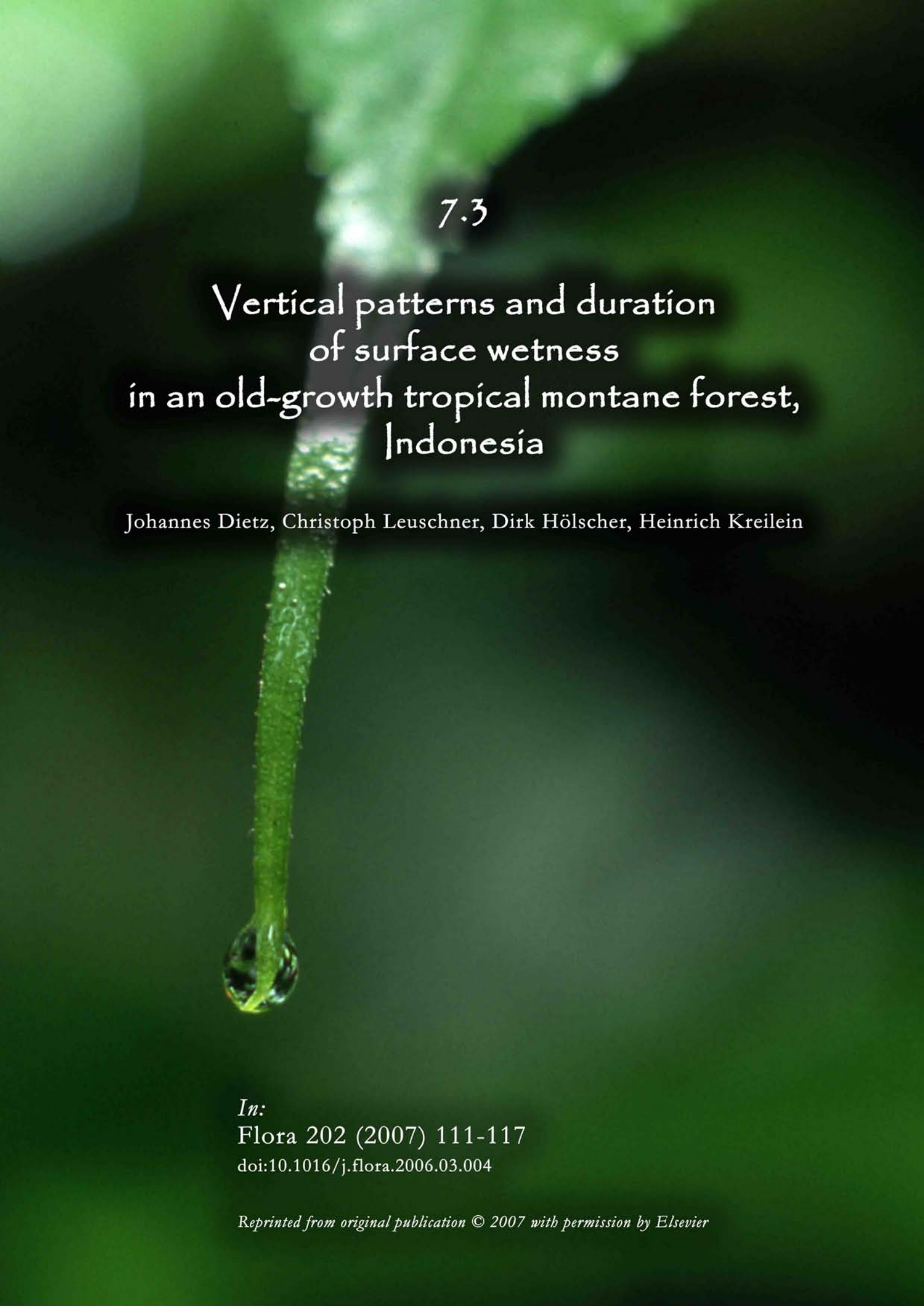


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Vertical patterns and duration of surface wetness in an old-growth tropical montane forest, Indonesia

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Abstract

In tropical montane forests, the wetness of leaf surfaces is an important parameter which may influence gas exchange, growth and vitality of leaves, and forest productivity. Thirty surface wetness sensors were operated during May–August 2004 in a vertical profile inside an old-growth lower montane rain forest of Central Sulawesi, Indonesia, with the objective to analyse spatial and temporal patterns of surface wetness and to relate wetness duration to the microclimate inside the stand. The canopy was wet during 25–30% of time in this study period. In a dry period, however, surface wetness lasted for only 5% of the time, whereas the canopy was wet during 45–55% of the time in a rainy period. In the lower shade canopy, surface wetness continuously existed for periods of up to 22 h and more, although rainfall occurred only during afternoon thunderstorms of limited duration. The long duration of surface wetness has implications for forest interception models, which assume a complete drying of the canopy between subsequent rainfall events. In periods with rainfall, leaf wetness typically occurred in the afternoon, evening and first half of the night because intercepted water persisted on the leaves until about midnight. In dry periods, in contrast, surface wetness was mainly caused by dewfall in the second half of the night, and it occurred mainly in the uppermost canopy where radiative heat losses resulted in a substantial under-cooling of the leaves. Ecophysiological and hydrological importance is suggested by the long duration of surface wetting in this stand with possible implications for gas exchange, leaf growth, leaf colonization by epiphylls and the forest water balance.
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Keywords: Dewfall; Dew point temperature; Microclimatology; Rainfall patterns; Saturation deficit

Introduction

Tropical montane forests exist in relatively cool and humid climates where high rainfall amounts prevail. On the slopes of tropical mountains, convective uplift of heated air masses forces water vapour to condensate at elevations of about 1,500–3,500 m (Hastenrath, 1991). Montane forests receive three different types of precipitation, i.e. vertical rainfall, fog interception (horizontal precipitation) and dewfall. Vertical rainfall may be as high as 6,000 mm yr^{-1}, and it can exceed 10,000 mm yr^{-1} at certain locations. Much less is known about the other two types of precipitation. Water loss with evapotranspiration most likely is comparably small in montane forests since temperature is lower than in the hot lowlands and cloud cover frequently reduces the radiation load. Therefore, tropical montane forests are

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typically characterized by a high water surplus, which plays an increasing role as a water source for the ever growing cities in tropical countries.

From an ecological perspective, tropical montane forests are characterized by their reduced tree size compared to lowland forests. A variety of hypotheses have been proposed to explain the structural and functional characteristics of tropical montane forests. They include (1) lowered temperatures at higher elevations (Kitayama and Aiba, 2002), (2) temperature-induced nutrient shortage (Tanner et al., 1998), (3) reduced insolation (Letts and Mulligan, 2005), (4) limited root aeration due to poor drainage (Odum et al., 1970), and other environmental constraints that could limit tree growth at higher elevations (Bruijnzeel and Veneklaas, 1998). Grubb (1977) has forwarded the hypothesis that the prevalence of high air humidities should reduce tree transpiration, thereby impairing nutrient uptake and causing nutrient deficiency.

Indeed, climate chamber experiments have shown that very high air humidities can reduce foliar nutrient levels of herbaceous plants (Leuschner, 2002). Letts and Mulligan (2005) present further field-based evidence for the inhibition of photosynthesis and productivity by leaf wetness in neotropical montane cloud forests. High air humidity can also favour pathogen attack of leaves which may reduce plant productivity (Magarey et al., 2005). On the other hand, there is substantial evidence that leaves expand more rapidly under high air humidities, and leaf conductance typically is higher under low saturation deficits which may enhance photosynthetic carbon gain (e.g. Gouvra and Grammatikopoulos, 2003; Hanba et al., 2004). Whether high levels of air humidity are significantly affecting tree growth in tropical montane forests and whether positive or negative effects on growth are prevailing, may largely depend on the duration of periods with saturation deficits close to zero.

Most terrestrial plants are not only exposed to high air humidities in part of their life, but frequently experience liquid water on photosynthetic surfaces as well (Barr and Gillespie, 1987; Harrington and Clark, 1989). In moist tropical environments, leaf surface wetness may be an important growth regulating factor for woody and herbaceous plants because epiphyllic lichens, mosses, fungi and also pathogens are thriving on wet leaf surfaces inhibiting light absorption by the leaf. On the other hand, transpiration rate and xylem water flux, and leaf carbon dioxide uptake may partly be inhibited by a water film covering the stomates (Brewer and Smith, 1994, 1995; Ishibashi and Terashima, 1995). The wetness of plant leaf surfaces is also an important parameter in the deposition process of atmospheric trace gases and pollutants (Klemm et al., 2002). Brewer et al. (1991) hypothesized that a strong selective pressure should exist for the repulsion of water films on leaf surfaces in environments with frequent leaf wetting events.

Until recently, remarkably little has been known about the occurrence of leaf wetness in tropical montane forests and its variation in time and space in the stand. Brewer and Smith (1997) analysed patterns of leaf wetness for montane and subalpine plants in the temperate Rocky Mountains, and Klemm et al. (2002) conducted similar measurements in temperate forests of Europe. We are aware of only very few studies that systematically monitored surface wetness in tropical montane forests for extended periods (Letts and Mulligan, 2005; Leuschner and Schulte, 1991). Here, we present data of a 3-month study with 30 leaf wetness sensors mounted in a vertical profile inside a lower montane rainforest in Central Sulawesi, Indonesia. Study objective was to analyse leaf wetness patterns in rainless and rainy periods and to relate wetness patterns to microclimate and rainfall regime.

Methods

Study site

The study was conducted in an old-growth tropical lower montane forests at about 1430 m elevation on the eastern fringes of Lore Lindu National Park near Bariri, province of Poso, Central Sulawesi, Indonesia (1.6579°S, 120.1735°E). The study site is located on a level plateau. A 70 m tall meteorological scaffolding tower inside the forest was used for mounting surface wetness and micrometeorological sensors in a vertical profile in the stand. The forest is a closed stand with a stem density (>10 cm in dbh) of 557 ha^{-1}, and a maximum tree height of 41.5 m. The undulating surface of the forest canopy reaches about 32 m, and the height of the average tree (according to dbh) is 24.7 m. With an estimated number of 100–150 tree species pre hectare, the forest is highly diverse (Kessler et al., 2005). The most species-rich tree family in the study region is the Lauraceae. A structural analysis inside the forest revealed that the mean height of the lowest branch was 12.2 m. The understorey contains a sparse layer of young tree individuals. Except for small-scale disturbances in the understorey during the tower construction phase, the forest shows no signs of major anthropogenic impact.

Leaf wetness and microclimatological sensors

We used surface wetness sensors of Skye Instruments Ltd. (Powys, UK) to estimate the duration of leaf surface wetness at different heights inside the forest. Wetness is recorded through changes in current output

that occur when a DC circuit is shortcut by a water film on the surface of a gold-covered horizontal plate of 80 mm × 80 mm in size. The sensors were mounted on horizontal poles that allowed positioning them inside the tree canopies close to the leaves. We installed 30 sensors in 1.5 m intervals from 1.5 to 33.0 m above the ground. At 1.5, 3.0, 4.5, 6.0, 27.0, 28.5, 30.0, 31.5 and 33.0 m height, two sensors were operated in parallel in order to obtain average values of surface wetness. To allow for measurements in the undisturbed understorey, all wetness sensors below 6.0 m height were mounted on a separate pole 12 m east of the tower base. Air temperature and air humidity were measured using radiation-shielded and ventilated dry and wet bulb thermometers (Friedrichs 3030.0000 BG sensors, Theodor Friedrichs & Co., Schenefeld, Germany). They were placed 2 m above ground on a separate weather station in the understorey approx. 15 m southwest of the tower base. Inside the canopy, temperature and air humidity were measured at 22 and 36 m above ground on horizontal poles protruding 1.5 m from the north-eastern corner of the tower. Precipitation was recorded with two Friedrichs 7041.0000 ombrometers placed at a distance of 3 m to each other on the top of the tower at 69 m above ground.

Surface wetness data were recorded during a 3-month period in 2004 using a CR10X logger combined with an AM16/32 relay multiplexer (both Campbell Scientific, Inc., Shepshed, UK). Data were read from all 30 sensors in 15 s intervals and stored as 5 min means. Microclimate data were recorded separately at each height with a Friedrichs Kombilog 1020 logger (Theodor Friedrichs & Co., Schenefeld, Germany). Sensors were scanned every 10 s and data were stored as 5 min means.

Results

Diurnal courses of microclimate parameters in wet and dry periods

Two example days from June 2004 with typical, but contrasting, weather conditions were selected for analysing the interdependency of air temperature (T_a), atmospheric saturation deficit (Δe) and measured surface wetness in the old-growth forest near Bariri. June 11 stands for days with a cloudless morning and subsequent formation of convective clouds around noon, followed by thunderstorms with heavy rainfall in the afternoon and evening (Fig. 1a). In contrast, June 22 exemplifies a bright cloudless day without rainfall as it is characteristic for about 30% of the days of a year at Bariri (Fig. 1b).

On rainy June 11, the vertical air temperature gradient from the forest floor through the canopy to the turbulent air layer above the canopy approached zero during the night-time hours (18 h to 6 h). On dry June 22, in contrast, the inner canopy at 22 m height remained by c. 0.5 K warmer than the air layer 6 m above the canopy (36 m height) for most of the night (unfortunately, the temperature sensor at 1.5 m above

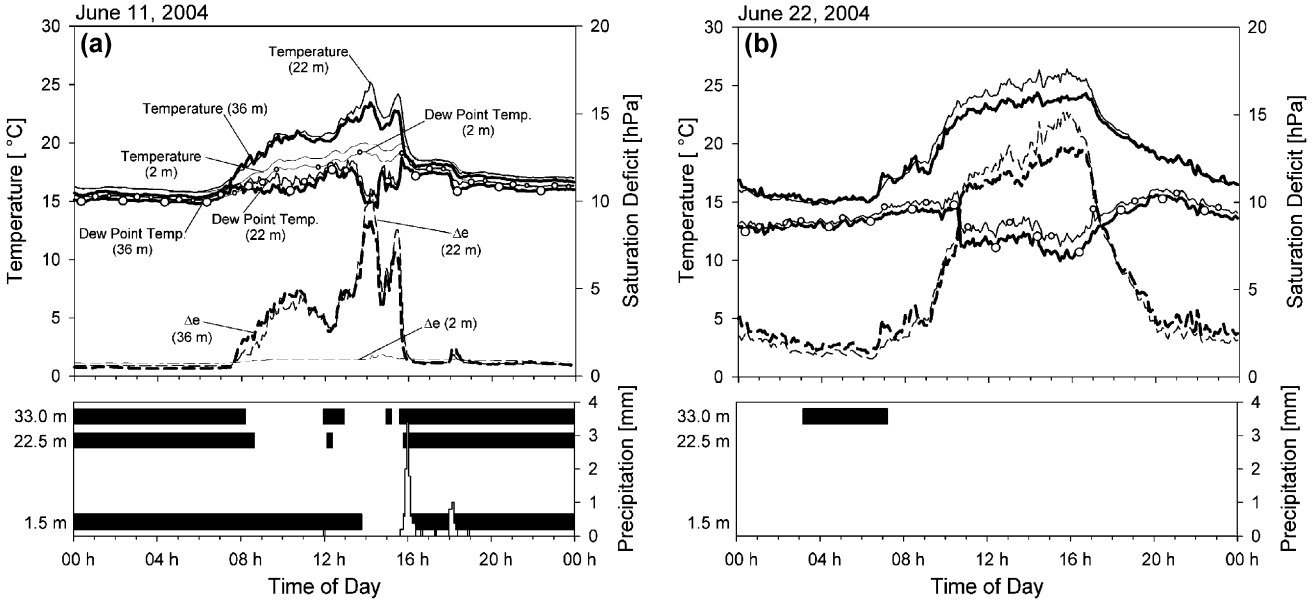


Fig. 1. (Upper panels) Daily courses of air temperature, dew point temperature and atmospheric saturation deficit (Δe) at 2, 22 and 36 m height inside and above the canopy of the Bariri forest on June 11 with afternoon rainfall (a), and on dry June 22, 2004 (b). (Lower panels) Duration of surface wetness at 1.5, 22.5 and 33.0 m height inside the forest and precipitation on June 11 (a) and June 22 (b).

the forest floor failed on this day). During the daylight hours of June 22, the inner canopy was by 1–2 K warmer than the air above the canopy revealing a substantial canopy over-temperature, whereas the canopy was only 0.5–1 K warmer than the air on rainy June 11 (Fig. 1a and b).

Striking differences between the wet and the dry days existed also with respect to the atmospheric saturation deficit. On rainy June 11, Δe remained close to zero during the night-time hours inside and above the canopy, and also did so at 1.5 m height close to the forest floor during the daytime hours. On dry June 22, in contrast, Δe remained at 2–3 hPa in and above the stand during the night (Fig. 1a and b). The saturation deficit reached daytime maxima of 15 and 10 hPa in the early afternoon of the dry and the rainy day, respectively. Remarkably, Δe maxima were by 2 or 3 hPa larger inside the canopy (22 m) than in the turbulent air above the trees (36 m) because the canopy maintained a significant over-temperature during the day.

Being determined by air temperature and saturation deficit, the dew point temperature (T_{DP}) remained very close to T_a during the night on rainy June 11, but it was below air temperature during the night of dry June 22 (Fig. 1a and b). Thus, on rainy June 11, dew point was approached during 24 h of the day (0–24 h) at the forest floor, and on 17–18 h of the day inside and above the canopy. In contrast, our temperature sensors did never record a drop of T_a to dew point temperature on dry June 22.

The results on the daily courses of T_a and T_{DP} closely match with the duration of recorded surface wetness. On rainy June 11, the wetness sensors indicated a surface water film on 22 of 24 h of the day at the forest floor, and on 16–18 h of the day inside and above the canopy. In contrast, on dry June 22, only the wetness sensors at maximum canopy height (33 m) gave a positive signal for about 4.5 h before sunrise when T_a dropped toward T_{DP} (although it never met dew point temperature, Fig. 1b).

Diurnal and seasonal variation of leaf surface wetness in the stand

In a 3-week period with average rainfall conditions (May 21–June 13, 2004), about 45% of the days received sufficient rainfall to moisten the entire forest canopy from the top to the forest floor in the afternoon. This is indicated by the frequency of surface wetness at sunset (7 p.m.) in Fig. 2a. On a typical evening of this measuring period, Δe was still larger than 1.5 hPa throughout the canopy thereby preventing the occurrence of dewfall in the first half of the night. During midnight, air temperature inside the canopy typically had dropped by 2–3 K, thereby reducing the

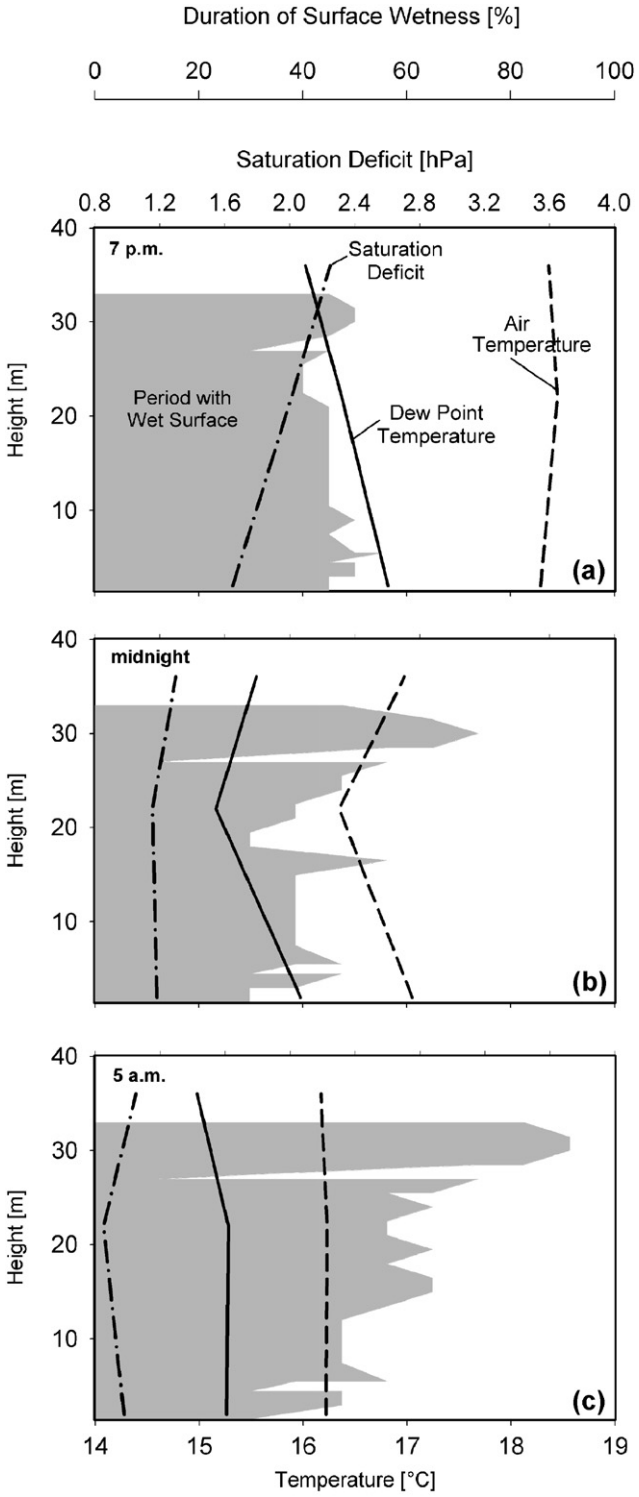


Fig. 2. Average duration of surface wetness (in per cent of the time) after sunset (7 p.m., a), at midnight (b) and before sunrise (c) in the period May 21–June 13, 2004, in a vertical profile inside the Bariri forest as measured with 30 surface wetness sensors mounted between 1.5 and 33.0 m height. Average vertical profiles of air temperature, dew point temperature and atmospheric saturation deficit after sunset, at midnight and before sunrise are also depicted for this period.

atmospheric saturation deficit to about 1 hPa. This allowed for the occurrence of dewfall in the upper canopy (Fig. 2b). In about 90% of the nights, surface wetness was recorded in the upper canopy (at about 30 m) shortly before sunrise at 5 a.m. This indicates that dewfall apparently is occurring regularly from midnight onwards in the upper canopy, but not in the lower canopy. After sunrise, surface wetness rapidly disappeared in the sun-lit canopy on all days (see Fig. 1, lower panel).

The average duration of surface wetness in the stand differed greatly in dependence of the rainfall regime. This is visible from a comparison of periods with different rainfall amounts in the 11-week measuring period. When analysing the whole study period (May 11–August 11, 2004), the canopy was covered by water during 25–30% of the time (Fig. 3d). In this period, upper and lower canopy strata behaved similar with respect to wetness duration. A comparison of 2-week periods with either very low (0.2 mm), low to medium (19.2 mm), or high rainfall amounts (101.4 mm) showed that surface wetness was highly different between dry and wet periods. Wetness lasted for less than 5% of the time in the dry period, and leaf wetness occurred for much longer in the uppermost canopy layer indicating the influence of occasional dewfall or fog interception (Fig. 3a). During the low-to-medium rainfall period, this trend along the vertical profile was inverted. While leaves remained wet for 20–25% of the time, wetness lasted longest near the forest floor, where insolation and turbulent energy exchange with the atmosphere is reduced (Fig. 3b). Finally, in the rainy period, the foliage remained wet for 45–55% of the time and the difference between upper and lower canopy strata disappeared (Fig. 3c). Remarkably, these vertical differences in wetness patterns inside the stand fade when leaf wetness is averaged over the entire study period (Fig. 3d).

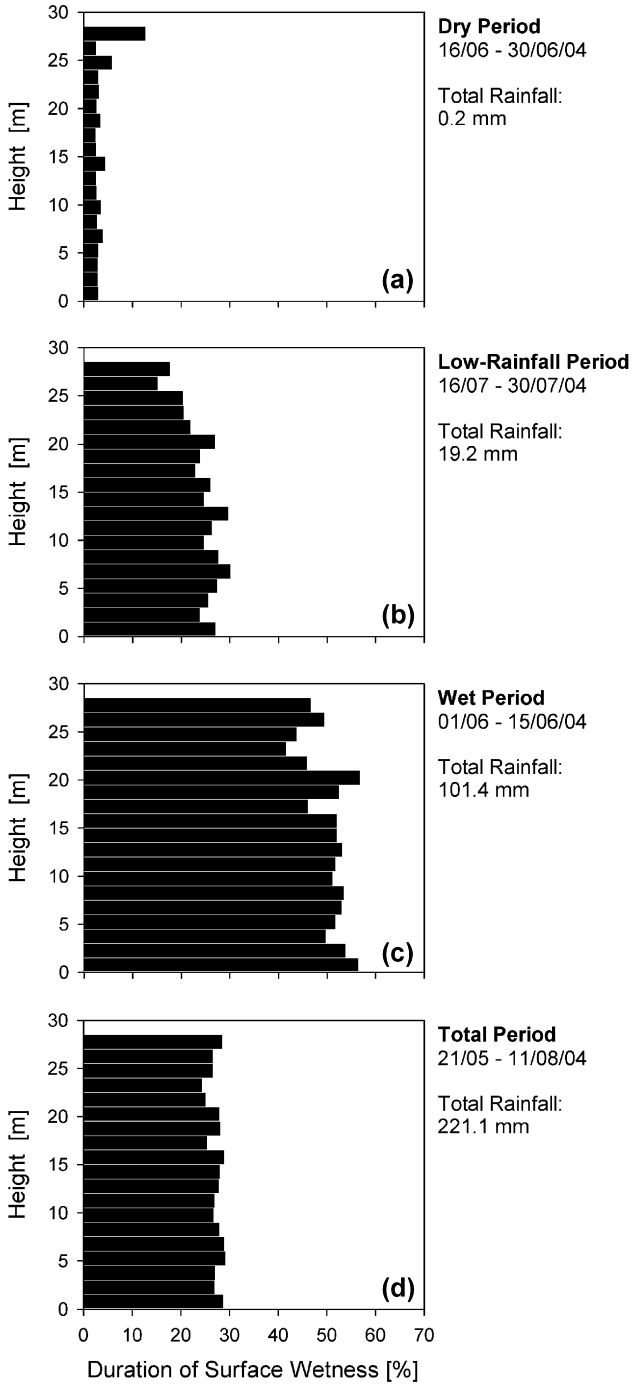


Fig. 3. Average duration of surface wetness (in per cent of the time) in a vertical profile inside the Bariri forest in a dry 2-week period (June 16–June 30, (a)), a low-to-medium rainfall period (July 16–July 30, (b)), a wet period (June 1–June 15, (c)), and during the entire measuring period (May 15–August 11).

Discussion

According to the rain gauge data, the study region receives only moderate annual amounts of vertical rainfall (1830 mm yr^{-1}) compared to other tropical lower montane or montane forests. However, this number does only cover rainfall collected in gauges; this situation occurs on about 65% of the days of a year in the study region. In tropical montane forests and especially in cloud forests, interception of wind-driven fog and rain by the vegetation may add substantial amounts of moisture to the system (Bruijnzeel, 2001; Kämmer, 1974). In a montane cloud forest of Guatemala at an altitude of 2550 m, an equivalent of fog precipitation of 203 mm was estimated by comparing throughfall and incident precipitation data. Fog precipitation was assumed during sampling periods when throughfall exceeded incident precipitation (Holder, 2003). However, the author himself states that the amount of fog precipitation in this study is underestimated. The quantification of the volume added by

fog is difficult and reliable data for tropical montane forest are lacking so far. By using a variety of methods including stable hydrogen and oxygen isotopes, Dawson (1998) estimated for Californian coastal redwood forests that 34% of the annual water input was derived from fog drip. Throughfall data from the Bariri forest in Sulawesi point at a relatively low importance of fog interception at this site probably because of the lower montane elevation.

Despite a comparably low frequency of fog during the day, leaf wetness is an important ecological factor in this forest. Surface wetness was present in about 30% of the time of the total measuring period, and in 50% or more of the rainy period. On rainy days, the upper canopy was often influenced by surface wetness for more than 16 h from the early afternoon onwards till the next morning. In the lower shade canopy close to the forest floor, wetness was continuously present for periods of 22 h and even more, although rainfall occurred only during thunderstorms of limited duration in the afternoon. Thus, epiphyllic liverworts, lichens and fungi are experiencing favourable moisture conditions on the leaf surface in this forest for several daylight hours and during the whole or most of the night as well. Vigorous growth of light-capturing epiphylls and, presumably, of pro- and eukaryotic pathogens on the leaf surface, that thrive in the water film on the leaf, may well explain why many trees in tropical montane forests have average leaf longevities not longer than about 16 months (Moser, pers. commun.).

In fact, the consequences for leaf growth of trees that follow from light competition by epiphyllic organisms may be more relevant than the effects on stomatal conductance and photosynthesis that are caused by the inhibition of gas exchange due to leaf wetness and high air humidity. Surveys of tropical montane trees at 1000–3000 m elevation in South Ecuador showed that the vast majority of species were hypostomatous (Schuldt, pers. commun.). Own observation in the Bariri forest suggests that most tree species are experiencing leaf wetness only at the upper, and not at the lower surface, unless leaf orientation is not vertically upward or downward which is rarely the case (Bohman, 2004). In fact, rainfall and cloud interception are occurring mainly on the upper (adaxial) leaf side, whereas the lower (abaxial) surface is moistened only by fine mist with water droplets in the μm scale (Letts and Mulligan, 2005). We assume that physical inhibition of gas exchange by leaf wetness should be of minor importance in this forest. Very low atmospheric saturation deficits, as are occurring in periods of leaf wetness, must result in very low or zero transpiration rates, whereas photosynthesis should proceed albeit at reduced rates. Therefore, leaf wetness should increase photosynthetic water use efficiency.

The surface wetness and microclimate data of this forest indicate that the occurrence of leaf wetness in the afternoon, evening and the first half of the night is normally a consequence of afternoon rainfall events of limited duration. Since we did not conduct direct measurements of fog interception, we cannot assess the relative contribution of horizontal precipitation to measured leaf wetness. If sufficient rainfall has occurred, the leaves may remain wet until the early morning. On days without rainfall, or when rain is followed by a late afternoon with sunshine sufficient to dry up the canopy, leaf wetness in night-time and morning is most often a consequence of dewfall. Dew formation seems to start around midnight as a consequence of under-temperatures of the upper canopy compared to the air in the course of substantial heat losses with long-wave radiation losses from the leaves. In such nights, leaf wetness often concentrates in the upper canopy and does not reach to the lowest canopy strata, probably because condensation heat from dewfall is preventing any further cooling of the lower canopy. We often recorded surface wetness in the canopy although air temperature remained 0.5–1.0 K above dewpoint temperature. Most likely, this situation is caused by significant under-temperatures of the leaves compared to the surrounding air due to radiative energy losses of the leaf surface.

Leaf wetness following afternoon rainfall events seems to last longer in the lower canopy because the sun canopy is drying more rapidly during the daylight hours. In contrast, surface wetness on more or less clear days as caused by night-time dewfall has a longer duration in the upper canopy because of the negative radiation balance of the leaves during the night.

Our results on leaf wetness patterns are not only relevant for understanding the ecophysiology of tropical trees, but they also have implications for the hydrology of tropical montane forests. The surprisingly long duration of surface wetness in this stand raises questions upon earlier modelling studies of rainfall interception. For example, the frequently applied Gash model of rainfall interception in forests (Gash et al., 1995) bases on the assumption that the canopy dries completely between subsequent rainfall events. In the Bariri forest, this seems not to be the case on many occasions. A possible conclusion would be that an application of the Gash model or its derivates (Gash, 1979; Gash et al., 1995) will fail. For canopies with long wetness periods, interception models that simulate changes in the amount of stored water on canopy and trunk surfaces by means of a running water balance seem to be more suitable. An example would be the Rutter model of rainfall interception (Rutter et al., 1971), which requires detailed information on the intensity of rainfall events together with meteorological variables related to evaporation.

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