while the above-canopy parameters were measured with one sensor each. For the WC at 8 m height data of the mosses are shown. Nighttime is shaded in grey (06:00 – 18:00 LT).


Legend: Wet Season
Frequency
lower compensation
upper compensation
optimum NP
Frequency [%]
a)
b)
c)
d)
e)
f)
g)
h)
i)
j)
k)
l)
Liverwort
Moss
23 m
18 m
8 m
1.5 m
PAR$_{avg}$ [µmol m^{-2} s^{-1} PPFD]
Temp [°C]
WC [% DW]

a)

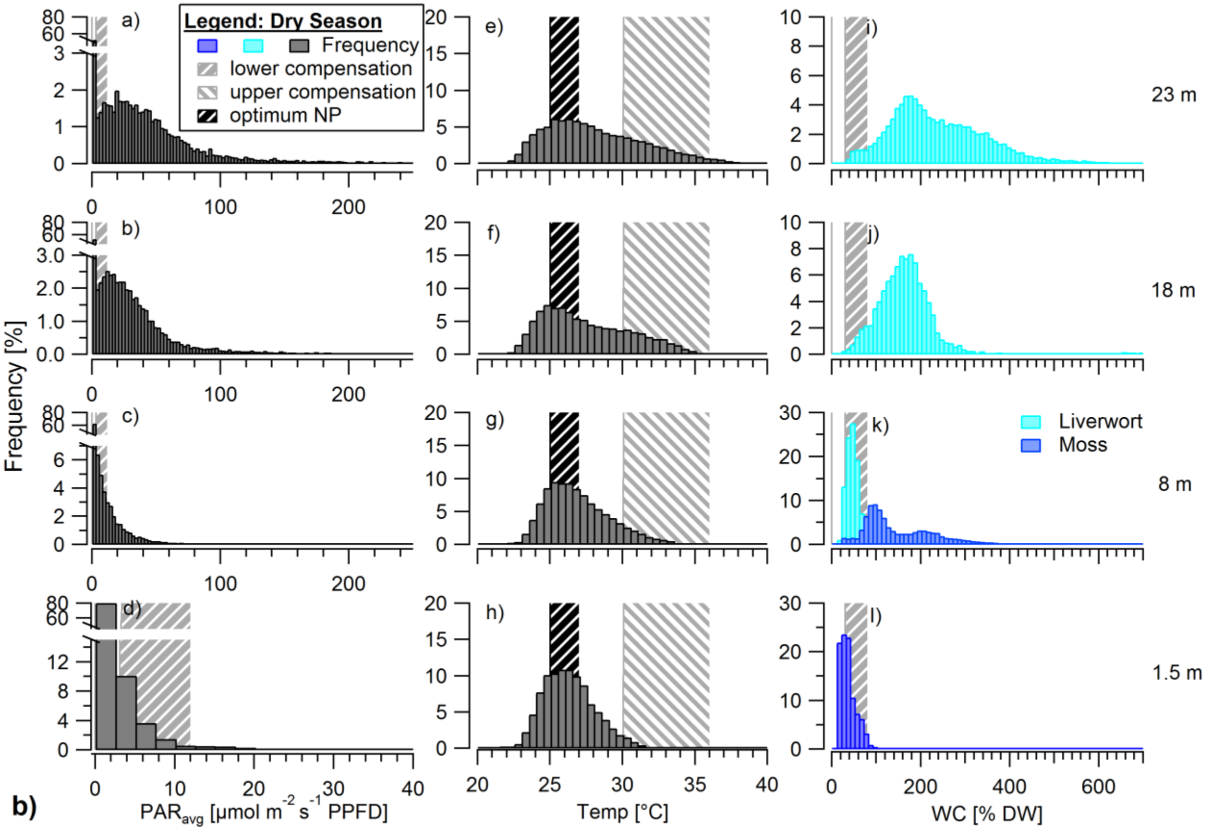


Figure 4: Frequency of mean photosynthetically active radiation (PAR_{avg}; a – d), temperature (Temp; e – h), and water content (WC; i – l) measured on top/within bryophytes at 1.5, 8, 18, and 23 m height during (a) the wet and (b) the dry season. Calculation of the histograms based on 30-minute intervals. Shaded areas represent the ranges
5 of lower compensation (PAR, WC), upper compensation (temperature), and the optimum (temperature) for net photosynthesis. Value ranges are adopted from Lösch (1994) and Wagner et al., (2013) (Table S5). Bin sizes: PAR: 2.5 µmol m^{-2} s^{-1}; temperature: 0.5 °C; WC: 10 %.