Epiphyte Diversity and Microclimate of the Tropical Lowland Cloud Forest in French Guiana

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Figure i. Tropical Lowland cloud forest and rain forest as seen from the top of the Inselberg in Les Nouragues Nature Reserve, French Guiana. Cover photo of Ecotropica 18 (2012).

1 Introduction

1.1 Preface

Tropical montane cloud forests (MCF) occur within the cloud belts of montane and submontane regions in the Tropics at elevations that may differ between regions, but generally lie between 1200 and 3000 m *a.s.l.* However, at island and coastal locations the level of cloud condensation tends to be much lower, with the lowest documented elevations being 450-500 m *a.s.l.* (Hamilton *et al.* 1995, Bruijnzeel *et al.* 2010). Characteristic of MCF are the frequent incidence of fog and low cloud and the abundance and high species richness of epiphytes (mosses, liverworts, lichens, ferns, flowering plants; Richards 1996). Indeed, it has been suggested that MCF may have more species of epiphytes than any other forest type (Richards 1996). Inventories of epiphyte diversity in a number of moist lowland and montane forests in tropical America have been carried out by S.R. Gradstein and his students since the late 1970s (e.g. Van Reenen & Gradstein 1983, Cornelissen & Ter Steege 1989, Montfoort & Ek 1990, Cornelissen & Gradstein 1990, Wolf 1993, Gradstein 1995, Gradstein *et al.* 2001, Holz *et al.* 2002, Acebey *et al.* 2003, Gradstein 2003). Special attention was paid to non-vascular epiphytes (bryophytes, lichens), which had been neglected previously because of difficulties with species identification and the occurrence of many species in the higher and less accessible parts of the forest canopy. Because of their poikilohydric nature, epiphytic bryophytes and lichens are excellent ecological indicators, especially of atmospheric humidity and quality (Bates & Farmer 1992, Gignac 2001). Their abundance is strongly influenced by local climatic conditions, and the degree of “mossiness” is a useful parameter to characterize tropical rain forest types (Frahm & Gradstein 1991).

These inventories revealed large differences between forest types in terms of species richness of epiphytic bryophytes. In most cases, species richness was higher in montane forests than in lowland forests, but in some lowland forests the number of epiphytic bryophyte species exceeded that of montane forest. For example, moist lowland forests at Saül (French Guiana) had up to 1.5 times more bryophytic species than did moist submontane forest at about 600 m *a.s.l.* near Sapecho (Bolivia) or lower montane forest at about 1500 m near Santa Rosa (Colombia), and up to three times more species than found in moist Amazonian lowland forest at Surumoni (Venezuela). At Surumoni, four species of tree had only 20 species of liverworts and fewer than 10 species of moss; whereas at Saül four trees yielded 60 species of liverwort and 40 of moss (Montfoort & Ek 1990, Gradstein 1995, 2006). Up to 50 bryophyte species occurred on a single tree. These figures are the highest ever recorded in tropical lowland rain forest and are similar to those recorded in montane cloud forest at about 2000 m *a.s.l.* in Colombia (Wolf 1993).

The marked differences in epiphyte diversity in the investigated lowland forests were surprising, because elevation (100-200 m *a.s.l.*) and annual precipitation (ca. 2700 mm) at the respective sites were similar (Gradstein 1995, Anhuf & Winkler 1999). A possible explanation of the difference in epiphyte abundance and diversity relates to the high incidence of fog at the Saül site, which is absent at Surumoni (Montfoort & Ek 1990, Gradstein 2003, 2006). The fog occurs typically during the night and early morning and is dispersed before noon. The fog development is probably due to eradiation and cooling beyond dew point at night during times of negligible wind, rather than to uplifting of air masses along mountains slopes (Bruijnzeel *et al.* 2005). Fog formation may be enhanced by the following factors: undulating terrain with many small hills and creeks, saturation of air during the night and early morning because of low turbulence (very low wind speeds) or occurrence of heavy rain during the night, and water-logging of valley-bottom soils (Brouwer 1996).

These mossy tropical lowland forests with high abundance of epiphytes and frequent fog may be called “Tropical Lowland Cloud Forests” (LCF) (Gradstein 2006). Lowland cloud forests are well known from temperate regions, e.g. the coasts of California and northern Chile (Bruijnzeel 2001), but in the Tropics their occurrence has been overlooked.

In order to further investigate LCF, an interdisciplinary project was established. Botanists from the University of Göttingen (lab of Prof. Dr. S.R. Gradstein) and climatologists of the University of Marburg (lab of Prof. Dr. J. Bendix) collaborated on this project, which incorporates two PhD-theses and was funded by the DFG (GR 1588/12-1, BE 1780/13-1).

1.2 Objectives of the collaboration

Our primary goal was to investigate the relationship between climate, especially fog, and epiphyte vegetation in French Guiana.

1.2.1 Objectives in botany (dissertation of C. Gehrig-Downie)

We compared epiphyte abundance (species diversity and biomass) in tropical lowland cloud forest and rain forest (LRF) in French Guiana in order to establish a botanical characterization of the tropical lowland cloud forest. Moreover, the suitability of epiphytes, especially bryophytes and ferns, as indicators for identifying forest types in the humid tropics was explored.

1.2.2 Objectives in climatology (dissertation of A. Obregón)

The causes of fog development in tropical lowland forests and the underlying meteorological processes were studied and the different microclimates of LCF and LRF characterized. An on-going analysis of spatiotemporal fog dynamics in French Guiana will answer whether lowland fog development is a local phenomenon or if it occurs throughout the country. Furthermore, an algorithm for the detection of fog at sub-pixel level of satellite measurements is being developed.

1.3 Establishment of markers for identifying LCF

As interest in LCF has increased since its first mention by Gradstein in 2006, reliable tools for identifying this forest type needed to be developed. Fog is generally considered to be a major driver of the diversity of epiphytic organisms in tropical forests (e.g., Grubb & Whitmore, 1966; Nadkarni, 1984). Surplus moisture by the interception of fog water in the forest canopy shortens the duration of desiccation of the epiphytic plants dwelling in the canopy and enhances their photosynthetic activity and growth.

The quantity of epiphytic biomass suspended on trees is strongly affected by the prevailing microclimate. In tropical montane cloud forests, epiphytic biomass is generally very high and may add up to 44 tons/ha (including suspended soil) in Andean cloud forests (Hofstede *et al.* 1993). In lowland forest, higher temperatures and longer periods with low RH usually lead to less bryophyte growth, leading to less accumulation of total biomass (Freiberg & Freiberg 2000).

The composition of epiphytic biomass differs greatly between MCFs and LRFs. The main components of epiphytic biomass in cloud forests are bryophytes, with smaller proportions of pteridophytes, lichens, and angiosperms (Nadkarni 1984, Ingram & Nadkarni 1993), while in drier forests, lichens are more abundant than bryophytes (Sillett & Antoine 2004). By analyzing the amount of epiphytic biomass suspended on trees and studying its components and respective cover, a general understanding of the microclimate can be established.

The coincidence of fog and high epiphyte diversity is well documented for tropical mountain forests (e.g. Hamilton *et al.* 1995, Richards 1996) but has only recently been recorded in tropical lowland forest (Gradstein 2006, Gradstein *et al.* 2010). Depending on their moisture requirements, diversity of epiphytes is affected differently. In general, lichens and bryophytes are differentially distributed along moisture gradients, with bryophytes thriving under moister conditions than lichens (Frahm 2003, Sillett & Antoine 2004). Cyanolichens take an intermediate position along the moisture gradient, between the drought-tolerant chlorolichens and the drought-intolerant bryophytes (Sillett & Antoine, 2004).

Due to the lack of a well-developed cuticle filmy ferns and liverworts are sensitive to water loss and hence dependent on moist habitats characterized by frequent precipitation and low evaporation (e.g. Bates & Farmer 1992, Proctor 2003). Because of their drought-intolerance, filmy ferns and liverworts commonly occur as epiphytes in tropical moist forests (Gradstein, 1995) and are considered sensitive indicators of high atmospheric humidity (Hietz & Hietz-Seifert 1995). In order to understand the role of fog events on establishing biodiversity of a forest, we compared diversity of these selected groups of epiphytes in LCF and in nearby lowland forest without fog (LRF).

To test the hypothesis that LCF and LRF are distinct forest types, I integrated epiphyte abundance and diversity of epiphytic macrolichens, filmy ferns and liverworts with microclimate measurements.

1.4 Study area

Fieldwork was conducted at two sites in central French Guiana in 2007. The first site was located in the vicinity of the village of Saül (3°37'20"N, 53°12'31"W), about 200 km southwest of the Atlantic coast at the headwaters of three of French Guiana’s major river systems. Soils in the fieldwork area are deep ferralitic well-hydrated soils (de Granville 1988).

The second site is in the Nouragues Natural Reserve (4°02'30"N, 52°40'30"W), *ca.* 100 km inland from the Atlantic coast (Figure 1).

Central French Guiana is hilly and considerably dissected, with small river valleys at about 200–250 m and hills to about 400 m in elevation in Saül, and varying in altitude from 50 to 200 m *a.s.l.* in Nouragues. Annual rainfall is *ca.* 2500 mm in Saül and *ca.* 3000 mm in Nouragues; there is a distinct dry season from late July to November and a less pronounced dry period for several weeks in February and March. Average temperature is 27°C (Mori *et al.* 1997, Grimaldi & Riéra 2001). In Saül, other than a zone of minor disturbance surrounding the village, the area is covered by mixed lowland rain forest (e.g. De Granville 1986, 2001, Mori & Boom 1987). The forest canopy varies in height from 20 to 45 m, with emergent trees reaching up to 55 m (Mori & Boom 1987). The flora is very rich, with about 5000 recorded species of vascular plants and over 300 of bryophytes (Mori *et al.* 1997, 2002, Buck 2003, Gradstein & Ilkiu-Borges 2009).

In Nouragues, the area is covered by dense, nearly undisturbed primary lowland forest, described as “old-growth terra firme dense rainforest” (Poncy *et al.* 2001). The forest is tall, with canopy trees reaching heights of approximately 50 m. Natural disturbances such as tree falls lead to canopy gaps in some places (Van der Meer & Bongers 2001). The forest is dominated by Burseraceae trees and represents one of the two main French Guianan forest types described by Sabatier and Prévost (1990) differing by the dominant tree family.

Lowland cloud forest (LCF) is common at both sites and occurs in valleys where fog develops during the night but clears well before noon (Gradstein 2006); LRF occurs higher up the slopes. The two forest types are very similar in overall stature (tree height, tree diameter) but emergent trees and gaps are more frequent in LCF.

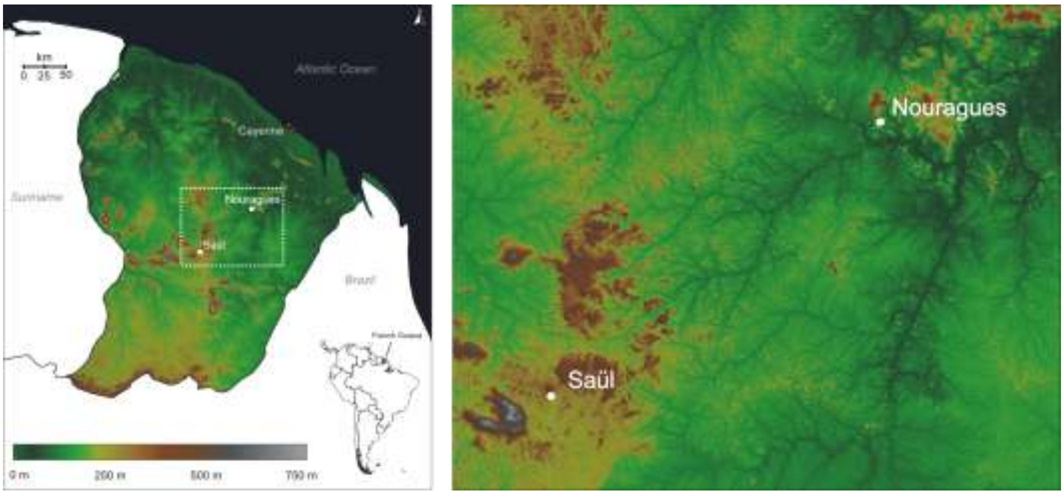

Figure 1. Map of the study area. Courtesy of A. Obregon.

1.5 Layout of this thesis

The following chapters of this thesis represent either papers published or manuscripts submitted, with the chapter style following the guidelines of the respective journal.

In chapter two, we explore epiphyte abundance and canopy microclimate in Central French Guiana. Are there differences in vertical distribution of epiphytic cover in LCF and in lowland rain forest (LRF) without fog? How is the epiphytic biomass distributed in the two forest types and what are its major components? Does canopy microclimate differ between LCF and LRF?

Chapter three focuses on fog frequency and the meteorological processes leading to fog formation in lowland valleys of central French Guiana. What is the diurnal course of fog frequency, persistence and visibility and how does this affect air humidity? What is the main trigger of fog development?

In chapter four, we analyze the macrolichen diversity of LCF and LRF in a lowland area near Saül, central French Guiana. Can epiphytic lichens be used as indicator taxa? Do cyanolichens and green-algal lichens differ in their distribution and preference for one forest type?

Chapter five deals with the diversity of epiphytic Hymenophyllaceae, a family of ferns dependant on frequent precipitation and low evaporation. How does the vertical distribution of species differ between the LCF and LRF? How does canopy microclimate correlate with filmy fern diversity? What are the best Hymenophyllaceae indicator species for LCF?

In chapter six, we analyze the diversity of bark-inhabiting liverworts in LCF, a group of organisms known to be sensitive indicators of humidity. Are LCF and LRF equally rich in liverworts? Which families are the most common? How does vertical distribution of liverworts and composition of assemblages differ? Which liverwort species are good indicators of LCF and LRF?

Finally, ***chapter seven*** summarizes the findings of the previous chapters and concludes with an outlook on future work in this field.

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2 Epiphyte Biomass and Canopy Microclimate in the Tropical Lowland Cloud Forest of French Guiana

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2.1 Abstract

Recent work on bryophyte diversity in lowland forests of northern South America has suggested the existence of a new type of cloud forest, the 'tropical lowland cloudforest' (LCF). LCF occurs in river valleys in hilly areas with high air humidity and morning fog, and is rich in epiphytes. We explored epiphyte abundance and canopy microclimate of LCF in a lowland area (200–400 m asl) near Saül, central French Guiana. We analyzed the vertical distribution of epiphytic cover and biomass on 48 trees, in LCF and in lowland rain forest (LRF) without fog. Trees in LCF had significantly more epiphytic biomass than in LRF; mean total epiphytic biomass in LCF was about 59 g/m^2, and 35 g/m^2 in LRF. In all height zones on the trees, total epiphyte cover in LCF exceeded that in LRF, with ca 70 percent mean cover in LCF and ca 15 percent in LRF. During both wet and dry seasons, mean diurnal relative air humidity (RH) was higher in LCF than in LRF, and persistence of high RH after sunrise significantly longer in LCF. We suggest that the prolonged availability of high air humidity in LCF and the additional input of liquid water through fog, enhance epiphyte growth in LCF by shortening the desiccation period and lengthening the period of photosynthetic activity of the plants.

2.2 Introduction

Cloud forests are widely distributed in montane and submontane regions of the tropics at elevations above 500 m, ranging normally between 1200 and 3000 m. These montane cloud forests are characterized by increased relative air humidity (RH) through frequent incidence of fog and low clouds, high abundance and species richness of epiphytes (Richards *et al.* 1996), and accumulation of large amounts of epiphytic biomass

(Nadkarni 1984, Veneklaas *et al.* 1990, Ingram & Nadkarni 1993, Freiberg & Freiberg 2000). Epiphytic biomass of tropical montane forests has received considerable attention (Nadkarni 1984, Veneklaas et al. 1990, Hofstede et al. 1993, Ingram & Nadkarni 1993, Wolf 1993). In tropical montane cloud forests, epiphytic biomass is generally very high and may add up to 44 tons/ha (including suspended soil) in Andean cloud forests (Hofstede *et al.* 1993). The main components of epiphytic biomass in cloud forests are bryophytes, with smaller proportions of pteridophytes, lichens, and angiosperms (Nadkarni 1984, Ingram & Nadkarni 1993).

Canopy-held epiphytic biomass plays a critical role in ecosystem processes in the forest by altering pools, pathways, and rates of nutrient and carbon fluxes (Nadkarni 1981, Coxson & Nadkarni 1995), and by influencing the forest hydrology through rainfall and cloud–water interception (e.g., Veneklaas & Van Ek 1990, Hölscher *et al.* 2004, Bruijnzeel *et al.* 2005). Epiphytes also greatly increase the structural complexity of tropical forest habitats, providing crucial resources for numerous arboreal and terrestrial organisms (Nadkarni & Longino 1990, Yanoviak *et al.* 2007).

Recent research on bryophyte diversity of central French Guiana has documented the occurrence of cloud forest in lowland areas, well below 500 m (Gradstein 2006). These cloud forests (‘tropical lowland cloud forest’ [LCF]) occur in valleys in hilly areas with high rainfall, which leads to almost daily morning fog. Fog in these forests presumably occurs due to nocturnal irradiation and cooling beyond dew point during night (Gradstein *et al.* 2010), rather than by uplifting of air masses along mountain slopes. Fog formation is enhanced by undulating terrain with many small hills and creeks, saturation of air during the night and early morning due to very low air turbulence or heavy rainfall, and waterlogging of valley-bottom soils. The radiation fog gradually lifts during early morning hours and clears by solar heating between 0700 and 1000 h. LCF has been observed in the Guianas, Colombia, Costa Rica, and Indonesia (Gradstein *et al.* 2010), but has received little scientific attention until now. Physiognomically, LCF resembles tropical lowland rain forest (LRF), but differs from the latter by the abundance of epiphytes, especially mosses and liverworts.

The purpose of this study was to analyze the epiphytic abundance and biomass of epiphytes in LCF relative to the microclimate (air temperature, air humidity) of the forest. We hypothesize that the occurrence of morning fog leads to decreased rates of vapor pressure deficit (VPD) enabling greater epiphyte abundance in LCF.

2.3 Methods

2.3.1 Study area

The study was carried out in central French Guiana, in the vicinity of the village of Saül (3°37'20" N, 53°12'31" W), located ca 200 km south of the Atlantic coast at the headwaters of three of French Guiana's major river systems. Soils in the fieldwork area are deep ferralitic well-hydrated soils (de Granville 1988). The terrain is undulating and varies in altitude from 200–400 m asl, with small rivers in the depressions. Annual rainfall averages 2000–3000 mm and is unevenly distributed over the year, resulting in a well-defined dry season from August through November and a shorter one from February to April. Average day temperature is about 27°C. Other than a zone of minor disturbance surrounding Saül, the area is covered by species-rich, mixed old growth LRF (de Granville 1986, 2001; Mori & Boom 1987). The forest canopy varies in height from 20 to 45 m, with emergent trees reaching up to 55m (Mori & Boom 1987). LCF is common in the area and occurs in valleys where fog develops during the night and early morning (Normann *et al.* 2010).

2.3.2 Sampling of biomass

Ten plots of 1-ha each were laid out in undisturbed, old growth forest in a 6×2 km area in the vicinity of Saül. The first two plots (I, II) were situated on the slope of a small hill adjacent to the valley of the Pelée river (‘Crique Pelée’), one in LCF on the bottom of the slope at ca 250 m elevation, the other in LRF on the upper portion of the slope at *ca* 325 m elevation. The remaining eight plots were laid out randomly as replicates in LCF and LRF at similar elevation on slopes of small hills adjacent to the valleys of ‘Crique Roche’ (III, IV), two smaller tributaries of ‘Crique Grand Fosseé’ (V–VIII) and ‘Crique Popote’ (IX, X). Distance between LCF and LRF plots was about 250 m. Following Gradstein *et al.* (2003), we sampled a limited number of mature canopy trees in each hectare plot; eight trees in plots I–II and two trees in the remaining plots were climbed using the single rope technique. Sampled trees were standing (N= 15) 20–30 m apart and were 20–45 m in height; dbh was 30–300 cm.

On each target tree, we removed all epiphytes growing in 24 sample plots of 600 cm^2. These plots were positioned at each cardinal direction in six height zones: trunk base (zone 1), lower trunk (zone 2), upper trunk to first ramification (zone 3), lower canopy (zone 4), middle canopy (zone 5), and outer canopy (zone 6). Sample plots were 20×30 cm on trunks and 20×30 cm or 10×60 cm on canopy branches according to branch diameter (Gradstein *et al.* 2003). Owing to the small size of the sample plots, which were laid out to investigate bryophyte species diversity and abundance (Gradstein *et al.* 2003), vascular plant individuals sampled represented a very limited fraction of the overall biomass of vascular epiphytes in LCF and LRF. For safety reasons, samples from height zone 6 were taken from cut branches. The biomass samples were divided into fractions of nonvascular epiphytes (bryophytes and lichens), pteridophytes, and angiosperm families, dried during 48 h at 70°C, and dry weight was measured. Owing to difficulties in removing bark from the nonvascular epiphyte samples, only part of these samples could be included in the analysis. In total, 56 nonvascular epiphyte samples of LCF and 52 of LRF were analyzed. For the analysis of vascular epiphytes, all samples of epiphytic biomass were taken into account. Angiosperms were contained in 154 LCF and 14 LRF samples, pteridophytes in 53 LCF and nine LRF samples.

2.3.3 Estimation of epiphyte cover

We visually estimated epiphyte abundance and cover per height zone and for each epiphyte type (bryophytes, lichens, pteridophytes, angiosperms). Mean total epiphyte cover was determined by summing up cover estimates of each component.

2.3.4 Microclimate and fog measurements

In plots I and II, air temperature (°C) and RH (%) were measured with 5-min intervals for 60 d during September and October 2007, using data loggers (HOBO ProV2 RH/Temp, Onset). The data loggers were installed in the middle of the crowns (zone 4) of 20 canopy trees (ten trees per site), at 15–25 m depending on canopy height (emergent trees excluded). In addition, loggers were installed in zone 4 of 20 canopy trees of plots I–VIII (two trees per site), at heights of 15–25 m, during November 2007–June 2008, and air temperature (°C) and RH (%) were measured with 20-min intervals for 230 d. Data were then divided into dry season (1 September 2007–15 November 2007) and wet season (16 November 2007–16 June 2008). Hourly and daily means per season were calculated and water VPD computed. The correlation between RH and fog events was studied by measuring horizontal visibility (km) and RH (%) at canopy level using sensors in the Nouragues Natural Reserve (approximately 75 km northeast of Saül, 4°2'30" N, 52°40'30" W, 75 m asl). Horizontal visibility was measured using sensor model HSS VPF-730 (Biral) installed in LCF on a platform of the Canopy Operating Permanent Access System. RH data for this analysis were retrieved during a 2-wk field campaign between June and July 2008 by means of a capacitive RH sensor (CS215, Campbell Scientific) installed in the inner crown of a nearby canopy tree. Persistence of high RH after sunrise was measured during 3 wk in the dry season in LCF and LRF at Saül using the CS215 RH sensors.

2.3.5 Data analysis

Epiphyte biomass, epiphyte cover, and canopy microclimate were statistically evaluated with unpaired t-tests. Because biomass of vascular epiphytes did not follow a normal distribution, nonparametric Mann–Whitney U tests were conducted. Three α-levels of significance were recognized: $P<0.05$, $P<0.01$, and $P<0.001$.

2.4 Results

2.4.1 Epiphytic biomass

Trees in LCF had significantly more epiphytic biomass than in LRF (LCF: $\bar{x}$= 58.5 g/m^2, SD= 48.7 g/m^2; LRF: $\bar{x}$= 34.5 g/m^2, SD= 51.4 g/m^2; $P<0.01$). Composition of epiphytic biomass was similar in both forest types and was largely made up of bryophytes and lichens (LCF 96%, LRF 99%). Contribution of vascular epiphytes to overall biomass was about three times greater in LCF than LRF, with pteridophytes being more common (LCF 3%, LRF 1%) than angiosperms (LCF 1%, LRF 0.4%). Furthermore, family composition of epiphytic angiosperms in the two forest types was different. While the amount of orchid biomass was similar in both forest types, bromeliads dominated in LCF biomass but were scarce in LRF. Moreover, Piperaceae, Cactaceae, and Gesneriaceae contributed to epiphytic biomass in LCF but were lacking in LRF.

Regarding the vertical distribution of biomass components, similar patterns were detected in both forest types but the amounts of biomass differed greatly. Biomass of bryophytes and lichens that in LRF, but differences were significant only for crowns ($\bar{x}$= 59.8 g/m^2, SD= 37.9 g/m^2; LRF: $\bar{x}$= 35.0 g/m^2, SD= 39.6 g/m^2; $P<0.05$). Vascular epiphytes were restricted almost exclusively to tree crowns in both forest types. The total amount of vascular epiphyte biomass on trunks and in crowns of LCF (trunks: $\bar{x}$= 1.6 g/m^2, SD= 6.7 g/m2; crowns: $\bar{x}$= 11.2 g/m^2, SD= 18.0 g/m^2) exceeded that of LRF (trunks: $\bar{x}$= 0.04 g/m^2, SD= 0.2 g/m2; crowns: $\bar{x}$= 3.3 g/m^2, SD= 11.1 g/m2). The difference was significant for trunks ($P<0.01$) and crowns ($P<0.001$).

2.4.2 Epiphyte cover

Throughout all height zones, total epiphyte cover in LCF exceeded that in LRF significantly (Fig. 2, $P<0.01$), with ca 70 percent mean cover in LCF and ca 15 percent in LRF.

Epiphytic cover consisted mainly of bryophytes, to a lesser extent of lichens and angiosperms, with angiosperms being prominent only in LCF. For all epiphyte components, differences in abundance were greatest in tree crowns, where epiphyte cover of LCF exceeded that of LRF significantly (Fig. 3, lichens: $P<0.01$; bryophytes: $P<0.001$; angiosperms: $P<0.001$).

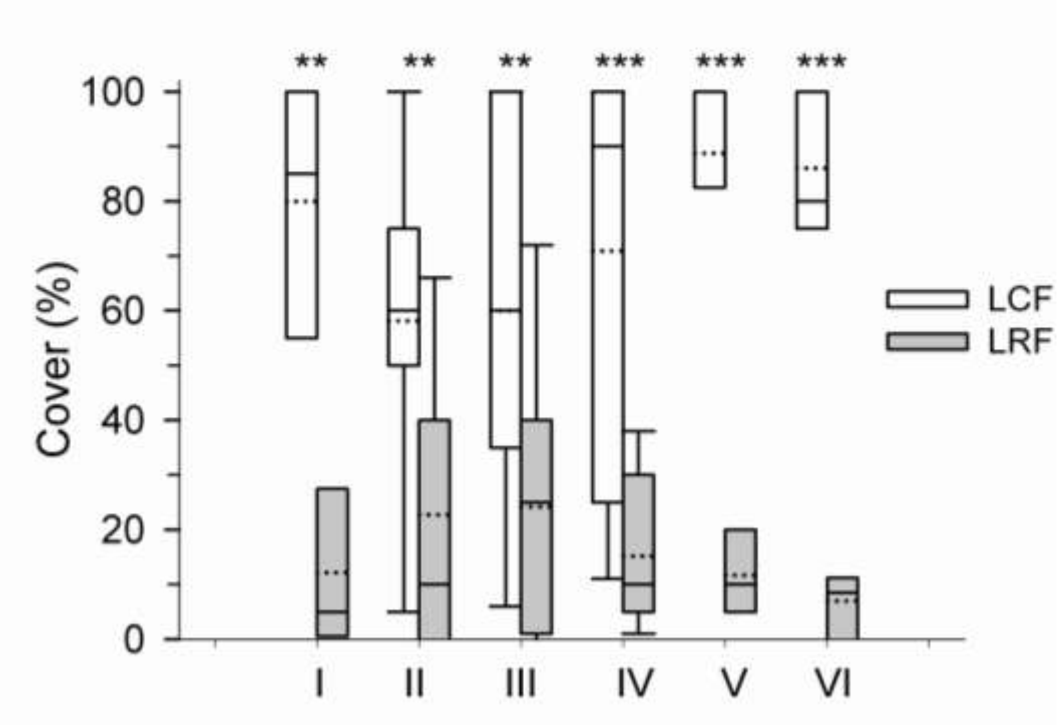

Figure 2. Abundance of all epiphytes in percentage of bark coverage in lowland cloud forest (LCF) (white) and lowland rain forest (LRF) (gray) in different height zones (I–VI) on the tree; N= 24 trees per forest type. Boxes indicate upper and lower quartile of data, unbroken line gives the median, dotted line the mean and whiskers 5th/95th percentile. Levels of significance are obtained with unpaired t-tests and shown by asterisks, $^*P<0.05$, $^{**}P<0.01$, $^{***}P<0.001$.

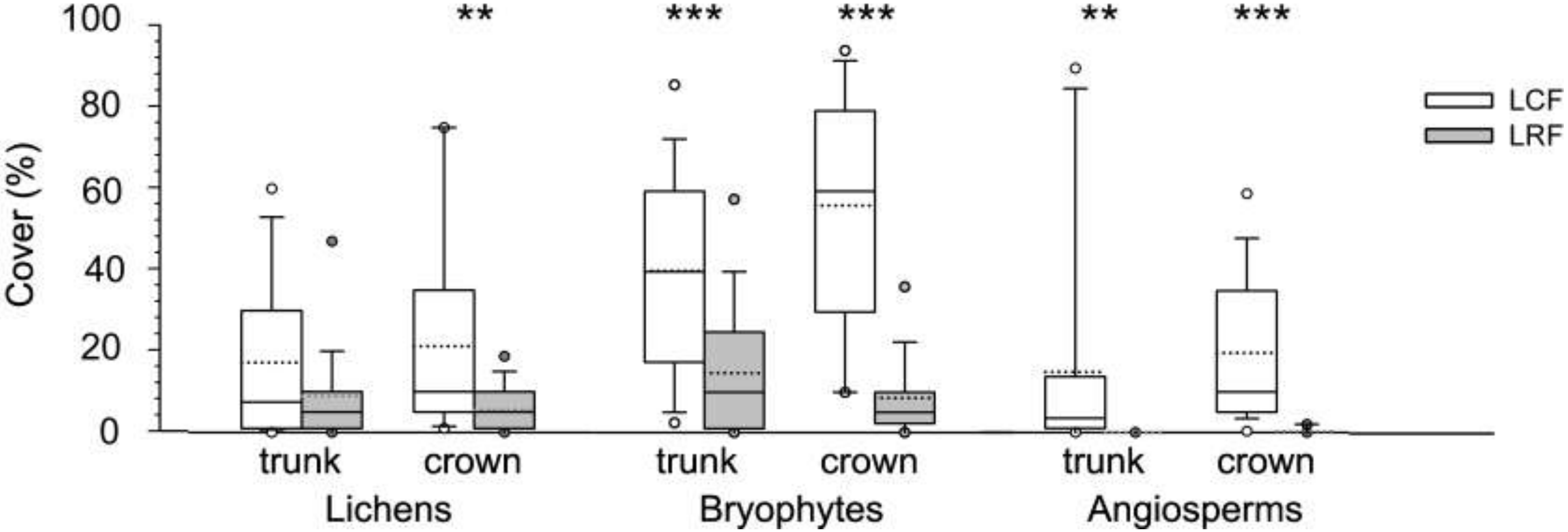

Figure 3. Abundance of epiphytic lichens, bryophytes, and angiosperms in percentage of bark coverage on trunks (zones I–III) and crowns (zones IV–VI) in lowland cloud forest (LCF) (white) and lowland rain forest (LRF) (gray); N= 72 estimates per forest type. Boxes indicate upper and lower quartile of data, unbroken line gives the median, dotted line the mean and whiskers 5th/95th percentile. Levels of significance are obtained with unpaired t-tests and shown by asterisks, *$P<0.05$, **$P<0.01$, ***$P<0.001$.

2.4.3 RH and temperature

In both forest types, microclimate measurements during the dry season (48 d) showed higher temperature (*T*) and lower RH than during the wet season (230 d) (Table 1). Throughout the two seasons, mean diurnal RH tended to be higher in LCF than LRF; during the dry season, however, differences between the two forest types were most pronounced. Maximum diurnal temperature and minimum RH occurred at noon (T_{LCF} = 26°C; T_{LRF} = 27°C; RH_{LCF} = 74%; RH_{LRF} = 72%). Temperature was lowest around 0400 h (T_{LCF} =22°C; T_{LRF} = 21°C) when air humidity was highest (RH_{LCF} = 97%; RH_{LRF} = 95%). Differences in RH were most pronounced from 1600 h to midnight when mean RH in LCF was 5–10 percent higher than in LRF, and from 0100 to 0700 h when mean RH constantly reached levels above 95 percent in LCF and was significantly higher than in LRF. The higher temperatures coupled with lower RH lead to higher VPD in LRF at all times (Fig. 4).

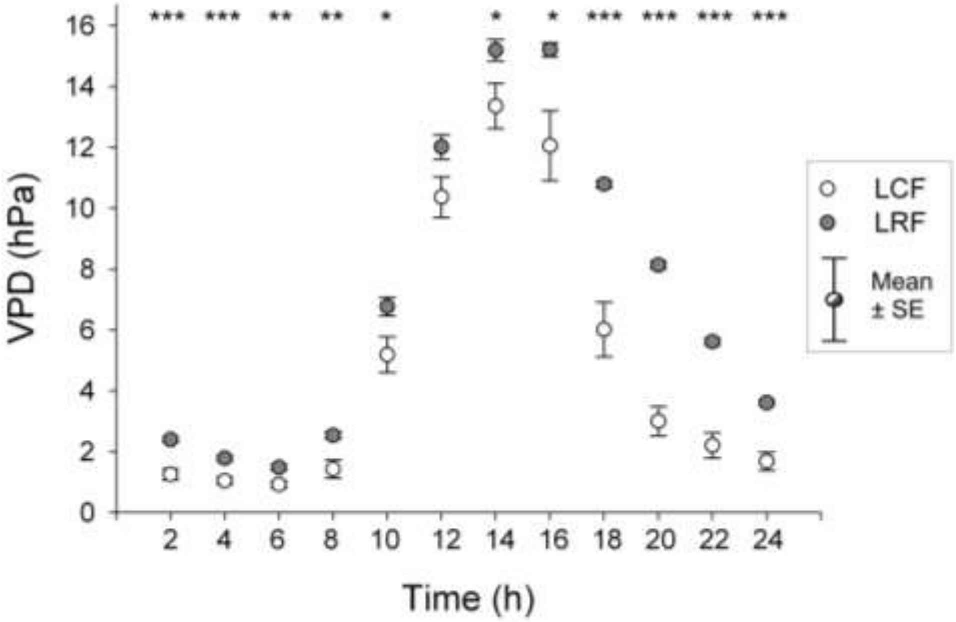

Figure 4. Diurnal course of vapor pressure deficit (VPD), calculated using hourly mean temperature and air humidity during 48 d of the dry season in lowland cloud forest (LCF) (white circles) and lowland rain forest (LRF) (gray circles). Levels of significance are obtained with unpaired t-tests and shown by asterisks, (*P<0.05, **P<0.01, ***P<0.001.

Table 1. Comparison of microclimatological factors measured in the middle canopy of lowland cloud forest and lowland rain forest of central French Guiana. RH= daily relative air humidity, t= daily air temperature. Top: 48 days of dry season September-October 2007. Bottom: 230 days of wet season November 2007-mid June 2008.

	t (°C)			**RH (%)**		
Dry season	**max**	**min**	**mean**	**max**	**min**	**mean**
Lowland cloud forest	30.86	21.51	24.63	96.77	59.36	86.35
Lowland rain forest	30.67	21.80	25.17	95.86	55.77	80.80

	t (°C)			**RH (%)**		
Wet season	**max**	**min**	**mean**	**max**	**min**	**mean**
Lowland cloud forest	29.37	21.20	23.66	97.93	69.32	92.79
Lowland rain forest	28.70	21.54	23.39	96.69	66.54	92.51

2.4.4 Relation of RH and fog events

Comparison of air humidity and horizontal visibility data showed a strong correlation between fog occurrence and >98 percent RH, with more than 80 percent of all recordings in this humidity class being fog situations (Fig. 5). The probability of fog occurrence was reduced to *ca* 50 percent at RH values between 97 and 98 percent and dropped to *ca* 10 percent, at 94 percent RH, becoming increasingly rare below this value. The measurements indicate that fog is very rare in LRF, being restricted to an occasional light fog with visibilities of ca 1 km during the wet season between 0400 and 0700 h. In LCF, on the other hand, dense fog events (indicated by RH <97%) should occur frequently in the second part of the night and in early morning hours, both in the wet and in the dry season.

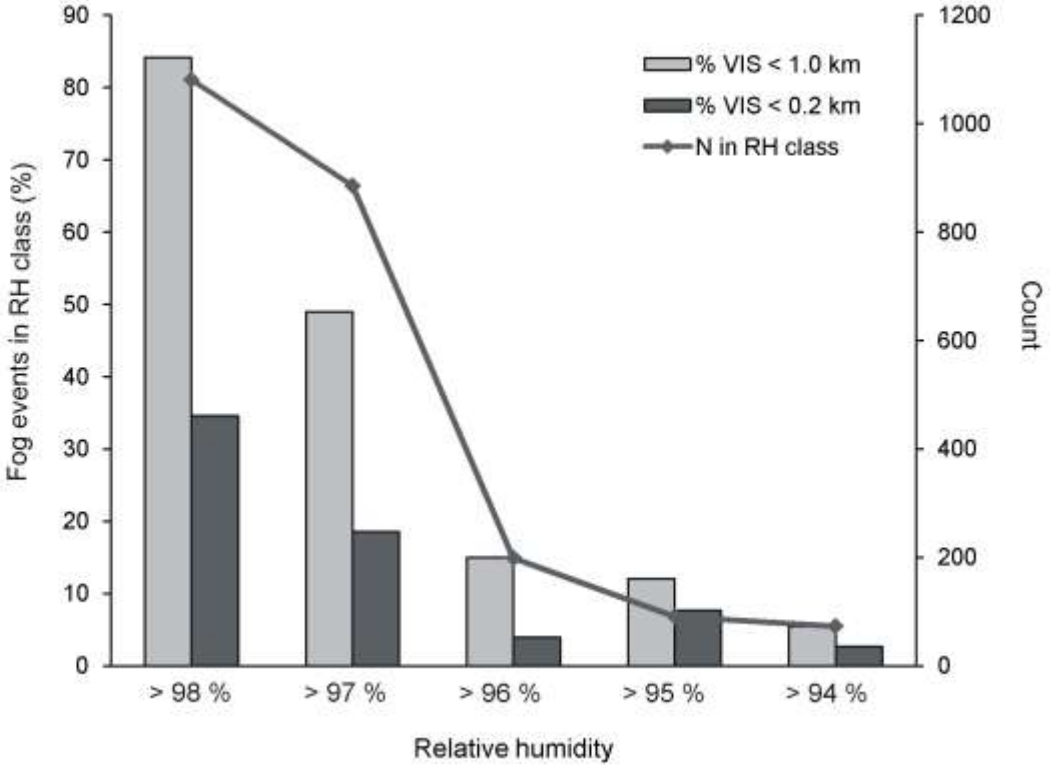

Figure 5. Relative (in percentage) and absolute (in N= number of total events) occurrence of light fog (visibility<1 km, light gray) and dense fog (visibility<0.2 km, dark gray) for classes of high relative humidity (RH) in lowland cloud forest at Canopy Operating Permanent Access System station, June–July 2008.

2.5 Discussion

There was significantly more epiphytic biomass suspended on trees in LCF than in LRF. We found less epiphytic biomass in the investigated forests, however, than is reported from other tropical lowland forests (Hietz-Seifert *et al.* 1996, Freiberg & Freiberg 2000). The discrepancy may be explained by the different methodologies used in our study and those of other authors. While our study only focused on holoepiphytes (Schimper 1888), Hietz-Seifert *et al.* (1996) also included the biomass of hemiepiphytes and climbers, and this probably holds true for the study of Freiberg and Freiberg (2000) as well. Although the amount of vascular epiphyte biomass analyzed in the present study was limited, we found that abundance of vascular epiphytes in LCF greatly exceeded that in LRF, both in terms of biomass and cover. In the latter habitat, epiphytic angiosperms and pteridophytes were very scarce, while occurring with high frequency in LCF.

As to biomass of epiphytic lichens and bryophytes, the amounts measured in LRF crowns are similar to those reported for lowland Ecuador (Freiberg & Freiberg 2000). Trees in LCF, however, hold over 30 percent more biomass than those in LRF. The amount of bryophyte biomass on LCF trunks is similar to that found in montane forest above 1000 m in the Andes of NE Peru (Frahm & Gradstein 1991). Comparison of the epiphytic bryophyte cover in LCF with that measured along altitudinal transects in Colombia (van Reenen & Gradstein 1983) and Borneo (Frahm 1990) yields even more striking results and shows a similarity of LCF with moist montane forest at 2000 m. The latter data coincide with those for species richness of liverworts, which in LCF are as high as in Colombian forests at 2000 m (Gradstein 2006, Gradstein *et al.* 2010).

We propose that the similarities between LCF and moist tropical mountain forests reflect the relatively high air humidity and occurrence of fog in the two forest types, in spite of the obvious differences in air temperature and radiation intensity. The general increase of bryophyte biomass with elevation has been explained by various climatic factors including precipitation, air humidity, frequency of fog, temperature, light intensity, and combinations of these (e.g., Seifriz 1924, Grubb & Whitmore 1966, Bayton 1969, Richards 1984). Apart from the obvious importance of moisture availability to bryophyte growth (Hosokawa *et al.* 1964), bryophytes reach their highest rates of net assimilation at temperatures below 25°C and light intensities between 500 and 900 lx. Therefore, production of biomass is considered to be restrained in lowland forests with temperatures above 26°C and light intensities below 500 lx (Frahm 1990). High (day and night) temperatures cause high rates of dark respiration (Lambers *et al.* 1998), causing bryophytes in hot conditions to lose greater parts of their assimilated carbon. With increasing elevation, bryophyte growth is considered to be favored by lower temperatures coupled with higher light intensities and longer periods of high humidity, as seen in tropical montane forests (Richards 1984, Zotz *et al.* 2003).

Nonvascular epiphytes are known to successfully colonize all height zones of trees in the humid tropics, but in terms of microclimate many bryophytes prefer the more shaded, humid habitats, where VPD is low, while lichens generally thrive on exposed bark, their majority being less tolerant against water over-saturation (Proctor 2000, Sillett & Antoine 2004, Green *et al.* 2008). The microclimate data gathered in this study demonstrate that RH is higher in LCF than in LRF, particularly at night and early mornings. We attribute the higher humidity in LCF to the prevalence of radiation fog in this forest type. During fog events, the moist environment should facilitate bryophyte growth in LCF but causes excessive water saturation in lichens, inhibiting photosynthesis and thus biomass gain (Lange *et al.* 1993, 2000; Zotz *et al.* 1998). As the day progresses, RH decreases, VPD increases, and lichens may again take up CO_2 and become photosynthetically active. For the majority of bryophytes, on the other hand, the ability to engage in photosynthesis is inhibited during periods of decreased air humidity (Proctor 2000). The occurrence of fog events in LCF, however, reduces the daily decrease of air humidity and the increase of VPD and, thus, would shorten the period of photosynthetic inactivity of the bryophytes. This, in turn, may explain why biomass of bryophytes in LCF is higher than in LRF. We suggest that the prolonged availability of high air humidity in LCF and the additional input of liquid water through fog, enhance epiphyte growth by shortening the desiccation period and lengthening the period of photosynthetic activity of the plants. The greater amount of nonvascular biomass in LCF, resembling that found in montane forests, may be explained by enhanced growth of bryophytes in response to additional water input by fog. The fog events may result in prolonged periods of photosynthetic activity in these organisms and thus improve conditions for bryophyte growth. Since lichens are water over-saturated during early morning in both forest types, the increased humidity observed in LCF would not affect these organisms.

The data on bryophyte and lichen abundance in the two forest types are paralleled by species richness, which is more strongly increased in bryophytes of LCF than in lichens, with exception of cyanolichens (Normann *et al.* 2010). Future studies may focus on the processes determining the high diversity and biomass of epiphytes that characterizes the tropical LCF.

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3 Canopy level fog occurrence in a tropical lowland forest of French Guiana as a prerequisite for high epiphyte diversity

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3.1 Abstract

Fog frequency and the meteorological processes leading to fog formation have never been studied in depth in tropical lowland forest areas. This study provides detailed evidence of frequent fog occurrence in lowland valleys of central French Guiana. Fog frequency showed a clear diurnal course, with a maximum before sunrise; average fog duration was 4.6 h. The diurnal course of visibility was positively correlated with the diurnal course of humidity in the above-canopy air. Fog persistence correlated significantly with atmospheric parameters during the dry season, but not during the rainy season. The main trigger of fog development in the lowland forest seemed to be precipitation, leading to higher soil moisture, greater evapotranspiration and, thus, higher water content of air. An increasing temperature difference between valley and hill sites after sunset, together with more frequent down-slope winds during nights with long fog periods, points at some influence of katabatic flows. The frequent occurrence of fog in the valleys correlated with significantly higher epiphyte diversities in valley forests as compared to hill forests, and supported the occurrence of the hitherto undescribed, epiphyte-rich “tropical lowland cloud forest” (LCF) in the valleys. The higher epiphyte diversity in LCF coincided with significantly higher relative air humidity in LCF than in hill forest. The ecological benefits of fog for the epiphytes in LCF are surplus of moisture and delayed onset of the stress period, particularly in the dry season.

3.2 Introduction

Fog as defined by a horizontal visibility of ≤ 1 km (Roach, 1994) is normally the result of very low cloud formation in the atmospheric boundary layer. It is an obstacle to traffic but, at the same time, can provide significant amounts of water to moistened surfaces by fog water interception. While a great number of studies on fog are available for the outer Tropics (e.g. Wanner and Kunz, 1983; Bendix, 2002; Gultepe *et al.,* 2007; Cermak and Bendix, 2008; Eugster, 2008) and for tropical montane cloud forests (e.g. Hamilton and Bruijnzeel, 2000; Bendix *et al.*, 2008), investigations in tropical lowland forest are virtually lacking. Low visibilities in Midlatitudes often occur in wintertime, frequently related to radiation fog which is formed predominately in valleys and basins due to nocturnal outgoing radiation and cooling of the boundary layer air to the saturation point. In tropical mountain forests, low visibility (and thus fog) is often the result of cloud formation/advection at/to the windward slopes, mostly at altitudes >500m a.s.l. (e.g. Shuttleworth, 1977; Cavelier and Goldstein, 1989; Hamilton *et al.*, 1995; Ataroff, 1998; Bruijnzeel, 2001; Rollenbeck *et al.*, 2006). In the lowland tropics and subtropics, fog occurrence is well documented for coastal waters, particularly in areas of cold upwelling of the coast (e.g. Olivier, 1995; Cereceda *et al.*, 2002; Shanyengana *et al.*, 2002; Osses *et al.*, 2005). In contrast, knowledge of temporal and spatial fog dynamics in tropical lowland forests is poor. Observations in the Amazon forest of Brazil suggest that radiation fog might occur in lowland river valleys (Bastable *et al.*, 1993; Klockow and Traga, 1998). Large scale atmospheric circulation patterns related to fog formation in eastern Brazil were recently described by Fedorova *et al.* (2008). However, no comprehensive study is available on the interaction of energy balance, local breeze pattern and fog occurrence in the tropical lowland forest.

Fog is generally considered to be a major driver of the diversity of epiphytic organisms in tropical forests (e.g., Grubb and Whitmore, 1966; Nadkarni, 1984, 2010). It is expected that the surplus of moisture by the interception of fog water in the forest canopy shortens the duration of desiccation of the epiphytic plants (mosses, liverworts, lichens, ferns, flowering plants) dwelling in the canopy, thus enhancing their photosynthetic activity and growth.

The coincidence of fog and high epiphyte diversity is well documented for tropical mountain forests (e.g. Hamilton *et al.*, 1995; Richards, 1996) but has not been recorded in tropical lowland forest, until recently by Gradstein (2006) and Gradstein *et al.* (2010).

Based on findings of high epiphytic bryophyte richness of lowland forest in valleys of central French Guiana (Gradstein, 2006), a new unique ecological habitat type, the "Tropical Lowland Cloud Forest" (LCF), is proposed, with exceptionally high richness of epiphytic bryophytes resembling epiphyte richness in tropical mountain forests. "Tropical Lowland Rain Forest" (LRF) with lower epiphyte richness is restricted to slope and hill sites. However, the specific mechanisms of low cloud formation are hitherto unknown. In this paper, we hypothesize that LCF is mainly related to radiation type valley fog formation, which is poorly documented for tropical lowland areas.

To test the hypothesis, the aims of the current study are:
1. To investigate fog frequency differences in valleys and ridges.
2. To analyze meteorological processes leading to fog formation.
3. To shed light on the relation between fog occurrence and species richness of LCF epiphytic vegetation.

The results are expected to be of great importance for the hydrological cycle of the Amazon lowland forest in a broader way because a high density of epiphytic vegetation in canopies can alter canopy storage capacity and interception efficiency significantly (e.g Veneklaas *et al.*, 1990).

3.3 Methods

3.3.1 Study area

The study was performed at research station Saut Pararé, Nouragues Natural Reserve (4°2'30" N, 52°40'30" W, 75 m a.s.l.) in the valley of the Arataye river, ca. 100 km inland from Atlantic coast (Fig. 6a).

The area is covered by dense, nearly undisturbed primary lowland forest, described as “old-growth *terra firme* dense rainforest” (Poncy *et al.*, 2001). The forest is tall, with canopy trees reaching heights of approximately 50 m. Natural disturbances such as tree falls lead to canopy gaps in some places (Van der Meer and Bongers, 2001). The forest is dominated by Burseraceae trees and represents one of the two main French Guianan forest types described by Sabatier and Prévost (1990) differing by the dominant tree family. The terrain is undulating, with many small hills and creeks, varying in altitude from 50 to 200 m a.s.l.

In terms of meteorological measurements, the Guiana Shield is one of the poorest monitored regions in the western hemisphere (Hammond, 2005). Generally, annual precipitation shows a latitudinal gradient from coastal regions to inland locations. Average annual precipitation ranges between 3500 mm at the Atlantic coast (Cayenne) and 2500 mm at Maripasoula on the border to Suriname (150 km west of the study site). The wind regime in 10 m (sigma-995 level) in the wider study area based on an analysis of NCEP–NCAR reanalysis data (Fig. 7, for data see Kalnay *et al.*, 1996) clearly shows that the wind direction is dominated by the easterly trade winds throughout the whole year at all times of the day.

Meteorological measurements in the Nouragues Natural Reserve are being conducted since 1996 at the “Inselberg” field station, at a distance of 7 km from the study site (Charles-Dominique, 2001). Grimaldi and Riéra (2001) provided meteorological data for November 1987–December 1996. Average annual precipitation at Inselberg field station is 2990 mm, with 310 days of rainfall. A relative dry season occurs from mid-August to mid-November, with less than 100 mm monthly rainfall during September–October, and a secondary decrease in rainfall between February and April. The rainy season lasts from November until August, with May being the wettest month (407 mm total rainfall). Air temperature exhibits little seasonal variation, mean monthly values ranging from 25.5°C in January to 27.5°C in October.

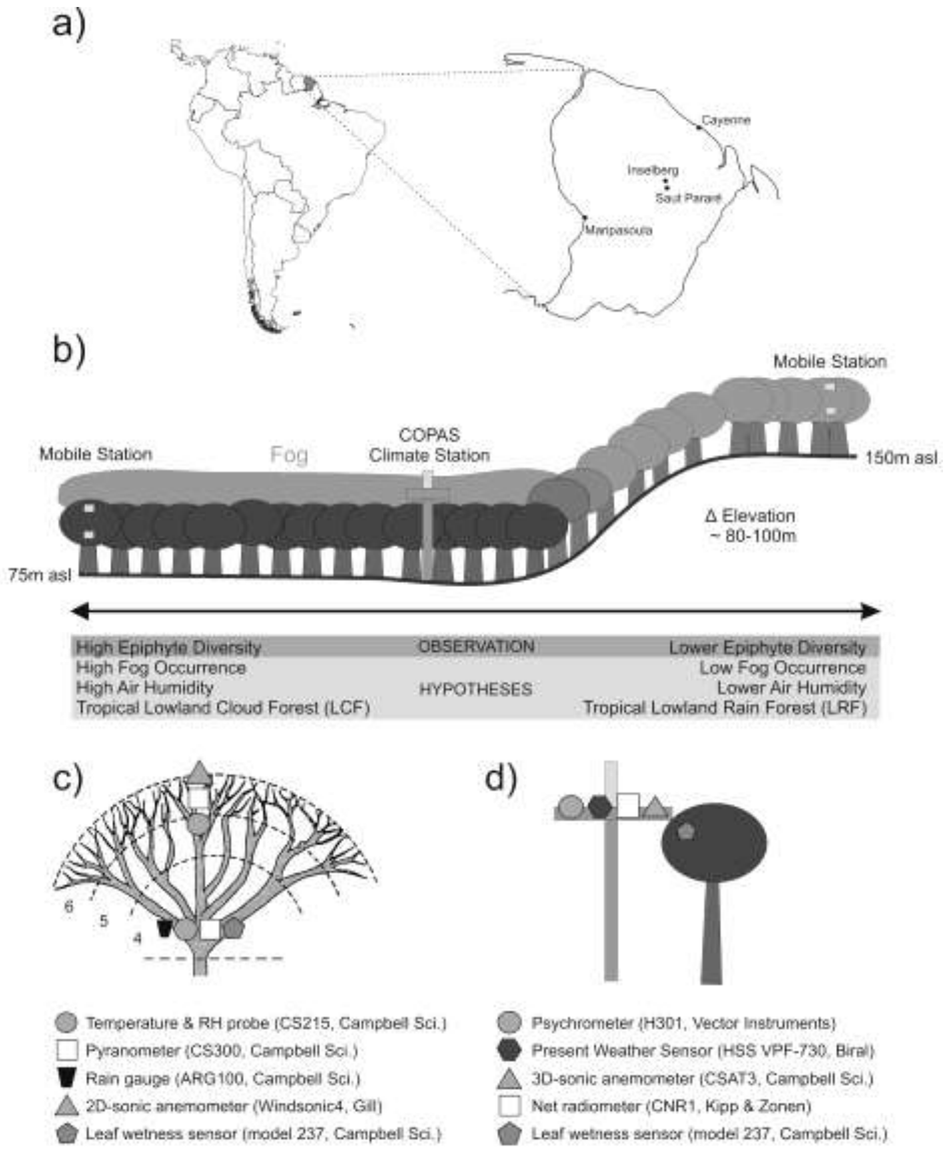

Figure 6. Measurement approach at the study site. (a) Location of the study site; (b) layout and visualization of hypothesis; (c) placement of mobile sensors in the canopy; (d) permanent measurements on COPAS platform.

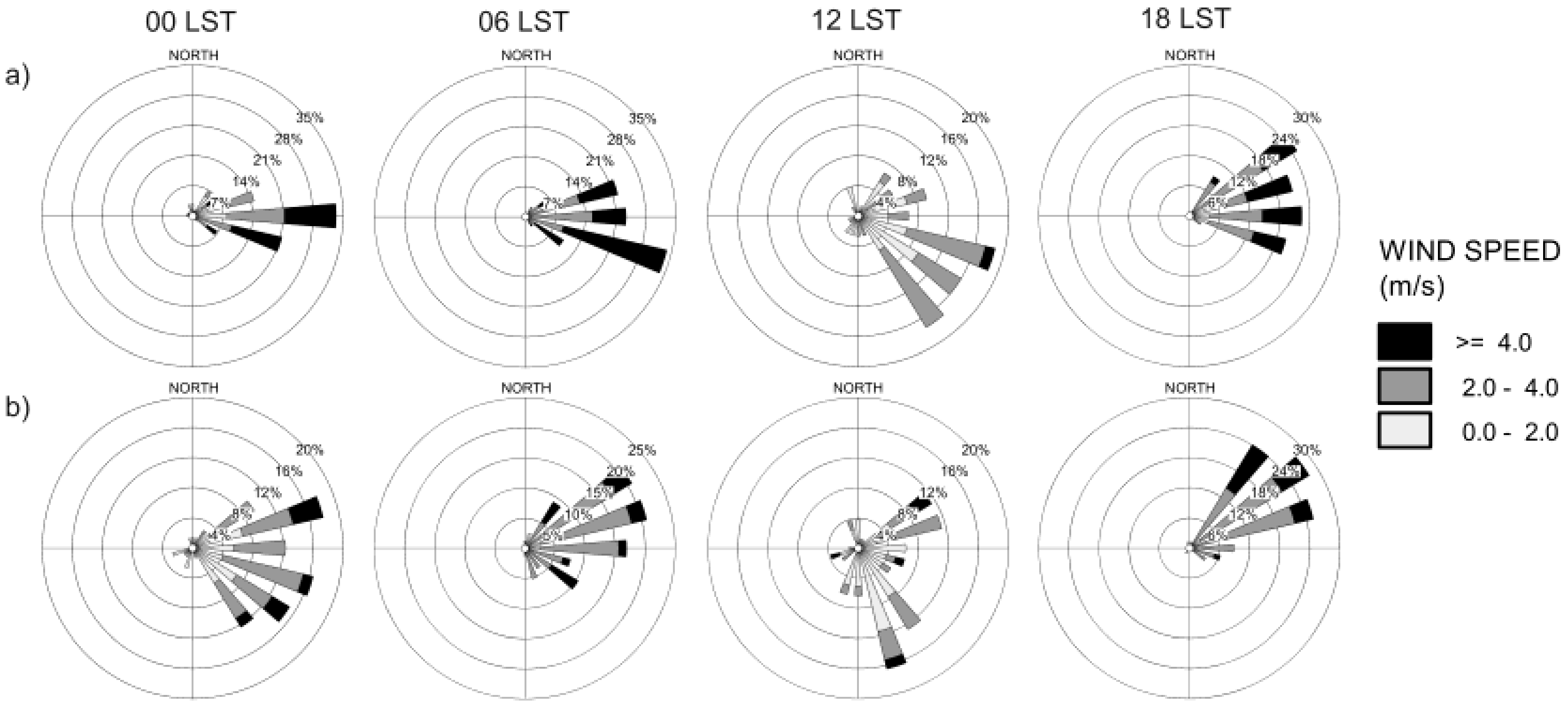

Figure 7. General streamflow patterns in 10m (sigma-995 level) from NCEP reanalysis data at different times of day for a) dry season (August–October 2007) and b) rainy season (May–July 2008).

3.3.2 Experimental setup

The measurement approach is illustrated in Fig. 6b. Permanent and mobile meteorological observations were conducted here between 2007 and 2009. In the valley of the Arataye river, data of important meteorological parameters were gathered directly above the canopy (45 m above ground) by installation of a climate station on one pylon of the “Canopy Operating Permanent Access System” (COPAS, 75 m a.s.l.; Fig. 6d) (Charles-Dominique *et al.*, 2002). The station encompassed a psychrometer (H301, Vector Instruments), a 3D-sonic anemometer (CSAT3, Campbell Sci.), a net radiometer (CNR1, Kipp and Zonen) and a leaf wetness sensor (Model 237, Campbell Sci.). Horizontal visibility (and thus fog occurrence) and rainfall was observed by using a visibility and present weather sensor (HSS VPF-730, Biral). All instruments were operated by solar and battery power. To compare the meteorological situation at ridge and valley locations, mobile meteorological stations were placed in the inner and outer canopy (ecologically relevant because of differences in epiphyte diversity, see Johansson, 1974; Gradstein *et al.*, 2003) of representative trees which were also sampled for epiphyte abundance and diversity (Fig. 6c). The single rope technique was used to access the tree crowns (Mitchell *et al.*, 2002). The topographic height difference between the two sites in the Saut Pararé area was about 100 m. Sensors installed were: (i) temperature and relative humidity probes (CS215, Campbell Sci.), (ii) pyranometer sensors (CS300, Campbell Sci.), (iii) a rain gauge (ARG100, Campbell Sci.), (iv) a 2D-sonic anemometer (Windsonic4, Gill), and (v) a leaf wetness sensor (model 237, Campbell Sci.). Leaf wetness sensors emulate the surface of a leaf and are primarily used to detect periods of leaf wetness caused by rain, dew or fog. They are often prepared with a thin coat of flat latex paint (Gillespie and Kidd, 1978). The leaf wetness sensor was field calibrated and the wet/dry threshold was determined at 100 kΩ.

The sensors at the COPAS system and the mobile sensors were connected to CR1000 data loggers (Campbell Sci.) computing 5-min averages from 60-s sampling intervals. A specific logger (NDL485 blueberry, Wilmers) was used for the visibility sensor operating with the same clock and intervals. Only the 3D-anemometer was used with a higher 3-s sampling interval.

Additional data loggers (HOBO ProV2 RH/Temp, Onset) were installed in 16 trees in hill and valley positions (eight trees per site) to measure air temperature (°C) and relative humidity (%RH) with 5 min intervals for 60 days during September and October 2007. The data loggers were installed in the middle of the crowns at 15–25 m depending on canopy height (emergent trees excluded). For each tree, diversity of epiphytic bryophytes and filmy ferns was determined.

3.3.3 Data analysis

Fog frequency was calculated on an hourly and daily base. Fog days were defined according to international standards by horizontal visibility falling below 1 km at least once a day. Similarly, fog hours were defined by visibility falling below 1 km within the respective hour. Duration of fog persistence was calculated by summation of all 5-min intervals of horizontal visibility below 1 km between 19:00 and 09:00 LST for each respective time period. Mean diurnal courses were computed for fog frequencies and various other meteorological parameters, including air temperature, relative air humidity, specific humidity deficit and wind direction.

Horizontal visibility as a measure of fog density was used for the estimation of fog liquid water content (LWC), although the correlation is dependent on drop size distribution. For stable fog, Eldridge (1971) found a non-linear decrease of fog liquid water content with increasing visibility based on drop-size distribution data, with a LWC of 0.35–1.8 gm^{-3} occurring in very dense fog (VIS = 50m) and 0.042–0.19 gm^{-3} in dense fog (VIS = 200 m). Towards the haze boundary (VIS = 0.5–1 km) LWC decreases to values <0.0005 gm^{-3}. Because “warm” fogs tend to contain greater droplets and liquid water contents (e.g. Stewart and Essenwanger, 1982), the upper boundary of LWC is more likely to be representative of the fog in the Arataye river valley. Visibility during the nocturnal fog period (19:00–09:00 LST) was determined for (i) the entire fog period, (ii) the time of maximum fog occurrence (05:00–06:00 LST) and (iii) the time of fog dissipation (08:00–09:00 LST).

To unravel atmospheric parameters responsible for fog occurrence/ persistence, a correlation analyses between fog persistence and other meteorological parameters was performed. During each night, fog persistence was compared with the following variables: (i) time of saturation (time when relative air humidity exceeds 99%), (ii) average relative humidity, (iii) average specific saturation deficit, (iv) average air temperature, (v) air temperature cooling rate, (vi) radiation balance, (vii) average wind speed and (viii) rainfall sum. The parameter “time of saturation” was derived by assigning low values to early saturation (1 = 15:00 LST, i.e. the earliest measured saturation time point on the day before fog formation) and high values to late saturation (14 = 04:00 LST, i.e. the latest measured saturation time point).

For averaging of the parameters, different time periods were used to unveil the importance of weather development on the day before/during fog formation on fog duration: (i) the entire day before the fog event (08:00–19:00 LST day-1), (ii) the evening hours (19:00–00:00 LST day-1) and (iii) the early morning (00:00–08:00 LST on the fog day).

Data of the mobile stations retrieved during a field campaign in March/April 2008 were used to compare meteorological parameters at valley and ridge sites. Median and median absolute deviation were calculated for the time between 00:00 and 08:00 LST.

Leaf wetness duration (LWD), defined as the length of time that deposited water (here only fog and dew periods), is retained on plant surfaces (Sentelhas *et al.*, 2007, 2008), was derived for valley and ridge sites using data of the leaf wetness sensors. Rainfall data of the mobile rain gauges were used to exclude rain periods when calculating LWD.

In order to study the relation between meteorological parameters and epiphyte diversity, and to verify the difference of LCF and LRF sites in terms of humidity, temperature and epiphyte diversity, a principal component analysis (PCA) was performed using data retrieved by the additional data loggers and botanic samplings of 16 trees.

3.4 Results

3.4.1 Fog frequency and fog density

Fog frequency at canopy level is presented in Fig. 8a. The data show that fog is a common phenomenon in the Arataye river valley. With regard to fog days (=at least one fog observation per day), visibilities of ≤1 km occurred on 96% of days in dry season and on all days in rainy season. Fog frequency shows a clear diurnal course, with a maximum at the early morning hours between 05:00 and 07:00 LST. A significant enhancement of frequency is detected after sunset (19:00 LST), followed by a steady increase during the night. Solar heating after sunrise leads to rapid fog clearance. Four hours after sunrise (10:00 LST), fog is almost completely cleared. During the rest of the day, until sunset, fog frequency is low, generally less than 10%. With regard to fog dynamics, the diurnal course of fog frequency clearly indicates that radiation fog formation and clearance is the most likely mechanism generating low visibilities (and thus, liquid water) in the canopy. However, clear differences are observed between the dry and the rainy season (Fig. 8a). Generally, higher fog frequencies occurred during the rainy season, with a marked increase of frequency observed after sunset. In contrast, a gradual and continuous increase of fog frequency during the night occurred in the dry season. While fog frequency reached high levels as early as 01:00 LST in the rainy season, highest fog frequency during the dry season appears just around sunrise.

The diurnal course of visibility was clearly related to the diurnal course of humidity and saturation conditions in the above canopy air (Fig. 8b). Average relative humidity was close to or at saturation during times of fog occurrence. The generally higher saturation deficit reflects the reduced fog frequency in the dry season. Average daily fog duration was 4.6 h but ranged from 4.4 h in the dry season to 6.2 h in the rainy season. Average relative humidity at canopy level for dry and rainy season was 87.1% and 93.4%, respectively.

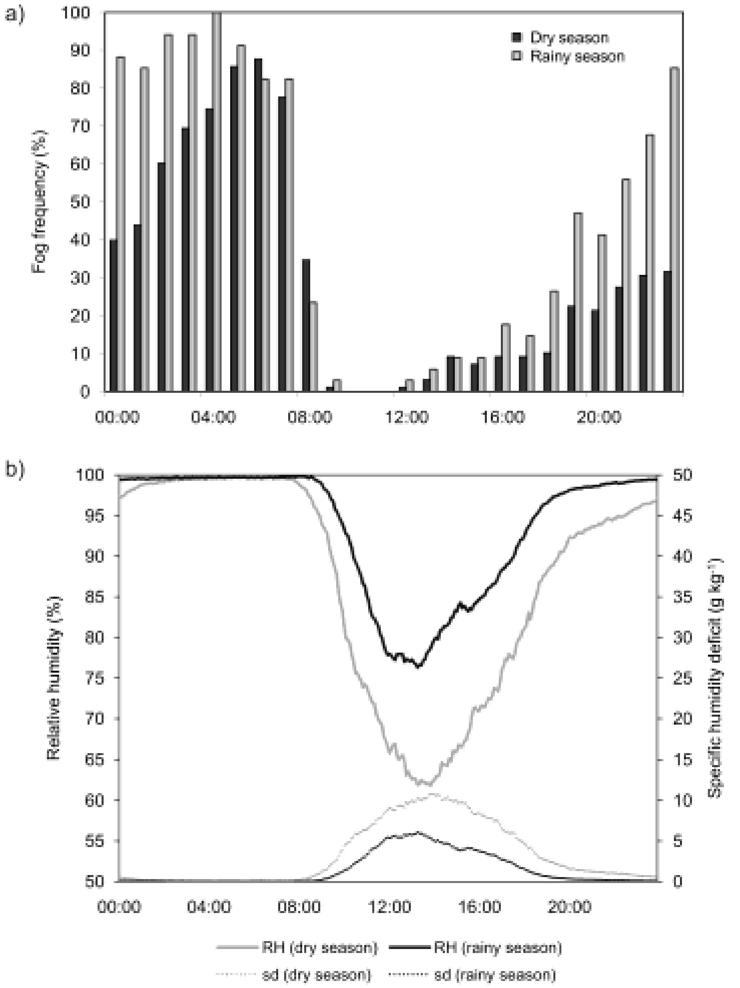

Figure 8. (a) Diurnal course of fog frequency in the dry (mid-August until mid-November 2007) and rainy (mid-June until mid-July 2008) season at the study site (present weather sensor) **(b)** diurnal course of average relative air humidity (RH) and specific saturation deficit (sd) for the rainy and dry season, both at the canopy–atmosphere interface level.

The frequency of fog density classes, as a parameter for liquid water content (LWC), is shown in Fig. 9. Very dense (and thus, moist) fog (VIS < 100 m) events are more frequent in the dry season than in the rainy season, even if the overall occurrence of fog during night is somewhat lower in comparison to the rainy season. The density differences hold also for the period of maximum average fog frequency around sunrise (05:00–06:00 LST), and even for the fog clearance time between 08:00 and 09:00 LST, when fog is more frequent than in the rainy season.

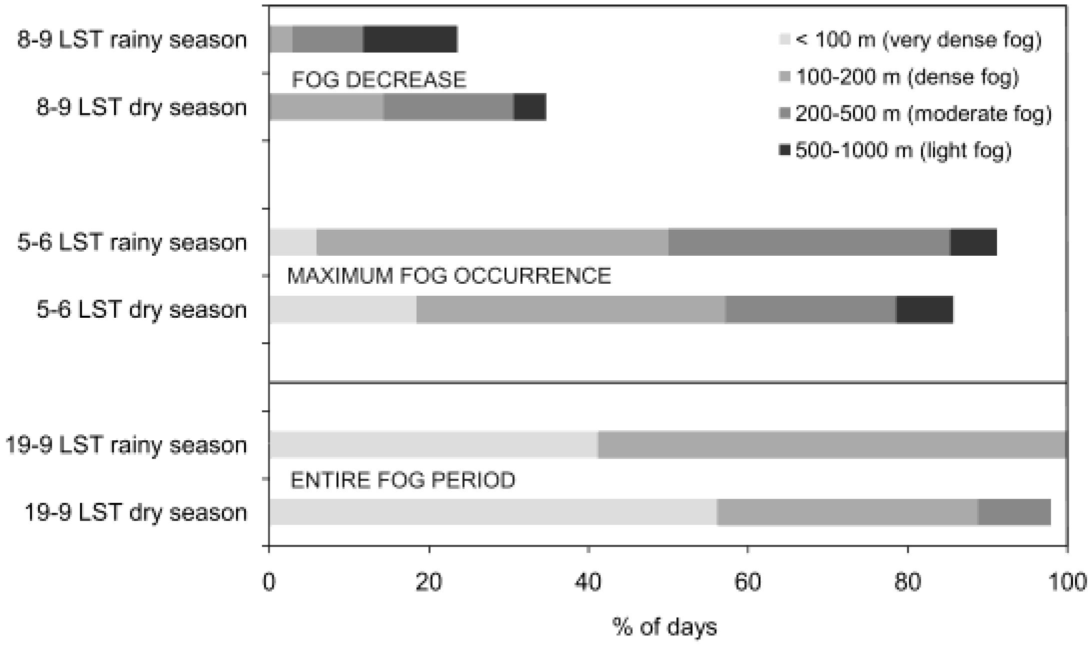

Figure 9 Frequency of visibility classes for the fog at the study site (present weather sensor) at canopy–atmosphere interface level.

Fig. 10 underpins the significant relation between mean visibility and fog persistence. Median global radiation during morning fog is linearly correlated to corresponding values during fog-free morning hours (Fig. 11). Global radiation during morning fog is reduced to 79.8±2% for light and moderate fog events (visibility 200–1000 m) and decreases to 66.3±2% during the occurrence of dense fog (visibility <200 m).

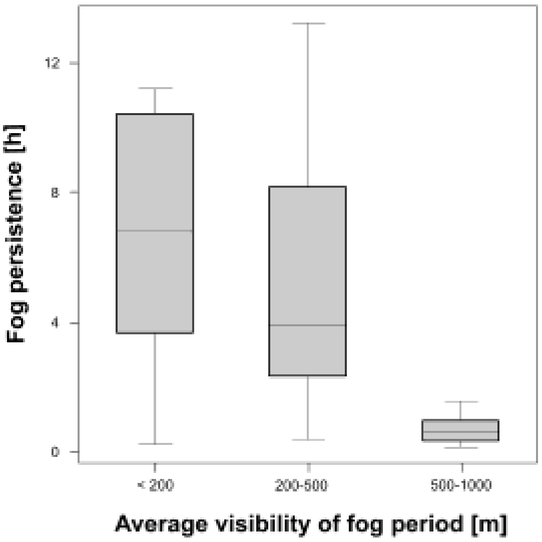

Figure 10. Box–Whisker plots of fog persistence shown for three fog density classes (dense fog: visibility <200 m, moderate fog: visibility between 200 and 500 m, light fog: visibility between 500 and 1000 m) in the dry season. Fog density (mean visibility) is calculated for each corresponding fog period.

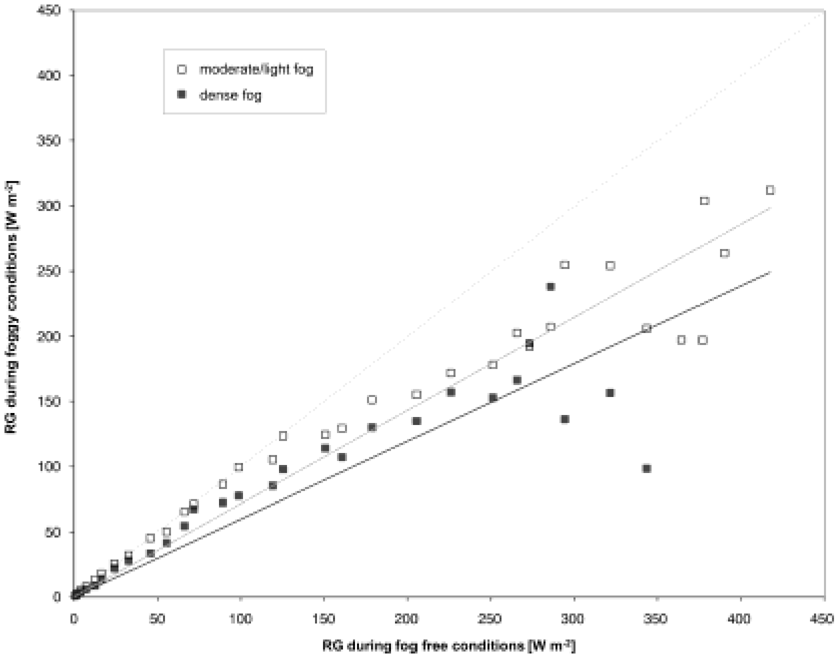

Figure 11. Median values of global solar radiation (RG) under foggy and fog-free conditions in the dry season. Data shown for 5-min intervals for the morning period from 6 to 9 LST (dotted line: 1:1 bisection); black line: regression line ($r^2 = 0.822$) for dense fog (visibility <200 m); grey line: regression line ($r^2 = 0.937$) for light and moderate fog (visibility 200–1000 m).

3.4.2 Relevant meteorological parameters of fog persistence

Significant correlations between atmospheric parameters and fog persistence were found for the dry season (Table 2). In this period, duration of fog persistence during night depends on the time when saturation conditions are reached (>99% relative humidity). Saturation at an early point in time (e.g. in the afternoon before the fog event) induces a high duration of fog. Also, relative humidity on the day before fog formation and specific saturation deficit correlate with fog persistence during the dry season. When the deficit on the day before the fog event (particularly before 18:00 LST) is low, persistence of fog is relatively high (r =− 0.73).

Table 2. Pearson's correlation coefficients of fog persistence (VIS≤1 km) at canopy level of the COPAS station in relation to meteorological parameters for time frames before (8:00–19:00 LST) and during fog formation (19:00–0:00 LST). Correlations are not significant if no p-value is given; α= 5%. Observation periods Aug–Nov 2007 (dry season, 98 days) and Jun–Jul 2008 (rainy season, 34 days).

Fog persistence vs.	Dry season			Rainy season		
	Specific time	8:00-19:00 LST	19:00-00:00 LST	Specific time	08:00-19:00 LST	19:00-00:00 LST
Relative humidity (mean)	-	0.7 (p<0.01)	0.76 (p<0.01)	-	0.1	0.25
Specific humidity deficit (mean)	-0.73 (p<0.01) (18:00 LST)	-0.66 (p<0.01)	-0.74 (p<0.01)	-0.27 (18:00 LST)	-0.11	-0.24
Air temperature (mean)	-	-0.62 (p<0.01)	-0.72 (p<0.01)	-	-0.14	-0.19
Radiation balance (mean)	-	-0.48 (p<0.01)	0.76 (p<0.01)	-	-0-03	0.13
Wind speed (mean)	0.3 (p<0.01) (00:00-08:00 LST)	-0.37 (p<0.01)	-0.17	0.06 (00:00-08:00 LST)	-0.14	-0.14
Rainfall (sum)	0.72 (p<0.01) (24 h day)	0.69 (p<0.01)	0.14	0.24 (24h day)	0.35 (p<0.02)	-0.17
Time of saturation	-0.83 (p<0.01)	-	-	-0.35 (p<0.02)	-	-
Cooling rate	0.5 (p<0.01) (12:00-18:00 LST)			0.17 (12:00-18:00 LST)		

Furthermore, a positive correlation is observed between fog persistence and specific humidity during daytime (08:00–19:00 LST), but not with specific humidity during late evening hours (19:00–00:00 LST). This suggests that a high water content of air on the day before fog formation promotes a greater length of the fog event. This conclusion is supported by the moderate positive correlation of fog duration with the rainfall sum on the day before fog formation (r = 0.72), and the low correlation with the rainfall sum at the evening of fog formation. Mean air temperature during afternoon and evening hours is negatively correlated to fog persistence due to the greater water holding capacity of air at higher temperature, leading to a delayed occurrence of the saturation point. A positive correlation is seen between afternoon cooling rate and fog persistence, indicating that a stronger cooling at sunset fosters an earlier onset of fog. Furthermore, the relation between fog persistence and radiation balance shows that a lower radiation (more clouds and rain) and a lower radiation balance on the day before fog formation might promote a longer duration of fog events. In contrast, radiation balance correlates positively with fog duration in the evening hours (r = 0.76) due to the fact that nocturnal counter radiation is enhanced by the fog layer. The correlation between fog duration and wind speed changes the algebraic sign from evening to morning hours (not significant).

No significant correlation between fog duration and meteorological parameters was found for the rainy season, but the overall tendencies are mostly the same as for the dry season (Table 2). Reason for the less strong correlation might be the generally high relative air humidity during the rainy season, reducing the effect of fog on humidity (Fig. 8b). Also, no significant relationships between average fog density (visibility) and atmospheric parameters were found, neither for the rainy season nor for the dry season.

3.4.3 Radiative cooling, katabatic flows and fog occurrence

The results of the correlation analysis suggest that fog occurrence at Saut Pararé could be induced by radiation processes and/or katabatic stream flow dynamics. Comparison of the diurnal course of air temperature inside and above the canopy with the development of wind direction indicates that the canopy acts as the main radiative transfer layer between the earth surface and the atmosphere (Fig. 12).

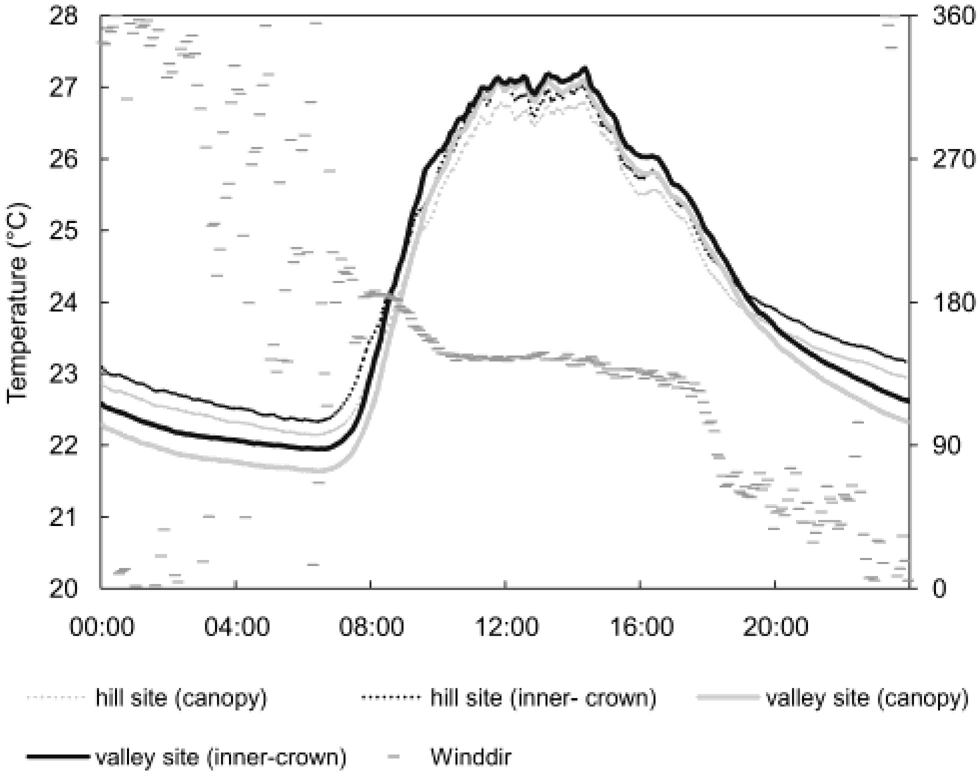

Figure 12. Average diurnal course of air temperature in two tree levels (canopy, innercrown) and wind direction (COPAS tower) on hill and in valley at the study site (field campaign March–April 2008).

During daylight, the lower valley site shows higher canopy level air temperatures than the slightly elevated hill site. The temperature difference between the above- and inside-canopy measurements oscillates, most likely due to the amount of evaporative cooling. Evaporative cooling of the canopy may be high at the very moist valley site. Consequently, the inner crown-area is slightly warmer than the above-canopy air around noon. After sunset, the situation changes completely. The valley site becomes clearly colder than the hill site. Because the top of the canopy acts as the main emitting surface for longwave outgoing radiation, the above-canopy air temperature further cools below the inner canopy air (valley site). The switch of the vertical temperature field coincides with the onset of descending vertical winds indicating cold air drainage flow. On average, the vertical wind vector turns negative between 19:00 and 20:00 LST. The penetration of cold air into the valley forest canopy during night is indicated by decreasing temperatures in the lower level of the canopy. Of interest is the reaction of the horizontal wind field, which is clearly changing with the evening switch towards a stable thermal stratification between the valley bottom and the hill top. During noon, the average wind direction is relatively aligned with the W–E running valley axis of the Arataye river so that a thermal up-valley wind is developed, most likely forced by the prevailing tropospheric easterly streamflow (see also Fig. 7). With the establishment of the temperature inversion, wind direction changes to northerly directions during early night hours and towards a streamflow oscillating around a westerly direction during the early morning hours until sunrise. The increase of the temperature difference between the valley and the hill site after sunset points to some influence of katabatic flows, with the initial northerly directions possibly resulting from the most elevated slopes in the north of the COPAS station (see topographical detail in Fig. 13). With increasing katabatic flows the wind system turns into a westerly down-valley flow along the axis of the Arataye river. After midnight until sunrise, the very weak winds ($>90\% < 0.5 ms^{-1}$) are oscillating around westerly direction, partly intermitted by northerly down-slope winds.

A comparison of the wind direction frequency of nights of persistent fog occurrence with mainly clear nights (Fig. 13) shows that northerly and westerly wind directions are frequent during foggy nights, representing upslope and down-valley drainage flows. Nights with short fog periods, or without fog, are characterized by the absence of these winds. It thus appears that diurnal changes in wind direction differ markedly from the diurnal course of the synoptic streamflow, evidencing the occurrence of katabatic systems in the valleys related to fog events.

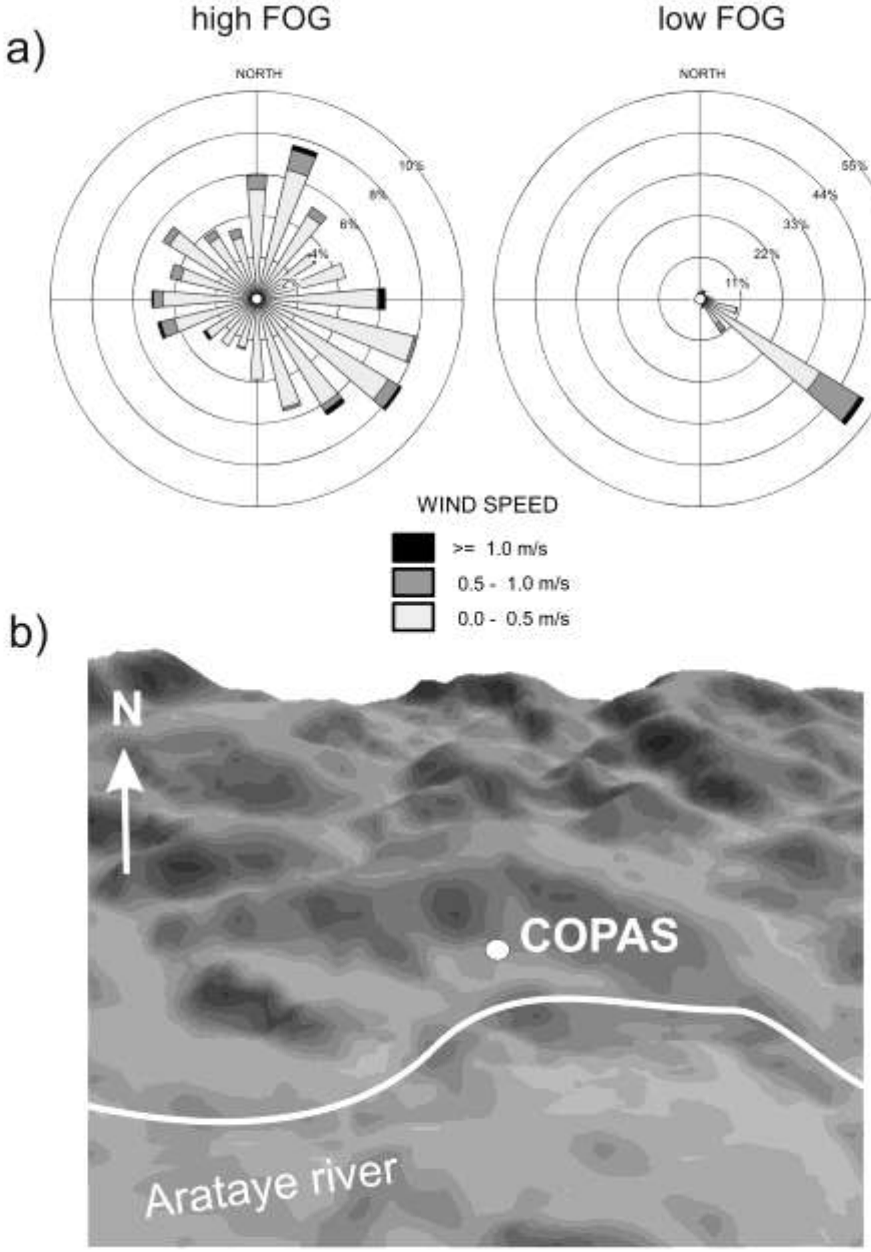

Figure 13. a) Distribution of wind directions (COPAS tower) in dry season for days of long (>6 h, high fog) and short fog persistence (<2 h, low fog) in the evening hours (19:00–00:00 LST) and **b)** terrain map of the surroundings.

3.4.4 Fog dynamics

Fig. 14 shows typical days of fog occurrence at the study site (valley) with four consecutive fog events differing in persistence and density. It appears that the initial fog event has low persistence and high visibility, the two consecutive events have increased duration, and the last event decreased persistence.

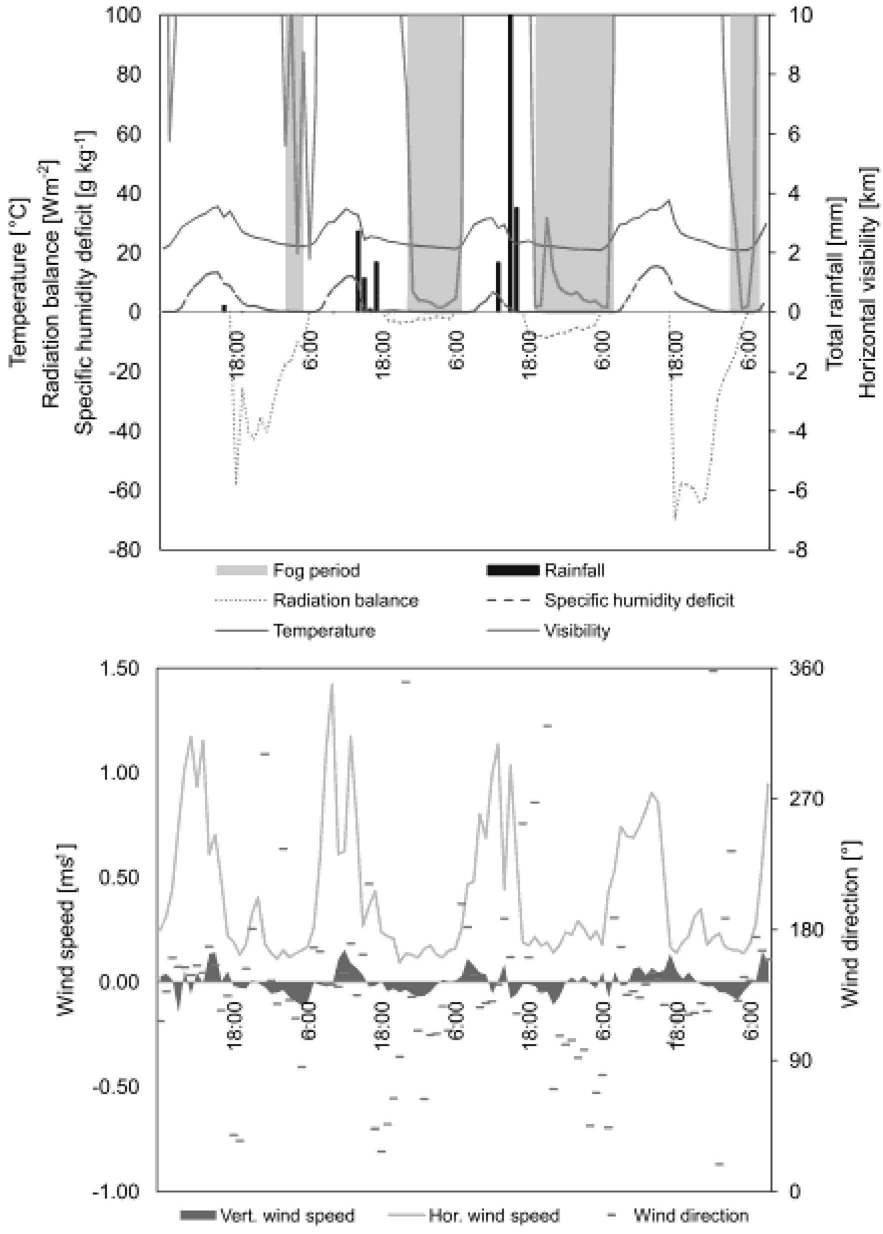

Figure 14. Fog dynamics for the period of 20–24 October 2007.

All events show some clear similarities: (i) Fog formation is related to equally reduced air temperature leading to saturation, (ii) low wind speed ($<0.2 ms^{-1}$) in the favourable range for fog formation, (iii) stable stratification (descending vertical winds) and (iv) wind turning to westerly down-slope/wind-valley directions before fog formation, simultaneously with the cooling process. Persistence, however, is greatest on the day with highest precipitation in the afternoon before fog formation. Both short fog events occur on days without any significant rainfall.

3.4.5 Fog occurrence and species richness at LCF & LRF sites

Data of the mobile stations retrieved at valley and ridge sites show clear differences for the time between 00:00 and 08:00 LST (Table 3). The valley forest is generally characterized by higher RH, lower temperatures and lower wind speed.

Table 3. Site comparison (median and median absolute deviation) of meteorological parameters measured during field campaign in March–April 2008 during nighttime (0–8 LST) and botanical data collected in 2007 (eight trees per site).

		valley site (LCF)		hill site (LRF)	
		median	MAD	median	MAD
COPAS station	Visibility 0-4LST (km)	8.24	6.49	*	*
	Visibility 4-8 LST (km)	0.789	0.67	*	*
	Fog persistence (h)	3.29	2.46	*	*
Mobile Stations	Leaf wetness duration (h)	7.75	0.17	1.25	1.25
	RH canopy (%)	98.3	0.3	95.3	1.6
	RH inner-crown (%)	97.2	0.3	95.3	1.4
	Temp canopy (°C)	21.95	0.49	22.79	0.53
	Temp inner crown (°C)	22.23	0.48	22.99	0.57
	Wind speed canopy ($m\ s^{-1}$)	0.11	0.04	0.27	0.1
Botanic collection	Liverworts (species per tree)	26	3	21	6
	Filmy ferns (species per tree)	2	1	0	0

The relation between fog occurrence and forest type is illustrated by the average diurnal course of relative humidity and LWD at both sites (Fig. 15). During noon the saturation deficit is nearly equally high in valley and hill sites. After sunrise, however, average relative humidity in the valley is very close to saturation in the above-canopy air, while in the hill site a saturation deficit between 10% and 5% occurs, which is generally unfavourable for fog formation.

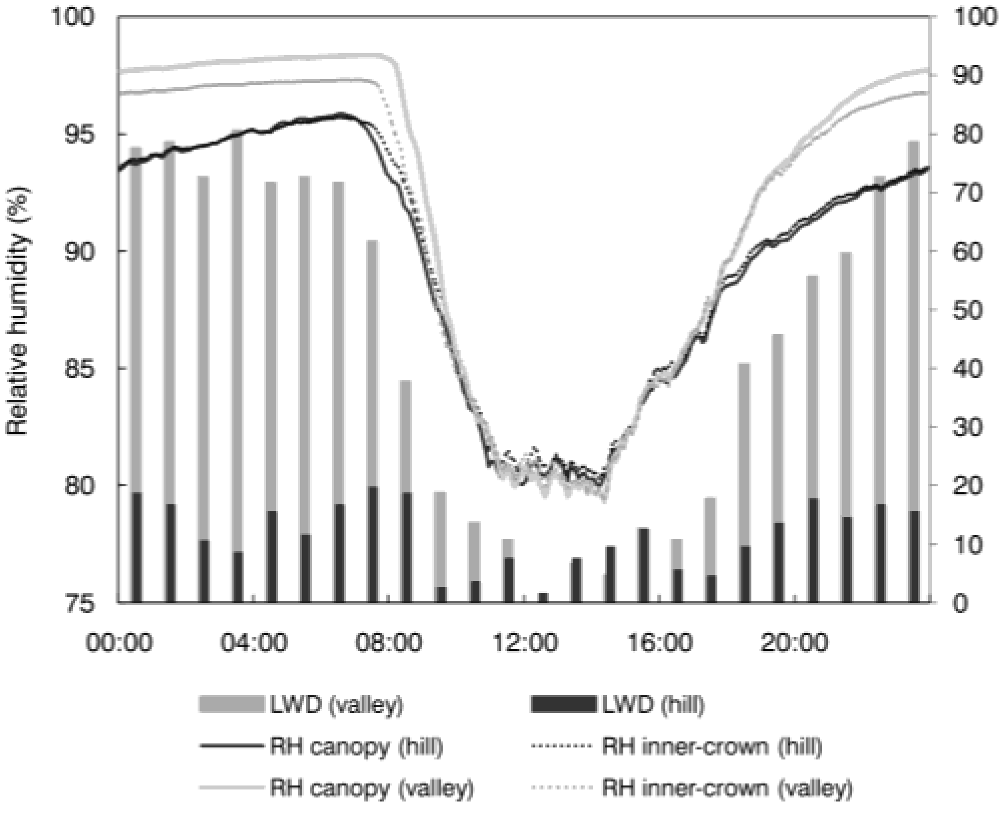

Figure 15. Mean diurnal course of relative humidity in two tree levels (canopy, inner crown) and leaf wetness duration (percentage of time per hour) on hill and in valley at the study site (field campaign March–April 2008).

LCF and LRF sites also show remarkable differences in leaf wetness duration, which is around three times higher at the LCF sites. Times of leaf wetness coincide with fog occurrence in LCF. During 97% of time when fog is reported, the leaf wetness sensor indicates a wettening of the surface. This onset of the wettening occurs on average 2 h before fog formation. In order to describe the relationship among relative humidity, temperature and epiphyte diversity, a principal component analysis was performed. The results are illustrated in Table 4 and the component plot is shown in Fig. 16.

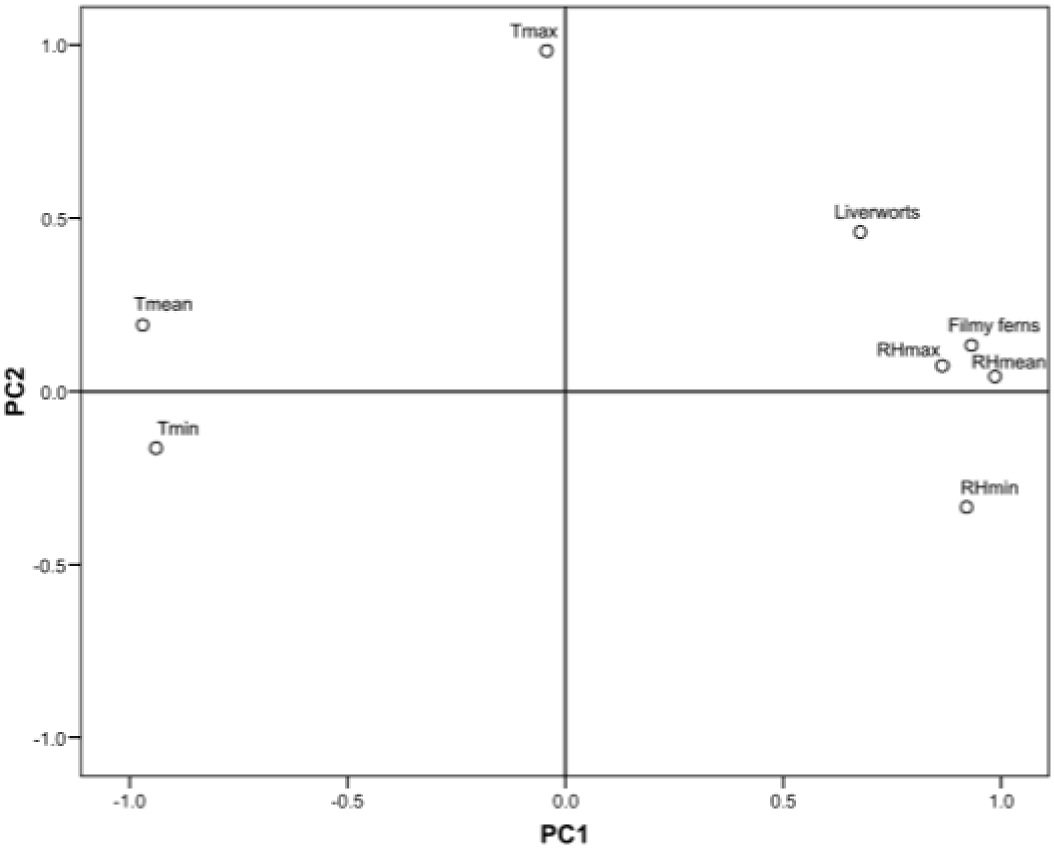

Figure 16. Component plot for the principal component analysis using air temperature, relative humidity and epiphyte diversity parameters.

Two main PCs explained 88.8% of the total variance. The first principal component, explaining 71.7% of the total variance, consists of all parameters except Tmax, which loads on the second principal component. The highest loading factor is observed for relative humidity. Interestingly, the loading of filmy fern richness and relative humidity is dominant in PC1 and points to the close relation between both parameters. The high negative loading of mean and minimum temperatures in PC1 might furthermore underline the importance of cold air drainage flow for fog formation. Liverwort diversity is obviously less affected by humidity in PC1 but also loads moderately high to PC2 which is dominated by maximum temperature.

Table 4. Principal component analysis using air temperature, relative humidity and diversity measured in 16 trees (eight in valley, eight in hill forest). Total variance explained and component matrix for eight parameters.

Component	Initial eigenvalues		
	total	variance (%)	cumulative (%)
1	5.734	71.677	71.677
2	1.373	17.159	88.836
3	.610	7.625	96.461
4	.142	1.779	98.240
5	.079	.983	99.223
6	.042	.530	99.752
7	.012	.148	99.900
8	.008	.100	100.000

Parameter	Component Matrix	
	PC1	PC2
RHmean	0.988	0.007
Tmean	-0.962	0.227
Tmin	-0.945	-0.130
Filmyferns	0.937	0.099
RHmin	0.909	-0.369
RHmax	0.869	0.042
Liverworts	0.694	0.434
Tmax	-0.007	0.984

3.5 Discussion and conclusions

The current study provides detailed evidence of the frequent occurrence of fog in river valleys of French Guiana. By using visibility data to represent fog occurrence it should be stressed that visibilities below 1000 m are not always related to fog conditions but can also be generated by strong precipitation events or aerosols. However, in the analysis of the visibility measurements, times of rainfall have been excluded when calculating fog occurrence. Furthermore, the study site is very remote to any industrial zones and only affected by background aerosols without any effect on a strong reduction of visibility. Thus, the presented visibility data is an excellent proxy for fog occurrence.

During the measurement period, fog occurred on nearly all days in the dry season and on every day in the rainy season. Comparable high fog frequencies are hitherto only reported from tropical montane cloud forests (e.g. Grubb and Whitmore, 1966; Gordon *et al.*, 1994; Chang *et al.*, 2002; Liang *et al.*, 2009). Fog frequency in the lowland cloud forest shows a clear diurnal course, with a maximum during early morning hours. Solar heating after sunrise leads to rapid fog clearance. Therefore, radiation seems to be the most likely cause of fog in the lowland cloud forest. The diurnal course of visibility is clearly related to the diurnal course of humidity and saturation conditions in the above-canopy air.

Very dense fog events (VIS < 100 m) are more frequent in the dry season than in the rainy season. The mechanism for the greater persistence of fog during dry season days could be as follows: (i) high evapotranspiration during a clear day, with high irradiance, before fog formation leads to high amounts of precipitable water in the air. (ii) Strong cooling due to unhampered nocturnal longwave radiation losses causes the formation of very dense fog with high LWC, resulting in (iii) longer duration of thermal fog clearance by sunlight.

The leaf wetness sensors indicate liquid water input by either dew or fog. Leaf wetness duration is about three times higher in LCF and periods of leaf wetness coincide with foggy episodes. Typically, water deposition on the leaf wetness sensor begins a few hours before the fog formation, which is probably attributed to dewfall. It has to be assumed that leaf wetness duration in LRF is mainly related to dew deposition rather than to fog water interception. It can be expected from the comparison of visibility and leaf wetness duration for the valley site that fog is an absolutely rare phenomenon at elevated terrain. This is also confirmed by personal observations in the field.

The main trigger of fog development in the lowland cloud forest seems to be precipitation, leading to higher soil moisture, greater evapotranspiration and, thus, a higher water content of air. Generally, in tropical lowland forests, air humidity close to saturation at canopy level has been shown to be related to soil moisture (Harris *et al.*, 2004; Kumagai *et al.*, 2005), which is highest in the rainy season (e.g. lowland forest of Venezuela, Rollenbeck, 2002). High soil moisture after rain may trigger air humidity in valleys and lead to the formation of fog. In another study, rainfall has proven to increase the tendency towards situations around the saturation point because the rain water lowers the canopy air temperature by evaporative cooling, resulting in a descent of the cloud base and a reduction especially of the nocturnal saturation deficit (Betts *et al.*, 2002). The present study shows that the time when saturation is reached is relevant to the beginning of the fog period. Saturation conditions in the afternoon favour the early formation of fog and enhance the probability of high fog persistence at night. With regard to the fog formation process, air humidity close to saturation and low wind speed/turbulence are known as prerequisites of fog formation (Findlater, 1985; Schilling, 1991; Pasricha *et al.*, 2003). Generally, cloud formation over the lowland forests is increased in comparison to open land (Lyons, 2002; Van der Molen, 2002). In the study area, valley and hill sites differ significantly during night in terms of temperature and humidity conditions. The canopy of the valley forest exhibits the lowest temperature and highest relative humidity, and constituting a cold air pool. In a Venezuelan lowland rain forest, Anhuf *et al.* (1999) and Szarzynski and Anhuf (2001) found that cold air production in the canopy was restricted to the nocturnal period (by outgoing longwave radiation) when thermal turbulence was very low, leading to air humidity close to saturation. However, no fog events were recorded at this site. Another study showed that the dense canopy of tropical lowland forests inhibits cold air diffusion to lower canopy levels (Kruijt *et al.*, 2000). Apparently, the canopy–atmosphere boundary layer of tropical forests is perfectly suited for the formation of radiation fog. In the presents study, the negative correlation between fog persistence and air temperature along with the positive correlation between fog persistence and afternoon cooling rate might also point at the specific role of cold air production and radiation fog formation. Furthermore, the increase of the temperature difference between the valley and hill sites after sunset, together with the more frequent down-slope winds during nights with long fog periods, points to some influence of katabatic flows. Fog formation could be triggered by a nocturnal down slope/valley-breeze as it is typical in complex terrains of the Midlatitudes. Although katabatic flows have rarely been recorded in the lowlands of northern South America (Oliveira and Fitzjarrald, 1993, 1994; Goulden *et al.*, 2006), cold air drainage regularly occurs in the study area. Komatsu *et al.* (2003) describe nocturnal drainage flows in a tropical monsoon forest of Thailand, where decoupling between canopy surface air and the overlying layers along with the formation of a stable stratification was observed. Stratification in the valley at Saut Pararé also switches in the evening towards a stable thermal situation between valley bottom and hill tops. A lower wind speed on the day before seems to trigger fog formation and persistence, most likely because of the required reduction of turbulences for fog formation (see e.g. Findlater, 1985; Pasricha *et al.*, 2003). On the other hand, nocturnal cold air drainage flow could favour fog formation due to cooling the air and thus reducing the saturation point. However, a strong inversion may hamper fog formation due to stronger cold air drainage, higher wind speed, and turbulence. In the present study, we observed that nights of high fog persistence coincide with a weaker temperature gradient between valley and hill sites. Subcanopy stratification at both valley and hill sites is mainly neutral or unstable at night, which often holds true for more closed canopies (Mahrt *et al.*, 2000). For open canopies, stable subcanopy stratification is often observed but is generally weaker in the absence of cold air drainage (Lee and Mahrt, 2005).

Overall, it can be concluded that the mechanisms behind fog formation described in this study are generally in good accordance with topographically inhibited radiation fog events in the Midlatitudes. The frequent occurrence of fog in the river valley at Saut Pararé correlated with significantly different epiphyte diversities in valley and hill forests in the study area. While epiphytes in valley forest (LCF) were very abundant both in biomass and cover, adjacent hill forest (LRF) harboured significantly less epiphyte mass ($p < 0.05$) (Gehrig-Downie et al., 2011). Also, species richness of epiphytes was significantly higher in LCF than in LRF, especially of epiphytic liverworts ($p < 0.05$) and ferns ($p < 0.001$). One single tree in LCF harboured on average 38 species of liverworts and 7 of ferns, compared to 27 liverworts and 1 fern in LRF.

The major differences in epiphyte diversity in the two forest types coincided with significantly higher relative air humidity in LCF. The principal component analysis confirmed the major influence of relative humidity on epiphyte richness. Although epiphytic liverworts and filmy ferns have similar ecological requirements regarding humidity, the PCA shows that species diversity of epiphytic liverworts seems to be less affected by relative humidity than the diversity of filmy ferns. Due to the lack of a well-developed cuticle and stomata, filmy ferns are sensitive to water loss and dependent on moist habitats characterized by frequent precipitation and low evaporation (Proctor, 2003). Significant influence is also exerted by the minimum temperature, providing evidence for the relevance of cold air drainage flows. Beside the correlation of humidity and temperature parameters with diversity, the PCA may indicate the difference of valley and hill sites in terms of relative humidity and epiphyte diversity.

Epiphytes are generally known for their potential to influence microclimate in tropical tree canopies by reducing water loss through evaporative drying (Stuntz *et al.*, 2002). High values of canopy epiphyte water storage capacities are reported for Tropical Montane Cloud Forests, in particular due to interception by bryophytes (Köhler *et al.*, 2007). Epiphytes contribute to higher canopy water storage even in temperate forests (Pypker *et al.*, 2006). Compared to LCF, canopy water storage is generally reduced in tropical lowland forests due to lower epiphyte mass (Köhler *et al.*, 2007). It is assumed that water storage capacity is much higher in LCF of French Guiana than in tropical lowland forests, which are lacking frequent fog events and high epiphytic biomass.

The results are suggestive of the major ecological relevance of fog as a source of additional water for ecosystems (Bruijnzeel *et al.*, 2005). In tropical montane rain forests and cloud forests, epiphytes, in particular, benefit from intercepted fog water (Hölscher *et al.*, 2004; Villegas *et al.*, 2008). Generally, canopy epiphytes heavily depend on atmospheric water deposition and are particularly stressed in the dry season by low humidity and high irradiance/temperature. The increased persistence of fog delays the onset of the stress period and, at the same time, provides more liquid water due to higher densities. Attenuation of global radiation by morning fog may reduce evaporative demand (Ritter *et al.*, 2009). Thus, the stress period for the epiphytic vegetation might be significantly shortened by fog, especially in the dry season, and prevent epiphytes from desiccation. The fog layer might function as a climatic shelter against unfavourable weather conditions for epiphytes.

It must be assumed that fog formation as observed in French Guiana is not an azonal phenomenon but could be widely distributed throughout the lowlands tropics, with significant consequences for vegetation. Liu *et al.* (2008) hypothesized that the frequent occurrence of radiation fog leads to a special type of rain forest in SW China (750 m a.s.l.). The frequent occurrence of fog at lower elevation is also reported from West Africa (Kamara, 1989). Yet, the occurrence of fog in tropical lowland forests (below 500 m a.s.l.) and its effect on vegetation has not been studied in-depth and certainly warrants more attention.

An open question remains the possible water source of fog drip. Environmental isotope analysis by using the oxygen isotopic composition ($\delta^{18}O$) of water and respired CO_2 could be a powerful tool to reveal the different water resources of the epiphytic vegetation (Ehleringer and Dawson, 1992). Using this method, Liu *et al.* (2007) attributed water sources of radiation fog in a tropical seasonal rain forest to evaporation from pond, river and soil, as well as to forest evapotranspiration. The latter factor was believed to contribute the largest fraction, which may also have been the case in the present study. In this study, measurement of fog was done indirectly by means of a scatterometer so that a detailed analysis of fog LWC and water fluxes is not possible at this point. With this respect, Eugster *et al.* (2006) could show that direct measurements of liquid water content yield better results to estimate fog water fluxes than only using visibility data. For locations without detailed information about fog droplet distribution, like in the present study, Eugster *et al.* (2006) provide simple empirical relationships using visibility data. The future use of a fog collector (e.g. Schemenauer and Cereceda, 1994) would permit analysis of water resources and fog chemistry. Also, estimates of fog deposition rates on epiphytes, by measurement of plant weight increase rates after exposure to fog (e.g. Chang *et al.*, 2002), would be a worthwhile approach.

Finally, efforts should be undertaken, and will be done in near future in the framework of the present research, to analyze the spatial distribution of lowland fog in the region of the Guiana Shield using remote sensing data (NOAA/AVHRR, AQUA-MODIS).

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4 Diversity and vertical distribution of epiphytic macrolichens in lowland rain forest and lowland cloud forest of French Guiana

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4.1 Abstract

Recent work on bryophyte diversity in lowland forests of northern South America has suggested the existence of a new type of cloud forest, the “tropical lowland cloud forest” (LCF). LCF occurs in river valleys with high air humidity and radiation fog, and is rich in epiphytes. We explored the lichenological characteristics of putative LCF in a lowland area (200–400 m a.s.l.) near Saül, central French Guiana, using macrolichens (including large crustose species) as indicator taxa. We analyzed macrolichen diversity on 16 trees in two 1 ha plots, in LCF and in lowland rain forest without fog (LRF). Sampling efficiency was ca. 80% in both forest types. Canopies of both LRF and LCF were richer in lichen species than understory trunks. Species richness of macrolichens was rather similar in the two forest types but species composition was significantly different. Cyanolichen richness in LCF was ca. 2.5 times higher than in LRF; in contrast, LRF had 4 times more species of green-algal Parmeliaceae. Our study suggests that cyanolichens except for Coccocarpiaceae serve as indicators of LCF. We explain the detected diversity patterns by differences in water availability due to fog precipitation and higher humidity. This is indicated by the higher relative air humidity in the lowland cloud forest, which was >6% higher than in the rain forest.

4.2 Introduction

Cloud forests are widely distributed in montane and submontane regions of the tropics, at elevations above 500 m and usually occurring between 1200 and 3000 m. Characteristic of these cloud forests are the frequent incidence of fog and low clouds, and the abundance and high species richness of epiphytes (Richards, 1996). Fog in these forests develops by uplifting of moist air masses along the mountain slopes and subsequent condensation of the saturated air.

Recent research on bryophyte diversity of central French Guiana has suggested the occurrence of cloud forest in lowland areas, well below 500 m (Gradstein, 2006). These cloud forests ("tropical lowland cloud forest"; LCF) occur in valleys in hilly areas with high rainfall, which leads to almost daily morning fog. Fog in these forests presumably occurs due to nocturnal irradiation and cooling beyond dew point during night (Gradstein *et al.*, 2010), rather than by uplifting of air masses along mountain slopes. It is enhanced by the undulating terrain with many small hills and creeks, saturation of air during the night and early morning due to very low air turbulence or heavy rainfall, and water-logging of valley-bottom soils. The fog gradually lifts during early morning hours and is cleared by solar heating well before noon. Putative LCF has been observed in the Guianas, Colombia, Costa Rica, and Indonesia (Gradstein *et al.*, 2010), but has not yet been formally described. Physiognomically, LCF resembles tropical lowland rain forest (LRF), but differs from the latter by the abundance of epiphytes, especially mosses and liverworts.

In this paper, we describe the epiphytic lichen assemblages of the poorly known tropical LCF. Lichens of tropical lowland forests have received considerable attention from taxonomists, but very little is known about lichen diversity and distribution within these forests (e.g., Cornelissen and Ter Steege, 1989; Montfoort and Ek, 1990; Komposch and Hafellner, 2000, 2002). Species diversity in these forests is very high and may include over 200 species in 1 ha. Much of the diversity is due to crustose, often tiny "microlichens", which contribute to ca. 90% of the total species number. Foliose and fruticose forms ("macrolichens") are a minor component of the total lichen species richness but by their relatively large size contribute disproportionally to lichen biomass of the forest. Lichens are not evenly distributed within these forests and the canopy flora differs from that of the understory.

Bark structure and microclimate have been identified as drivers of epiphytic lichen distribution in temperate forests (e.g., Barkman, 1958 a,b; Sillett and Antoine, 2004; Hauck and Spribille, 2005) and in the tropics (e.g., Cornelissen and Ter Steege, 1989; Wolf, 1993; Wolseley and Aguirre-Hudson, 1997). Chemical bark factors also play an important role (Hauck, 2003), but these have not been studied in tropical forests. Stochastic effects of species dispersal (Wolf, 1994; Caceres *et al.*, 2007) and competition with epiphytic bryophytes (Frahm, 2003) may also play a role in shaping epiphytic lichen distribution. In general, however, lichens and bryophytes are differentially distributed along moisture gradients, with bryophytes thriving under moister conditions than lichens (Frahm, 2003; Sillett and Antoine, 2004). Due to their poikilohydric physiology, epiphytic lichens are sensitive indicators of climatic conditions. Changes in the microclimate, e.g., light exposure or air humidity, may result in rapid composition changes of lichens assemblages on host trees. Consequently, lichens can be used as indicators of forest disturbance and succession (e.g., Nöske, 2005; Holz and Gradstein, 2005; Rivas Plata *et al.*, 2008). Moreover, many lichens are very sensitive to atmospheric pollutants, reinforcing their use as indicators of air quality (Bates and Farmer, 1992; Nash, 1996).

The purpose of this paper is to analyze the macrolichen diversity of LCF. By comparing the diversity in putative LCF and nearby LRF we will elucidate the usefulness of macrolichens as indicators of lowland cloud forest.

4.3 Methods

4.3.1 Study area

The field study was carried out in central French Guiana in the vicinity of the village of Saül (3°37'20" N and 53°12'31" W), about 200 km south of the Atlantic coast. The area is hilly and considerably dissected, with small river valleys at about 200–250 m and hills to about 400 m in elevation. Annual rainfall is *ca.* 2500 mm and there is a dry season from late July to November, with a less pronounced dry period for several weeks in February and March. Average temperature is about 27°C (Mori *et al.*, 1997). Other than a zone of minor disturbance surrounding the village, the area is covered by species-rich, mixed lowland rain forest (De Granville, 1986, 2001; Mori and Boom, 1987). Lowland cloud forest is common in the area and occurs in valleys where fog develops during the night and early morning (Gradstein, 2006). The flora is very rich, with about 5000 recorded species of vascular plants and over 300 of bryophytes (Mori *et al.*, 1997; Mori *et al.*, 2002; Buck, 2003; Gradstein and Ilkiu-Borges, 2009). The lichens of the study area have not been treated comprehensively; a first inventory of about 1.5 ha of forest was carried out by Montfoort and Ek (1990) and foliicolous lichens were recorded by Lücking (2006).

4.3.2 Sampling

Two plots of 1 ha each were laid out in almost undisturbed, old growth forest on the slope of a small hill adjacent to the valley of the Pelée river (“Crique Pelée”), one in putative LCF on the bottom of the slope at *ca.* 250 m elevation, the other in LRF on the upper portion of the slope at ca. 325 m. Henceforth in this paper “LCF” stands for putative tropical lowland cloud forest. Distance between the two plots was ca. 250 m. The forest canopy is undulating and varied considerably in height in both forest types. In LRF, canopy height varies from 25 to 40 m, emergent trees are lacking and gaps are scarce. In LCF, canopy height varies from 20 to 40 m, emergent trees are present, and gaps are more frequent. Stand-level sampling of epiphytic lichens followed Gradstein *et al.* (2003). In each plot, we climbed eight mature canopy trees minimally 15 m apart and differing in bark structure (smooth, rough, peeling off) using single rope technique (Ter Steege and Cornelissen, 1988). Sampled trees were 20–45 m in height and diameter at breast height (dbh) was 30–90 cm.

We collected all epiphytic macrolichens in sample plots of 600 cm^2 positioned at each cardinal direction in six height zones on canopy trees (Johansson, 1974; Cornelissen and Ter Steege, 1989): trunk base (zone 1), lower trunk (zone 2), upper trunk to first ramification (zone 3), lower canopy (zone 4), middle canopy (zone 5), outer canopy (zone 6). Because foliose and fruticose taxa were rather scarce, we also sampled large crustose species of Arthoniaceae (*Herpethallon*) and Roccellaceae (*Dichosporidium*, *Sagenidiopsis*); the term “macrolichens” is therefore used in a somewhat wider sense than usual in this paper. Sample plots were 20 cm × 30 cm on trunks and 20 cm × 30 cm or 10 cm × 60 cm on canopy branches according to branch diameter. For safety reasons, thin canopy branches (zone 6) were cut and carefully lowered to the ground for sampling. We estimated total lichen cover (%) for each plot. Lichens were identified with relevant taxonomic literature (e.g., Sipman, 1996) and reference collections from the herbaria of the University of Göttingen (GOET) and Berlin (B). Vouchers were deposited in GOET.

4.3.3 Microclimate measurement

In each study site, we measured air temperature (°C) and relative humidity (% RH) with 5 min intervals for 60 days during September and October 2007, using data loggers (HOBO ProV2 RH/Temp, Onset). The data loggers were installed in the middle of the crowns (zone 4) of 20 canopy trees (10 trees per site), at 15–25 m depending on canopy height (emergent trees excluded). Hourly means as well as average diurnal minimum and maximum values were calculated for each site (Table 7).

4.3.4 Statistical analysis

We calculated sampling completeness with the Chao2 and MMMeans species richness estimators (Colwell, 2004; as recommended by Herzog *et al.*, 2002). Species richness of height zones and plots were compared using the Shannon Index and by calculating evenness (Magurran, 1988; Chao *et al.*, 2005). To obtain a graphical depiction of community relationships, we analyzed plot data with principal component analysis (PCA) as justified by a gradient length of 2.66 for the first axis of detrended correspondence analysis (DCA).

4.4 Results

4.4.1 Species richness

In total, we collected 39 taxa of macrolichens (21 genera, 12 families) with 28 in LCF and 30 in LRF (Table 5). Large crustose species included 8% (5 species) of the total number of species collected. Sampling efficiency was about 80% in both forest types (Fig. 17).

Ramalinaceae were by far the largest family with 13 species, representing almost 40% of all species recorded. Next in importance were Parmeliaceae (6 species) and Coccocarpiaceae (5 species). The remaining families were present by 1–3 species each. About 30% of the species (12) were associated with cyanobacteria (cyanolichens) and included the members of Coccocarpiaceae, Collemataceae, Dictyonemataceae, Pannariaceae and Lobariaceae (Table 5); all other species had green algae as photobiont (chlorolichens).

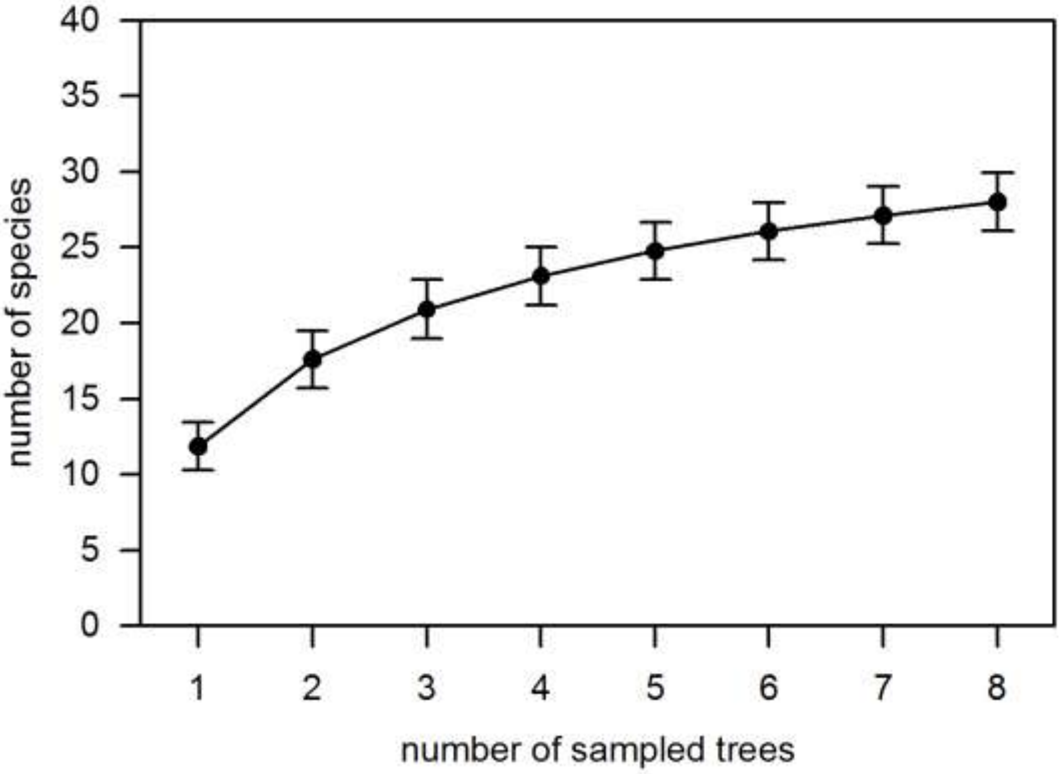

Figure 17. Species accumulation curve of macrolichens in lowland cloud forest of central French Guiana. Graph smoothened with Mao Tau.

The mean number of species per tree was very similar in both forest types, 11.9±3.8 in LCF (maximum = 18; minimum= 7) and 12.1±3.1 in LRF (maximum = 18; minimum= 9). The Shannon Index and Evenness of diversity reached slightly higher values in LRF (1.25 and 0.86 respectively) than in LCF (1.18 and 0.82 respectively). Bark structure, trunk dbh, and plot exposition did not correlate significantly with species richness.

Table 5. Occurrence and vertical distribution of macrolichens in lowland cloud forest (LCF) and lowland rain forest (LRF) in central French Guiana. Arabic numbers refer to height zones on the tree, roman numbers to abundance (see text). Relative abundance classes: I = <10%; II = 10–24%; III = 25–49%; IV = 50–74%; V= 75–100%. Nomenclature of taxa follows Sipman *et al.* (2008) and other sources. Cyanolichens are marked by an asterisk.

	LCF							LRF						
taxa / **height zone**	1	2	3	4	5	6	n	1	2	3	4	5	6	n
Arthoniaceae														
Herpothallon cf. *brialmonticum* Aptroot & Elix	-	-	IV	IV	-	-	4	-	-	-	-	-	V	1
Herpothallon roseocinctum (Fr.) Aptroot *et al.*	-	I	III	III	II	-	11	I	II	II	III	II	III	18
Herpothallon rubrocinctum (Ehrenb.: Fr.) Aptroot, Lücking & G. Thor	-	-	-	-	-	-	0	II	-	-	V	-	-	7
Cladoniaceae														
Ramalea sp.	V	-	-	-	-	-	3	-	III	II	II	III	I	20
Coccocarpiaceae														
*_Coccocarpia domingensis_ Vain.	-	-	-	IV	-	IV	2	-	-	-	-	-	V	4
*_Coccocarpia erythroxyli_ (Spreng.) Swinsc. & Krog	-	-	-	-	-	V	4	-	-	-	-	-	-	0
*_Coccocarpia_ cf. *imbricascens* Nyl.	-	I	-	III	II	III	11	-	I	II	II	III	II	23
*_Coccocarpia palmicola_ (Spreng.) Arvidss. & D. Galloway	-	-	-	-	III	IV	10	-	-	-	-	-	-	0
*_Coccocarpia pellita_ (Ach.) Müll. Arg.	-	-	II	III	II	III	17	-	-	-	V	-	-	2
Collemataceae														
*_Leptogium azureum_ (Sw.) Mont.	-	-	II	II	IV	-	10	-	-	-	-	-	-	0
*_Leptogium cyanescens_ (Rabenh.) Körb.	I	I	II	III	II	III	36	-	-	-	-	-	-	0
*_Leptogium reticulatum_ Mont.	-	III	II	III	II	-	7	-	-	-	-	-	-	0
Crocyniaceae														
Crocynia gossypina (Sw.) A. Massal.	-	-	-	-	-	-	0	V	-	-	-	-	-	2
Dictyonemataceae														
*_Dictyonema sericeum_ (Sw.) Berk.	-	-	-	V	-	-	1	-	-	-	IV	-	IV	2
Gyalectaceae														
Coenogonium cf. *linkii* Ehrenb.	II	III	II	II	II	III	44	III	III	I	I	I	I	36

Lobariaceae														
**Sticta weigelii* (Ach.) Vain.	-	-	-	III	IV	II	14	-	-	-	-	-	-	0
Pannariaceae														
**Pannaria* cf. *prolificans* Vain.	-	-	-	-	V	-	2	-	-	-	V	-	-	1
**Parmeliella pannosa* (Sw.) Müll.Arg.	-	-	-	-	-	V	1	-	-	-	-	-	-	0
Parmeliaceae														
Bulbothrix sgoebelii (Zenker) Hale	-	-	-	-	-	-	0	-	-	-	II	II	IV	7
Canoparmelia sp. 1	-	-	-	-	-	-	0	-	-	-	-	-	V	1
Parmotrema endosulphureum (Hillm.) Hale	-	-	-	-	-	-	0	-	V	-	-	-	-	1
Parmotrema sp. 1	-	-	-	-	-	-	0	-	-	-	-	-	V	1
Pseudoparmelia relicinoides Elix & Nash	-	-	-	-	-	-	0	-	-	-	-	-	V	1
Pseudoparmelia cf. *cubensis* (Nyl.) Elix & Nash	-	-	-	-	-	V	1	-	-	-	-	-	-	0
Ramalinaceae														
Eschatogonia dissecta Timdal & R. Sant.	III	III	I	II	II	I	26	III	II	III	II	II	-	25
Eschatogonia minuta Timdal & R. Sant.	-	-	V	-	-	-	3	II	I	II	III	II	II	33
Eschatogonia prolifera (Mont.) R.Sant.	I	II	II	III	I	II	32	III	III	I	II	-	II	36
Phyllopsora cf. *buettneri* (Müll.Arg.) Zahlbr.	-	-	-	-	-	-	0	IV	III	-	-	-	-	5
Phyllopsora cf. *corallina* (Eschw.) Müll.Arg.	-	-	-	IV	III	-	5	-	-	-	IV	IV	-	4
Phyllopsora sp. 1	-	-	III	-	IV	-	3	II	II	II	III	II	-	15
Phyllopsora sp. 2	-	V	-	-	-	-	6	-	-	II	-	V	II	9
Phyllopsora sp. 3	-	V	-	-	-	-	1	-	-	III	III	-	II	5
Phyllopsora sp. 4	-	III	IV	-	-	-	3	-	-	-	-	-	-	0
Physcidia sp.	-	-	-	-	-	-	0	I	-	I	III	III	-	11
Ramalina sp. 1	-	-	-	III	IV	II	14	-	-	II	II	III	II	5
Ramalina sp. 2	II	-	II	III	II	I	18	I	-	III	I	II	III	12
Triclinum cinchonarum Fée	-	-	-	-	-	-	0	-	-	-	IV	IV	-	2
Roccellaceae														
Dichosporidium nigrocinctum (Ehrenb.) Thor	II	II	II	II	II	II	80	III	II	II	III	I	-	14
Sagenidiopsis undulatum (Fée) Egea et al.	-	-	-	-	-	-	0	-	-	-	-	V	-	1

4.4.2 Species composition

Although species richness of macrolichens in LRF and LCF were similar, species composition of the two forest types differed significantly. About half of the species occurred in only one forest type (Table 5). Species recorded only from LCF included, among others, *Parmeliella pannosa*, *Sticta weigelii*, 2 species of *Coccocarpia* (*Coccocarpia erythroxyli*, *Coccocarpia palmicola*) and all Collemataceae (*Leptogium azureum*, *Leptogium cyanescens*, *Leptogium reticulatum*). Exclusive to LRF were a.o. *Herpothallon rubrocinctum*, *Crocyna gossypina*, *Phyllopsora* cf. *buettneri*, *Physcidia* sp., *Triclinum cinchonarum*, *Sagenidiopsis undulata* and most Parmeliaceae (5 species). In addition, some species were significantly more common in one forest type than in the other. For example, *Coccocarpia pellita* and *Dichosporidium nigrocinctum* were more abundant in LCF where they were recorded in 6 times more plots than in LRF. Species of *Eschatogonia* and of *Phyllopsora*, on the other hand, were about 5–10 times more common in LRF.

More than 80% of the species exclusive to LCF were cyanolichens (Collemataceae, Pannariaceae, Lobariaceae; some Coccocarpiaceae) (Table 5 and Fig. 18).

They were represented in LCF by 12 species (43% of the total number of species recorded), and 7 of them were exclusive to LCF.

In contrast, only 5 cyanolichen species (17%) occurred in LRF, and none of them was exclusive to this forest type (Table 5). In all, LCF had about 2.5 times more species of cyanolichens than LRF. In contrast, Parmeliaceae and Ramalinaceae were clearly more abundant in the LRF. Members of Parmeliaceae, however, were generally scarce and mostly restricted to the outer canopy.

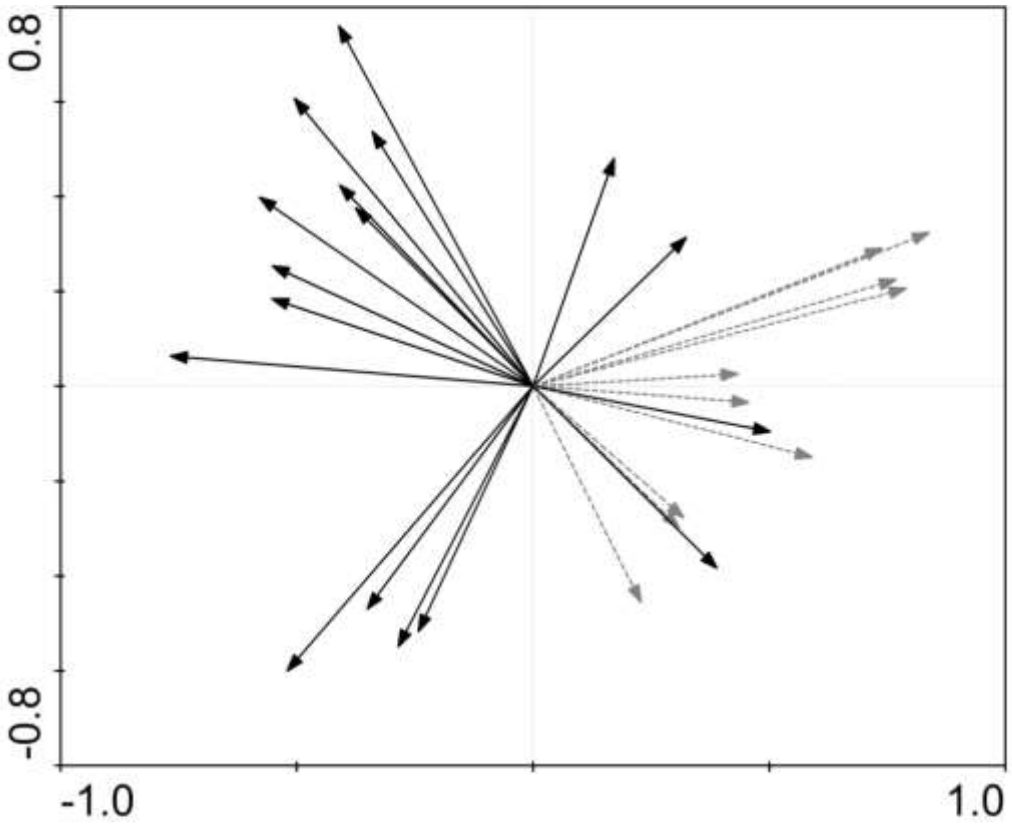

Figure 18. Ordination of macrolichen species in lowland cloud forest (LCF) and lowland rain forest (LRF), using PCA. The right hand side of the diagram corresponds to LCF, the left hand side to LRF. Unbroken lines indicate chlorolichens, broken ones cyanolichens. PCA axes 1 (21.7%) and 2 (14.3%) are shown. Species with correlations < 20% are excluded.

4.4.3 Vertical distribution

In both forest types, canopies were richer in species than trunks (Fig. 19 and Table 5). In total, we recorded 34 species from the canopy, 16 of them exclusively so including *Dictyonema sericeum*, *Pannaria prolificans*, *T. cinchonarum*, *S. weigelii*, and most of the Parmeliaceae and Coccocarpiaceae. In contrast, 22 species occurred in the understory, four of them exclusively so: *Crocynia gossypina*, *Parmotrema endosulphureum* and two species of *Phyllopsora* (*P. buettneri*, *P.* sp.). Eighteen species were ecological generalists and occurred in the understory and the canopy. Of these, *Coccocarpia* cf. *imbricascens*, *Coenogonium* cf. *linkii*, *D. nigrocinctum*, *Eschatogonia prolifera* and *Ramalina* spp. were common generalists in both forest types.

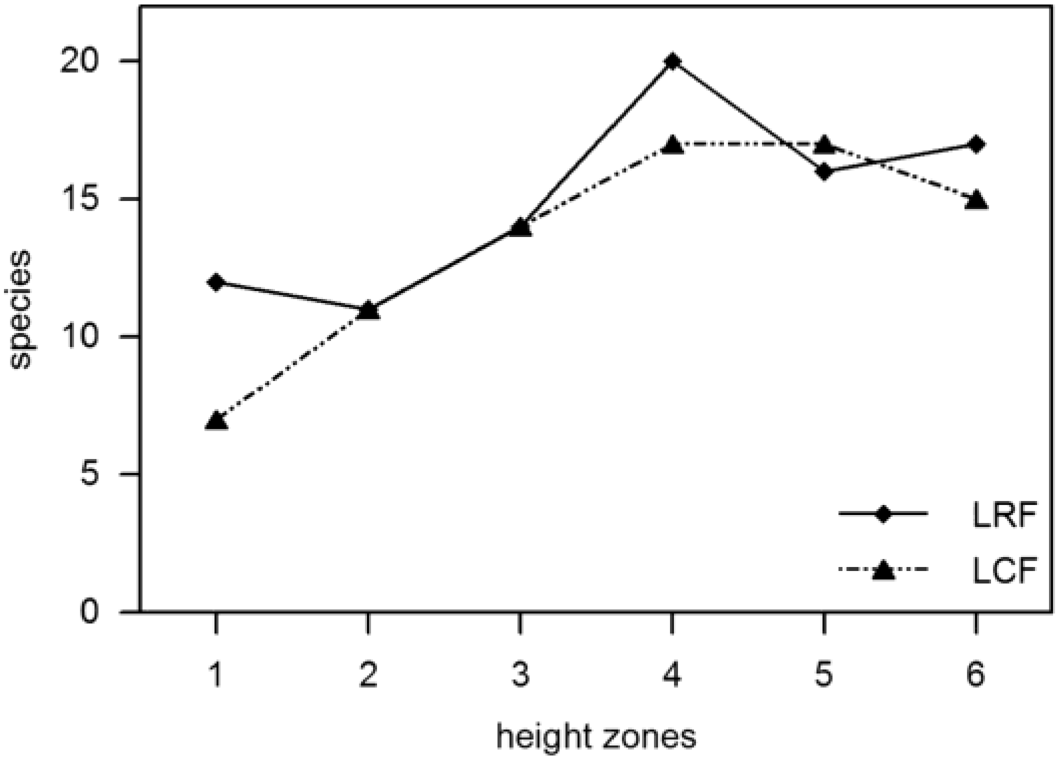

Figure 19. Vertical distribution of macrolichen species on mature trees in lowland cloud forest (LCF) and lowland rain forest (LRF). Explanation of height zones: see text.

Comparison of the two forest types showed that trunk bases in LRF (12 species) had almost twice as many species as in LCF. Moreover, the canopy of LRF was slightly richer in species than that of LCF. The number of ecological specialists (canopy epiphytes, understory epiphytes) and generalists was about the same in the two forest types even though species were not always the same. Specialists exclusive to one forest type included *C. erythroxyli* and *C. palmicola* in LCF (canopy) and *C. gossypina*, *P. endosulphureum* and *P. buettneri* in LRF (understory). Two species, *E. prolifera* and *Coenogium* cf. *linkii*, showed a significant upward shift towards the canopy in LCF as compared with LRF (Fig. 20).

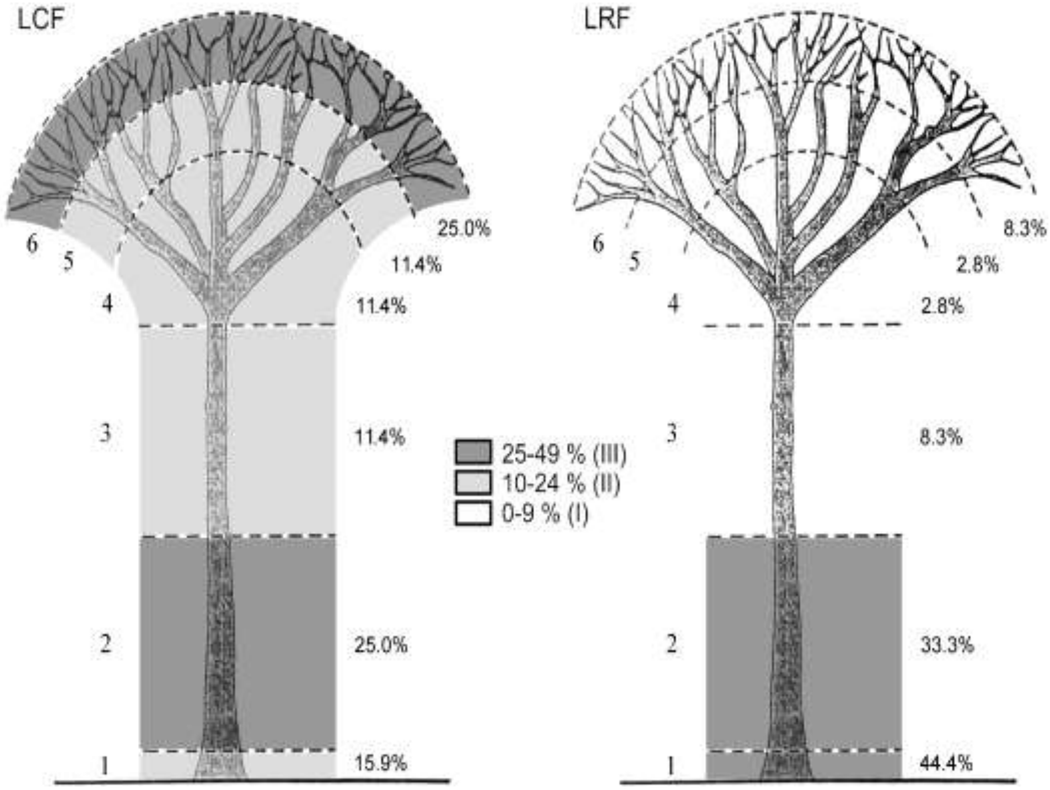

Figure 20. Vertical distribution of *Coenogonium* cf. *linkii* in lowland cloud forest (LCF) and lowland rain forest (LRF).

4.5 Discussion

4.5.1 Species richness

Only a few studies have been carried out on lichen diversity of tropical evergreen lowland forests that included sampling in the canopy (Cornelissen and Ter Steege, 1989; Cornelissen and Gradstein, 1990; Montfoort and Ek, 1990; Komposch and Hafellner, 1999, 2000, 2002; Table 6). All inventories are from sites in northern South America (central French Guiana: Saül; northern Guyana: Mabura Hill; Amazonian Venezuela: Surumoni) with annual rainfall of ca. 2500–3000 mm and a dry season of up to 3 months. Cornelissen and Ter Steege (1989) studied a forest in Guyana on white sand, the other investigated forests were on loamy soil. The study site of Montfoort and Ek (1990) was in LCF very close to our study area.

Table 6. Species richness of epiphytic macrolichens in tropical evergreen lowland forests based on whole tree inventories.

	Country	Forest type	Nr. of trees sampled (nr. of tree spp.)	Nr. of spp. of macrolichens	Nr. of spp. of cyanolichens (% of total macrolichen spp.)	Ibid., excl. *Coccocarpia*
Cornelissen & Ter Steege, 1989	Guyana	LRF[a]	11 (2)	34[b]	16 (47%)	10 (29%)
Cornelissen & Gradstein, 1990	“	LRF[a]	5 (5)	17[b]	11 (65%)	6 (35%)
Komposch & Hafellner, 1999, 2000	Venezuela	LRF	9 (4)	22	8 (36%)	1 (5%)
Montfoort & Ek, 1990	Fr. Guiana	LCF[c]	28 (24)	53	20 (38%)	13 (25%)
id., tree 1-8[d]	“		9 (9)	40	16 (40%)	12 (30%)
id., tree 9-18[d]	“		9 (8)	42	15 (36%)	9 (21%)
id., tree 19-28[d]	“		10 (9)	31	14 (45%)	10 (32%)
This study	“	LRF	8 (?)	29	5 (17%)	2 (7%)
This study	“	LCF	8 (?)	28	12 (43%)	7 (25%)

[a] Forest with occasional occurrence of mist (see text).

[b] These studies do not include large crustose lichens (*Dichosporidium, Herpothallon,*

Sagenidiopsis). When included, figures may rise up to 10%. [c] Described as "rain forest".
[d] Data based on a revision of the Montfoort & Ek vouchers in herbarium U (Sipman, unpubl.).

Species richness varied from 17 species on 5 trees in LRF of Guyana to 53 on 28 trees in LCF in French Guiana (Table 6), and increased with the number of trees sampled. This variation shows the need for standardization of sample size in epiphyte studies (Gradstein *et al.*, 2003). Lowest species richness relative to number of trees was reported by Komposch and Hafellner (1999, 2000), who detected no more than 21 macrolichen species (including large crusts) on 9 trees in LRF at Surumoni in Amazonian Venezuela.

Because sampling in the latter study was done very carefully, we suggest that the more severe dry season in Surumoni as compared with the Guianan rain forest site played a role. The different climate correlates with the different synoptic situation and its relation to rainfall (and thus air humidity) variability at the two forest sites. Enfield and Alfaro (1999) recorded a higher interannual variability with respect to the main rainy season in the Surumoni area as compared to the Guianas. From a synoptical point of view this may be explained by two factors: (1) high level wind shear during westerly streamflow can suppress deep convection and thus, rainfall over the Surumoni area, which is frequently related to Pacific El Niño-like situations and (2) high pressure events over the Caribbean with easterly streamflow can enhance deep convective rainfall over the Surumoni area. This rainfall occurs very locally, leaving other sites without rain (Riehl, 1973; Ross *et al.*, 2007).

Weather situations with westerly high level streamflow can lead to monthly rainfall <50 mm (as in January 1998) and very low air humidities <40% in the Surumoni area (Rollenbeck, 2002; Rollenbeck and Anhuf, 2007). Such low values have not hitherto been reported for the dry season at Mabura Hill (RH generally >70%; Cornelissen and Ter Steege, 1989) and Saül. Thus, the greater rainfall and humidity variability at Surumoni presumably generate the more severe dry seasons characteristic of Surumoni. The dryer conditions at the latter site are also reflected in the larger share of deciduous trees in the forest (H.J. Sipman, pers. obs.).

Table 7. Comparison of microclimatological factors measured during 60 days in the middle canopy of lowland cloud forest and lowland rain forest of central French Guiana. RH: daily relative air humidity; t: daily air temperature.

Site	**t (°C)**			
	max	**min**	**mean**	**SD**
Lowland cloud forest	30.69	21.38	24.63	3.15
Lowland rain forest	30.51	21.8	25.23	2.81
t-test			p<0.01	
	RH (%)			
	max	**min**	**mean**	**SD**
Lowland cloud forest	96.95	59.24	86.33	12.21
Lowland rain forest	95.57	54.98	80.13	13.93
t-test			p<0.01	

4.5.2 Species composition

The most interesting find of this study was the richness of cyanobacterial lichens in LCF, which was about 2.5 times higher than in LRF. In LCF, cyanolichens represented almost half of all species recorded (12), whereas in LRF, less than 20% (5 species) were cyanolichens. Most of them were associated with *Nostoc* sp. as photobiont (often in condensed, glomerule-like colonies), except for *D. sericeum*, which is associated with a new and previously unrecognized genus of cyanobacteria related to *Scytonema* (Lücking *et al.*, 2009). In contrast, LRF had 4 times more species of the green-algal Parmeliaceae than LCF, which may reflect the dryer microclimate in LRF. Species of this family were generally present at low density, however, and were mostly restricted to the outer canopy, which reflects their general preference for high-light conditions (Sipman and Harris, 1989).

The abundance of cyanolichens in LCF, in contrast to LRF, may be due to the more humid microclimate in LCF (Table 7). Mean daily relative air humidity in LCF was about 6% higher in LCF than in LRF. This indicates on the one hand that potential fog precipitation events occur more often leading to an input of liquid water by fog droplets. On the other hand higher humidity will reduce evaporation rate leading in poikilohydric lichens to a prolonged photosynthetic active time. Cyanolichens profit from this higher water availability, since they require liquid water to initiate photosynthesis while chlorolichens can be activated by high humidity only (Lange *et al.*, 1986, 1993; Bilger *et al.*, 1989). Therefore, cyanolichens are usually more abundant in sheltered and humid sites, and in humid montane forest rather than lowland forest (Forman, 1975; Sipman and Harris, 1989; Smith, 1995). The higher air humidity and frequent interception of fog droplets in our LCF may thus have favoured cyanolichen growth in this forest type. A preference of cyanolichens for tropical (montane) cloud forest has earlier been observed on Hawaii (Smith, 1995). Forman (1975) observed that cyanolichens were mainly restricted to the outer canopy of humid tropical lowland forest in Costa Rica, but our results do not support this observation. Cyanolichens are also known to have a preference for humid sites in the epiphyte-rich temperate conifer forests of the Pacific Northwest, where they take an intermediate position along the moisture gradient, between the drought-tolerant chlorolichens and the drought-intolerant bryophytes (Sillett and Antoine, 2004). In montane watersheds of the Northwest, biomass of cyanolichens tends to be largest in riparian forests, near to streams (Sillett and Neitlich, 1996; McCune *et al.*, 2002), under conditions which resemble those in LCF.

Our finding that high cyanolichen richness is characteristic of LCF is supported in part by the results of lichen inventories in other tropical evergreen lowland forests (Table 6). Montfoort and Ek (1990) found almost similarly high cyanolichen richness (40%) in LCF of central French Guiana, in spite of the much larger number of trees (28) sampled. Subsets of 9–10 trees yielded similar results (Table 6). A high representation of cyanolichens was also recorded in LRF of Guyana (Cornelissen and Ter Steege, 1989; Cornelissen and Gradstein, 1990), both in the "dry evergreen forest" (47%) and the "moist mixed forest" (65%). Since these Guyanan forests were also unusually rich in liverworts (Cornelissen and Gradstein, 1990), much more so than in the Venezuelan site (Gradstein *et al.*, 2010), we suggest that the microclimate of those Guyanan forests was also humid and may have featured some morning fog. The occasional occurrence of mist at the Guyanan rain forest sites has been confirmed by Dr. H. ter Steege (pers. comm., 2007). Another explanation for the high percentages of cyanolichens in the Guyanan forests is the omission in the inventory of large crustose lichens (*Dichosporidium*, *Herpothallon*, *Sagenidiopsis*), all of which are chlorolichens. If these had been included, the percentages of cyanolichens would have been up to 10% lower.

The high percent richness (36%) of cyanolichens in LRF of Surumoni, Amazonian Venezuela (Komposch and Hafellner, 1999, 2000) was unexpected. This forest was relatively poor in bryophytes and lacked any morning fog (Engwald, 1999). However, species composition of cyanolichens at Surumoni was very different from that in LCF, with almost all cyanolichen species belonging to Coccocarpiaceae (genus *Coccocarpia*) (Table 6). In contrast, Pannariaceae, Collemataceae and Lobariaceae were lacking at this site. Except for the absence of the latter three families, the forest at Surumoni was similar to our LRF site. Published information on the ecology of the genus *Coccocarpia* is lacking (Arvidsson, 1982). According to our field observations, species of this genus usually occur in relatively dry and open habitats in the lowland tropics and are not often found in the shaded, humid habitats characteristic of other cyanolichens taxa. In view of their different distributions, we have calculated the cyanolichen composition of LRF and LCF without *Coccocarpia*. In the latter case, the cyanolichen ratio is less than 10% in LRF of French Guiana and Venezuela, and more than 20% in LCF and the humid forests of Guyana (Table 6, rightmost column). These data indicate that cyanolichen richness without Coccocarpiaceae serve as an indicator of LCF.

4.5.3 Vertical distribution

The vertical distribution we documented confirms that the canopy of the tropical evergreen lowland forest is richer in lichen species than the understory, both in LRF and in LCF (Cornelissen and Gradstein, 1990; Montfoort and Ek, 1990; Komposch and Hafellner, 2000, 2002). Inventories of tropical forests would therefore be incomplete without detailed analysis of the tree crowns. About 50% of the species recorded there were exclusive to the canopy and the upper portion of the trunk (zones 3–6), and about 65% to zones 2–6. Thus, we would have missed about 2/3 of the macrolichen flora if only trunk bases had been inventoried. Even higher percentages have been reported in other studies: in a Venezuelan lowland forest, 87% of all lichen species (including microlichens) occurred from height zone 2 upward (Komposch and Hafellner, 2000); in a Guyanan lowland forest, 86% of all macrolichens occurred from height zone 3 upward (Cornelissen and Gradstein, 1990).

The differences between LCF and LRF in terms of species composition are also notable for the different height zones and reflect the microclimatic requirements of the species. The higher species richness on tree trunks in LRF presumably reflected the avoidance of conditions of reduced light plus constantly high air moisture, characteristic of LCF, by most lichens (exceptions are the cyanolichens) (Zotz and Winter, 1994; Lange *et al.*, 2000; Lakatos *et al.*, 2006). The drier microclimatic conditions in LRF (Table 7) may also explain the vertical range shifts towards lower elevations on the tree in LRF, which can be observed in some species. These distributional shifts have not yet been shown for lichens, but have been documented for bryophytes and vascular epiphytes along a successional gradient in submontane rain forest of Bolivia (Acebey *et al.*, 2003; Krömer, 2003). These authors found that epiphyte species occurred at much lower heights on trees in young regenerating forest than in the mature forest. The range shifts correlated with higher average temperatures (2°C) and lower relative air humidity (*ca.* 7.5%) in the young secondary forest, where microclimatic conditions on tree bases were similar to those in the lower canopy of the primary forest. The differences in relative air humidity between the Bolivian forest habitats were similar to those between LCF and LRF in this study.

In conclusion, our study suggests that tropical lowland cloud forest can be distinguished from lowland rain forest by its different macrolichen assemblage (including large crusts). The most notable difference is the richness of cyanobacterial lichens (excl. *Coccocarpia*) in LCF, which make up 20–35% of the macrolichens, in contrast to <10% in LRF. A significant upward shift of the vertical ranges of some rain forest species towards the canopy is another characteristic feature of LCF. We propose that these diversity patterns may be explained by the higher water availability indicated as differences in air humidity, which was >6% higher in the cloud forest than in the rain forest.

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5 Diversity and vertical distribution of filmy ferns as a tool for identifying the novel forest type "tropical lowland cloud forest"

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5.1 Abstract

Recent studies on bryophyte and macrolichen diversity in lowland forests of northern South America have shown the existence of a novel forest type, the “tropical lowland cloud forest” (LCF). LCF is very rich in epiphytes and occurs in lowland river valleys where radiation fog in the morning provides an additional input of liquid water. Because of their dependence on frequent precipitation and low evaporation, Hymenophyllaceae (filmy ferns) are a suitable group for studying moisture availability. We sampled epiphytic Hymenophyllaceae on 32 trees in French Guiana, 16 in LCF and 16 in adjacent rain forest (LRF). Abundance of Hymenophyllaceae was significantly higher in LCF than in LRF. Only 10% of trees in LRF were inhabited by filmy ferns, in contrast to 70% in LCF. Moreover, the number of species recorded in LCF (9) was more than twice as high than in LRF (4), and the mean number per tree 8 times higher. Species restricted to the understory of LRF occurred in the canopy of LCF. We attribute the detected differences in diversity and vertical distribution of Hymenophyllaceae in the two forest types to the occurrence of fog in LCF, enhancing the availability of liquid water and thus facilitating the establishment and growth of the filmy ferns. Also, radiation protection against evaporative loss seems to play a crucial role in the vertical distribution of filmy fern diversity. The observed differences in filmy fern diversity and distribution in LCF and LRF represent novel traits separating the two forest types, and indicate that Hymenophyllaceae species are sensitive indicators of lowland cloud forest.

5.2 Introduction

Recent work on bryophyte and lichen diversity in French Guiana has demonstrated the existence of a new type of tropical forest, the "tropical lowland cloud forest" (LCF) (Gradstein 2006, Normann *et al.* 2010, Gradstein *et al.* 2010, Gehrig-Downie *et al.* 2011, Obregón *et al.* 2011). LCF occurs in lowland river valleys with high air humidity and radiation fog. The process of fog formation in LCF is different from that in montane cloud forests (MCF). While in MCF, fog formation is mainly due to advective orographic clouds touching the ground, canopy fog formation in valleys characterized by LCF is a result of nocturnal radiation processes (radiation fog). The formation of this type of fog is catalyzed by the nocturnal cold air drainage flow from small hills and crests bordering the river valleys, causing saturation of air humidity during the night and early morning in situations of low air turbulence. Heavy rainfall the day before and waterlogging of valley-bottom soils are additional factors fostering condensation in the valleys. Fog in LCF gradually lifts during early morning hours and clears well before noon by solar heating (Obregón *et al.* 2011). Botanically, LCF resembles lowland rain forest but differs by higher species richness and biomass of epiphytes, especially bryophytes (Gradstein 2006, Gehrig-Downie *et al.* 2011). Microenvironmental conditions within the tropical rain forest are very heterogenic. Air temperature, light availability and wind speed generally increase from understory towards outer canopy while air moisture and nutrient availability decrease (Johansson 1974, Meinzer & Goldstein 1996, Parra *et al.* 2009). The vertical distribution of epiphytes depends on their physiological requirements and is related to microclimatic conditions and branch characteristics (ter Steege & Cornelissen 1989, Hietz & Hietz-Seifert 1995, Freiberg 1997, Cardelús & Chazdon 2005, Cardelús 2007, Krömer *et al.* 2007). For vascular epiphytes species richness usually increases from lower trunk to inner crown before decreasing again towards the periphery of the canopy (ter Steege & Cornelissen 1989, Acebey *et al.* 2003, Krömer *et al.* 2007, Pos & Sleegers 2010).

This study focuses on the filmy ferns (Hymenophyllaceae) of LCF. Hymenophyllaceae are a large and speciose family of leptosporangiate ferns, containing more than 600 species and occurring commonly as epiphytes in humid lowland to montane forests throughout the tropics (Lellinger 1994, Dubuisson *et al.* 2003). Due to the lack of a well-developed cuticle and stomata, filmy ferns are sensitive to water loss and hence dependent on moist habitats characterized by frequent precipitation and low evaporation (Proctor 2003). Because of their drought-intolerance, filmy ferns are good indicators of high atmospheric humidity (Hietz & Hietz-Seifert 1995). Even though physiologically perceived as shade plants (Gessner 1940, Evans 1964, Richards & Evans 1972, Johnson *et al.* 2000, Proctor 2003), shady conditions are not obligatory for all filmy ferns and some are even desiccation-tolerant (Benzing 1990, Iwatsuki 1990).

Recent molecular work on Hymenophyllaceae (Pryer *et al.* 2001) has shown the existence of two major lineages: the Hymenophyllum clade (= genus *Hymenophyllum* s.l.) and the Trichomanes clade (genus *Trichomanes* s.l.). The two clades differ somewhat in elevational distribution, *Trichomanes* s.l. occurring mainly in lowland and submontane forests whereas *Hymenophyllum* s.l prevails in montane forests, with a wide elevational overlap between the two groups (Kessler *et al.* 2001, Krömer & Kessler 2006). The species primarily grow in the forest understory (Kelly 1985, Hietz & Hietz-Seifert 1995) except in the mountains where species of *Hymenophyllum* may occur in all forest strata, with a high relative abundance in the canopy (Krömer *et al.* 2007). Indeed, some species in these forests may be considered canopy specialists (Krömer & Kessler 2006). In contrast, *Trichomanes* species seem to be largely restricted to the lower portions of the tree trunks.

The aim of this study is to analyze the diversity of Hymenophyllaceae in LCF. By comparing species richness, composition, and vertical distribution in LCF and nearby LRF, we explore the usefulness of filmy ferns as indicators of tropical lowland cloud forest.

5.3 Methods

5.3.1 Study area

Fieldwork was conducted in central French Guiana in the vicinity of the village of Saül (3°37'20"N, 53°12'31"W), about 200 km southwest of the Atlantic coast, and in the Nouragues Natural Reserve (4°02'30"N, 52°40'30"W), *ca.* 100 km inland from the Atlantic coast. Annual rainfall is *ca.* 2500 mm in Saül and *ca.* 3000 mm in Nouragues; there is a distinct dry season from late July to November and a less pronounced dry period for several weeks in February and March. Average temperature is 27°C (Mori *et al.* 1997, Grimaldi & Riéra 2001). For more detailed climate data see Obregón *et al.* (2011). The area is very undulated, with small river valleys at about 100-250 m and hills to about 400 m a.s.l. Other than a zone of minor disturbance surrounding the village, the area is covered by mixed lowland rain forest (e.g. De Granville 1986, 2001; Mori & Boom 1987). The flora is very rich, with about 5000 recorded species of vascular plants and over 300 of bryophytes (Mori *et al.* 1997, 2002; Buck 2003, Gradstein & Ilkiu-Borges 2009). Lowland cloud forest (LCF) is common in the area and occurs in valleys where fog develops during the night but clears well before noon (Gradstein 2006); LRF occurs higher up the slopes. The two forest types are very similar in overall stature (tree height, tree diameter) but emergent trees and gaps were more frequent in LCF.

5.3.2 Epiphyte sampling

Twelve plots of 1 ha each (Gradstein *et al.* 2003) were laid out in almost undisturbed, non-flooded old growth forest in a 6 x 2 km area in the vicinity of Saül. Four plots were situated on the slope of a small hill adjacent to the valley of the Pelée creek ("Crique Pelée"), two in LCF at the bottom of the slope at *ca.* 250 m elevation, the other two in LRF on the upper portion of the slope at *ca.* 325 m. The remaining eight plots were laid out randomly as replicates in LCF and LRF at similar elevations on slopes of small hills adjacent to the valleys of "Crique Roche" and the two smaller tributaries of "Crique Grand Fosseé" and "Crique Popote". Distance between LCF and LRF plots was about 250 m. In order to explore the occurrence of LCF over a wider area, four additional plots (2 in LCF, 2 in LRF) were laid out in the Nouragues Natural Reserve, 80 km northeast of Saül. A total of 32 mature canopy trees, two in each plot, were climbed using the single rope technique (ter Steege & Cornelissen 1988). Sampled trees were selected randomly, standing (15)20-30 m apart, and were 20 to 45 m in height; diameter at breast height (dbh) was 30-300 cm (Table 8).

Table 8. Tree height and diameter at breast height (dbh) of trees sampled in lowland cloud forest (LCF) and lowland rain forest (LRF) in central French Guiana. Tree species name and family are provided where available.

Forest type	Height (m)	Dbh (cm)	Species	Family
LCF	30	61	*Schefflera* sp.	Araliaceae
	32	47	*Jacaranda* sp.	Bignoniaceae
	45	313	*Eriotheca* cf. *globosa*	Bombacaceae
	17	50	*Dimorphandra* sp.	Caesalpiniaceae
	25	40	*Eperua falcata*	Caesalpiniaceae
	25	65	*Eperua falcata*	Caesalpiniaceae
	45	95	*Goupia glabra*	Celastraceae
	30	50	*Licania heteromorpha*	Chrysobalanaceae
	35	69	*Inga paraensis*	Mimosaceae

	25	96	*Ficus insipida scabra*	Moraceae
	30	32	Unidentified 1	
	30	50	Unidentified 2	
	33	48	Unidentified 3	
	35	56	Unidentified 4	
	35	76	Unidentified 5	
	35	42	Unidentified 6	
LRF	40	60	*Thyrsodium spruceanum*	Anacardiaceae
	25	32	*Jacaranda copaia*	Bignoniaceae
	40	92	*Dimorphandra multiflorum*	Caesalpiniaceae
	33	67	*Eperua falcata*	Caesalpiniaceae
	25	60	*Tachigali amplifolia*	Caesalpiniaceae
	30	55	*Caryocar glabrum*	Caryocaraceae
	22	35	*Inga* cf. *alata*	Mimosaceae
	30	26	*Inga* sp.	Mimosaceae
	25	65	*Sterculia* sp.	Sterculiaceae
	25	41	Unidentified 7	
	25	53	Unidentified 8	
	28	45	Unidentified 9	
	30	80	Unidentified 10	
	30	35	Unidentified 11	
	35	65	Unidentified 12	
	40	75	Unidentified 13	

We collected all epiphytic Hymenophyllaceae from trunk base to outer canopy and subdivided the samples according to location in six tree-height zones (Johansson 1974, Cornelissen & ter Steege 1989): trunk base (zone 1), lower trunk (zone 2), upper trunk to first ramification (zone 3), lower canopy (zone 4), middle canopy (zone 5), and outer canopy (zone 6). For safety reasons, thin canopy branches (zone 6) were cut and carefully lowered to the ground for sampling.

The collected Hymenophyllaceae were identified with relevant taxonomic literature (e.g. Lellinger 1994, Cremers 1997) and using reference collections from the Herbarium of the University of Göttingen (GOET). Vouchers were deposited in GOET. Nomenclature follows Lellinger (1994) and Cremers (1997), using the traditional subdivision of the filmy ferns into two broad genera *Hymenophyllum* and *Trichomanes*.

5.3.3 Microclimate measurements

Air temperature and relative humidity were measured for 60 days during September and October 2007 using data-loggers (HOBO ProV2 RH/Temp, Onset). The sensors were installed in the middle of the crowns (zone 4) of seven canopy trees per site in Saül (for detailed description of study design see Gehrig-Downie *et al.* 2011). Additional meteorological stations were placed in the inner crown (zone 4) and outer canopy (zone 6) of two representative trees in LCF and LRF during 33 days in September and October. The stations encompassed: (i) temperature and relative humidity probes (CS215, Campbell Sci.), (ii) pyranometer sensors (CS300, Campbell Sci.), and (iii) 2D-sonic anemometers (Windsonic4, Gill). The latter were installed in the outer canopy (zone 6), while temperature, relative humidity, and radiation sensors were installed in height zones 4 and 6.

5.3.4 Statistical analysis

The Nouragues plots were pooled with the Saül plots because they shared the same Hymenophyllaceae species and similar levels of diversity. Species richness of height zones and plots was compared using the Shannon Index and by calculating evenness (Magurran 2004, Chao *et al.* 2005). Differences in species number between plots were analyzed with unpaired t-tests. Floristic similarity between epiphytic Hymenophyllaceae in LRF and LCF was tested with the Sørensen coefficient (Banaticla & Buot Jr. 2005). We analyzed the relation between average relative humidity and diversity of Hymenophyllaceae by correlating a species inventory of epiphytes on 14 trees on the Pelée hill with the microclimate data derived by the HOBO loggers. The pyranometer measurements were used to calculate daily global radiation (MJ m^{-2} d^{-1}) by summation over each respective day. Evaporation was estimated using a simplified version of the Penman equation provided by Valiantzas (2006), incorporating daily global radiation, relative humidity, air temperature, and the latitude of the site. Mean diurnal courses were computed for relative humidity and global radiation.

5.4 Results

5.4.1 Species richness

On 32 trees we collected in total 9 species of Hymenophyllaceae (2 genera), 9 in LCF and 4 in LRF (Table 9). *Trichomanes* was the largest genus with 6 species; 3 species belonged to *Hymenophyllum*. The latter species were relatively rare and represented only 7% of all specimens collected. *Trichomanes punctatum* was the most abundant species, followed by *T. angustifrons*; together these two species represented more than half (58%) of all Hymenophyllaceae samples. The mean number of species per tree was 8 times higher in LCF than in LRF, with 2.4 ± 2.2 species in LCF (max. = 6, min. = 0) and 0.3 ± 1.0 in LRF (max. = 4, min. = 0) ($P<0.01$). The Shannon Index of α-diversity was higher in LCF (H' = 1.90) than in LRF (H' = 1.33) whereas evenness was slightly higher in LRF (E = 0.96) than in LCF (E = 0.87).

Table 9. Occurrence and vertical distribution of Hymenophyllaceae in lowland cloud forest (LCF) and lowland rain forest (LRF) in central French Guiana. Numbers refer to the number of samples in which the species was recorded. For further explanation see text. z1 = trunk base, z2 = lower trunk, z3 = upper trunk, z4 = lower canopy, z5 = middle canopy, z6 = outer canopy. Nomenclature of taxa follows Lellinger (1994) and Cremers (1997).

		LCF							LRF						
Taxa	Height zone	z1	z2	z3	z4	z5	z6	n	z1	z2	z3	z4	z5	z6	n
Hymenophyllum decurrens		1	-	-	1	1	-	3	-	-	-	-	-	-	0
Hymenophyllum hirsutum		-	-	1	-	1	-	2	-	-	-	-	-	-	0
Hymenophyllum polyanthos		-	-	-	-	1	-	1	-	-	-	-	-	-	0
Trichomanes angustifrons		4	6	3	4	4	-	21	-	1	-	-	-	-	1
Trichomanes diaphanum		1	-	-	-	1	-	2	-	-	-	-	-	-	0
Trichomanes kapplerianum		6	1	-	-	-	-	7	-	-	-	-	-	-	0
Trichomanes krausii		-	-	1	3	4	3	11	-	1	1	1	-	-	3
Trichomanes pinnatinervum		-	-	-	2	1	1	4	1	1	-	-	-	-	2
Trichomanes punctatum subsp. *labiatum*		6	6	3	6	2	2	25	1	1	-	-	-	-	2
Hymenophyllaceae total		18	13	8	16	15	6	77	2	4	1	1	-	-	8

5.4.2 Species composition

Floristic similarity of the two forest types in terms of filmy ferns was low (Ss = 0.33). *Trichomanes angustifrons*, *T. krausii*, *T. pinnatinervium* and *T. punctatum* subsp. *labiatum* occurred in both forest types, while *T. diaphanum*, *T. kapplerianum*, *Hymenophyllum decurrens*, *H. hirsutum* and *H. polyanthos* were exclusive to LCF. The abundance of Hymenophyllaceae was much lower in LRF than in LCF. In LRF only 10% of trees were inhabited by filmy ferns in contrast to 70% in LCF.

5.4.3 Vertical distribution

The vertical distribution of the species on trees in the two forest types was remarkably different (Fig. 21). In LRF, Hymenophyllaceae were only found up to the inner tree crown (zones 1-4). The trunk base (zone 1) was inhabited by two species (*T. pinnatinervium* and *T. punctatum* subsp. *labiatum*), the lower trunk (zone 2) by four species (*T. angustifrons*, *T. krausii*, *T. pinnatinervium*, *T. punctatum* subsp. *labiatum*) and the upper trunk and inner crown (zones 3 and 4) only by *T. krausii*. In contrast, in LCF filmy ferns were present in all height zones, and number of species per height zone was higher and more constant (3-8 species). Within-tree distributions of the species differed, however, some species being restricted to the trunk base (e.g. *T. kapplerianum*), others being crown-centred (e.g. *T. polyanthos*) or occurring evenly throughout the tree (e.g. *T. punctatum*).

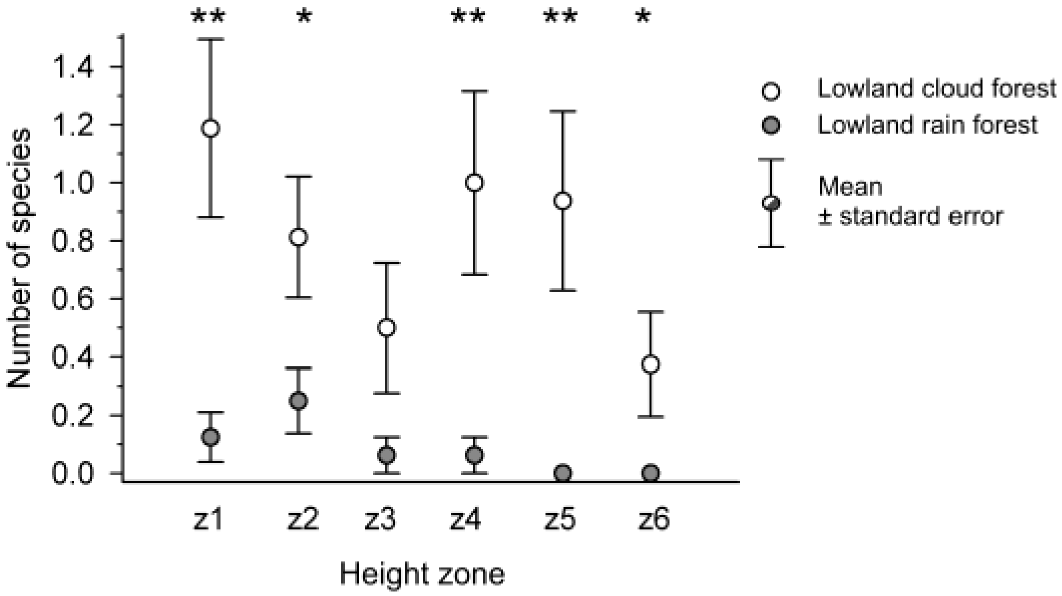

Figure 21. Number of epiphytic Hymenophyllaceae species per height zone in lowland cloud forest and lowland rain forest; n = 16 trees per forest type. Asterisks indicate level of probability calculated with unpaired t-test (* $p<0.05$, ** $p<0.01$). z1 = trunk base, z2 = lower trunk, z3 = upper trunk, z4 = lower canopy, z5 = middle canopy, z6 = outer canopy.

5.4.4 Canopy microclimate

During 60 days in the dry season the diurnal mean relative humidity (RH) was positively correlated with species diversity of filmy ferns (Fig. 22; $r^2 = 0.81$, $P<0.001$). Estimated mean daily evaporation was highest in the outer canopy in LRF, while smallest values were related to the inner crown in LCF (Fig. 23). Global radiation was clearly reduced in the canopy of LCF as compared with LRF. Interestingly, the diurnal course of global radiation showed a strong decrease in the early afternoon in LCF, coinciding with a sharp increase in relative humidity. At the LRF site, this transition is delayed for some hours. The inner crown zones showed a similar diurnal course of global radiation at both LCF and LRF sites (Fig. 24). Average daily wind speed was 0.65 m s^{-1} in LRF and 0.17 m s^{-1} in LCF.

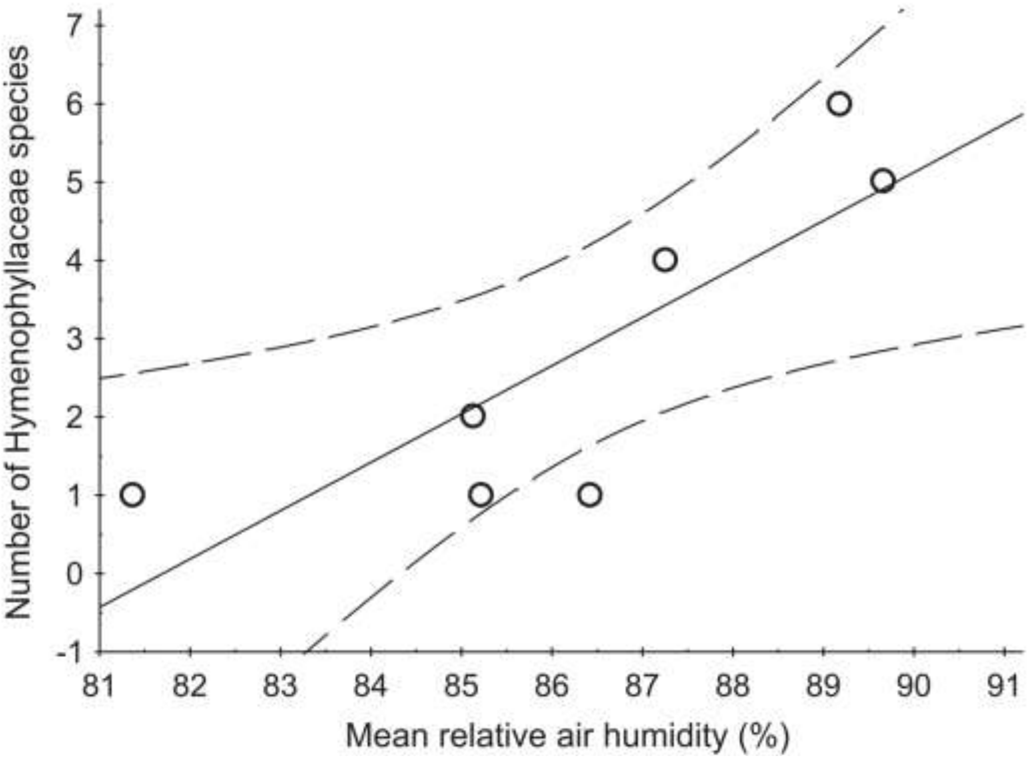

Figure 22. Correlation between number of Hymenophyllaceae species per tree and mean diurnal relative air humidity for 60 days of the dry season in the canopy of 7 trees in lowland cloud forest. Unbroken line indicates the regression, dotted line the 0.95 confidence interval. $R = 0.82$, $P<0.05$.

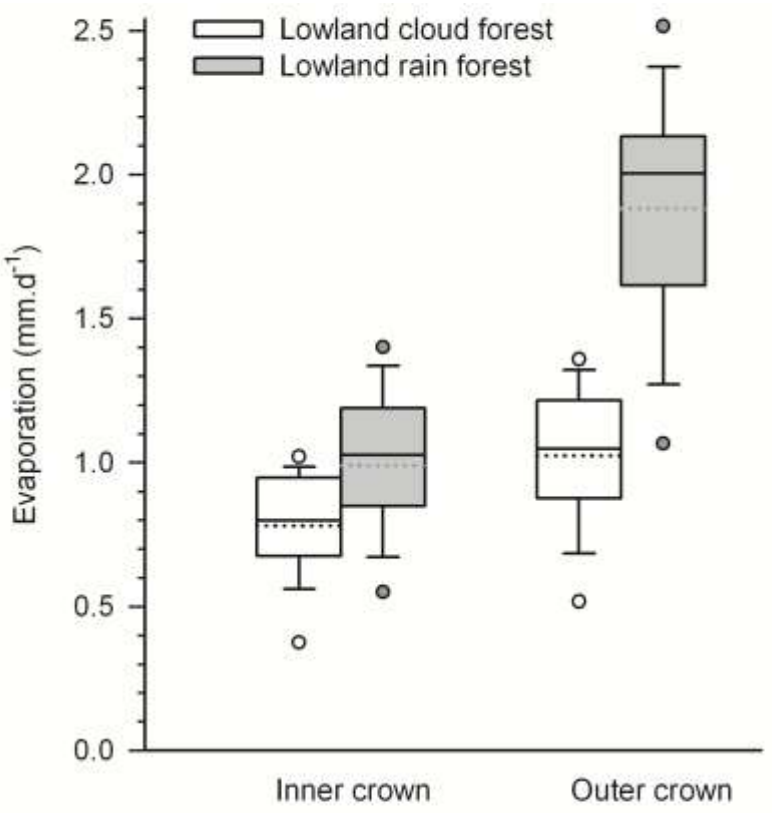

Figure 23. Evaporation per day in the inner and outer canopy of lowland cloud forest and lowland rain forest, calculated using a simplified version of the Penman equation provided by Valiantzas (2006), incorporating daily global radiation, relative humidity, air temperature and the latitude of the site. Boxes indicate upper and lower quartile of data, unbroken line indicates the median, dotted line the mean, whiskers 5th/95th percentile, and circles mark outliers.

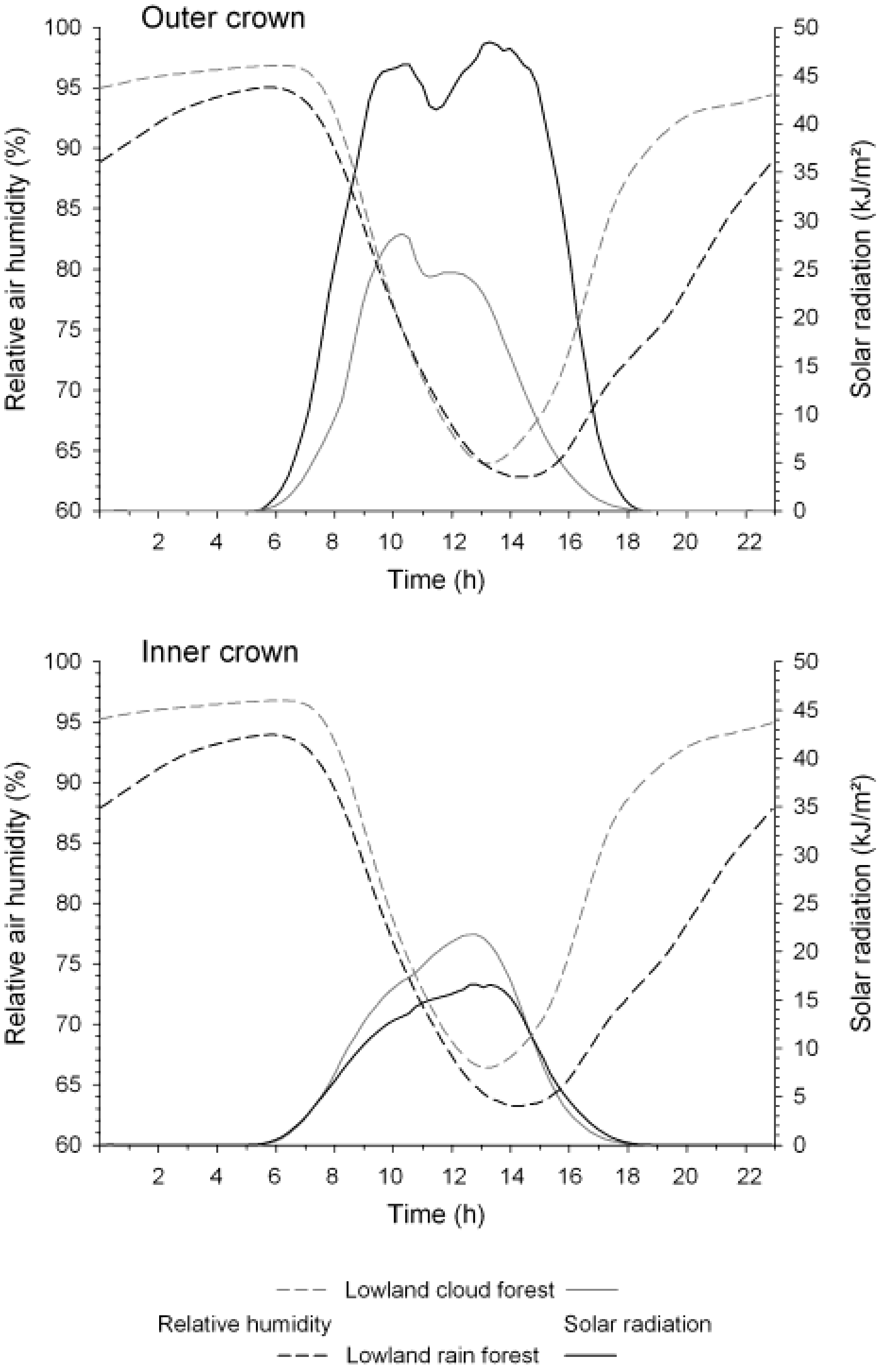

Figure 24. Mean diurnal course of global radiation and relative humidity in lowland cloud forest and lowland rain forest in the inner and outer canopy during 22 September – 24 October 2007.

5.5 Discussion

Because they lack a well-developed cuticle and stomata, Hymenophyllaceae are sensitive to water loss and so are dependent on moist habitats (Proctor 2003). Since humidity is a key driver of filmy fern diversity, Hymenophyllaceae are considered good indicators of high atmospheric humidity (Hietz & Hietz-Seifert 1995). With 9 species of filmy ferns recorded on 16 trees in LCF, the lowland cloud forests of central French Guiana are a rich habitat for Hymenophyllaceae. In comparison, only a single species was found on 25 trees in LRF of Guyana (ter Steege & Cornelissen 1989) and in 1.5 ha of LRF in Venezuela (Nieder *et al.* 2000). In Amazonian Brazil only 3 species were found on 10 trees (Pos & Sleegers 2010). These data agree with our findings, even though the number recorded in LRF of French Guiana was higher. The highest species number hitherto recorded in moist lowland forest is from Amazonian Ecuador, where an inventory of about 650 ha of forest yielded 12 species of filmy ferns (Kreft *et al.* 2004), or only a few more than recorded for LCF in this study.

Not only the total number of species but also their number per height zone was higher in LCF than in LRF (Fig. 21). The scarce occurrence of Hymenophyllaceae in LRF agrees with the observations of Zotz & Büche (2000), Köster (2002), and Pérez Peña & Krömer (2011), who found that filmy ferns were primarily restricted to the lower strata of LRF. By contrast, in LCF filmy ferns frequently occur in the forest canopy, even in the outer periphery of tree crowns (Table 9).

Within the tropical rain forest, air temperature, light availability, and wind speed generally increase with tree height while air moisture and nutrient availability decrease (Johansson 1974, Meinzer & Goldstein 1996, Parra *et al.* 2009). The sharp decrease of filmy fern diversity towards the canopy in LRF can readily be explained by the vertical changes of the microclimate in this forest type. The high frequency of filmy ferns in LCF crowns, on the other hand, is suggestive of the moister microclimate in this forest type and the availability of surplus water in the canopy attributable to fog events (Obregón *et al.* 2011). Further, radiation protection against evaporative loss seems to play a crucial role in the vertical distribution of filmy fern diversity. The relative maximum of diversity in the inner crown (zone 4) in LCF coincides with low values of daily evaporation, which is clearly reduced compared with the canopy. In LCF, epiphytes also benefit from throughfall in the inner crown (zone 4) and in particular from fog events in the outer canopy (zone 6). However, because the highest values of global radiation and hence evaporative loss are in the outer canopy, the inner crown seems to be the most favorable region for filmy ferns in the upper forest stratum (see also Krömer & Kessler 2006). This pattern is also well reflected in the abundance of some filmy fern species. For the lower stratum, the high diversity of filmy ferns in the trunk zone (z1) in LCF may be explained by both radiation protection and high soil moisture. Microclimatic conditions on the hill sites (LRF) are generally less suitable for epiphytes due to higher wind speed, higher evaporation caused by more open canopies, and the lack of fog events. The strong correlation between mean diurnal RH and number of Hymenophyllaceae species per tree reveals the dependence of filmy ferns on humidity (Fig. 2).

Interestingly, we found that species restricted to trunks in the understory of LRF occurred in the canopy of LCF (Table 9; Fig. 25). Shifts in vertical distribution between climatically different habitats have also been observed in epiphytic bryophytes by Acebey *et al.* (2003). Moreover, a similar upward shift in distribution in LCF has been observed in epiphytic macrolichens (Normann *et al.* 2010). The latter study also found that lichens with cyanobacteria as photobionts (“cyanolichens”) are sensitive indicators of LCF. Based on our observations, we suggest that species with upwards-shifting distributions (*Trichomanes krausii, T. pinnatinervium*, *T.punctatum* subsp. *labiatum*) as well as those exclusive to LCF (*Hymenophyllum decurrens*, *H. hirsutum*, *H. polyanthos*, *T. diaphanum*, *T. kapplerianum*) may be used as indicators of LCF. Furthermore, the upward shift of *T. krausii* and *T. punctatum* is remarkable, as Krömer & Kessler (2006) have classified both species as trunk epiphytes. *Trichomanes kapplerianum* seems to be the best indicator species of LCF based on our study. The species is readily recognized by its simple fronds with glabrous margins and uniformly-colored involucres, and can be easily collected due to its occurrence on tree bases.

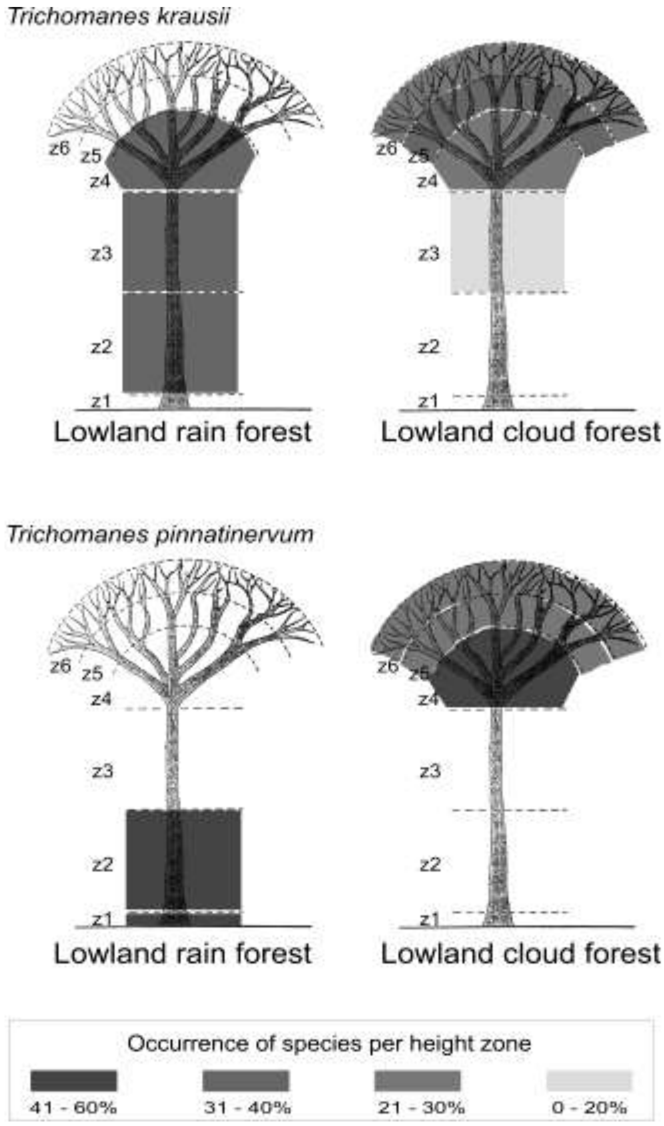

Figure 25. Vertical distribution of two Hymenophyllaceae species in lowland rain forest and lowland cloud forest, expressed by percent occurrence per zone as compared with occurrence on whole trees. z2 = lower trunk, z3 = upper trunk, z4 = lower canopy, z5 = middle canopy, z6 = outer canopy.

LCF and LRF are two different types of tropical lowland forest that were traditionally viewed as a single formation (Gehrig-Downie *et al.* 2011). Discrimination of the two forest types had long been overlooked by the absence of traditional traits separating them, such as differences in tree composition. We present evidence indicating that the presence of morning fog in forest valleys favors the establishment of hygrophilous epiphytes such as filmy ferns. The observed high diversity of filmy ferns in the canopy of LCF and their occurrence in the outer crowns of the trees correlates with the presence of a surplus of liquid water resulting from episodes of fog. The scarcity of Hymenophyllaceae in LRF, in contrast, reflects the drier microclimate in this forest type. The observed differences in filmy fern diversity and vertical distribution in LCF and LRF represent novel traits separating the two forest types and indicate that Hymenophyllaceae are sensitive indicators of lowland cloud forest. Further studies in other sites should verify our observations, and should further explore the usefulness of filmy fern species as indicators of LCF.

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6 Diversity and vertical distribution of epiphytic liverworts in lowland rain forest and lowland cloud forest of French Guiana

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6.1 Abstract

Recent evidence is emerging that tropical cloud forests are not restricted to mountains but may also be found in tropical lowland areas, the so-called "tropical lowland cloud forest" (LCF). LCF occurs in river valleys with high air humidity and morning fog, and is rich in epiphytes. We explored the diversity of bark-inhabiting liverworts in LCF, a group of organisms known to be sensitive indicators of humidity. To test the hypothesis that LCF differs in species richness and species composition from lowland rain forest without fog (LRF), we sampled liverwort diversity in LCF and LRF on 48 whole trees in two sites in French Guiana. Sampling efficiency (= nr. of species found as percentage of estimated total species richness) was about 90% in both forest types. Species richness in LCF was significantly higher than in LRF and species composition differed in all height zones; moreover, LCF had three times more indicator species. Indicators of LCF included shade epiphytes and generalists that occurred also in montane forests, those of LRF were sun epiphytes characteristic of rather dry, open sites. The detected differences in liverwort diversity of LCF and LRF are explained by the more humid conditions in LCF as compared with LRF. A comparison of liverwort richness along elevational gradients in the Neotropics showed that species richness differs more strongly among forest type (rain forest, cloud forest) than among elevation and that lowland cloud forests may be richer in species than montane rain forests. The data indicate that elevational comparisons of bryophyte species diversity in the Tropics should make a distinction between rain forests and cloud forests.

6.2 Introduction

Although covering only about 0.25% of the Earth's land surface, tropical cloud forests are amongst the biologically richest ecosystems worldwide, both in terms of plants and animals (Bruijzeel *et al.*, 2011). These forests occur in areas of frequent or persistent ground-level cloud or fog and are usually found in montane environments, above 500 m elevation. Because of their predominance in mountain areas, tropical cloud forests are usually described as "montane cloud forests" (Hamilton *et al.*, 1995; Bruijnzeel, 2005; Bruijnzeel *et al.*, 2011).

Recent evidence is emerging that tropical cloud forests are not restricted to mountains but may also be found in the lowland areas, well below 500 m (e.g. Normann *et al.*, 2010; Gradstein *et al.*, 2010; Obregon *et al.*, 2011; Gehrig-Downie *et al.*, 2011, 2012). Meteorological observations in evergreen lowland forest in central French Guiana showed almost daily occurrence of morning fog in river valleys and a clear diurnal course of fog frequency (Obregon *et al.*, 2011). In contrast, fog events were largely absent on hill sites. Fog development in the valleys was apparently triggered by nocturnal cold air drainage flow from the hills bordering the valleys, causing saturation of air humidity during night and early morning in situations of low air turbulence. Heavy rainfall and water logging of valley-bottom soils were additional factors enhancing condensation in the river valleys. The frequent occurrence of fog correlated with significantly higher epiphyte diversities in the valley forest as compared to the hill forest, and supported the occurrence of the hitherto undescribed "tropical lowland cloud forest" (LCF) in the valleys. The high epiphyte diversity in LCF coincided with significantly higher relative air humidity in LCF than in the rain forest on the hills (LRF). It was hypothesized that the epiphytes in LCF benefitted from the surplus moisture and delayed onset of the stress period, particularly during the dry season (Obregon *et al.*, 2011).

Recent studies on epiphyte diversity in LCF and LRF of central

French Guiana found significantly higher amounts of epiphyte biomass in LCF, both of bryophytes and lichens, ferns and of angiosperms (Gehrig-Downie *et al.*, 2011). Moreover, epiphyte cover was much higher in LCF than in LRF, in all height zones on the trees, with about 70 % mean cover in LCF and 15 % in LRF. The epiphyte work furthermore showed that cyanolichens and filmy ferns are excellent indicators of lowland cloud forests (Normann *et al.*, 2010; Gehrig-Downie *et al.*, 2012), with cyanolichen species richness in LCF exceeding that in LRF about 2.5 times.

In this paper we explore the diversity of epiphytic liverworts in LCF. Liverworts (Marchantiophyta) are the second largest groups of the bryophytes, after the mosses, and contain more than 5000 species worldwide. They commonly occur as epiphytes in tropical moist forests (Gradstein, 1995) and are considered sensitive indicators of microclimatic conditions, especially humidity, due to the lack of a protective cuticle (e.g. Bates & Farmer, 1992). Studies on bryophyte diversity along elevational gradients in tropical mountains have indicated that the contribution of liverworts to overall bryophyte diversity increases with humidity, more strongly so than that of mosses (Gradstein *et al.,* 1989, 1996; Wolf, 1993b). Several recent studies have described the species composition and richness of epiphytic liverworts in tropical moist forests and at different height levels on the forest trees (Cornelissen & ter Steege, 1989; Montfoort & Ek, 1990; Wolf, 1993 a, b; Gradstein *et al.*, 2001 a; Holz *et al.*, 2002; Acebey *et al.*, 2003; Sporn *et al.*, 2010). These studies have identified bark structure and microclimate as key drivers of liverwort diversity within the forest. Host preference, on the other hand, was found to play no role of importance in tree species-rich tropical forests (Richards, 1984; Frahm, 1990). Changes in insulation or air humidity may result in rapid composition changes of epiphytic species assemblages on host trees (e.g. Acebey *et al.*, 2003; Frego, 2007), and epiphytic liverworts can therefore be used as indicators of forest disturbance and succession (Holz & Gradstein, 2005).

In spite of the recent upsurge in ecological research on these tropical forest organisms, our knowledge of diversity and vertical distribution of epiphytic liverworts in tropical evergreen forests remains incomplete. Most of the studies focused on tropical montane forests; very few have dealt with lowland forests (Cornelissen & ter Steege, 1989; Montfoort & Ek, 1990; Cornelissen & Gradstein, 1990; Gradstein, 2006; Mota de Oliveira, 2010). Moreover, descriptions of diversity and vertical distribution patterns were usually observational; none of the studies in lowland forests with exception of Mota de Oliveira (2010) included statistical analysis of these data.

The aim of the present study was to analyze the diversity of epiphytic liverworts in LCF. By comparing species richness, composition and vertical distribution in LCF and nearby LRF, we explore the usefulness of liverworts as indicators of tropical lowland cloud forest.

6.3 Methods

6.3.1 Study area

Field work was conducted in central French Guiana in the vicinity of the village of Saül (3°37'20"N, 53°12'31"W), about 200 km southwest of the Atlantic coast, and in the Nouragues Natural Reserve (4°2'30"N, 52°40'30"W), ca 100 km inland from the Atlantic coast and 80 km northeast of Saül. Annual rainfall is ca. 2500 mm in Saül and ca. 3000 mm in Nouragues, with a distinct dry season from late July to November and a less pronounced dry period for several weeks in February and March. Average temperature is 27°C (Mori *et al.*, 1997; Grimaldi & Riéra, 2001). For details on the local climate see Obregon *et al.* (2011). Lowland cloud forest (LCF) occurs in valleys and lowland rain forest (LRF) on slopes (Normann *et al.*, 2010; Obregon *et al.*, 2011; Gehrig-Downie *et al.*, 2012).

6.3.2 Epiphyte sampling

Species richness of corticolous liverworts was sampled on randomly selected, climbable trees following the standard protocol for epiphyte sampling in tropical forests (Gradstein *et al.*, 1996, 2003). All trees belonged to the age class of mature canopy trees (Hallé *et al.*, 1978; Richards, 1996). Plots of one hectare were laid out in almost undisturbed, old growth forest in each forest type, on the bottom of slopes in LCF and higher up slopes in LRF. We sampled trees in six hectare plots in each forest type: five plots in each forest type at Saül, which was the principal site in this study, and one plot in each forest type at Nouragues. The purpose of the latter study site was to test further occurrence of LCF in French Guiana. At Saül one ha plot with 8 sampled trees and four additional ha plots with 2 sampled trees (as statistical replicas) were inventoried in each forest type. At Nouragues one ha plot with 8 sampled trees was inventoried in each forest type. The plots at Saül were situated in valleys at ca. 250 m (LCF) and on slopes at ca. 325 m (LRF) along "Crique Pelée" and "Crique Roche"; at Nouragues they were situated in valleys at ca. 100 m (LCF) and on slopes at ca. 220 m (LRF). Distance between adjacent plots in LCF and LRF was about 250 m. Sampled trees were standing about 20-30 m apart and were 20 to 45 m in height (mean height was 31.4 m ± 7.3 m in LCF and 30.2 m ± 5.9 m in LRF); dbh was 30-300 cm (mean dbh excluding one tree with buttresses was 58.3 cm ± 19.6 cm in LCF and 54.1 cm ± 20.3 cm in LRF). Details on height, dbh and species identity of all sampled trees are given in Gehrig-Downie *et al.* (2012).

Trees were climbed using the single rope technique (ter Steege & Cornelissen, 1988) and on each of the 48 target trees all corticolous liverworts growing in 24 sample plots of 600 cm^2 were removed. The sample plots were positioned at each cardinal direction in six height zones (Johansson, 1974; Cornelissen & ter Steege, 1989): trunk base (zone 1), lower trunk (zone 2), upper trunk to first ramification (zone 3), lower canopy (zone 4), middle canopy (zone 5), and outer canopy (zone 6). Sample plots were 20 x 30 cm on trunks and 20 x 30 cm or 10 x 60 cm on canopy branches according to branch diameter (Gradstein *et al.*, 2003). For safety reasons, thin canopy branches (zone 6) were cut and carefully lowered to the ground for sampling. The collected liverworts were identified using the relevant taxonomic literature (Gradstein & Ilkiu-Borges, 2009) and reference collections in the herbarium of the University of Göttingen. Vouchers were deposited in the herbarium of the Muséum National d'Histoire Naturelle, Paris (PC).

6.3.3 Statistical analysis

Species presence absence matrices were prepared for all six height zones per tree as well as per plot. Species richness of height zones and plots was compared using the Shannon Index and by calculating evenness (Magurran, 2004; Chao *et al.*, 2005). Differences in species number between trees and plots were analyzed with Mann-Whitney-U-tests. The floristic similarity between epiphytic liverworts in LRF and LCF was tested with the Sørensen coefficient (e.g. Banaticla & Buot, 2005). To calculate sampling efficiency (= nr. of species found as percentage of estimated total species richness in the area), the number of species found on 24 trees compared to projected total species richness at the two sites was calculated with MMMeans.

Indicator species analysis (ISA; Dufrene & Legendre, 1997) was used to investigate the preference of species for each forest type. This method takes into account the information on the concentration of species abundance in a particular group (here forest type) and the relative frequency of the species in this group. These two measures combined produce in indicator value (IV) that weighs the preference of a species for a particular group. The indicator value ranges from 0 to 100, according to the strength of the preference. Randomization procedures test for the significance of the indicator value obtained for each species. Species composition of epiphytic liverworts was analyzed by means of a multi-response permutation procedure (MRPP) applying a natural weighting factor (n/sum(n)) as recommended by Mielke (1984). MRPP was carried out to calculate similarity among liverwort communities, and to test whether the similarities among communities in the a-priori forest types and the two study sites were significantly different from similarities among communities drawn at random. The resulting test statistic 'A', the chance-corrected within-group agreement, is a sample size-independent measure of ‘effect-size’. When all items are identical within groups, then the observed $A = 1$ is the highest possible value for A. If heterogeneity within groups equals expectation by chance, then $A = 0$. If there is less agreement within groups than expected by chance, then $A < 0$. The p-value is useful for evaluating how likely an observed difference is due to chance.

To analyze differences in floristic composition of plots we applied non-metric multidimensional scaling (NMDS) based on relative Sørensen distance. Tree height zones 1-3 were pooled in the group "trunk", zones 4-6 in the group "crown". Validity of a 2-dimensional solution was assessed by means of Monte Carlo randomizations. The representation of the distances was evaluates by calculating the coefficient of determination R^2 between distances in the ordination space and distances in the original space. Simultaneous plotting of environmental variables was done by weighted averaging (Whittaker, 1967). The scores of the plots on the first axis of the ordination were correlated with the forest type and of the second axis with position in tree, as these were the expected environmental gradients.

All analyses were carried out with PCORD 5 (McCune & Grace, 2002).

6.4 Results

6.4.1 Species richness

In total we found 129 species of liverworts (8 families, 39 genera), including 113 in LCF and 96 in LRF (Table 10). At Saül we collected 99 species on sixteen trees in LCF and 84 on sixteen trees in LRF, at Nouragues 86 species in LCF and 62 in LRF (on eight trees each). Sampling efficiency was about 90% in both forest types. In LCF, 85% of species were found in more than one relevé and 75% in more than one plot. In LRF singletons were more common with 77% of species found in more than one relevé and 66% in more than one plot. Lejeuneaceae were by far the largest family with 95 species, representing more than 80% of all samples. Next in importance were Plagiochilaceae (9 species) and Frullaniaceae (7 species). The largest genera was *Lejeunea* Lib. (14 species) followed by *Ceratolejeunea* (Spruce) J.B. Jack & Steph., *Cololejeunea* (Spruce) Schiffn. (Lejeuneaceae) and *Plagiochila* (Dumort.) Dumort. (Plagiochilaceae) with 9 species each.

The mean number of species per tree was significantly higher in LCF than in LRF, with 33.6 ± 8.3 species in LCF (max. = 47; min. = 20) and 25.0 ± 10.2 in LRF (max. = 48; min. = 7) ($p<0.01$). The Shannon Index of α-diversity was slightly higher in LCF ($H'=4.4$) than in LRF ($H'=4.1$), whereas evenness was similar in LRF ($E=0.90$) in LCF ($E=0.92$).

Table 10. Occurrence and vertical distribution of liverworts on 48 trees in lowland cloud forest (LCF) and lowland rain forest (LRF) of Nouragues (Nou) and Saül in French Guiana. Numbers refer to the number of samples in which the species was recorded. For further explanation see text. z1= trunk base; z2= lower trunk; z3= upper trunk; z4= lower canopy; z5= middle canopy; z6= outer canopy. Nomenclature of taxa follows Gradstein & Ilkiu-Borges (2009). Species marked with two stars (**) are new to French Guiana, those with one star (*) new to Central French Guiana (see also Gradstein & Ilkiu-Borges, 2009).

	LRF								**LCF**							
	Saül	**Nou**	**z1**	**z2**	**z3**	**z4**	**z5**	**z6**	**Saül**	**Nou**	**z1**	**z2**	**z3**	**z4**	**z5**	**z6**
Cephaloziellaceae																
Cylindrocolea planifolia	+	+				3	4		+	+		2		3	2	3
Frullaniaceae																
Frullania apiculata	+	+		1	4	7	9	7	+	+		1	2	5	5	8
F. brasiliensis	+							1	+					1	1	1
F. caulisequa	+	+		3	5	6	12	2	+	+				3	5	5
F. ericoides	+					1										
F. kunzei	+	+		1	1	5	8	12	+					1	1	2
F. nodulosa										+					1	1
*F. (*subgen. *Diastaloba)* sp.	+	+	1	6	5	9	14	9	+	+				2	7	6

Lejeuneaceae																
Acrolejeunea emergens										+			1	1	1	
A. torulosa	+	+				1	1	2		+						1
Anoplolejeunea conferta	+				1	2										
Archilejeunea auberiana									+							1
**_A. badia_		+			1											
A. fuscescens	+	+	6	6	6	5	3	2	+	+	2	2	7	9	7	4
A. parviflora	+	+	4	1	2	1	1		+	+	7	5	4	2	2	3
*_Ceratolejeunea ceratantha_										+			1	1		
_C._ cf. _laetefusca_		+	1	1	1	1										
C. coarina									+	+				5	5	5
C. confusa	+	+	1	2	3	5	9	9	+	+	1		1	5	7	6
C. cornuta	+	+	8	7	9	18	16	9	+	+	8	11	15	2	2	2
C. cubensis	+	+	11	1	6	1	8	6	+	+	6	13	13	13	19	13
C. deciscens	+				1				+		1		1	1	1	
C. guianensis	+	+			1	3	3		+	+	1	3	6	4	4	2
C. minuta	+	+	1	7	3	4	1	2	+	+	2	2	1	1		
Cheilolejeunea adnata	+	+	17	19	18	22	21	19	+	+	9	15	13	2	19	2
C. clausa	+	+	1	1	3	1		4	+	+		2	3	5	3	2
C. holostipa	+	+	1	6	1	16	16	12	+	+	1	3	6	11	1	9
**_C. oncophylla_	+	+		3	3	5	3	2	+		1			1	1	
C. rigidula	+	+	8	6	1	9	9	8	+	+	2	5	13	14	13	15

C. trifaria	+	+	4	8	8	12	15	7	+	+	4	2	8	13	13	11
Cololejeunea cardiocarpa	+							1								
C. clavatopapillata	+					1			+	+	1	4	1			
C. contractiloba		+	1							+			1			
C. microscopica	+	+	1			1	1		+	+			1	2	1	1
C. obliqua									+					1		
C. papillosa	+		2						+	+	2	1		1	1	
C. sicaefolia										+	1					
C. sp.										+				1		
C. verrucosa									+		1					
Colura cylindrica	+	+			1			3	+						1	2
C. sagittistipula	+	+			1	6	5	4	+	+				2	4	1
C. tortifolia	+							1	+			1			1	
Cyclolejeunea chitonia									+	+	1	1	1	8	7	12
C. convexistipa	+		1						+	+		2		3	3	6
C. luteola	+					2			+	+	2	1	1			
C. peruviana									+							1
Diplasiolejeunea cf. *cavifolia*	+	+						3								
D. rudolphiana	+					1		3								
Drepanolejeunea bidens	+	+		1	1	3	5	3	+	+				1	3	2
D. crucianella	+	+	1	3	2	2	2	2	+	+				2		3
D. fragilis	+	+		2	4	1	15	13	+	+			3	5	6	12

D. lichenicola		+				1		1	+	+				1	2	2
D. orthophylla		+		1		1	1									
Harpalejeunea oxyphylla	+	+	8	6	5	11	11	3	+	+		4	3	1	6	9
H. stricta	+	+	2	5	5	12	13	7	+	+			6	7	5	5
H. tridens	+			1	2	2	1	1	+	+			1	5	3	1
Lejeunea aphanes	+	+	2	3	2				+	+	3			1		1
L. asperrima		+	2						+					1		
L. boryana	+	+	2	2					+	+	3			1	2	
L. cancellata	+		1							+			1	1		
L. caulicalyx	+		1					1		+		2				1
L. cerina	+		3	1		1	1	2	+	+	5	7	6	8	4	5
L. cf. *adpressa*	+	+		1	3	2			+	+			1	1	1	
L. flava		+		1		1			+	+	3	2	5	5	2	2
L. huctumalcensis	+	+	1	1	2			1	+		2	2	1			3
L. laetevirens	+	+	5	3		4	1	4	+	+	6	6	5	5	8	9
**L. phyllobola*										+			1			
L. reflexistipula									+					1		
L. sp.										+						1
L. tapajoensis	+	+	1					1	+	+		2	2			2
Lepidolejeunea involuta	+		1						+	+	2	5	1	1	1	
Leptolejeunea elliptica										+				1		
Lopholejeunea eulopha	+	+			2	3	4	2	+	+	1			1	5	3

L. nigricans	+						1		+	+				4	2	5
L. subfusca	+	+	2	3	6	6	5	7	+	+	1	5	5	1	15	12
Mastigolejeunea auriculata	+	+	1	1	1			1	+			1	1	1	1	1
M. innovans		+					1									
M. plicatifolia	+		1						+	+		4	5	6	2	2
Metalejeunea cucullata	+	+	5	3	5	7	6	2	+	+	2	1	2	5	1	6
Microlejeunea acutifolia	+		1	1	1	3	3		+	+	5	6	8	12	12	13
M. epiphylla	+	+	6	5	7	1	12	13	+	+	3	5	4	15	15	17
Neurolejeunea breutelii	+	+	1	2	3	4	5	3	+	+	1	2	4	9	11	9
N. sastreana	+						1									
N. seminervis	+	+	1	2	3	5	7	3	+			1	1	1	1	1
Odontolejeunea lunulata	+							2	+						1	
O. rhomalea									+	+	1			1	1	
Pictolejeunea picta									+	+	4	1	1			
Prionolejeunea denticulata	+		1	1					+	+	4	3	2	3	3	2
P. muricatoserrulata	+		2		2	1			+	+	9	8	5	3	4	1
P. scaberula	+	+	1					1	+	+	1	2	2	1		2
P. trachyodes		+		1												
Pycnolejeunea contigua	+	+		3	7	1	13	13	+	+			1	5	4	5
P. macroloba	+	+	1	4	2	6	8	7	+	+	1			3	4	4
***P. papillosa*	+	+			1	4	7	5	+						1	
Rectolejeunea berteroana	+	+	5	5	4	5	3	5	+	+	1	3	2	5	3	1

R. flagelliformis	+	+	6	4	2	4	3	8	+	+	1	2	1	2	3	9
Stictolejeunea squamata	+		2	1		1			+	+	5	7	7	8	9	9
Symbiezidium barbiflorum	+	+	1	2	1	3	2	5	+	+	3	7	8	1	12	15
**S. transversale*	+	+	4	2	1	3	3	1	+	+	2	3	3	5	11	7
Taxilejeunea sp.									+	+			2	2	1	
Thysananthus amazonicus	+	+		3		2	2	5	+	+			1	3	6	5
Xylolejeunea crenata										+					1	1
Lepidoziaceae																
Bazzania cuneistipula		+	1		1	2	2	2	+				1	1		1
B. diversicuspis									+					1	1	
B. hookeri									+		1	1	2	2	1	
Telaranea nematodes	+					1			+		1				1	
Lophocoleaceae																
Chiloscyphus coadunatus	+			1					+		1	1	1	1		
C. liebmannianus	+			1					+	+	5	3	1	1		1
Leptoscyphus porphyrius	+						1		+					1		
Metzgeriaceae																
Metzgeria decipiens	+							1	+	+	2	1	1	2	1	1
M. leptoneura									+		2	1		1	1	

Plagiochilaceae																
Plagiochila disticha	+			1			1	1	+	+	6	4	3	3	6	6
P. gymnocalycina										+	2					
P. montagnei	+		1			1			+	+		1	1	2	6	4
P. patentissima									+			1		1		
P. raddiana									+	+	4		1	2	2	2
P. rutilans									+	+	2					
P. simplex	+	+		1	4	7	7	1	+	+	5	5	4	9	5	4
P. subplana		+	1			1		1	+	+	11	5	6	5	4	3
P. tenuis	+						1		+		1	1	1	2		
Radulaceae																
Radula aurantii									+					1		
R. flaccida									+		2	2				
R. javanica	+		4	4	2	2	2		+	+	12	17	16	14	14	12
R. kegelii	+		2	1	2				+	+	6	7	4	5	5	3

6.4.2 Species composition and indicators

About one third of the species found in LCF were only collected in this forest type, while about one tenth of the species found in LRF were exclusive to it (Table 10). Species recorded only from LCF, and found on more than one tree, included *Bazzania hookeri* (Lindenb.) Trevis., *Ceratolejeunea coarina* (Gottsche) Steph., *Cyclolejeunea chitonia* (Tayl.) A. Evans, *Metzgeria leptoneura* Spruce, *Pictolejeunea picta* (Steph.) Grolle, three species of *Plagiochila* (*P.* cf. *gymnocalycina* (Lehm. & Lindenb.) Lindenb., *P. raddiana* Lindenb., *P. rutilans* Lindenb.) and *Radula flaccida* Lindenb. & Gottsche. Exclusive to LRF, and collected on more than one tree, were *Anoplolejeunea conferta* (Meissn.) A. Evans, *Diplasiolejenea* cf. *cavifolia* Steph. and *D. rudolphiana* Steph.

Some species were significantly more common in one forest type than in the other. For example, *Cololejeunea clavatopapilata* Steph., *Cyclolejeunea convexistipa* (Lehm. & Lindenb.) A. Evans, *Lejeunea flava* (Sw.) Nees, *Mastigolejeunea plicatifolia* (Spruce) Steph., *Microlejeunea actutifolia* Steph. and three species of *Prionolejeunea* (Spruce) Schiffn. were recorded in ten times as many LCF samples as in LRF. On the other hand, three species of *Frullania* Raddi (*F. caulisequa* (Nees) Nees, *F. kunzei* (Lehm. & Lindenb.) Lehm. & Lindenb., *F.* sp.) were much more common in LRF than LCF. *Ceratolejeunea cubensis* (Mont.) Schiffn. was the commonest species in LCF, being present in more than 50 % of LCF samples. In contrast, this species was only found in about 20 % of LRF samples. The most common species in LRF was *Cheilolejeunea adnata* (Kunze) Grolle being present in 80 % of LRF samples (40 % of LCF samples).

Although only 60 % of all liverwort species were found both at Saül and Nouragues, 28 % exclusive to Saül vs. 20 % exclusive to Nouragues, MRPP of species composition indicated a greater similarity of LCF resp. LRF samples among study sites (A = 0.007, p<0.001) than between LCF and LRF within study sites (*A* = 0.02, *p*<0.001, Table 12).

Using the ISA approach we identified 21 indicator species of LCF, with *Cyclolejeunea chitonia*, *Microlejeunea acutifolia*, *Plagiochila disticha* (Lehm. & Lindenb.) Lindenb., *P. subplana* Lindenb., *Radula javanica* Gottsche, *Stictolejeunea squamata* (F. Web.) Schiffn. and *Symbiezidium barbiflorum* (Lindenb. & Gottsche) A. Evans showing highly significant indicator values (IV) of *p*<0.001. In contrast, for LRF we detected only eight indicator species including only a single one, *Frullania kunzei*, with a highly significant indicator value (Table 11).

Table 11. Indicator values (IVs) for liverwort species of lowland cloud forest (LCF) and lowland rain forest (LRF) in central French Guiana. IVs are ranging from 0 (no indication) to 100 (perfect indication), their significance was calculated with randomization procedures (* p<0.05, ** p<0.01, *** p<0.001).

LCF Indicator species	IV	P	LRF Indicator species	IV	P
Radula javanica	68.1	***	*Frullania kunzei*	56.1	***
Microlejeunea acutifolia	66.7	***	*Pycnolejeunea contigua*	51.9	**
Stictolejeunea squamata	63.4	***	*Harpalejeunea stricta*	48.2	*
Cyclolejeunea chitonia	62.5	***	*Frullania sp.*	46.3	*
Symbiezidium barbiflorum	56.2	***	*Frullania caulisequa*	42.6	*
Lopholejeunea subfusca	55.7	*	*Pycnolejeunea macroloba*	41.4	*
Plagiochila disticha	55.1	***	*Ceratolejeunea minuta*	40.0	*
Plagiochila subplana	50.3	***	*Pycnolejeunea papillosa*	29.6	*
Lejeunea aphanes	49.3	**			
Lejeunea laetevirens	48.2	*			
Radula kegeli	46.9	**			
Plagiochila simplex	46.3	*			
Lejeunea flava	38.8	**			
Cyclolejeunea contigua	37.9	**			
Lopholejeunea nigrescans	33.7	**			
Plagiochila raddiana	33.3	**			
Prionolejeunea denticulata	30.7	*			
Chiloscyphus liebmannianus	29.6	*			
Mastigolejeunea plicatifolia	29.6	*			
Ceratolejenea coarina	29.2	**			
Pictolejenea picta	20.8	*			

6.4.3 Vertical distribution

In both forest types, the number of liverwort species increased with height zone. In LCF the middle and outer crowns were richest in species while in LRF highest diversity was found in the middle crowns. Throughout all height zones LCF trees harbored a higher number of liverwort species than trees in LRF, though only significantly so for the crown (Figure 26). However, MRPP of liverwort composition of height zones showed significant differences between the forest types for all zones (Table 12).

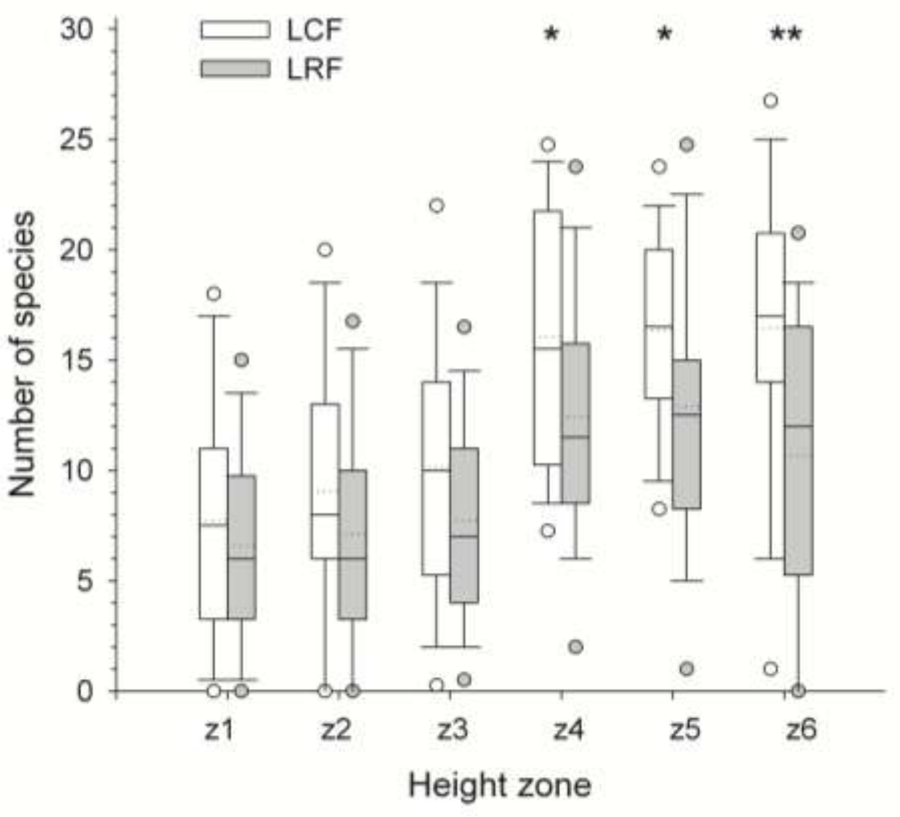

Figure 26. Number of epiphytic liverwort species per height zone in lowland cloud forest (LCF, light bars) and lowland rain forest (LRF, grey bars). n=24 trees per forest type. Boxes indicate upper and lower quartile of data, unbroken line gives the median, dotted line the mean and whiskers 5th /95th percentile. Levels of significance are obtained with unpaired t-tests and shown by asterisks, $P<0.05$*; $P<0.01$**. z1= trunk base; z2= lower trunk; z3= upper trunk; z4= lower canopy; z5= middle canopy; z6= outer canopy.

Table 12. Similarity among liverwort assemblages in lowland cloud forest (LCF) and lowland rain forest (LRF) in central French Guiana analysed by means of a multi-response permutation procedure (MRPP). The lower the test statistic *A*, the more different is species composition in the two forest types. For further explanation see text. z1= trunk base; z2= lower trunk; z3= upper trunk; z4= lower canopy; z5= middle canopy; z6= outer canopy. * p<0.05, ** p<0.01, *** p<0.001.

LCF vs. LRF	*A*	P
z1	0.019	***
z2	0.018	**
z3	0.018	***
z4	0.016	***
z5	0.033	***
z6	0.030	***
total	0.043	***

Non-metric multidimensional scaling (NMDS) of 32 samples (16 plots with trunk and crown, respectively) and 124 species of liverworts resulted in a two-dimensional solution with final stress of 18.25 and final instability of 0.018 (Figure 27). A Monte-Carlo test comparing stress in randomized data with stress in real data stated a level of significance $p<0.01$.

Axis 1 correlates with forest type (r=0.65, tau=0.56), Axis 2 correlates with position in the tree (r=0.50, tau=0.50). The correlation between ordination distances and distances in the original n-dimensional space is $R^2=0.493$ for Axis 1 and $R^2=0.329$ for Axis 2 (cumulative $R^2= 0.822$).

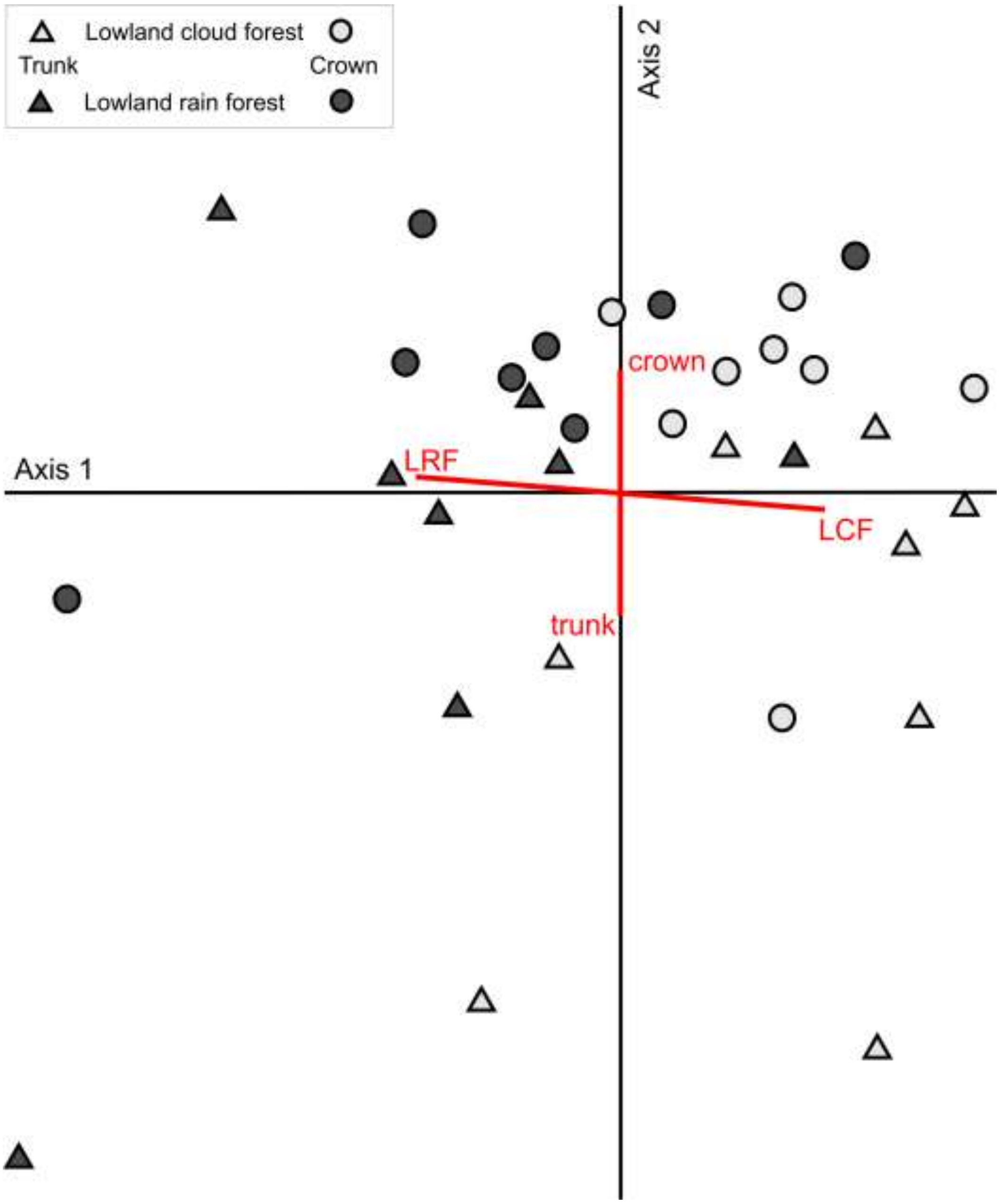

Figure 27. Non-metric multidimensional scaling (NMDS) of liverwort species composition in crown (circles) and trunk (triangles) plots of lowland cloud forest (light symbols) and lowland rain forest (grey symbols). Axis 1 correlates with forest type (r=0.65, tau=0.56), Axis 2 with position in the tree (r=0.50, tau=0.50).

6.5 Discussion

6.5.1 Species richness and composition

With 129 corticolous species (including 3 morphospecies) recorded from 48 trees in two lowland forest sites ca. 80 km away from each other, this is the highest number of liverwort species recorded from evergreen lowland forest in a relatively small area. Mota de Oliveira (2010) recorded 162 corticolous species (including 30 morphospecies) or only 25% more species from nine lowland forest localities across the entire Amazon basin, stretching from French Guiana and the Brazilian state of Pára in the East to Ecuador in the West. The number sampled in this study represents about two third (63%) of the entire liverwort flora of French Guiana; this percentage would be even higher when *ca.* 35 non-corticolous species recorded from French Guiana would be excluded from the calculation. The figures are clearly suggestive of a high species density of epiphytic liverworts in tropical forests (see also Gradstein, 1992 a). In addition, they show the important contribution of bark-inhabiting taxa to the total diversity of liverworts in tropical forests. As expected, Lejeuneaceae were the most speciose family by far. With more than 80% of all species, the dominance of Lejeuneaceae was even greater than reported from other lowland forests (70-75%; Gradstein, 1995, 2006). The data clearly show the overriding importance of this family in the liverwort flora of tropical lowland forests (Schuster, 1983).

On average, the Nouragues site was slightly richer in liverwort species per tree than the Saül site (LCF: 38 spp. per tree at Nouragues vs. 31 at Saül; LRF: 28 spp. per tree at Nouragues vs. 25 in Saül). This might reflect the higher annual rainfall at Nouragues (3000 mm) than at Saül (2500 mm) and the close proximity of an inselberg at Nouragues, which may have somewhat altered the climate of the adjacent LRF and may have caused short episodes of fog through uplifting of moist air along the slopes of the inselberg (P. Forget, oral com.). However, during our fieldwork the rain forest was always free of fog. In addition, species assemblages of the two sites differed considerably and only slightly more than half (60%) of all species sampled were found at both localities.

MRPP of species composition showed more similarity for forest type than for location. In a study on epiphytic bryophyte diversity in the Amazon region (nine study sites), Mota de Oliveira (2010) found that species assemblages of the region were rather similar and comprised in a single metacommunity, with species apparently dispersing freely across the entire region. The structure of a majority of the local assemblages could be explained by Hubbel's neutral theory of species diversity (Hubbel, 2001), stating that local species communities are built as random samples of the metacommunity. For those sites where neutral dynamics could not account for species composition (Ecuador: Tiputini), environmental factors (humidity) were assumed to play a major role. Based on the results of Mota de Oliveira (2010), we conclude that the compositional similarities between the same forest type in Nouragues and Saül indicate the presence of a single metacommunity, and the differences between LCF and LRF in each site reflect the climatic and ecological differences between the two forest types.

As expected, species richness of liverworts was significantly higher in LCF than in LRF. On average, we found about 25% more species in the cloud forest than in the rain forest, both at Nouragues and Saül. The percentage might have even higher when epiphyllous liverworts, considered to be very sensitive indicators of humidity (Pócs, 1996), had also been included in the study. These results clearly suggest that liverwort richness is an excellent trait separating tropical lowland cloud forests from rain forests, additional to richness of cyanolichens and filmy ferns (Normann *et al.*, 2010; Gehrig-Downie *et al.*, 2012). The high liverwort richness in LCF of Central French Guiana was earlier hinted at by Gradstein (2006) and Gradstein and Ilkiu-Borges (2009), based on the pioneering work of Montfoort and Ek (1990), but these studies did not include local comparisons with LRF. The high liverwort diversity of LCF is substantiated in this study by a first comparison between diversity in LCF and LRF, as supported by statistical analysis. The detected differences in epiphyte diversity patterns of LFC and LRF are explained by the more humid conditions in LCF as compared with LRF (Obregon *et al.*, 2011). During both wet and dry seasons, mean diurnal relative air humidity (RH) in higher in LCF than in LRF, and persistence of high RH after sunrise significantly longer in LCF. The latter authors suggested that the prolonged availability of high air humidity in LCF and the additional input of liquid water through fog, enhance epiphyte growth in LCF by shortening the desiccation period and lengthening the period of photosynthetic activity of the plants. Support for this hypothesis was presented by Pardow and Lakatos (2012) based on desiccation tolerance measurements of epiphytic bryophytes in evergreen lowland forest. These authors also presented first ecophysiological support for the notion that shade epiphytes are less desiccation-tolerant than sun epiphytes (e.g. Gradstein, 1992b; Gradstein & Sporn, 2010).

6.5.2 Indicators

In contrast, all exclusive species and ISA indicators of LRF are desiccation-tolerant sun epiphytes, adapted to thrive in relatively dry conditions (Tables 10 and 11). They included a.o. *Anoplolejeunea conferta* (Meissn. ex Spreng.) Evans, *Cheilolejeunea oncophylla* (Ångstr.) Grolle & E. Reiner and several members of the genera *Diplasiolejeunea* (Spruce) Schiffn., *Pycnolejeunea* (Spruce) Schiffn. and *Frullania* which are characteristic canopy epiphytes of the neotropical tropical lowland forest Gradstein *et al.*, 2001 b). *Frullania kunzei* was resolved as the most significant indicator of LRF (***) and this concurs with its common occurrence in rather open, dry lowland sites in the Neotropics (Gradstein & Costa, 2003). Beside its occurrence on bark, this species is frequently found on rock as well.

6.5.3 Vertical distribution on host trees

Liverwort diversity increased with height in the tree in both forest types. Highest number of species per height zone was found in the middle crown in LRF and in the outer crown in LCF. We attribute the high richness in the middle crown of LRF to the overlap in this zone of shade-loving species characteristic of the inner zone with xerophytic species from the sunny outer crown. In LCF, occurrence of fog in the outer canopy should have triggered high liverwort richness in this zone. The latter observation agrees with Wolf (1995) who found that species richness of cryptogamic epiphytes was highest in the outer canopy of montane cloud forests of Colombia.

The data on vertical distribution of liverwort species in LCF and LRF confirm that the canopy of the tropical evergreen lowland forests is richer in bryophyte species than the understory (Cornelissen & Gradstein, 1990; Gradstein, 1992 a). Similar results have been obtained for epiphytic lichens (Komposch & Hafellner, 2000; Normann *et al.*, 2010). The data clearly indicate that inventories of non-vascular epiphytes of tropical lowland forests are seriously incomplete without detailed analysis of the forest canopy.

The analysis of the different height zones in LCF and LRF in terms of species composition showed distinct differences among height zones. These findings also agree with observation in other neotropical rain forests (e.g. Cornelissen & ter Steege, 1989; Acebey *et al.*, 2003) and in Indonesia (Sporn *et al.*, 2009). The latter study also included understory treelets, which appeared to be rather similar to tree trunks (zones 1-3) in terms of species compositition and added 12 % to total species richness of the forest.

In a study of epiphytic bryophyte diversity in three lowland forest sites across the Guianas, including Saül in French Guiana, Mota de Oliveira *et al.* (2009) found that species assemblages of one height zone between different sites was more similar than between height zones in one site. The results indicated that epiphytic bryophyte communities in tropical lowland forest at the local and regional scale are driven by niche assembly rather than by dispersal. The predominance of niche assembly at these scales distinguishes the bryophyte communities from those of the seed plants, which are mainly driven by dispersal limitation.

In our study, trunk and crown can be clearly distinguished in NMDS of species composition (axis 2), consistent with the observation of Mota de Oliveira (2010). In addition we observed a separation of assemblages along the first axis, reflecting forest type (Figure 27). Moreover, MRPP analysis of LCF and LRF showed significant differences for all height zones reflecting the importance of forest type for species composition (Table 12).

6.5.4 Regional and elevational comparisons

Several studies have been carried out on liverwort diversity in evergreen tropical lowland forests that included sampling of the canopy (e.g. Cornelissen & ter Steege, 1989; Montfoort & Ek, 1990; Cornelissen & Gradstein, 1990; Mota de Oliveira, 2010). These inventories have revealed large differences between forest types in terms of species richness. In most cases, species richness was higher in montane forests than in lowland forests, and this supporting the generally accepted notion that bryophyte diversity in montane forests is higher than in evergreen lowland forests (e.g. Richards, 1984; Frahm & Gradstein, 1991). However, evidence has been arising that in some lowland forests the number of species exceeded that of montane forest (Gradstein, 1992; 2006; Gradstein *et al.*, 2010).

A synthesis of species richness data of liverwort species richness on four trees in neotropical evergreen forests is provided in Figure 28. The data are similar as those provided by Gradstein *et al.* (2010: Fig. 1) except for the addition of three further neotropical sites: Ecuador, 1900 m (Nöske, 2005), Costa Rica, 2900 m (Holz & Gradstein, 2005) and this study. A further difference is the separation in the graph between rain forest and cloud forest sites. The results are remarkable. The figure indicates, for the first time, that species richness along the elevation gradient, from sea level to 3000 m, is consistently lower in rain forests than in cloud forests, in spite of considerable richness variation per site. It shows that montane rain forests are poorer in species than lowland cloud forest and that some lowland rain forests are richer in species than montane rain forests.

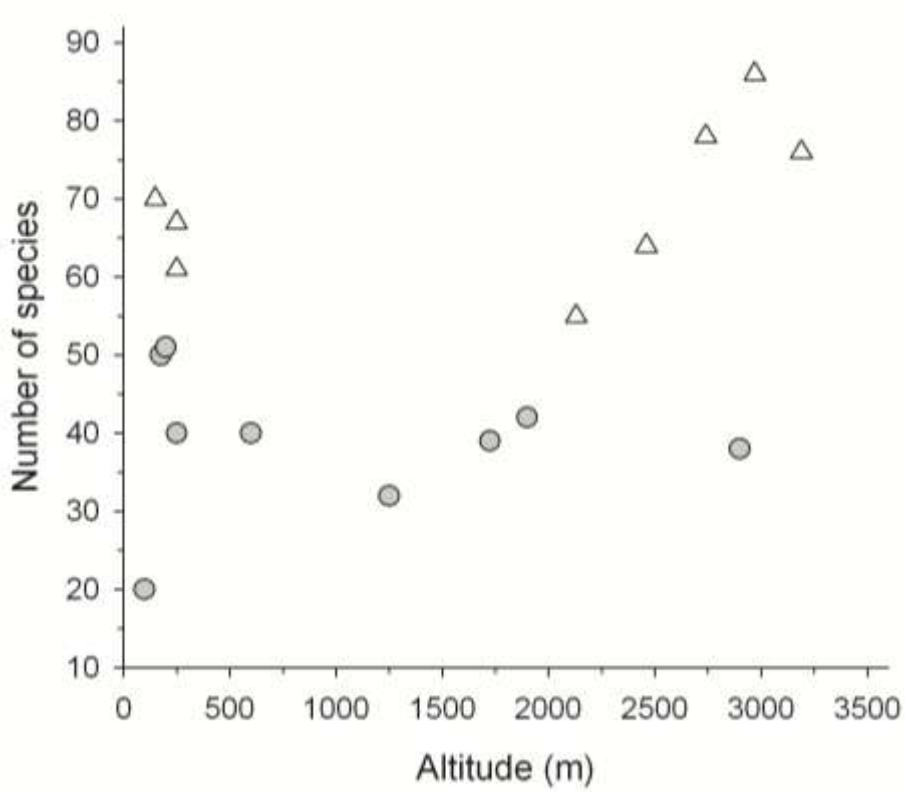

Figure 28. Species richness of epiphytic liverworts on four trees in cloud forest (triangles) and rain forest (circles) along an elevational gradient in the Neotropics. Cloud forest data from below 500 m are from French Guiana (Montfoort & Ek, 1990; this study), those from higher elevations from Wolf (1993). Rain forest data from below 500 m are from Venezuela (lowest number of species; Gradstein, 2010), Guyana (intermediate numbers of species; Cornelissen & Gradstein, 1990) and French Guiana (highest numbers of species; this study), those from higher elevations are from Bolivia (Acebey *et al.*, 2002), Colombia (Wolf, 1993), Ecuador (Nöske, 2005) and Costa Rica (Holz & Gradstein, 2005). Trees were usually sampled as described by Gradstein *et al.* (1996, 2003). All data are from randomly selected, climbable mature canopy trees, standing well apart from each (more than 15 m) in one hectare of dense primary tropical forests on flat or sloping ground. Sampling completeness per stand was about 75-80% of total estimated species richness.

As shown in Figure 28, liverwort richness in lowland rain forests of French Guiana and Guyana is higher than in montane rain forests of the Andes and Costa Rica. We speculate that the higher richness in these lowland forests may be due to their higher and more complex architecture as compared to the montane forest. However, regional ecological and historical factors leading to a very rich lowland liverwort flora in the Guianas (Gradstein *et al.*, 1990), or site factors and sampling intensity at the Andean localities may also have played a role here. Finally, it should be noted that the Guyana site in Figure 28 (Mabura Hill; Cornelissen & ter Steege, 1989) was earlier classified as tropical lowland cloud forest based on lichen data and the "occasional" occurrence of mist. Because the liverwort data for Mabura Hill are similar to those for LRF in French Guiana and precise information on fog at Mabura Hill is lacking, we classify the latter site as rain forest in this paper. We recommend a careful study on the putative presence of fog in the Mabura Hill forests.

6.5.5 Conclusion

This study has confirmed that evergreen tropical lowland forests are a rich habitat for epiphytic liverwort species, with Lejeuneaceae being the dominant family in this habitat. Canopies of evergreen tropical lowland forests are clearly richer in liverwort species than the forest understory, and inventories of tropical lowland forests must therefore include detailed analysis of the forest canopy. We have been able to show that lowland cloud forests (LCF) differ significantly from lowland rain forest (LRF) by the greater total richness of liverwort species and their far greater number of indicator species. These results complement our earlier findings for lichens and filmy ferns. Indicators of LCF and LRF clearly differ by their ecological preferences: those of LCF are shade epiphytes and generalists, and occur also in montane forests, while those of LRF are sun epiphytes and also occur in dry, rather open sites. The detected differences in liverwort diversity of LCF and LRF are explained by the more humid conditions in LCF as compared with LRF. Height zones on trees differ significantly in terms of species assemblages of liverworts, and the differences between the two forest types are as pronounced as the differences along the vertical gradient.

Finally, we have been able to show for the first time that species richness of liverworts along the elevation gradient in the Neotropics differs more strongly among forest type (rain forest, cloud forest) than among elevation, and that lowland cloud forests may be richer in liverwort species than neotropical montane rain forests. The data indicate that elevational comparisons of bryophyte species diversity in the Tropics should make a distinction between rain forests and cloud forests.

Future studies in other sites may unravel the distribution of lowland cloud forests in the Neotropics. Moreover, we recommend across-tropics comparisons of liverwort species diversity in cloud forests and rain forests along elevational gradients.

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7 Summary and Outlook

Lowland cloud forests are well known from temperate regions, e.g. the coasts of California and northern Chile (Bruijnzeel 2001), but in the Tropics have remained uninvestigated. We tested the hypothesis that tropical lowland cloud forest (LCF) and lowland rain forest (LRF) exist as distinct forest types with a higher abundance of epiphytes in LCF and differing in epiphyte species composition and microclimate. Furthermore, these forest types seem to occur in close proximity to one another, with LCF in valleys and LRF on adjacent slopes.

To validate this hypothesis, we compared epiphyte diversity and abundance at two localities in Central French Guiana (Saül, Nouragues Nature Reserve). Using the single rope technique (ter Steege & Cornelissen 1988), we climbed 48 canopy trees from putative LCF and LRF during a 6 month field trip to French Guiana. On each of the 48 target trees, we removed epiphytes growing in 24 sample plots of 600 cm^2. The plots were positioned at each cardinal direction in six height zones (Johansson 1974, Cornelissen & ter Steege 1989): trunk base, lower trunk, upper trunk, lower canopy, middle canopy, and outer canopy. Biomass of epiphytic angiosperms, pteridophytes, lichens and bryophytes was determined and three groups of epiphytic plants identified at species level: macrolichens, filmy ferns and liverworts. Trees were classified as belonging either to LCF or LRF based on geography and validated by microclimate measurements. Species were identified using appropriate methods for the different taxa, and overall forest species composition evaluated for each forest type and statistically compared.

In total we found 39 (morpho-) species of macrolichens, 9 species of Hymenophyllaceae, and 129 liverwort species. LCF contained a significantly higher mean species number per tree for both liverworts (LCF:

33.6; LRF: 25.0) and Hymenophyllaceae (LCF: 2.4; LRF: 0.3) than LRF. Moreover, 8 species of Hymenophyllaceae and 21 of liverworts were statistically determined as indicator species for LCF. These indicators of LCF included shade epiphytes and generalists that also occur in montane forests. As LCF is more humid than LRF, the differences in liverwort and filmy fern diversity can be attributed to the greater atmospheric water content. Although the number of macrolichen species per tree was similar in both forest types, lichens with cyanobacterial photobionts (cyanolichens) were 2.5 times more common in LCF. Cyanolichens are known to prefer humid habitats and this study showed that they are good indicators for LCF. The observed differences in species diversity of liverworts, filmy ferns and cyanolichens support the hypothesis that LCF and LRF contain distinguishable epiphytic biodiversity, a finding which is further supported by the measurement of higher overall epiphyte biomass in LCF and more tree surface area covered by epiphytes (70 % in LCF, 15 % in LRF).

Species composition differed greatly in all height zones for all studied groups of epiphytes. Hygrophilous taxa (shade epiphytes) were more common in LCF, while LRF harbored more xeric taxa (outer canopy specialists). Moreover, comparison of the vertical distribution of epiphyte species in LRF and LCF showed an upward shift of certain species of lichens, bryophytes and ferns inhabiting lower strata in LRF towards higher strata in LCF.

It had been previously observed that morning fog was present in LCF of Saül (Montfoort & Ek 1990). Fog can lead to higher humidity by providing a surplus of liquid water. To investigate whether there was an increased incidence of fog in LCF over LRF, we measured air humidity, calculated vapor pressure deficit, and frequency and duration of fog. LCF plots were more humid than LRF plots during both wet and dry season. LCF experienced higher overall mean air humidity, while high humidity events occurred both more frequently and longer than in LRF. The overall higher humidity is caused by fog formation in LCF at night; at early morning the moist air lifts into the canopy and acts as a radiation shield. Vapor pressure deficit in LCF was calculated to be lower than in LRF, especially in the early morning and significantly longer in duration. The prolonged availability of high air humidity in LCF and the additional input of liquid water through fog enhance epiphyte growth and influence species composition and diversity in LCF by shortening the desiccation period and lengthening the period of photosynthetic activity of the plants.

The studies representing this thesis have further clarified and brought into light the tropical lowland cloud forest as a new and neglected tropical lowland forest type. LCF occurs in close proximity to LRF, but differs dramatically in epiphyte species diversity, composition, and abundance due to differences in microclimate. This cloud forest type appears to be prolific, as other scientists have informed me that similar forest types occur in their study sites as well. If these observations hold true, distinguishing LCF from LRF may help tropical biologists to better understand the ecosystems they study. Such an improved understanding will also help policy makers to protect this unique forest type, which is a lowland hotspot for epiphytic liverworts and could represent a unique refuge for montane taxa in the lowlands.

Future work should include comparing epiphyllous liverwort diversity of the understory of LCF and LRF, and determine their possible use as indicators. Because epiphylls generally require humid conditions and are sensitive to small-scale local variation in light and humidity (Richards 1984, Marino & Allen 1991), an inventory of the epiphylls of the understory should reflect the moisture regime and further elucidate the mosaic of LCF and LRF occurrence.

Comparing epiphytic flowering plant and fern diversity (other than Hymenophyllaceae studied in this thesis) is also an important subject for future study. Being mostly homoiohydrous, vascular epiphytes should be less affected by the differences in microclimate of LCF and LRF than poikilohydric non-vascular epiphytes. Surprisingly, analyses of epiphytic cover and biomass showed large differences in the amount of vascular plant mass suspended in LCF and LRF trees. Studying the differences in species composition of the two forest types should clarify those differences and complete the inventory of the LCF epiphyte flora.

A further future goal should be generating a model to predict LCF occurrence based on satellite data, in collaboration with the AG Bendix at the University of Marburg. Additionally, an index of likely indicator taxa should be generated to help field scientists identify new LCFs in their own regions of interest. Using the climatologic and botanic expertise established in our studies, putative LCF could be studied in detail. Given the proper support, a new project could be initiated with the goal of constructing a global map of tropical lowland cloud forest distribution.

LCF could also be interesting for zoologists. Canopy-held epiphytic biomass plays a critical role in ecosystem processes in the forest by altering pools, pathways, and rates of nutrient and carbon fluxes (Nadkarni 1981, Coxson & Nadkarni 1995), as well as by influencing forest hydrology through rainfall and cloud–water interception (e.g., Veneklaas & Van Ek 1990, Hölscher *et al.* 2004, Bruijnzeel *et al.* 2005). Epiphytes also greatly increase the structural complexity of tropical forest habitats, providing crucial resources for numerous arboreal and terrestrial organisms (Nadkarni & Longino 1990, Yanoviak *et al.* 2007). It would be interesting to study whether the fauna also differs between LCF and LRF, and if so, whether ground vegetation is also affected (e.g. by different pollinators and seed dispersers). To clarify this question, an in-depth study of the entire LCF ecosystem should be conducted.

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9 Appendix

9.1 List of publications and conference proceedings

Publications

Gehrig-Downie, C., Obregon, A., Bendix, J., S.R. Gradstein. Diversity and vertical distribution of epiphytic liverworts in lowland rain forest and lowland cloud forest of French Guiana. *Accepted at* Journal of Bryology.

Gehrig-Downie, C., Marquardt, J., Obregón, A., Bendix, J., Gradstein, S.R. 2012. Epiphyte Diversity and vertical distribution of filmy ferns as a tool for identifying the novel forest type "Tropical Lowland Cloud forest". Ecotropica 18(1): 35–44.

Pardow, A., Gehrig-Downie, C., Gradstein, R., Lakatos, M. 2012. Functional diversity of epiphytes in two tropical lowland rainforests, French Guiana: using bryophyte life-forms to detect areas of high biodiversity. Biodiversity and Conservation 21: 3637-3655.

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Conference proceedings

Gehrig-Downie, C., Obregon, A., Bedix, J., & S.R. Gradstein. 2011. The Tropical Lowland Cloud Forest: a lowland forest with montane epiphyte richness. Invited lecture. Annual meeting of the Society for Tropical Ecology (GTÖ), Frankfurt, Germany.

Obregon, A., Bendix, J., Gehrig, C., & Gradstein, S.R. 2011. The role of fog in the spatial distribution of a new tropical lowland forest type. Invited lecture. Annual meeting of the Society for Tropical Ecology (GTÖ), Frankfurt, Germany.

Gehrig, S., Obregon, A., Bendix, J., & Gradstein, S.R. 2009. The tropical lowland cloud forest: Epiphytic biomass and canopy microclimate. Poster. Joint Meeting of the Association for Tropical Biology and Conservation (ATBC) and the Society for Tropical Ecology (GTÖ), Marburg, Germany.

Hofstaetter, M., Gehrig, S., Obregon, A., Bendix, J., & Gradstein, S.R. 2009. Epiphyllous bryophyte diversity in lowland rain forest and lowland cloud forest of French Guiana: first results. Poster. Joint Meeting of the Association for Tropical Biology and Conservation (ATBC) and the Society for Tropical Ecology (GTÖ), Marburg, Germany.

Marquardt, J., Gehrig, S., Obregon, A., Bendix, J., & Gradstein, S.R. 2009. Epiphytic filmy ferns as indicators of Tropical Lowland Cloud Forest. Poster. Joint Meeting of the Association for Tropical Biology and Conservation (ATBC) and the Society for Tropical Ecology (GTÖ), Marburg, Germany.

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9.2 Curriculum vitae

Personal Details

Name	Christine Gehrig-Downie
Date and place of birth	14.10.1980 in Northeim
Nationality	German

Education and professional experience

Since 10/2008	Georg-August-University of Göttingen, certificate program in University Didactics (120 teaching units à 45 minutes)
Since 05/2007	Georg-August-University of Göttingen, Doctoral Studies Dissertation Title “Epiphyte diversity of the Tropical Lowland Cloud Forest of French Guiana”
10/2006-04/2007	Scientific Assistant, Univ. Göttingen, Systematic Botany
10/2006	Diploma in Biology with honors
11/2000-10/2006	Georg-August-Univ. of Göttingen, undergraduate studies in Biology with a major in Botany and minors in zoology and nature conservation Title of diploma thesis „Epiphytische Biomasse auf in Weiden isolierten Bäumen im Bergwaldgürtel Südecuadors“
04-05 & 10-11/2006	Teaching Assistant, Univ. Göttingen, Biology for Medicine Students

Language skills

German	Native
English	Fluent
French	Basic
Spanish	Basic

Computer skills

Windows Microsoft Systems (Word, Excel, PowerPoint)
Statistic programs (Xact, Systat, Statistica, PCOrd)
Graphic programs (CorelDraw, Sigma Plot)

Interests

Outdoors	Hiking, climbing, diving
Travelling	Backpacking in tropical countries
Socials	Board and card games, movie nights
Literature	Travelling reports, crime novels

Publications

Gehrig-Downie, C., Obregon, A., Bendix, J., Gradstein, S.R. Diversity and vertical distribution of epiphytic liverworts in lowland rain forest and lowland cloud forest of French Guiana. *Accepted at* Journal of Bryology.

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