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 fluctuations 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 in 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

Epiphytic bryophyte communities widely cover the stems and branches of trees in the tropics (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). Whereas studies in temperate zones address the importance of cryptogamic communities for the ecosystem (Gimeno et al., 2017; Rastogi et al., 2018), only few reports for the tropical region can be found in the literature.

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). Up to now, the relevance of cryptogamic communities in these regional cycling processes are largely unknown (Hargis et al., 2019). This data are urgently needed, as this ecosystem is under severe pressure and it is 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).

In the current study, long-term continuous measurements of temperature, light and water content inside bryophyte communities have been conducted along a vertical gradient. To our knowledge, our study is the first one measuring microclimatic parameters and the water status inside bryophyte communities in a rainforest environment. With these data on the microclimate along a vertical profile and during different seasons, we believe to provide a unique dataset, combined with an estimation of the activity patterns of bryophyte communities in a tropical rainforest.

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 bryophyte communities 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, and 23 m above the ground on one tree, corresponding to the zones 1, 2 and 4 (i.e., at the base, the lower trunk, and at the base of the crown) described by Mota de Oliveira and ter Steege (2015), to investigate the variation within the story structure of the forest. 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 three 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* (2 sensors) and *Symbiezidium barbiflorum* (1 sensor), and at 23 m in *Symbiezidium barbiflorum* (3 sensors; Fig. S2, Fig. S3). Additionally, at each height level two temperature and two light sensors (except for 1.5 m with only one light sensor) were installed in/on top of the bryophyte communities located on the approximately 26 m high tree (Fig. S2, Table S1). The temperature sensors were installed in the same communities as the WC sensors, 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 contents were observed (Tab. S1, S2). At 1.5 and 8 m the sensors were installed vertically along the trunk, whereas at 23 m they were placed 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. Additionally, during some episodes the sensors showed unreliable data, which had to be removed from the overall dataset. All data, which could be used for data analysis, are shown in Fig. S5.

The EC values were oscillating, causing an inaccuracy corresponding to approximately 20 mV. Besides the specific position in the substrate, the EC 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 $\mu mol\ m^{-2}\ s^{-1}$ photosynthetic photon flux density (PPFD). To smoothen the microclimate data, 30-minute averages were calculated and used for all further calculations. 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):

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

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 has a fixed distance between the sensor pins, which ensures that in all sensors the resistance is equal. This guarantees that the electrical 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, given as dry weight percentage, as explained below.

To determine the maximum water content of the different bryophyte communities, 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 maximum 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 a water content of 0%, as we assumed that all samples dried at least once over the whole measurement period. Accordingly, the water content (WC) was calculated as follows:

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

with WC_{max} corresponding to the maximum WC measured in the laboratory, EC_i as electrical conductivity, EC_{min} as the minimum electrical conductivity , and EC_{max} as the maximum electrical conductivity measured in the field. The measured electrical conductivity values showed short-time oscillations, which might be caused by the fact that the bryophytes cushions have some air spaces in-between, as we observed that these oscillations are less pronounced in denser substrate. Nevertheless, the overall functionality of the sensors is still ensured also in less dense material, and the short-term fluctuations could be removed with a 30-minute smoothing algorithm. Thus, for all calculations the 30-minute averages were used. The electrical conductivity data of replicate samples at the same height 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 $\text{m}^{-2}\,\text{s}^{-1}$ 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 data are presented as accumulated values in millimeters per month, season, or year, which were calculated by an integration of 30-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.

Based on the climate data, we calculated the dew point temperature, at which saturated air humidity levels are reached. If the temperature drops below the dew point, condensation might occur and form liquid water. The dew point spread is the temperature difference between a surface temperature and the dew point of the surrounding air and can be used to assess potential condensation processes at surfaces. If the difference between the surface temperature T_s and the dew point of the surrounding air T_d is negative, water vapor is able to condense at the colder surface. The calculations were performed according to the following equations:

$$\Delta T_d = T_s - T_d \tag{5}$$

and

$$T_d = \frac{241.2\ \ln\left(\frac{\varphi}{100}\right) + \frac{4222.03716\,\vartheta}{241.2 + \vartheta}}{17.5043 - \ln\left(\frac{\varphi}{100}\right) - \frac{17.5043}{241.2 + \vartheta}} \tag{6}$$

With ΔT_d = dew point spread [°C], T_s = surface temperature (bryophyte sensors, 23 m or 1.5 m) [°C], T_d = dew point temperature air [°C], ϑ = temperature [°C], φ = relative humidity [%]. The dew point spread calculation was performed for the levels of 23 m and 1.5 m height. As a data source for air temperature and humidity, meteorology data assessed at the walk-up tower at 26 m and 1.5 m were used. For surface temperature (T_s), the temperature data measured within the bryophyte communities at 23 m and 1.5 m height were applied. The dew point calculations were performed with R version 3.6.1 (2019-07-05).

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 S4).

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 S3).

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 S3). 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. 1, Table. S5). 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, Fig. S7). 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 S3). 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 monthly WC values of epiphytic bryophyte communities at 1.5 and 8 m varied between seasons in parallel to the monthly rain amounts, whereas at 23 m the values remained relatively stable over the complete measurement time. During the dry seasons, the WC of the mosses at 1.5 m tended to be lowest, whereas during the wet season this was the case for the liverworts at 23 m height (Fig. 1, Tab. 2).

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 % (Fig. 2, Table 2, Fig. S6). 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 %. 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 (Fig.

3). While the microclimatic temperature and light conditions within and on top of the epiphytic bryophyte communities mostly 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 somewhat stronger fluctuations in the dry season than in the wet season (950 ± 93 µmol m^{-2} s^{-1} vs. 738 ± 46 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: 25.7 ± 0.7 °C, dry season: 27.2± 1.0 °C) towards the understory (wet season: 24.9 ± 0.4 °C, dry season: 26.0± 0.8 °C) and the differences among heights and diel amplitudes were more pronounced during the dry season (Fig. 2, 3, Table 2). During the dry season, temperatures within the bryophyte communities at 23 m height were frequently higher than the above-canopy values, and even the seasonal average temperature was 0.6°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 (Table S3). During the wet season, an average RH of 94 ± 2 % and frequently even full saturation was reached, while during the dry season the RH reached an average value of 84 ± 6 % (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, Table S3). According to our observations, fog observed above the canopy normally also occurred (at least to some extent) within the forest.

The WC of the bryophytes at 1.5 and 8 m responded consistently to rain events, while for the liverworts at 23 m height only sometimes an immediate response was observed. During the wet season, the bryophytes at 1.5 and 8 m height contained an increased WC over several days after a rain event, while in the dry season the samples tended to dry quickly again. Overall, the bryophytes at 8 m and 23 m showed a regular and pronounced nightly increase of the WC, especially during the dry season (Fig. 2). Nightly condensation might serve as an additional source of water, as in ~50 % of the wet season and ~30% of the dry season days the surface temperatures of the bryophytes at 23 m height went below the calculated dew point temperature (Fig. S8, Fig. S9). Contrastingly, at 1.5 m height dew point temperatures were only surpassed during ~9 % of the days, independently of season. This occurred preferably in the early morning hours and lasted for ~ 2 h in the canopy (23 m), but only ~ 1 h in the understory (1.5 m).

3.2 Potential physiological activity of bryophytes

Whereas overall light intensities at the upper two height levels were rather similar, with values below 108 and 147 µmol m^{-2} s^{-1} (at 8 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 (Fig. 4). 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). If we assume a lower light compensation point (LCP_l) ranging between 3 and 12 µmol m^{-2} s^{-1} (Lösch et al., 1994), the understory samples (1.5 m) exceeded that range only in less than 20 % of the time during both the wet and the dry season. , whereas at the uppermost height level the bryophytes exceeded these values in during one third to almost half of the time (Table 3).

The temperatures inside the moss stands at different height levels mainly ranged between 22 °C and ~28 °C during the wet and between 23 °C and ~33 °C during the dry season (Fig. 4). For tropical lowland regions, the optimum temperatures for bryophytes (T_{opt}) have been suggested to range between 24.0 °C and 27.0 °C (Wagner et al., 2013). If we assume this range for our study, the temperatures in the understory remained within these limits in 2-77 % of the time during the wet season and in 9-60 % of the time during the dry season (Table 3). In the canopy, temperatures remained in this range in 4-54 % of the time during the wet and in 6-35 % of the time during the dry season (Table 3). For an upper temperature compensation point (TCP), above which respiration exceeds photosynthesis, Wagner and co-authors suggested 30.0 °C – 36.0 °C (Wagner et al., 2013). In the understory, this TCP was never surpassed during the wet season and only rarely 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 0-27 % 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 smaller values in the understory at 1.5 m height than in the canopy (8 m and 23 m), particularly during the dry season (Fig. 4). Considering a lower water compensation point (WCP) between 30 and 80 % according to the literature (Wagner et al., 2013), bryophytes at the uppermost level surpassed these values during 3-80% of the time during the wet and 6-64 % of the time during the dry season. Contrastingly, at 1.5 m and 8 m height there were larger differences between seasons, as the assumed upper range of the WCP was only rarely reached during the dry but during ~ 40% of the time during the wet season. (Fig. 4; Table 3).

4 Discussion

4.1 Microclimatic conditions

In the current study we measured the microclimatic conditions experienced by epiphytic bryophyte communities along a vertical gradient over the course of more than two years. In previous studies, microclimatic data on the light, temperature, and air humidity have been assessed at different height levels within the forest (Chazdon and Fetcher, 1984; Lösch et al., 1994; Romero et al., 2006), but long-term measurements of the water content and the light and temperature on top and inside the cryptogamic communities and have been missing up to now.

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.

Within one height level, the small-scale environmental conditions, such as radiation and shading, water conditions, and wind velocity vary, depending on the specific habitat conditions, as e.g. exposition, tree foliage and inclination of the substrate (Barkman, 1958; Campos et al., 2019; Cornelissen and ter Steege, 1989; Oliveira and Oliveira, 2016; Sierra et al., 2018). These small-scale patterns also explain the variability observed within one height level.

Over the measurement period, the monthly averages of above-canopy light conditions (PAR_{avg}) were rather stable (Fig. 1, Table S3). 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 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, whereas 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 23 m, probably also caused by canopy shading effects at the upper two height levels (Fig. 2). 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 (Fig. 1, Table 1, 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 bryophyte communities at the lower levels (1.5 and 8 m), whereas those in the canopy showed similar water contents during all seasons (Fig. 2, Fig. S6a, Table 2).

The data also suggest that the position of the measured communities and the tree foliage played a crucial role for rainwater absorption and the subsequent drying process. Whereas the sensors at 1.5 m and 8 m height responded quite reliably to rain events during all seasons, these at 23 m responded quite reliably during the dry but only rarely during the wet seasons. This might be caused by a dense foliage during the wet season, shading the communities at 23 m from direct inundation, whereas during the dry season the canopy foliage changes a lot and intense leave shedding takes place before new leaves develop, which seems to allow rain to also reach the samples directly below the canopy (Lopes et al., 2016).

During the wet season, the WC of bryophytes in the understory and at 8 m height responded strongly to rain events and subsequently, the water was lost gradually with bryophytes staying wet and active over prolonged time spans, indicating that large amounts of water were taken up during prolonged rain events (Fig. 2, Fig. S6). In contrast to that, during the dry season the drying of the samples occurred quite rapidly after the rain during the dry season. 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 strong rain events occurring more frequently during the wet season.

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 water content data at 8 m and 23 m height showed diel fluctuations, particularly during the dry season, with the highest water contents reached during the morning hours. This might be caused by condensation, as our data suggest that at 23 m height bryophyte temperatures regularly fall below dew point temperatures in the early morning hours. The WC of bryophytes could increase upon fog, which has also been shown in some other studies (León-Vargas et al., 2006).

In addition, also the water holding capacity of different bryophyte species, which is influenced by the life form and has been described in several other studies (Lakatos et al., 2006; Romero et al., 2006; Williams and Flanagan, 1996; Proctor, 1990), may play a role in the WC patterns observed by us. At 23 m height, the WC sensors were placed in communities dominated by the liverwort *Symbiezidium barbiflorum* (Lejeuneaceae), which has been described to have the life-form of a mat (Batista and Santos, 2016; Mägdefrau, 1982; Valente et al., 2017). Mats have been described to have a high capillarity retention of water, which may support an uptake and particularly storage of condensed water. In addition, mats have an increased drought-tolerance, being more adapted to dry conditions as well as to extreme changes (Gimingham and Birse, 1957), which occur below the canopy as observed by us. In the understory at 1.5 m height, *Sematophyllum subsimplex* (Sematophyllaceae) and *Leucobryum martianum* (Dicranaceae) occur, which belong to the life-forms of wefts and turfs, respectively (Mägdefrau, 1982, Batista and Santos, 2016; Valente et al., 2017). They have been described to show high values of capillary water conduction and lower values of water retention (Mägdefrau, 1982). Wefts have been characterized as life forms characteristic of humidity areas (Gimingham and Birse, 1957).

The distribution of bryophytes among height zones exhibit a well-known pattern for the Amazon rainforest (Cornelissen and ter Steege, 1989; Mota de Oliveira, 2010; Mota de Oliveira and ter Steege, 2015; Pantoja et al., 2015). Studies describe that Lejeuneaceae (common liverwort family registered for Amazonian region) are more diverse and abundant in the canopy area, while mosses are mainly concentrated at the tree base and trunk in a plateau ecosystem (Campos et al., 2019; Mota de Oliveira, 2010, 2018). The species identified by us (Table S1) 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).

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).

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.

Utilizing the compensation points of water, light, and temperature taken from the literature, one can make rough estimates of the time fractions when NP and DR occur at the different height levels (Table 3).

These data suggest that at the upper height level NP occurred in 1-30 % and DR in 2-52 % of the time during the wet season and in 1-24 % (NP) and in 4-45 % (DR) of the time during the dry season, respectively (Table 3). These estimates suggest that the duration of DR was about twice as long as that of NP. For the samples at 8 m height the results were similar, whereas for those in the understory the duration of DR was about 5- to 30-fold higher than the duration of NP. The large discrepancy between the time ranges for NP and DR calculated for the bryophytes in 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 upper height levels. For other habitats, LCP_l values 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 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 responded reliably upon rain events, and after major rain events, the samples could stay wet for several days before they dried out again. In contrast to that, the WC of the bryophytes in the canopy responded only very rarely to rain events during the wet season, probably caused by the dense foliage, and kept relatively stable low water contents. During the dry season, probably due to the less dense foliage, they responded to some rain events and showed a regular nightly increase in water contents, which might be a combined effect of nightly condensation and thallus morphology (life form). Thus, our data suggest that the relevant water source for bryophytes in the understory might be rain, while for the bryophytes in the canopy nightly condensation 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, RPA 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 deviations (± SD) of mean daytime photosynthetically active radiation (PAR_{avg}), temperature, and water contents (WC) of bryophytes at the three 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 30-minute intervals. 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). Values for PAR_{max} can be found in Table S6.

(a)

Height	**2015**		**2016**	
	Mean	**SD**	**Mean**	**SD**
PAR_{avg} daytime[µmol m^{-2} s^{-1}]				
above-canopy	819	596	824	599
23 m	32	37	49	52
8 m	43	50	8	14
1.5 m	5	15	3	8
Temperature [°C]				
above-canopy	26.6	3.4	26.4	3.1
23 m	26.1	3.0	26.8	3.3
8 m	25.8	2.3	25.8	1.9
1.5 m	25.4	1.8	25.5	1.5
Water content [%]; above canopy RH [%]				
above-canopy	86	15	90	13
23 m	39	30	47	69
8 m	70	45	73	72
1.5 m	64	85	38	53

(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 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 30-minute intervals from October 2014 to November 2016 Values for PAR_{max} can be found in Table S7.

Height	**PAR_{avg} daytime [µmol m^{-2} s^{-1}]**		**Temperature [°C]**		**RH (above-canopy) [%], WC [%]**	
[m]	Mean	± SD	Mean	± SD	Mean	± SD
Wet season						
above-canopy	738	46	25.7	0.7	94	2
23 m	27	17	25.3	0.6	41	3
8m	41	24	24.9	0.4	93	21
1.5	3	1	24.9	0.4	83	26
Transitional season Wet-Dry						
above-canopy	860	53	25.6	0.5	91	2
23 m	38	29	25.7	0.7	49	4
8 m	63	14	24.9	0.4	72	27
1.5 m	2	1	24.6	0.2	31	6
Dry season						
above-canopy	950	93	27.2	1.0	84	6
23 m	54	21	27.8	1.2	45	10
8 m	24	17	26.6	0.9	58	20
1.5 m	5	4	26.0	0.8	30	31
Transitional season Dry-Wet						
above-canopy	784	111	26.5	1.6	87	8
23 m	52	34	27.1	2.2	37	2
8 m	23	5	26.2	1.7	58	13
1.5 m	4	1	25.9	1.4	52	53

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, 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. Thirty-minute averages of measurements during the entire measurement period from October 2014 to November 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**
		≥ 3-12	24.0-27.0	≥ 30.0-36.0	≥ 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	33-43	4-54	0-3	3-80	1-30	2-52
8	M & L	24-31	2-74	0	42-94	14-35	29-59
1.5	M	2-19	2-77	0	32-80	1-13	32-67

b) Dry season

Height	**Division**	**LCP_l**	**T_{opt}**	**TCP**	**WCP**	**NP**	**DR**
		≥ 3-12	24.0-27.0	≥ 30.0-36.0	≥ 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	40-46	6-35	0-27	6-64	1-24	4-45
8	M & L	18-35	8-51	0-11	5-84	2-34	7-51
1.5	M	3-16	9-59	0-4	2-21	0-5	10-26

Figures

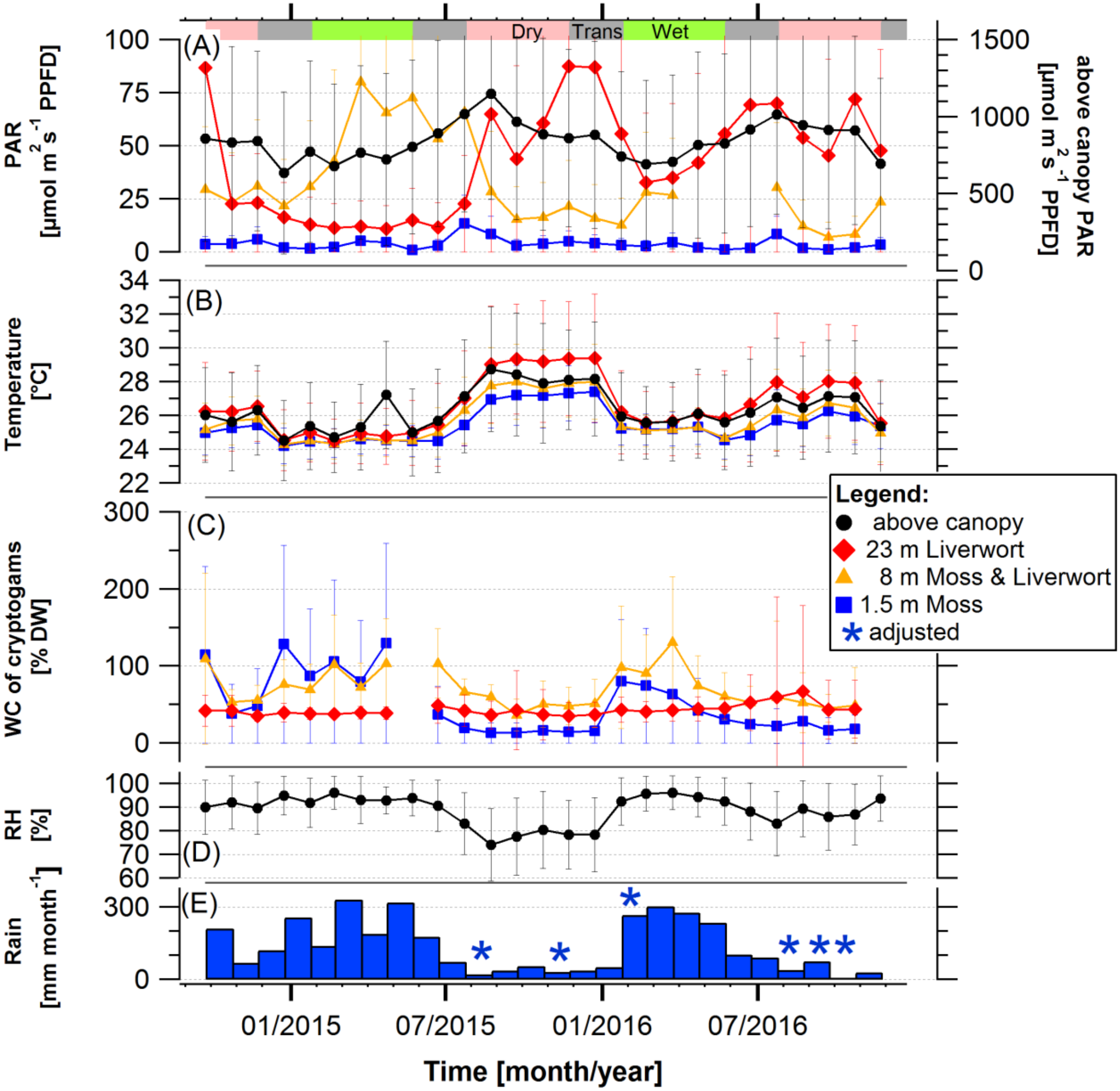
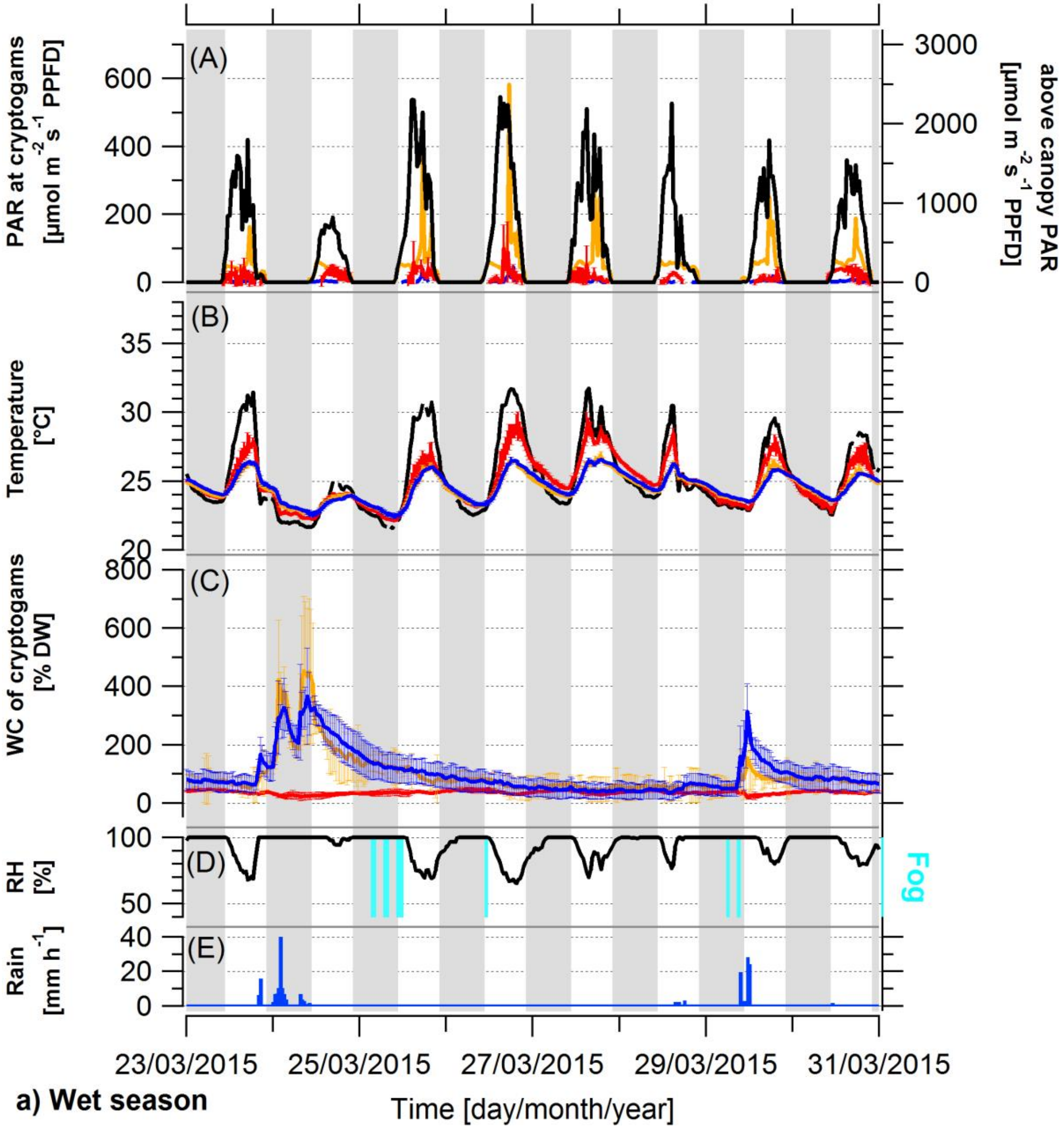


Figure 1: Mean light condition (PAR), temperatures, and water content (WC) experienced by bryophyte communities, and above-canopy meteorological conditions in the Amazonian rain forest. The micrometeorological parameters on top/within epiphytic cryptogamic communities represent monthly mean values ± SD of (A) daily average (06:00 – 18:00 LT) of photosynthetically active radiation (PAR) 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 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 S3 and S5.


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

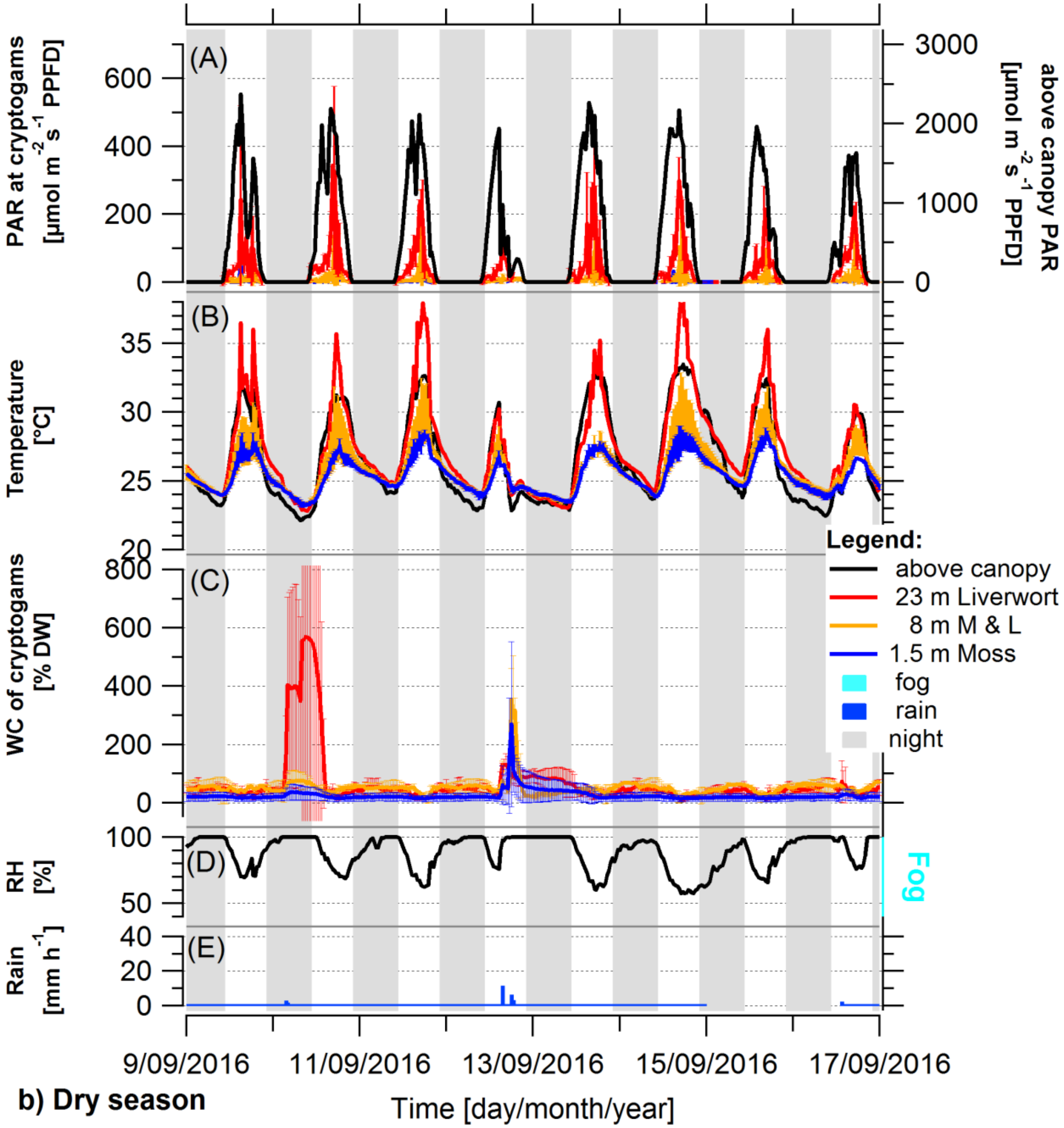
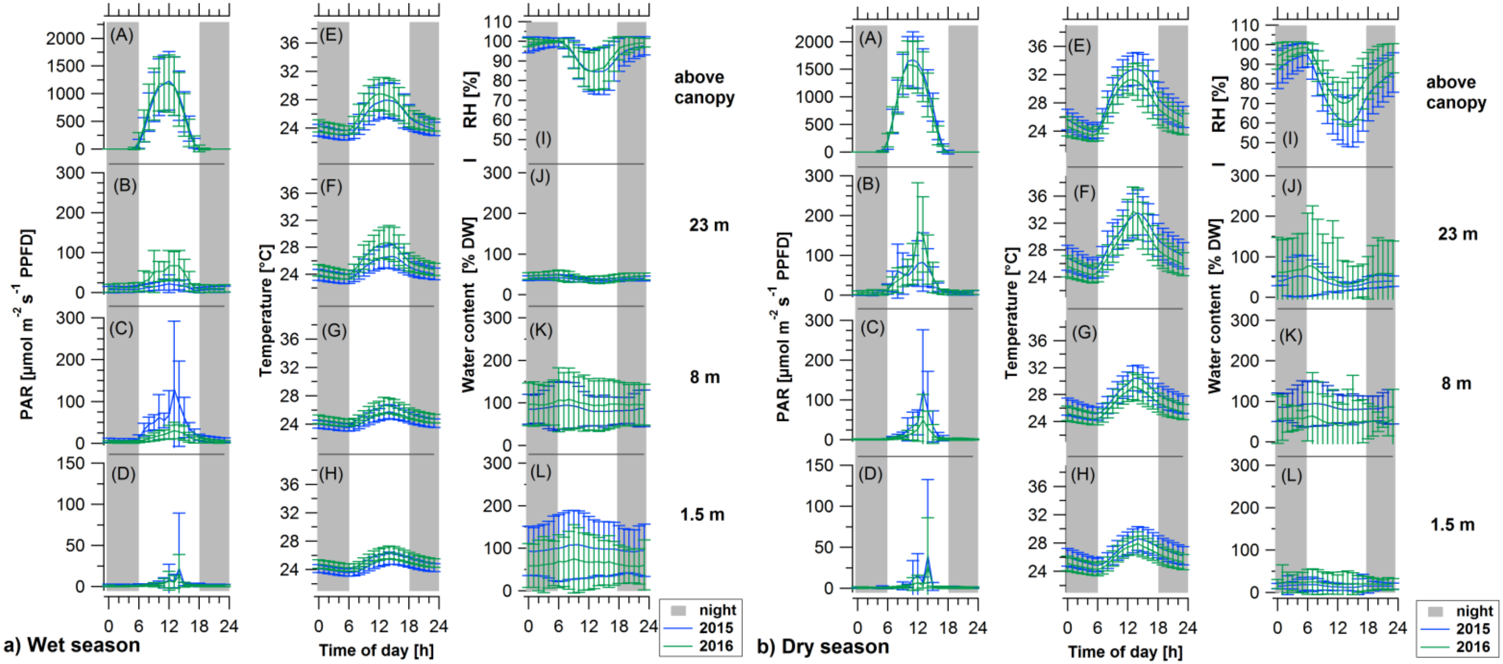


Figure 2: Representative periods during the wet and dry season under average conditions, showing light condition (PAR), temperature, and water content (WC) of bryophytes, and above-canopy meteorological conditions in the Amazonian rain forest. Shown are 8-day periods during (a) the wet season 2015 and (b) the dry season 2016. The micrometeorological parameters on top/within epiphytic cryptogamic communities represent (A) the photosynthetically active radiation (PAR) 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

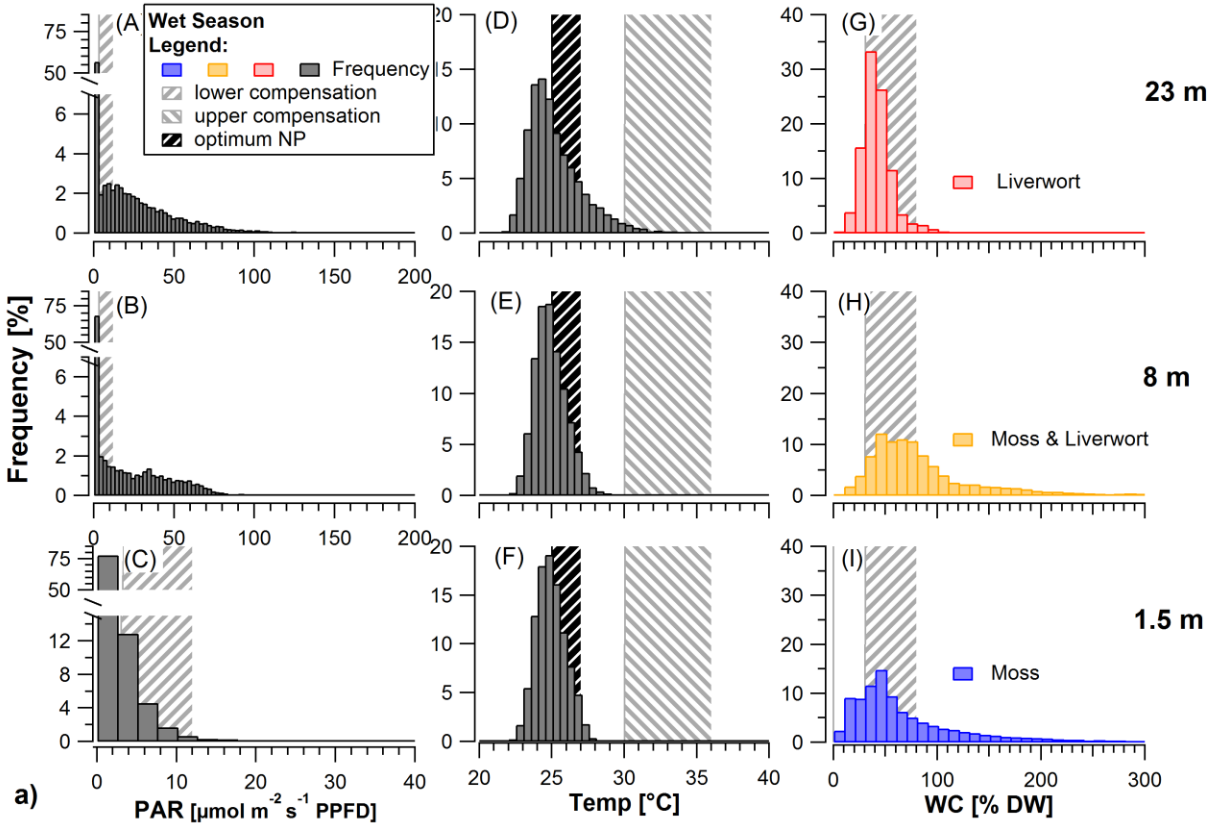
(PAR at 75 m), (B) above-canopy temperature (at 26 m), (D) relative air humidity (RH at 26 m height), presence of fog events, and (E) rain amount. The data show 30-minute averages ± SD except for rain, which shows hourly sums. Data of replicate sensors installed within communities at the same height level were pooled, while above-canopy parameters were measured with one sensor each. The nighttime is shaded in grey (06:00 – 18:00 LT).



a) Wet season

b) Dry season

Figure 3: Mean diurnal cycles of light conditions (PAR), 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 at 75 m), (E) the temperature (at 26 m), and (I) the relative air humidity (RH at 26 m height). The micrometeorological parameters measured on top/within epiphytic cryptogamic communities comprise (B – D) the photosynthetically active radiation (PAR) on top, (D – H) the temperature within, and (J – L) 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. Nighttime is shaded in grey (06:00 – 18:00 LT).


Wet Season
Legend:
🟦 🟨 🟥 ⬛ Frequency
▨ lower compensation
▨ upper compensation
▨ optimum NP
(A)
(B)
(C)
(D)
(E)
(F)
(G)
(H)
(I)
23 m
8 m
1.5 m
Liverwort
Moss & Liverwort
Moss
Frequency [%]
75
50
6
4
2
0
12
8
0
50
100
150
200
0
10
20
30
40
20
15
10
5
0
20
25
30
35
40
40
30
20
10
0
0
100
200
300
a)
PAR [µmol m^-2 s^-1 PPFD]
Temp [°C]
WC [% DW]

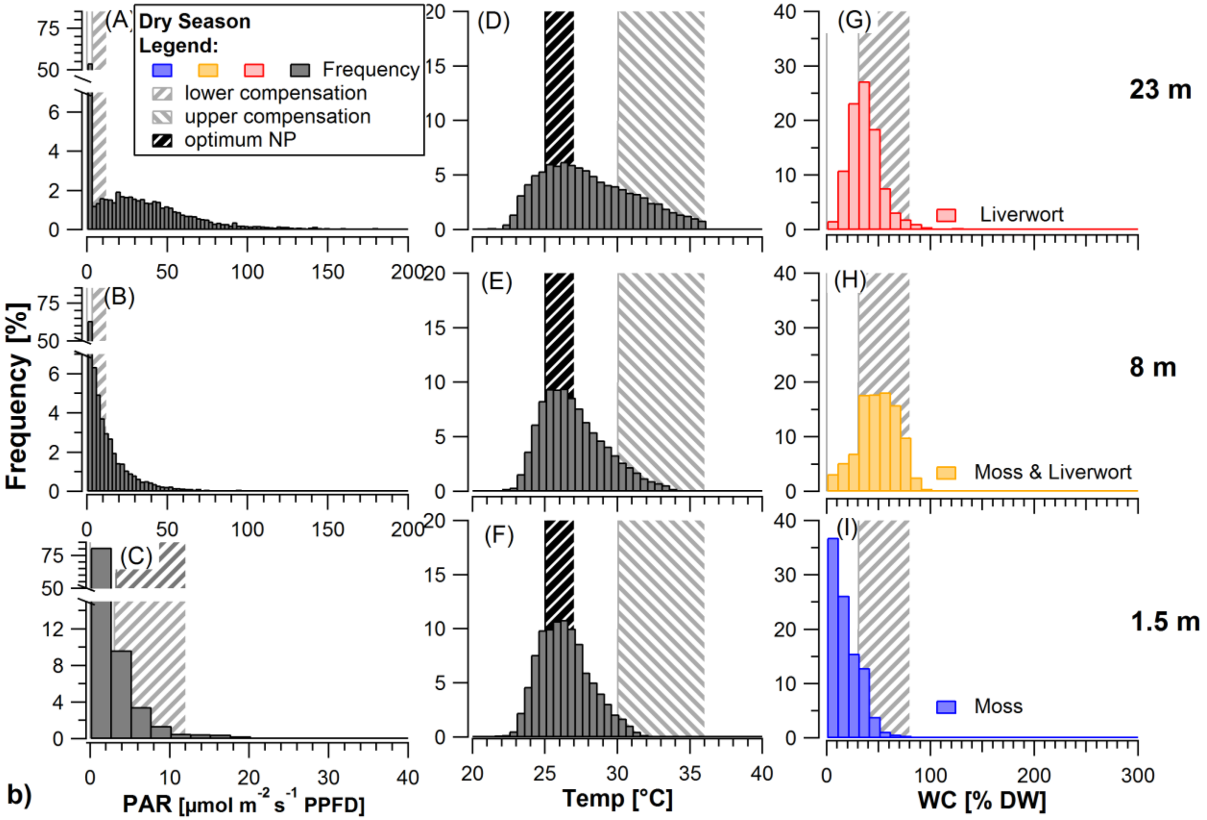


Figure 4: Estimated frequency of mean photosynthetically active radiation (PAR; A – C), temperature (Temp; D – F), and water content (WC; G – I) measured on top/within bryophytes at 1.5, 8, and 23 m height during (a) the wet and (b) the dry season. Calculation of the histograms based on 30-minute intervals. Shaded areas represent the ranges of reference values for lower compensation (PAR, WC), upper compensation (temperature), and the optimum (temperature) for net photosynthesis, as measured by Lösch (1994) and Wagner et al., (2013) (Table S4). Bin sizes: PAR: 2.5 µmol m^{-2} s^{-1}; temperature: 0.5 °C; WC: 10 %.