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

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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 98 % 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 higher levels were affected by frequent wetting and drying events, those close to the forest floor remained wet over longer time spans during the wet seasons. 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. These data may be used as a starting point to investigate the role of bryophytes in various biosphere-atmosphere exchange processes, such as measurements of CO_2 gas exchange, 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 equally 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). It has been described to play important roles in the water cycle, as well as for 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 changes will still ensure its ecological services as “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, few reports can be found in the literature. There is a lack of information regarding the functioning of such communities in an environment with an almost constant high relative humidity and temperature range. 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 bryophytes communities along a vertical gradient and an estimation of their activity patterns in response to annual and seasonal variations of 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) (Pöhlker et al., 2018). 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 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. Generally, 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). 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 vertical branch. Thus, also the orientation at the stem may influence the WC of the bryophyte communities, not only the species and the canopy structure. Whereas bryophytes were selected as cryptogamic exemplary organisms to be measured, similar microclimatic conditions and activity patterns are expected for all cryptogamic organisms due to their poikilohydric nature (Raggio et al., 2017). 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 6 (1.5 m) was repositioned in January 2015, WC sensor 1 (1.5 m) in November 2015, WC sensor 1, 6 to 24 and all temperature sensors in November 2016. The periods when the sensors have not been 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 depended 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 measurement, 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 $\mu mol\ m^{-2}\ s^{-1}$ photosynthetic photon flux density (PPFD), thus an averaging of 30-minute intervals allowed a smoothening of the data (Fig. S4). The smoothened data were used for detailed illustrations of seasonal variability (Fig. 2 and S5), whereas the 5-minute data were used for calculations in order to also consider short light fleck events.

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):

$$EC_{25} = f_T * EC_t, \tag{1}$$

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

$$f_T = 0.447 + 1.4034\ e^{-T/26.815}. \tag{2}$$

The WC sensor was designed in the manner that the electric voltage is proportional to the electrical conductivity, which is the inverse resistance, due to the fixed distance between the sensor pins. 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). The dry weight was determined after drying at 60 °C until weight consistency was reached (Caesar et al., 2018).

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. 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):

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

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

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 assume, that the maximum electrical conductivity achieved in the field equals the maximum WC achieved in the laboratory due to water saturation of the samples during the laboratory measurement. Minimum electrical conductivity values reached in the field were assumed to correspond to air-dry samples, as we are confident that the samples dried out at least once during the dry season of the year. Accordingly, the water content (WC) was calculated as follows:

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

with EC_i as electrical conductivity, EC_{min} as minimum electrical conductivity, EC_{max} as maximum electrical conductivity in the field, WC_{max} as the maximum WC in the laboratory, and WC_{min} as the minimum WC in the laboratory.

8The measured electrical conductivity values showed short-time oscillations, which could be removed with a 30-minute smoothing algorithm (Fig. S4). Thus, for all calculations the 30-minute averages have been 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 collected 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) data assessed 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 (PAR_{avg} month, PAR_{avg} season, PAR_{avg} year) only values during daytime (6:00 – 18:00 local time) were considered. Rainfall is presented as accumulated values in millimeters per month, season, or year, which was calculated by an integration of 5-minute intervals. As there were gaps in the readings of the rain gauge, additional information from the WC sensors was 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 rain gauge readings 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 S2).

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).

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 tropical species in lowlands near sea level in Panama, values in the range between ~ 30 and ~ 80 % have been determined (Wagner et al., 2013) (Table S3).

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 in African tropical lowland rain forests (Lösch et al., 1994). At light intensities below the compensation point and WCs above 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}; 95 % of maximum NP rate reached) and an upper compensation point, where NP equals DR, (TCP), can be defined. For tropical bryophytes, T_{opt} ranges between 24 and 27 °C and the TCP between 30 and 36 °C (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. 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 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 S2).

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 315 and 570 µmol m^{-2} s^{-1} during the daytime (Fig. 1, Table 1a). Within the canopy, the PAR_{avg} values at 1.5 m also showed only minor seasonal variation, whereas those at higher levels revealed larger variations (Table S4). At 23 m height, PAR_{avg} values tended to be higher during the dry seasons. Comparing the two subsequent years, the annual mean values of the monthly PAR_{avg} tended to be higher at 1.5, 8, and 18 m, but lower at 23 m in 2015 compared to 2016.

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. S6). Overall, temperatures at all height levels were lower and more similar during the wet than the dry seasons. Maximum differences of monthly mean temperatures between the wet and the dry season were 5.0 °C at 23 m height, 3.0 °C at 1.5 m height, and 4.0 °C for above-canopy values (Tab. S2, Tab. S4).

The monthly rain, RH, and WCs of epiphytic bryophytes showed similar patterns over the course of the years. During the dry season 2015, it rained on 25 % of the days per month, while in the previous and subsequent years rain occurred at a higher frequency (58 % and 31 % of the days per month, respectively; Fig. 1, Table S2). 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 detected 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 tended to be the lowest, whereas during the wet seasons they were rather similar to the WCs of mosses at 8 m, whereas those of the liverworts at 8 m height had the lowest values (Fig. 1). 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. Furthermore, the liverworts at 8, 18, and 23 m height showed particularly high WC values in November and December 2016, which might be caused by a previously required 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 reached values below 60 % (Fig. 2, Fig. S5). The temperature and light conditions within and on top of the epiphytic bryophyte communities followed the above-canopy climatic conditions, modified by canopy shading.

The above-canopy light intensity tended to be higher in the dry season as compared to the wet season (970 ± 650 vs. 740 ± 570 µmol m^{-2} s^{-1}) and the values showed stronger fluctuations. During both main seasons the average light intensity 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, with values at 23 m being lower than at 8 m or 18 m height (Fig. 2, Table 2).

The temperatures showed larger diel amplitudes in the dry compared to the wet season. Temperatures reflected a decreasing gradient from the canopy towards the understory and differences among heights were more pronounced during the dry season (Fig. 2, 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 (Tab. S2).

During 2015 and 2016, rain occurred in the wet season on 81 and 87 % of the days and in the dry season on 25 and 31 % of the days, respectively. During the dry season the RH reached on average 87 ± 14 %, while in the wet season the average RH was 95 ± 9 % and frequently even full saturation was reached. Fog was recorded on 56 and 67 % of the days during the wet seasons of 2015 and 2016 and on 27 and 16 % of the days during the dry seasons, respectively (Fig. 2, Table 2).

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. The mosses at 1.5 m height had an increased WC over several days during the wet season, while in the dry season they had lower WC values. The bryophytes at the upper three heights showed a regular and pronounced nightly increase of WC (Fig. 2, Fig. S5). Nightly fog might serve as an additional source of water, as the WC of the bryophyte communities increased upon fog events (Fig. S7).

3.1.3 Diel cycles in different seasons and years along a vertical gradient

The diel cycles of WC, temperature, and light conditions experienced by epiphytic bryophyte communities showed varying characteristics during the wet and the dry seasons (Fig. 3). The diel variability of light and temperature was larger in the canopy than in the understory, while for WC of bryophytes the diel variability was the largest at the two uppermost height levels. Comparing the seasons, the diel amplitudes of light, temperature, and RH were larger in the dry compared to the wet season, while for the WC of bryophytes the results did not present a clear pattern. The liverworts in the canopy tended to follow a higher amplitude of the WC during the dry season, while the mosses in the understory (at 1.5 m height) tended to show larger variations during the wet season.

The average daily above-canopy light intensities (PAR_{avg}) were higher in the dry than in the wet season, and also the PAR_{avg} on top of the epiphytic bryophytes at different height levels predominantly reached higher values during the dry season (Fig. 3). This mostly corresponds well with the daily maximum and amplitude values measured by the above-canopy climate and the microclimatic sensors, as these mostly were also higher during the dry seasons. Exceptions from that were the lower above-canopy values during the dry season 2015 and relatively low values at 8 m and 1.5 m height during the dry season 2016 (Table S5, S6, S7).

The above-canopy temperatures showed larger diel amplitudes and higher values in the dry compared to the wet seasons (Fig. 3). Also mean daily maxima were higher with 33.5 ± 2.0 and 32.5 ± 2.0 °C during the dry compared to 29.0 ± 2.5 and 30.5 ± 2.0 °C reached during the wet seasons of 2015 and 2016, respectively. The microclimatic mean temperatures measured within the epiphytic bryophyte communities showed an increasing daily amplitude and increasing maximum temperatures from the understory to the canopy. Daily maxima, minima, and amplitudes were larger in the dry than the wet seasons.

The mean RH values showed larger daily amplitudes in the dry compared to the wet seasons with particularly large amplitudes during the dry season 2015 (Fig. 3). Also the mean daily maxima of RH reached only 96 % in the dry season 2015, whereas in all other seasons (i.e., dry season 2016 and both wet seasons) values above 99 % were reached. The diel mean WC of epiphytic liverworts was the highest at 23 m and also daily maxima, minima, and amplitudes were the highest at this level. At 23 m height, also the daily amplitudes tended to be higher during the dry compared to the wet seasons, whereas for the mosses at the lowest height level the amplitude tended to be higher during the wet season. For bryophyte communities at the other height levels the amplitudes during the different seasons were less clear.

3.2 Potential physiological activity of bryophytes

While the availability of water determines the overall time of physiological activity, light is essential for net photosynthesis to occur. Furthermore, high nighttime temperatures cause increased carbon losses due to increased respiration rates.

Whereas overall light intensities at the upper three height levels were similar, with values mostly ranging between 0 and 100 µmol m^{-2} s^{-1} and maximum light intensities of 1,500 (8 m), 1,040 (18 m), and 950 µmol m^{-2} s^{-1} (23 m), intensities at 1.5 m height were extremely low, mostly reaching 0 – 10 µmol m^{-2} s^{-1}, although maximum values of 1,550 µmol m^{-2} s^{-1} were measured (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 only reached during 2 – 15 % of the reported time, whereas at higher canopy height levels the bryophytes reached these values during 29 – 47 % of the time (Table 3).

The microclimatic temperatures at different height levels within the canopy mainly ranged between 23.0 and 33.0 °C (Fig. 4). In tropical lowland regions, the optimum temperatures for bryophytes (T_{opt}) range between 24.0 and 27.0 °C (Wagner et al., 2013). In our studies this optimum was matched during 6 – 51 % of the time (Table 3). The upper temperature compensation point (TCP) of 30.0 – 36.0 °C (Wagner et al., 2013), above which respiration exceeds photosynthesis, was surpassed during 0 – 11 % of the time in the understory and 0 – 17 % in the upper three canopy levels. Overall, the highest temperatures were reached when the bryophytes were relatively dry (Fig. S8).

The WC of bryophytes differed along the vertical profile, with substantially 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 reached during 0 – 88 % of the time by mosses (1.5 and 8 m), during 2 – 33 % by liverworts (8 m) in the understory, and during 2 – 100 % of the time by liverworts in the canopy (18 and 23 m; 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 only been assessed only over short time-spans of hours or days (Romero et al., 2006; Wagner et al., 2013; Zotz et al., 1997).

The microclimatic conditions experienced by 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 water content and temperature readings mostly followed the patterns of the meteorological parameters precipitation and temperature, the light intensities were clearly altered, particularly at the lower levels of the canopy.

Over the course of two years, the above-canopy average monthly light conditions (PARavg) were rather stable. In previous studies, increased biomass burning activities during El Niño in 2015 were reported to cause an increase of smoke and soot particles in the atmosphere (Saturno et al., 2017), and our data also suggest a slight reduction of monthly PAR_{max} during the dry season 2015 (Table S2). 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 vertical 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.

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 during 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 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 microclimatic temperatures measured within 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. At the uppermost height level, mean temperatures within 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 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 diurnal and seasonal temperatures were the most stable in the understory, whereas the largest variations were observed in the canopy. The daily amplitude of the temperature was about twice as large in the canopy as compared to the understory (Tab. S6). 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).

The two consecutive years 2015 and 2016 were by no means identical, as rainfall amounts and relative air humidity values were considerably higher between October 2014 and February 2015 as compared to the following year. The dry season of 2015/2016 was affected by an El Niño event, causing air humidity and WC of bryophytes to be substantially lower compared to the previous dry season (Fig. 1, Table 1).

As expected, the response of the WCs of bryophytes upon rain, fog, and high RH differed between seasons. During the wet season, the RH and the WC of the moss communities at 1.5 and 8 m and the liverwort communities at 23 m tended to be higher as compared to the dry season (Table 2), when the RH values showed lower values during the daytime. During the wet season, the frequency of rain was higher, and thus affected especially the moss communities at the lower levels (1.5 and 8 m; Fig. S5a).

Furthermore, 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., 2018). 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. S5). It can be expected that, besides the dominating wind direction, also the tree foliation and epiphytic vascular plants might shield 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 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 cause no complete water saturation of the bryophytes. Consequently, the organisms dry much quicker than after a strong rain event that fully saturates the community. Besides solar radiation, probably also the higher wind velocities accelerated the desiccation of the epiphytic cryptogams in the canopy (Oliver, 1971). The diel above-canopy RH amplitudes were larger and reached lower values during the dry season, thus also promoting quicker drying of samples.

In a rainforest 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 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 showed a high variability during the wet season, indicating that large amounts of water were taken up during prolonged rain events, which were subsequently lost again in a stepwise manner, with bryophytes often staying wet and active over long time spans (Fig. 2, Fig. S5). The high WC of the bryophyte samples in the canopy might be partly explained by the different water holding capacity of different bryophyte species (Lakatos et al., 2006; Romero et al., 2006; Williams and Flanagan, 1996). The species dominating the measurements in the canopy (23, 18, and 8 m) was a liverwort, while in the understory (1.5 and 8 m) moss species were dominating the measurements.

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.

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 long-term adaptation of the metabolic properties, the performance of species under differing microenvironmental conditions can also be modulated by acclimation processes (intraspecific variability), as, e.g., shown for bryophytes and lichens (Cornelissen et al., 2007; Pardow et al., 2010). These two aspects help to understand the occurrence of bryophytes under widely varying microclimatic conditions within the canopy. It was recently demonstrated that a prediction of the physiological activity patterns of cryptogamic organisms and communities was possible on the basis of climatic conditions alone (Raggio et al., 2017). During our study, we also observed bryophyte taxa to vary depending on the microenvironmental conditions. 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, the organisms need to react rapidly and efficiently to changing light conditions to reach overall positive net photosynthesis rates, and it has been reported that understory mosses and lichens indeed 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 are also known to have lower LCP_l values under low-light conditions in the understory compared to the canopy, as documented for epiphytic lichens in French Guiana (Lakatos et al., 2006).

The temperature regulates the velocity of metabolic processes, hence it has a strong impact on the respiration, while the photosynthetic light reaction is by far less sensitive (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. S8). Similarly, Wagner and coauthors (Wagner et al., 2013) stated that the temperature likely was not a limiting factor for NP and growth of the bryophytes investigated by them in a lowland and highland rainforest in Panama. The WC of bryophytes has been shown to be higher in the canopy than in the understory. In the understory, the WCP was reached between 1 and 36 % of the time, depending on the literature value being considered, whereas at 18 and 23 m it was reached during ~3 – 100 % of the time. In the understory, the WC of cryptogams seems to be predominantly regulated by rain events and the vegetation reduces the evaporation by its shadowing effect. An increased RH slows down the drying process, causing the samples to dry over a longer time-range, especially during the wet season (Fig. 2). In the canopy, the samples stayed relatively homogeneously wet over long time spans. 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 on top of nearly vertical stems, they probably could store the water over longer times.

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 bryophyte WC could increase upon fog (Fig. S7), 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 that similar processes 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.

Based on our measurements combined with the compensation points of water, light, and temperature, one can make rough estimates of the potential time of NP and DR for bryophytes at the different height levels (Table 3). Whereas the lower end of the WCP range (30 % DW) was reached during 100 % of the time by the liverworts at the upper two height levels, the liverworts at 8 m reached this value only during 33 % of the time, and the mosses at 1.5 and 8 m height reached it only during 36 and 88 % of the time, respectively. For the LCP_l an even more critical pattern was observed, as the data suggest that it was reached only during 2 % of the time by communities at the ground level, whereas those at higher levels reached it during ~30 – 40 % of the time. In contrast to these factors, the temperature was only rarely limiting and there were no major differences between the height levels. Combining the ranges of the environmental factors needed for NP and DR to occur, our data suggested that NP and DR at the upper two height levels occurred during ~30 – 60 % and ~30 – 50 % of the time, respectively, thus being in a reasonable range. At the lower levels, however, the durations of NP and DR were relatively short and the results for the ground level suggested that NP occurred only during ~5% and DR during~10 – 25% of the time. These results appear highly unrealistic and thus we expect the LCP_l and the WCP at the lower levels and particularly at the ground level to be lower than the values that have been published up to now. For other habitats, light compensation points 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.

In the environment studied, the adaption 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, while 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 bryophyte WC is mostly relatively low, but stays high for a longer time after intense rains. In contrast to that, the water content of the bryophytes at higher levels remains high and at similar values over most of the time, probably caused by the bryophyte morphology and also their growth habitat on top of a vertical stem. 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, it might 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 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

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Tables

Table 1: Annual mean values and standard deviation (± 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, except for PAR_{max}, where the daily maximum values were considered. Due to data gaps in the measured rain (shown in brackets) 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	27	42	116	44
18, Liverwort	107	40	170	172
8, Liverwort	25	7	67	119
8, Moss	55	24	57	38
1.5 Moss	41	50	31	35

(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 different parameters, photosynthetically active radiation (PAR_{avg}), daily maximum of photosynthetically active radiation (PAR_{max}), temperature, and above-canopy relative humidity/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	**PAR_{avg} daytime [µmol m^{-2} s^{-1}]**		**PAR_{max} [µmol m^{-2} s^{-1}]**		**Temperature [°C]**		**RH (above canopy), WC [%]**	
[m]	Mean	± SD	Mean	± SD	Mean	± SD	Mean	± SD
Wet season								
above-canopy	738	566	2086	515	25.6	2.5	143	36
23 Liverwort	30	3	248	194	25.3	2.0	125	33
18 Liverwort	39	12	282	175	25.2	1.9	113	37
8 Liverwort	31	26	144		24.9	1.1	31	10
8 Moss							64	29
1.5 Moss	4	15	114	224	24.9	1.0	60	50
Transitional season Wet-Dry								
above-canopy	861	649	2227	182	25.8	3.0	143	57
23 Liverwort	41	72	414	252	25.7	2.8	128	41
18 Liverwort	44	54	351	123	25.4	2.3	127	20
8 Liverwort	66	88	165	218	24.9	1.4	25	5
8 Moss							54	21
1.5 Moss	2	12	61	102	24.6	1.1	24	15
Dry season								
above-canopy	973	647	2100	609	26.7	3.4	119	52
23 Liverwort	55	9	503	231	27.2	3.5	122	52
18 Liverwort	41	13	412	190	26.5	2.9	107	52
8 Liverwort	23	16	295	268	26.0	2.1	32	28
8 Moss							51	33
1.5 Moss	6	25	209	299	25.5	1.7	23	20
Transitional season Dry-Wet								
above-canopy	785	617	1988	509	26.5	3.3	141	67
23 Liverwort	55	91	530	297	27.2	3.7	130	48
18 Liverwort	37	28	185	109	26.6	3.0	137	75
8 Liverwort	21	47	269	178	26.3	2.5	61	49
8 Moss							56	24
1.5 Moss	4	20	107	113	26.0	2.1	35	33

Table 3: The potential time ranges [%], during which the epiphytic bryophytes reached the lower compensation points of light (LCP$_l$), the optimal temperature for net photosynthesis (T$_{opt}$), the upper compensation points for temperature (TCP), and the lower compensation points for water (WCP). The conditions at which the compensation points were reached are listed, and the potential time ranges, during which NP and DR might occur were listed. Values are given for the different height levels and bryophyte divisions (M=moss, L=liverwort). 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 optimal ranges (opt) were reported in Lösch (1994) and Wagner et al. (2013) (see Table S3).

Height	**LCP$_l$** 3-12 µmol m^{-2} s^{-1}	**T$_{opt}$** 24.0-27.0 ° C	**TCP** 30.0-36.0 ° C	**WCP** 30-80 % DW	**Conditions** for NP and DR LCP$_l$/TCP/WCP	**NP** WC > WCP & PAR > LCP$_l$ & T < TCP	**DR** WC > WCP & PAR < LCP$_l$ or WC > WCP & T > TCP
[m]	**Time fraction when cardinal points are reached [% of time]**				**µmol m^{-2} s^{-1}/°C/%DW**	**Time fraction when cardinal points are reached [% of time]**	
23 L	36-45	6-46	0-16	2-100	3-12/30-36/30-80	28-58	40-47
18 L	39-47	6-51	0-13	4-100	3-12/30-36/30-80	27-59	30-33
8 L	29-40	13-29	0-17	2-33	3-12/30-36/30-80	1-23	3-16
8 M				0-88	3-12/30-36/30-80	5-46	9-30
1.5 M	2-15	14-30	0-11	1-36	3-12/30-36/30-80	0-6	10-26

Figures

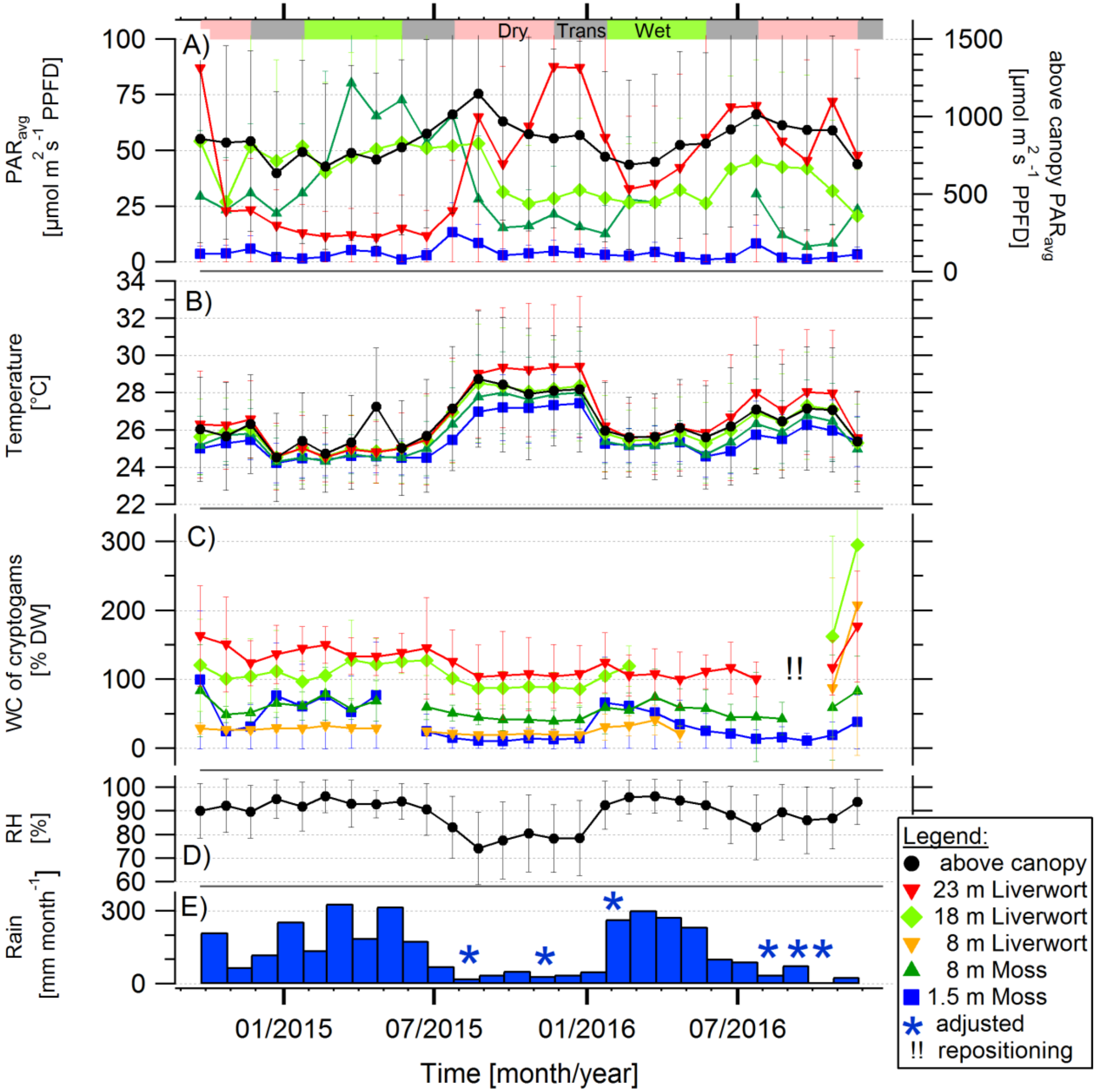


Figure 1: Water content (WC), temperature, and light conditions experienced by bryophyte communities, and above-canopy meteorological conditions in the Amazonian rain forest. The micrometeorological parameters on top/within epiphytic the cryptogamic communities represent monthly mean values ± SD of (A) average by day (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 (A) the monthly mean value of the average by day (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 S2 and S4.

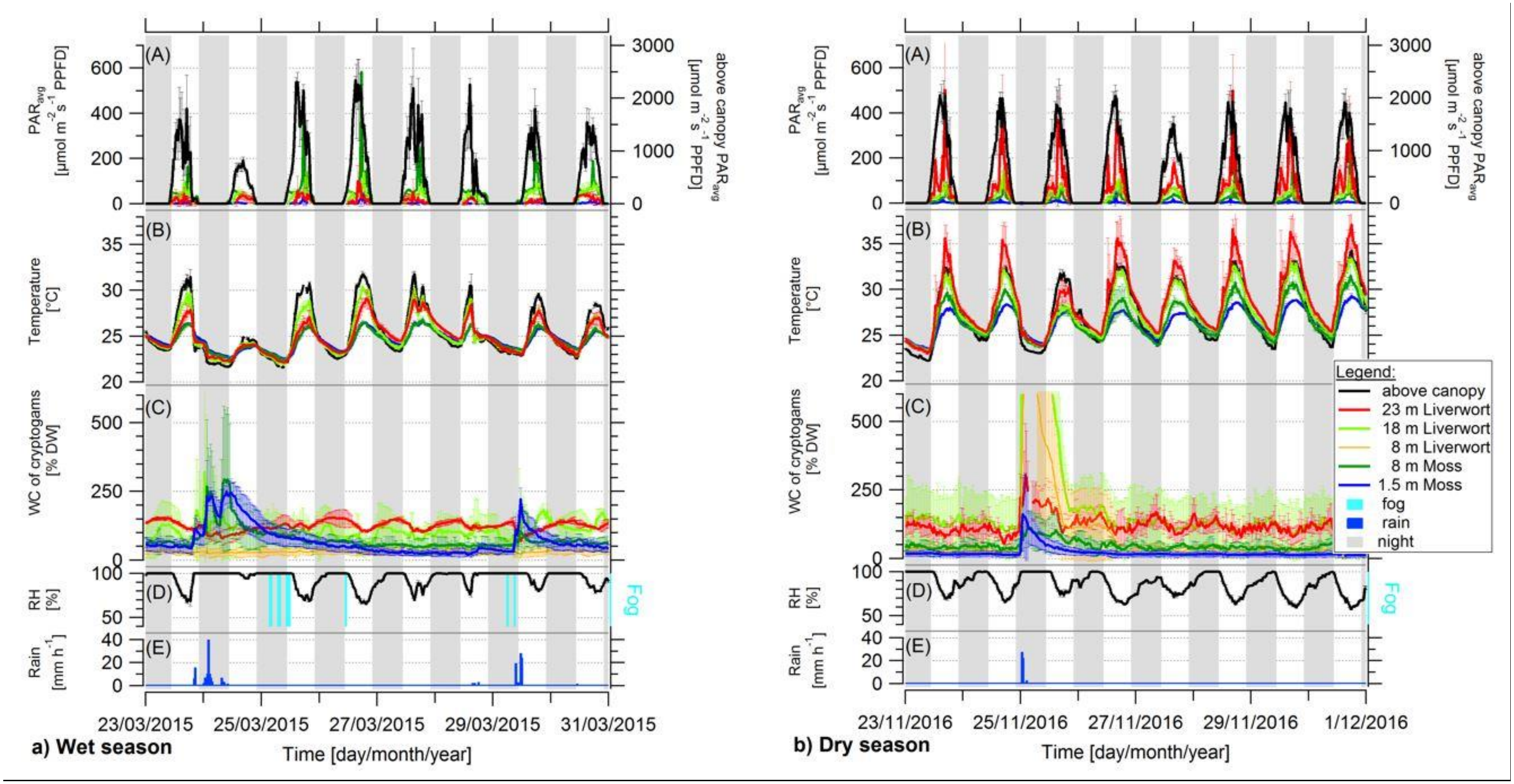
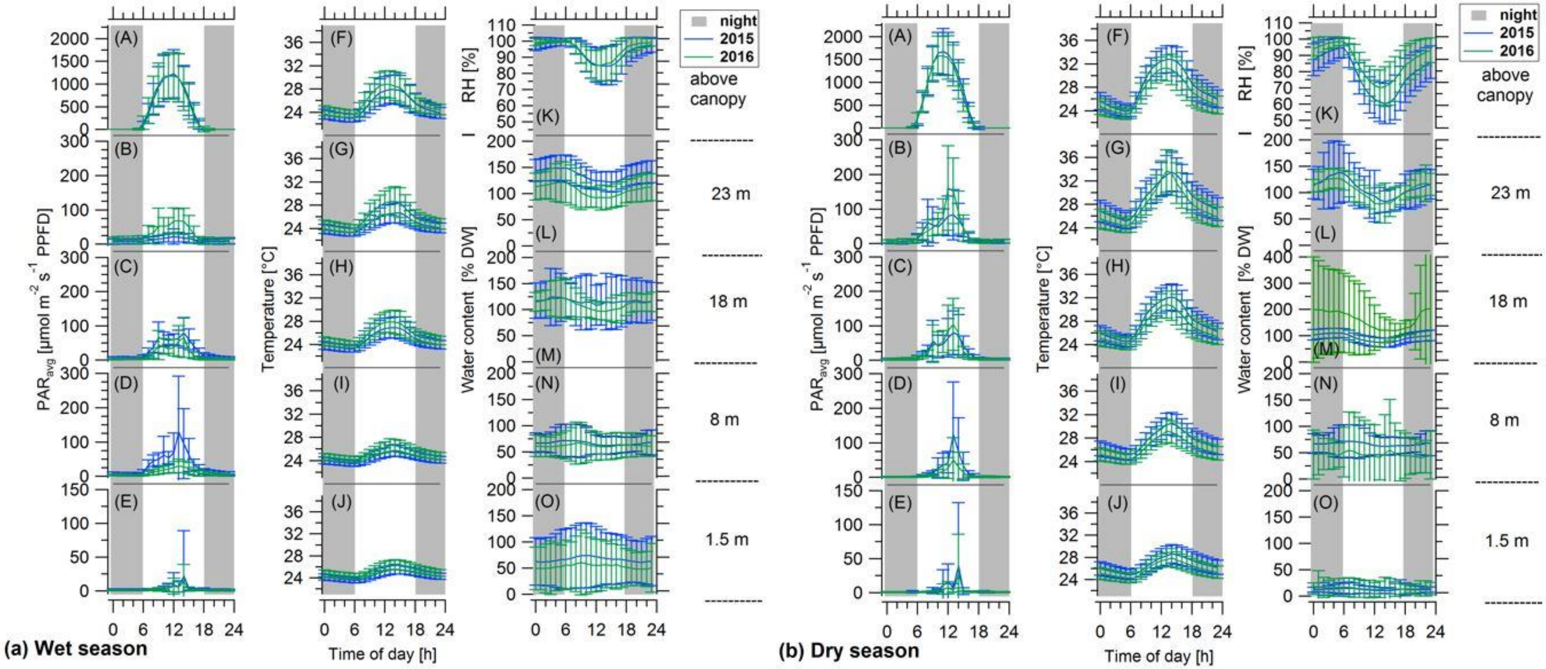


Figure 2: Representative periods during the wet and dry season under average conditions, showing water content (WC), temperature, and light condition (PAR$_{avg}$) of bryophytes, and above-canopy meteorological conditions in the Amazonian rain forest. Shown are 8-day periods during (a) the wet season 2015 and (b) the dry season 2016. The micrometeorological parameters on top/within epiphytic cryptogamic communities represent (A) the photosynthetically active radiation (PAR$_{avg}$) 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 (PAR$_{avg}$ 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. 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 night time is shaded in grey (06:00 – 18:00 LT).


(a) Wet season

(b) Dry season

Figure 3: Mean diurnal cycles of water content (WC), temperature, and light conditions 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) based on 30-minute intervals. The above-canopy meteorological parameters comprise (A) the above-canopy photosynthetically active radiation (PAR$_{avg}$ at 75 m), (F) the above-canopy 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 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. Nighttime is shaded in grey (06:00 – 18:00 LT). Comparisons of maximum and minimum values and diel amplitudes of light, temperature, and humidity between seasons are shown in Table S5 – S7.

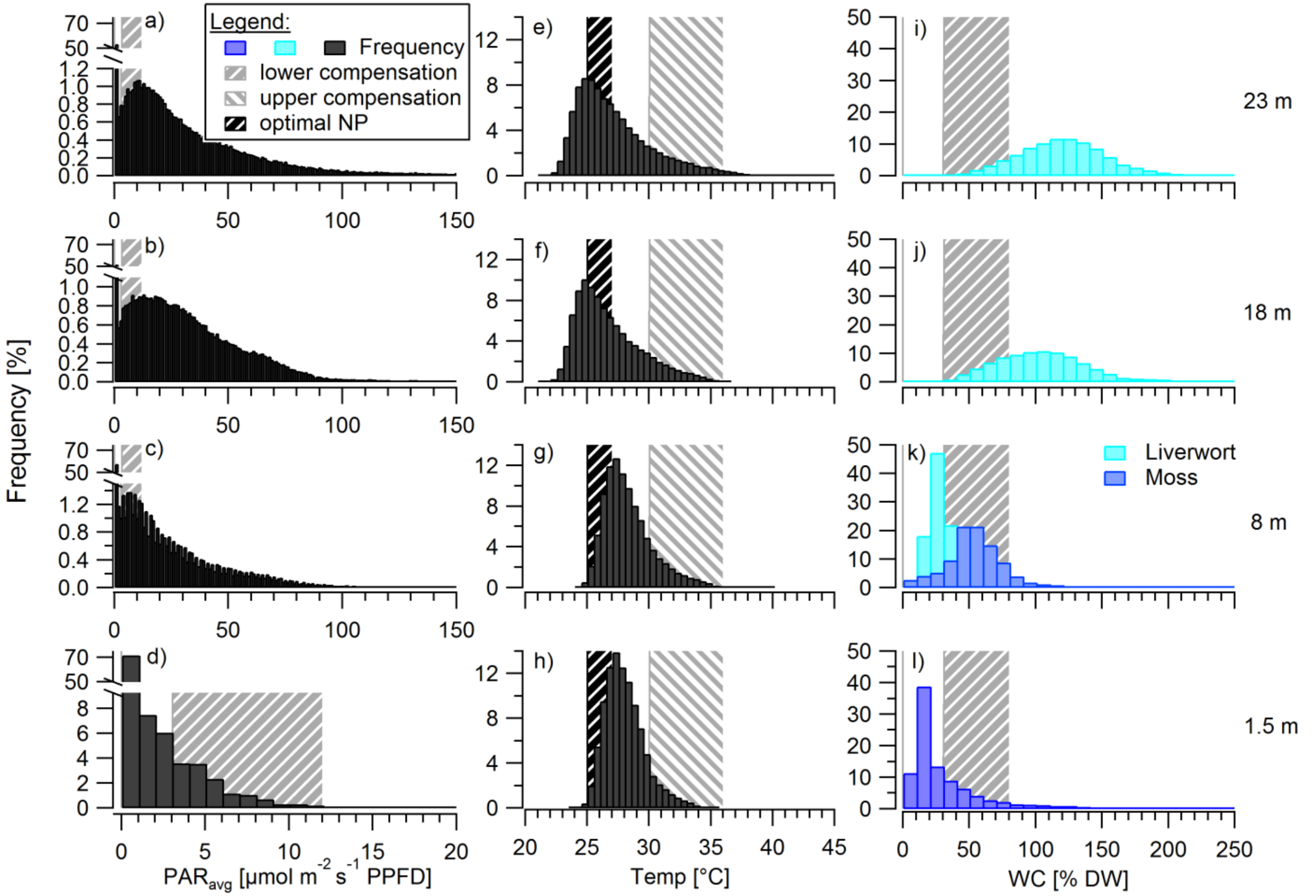


Figure 4: Frequency of photosynthetically active radiation (PAR$_{avg}$; a – d), temperature (Temp; e – h), and water content (WC; i – l) measured on top/within bryophytes at 1.5, 8, 18, and 23 m height within the canopy based on 30-minute intervals. Shaded areas represent the ranges of lower compensation (PAR, WC), upper compensation (temperature), and temperature for optimum net photosynthesis (black shading). Value ranges are adopted from Lösch (1994) and Wagner et al., (2013) (Table S3). Bin sizes: PAR: 1 µmol m^{-2} s^{-1}; temperature: 0.5 °C; WC: 10 %. 5